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AVANT-PROPOS / FOREWORD

Quand nous avons entrepris, en novembre 1971, les premières démarches pour organiser une rencontre internationale des chercheurs intéressés à l'écologie de l'orignal, nous avions déjà l'objectif majeur de regrouper sous une même couverture des articles de synthèse couvrant de manière exhaustive tout le champ des recherches contemporaines sur l'écologie, le comportement et l'aménagement de l'orignal. Aussi, le lecteur ne trouvera-t-il pas dans les pages qui vont suivre, un assemblage hétéroclite de travaux sur l'orignal, mais plutôt une monographie qui fait, nous l'espérons, un tour d'horizon très complet des connaissances actuelles sur cet important ongulé de la forêt boréale. Pour atteindre ce but, nous avons sollicité l'aide de six éditeurs adjoints: chacun d'eux avait la responsabilité de recruter ses propres collaborateurs; chacun avait également la responsabilité de coordonner la participation des auteurs à l'intérieur du chapitre qui lui était assigné de façon à restreindre au minimum la redondance et l'enchevêtrement.

In view of its vastness, not all aspects of the subject could be covered. For example, the reader will notice the absence of a chapter on the relationships between moose and caribou; he will also notice the lack of treatment given a new and increasingly important aspect of moose management, management for non-consumptive use. We invited papers on these themes as well as on several others: however, for a number of reasons, these did not develop. Review papers on such subjects as taxonomy or paleontological history that have changed little in the past fifteen or twenty years were not included because of limited space.

On hundred and fifty five participants from seven different countries registered for the symposium which was made possible through the generous financial assistance of the following organizations: the National Research Council of Canada, the Association canadienne-française pour l'avancement des sciences, the Université Laval, the Council of Pulp and Paper producers of Québec, the Société zoologique de St-Félicien and the Daaquam Lumber Company. La Société zoologique de Québec Inc. also made a substantial contribution towards publishing costs of the present proceedings as a special issue of Le Naturaliste canadien.

Les personnes dont les noms suivent ont pris une part active et essentielle à l'organisation du Symposium: Emile Audy, Rodrigue Bouchard, Michel Crête, Pascal Grenier, Jean-Luc Grondin, Jean Huot, Jean Munro, Claude Minguy, Gaston Moisan, Magella Morasse, Charles Pichette, François Potvin, Yvon Roussel et Benjamin Simard.

Il convient également de remercier un pionnier dans les recherches sur l'orignal en Amérique du Nord, qui a bien voulu accepter notre invitation de présenter la conférence inaugurale et de lier ainsi ses importants travaux réalisés, il y a une vingtaine d'années, à ceux d'aujourd'hui. Nos remerciements les plus sincères s'adressent également au docteur Ian McTaggart-Cowan qui a accepté de nous entretenir, avec son éloquence coutumière, lors du banquet de clôture du Symposium.

Finally, thanks must be given to Emile Audy, Jean Huot, Michel Crête and the regular editorial staff of Le Naturaliste Canadien who worked extremely hard to help an overburdened general editor put together these proceedings. I hope they will will be a valuable reference to all those concerned with the moose itself or with the ecology of the boreal forest.

J. B.

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MOOSE: YESTERDAY, TODAY AND TOMORROW

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Yesterday

My «yesterday» association with moose began in the spring of 1946, then as a fresh graduate student seeking a Ph.D. at the University of Toronto and as a somewhat younger acting curator of the Department of Mammalogy at the Royal Ontario Museum. This association essentially culminated with the publication of my modest efforts "North American Moose" in 1955. Although my subsequent research program turned to a faunal study of the mammals occurring in eastern Canada, followed by a geographical shift to tropical mammalogy and the systematics of bats in particular, my early love of moose has really never waned. I regard this opportunity to refocus my attention on moose in the lead-off position for this International Symposium on Moose Ecology and Ninth North American Moose Workshop as a singularly great honor that I shall long remember. Therefore, I would like herewith to express my gratitude to Dr. Jean Bédard and the Organization Committee for extending the invitation to me to speak to such an august body of leading world authorities on moose. After having been away from active field research on moose for more than 20 years, I must admit to a great deal of apprehension in speaking to such a knowledgeable group. I feel somewhat like a "has-been" that is no longer "with-it". Having been naive enough to set down in print all I could find out about moose, I now find myself having to "face the music" as an easy target to be "shot down in flames" by subsequent moose researchers who have

Naturaliste can., 101: 1-8 (1974).

been able to carry out detailed and more thorough studies of many aspects of moose, whereas my earlier attempts merely scratched the surface.

Nonetheless, and perhaps in self defence, I have felt that a very brief resumé of the state of our knowledge of moose at the beginning and end of my own attempts might be helpful. By 1946 much had been written about moose but I still recall quite vividly the reams and reams of printed pages that I searched through ever hopeful of screening out a few "kernels" of reliable information that would withstand critical tests of authenticity. Some 600 references were found that provided information on moose; some of historical interest, some as a background matrix, some proved to be unreliable opinions and some even appeared to be fiction. Nonetheless, some of the earlier publications contained specific observations of varying levels of value. By modern standards, monographic studies of moose were rare indeed, with the studies of Adolph Murie (1934) being the major keystone on which to build my own studies. This Isle Royale study was further expanded by works of Hickie (undated, 1936, 1937), Kellum (1941) and Aldous and Krefting (1946). Most other available data on North American moose were included in faunal reports, notes, review articles or perhaps buried in accounts dealing primarily with other species or related, as well as unrelated topics. Some moose studies had been carried out in Montana by people like McDowell, Moy and Schultz but their results had not been published. Similarly a few studies had already been carried out in Alaska (Sarber, 1944). Studies of the diseases and parasites of moose had been underway for some time in Minnesota by Fenstermacher and his associates including Cahn, Olsen, Thomas and Wallace.

During the period 1946-55 when I was working in Ontario, several other moose studies were also in progress. Pimlott in Newfoundland; Hosley and Krefting in Michigan; Denniston and McMillan in Wyoming; Cowan, Hatter, Hoar and Edwards in British Columbia; and Chatelaine, Raush and Spencer in Alaska.

Considerable work on moose was also prodeeding in Europe and Asia and the publication of the book by Skuncke (1949) provided us with the first comprehensive review of the moose in Sweden using modern standards.

In an attempt to put into some perspective the advances in our knowledge of moose since 1955, I propose to review briefly the major chapter topics discussed in my book as points of departure to bring us to the present.

NORTH AMERICAN MOOSE — 1955

1. *Introduction*
2. *Taxonomy and distribution*

The genus *Alces* (Gray) is circumpolar in distribution occupying the boreal forests of the northern hemisphere. Formerly the Old and New World populations were thought to represent two distinct species but more recently there seems to be general agreement (Hall and Kelson, 1959; Walker *et al.*, 1964 and 1968) that the genus is monotypic with the single species being represented by a number of geographic races (Peterson, 1952). There appears to have been some further general expansion northward in both the Old and the New World in recent years although a part of this apparent expansion may be a reflection of more precise knowledge of distribution in remote areas (see Fig. 1), as shown by Kelsall (1972).

There has been no recent critical systematic review of the genus subsequent to that of Peterson (1955), a much needed task that is still hindered by an insufficient number of specimens to allow modern methods of statistical analysis of data, based on adequate sample sizes. In addition to the traditional morphological measurements of skull and body, there are now a number of new tools available to the taxonomist which include comparative ethology, comparative biochemical studies of blood and other tissues, specificity of external and internal parasites as well as karyotype studies.

Aula and Kaariainen (1964) were the first to describe the karyotype of *Alces alces alces* from kidney tissue culture and found $2n = 68$, with 6 metacentric and 62 acrocentric chromosomes. These results were later confirmed by Nes, Amrud and Tondevold (1965), Wurster and Benirschke (1967) and Gustavsson and Sundt (1965 and 1968). The latter defined the fundamental number as 74.

Hsu and Benirschke (1969) have reviewed the karyotype of North American moose based on skin biopsies of a pair of *A. a. shirasi* and one male of *Alces a. americana* from "northeastern Canada". In both races they found general agreement of $2n = 70$ (rather than 68 as in Europe) with 2 submetacentric, and 66 acrocentric chromosomes (compared with 6 metacentric and 62 acrocentric in Europe). This difference in karyotype number and morphology provides an avenue worthy of further investigation.It will be highly interesting to learn what the karyotype picture of the other races of *A. alces* will reveal, especially that of

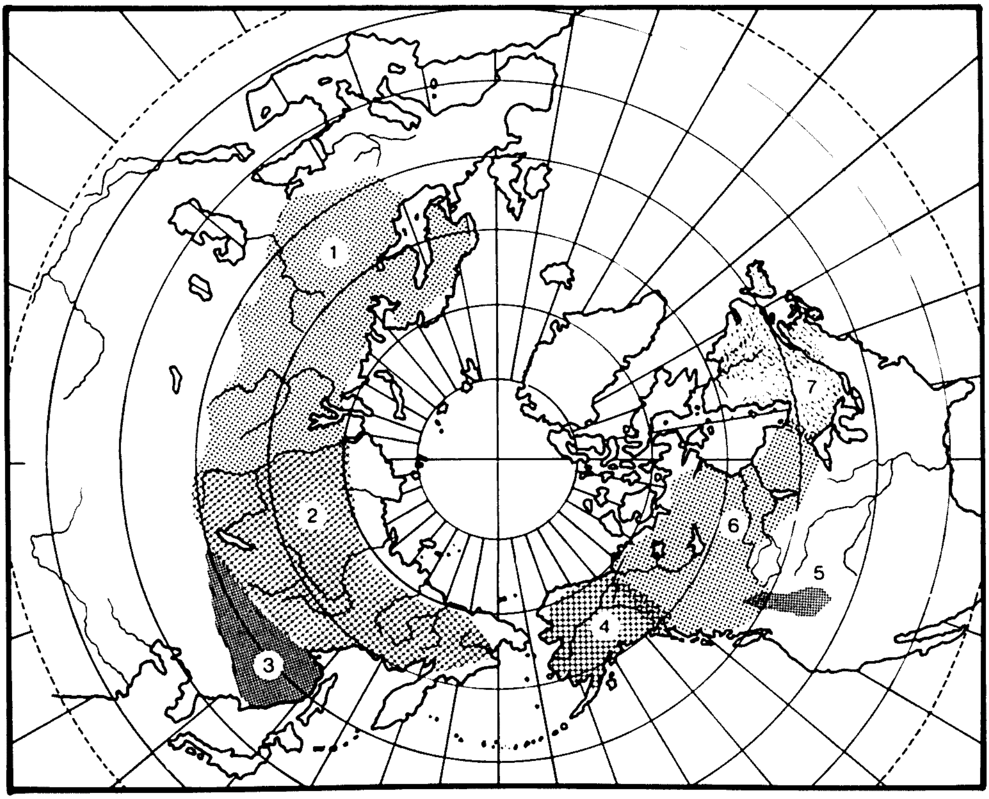

Figure 1. Distribution of moose, *Alces alces*. 1. *A. a. alces* 2. *A. a. pfizenmayeri* 3. *A. a. cameloides* 4. *A. a. gigas* 5. *A. a. shirasi* 6. *A. a. andersoni* 7. *A. a. americana.*

Alces a. pfizenmayeri from northern Siberia and that of *Alces a. gigas* from Alaska. Based on cranial morphology, *A. a. alces* is more distinct from all other races than any other (see Peterson, 1955, Fig. 2). One is tempted to speculate the karyotype of *A. a. pfizenmayeri* and *A. a. gigas* will prove to be similar to each other as well as to other North American races ($2n = 70$). Perhaps other workers will be encouraged to determine the karyotype characteristics of moose from these other areas to clarify this interesting genetic relationship within the genus.

3. *Palaeontological history*
4. *Post-glacial dispersal in North America*
5. *Moose in the early history of North America*

To my knowledge, these three topics have not been the subject of recent research. There has been a great deal of new background data that relate to these topics and perhaps the time is approaching, if not at hand, to re-examine all new evidence with the view of confirming or modifying earlier theories or perhaps to develop entirely new concepts more compatible with available evidence.

6. *General population status*
7. *Distribution and status of Moose in Ontario*

These subjects will be reviewed in this symposium in the section "Habitat distribution". The ten papers cover not only North America but Europe and Asia as well.

8. *Rate of reproduction*

This topic has been the subject of considerable research by a number of workers in the Old as well as the New World and are reviewed in detail by five different authors in the section "Population dynamics".

9. *General life history*

I have been assigned the task of reviewing this general topic (Peterson, 1974) except for those aspects that are covered in the "Behavior" section where aspects of this and the following chapter are discussed in detail.

10. *General behavior and activities*

In addition to the section on "Behavior" this general topic is touched upon in other sections. Studies in ethology have opened up a whole new field of active interest and specialization with most of the advances coming after 1946.

11. *Food habits*
12. *Food plants in Eastern North America*
13. *Food plants in Western North America*

In my own field studies, I placed a high priority on these aspects of moose ecology because of their obvious fundamental importance. I attempted to carry out a moose browse analysis based on techniques developed by Aldous (1944) for deer. A special section is devoted to "Nutrition" in which the summary results of several more sophisticated studies essentially render some of our earlier efforts obsolete.

14. *Habitat studies*

The interactions of this broad topic are discussed in most of the sections of the Symposium as well as the Workshop. Here we have an opportunity to relate the moose with current philosophies and concepts of the environment.

15. *Relationships with other animals*

The modern term for this topic is now "Moose coactions" and we have two entire session periods devoted to this broad topic. I merely scratched the surface of this topic in 1955 whereas we have eight authors to provide in-depth reviews of different aspects of the relations of moose with other animals in its environment.

16. *Diseases, parasites and insect Pests*

A review of infectious and parasitic diseases of moose in North America is provided by Anderson and Lankester (1974). Here again we see the role of a specialized discipline contributing to the overall understanding of the ecology of moose.

17. *Accidents*

Grenier (1974) is concerned with the question of accidents as a factor in moose losses.

18. *Population studies*

For those concerned with management of moose as a natural resource, this is the "name of the game" and figures in several papers cutting across several sessions including the workshop. The section on "Population dynamics" is particularly concerned with this subject. Each individual locality presents a unique set of conditions that interact to affect resident populations of moose. One of the important functions of this symposium will be the identification of those factors which appear to be common to all areas.

19. *Management*

Here we come to the "nitty gritty" of major thrust of interest on the part of most of the people attending this symposium and we shall attempt to come to grips with several aspects of this problem in the "Moose management" session. We will be trying to rationalize all of the information articulated in these sessions and to come up with concepts, policies and procedures which hopefully will insure future sustained populations of healthy moose.

APPENDIX A — *Tooth wear as an index to age*

In the absence of any known way to establish the age of moose, in 1955 my colleagues and I attempted to establish some guideline criteria by which moose specimens could be classified into roughly comparable age-classes based on relative amount of wear on the teeth. We proposed a series of what we called "Wear-classes" (Passmore, Peterson and Cringan, 1955). We felt that, at the younger end of the scale, these wear-classes appeared to correspond reasonably well with age-class, but in the absence of actual known age material, we felt certain that the actual age spread for the higher wear-classes would tend to become progressively larger in older populations. Sergeant and Pimlott (1959) subsequently developed an aging technique based on counting the cement layers of incisor teeth of moose which appears to provide greater accuracy in age determination particularly at the older end of the age spectrum. The relative accuracy of the two techniques still requires the confirmation from an adequate series of known age specimens. The interpretation of both the number of annuli and the degree of wear remains somewhat subjective and the results may vary from worker to worker. The rate of wear on teeth is subject to a number of factors and cannot be assumed to be uniform from region to region. We still require some practical method of ascertaining the age structure of moose populations and of determining the relative age of individual specimens. Unfortunately the tooth sectioning technique, while obviously providing a more precise technique, is more difficult and time consuming when considered as a routine management tool. In our attempt to develop a meaningful aging technique we specifically referred to our grouping as "wear-classes" – not age-classes – as some have interpreted our results. While we did speculate on the possible correlation of wear-classes with ages we were explicit in the concept that the older wear-classes contained more than one calendar year age group. If the wear rate in Newfoundland moose is comparable to that of Ontario moose, the work of Sergeant and Pimlott (1959) suggests that our original suggested age spans of the higher wear-classes should be revised upward.

APPENDIX B — *Antler development in relation to age*

The earlier review of this subject demonstrated a wide range of variation in size and confirmation of antler development in relation to age and therefore does not appear to be a fruitful avenue for further study in that context. In the Workshop Session a most interesting hypothesis concerning the morphogenesis in antlers of moose is provided by A. B. Bubenik (1974).

Timmermann (1971) carried out further studies of moose antlers in relation to age using a reasonably adequate sample size, especially of the younger age groups, and checked the results against ages determined by cementum ring counts. His results essentially confirmed the great amount of variability found earlier by Cringan (1955).

Today

With this brief over-view of the state of knowledge during the period 1946-55 and with an indication of the topics that will be reviewed in detail from 1955 to date, I would like to reflect briefly on the ever-fleeting present.

Perhaps it is just as well that I was younger and more naive when I attempted to bring together analyses, and to synthesize the existing knowledge of North American moose back in 1955. At that time there were not many of us devoting our full efforts toward moose studies and the data base we had to work from was not very extensive. We were operating in a transitional period when we were attempting to apply critical scientific methods to a field in which the literature had been dominated by the concepts of trophy hunters, amateur naturalists, and poorly qualified observers and uncritical natural history writers. With the gradual upgrading of resource management from the policial and emotional biases of earlier years toward a more soundly based approach using scientific methods, it is now essential that we review our concepts and philosophies and critically re-examine in detail the data base upon which we have founded these concepts and philosophies. In the period since 1955 we have witnessed a mushrooming interest in the environment with all its complex components.

This symposium provides us with an excellent opportunity to bring together specialists in various aspects of moose research as well as authorities from the various geographic areas within the range of moose. By synthesizing the specialized knowledge brought to this symposium, by exchanges of ideas, data, philosophies, techniques and new as well as old concepts, surely we shall gain deeper insight, stimulation and renewed enthusiasm for satisfying our search for knowledge of all aspects of the moose and its environment.

Tomorrow

What about tomorrow? Where do we go from here?

In order to avoid being swamped with all the complex interrelationships that impinge on our understanding of moose, it has become necessary to specialize on limited selected aspects in order to focus our attention on a manageable body of information. We are rapidly reaching the stage where the proliferation profile of specialized knowledge of moose and its environment will have expanded beyond the ability of any one individual to comprehend, evaluate and articulate the multitude of bits of information that fit together to make the whole. Perhaps we are approaching the point when it will be necessary to feed all of our accumulating data into a giant computer programmed to store, integrate, analyze, and compute causes and effects as well as define interrelationships to provide us with the answers to specific questions for which we require answers.

Looking back to what we knew in 1946, in 1955 and reviewing the accumulation of knowledge from 1955 to date, it is patently obvious that we have come a long way — but I would like to close my remarks with a statement of firm conviction that in relation to a total understanding of the interactions of the moose with its environment, we still have a long way to go, in many areas we still have only scratched the surface.

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A REVIEW OF THE GENERAL LIFE HISTORY OF MOOSE

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Résumé

La reproduction est bien synchronisée chez toutes les sous-espèces d'orignal (*Alces alces*) puisque la grande majorité des accouplements ont lieu durant le même cycle oestrien; seulement quelques gestations seront amorcées durant le cycle oestrien précédant ou durant l'un ou l'autre des deux cycles oestriens suivant le sommet de l'activité reproductrice. Une proportion variable des femelles est capable d'ovuler et de se reproduire à l'âge de 16 mois tandis que la plupart des mâles, bien que produisant des spermatozoides à cet âge, sont probablement empêchés de prendre part à la reproduction à cause de l'intervention des mâles plus âgés. La pleine maturité est atteinte vers l'âge de cinq ou six ans et la période de fécondité maximale s'étend jusqu'à l'âge de 10 ou 11 ans. La longévité maximale dépasse 20 ans (un cas jusqu'à 27 ans). L'auteur regroupe des données sur les mensurations et le poids d'embryons à divers stades de la gestation et de veaux depuis la naissance jusqu'à l'âge de trois mois. Il analyse les facteurs permettant de transformer le poids des carcasses éviscérées et le poids des carcasses préparées pour le dépeçage (viscères, peau, pattes et tête enlevées) en poids entier. Le poids des animaux d'un an («yearlings»: âge de 16 à 18 mois) est le même, aussi bien en Alberta et au Québec qu'en Suède. L'auteur propose un ensemble de mensurations qui seraient d'une grande utilité dans les études de populations. Des photographies au microscope électronique à balayage du poil chez l'orignal, le wapiti, le cerf de Virginie et le caribou sont présentées et comparées.

Abstract

This paper attempts to review the most noted progress that have been made since 1955 in our knowledge of the general life history of *Alces*. We will briefly survey: the breeding habits, the size and the growth of the animal as well as some new information on pelage and antlers.

The peak of the breeding season in all races of moose (*Alces alces*) falls within one oestrus period; one early and perhaps, one or two late oestrus periods account for a small percentage of total pregnancies. A variable number of females ovulate and are bred at about 16 months and most males develop spermatozoa at the same age but may be prevented from breeding by older bulls. Full maturity is reached at about five or six years of age with maximum fecundity lasting until age 10 or 11. Maximal life span is known to exceed 20 (up to 27) years. Data on growth and weights are presented for embryos from two weeks old to birth, and for calves from two or three days to 91 days of age. Data on conversion from eviscerated carcasses and dressed carcass to whole (or live) weights of moose are reviewed. Weights of yearlings (16-18 months old) from Alberta, Québec and Sweden are shown to be similar. Much needed standard external body measurements are defined and illustrated. Scanning electron microscope photographs of moose hair are presented and compared with wapiti, white-tailed deer and caribou.

Breeding habits

BREEDING SEASON

Since several aspects of breeding behaviour have been recorded by Altmann (1959) and are treated elsewhere (Lent, 1974) only a synoptic review of data subsequent to Peterson (1955) will be presented here. The rutting or breeding season usually lasts from early September to mid-or late October. Flerov (1952) stated that in Siberia, the rut takes place in September although Egorov (1965) observed the first signs of the rut in *Alces alces pfizenmayeri* between September 5 and 10 with the peak of mating from September 20 to October 10. He noted no sign of rut after October 15 but suggests that some mating might take place after that date. Markgren (1969) has reviewed data from Europe and found some variation in time of the rut depending upon latitude, with a great deal of sexual activity in early September. He found that the peak begins somewhere at the end of September and extends far into October for the largest part of Sweden. In one area (Gavleborg county) the main oestrus appeared to be in the first half of October, normally between the 5th and 10th.

Dodds (1958) discussed pre-rutting behaviour of Newfoundland moose and found that breeding activity had begun by September 9 but no indication was given for the duration of the actual rut. Denniston (1956) concluded that Wyoming moose mate from mid-September through early November although Altmann (1959) found that it "starts in early September and extends through late October," in the same general region. On the basis of examination of embryos, Edwards and Ritcey (1958) concluded that breeding in British Columbia might extend from early September to late November but that 89 percent bred in late September and early October.

In summary, it appears that the peak of the breeding season in all races of moose fall within one oestrus period with one early and perhaps one or two later oestrus periods accounting for only small percentages of total pregnancies. There appears to be considerable variation from area to area with respect to early and late conceptions which Markgren (1969) has shown to be influenced by several factors such as nutrition and other habitat factors as well as by population density, age and physiological conditions of the animals themselves.

The duration of the oestrus in individual females needs further confirmation. Data summarized by Markgren (1969) indicated that the cow is receptive for about 7 to 12 days but that the actual "heat" lasts less than 24 hours. The interval between oestri has been reported to be about 21 days in Europe and 18 days from zoo records (Markgren, 1969) to 30 days in North America (Edwards and Ritcey, 1958).

The length of the gestation period has been reviewed by Markgren (1964) who found a mean of 234 varying from 226 to 244 days with over 75 percent calculated to fall between 232 and 238 days. This is slightly shorter than the 240 to 246 days that has been reported for North America (Peterson, 1955).

AGE AT FIRST BREEDING

Recent studies of ovaries indicate that calves do not ovulate in the year of birth (Pimlott, 1959; Simkin, 1965; Markgren, 1969). It has been assumed for sometime that at least a few females are successfully bred at the age of 16 months (Lonnberg, 1923; Peterson, 1955). More recently detailed studies of ovaries and uteri have confirmed the incidence of both ovulation and pregnancies in yearlings in the Old as well as New World; the results of these studies have been ably reviewed by Markgren (1969). There appears to be considerable regional variation in the rate of ovulation and pregnancies in yearlings. "In some areas practically none of the female yearlings will ovulate, in others, ovulation is the rule in this age group" (Markgren, 1969, p. 197). In general yearlings have a distinctly lower fertilization rate than older cows (Simkin, 1965; Houston, 1968). There is also evidence that some yearlings which reach puberty will come into oestrus later in the season than older cows, although Markgren (1969) found that most of the yearlings which ovulate will do so in the general period when the majority of the adults do.

In a study of 13 yearling males, Houston (1968) found that 92 percent had developed spermatozoa by September 21 and were assumed to be physiologically capable of breeding although their opportunity to breed may be limited by the domination of available cows by older bulls. Markgren (1969) obtained similar results in Sweden.

MATURITY AND OLD AGE

Precise information on age-related development in moose has advanced but little in recent years. The most significant recent review of the subject has been provided by Markgren (1969) based on his studies in Sweden. He found that "...full maturity is not reached until about 5 or 6 years of age in these regions, and a cow moose may evince a maximal fecundity till the age of 10-11 years or longer" (p. 203). He presents evidence that "...maximal reproductive capacity in female moose is found in fairly older ages, considerably older than formerly believed in Sweden. Also among 211 cows reported to be accompanied by calves, there was a significantly higher proportion of cows with two calves between 6 to 11 years of age than between 2 and 5 years" (p. 203). Markgren found no available data to suggest that there is a definite age in moose when reproductive capacity ceases. Houston (1968) has reported senile cows of 18 and 22 years of age in Wyoming based on age determination by incisor sections, and a cow of apparent senility has been reported from Ontario by Simkin (1965).

LIFE SPAN

The normal maximal life span of moose is still a matter of conjecture. An age of 22 years for a Wyoming moose has been recorded (Houston, 1968). Earlier reports of moose exceeding 20 years of age in Sweden are supported by an East Prussian record of 27 years (Gardell, 1958) based on an animal tagged as a calf.

MATING BEHAVIOUR

Details of rutting activity have been recorded by Altmann (1959) and Geist (1963) and recently reviewed by Markgren (1969), and are further discussed by Lent (1974). There seems to be general agreement that bulls will mate with more than one cow, normally staying with one at a time, sometimes up to a week, before searching out another mate. Whether or not this is true polygamy has been questioned by Markgren (1969).

Growth and weights

Data on the growth and development of moose embryos and foetuses in Sweden have been provided by Markgren (1969) and are summarized in Table I.

Accurate weights of new born young have remained largely unavailable. In general most workers estimate the average weight usually falls between 11.3 and 15.9 kg (25 and 35 lbs) with some records falling as low as 5 to 6.8 kg (12 to 15 lbs) but these are regarded as "runts" with little survival potential.

The growth of calves of *A. a. shirasi* has been documented by Denniston (1956) and Peek (1962) (Table I). Accurate live weights of older moose of any race have been based on extremely small samples. Blood *et al.* (1967) provided the first reasonable sample of *A. a. andersoni* recording both whole weights and dressed weights[1] based on 35 specimens (nine

TABLE I

Growth of moose embryos, foetuses and calves. A. Embryo/foetus growth (from Markgren, 1969). B. Calf growth (from Denniston, 1956 and Peek, 1962)

A. Growth of moose embryos and foetuses

Age (weeks)	*Sex*	*Embryo crown-rump length (mm)*	*Foetus forehead rump (mm)*	*Weight (g)*
4		7		
4-5		11		
5		14.5-15.5		
5-6		19-28		
7		42-44.5		
7-8	♀ ♂	56-57	68	
10	♀ ♂		105-112	84
13-14	♂		174	240
18-19	♂		304	1521
21-22	♀		407	
24-25	♂		462	5490
26-27	♀		509	6150
30-31	♂		660	13200
32-35	♂ ♀	Neonate		11-16 kg

B. Growth of moose calves

Age (days)	*Sex*	*Total length (cm)*	*Shoulder height (cm)*	*Tail length (mm)*	*Hind foot length (mm)*	*Ear length (mm)*	*Weight (kg)*
2-3	♂[1]	85-99		25-51	414-432	147-152	
2-3	♀[1]	101.6		38	427	147	14.9
4-5	♂[1]	104.1		38	444	160	20.4
4-5	♀[1]	105.6-111.2		33-51	429-432	165-173	20.8
5-7	♂[1]	111		38	444	165	
7-10	♀[1]	104.1		58	465	190	28.1
14	♀[2]	91.4	81.3			127	17.7
21	♀[2]	99.1	83.8			152	20.8
28	♀[2]	106.7	86.4			152	23.6
35	♀[2]	109.2	87.6			152	25.8
42	♀[2]	118.1	87.6			152	32.6
49	♀[2]	118.1	94.0			178	38.1
63	♀[2]	134.6	109.2			190	49.9
77	♀[2]	144.8	111.8			203	58.0
91	♀[2]	162.6	114.3			203	

[1] From Peek, 1962.

[2] All measurements and weights of same individual hand reared orphan. From Denniston, 1956.

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[1] Dressed weight is defined as the carcass with the viscera, skin, head and feet removed.

calves, six yearlings of 18 months, eleven 2 1/2 year olds and 9 adults). Their sample included only 3 adult bulls (442-476 kg) which represent the younger end of the adult scale. They found that the carcass yield in animals over 18 months of age varied from 46.7 to 56.7 percent of the live weight which is somewhat lower than the 55 to 60 percent that I reported earlier on the basis of four adults (Peterson, 1955). Markgren (1964) also reported that in Sweden the dressed weights of *A. a. alces* represents some 55 to 60 percent of the live weight. He showed that the dressed weight of 65 yearling bulls (*ca.* 16 months old) had a three year mean of 154.4 ± 16.5 kg (118–215) whereas 57 yearling females averaged 153.3 ± 13.2 kg (129–190). By converting these figures to live weight using a 55 percent yield, the males averaged 280.1 kg (214.1–390.1) and the females 278.1 kg (234–344.7). Comparable figures for yearlings of *A. a. andersoni* (perhaps a month older) from Alberta (Blood *et al.*, 1967) are two males 310.7 kg (292.1–329.3) and four females 336.1 kg (304.8–354.7) based on actual whole weights. Using dressed weights for *andersoni* Blood *et al.*, (1967) calculated live weight for 34 males at 305.7 kg (230.4–386.5) and 323.9 kg (255.8–371.9) for 28 females on the basis of 50 percent carcass yield. If based on a 55 percent carcass yield, the figures for Alberta males would be strikingly similar (Table II) except that the males would be lighter and the females heavier in weight than the Swedish sample.

DesMeules (1966) listed the average weights of moose of various ages based on the work of Heyland (1964) which included 110 cows and 101 bulls weighed during the controlled hunt period between 1962 to 1964. The weight data of the above, plus additional data secured during additional controlled hunts in Laurentide, La Vérendrye and Matane Provincial Parks, Québec, in 1965 and 1966 (Heyland, 1966) provides the first reasonable sample of weights from all age classes of *A. a. americana.* Since the controlled hunts in the Provincial Parks were carried out from about mid-September to the third week of October the weights of the bulls are affected by a weight loss brought about by rutting activities with reduced feeding. Total weights (live weight less, variable blood losses) and visceral weights were obtained for eight road-killed and one hunter-killed specimens, six males and two females, with estimated ages of five ranging from one to eight years of age. The visceral weight varied from 34.2 percent for a young 193 kg bull of unknown age to 20.5 percent of the total weight for a 443 kg bull (estimated age at wear class VIII) with a mean of 28.0. The total weight estimated for yearling moose (16–18 months of age) from Québec are compared with those of Alberta and Sweden in Table II. The mean of the first sample of 24 males (1962-64) was slightly less than that of either Alberta or Sweden but when the sample was increased to 51 by including data obtained in 1965 and 1966 they exceeded the other two areas. Similar comparisons for female yearlings, 28 Alberta specimens with a mean substantially heavier than any of the male or the female samples from Québec and Sweden, suggest an unusual bias toward heavier animals in the sample in that the observed range (min.-max.) was subtantially similar to that of Québec and Sweden. Egorov (1965) records the live weight of two females (*A. a. pfizenmayeri*) of about the same age as 249.5 and 254.5 kg which falls within the range listed in Table II.

Moose weights are obviously affected by the seasons as well as by physical conditions of each individual. Conversion from dressed to live weights includes still further factors which make critical statistical analysis of most available weight data on adults suspect, if not meaningless. Only with the accumulation of large numbers of weights taken under controlled conditions, can we properly assess weight in relation to age classes or to geographic populations.

To date, accumulation of weight data for older moose has been based on extremely small samples of actual total weights with even fewer classified by even roughly estimated age groups. The weight data for Alberta moose provided by Blood *et al.* (1967) involved a conversion of dressed weights to whole weights based on a formula derived from whole weights of 35 specimens which were heavily biased toward the younger age groups (see above). The weight data on Québec moose (Heyland, 1964 and 1966) involved a conversion from eviscerated or hog dressed weight[2] to total weight, again based on a formula derived from total weights of only nine specimens. It would appear that the formulas used for both of these conversions should be critically checked against larger samples of actual total weights. For example, when we examine the visceral weight mean of 28 percent of total weight (Appendix 1 of Heyland, 1964), the sample includes only three individuals over 385 kg (850 lbs) in total weight. If the heavier weight end of the sample is extended by including the data from Peterson (1955, Table XI) and the males arranged in order of total weight, the following trends in Visceral Weight/Total Weight relationships result: 42.6/

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[2] Hog dressed weight is the weight of whole carcass with only the viscera (and most of the blood) removed.

TABLE II

Estimated total weight (kg) of yearling (16-18 months old) *A. alces* based on a 55 per cent carcass yield for Alberta and Sweden and a 28 percent visceral weight from Québec. (Blood *et al.* 1967; Markgren 1964; Heyland, 1964 and 1966)

Weight[3]	*A. a. andersoni* Alberta				*A. a. americana* Québec				*A. a. alces* Sweden			
	X̄	Min.	Max.	N	X̄	Min.	Max.	N	X̄	Min.	Max.	N
Dressed weight												
Males	152.9	115.1	193.2	34					154.4	118.0	215.0	65
Females	161.9	127.9	186.1						153.3	129.0	190.0	57
Eviscerated weight												
Males 1962-64[1]					199.3	117.2	253.1	24				
Males 1965-66[2]					204.0			51				
Females 1962-64[1]					192.6	130.9	257.7	11				
Females 1965-66[2]					203.4			34				
Total weight												
Males	277.9	209.5	351.3	34	276.8	162.8	351.5	24[1]	280.1	214.1	390.1	65
Males					283.4			51[2]				
Females	294.4	232.6	338.1	28	267.5	181.9	357.9	11[1]	278.1	234.0	344.7	51
Females					282.5			34[2]				

[1] Heyland, 1964.

[2] Heyland, 1964 and 1966.

[3] Dressed weight is based on carcasses with viscera, hide, feet and head removed. Eviscerated weight is based on carcasses with only viscera removed.

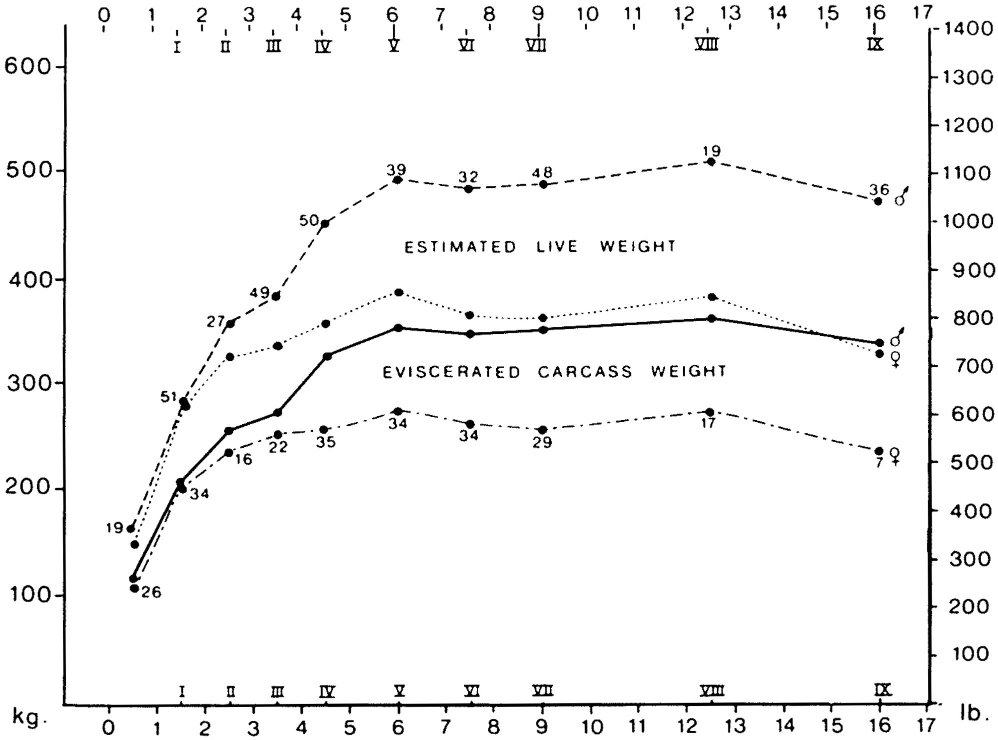

Figure 1. Mean eviscerated carcass and calculated total weights of Québec moose, *Alces a. americana*, plotted by sex and wear-class ages (data from Heyland, 1964, 1966). Numbers on the graph indicate sample sizes. The roman numbers represent the wear-classes and are positioned to represent their approximate average age on the abscissa along with calendar year ages in arabic numbers. This age assignment corresponds with that of Peterson (1955, fig. 65) based on tooth wear.

TABLE III

Weights (kg) of Québec moose based on summary of data from harvests during controlled hunts 1962-1966 (Heyland, 1964 and 1966)

Wear class age	*Males*			*Females*		
	Eviscerated carcass wt.		*Total wt.*[1]	*Eviscerated carcass wt.*		*Total wt.*[1]
	N	$\overline{X}$	$\overline{X}$	N	$\overline{X}$	$\overline{X}$
6 months	19	119.6	166.0	26	108.6	150.7
I	51	204.3	283.6	34	203.4	280.7
II	27	260.6	361.7	16	239.4	332.3
III	49	278.3	386.3	22	246.6	348.1
IV	50	328.7	456.2	35	260.6	361.7
V	39	357.4	496.1	34	280.5	389.3
VI	32	351.5	487.9	34	265.8	368.9
VII	48	353.9	491.2	29	262.4	364.2
VIII	19	368.6	511.6	17	277.8	385.6
IX	36	342.8	475.8	7	239.3	332.1

[1] The total weight has been calculated with a constant 28 percent visceral weight.

136.1 kg (31.3 percent), 65.8/192.8 (34.2 percent), 59/213.2 (28.7 percent), 84.3/394.6 (23.9 percent), 113.4/408.2 (27.8 percent), 90.7/442.3 (20.5 percent), 108.4/469.5 (23.0 percent), 113.4/523 (22.0 percent).

Visceral weights are obviously greatly influenced by the volume of food in the digestive tract. Apart from any pathological condition that might affect weight, the next most variable factor would appear to be the amount of visceral fat present. Although only a small sample, the above data suggest that the ratio of visceral weight to total weight tends to be greatest in the lower (younger?) weights and least in the heavier (older?) individuals. It is also of interest that of the six individuals weighing over 385 kg the visceral weight varied only between 90.7 and 113.4 kg or (20.5 to 28.7 percent) for a mean of 24.3 percent rather than 28 percent as used for an average. The total and visceral weights of the two cow moose for Québec were 47.7-181.4 kg (26.2 percent) and 56.7-204.1 (27.8 percent) which again represents the lower end of the weight range. It would seem logical that the development of antlers and the related supporting neck and shoulder muscles would have the effect of bulls manifesting a more variable Visceral Weight/Total Weight relationship at perhaps a slightly lower average percentage than for cows of comparable ages especially in older age categories.

The data on moose weight compiled by Heyland (1964 and 1966) provides the first reasonable sample of *A. a. americana* of weights by sex and age classes (wear classes) and is summarized in Figure 1 and Table III. The eviscerated carcass weight has been calculated and plotted separately so that it might be possible in the future

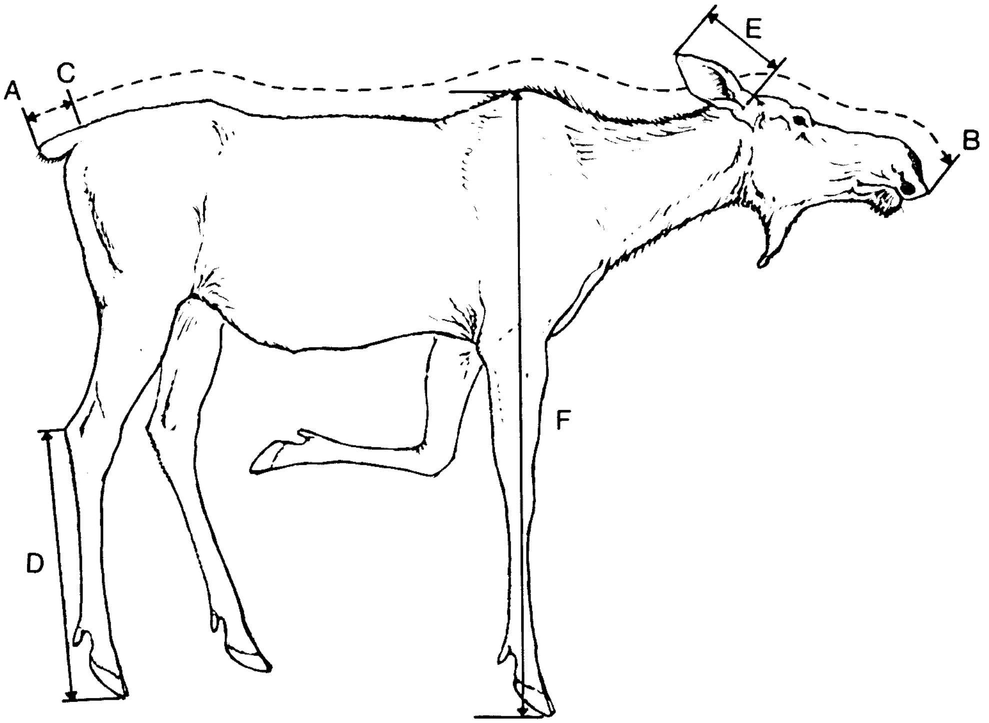

Figure 2. Standard external measurements for moose. Total length, A to B. Tail length, A to C. Hind foot, length, D. Ear from notch, E. Height at shoulder, F.

to establish a more precise Visceral Weight/Total Weight relationship based on further accumulations of actual total weights with precise visceral weights for comparisons.

In summary, the data graphed in Figure 1 can be divided into a pattern of four growth rates: 1) A steep growth period extending from birth to about 18 months with no significant differences between males and females. 2) From 18 months to wear class V growth continues at a less accelerated rate in both sexes, but with females increasing at a slower rate. 3) From wear class V to VIII weight tends to stabilize with the probability that the observed variation in both sexes result from responses to both individual (internal) and environmental (external) factors. 4) After wear class VIII both sexes begin a similar decline in weight. Limited additional weights have been reported as follows: *A. a. andersoni* — Timmermann (1972), *A. a. shirasi* — Doutt (1970), *A. a. gigas* — Rausch (1958), *A. a. pfizenmayeri* — Egorov (1965).

Measurements

As in the case of published weights, body measurements have not accumulated sufficiently in recent years to provide sufficient data for meaningful critical analysis in relation to age, sex or geographic variation. Blood *et al.* (1967) have recorded measurement summaries for 25 to 35 individuals from Alberta. Other recent records include those of Denniston (1956) and Doutt (1970) for *A. a. shirasi*, and those of Egorov (1956) for *A. a. pfizenmayeri* from Siberia. Undoubtedly there has been an accumulation of body measurements of moose in unpublished files. These data are seriously needed for an adequate assessment of growth rates in relation to age and/or size in relation to geographic variation. As with all field measurements of mammals, the variation of technique used in measuring limits the degree of accuracy obtainable with these data but larger samples will provide increased confidence and usefulness in future studies.

In order to standardize measurements that can be accumulated by various workers it is recommended that a flexible steel metric tape be used to take the following standard external measurements as illustrated in Figure 2:

TOTAL LENGTH — tip of nose to tip of tail vertebrae (A-B)

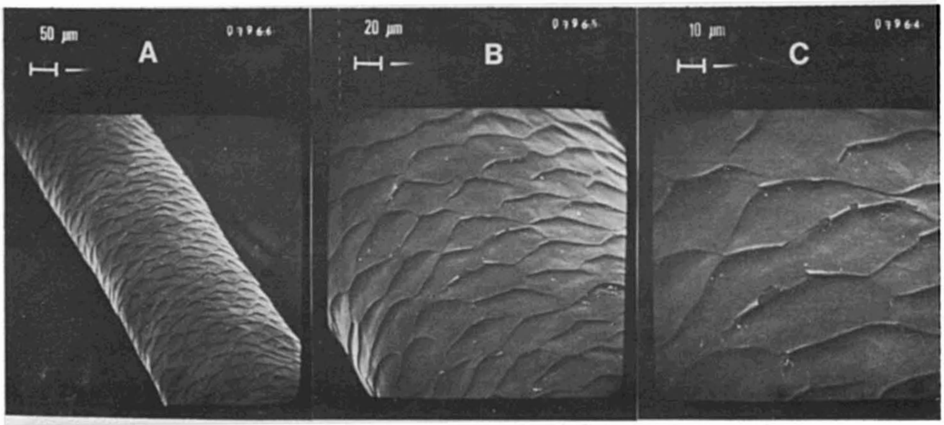

Figure 3. Moose hair at three magnifications photographed with a scanning electron microscope. A. 220X; B. 550X; C. 1100X.

TAIL LENGTH — tip of tail vertebrae to base of tail (A-C)

HIND FOOT LENGTH — top of heel joint to tip of hoof (D)

EAR LENGTH — top of ear to bottom of notch (E)

SHOULDER HEIGHT — top of shoulder above shoulder blade to tip of front hoof.

A number of girth measurements can also be taken when desired but these tend to be less precisely reproducable and subject to greater variability than the standard measurements.

Pelage

There does not appear to have been any noteworthy advances in recent years in our understanding of the pelage growth, molt patterns or seasonal changes in hair colour or structure

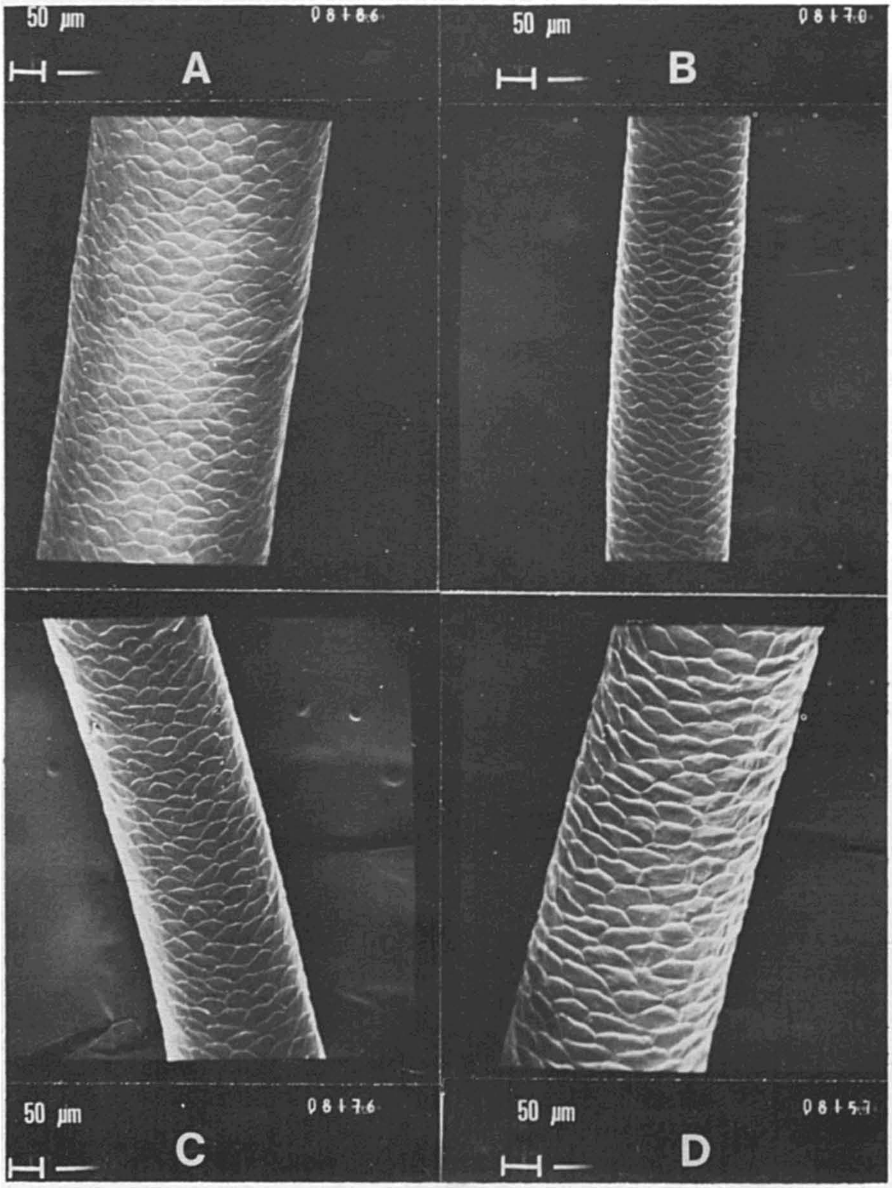

Figure 4. Cervid hairs compared at a lower magnification with a scanning electron microscope. A. moose, 160X; B. wapiti, 185X; C. white-tailed deer, 155X; D. caribou, 200X.

due to fading and/or wear. Adorjan and Kolenosky (1969) have included moose (adult in winter and calf in summer) in their manual for identification of hairs. They use the scale impression technique.

We have recently carried out a preliminary examination of the hair of moose, wapiti, deer and caribou using a scanning electron microscope. Our initial results (Fig. 3) indicate that the hair morphology can be vividly illustrated with the scale patterns clearly outlined in moose. Much more work will have to be carried out before we can define the normal variation in scale pattern that is manifested not only in the various portions of the individual hair examined but also in the hairs from various parts of the body.

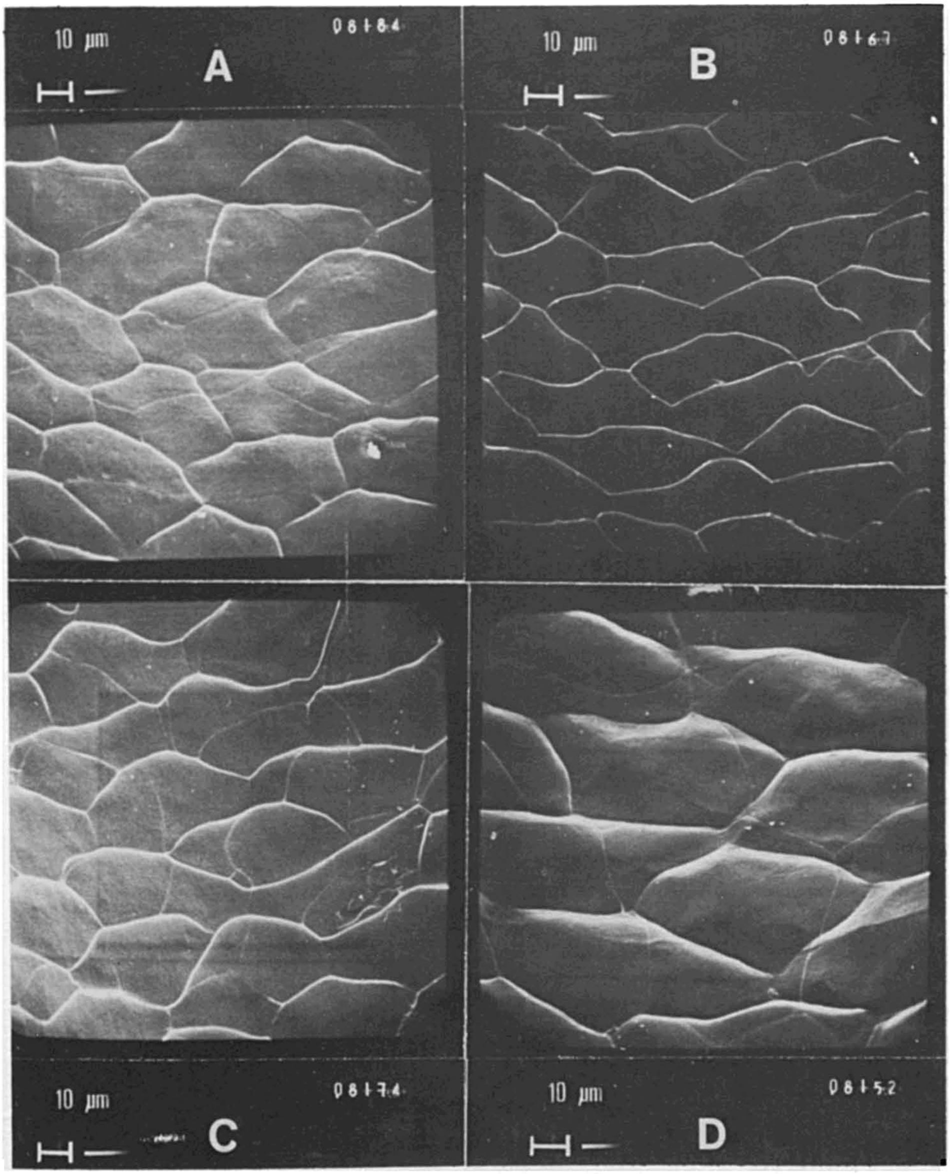

Figure 5. Cervid hairs compared at a higher magnification with a scanning electron microscope. A. moose, 800X; B. wapiti, 920X; C. white-tailed deer, 800X; D. caribou, 1000X.

Comparisons of wapiti (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), moose and caribou (*Rangifer tarandus*) are shown in Figures 4 and 5. Our preliminary results suggest that there may be a tendency for the cervid hair scale pattern to vary from rather elongate, irregular shaped and tightly flattened scales in wapiti, to less elongate but irregular shaped scales in deer, to more regularly shaped less flattened imbricated scales in moose, to deeply imbricated, thicker and more raised scales in caribou.

Antlers

Knowledge of the basic morphology, growth and development of Cervid antlers has been greatly advanced in recent years by the studies of Bubenik (1966, 1973). (For an English review of this important work, see van Zyll de Jong, 1967). Dr. Bubenik has continued his research on antlers and has published on the significance of antlers in the social life (Bubenik, 1968) as well as the general biological function of antlers in moose and other deer (Bubenik, 1971). He has also carried out some most interesting and fundamentally important studies involving the ethology of moose in relation to antlers which is yet to be published.

Dr. Bubenik has carried out a series of experiments using maniken moose heads with antlers of varying sizes in which he carried these "dummies" on his own head while approaching moose quite closely. He has found that the antlers provide visual stimuli of primary importance, ranking above most other stimuli. He found that the social significance of antlers of cervids reaches its highest development in moose. The ultimate publication of his findings will surely provide a major advancement in our knowledge of the real significance of the large palmate antlers of moose.

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INFECTIOUS AND PARASITIC DISEASES AND ARTHROPOD PESTS OF MOOSE IN NORTH AMERICA

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Résumé

Cet article comprend un répertoire de toutes les maladies infectieuses, des parasitoses ainsi que de tous les arthropodes observés chez l'orignal (*Alces alces*) en Amérique du nord :

(1) Arbovirus — Encéphalite de Saint-Louis, Encéphalite occidentale, Encéphalite de Californie. (2) Tumeurs épidermiques. (3) Diarrhée à virus des bovins. (4) Parainfluenza 3. (5) Leptospirose — *Leptospira pomona, L. autumnalis, L. biflexa, L. grippotyphosa.* (6) Brucellose — *Brucella.* (7) Listeriose — *Listeria monocytogenes.* (8) Charbon — *Bacillus anthracis.* (9) Nécrobacillose — *Spherophoros necrophorus.* (10) Actinomycose — *Actinomyces.* (11) Paratuberculose — *Mycobacterium paratuberculosis.* (12-17) Bactéries diverses — *Bacillus* spp., *Micrococcus* spp., *Corynebacterium* spp., *C. pyogenes, Streptococcus fecalis, S. salivarius.* (18) Sarcosporidiose — *Sarcocystis.* (19-20) Trematodes — *Paramphistorum* sp., *Fascioloides magna.* (21-25) Cestodes — *Taenia hydatigena, T. krabbei, Thysanosoma actinoides, Moniezia benedeni, Echinococcus granulosus.* (26-35) Nematodes — *Dictyocaulus viviparus, Haemonchus contortus, Nematodirella longispiculata, Oesophagostonum venulosum, Parelaphostrongylus tenuis (+Pneumostrongylus tenuis), Ascaris* sp., *Elaeophora schneideri, Setaria yehi, Wehrdikmansia cervipedis, Trichuris* sp. (36-38) Tiques — *Dermacentor albipictus, D. andersoni.* (39-40) Oestres — *Cephenemyia jellisoni, C. phobifera.* (41-68) Insectes — *Lyperosiops alcis, Simulium venustum, S. pictipes, Chrusops celvus, C. cincticornis, C. cuclux, C. excitans, C. frigidus, C. lateralis, C. mitis, C. montanus, C. niger, Hybomitra affinis, H. arpadi, H. criddlei, H. epistates, H. illota, H. lasiophthalma, H. lurida, H. microcephala, H. nuda, H. trepida, H. trispila, H. typhus, H. zonalis, Tabanus marginalis,* et *T. nigripes.*

A son arrivée de la région paléarctique, l'orignal semble avoir apporté peu de parasites et de maladies. Les affections dont souffre cet ongulé sur notre continent semblent lui avoir été transmises par le bétail et surtout par les cerfs indigènes (genre *Odocoileus*). Des changements dans l'aire de répartition géographique de ces derniers ont permis la transmission de certains agents pathogènes à l'orignal. Il est important d'intensifier les recherches sur les maladies de l'orignal.

Abstract

The literature on the following infectious and parastic diseases and insect pests of moose (*Alces alces*) in North America is reviewed :

(1) Arboviruses — St. Louis encephalitis, Western encephalitis, California encephalitis. (2) Skin tumours. (3) Bovine Virus Diarrhea. (4) Parainfluenza 3. (5) Leptospirosis — *Leptospira pomona, L. autumnalis, L. hardjo, L. biflexa, L. grippotyphosa.* (6) Brucellosis — *Brucella.* (7) Listeriosis — *Listeria monocytogenes.* (8) Anthrax — *Bacillus anthracis.* (9) Necrobacillosis

— *Spherophoros necrophorus.* (10) Actinomycosis — *Actinomyces.* (11) Johne's Disease — *Mycobacterium paratuberculosis.* (12-17) Miscellaneous bacteria — *Bacillus* spp., *Microccus* spp., *Corynebacterium* spp., *C. pyogenes, Streptococcus fecalis, S. salivarius.* (18) Sarcosporidiosis — *Sarcocystis.* (19-20) Trematodes — *Paramphystomum* sp., *Fascioloides magna.* (21-25) Cestodes — *Taenia hydatigena, T. krabbei, Thysanosoma actinoides, Moniezia benedeni, Echinococcus granulosus.* (26-35) Nematodes — *Dictyocaulus viviparus, Haemonchus contortus, Nematodirella longispiculata, Oesophagotonum venulosum, Parelaphostrongylus tenuis (+ Pneumostrongylus tenuis), Ascaris* sp., *Elaeophora schneideri, Setaria yehi, Wehrdikmansia cervipedis, Trichuris* sp. (36-38) Ticks — *Dermacentor albipictus, D. andersoni.* (39-40) Nasal bots — *Cephenemyia jellisoni, C. phobifera.* (48-68) Biting insects — *Lyperosiops alcis, Simulium venustum, S. pictipes, Chrysops celvus, C. cincticornis, C. cuclux, C. excitans, C. frigidus, C. lateralis, C. mitis, C. montanus, C. niger, Hybomitra affinis, H. criddlei, H. epistates, H. illota, H. lasiophthalma, H. lurida, H. microcephala, H. nuda, H. trepida, H. trispila, H. zonalis, Tabanus marginalis,* and *T. nigripes.*

The moose probably brought few parasites and diseases from the Old World. Those reported from moose in North America seem mainly to have been acquired on this continent from livestock and especially from native deer of the genus *Odocoileus.* Changes in the distribution of strictly native deer have brought some disease agents into contact with moose populations and this has apparently resulted in the main disease problems of moose in North America. Much more research on the diseases of moose is required.

Introduction

In general our knowledge of the infectious and parasitic diseases of moose (*Alces alces*) in North America is still fragmentary. A considerable number of parasites and disease-causing organisms have been found in this host but there is a dearth of detailed distributional and quantitative information. Also the list of parasites occurring in moose is undoubtedly incomplete especially as it concerns the intestinal round worms (which are difficult to collect in such a large host), the biting insects, and the ectoparasites. There are, for example, no reports of lice, mites or louse flies although they occur commonly on various other cervids in North America. Also, no blood Protozoa have been reported and there is no report of the species of mosquitoes which feed on moose although they probably transmit at least one of the filarial worms occurring in this host.

The present article attempts to provide a summary of the present status of our knowledge of the infectious and parasitic diseases of moose in North America. Recent investigations of parelaphostrongylosis have suggested that an helminth can be responsible for significant declines in moose populations under certain conditions. This indicates the need to consider disease in management in a way unforeseen even a decade ago. Apart from its practical importance a more complete knowledge of the diseases and parasites of moose may help to shed further light on the history of moose on this continent and the relationship of moose to other wild ruminants. In a brief concluding section the authors will point out that the diseases and parasites of moose in North America tend to reflect the peculiar history of the species as a relatively recent immigrant to this continent. It is striking that the major diseases of moose in North America seem to be acquired from strictly native cervids of the genus *Odocoileus,* and also from livestock.

Viral, bacterial, and protozoan diseases

Arboviruses

It is characteristic of arboviruses that they multiply within the body of an arthropod vector ; yellow fever, and eastern and western equine encephalitis are well known examples (Karstad, 1970).

Trainer and Hoff (1971) obtained one reactor to St-Louis encephalitis, two reactors to western encephalitis, and 16 reactors to California encephalitis in a total of 23 sera tested from moose from the Cypress Hills Provincial Park in southeastern Alberta.

Skin tumours (papilloma, fibroma)

Most cutaneous tumours in deer and moose seem to be associated with a virus (for review see Fay, 1970). The mode of transmission is not clear but may be by contact of animals (Friend, 1967) or possibly by arthropod vectors. The tumours are not considered deleterious unless they are massive and interfere with sight and feeding. Murie (1934) reported skin tumours on moose on Isle Royale, Ritcey and Edwards (1958) noted them on two moose from British Columbia, and Fyvie (1968) has reported a case in Ontario.

Bovine Virus Diarrhea and Parainfluenza 3

Thorsen and Henderson (1971) reported antibodies to these viruses in a few adult and juvenile moose from the Cypress Hills in Alberta (see also Barrett, 1972). Transmission is by direct contact of infected and uninfected animals. Livestock probably serve as the main source of the infections.

Leptospirosis

The disease is caused by antigenically distinct serotypes of the spirochaete genus *Leptospira* (see Roth, 1970) and is widespread in domesticated as well as a great variety of wild animals. Skunk and raccoon may be important reservoirs of the disease in North America (McGowan *et al.*, 1963).

The organism usually enters the host through the mucous membranes of the eye, nose, mouth or abrasions on the skin. Infected animals pass the leptospire in their urine and drinking water is probably an important source of the infection. Little is known about the signs and pathogenesis of the disease in wild animals but anorexia, weakness, anaemia, haemoglobinuria, icterus, fever, death (Reilly *et al.*, 1962 ; Roth, 1970) as well as abortion (experimentally, see Trainer *et al.*, 1961) associated with the serotype *L. pomona* have been reported in white-tailed deer. For a recent review of the subject the reader is referred to Roth (1970).

McGowan *et al.* (1963) were the first to present serologic evidence of leptospirosis in wild moose (in 4 of 58 moose from the Kenora district, Ontario) and they also reported that one captive moose became infected through exposure to contaminated water. Between 1965 and 1968, 25 moose sera from northern Ontario were tested at the Ontario Veterinary College. Low titers to *L. pomona, L. autumnalis, L. hardjo,* and *L. biflexa* antigens were found in 3 of these moose (Kingscote, 1971). The Report of the Committee on Leptospirosis (1971) reported *L. grippotyphosa* and *L. pomona* antibodies in moose in Minnesota.

Brucellosis

Brucellosis is caused by a bacterial *(Brucella)* infection of many animals including man. It is known throughout the world and is a major disease of livestock. Transmission is usually oral but eyes, the genital tract, and wounds can be the source of entry of the bacillus. There is evidence of the disease being transmitted during coitus and during a period of bacteraemia blood-sucking arthropods may transmit the agent (Witter and O'Meara, 1970). The bacterium localizes in the uterus and results in abortion. There are apparently only three published reports of brucellosis in moose namely, Jellison *et al.* (1953) in a moose from Montana, Fenstermacher and Olsen (1942) in a moose from Minnesota, and Corner and Connell (1958) who examined animals in Elk Island Park, Alberta. For a detailed review of the disease as it relates to wild animals see Witter and O'Meara (1970).

Listeriosis

Listeriosis, caused by the bacterium *Listeria monocytogenes*, is a widespread disease of many wild and domesticated animals. Animals contact the bacterium in the environment, from each other, and possibly by way of biting arthropods. The infection was reported by Archibald (1960) in a moose from Nova Scotia with clinical signs of parelaphostrongylosis. Later studies by Benson (1958) and Gray (1955) failed to detect *L. monocytogenes* in the brain of several moose with neurologic disease. The pathogenesis and clinical characteristics of the disease are poorly understood and require more study. For a review of the subject as it relates to wild animals, the reader is referred to Eveland (1970).

Anthrax

The causal agent of anthrax is *Bacillus anthracis* which on exposure to air forms resistant spores which may persist in the soil for many years. Animals contract the disease usually by ingesting contaminated food and water. Biting insects and blow flies may also transmit or disseminate the bacterium. The course of the disease may be rapid with the animal succumbing to septicaemia or it may be more prolonged and the animal may recover. Anthrax has been reported in moose in northwestern Canada (Choquette, 1970) and in Wyoming (Good, 1956). For a review of anthrax as it relates to wild animals see Choquette (1970).

Necrobacillosis

This disease is associated with the bacterium *Spherophoros necrophorus*. The best known sign of the disease is inflammation and necrosis of the foot (foot rot) but buccal abcesses may also occur and be associated with excessive salivation. The bacterium may eventually invade the respiratory and alimentary tracts and associated organs. Necrobacillosis is usually associated with animals which are crowded about water holes, and it is suggested the bacterium invades the foot by way of tiny lesions. Murie (1934) reported foot rot in moose on Isle Royale (see also below under *Miscellaneous Bacteria*). For a review of the subject as it relates to wild animals the reader is referred to Rosen (1970).

Actinomycosis

The disease, caused by the bacterium *Actinomyces*, manifests itself mainly by granulomatous lesions in the mandibular region (i.e. lumpy jaw). Cowan (1951) and Ritcey and Edwards (1958) have reported this disease in moose in British Columbia. The latter authors associated actinomycotic-like lesions with food impaction and worn teeth in older moose. For a more detailed review of the disease see Howe (1970).

Johne's disease

Soltys *et al.* (1967) reported a clinical case of Johne's disease in a young captive moose from a zoological park in Ontario. The disease, which causes diarrhea and emaciation, is associated with the presence of the bacterium *Mycobacterium paratuberculosis*.

Miscellaneous bacteria

Barrett (1972) reported that nasal swabs from moose from the Cypress Hills in Alberta contained *Bacillus* spp., *Micrococcus* spp. *Corynebacterium* spp., *Streptococcus fecalis*, and *S. salivarius*. The significance of such findings is unknown. *Corynebacterium pyogenes* was also cultured from a diseased foot of a moose from the same region (cf. *Necrobacillosis* above).

Sarcosporidiosis

Sarcocystis, a protozoon of uncertain affinities, forms small whitish streaks in the muscle of a great many birds and mammals. Its mode of transmission and pathogenicity are not understood. De Vos and Allin (1949) reported the parasite in the myocardium of a moose from Ontario. Kelly *et al.* (1950) reported *Sarcocystis* in the myocardium of a moose from British Columbia. The parasite is probably a coccidian of canids.

Flatworms (Platyhelminthes)

FLUKES (TREMATODES)

Paramphistomum sp.

Members of the genus *Paramphistomum* are cosmopolitan rumen flukes of sheep, goats, cattle, deer and other ruminants. The species in moose is probably *P. liorchis* although it has generally been referred to *P. cervi* (Schrank, 1790). In North America various aquatic and amphibious snails (e.g. species of *Stagnicola, Fossaria* and *Pseudosuccinea*) serve as intermediate hosts and the metacercariae are found encysted on vegetation where they are readily available to grazing animals, including the moose. When ingested the metacercariae penetrate the duodenum before establishing themselves in the rumen. Invasion of the duodenum is considered a major cause of the pathogenesis of the infection in livestock. Nothing is known of the pathology of paramphistomes in moose although the parasite has been reported in this host in Minnesota (Wallace, 1934 ; Olsen and Fenstermacher, 1942 ; Fenstermacher and Olsen, 1942), Ontario (Peterson, 1955), and Newfoundland (Threlfall, 1967). It is probably a widespread parasite of moose throughout North America.

Fascioloides magna (Bassi, 1875)

The large American liver fluke was originally described from captive deer near Turin, Italy but there is now general agreement that its spotty distribution in captive and wild cervids in Europe resulted from the importation of infected American wapiti and that *Fascioloides magna* originated in North America (Swales, 1935 ; Price, 1953). According to Swales (1935), eggs passed in faeces hatch in water after approximately 35 days at summer field temperatures releasing miracidia which penetrate and develop in aquatic snails of the genera *Lymnaea (Stagnicola), Fossaria* and *Pseudosuccinea* (Krull, 1933a, 1933b ; Swales, 1935 ; Griffiths, 1959 ; Dutson *et al.*, 1967). Cercariae emerging from snails after 56 days at 24°C quickly encyst on aquatic vegetation and in a matter of hours are infective to ruminants. Recent reviews (Price, 1953 ; Becklund, 1964) report *F. magna* in cattle, sheep and wild ungulates in almost half the states of continental United States and the Canadian provinces of British Columbia, Alberta, Ontario, Québec (Choquette and Gibson, 1971) and Manitoba (Lankester, 1972, 1973).

F. magna was first recorded in moose in northern Minnesota where during a ten year period 4 of 33 sick animals examined harboured liver flukes (Fenstermacher and Jellison, 1933 ; Wallace, 1934 ; Fenstermacher, 1934a, 1934b, 1937 ; Fenstermacher and Olsen, 1942 ; Olsen and Fenstermacher, 1942). Dillon in correspondence (see Kingscote, 1950) mentioned the occurrence of *F. magna* in moose of northern Michigan and Cowan (1951) found the parasite in one moose near Golden, British Columbia. Kingscote (1950) found eggs believed to be those of *F. magna* in 4 of 10 samples of moose droppings in Ontario. Peterson (1955) reported an infected animal from the Kenora district of Ontario. Fyvie (1966) recorded 8 infected animals during a 15 year study in Ontario.

In a more recent study of moose in Minnesota (Karns, 1972), 87 per cent of 111 animals taken by hunters in one season from the northwestern portion of the state were infected while only 17 per cent of 11 moose from northeastern Minnesota had flukes. In adjoining southeastern Manitoba 7 of 11 moose examined during a 12 month period were infected (Lankester, 1972, 1974); *F. magna* had not previously been reported from this province.

Clinical disease caused by *F. magna* is rarely seen in white-tailed deer and wapiti (Swales, 1936 ; Fenstermacher *et al.*, 1943; Cowan, 1951; Griffiths, 1962; Flook and Stenton, 1969) although Cheatum (1951) believed heavy infections accompanied by inanition may contribute to death of deer during periods of winter hardship. In deer and wapiti, *F. magna* matures in thin-walled cavities which are continuous with bile ducts allowing fluke vomitus and eggs to pass to the intestine (Swales, 1935, 1936).

The death of one moose examined by Fenstermacher and Olsen (1942) was believed due to liver damage caused by a large number of migrating *F. magna*. Karns (1972) reported extensive liver damage in infected moose in Minnesota and Lankester (1972) found liver lesions caused by *F. magna* in moose similar to « liver rot » produced in infected cattle, a host in which *F. magna* cannot complete its life cycle (Swales, 1935, 1936). In moose, extensive hepatic fibrosis results from invasion by even a few flukes ; thick-walled closed cysts are common, and apparently flukes rarely mature and produce eggs (Lankester, 1972, 1973).

Although evidence presently available is insufficient to evaluate the importance of liver flukes as a pathogen of moose, it appears that moose, like cattle, may be unsuitable hosts for *F. magna*. Liver fluke may not persist in moose populations in the absence of more suitable cervid hosts such as white-tailed deer. Because of their intensive aquatic feeding habits during summer, moose co-habiting with white-tails may be particularly vulnerable to infection. The significance of this parasite in relation to the health of moose should be examined more closely.

TAPEWORMS (CESTODES)

Taenia hydatigena Pallas, 1766

The larval stage *(Cysticercus tenuicollis*, the thin-necked bladder worm*)* of *Taenia hydatigena*, a parasite of canids and felids, occurs in rodents as well as in wild and domesticated ruminants, including moose. The adult stage of the parasite has been reported in coyotes, wolves, and lynx from many parts of North America (see Leiby and Dyer, 1971). Freeman *et al.* (1961) have shown it is the common cestode of wolves in Ontario. Gravid proglottids are eliminated in the faeces of the definitive host. When eggs are ingested by the vertebrate intermediate host, larvae penetrate the gut wall and reach the liver by the portal system. Some larvae develop into cysticerci in the liver (especially in moose) but others may move to other sites in the body. The cysticerci are infective to the final host about 7-8 weeks after they have reached the liver. The prepatent period in the final host is about 2 1/2 months.

The parasite has been reported in moose in Minnesota (Fenstermacher and Jellison, 1933 ; Wallace, 1934 ; Fenstermacher, 1937 ; Fenstermacher and

Olsen, 1942), Alberta and British Columbia (Hatter, 1948 ; Cowan, 1951 ; Ritcey and Edwards, 1958 ; Stelfox, 1962 ; Barrett, 1972), Ontario and Saskatchewan (Sweatman and Plummer, 1957) and Alaska (Rausch and Williamson, 1959 ; Voge, 1962). Cysts in the myocardium of a moose from Ontario examined by DeVos and Allin (1949) may refer to this species or *T. krabbei.*

There is little evidence that these parasites are significant pathogens of moose. For a more detailed review of the biology of *T. hydatigena* and its prevalence in moose the reader is referred to Leiby and Dyer (1971). Dikmans (1939) included *T. hydatigena* in his list of parasites of moose.

Taenia krabbei Moniez, 1879

Larval stages (cysticerci) have been reported in the muscles of the legs, shoulders, tongue and heart of various wild cervids, including moose. The adult stage is reported in coyotes, wolves, lynx and bears which become infected from eating flesh with cysticerci (Leiby and Dyer, 1971 ; Samuel, 1972). The prepatent period in the final host is 34-37 days (Sweatman and Henshall, 1962). Infected moose have been found in Alaska (Dunagan, 1957), British Columbia (Ritcey and Edwards, 1958), Alberta (Stelfox, 1962 ; Samuel, 1972), Saskatchewan and Ontario (Sweatman and Henshall, 1962), Maine (Lamson, 1941) and Minnesota (Fenstermacher, 1934b). There is no evidence that the parasite is significantly pathogenic in moose but the presence of cysticerci in the flesh is undesirable from the point of view of the hunter (the condition is often referred to as measles). For a recent more detailed review of *T. krabbei,* the reader is referred to Samuel (1972).

Thysanosoma actinoides Diesing, 1835

The fringed tapeworm is a cosmopolitan parasite of the bile ducts and small intestine mainly of domesticated ruminants. Larval stages occur in psocid insects (Allen, 1959). Dikmans (1939) recorded it as a parasite of moose without comment but according to Olsen and Fenstermacher (1942) the specimens came from Wyoming. Barrett (1972) reported this parasite in moose from the Cypress Hills of Alberta. Infected bile ducts may become dilated, thickened, and sometimes occluded (Allen and Kyles, 1960).

Moniezia benedeni Moniez, 1879

This is a cosmopolitan tapeworm of the intestine of wild and domestic ruminants. The larval stage (cysticercoid) occurs in oribatid mites. It has been reported in moose in Minnesota (Wallace, 1934 ; Jellison, 1939 ; Fenstermacher and Olsen, 1942), Alberta (Barrett, 1972) and British Columbia (Cowan, 1951). It is probably harmless.

Echinococcus granulosus (Batch, 1786)

The larval stage (hydatid cyst) occurs commonly in the lungs and occasionally the liver of moose whereever moose and large canids co-exist. In Canada and northern United States the sylvatic cycle includes wolves and to some extent coyotes as final hosts in which the small adult tape-worm occurs in the intestine (Holmes and Podesta, 1968). In addition to moose, a variety of ungulate intermediate hosts may become infected by ingesting eggs in the faeces of canids or on contaminated vegetation (see Leiby and Dyer, 1971). The larvae released from the egg in the small intestine penetrate the mucosa, enter the circulation, and eventually lodge in the lung or liver where the hydatid cyst matures slowly attaining a diameter of 1 cm in elk after 5 months (Green, 1949). Pulmonary hydatid cysts are most numerous in older animals (Green, 1949 ; Rausch, 1952). In canids infected by eating organs with cysts, the adult tapeworm matures to produce eggs in 6 to 7 weeks and is known to live up to 20 months in the dog (Leiby and Dyer, 1971).

Hydatid cysts have been reported in moose in Minnesota (Riley, 1933 ; Fenstermacher and Jellison, 1933 ; Wallace, 1934 ; Fenstermacher, 1937 ; Riley, 1939 ; Olsen and Fenstermacher, 1942 ; Karns, 1971), Isle Royale (Sweatman, 1952 ; Mech, 1966), Alaska (Rausch, 1952 ; Spencer and Chatelain, 1953 ; Rausch, 1959), Canada generally (Sweatman, 1952 ; Wolfgang and Poole, 1956), British Columbia (Hatter, 1948 ; Cowan, 1948 ; Ritcey and Edwards, 1958), Alberta (Stelfox, 1962), Saskatchewan (Harper *et al.*, 1955), Manitoba (Hadwen, 1932), and Ontario (Law and Kennedy, 1933 ; Peterson, 1949 ; de Vos and Allin, 1949 ; Fyvie, 1966).

Sylvatic echinococcosis may have been introduced to North America by moose as already suggested by Sweatman and Williams (1963) but the possible importance of other cervids in this respect, such as caribou and wapiti which also immigrated fairly recently to the New World cannot be ignored (Rausch, 1967). Nevertheless, it is presently evident that *E. granulosus* is firmly established in the boreal forest region by the mediation of moose which is the cervid most commonly found infected.

Cowan (1951) suggested heavy infections in wapiti might impair an animal's ability to survive adverse conditions. Ritcey and Edwards (1958) reported the sudden death of a young cow moose with numerous pulmonary cysts. Cowan (1951), Fenstermacher (1937), Peterson (1955), and Mech (1970) have suggested that animals with many pulmonary hydatid cysts may be more vulnerable to predation and other environmental pressures than uninfected animals. According to Rausch (1952), however, the hydatid cyst of *E. granulosus* is essentially non-pathogenic in moose and as numerous cysts are usually seen only in older animals, the poor physical condition often associated with such infections can usually be attributed to the age of the host.

As man is also a suitable intermediate host of *E. granulosus*, care should be taken by wildlife personnel in handling specimens of wolf faeces and hunters should be cautioned against feeding organs of moose containing cysts to domestic dogs in which the adult tapeworm can develop and pass eggs.

Roundworms (Nematodes)

Dictyocaulus viviparus (Bloch, 1782)

This is a cosmopolitan trichostrongyloid parasite of the trachea, bronchi, and bronchioles of livestock (cattle, sheep) and various wild ruminants. *D. hadweni* and *D. eckerti* are regarded as synonyms of this species (Chapin, 1925 ; Dikmans, 1936) but Gupta and Gibbs (1971), Presidente *et al.* (1972), and Presidente and Knapp (1973) have recently marshalled experimental evidence to suggest the species in cervids in North America is at least a different strain from that in livestock. Eggs containing first-stage larvae pass up the bronchial escalator, are swallowed, and the larvae develop in the external environment to the third stage which is ingested with the food of the final host.

D. viviparus has been reported in moose in western Canada (Cowan, 1951), Minnesota (Fenstermacher, 1934a, 1934b ; Fenstermacher and Olsen, 1942 ; Olsen and Fenstermacher, 1942 ; Wallace, 1934), Newfoundland (Threlfall, 1967), Maine (Lamson, 1941), and Ontario (Anderson, unpublished data).

There is little evidence that *D. viviparus* is an important pathogen of moose. Fenstermacher and Olsen (1942) examined a moose with many worms associated with lung congestion. The parasite is an important pathogen of deer and livestock and under suitable conditions one would expect it to be pathogenic in moose but there is not yet sufficient information.

Haemonchus contortus (Rudolphi, 1803)

Haemonchus contortus is a cosmopolitan abomasal worm of livestock and wild ruminants. It is regarded as one of the most important parasitic pathogens of sheep especially in warm moist climates. The parasite sucks blood and its life cycle is direct with the eggs developing in the external environment. The first-stage larvae, which hatch, and subsequent stages up to the infective third are attained in a few days. The infective larvae are long-lived and persist in the ground or on vegetation. The final host ingests the infective stage with its food. There is apparently only one report of this parasite in moose, that of Ransom (1911) who apparently identified it from several animals.

Nematodirella longispiculata Yorke and Maplestone, 1926

N. longispiculata is a widespread cosmopolitan parasite of the small intestine of sheep, goats, and various wild ruminants (*N. alcidis* is regarded as a synonym). According to Levine (1968) eggs are passed in the faeces and development, including two larval moults, takes place in the egg. The infective third-stage larvae hatch and contaminate the ground and vegetation from which they are ingested by the final host. There is apparently no evidence that the species sucks blood.

A number of authors have reported this nematode from moose, sometimes in great numbers, but nothing is known about its pathogenicity in this host. The reports may be summarized as follows : Minnesota — Dikmans (1932), Wallace (1934), Fenstermacher (1934a, 1934b), Olsen and Fenstermacher (1942), Fenstermacher and Olsen (1942) ; Newfoundland — Threlfall (1967) ; British Columbia — Cowan (1946) ; Alberta — Cowan (1951), Barrett (1972) ; Ontario — Peterson (1955). It can probably be assumed that the parasite occurs in moose everywhere in North America.

Oesophagostomum venulosum (Rudolphi, 1805)

This species occurs mainly in the large intestine of sheep, goats and deer throughout the world. Eggs are passed in faeces. These develop in the external environment into the third infective stage which is ingested by grazing animals.

Olsen and Fenstermacher (1942) and Fenstermacher and Olsen (1942) collected 22 specimens from a moose in Minnesota. There appears to be no further reports of the species in moose in North America.

Ostertagia spp.

Members of this genus are common abomasal trichostrongyles of ruminant animals. The life cycle is similar to that of *O. venulosum*. Barrett (1972) reported this genus in one of 22 moose examined from the Cypress Hills, Alberta.

Parelaphostrongylus tenuis (Dougherty, 1945) *(=Pneumostrongylus tenuis)*

Parelaphostrongylosis is a neurologic disease associated with the presence of *P. tenuis* in the central nervous system of the host. The disease has been reported in wild moose in Minnesota (Thomas and Cahn, 1932 ; Fenstermacher and Jellison, 1933 ; Fenstermacher, 1934, 1934a, 1937 ; Fenstermacher and Olsen, 1942 ; Loken *et al.*, 1955 ; Kurtz *et al.*, 1966 ; Karns, 1967), Maine (Lamson, 1941; Gilbert, 1974), Nova Scotia (Cameron, 1949 ; Benson, 1955, 1958 ; Smith and Archibald, 1967 ; Smith *et al.,* 1964 ; Telfer, 1967), New Brunswick (Smith *et al.,* 1964 ; Smith and Archibald, 1967 ; Kelsall and Prescott, 1971), Ontario (Thomas and Cahn, 1932 ; Anderson, 1965c) and Manitoba (Lankester, 1972, 1973). The disease has been produced experimentally in moose (Anderson, 1964), caribou (Anderson and Strelive, 1968), wapiti and mule deer (Anderson *et al.,* 1966), occurs in wild wapiti in eastern North America (Anderson *et al.,* 1966; Carpenter *et al.,* 1973), and has been reported in European reindeer and caribou introduced into Ontario (Anderson, 1970b), Maine (Behrend and Witter, 1968) and Wisconsin (Trainer, 1973).

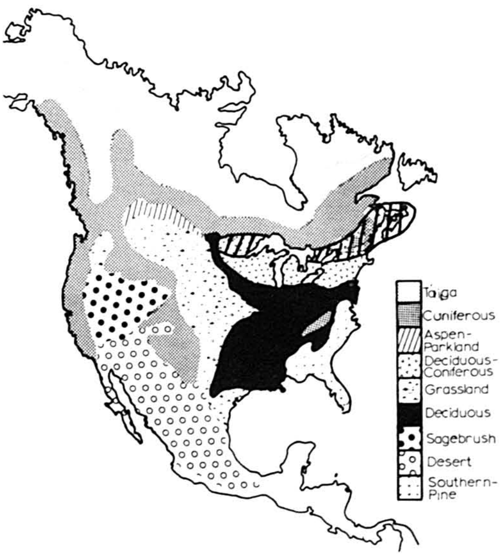

Figure 1. A schematic map of the major biomes in North America, adapted from *Ecology and Field Biology* by Robert L. Smith (Harper and Row 1966). *Parelaphostrongylus tenuis* occurs in white-tailed deer throughout the Deciduous Biome and the Deciduous-Coniferous Ecotone, some southern parts of the Coniferous Biome, and in the Aspen-Parkland Ecotone probably as far west as central Saskatchewan. As indicated on the map, (heavy vertical lines), the main potential endemic zone for parelaphostrongylosis in moose includes the northern one half to one third of the Deciduous-Coniferous Ecotone where the ranges of moose and deer overlap in eastern North America. Moose neurologic disease has not been reported, however, from all parts of the zone indicated on the map and is still unreported from the Aspen-Parkland.

P. tenuis is a common but clinically silent parasite of white-tailed deer over much of its range in eastern North America (for reviews see Anderson 1965b, 1968, 1971 ; Prestwood and Smith, 1969 ; Bindernagel and Anderson, 1972a, 1972b). It occurs generally in deer throughout the deciduous forest biome and the deciduous-coniferous ecotone (Fig. 1). The parasite has spread northward with deer within the last 100 years into the latter regions as well as the coniferous biome all of which have frequently been turned back to earlier successional stages by human activities (forestry, agriculture, fires), and it is principally here that the parasite transfers to moose and is associated with neurologic disease in this host. The parasite has been reported in deer in the aspen parklands of Manitoba and perhaps Saskatchewan and it has been suggested that this may be the only natural route for it to reach western North America (Bindergel and Anderson, 1972). The apparent absence of *P. tenuis* in Alberta has been reported by Samuel and Holmes (1974). Anderson (1972) has summarized knowledge of the ecological relationships between white-tailed deer, the parasite, and native cervids in North America. Karns and Jordan (1969) examined 221 faecal samples from moose on Isle Royale and reported finding a single larva of *P. tenuis* in each of two samples. However, larvae cannot be idenfified with such confidence and the existence of *P. tenuis* on this deer-free island could only be demonstrated by the discovery of adult worms in the cranium of moose. A substantial body of sound data suggests the parasite occurs only in those moose sharing range with infected white-tailed deer.

In the adult stage, *P. tenuis* inhabits the subdural space and the cranial venous sinuses of deer (Anderson, 1963,

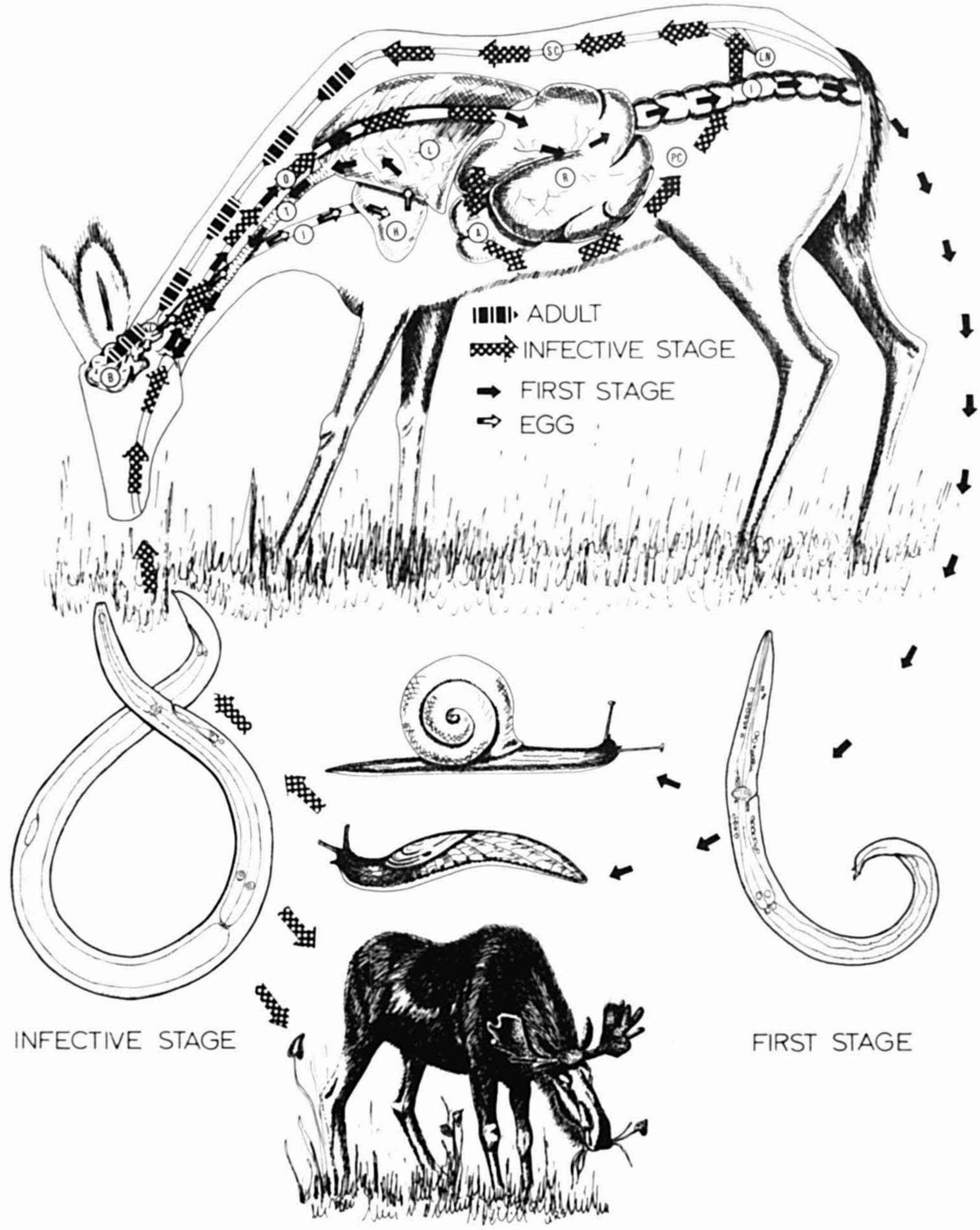

Figure 2. The life cycle of *Parelaphostrongylus tenuis* and the relationship of the parasite, white-tailed deer, and moose. Adult worms occupy the cranial venous sinuses. Eggs reach the heart via the jugular veins and are pumped to the lungs in which they develop to the first stage. The latter migrate up the respiratory tract, are swallowed, and passed in faeces. First-stage larvae develop in terrestrial gastropods to the infective stage. Infected gastropods containing infective larvae are accidently ingested by deer. The infective larvae migrate through the wall of the abomasum, across the peritoneal cavity, and along spinal nerves to the spinal cord where development to the adult stage takes place. Adults migrate towards the head region and many eventually invade the cranial sinuses. Moose on deer range become involved by ingesting gastropods containing infective larvae. The latter behave in moose as they do in deer. The developing worms in the central nervous system as well as adult worms which have repenetrated the brain and spinal cord cause, however, the characteristic neurologic signs associated with parelaphostrongylosis in moose. A = abomasum; B = brain; H = heart; I = intestine; J = jugular vein; L = lung; LN = lumbar nerves; O = oesophagus; PC = peritoneal cavity; R = rumen; SC = spinal cord; T = trachea.

1965a). Eggs and larvae are carried by the venous system to the lungs. Eggs develop in the lungs and first-stage larvae pass up the bronchial escalator, are swallowed, and passed in the faeces (Fig. 2). The larvae are resistant to dry conditions and can withstand freezing temperatures. They are, therefore, easy to detect by floating faeces (even those which have been frozen) in warm water in a funnel and examining the material in the bottom of the funnel (the Baermann technique). Larvae penetrate into the foot of terrestrial gastropods and develop to the infective stage in a few weeks at summer temperatures. Infective larvae survive winter in the intermediate host (Lankester and Anderson, 1968). Moose apparently become infected by accidently ingesting gastropods while feeding. Important intermediate hosts, at least in Ontario, appear to be species of snails of the genus *Zonitoides* and the common woodland slug *Deroceras laeve (= gracile)* (Lankester and Anderson, 1968). Infective larvae penetrate the stomach of deer, enter the body cavity, and migrate to the spinal cord where they grow to the subadult stage in the dorsal horns of grey matter. They eventually migrate into the subdural space and from there to the cranial region where eggs are produced (Fig. 3). The parasite behaves similarly in moose but the activities of the worms in the central nervous system result in tissue damage which produces the striking clinical disease associated with the infection in this host. The evidence indicates that small numbers of worms (1-3) can cause fatal disease in moose and cervids other than white-tailed deer.

Signs of parelaphostrongylosis in moose (Figs. 4, 5 and 6) consist of locomotor incoordination (ataxia), lameness, stiffness, listlessness, loss of fear, lumbar and general weakness, circling associated with blindness and/or abnormal positions of the head and neck, and eventually paraplegia and death (An-

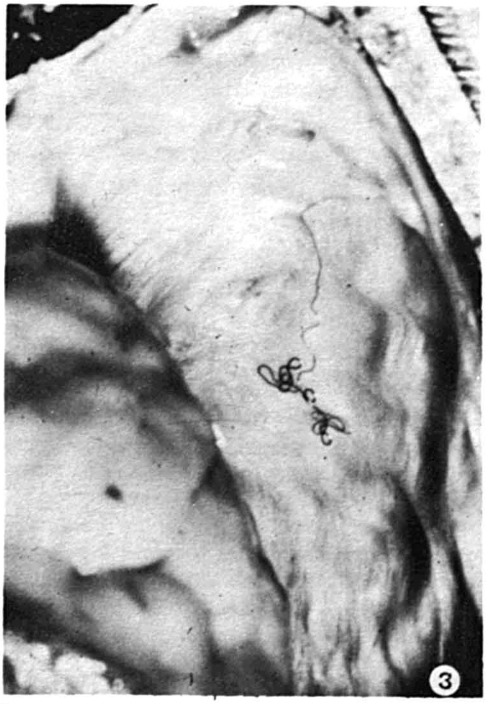
③

Figure 3. *Parelaphostrongylus tenuis.* Female worm on cranial dura mater of moose from Manitoba, Canada.


④

Figure 4. Wild moose with typical signs of parelaphostrongylosis. Note listlessness, fearlessness, and abnormal positions of the head and limbs (Courtesy of the Maine Department of Inland Fisheries and Game).

derson, 1964). The disease occurs in all age groups (except unweaned calves) and at any time of the year. Clinical signs in moose in winter are probably the result of the activities in the central nervous system of worms acquired in the previous year. Adult worms may penetrate the neural parenchyma or eyes (presumably via the optic nerve) (Dikmans and Wehr, 1935 ; Anderson, 1965c) at any time and produce clinical disease ; there is ample evidence that some moose survive the initial phase of the infection involving development in the neural parenchyma.

Careful necropsy procedures and histologic examination of the central nervous system of moose showing characteristic clinical signs in endemic areas can usually reveal a few adult or subadult worms in the subdural space, the neural parenchyma of the brain and spinal cord (Figs. 7 and 8), and less commonly in the eyes. Histologic sections of various parts of the central nervous system will often reveal sections of worms, eggs, larvae, and various lesions associated with the presence of the parasite. The latter consist of focal malacia, perivascular infiltrations (often with many eosinophils), focal

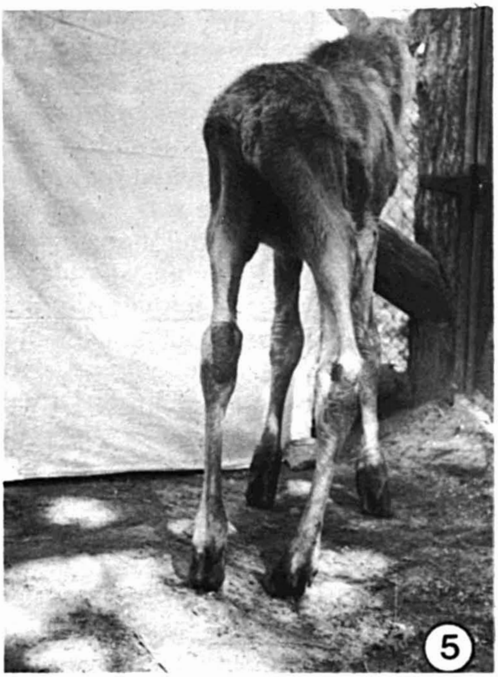

Figure 5. Paresis and ataxia in right hind leg of female moose calf experimentally infected 38 days previously with *Parelaphostrongylus tenuis* (from Anderson, 1964).

Figure 6. Severe lumbar weakness in female moose calf experimentally infected 38 days previously with *Parelaphostrongylus tenuis* (from Anderson, 1964).

Figure 7. *Parelaphostrongylus tenuis* in dorsal horn of grey matter and central canal of spinal card (thoracic region) of moose calf infected 60 days previously (from Anderson, 1964).

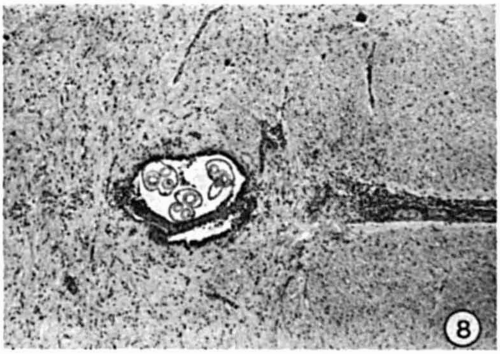

Figure 8. *Parelaphostrongylus tenuis* in central (ependymal) canal of spinal cord (sacral region) of moose calf infected 60 days previously (from Anderson, 1964).

haemorrages, myelin sheath and neuron degeneration, ballooning of axis cylinders, foreign body reactions, and traumatic lesions such as microcavitations (Anderson, 1964, 1965c).

Prior to the discovery of its etiology, neurologic disease in moose was for many years associated with marked declines in moose populations, particularly in Nova Scotia (Benson, 1955, 1958 ; Dodds, 1963), Maine (Lamson, 1941) and Minnesota (Karns, 1967). These disease outbreaks and declines in moose populations were all coincident with spectacular rises in populations of white-tailed deer which were related by specialists to long range climatic changes, and to man-made changes in the environment by forestry, agriculture and other activities.

A number of more recent studies emphasizing population dynamics and the ecological relationships between moose and deer are now beginning to provide some insight into the effects of parelaphostrongylosis on moose populations. Thus Telfer (1967) has reported that in Nova Scotia moose surviving in certain elevated areas, or refugia, appear ecologically separated from surrounding deer populations. He suggested that these populations escaped parelaphostrongylosis because they were not in close contact with surrounding deer populations.

Kelsall and Prescott (1971), working in Fundy National Park, New Brunswick, have suggested that the ecologic separation of moose and deer may be related to a combination of snow depth and crust conditions and the action of parelaphostrongylosis; since deer cannot tolerate as great snow depths as moose they are unable to build up in refugia with moose populations. They suggest that when surplus moose in elevated refugia move down on to deer range they invariably succumb to parelaphostrongylosis. Gilbert (1974) has identified three refugia in Maine where moose populations have remained relatively stable, again because they seem ecologically isolated from surrounding deer populations

Karns (1967) in Minnesota and Behrend and Witter (1968) in Maine have suggested that the prevalence of *P. tenuis* in deer is related to deer density. At the same time Karns (1967) has noted that in Minnesota the prevalence of parelaphostrongylosis in moose is related to deer density. Recent increases in moose populations in this state appear to be coincident with marked reductions in deer populations. He has concluded « that the large deer population with the attendent parasite, *P. tenuis*, was a factor and perhaps a major factor in the past decline of the moose populations in Minnesota and perhaps other southern fringe areas of the eastern moose range ». Gilbert (1974) has shown that in Maine the prevalence of parelaphostrongylosis in moose is related to the size of deer populations although in 1973 he showed that the prevalence of *P. tenuis* in deer was not necessarily dependent on deer density. He noted that recent increases in moose populations in Maine were the result of the expansion of moose from one refugia into areas where deer populations had declined and suggested that parelaphostrongylosis increases the chances of moose being killed by hunting and predation. He observed a higher prevalence of *P. tenuis* in younger moose than in older moose and stated « as young animals move out of the maternal range, the likelihood that contact will be made with infected intermediate hosts probably increases. The ecological separation from deer that helps to protect the breeding stock in refugia (Telfer, 1967) is less likely to exist». Gilbert (1974) concluded that parelaphostrongylosis is probably a limiting factor in moose populations in endemic areas and the prevalence of the disease is related to the density of deer populations with the parasite.

Bindernagel and Anderson (1972) have reported evidence of *P. tenuis* in white-tailed deer in the aspen parklands, including such areas as Prince Albert National Park in Saskatchewan where deer and moose apparently live in close association, although neurologic disease has not been reported in moose west of southern Manitoba. They have pointed out, however, that the prevalence of *P. tenuis* in deer is only about 24% (8% elsewhere in the aspen parklands), much lower than in areas in eastern North America where parelaphostrongylosis is an obvious problem in moose. This raised the possibility that the disease in moose is related not only to deer density as reported by Karns and Gilbert, but also to the prevalence of the parasite in deer populations. Saunders (1974) has now shown that in Northwestern Ontario prevalence of meningeal worm varies markedly in deer populations. Morever, in areas where prevalence was high, moose population densities tended to be markedly lower than in areas where prevalence in deer was lower. This extremely important study may give some indication of the subtle effects of parelaphostrongylosis on moose populations, effects not readily apparent from the rather small numbers of infected moose reported showing clinical signs in the area. This bears out Anderson's (1972) suggestion that «...possibly the existence of clinical disease in moose in an area should be regarded as evidence of a much more widespread disease problem which may have a serious impact on the population ».

Ascaris sp.

Two female worms identified as *Ascaris* sp. were found by Olsen and Fenstermacher (1942) in a moose from Minnesota.

Elaeophora schneideri Wehr and Dikmans, 1935.

Worley *et al.* (1972) have recently reported this helminth in four moose in Montana. One moose was blind, probably as a result of damage to the central nervous system. The other three did not show clinical signs. Worms were found in arteries of the optic nerve sheath and sclera, leptomeningial arteries and in the carotid arteries. The discovery of *E. schneideri* in moose is important because of the work of Hibler and Adcock and their associates (Adcock and Hibler, 1969; Adcock *et al.*, 1965; Clark and Hibler, 1973; Hibler and Adcock, 1968, 1971; Hibler *et al.*, 1969, 1970, 1971) which has shown that the parasite is one of the major pathogens of big game in North America. Up until recently *E. schneideri* was considered to be restricted to the western parts of the continent (including British Columbia, Cowan 1951) but Prestwood and Ridgeway (1972) have now established its presence in certain restricted localities in Florida, Georgia, and South Carolina. They also raised the possibility that the parasite was introduced there but the source of the infection has not been determined.

E. schneideri has been reported in domestic sheep, white-tailed deer, mule deer, and wapiti especially at higher elevations. The adult worms inhabit the carotid arteries and their branches. Microfilariae released into the blood by female worms tend to accumulate in capillaries of the skin especially on the pole, forehead, and face. Vectors are horseflies (Tabanidae) of the genera *Hybomitra* and *Tabanus*. Clinical signs are rare in infected deer but in wapiti the parasite is associated with blindness and other ocular abnormalities, circling, incoordination, nystagmus, necrosis of the muzzle and nostrils, dry gangarine of the ear tips, abnormal antler growth, and emaciation. In wapiti, in particular, the presence of worms in the cephalic arterial system causes lesions which impede blood flow to the head region resulting in ischaemic necrosis which accounts for the lesions observed and clinical signs. For a detailed review of the present state of our knowledge of this helminth the reader is referred to Hibler and Adcock (1971). The significance of elaeophorosis in the population dynamics of moose is unknown but should now obviously be investigated in endemic areas.

Setaria yehi Desset, 1966

This filarial worm is a fairly common parasite of the abdominal cavity of deer throughout North America (Anderson, 1962 ; Becklund and Walker, 1969 ; Cowan, 1951 ; Shoho, 1958 ; Yeh, 1959). It has been reported rarely in moose (Dikmans, 1939 ; Becklund and Walker, 1969 ; Fenstermacher and Olsen, 1942 ; Olsen and Fenstermacher, 1943 ; Shoho, 1958) and is undoubtedly much more common than indicated by these few reports. This helminth has been referred in the past to *S. cervi*, *S. labiatopapillosa*, and *S. tundra* but is now regarded as a distinct species characteristic of cervids in North America. Its life cycle is unknown but presumably involves mosquito vectors which ingest microfilariae in their blood meal. Its pathogenicity is unknown. Anderson (1968) has suggested the possibility that species of *Setaria* may be neurotropic.

Wehrdikmansia cervipedis (Wehr and Dikmans, 1935)

This species is found commonly in the subcutaneous tissues, especially in the leg region, of various cervids in North America, including the moose. This filarioid has been reported in moose in British Columbia (Hatter, 1948 ; Cowan, 1951 ; Ritcey and Edwards, 1958) and Alaska ; the *Onchocerca* sp. reported in moose in Alaska by Williams and Babero (1958) is presumably referable to this species.

The life cycle of *W. cervipedis* is unknown but systematically its affinities lie with the genus *Onchocerca* species of which are transmitted by Simuliidae and Ceratopogonidae. Hibler (1965) reported adult worms under skin at the base of the ear in mule and white-tailed deer and suggested this was the preferred site of the worms. Microfilariae do not appear in the blood stream and seem to accumulate in skin near the site of adult female worms.

Trichuris sp.

Whipworms occur in the caecum and colon of their hosts. Resistant eggs passed in the faeces embryonate in the external environment to infective first-stage larvae. The eggs containing infective larvae are ingested by the final host with its food.

Lamson (1941) reported whipworms in moose from Maine, Fenstermacher and Olsen (1942) from Minnesota, Honess and Winter (1956) from Wyoming, and Barrett (1972) from Alberta. One might expect the specimens to belong to *T. ovis* (Abildgaard, 1795) since this is apparently widely distributed in wild and domesticated ruminants.

Arthropoda

TICKS (IXODOIDEA)

Dermacentor albipictus (Packard, 1869)

Packard (in Hayes and Packard, 1869) originally described *D. albipictus* from a moose from Nova Scotia and *D. nigrolineatus* from deer in New York. Some authors (McIntosh and McDuffie, 1956) regard the two species as distinct *(D. nigrolineatus* a more southerly species) but others regard them as synonyms and this is accepted here mainly on the authority of Cooley (1938), Bequaert (1945) and

Gregson (1956) who have reviewed the problem in detail.

D. albipictus, the moose, winter or horse tick, is mainly an ectoparasite of moose and other cervids but horses are sometimes severely attacked. Cattle and beaver are also reported as hosts. The first observations on the biology of winter tick were recorded by Hayes (in Hayes and Packard, 1869) who gave specimens to Packard for description. He stated : « On the 13th of April a pair of young moose were brought through New York on their way to Europe. They were raised in Nova Scotia and being very tame were allowed to run at large. The cow moose would ramble off in the woods and while there, had become infected with ticks ; the bull had escaped contact with these insects. When the cow arrived in New York, her side and back were almost covered with adult ticks. The insects were removed very much to the relief of the animal, and the ticks were placed in a bottle without food or water. On the first of May they commenced to lay eggs, and continued to do so until the 25th of June, when they died. The eggs were forced out in large masses. On the 3rd of July, the day after I sent the drawings to you, the entire mass of eggs seemed to hatch out at once, the shell opening like a clam, and releasing a six-legged insect ».

D. albipictus is a one-host tick, all stages moulting on the one host (Bishopp and Wood, 1913). Engorged females fall to the ground in the spring and lay their eggs under rocks, leaves etc. Larvae remain inactive during the summer months but become active with the approach of cooler weather in the fall. They ascend vegetation and continually move their fore-legs. They rapidly attach to moose and other animals that come in contact with them. Nymphs become numerous on the host around the end of November and the first of December ; two weeks after the larval moult the nymphs moult to give rise to young adults (Bishopp and Wood, 1913 ; Cameron and Fulton, 1926-7 ; Howell, 1940).

The winter or moose tick is widely distributed in North America and is especially abundant in the northern states and Canada (Bishopp and Wood, 1913 ; Hewitt, 1915 ; Bishopp and Trembley, 1945 ; Hearle, 1938 ; Gregson, 1956).

There are many reports of *D. albipictus* on moose and Canadian reports show that the parasite occurs from British Columbia to Nova Scotia (Cowan, 1951 ; Gregson, 1956 ; Ritcey and Edwards, 1958 ; Cameron and Fulton, 1926-7 ; Bradshaw, 1916 ; Hadwen, 1917 ; Hewitt, 1915 ; Hearle, 1938). In the United States early work in Minnesota focused attention on winter tick as a possible cause of moose neurologic disease (Thomas and Cahn, 1932 ; Fenstermacher and Jellison, 1933 ; Fenstermacher, 1934a, 1934b, 1937 ; Fenstermacher and Olsen, 1942). The tick is also reported from moose in Montana (Jellison *et al.,* 1953) and undoubtedly occurs on this host throughout its entire range in the U.S.A. (Banks, 1908 ; Hickie, 1936 ; Howard, 1917).

Hardy (1869) was among the first to record the effects of winter tick on moose in field. He stated «tick affect moose especially in winter and early spring. The animal strives to free itself from its irritation by striding over bushes and brambles. The ticks may often be seen on the beds in the snow where moose have lain down, and whence they are quickly picked up by the ever attendant moose birds or Canada jays... ».

Cameron and Fulton (1926-7) reported that some heavily infested moose in Saskatchewan were weak and some dead animals covered with ticks although they were not certain of the cause of death of the animals.

Wallace (1934) pointed out that ticks were found mainly on the ears, between the legs, on the belly, and around the anus. He believed moose often rubbed ticks from other parts of the body leaving scab-covered areas.

Hatter (1948) and Cowan (1951) believed winter tick was a major pathogen of moose in western Canada and the former attributed death of some moose to their attacks. Cowan (1951) suggested that winter tick was especially damaging because it attacked animals, especially younger animals, during a period of food scarcity and severe weather. He felt infested animals tended to become weak and die by February and March.

Ritcey and Edwards (1958) observed moose apparently attempting to dislodge ticks from their heads and they pointed out that moose beds often contained live ticks and bloody patches. They observed sizeable areas of snow spotted with blood from moose which had shaken themselves. They concluded, however, that heavily infested moose were not seriously weakened by the ticks but that animals weakened by other conditions often carried unusually heavy tick burdens.

Cahn *et al.* (1932), Thomas and Cahn (1932) and Wallace *et al.* (1932, 1933) attempted to show that moose neurologic disease (parelaphostrongylosis) was associated with a bacterium, *Klebsiella paralytica,* transmitted in some way by winter tick but this work has not been substantiated by numerous subsequent bacteriological studies. Although it is often true that animals exhibiting signs of neurologic disease (in the winter) are heavily infested with ticks this is more likely the result of their weakened condition which makes it difficult to dislodge ticks from the body. It is now well established that neurologic disease is not confined to the winter months but occurs the year around whether or not moose are infested with ticks.

The literature indicates that winter tick is one of the most important parasites of moose. There is, however, little data to show that it is a mortality factor although comparisons with the literature on livestock ticks suggest it may be.

Dermacentor andersoni Stiles, 1908

The Rocky Mountain wood tick, also known as the paralysis or spotted fever tick, is western in distribution especially in drier parts of the continent (Cooley, 1932, 1938 ; Gregson, 1956). It is a serious pest of livestock and the vector of tularaemia, Colorado tick fever, and Rocky Mountain spotted fever. Adult activity is during the spring. At this time the ticks attach to a variety of animals especially large mammals. Mating occurs on the host. The engorged female drops to the ground and lays her eggs. The larvae, like nymphs, attack rodents.

Cowan (1951) reported this tick on moose in drier parts of Alberta and British Columbia.

NASAL BOTS (OESTRIDAE)

Cephenemyia spp.

Larval stages (nasal bots) of members of the genus *Cephenemyia* are parasitic only in Cervidae and five species are known from deer in North America (Bennett and Sabrosky, 1962). The various species seem to display little host specificity since larvae of the same species can be found in moose, white-tailed deer, wapiti, etc. There are, however, specific differences in their geographic distribution and any one species tends to infest any species of Cervidae within its range.

Bennett and Sabrosky (1962) record *C. jellisoni* (Townsend) from moose in Montana and Ontario, and point out that this fly « ...is a species of the northwest, extending southwards along mountain chains. » The same authors report *C.*

phobifera (Clark) from moose (as well as white-tailed deer) in Ontario. This fly has an eastern distribution and extends from Ontario south to the Gulf coast states.

The life cycle of *C. phobifera* has been studied by Bennett (1962) in white-tailed deer in Algonguin Park. Larvae of the first instar are usually found in nasal cavities but second stages migrate to the pharynx. The fully grown bot, which leaves the nostrils mainly when the host sneezes, pupates in the soil. In Algonquin Park *C. phobifera* has two generations a year, a rapid summer cycle of 3 months starting in May and June, and a retarded winter cycle of at least 6 months starting in October and early November. Thus, larvae are scarce in September and October and become common in November. Growth is retarded during the winter and early stages of the parasite may persist until spring. Anderson (1962) and Capelle (1971) have reviewed the studies of Bennett and others.

There is little evidence that nasal bots are significant pathogens. Bennett (1962) reported enlargement of the retropharyngeal pouches, and erosion of the epithelium in infected deer. Gaab (1948) associated swelling of the jaws, throat, and the bell region in a moose calf prior to its death with the presence of bots in the larynx and nasal and pharyngeal region.

BITING INSECTS

A number of authors have noted that moose are greatly bothered by biting flies in the summer months (Murie, 1934 ; Peterson, 1955 ; Flook, 1959), but there is remarkably little specific information concerning the species involved.

Muscidae

The moose fly, *Lyperosiops alcis* (Snow, 1891), originally described by Snow as *Haematobia alcis*, was first collected from moose in Minnesota. Snow believed the fly preferred to feed around the head, rump and legs. Murie (1934) collected specimens from moose on Isle Royale. Peterson (1955) regarded *L. alcis* as the most serious pest of moose in Ontario. The fly is also reported from Alaska and Newfoundland. Both Murie and Peterson associated cutaneous lesions on the hind legs with attacks of this fly.

Simuliidae and Culicidae

Olsen and Fenstermacher (1942) collected *Simulium venustum* (Say) from moose in Minnesota. Nicholson and Mickel (1950) reported *Simulium pictipes* (Hagen) feeding on moose in Minnesota. Smith (1972, personal communication) has observed *Simulium venustum* feeding on a captive moose in Algonquin Park, Ontario. He stated that the favourite feeding site was around the eyes and they were often there in great numbers.

Some authors (Snow, 1891 ; Peterson, 1955 ; Smith, 1972) have noted that mosquitoes feed on moose but there are apparently no published reports of the species involved.

Tabanidae

Smith *et al.* (1970) have carried out an important study of Tabanidae in Algonquin Park, Ontario, including an analysis of the flies attracted to, and feeding on, a captive moose. They collected *Chrysops celvus* Pechuman and Teskey, *C. cincticornis* Walker, *C. cuclux* Whitney, *C. excitans* Walker, *C. frigidus* Osten Sacken, *C. lateralis* Wiedemann, *C. mitis* Osten Sacken, *C. montanus* Osten Sacken, *C. niger* Macquart, *Hybomitra affinis* (Kirby), *H. arpadi* (Szilady), *H. criddlei* (Brooks), *H. epistates* (Osten Sacken), *H. illota* (Osten Sacken), *H. lasiophthalma* (Macquart), *H. lurida* (Fallen), *H. microcephala* (Osten Sacken), *H. nuda* (McDunnough), *H. trepida* (McDunnough), *H. trispila sodalis*

(Williston), *H. typhus* (Whitney), *H. zonalis* (Kirby), *Tabanus marginalis* Fabricius, and *T. nigripes* Wiedemann. Members of the Tabaninae (with the genus *Hybomitra)* were by far the most important pests of moose in this study. Smith *et al.* (1970) also provide data on the seasonal succession of the various Tabanidae in Algonquin Park.

Discussion

The parasites and diseases of moose in North America tend to reflect this animal's unusual history on this continent. The moose is a relatively recent arrival to North America (Peterson, 1955) and it harbours a number of parasites apparently brought with it from the Old World. One wonders, for example, if sylvatic hydatid *(Echinococcus granulosus borealis)* was not introduced by moose as already suggested by Sweatman and Williams (1963) ; the almost perfect relationship between the parasite, moose and wolves certainly indicates the association of the three species is an ancient one. On the other hand, the apparent absence of metastrongyloid lungworms specific to moose suggests that some parasites may not have been able to transfer to the New World with their host ; in the case of metastrongyloids perhaps suitable molluscan intermediate hosts were absent in the new environment. Similarly, the nasal bot *(Cephenemyia ulrichi)* of Old World moose did not apparently transfer to the New World.

The moose has, especially in the southern parts of its range in North America, come into contact with strictly native cervids of the genus *Odocoileus* and acquired some of their parasites, often with unfortunate results. The most obvious examples of the latter phenomenon are parelaphostrongylosis *(Parelaphostrongylus tenuis)* and liver rot *(Fascioloides magna)* which result from parasites well adapted to species of *Odocoileus* but poorly adapted to moose. The existence of parelaphostrongylosis and liver rot in moose seems dependent largely upon the presence on moose range of reservoir hosts in which the parasites can complete their life cycles since this cannot apparently be achieved with any success in moose. The acquisition of elaeophorosis *(Elaeophora schneideri)* from species of *Odocoileus* or *Cervus* could pose a serious disease problem in moose.

Winter tick, often regarded as the scourge of moose, is probably also derived from species of *Odocoileus* which are, however, rarely as massively infected as the more poorly adapted moose. Moose may be much less successful than deer in removing the parasites by rubbing and grooming behavior. Winter ticks, unknown in the Old World, may be an example of a parasite which is much more successful on a newly acquired host than on the original one.

The importation of livestock to the New World introduced a number of viral, bacterial, and helminth agents many of which have readily transferred to wild ruminants, including the moose. Brucellosis, anthrax, cestodes of the alimentary tract, and a number of round worms such as *Haemonchus contortus* probably fall into this category.

In general, therefore, it can be stated that the major diseases of moose in North America are relatively recently acquired, especially from cervids long native to the continent but also from imported livestock. At the same time, human interference with the environment which has profoundly affected the distribution and abundance of the deer family is reflected in the diseases of moose. For example, the distribution of parelaphostrongylosis and liver rot in moose has probably been greatly expanded by historical changes in the numbers and distribution of white-tailed deer. Thus, some of the most important disease problems in moose in North America tend to be rather unique in that they do not occur in this species elsewhere in the world.

It should also be mentioned that the parasites of moose also reflect the latter's ancient role as prey of the larger carnivores, especially the timber wolf. In vast areas of North America the existence of various taenid parasites is probably dependent upon the relationship between the wolf, the final host, and the moose, the intermediate host.

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DISTRIBUTION, HABITAT AND STATUS OF MOOSE IN THE ATLANTIC PROVINCES OF CANADA AND NORTHEASTERN UNITED STATES

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Résumé

A l'arrivée de l'homme blanc en Amérique du Nord, l'aire de distribution de l'orignal s'étendait jusqu'au sud de la Nouvelle-Angleterre et au nord de la Pennsylvanie; de nos jours, cette aire s'est rétrécie et on ne trouve plus de populations valables qu'au Maine, au Nouveau-Brunswick et en Nouvelle-Ecosse ainsi que sur l'île de Terre-Neuve, où on l'a entretemps introduit. Des populations isolées subsistent au New Hampshire et au Vermont de même que dans la partie terre-neuvienne de la péninsule du Labrador, où on l'a aussi introduit. L'orignal préfère les étapes successionnelles menant à des peuplements mixtes de conifères et de feuillus. Sans être essentielle, la présence de végétation aquatique augmente la qualité de l'habitat. Au début du 19ème siècle, l'exploitation commerciale a eu des effets sur la distribution de l'orignal. La chasse, tant légale qu'illégale, peut altérer les patrons de distribution. Au Maine et sans doute aussi au Nouveau-Brunswick, le principal agent influençant la distribution de l'orignal est le ver nématode *Parelaphostrongylus tenuis*, lequel est un parasite inoffensif chez le cerf de Virginie, mais pathogène chez l'orignal. Avant 1900, les feux de forêt à grande échelle entamaient périodiquement l'habitat de l'orignal; suite à de tels feux, les conditions de milieu s'amélioraient durant la régénération des peuplements forestiers avec des conséquences favorables pour l'orignal. Mais depuis 1900, des feux de forêt de plus faible envergure ont eu pour effet d'améliorer la mosaïque que constituent ces deux éléments de base de l'habitat de l'orignal, le couvert offert par des peuplements mûrs et la nourriture par des étendues en régénération. Au début du siècle, le cerf de Virginie a tiré profit des exploitations forestières à grande échelle, étendant beaucoup sa distribution et amenant avec lui le parasite *P. tenuis*, ce qui eut pour conséquence de décimer les populations d'orignal avec lesquelles il entrait en contact. De manière générale, les exploitations forestières ont eu des effets favorables pour l'orignal et ce, tant en Nouvelle-Ecosse, au Nouveau-Brunswick qu'à Terre-Neuve. Certains indices permettent de croire que le cerf de Virginie ne fait présentement qu'envahir de nouveau, dans le nord-est du continent nord-américain, des régions qu'il occupait déjà il y a 900 ans.

Abstract

Moose occurred as far south as southern New England and northern Pennsylvania at the time of white settlement. Today, good moose populations are found only in Maine, New Brunswick, and Nova Scotia of the former range in the region and on the Island of Newfoundland through introduction. Low density populations are also found on the mainland of Newfoundland-Labrador from an introduction and in the State of New Hampshire. A few still occur in Vermont.

Mixed stands of conifers and hardwoods in continuous succession are favored by moose. The presence of aquatic vegetation improves moose habitat but is not essential. In winter, moose tend to select sites where snow depths allow for bedding in comfort, and which do not restrict movement to feeding areas.

Commercial killing affected moose distribution prior to the latter part of the 19th century. Illegal and legal killing may alter distribution patterns.

In Maine and probably in New Brunswick and Nova Scotia the primary factor determining the present distribution of moose is the nematode *Parelaphostrongylus* *tenuis*, a parasite pathogenic in moose and essentially non-pathogenic in white-tailed deer.

Large scale cutting in the early 1900's encouraged the spread of white-tailed deer, introducing the complex *P. tenuis* problem and provoking moose decline. Logging practices have been generally beneficial to moose habitat in Nova Scotia, New Brunswick and Newfoundland.

Evidence is provided suggesting that white-tailed deer may be reinvaders into some portions of the northeastern moose range, having been present there prior to 1100 A. D.

Historic status and distribution

The range of the eastern moose (*Alces alces americana*) extended south into Pennsylvania in the 18th Century (Peterson, 1955, from Goodwin). It was rare in southern New England but common in northern New England (Peterson, 1955). There are conflicting reports in the literature concerning the extent of the range in New York prior to white settlement; however, if moose were present in Pennsylvania it seems likely that they also extended through the Catskill and perhaps the southern tier region of New York State.

From an extensive review of the literature, Benson (unpubl. ms.) noted that in the provinces of New Brunswick and Nova Scotia, the moose was the dominant big game species in the 1700's, providing meat and hides for Indians, the white settlers and merchant vessels. Moose were not indigenous to Newfoundland, and if once present on Prince Edward Island, were no longer there in 1700 (Peterson, 1955; Cameron, 1958).

As the 19th century dawned, the status and distribution of the moose reflected the beginnings of the most rapid continental human development and exploitation in the history of man. Moose were now gone from Pennsylvania, rare in New York, near extirpation from Massachusetts south, in New England and rapidly declining in Vermont and New Hampshire (Foote, 1946; Peterson, 1955; Silver, 1957). A period of reported scarcity also existed in Maine, New Brunswick and Nova Scotia during the early to mid part of the century, lasting for perhaps 30 years when a gradual increase became apparent (Peterson, 1955; Wright, 1956; Benson, unpubl. ms.).

During the 1800's, the first major changes in moose numbers also occurred in many parts of the present range. By 1850, moose were absent from most of Vermont and New Hampshire, with low numbers remaining in the northern parts of those states, while by the end of the century, moose were found only in the northern counties of Maine. The last recorded kill in northern New York was in 1861 (Foote, 1946; Peterson, 1955). A mid century increase was recorded in New Brunswick by Squires (1946 *in* Peterson, 1955), followed by a decline lasting until the final decade (Wright, 1956). An increase, beginning about 1825 and lasting until about 1870 occurred on mainland Nova Scotia, was also followed by a decline lasting until about 1890 when a steady increase began. On Cape Breton Island, Nova Scotia, however, the early century decline was apparently not arrested and at the end of the 1800's moose were reportedly scarce in that portion of Nova Scotia (Boyer, 1950; Benson, unpubl. ms.).

Then the 20th century began and the pressures created by man on the moose and its habitat increased. Now, moose wandered into Vermont and New York only occasionally while New Hampshire's population was probably in the order of a few hundred animals and would drop below 100 during the first three decades of the century. In Maine, moose were still common in the northern counties early in the century; however, the scene had changed by 1940 when the northwestern portion of the state contained relatively few animals. In New Brunswick and Nova Scotia, the increase in moose numbers which began in the 1890's, continued through the early part of the century until perhaps 1920, when regional population changes within the provinces became prominent. Areas of relatively high numbers, areas of scarcity and areas where no moose occurred at all became the pattern throughout these provinces and to a lesser extent in Maine. In addition, local population fluctuations were indicated over periods of a relatively few years (Peterson, 1955; Wright, 1956; Dodds, 1963; Benson, unpubl. ms.).

In the meantime, another area of moose range in Atlantic Canada became important. In 1878, a bull and a cow from Nova Scotia were released at Gander Bay, Newfoundland, and in June 1904, two bulls and two cows were released near Howley at the northern end of Grand Lake. Subsequent kill and sight records indicate that both introductions met with success (Pimlott, 1953). A gradual increase and spread of moose allowed the entire island to be populated by 1945, nine years after the first limited open season (Pimlott, 1953).

Then, in 1953 seven cows and five bull moose from the island of Newfoundland were introduced to Newfoundland-Labrador at St. Lewis River (Pimlott and Carberry, 1958). The successful results of this introduction were discussed by Mercer and Kitchen (1968).

Re-introductions into areas previously inhabited by moose did not fare as well, however. In 1894 and 1895, 10 adults and one "young" were liberated near Nehasane, New York and again in 1902-1903, 12 were released near Racquette Lake; a few animals were also liberated near Saranac Inn in 1903 (Severinghaus and Jackson, 1968). These efforts ended in failure and scattered reports of moose in the Adirondack region since then are likely the result of occasional long-ranging animals moving from Canada or northern New England.

In Nova Scotia seven moose from the mainland were released in Inverness County, Cape Breton Island, in 1928 and 1929 (Peterson, 1955). The results of this transplantation are difficult to assess since records are scant; however, a second successful release, this time at Roper's Brook, Cape Breton Highlands National Park, was made in two operations in 1947 and 1948 (Boyer, 1950). Eighteen animals of the sub-species *andersoni* were successfully liberated after being trucked from Elk Island National Park, Alberta.

An early introduction (1784) of a pair of moose from the New Brunswick mainland to Grand Manan Island resulted in an increasing population for several years. However, the last moose was recorded there sometime after 1835 (Wright, pers. comm.).

Present status and trends

Today moose occasionally move into the Adirondacks of New York but there is no resident population. In Vermont, the population is "probably less than two dozen" according to Garland (pers. comm.), and these animals are mostly restricted to Essex County in the extreme northeastern portion of the state, bordering New Hampshire.

Severinghaus and Jackson (1968), refer to estimates of between 75 and 300 moose in New Hampshire and signs of a slowly, but steadily increasing population. Silver (pers. comm.) also indicates that moose are believed to be increasing with an estimated population of 50 in 1962 and 200 in 1972: this population is "probably centered" in Carrol County of central eastern New Hampshire bordering Oxford County, Maine. Silver also notes that moose are being seen more often in southern New Hampshire.

In Maine, Dunn (pers. comm.) states that moose are found in all sections of the state from occasional sightings in the south to areas where they are very common. Relatively high density populations are found primarily in northern Maine, except in intensively cultivated areas, and the 1971 statewide population estimate based on an aerial census exceeded 13,000 (Dunn, 1972). The population in northern Maine and possibly throughout the state is increasing, according to all census data.

As in Maine, to the moose north and east in New Brunswick are also increasing. The annual kill in that province's restricted season is climbing and in 1972, 2,460 hunters accounted for 1,041 moose (about 42 percent hunter success). The increase is general throughout the province, according to Carter (pers. comm.).

In Nova Scotia, an increase in moose has also been observed with animals appearing more commonly in western interior portions of the province from Yarmouth County to Kings and Lunenburg Counties. Biologists travelling throughout a large section of this essentially low productivity-granite based interior in November 1972 reported extensive indications of growing moose populations. Similarly, in northern Inverness and Victoria Counties of Cape Breton, Lands and Forest staff reported moose increasing and within the limited open season area of eastern mainland Nova Scotia, 409 moose were killed by 1,000 hunters in the 10 day season this past (1972) fall. The 1972 kill was a substantial increase over previous recent seasons. All indices available indicate a general increase in Nova Scotia and aerial census work will be carried out in the winter of 1972-73 to further check this condition.

The island of Newfoundland presents a different picture. There, Mercer (pers. comm.) indicates a general decrease since 1960 from all indices with certain exceptions in areas most recently penetrated by moose or in some sections of low human accessibility. The population in the mainland part of Newfoundland-Labrador, however, is increasing and slowly extending its range.

The overall picture at present, then, is that in areas of extensive forests from Maine through New Brunswick and Nova Scotia moose are increasing. They are slowly declining on the island of Newfoundland and slowly increasing on mainland Newfoundland-Labrador. Elsewhere in the region covered by this review, moose are now unimportant as either a consumptive or a non-consumptive wildlife resource except in limited local areas.

Habitat preference

Peterson (1955) notes that the basis of a favourable moose habitat is continual forest succession and that mixed rather than pure stands are desirable. Pimlott (1953) classified Newfoundland moose range into "good", "marginal" and "sub-marginal". His "good" range is indicated as the commercial forest areas of the island and he notes that mixed stands of balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) are preferred by moose, particularly where the habitat is interspersed with muskegs and barrens. In another paper, Pimlott (1961) notes that in the eastern North American moose range, key browse species are balsam fir, white birch and trembling aspen (*Populus tre-*

muloides) and that seral stages from logging or fire are important in providing good habitat. Mercer (pers. comm.) indicates that the best moose habitat in Newfoundland is the harvestable commercial forests (the mixed stands referred to by Pimlott).

In Nova Scotia, Dodds (1963) noted that moose inhabited areas of mixed forests with coniferous stands at lower elevations, stands of balsam fir and white birch at higher elevations and stands of tolerant hardwoods on upper slopes. On the island of Newfoundland, aquatic areas with great diversity of summer foods are used heavily where available (Dodds, 1955). In our studies of an aquatic moose habitat area in 1954 (unpublished data) in Newfoundland, moose were observed to feed extensively on aquatic vegetation. The presence and use of aquatic vegetation in moose range is well documented (Peterson, 1955; deVos, 1958). The reduction in use of aquatics by late summer noted by Peterson and, to a lesser extent by deVos in Ontario, was also observed in our 1954 Newfoundland studies. Although not essential to summer moose habitat, aquatic areas greatly increase the value of the range.

Winter habitat selection by moose has been described by Telfer (1965, 1967a, 1967b), Kelsall and Telfer (1971) and DesMeules (1962, 1964) in the eastern moose range. That moose inhabit areas where snow depth allows for bedding in comfort and unimpeded movement to feeding areas is well documented. Yet, before the increase in deer (*Odocoileus virginianus*) densities in the region, moose were found in areas with much less severe snow conditions, particularly in western Nova Scotia (Benson, unpubl. ms; Nova Scotia, Annual Reports; Canada, Department of Transport). That moose and deer yarded together when deer most recently invaded eastern moose range cannot be doubted: in fact, they still did so in the early 1950's on Anticosti Island (Pimlott, 1954) and do so now in Nova Scotia (the James River Yard, Antigonish County). Peterson (1955) and others have also noted that the two cervids yard together in North American moose range. Thus, climate, weather and general habitat tolerances of deer and moose not only overlap but, in the absence of deer, with its accompanying parasite, *Parelaphostrongylus tenuis*, moose would doubtless exhibit a broader range in selecting winter quarters.

Factors affecting status, distribution and habitat

MORTALITY FACTORS

Mortality factors, by reducing local populations, can temporarily, and if consistently operating, permanently affect moose distribution. The direct mortality factors of most probable importance in affecting status, distribution and possibly habitat selection in Atlantic Canada and the northeastern states since settlement are: market (commercial) killing, illegal hunting and snaring, legal killing and the effect of diseases and parasites, particularly the roundworm *Parelaphostrongylus tenuis*.

Although little evidence is available, I doubt that predation from animals other than man (i.e. black bear, *Euarctos americanus*; wolf, *Canis lupus*; cougar, *Felis concolor*) has been a major factor in this region. Bears occasionally kill moose calves but their effect is presently minimal and we have no historical evidence to indicate that bear, wolves or cougar have exerted major pressures upon these moose populations since white settlement, even though wolves were recorded as killing moose often during the early settlement period. Whatever effect wolves may have had would have been limited to the northeastern states and New Brunswick, since permanent breeding populations of wolves in Nova Scotia probably did not occur after settlement by Europeans (Hardy, 1869; Duvar, 1867; Hollingsworth, 1787).

Commercial killing

During the period of exploration and settlement in the 17th and 18th centuries, moose were killed by the thousands for their skins, tallow and their nose (moose mosel) which was known as a delicacy for epicures. Meat was usually, but not always, sold or used by the hunters for food for themselves and their dogs (dogs often being used in the hunt). Killing was most often accomplished in late winter (March) when the snow was deepest, or when a crust had formed for dogs to run on. There are many references to such slaughter with trading firms and posts reported as buying and exporting skins. In 1760, the moose skin was equal to "1½ beavers" in Atlantic Canada at "truck houses" in Fredericton, St. John, and Halifax, compared to the bear (1⅓ beavers) and silver fox (2½ beavers). Although partly out of the region covered by this review, the Sieur d'Aunay traded 3,000 moose skins annually on the lower St. Lawrence between 1645 and 1650. Similarly, Pierre Radisson was reported as killing 600 moose around 1660 near Trois-Rivières and in a single winter one Nathan Caswell killed 99 near Lancaster, New Hampshire in the early 1700's (Silver, 1957; Benson, unpubl. ms.). Wright (1956) also lists numerous records from the literature, relative to commercial killing in New Brunswick.

There can be little doubt that such extensive killing was the first of man's major influences in the "new world" which altered the status, and caused local extirpation of moose in areas hunted most heavily in the Maritime Provinces and New England. Along with fire, such commercial slaughter helped set the stage for a struggle against odds less tolerant mammals would have succombed to.

Illegal killing

As a result of the effects of man's influences in 17th, 18th and early 19th centuries, jurisdictions began to strengthen legislation beginning in the late 1800's. Seasons were shortened (as in 1873 in Nova Scotia, 1877 in New Brunswick and 1895 in New Hampshire) or closed (as in 1901 in New Hampshire, 1935 in Maine and 1937 in New Brunswick and Nova Scotia). However, protective legislation affects game populations only by removing whatever direct effect the legal hunter has been responsible for. Illegal killers are not only less affected by restrictive legislation but the restrictions thus applied, reduce competition from the legal hunter. Thus, the illegal hunter and the snare setter have fuller access to the population.

From a review of historical records including Silber (1957), Benson (unpubl. ms.), and Annual Reports of the Nova Scotia Game and Inland Fishery Protection Society for the years 1898, 1900, 1902, and 1903, illegal killing was a mortality factor of some importance in the past. It is still a factor today in Nova Scotia and probably in New Brunswick and Maine. Poaching was also a well established art in Newfoundland during my years in the province (1953-1958). However, poaching cannot be considered as important a factor in determining distribution as commercial killing since the numbers of animals removed by this means has been far lower. It also seems unlikely that illegal killing prevented moose from occupying traditional seasonal habitats except, perhaps, temporarily in local instances.

Legal hunting

Legal kill data examined from the three Atlantic Provinces presently offering open seasons suggests that hunting pressure tends to be concentrated annually in certain areas because such areas are (a) accessible and (b) have a reputation among hunters as good moose country. Because of this, local densities may well be reduced, altering the overall distribution picture. The limited seasons in New Brunswick (since 1960) and Nova Scotia (since 1964) do not yet appear to have altered the distribution pattern, although slight changes may be occurring in Nova Scotia. However, Mercer (pers. comm.) has noted that on the island of Newfoundland, "In most accessible areas the population has decreased through human predation — the accessible areas include the best moose habitat — most of the harvestable commercial forests." Mercer states further that, "in inaccessible areas, especially the South Coast, which are also usually the poorest moose habitat, the moose have surpassed the carrying capacity of the range..."

Thus, combined legal and illegal hunting pressure can reduce population densities locally, altering the overall distribution picture. The presence of moose populations existing at densities above carrying capacity even temporarily, on poorer range is more likely to be a result of under harvesting through inaccessability than the result of movement from neighbouring areas due to disturbance by hunters.

Disease and parasites

The only parasite influencing distribution and habitat use in the region covered by this review is the nematode *P. tenuis* the causative agent of "moose sickness".

In a 1954 paper, Pimlott considered the question of white-tailed deer (*Odocoileus virginianus*), dominance in some length and summarized his findings that though deer "...do appear to be the dominant species in parts of the Canadian biotic province (of Dice, 1942)... it cannot be considered a general rule." He further noted that on Anticosti Island in Dice's Hudsonian biotic province deer appear to be the dominant species. In continuing his discussion, Pimlott (1954) provided information supplied to him by Mr. Bruce Wright (New Brunswick) and Mr. Denis Benson (Nova Scotia) that the areas where moose were increasing or were the dominant species were the mountainous regions of the provinces which, he suggested were "probably outposts of the Hudsonian biotic province."

Notwithstanding the importance of climate, weather and cover type relating to specific biotic provinces, moose biologists increasingly mentioned the presence of moose in areas of low deer density or in areas where deer were absent and the contradiction Pimlott (1954) indicated of deer being dominant in one Hudsonian area (Anticosti) may well have stimulated workers to search for other reasons for the obvious separation of these two cervids in the eastern range of the moose.

Benson (1953-1958), Kelsall (undated), Dodds (1963), Telfer (1965) and Parker (1966) all investigated moose distribution and found that high densities were limited to forests above 150 m or more in elevation in several areas of New Brunswick and Nova Scotia. Historical records (Benson, unpubl. ms.) and Annual Reports of the Nova Scotia Department of Lands and Forests indicate that in the province, the traditional and, presumably, the best moose habitats were, by 1932, sparsely inhabited by moose. Data provided by Peterson (1955) indicate that the average number of square kilometres per kill was lower (39) in Nova Scotia than in New Brunswick (78) during the period of 1920 to 1937. The ratio of 39 square kilometers per kill is derived using the land area of the entire province, not only the land area corresponding to effective moose range. Thus, Nova Scotia in particular, produced large quantities of moose from a relatively small area and from counties where moose were subsequently scarce or absent. As early as 1932, officials in Nova Scotia expressed alarm at the possible effect of increasing deer numbers upon the moose population. Moose sickness outside the region was noted as a mortality factor at least as early as 1932 (Cann *et al.*, 1932); Benson (1958) and Dodds (1963) linked moose sickness to moose declines in Nova Scotia, but it was not until Anderson's studies (Anderson 1964a, 1964b, 1964c, 1965a, 1965b) that *P. tenuis* was described and considered to be responsible for moose population declines associated with deer densities.

Telfer (1965) and Prescott (1968b) suggested that the altitudinal separation of moose and deer over a part of the year might be significantly involved in the survival of moose midst general areas of deer dominance in Nova Scotia.

DesMeules (1962, 1964) discussed moose adaptations to snow and described moose winter yards in Québec in detail. Telfer (1967a, 1967b) and Kelsall and Telfer (1971) presented detailed data concerning the differences between moose and deer yards relative to shelter components and snow depths, as well as the comparative physical adaptations of big game for snow. Telfer (1965) and Parker (1966) considered the possible link between the seasonal separation of deer and moose and the incidence of *P. tenuis* in the latter but, although it has been generally accepted that the incidence of *P. tenuis* is higher in moose where deer are dominant throughtout the year, it was not until Gilbert (1974) compared the incidence of *P. tenuis* in moose among areas of varying moose and deer densities in Maine that more positive evidence concerning *P. tenuis* and moose distribution has been available. Gilbert (pers. comm.) states, "The prime factor governing distribution, at least in my mind, has been *Parelaphostrongylus tenuis*, the meningeal worm in white-tailed deer. In effect, the distribution and density of deer has determined moose distribution in Maine."

In areas where deer are undergoing a general decline (Maine, New Brunswick and Nova Scotia) moose are increasing, whereas in Newfoundland, where deer do not exist, moose are slowing decreasing. However, as indicated by Anderson (1972), the ecological relationship between incidence and transmission of *P. tenuis* and the possible connection with seasonal separation of the two cervids has yet to be worked out.

Summary of mortality factors

The first direct mortality factor which affected the distribution of moose in the areas covered by this review was commercial killing. Restrictive legislation reduced the importance of this factor in the late 19th century. Illegal and legal killing may alter distribution patterns under excessive pressure.

In Maine and probably in New Brunswick and Nova Scotia, the main factor determining the present distribution of moose is probably *P. tenuis* associated with deer density.

Moose seasonally occupy areas uninhabited by deer, not only because of their apparent preference for these areas but also because deer are not as well adapted as moose to cope with the climatic conditions there, particularly the presence of deep snow on the ground.

HABITAT CHANGES

Alteration of habitat, as considered here, refers to changes caused both by man's influences and seasonal or long term natural influences. There are five major areas we may examine: white settlement, fire forest cutting, forest insects and diseases, climate and weather.

White settlement

The first, white settlement and development, we can dispose of briefly. Early settlement by itself had little effect on the status, distribution or habitat of moose. As extensive land areas were cleared for agriculture in the 19th century, however, moose movement and distribution were altered. In the 20th Century moose were further restricted in distribution, first in New England and then in the Maritime Provinces, by land clearing, cultivation, urbanization and development in general.

Changes due to human development are easy to appreciate; however, it is the effects of fire, commercial logging, climatic factors and the alteration of habitat by both moose and other browsers that we should consider in greater detail.

Fire

Fire has always been a natural influence on forests and wildlife. Prior to man's emigration into the Atlantic Provinces and northeastern states, fire was a major factor in increasing interspersion of cover types. The American Indian started fires accidentally and purposely to clear lands and fell trees, but it was not until white settlement that fire became one of the dominant influences on moose habitat in eastern North America. It should be noted, however, that the American Indian's seasonal movements, need for wood and agricultural practices (in New England particularly) did result in increased forest type interspersion (Thompson and Smith, 1970; Silver, 1957; Benson, unpubl. ms.).

Fire may kill game but, for moose, the fact that some animals are killed or forced to move is secondary to the long term improvement in moose range that fire normally causes in temperate and boreal North American regions (Pimlott, 1961; Peterson, 1955; Leopold and Darling, 1953). However, repeated high temperature, deep burns may have destructive effects on shallow soils.

Fire from settlement activities was a major factor in altering moose habitat, beginning in the 17th century in the region covered by this review. Wright (1956) quotes historical documentation of fires before 1677 and in 1761 and 1825. The latter date reflects the Miramichi fire which Wright (1956) states was "the greatest single factor in the status of big game in the province for the next one hundred years."

In the same year, 1825, the greatest fire in Maine's history burned 3,400 km^2 of the central woodlands of the state and another 600 km^2 burn destroyed some of Maine's best white pine (*Pinus strobus*) stands in 1837 (Stanton, 1963).

Benson (unpubl. ms.) states that "by 1784 most of the interior (of Nova Scotia) had been burned." And records of the Nova Scotia Game and Inland Fishery Protection Society (1898, 1900, 1902, 1903) are dotted with references to fires in those years.

Pimlott (1953) indicates that records of fire history for Newfoundland before 1944 are difficult to obtain but notes that from 1944 to 1952 about 100 km^2

of productive forests were burned annually. He further notes that many of the fires were small and resulted in favourable habitat changes for moose.

The effects of fire have been generally beneficial to both moose and deer in the region, with certain local exceptions. Severe and repeated burning has produced a relatively stable sub-climax of ericaceous vegetation in portions of western Nova Scotia (Strang, 1972) while in portions of central Newfoundland (Dodds, 1955) and New Brunswick, past repeated burns have retarded succession favourable to moose.

Fire alters distribution of moose when extensive and severe, by restricting them to the remaining forest stands. Regeneration of pioneer plants providing food and increasing shelter allows them to reinhabit the burn. A specific example of the importance of small fires providing ideal interspersion between new growth and old growth coniferous canopy in Newfoundland is described by Dodds (1955).

Forest cutting

Data concerning the effects of forest cutting on eastern moose habitat and distribution are conflicting. There are several synergistic effects, making it difficult to determine the precise environmental parameter affecting moose and research on the impact of forest cutting is badly needed. Cutting affects snow cover depth and condition (DesMeules, 1964) and therefore an area's use by moose. Forest cutting may also affect the degree of use of cutovers by other browsing animals (Dodds, 1960). More important than these complexes in eastern moose range, however, are the following effects of harvesting forests.

In the first instances, the extensive lumbering and pulpwood operations from the mid 19th through the 20th century until the present, have been a major factor in the northward extension of white-tailed deer (deVos, 1962) and the ensuing interrelations with moose and *P. tenuis*. Thus cutting practices have affected both the population density and the distribution of moose in the region (outside of Newfoundland) adversely. Although the cutting *per se* only initiated a complex chain of ecological events.

On the other hand, cutting has been beneficial in many instances. Peterson (1955) considered "smaller" clear cuts to be advantageous and noted that regeneration following cutting is similar to that following fire. For specific cases of cutting benefitting moose habitat, we can refer to Telfer (1967b) who described a moose yard cut for pulpwood "15-20 years ago" in Nova Scotia, to Bergerud and Manuel (1968) who relate cutting practices in Newfoundland to improved moose range, and to Prescott (1968a) again in Nova Scotia, who stated that winter concentration areas were found where the "most frequent disturbance factor was a partial cut approximately 15 years old." It was, in fact, the concern that extensive cutting in Nova Scotia's present winter moose range might force moose into wintering areas occupied by deer that initiated Prescott's (1968b) study.

Telfer (1972) suggests that clear cuts of about 130 ha might be tolerated in boreal forests; but, the size of clear cut areas that will be large enough to be beneficial to moose, yet, not large enough to reduce interspersion and create a homogeneous stand which would probably be less beneficial, at least temporarily, must be determined in future research.

FOREST INSECTS AND DISEASE

Although noted by Peterson (1955) and by de Vos (1962) the effects of spruce budworm (*Choristoneura fumiferana*) on moose habitat through their destruction of balsam fir are also largely unknown in this region. Depending upon the extent of the damage of fir and the forest area destroyed and the regeneration in relation to adjacent cover types, we might expect the long term effect to be generally beneficial to moose, although one exception has been recorded. In New Brunswick, Wright (1956) noted a record of "moose leaving heavily damaged budworm areas in the northern part of the province (1922)." Since the majority of New Brunswick's spruce-fir forests are in their second decade of a major budworm infestation now, the effects of this insect on distribution and habitat of moose might well be studied there.

The disease known as birch "die back" (Hawboldt, 1952) was noted by Prescott (1968a) as one of the disturbance factors creating small openings that regenerated to successional species preferred by moose. Prescott (pers. comm. to E.S. Telfer, 1972) stated that killing of patches of trees by spruce budworm and by balsam wooly aphid (*Adelges piceae*) was also a beneficial factor in improving interspersion in Nova Scotia winter moose range.

The eastern hemlock looper (*Lambdina fiscellaria*) is also prevalent at times in the region but no data are available relative to its effect on moose habitat.

CLIMATE AND WEATHER

Benson (1952) and Hawboldt and Benson (1953) and Benson (unpubl. ms.) considered long term climatic changes as possible causes of change in distribution of moose and deer and other animals in this region. In his unpublished manuscript, Benson reviewed the climatic changes from historical data relating to Nova Scotia and indicated that beginning about 1100 A.D. a cold trend was evident. He correlated this trend with the decline of deer, known to be present in Nova Scotia in 500 A.D., the increase of caribou and probably moose which were also known to be present but believed to have existed in lower densities before the cooling trend.

Wright (1956) also refers to a warmer climate in New Brunswick for a period in the late 1800's but does not specifically relate this to changes in deer and moose distribution or numbers.

Snow as a factor in determining winter distribution and movements of moose has been considered in detail by DesMeules (1964) who noted that the optimum depth of soft snow preferred for bedding was 60 cm and the maximum depth for unimpeded movement was 100 cm. Kelsall and Telfer (1971) found moose and deer to be restricted in movement in snow which exceeded two thirds of chest height.

In the Atlantic Provinces, Telfer (1967a) noted differences in snow cover between moose and deer yards, with thinner snow cover in deer yards which had a denser coniferous crown canopy. Telfer (1965) noted 55 cm of snow in deer yards studied in Nova Scotia and 85 cm in moose yards. Telfer also indicated that average daily maximum temperature in a deer wintering area was 2.2°C higher than in a comparable forest stand used by moose.

The superior capability of moose compared to deer for locomotion in snow enables them to select greater depths for insulation (DesMeules, 1964). However, conditions can become too extreme, and Mercer and Kitchen (1968) suggested the slow dispersal of the introduced mainland Newfoundland-Labrador moose population may be caused by the thick snow covers there.

Wright (1956) refers to a severe winter causing a die-off of moose in New Brunswick in 1922, and Benson (unpublished manuscript) quotes from the diaries of Simeon Perkins of Liverpool, Nova Scotia (1789): "The snow storm has continued all right — it is much drifted and has fallen considerable depth — the moose have been remarkably plenty for some days past (about the village) — the people of the falls and about the town have killed 20 besides what the Indians have killed".

The moose is well adapted to snow depths of up to one m yet there have apparently been instances in the region we are concerned with when snow depths have forced moose to move and be killed, and when combinations of snow depth and severe temperatures have created conditions where the nutritional intake was inadequate and die-offs occurred.

Winds severe enough to blow down extensive stands of mature or over mature timber may create favourable plant succession for moose and improve interspersion of food and cover types. Throughout the region, areas of blown down forest are common in moose range, particularly in Newfoundland and Nova Scotia. Wright (1956) refers to the Saxby Gale of 1869 causing extensive blowdown in the southern region of New Brunswick and Silver (1957) presents records from 1639 of gales causing extensive blowdowns in New England. Prior to white settlement, blowdowns along with fire doubtless helped improve interspersion and improve moose habitat. Both blowdown areas and insect damage areas were also prime areas for natural, lightning caused, fires to start.

Summary of alterations of habitat

Prior to 1900, wildfire periodically restricted moose habitat and distribution and then, increased it as regeneration occurred. Repeated intensive burns on shallow soils have in some areas created poor moose range deficient in shelter and in preferred food species, which may require centuries to recover. Since 1900, smaller fires probably improve interspersion of food and cover and are beneficial to moose habitat.

Large scale cutting in the early 1900's encouraged the spread of deer, bringing about the complex *P. tenuis* problem and resultant moose decline. Logging practices have been beneficial to moose habitat in Nova Scotia, New Brunswick and Newfoundland but the size of cuts which may prove beneficial in both the long and short term has yet to be determined.

The effects of forest insect pests and tree diseases have been described in the literature as both harmful and beneficial to moose habitat, depending on the type of insect or disease and the extent of damage incurred.

Snow depths of 60 to 100 cm are often chosen by moose in winter but depths exceeding two thirds of their chest height tend to impede movement. Extensive snow may reduce dispersal or alter distribution. One historical record of a winter "die-off" in New Brunswick is noted.

INTERSPECIFIC AND INTERASPECIFIC FACTORS

Other than deer, few mammals are noted in the literature relating to the area covered by this review as influencing moose habitats and or distribution. Dodds (1960) noted that extensive browsing by moose in cutovers, where balsam fir and white birch are dominant successional species, may reduce available browse for the hare *(Lepus americanus)*. I found no indication in the literature, except for historical notes, (Benson, unpubl. ms.), that caribou

(Rangifer caribou) might have been a factor in altering habitat for moose or vice versa. Prescott (1968a), however, noted porcupine *(Erithizon dorsatum)* to be a positive disturbance factor favoring improved browse conditions for moose.

Moose may affect their own habitat as reported in Newfoundland (Bergerud and Manuel, 1968). And, as Mercer has noted (pers. comm.) moose may now exist in numbers above carrying capacity in marginal, less accessible (to humans) range in Newfoundland. If so, the biomass of moose this habitat will support in the future must decline.

As a closing thought, I would like to refer to Anderson (1965a) who suggested that moose may first have been exposed on a large scale to *P. tenuis* within recent times since deer are believed to be a more recent invader into northern ranges. From archeological data, however, (Wintemberg, 1919; Benson, unpubl. ms.) we have a part of a puzzle: white-tailed deer were apparently dominant in Nova Scotia, although moose were also present, for several centuries prior to about 1100 A.D. when a period of colder climate began. From 1100 A.D. until about 1900 the moose was the dominant ungulate except for short periods when caribou were apparently more numerous. White-tailed deer again became the dominant species soon after 1900 from ingress and introductions and still are, while caribou declined gradually from 1800 until extirpation about 1920.

If white-tailed deer were the dominant or even a sub dominant ungulate species until around 1100 A.D., was it because of climatic conditions only or was *P. tenuis* present even then? And should we not consider white-tailed deer to be recent re-invaders of the moose range or the northeast?

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DISTRIBUTION AND WINTER HABITAT OF MOOSE IN QUÉBEC

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Résumé

Les documents historiques ne permettent pas de préciser la distribution passée de l'orignal (*Alces alces*) au Québec. Cependant, ces informations portent les auteurs à croire que l'orignal occupait dans le passé la même aire de distribution qu'actuellement. Les populations d'orignaux ont fort probablement subi des fluctuations numériques importantes attribuables aux épidémies d'insectes, aux incendies forestiers et à l'exploitation de plus en plus septentrionale des ressources naturelles.

Au Québec, les zones forestières 2 et 3 supportent les plus fortes populations d'orignaux. Ces deux zones forment une large bande de transition entre la forêt feuillue méridionale et la forêt coniférienne septentrionale. La composition de ces forêts et les perturbations nombreuses qu'on y rencontre en font les zones à meilleur potentiel. L'importance de la strate de protection semble principalement conditionnée par l'abondance des chutes de neige. Ainsi, dans les régions de l'ouest et du nord de la province où les chutes de neige sont peu considérables, la qualité du couvert ne revêt pas la même importance que dans la partie orientale du Québec, où l'épaisseur du manteau nival peut même devenir un facteur limitant. L'effet des perturbations du couvert forestier sur l'orignal se fera certainement sentir beaucoup plus rapidement dans les zones où les précipitations nivales sont optimales.

Dans les régions étudiées, les espèces végétales les plus importantes dans la diète hivernale de l'orignal sont l'érable à épis et le sapin baumier. Il existe une relation nette entre le degré d'utilisation des sites d'hivernage et la quantité de tiges feuillues disponibles. Cette dernière variable serait alors un des paramètres déterminant la capacité de support pour la zone forestière 2.

Abstract

Historical documents do not enable us to precisely outline the past distribution of moose in Québec. However, we believe that moose have always been present in the same areas. Moose populations have probably fluctuated following insect epidemics, forest fires and the increasing northern exploitation of natural resources.

In Québec, the densest moose populations occur within Forest zones 2 and 3. These two zones form a transition between southern deciduous forests and northern coniferous forests. The vegetation and disturbances found within these forest zones make them the best potential regions for moose. The significance of cover is related to the amount of snowfall. That is, in the western and northern parts of Québec, where snowfall is light, the cover quality does not affect moose density and distribution as much as in the eastern part where snow can become a limiting factor. Definitely, the consequences of cover perturbations will be more rapid in regions of light snowfall.

In the regions studied, the most important tree and shrub species forming the winter diet of moose were mountain maple and balsam fir. There was a direct relationship between the degree of occupation of the wintering areas and the quantity of available deciduous stems. Thus, availability of deciduous stems should be one of the variables determining the carrying capacity of Forest zone 2.

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Introduction

The first studies on the distribution and habitat of moose *(Alces alces)* in the Province of Québec were initiated in 1960 when the Québec Wildlife Branch was formed by a reorganization of the Department of Tourism, Fish and Game. An aerial survey program was established at that time (DesMeules and Brassard, 1963, 1964) and thereafter applied throughout the province (DesMeules and Brassard, 1967a,b; Brassard and Bouchard, 1968; Brassard, 1968, 1972).

By 1965, researchers for the Canada Land Inventory Program, were seeking a correlation between moose density and the nature of the habitat being utilized (Brassard, 1967a,b; Anonymous, 1969; Bouchard and Brassard, 1971). During this period local studies on moose winter habitat were being carried out (DesMeules, 1962, 1964, 1965, 1968; Audy, 1974; Crête, 1973).

This paper summarizes our knowledge of moose habitat in Québec. The first section briefly describes the past and present distribution of moose. The second deals with the population density and distribution as they relate to habitat quality.

Only the winter habitat has been considered, as limiting factors are most predominant during this season.

Moose distribution in Québec

According to Stephens (1980) and Merril (1920), moose were established within the province before the arrival of the first explorers. Champlain, in 1603, was the first to give a description permitting a positive identification of moose (Bourne and Bourne, 1911; Merril, 1920). At that time, the southern limit of moose extended south of the present Québec-United States border (Ganong, 1908). From data gathered at the Tadoussac fur trading post from 1646 to 1648, it appears, although some doubt exists as to the correct identification of the pelts, that the northern limit was slightly north of the 48° latitude. Chenu (1874) and Peterson (1955) suggest the 53° latitude and the 48° latitude respectively as being the northern limits. Recently, moose have been observed as far north as the 57° latitude (Fig. 1).

It is possible that moose have always occupied the same regions. This statement is in close agreement with the hypothesis proposed by Kelsall (1972). He believes that the northward range expansion in the Norhwest Territories is largely a reflection of increased human travel and not an actual expansion of moose range. It is also possible, but less likely, that moose extended their range northward within the last century, following local habitat improvements. For example, in northeastern Québec, between 1963 and 1972, an extension of the moose range was correlated with disturbances caused by forest fires (Fig. 1).

HABITAT

General aspects

Three parameters were considered in the study of moose habitat in Québec: vegetation (Fig. 2), snowfall (Fig. 3) and relative density of moose populations (Fig. 4).

The map illustrating the forest zones has been modified from Rowe's (1959). Sections of homogeneous vegetation have been grouped. The use of six forest zones is based upon the knowledge gained while preparing classification studies for the Canada Land Inventory (Fig. 2).

This stratification was used as a basis for small-scale moose habitat studies. The map illustrating snowfall patterns in Québec is reproduced from Wilson

(1971). The map depicting moose density was prepared using aerial survey data obtained by the Québec Wildlife Service from 1964 to 1972. These were obtained in 450, 10 mi² (26 km²) block quadrats, systematically distributed south of 50° latitude. Also included are data from 23,000 miles (36,800 km) of parallel transect lines spaced at ten mile (16 km) intervals. These data were obtained principally in 1972, encompassing the region north of the 50° latitude for which no large scale topographic maps exist. These samples represent about 3% of the total moose range.

Forest zone 1

This section involves the majority of Québec's deciduous forests which surround the St. Lawrence and Ottawa

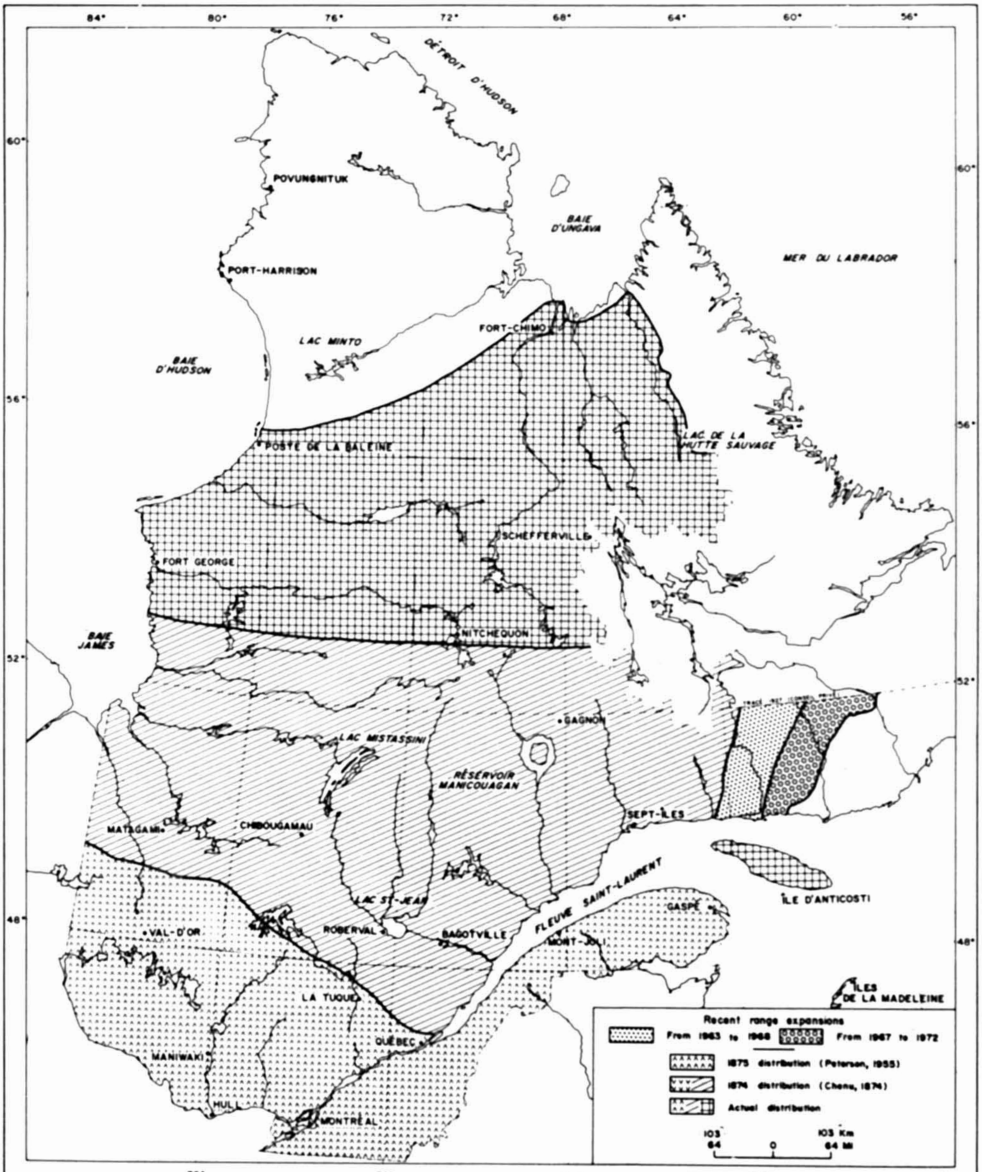

Figure 1. Past and present distribution of moose in Québec

rivers. Here, agricultural practices and urbanisation are well-developed. Moose, for all intensive purposes, are absent from this habitat.

Forest zone 2

This unit of vegetation forms a transition between boreal coniferous forests and the deciduous forest of the St. Lawrence lowlands. The main tree species occuring in this zone are yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), white spruce (*Picea glauca*), white pine (*Pinus Strobus*) and hemlock (*Tsuga canadensis*). Snowfall rarely exceeds 160 inches (400 cm) which corresponds to 35 to 40 inches (87.5 to 100 cm) accumulation on the forest floor. At this depth, moose movement is somewhat impeded (DesMeules, 1964).

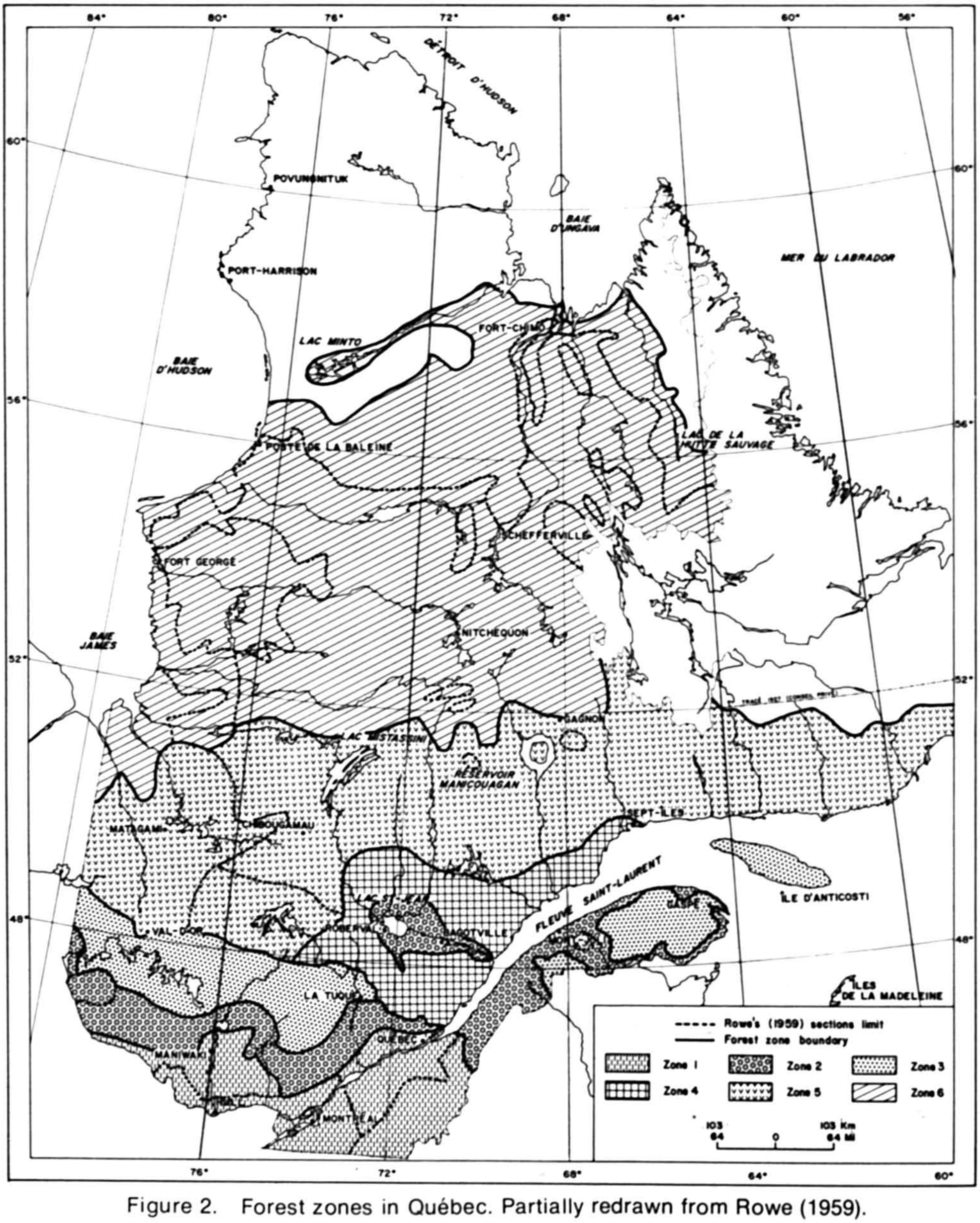

Figure 2. Forest zones in Québec. Partially redrawn from Rowe (1959).

Moose are present in this forest zone, the highest densities being in the western area. The mean density is 4.6 moose per 10 mi^2 (1.8 moose/km^2). In the western part of this zone, the southern boundary delimits a rapid transition between low and high moose density. In the eastern part, the lower densities are related to the agricultural development.

Forest zone 3

This zone of boreal forest is characterized by the occurrence of balsam fir, black spruce (*Picea mariana*), white spruce and paper birch *(Betula papyrifera).* Plant diversity is lower than in in the preceeding zone. Except for the moutains of the Gaspé peninsula, where snowfall exceeds 200 inches (500 cm), snow accumulation is comparable to

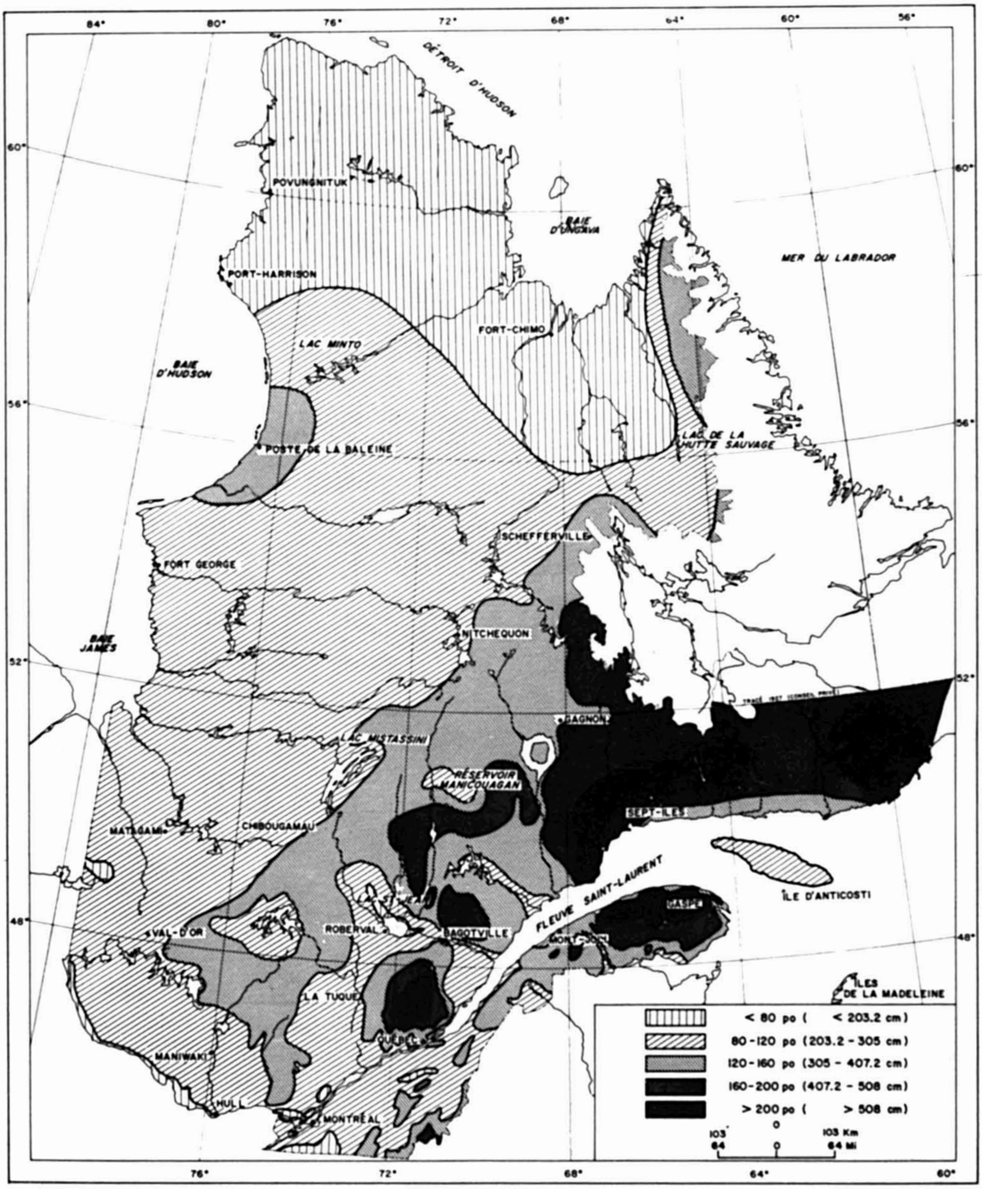

Figure 3. Distribution of snowfall in Québec.

that recorded in Forest zone 2. The best potential for moose is in this third zone and the mean density approximates 6.8 moose per 10 mi^2 (2.6 moose/10 km^2).

Forest zone 4

The vegetation in Forest zone 4 is comparable to that in Forest zone 3. However, the rougher topography and more shallow soils lower the productivity. Snowfall ranges from 120 to 200 inches (300 to 500 cm) yearly; scattered observations indicate that snow accumulation varies from 25 to 60 inches (62.5 to 150 cm) impeding the movement of moose particularly along the Saguenay river. Moose density is low in this zone: 3.0 moose per 10 mi^2 (1.1 moose per 10 km^2).

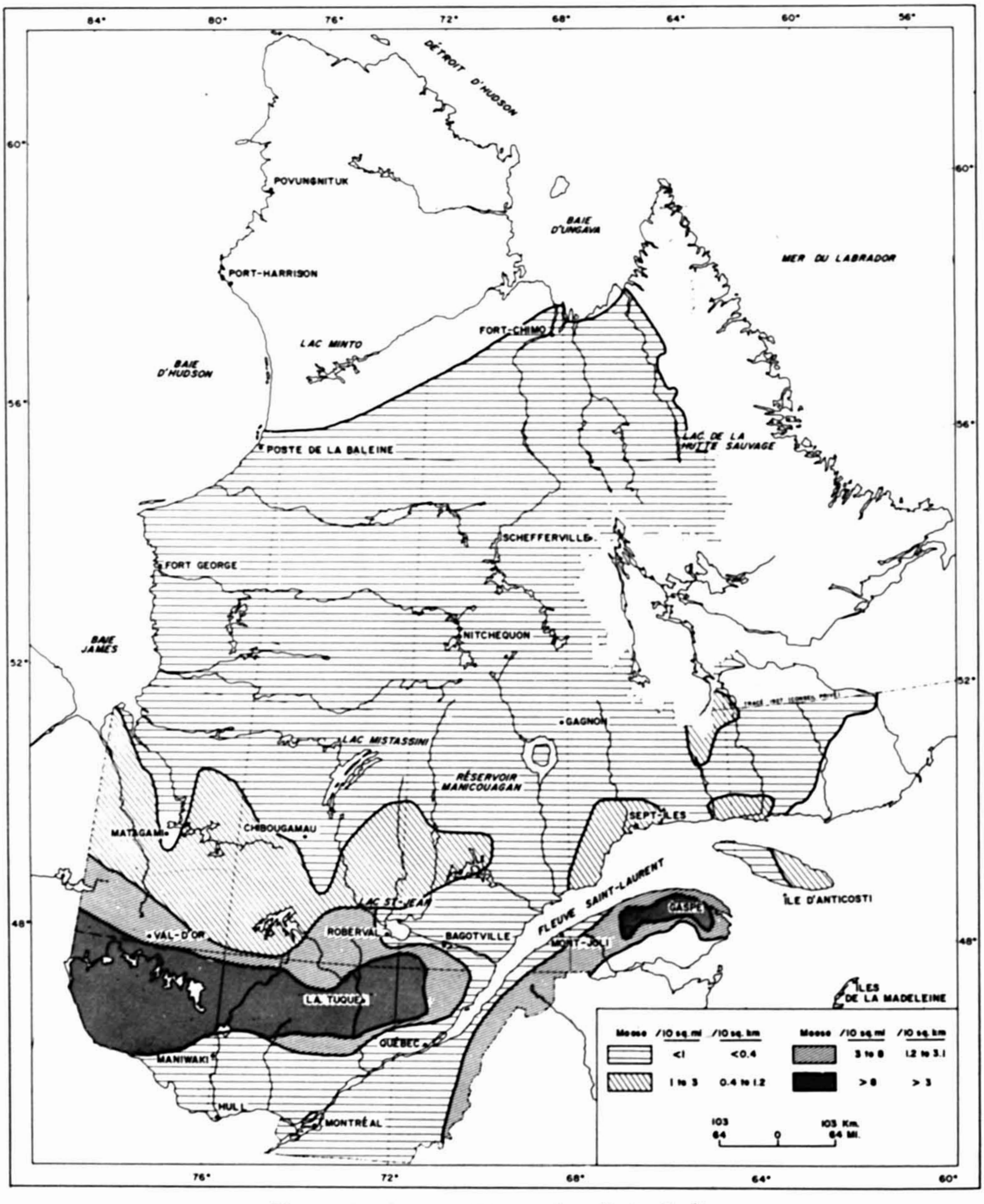

Figure 4. Relative moose density in Québec.

Forest zone 5

Black spruce is dominant in this zone. Relatively dense forests in the southern sections of this zone give way to more open stands near the forest-tundra transition. Numerous bogs are present in the northernmost sections. In the western area, snowfall is less than 120 inches (300 cm). In the east, snowfall may exceed 200 inches (500 cm) which hinders moose movement. This lowers the carrying capacity of the eastern region and moose density averages only 1.4 moose per 10 mi^2 (0.6 moose per 10 km^2). Moose density is higher in the western part, possibly due to lower snow accumulation.

Forest zone 6

The dominant tree species in this forest-tundra transition area is the black spruce. Snowfall averages 120 inches per year (300 cm), but in the southeast section of this zone it may exceed 160 inches (400 cm). The moose population is low and it relates to the more productive closed forest stands. The mean density is about 1.0 moose per 10 mi^2 (0.4 per 10 km^2).

Local studies of moose yards

In Québec, moose winter habitat has been studied in La Mauricie National Park (Audy, 1974), Mont-Tremblant and La Vérendrye Provincial Parks (Joyal, pers. comm.), in Matane Fish and Game Reserve (Crête, 1973) and in the Laurentides Provincial Park (DesMeules, 1965) (Fig. 5).

La Mauricie and Mont-Tremblant parks are within Forest zone 2, which is characterized by a transition vegetation between boreal and deciduous forests. The Matane Reserve and La Vérendrye Park are located within Forest zones 2 and 3, the latter zone being dominated by balsam fir. The Laurentides Park is situated within Forest zone 4.

DISTURBANCES IN FOREST STANDS UTILIZED BY MOOSE

Moose do not select wintering sites randomly but actively search out suitable habitat. This was studied in Forest zone 2 (La Mauricie Park).

During the winters of 1970-71 and 1971-72, this region was entirely surveyed from the air twice each year. Using the forest survey maps of Darveau (1971), vegetation disturbance was noted for a 0.5 mile (0.8 km) radius from the center of each moose yard. The percentage of the total area of La Mauricie Park affected by these disturbances was then compared to the percentage of occurrence of moose yards within and around these disturbances.

A Mann-Whitney non-parametric test showed a significant difference ($P<0.01$) between the two frequency distributions (Table I) and thus illustrates the selectivity by moose in choosing a wintering site.

These results for La Mauricie Park, indicate that moose prefer those areas affected by partial cuts and insect epidemics.

DENDROMETRIC CHARACTERISTICS OF FOREST STANDS UTILIZED

Cover

The cover stratum is composed of trees which furnish shelter to moose, facilitating their movement under the crowns and diminishing wind effects (DesMeules, 1965). In the tree canopy, only coniferous stems of a diameter at breast height (DBH) larger than 4 inches (10 cm) were considered. Coniferous stems less than four inches (10 cm) DBH are generally too small and hardwoods do not prevent the snow from reaching the forest floor (DesMeules, 1965). The cover stratum is characterized by the number of stems per acre (0.4 hectare), their mean DBH, and their mean basal area. Data have been gathered from Forest zones 2 and 3 (La Mauricie Park and Matane Reserve). All parameters have been evaluated using the method of Grosenbaugh (1952).

The data from La Mauricie Park were obtained in a systematic survey of two winter yards and those from Matane Reserve were obtained by sampling 16 yards within Forest zone 2 and 15 within Forest zone 3.

When comparing Forest zone 2 with 3, we find that the mean number of stems per acre (0.4 hectare) is greater,

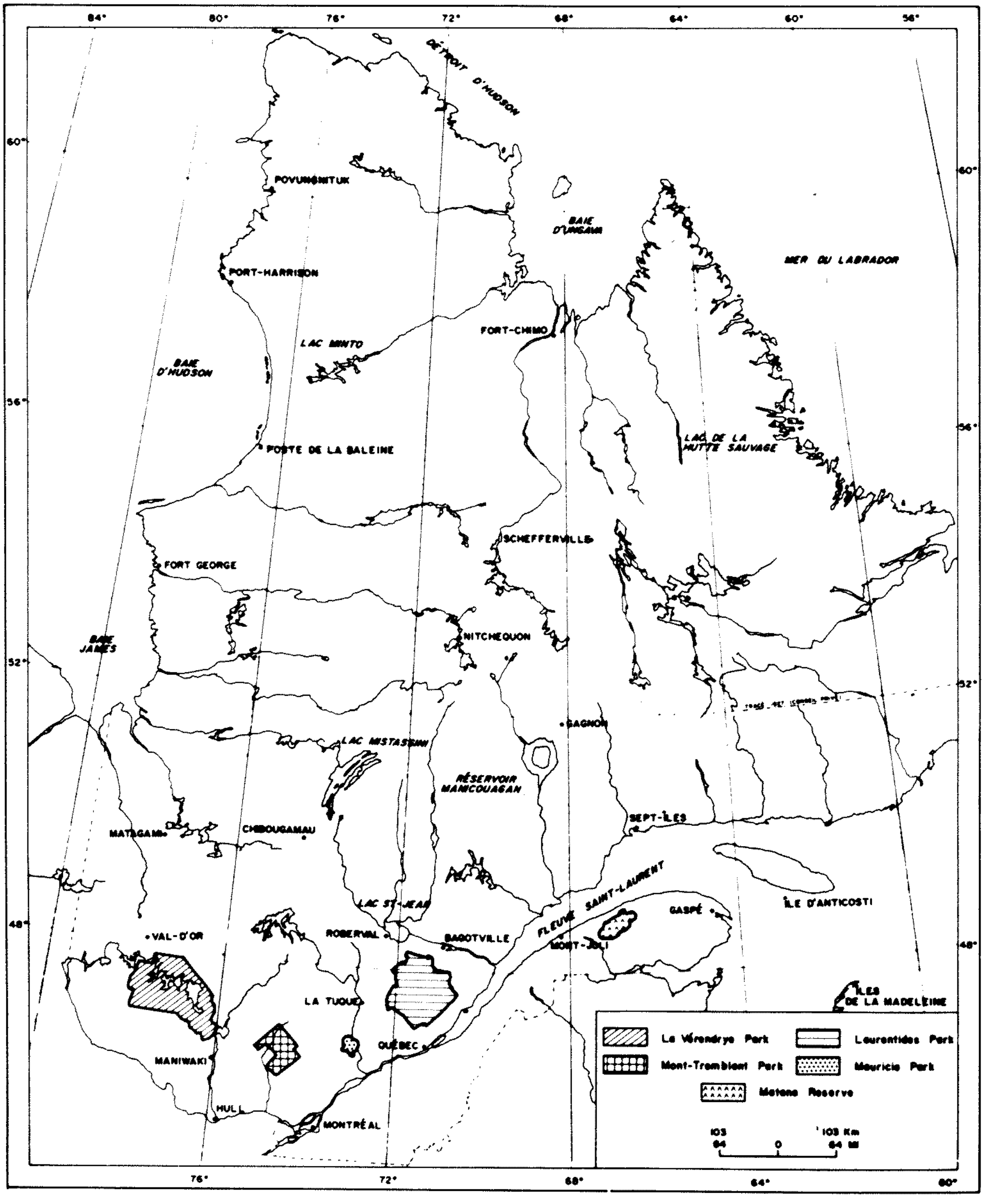

Figure 5. Location of specific habitat studies in Québec.

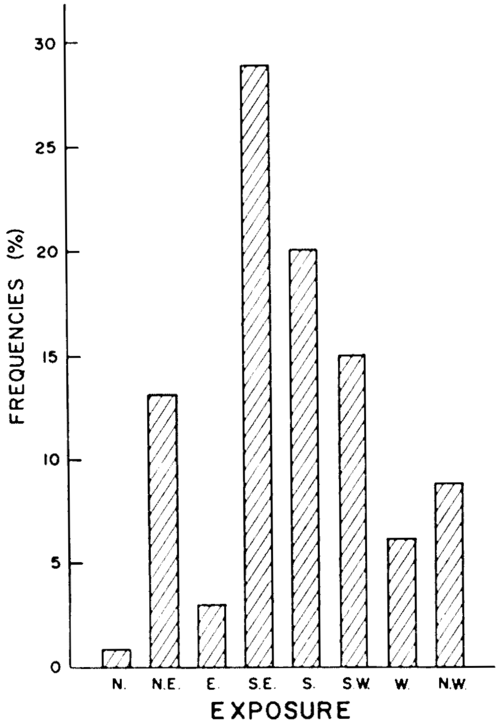

Figure 6. Relative frequency of exposure encountered in 106 moose yards in La Mauricie and Mont-Tremblant parks, Québec, Forest Zone 2 (Audy, 1974; Joyal, pers. comm.).

while the mean DBH is smaller in Forest zone 3, (Table II). The method used prevents statistical comparison of the mean number of stems per acre (0.4 hectare) in the two zones. However, there is a significant difference ($P \leq 0.05$) between the three mean DBH values for Forest zones 2 and the same parameter for Forest zone 3.

Thus, a suitable cover for moose within Forest zone 2 would be 150 to 200 stems by acre (0.4 hectare), with a mean DBH greater than 6.8 inches (17.0 cm), giving a mean basal area of 50 to 70 square feet per acre (11.3-15.8 m^2 per hectare). Within areas used by moose in Forest zone 3 there are some 300 stems per acre (0.4 hectare) with a mean DBH of approximately 6.3 inches (15.8 cm) and occupying a mean basal area of 79.8 feet^2 per acre (17.9 m^2 per hectare). These differences indicate that moose seek wintering sites in Forest zone 3 where the coniferous stems are more numerous but smaller than those in Forest zone 2.

Feeding stratum

A survey of the woody stems of this stratum was made using the browse survey method of Passmore and Hepburn (1955).

Table III illustrates the abundance of the major tree species in the moose yards studied and the total available stems per acre (0.4 hectare). In Forest zone 2, the number of browsed species varied from 8 to 12 per yard, the main species being balsam fir and mountain maple (*Acer spicatum*). The abundance of beaked hazelnut (*Corylus cornuta*) and red maple varied between the study areas. The total number of avail-

TABLE I

Percent disturbance in forests within the total study area and within a 0.5 mile (0.8 km) radius from the center of the moose yards. Data from 175 mi^2 (450 km^2) La Mauricie National Park, Québec.

Disturbance[1]	*% of the park area covered by disturbance*	*% of yards having a disturbance within a 0.5 mi (0.8 km) radius*
Partial windfalls	0.1	1.4
Partial cuts	5.5	46.6
Insect epidemics	0.6	12.3
Forest fires	11.7	24.7
No perceptible disturbances	82.0	15.1
Total	99.9	100.1

[1] The disturbances, except forest fires, have occurred within the past 15 years.

able stems per acre (0.4 hectare) ranged from 4,000 to 9,000 (10,000 to 22,5000 stems per hectare).

In Forest zones 3 and 4, the number of browsed species varied between one and eleven. In these zones balsam fir was most abundant. White birch, mountain maple and willows (*Salix* spp.) remained very important locally, while the total number of available stems fluctuated from 700 to 13,000 per acre (1,750 to 32,500 stems per hectare).

In the regions of Québec where the feeding layer was studied, balsam fir and mountain maple were found to be the most common. Occasionnally, balsam fir appeared to be of sole importance in moose yards (DesMeules 1965). This was observed when moose activity was hindered by snow accumulation and explains the variation in the data obtained for Forest zones 3 and 4.

Intensity of utilization

An index of moose yard carrying capacity was calculated by expressing the intensity of utilization in terms of moose-days per unit area. The use of this expedient became necessary as it was often imposible to directly determine the amount of time the animals spent in the wintering grounds.

The data were derived from pellet-group counts. The sample unit was 0.02 acre (0.081 hectare). Mean numbers of sampled units per yard averaged 125. The mean number of moose-days per acre (0.4 hectare) was obtained by dividing the mean number of pellet-groups per acre by 10.7, the daily defecation rate determined by DesMeules (1968).

Intensity of occupation within these moose yards varied from three to fourteen moose-days per acre (13 to 35 moose-days per hectare) (Table IV). There was a positive correlation between the intensity of occupation and the abundance of available deciduous stems. The correlation coefficient for all deciduous stems in all the Forest zones was 0.69 ($P \leq 0.01$) (Table IV). This relationship becomes more evident

TABLE II

Dendrometric characteristics[1] of moose yard cover in Forest zones 2 and 3 (La Mauricie Park and Matane Reserve)

Forest zone	*Study area*	*Mean number of stems per acre (0.4 hectare)*	*Mean basal area per acre (0.4 hectare) (square feet)*	*Mean DBH[2] (inches)*	*Sample size*
2	La Mauricie Park (Audy, 1974)				
	Edouard yard	164	68.8	8.2	56
	Ecarté yard	171	52.9	7.1	43
	Matane Reserve (Crête, 1973)	193	55.1	6.8	63
3	Matane Reserve (Crête, 1973)	337	79.8	6.3	60

[1] Softwoods >4 inches (10 cm) DBH.

[2] X ± 10% ($P < 0.20$).

TABLE III

Available stems per acre (0.4 hectare) for the main species of the feeding stratum

Forest zone	*Location and identification of yards*	*Number of browsed species*	*Available stems per acre (0.4 hectare)*						*Total number of stems*
			Abies balsamea	*Acer rubrum*	*Acer spicatum*	*Betula papyrifera*	*Corylus cornuta*	*Salix sp.*	
2	La Mauricie Park (Audy, 1974)								
	Hamel	10	2584	250	1264	122	1240	125	6624
	Fou	11	2203	1878	2103	581	107	143	7029
	Jumior	8	1609	949	2784	62	505	52	7497
	Ecarté	10	2072	238	2544	297	100	201	6546
	Edouard	10	1739	647	2014	126	143	0	6149
	Matane Reserve (Crête, 1973)								
	A-71	11	467	T[1]	2955	T	676	T	4502
	A-72	9	1355	173	2543	42	626	67	5321
	B-72	12	1191	0	5210	318	1931	T	9301
	D-72	10	1280	39	3787	73	1153	0	7019
	Mont-Tremblant Park (Joyal, pers. com.)								
	Lac à l'Ours	10	396	33	3003	462	198	33	5280
	La Vérendrye Park (Joyal, pers. com.)								
	Lac Marin	12	300	138	680	T	2049	0	3770
3	Matane Reserve (Crête, 1973)								
	B-71	11	969	T	2691	110	1094	T	5204
	D-71	8	1443	0	1445	584	0	24	4065
4	Laurentides Park (DesMeules, 1965)								
	Cyriac 1	11	348	66	3750	T	660	1080	5362
	Cyriac 2	10	58	36	1636	298	76	0	1720
	Ecorces	5	1971	0	0	8487	0	0	12599
	Epaule	9	889	0	1460	508	0	0	4076
	Enfer 1	1	1452	0	0	0	0	0	1465
	Enfer 2	2	656	0	0	0	0	0	671
	Enfer 3	2	542	0	0	389	0	0	931
	Enfer 4	2	633	0	0	348	0	0	981
	Enfer 6	1	796	0	0	0	0	0	796

[1] T = < 25 stems per acre (0.4 hectare).

when the data from Forest zone 2 alone are considered (r = 0.92, P ≤ 0.01). Lack of data from Forest zones 3 and 4 precluded the use of statistical analysis. No relationship was evident between the intensity of occupation and the numbers of available coniferous stems.

Therefore, the carrying capacity of moose yards within Forest zone 2, depends above all upon the availability of deciduous stems in the feeding layer.

The carrying capacity of these yards is also related to cover quality. However, the absence of appropriate information pertaining to this aspect prevents us from drawing any conclusions.

TOPOGRAPHIC CHARACTERISTICS

Moose yards exhibit certain common topographic characteristics. The location of the moose yards found during the aerial surveys of 1970-71, 1971-72 and 1972-73 in La Mauricie and Mont-Tremblant Parks were plotted on topographic maps (Scale: 1:50,000). Only the dominant slopes and exposures of moose yards were considered. We found that most moose yards were located on moderate slopes averaging 6.5% ± 0.8 ($P \leq 0.05$) and having a southerly exposure (Fig. 6).

We therefore concluded that moose seek wintering areas on southfacing slopes, where they benefit from favorable exposure to the sun. Good drainage

TABLE IV

Number of available stems per acre (0.4 hectare) and intensity of occupation of moose yards

Forest zone	*Location and identification of yards*	*Available stems per acre*		*Moose-days per acre*
		coniferous	*deciduous*	
2	La Mauricie Park			
	(Audy, 1974)			
	Hamel	2584	4040	2.41
	Fou	2203	4826	5.63
	Junior	1609	5888	9.77
	Ecarté	2072	4474	7.75
	Edouard	1739	4410	8.92[1]
	Matane Reserve			
	(Crête, 1973)			
	A-71	467	4035	4.85[1,2]
	A-72	1353	3968	4.32[1]
	B-72	1191	8110	16.59[1]
	D-72	1280	5739	11.68[1]
3-4	Matane Reserve			
	(Crête, 1973)			
	B-71	968	4236	4.85[1,2]
	D-71	1443	2622	4.85[1,2]
	Laurentides Park[3]			
	(DesMeules, 1965)			
	Cyriac 1	348	5014	9.77[1]
	Enfer 3	542	389	6.59[1]

[1] X ± 20%(P<0.20).

[2] Combined mean (no statistical difference (P>0.05) between yards).

[3] No data available for the other yards.

likely provides a higher quality of vegetation.

Conclusion

Moose are present over most of the province of Québec but their density is far from being uniform. They abound in Forest zones 2 and 3, two zones that are, broadly speaking, transition zones between almost pure coniferous stands to the north and almost pure deciduous stands to the south. Within these two zones moose select those areas that have suffered perturbations as a consequence of logging, fire or insect outbreaks and are in fairly early transitional stages.

Generally speaking, Forest zones 2 and 3 have the highest potential in the province for pulpwood (Lafond and Ladouceur, 1970). No doubt, forest exploitation there has benefited moose during the past and contributes at least a partial explanation to the animal's abundance. This benefit has not necessarily been the best one could have hoped for. The tendency of the logger has sometimes been to extract more from the land than it can return and sometimes to do it on such a broad scale that the forest surging back lacks in at least two basic respects: its diversity, both floristic and physionomic, has been reduced, and its evolution into immense and monotonous, single-species (usually balsam fir) tracts will not benefit moose more than for a short while. It would seem urgent to design a plan for forest exploitation that would incorporate more than accidentally, as many as possible of the prerequisites of moose.

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MOOSE DISTRIBUTION AND HABITAT SELECTION IN NORTH CENTRAL NORTH AMERICA

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Résumé

La distribution de l'orignal (*Alces alces andersoni*) coïncide principalement avec celle de la forêt boréale et les tout premiers stades de la sère chronologique suivant une perturbation dans cette forêt constituent un habitat de choix pour cet ongulé. Mais à mesure que la succession progresse, on observe une diminution de la qualité de l'habitat et, partant, une diminution dans l'abondance de l'orignal. En effet, la fermeture graduelle de la synusie arborescente, en même temps qu'elle passe hors de portée de l'orignal, va, en interceptant la lumière qui normalement y parvient, entraîner la disparition de la synusie arbustive. De tous les facteurs du milieu, le feu est sans doute celui qui a le plus influencé la distribution de l'orignal et ce, probablement depuis plusieurs siècles; des incendies forestiers dont on connaît le moment et l'étendue ont, en détruisant des milliers de kilomètres carrés de forêt, amené le développement d'un stade successionnel arbustif, lequel est essentiel à l'orignal. De nos jours, l'exploitation commerciale de la forêt est l'élément le plus important capable de ramener la succession au début de la sère chronologique. La tordeuse du bourgeon de l'épinette *(Choristoneura fumiferana)* affecte indirectement l'orignal en détruisant la synusie arborescente, ce qui favorise la synusie arbustive dans laquelle l'orignal trouve sa nourriture; inversement, la tordeuse détruit parfois de jeunes pousses de sapin destinées à devenir une ressource hivernale importante de nourriture. En somme, l'habitat qu'occupe l'orignal dans la forêt boréale est naturellement instable et les variations de niveau dans ses populations assez naturelles. Il semble bien que le feu ait toujours agi avec assez de régularité dans le milieu forestier boréal pour empêcher que toute la forêt atteigne la maturité; mais une protection efficace contre les feux de forêt a eu pour résultat net de réduire la disponibilité d'un habitat de qualité pour l'orignal. Le domaine vital de l'orignal incorpore des biotopes passablement différents selon la saison. En hiver, l'épaisseur et la qualité de la neige au sol vont influencer les déplacements et la sélection de l'habitat. A mesure que l'hiver progresse, l'orignal va se déplacer et passer de peuplements ouverts vers des peuplements plus fermés; en règle générale, les peuplements d'épinettes et de sapin seront davantage utilisés en fin d'hiver, chaque fois que l'épaisseur de neige au sol atteint ou dépasse 90 cm.

Abstract

The moose (*Alces alces andersoni*) is mostly confined to the boreal forest where important habitats are produced in the early seral stages of plant succession. As forest succession advances, the quality of the habitats and populations decrease accordingly because at maturity the boreal forest shades out the understory browse, and the overstory trees grow beyond the reach of moose. Wild fire is the most important factor that has influenced moose distribution and habitat selection for at least several hundred years; historic fires that covered thousands of square kilometers created seral shrub stages needed by moose. Timber cutting is presently the most important factor improving moose habitat by creating vegetation in the seral stage. The spruce budworm *(Choristoneura fumiferana)* destroys the overhead canopy of balsam fir *(Abies balsamea)* and white spruce *(Picea glauca)*, and removal of the overstory benefits moose by increasing the browse supply although budworms sometimes kill young balsams, an important source of winter browse. Therefore, moose habitats within the boreal forest are unstable, and natural population fluctuations occur. Natural fire apparently occurred often enough in many parts of the boreal forest to prevent the forest from reaching maturity, but fire protection during the past half-century has reduced the amount of good moose habitat. Summer and winter home ranges for moose require different kinds of habitats. In winter, movements and habitat selection are influenced by the depth and quality of snow. As the winter advances, moose gradually move from the more open stands to denser cover; usually snow depths of 36 inches (90 cm) or more result in greater use of spruce-fir stands in late winter.

Introduction

The most important habitats within the boreal forest are produced in the early stages of plant succession. "Many factors combine to influence the plant life and thereby become important in the ecology of the moose. Climate, soils, and time combine to shape the basic factors in the environment. However, several additional factors become interrelated to create considerable variation in local habitats" (Peterson, 1955). The quality of moose habitats are constantly changing because of forest succession and the populations fluctuate accordingly. The highest moose densities are usually associated with the subclimax type, with populations gradually declining as the forest reaches maturity.

The purpose of this paper is to bring together the available information pertaining to moose distribution and habitat selection in Manitoba, Ontario, and the Lake States. Special reference will be made to unpublished habitat studies on Isle Royale, Lake Superior, where information on moose-habitat interrelationships was obtained.

Moose populations have been affected by such factors as forest fires, defoliation by the spruce budworm, and commercial timbercutting operations, all of which produce second-growth forests that moose prefer.

Post-glacial dispersal

According to Peterson (1955), the Wisconsin stage of glaciation influenced the redispersal pattern of the moose from north central United States. He noted there were four refugia in North America in which the four modern subspecies originated, the three southern races being separated by grassland barriers for at least the last 8,000 years. In eastern United States two subspecies were recognized, *Alces alces americana* and *A. a. andersoni*. The differentiation may have been caused by an eastward extension of grassland (Schmidt, 1938) that created a barrier in combination with the large post-glacial lakes in the mid-continental region. When the glacier receded the central continental section became ice-free but the Cordilleran and Laurentide sheets of ice receded more slowly, permitting an earlier range extension for *A. a. andersoni* than for the other North American subspecies. With the passage of time, the two subspecies *(A. a. andersoni, A. a. americana)* dispersed northward and around the Great Lakes and the east-west movements met around 1900.

Present and historic status

In 1870 no moose were reported from the northern shore of Lake Superior (Shiras, 1921) and, according to the same author, "About 1885 a steady movement of the moose westerly from Québec was observed and a slower easterly migration from northern Minnesota. Eventually these animals commingled and took possession of the entire shore, later extending into the interior until they reached the waters flowing into Hudson Bay."

Gradually the moose spread northward in the forested areas of Ontario until the Hudson Bay lowlands was reached in the 1950's; although early settlers claim moose were present earlier, they could have dispersed from the west where they were reported earlier (Cumming, 1972). The movement from east and west around the Great Lakes has resulted in the overlap of the two subspecies now found through central Ontario (Cumming, 1972). The range they now occupy coincides reasonably well with the distribution of balsam fir except that fir extends further south along the Appalachian Mountains, and that in western Canada, moose cover a more extensive range than does balsam fir (Bakuzis and Hansen, 1965).

STATUS OF MOOSE IN ONTARIO

Champlain, in about 1603, is credited with first describing the moose or "orignac" as being similar to the European elk although Jacques Cartier had previously made an ambiguous reference to the animal (Cumming, 1972). The first recorded observations of moose in Ontario were by Gabriel Sagard between 1623 and 1624. He reported that moose were rare in the Huron region south of Georgian Bay (Wrong and Langton, 1939; cited in Peterson, 1955, p. 45). In 1731, writings by French traders indicate that moose were fairly abundant in the region around Lake of the Woods (Burpee, 1927; cited in Peterson, 1955, p. 45). Churcher (1965) found the remains of one moose at the Fishing Creek site near Fort Albany on James Bay that dated to approximately 1700 A.D., and Kenyon and Churcher (1965) reported a worked antler fragment from the Rainy Lake district dating to 7861 ± 423 years B.P., which they thought belonged to *Alces* although they did not rule out *Cervalces*. Excessive hunting of moose for hides and meat by explorers, Indians, settlers, survey crews, prospectors, and railroad builders resulted in a closed season from 1888 to 1895. An 1892 investigation noted that moose were endangered if poaching was not stopped; but in spite of this, the moose population began increasing again. Research by the Royal Ontario Museum of Zoology suggested that "moose decreased from 1935 to 1939, increased from 1940 to 1943 and decreased again from 1944 to 1946, remaining low until 1949. [...] the season for moose hunting was closed across the entire Province during 1949 and 1950 to facilitate moose studies" (Cumming, 1972). Apparently moose have increased since then as moose were known to have moved to the Hudson Bay lowlands as well as into southern Ontario. Currently they are present in the better habitats north of Sault Ste. Marie, Sudbury and North Bay, and south of the lowlands of Hudson Bay. To the south, moose are scattered in suitable habitats as far south as Parry Sound, Bracebridge, Bancroft, and Pembroke. The estimated population is 125,000 and from 12 to 15 thousand moose are killed each year by 50 to 60 thousand hunters (Cumming, 1972).

STATUS OF MOOSE IN MANITOBA

Bryant (1955) has reviewed the historic status of the moose in Manitoba from the 17th century through the 20th century. He reported: "In the past 200 years, moose extended their range from the 55th parallel and 97th meridian to the northern and eastern limits of the boreal forest. The advance is considered to have been part of a "normal" post-glacial movement accelerated by the concurrent extension of the range of the Cree Indians which increased the number of fire-produced openings" (Doughty and Martin, 1929; Douglas and Wallace, 1926; Burpee, 1927; Mendelbaum, 1941; Thompson, 1886; Seton, 1927). Soper (1946; cited in Peterson, 1955, p. 37-38) reported: "In primitive times the moose was widely distributed in the southern extremity of

Manitoba, but is now confined to the coniferous forest along the Ontario border, and Spruce Woods Forest Reserve."

Between 1694 and 1714, Jeremie reported many moose north of Lake Winnipeg in the Split Lake and Grass River area (Douglas and Wallace, 1926, cited in Peterson, 1955, p. 36). Small populations occurred in the Duck and Riding Mountains and Lake Manitoba in 1886 (Thompson, 1886, cited in Peterson, 1955) and about the same time they were present in satisfactory habitats from Lake Winnipeg almost to Hudson Bay (Preble, 1902).

Seton (1927) stated the province had 160 to 180 thousand km^2 (60 to 70 thousand mi^2) of moose range with a density of 0.38 moose per km^2 (or one moose per mi^2); early kill records provide some basis for estimating moose populations. From 1914 to 1924 the kill ranged from 2,447 to 247 (Jackson, 1926, cited in Peterson, 1955); from 1932 to 1936, it ranged from 248 to 75 (Manitoba, 1942), and in 1943 and 1944 the kill was 160 to 170 moose (Manitoba, 1947). Approximately 8,000 Manitoba hunters have harvested 3,500 - 4,000 moose annually in recent years (Howard, pers. comm.). Currently, Manitoba's moose population has been estimated at 64,000 animals; highest densities in the boreal forest reach only 0.1 moose per km^2 (0.25 moose per mi^2) but in the transitional parkland, aspen parkland, and shrub meadow the highest densities are about 1.1 moose per km^2 (3 moose per mi^2) (Howard, pers. comm.)

STATUS OF MOOSE IN MINNESOTA

Peat bogs near Crosby, Minnesota, have produced the skeletal remains of early moose (Swanson *et al.*, 1945). Historically, they have occurred mostly in the coniferous forest north of a line extending from the southern tip of Pine County in the east-central region to the northwest corner of the state (Karns, 1967).

Peek (1971) has reviewed the literature pertaining to the prehistorical aspects of moose distribution in northeastern Minnesota and noted that their presence may be shown by Indian records, fossil remains, and prehistoric vegetation. In the Great Lakes area, Indian pictographs (Dewdney and Kidd, 1962, cited in Peek, 1971) were probably the work of late Woodland Culture peoples (1000-1650 A.D.), or Eastern Woodland culture peoples (1650-1750 A.D.). Pictographs representing moose were most common along the waterways between Lake Superior and the Manitoba border and they were also found in the Quetico-Superior area, the Rainey Lake area, and north of Rainey Lake in Ontario, as well as in the area east of Lake Superior. The pictographs were absent in the Nipigon area north of Lake Superior.

Archaeological sites indicates prehistoric occurrence of moose at the McKinistry sites, the Nett Lake site, and the Pike Bay site (500 B.C. — 100 A.D.) in northern Minnesota (Lukens, 1963). Paleobotanical information gathered by Fries (1962) at the Weber Lake sites indicates the presence of spruce-fir pollen along with charcoal showing the presence of fire and the early seral stage vegetation which probably furnish moose habitat. Radiocarbon dates for *Betula* profiles were 10,180 ± 160 and 10,550 ± 300 B.P.

In their writings about Minnesota, Surber and Roberts (1932) noted that Radisson hunted in the region of Kanabec County in 1660 or 1661 and killed many big game animals including *Oriniaks* (moose). The party of Radisson and Des Groseillers reported killing more than 600 moose in 1660 (Peterson, 1955). In the 1800's John Tanner recalls moose were abundant in northwestern Minnesota and adjacent Canada (James, 1830); in northeastern Minnesota, in 1885, moose were considered to have been rare in 1880 in eastern St. Louis County, most of Lake County and all of Cook County; the southern edge of the range extended from Marine-on-St. Croix northwesterly to Staples and the Ontario border (Surber and Roberts, 1932). Lake and Cook County residents maintained moose were scarce in this area in the 1870's and early 1880's (Surber and Roberts, 1932; by 1890 they were unknown around Lutsen in Cook County, became abundant again, declined again and then increased (Swanson *et al.*, 1945).

The state population was estimated at 2,500 moose in 1922. They were concentrated in 1120 km^2 (432 mi^2) of range; one 104 km^2 (40 mi^2) area had an estimated density of 3.9 animals per km^2 (10 per mi^2) (Surber and Roberts, 1932). About 1930 the total Minnesota moose population was estimated at 3 to 4 thousand and they were common along the Ontario border (Surber, 1929). Currently the major moose range along the Ontario border occupies 20,700 km^2 (8000 mi^2) and the southerly peripheral range about 23,300 km^2 (9000 mi^2). Within the major moose range there are two distinct populations, one in the northeast conifer forest, and one in the bogs north of Upper Red Lake (Idstrom, 1965). The present population has been estimated at 7 to 8 thousand (Nelson, pers. comm.).

STATUS OF MOOSE IN MICHIGAN AND WISCONSIN

The past status of moose in Michigan, except Isle Royale, is poorly known. According to Hickie (*ca.* 1943), "possibly the earliest account which would place moose within the present boundary of Michigan is by Radisson in the year 1652." Other information gathered by Hickie shows moose were present in the Upper Peninsula in 1661, 1671, 1864, 1881, 1889 and 1899. Burt (1946) noted moose were: "Formerly over most of the state, but now confined to Isle Royale and a few places in the Upper Peninsula, where the Conservation Department is attempting to reestablish them... It is doubtful if they will ever become an important game animal in the state again." A total of 71 moose were released at three different places in Upper Michigan between 1934 and 1937; they were live-trapped on Isle Royale (Hickie, *ca.* 1943). Occasional moose are still sighted in various parts of Upper Peninsula; in 1972 the estimate was 25 to 50 animals (Voight, pers. comm.). In northern Wisconsin moose apparently were quite common around 1860 (Upham, 1905). Cory (1912) noted: "Moose were abundant in Wisconsin up to the middle of the last century, and more or less common in a few localities at a much later date. It is not unlikely that even at the present time one or two individuals may still be found in the extreme northwestern part of the state." Schorner (1956) concluded: "The year 1900 may be considered as approximately the time of the near extinction of the moose in Wisconsin. The last moose to arrive unaided in Wisconsin was drowned near Superior in 1921". However, Schorger's prediction proved incorrect since Dahlberg (1964) reported that there has been a scattered movement of moose into northwest Wisconsin from Minnesota from the late 1950's through 1963. During that period, thirty-five reports were obtained: 1 in 1960, 3 in 1961, 16 in 1962, and 15 in 1963. A recent estimate by Dahlberg (pers. comm., 3 Jan. 1973) from area game managers indicates 24 to 32 moose in the northwest counties of Wisconsin.

STATUS OF MOOSE ON ISLE ROYALE

Isle Royale, the largest island in Lake Superior, is a National Park and is part of the State of Michigan. It covers approximately 544 km^2 (210 mi^2) and consists of the main island which is 72 km long (45 mi) by 13 km (8 mi) wide at its widest point, with about 200 small islands and rock outcrops. The closest point to Ontario, Canada, is 21 km (13 mi), while the distance to Minnesota is about 29 km (18 mi).

The date of arrival of the moose and the literature pertaining to arrival is highly speculative. Hickie (*ca.* 1943) noted that ..."it seems probable that a few moose came to Isle Royale from the north shore of Lake Superior, either by swimming or walking on the ice, sometime around 1905. Although some moose may have crossed over in 1912-13, it seems doubtful that these were the first to reach the island." Murie (1934) cited J. Abner Sherman who reported seeing four or five moose out on the ice prior to 1880 and in 1880 noted moose were very scarce. Adams (1909) and his crew spent much time on the island in 1904 and 1905 but did not include moose on the list of mammals present. However, Max Peet, a member of Adam's party reported browsing on maples which he attributed to caribou but Murie (1934) felt that this browsing was probably the work of moose. He also noted: "...the last influx of moose occurred during the winter of 1912-13. The presence of moose on the island the following summer is correlated with conditions of the previous winter, and it is presumed that a few moose crossed over on the ice. Since 1913, the moose has increased in numbers untils now it is very abundant." Estimates by the State of Michigan showed: 250 by 1915-16, 300 by 1917-18, 300 in 1919-20, 1,000 by 1921-22, no estimate for 1923-24, and 2,000 by 1925-26 (Hickie, *ca.* 1943). For 1930, Murie (1934) noted: "Without an organized count or some sort it is practically impossible to know the moose population. From general observations I should estimate that in 1930 there were at least a thousand moose on Isle Royale, and I think that a count would give a figure far above the estimated minimum. As a rule, wild populations are greatly underestimated so it would not be surprising if the actual number of moose in 1930 proved to be two or three thousand." While Murie's population estimates may appear to be unrealistic, his observations on overbrowsing tend to confirm his highest estimate. Hickie (*ca.* 1943) noted Murie stated (p. 12): "On Isle Royale all of the important winter foods as well as several species eaten only in summer are overbrowsed — if the population is not reduced, the rate at which the vegetation is destroyed will rapidly increase, and in the future, the moose will begin to be eliminated by disease and starvation.' Hickie (*ca.* 1943) also noted: "In support of this contention, Murie's report lists the disappearance of water lilies *(Nymphaea* spp.), and pondweeds (*Potamogeton* spp.), the exhaustion of group hemlock (*Taxus canadensis*), the extensive depletion (over 50 percent) ob balsam fir, and severe overbrowsing on poplar (*Populus tremuloides*), birch (*Betula* spp.), mountain ash (*Sorbus americana*), and most of the shrubs." Later observations in 1945 by Aldous and Krefting (1946) support Murie's contention that the population probably exceeded 1,000 or more moose. Browse lines on older white cedar (*Thuja occidentalis*), a species disliked by moose, and on older balsams, were evident everywhere along with a depleted supply of balsam fir reproduction. The widespread distribution and dense growth of ground hemlock reported on by Ives (1848) and Holt (1905) was reduced to scattered small sprigs and aspen reproduction was nonexistent.

Murie's prediction that the population would decrease proved correct since: "During the period from about 1929 to 1935 the moose herd on Isle Royale underwent a drastic reduction due to the effects of a depleted food supply" (Aldous and Krefting, 1946; Titus, 1941). From a low of about 200 in 1935, the herd began a slow but steady increase because of an abundant food supply which followed the extensive 1936 burn that covered about 100 km² (about 40 mi²). Airplane strip-counts indicated there were about 500 animals in 1945 and 600 in 1947; by the fall of 1948 the herd was estimated at 800 moose (Krefting, 1951). A second die-off followed and the estimated population decreased from about 800 to about 500 by the spring of 1950 (Krefting, 1951).

Pellet group counts were made in the spring of 1948 on 0.004 ha (0.01 acre) plots at 200 m (10-chain) intervals on transects in representative cover types on the island. Similar counts were repeated about the same time each spring on a total of 844 plots for 1950, 1961, 1965 and 1970 to measure the population trend Table I). From 1948 to 1950 the counts decreased significantly ($\chi^2 = 119$, $P < .01$) and reflected the known die-off of the herd. Between 1950 and 1970 the counts showed a steady significant population trend increase $\chi^2 = 206$, $P < .01$) in spite of depredations by the wolf. These data are in contrast to the findings of Jordan *et al.* (1971) who reported, on the basis of other studies, that the population appeared to have remained stable from 1959 to 1969.

Factors affecting the range

FOREST FIRES

Fires have largely been responsible for generating the vegetation needed by moose, deer, beaver, and most other forest wildlife. "It may be agreed that fire has been an ecological factor, even in the forest primeval, and that in favoring certain types of forest and wildlife, it produces a natural condition" (Hayes, 1938). "There is some direct evidence for the long-term presence of fire and fire-adapted tree species in North America. Charcoal layers are common in peat bogs in the north, and some layers in Minnesota have been shown by carbon-14 dating to be 3,000 to 8,000 years old or more" (Heinselman, 1970). "A collection of tree fossils from early glacial drift in Minnesota, carbon-dated at more than 38,000 years old, contained cones and wood of jack pine and black spruce — both common post-fire species. Some of the wood was charred" (Heinselman and Roe, 1963). In northern Manitoba, the

TABLE I

Moose population trends on Isle Royale based on pellet group counts

Area	*Number of 0.01 acre plots (0.004 ha)*	*Mean number of pellet groups per acre (0.4 ha)*				
		1948	*1950*	*1961*	*1965*	*1970*
Entire island	844	82	36	63	83	113
Habitat types:						
Sugar Maple — Yellow Birch	77	44	8	9	8	31
1936 Burn:						
Siskiwit Lake	153	125	57	35	30	31
Feldtmann	36	83	50	86	111	122
Aspen-Birch-Fir-Spruce	471	70	33	68	93	125
Birch-Fir-Spruce	107	98	34	109	150	229

modification of the range, mostly by forest fires, was found to be the most important factor in moose abundance and distribution (Bryant, 1955). A record of fires in the province from 1945 to 1970 has shown there were 8,603 fires that burned 3,340,745 ha (8,254,868 acres); the largest number was 707 in 1961 and the largest area that year was 1,102,799 ha (2,424,978 acres) (Howard, pers. comm.). Although moose and deer benefited by these fires, only one Manitoba fire has been documented. A study of the Swan Pelican fire of 1961, which started in 1968, has shown both higher reproduction per 100 cows and a higher twinning rate than the Duck Mountain area which had the poorest habitat (D.L. Davies, pers. comm.).

In Ontario large fires ranging in size from 182 to 7,800 km^2 (70 to 3,000 mi^2) burned over 57,000 km^2 (22,000 mi^2) between 1855 and 1861 (Ontario Dept. Lands and Forests, 1971). From 1917 to 1961 there were 14 years with burned areas of more than 12,000 ha (300,000 acres). Peterson (1955) concluded that fire was the most important agent affecting forest succession, but that extensive burned-over tracts do not support large moose populations until the summer and winter habitat are in balance. Cumming (1972) also reported: "It has been observed over and over again that some of the greatest moose concentrations are in areas previously burned. It seems likely that nutrients released in ashes from burned vegetation enrich the area and produce more nutritious foods."

In the Lake States the severest fires occurred during droughty periods but most of them were outside the range of the moose and the white-tailed deer probably benefited most. Within the moose range in northeastern Minnesota, a fire history study showed that the oldest stand dated from 1595 and the youngest of any size from 1936. Major fires recurred at 5-50 year intervals from 1600 A.D. to 1920, others reburned at intervals as short as 10 years, and some as long as 200 to 300 year intervals (Heinselman, 1969, 1970). Regarding wildlife, Heinselman noted: "The animal component of these forest ecosystems was adapted to a fire ecology. Some of our most abundant herbivores — deer, moose, elk, snowshoe hare, and the beaver — are best adapted to recent burns and the early successional stages of the forest — not climax forests." In May 1971, the largest single fire in the recent history of northeastern Minnesota (Little Sioux) burned over 6,100 ha (15,000 acres). Ruffed grouse were drumming within a week, and moose were observed browsing a few weeks later (Stenlund, 1971). Peek (1972) classified moose on this burn and made comparisons with his Kawishiwii River-Isabella study area; aerial counts showed a density of 0.4 to 0.8 moose per km^2 (1.0 to 2.0 per mi^2), compared to 0.8 to 2.0 per km^2 (2.0 to 5.0 per mi^2) on the study area. He found the percentage of yearlings (18 months old) was 34 percent (77 observations) in the burn compared to 13 percent (348 observations) on the unburned study area.

Although information on the fire history on Isle Royale is rather sketchy, a recent vegetation-type map demonstrates that the island has a mosaic of varied forest cover types of different sizes due to past fires (Krefting *et al.*, 1970). The field notes of the linear survey of 1847 made reference to burned-over areas at various locations (Ives, 1848). From 1843 to 1855, and again in the 1870's and 1890's, fires were set intentionally by prospectors in search of copper deposits (Brown, *ca.* 1935). The last and most severe and extensive fire occurred in 1936 when about 100 km^2 (40mi^2) burned. Regarding this fire Aldous and Krefting (1946) noted: "In 1936 fires burned over approximately one-fourth of the island. These eliminated a large part of the browse supply for 2 or 3 years, but in the long run have been one of the greatest factors in permitting a comeback of the moose. Today (1946) the 1936 burned area supplies more browse than the remainder of the island combined." Documentation of this fire has been included in the habitat section of this publication.

To date, there have been no prescribed burning studies in the region designed specifically for moose habitat improvement. Sando and Dobbs (1970) have outlined the precautions and procedures to be followed to execute prescribed burns to regenerate jack pine on logged areas in Manitoba and Saskatchewan. In northeastern Minnesota, Ahlgren (1970) has used prescribed burns on logged areas to regenerate jack pine. Only one prescribed burning study has been designed specifically for wildlife habitat improvement purposes in this region (Sando, 1972). The study area is located in north central Minnesota, outside of the moose range, within the aspen-birch type which is important to white-tailed deer and ruffed grouse (Byelich *et al.*, 1972; Gullion and Svoboda, 1972).

LOGGING

"When a forest is either logged or burned over, or both, the newly developing vegetation will not only be in an early successional stage, but it will, particularly during the first few years, contain a much greater variety and quantity of available food for most wildlife species than a mature forest. Particularly from three to ten years after logging or burning, the available food is vastly superior both in quantity and quality" (de Vos, 1962).

Over much of the moose range in eastern North America, logging is the principal method by which older-age classes of timber are removed and young browse-producing stands are created; both the pattern and extent of the logging have a direct influence on the moose and deer populations produced (Telfer, 1970b) "In eastern Canada, various factors have led to a pattern of clear-cut areas replacing large, pure soft-wood stands (conifer), and partial cuts of mixed-wood stands, leaving patches of hardwood and patches of soft-woods that are too small for profitable handling" (Telfer, 1970b). A New Brunswick study showed the annual growth of browse on 1.6 ha (4 acres) uncut stands would feed a moose for one day and in contrast five to seven year old cuts provided browse at the rate of 32 moose-days per ha (13 per acre) (Telfer, 1970b).

In northwestern Ontario, one company cut 25,980 ha (64,190 acres) of pulpwood (1948 to 1961) on a moose study area; these operations not only produced more moose browse but they also provided greater access to hunt moose because of the roads that remained after logging (Simkin, 1963).

The commercial forest-land area within the moose range in northern Minnesota embraces about 5,658,100 ha (13,981,000 acres) and the area of the major forest types include 3,737,700 ha (9,235,700 acres) of upland types 274,800 ha (3,150,000 acres) of swamp types and 645,300 ha (1,594,500 acres) classified as upland and lowland brush (Zasada, 1971). The upland type consists of 52 percent aspen-balsam, 19 percent northern hardwoods, 13 percent balsam fir-white spruce, 10 percent jack pine, and 4 percent red and white pine. From 1966 to 1970 a total 294,000 ha (726,500 acres) was cut (5.1 percent); the annual cut averaged about 1 percent, ranging from 54,840 to 61,920 ha (135,500 to 153,000 acres). Since the predominant species on about 60 percent of the area consist of aspen, paper birch, jack pine, and balsam fir, it is important that harvesting of those species be increased if the crop is to be cut at maturity (50 to 60 years) and still maintain desirable habitat for moose. About 87 percent of the land logged between 1966 and 1970 was clear-cut of merchantable timber, which produced the most browse, while 13 percent was thinned or partially cut. The area burned in northern Minnesota between 1966 and 1970 ranged from 937 to 4,767 ha (2,319 to 11,779 acres) so it appears that logging had a greater impact on the habitat for moose and deer than fire.

Heinselman (1969) mapped areas that had been logged between 1895 and 1940 on the Boundary Waters Canoe Area in northeastern Minnesota and reported: "It was the big pine that the early lumbermen sought, at first little else was cut. Later some spruce was taken for pupwood, fir for lath and studs, and cedar and tamarack *(Larix laricina)* for poles and posts." In northeastern Minnesota, Peek (1971) also felt that cutting on his moose study area (1948 to 1967) was largely responsible for maintaining the high moose population; one large operation covered 25,900 (64,000 acres).

On Isle Royale most logging occurred before the arrival of the moose in the early 1900's. Most of the mature white pine apparently was cut from 1835 to 1837 when the American Fur Company (1835-37) operated field stations on the island (Ives, 1848). Some logging was carried on at various times during the copper mining period which extended from 1844 to 1899 (Pietila, 1965). In 1935 about 1,000 ha (2,500 acres) pulpwood was clear-cut within the proposed national park (Hickie *ca.* 1943). Therefore, it can be concluded that logging had little impact on the island's moose herd.

FOREST INSECTS

Moose habitat is sometimes affected by severe defoliation by forest insects (Peterson, 1955). Case history outbreaks of the spruce budworm *(Choristoneura fumiferana)* have been reported on by Blais (1968) for eastern North American forests. Also, Kulman (1971) has pointed out that budworm attacks have occurred throughout the range of balsam fir since the early 1700's and during the period 1920 to 1958 nearly all balsam fir stands have been attacked. Outbreaks of epidemic proportions have been reported by various observers (Bakuzis and Hansen, 1965) from nearby Ontario and Minnesota locations about 1880, from 1909 to 1913, from 1937 to 1955, in 1954, and in 1956. Budworm attacks in Ontario in 1946 and before had killed 50 percent of the balsam fir in some areas and in others 100 percent (Peterson, 1955). The 1952 infestation in Ontario was formed by the merging of outbreaks in the Hudson, Lac Seul and Lake of the Woods areas and extended into northeastern Minnesota (McGugan *et al.*, 1953; Batzer, 1969). After 1961 the Minnesota infestation decreased until 1966 but since 1970, an increase has been noted (Batzer, pers. comm.). Budworm defoliation increased in the spruce-fir type in northeastern Minnesota from 38,851 ha (96,000 acres) in 1960 to 97,100 ha (240,000 acres) in 1961 (Batzer and Bean, 1962). Although the insect destroys balsam fir, an important winter browse species, the removal of overstory trees increases the browse production in the long run. In writing about the moose browse increase following budworm attacks, Cumming (1972) stated: "High densities of moose which built up in northeastern Ontario some 10 to 20 years ago, probably resulted from the great spruce-budworm outbreak which had previously occurred in that area." Also, in northwestern Ontario, Simkin (1963) noted that when budworm-killed stands are burned, the successional growth (seral stage) provides an excellent moose-habitat. He reasoned that even without fire the budwormkilled stands permit more sunlight to reach the forest floor and enhances the growth of such browse species as quaking aspen, white birch (*B. papyrifera*), willow (*Salix spp.*), juneberry (*Amelanchier spp.*), mountain ash and beaked hazelnut (*Corylus cornuta*). In northeastern America it has indeed in the past created good moose food supplies (E.S. Telfer, pers. comm., 15 May, 1973).

On Isle Royale, the first known budworm attack occurred in the early 1930's and 75 to 100 percent of the balsam fir stands along the south shore of the island from the northeast to the southwest end were damaged (Brown, *ca.* 1935). Ninety to 100 percent of the young balsams that projected above the snow were killed and since balsam was regarded as a high preference winter browse species, and the older stands provided important winter cover, the attacks were regarded as detrimental (Hickie, 1936). However, the budworm-killed trees probably furnished added fuel for the fire which burned about 40 mi^2 (104 km^2) of the island in 1936 and reduced the succession to the early seral stages responsible for the marked increase in the moose herd.

While the spruce budworm outbreaks are natural events which will undoubtedly continue to affect the forest types having large proportions of balsam fir, their future incidence is difficult to predict as to extent, periodicity, or severity. While understories under fir-killed trees may sometimes be dominated by raspberries, the duration is usually only a few years before browse plants become established. However, the outbreaks must be considered beneficial to moose in the long run.

Moose habitat selection and distribution

HABITAT SELECTION AND SNOW RELATIONSHIPS

In winter, movements and habitat selection are influenced by the depth and quality of the snow (Peek, 1971; Kelsall and Prescott, 1971). Québec and New Brunswick studies have shown that, as the winter advanced, the moose gradually moved from the open timber stands to the more dense cover (DesMeules, 1964 and Telfer, 1970a). In January, New Brunswick moose favored the more open stands of timber while the white-tailed deer favored the dense conifer belts. By March, both species used the more dense conifer stands. In Québec, DesMeules (1964) reported that moose shift from cut-overs to small medium openings when the snow depth reached 76 to 86.4 cm (30 to 34 inches), and in New Brunswick uncrusted snow over 90 cm (36 inches) deep resulted in high use in soft-wood (conifer) cover types (Telfer, 1968).

The shift from open to dense cover in northeast Minnesota took place at lower snow depths than reported on in New Brunswick and Québec (Peek, 1971). While most studies make reference to snow depth only in relation to movements of moose and other big game (DesMeules, 1964; Edwards, 1956; Kelsall 1969; Telfer, 1967), very few studies stress the importance of additional snow quality factors such as compactness, density, and hardness as they relate to big game movement (Kelsall, 1969; Kelsall and Prescott, 1971; Ozoga, 1968; Peek, 1971; Pruitt, 1959).

Recent studies on moose habitat selection in northeast Minnesota indicated areas logged less than 20 years previously were responsible for maintaining a high moose population. Peek (1971) found the logged areas were used in June when the protein levels in key species were highest, and in late fall and early winter when fat and carbohydrate levels were highest. The more mature quaking aspen and white birch stands were favored in late summer; spruce-fir stands were used most in late winter.

Use in June was oriented towards aquatic communities and the more open and poorly stocked stands; the presence of preferred forage species seemed to govern habitat use. Upland stands of quaking aspen and white birch were used throughout the summer period; these relatively mature stands were usually moderately to sparsely stocked. And in late summer and early winter, use was centered on upland deciduous tree stands. During the late November to April period, the most drastic changes in habitat occurred. These shifts from January to March were geared mostly to snow quality and weather conditions; in moderate weather periods; use of more open areas occurred, and in severe weather periods use of the upland spruce-fir type was most common. Peek's data indicated that early winter forage selection may be more critical than mid-winter, when cover requirements may also become important. In Ontario, Peterson (1955) concluded that 75 cm (30 inches) of snow did not hinder moose movement unless it was crusted.

On Isle Royale snow depths seldom reach 90 cm (36 inches) and with the exception of some of the northwest-facing ridges, snow is not a hindrance to moose movement. Mech (1966) reported the depth did not exceed 66 cm (26 inches) in the wind-protected areas in 1959, 1960 and 1961; in the winter of 1963 they ranged from 45 to 90 cm (18 to 36 inches) in depth. Records for the period 1966 to 1972 showed the depths exceeded three feet only for short periods of time in 1966, 1969 and 1972 (Park Service weather records).

THE ISLE ROYALE HABITAT STUDY

The 544 km^2 (210 mi^2) archipelago has a relatively undisturbed terrestrial community that has been dominated by the moose for about 60 years. Major changes in the vegetation have resulted because of moose browsing, activities of the beaver, and forest fires over the past 125 years, especially the extensive 1936 fire. Fire alone has been responsible for producing a good interspersion of vegetation types along with a wide assortment of diverse high quality seral stage habitats for the moose.

The forest cover types on the island are relatively homogeneous assemblages of species which can be distinguished from adjacent types on the basis of species, age, size or developmental differences. A cover type was named after the species or combination of species making up over 50 percent of the total tree stand. Because of the great variety of cover types, they have been grouped into type complexes that contain a wide range of conditions. However, almost all of them provide a wide variety of high quality moose habitats that are used at different seasons of the year. Data on the density of piles of pellets have been summarized for four major habitats as an index of winter use (Table I).

Habitat preferences

Sugar maple — yellow birch type. This type covers an estimated 4,030 ha (9,950 acres) or about 7 percent of the island and is climax because it is self-supporting under present conditions. Most stands in this type have not been disturbed for 120 years or more and the annual ring counts have shown some sugar maple (*Acer saccharum*) over 220 years old and yellow birch (*Betula alleghaniensis*) over 150 years of age. The largest trees are 63.5 to 76 cm (25 to 30 inches) in diameter, while the basal area ranges from 32.1 to 36.7 m^2 per ha (140 to 160 square feet per acre) and the heights are from 21.4 to 24.4 m (70 to 80 feet). Pollen data by Potzger (1954) and research by Linn (1957) suggest that the type is a relic of the xerothermic period. Understory reproduction is mostly sugar maple; yellow birch, white cedar, and balsam fir are scattered. Shrub species are ground hemlock (*Taxus canadensis)*, juneberry, round-leafed dogwood (*Cornus rugosa*), beaked hazelnut, and mountain maple (*Acer spicatum*).

Pellet group counts showed there was a significant downward trend in the use of this type from 1948 to 1950 (χ^2=40, P<.01) and reflects the known die-off of moose on the island during that period (Table I). The counts from 1950 to 1965 were at a uniformly low level of about 3.2 per ha (8 per acre), but from 1965 to 1970 there was a significant upward trend (χ^2=34, P<.01). The low pellet count data for this type, the lowest of all the types, indicates that the type is un-important to moose in winter.

1936 burn type. The 10,520 ha (26,000 acre) burned-over area covers 19 percent of the island and contains two separate burns: the Feldtmann burn in the southwest section of the island (1210 ha or 3000 acres) and the Siskiwit Lake burn in the central section (93000 ha or 23,800 acres). Paper birch is more widely distributed than aspen in the burn area (Fig. 1). White cedar and white spruce are scattered in this type, and balsam fir is largely absent. Tree diameters are 7.6 to 12.7 cm (3 to 5 inches) for quaking aspen and 2.5 to 17.8 cm (1 to 7 inches) for white birch and white spruce. The quaking aspen and white birch are not uniform in age, relating to the history of previous moose browsing. Understory shrub species include fire cherrey *(Prunus pennsylvanica),* redosier dogwood *(Cornus stolonifera),* willow *(Salix spp.),* juneberry, beaked hazelnut, rose (*Rosa spp.),* and mountain maple. On the Feldtmann burn, the pellet counts showed a significant decrease from 1948 to 1950 (χ^2=15, P < .01). However, a significant increase occurred from 1950 to 1970 (χ^2=22, P < .01).

The Siskiwit Lake burn also showed a significant decrease from 1948 to 1950 (χ^2 = 84, P < .01). However, unlike the Feldtmann burn, the data showed a significant decrease from 1950 to 1961 (χ^2=24, P < .01), leveling off from 1965 to 1970. These population trends also relate to changes in the availability of browse on the burn from 1945 to 1970. This burn was attractive to the moose herd for about 14 years (1936 to 1950). Apparently the better interspersion of unburned patches of cover in the Feldtmann burn sustained longer use than the Siskiwit Lake burn.

Aspen-birch-fir-spruce type. Due to its fire origin, the type has extensive stands of quaking aspen and white birch about 80 to 100 years old and is heavily invaded by white spruce and balsam fir (Fig. 2). The type occurs mostly in the northeast end of the island and covers 43 percent or about 23,200 ha (58,000 acres); it averages about 642 trees per ha (260 per acre) and a basal area of about 23 m^2 per ha (100 square feet per acre). Species ages vary from 43 to 83 years for quaking aspen, 33 to 115 years for paper birch, 26 to 100 years for balsam fir, and 51 to 100 years for white spruce. Balsam fir reproduction has increased strikingly during the past 10 years in some areas; quaking aspen reproduction is scattered, but moose browsing is preventing its establishment. The shrub understory consists of beaked hazelnut, juneberry, mountain alder *(Alnus crispa),* mountain ash, redosier dogwood, highbush cranberry *(Viburnum trilobum)* and willow. Pellet counts in this type from 1948 to 1950 indicate there was a significant decrease in the population (χ^2 = 198, P < .01); from 1950 to 1970 there was a significant upward trend (χ^2 = 358, P < .01).

Birch-fir-spruce type. About 8,900 ha (22,000 acres) or 16 percent of the island is covered by this type consisting mainly of three overstory species: balsam fir, white birch, white spruce and scattered quaking aspen. Without fire, it represents the boreal climax stage toward which other plant communities evolve (Cooper, 1913). However, the forest classifications by Halliday (1937) and Rowe (1959) suggest that Isle Royale is not typically boreal and that it relates more to the Great Lakes — St. Lawrence region (Rowe, 1959). Because of more than 60 years of severe moose browsing, the type has become quite open and park-like (Fig. 3). Balsam firs 30 years of age are less than three feet tall, and a distinct browse line on the overstory balsams still persists from the 1930's. The spruce budworm epidemic in the 1930's also thinned out the older balsam fir. The openness of this type has encouraged more shrub browse than is typical in the boreal type.

The pellet counts in this type in 1970 were 566 per ha (229 per acre) the highest on the island. In 1948 it was the second highest 242 per ha (98 per acre).

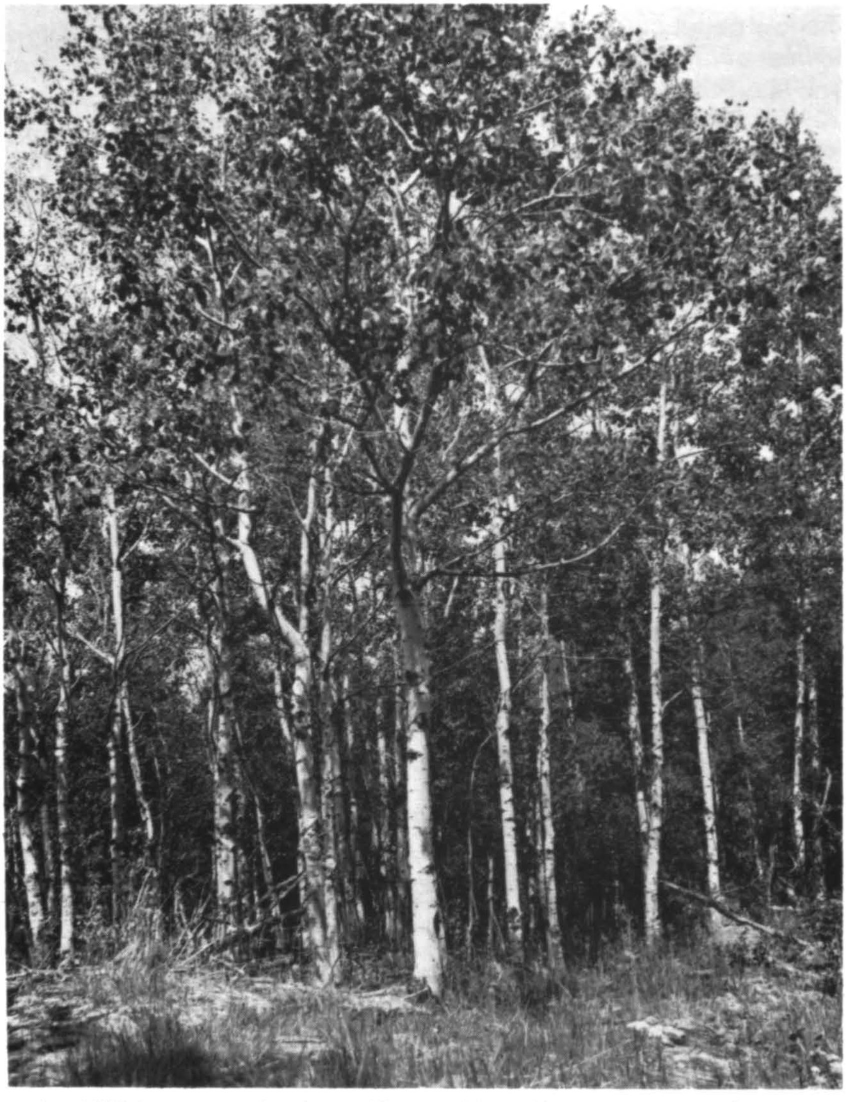

Figure 1. 1936 burn type showing a 36-year-old quaking aspen stand. Quaking aspen is less common than paper birch and is usually confined to smaller areas on better sites. U.S. Fish and Wildlife Service photo by author.

Like other types, the counts decreased significantly from 1948 to 1950 ($\chi^2 = 72$ $P < .01$) and increased significantly from 1950 to 1970 ($\chi^2 = 214$, $P < .01$).

Home range

Telemetry studies in northeast Minnesota revealed that moose winter ranges consisted of a series of high-use areas where moose stayed for a period, then moved to establish themselves in new locations between 0.4 and 4.8 km (0.25 to 3.0 miles) away; the ranges were found to be 1.8 to 3.4 km^2 (1.1 by 2.1 mi^2) in area (van Ballenberghe and Peek, 1971). Observations of unmarked but recognizable moose in Ontario suggested that summer movements were limited and the home range was 0.8 by 7.6 km (0.5 by 4.7 miles) (De Vos, 1956); another study of marked moose in Ontario indicated that summer and winter home ranges were quite small (Goddard, 1970). Two moose in Finland had a winter home

Figure 2. Aspen-birch-spruce type. Quaking aspen overtops white spruce on the better sites; others have extensive stands of paper birch 80 to 100 years of age which are gradually invaded by white spruce and balsam fir. U.S. Fish and Wildlife Service photo by author.

range that was less than 2.6 km² (one square mile) in size (Loisa and Pulliainen, 1968). Studies in western United States have shown that the summer and winter home ranges in Wyoming were less than 1.5 square mile (3.9 km²) (Houston 1968); a second Wyoming study showed the summer range was 1.0 by 5.3 km (0.6 by 3.3 miles) (McMillan, 1953). Knowlton (1960) concluded the extent of the summer range was 1.1 by 1.9 km (0.7 by 1.2 mile) in Montana.

On Isle Royale, the moose restricts its wanderings to a very limited area, if food is plentiful. Observations made during the summer of 1929 (Murie, 1934) indicate that the moose at this season likewise tends to confine his movements to a small area; recognizable bulls in August and September provided the information on summer home ranges. Hickie (*ca.* 1943) also concluded that in late winter they tended to congregate into moose "yards". Murie (1934) noted: "There may be some travel from a summer to a winter range, but it seems probable that many of the animals remain in the same general region the year round." Hickie (1938) felt that seasonal movements of moose were short and that availability and palatability of browse had more influence on movement than topography. The writer is also of the opinion that in the spring there is a noticeable shift of moose into the northeast end of the island; apparently the aquatic plants in beaver impoundments attract the moose to this area.

Figure 3. Birch-fir-spruce type. Note the severe browsing by moose, especially on balsam fir reproduction (30 years of age), mountain ash, aspen, and paper birch. Sixty years of moose browsing has resulted in a lack of different age classes of young balsam fir and an open park-like habitat. U.S. Fish and Wildlife Service photo by author.

Conclusions

An extensive survey of the literature demonstrates a lack of information on moose distribution and habitat selection that is needed to manage moose. While various authors have shown that such environmental factors as fire, logging, and spruce budworm damages in the boreal forests, apparently increased moose populations because they provided the early seral stage of plant succession, many of the observations are unfortunately not well documented. On two burns, some preliminary results are available pertaining to moose productivity studies for the Swan-Pelican fire in Manitoba and the recent Little Sioux fire in Minnesota. On Isle Royale the 1936 burn has been documented, starting in 1944 with emphasis on available browse, and with a study of population trends based on pellet counts started in 1948. The observations made on burns not only point out the need for documenting burns of different sizes but also demonstrate the need of prescribed burns designed specifically for moose. Because the moose is a fire-adapted species, there is a need to reintroduce fire into the ecosystem.

Data on the protected commercial forest lands in northern Minnesota suggest that logging in recent years has had a greater impact on the moose and deer populations by improving habitat than fire. The data also show the need to document the effects of cutting on the habitat by measuring the browse supply, cover, and population before and after cutting. Because the current timber-cutting practices are geared towards cutting smaller areas than required by moose, research should be conducted on various sizes of areas that are cut as they relate to both moose and deer. Northeastern Minnesota studies suggest that primary moose habitats appear to be rather open cutovers which are used in early summer and late fall. At other times of the year, preferred habitats are the mature quaking aspen-white birch and spruce-fir types. The radio telemetry study in the area also showed the summer range was about 1.6 by 3.2 km (1 by 2 miles) in size and the winter range was a series of wanderings in an area about 0.4 by 4.8 km (0.25 to 3.0 miles).

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HABITAT USE BY MOOSE IN NORTHWESTERN MINNESOTA WITH REFERENCE TO OTHER HEAVILY WILLOWED AREAS

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Résumé

Cet article décrit les relations entre l'orignal (*Alces alces andersoni*) et son habitat dans le Refuge national de la faune d'Agassiz au nord du Minnesota, et établit des comparaisons avec d'autres biotopes. Entre 1968 et 1971, on a pu recueillir 3,881 observations — rattachées aux différents types d'habitats — par le moyen d'émetteurs portés par 23 orignaux et de colliers d'identification portés par 14 orignaux. Dans 83.8% des cas, les animaux se trouvaient dans l'une ou l'autre des catégories de saulaies. L'habitat constitué de futaies dominées par des trembles (*Populus tremuloides*) et de gros *Salix* (tall-mature habitat) est fréquenté du 1er janvier au 15 avril, comme l'indiquent 76% des observations. Il fut possible d'établir une corrélation entre l'utilisation d'un tel habitat et l'épaisseur de la neige ($r = 0.84$ pour 1970; 0.39 pour 1971). A la mi-avril, les animaux passent à un autre type d'habitats (low-open), constitués surtout par des saules arbustifs prostrés et un sol marécageux; 60% des observations d'été proviennent de ce type d'habitat. Les marécages eux-mêmes sont peu fréquentés. Du premier septembre au 31 décembre, les deux types d'habitats (tall-mature; low-open) présentent un même taux de fréquentation. De façon générale, la préférence de l'orignal va au premier type; le second est évité, sauf quand les sites sont dominés par *Salix interior*. On a noté certaines préférences pour des espèces déterminées de saules, plantes qui de toute façon constituent la presque totalité du contenu du rumen.

L'auteur fait ensuite des comparaisons avec des observations analogues provenant d'autres régions: les deltas des rivières Peace-Athabasca (Alberta) et Saskatchewan. Du point de vue écologique et géologique, il y a beaucoup de ressemblance avec le nord-ouest du Minnesota. Les résultats, encore peu nombreux, permettent de faire des rapprochements: 1) les saules sont les plantes les plus recherchées par l'orignal, sans toutefois être l'objet d'une sur-utilisation; 2) les saulaies du type «prostré» (low-open) sont souvent fréquentées en été et en automne; 3) les saulaies du type «dressé» (tall-mature) et les peuplements de conifères le sont surtout pendant l'hiver.

Dans le nord-ouest du Minnesota, on se sert souvent du feu pour retarder la succession naturelle au sein des communautés arbustives. Il y a, dans cet Etat, transformation rapide des saulaies marécageuses en zones agricoles. Il se peut bien que, dans l'avenir, on ne retrouve plus que des vestiges des populations actuelles d'orignaux.

Abstract

This paper presents findings of moose (*Alces alces andersoni*) habitat relationship studies on the Agassiz National Wildlife Refuge in northwestern Minnesota and, where possible, compares these results to those from other ecologically similar areas. During 1968-1971, 22 transmitter-equipped and 14 collar-marked moose provided 3,881 observations to which a habitat type could be assigned. Over the 3-year period, 83.8 percent of the total observations were in willow and associated willow habitats. «Tall-mature» habitat types consisting of tall willow (*Salix* spp.) and willow-aspen (*Populus tremuloides)* were extensively used from January 1 to April 15, and accounted for 76 percent of the total observations. Use of the tall-mature habitat was correlated with snow depth ($r = 0.84$ for 1970 and 0.39 for 1971). In mid-April, use shifted to «low-open» habitats, consisting mainly of willow, open willow and marsh and for the duration of the summer, 60 percent of the observations were in the low-open types. Little use was made of the vast marsh areas available. «Tall-mature» and «low-open» habitats were used on approximately a 50 : 50 basis from September 1 to December 31. «Tall-mature» habitats were generally preferred, and the «low-open» types with the exception of sandbar (*Salix interior)* and open willow, were avoided. Preferences for certain willow species were noted, and willow comprised the bulk of the rumen volume. Results from our study were compared with information known about other marsh-willow areas: the Peace-Athabasca and Saskatchewan River Deltas of Alberta and Saskatchewan, respectively. These areas are similar geologically and ecologically to northwestern Minnesota. Results of limited moose investigations in these deltas suggest that patterns of use are similar in the marsh-willow expanses of North America in that : 1) willows are the preferred browse species but are seldom over-browsed, (2) low willow habitats are frequently used during the summer and autumn and (3) tall willows and deciduous and coniferous forests are most used during the winter. Fire is often used in northwestern Minnesota to retard succession of the shrub community. The willow-marsh areas of northwestern Minnesota are rapidly being developed for agriculture and, as a result, only remnant moose populations may remain in future years.

Introduction

Across the North American Continent, moose inhabit three markedly different areas. The first consists of the mountainous regions of Wyoming, Montana, British Columbia, and Alaska, and their associated willow lowlands. Habitat use in these areas has been documented by Denniston (1956), Harry (1957), Knowlton (1960), Houston (1968), Milke (1969) and Stevens (1970).

The second type is the northern boreal forest. Here, habitat use has been described by Peterson (1955), DeVos-(1958), Pimlott (1961), Telfer (1967), and VanBallenberghe and Peek (1971).

The third type frequented by moose consists of the relatively level, broad expanses of willow and marsh such as those commonly found in northwestern Minnesota, east-central Saskatchewan, and north-central Alberta. These geologically similar areas are associated with glacial lake beds or deltas. Little information is available concerning moose habitat use in these areas.

The purpose of this paper is to present findings of moose-habitat relationships studies in northwestern Minnesota and, where possible, relate this information to areas of similar geologic histories and physiographic and floristic composition.

Description of the area

Skeletal remains (Swanson *et al.*, 1945) and historical evidence (James, 1830) indicate that moose have frequented northeastern and north-central Minnesota for hundreds and perhaps thousands of years. Populations likely fluctuated dramatically during this time

(Idstrom, 1965). Just 40 years ago, moose were practically non-existent in the northwestern corner of Minnesota except for an occassional wanderer from the main herd farther to the east (Swanson *et al.*, 1945). Interviews with original settlers confirm these observations. Today, however, a portion of northwestern Minnesota having an area of about 12,400 km² (4,800 mi²) supports about 3,100 moose, or approximately 40 percent of the state moose population (Fig. 1).

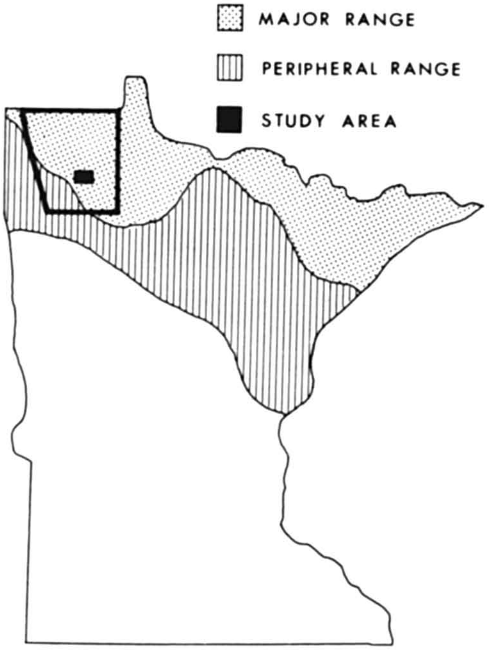


Figure 1. Area inhabited by moose in Minnesota. Area enclosed by solid line includes the main moose range of northwestern Minnesota (after Idstrom, 1965).

Northwestern Minnesota is characterized by three major vegetation types (Ewing, 1924). The westernmost type, formerly grassland-prairie, is today nearly 100 percent farmland. Eighty to 110 km (50 to 70 miles) to the east lies dense forest consisting mainly of aspen, balsam poplar (*Populus balsamifera),* and black spruce (*Picea mariana)* in association with large expanses of marsh and bog. Between these two types lies the area with which we are primarily concerned — a narrow ecotone consisting of agricultural land together with large expanses of willow brush, marsh, and scattered deciduous forest.

The area lies in the bottom of Glacial Lake Agassiz. Approximately 11,000 years ago, this lake drained northward and left behind a 210,000 km² (80,000 mi²) deposit of organic and alluvial soils. Soils in our study area were mainly silty loam and peat underlain by clayey glacial drifts (McMiller *et al.*, 1942). Topography is extremely flat, with a mean drop in elevation of 0.29 m/km (1.5 feet/mi) toward the west.

Agricultural development in northwestern Minnesota has greatly influenced moose habitat. In the western prairie areas, development was intensive and very successful. In contrast, attempts to clear and farm the deciduous and coniferous forests to the east failed, despite extensive ditching. Although some land was cleared, all farmers left by 1941, and most farmland subsequently reverted to brush.

In the ecotone, agriculture was only mildly successful, despite a vast network of drainage ditches and extensive land clearing during the early 1900's. Many farms were abandoned or taken by state and local governments for delinquent taxes and much of this land grew back to brush. Today, cultivated land occupies about 48 percent of this 12,400 km² (4,800 mi²) area. The remainder consists of deciduous and coniferous forest (21 percent); open brush, pasture, and meadow (19 percent); marsh (11 percent); and water (1 percent) (Orning and Maki, 1972).

Our principal study area was the Agassiz National Wildlife Refuge and two adjoining state Wildlife Management Areas, which together comprised

33,600 ha (83,000 acres). This area consisted of large expanses of willow and marsh, deciduous hardwoods, conifers and old fields in various stages of succession. Farms specializing in small grain and cattle-raising surrounded the area, and interspersed with these farms were scattered marshes and abandoned land that had reverted to brush and trees.

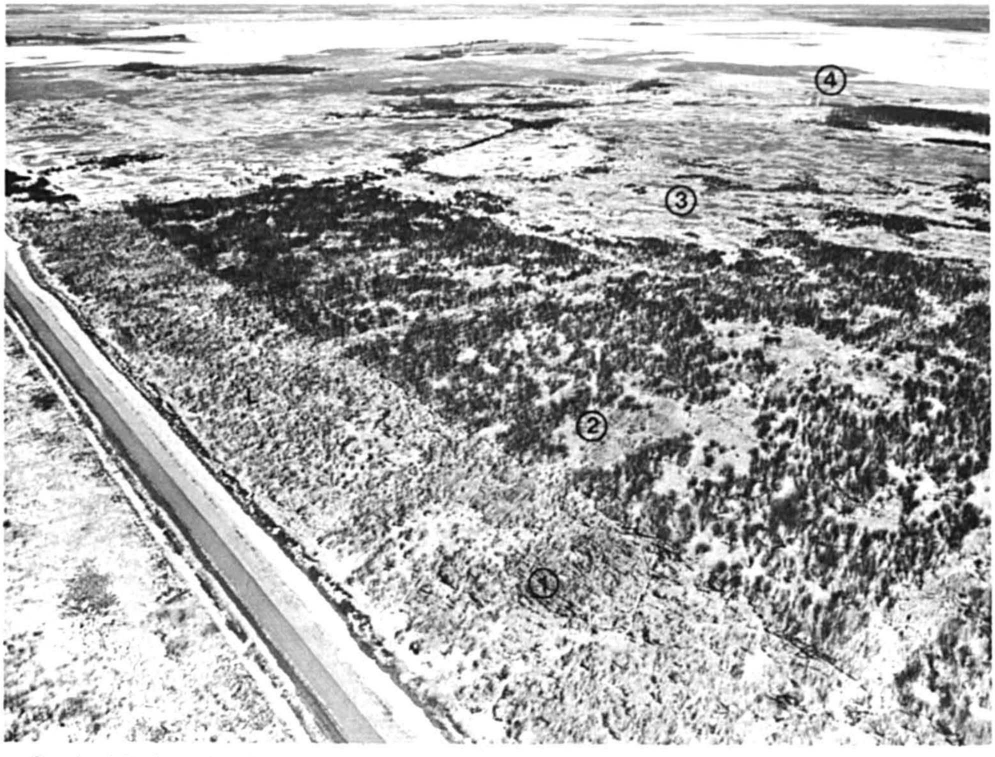
Vegetation description

Habitat categories found on our study area are representative of those found in the moose range of northwestern Minnesota (Fig. 2). Defined categories are as follows: (1) dense willow, (2) open willow, (3) aspen-willow, (4) aspen-balsam poplar, (5) marsh, (6) grass (Gramineae) and sedge (*Carex* spp.), (7) phragmites (*Phragmites communis*), (8) tamarack (*Larix laricina*) and black spruce, (9) cultivated fields, (10) open water.

DENSE WILLOW

This category consisted of areas with 20 percent, or more, of willow and 80 percent, or less, of openings, where sedge and grasses were usually dominants. Willow species consisted of sandbar, slender *(Salix petiolaris)*, pussy (*S. discolor)*, heart-leafed (*S. cordata)*, Bebb's (*S. bebbiana)*, shining (*S. lucida*), peach-leaf (*S. amygdaloides*), and the only tree, black willow *(S. nigra)*.

Sandbar willow: this species was found in extremely dense, uniform stands on dry sites such as ditch banks and the perimeter of aspen clones, and as an invading species in the succession of old fields.



2. Aerial view showing interspersion of habitat types on the Agassiz National Wildlife Refuge study area. Habitat types from lower left to upper right corner are (1) mixed willow less than 3m (10 feet), tall, (2) mixed willow greater than 3m (10 feet) tall, (3) open willow, (4) marsh. Note mature hardwood stand in upper right corner.

Mixed willow less than 3m (10 feet) tall: all willow species except black willow were pooled into this category. Slender willow was frequently dominant, but usually, all willow species were found in the mixed stand (Fig. 3a).

Mixed willow more than 3m (10 feet) tall: this category was similar to the preceding, except that pussy willow was usually dominant (Fig. 3b).

Black willow: this species, found as mature trees growing in small stands, occupied an insignificant area. However, its association with sandbar willow made independent classification necessary.

OPEN WILLOW

This category consisted of willow clumps growing in an open, parklike situation in which 80 percent or more of the area was dominated by grass and sedge, phragmites, cattail (*Typha latifolia* and *T. angustifolia)* or forbs.

ASPEN-WILLOW

The aspen-willow category was represented by association of any height class of willow with any height class of aspen or balsam poplar.

ASPEN-BALSAM POPLAR

Rather than an association with willow, aspen and balsam poplar in this category were associated with a shrub understory consisting of hazel *(Corylus americana* and *C. cornuta),* red-osier dogwood *(Cornus stolonifera),* amelanchier (*Amelanchier* spp.) and highbush cranberry (*Viburnum opulus).*

Closely related was the mature hardwood category, which consisted of mature American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), white oak (*Quercus alba*), and black cherry (*Prunus serotina*). Mature hardwoods contained the same shrub understory as did aspen-balsam poplar, with the addition of *Viburnum affine* and choke cherry (*Prunus virginiana*).

MARSH

Nearly one-quarter of the area was marsh, characterized by water less than 1.5 m (5 feet) deep containing cattail, phragmites, sedge, rush (*Scirpus validus* and *S. acutus),* and occassionally willows. Submergent vegetation consisted of sago pond weed *(Potamogeton pectinatus),* water millfoil (*Myriophyllum exalbescens),* coontail *(Ceratophyllum demersum),* and several species of broad and narrow-leaf pond weeds (*Potamogeton* spp.).

GRASS-SEDGE

This category included all open areas such as old fields composed of grass, sedge, and forbs dominated by goldenrod (*Solidago* spp.).

The remaining categories (7-10) are self-descriptive. The tamarack and black spruce stands were concentrated in two large island-like areas in the northern portion of the study area. The large open water areas, usually less than 1.5 m deep (5 feet), were rich in submergent vegetation.

Methods

Most habitat information was obtained by monitoring transmitter-equipped moose with a vehicle-mounted antenna system similar to that described by Verts (1963). Each radio location was assigned to a habitat type. These data were then partitioned by habitat and the following seasons: 1) late spring-summer (April 16-August 31), 2) autumn-early winter (September 1-December 31), and 3) winter-early spring (January 1-April 15).

3a Mixed willow less than 3m (10 feet) tall on Agassiz National Wildlife Refuge, Minnesota: this view is typical of the «low open» habitat type.

3b Mixed willow more than 3m (10 feet) tall: this view is typical of the «tall-mature» habitat type.

Frequent mention is made in the text of «tall-mature» and «low-open» habitats. All habitat categories previously described were grouped into these two broad types on the basis of structural similarities as follows: 1) the «tall-mature» type consisted of mixed willow more than 3m (10 feet) tall, aspen, aspen-willow, mature hardwoods, black willow and conifers (Figure 3b); 2) the «low-open» type consisted of sandbar willow, mixed willow less than 3m (10 feet) tall, open willow, marsh, fields, grass, sedge, phragmites, and open water (Figure 3a). Understandably, those habitats in the «tall-mature» type provided less forage and more cover than the "low-open" type.

The relationship between the area of habitat used and the amount of habitat available is expressed as the difference between the percentage of moose observations in each habitat type and the percentage of each habitat type available. «Available habitat» for a moose was defined as all habitats within the polygon described by connecting the outermost locations of the minimum home range (Mohr, 1947). The entire study area was not available to each moose, as individual differences in habitat preferences and movements were apparent.

Food habits were investigated by using feeding site analyses during the summer, and progressive browse utilization of permanently marked plants during the winter. Shrub and tree densities were determined by using the point-centered quarter method (Cottam and Curtis, 1956).

Results

Thirty-six marked moose (21 bulls and 15 cows) were relocated 3,881 times over a period of 3 years. Those with transmitters (13 bulls and 9 cows) provided 94 percent of these observations.

SEASONAL USE PATTERNS

Winter and early spring

Moose moved into the «tall-mature» habitat types during December and continued to inhabit this type through mid-April (Fig. 4). Habitat categories receiving the greatest use were mixed willow over 3 m (10 feet) tall, aspen-willow, aspen, and mature hardwoods (Table I). «Tall-mature» types accounted for 79 percent of the winter observations in 1970, and 75 percent in 1971. While coniferous cover made up 3 per-

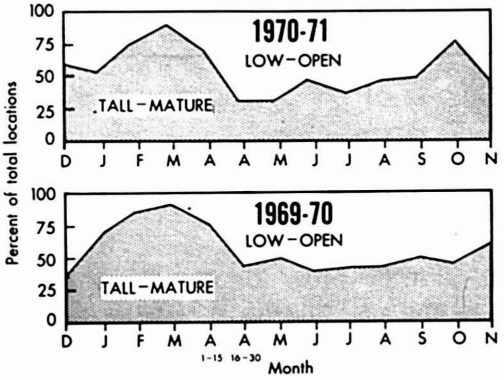


Figure 4. Annual use pattern of the low-open and tall-mature habitat classifications on Agassiz National Wildlife Refuge, 1969-1971.

TABLE 1

Moose observations in various habitat types and categories during the late winter and early spring period, 1970 and 1971, expressed as the percent of the total observations. Total numbers of observations are shown in parentheses

Habitat classification	*1970*	*1971*
«*Tall mature*»		
mixed willow > 3m (10′)	36	17
aspen-willow	27	33
aspen	9	19
hardwoods	7	5
other	0	1
TOTAL	79 (333)	75 (453)
«*Low-open*»		
(all categories combined)	21 (87)	25 (160)

cent of the toal area, it was completely avoided during the winter as well as other seasons. In the boreal forest areas, however, coniferous forests are heavily used by moose (Telfer, 1970; Peek, 1971; van Ballenberghe and Peek, 1971).

Shrub densities in the aspen-willow areas varied from 1,042 to 3,310 clumps per ha (422 to 1,340 per acre). A representative mature hardwood stand had a shrub density of 19,491 stems per ha (540 per acre) and a tree density of 1,334 per ha (540 per acre). One area, consisting entirely of slender willow greater than 3m (10 feet) tall, had a density of 852 clumps per ha (345 per acre). Thus, « tall-mature » habitats were characterized by dense, neraly mature vegetation which provided excellent cover.

In 1969-1970, use of the « tall-mature » habitat was highly correlated ($r = 0.84$, $P = 0.01$) with snow depth. In 1970-1971, snow depth decreased from January to mid-April, yet the haditat use followed the pattern of the previous winter (Fig. 5), but this time revealing no correlation between habitat use and snow depth ($r = 0.39$). These data suggest that in the willow type, snow depth apparently is not the single factor forcing moose to use dense cover. Peek (1971) noted that moose in northeastern Minnesota moved to dense cover at snow depths of less than 75 cm (30 inches); however, others have not observed this shift until depths exceeded this value (DesMeules, 1964; Telfer, 1968).

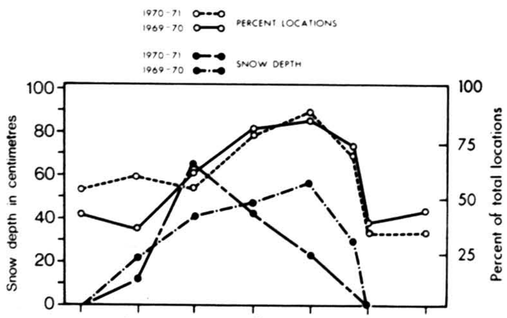


Figure 5. Snow depth versus the percent of moose observations in the tall-mature habitat types during the winter and early spring, 1969-70 and 1970-71. Points on abscissa represent mid-month with the exception of two additional points for April 7 and 22.

Late spring and summer

A dramatic change in habitat use occurred during mid-April (Fig. 4). Habitat use shifted abruptly to the more open categories such as open willow and mixed willow less than 3m (10 feet) tall. Moose were often observed browsing on the first emergent green vegetation. The change to more open, park-like habitats at the first sign of spring has also been documented in Montana (Knowlton, 1960) and Wyoming (Houston, 1968).

Habitat use during the summer showed little change from the pattern established during mid-April. During both 1970 and 1971, use was about 60 percent for the « low-open » types and about 40 percent for the « tall-mature » types (Table II).

Moose were seen using aquatic areas during the entire summer. With the numerous drainage ditches and water-filled peat burn-outs, marsh use may have been higher than detected in our radio-tracking efforts. Researchers in other areas have observed an extensive use of aquatic habitats (Peterson, 1955, Denniston, 1956; De Vos, 1958; Ritcey and Verbeek, 1969; van Ballenberghe and Peek, 1971).

Autumn and early winter

The change to « tall-mature » habitats as the winter progressed was more gradual than the abrupt mid-April move to the more open types (Fig. 4).

The use of sandbar willow was at its highest during the autumn-early winter period (Table III). The high use detected by telemetry, combined with several observations of moose feeding on sandbar willow, suggests that this species may be the key to moose distribution during this period.

TABLE II

Moose observations in various habitat types during the late spring and summer period, 1970 and 1971, expressed as the percent of the total observations. Total numbers of observations are shown in parentheses

Habitat classification	*1970*	*1971*
«*Tall-mature*»		
mixed willow > 3m (10′)	20	17
aspen-willow	14	16
aspen	4	6
hardwoods	0	0
other	2	0
TOTAL	40 (533)	39 (188)
«*Low-open*»		
sandbar willow	4	16
mixed willow < 3m (10′)	25	16
open willow	27	16
marsh	2	10
other	3	3
TOTAL	60 (808)	61 (290)

TABLE III

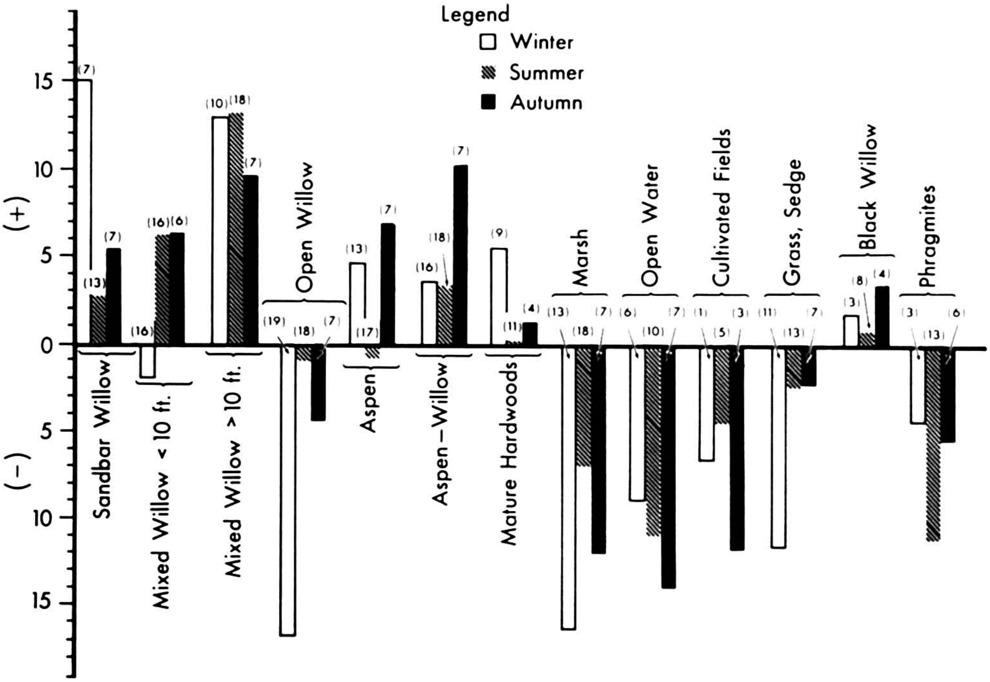
Moose observations in various habitat types during the autumn and early winter period, 1970 and 1971, expressed as the percent of the total observations. Total numbers of observations are shown in parentheses

Habitat classification	*1970*	*1971*
«*Tall-mature*»		
mixed willow > 3m (10′)	17	13
aspen-willow	15	22
aspen	12	14
hardwoods	1	1
other	3	9
TOTAL	48 (328)	60 (46)
«*Low-open*»		
sandbar willow	9	3
mixed willow < 3m (10′)	19	24
open willow	18	8
marsh	4	4
other	2	
TOTAL	52 (353)	40 (30)

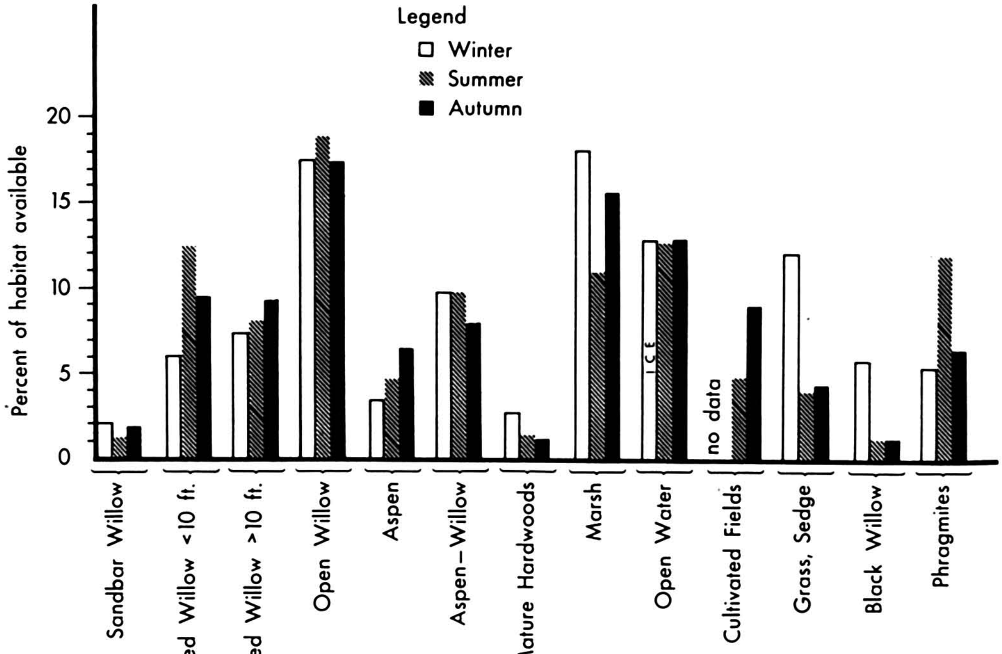
HABITAT USE RELATED TO HABITAT AVAILABILITY

Habitat categories in the «low-open» type were generally avoided during the entire year (Fig. 6). However, this avoidance was less pronounced during the summer than during the autumn and winter. Two exceptions were sandbar willow and mixed willow less than 3m (10 feet) tall. Browse studies (to be covered in a later section) indicated that sandbar willow was the most preferred browse species during the winter months, despite its apparently poor value as winter cover. Mixed willow less than 3m (10 feet) tall was also not suitable for winter cover and thus was slightly avoided during the winter months. However, this type was highly preferred during the summer and autumn. During all seasons, utilization of habitats in the «tall-mature» type equalled or exceeded their relative availability.

The average amount of habitat available to each moose varied seasonally, with the least differences between availability and use occurring between summer and autumn (Fig. 7). The average amount of habitat available during the winter per moose was 805 ha or 1,988 acres and represented 61.3 and 58.4 percent of the area available during the summer and autumn, respectively. Despite the fact that habitats such as open willow, marsh and grass-sedge were available in as great or greater proportions during the winter than other seasons, they were the most avoided during the winter (Fig. 6). Coniferous cover was available to, at most, three transmitter-



6. Selection for (+) or against (−) habitat types expressed as the percent difference between the amount of habitat available and the number of moose observations in each habitat type. Winter and summer differences are combined 1970-71 totals; autumn data is for 1970 only. Moose sample size in parentheses.



7. Amount of each habitat type available per moose expressed as the percent of the total available area.

equipped moose during the study, and all three avoided it.

The average amount of habitat available was not representative of the proportions of habitat types present on the entire study area (Table IV). Whereas some habitats available to our marked sample of moose were in approximately the same proportions (such as most willow types), others such as marsh and open water were much more abundant over the entire study area than in the available area.

TABLE IV

Proportions of moose observations in each habitat category, average amount of habitat available per moose and habitat composition of the entire study area. Figures expressed as percent of the total

Habitat type	*Total observations*	*Habitat available per moose*	*Habitat available in total study area*
Sandbar willow	7.4	1.4	1.0
Mixed willow < 3m (10')	17.6	8.8	6.0
Mixed willow > 3m (10')	20.2	9.1	12.0
Open willow	17.8	20.3	9.0
Aspen	8.9	4.3	8.0
Aspen-willow	19.3	8.2	10.0
Hardwoods	2.0	1.3	0.5
Marsh	3.2	12.3	24.0
Open water	0.0	11.9	17.0
Cultivated fields	0.1	6.5	2.0
Grass-sedge	1.3	5.2	6.0
Black willow	1.5	1.4	0.5
Phragmites	0.4	9.3	1.0
Conifers	0.1	0.1	3.0
	100.0	100.0	100.0

FOOD HABITS

Seasonal preferences were noted for certain browse species. All willow species were browsed to some extent during the winter, but sandbar willow was the most heavily browsed (Table V). A high preference for sandbar willow was also noted in central Alaska (Milke, 1969).

During the summer months, two broad-leafed willow species (Bebb's and pussy willow) were the most heavily browsed (Table VI). This was in contrast to the winter period, when twigs from the two narrow-leafed species, sandbar and slender willow, were used to a greater extent.

Willows formed the bulk of the moose's diet, but their use varied sea-

TABLE V

Progressive browse utilization by moose on 347 plants belonging to the genera *Salix* and *Populus* during the winter of 1970

Browse species	*Sample size*	*Percent of leaders browsed*	
		January	*April*
		1970	*1970*
Salix interior	51	75.5	85.2
S. bebbiana	54	11.4	34.0
S. discolor	56	22.9	37.5
S. petiolaris	107	21.9	32.2
S. cordata	33	59.2	74.8
Populus tremuloides	26	3.7	14.8
P. balsamifera	20	27.1	47.6

TABLE VI

Summer browse preferences by moose on 178 feeding sites on Agassiz National Wildlife Refuge

Browse species	*Percent of plots in which species occurred (A)*	*Percent of plots in which species was utilized (B)*	*Preference rating B/A × 100*
Salix discolor	73	58	79.4
S. bebbiana	39	29	74.3
S. interior	13	3	23.0
S. petiolaris	94	12	12.7
S. cordata	45	13	28.8
Populus tremuloides	9	1	11.1
P. balsamifera	13	1	7.6

sonally, based on analysis of rumens collected during the 1971 moose season. Willows made up 80 percent of the rumen contents in October, and 63 percent in December (P. Karns, pers. comm.)

Discussion and conclusions

Willow and associated willow habitats were used much more than the non-willow habitats in northwestern Minnesota, and for the period of our study accounted for 83.8 percent of the total number of observations. Use of willow in the mountainous areas of western and northwestern North America has been described by Harry (1957), Knowlton (1960), Pimlott (1961), Houston (1968) and Milke (1969). In non-mountainous willow areas, however, knowledge of moose habitat requirements is practically non-existent. The following discussion compares northwestern Minnesota moose habitat with other ecologically similar areas.

The transition zone between the prairies and forest of northern North America consists mainly of marsh, willows, aspen parkland, and portions of deciduous and coniferous forests. This zone extends northwest from our study area through southern Manitoba, westward through central Saskatchewan and again northwest, ending in northwest Alberta (Fig. 8). In the transition zone and on its northern fringes lie many other willow areas that support substantial moose populations.

Two of these areas are the Peace-Athabasca Delta in Alberta, and the Saskatchewan River Delta west of The Pas. Here, habitat use by moose has been studied to some extent, which permits direct comparisons to be made. These areas differ from northwestern Minnesota in that: 1) the deltas have been modified greatly by erosion and deposition activity of rivers; 2) there has been little or no agricultural development; and 3) coniferous forests, usually black spruce and tamarack, are much more prevalent.

Despite these differences, all areas are similar in that: 1) the soils are alluvial, fertile and often covered with peat (Dirschl and Dabbs, 1969; Dirschl, 1972); 2) the slight changes in the generally flat terrain greatly influence the vegetation patterns; and 3) large expanses of willow and marsh predominate, interspersed with upland deciduous and coniferous trees. It is these willow-marsh areas, interspersed with upland forests, that are largely responsible for supporting the present moose populations.

PEACE-ATHABASCA

More than one-half of this 4,400 km^2 (1,700 mi^2) delta consists of open water and marsh of little value to moose (E. S. Telfer, pers. comm.). Willow and alder (*Alnus rugosa)* shrub areas account for 35 percent of the delta area. The delta presently supports about 500 moose.

Information on habitat use in scant. During the summer, 78 percent of the moose observed from aircraft were in marsh and open willow habitats (L. Allison, pers. comm.). Moose were most often observed in tall willows during the autumn and in coniferous and deciduous forests with nearby willow stands during the winter. Despite abundant marsh vegetation, rumen analysis showed that aquatic plants were nearly absent from the diet.

SASKATCHEWAN RIVER DELTA

This 4,144 km^2 (1,600 mi^2) area is somewhat older geologically than Peace-Athabasca and consequently less active hydrologically (H. J. Dirschl, pers. comm.). About one-third of this area consists of willow, much of which is interspersed with white spruce (*Picea glauca*), black spruce and deciduous forest. Approximately 2,000 moose inhabit the area (M. C. Dennington, pers. comm.).

Moose observed on aerial transects frequented willow or willow edges. High willow use was substantiated by the fact that rumens contained 60 and 71 percent willow during the winter and summer, respectively (M. C. Dennington, pers. comm.). Extensive use of marsh areas as suggested by Peterson (1955) in Ontario was not observed, and aquatics accounted for less than 1 percent of the rumen volume.

COMPARISON OF THE THREE AREAS

It is evident from the foregoing descriptions of three marsh-willow areas of North America that, while separated by hundreds of miles, broad ecological similarities exist. The four most common and highly preferred willow species in northwestern Minnesota: *S. beb-*

8. Transition zones (aspen-parkland and deciduous-coniferous forests) cutting across the Canadian Provinces and Minnesota. (After Rowe 1959).

biana, S. discolor, S. interior, and *S. petiolaris,* are also found in the Canadian deltas (Dirschl and Dabbs 1969, G. C. Gentle, pers. comm.). *Populus* species present in our area abound in the northern deltas as well.

In our study area, very few plants could be found which had been browsed during the current year, and overbrowsing was non-existent. This was also true in the Peace-Athabasca, where a maximum of 16.5 percent of the willow twigs had been browsed (L. Allison, pers. comm.). In the Saskatchewan River Delta, 50 percent of the willows had not been browsed, and an additional 25 percent of the willows had 90 percent of the current year's twigs remaining (M. C. Dennington, pers. comm.).

The aspen and aspen-willow areas of northwestern Minnesota apparently satisfy the moose's need for winter cover just as well as deciduous-coniferous forests growing on the levees of the northern deltas. However, winter migrations by approximately 20 percent of the herd from the Agassiz study area to agricultural zones with more cover but less browse may mean that winter cover on Agassiz is somewhat lacking (Phillips *et al.,* 1973. Because of intraspecific social pressures that appear to space individuals, the amount of available winter habitat interspersed with willow may thus be somewhat less than optimum (Berg and Phillips, 1972).

The willow community may be maintained in several ways. It has been suggested that, in Peace-Athabasca, water levels can be lowered, thereby encouraging shrub growth on existing meadows and mudflats, which in turn would increase the carrying capacity of the range (E. S. Telfer, pers. comm.). Logging is another means, and one logged area in Peace-Athabasca can reportedly support eight moose per square mile. Logging has also been suggested as a practical method in the Saskatchewan River Delta, as has winter dozing of subclimax communities (M. C. Dennington, pers. comm.).

In Peace-Athabasca, wild fires 20 to 30 years ago created range that is still excellent moose habitat. Fire is mentioned only in passing as a habitat improvement tool in the Saskatchewan River Delta, however. In northwestern Minnesota, a combination of wild and controlled fires is largely responsible for maintaining the willow community. Controlled burning is used extensively by State and Federal conservation agencies to improve wildlife habitat on public lands. Spring and autumn wild fires on private and public lands also do their part to perpetuate the willow areas.

The delta areas of Alberta and Saskatchewan are relatively free from any possibility of agricultural development and with proper management, seem secure as good moose habitat for some time to come. However, this is not the case in northwestern Minnesota. Much of the undeveloped and earlier abandoned land is now being developed for agricultural purposes by draining and dozing. Whereas some areas such as marshes and bog meadows have no agricultural potential, much of our best moose habitat — the vast expanses of willow, aspen-willow, and aspen — is rapidly disappearing. In time, few areas will be able to support moose except lands publicly owned for wildlife management purposes. Thus, the excellent and highly productive marsh-willow habitat of northwestern Minnesota may be a temporary phenomenon. However, we hope that our findings may be applicable to other similar areas, and that the Canadian Provinces will preserve their marsh-willow areas as a valued resource.

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BIOGEOGRAPHY OF MOOSE WITH PARTICULAR REFERENCE TO WESTERN NORTH AMERICA

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Résumé

Cet article reconstitue, à la lumière des informations les plus récentes, ce que fut la distribution post-pléistocène de l'orignal (*Alces alces*) dans la partie occidentale de l'Amérique du Nord. Presque toutes les régions forestières de l'ouest sont effectivement occupées par l'orignal. Vers le nord, dans la toundra, sa distribution semble freinée par l'absence de plantes ligneuses pouvant servir de base à son alimentation; l'absence de plantes ligneuses ainsi que la grande accumulation de neige au sol empêcheraient l'animal d'occuper l'étage montagnard de la cordillière occidentale; la chaleur torride de l'été et la rareté de l'eau et d'une nourriture appropriée l'empêcheraient d'occuper les vallées arides du sud et de l'ouest des provinces canadiennes; enfin le ver des méninges (paraléphostrongylose) l'empêcherait d'augmenter son aire de distribution en direction sud-est.

Les récentes expansions de l'aire de l'orignal au nord du lac Supérieur et en Colombie-Britannique, associées à une augmentation des nombres, seraient des conséquences de la modification de l'habitat forestier par l'homme et peut-être aussi, en partie, de l'amélioration climatique en cours. Toute population d'orignal fluctue en réponse dynamique aux conditions changeantes du milieu ce qui donne naissance à de grandes variations dans l'abondance de l'animal, à divers moments, en un lieu donné.

Abstract

Post-Pleistocene distribution of moose (*Alces alces*) in western North America, excluding Alaska, is reviewed in the light of recent information. Most of the forested Canadian west is suited to, and populated by moose. The range seems limited in the north principally by an absence of woody food plants on the tundra; by a lack of woody plants and by excessive snow depths in many high altitude areas in the western cordillera; by combinations of excessive summer heat with absence of shade, water and suitable food on the prairies and in the arid valleys of the south and west; and by neurologic disease in the southeast.

Recent population increases and range expansions north of Lake Superior, and in British Columbia, are thought to have resulted from human influence on habitat, perhaps abetted by climatic warming trends. Moose populations everywhere fluctuate dynamically in response to environmental changes, and there are great local variations in abundance in time within the animal's range.

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Introduction

This paper discusses the prehistoric and present distribution of moose with special reference to western North America, excluding Alaska, and certain biogeographical aspects of their distribution. We have relied upon the literature, and upon personal knowledge and communications from others, in charting present distribution. Moose populations are constantly expanding or contracting. Because little current information is available on their status in many localities, this review is not necessarily exhaustive.

Three sub-species of moose occur in western Canada, *A. a. gigas, A. a. shirasi*, and *A. a. andersoni* (Peterson, 1955). We have no contribution to make on taxonomy, and no reason for believing that the presence of three subspecies invalidates any of our comments.

There are several problems regarding the distributional limits of moose in the area under consideration:

1. Why have moose been restricted to the northen Rocky Mountains, not colonizing the inter-mountain shrub deserts or the brushy coulees and river valleys of the Great Plains?

2. Why were moose not found in the deciduous biome-specifically the oak-hickory *(Quercus-Carya)* and maple-basswood *(Acer-Tilia)* forests south of their earliest historical range in Minnesota?

3. What enabled moose to increase to dense populations in the interior of British Columbia and north of Lake Superior, where they were absent or extremely scarce until the past century?

4. Why have moose occupied so little of the coniferous rain-forest on the coast of western North America?

5. What factors control the colonization of the northern tundra by moose?

These problems will be reviewed and some hypotheses proposed to explain them in the hope that our comments will stimulate further work on the physiological and ecological requirements of moose.

Prehistoric and present distribution

Peterson (1955) described moose distribution during the maximum expansion of the Pleistocene glaciation. He suggested that there were major refugia in central Alaska, in the west central United States, south of the present location of the Great Lakes, and along the Atlantic seaboard. Peterson believed that subspeciation occurred in those refugia, and that the three southern races were isolated by the presence of intervening barriers of grassland. With the retreat of the glaciers, the Alaskan moose moved into the Yukon Territory, and the Shiras moose of the central west moved north. However, according to Peterson, the great thrust of repopulation of most of the area under consideration was by *A. a. andersoni* which expanded from south of the Great Lakes north and west through western Ontario and the Prairie provinces, along treeline to the Mackenzie River, and south through much of the Yukon Territory and British Columbia.

Additional information is now available on the distribution of vegetation zones in Wisconsin and post-Wisconsin time, including the major work of Flint (1957). Peterson's (1955) hypothesis that moose originated in Asia was probably correct, but their evolution and dispersal during and after Wisconsin time was complex and may possibly have followed a pattern analogous to that suggested by Geist (1971) for sheep *(Ovis* spp.*)*.

At the greatest extent of Wisconsin glaciation moose populations occurred south of the icefield and tundra zones both in North America and Eurasia. Additionally, moose were present in the unglaciated region of central Alaska and perhaps adjacent areas of east Siberia and the Bering land bridge. At that time (*circa* 12,000 B.P.), a broad zone of boreal forest with *Picea* and *Salix* covered the North American Great Plains including Nebraska, Iowa, and the Ozark Plateau (Durkee, 1971; Mehringer *et al.*, 1968; Watts and Wright, 1966). A similar, though not identical, flora to that now found in northern Maine existed in northwest Georgia (Watts, 1970). This evidence, as well as fossil finds reviewed by Peterson (1955), suggests that moose ranged over a broad belt of the Great Plains and the eastern United States, both then forested. Following the retreat of the ice and the northward spread of the boreal forest, moose moved northward. In North America, boreal forest existed in southern Saskatchewan until after 10,000 B.P. (Ritchie and de Vries, 1964). Moose probably moved north on a broad front across the continent. However, those dispersing into the northern Great Plains would have been separated from those to the east, first by the huge barrier of Lake Agassiz, later by the Great Lakes (Schuchert and Dunbar, 1947) and, after 8,000 B.P., by the spread of grasslands over the central Great Plains and into the region south of the Great Lakes. The population of the northwestern glaciated region, thus isolated for nearly 8,000 years, became a separate form, *A. a. andersoni*. (Fig. 1).

Deglaciation of the northern Rocky Mountains began about 10,000 B.P. and was completed by 7,000 B.P. Forests along the eastern flank of the mountains were dryer from the start, with *Pinus* and *Pseudosuga* prominent (Heusser, 1956). It remains a mystery why moose did not move north along the mountains and through them to the interior plateaux of British Columbia at an early period. Possibly moose populations were reduced by primitive hunting,

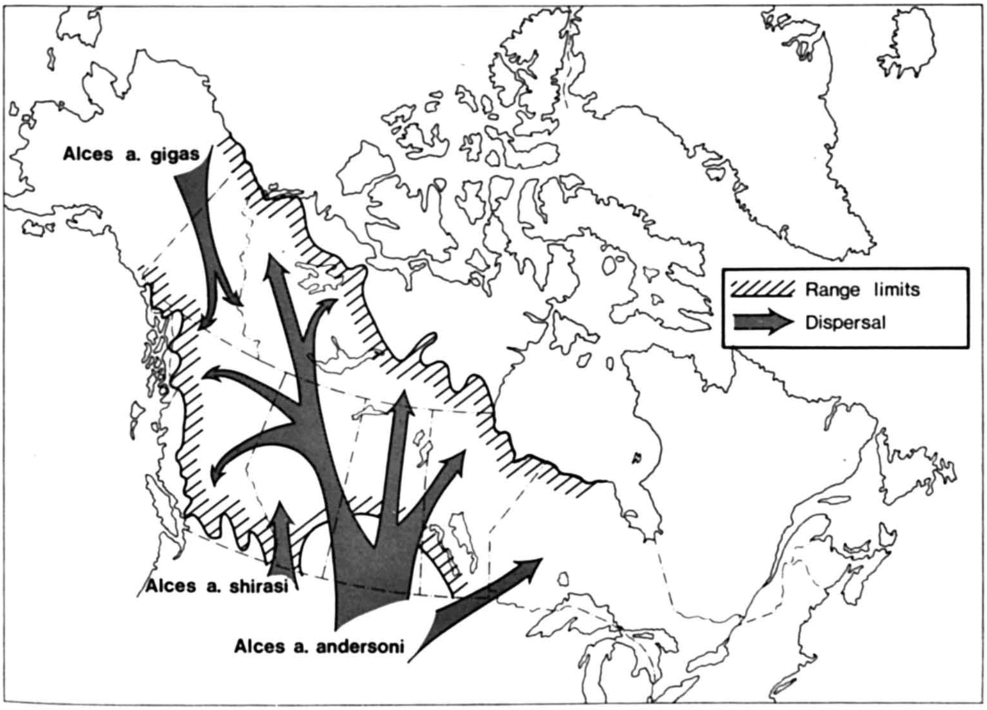

Figure 1. Current limits of moose in western Canada, and lines of postglacial dispersal.

or their dispersal discouraged by the aridity of the hypsithermal period.

As glaciers receded, *A. a. gigas* from the Alaska refugium invaded deglaciated regions which today constitute over half its range and probably support much more than half of its population (Flint, 1957; Le Resche *et al.*, 1974). Geist (1971) suggests that big, large-horned sheep must have evolved repeatedly with every major glaciation in the Pleistocene. A similar evolution is possible for moose. If larger races did indeed evolve in the areas glaciated by the Illinoisian ice sheets, it is probable that they were ancestral to *A. a. gigas,* and that while some survived in the Alaskan refugium the rest were eliminated, along with their habitat, by the Wisconsin glaciation.

Peterson (1955) shows that *A. a. andersoni, shirasi* and *gigas* have all colonized huge tracts of land in the past hundred years, to the point where they now overlap. Peterson believes that, before 1875, the three sub-species were still geographically separated, and that most of the eastern Yukon Territory and virtually all of British Columbia and southern Alberta had no moose at all. It should not, perhaps, be assumed that moose were completely absent from those regions, and from Ontario north of Lake Superior, before the documented changes in status during the past century. Because adult moose are usually quite sedentary, a low population of individuals or groups may exist in widely scattered locations. It would be possible for an extensive exploration to be made at such a period of scarcity without reporting moose. Following the die off of the moose population in southwestern Nova Scotia from «moose sickness» in the 1940's (Benson, 1958), one of us (Telfer) often travelled the forests for months without encountering the animals. However, on several occasions localities containing one or more moose were discovered.

The present range of moose in western Canada (Fig. 1) is based generally on Peterson (1955), on Kelsall (1972) in the north, and in local areas on personal observation and communications from others. Within the delineated range, there are many localities not habitable by moose, such as developed areas, alpine areas and mountainous terrain having great depths of snow.

Today *A. a. andersoni* and *A. a. gigas* probably overlap in northern British Columbia and in the Yukon (Peterson, 1955; Le Resche *et al.*, 1974) and have invaded the coastal rain forest of southeastern Alaska and British Columbia, moving down river valleys some time before 1900 (Klein, 1965; Cowan and Guiguet, undated and R.W. Ritcey, pers. comm.).

Although a few moose have been reported in north-eastern Washington (Dalquist, 1948), *A. a. shirasi* has not dispersed westward along the corridor of the Okanagan Highlands in southern British Columbia and northern Washington. Dispersal in that direction would have made available large areas of apparently suitable habitat in the Cascade Mountains and provided an opportunity for invasions of the central part of the coastal rain forest. The presence of moose in those forests in Alaska and British Columbia suggests that they provide acceptable habitat, especially in the early successional stages.

Adaptive and limiting factors

THE BROWSING ECONOMY

Moose eat a wide variety of plants including mosses, sedges, grasses, herbs, shrubs and trees (Sablina, 1970). However, few of the plants eaten are available to the animals in winter, and winter food profoundly influences distribution. The important winter food plants are found among the shrubs and trees, and their use has been discussed by Hatter (1950), Houston (1968), and Peterson (1955). On the southern extremities of the range there are a wide variety of, apparently palatable, plant species available during winter months. They include one or more shrub or tree-form species of the genera *Cornus, Betula, Salix, Populus, Pyrus, Amelanchier, Abies, Purshia, Viburnum, Acer, Alnus, Shepherdia, Lonicera, Prunus, Sambucus, Spiraea,* and *Symphoricarpos.* Some other genera, for example *Pinus,* are eaten in local areas.

Even where many winter food plants are available, only a few species are eaten in large quantities. Throughout the western range of moose the important food plants are willows (*Salix* sp.) of several species, quaking aspen *(Populus tremuloides),* paper birch *(Betula papyrifera)* and dwarf birch *(B. nana* and *B. glandulosa),* in roughly that order of preference. Some genera are important both at the southern extremities of the range, where there are many plants to choose from, and at the northern limits where the choice is reduced. Along the northern periphery of the range available winter food is reduced to one or two species of willows and dwarf birch. Even there, moose may be abundant, and they have been frequently observed to winter beyond tree-line, on the tundra, in areas having no winter food except tall-growing willows in river valleys (Kelsall, 1972). Houston (1968) reported that *Salix* was also the key genus of forage plants on the southerly moose range in Jackson Hole, Wyoming. The importance of willows to moose is strikingly shown by the name for moose in the language of the Evenki people of the U.S.S.R., «shektaty» meaning «willow eater» (Sablina, 1970, p. 81).

One or more species of willow, poplar and birch are found throughout the western Canadian moose ranges. However, considering the adaptiveness of moose to new food plants in local areas of their circumpolar range, it seems unusual that they have not successfully invaded the arid regions of northwestern America such as the Columbia Plateau, the Wyoming Basin, the Great Basin and the many arid valley bottoms in Idaho, Washington and British Columbia, where shrubs are the dominant life form (Oosting, 1956). Moose make some use of arid shrublands for winter range (Ritchie, 1972; Ritchie and Barney, 1972; Houston, 1968) but have never adapted to fully utilize the huge resource available.

Similarly, the forests of the North American deciduous biome produce substantial quantities of woody browse (Murphy and Crawford, 1970) that should be adequate to support moose, and yet moose are absent there, as well as from the southern extension of the deciduous-coniferous transition in the Appalachian Mountains. South of the deep snow region, in the Midwest States, white-tailed deer *(Odocoileus virginianus)* eat a high proportion of mast and herbage (Murphy, 1970). The scattered population of wapiti *(Cervus canadensis)* that existed in pre-settlement times in the deciduous forests were probably concentrated on interspersed areas of grasslands (Murie, 1951). Wapiti reintroduced into the deciduous forests of Virginia also depend largely on herbage (Baldwin and Patton, 1938), leaving a food niche for a large mammal capable of subsisting on browse.

Although moose food plants are widely distributed, local availability of large quantities is variable. Willows are generally restricted to wet lands and forest edges and to the tree-line at high altitudes and latitudes, but are probably the most ubiquitous of all the highly preferred food plants. Quaking aspen, also a preferred food, is a dominant in the parklands fringing the prairies, and in parts of the mountainous west (Maini, 1968). It is one of the commonest taxa to follow fire in the northern boreal forest and the coniferous forests of the western mountains. There, moose usually increase in number with the growth of deciduous shrubs and trees following fire (Cowan *et al.*, 1950).

The paper birches are scattered in the west, but are a preferred food plant where they are found in a size suitable for browsing. They are component of early succession following fire in northern boreal forests. The dwarf or glandular birch is abundant in some northern forests, and particularly in the forest-tundra section of the northern boreal forest (Rowe, 1959). Dwarf birch is often considered highly palatable to moose, but our observations suggest that it is rarely important in the diet of moose in northern Canada and has little influence on their distribution. Observations along tree-line (by Kelsall) for over 10 years, suggest that moose are uncommon in areas of extensive glandular birch that have no willow. Where willow, glandular birch and moose are all abundant, the willow was browsed rather than the birch.

Many studies have shown the importance of early successional growth to moose. Speaking of the Saskatchewan boreal black spruce and white birch forests, Scotter (1964) noted that «...49 moose pellet groups per acre were present on 1 to 10 year age-class and only nine were present in forests over 120 years old. Moose apparently prefer habitat less than 50 years old...» He found no moose pellet groups at all in jackpine forests five or more years following a forest fire. Preferred browse is scarce in thick young jackpine. In all cases he had positive correlations between quantity of deciduous browse, which is greatest in young forests, and numbers of pellet groups.

Hatter (1950) concluded that a combination of extensive burning and lumbering created huge areas of young forest that permitted the invasion of much of British Columbia by moose in recent times. The wandering characteristics of moose, particularly yearlings, make them efficient colonizers when habitat changes permit (Geist, 1971).

It is apparent that suitable food plants are found throughout forested sections of western North America, but availability of food plants varies in space and time with site characteristics, and fire. Therefore the browsing economy places only local limitations on moose distribution.

CLIMATE

Climate is probably the most important factor limiting the distribution of moose in western North America and adjacent regions. One important climatic factor is snow — its depth, density, hardness, and duration. The effects of snow on large ungulates were first studied systematically in the U.S.S.R. (Formozov, 1946; Nasimovitch, 1955) and, subsequently, by North American workers (Pruitt, 1959; DesMeules, 1964; Telfer, 1967; Kelsall and Prescott, 1971). Studies in both U.S.S.R. and Canada suggest that moose can travel more or less freely through soft snow up to about 60 cm (Telfer, 1970). Moose are increasingly impeded and restricted by depths of soft snow up to 100 cm (about the chest height of an adult animal).

We have studied the relationship of some aspects of the external morphology of moose and other large mammals to survival (Kelsall, 1969; Kelsall and Telfer, 1971; Telfer and Kelsall, 1971). Chest heights and foot loads (the weight exerted by an animal per unit area of foot) are indices of mammalian ability to cope with snow. In Alberta, chest height increases with age for both male and female moose, although the differences are statistically significant only between the youngest and older year-classes (Table I). The chest heights of females are slightly less than those for males, except in the 1½ year age-classe, but the differences between sexes are not statistically significant. The legs of young animals are 10 percent shorter than those of adults, putting them at a disadvantage in deep snow. In some winters the disadvantage could increase juvenile mortality. There is compensation for this, in part, by the animals having the least chest height also having the least load on their feet, an advantage on dense or crusted snow. While both male and female calf moose have foot loadings of about 400 g/cm^2, the loadings for male and female adults, 4 1/2 years old or more, are 710 and 652 g/cm^2 respectively. The density of the snowcover usually increases as the snow matures during the course of the winter (McKay, 1968) and increasingly dense snow provides increasing support to large mammals. When snow densities exceed 0.30, moose sink through only 52 to 63% of the thickness of the snowcover (Kelsall and Prescott, 1971).

Moose probably cannot survive in areas where soft snow of 70 cm or more is common and of long-lasting occurrence, according to Nasimovitch (1955), who describes areas in the northern U.S.S.R. where such snow conditions prevail and where there are no moose. Kistchinski (1974) mentions that moose are rare in the mountains having deep snowcover adjacent to the Okhotsk Sea, and that in the region of deepest snowcover in eastern Siberia (Koryak Highlands, Kamchatka) moose do not occur. In North America, depths greater than 70 cm regularly occur on the higher parts of the western cordillera and in high regions in the east, especially the plateau of Ungava in central

TABLE I

Chest height and foot loading for moose from Elk Island National Park, Alberta, Canada[1]

Sex	*Age (years)*	*Chest height ± SE (cm)*	*Foot load ± SE (gm/cm²)*
Male	½	87.8 ± 1.14 (12)	400.4 ± 11.60 (12)
	1½	98.8 ± 0.80 (4)	504.4 ± 18.79 (4)
	2½	103.2 ± 1.84 (5)	572.9 ± 38.32 (5)
	3½	106.5 ± 0.75 (13)	644.7 ± 21.68 (13)
	4½	106.7 ± 0.50 (37)	710.0 ± 12.63 (38)
Female	½	87.4 ± 1.13 (7)	403.2 ± 5.54 (7)
	1½	101.6 ± 2.39 (4)	492.5 ± 18.14 (4)
	2½	102.8 ± 0.91 (12)	578.0 ± 19.06 (12)
	3½	103.0 ± 1.50 (9)	612.6 ± 22.56 (11)
	4½	105.2 ± 0.59 (39)	651.6 ± 12.42 (38)

[1] The numbers examined are in parentheses.

Québec and Labrador (Fig. 2) where snow depths greater than 70 cm may be expected to last more than 2 months in 2 out of 3 winters (Potter, 1965). Moose have been scarce, if present at all, in Ungava in historic time (Brassard *et al.*, 1974). In the cordillera of western North America moose move down to lower slopes or up to windswept alpine areas as snow accumulates (Ritcey, 1967).

Moose are absent from small areas in the mountains of western Canada which have greater snowfall than shown on Figure 2, although moose are also absent from areas in British Columbia where snow depths are not limiting. Edwards (1956) presents evidence of moose mortality due to deep snowcover in marginal regions of the western cordillera.

As with most dynamic situations, one factor affects another. Moose can occupy regions having deep snow if there is also abundant food, but they cannot if food is so scattered that the laborious process of wading through snow to get to it results in deficit energy balances. Also, moose are able to occupy some forest areas having deep snow, by taking advantage of lesser snow depths under tree canopies for travelling (DesMeules, 1964; Telfer, 1970). At high latitudes and altitudes, where trees tend to be open-growing and branched to the ground, this behaviour cannot occur.

In regions subject to winter thaws and rainfalls, such as the Atlantic Provinces of Canada, parts of Québec, and New England, thick crusts may form in the snow-cover, permitting moose to travel without sinking very deeply, even when the snow is well over 100 cm in total depth. This likely occurs on some western moose ranges as well.

A second climatic factor which may restrict moose is temperature. There

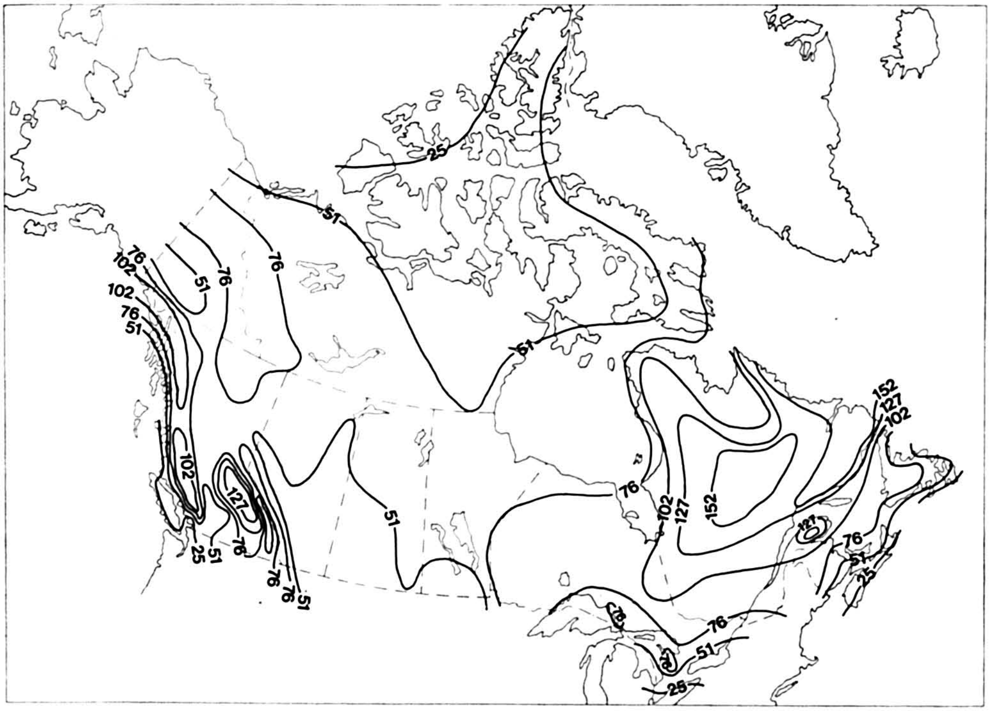

Figure 2. Mean annual maximum depth of snow in Canada, in centimetres (from Canada Dept. of Mines and Technical Surveys, 1957).

is no evidence that extreme cold *per se* has any adverse effect, for short periods, if there is shelter from wind. Moose winter successfully in some of the coldest portions of the Canadian north. However, Knorre (1959) reports mortality of calf moose due to a prolonged cold spell, and to deep cold following a winter rain. Knorre (1959) and DesMeules (1964) show that, when resting, moose often seek areas of relatively deep soft snow, probably to benefit from its insulating effect and to escape the wind. It may be significant that the area from which Miller *et al.*, (1972) examined a moose, that they believed died of exposure, is one of the highest windchill areas on the Canadian tundra (Thomas, 1960).

Moose are not well adapted to high temperatures (Knorre, 1959). Regions where temperatures exceed 27°C for lengthy periods, particularly without tall trees to provide shade, or other refugia such as lakes and rivers, do not support moose.

Moose frequent water bodies where they exist in the range, feeding on aquatic vegetation (Peterson, 1955). They are thought to seek relief under water from the attacks of insects. It is also probable that they frequent water to cool themselves. During a hot spell in August 1971, on a day when the temperature was over 26°C on a research area in the Porcupine Hills of Alberta, one of us (Telfer) observed a female moose and her twin calves lying in a small stream 5 cm deep and 60 cm wide coming from a cold spring. Investigation showed several moose beds in the stream within a hundred metres of its emergence from the spring. Later in the day another female moose was observed standing in a somewhat larger spring-fed stream. During the week of hot weather several moose were observed standing in streams or beside them. No large streams or lakes exist in the Porcupine Hills.

Temperatures in excess of 25°C and even 30°C can occur during a few days annually even far to the north. This may explain, in part, some of the behaviour observed by Flook (1959) who reported nine of 18 moose (observed during a canoe trip down a fast, shallow river in the Northwest Territories) in the water, six standing in deep water and three lying down in the shallows. Only one moose was near aquatic plants. Flook attributed their behaviour entirely to an attempt to escape flies, but they may have also been cooling off. Knorre (1959) describes a similar behavior, which he ascribes to both cooling and insect avoidance.

Moose may well have problems similar to those found among sheep and cattle introduced in tropical arid areas. Domestic animals of temperate climatic origin cannot thrive as do native mammals such as euros *(Macropus robustus)* in Australia (Ealey and Suijdendorp, 1959; Ealey, 1962) and the water buffalo *(Bubalus arnee)* (Kamal and Ibrahim, 1969; Kamal and Seif, 1969). Food intake, water balance, body weights, nitrogen digestion and reproduction may be adversely affected by heat stress (Wiersma and Stott, 1969; Smith, 1971; Kamal *et al.*, 1970; Bianca, 1962). Mammals native to hot and arid regions generally possess behavioral and physiological adaptions to those environments (Folk, 1966).

Teal (pers. comm.), in domesticating muskoxen (*Ovibos moschatus*), found that the animals thrive and reproduce well under captive conditions near Fairbanks, Alaska, within the latitudinal and temperature range for the species. The muskoxen survived, but reproduced poorly and fell prey to exotic parasites, in Vermont, U.S.A., where he first tried to keep them. Knorre (1959) remarked that in cold, rainy summers the growth rate of the young moose was greater and the condition of the adult animals was best, due in his opinion to the opportunity to feed any time during the 24 hours of the day.

Heat may prevent moose colonization of western shrub deserts, prairies, and perhaps some of the arid valleys in British Columbia. Summer temperatures in these valleys of southern British Columbia are among the highest in Canada (Canada Dept. of Mines and Technical Surveys, 1957), possibly discouraging moose dispersal westward.

A warming trend has been evident in the climate from at least 1885 to 1940 (Flint, 1957). Data for northwestern Ontario show a rise of over 2°C in the mean annual temperature between 1890 and 1910, with the higher temperature continuing until at least 1955 (Urquhart, 1957). A rise in mean annual temperature might affect moose by producing crusted and dense snow, making locomotion easier, and by drying the forests in summer, increasing the likelihood of extensive fires.

Alaskan glaciers reached a maximum about 1750, receded greatly by 1800, then advanced prior to a further recession between 1850 and 1950 (Flint, 1957). Mean annual temperature increased more than 1.1°C in Alaska between 1910 and 1950 (Hamilton, 1965). The net gain since the late 1800's has been almost 0.8°C. Glaciers in the Canadian Rockies receded after 1870, except for a modest advance in the early 1900's. Snowfall at Banff averaged less between 1920 and 1940 than previously (Heusser, 1956). Glacial recession possibly indicated milder winters with shallower and harder snowcovers over a wide area of northwestern America, thereby encouraging the spread of moose into central British Columbia.

ALTERATION OF HABITAT

Man has both restricted and benefited moose by altering habitat in western Canada. Huge areas of habitat have been eliminated by clearing and cultivation in the prairie-fringing aspen parklands and adjacent boreal forests. The removal of aspen has rendered moose vulnerable to human hunting, extirpating them locally.

Man has also affected moose through forestry practices. Wherever the cutting of coniferous forest results in regeneration containing a large proportion of deciduous trees and shrubs, moose populations benefit. This is true not only of logging operations but also of cuttings for seismic lines, oilfields, pipelines and hydro-electric lines. Peterson (1955) hypothesized that logging and wildfire associated with opening up of the country north of Lake Superior led to the expansion of moose into that area. Hatter (1950) and Cowan *et al.* (1950) presented the same hypothesis to explain the invasion of central British Columbia by moose during the past century. The appearance of moose in both regions followed railroad building and intensive prospecting, both notorious causes of wildfire. Scotter (1964) documented increases in fire occurrence, especially near settlements, in a remote area of the boreal forest. The increases appeared to be associated with expanding economic development activities. It should be noted, however, that fire has always been a dominant factor in all northern conifer forests and that years of widespread burning have occurred periodically (Heinselman, 1971). Burning associated with development may have combined with increased temperature to make the area north of Lake Superior suitable for moose.

OTHER FACTORS LIMITING DISTRIBUTION

Certain parasites, that have evolved a stable relationship with North American deer of the genus *Odocoileus*, cause serious illness accompanied by a high rate of mortality in genera of cervids that are considered to have invaded North America during the Pleistocene. *Elaeophora schneideri* does not appear to harm mule deer *(Odocoileus hemionus)* but is deadly to wapiti (Hibler and Adcock, 1971). The parasite *Parelaphostrongylus tenuis*, which produces only occasional mild symptoms in its principal host, white-tailed deer, causes heavy mortality in moose (Anderson, 1971 and 1972). Dense populations of white-tailed deer in parts of the deciduous-coniferous transition zone inhabited by both these cervids, have led to outbreaks of neurologic disease in moose, apparently caused by *P. tenuis* (Benson, 1958; Smith *et al.*, 1964; Karns, 1967; Anderson, 1972). The outbreaks may well be a limiting factor for moose (Bindernagel, 1972) and Gilbert (1974) demonstrates the effective restriction of moose in Maine due to this factor.

We have previously stated our opinion that, as far as food was concerned, a niche existed in the deciduous forest of the Midwest States that moose might have filled. The fact that moose did not do so, but appear to have moved north with the deciduous-coniferous transition belt after having occurred in Oklahoma, Iowa, Illinois and Ohio, as well as more eastern areas during the Quartenary (papers cited by Peterson, 1955), suggests that some critical factor excluded them from the deciduous forest. Neurologic disease caused by *P. tenuis* may have been that factor. Heat stress may also have been a factor at lower elevations, but shade and water would have been plentiful in the deciduous forests.

The factors of predation by wolves, human hunting and competition with other wild ungulates seem not to have had wide geographical implications in our region. We subscribe to the thesis that predators do not eliminate their prey under natural conditions. Man, however, can reduce or even eliminate moose through hunting. The advent of the motor toboggan has provided the means for the extirpation of moose populations in some peripheral northern areas, and adjacent to settlements (Kelsall, 1972; Prescott, pers. comm.).

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ON THE NATURE OF WINTER HABITATS OF SHIRAS MOOSE

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Résumé

L'orignal (*Alces alces*) appartenant à la sous-espèce *shirasi* semble préférer, durant l'hiver, une série d'habitats stables ou climaciques alors que les autres sous-espèces dépendent dans une large mesure à cette saison de divers stades successionnels précédant la forêt boréale. L'auteur suggère que le principal facteur de régulation des nombres est la condition physiologique des animaux, laquelle est déterminée par la qualité et la quantité de nourriture disponible durant l'hiver. C'est peut-être ainsi qu'on pourrait expliquer pourquoi les bois, les groupes sociaux et le pourcentage de jumeaux à la mise bas sont tous plus petits chez cette sous-espèce que chez les sous-espèces plus septentrionales habitant la forêt boréale. Le caractère permanent des aires d'hivernage permet un programme d'aménagement basé surtout sur l'évaluation de la qualité et sur le sens des changements à long terme dans l'abondance de la nourriture. Par opposition, il est très difficile de pratiquer quelque aménagement que ce soit dans l'habitat de transition occupé par les orignaux plus au nord puisque leur habitat contient des essences qui croîtront rapidement hors de leur portée ou encore seront remplacées par des espèces non recherchées dans le cadre des processus normaux de la succession. L'objectif premier d'un programme d'aménagement de ces populations exploitées (*shirasi*) consiste donc à essayer de préserver la stabilité des populations et à freiner l'invasion progressive des quartiers d'hivernage de l'homme.

Abstract

Important habitats occupied by Shiras Moose (*Alces alces shirasi*) in winter are generally a more permanent part of the landscape than are seral stages of boreal forest commonly used by other moose. Nutritional status of individuals relative to winter forage availability and quality may be the primary natural population regulation mechanism. This situation may be a major reason why twins are less frequently seen, antler sizes are smaller and aggregation size is smaller among Shiras moose than for races occupying the seral stages of boreal forest. The more permanent winter ranges of Shiras moose lend themselves to management system based upon assessment of condition and trend of forage supplies. The transitory seral boreal forest, containing species which either grow beyond browsing range or are rapidly replaced through succession are less suited to such management. A practical management objective for hunted Shiras moose populations appears to simply be maintenance of a suitable population density and preservation of wintering habitats from human encroachment.

Introduction

Enough information has become available on winter habitat selection by Shiras moose to provide an estimate of the variation involved. Shiras moose occupy montane woodland, while the three more northerly subspecies occupy boreal or coastal rain forests (Peterson, 1955: 17; for map of North American

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biomes, see Aldrich, 1967). The purpose of this review is to describe Shiras moose winter habitats and point out the possible implications of the differences between these and boreal forest habitats.

Shiras moose presently occur in southern Alberta, southern British Columbia, western Montana, eastern Idaho, eastern Wyoming, northeastern Utah, northwestern Colorado and in northeastern Washington (Hall and Kelson, 1959). Wilson (1971) stated that the Shiras moose has extended its range south since about 1950 and moose in the Uinta Mountains, Utah, increased over 500% from 1965 to 1971. Denniston (1956) felt that the occasional moose in Colorado came from Utah and Wyoming.

Poelker (1972) reported a resident population of about 60 moose (probably *A a. shirasi*) in the extreme northeastern portion of Washington. Evidence of moose was found in that area in 1954. Moose within the established range of the subspecies have made local range extensions in Montana from 1940-1970 (Fig. 1); it thus appears that this race has extended and filled in many areas not previously occupied since 1950 (Stevens, 1971).

Although the Boone and Crocket Club (Waters, 1971) recognizes that the Shiras moose has smaller antlers than the Canadian subspecies (*A. a. andersoni* and *A. a. americana*), Peterson (1952) reported that the three southerly races of moose in North America (*A. a. americana, A. a. andersoni, A. a. shirasi*) do not differ significantly in skull size. Weights presented by Blood *et al.* (1967), Houston (1969) and Stevens (1967) suggest that differences in size among individuals and local populations may be more significant than between the three races. However, a series of 20 skulls of adult moose collected in Montana by Stevens (1967) were considerably smaller than those of nine Shiras moose reported by Peterson (1952).

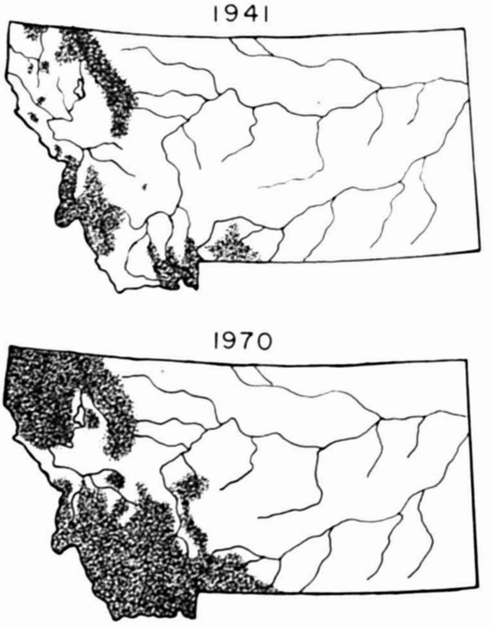

Figure 1. Montana map showing distribution of moose in 1941 and 1970 (after Stevens, 1971).

Apparently, a substantial area unoccupied by moose existed in British Columbia and Alberta as recently as 1875, attributable to the Wisconsin glaciation (Peterson, 1955:17). Parts of the current Shiras moose range were not included in this glaciation (Flint, 1945), suggesting that this subspecies has been isolated from other subspecies and has long occupied much of its current range. Evidence of size differences between subspecies is not conclusive, but investigation may confirm the "dispersal theory" of Geist (1971a) which predicts that body and antler size of races from glacial refugia are smaller than those forms from formerly glaciated terrain. This may account for the difference in antler size between the Shiras moose and its more northerly conspecifics.

Description of shiras moose winter habitat and habitat use

Areas used by Shiras moose in winter are of five different types. The most commonly used winter range, Type I, is the willow bottom stream conifer complex occurring along the typical high-gradient streams throughout the range of the race (Table I). Moose usually arrive on these bottoms between mid-December and mid-January, but during milder winters, not until March (Knowlton, 1960). Use of these limited stream bank communities has also been reported by Smith (1962), Stevens (1965) and McDowell and Moy (1942). Conifers, including Engelmann spruce (*Picea engelmanni)*, Douglas fir (*Pseudotsuga menziessi*), and lodgepole pine (*Pinus contorta*), are used for bedding (Stone, 1971) and escape cover (Knowlton, 1960). Willow bottoms commonly contain thinleaf alder (*Alnus tenuifolia*), red-osier dogwood (*Cornus stolonifera*), silverberry (*Eleagnus commutata*), and willows (*Salix drummondiana, S. geyeriana*, and *S. myrtillifolia* are especially important to moose), as well as some Rocky Mountain juniper (*Juniperus scopulorum*) and an occasional Engelmann spruce. Prior to arrival on the bottoms, subalpine fir (*Abies lasiocarpa*) and spruce stands at high elevations near drainage heads may be commonly used (Peek, 1963).

Another wintering habitat (Type II) occurs on floodplain, riparian communities containing extensive willow stands, as in the Centennial Valley, Montana (Dorn, 1970), Jackson Hole, Wyoming (Houston, 1968), and the Big Hole, Montana (Stevens, 1965). Use of willow and related types for feeding and resting appears to be more extensive in Type II than in Type I winter ranges (Table I). Also, Type II areas may support a year-long resident moose population. Variation in winter's onset, controls the time of arrival and length of stay on such areas. At the peak of winter use, Type II areas may support over 15 moose per km² (40 per mi²) (Houston, 1968:47).

The Jackson Hole Type II region contains the following vegetation types

TABLE I

Winter use of main habitat types by Shiras moose (see text for details on habitat types); in percentage of all observations by cover category

	Gravelly Range, Mo. (Stevens, 1965)	*Rock Creek, Mo. (Stone, 1971)*	*Centennial Valley, Mo. (Dorn, 1970)*	*Big Hole Valley, Mo. (Stevens, 1965)*	*Jackson Hole, Wy. (Houston, 1968)*	*Gallatin Mtns., Mo. (Stevens, 1970)*
Cover *Winter range type*	I[1]	I[2]	II[3]	II[1]	II[4]	III[1]
Willow	79	33	93	90	68	22
Aspen	12		3	1	6	28
Conifers	10	26	3	9	13	36
Open		17			9	19
Other		20			4	5
Total No. Moose Seen	85	—[5]	413	223	3343	976

[1] Aerial observations. [2] Track locations. [3] Ground observations. [4] Ground marked animals.

[5] Based on percentage of tracks encountered in each type rather than upon direct observation of animals.

(Houston, 1968:23): willow type with *Salix pseudocordata*, and *S. interior*, upland forest with *Picea engelmanni*, *Abies lasiocarpa*, *Pseudotsuga menziessi*, *Pinus contorta*, and *Populus tremuloides*, floodplain forest type with *Picea pungens* and *Populus angustifolia*, sagebrush grassland type with *Artemesia tridentata* and *Purshia tridentata* (bitterbrush) and bunchgrass shrub with various grasses and *Amelanchier alnifolia*. The Centennial Valley winter range contained the willow type, spruce type, douglas fir type, spruce fir type and aspen type (Dorn, 1970).

Type III winter range occurs in drainage where willow-bottom communities are very limited and of little importance to moose (Stevens, 1970). Here, the conifer and aspen types are important (Table I), and food habits resemble those described by Aldous and Krefting (1946) and Peterson (1955:127) for eastern ranges where more species form the major portion of the moose winter diet. Some Montana areas are Type III (Stevens, 1970), as is the winter range in eastern Washington where moose did not appear to concentrate on willow bottoms (Poelker, 1972).

Type IV winter range included the arid Juniper Hills in southeastern Idaho and appears to be unique as winter moose range (Ritchie, pers. comm.). Here, chokecherry (*Prunus virginiana*) and bitterbrush dominate the vegetative types (Chadwick and Dalke, 1965), which appear more characteristic of the northern desert scrub biome (Aldrich, 1967).

Type V winter range exists in the Hellroaring-Slough Creek area north of Yellowstone Park in Montana. McDowell and Moy (1942) reported that the willow bottoms in this area were being heavily grazed as early as 1935 by moose; a minimum of 194 moose were seen in the area in summer 1942. Moose used the willow bottoms in November and December, feeding mainly on willows. When the willow forage became exhausted, or snow conditions became too adverse in the bottoms, moose moved to the adjacent forested slopes where they ate conifers, probably Douglas fir and subalpine fir. Ellig (1962) reported willows virtually non-existent in the bottoms by 1960. Stevens (1965) verified this observation and saw only 22 moose in this area, all using spruce-fir vegetation in smaller drainages away from the large bottoms. Use of spruce-fir stands by a small population in the 1960's may have resulted from overbrowsing by a much higher population before 1960. Apparently, subalpine spruce-fir stands will, however, support a low density moose population in winter.

This brief review of winter habitats supports the contention of Hosley (1949) that willow communities are important wintering areas for Shiras moose, but also confirms the observations of Stevens (1970) in that willow is not always an important component of Shiras moose winter range. The review suggests that winter habitat preferences of moose must be determined with care. There is enough variation in habitat use between areas to render generalizations misleading. The problem of determining preference is further complicated because variation in winter severity also affects use of habitat types.

Stability of Shiras Moose Winter Habitats

The foregoing review establishes the importance of riparian plant associations containing willow as winter range for Shiras moose. The optimum moose habitat in boreal forest is primarily the young seral stages which contain abundant woody browse (Aldous and Krefting, 1946; Cowan *et. al.*, 1950). Both logging and fire can create the seral shrub stages, but in neither case does the stage last more than a few years. Although succession is highly variable from place to place, a 20 year postdisturbance interval probably encompasses the major forage producing period for a given area (Cooper, 1913), and it may be as little as 5 or 6 years (Cowan *et. al.*, 1950).

In northeastern Minnesota, use of recent cutovers was most common in early summer, late fall and early winter (Fig. 2). Aspen-white birch (*Betula papyrifera)* stands over 50 years old were frequented during late summer, and mature spruce-fir communities were important in late winter (Peek, 1971). Use of seral communities was important at several critical times of the year in this area, although not throughout the year.

Riparian communities, on the other hand, are frequently disturbed by

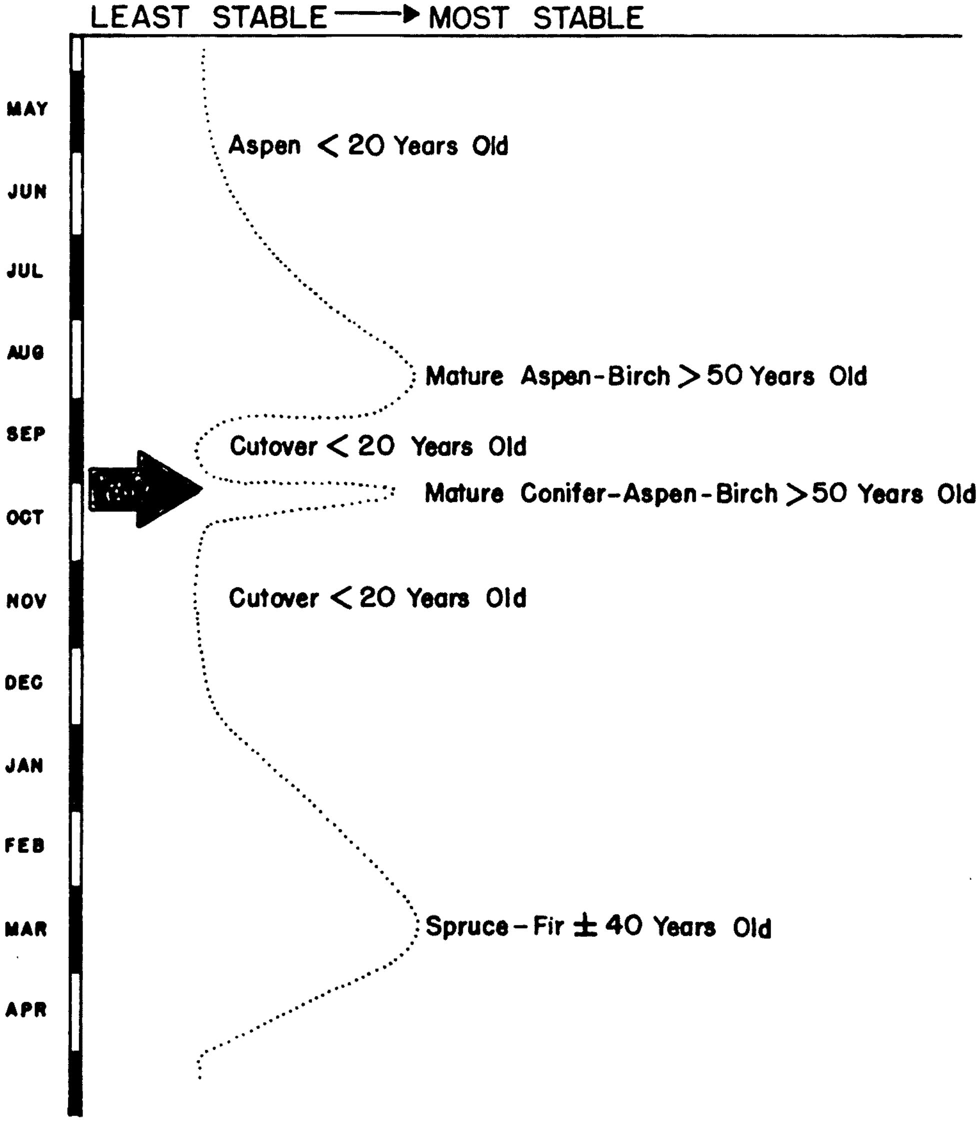

Figure 2. Selection of various habitats according to their relative stability in northern Minnesota (modified after Peek, 1971).

flooding, stream channel changes and ice damage and are thereby maintained in a seral stage of succession. Species such as sandbar willow (*Salix interior)* pioneer newly created sand outwashes (Fassett, 1969). Patten (1968) demonstrated a willow continuum extending from river edge and dominated by *Salix farrae* to a community dominated by *S. lutea* and *S. drummondiana* to a community 40 m from the stream dominated by *Salix exigua*, along the Gallatin River, Montana. He considered these stands relatively stable before they were heavily browsed by elk (*Cervus canadensis*). Houston (1968:33) found no significant change in willow density on a moose winter range in the Jackson Hole from 1950-1967. Very slow successional changes of floodplain vegetation in that area provided increasingly less willow as the climax *Picea pungens* community was attained.

A somewhat similar pattern of succession of river-bank vegetation occurs along the Chena River of Alaska (Viereck, 1970). Initial vegetation which establishes on newly created coarse gravel consists of willows (*Salix alaxensis, S. pseudocordata, S. pulchra).* As gravels accumulate silt and sand, balsam poplar (*Populus trichocarpa)* dominates. As organic matter accumulates and soil temperatures cool, white and black spruce (*Picea glauca* and *P. mariana)* dominate and maintain themselves. While succession, if allowed to progress, will reduce the willow-containing communities, the process is slower than would be expected to occur on secondary succession on boreal forest upland.

While floodplain succession should be more fully investigated, these riverside communities may persist because of periodic disturbance which retains willow a variable but lengthy period. In this sense, they are a relatively stable part of the local vegetative complex.

Coniferous habitats used by Shiras moose include Douglas fir, lodgepole pine, and spruce-fir. Douglas fir and spruce-fir are considered climax types and lodgepole pine a long-lived seral stage (Daubenmire, 1952; Patten, 1963). These areas may resemble the "permanent" habitat of Geist (1971b:122). Cowan *et. al.* (1950) reported that a climax Engelmann spruce forest supports as many moose as can be fed on the deciduous browse produced by lake shores, streams and clearings. Such habitats may be important in early winter in some areas (Peek, 1963) and in late winter on other ranges (Stevens, 1970). The chokecherry-bitterbrush type used as winter range in southeastern Idaho appears to be a stable community also (Chadwick and Dalke, 1965).

It is hypothesized that the essential winter habitats presently occupied by most Shiras moose are a more permanent part of the landscape than are the seral stages of boreal forest used commonly by other races, although exceptions do occur.

Adaptive significance of winter habitat stability

Twinning rates among Shiras moose populations have, at least in recent years, run lower than in other races, leading Houston (1968) to speculate that some genetic influence may retard twinning in the Jackson Hole area. A more traditional line of thought is that forage quality and quantity, especially on winter ranges, results in decreased production and survival (Klein, 1970) a phenotypic adjustment. However, investigations with domestic pigs (King and Young, 1957) and laboratory mice (Hull, 1967) have demonstrated that, within the genetically determined limits of fecundity for a species, there is also heritable variation in the number of young individuals produced. Lack (1958) stated that although a hereditary basis for variation in clutch sizes of birds is presumed. "There is as yet little proof of this though it seems likely on general grounds that specific differences in clutch size have a hereditary basis." Lack (1954) considered that clutch and litter size has been adapted by natural selection to correspond to the largest number of young for which parents can, on the average, provide enough food. Houston (1968:80) felt that moose populations in Jackson Hole may be regulated by winter forage availability and quality, which were, in turn, influenced by snow conditions and moose distribution.

Houston's conclusion may not apply to long-term natural population regulation. The role of predation in regulating ungulates must be given consideration (Pimlott, 1967). Moose in Jackson Hole have existed virtually without significant predation, most especially that of the timber wolf, (*Canis lupus)* for at least 60 years. The presence of several ungulate species, including elk, mule deer (*Odocoileus hemionus)* and bighorn sheep (*Ovis canadensis)* on many Shiras moose ranges would reduce the importance of predation as a limiting factor to many Shiras moose populations, even in primitive times. An analogous situation has been reported from Banff and Jasper National Parks, Canada (Cowan, 1947).

The ultimate limiting factor for most Shiras moose populations may be condition and availability of winter forage supplies occurring in plant communities which are long-lived or are effectively maintained through natural phenomena. The high occurrence of singletons could reflect the ability of the cow to successfully bring only one calf through to maturity, due to scarcity of winter forage sources. This implies that Shiras moose most commonly occupy stable winter habitats where utilization is heavy enough to prevent production and survival of most twins to maturity. The present range expansion by Shiras moose does not contradict this hypothesis. Either mortality or emigration may serve as a means of eliminating a surplus of individuals from an area filled to carrying capacity.

On less stable habitats such as seral boreal forest, the premium placed on rapid colonization of quickly created habitats would favor the cow which left the greatest number of offspring to disperse into such areas and reproduce. Burning or logging in a boreal forest area may produce as much as a five-fold increase in forage (Telfer, 1970) Under such conditions, forage supplies doubtlessly exceed the requirements of the moose population for a considerable length of time.

Differences in habitat permanency do not necessarily indicate that heritable differences in fecundity between populations or races exist, although the consistency in differences in twinning rates implies a genotypic difference. Most certainly, high post-natal mortality, which can often be detected by checking to determine if the percentage of calves decreased during winter, would suggest environmental influences. Such influences could operate through affecting lactation and maternal behavior, or through reducing the ability of the young to cope with deep snows and cold. Even if ovarian analysis indicated a low incidence of multiple ovulations, environmental influences may still be responsible.

In summary, while twinning rates among Shiras moose appear lower than for the other subspecies, the cause is in doubt. The existence of heritable differences in fecundity between the several subspecies would be difficult to demonstrate.

There are several other possible effects of habitat stability on Shiras moose populations. Even though the weight and general size of Shiras moose and the two Canadian subspecies is similar, Shiras' antlers are usually smaller and such differences may be environmentally related. Antlers are among the most recently evolved weapons and Ewer (1968) considered them to be of predominant importance as a means of communication through body expression. Antlers may serve as display organs for establishing rank in dominance hierarchies among Cervidae (Bubenik, 1966). Presumably, the largest antlered males assume the higher ranks in a dominance hierarchy (Ewer, 1968). It is then possible that larger antler size of one race over another may serve as an indication of intensified intraspecific behaviour involving adjustment or maintenance of social rank in the larger antlered race.

In colonizing areas of early stages in the boreal forest, social systems would be more frequently in need of adjustment or re-establishment than would be necessary in a more stable environment. Thus, Shiras moose may either have not evolved as large antlers, or their antler size may have decreased relative to the Canadian subspecies. The necessity of obtaining sufficient forage for maintenance and survival would preclude the development of large antlers and quite possibly the development of as competitive a social system among populations existing on limited forage supplies.

This is tentatively supported by observations on relative size of groups of moose in Montana, Minnesota, and Alaska by Peek *et al.* (1974). The largest aggregations occured on the Kenai Peninsula, Alaska, while Shiras moose were least aggregated, suggesting more opportunity for intraspecific interaction among the boreal forest subspecies than within the Shiras subspecies. Such factors as population density, habitat selection, migratory behaviour, sex and age, terrain, snow conditions and forage supplies were found to affect aggregation size (Peek *et al.*, 1974). Implications concerning variation in sociality among the subspecies are put forth here only as an hypothesis worthy of investigation.

Implications for management

A major objective of management of big game populations should be to retain as intact as possible the natural dynamic processes and interrelationships between the population and its environment. It is recognized that some artificiality inevitably replaces some parts of natural processes, reflecting the degree of habitat modification and local management needs. Shiras moose wintering habitats are encroached upon by grazing, highway construction, logging and fire prevention, but appear to be less subject to the artificial modification which occurs, often through logging, on boreal forest habitats. Many Shiras moose populations exist on relatively unaltered winter habitats. It seems logical to attempt to retain this situation rather than modify it through artificial means, even though carrying capacities may increase as a result. Shiras moose are usually only one of several cervid species occupying an area, and more attention must often be given to the other species. Conversely, Canadian moose are frequently the major game animal in areas subject to extensive modification. In fact, such modification is needed to retain the desired habitats and population levels.

There are two somewhat divergent approaches to moose management which may be related, among other reasons, to habitat stability. Management based upon assessment of condition and trend of winter foraging areas appears to be most adapted to relatively stable vegetation which will not be rapidly replaced through natural succession. This approach, used in conjunction with production-survival and harvest data, was emphasized by Cole (1961). Since variation in productivity and survival of young can be great if populations are allowed to periodically over-browse winter forage supplies, harvests may be directed toward maintaining a relatively constant population level, probably more stable than might be expected to occur otherwise. Such an objective would benefit the non-consumptive user as well by insuring the presence of a reasonably high population.

On boreal forest moose range, forage species either grow out of reach quickly if not browsed heavily or are replaced rapidly through succession whether browsed or not. Condition and trend data may be less important in management while assessment of production and survival may be emphasized (Robinson, 1962; Rausch and Bratlie, 1965). In effect, the population itself is then used as an index to the quality of the habitat. Boreal forest ranges are often relatively inaccessible, generally more extensive than those occupied by Shiras moose, and winter moose distributions may be variable enough to preclude reliance on condition-trend data for specific areas. The naturally transitory nature of important boreal forest moose habitat implies that dramatic fluctuations in populations on any given area will probably occur naturally, suggesting that less concern about retention of stable populations and heavy browsing is necessary. However, if management objectives center on production and retention of high moose populations for intensive harvest on local areas, then consideration of habitat condition-trend would become important in judging when habitat modification should proceed.

There are no recorded situations where Shiras moose have overbrowsed their winter range so consistently that permanent population declines have resulted, with the possible exception of the Buffalo-Hellroaring-Slough Creeks area, a situation confounded by the close proximity of a large elk population. The Jackson Hole winter range, considered to be heavily browsed by Harry (1957) has apparently experienced fluctuations in willow condition and moose populations over the 1950-1966 period, with little permanent damage to willow (Houston, 1968). A similar situation may have occurred on the Ruby River winter range in southwestern Montana (Peek, 1963; Stevens, 1966).

Conclusions

This review concerns rather subtle, differences in habitats which are related to equally subtle, variations within a species which in widely adaptable as evidenced by holarctic distribution. We are, in effect, considering possible adaptations of a species to the biotic complex of vegetation types which are themselves continually evolving. A much greater proportion of Shiras moose range can be considered stable than that occupied by the other subspecies: therefore, the postulated adjustments to relative environmental stability appear to reinforce the subspecific identity of the Shiras moose. The variation in environments occupied with regard to habitat stability has practical implications in management of Shiras moose.

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DISTRIBUTION AND HABITATS OF MOOSE IN ALASKA

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Résumé

L'orignal *(Alces alces)* occupe l'Alaska depuis le milieu du Pléistocène. Durant cette période, l'Alaska consistait en un vaste refuge glaciaire recouvert de formations végétales intermédiaires entre la steppe et la toundra; l'orignal se répartissait probablement alors en petits groupes isolés dans les parcelles d'habitat approprié. A la fin de la période glaciaire, la prolifération d'associations dominées par les arbustes et le développement de la forêt véritable permit à l'animal d'envahir la presque totalité de l'Alaska. Par la suite, les saulaies ripariennes ou sous-alpines ont joué le rôle de réservoirs à partir desquels l'orignal envahissait l'habitat de transition engendré par les feux ou par d'autres facteurs: c'est encore la situation qui prévaut de nos jours. Tout récemment, on a été témoin d'extensions de l'aire de l'orignal aux deux extrêmes géographiques de l'Alaska: dans le sud-est de l'État, le recul des glaciers lui a permis d'envahir le bassin des principales rivières au delà de la cordillière cotière tandis que dans le nord-ouest, l'orignal envahissait la péninsule de Seward et le versant nord de la rivière Noatak. Envahisseur récent dans cette dernière région de toundra, l'orignal semble au contraire être un résident de longue date du plateau arctique au nord des monts Brooks et ses populations là-bas sont présentement en pleine expansion. Presque partout, l'orignal a subi de remarquables changements d'abondance au cours des 150 dernières années, les grandes augmentations prenant surtout place dans les brûlis d'un certain âge. Les auteurs suggèrent d'interpréter les compte-rendus historiques faisant état de l'absence d'orignal dans une région donnée plutôt comme la conséquence de l'absence prolongée de feux dans la région: on rencontre de nos jours de telles populations à très basse densité dans les secteurs dominés par de vastes peuplements d'épinettes (pessières). Aussi, faudrait-il considérer les prétendus changements dans la distribution de l'orignal en Alaska plutôt comme des changements dans la densité relative des populations.

Les habitats les plus utilisés par l'orignal en Alaska correspondent surtout à des communautés climaciques et sous-climaciques. La densité de l'orignal est très basse dans la taïga climacique du nord de la forêt boréale. La densité est plus forte dans les communautés climaciques de saules et de bouleaux arbustifs et les communautés caractéristiques des fondrières, tout comme dans les communautés ripariennes ou les brûlis à divers stades de leur évolution. Des communautés arbustives dominées par les saules et les bouleaux et comprenant un sous-étage de plantes herbacées et d'Ericacées couvrent de vastes superficies un peu au-dessous de la limite des arbres, en altitude, et constituent des habitats très importants pour l'orignal. Ordinairement, ces habitats sont fréquentés surtout durant l'été et l'automne mais, dans certaines régions, l'orignal peut y habiter l'année durant. Les vastes plaines alluviales au sud des monts Brooks sont recouvertes d'une grande variété de formations végétales. Ces communautés ont une grande importance pour l'orignal au printemps et à l'été mais principalement durant la mise bas. Les communautés ripariennes sont fort importantes en dépit de leur caractère transitoire parce qu'elles sont en perpétuelle régénération. Dans bien des régions, les quartiers d'hiver de l'orignal sont localisés dans ces communautés tandis que, dans la partie la plus septentrionale de l'État, ces formations ripariennes sont les seuls refuges de l'animal durant toutes les saisons. Bien que les brûlis constituent le plus éphémère de tous les habitats étudiés, c'est néanmoins celui dans lequel on rencontre les plus fortes densités d'orignal. L'utilisation d'un brûlis par l'orignal dépend de toute une série de facteurs: l'identité des espèces végétales présentes, la dimension du brûlis, le taux de régénération, la diversité des communautés présentes avant le feu et le morcellement créé (écotone) par celui-ci. Les auteurs sont d'avis que, de façon générale, l'orignal ne peut ralentir de façon significative l'évolution de la succession végétale à la suite d'un feu mais qu'il peut dans une certaine mesure influencer la direction que va prendre cette succession en détruisant, par broutement sélectif, certaines des essences pionnières. De tous les habitats créés par l'homme, seuls les brûlis ont une importance quelconque pour l'orignal.

Abstract

Moose *(Alces alces)* have been present in Alaska since mid- to late-pleistocene times. They probably survived in relatively small, disjunct groups wherever suitable habitat could be found throughout this period, when a tundra-steppe community dominated much of the Alaska refugium. With the close of the glacial period and proliferation of shrub and forest communities, they spread throughout much of Alaska. In more recent times riparian and subalpine willow communities have provided a means of maintaining minimal populations able to exploit new range produced by fire and other disturbances: this pattern persists today. Very recent extensions of moose distribution have occurred in the geographic extremes of Alaska: in Southeastern Alaska, where glacial recessions have allowed moose to expand along major river valleys crossing the coastal range and in northwestern Alaska, where moose have become established on the western Seward Peninsula and north of the Noatak River. On the Arctic Slope moose seem to have been established for a longer time than on the western tundra areas, but are currently increasing in numbers. In most of Alaska, moose numbers have risen and declined dramatically in local areas over the last 150 years, largely in response to creation and maturation of fire-caused seral range. Historical accounts that moose were absent from a particular locale most likely reflect only a period of very low moose numbers resulting from a prolonged absence of fires in that area. Extremely low densities of moose presently exist in some areas where extensive spruce stands are dominant. Thus in most of Alaska the purported variations in moose distribution have in reality been only variations in relative abundance.

The most important moose habitats in Alaska include both climax and subclimax communities. Moose are present in low densities throughout the climax taiga communities of the northern boreal forest. Climax upland birch — willow communities and lowland bog communities support greater densities of animals, as do continuously-renewed riparian seral communities and more transient post-burn communities. Upland moose habitats are very important in many areas of the state. These habitats are timberline shrub communities characterized by birch and willow, with heath and forb understories. These habitats are used most intensively in summer and autumn, but are year-round residences for moose in some areas. Lowland climax communities are many and diverse, occurring on the broad alluvial plains common south of the Brooks Range. These communities are especially important during spring and summer, and support large concentrations of moose during calving. Riparian willow communities, although seral in nature, are consistently present because of constant renewal. They are key winter ranges in much of Alaska and are the only habitat consistently occupied by moose in Arctic areas. Fire created communities have been responsible for the greatest densities of moose achieved in Alaska, but are the least permanent of the habitats discussed. Species composition, size of burn, rate of growth, diversity of communities and ecotone created together determine the impact of a burn on moose populations. Moose are generally unable to alter the rate of post-burn succession, but may alter its course, by destroying some favored forage species. With the exception of burns, man-made habitats have been negligible in Alaska as a whole, although local moose populations have been affected in recent times.

Introduction

Moose in most of Alaska as well as in adjacent portions of Canada are considered *Alces a. gigas*, but intergradation with *A. a. andersoni* probably does occur in Southeastern Alaska (Klein, 1965).

The present review describes probable past and known present distribution of moose in Alaska and describes and discusses the major habitats important to moose in the state.

I. DISTRIBUTION

Pleistocene distribution

Moose are Alaskan and North American residents of long standing. Flerow (1967) surmised that larger Pleistocene mammals originating in Eurasia crossed the Bering Land Bridge readily, perhaps as early as the Kansan glacial period. Moose remains have been identified from sediments of Illinoian age (100,000-175,000 years old) in central Alaska (Péwé and Hopkins, 1967). Repenning (1967) indicates *Alces* immigrated from Palearctica early in the Rancholabrean mammalian age (between the Illinoian and Wisconsin glaciations) and are known from an earlier period (Günz glaciation) in northeastern Siberia. Later immigrations during the Wisconsin (10-35,000 years ago) glaciation are implicit in these observations, and probably contributed to development of subspecies among *Alces.* Klein (1965) recorded the relatively recent penetration of the Coast Range icefields of Southeastern Alaska by moose from the Alaska-Yukon refugium as far south as the Taku River, where they intergrade with *A. a. andersoni.* Progenitors of *andersoni* were likely earlier immigrants than those of *gigas,* for moose remains are known from the refugium south of the Continental ice sheet (Osburn, 1921, cited by Klein, 1965).

Hopkins (1967) characterized climatic changes produced by Illinoian and Wisconsin glaciations as ''severe refrigerations'' that resulted in a lowering of treeline by 400 m or more (Péwé, 1965; Repenning *et al.*, 1964) and produced a considerably drier climate than exists today. On the basis of several lines of evidence various authors agree that Alaska and Beringia in general supported largely steppe and tundra during these glaciations (Colinvaux, 1964a 1964b, 1967; McCulloch, 1967; Repenning, 1967). Repenning (1967) noted that most of the Rancholabrean immigrants to Alaska were boreal forms, already adapted to an arctic-subarctic environment. Guthrie (1968) studied data on collections of Pleistocene large mammal remains from four mining areas near Fairbanks in central Alaska. Sediments containing the remains were of Wisconsin age at three sites,.and pre-Wisconsin at the fourth. Remains of grazing mammals predominated at all sites, and browsing mammals were very scarce. Moose comprised less than one percent of the remains except at one site, where they approached five percent. Guthrie concluded that the habitat of this mammalian complex was a grassland supporting a substantially larger biomass than the present vegetation complex, typical of Interior Alaska moose habitat.

Recent prehistoric distribution

On the basis of former forest extension with beaver *(Castor* spp.*)* present on the Seward Peninsula, and of glacial recession in the Brooks Range, McCulloch (1967) concluded an early Recent warming trend occurred in Northwestern Alaska 8,000 to 10,000 years ago. A cooler period followed with reverse effects. Following this, McCulloch believed the Postglacial thermal maximum occurred in Alaska 3,000 to 6,000 years ago. Since then, brief thermal fluctuations have occurred, with the most interesting note from our viewpoint that small glacial advances occurred in the Brooks Range about 1,000 to 1,500 years ago, and again during the first half of the 18th century (Porter, 1964). During the last 200 years the climate has grown warmer.

Although there is little direct evidence of moose distribution from this period, it is clear from this brief summary that climatic trends were conducive to improved habitat conditions for moose. If beaver invaded western Seward Peninsula, it is very likely moose did also. Although both subsequently disappeared from that area, the response of forest and beaver to the early Recent warming is indicative of change that surely occurred in vegetation and in distribution of browsers such as moose as climatic warming ensued.

In summary, moose survived in Alaska during Wisconsin and pre-Wisconsin times on limited and marginal habitat. During the last few thousand years, development of extensive shrub and forest communities favored increased moose densities throughout much of Alaska. As taiga developed, pioneering willow communities (in areas of glacial recession, unstable slopes and riparian situations) probably assumed increasing importance as "reservoir habitats" for moose since the taiga is basically incapable of supporting high densities of moose. Nevertheless, overall trends in plant communities undoubtedly favored moose.

Early historic distribution: 1800-1950

Post-Pleistocene moose remains and written records of moose distribution prior to 1800 are scarce. The record is little better since that time for many parts of the state because few people possessing written language travelled or lived in those areas. Some information has been gained from early explorers and archaeological work, and inferences can be made on the basis of native cultures. Major places or area names referred to in the following pages appear in Figure 1.

INTERIOR AND SOUTHERN ALASKA

In a comprehensive review of the subject, Lutz (1960) concluded that moose have long been residents of most of Alaska and in particular of Interior and Southern Alaska. Wrangell (1839) noted that Indians of the Copper River used moose hides and sold them, and that moose occurred throughout the Copper River Basin, a large area in southcentral Alaska. Lutz (1960) gives many references reporting upon the presence of moose at various times on the Alaska Peninsula as well as on the upper Yukon and on most of its tributaries (Howard, 1868; Raymond, 1871; Sheldon, 1930; Turner, 1886; Wickersham, 1938; Zagoskin, 1967).

Lutz (1960) also gives many references to show that moose were known on the Kenai Peninsula since the early 1800's and in fact were present in archaeological sites dated to about 750 B. C. He concluded that the often repeated story that moose were absent from the Kenai prior to 1870-1900 had no basis in fact.

Athabascan Indians in some areas of Interior Alaska depended on moose for a substantial proportion of their food and clothing, particularly in winter when moose tended to congregate in riparian willow stands. These observations and the probable evolution of biotic communities since Pleistocene times (Hopkins, 1967) support Lutz's contention that moose have long been residents of most of Alaska.

ARCTIC ALASKA

In the Brooks Range, on the Arctic Slope, and on the tundra of northern and western Alaska moose were apparently very scarce at the turn of the 20th century. Leopold and Darling (1953a) suggest moose were rare on the North Slope in the early 1900's because most travellers on the Colville River failed to mention moose or their signs. Moose did not inhabit the Colville River Delta until about 1890 to 1910, were seen rarely through about 1930, and became common by the early 1950's, based on our interpretation of events reported by Bee and Hall (1956). R. O. Stephenson (pers. comm.) has also obtained information from the Nunamiut Eskimo of Anaktuvuk Pass which largely corroborates our interpretation of the changes in the abundance of moose in the area north of the Brooks Range.

Stephenson further feels that native hunting along the well-travelled Colville River may have retarded growth of the moose population prior to 1920. Most of the Nunamiut moved to the coast in the 1920's and early 1930's, removing much of whatever hunting pressure they had applied, and the moose population subsequently increased. Wolves may well

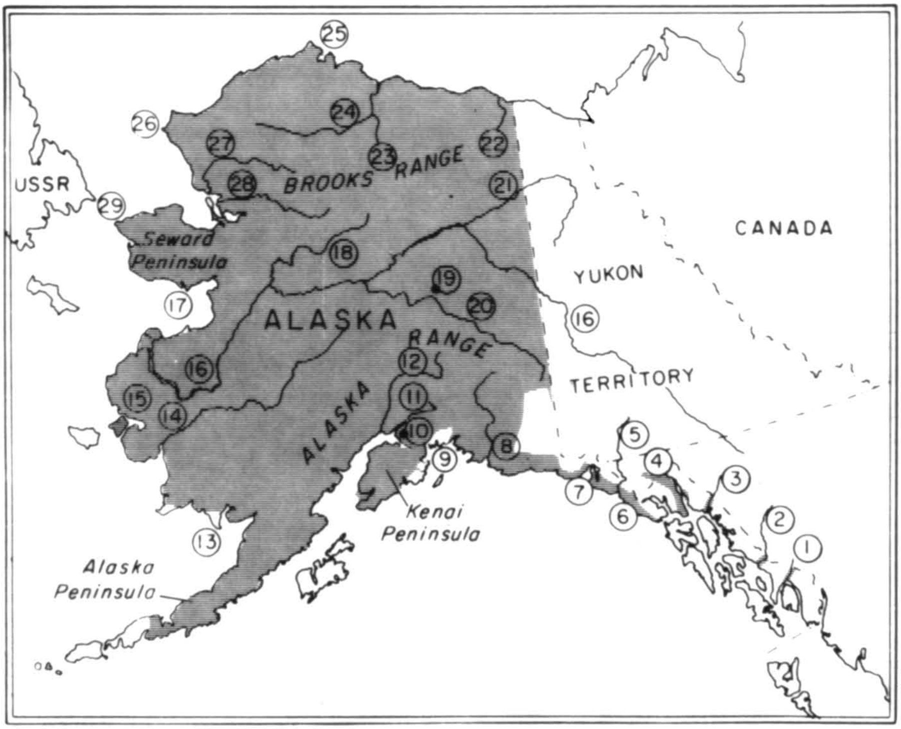

Figure 1. Present (shaded area) distribution of moose in Alaska and major place and area names referred to in the text. Numbers indicate: 1. Unuk River; 2. Stikine River; 3. Taku River; 4. Chilkat River; 5. Alsek River; 6. Cape Fairweather; 7. Yakutat Bay; 8. Copper River; 9. Prince William Sound; 10. Anchorage; 11. Matanuska River; 12. Susitna River; 13. Bristol Bay; 14. Kuskokwim River; 15. Yukon-Kuskokwim Delta; 16. Yukon River; 17. Norton Sound; 18. Koyukuk River; 19. Fairbanks; 20. Tanana River; 21. Porcupine River; 22. Kongakut River; 23. Anaktuvuk River; 24. Colville River; 25. Pt. Barrow; 26. Pt. Hope; 27. Noatak River; 28. Kobuk River; 29. Cape Prince of Wales.

have contributed to control of moose until the late 1940's and early 1950's when extensive predator control work was done on the Arctic Slope.

Trends in moose numbers followed a similar pattern south of the Brooks Range in the upper Koyukuk River drainage. Observations gathered from older residents of the Koyukuk by Stephenson (pers. comm.) indicate moose were first seen around Wiseman (upper Koyukuk River) in 1922 to 1924, after virtual absence for perhaps 20 years.

In summary, available records for the south side of the central Brooks Range, the range itself and the Arctic Slope indicate few moose about 1900, with a very slow increase resulting in moose becoming common and in some locations abundant by the early 1950's.

WESTERN ALASKA

Along the northwestern and western coast of Alaska moose seem to have been essentially absent beyond treeline at the turn of the century, but few records exist. Hadleigh-West (1966) found no moose remains in archaeological excavations of two houses at Ogotoruk Creek, near Cape Thompson on the northwest coast. The houses had been occupied from about 1880-1900 until recently. Remains of various other terrestrial and marine animals were abundant. What accounts are available concerning the Noatak and Kobuk Rivers suggest a gradual increase in moose numbers similar to that in the central Brooks Range. On much of the Seward Peninsula moose were absent until perhaps as recently as the last 30 years. South of the Seward Peninsula moose probably occurred in small, disjunct groups along streams flowing into Norton Sound where treeline extends to the coast along many streams. Moose have evidently been residents for some time, because in the local Eskimo dialect there is a specific word for moose. By comparison, the local Eskimo word for moose on the Seward Peninsula is a modification of the word for caribou (J. J. Burns, pers. comm.). Nelson (1887) noted that a few years prior to 1881 a moose was killed on the Yukon Delta quite near the Bering Sea, which suggests moose occasionally wandered west from better habitat along the Yukon River, much as they do today.

To the best of our knowledge the Yukon-Kuskokwim Delta has never supported more than the occasional wandering moose.

Contemporary distribution: 1950-1972

Efforts to document distribution and relative abundance of moose throughout the state have increased considerably within the last 30 years. Several transplants of moose have also been made, which extended the distribution of moose in Southeastern Alaska. In general, moose appear to be increasing and extending their distribution in extreme northern and western Alaska and in local southeastern areas, while in much of Southcentral and Interior Alaska current population trends are stable or downward.

SOUTHEAST ALASKA

Moose naturally invaded Southeastern Alaska (the area south of Cape Fairweather) via the Chilkat, Taku, Stikine, Unuk, and Alsek Rivers from Canada (Klein, 1965). A small natural population also exists at Thompson Bay, north of the Stikine River. It is apparently dependent on secondary succession following clearcutting of timber (Alaska Department of Fish and Game, 1973). Timing of moose invasions in the Chilkat, Taku and Unuk Rivers is not known, but they must have occurred well before 1900. Small populations limited by restricted habitat have persisted.

Moose probably invaded the Yakutat area by the Alsek River valley 40 to 50 years ago, following recession of glaciers that previously blocked access (Klein, 1965). Since then, the population has grown rapidly, and may have approached 4,000 to 5,000 (Alaska Department of Fish and Game, 1973) prior to the winter of 1971-72, when substantial losses occurred due to deep snow. The Icy Cape-Yakutaga area north of Yakutat may have been colonized by moose from Yakutat, or from the Copper River Delta population.

Moose apparently became established in the Stikine River valley between 1875 and 1900 (Klein, 1965). Habitat is limited, but a small population thrives there. Twenty-one moose calves were transplanted to Berner's Bay, 34 miles north of Juneau, in 1958 and 1960 (Burris, 1965). This population grew rapidly and needs control by continued sport hunting to avoid over-use of its range (Alaska Department of Fish and Game, 1973).

Fourteen moose calves were released at Chickamin River on the east side of Behm Canal, east of Ketchikan, in 1963 and 1964 (Burris, 1965). Moose have been observed there since that time, but the population does not seem to be increasing. Moose persist at low densities in the Unuk River valley (Robert Wood, pers. comm.).

With the exception of Yakutat, none of the Southeastern areas can sustain large populations of moose, but all populations do support limited sport hunting. Habitat is limited to relatively small areas in and adjacent to river valleys, where coastal and interior influences mingle.

SOUTHCENTRAL ALASKA

For discussion purposes, Southcentral Alaska includes the area south of the Alaska Range, the Bristol Bay drainages, and the Alaska Peninsula. It includes a striking diversity of ecotypes, ranging from coastal rain forest in Prince William Sound, to taiga south of the Alaska Range, to coastal tundra on the Alaska Peninsula.

Prince William Sound

Moose were probably effectively isolated from Prince William Sound by glaciation and by Miles Canyon on the Copper River (Klein, 1965). The largest extant population was established on the Copper River Delta by a series of transplants between 1948 and 1958 (Burris, 1965). This population is largely dependent upon riparian willow communities, and now occupies essentially all available range (Alaska Department of Fish and Game, 1973).

A few moose inhabit the Valdez area, and they occasionally reach western Prince William Sound via the Nellie Juan River (Ronald Somerville, pers. comm.).

Kenai Peninsula

Moose are absent from much of the southern coast of the Kenai Peninsula, which is isolated by the Kenai Mountains and the Harding Icefield. The eastern portion of the Kenai Peninsula is mountainous, available habitat is limited, and in many areas browse is decadent. Moose numbers have declined here since the late 1950's, although distribution has probably changed little.

Chatelain (1952) stated moose numbers on the Kenai Peninsula probably peaked in 1925 and had declined somewhat by 1950. He cited major fires in 1871, 1891, and 1910 as the probable cause for subsequent moose increase. His comments do not relate directly to the eastern Kenai Peninsula, but rather to the foothills and broad flats extending west from the Kenai Mountains. Large fires in 1947 and 1969 have resulted in a recent peak of moose densities in this area.

Moose are found throughout the western portion of the Kenai Peninsula. They exhibit strong seasonal movement patterns (LeResche, 1973, 1974), in which substantial numbers alternately use upland willow communities and lowland birch-spruce second growth. General distribution and movement patterns probably have changed little since 1950, but succession following fire has undoubtedly produced spatial readjustments in seasonal use patterns as well as an increase in moose numbers.

On the southwestern portion of the Kenai seasonal distribution and movements have probably changed little in the last 20 years. However, certain winter ranges are currently very decadent and little used. Fires have been rare in the area. Total moose population on the Kenai probably exceeds 15,000.

Six moose were released on Kalgin Island in Cook Inlet near the Kenai Peninsula between 1958 and 1960 (Burris, 1965). A small population persists there.

Alaska Peninsula

Chatelain (1952) noted moose numbers were increasing on the Alaska Peninsula through the late 1940's. The increase continued in certain areas, principally south of Mother Goose Lake, through the early 1960's to a present total estimate of 7,500 animals (Alaska Department of Fish and Game, 1973). Greatest densities of moose presently are associated with willow communities on and adjacent to drainages from King Salmon River to Meshik River.

Moose have been seen on the Alaska Peninsula as far west as Port Moller and Pavlof Bay (Murie, 1959; Alaska Department of Fish and Game, 1973).

Upper Bristol Bay drainages

The status of moose populations in this area is poorly known. General observations indicate similar distribution but lower densities than on the Alaska Peninsula.

Matanuska and Lower Susitna Valleys

This broad area forms an arc surrounding upper Cook Inlet, and originally supported mainly taiga vegetation. Agriculture, other development, and associated fires beginning in the 1920's and 1930's prompted substantial production of browse species in much of the Matanuska Valley and adjacent Susitna Valley (Hatter, 1948; Chatelain, 1952; Alaska Department of Fish and Game, 1973). In remote areas west of the Susitna River, riparian and subalpine willow communities, old burns and glacial outwash areas provide prime moose habitat. Moose populations reached their highest recorded densities over much of the area in the late 1950's. Maturation of browse communities and continued human development have since impinged on available moose winter range, particularly in the immediate Anchorage area.

Moose numbers have been variable in the area but are presently high with an estimated 15,000 moose east of the Susitna River, and unknown but substantial numbers to the west (Alaska Department of Fish and Game, 1973).

Copper River and Upper Susitna River

This vast area lies between summits of the Alaska Range on the north and west, the Chugach Mountains on the south, and the Wrangell Mountains on the east. Much of the region lies above timberline, but a considerable area supports predominantly taiga. Moose are found in plant communities ranging from subalpine willow to old burns and riparian communities. Greatest concentrations of moose occur in subalpine climax willow communities in October and November, and in lowland riparian willow communities later in winter. Substantial numbers of moose occur at low densities throughout areas supporting predominantly spruce, but with willows, birch and other shrubs comprising a sparse understory.

Chatelain (1952) observed that moose were increasing rapidly in this general area in response to extensive fires over the preceding 30 years. Additional factors that may have contributed to marked increases were cessation of market hunting and virtual elimination of wolves in much of the area (Alaska Department of Fish and Game, 1973). An estimated 25,000 to 30,000 moose occupied the western and northern two-thirds of this area in 1965. Since then, a considerable decline occurred primarily in response to severe snow conditions (Bishop and Rausch, 1974). Predation combined with heavy hunting pressure in certain areas have contributed to a continuing decline. Range conditions may have been affected by high moose populations, and in some areas high snowshoe hare *(Lepus americanus)* populations in 1963-1964 did kill substantial numbers of willows (Alaska Department of Fish and Game, 1973). Although wildfire has been of only local and limited importance in creating moose range, the acreage burned in the last 15 to 20 years (Barney, 1969) has declined to near zero due to effective fire suppression and therefore has made virtually no contribution to support of moose.

NORTHERN ALASKA

Interior Alaska

Interior Alaska comprises the drainages of the Yukon and Kuskokwim Rivers. In contrast to the Copper River-upper Susitna River area discussed above, a large proportion of Interior Alaska is below timberline (Viereck and Little, 1972; Warhaftig, 1965). Moose inhabit all of the Interior except alpine areas.

In the broadest sense, Interior Alaska moose distribution has changed little in the last 20 years; that is, no previously unoccupied range has been occupied. Changes in abundance have occurred, however. During the late 1950's moose numbers appeared to be rising throughout much of Interior Alaska (U.S. Fish and Wildlife Service, Alaska Department of Fish and Game unpublished reports, and Alaska Department of Fish an Game, 1973). Quantities of additional seral range were created through relatively regular and extensive wildfires (Hardy and Franks, 1963; Lutz, 1956; Barney, 1969).

Because the quantity of climax alpine and riparian winter range is relatively constant, seral range created by disturbance is the major agent for increase in carrying capacity. As Geist (1971) succinctly states, climax-type ranges support a nucleus population from which individuals can rapidly colonize newly created transient (seral) habitat. In Interior Alaska, fire is the chief disturbance.

Many of the Interior Alaska areas now most heavily used by moose in fall and early winter are burns that date from 1957, when an estimated 12.5 million hectares burned in Alaska (Hardy and Franks, 1963). Local distribution of moose is materially affected by the prevalence and successional stage of fire site vegetation dating from that year.

Annual concentrations of moose in old burns usually occur from October into December.

Similar effects occur on a broader scale. Chatelain (1952) reported low numbers of moose along the Kuskokwim River in the taiga zone. Today, moose are abundant, although areas of abundance are discontinuous. In contrast, moose in the Big Delta area south of Fairbanks have declined from the abundance reported by Chatelain largely in response to successional changes in seral range.

The importance of snow characteristics must be emphasized in any discussion of moose distribution or abundance (Coady, 1974). Rapid accumulation of snow on higher seral and subalpine ranges appears to accelerate movement to lowland seral and riparian ranges. Deep snow for extended periods can substantially lower productivity, calf survival, and adult survival (Bishop, 1969).

In summary, general distribution of moose in Interior Alaska has not changed materially in the last 20 years, but local distribution and abundance have been substantially affected by creation and maturation of primarily fire-caused seral ranges. In addition, a series of relatively severe winters (in terms of snow depth) has recently caused reductions of moose numbers in much of the Interior.

Western and Arctic Coastal Alaska

The only area where moose have significantly extended their range in the past two decades appears to be northwestern coastal Alaska, including the Seward Peninsula north to the vicinity of Point Hope.

Moose have occurred commonly in and near the limit of timberline on the eastern Seward Peninsula for an indefinite but long period (Alaska Department of Fish and Game, 1973). Within the last 20 to 30 years, however, they have gradually become common on the western, treeless portion of the Peninsula. Brooks (1953) reported shooting a bull moose near Cape Prince of Wales in 1948, one of the earliest documented occurrences of moose on the Seward Peninsula. Chatelain (1952) commented that a few moose were found on the Seward Peninsula. Although densities are low compared to Interior Alaska populations, moose are now permanent residents throughout most of the Peninsula. Beyond treeline, moose depend upon upland willow communities for much of their summer range, and upon riparian willow communities in winter.

In the Kobuk and Noatak River drainages to the north, moose were apparently scarce or absent until 50 to 75 years ago (Alaska Department of Fish and Game, 1973). In coastal areas north of the Noatak River moose were definitely absent as noted earlier. They have reached the Point Hope area only within the last five years (Alaska Department of Fish and Game, 1973). Beyond treeline they concentrate in riparian willow habitat during winter.

Thus, the western Seward Peninsula and the northwest coastal areas of Alaska are the only actual extensions of moose distribution that have occurred in the last 20 to 30 years in Alaska.

Although moose have increased in number on the Arctic Slope over the last 20 years, their distribution has changed little. Within the last five years, many more sightings of moose have been reported, largely because of increased activities related to the developing oil fields. On the basis of these various reports, limited surveys by the Alaska Department of Fish and Game, and reconnaissance by Renewable Resources Consulting Services Ltd., moose population densities appear highest from the Colville River east to the Canning River. Moose do occur outside of this area along essentially all major streams. Records are fewer from the west, but Chesemore (1968) recorded several sightings from the Barrow vicinity and Meade River for the period 1958-1963.

Yukon-Kuskokwim Delta

Moose distribution apparently has not changed appreciably over the last 20 to 30 years in the Yukon-Kuskokwim Delta area, where occasional wanderers are the rule, nor in Norton Sound, where moose regularly approach the coast along timbered valleys.

II. HABITATS

Because moose occupy perhaps 1,350,000 km^2 of Alaska's 1,518,000 km^2 of very diverse wild land, it is necessary to generalize considerably in this discussion of their habitats in the state. The most important of these habitats can most simply be considered as being composed of four major "types" occurring relatively distinctly or intergraded. Each "type" represents a continuum of rather similar communities. Climax communities utilized are (1) upland willow (*Salix* spp.) or birch (*Betula* spp.) dominated communities and (2) lowland bog areas; seral communities include those created by (3) fire and by (4) glacial or fluvial action. This discussion will deal with these four types, but it must be emphasized that the types are seldom discrete, are very often mixed and are sometimes hybridized with each other or with the coniferous, mature deciduous, or tundra types also abundant in the state. Further, although the value of these four types to moose varies between parts of the state, many moose populations migrate between two or more types annually. In contrast, some populations exist entirely within a sometimes very small area of only one type community, and survive year-round on it. In addition to these four types, other taiga communities are very widespread, but support only low densities of moose wherever they occur.

Upland climax communities

These communities have been little studied but are important throughout the Alaska and Seward Peninsula, Southcentral Alaska (including the Kenai Peninsula and Matanuska highlands) and southern Interior Alaska, as well as on the south slopes of the Brooks Range. They are essentially timberline shrub complexes containing both birch (predominately *Betula glandulosa* and *B. nana*) and several species of willow mixed with heaths and forbs, and often intergraded with coniferous taiga communities growing at lower elevations.

The type extends from sea level to elevations of 1200-2000 m, depending upon local timberline. Upland streamsides usually support the densest and tallest willow shrub stands, with birch dominated communities being more common in the drier sites between. The upland shrub type most often intergrades with alpine tundra or heath-mountain avens communities at higher elevations, and with spruce (*Picea* spp.)-birch taiga below. The upland shrub communities often contain scattered white spruce (*Picea glauca*) at their lower reaches.

Hanson (1951) likened the birch shrub type ("scrub birch") to communities described in Norway by Nordhagen (1943) as "dwarf heath shrub on lime — poor rock" and to communities in northern Siberia and northwestern Manchuria called "jernik" or "shurb tundra" by Imaniski (1950). Birch shrub communities may be created by repeated fires in spruce-paper birch (*Betula papyrifera*) stands, or by pecularities of topography and elevation alone. Upland willow stands along streams are the rule in areas both with and without recent fire history and are primarily products of topography, soils and elevation.

Table I lists floristic characteristics of typical upland willow and shrub birch stands from Southcentral Alaska. These communities are often interwoven along stream-cut rolling hills and upland plateaus. Forb species present vary considerably by area of the state and specific site, but the woody shrub and heath species listed are representative of most upland moose habitat in Alaska.

WILLOW COMMUNITIES

These communities are concentrated at streamsides above timberline or in low coastal tundra areas. Shrubs may be decumbent, at higher elevations, growing no more than 20-30 cm tall. In the more vigorous stands at lower elevations, willow species are tree-shrubs, often more than 1.5 m tall. Density of willow stems may be very high: Milke (1969) has found, in lush upland willow stands from Interior Alaska, that some species of *Salix* could be represented by as many as 34,000 stems per hectare. The average height of the willows in such stands varied between 50 and 140 cm.

SHRUB BIRCH COMMUNITIES

These communities also occur at and just below timberline, but on drier sites than upland willow stands (Fig. 2). Shrub height may vary from 20-30 cm to over 2 m, depending upon location and elevation. Densities of shrubs within the type are quite variable, but generally decrease with increased elevation. Dominant and characteristic species for such a community appear in Table I.

MOOSE USE

Most upland shrub communities are important to moose in summer and autumn; however, in some areas of light snowpack they support moose throughout the year. In the Kenai Peninsula and Matanuska Valley and many areas of Interior Alaska, moose migrate to these areas in June and July, breed in these communities or slightly below in mixed shrub birch-white spruce stands, and return to upland shrub areas until driven out by snow in November or later. Mature bulls and cows without calves are most characteristic of these upland areas, for cows with calves and young bulls tend to remain in lowland areas throughout the summer (LeResche, 1973, 1974). In contrast, in some Interior Alaska areas, moose desert lowland summering areas and move upward to shrub communities in winter (LeResche, 1974).

With the exception of temporary aggregations, moose density seldom reaches extreme levels on upland ranges, but densities of 0.8-1.6 moose per km^2 are not uncommon over vast upland areas. As a result and because the range is seldom occupied throughout the year, we know of no major instances where upland shrub communities have been over-utilized by moose. One such case possibly exists in the Nelchina Basin, south of the Alaska Range, where moose populations have decreased drastically since 1965. A series of severe winters has occurred, along with a general drying trend, and many upland shrub stands are in low vigor today (Pegau, 1972). Specific moose-habitat relationships in the area remain unclear, however.

Upland ranges are permanent refugia for moose populations and are among the most luxurious in Alaska. Due to their topography they have seldom been encroached upon by man, and the limited use received relative to standing biomass insures their continued high quality. Upland ranges are very extensive in some areas (see Fig. 2). Skoog (1968) estimated that shrub birch and willow communities made up 18.7 percent of the 44,800 km^2 of moose and caribou range he studied in the Nelchina Basin. Only a few moose winter in these ranges in normal years. During years of light snowfall, moose remain in upland areas well into winter, thereby relieving pressure on heavily used lowland wintering areas (LeResche, 1974).

Lowland climax communities

CHARACTERISTICS

This habitat type contains a broad spectrum of communities particularly important to moose during summer. In addition, all the major calving concentrations we know of in Alaska occur in boggy lowland climax communities (Fig. 3). These communities are an integral part of taiga vegetational complexes throughout Interior and Southcentral Alaska.

Extensive lowlands, locally referred to as "flats" or "muskeg" occur on broad alluvial plains from the south slopes of the Brooks Range to the southern coastal forests, and from the Alaska-Canada border nearly to the Bering and Chukchi Seas (Wahrhaftig, 1965; Johnson and Hartman, 1969). Approximately 30 percent of this area is forested, while the remaining land consists of bogs, shrub thickets, and tundra (Viereck, 1973).

Figure 2. Upland climax communities of shrubby birch and willow are extensive and important habitats in many areas. R. Bishop photo, central Alaska Range.

Surface features in lowland areas frequently include extensive flood plains with little relief, meander scars and oxbow lakes, terraces, and alluvial outwash deposits (Black, 1958; Wahrhaftig, 1965). Loess, sand, and outwash of Quaternary age, organic deposits formed in bogs, and recently deposited alluvium frequently overlay a micaceous schist bedrock (Dutro and Payne, 1957; Viereck, 1973). Forest soils are generally shallow with poorly developed profiles. Piedmont streams, many of glacial origin, change from braided to tightly meandering tributaries as they enter lower elevations.

Geologically and vegetatively the lowland climax communities or flats of Interior Alaska consist of treeless or nearly treeless bogs and more or less forested areas surrounding or occurring within the bogs. Between the Alaska Range and the Brooks Range, permafrost oc-

TABLE I

Mean composition and cover of 10 upland shrub ("shrub birch") stands measured in the Nelchina Basin, Alaska by Hanson in 1957 and 1958: modified from Pegau, 1972. Average cover was measured by the modified Hult-Sernander scale

Species	*Average cover*	*Frequency of occurrence in 100 m² quadrats*	*Frequency of occurence in 10 stands*
Betula glandulosa	2.5	92	100%
Salix arctica	0.2	11	40%
S. pulchra	0.5	26	70%
S. glauca	0.2	6	20%
Vaccinium uliginosum	1.5	73	100%
V. vitis-idaea	1.6	99	100%
Empetrum nigrum	1.6	74	100%
Ledum decumbens	1.1	57	90%
Diapensia lapponica	0.1	8	30%
Arctostaphylos alpina	0.1	2	10%
Dryas octopetala	0.2	8	30%
Loiseleuria procumbens	0.0	1	10%
Rubus chamaemorus	0.1	6	20%
Spirea beauverdiana	0.1	6	10%
Calamagrostis canadensis	0.6	61	90%
Festuca altaica	0.4	33	60%
Hierochloe alpina	0.6	50	80%
Arctagrostis latifolia	0.0	1	10%
Carex bigelowii	0.7	48	70%
C. montanensis	0.1	8	10%
C. podocarpa	0.0	1	10%
Anemone narcissiflora	0.4	31	60%
Artemisia arctica	0.2	17	50%
Pedicularis spp.	0.1	13	50%
Polygonum bistorta	0.4	33	60%
Cornus canadensis	0.0	3	20%
Lycopodium annotinum	0.0	1	10%
Antennaria monocephala	0.0	4	20%
Arnica lessingii	0.0	2	10%
Gentiana glauca	0.1	5	20%
Stellaria laeta	0.0	1	10%
Mosses	3.9	99	100%
Lichens	4.4	100	100%

curs in all areas except underneath south facing slopes and recently deposited alluvium. South of the Alaska Range, permafrost is sporadic in occurrence and is found only in bogs and on north facing slopes (Viereck, ms). Permafrost affects vegetation patterns and types by preventing lateral movement and downward percolation of soil water (Benninghoff, 1952) while vegetation affects permafrost by providing an insulating layer which prevents or at least influences the rate of melting of permafrost during the summer months (Benninghoff, 1952; Drury, 1956).

Drury (1956) and Viereck (1970a, 1970b) have discussed at length lowland forest succession and origin of bogs along braided or meandering streams in Interior Alaska. Freshly deposited alluvium is first colonized by willow or alder (*Alnus* spp.) and later by balsam poplar (*Populus balsamifera*). An understory of low shrubs, horsetails (*Equisetum* spp.) and white spruce seedlings may develop beneath the poplars. As the white spruce mature, an organic ground layer of mosses, herbs, and low shrubs develops, permafrost forms and after 200 to 300 years, the substrate becomes more favorable to black spruce than to white spruce.

Local disturbance of the insulating organic layer in black spruce forests may result in shallow thawing of the permafrost, water accumulation, and bog formation (Benninghoff, 1952; Drury, 1956). Development and expansion of bogs is frequently indicated by angular growth of trees due to soil instability.

Figure 3. Spruce-bog habitats is typical of the lowland climax communities of Interior Alaska. Here, moose concentrate during calving. R. Bishop photo.

The resulting vegetation over extensive lowland areas becomes an intricate mosaic of black spruce forests, bogs, shrubs, and sub-climax hardwood communities, as well as numerous intermediate stages.

Floristics of northern lowlands have been reported by Ritchie (1959) and Larsen (1965) in subarctic Canada, Hanson (1951, 1953) in western Alaska, Drury (1956) in the upper Kuskokwim River region of Alaska, and Johnson and Vogel (1966) in the Yukon Flats of Alaska. In addition, Anderson (1959), Hultén (1968), and Viereck and Little (1972) have described the circumpolar distribution of trees, shrubs, and herbs found in Alaska.

Recent alluvial deposits on lowland floodplains throughout Interior Alaska are generally colonized first by horsetails (*Equisetum arvense*), Canada reedgrass (*Calamagrostis canadensis*), willows (*Salix alaxensis, S. arbusculoides, S. bebbiana*) and alder (*Alnus tenuifolia*).

As balsam poplar and later, white spruce or mixed white spruce-paper birch become established, herbs such as wintergreen (*Pyrola secunda*) and fireweed (*Epilobium angustifolium*), and low shrubs such as rose (*Rosa acicularis*), currant (*Ribes triste*), and highbush cranberry (*Viburnum edule*) appear.

Accompanying the replacement of white spruce and birch by black spruce is a gradual increase in the sphagnum moss (*Sphagnum capillaceum, S. girgensohnii, S. fuscum,* and *S. rubellum*) cover and growth of a dense shrub layer of blueberry (*Vaccinium uliginosum*), Labrador tea (*Ledum groenlandicum, L. decumbens*) and birch (*B. glandulosa, B. nana*).

A dense ground cover of sphagnum and low shrubs, along with willow thickets (*S. pulchra, S. bebbiana*), and widely spaced paper birch, black spruce, or tamarack (*Larix laricina*) may replace stands of black spruce. The recurring process of bog formation and subsequent reforestation has been described in detail by Drury (1956).

Tanana Flats, Interior Alaska

The vegetation of the Tanana Flats, a 7200 km^2 alluvial lowland lying immediately south of Fairbanks, Alaska, has been recently studied (Coady and Simpson, unpubl.) and the main features of the area will be reviewed as it typifies the lowland community. The area is bounded on the south by the rugged Alaska Range, on the north and east by the glacial Tanana River, and on the west by the glacial Wood River, and is part of the much larger Tanana-Kuskokwim physiographic province described by Wahrhaftig (1965).

Surface deposits from glacial streams flowing into the Tanana Flats on the south form a belt of broad coalescing fans that grade from coarse sand and gravel near the mountains to fine sand and silt at lower elevations. Material manteling the eastern and northern portion of the Flats has been deposited by the Tanana River (Andreasen *et al.*, 1964). Except for scattered low hills of granite, ultramafic rocks and possibly Precambrian schist, the Flats are an area of little relief (Andreasen *et al.*, 1964). The entire region is underlain by permafrost (Black, 1958; Wahrhaftig, 1965), and drainage is poor, resulting in numerous small, shallow ponds, extensive bogs and meander scars. Five major vegetation types were identified in the course of exhaustive surveys conducted in the area: herbaceous bog, heath bog, tall shrub, deciduous tree and conifer tree.

Herbaceous bogs occur primarily in the northern portion of the Flats and cover approximately 7 percent of the area. Vegetation is dominated by emergent species, and live trees and shrubs are totally absent (Table II). Stagnant or slowly flowing water depths vary seasonally, ranging from several cm to several m after spring run-off. Bog bottoms consist of a meter or more of dead and decaying vegetation, and permafrost depths are presumably well below the upper surface of organic material.

Heath bogs occupy approximately 40 percent of the land. Dominant vegetation consists of mosses and shrubs, although scattered trees and various herbs rooting on precipitous sedge hummocks are common (Table II). Both mineral soil and permafrost tables occur within a meter of the surface, although seasonal thaw may extend to greater depths in some areas. Soil moisture is high and shallow standing water is common in many areas.

Tall shrub communities occur throughout approximately 10 percent of

TABLE II

Dominant plant species in 5 vegetation types in the Tanana Flats, Alaska

Type	*Dominant species*			
	Trees	*Tall shrubs*	*Low shrubs*	*Herbs*
Herbaceous Bog	None	None	None	Gramineae *Carex* spp. *Equisetum* spp. *Eriophorum* spp. *Potentilla palustris*
Heath Bog	*Picea mariana* *Larix laricina* var. *alaskensis* *Betula papyrifera* subsp. *humilis*	*Salix bebbiana* *Salix planifolia* subsp. *pulchra* *Salix arbusculoides* *Betula papyrifera* x *glandulosa*	*Betula nana* *Salix myrtillifolia* *Salix brachyocarpa* subsp. *niphoclada* *Ledum palustre* subsp. *groenlandicum* *Vaccinium uliginosum* subsp. *alpinum*	Gramineae *Eriophorum* spp. *Equisetum* spp. *Potentilla palustris* *Pyrola* spp.
Tall Shrub	*Populus balsamifera* subsp. *balsamifera* *Betula papyrifera* subsp. *humilis* *Picea mariana* *Picea glauca*	*Salix bebbiana* *Salix monticola* *Salix arbusculoides* *Alnus incana subsp. tenuifolia* *Alnus crispa* subsp. *crispa*	*Rosa acicularis* *Potentilla fruticosa* *Ledum palustre* subsp. *groenlandicum* *Vaccinium uliginosum* subsp. *alpinum* *Viburnum edule*	*Equisetum* spp. Gramineae *Epilobium angustifolium* subsp. *angustifolium* *Pyrola* spp. *Cornus canadensis*
Deciduous	*Betula papyrifera* subsp. *humilis* *Populus tremuloides* *Populus balsamifera* subsp. *balsamifera*	*Alnus crispa* subsp. *crispa* *Alnus incana* subsp. *tenuifolia* *Salix alaxensis* *Salix novae-angliae*	*Rosa acicularis* *Viburnum edule* *Ribes triste* *Ribes hudsonianum*	*Equisetum* spp. Gramineae *Epilobium angustifolium* subsp. *angustifolium* *Pyrola secunda* *Trientalis europea* subsp. *arctica*
Coniferous	*Picea glauca* *Picea mariana* *Larix laricina* var. *alaxensis*	*Alnus crispa* subsp. *crispa* *Alnus incana* subsp. *tenuifolia* *Salix alaxensis* *Salix bebbiana* *Salix arbusculoides*	*Rosa acicularis* *Vaccinium vitis-idaea* subsp. *minus* *Linnaea borealis* *Arctostaphylos uva-ursi* *Ribes* spp.	*Equisetum* spp. *Cornus canadensis* *Pyrola* spp. *Trientalis europea* subsp. *arctica* *Mertensia paniculata*

the Flats but are most frequent along rivers, streams, sloughs and along margins of ponds and meander scars (Fig. 4). Recently burned areas may also support tall shrub communities. Vegetation ranges from pure to mixed stands of willow and alder with a dense understory of mosses, herbs, and low shrubs in poorly drained sites (Table II). Exposed mineral soil, low moisture content, and absence of permafrost are common on recent alluvial deposits, while a thick organic layer, impeded drainage, and high permafrost tables are found in other areas.

Discontinuous pure or mixed stands of paper birch, aspen, or balsam poplar occur on approximately 8 percent of the Flats, particularly on slightly elevated land and on coarse river alluvium. Understory vegetation ranges from a dense herbaceous cover in cottonwood (*Populus balsamifera*) stands to mixed herbs and low shrubs in aspen and birch stands. Scattered willows and alders are common among cottonwood communities (Table II). Well-drained mineral soil lies close to the surface and permafrost tables are deep or nonexistent.

Scattered conifer stands in the western portion and extensive low, dense black spruce and occasional tamarack forests in the southern area cover approximately 35 percent of the Flats. Mature white spruce forests with a ground vegetation of low shrubs and mosses are common on elevated areas

Figure 4. The Tanana Flats, a typical Interior lowland area supports diverse vegetation types that are important to moose as calving and wintering habitats. Note the tall shrub community along the river margin in the center. J. Coady photo.

near streams. Black spruce forests underlain by a dense mat of moss, herbs, and low shrubs grow in poorly drained areas (Table II). Soil organic layer, moisture content, and permafrost tables range from low in young white spruce stands to high in black spruce and tamarack stands.

MOOSE USE

The seasonal importance to moose of local flatlands south of the Brooks Range is variable. Lowland areas, by virtue of their abundant herbaceous vegetation, are generally important summer ranges for moose of all sex and age groups (Fig. 5). Furthermore, interspersion of escape cover with prime feeding habitat create favorable calving areas for large numbers of moose (Rausch and Bratlie, 1965; Bishop, 1969).

In the Tanana Flats moose commonly feed in herbaceous bogs from spring thaw to late summer. However, greatest use of this habitat appears to be during early to mid-summer. During late summer moose may feed more frequently on herbaceous and woody browse in heath bog and tall shrub communities.

Generally, the Tanana Flats do not seem to be good winter moose range, and there is large scale emigration of animals during fall and early winter. Although several species of willows are widely scattered throughout portions of the Flats, most plants are old and extremely decadent. Apparently, changes in local edaphic factors (e.g. soil temperature, moisture, and organic content) due to the dynamic nature of bog formation frequently create substrates unfavorable to continued growth of tall

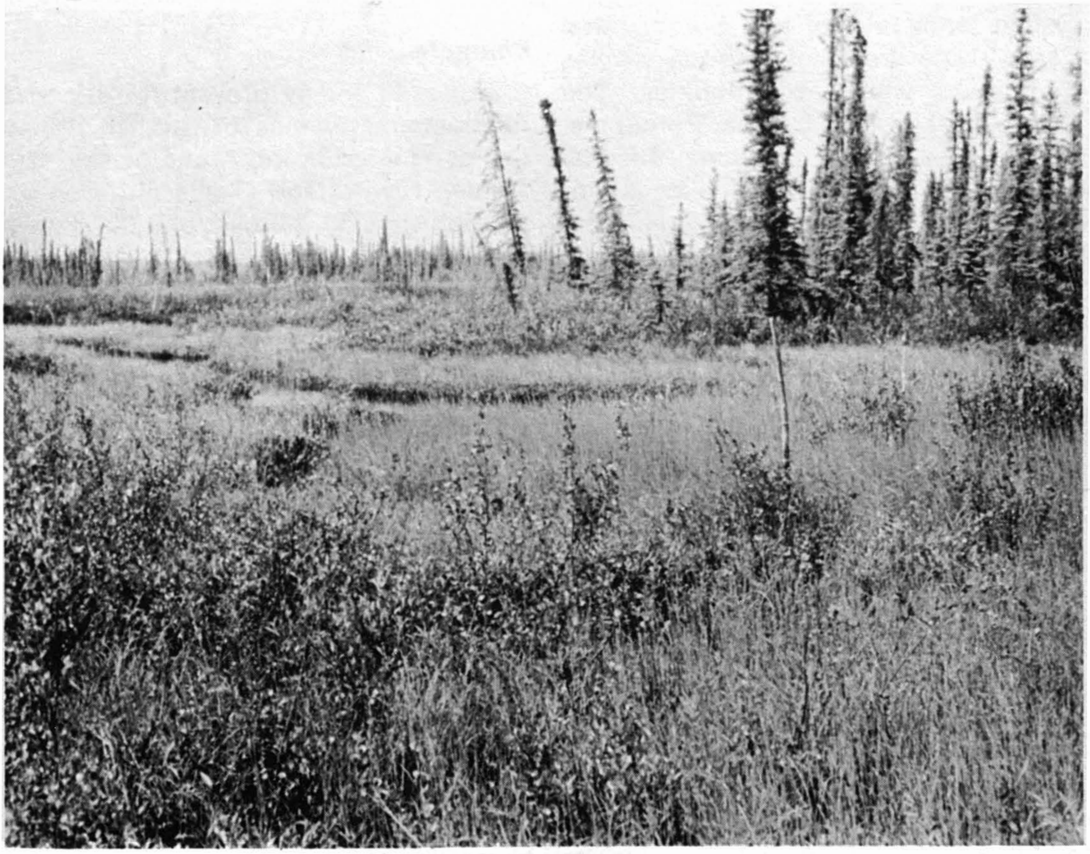

Figure 5. The generally abundant herbaceous vegetation of the lowland areas increases their importance as summer habitat for moose. Tanana Flats, J. Coady photo.

shrub and other sub-climax communities. However, vigorous growth of shrubs occurs in burned areas and on well drained recent deposits along some streams, and these areas do support modest numbers of moose during winter.

Glacial and riparian seral communities

These predominately willow communities are key winter ranges in much of Alaska and are the only habitat consistently occupied by moose on the North Slope and Arctic coastal plain. They differ from fire-created seral communities in that many are constantly renewed by erosion, flooding and/or ice scouring. Thus they provide relatively permanent (if dynamic) moose range.

Most large Interior and Southcentral Alaska rivers create many square miles of riparian willow communities. The Yukon, Kuskokwim, Tanana, Porcupine, Kobuk, Koyukuk, Chandalar, Susitna, Copper and scores of smaller drainages are all lined with these communities. Arctic rivers, notably the Colville, Chandler, Anaktuvuk, Sagavanirktok and Canning, likewise have created riparian willow stands which have allowed moose to disperse to the Arctic Ocean. Glacially scoured and still active deltas and outwash plains such as at Yakutat, Redoubt Bay and Cordova support similar communities (cf: Cooper, 1942; Crocker and Dickson, 1957; Crow, 1968) and sustain substantial moose populations.

Throughout Alaska, glacial-riparian stands occur on predominately coarse gravel substrate on riverine and glacial flood plains. *Salix alaxensis* is the dominant shrub species, and is associated with several willow species, most notably *S. arbusculoides*, and occasionally with *Alnus crispa* or *Populus balsamifera* (in Interior and Southcentral Alaska). Herbs and grasses form the understory. Adjoining these communities on more poorly drained soils further from the river in tundra areas are *Salix pulchra, S. glauca, S. lanata* dominated stands, similar to those described as upland shrub types. Hanson (1951) describes such communities from the Seward Peninsula, and we have studied them on the Arctic Coastal Plain and in the Interior. Willow heights in these stands vary from 1-7 m, depending upon the site (Fig. 6).

In the Interior, riparian willow stands commonly grade into Balsam poplar and white spruce communities (Viereck, 1970a); whereas, in tundra areas willow stands typically adjoin terraced heath or dwarf shrub communities (Spetzman, 1959).

Characteristics

Tables III and IV present floristic and other characteristics of riparian willow stands in Interior and Arctic Alaska. The Tanana River stand (Table III) is on an alluvial island in a broad, braided glacial river, and is representative of these dense stands along all major Interior rivers which may flood and ice-scour annually. The Chena River stand (Table IV) is on a gravel bank on the upper reaches of a smaller, clear stream, and represents a less extreme situation where flooding is less persistent.

On the eastern Arctic north slope feltleaf (*S. alaxensis*) communities are found on coarse gravel bars of clear braided streams as they flow onto the Arctic coastal plain. These streams normally flood only in spring, and many produce considerable *aufeis* in most years. Bliss and Cantlon (1957) describe intergrading young and decadent feltleaf willow communities occurring between gravel bar herb communities and terrace communities. The communities differed chiefly in height and vigor of the dominant *S. alaxensis* plants (1-1.6m in young communities; up to 7m, with many dead stems, in decadent communities) and a shift from herb (typically *Lupinus arcticus* and *Deschampsia caespitosa*) to moss understory.

TABLE III

Shrub characteristics of a riparian willow community on an island in the Tanana River, Interior, Alaska (64° 47'N 147° 45'W; elevation 140m). Modified from Milke, 1969

Species	*$\bar{X}$ height (cm)*	*Stems/ hectare*	*Oven-dried wt. "available browse"* (g/hectare)*
Salix alaxensis	131.3	1,497	36,850
S. lasiandra	52.5	499	—
S. interior	69.3	8,485	19,980
S. myrtillifolia	77.3	3,244	15,100
S. niphoclada	70.0	14,725	131,870
Totals		28,450	203,800

* All twigs above minimum browsed height were clipped at mean browsed diameter for the species.

MOOSE USE

Riparian willow communities are the year-round habitats of moose at the edges of their range, (in the Arctic, for example) and are important winter habitats wherever they occur (see Fig. 6). In addition, they serve as calving and summering areas for moose in Interior Alaska. Since these stands are relatively permanent features, they serve as reservoirs from which moose populations can expand into newly-burned area and as avenues for dispersal into new range.

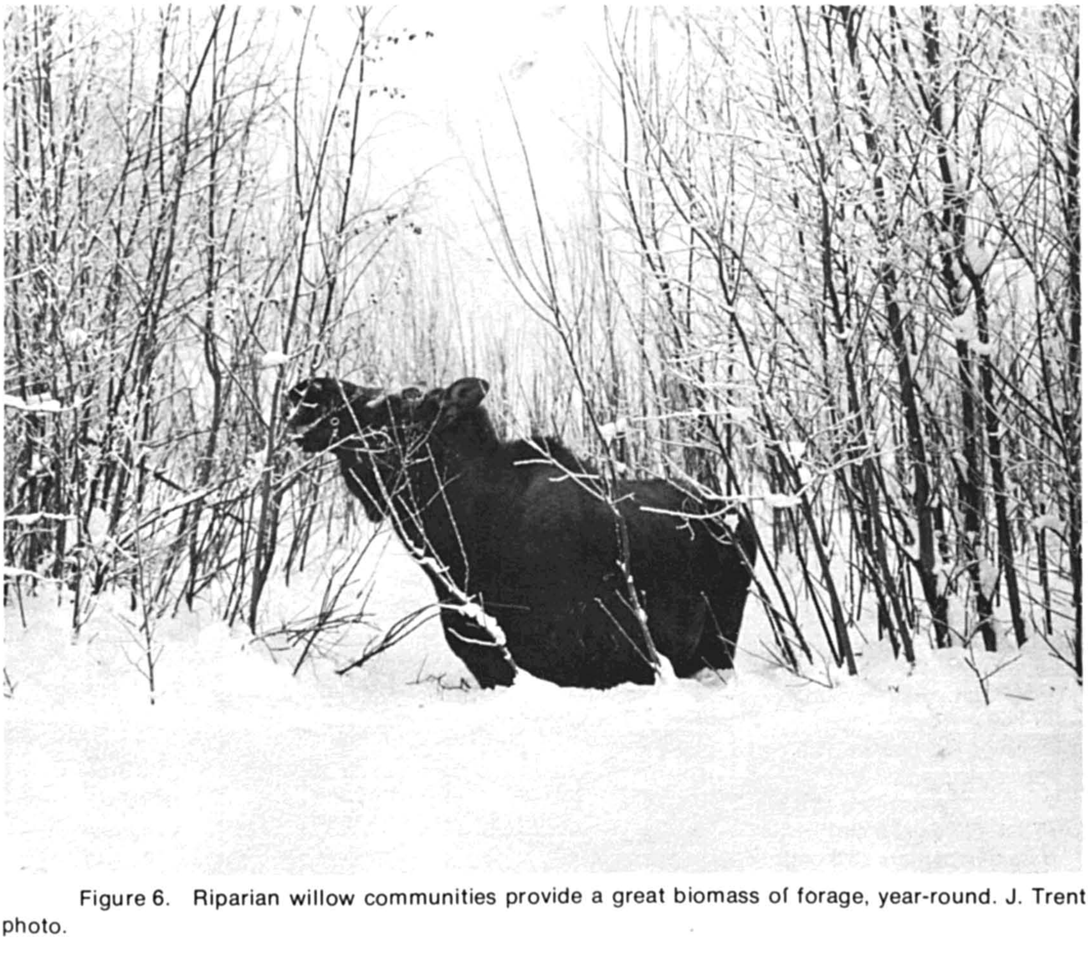

Figure 6. Riparian willow communities provide a great biomass of forage, year-round. J. Trent photo.

Movement into riparian willow habitats from upland and lowland summer ranges usually occurs in November or later, apparently depending upon snow characteristics. During harsh winters, river "bottoms" become yarding areas for high densities of moose. When deep snow persists, overbrowsing may occur, and these areas have been the scenes of the most spectacular moose die-offs recorded in Alaska. Where extensive burned areas are lacking, riparian communities are the habitat of last resort for wintering moose. Their extent and vigor ultimately determine at what level moose populations will persist in the area.

Fire-created seral communities

Fire-mediated habitats are the most ephemeral of Alaskan moose habitats; yet, they support the greatest population explosions and among the greatest densities of moose in the state. The earliest specific publications concerning moose management in Alaska (Spencer and Chatelain, 1953; Leopold and Darling, 1953a and 1953b; Chatelain, 1951, 1952) correctly stressed the correlation between dense moose populations and forest fires.

The ecological effects of fires in Alaska are extremely complex (cf. Lutz, 1956; Slaughter *et al.*, 1971; Viereck,

TABLE IV

Characteristics of a riparian willow stand on the Chena River, Interior Alaska (approx. 64°55'N 147°W; elevation 200m). Modified from Viereck, 1970a

Species	*Frequency of Occurrence (%)*	*$\bar{X}$ Cover (%)*	*Stems/hectare*
FORBS AND GRASSES			
Galium boreale	40	3	
Poa alpina	40	2	
Epilobium angustifolium	40	2	
Artemisia tilesii	40	1	
Agrostis scabra	20	1	
Agropyron macrourum	10	1	
Stellaria laeta	10	1	
Wilkelmsia physodes	10	1	
Arabis lyrata	10	1	
Mertensia sp.	10	1	
Calamagrostis canadensis	10	1	
MOSSES AND LICHENS	10-80	21	
SHRUBS			
Salix alaxensis	60	15	1,220
S. pseudocordata	10	1	40
Rosa acicularis	40	3	
Alnus incana	10	6	540
Viburnum edule	10	2	
Rubus idaeus	10	1	
Populus balsamifera (3.8 cm)			420
Picea glauca (3.8 cm)			40
Populus balsamifera (3.8 cm)			7,280
Picea glauca (3.8 cm)			10,660
Betula papyrifera (3.8 cm)			540
TOTAL STEMS/HECTARE (SHRUBS)			20,740

1973) and cannot be considered in detail here. Lutz (1956) presented a diagrammatic representation of normal courses of post-fire succession in Alaskan taiga. Viereck (1973) modified the chart and we reproduce his chart here (Fig. 7). The course of succession and the seral community's value to moose are determined by a multitude of site (soils, temperature, moisture, slope and exposure), fire (severity, mode of travel, duration) and miscellaneous (natural reseeding sources, size of openings created) factors. The general successional courses producing maximum benefits to moose populations are those involving paper birch-willow-aspen shrub thickets.

Fires have probably always been common in Alaska, but have increased in frequency and area burned since modern settlement (Hardy and Franks, 1963). Viereck (1973) maintains there are very few Interior forests that survive burning long enough to reach what can be considered climax stage. Barney (1971) suggests that 600,000 to 1,000,000 ha burned annually from 1900-1940. Even with modern fire control, a mean of approximately 400,000 ha annually have burned between 1940-1969 (Barney, 1971). The general trend in the past three decades has been toward an increase in numbers of fires (1,138 in the 1940's, 2,583 in the 1950's and 2,380 in the 1960's in Interior Alaska) but a decrease in the total area burned (5,018,000 ha in the 1940's, 4,330,000 ha in the 1950's, 2,590,000 ha in the 1960's) and the area burned per fire. Increased fire control capabilities have thus perhaps decreased the benefits of civilization to moose.

CHARACTERISTICS

Several factors determine the impact a fire-created successional community will have on moose populations: 1) species composition, 2) size of burn and per-area standing biomass and production of available browse, 3) rate of attaining a) above snow and b) above

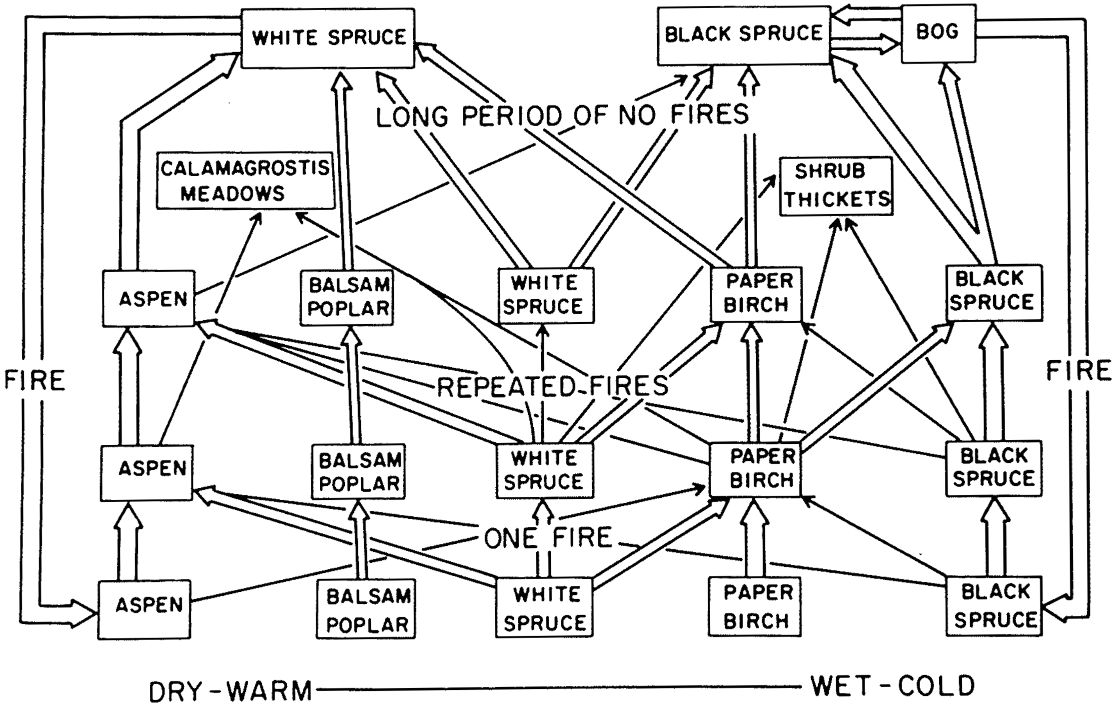

Figure 7. Usual successional sequences following fires in Alaska. From Viereck, ms.

moose-reach heights, and 4) extent and diversity of the resulting pattern of mature and seral communities.

Composition

Burned areas in Alaska are frequently reinvaded by the same species present before the fire (Fig. 7). This results from re-sprouting or growth of root suckers (Spencer and Hakala, 1964; Viereck, 1973). Stands are often nearly monotypic in shrub species (cf. Table V), with birch or aspen (on the warmest, driest sites) predominating. Spruce encroachment occurs usually slowly (Viereck, 1973) in the Interior but sometimes almost immediately (e.g.: on some stands on the Kenai Peninsula). Although willows are often among the first recolonizers, they generally do not achieve great numbers or production, perhaps because of consistent utilization by moose. Aspen may be similarly affected. Spencer and Hakala (1964) described how moose and plant competition had altered the proportion of aspen in the 1947 Kenai burn. It apparently decreased from 96.5 percent of the standing shrub biomass in 1952 (Spencer and Chatelain, 1953) to less than one percent in 1967 (Table V). Wet lowland and permafrost sites are usually less thoroughly burned (Viereck, 1973) and thus may rapidly recover by vegetative reproduction to a composition similar to that existing before the fire.

TABLE V

Characteristics of shrub standing crop and production on Kenai Burn twenty years after the 1947 fire. Modified from Seemel, 1969

Species	*Community*	*Stems/hectare*	*Annual production*[1] *g/hectare*
Betula papyrifera	Dense Birch	80,046	479,348
	Medium Birch	47,221	315,987
	Thin Birch	34,381	249,316
	Spruce-birch	19,296	118,118
	Spruce Regrowth	6,775	35,226
Populus tremuloides	Dense Birch	237	202
	Medium Birch	339	348
	Thin Birch	541	875
	Spruce-birch	200	224
	Spruce Regrowth	168	224
Viburnum edule	Dense Birch	114	101
	Spruce-birch	89	90
Salix spp.	Dense Birch	1,641	9,233
	Medium Birch	1,196	6,193
	Thin Birch	692	3,747
	Spruce-birch	469	2,255
	Spruce Regrowth	652	2,109
Alnus crispa	Thin Birch	319	718
Betula nana	Spruce Regrowth	8,772	9,008
TOTALS:	Dense Birch	82,038	488,884
	Medium Birch	48,756	322,528
	Thin Birch	35,933	254,656
	Spruce-birch	20,054	120,687
	Spruce Regrowth	16,367	46,567

[1] Terminal twig growth at all heights.

Willows, blueberry and dwarf birch tend to be more numerous in these stands.

The exact composition of species recolonizing a burn may depend upon the timing of the fire relative to plant phenology (Viereck, ms). Willow species produce seeds that are viable for only a matter of weeks, and various species produce seeds at different times of year. Further, some species (paper birch, white spruce) produce "bumper" seed crops only once in several years, (Viereck, ms) and the year the burn occurs might thus affect species composition of the resulting seral community.

There is little detailed information directly relating species composition of burn regrowth to subsequent moose population densities. However, observations suggest that the higher the proportion of first, willow, and second, birch shrubs produced, the greater the moose densities that will result during early years of succession.

Production

Biomass production of shrubs can be prodigious following burns in Alaska (Fig. 8). Seemel's (1969) studies 21 years after the 1947 Kenai burn indicate annual production of nearly 500 kg/ha in the densest shrub *B. papyrifera* stands (Table V). Standing crop is also large, with 82,000 shrub stems/ha estimated in the densest stands. Both production and standing crop, as well as composition, vary considerably between individual stands (Table V), and thus the relative proportions of various communi-

Figure 8. Dense shrubs re-invading burns in Interior Alaska create large amounts of forage and excellent fall-winter ranges for moose. J. Coady photo.

ties occurring in a burn also influence moose numbers.

Biomass of available browse is seldom a limiting factor to moose densities in large burns in Alaska. In the 1947 Kenai burn of 127,600 ha, Seemel (1969) estimated that more than 8 moose/km^2 in a 2.6 km^2 enclosure used only 18.3–22.8 percent of the estimated annual shrub production, depending upon community. Spencer and Chatelain (1953) in contrast, had estimated that utilization by only 1.7 moose per km^2 on the same burn in 1952 was 45 percent of the annual production of aspen, then virtually the only shrub present. Since then, plant production has exceeded moose production in relative terms, even though moose densities achieved the highest level ever recorded. Spencer and Hakala (1964) suggested that adequate densities of moose might retard succession in seral shrub habitats under certain conditions. We feel that these densities are seldom reached and never persist. Although moose may alter relative abundance of species in seral communities, we know of no instance where they have retarded succession over a large burned area. In the case of the Kenai burn, moose populations appeared to peak at the very high level of 4-6 moose/km^2 in the most productive habitat, at about the same time Seemel made his estimates. Within four 2.6 km^2 enclosures, populations remained relatively static at 4.6–5.4 moose/km^2 (before calving) over a three-year period, and utilization probably did not exceed Seemel's estimate (LeResche and Davis, 1971).

Isolated smaller burns serving as winter concentration areas for moose are sometimes retarded in succession and, on occasion, "over-utilized" by immigrant moose. Succession on the 1320 ha 1959 Kenai Lake burn has been effectively retarded by wintering moose, with most shrubs being browsed to snowline annually (Fig. 9). This burn is unusual in that it is situated in the midst of nearly-mature range that wintered many moose until the late 1950's, and is about 20 km from the nearest edge of the larger 1947 Kenai burn. Because fires are frequent throughout most of Alaska, small burns are often near other burns of various ages, and are therefore not subjected to intensive use by large concentrations of moose from a vast area. Furthermore, small isolated burns do not produce widespread moose population explosions sufficient to alter succession. Thus, in most cases, post-burn succession in large burned areas seems to proceed at a rate little different from what it would in the absence of moose. The course of succession may well be altered, however.

Rate of growth

The sooner recolonizing shrubs achieve a height that makes them available to moose during winter, the sooner moose population explosions occur. Conversely, the more rapidly shrubs mature into trees, the shorter is the productive life of the burn. Spencer and Chatelain (1953) estimated that the 1947 Kenai burn produced significant browse by 1950, and that by 1953, moose had increased four-fold. Moose densities peaked on the burn about 1967-1969, and may have experienced the first stages of a decline in the winter of 1971-1972; however, they remain very high today.

Rates of growth differ between burns and within large burns, depending upon species present and site and climatological variables. Within the 1947 Kenai burn, heights of *B. papyrifera* plants in adjacent stands ranged from 1 m to almost 7 m in 1970. We do not know whether some sites were recolonized by paper birch later than others or whether growth rates alone account for the differences.

Hakala *et al.* (1971) predicted that browse would "continue to improve" on areas burned on the Kenai Peninsula (1969) for 23-25 years after the burn, as has been the case with the 1947 Kenai burn area. Moose densities could be expected to remain high for this period and then decline as happened after a series of fires in the 1880's and 1920's (Spencer and Hakala, 1964). The limited information available, then, suggests that the "useful life" of a burn as moose habitat in Alaska is usually less than 50 years, and that moose densities peak 20-25 years after the burn.

Shape of burn, diversity and "edge effect"

The degree of interspersion of communities, or amount of "edge effect", produced by a fire is very important in determining the fire's effect on moose populations. Great discontinuity of burning is desirable because it provides, 1) cover (mature) habitat close to feeding habitat, 2) increased variety of alternate forage species and 3) staggered maturation rates of individual stands.

The forest edge ecotone allows moose both to invade a heterogeneous burn sooner than a large homogeneous burn and to achieve higher year-round densities. The distance a moose will continually move from cover into open feeding areas likely varies with season, age, sex, reproductive status, snow characteristics and a multitude of other factors. It appears certain, however, that increased mature forest edge will hasten establishment of moose in a new burn. The rate of moose increase on the Ke-

Figure 9. Moose have retarded succession in the 1320 ha Kenai Lake burn, now 14 years old. R. Bishop photo.

nai 1947 burn, described by Spencer and Chatelain (1953) as 400 percent in 5 years, was probably near the maximum attainable because of the tremendous amount of edge created. Immigration from nearby areas was probably not significant (LeResche, 1974).

Once the moose population is established, small stands of mature timber (30-40m tall birch, white spruce and aspen in the 1947 Kenai burn) provide year-round escape cover and winter refugia from deep snow. In addition, these stands provide alternate food sources that may be of considerable importance to the maintenance of high moose densities. LeResche and Davis (1973) showed that *Vaccinium vitis-idaea* plants were important to moose in winter and remained available more consistently in mature stands than in adjacent seral stands on the Kenai.

Shrub-forest ecotones are not the only important edges created by fires. Shrub-sedge and shrub-aquatic ecotones are also important at various times of year. Brush bordering summer feeding bogs, for example, can be excellent cover habitat for young calves (LeResche, 1966). Dense shrubs bordering small, drying potholes is preferred habitat for adults in late fall, when they dig craters in snow to feed on cured sedge leaves.

The optimum amount of edge and/or the optimum size and shape of individual burned stands in Alaska is difficult to determine because moose densities depend upon so many variables. The 1947 Kenai burn, however, appears to represent, if not the ideal, at least the most productive large area of moose habitat known to us. Densities of moose exceeding 4/km² have been achieved over most of the burn (vs densities of ca 0.08/km²) in similar unburned areas (Spencer and Chatelain, 1953) through a combination of high forage production, generally mild winters, abundant alternate foods (especially *V. vitis-idaea*), edge effect, and adjoining upland ranges.

The fire burned 127,600 ha of approximately 260,000 ha, and has regenerated into several paper birch and birch-spruce communities (Table V). The entire burn has not been analyzed, but detailed type maps have been constructed of the reasonably-representative 1024 ha enclosed by the Kenai Moose Research Center[1] enclosures.

A map of 254 ha of this mixed habitat, prepared 20 years after the burn, (Fig. 10) was analyzed for sizes of individual stands and amount of ecotone between each of the 11 communities distinguished (Tables VI and VII). A "stand" was defined as a contiguous area of one community, regardless of shape, and ecotone was simply taken as the length of mapped margin between stands.

The 254 ha contains 624 individual stands ranging in size from .02 ha to 18.4 ha (Table VI). Mean stand size is 0.41 ha, and 86 percent of all stands are less than 0.5 ha in area; only 8 percent of the stands are larger than 1 ha, and only 2 percent larger than 5 ha. Remnant mature stands comprise 118 ha, or 46 percent of the area. This mature forest is extremely segmented, comprising 411 stands distributed throughout the area.

The large number of stands and their irregular shapes have produced tremendous amounts of ecotone (Table VII) — 112 km in the 2.5 km² area. Mature communities have about 99 km of "edge", sharing 59 km of this with the various seral shrub communities. Shrub communities themselves are surrounded by about 103 km of ecotone, border-

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[1] A joint project of Alaska Department of Fish and Game and U.S. Fish and Wildlife Service.

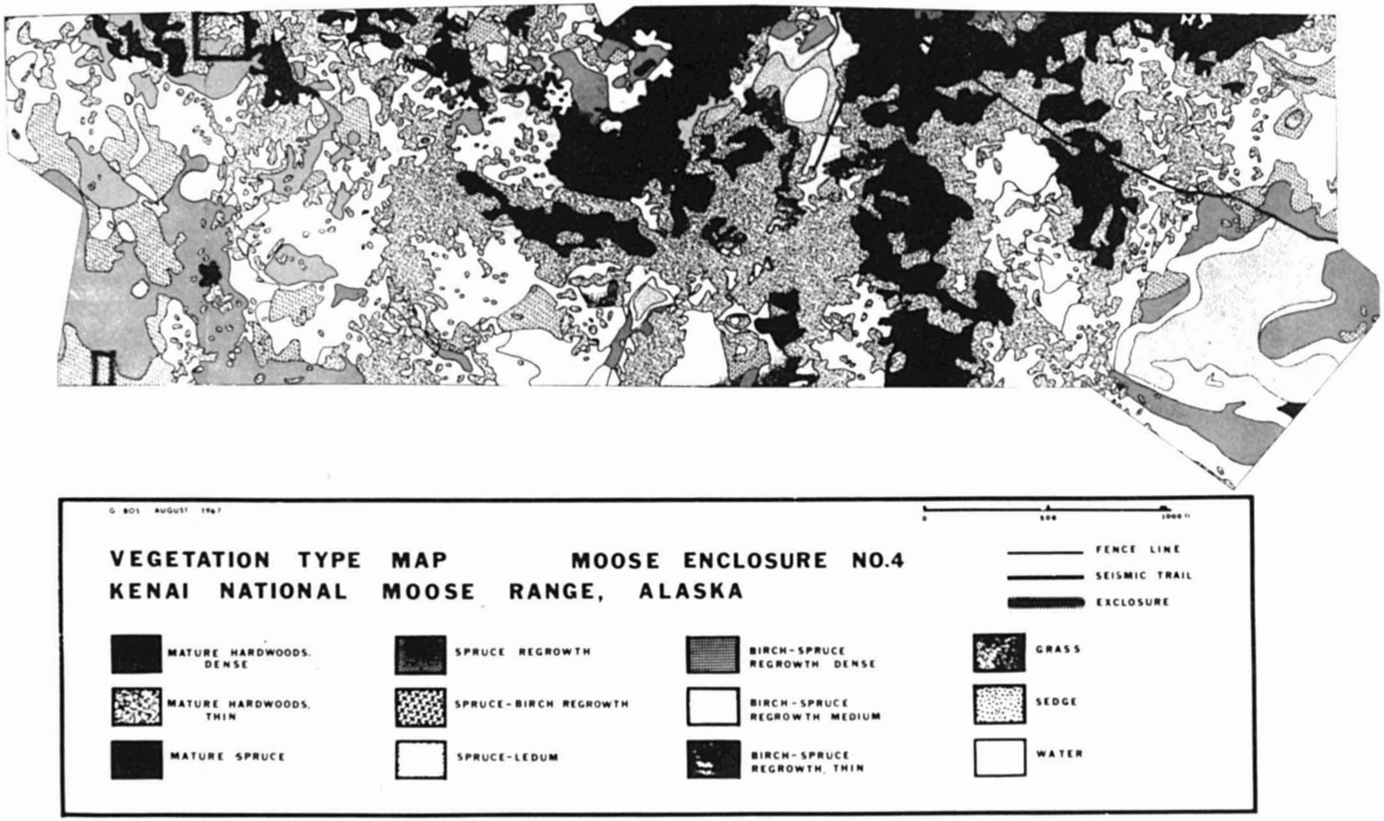

Figure 10. Vegetation type-map of 2.5 km^2 area of the 1947 Kenai Alaska burn, mapped in 1967. This area contains 624 separate stands and 112 km of ecotone.

TABLE VI

Sizes of 624 stands of 11 communities in 254 ha of the 1947 Kenai, Alaska burn, mapped in 1967, Kenai Moose Research Center, Pen 4

Community	*Number of stands*	*Total area (ha)*	$\bar{X}$ *stand area (ha)*	*Range ha/stand*	*No. of stands of area*					
					<0.5 ha	*.5-1.0 ha*	*1.1-2.0 ha*	*2.1-5 ha*	*5-10 ha*	*>10 ha*
Dense Mature Hardwoods	22	43.07	1.96	.05-12.9	9	5	2	3	2	1
Thin Mature Hardwoods	383	70.69	0.18	.02-18.4	368	7	4	1	1	2
Mature Spruce	6	4.54	0.76	.02- 3.9	5				1	
Spruce Regrowth	10	19.29	1.93	.14-11.6	4	2	2	1		1
Spruce-Birch Regrowth	33	17.83	0.54	.02- 2.3	22	5	5	1		
Spruce-Ledum	6	5.39	0.90	.23- 2.5	3	1	1	1		
Dense Shrub Birch	23	7.30	0.32	.21- 1.3	20	1	2			
Medium Shrub Birch	40	41.16	1.04	.03- 8.9	24	7	4	2	3	
Thin Shrub Birch	77	31.28	0.41	.02- 6.2	62	7	5	2	1	
Grass	19	1.82	0.10	.02- 0.4	19					
Sedge	5	12.05	2.41	.07-10.2	3	1	0			1
Totals	624	254.42	0.41	.02-18.4	539	36	25	11	8	5
Percent of total stands					86	6	4	2	1	1

ing on mature forest and on other seral communities.

This 2.5 km^2 area by no means represents an extreme case, but rather is a fair sampling of the entire 260 km^2 area affected by the burn. By extrapolation, then, the 1947 Kenai burn probably produced over 60,000 separate stands having more than 11,000 km of ecotone and 128,000 ha of new shrub communities. It is not surprising that moose densities achieved such a high level as a result of this fire.

MOOSE USE

Seral burn habitats are extremely important wintering ranges once growth is sufficient to provide available browse above the snow. Some burns (the 1947 Kenai burn, for example) receive an influx of moose from upland ranges in early winter, and support very dense wintering concentrations (on the Kenai burn, winter density sometimes reaches 6.0 animals per km^2). Others (in the upper Little Chena drainage near Fairbanks, for example) support moose during late summer and fall, but may be virtually deserted when moose move down into denser forests and riparian stands in November and December. The most diversified burns, such as the 1947 Kenai burn also support significant densities of moose during calving, summer and rutting periods and have relatively high resident populations throughout the year.

Anthropogenic habitats and effects of development

The greatest part of man-caused moose habitat in Alaska has been, and continues to be created through accidental fires. From 1940 through 1969, 70 percent of the fires in Alaska were man-caused, and these fires accounted for 22 percent of the area burned (Viereck, 1973). This amounts to a mean of approximately 88,000 ha of largely seral brush moose habitat created annually by man in the last three decades. Other human activities, by comparison, today have little effect on available moose habitat in Alaska.

Two short-lived activities of man, mining and homesteading, have been of some importance to moose in the last century. Both increased man-caused fires, and both created habitat by physical disruption of forests. Placer mining from 1900 to as recently as 1965, although it destroyed some riparian habitat, created a much greater area of dense, productive seral shrub communities along stream courses in many parts of the Interior. This disturbance had an especially great effect on moose distribution because it occurred in many areas where there were low densities of moose before mining. The Kuskokwim Mountains and Yukon-Tanana highlands are two regions where mining probably contributed significantly to increased moose densities. Dredged "tailing" piles near Fairbanks still support stands of birch and willow shrubs important to wintering moose.

Several thousand hectares of maturing spruce forest have recently been cleared mechanically on the Kenai National Moose Range. This program has resulted in increased moose winter range, and may be expanded (Hakala *et al.*, 1971).

Most land clearing in Alaska today is for road and building construction and oil exploration. Seismological trails have been bulldozed through many forests of the state and provide some shrub-forest ecotone. Road and building construction, similarly, create some new brush communities. Depending upon their location, they may also remove productive moose habitat.

Perhaps the greatest effect of these activities on moose is to increase ac-

TABLE VII

Amount of ecotone (in meters) between 11 plant communities in 254 ha of the Kenai, Alaska (1947) burn mapped in 1967, Kenai Moose Research Center, Pen 4.

Community	*Dense mature Hardwoods*	*Thin mature Hardwoods*	*Mature Spruce*	*Spruce Regrowth*	*Spruce-Birch Regrowth*	*Spruce Ledum*	*Dense shrub Birch*	*Medium shrub Birch*	*Thin shrub Birch*	*Grass*	*Sedge*	*Walter*
Dense Mature Hardwoods		17,581	325	206	356		711	1,728	2,642	51		
Thin Mature Hardwoods			305	2,541	2,795		3,150	22,764	22,967	508	178	
Mature Spruce				—	—	76	203	1,016	406	—	76	
Spruce Regrowth					3,455	1,524	305	457	1,524	661	356	
Spruce-Birch Regrowth						203	1,067	4,522	4,472	813	102	
Spruce-Ledum							—	102	280	—	1,931	
Dense Shrub Birch								3,303	1,016	—	—	
Medium Shrub Birch									3,303	457	508	
Thin Shrub Birch										457	102	
Grass											—	152
Sedge												356
Total edge-m	23,600	72,789	2,407	11,029	17,785	4,116	9,755	38,167	37,169	3,099	3,609	508
Total area-h	43.1	70.7	4.5	19.3	17.8	5.4	7.3	41.2	31.3	1.8	12.1	
km edge/km²	54.9	103.0	53.5	57.2	99.9	76.2	133.6	92.6	118.8	172.2	29.8	

Total edge = $\frac{224{,}033\ \text{m}}{2^{*}}$ = 112 km/2.54 km^2 = 44.1 km/km^2

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* Divided by a factor of two because two stands share each meter of edge.

cidental mortality by attracting them to areas occupied by motor vehicles, trains, and occasionally aircraft. In some years, moose mortalities from such collisions may exceed 750-1000 animals throughout the state.

With these exceptions, developmental activities have as yet had little effect on Alaska moose distribution and habitat. The proposed Prudhoe Bay — Valdez oil pipeline and a possible Prudhoe Bay — Mackenzie River gas pipeline would both pass through forested areas. Their effects on habitat will likely be minimal due to the small area actually disturbed, but if they restrict free passage of moose they could significantly affect moose movements and distribution.

Other habitats

The northern boreal forests in Alaska, referred to by the general term "taiga," consist primarily of low elevation open-growing spruce forests, occasional stands of well developed spruce and hardwoods, and frequent tracts of treeless or sparsely treed bogs. On south facing slopes and well drained sites the forest consists of white spruce and hardwood stands of mature aspen and paper birch; on cool north facing slopes and poorly drained lowlands climax vegetation is generally black spruce and bogs.

Most of forested Alaska north of the Gulf of Alaska consists of a matrix of taiga communities within which most other habitats discussed earlier have developed, each due to a particular set of special circumstances. Because the taiga is so extensive, it supports substantial numbers of moose even though densities are very low. In many areas, moose densities may not exceed one moose each 5-10 km^2, but some animals are generally present. The most important taiga habitats, in addition to the bog communities discussed above, are those bordering upon riparian or upland shrub habitats or interspersed with seral fire-created communities. These areas provide cover and some food for moose spending most of the year on more preferred habitats.

Acknowledgments

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THE MOOSE IN NORTH-EAST SIBERIA

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Résumé

L'orignal (*Alces alces*) occupe de nouveau une vaste aire de distribution à l'est du fleuve Lena, en Sibérie après avoir presque disparu de ce territoire à la fin du siècle dernier. La population totale est estimée à quelques 22,000 ou 24,000 individus tandis que la densité varie de 2.3 à 13.3 animaux par 100 km^2. Dans des habitats particulièrement favorables comme par exemple les brûlis ou les vallées de rivière dominées par une végétation arbustive, la densité peut atteindre 62 animaux par 100 km^2. La sous-espèce *A. a. gigas* occupe toute la Sibérie à partir du fleuve Indigirka, vers l'est. Les animaux de ces populations incorporent une proportion relativement élevée de plantes herbacées dans leur diète. La productivité du cheptel est passablement élevée puisque la proportion de jeunes âgés d'un an atteint environ quinze pour cent de la population. L'auteur est d'avis que le territoire peut supporter une densité plus élevée d'orignaux et les populations y sont en expansion numérique.

Abstract

Moose (*Alces alces*) are now widely distributed in Siberia east of the Lena River, following a period of scarcity at the end of the last century. The total population is probably between 22 and 24 thousand, with densities ranging from 2.3 to 13.3 per 100 km^2. Moose are concentrated in suitable habitat such as burns and riparian brush, where densities may reach 62 per 100 km^2. The subspecies *A. a. gigas* is present in the Indigirka Basin and eastward. These moose have adapted their food habits to include a relatively high proportion of herbaceous plants. Herd productivity is relatively high, with the net increment of yearlings amounting to about 15 percent. It is believed that the region can support a larger moose population, and numbers continue to increase.

Introduction

Moose live throughout the forest zone of northeast Siberia, occupying mainly that part of the forest-tundra biome corresponding with the distributional limits of the Dahurian larch (*Larix dahurica*). In summer, they also penetrate into the tundra following riparian brush along river valleys — sometimes up to the shores of polar seas (Fig. 1). Long-term range fluctuations are known, especially in the extreme north-east. At the end of the XVIIIth and the beginning of the XIXth centuries, moose inhabited river valleys up to the mouth of the Kolyma River, to the watershed between the Malyi Anyui and Tchaun rivers, and to the middle reaches of Anadyr and Penzhina rivers. In extreme cases, some animals even reached Cape Schmidt (Nasimovitch, 1955) and the mouth of the Anadyr (Portenko, 1941). According to Ditmar (1901), moose were occasionally met with, even in Kamtchatka, but it is unlikely that they lived there constantly during historic times. During the first half of the XIXth century, moose range began to decrease and at the end of the century it reached a nadir. At the beginning of the XXth century, moose began to expand their range, which during the past 70 to 80 years has reached its present limits (Fig. 1). In the north-east of Yakutia such fluctuations were not recorded. Moose penetrate there into mountains up to the timberline, and into the alpine tundra beyond on occasion.

Habitats

In north-east Siberia, both in the "snowy" and "snowless" seasons, moose mainly occur in the willow thickets along river valleys (Table I), in burns of different ages, on river terraces and gentle slopes, and in young larch (*Larix* spp.) stands with those shrubs like willow (*Salix* spp.) and birch (*Betula*

TABLE I

Proportions of observations of moose (from aircraft) in different habitats in the basins of Kolyma and Indigirka rivers, April 3-15, 1965: n = 161*

Habitats	*Frequency of moose observations (percent)*
Burns of different age	34.8
Larch forest	12.4
Floodplains of rivers and streams (riparian brush)	44.8
Shrubby and grassy clearings	3.7
Swamps	4.3
	100.0

*According to Tavrovski *et al.* (1971).

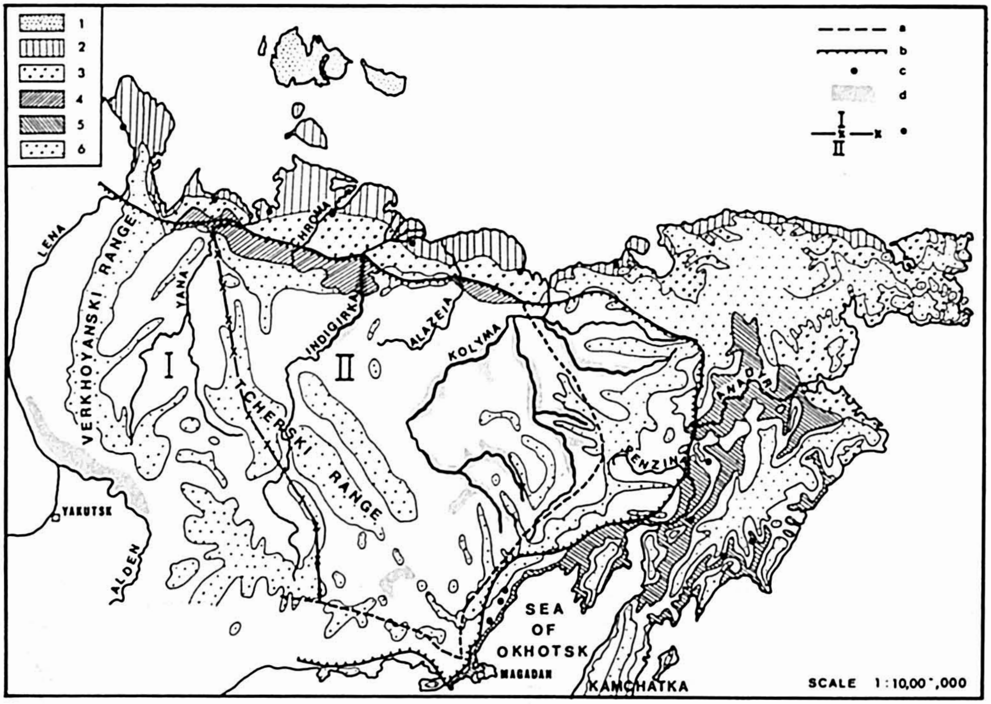

Figure. 1. Distribution of the moose in North-East Siberia. Definitions: 1) "arctic deserts", 2) arctic tundras, 3) subarctic tundras, 4) forest-tundras with *Larix dahurica*, 5) forest-tundras with *Pinus pumila*, 6) alpine tundras: a) eastern limit of the moose range at the end of the XIXth century (at the time of its maximum reduction), b) present limits of the year-round moose range, c) summer observations outside the normal range, d) some areas of high density, e) boundary between the subspecies: I. *A. a pfizenmayeri* Zukowski, II. *A. a. gigas* Miller (According to Portenko, 1941; Kistchinski, 1967; Tavrovski *et al.*, 1971; Vershinin, 1972; Yegorov, 1972, with some additions). tions).

spp.), that often appear after logging or other disturbance. In the continental parts of the north-east (*i.e.*, in Yakutia), snow cover probably does not limit moose distribution. In the mountains adjacent to the Sea of Okhotsk, where snow is deep, moose are rare, and in the most "snowy" areas (Koryak Highlands, Kamtchatka) they do not live at all. In mountain-taiga areas, orography is important (Tavrovski *et al.*, 1971): moose are absent from extremely broken terrain poor in forest, preferring valleys and gentle slopes. In the forest-tundra, moose, as a rule, are rare, but in some places (for example, in the Yana delta, my observations in 1972) there are local concentrations in the riparian willow thickets along the northern timberline. Similar local concentrations are known along the timberline in Canada (Kelsall, 1972). Long seasonal migrations are not recorded in north-east Siberia; however, in the middle and lower reaches of the Kolyma River, moose regularly move for winter from the lowlands of the left bank to the uplands (the Yukagir Plateau) of the right bank (Yegorov, 1965).

Habitat changes due to human activities (fellings, forest fires) in sparsely populated areas are, as a rule, favourable for moose, because the secondary succession that follows provides more food. Perhaps continuing increase of numbers and range expansion of moose in north-east Siberia are connected with the increase of the area of glades and burns. These effects, however, are hard to evaluate in relation to other factors such as decreasing hunting pressure and conservation measures.

Population density and numbers

Population data, obtained from aerial, surveys were gathered mainly by Dr. O. V. Yegorov and his colleagues, and by the staff of Yakutian and Magadan game departments (Table II). Counts were timed to take advantage of high moose visibility during the period of snowcover, mainly early spring when moose live in larch stands and shrub habitats in which they can be easily seen. However, ground counts made some years earlier resulted in larger estimates (Table II) — probably because they were mostly made in favourable habitats.

Population density is greatest along the south-west slopes of the Verkhoyanski Range, in parts of the Indigirka river valley, and especially in the valleys of the Kolyma river (middle reaches) and its main tributaries — Bolshoi Anyui, Omolon, Oloi, Korkodon, Sugoi, Berezovka, etc. (see also Kistchinski, 1967). Areas of high density in the Kolyma and Indigirka basins are separated by the high mountains (Tcherski Range, Verkhoyanski Range) from other areas where moose are abundant, i.e., basins of the Aldan River and Middle Lena River. Total moose numbers in north-east Siberia seems to be near 22-24 thousand (Table II). This is below the optimum level and further increase is expected.

Taxonomy

Moose of the Kolyma and Indigirka basins differ from the moose of central Yakutia and Yana basin in morphology, having large body size, large skulls with especially elongated facial parts, very massive antlers and shortened massive matapodia. They also differ in ecological relationships. In winter they eat horsetails (*Equisetum* spp.) in large quantities, as well as grasses (*Gramineae*) and sedges (*Cyperaceae*) which they take from under the snow. Adult moose from central Yakutia weigh 385-440 kg, and ones from Kolyma and Indigirka 510-600 kg. In contrast to the moose of central Yakutia and Yana basin which belong to

TABLE II

Population densities and numbers of moose in north-east Siberia

Territory	*Year*	*Moose numbers per 100 km² of:*		*Total moose numbers (× 1000)*	*Source*
		total area	*moose habitats*		
Lands on the right bank of Aldan river and southern foothills of the Verkhoyansk Ridge*	1964	10.9		3.80	Tavroski *et al.*, 1971
South-western slopes of the Verkhoyansk Ridge*	1958-1960	11.3-13.3			Yegorov, 1965 (our recalculation)
Basin of the Yana River*	1964	2.3		0.42	Yegorov and Popov, 1970
Middle reaches of the Adycha River (Yana basin)**	1959	6.5			Yegorov, 1965 (our recalculation)
Kolyma-Indigirka Lowlands, total* including:	1965	3.4		7.66	Yegorov and Popov, 1970
Uplands		6.7		5.70	"
Valley of Indigirka River from Druzhina to Tchokurdakh		10.8		0.68	"
Yukagir Plateau*	1966	4.0		1.80	"
All the north-east Yakutia except the middle and upper parts of Yana basin*	1968	3.1		8.10	Yakutian Game Dept. (our recalculation)
Basin of the middle reaches of the Kolyma River and its main tributaries (Anyui, Omolon and others)*	1969-1970	62.0			Magadan Game Dept.
Basins of upper reaches of the Kolyma River and Anadyr*	1969-1970	16.0	9.0-9.5		"
Mountains adjacent to the Okhotsk Sea*	1969-1970	1.0			"
Upper reaches of the Penzhina River and Oklan River (its right tributary)*	1970		0.5		Vershinin, 1972

* Aerial counts. ** Ground counts.

the subspecies *Alces alces pfizenmayeri* Zukowski, populations from Kolyma and Indigirka basins are referred by O. V. Yegorov (1972) to the subspecies *A. a. gigas* Miller, which occurs also in Alaska and belong therefore to the category of Beringian forms. Moose inhabiting areas eastwards of Kolyma basin probably also belong to *A. a. gigas.*

Ecological peculiarities

These features have been mainly studied in north-eastern Yakutia. (Tavrovski *et al.*, 1971). During the period of snowcover, trees and shrubs predominate among the moose foods in north-east Siberia — mostly different species of willows (*Salix*) and to a lesser extent of birches (*Betula* spp.). In summer, leaves of willows are also very important food, but herbs are also eaten in large quantities. The summer diet of moose from central Yakutia and the Yana basin consists mainly of *Salix* and *Epilobium,* which grow on burned areas, whereas moose in Kolyma and Indigirka basins prefer aquatic and coastal plants: *Salix* spp., *Arctophila fulva, Menyanthes trifoliata,* and *Equisetum heleocharis.* Kolyma — Indigirka populations consume as well large quantities of horsetails, grasses, and sedges in winter (Table III) when these foods are taken from under the snow. *A. fulva* and *E. heleocharis* (which are in the green state when being covered by snow in autumn) are very important winter foods, as are willows.

The herd structure of moose in Yakutia, in summer, is on the average as follows: adult males 26.0 percent, adult females 26.4 percent, animals 1.5 years old 17.9 percent, calves 29.7 percent. In October-November, calves comprise 22 percent of the population. Calf mortality is approximately 40 percent leaving an annual increment of about 15 percent (Tavroski *et al.*, 1971). In the basin of the Adycha River (a tributary of the Yana River), 47.2 percent of females counted in June-July had 2 calves each, compared to 35,7 percent on the western slopes of the Verkhoyanski Range (Yegorov, 1965). A large proportion of females 1.5 years old probably conceive. This fact as well as the rather high proportion of twins may be linked with the comparatively low population densities of moose which are certainly below the optinum level.

The main enemies of the moose in north-east Siberia are the wolf (*Canis*

TABLE III

Main foods of the Yakutian populations of moose in the "snowy" and "snowless' periods oy the year* — per cent frequency of occurence

Foods	*Central Yakutia, basin of Middle and Upper Yana river*		*Basins of Kolyma and Indigirka rivers*	
	"snowy" period (n =11)	*"snowless" period (n = 14)*	*"snowy" period (n = 4)*	*"snowless" period (n = 10)*
Trees and shrubs	91.4	51.1	46.4	25.5
Horsetails	3.9	4.0	11.3	12.5
Grasses and sedges	1.2	6.0	40.8	23.0
Other herbs	2.2	37.9	1.3	37.0
Other foods	1.3	1.0	0.2	2.0

*Based on Yegorov (1972).

lupus) and the brown bear (*Ursus arctos*). In the Yana besin, wolves often kill moose more in years of low hare numbers. In eight of 12 cases observed, animals less than 1.5 years old were taken (Tavrovski *et al.*, 1971). In the Yana basin, remains of moose were found in four of 109 specimens of brown bear feces; probably animals already dead were eaten. In the Kolyma-Indigirka lowlands, moose suffer severely from blood-sucking insects, especially mosquitoes (*Culicidae*). Gadflies (*Oedemagena* sp. and *Cephenomyia* sp.) have not been found in moose in north-east Siberia. Cases of moose death due to high floods are known and some cases of calf mortality in winters with especially deep snow in the Kolyma Basin (Jochelson, 1898).

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THE MOOSE IN FENNOSCANDIA

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Résumé

L'auteur passe en revue l'évolution passée et les changements contemporains dans les populations d'orignaux de même que les préférences de l'orignal dans le choix de l'habitat en Finno-Scandinavie. Une très forte pression de chasse avait entrainé du moins en partie, une réduction marquée de la population au début du XIX ème siècle. Mais, grâce à une réglementation de la chasse, les populations d'orignaux augmentèrent à nouveau. Cet accroissement a été particulièrement marqué durant la période 1940-1960. Il semble faire suite à l'utilisation de nouvelles méthodes d'exploitation forestière, lesquelles n'auraient pas fait qu'augmenter les ressources alimentaires disponibles, mais auraient aussi probablement amélioré la qualité nutritive de ces ressources et auraient eu, par le fait même, un effet sur la reproduction. Aujourd'hui, l'abondance du cheptel d'orignaux en Finno-Scandinavie, évaluée pendant l'hiver, s'établit à 200,000 têtes. Les densités les plus fortes s'observent dans le sud-est de la Norvège, le centre de la Suède et le sud de la Finlande.

Abstract

The history, recent population developments and habitat preferences of moose in Fennoscandia are reviewed. There was a marked decline of the moose population at the beginning of the 19th century, at least due in part to a very heavy hunting pressure. Thanks to hunting regulations, the moose populations increased afterwards. A very pronounced rise was noted in the period 1940-1960. This seems to have been connected with new forest exploitation practices which have increased the available forage tremendously and have also probably improved the quality of the nutrition which may, in turn, have affected reproduction. Today, the wintering moose population in Fennoscandia is estimated at 200,000 animals. The greatest densities are to be found in southeastern Norway, central Sweden and southern Finland.

Introduction

Geographically, Fennoscandia comprises Norway, Sweden and Finland and represents a total land area of 1,110,535 km^2. Moose is the most important game species in all three countries. Moose hunting is of great economic value to many countryside households and also the object of an enormous interest. In the regulating of hunting in Fennoscandia, hunting organizations have a rather unusual role. In Sweden, the Swedish Sportsmen's Association has exerted influence on the game regulations all since it was formed in 1830.

Early history of moose in Fennoscandia

As regards the recent form of moose *(Alces alces)*, it is generally believed that Asia was the centre of dispersal with the Siberian subspecies *(Alces a. pfizenmayeri)* approaching the ancestral type (Peterson, 1955). According to Kurtén (1964), moose were common in the temperate faunas of Europe from the so-called F-Eem period, that is beginning some 80,000 years ago. It existed on the European continent all through post-glacial times (Reynolds, 1934). Southern Sweden was the first ice-free part of the Scandinavian peninsula at the end of the last glaciation period about 8,000 B.C. There existed then a land connection with Denmark and moose as well as many other land animals invaded the Scandinavian peninsula from the south. Later on, there was an immigration also from the northeast, so that northern Finland, Sweden, and Norway got some of their moose that way (Ekman, 1922). This double route of immigration has caused speculation on the possibility of two different moose forms existing in Scandinavia. However, all recent European moose have been assigned by Peterson (1952) as belonging to the typical subspecies.

Records of the abundance and distribution of moose in early historical times are difficult to get. The species was discussed regarding characteristics, habits, methods of hunting, etc. by some authors such as Olaus Magnus (1555). The moose was treated also in the old provincial laws that were written in both Norway and Sweden in the 12th through the 14th century. For a long time moose hunting was restricted to nobility and poaching was severely punished.

The moose populations seem to have declined markedly from unknown causes during the 15th and 16th centuries (Lykke and Cowan, 1968). In Sweden a famous edict of 1789 gave hunting rights to commoners who owned taxable land. This was very democratic but fatal to the already scarce moose population. A very heavy hunting followed and by 1825, the Swedish moose population was nearly exterminated. According to Collett (1912), the situation was much the same in Norway, and an unpublished note tells that the Finnish moose population had almost disappeared by 1850. Immigrants from the southeast were regularly poached.

The development of the Swedish moose population after 1830 till the beginning of the 20th century has been described by Ekman (1918): completely closed seasons, maximally for a ten-year period, gave the moose a possibility to recover and start the upward trend. Later, the hunting season was restricted to 1 August — 30 November, which implied that the destructive ski hunting on crusty snow stopped. At the end of the 19th century the moose had dispersed almost to its present limits in Scandinavia. In Finland the moose was under protection between 1868 and 1898.

Recent changes in the moose populations

Annual moose harvest statistics exist for Norway and Sweden from the end of the 19th century and for Finland from 1906 when licensed hunting was permitted for the whole country. The Norwegian data have been summarized and discussed by Olstad (1934) and by Hohle and Krafft (1962), the Swedish data by Skuncke (1949).

It seems reasonable to assume that the data on annual harvest reflect the general

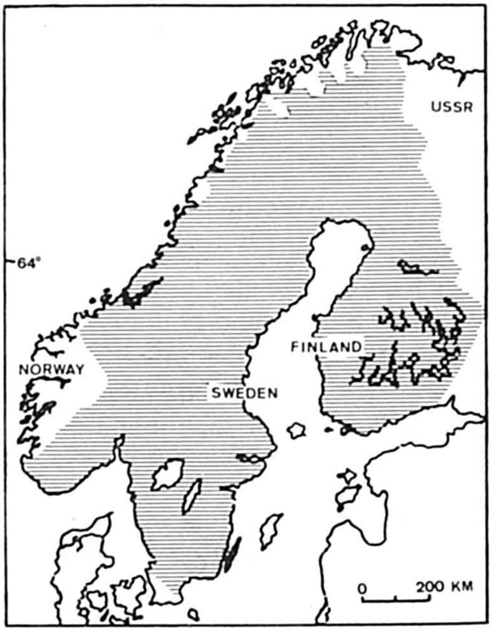

Figure 1. Distribution of moose (shaded area) in Fennoscandia.

population trend, particularly as the moose hunting in these countries is carried out very regularly by local teams. Irregularities in hunting activity have occurred during exceptional conditions, e.g. during the second world war.

Moose harvest statistics for Norway and Sweden are presented in graphic form in Lykke (1974); according to these statistics, the harvest remained at a comparatively low level until about 1930, when a rise began in Sweden. The rise started some 10 years later in Norway, but particularly between 1950 and 1960-65 there was a period of strong growth in all three countries (Lykke, 1974).

Partially closed seasons were established in Finland, Norway and Sweden after a period of heavy hunting during the world war 1914-1918. It seems likely that these restrictions at least contributed to the initial phase of the subsequent marked rise of the population curve. The second world war caused a peak in hunting activity in the neutral Sweden about 1940, while there was a marked decline in Norway which was involved in the war. In all three countries, there has been a decline in the harvest curve between 1960 and 1970. In Finland, the very strong descending tendency prior to 1970 is due to a partially closed season in 1969. The rising curve in Sweden, after 1967, is connected with a new hunting policy under which a higher percentage of calves are harvested.

Lykke and Cowan (1968) who made a survey of moose population dynamics in Scandinavia pointed out that the rapid increase of moose during the last decades is not confined to Scandinavia. Western North America had a similar increase accompanied by an extension of range. Also in European Russia and western Siberia, there has been an increase in number and an extension of the range northwards throughout the taiga zone (Heptner and Nasimovitch, 1967 ; Bannikov, 1970).

Factors involved in the growth of the moose population

HUNTING

It is obvious that above all, a ruthless hunting had caused the very marked decline of the Fennoscandian moose population at the beginning of the 19th century. It is equally obvious that hunting restrictions, such as closing or shortening the hunting season, made the subsequent population growth possible. Hunting pressure on moose is rather heavy in many Fennoscandian areas. Rajakoski and Koivisto (1970) considered it likely that the decline of the Finnish moose population by the middle of the 1960's was caused, at least partially, by too excessive harvesting. Hunting is normally carried out all over the areas where moose occur and periods of heavy hunting pressure can bring a moose population down within a rather short time. There are several local examples of that. On the other hand, hunting restrictions may contribute to a population rise, but certainly cannot explain the marked population growth in the Fennoscandian countries between 1930 and 1960.

DECREASING NUMBERS OF PREDATORS

There has been a continuous reduction in the numbers of the large predators in Fennoscandia during the period of moose population growth from about 1830 and onwards. This is particularly true of the wolf *(Canis lupus)* and the wolverine *(Gulo gulo)*. The wolf is now practically extinct in Norway and Sweden and very rare also in Finland. The wolverine begins to approach the critical point at which protective measures will be necessary if the species is to be saved (Haglund, 1968 ; Myrberget, 1969, 1970). Up until about 1840, wolves were still seen in southernmost Scandinavia (Hanström, 1960). The brown bear (*Ursus arctos*) and the lynx *(Lynx lynx)* were also reduced by hunting during the last hundred years and pressed back to the far north and the mountain areas between Norway and Sweden. Yet, these two species have shown in the last decades a tendency to increase in numbers and to disperse over wider regions.

The wolf and the brown bear have been the principal predators upon moose. Studies in North America, e.g. on Isle Royale (Mech, 1966) show that a wolf pack can act as an effective regulator on a moose population. The bear is most successful during certain snow conditions in the early spring, namely when there is still fairly deep snow with a thin crusty layer. The crust supports the bear but not the moose.

The gradual reduction of the main predators certainly have favoured the life conditions of the moose and have been a contributing factor in the positive population growth. However, changes in the abundance of the predators have not had much to do with the rise of the last two or three decades.

CLIMATE

Meteorological data show that there has been a continuous climatic change over the North Atlantic and adjacent land areas in the last hundred years (Eriksson, 1943). The change has involved reduced severity of the winters and an increasing proportion of the annual precipitation falling in the summer. This has implied at least one favourable condition for moose, namely a lower depth of snow, on an average. A period of weather warmer than normal in Scandinavia in the 1930's (Hesselberg and Birkeland, 1956) also caused lower snow depths, and above all, significantly shorter winters. This ought to have resulted in better food supply in winter and increasing survival of foetuses and calves. High losses of embryos, foetuses, and calves have been reported from hard-winter regions in the USSR (Heptner and Nasimovitch, 1967; Bannikov, 1970).

COMPETITION FOR FOOD

Attention has been drawn to the competitive role of domestic livestock in forest habitats in former days. Ahlén (1965) pointed out the great changes in land use during the last hundred years in Fennoscandia. The changes have involved the abandonment of small farms, the disappearance of extensive cattle-raising, and also the advancement of modern forestry. In this connection, the pasturage and haymaking in non-agricultural land is of particular importance. In the 19th and still in the beginning of the 20th century, a large biomass of domestic animals were feeding in forest areas; particularly sheep and goats, and in some regions also cattle, were competing with the wild herbivores thereby strongly reducing available herbaceous vegetation and either keeping the deciduous seedlings down, or else, killing them.

The stocks of sheep and goats have been very drastically reduced in Finland and Sweden (not so much in Norway) during the last fifty years, but significantly the so-called chalet type of husbandry, which involved keeping the animals in the forests for most of the summer, has now largely ceased. Lykke and Cowan (1968) also discussed these striking changes in husbandry management and concluded that they must have been of noticeable importance in the ecology of moose.

Competition with other cervids may be of less importance. The main range of the red deer *(Cervus elaphus)* in Fennoscandia is on the Norwegian west coast where moose do not occur. The minor regions of overlap are not very important. Most wild reindeer *(Rangifer tarandus)* are confined to the high mountains, but semi-wild and domesticated herds feed periodically in forest habitats. The roe deer (*Capreolus capreolus*) occupies very much the same habitats as moose, but in winter, when competition would be of any importance, the roe deer feed mostly on the vegetation of the field layer and spend much time in dense spruce forests where moose are rarely seen. Furthermore, the roe deer have increased in number and extended their range enormously in Scandinavia parallel with the moose, which indicates that they are not serious competitors.

SYLVICULTURAL PRACTICES

When considering the last few decades, the most thorough alterations in forest habitats have been in connection with forestry operations. The harvested forests consist mainly of mixed conifers, namely Scots pine *(Pinus silvestris)* and spruce *(Picea abies)*, with intermixture of birch *(Betula verrucosa* and *B. pubescens)* and some other deciduous tree species but the latter are hardly cut at all.

In Fennoscandia there has been a shift from a selective-cutting system to a clear-cutting system. Moderately large clearings produce a succession of rich vegetation that is utilized as food by moose (Cowan *et al.*, 1950). During the first summer, the vegetation in clear-cut areas may be dominated by nitrate-collecting species, such as fireweed (*Chamaenerion angustifolium*) and raspberry (*Rubus idaeus*). Later on, deciduous seedlings may grow in dense stands over large areas. In Sweden, aspen (*Populus tremula*) is a particularly fast invader in clearings. The vigorous regrowth following clear-cutting and intentional burning, or forest fires, is believed to be made possible through the freeing of nitrogen compounds from the old root-soil system of the forest trees [the so-called « assart effect » (Romell, 1957)].

At present, however, it is common to use herbicides to prevent the growth of undesirable deciduous shrubbery, particularly in the state forests, although the use of such compounds has now been somewhat restricted by law in Sweden.

The size of the clear-cut areas is another debatable question. The moderate clearing size of approximately 2 hectares (5 acres) that was common in Sweden less than 10 years ago, seemed favourable for regeneration of preferred browse. Lately, with more general use of forest machines the economic size of the clear-cut areas has increased markedly and areas of 5 or more hectares (> 12 acres) are now normal. This again may have had a negative influence on the nutrition for browsers, due to a changing of the local climate involving a gradual drying-up of the soil. This is an opinion in some forestry personnel. Furthermore, cover is greatly reduced in such areas. The recent method of macro-ploughing in clearings in northern areas seems to have had a similar negative effect as regards the local climate of the areas.

On the whole, forestry operations have been very positive. Telfer (1970) showed, for Eastern Canada, that logging may result in a greater than 50-fold increase in browse yield seven years after the cut. In Fennoscandia, the greatly increased food supplies created by the first shift in cutting practices coincides with the most marked rise of the moose populations, and has probably been one of the main factors behind it.

QUANTITY AND QUALITY OF NUTRITION

A marked population rise may be connected with a drop in mortality. In such a case increased food supplies could have reduced winter mortality, particularly that of calves. However, it is hard to believe that such a pronounced population growth would have been possible without an actual rise in productivity. There are indications that Fennoscandia has had such a rise. Recent studies (Rajakoski and Koivisto, 1966 a, 1966b ; Markgren, 1969 ; Stalfelt, 1969, 1970 ; Haagenrud, 1972) show early puberty in females, high ovulation rate, and high twinning rate, particularly in older cows. In fact, the data presented by Stalfelt (1969, 1970) from two Swedish counties reveal the highest productivity known for any moose population. Censuses during two consecutive winters and the kill statistics suggested an annual increase of approximately 60 percent calculated on the population of the former winter.

A recent increase in productivity of the moose populations might have something to do with hunting policy, above all a saving of cows in the prime age of 5 to 10 years (Markgren, 1969). Comparative studies between different regions indicate, however, that not only food supplies but also the quality of nutrition is involved. We know from studies on deer that the level of protein in the diet is very important for reproduction (Murphy and Coates, 1966). Nitrogen may be the critical element in many ranges as it affects directly the protein level of the forage. The so-called « assart effect » mentioned earlier implies increasing amounts of nitrogen being released for the new vegetation on clear-cut areas.

Thus, forestry may have contributed directly to an increased productivity in moose. Relatively small shifts in any of the components of reproduction, such as initial breeding age, numbers of young, and incidence of pregnancy have important consequences on the rate of population increase (O'Roke and Hamerstrom, 1948).

Present distribution and status in Fennoscandia

Today, moose are distributed over most of Fennoscandia with the exception of westernmost and parts of northern Norway and a few other minor areas (Fig. 1). According to Myrberget (1972), there is an increase going on in some coastal districts of northern Norway.

Densities vary greatly, locally as well as periodically. When considering large regions such as counties or provinces, moose densities will only rarely exceed one animal per square kilometer in Fennoscandia. There is a general tendency for densities to be at the lowest in the north. Southeastern Norway, central Sweden, and southern Finland show the highest densities, but these are not as high as those reported from certain North American regions (see Bergerud and Manuel, 1968). However, it should be remembered that human settlement, cultivated regions and industrial areas are scattered over most parts of the Fennoscandian countries, although broad wilderness expanses when found, are mostly in the far North or in high mountain areas.

As regards total numbers, extensive counts have been carried out in Finland and Sweden, and estimates have been made on the basis of local censuses in Norway (Koivisto, 1962, 1966 ; Hamilton, 1962; Lykke pers. comm.). It appears that Finland would have had some 40,000 animals in 1966, Norway probably about an equal number, while in 1962 the Swedish moose population amounted to about 120,000. That is, the total moose population in Fennoscandia may be about 200,000.

The last few years seem to have been marked by fluctuations but the sinking numbers in total harvest in Finland and Norway are probably not to be interpreted as a definite decline. By hunting regulations, the moose populations in the Fennoscandian countries can be controlled fairly well as long as there is no risk of heavy overbrowsing over large regions, and this is not the case.

Food and habitat preferences

Studies on moose feeding habits have been carried out in all Fennoscandian countries and research is continuing on various aspects of the subject. In the 1950's, there was much concern about the damage caused by moose to young forest stands, particularly of Scots pine. This tree species makes up a large percentage of the forests in northern Europe, and young stands of pine is an important winter food for moose, at least quantitatively. This is mainly true of Finland and Sweden. In Norway the damage to spruce is of greater importance because pine forests make up only 7 percent of the area. Studies on these questions have been carried out in Sweden by Westman (1958), in Norway by Lykke (1964), and others, in Finland by Kangas (1949), and other workers. However, the long-time effects of moose browsing on conifers have been found to be less serious than was feared. Mostly, a very low percentage of the stems are killed, some are heavily retarded, but the majority recover, and after having reached beyond the critical browsing height, they show a tendency to grow rapidly (see discussion in Lykke, 1964).

Winter food studies in Fennoscandia have been published by Sainio (1958), Hagen (1962), Ahlén (1968), Andersson (1971), and others. Little exact information exists on summer food. In the following discussion I have to restrict myself mainly to experiences from Sweden.

One of the most striking features as regards the distribution of moose in Fennoscandia is that it has been able to accept widely varying types of habitat. It is found from cultivated plain landscape with clumps of trees and parklike woods in the south, to small, thinly forested islands in the sea and the slopes of the high mountains between Norway and Sweden. However, its main summer habitat is wet regions of mixed coniferous forest with young deciduous vegetation in the shrub layer. The moose spends much of its life at the edge between mature forest and open areas, such as clearings, lakes, or rivers (Fig. 2). In

Figure 2. Preferred summer habitat of moose in Hälsingland, central Sweden. Edge of mixed forest (pine, spruce, birch, aspen) and boggy lake shore with *Menyanthes* and low *Salix* shrubbery.

winter, its distribution is guided by snow conditions and food supply, which is an old truth (Formozov, 1946 ; Telfer, 1967 ; Kelsall and Prescott, 1971) Snow depths will drive moose from higher summer range into river valleys where large aggregations may be found in mid-winter. This is particularly true of Norway, in regions where altitudinal differences are great. On the Swedish east coast, there is a comparable shift from the inner coast regions out to the shores and islets near the coast. Such localities may have moderate snow depths due to exposure to sun and wind and, periodically, the overflowing of water. However, by the end of the winter the islands may show heavy overbrowsing.

In summer, a great variety of herbaceous plants are eaten and the leaves of several common deciduous species are browsed. I cannot give a list of the forbs grazed in summer, but it may be mentioned that some aquatic or semi-aquatic species seem highly palatable, such as *Menyanthes trifoliata*, pondweed (*Potamogeton* spp.), and yellow pond lily (*Nuphar luteum*). In the mountain areas *Mulgedium alpinum* is an important and favoured food. Among the broad-leaved species the most palatable are willows (*Salix* spp.), rowan or mountain ash (*Sorbus aucuparia*), aspen (*Populus tremula*), maple (*Acer platanoides*), and in the southern parts of Fennoscandia oak (*Quercus robur*), and ash (*Fraxinus excelsior*).

In the autumn, there is a period after the falling of the leaves when moose are found in mature coniferous woods with little or no shrub layer. There the object of interest is dwarf-shrubs, such as blueberry *(Vaccinium myrtillus)* and heather (*Calluna vulgaris*, Fig. 3) Moose killed in October always have large amounts of blueberry plant parts in the rumen.

With the arrival of the snow cover, moose rather suddenly seem to lose inter-

Figure 3. Low shrubs such as blueberry *(Vaccinium myrtillus)* are an important food for moose after the falling of leaves in autumn.

est in the field layer. They are very rarely observed to paw into the snow with a front foot, as do, for instance, reindeer. In winter, nearly all feeding is browsing. Much the same deciduous species are preferred as in summer. Besides, there is periodically and locally heavy browsing on conifers, such as juniper *(Juniperus communis)*, Scots pine, and in some regions (mainly in Norway) spruce. A list of preference in northern Sweden would be of this order : willows, mountain ash, aspen, juniper, birch, Scots pine, and alder (*Alnus incana*). Willows (*Salix* spp.), are among the most important moose food in all seasons. The same statement was made by Peterson (1955) for North America. Although pine and birch are near the bottom of the preference order, they play a very important role quantitatively in winter, as they are found nearly everywhere in forest habitats and may during some periods be the only trees with browsable twigs above the snow. All the most palatable species may be pruned down to a level below the surface of the snow.

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A REVIEW OF MOOSE FOOD HABITS STUDIES IN NORTH AMERICA[1]

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Résumé

Cet article passe en revue 41 études portant sur les habitudes alimentaires de l'orignal, dont 13 ont été effectuées dans la cordillière intérieure, 6 en Alaska et 22 au Canada, au Minnesota, à l'Isle Royale et dans le Maine. Seulement neuf de ces études traitent des habitudes alimentaires estivales, alors que seulement quatre de celles-ci traitent de la phénologie annuelle des habitudes alimentaires de l'orignal et seulement deux études s'étendent sur plus d'un an. Les variations locales des habitudes alimentaires sont très importantes et des généralisations concernant les espèces préférées, sans que soit corroborée l'information pour une région donnée, apparaissent risquées. Une combinaison des méthodes utilisées semble pertinente, car chaque méthode a ses restrictions propres. Bien qu'une vue d'ensemble pour l'Amérique du Nord puisse être tracée à partir de l'information disponible, l'auteur conclut néanmoins que les données manquent pour comparer, entre différentes régions, les patrons d'utilisation annuels, saisonniers de même qu'en fonction des différents types d'habitats. L'auteur estime qu'il est essentiel d'évaluer les habitudes alimentaires avant d'apprécier les conditions du milieu et leurs changements, ou, avant d'entreprendre des recherches portant sur la valeur nutritive et la digestibilité des différentes espèces végétales concernées.

Abstract

This review covers 41 studies of moose food habits, including 13 from the intermountain west, 6 from Alaska, and 22 from Canada, Minnesota, Isle Royale, and Maine. Only nine of these studies include information on summer food habits, only four on year-long food habits and only two studies were longer than one year. Local variations in forage preferences were very important, and generalizations about preferred food items without confirming data for any given area appeared risky. A combination of methods for obtaining food habits data appears the most useful, since any given method in use has limitations. It was concluded that, although a generalized picture of moose forage preferences for the North American ranges can be obtained from the data on hand, there was not enough information to compare the annual, seasonal, or habitat-type forage use patterns between areas. Evaluation of forage preferences is a prerequisite to evaluating habitat conditions and trends, and investigations of nutritive values and forage digestibility.

Introduction

Food habits express a fundamental relationship between animals and their environment. The feeding habits and plants used by moose for food should be ascertained in order to fully understand the interspecific, intraspecific and environmental relationships of the species. A variety of moose food habit studies have become available since Peterson (1955) compiled the availa-

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ble data in the 1950's for North America. The purpose of this review is to bring all known studies together for the continent and summarize the major findings.

It has been well established that moose are primarily a browsing species, especially during winter. Moose occupying western ranges seem to use willows (*Salix* spp.)[3] as a primary food source (Hosley, 1949), while trees such as paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*) and balsam fir (*Abies balsamea*) assume importance on the eastern ranges (Pimlott, 1961). Forbs and aquatic plants may be important during the growing season, while grass and grass-like plants assume relatively little importance, with some exceptions. Food habits studies have been summarized according to general region as follows : (1) Alaska ; (2) the mountain states of Idaho, Montana, Utah, Washington and Wyoming; (3) western Canada (British Columbia-Manitoba) ; (4) eastern Canada, Isle Royale, Maine and Minnesota.

Alaska food habits studies

Spencer and Chatelain (1953) provide data on moose food habits in south-central Alaska based on spring browse surveys (Aldous, 1944). Willows and Kenai birch (*Betula kenaica*) head the winter preference list, and quaking aspen was considered important because of the quantity of forage it produced. Cottonwoods (*Populus balsamifera*), high bush cranberry (*Viburnum edule*), red elder (*Sambucus racemosa*), rose (*Rosa* spp.) and raspberry (*Rubus idaeus*) were less important browses in the diet. Willow, birch, aspen and cottonwood supplied 95 percent of the winter forage in their studies. Conifers were apparently not important in the diet of Alaskan moose, primarily because the two major species present, white spruce (*Picea glauca*) and black spruce (*Picea mariana*), were not palatable (Murie, 1944).

Spencer and Hakala (1964) recorded *Salix depressa*, *S. scouleriana*, *S. arbusculoides*, and *S. barclayi* as particularly important willow species on the Kenai peninsula. These species attain small tree size in that area. Bog birch (*Betula glandulosa*), dwarf birch (*B. nana*), serviceberry (*Amelanchier alnifolia*), mountain ash (*Sorbus scopulina*), and high-bush cranberry were considered of minor importance. Hosley (1949) reported work done by L. J. Palmer on the Kenai in the 1930's which indicates that tree and ground birches, willows, mountain ash, red and black currant (*Ribes* spp.) and serviceberry were highly palatable. The winter diet according to Palmer was mainly willows, ground birches, cottonwood and the green bases of bunch and marsh grasses.

LeResche and Davis (1973) provide information on moose food habits from Kenai peninsula. Summer foods of three semi-tame moose were two thirds birch leaves, one fourth forbs, including cloudberry, (*Rubus chamaemorus*), sundew (*Drosera rotundifolia*), fireweeds (*Epilobium angustifolium* and *E. latifolium*) and lupine (*Lupinus nootkatensis*). Mushrooms were eaten whenever encountered and grasses, sedges and aquatics constituted about ten percent of the observed diet.

Winter forages varied according to conditions of winter range. When snow depths were less than 30 cm sedges were used. After snow depths increased beyond that figure, birch stems

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[3] Scientific plant names follow Fernald (1950) for eastern North America, Davis (1952) for the mountain states and Hultén (1968) for Alaska.

comprised 72 percent of the use from February to May, low-bush cranberry (*Vaccinium vitis-Idaea*) 26 percent, willows and alder (*Alnus* spp.) 6% each, and occasionally a fruticose lichen (*Peltigera sp.*) was taken on range considered to be representative of the wintering area.

On depleted ranges, browse consumption declined to 23 percent of the diet between February and May, with birch predominant, while lichen consumption increased to 24 percent. In late April and May, when snow depths declined, lichens and low bush cranberry comprised most of the diet. The northern Kenai Peninsula wintering area exhibits moderate snow conditions, which provide access to low-growing shrubs and forbs and lichens. The more persistent snows of interior Alaska require that taller browse species be available for moose in winter. The Kenai work also reflects changes in food habits relative to availability, where lower-growing forms were used more on heavily used range. Murie (1944) considered willows the major summer and winter food of moose in Mt. McKinley Park. Dwarf birch was regularly browsed. Quaking aspen (*Populus tremuloides*) and cottonwood were used, but were less important because of their limited occurrence. Murie (1944) started that grasses, sedges, various herbs and submerged vegetation was eaten in summer.

The following willows, listed in order of decreasing preference, were important forage species in interior Alaska near Fairbanks (Milke, 1969): *Salix interior, S. alaxensis, S. arbusculoides*, and *S. pulchra*. The relative abundance of a species did not seem to affect the utilization, perhaps due to inherent palatability differences detectable to the moose. However, less palatable species were more heavily utilized when in proximity to species of higher palatability. Milke's analysis showed that the tallest plants (over 151 cm) were preferred. A positive correlation between plant density and intensity of browsing was also noted, suggesting that the stands were not acting as barriers to moose. A combination of high moisture, protein, and caloric contents were possibly related to the high preference for *Salix alaxensis*, and the low values of *S. niphoclada* could explain its low palatability, although such conclusions were considered tentative.

Montana, Utah, Washington and Wyoming food habit studies

Since Peterson (1955) mentioned the lack of detailed moose food habit studies on western ranges, several studies have become available. These studies generally support the contention that moose primarily depend upon willows for forage on western ranges. The feeding site examination method (Cole, 1956) and rumen analysis (Martin *et al.*, 1946) have been the main means of obtaining data in the following studies.

Comprehensive food habits studies have been done in Jackson Hole, Wyoming and southwestern Montana areas. These areas represent two generally different types of moose winter range in the intermountain west. The Jackson Hole winter range (Harry, 1957; Houston, 1968) was mostly an extensive valley wherein floodplain vegetation was the major area used by moose. Some use of adjacent forest communities was also recorded (Houston, 1968). Knowlton (1960) reported that willow bottoms, the most extensively used winter range, were limited to moist areas along streams and springs in the Ruby River area of Montana.

This study area of 148 km² contained 58.3 hectares of willow bottom communities along 33.5 km of streams (Peek, 1961). While willow communities generally typify moose winter range in the mountain west, some areas are much more extensive than others. This causes considerable variation in length of time used, and degree of concentration of moose on the willow. Densities on the extensive willow community in Jackson Hole, ranged up to 19.3 moose per km² in winter (Houston, 1968). Harry (1957) and Houston (1968) reported winter moose food habit studies in Jackson Hole. Harry (1957) rated serviceberry (*Amelanchier alnifolia*), red osier dogwood (*Cornus stolonifera*), mountain ash (*Sorbus scopulina*), bog birch (*Betula glandululosa*), snowbrush (*Ceanothus velutinus*) and bitterbrush (*Purshia tridentata*) as "very highly palatable" to moose in winter. Since willows (*Salix* spp.) made up over three quarters of the winter diet and were extensively distributed on winter ranges, he considered these the most important forage species. Houston (1968) regarded blueberry willow (*Salix pseudocordata*) as the "key" forage plant. Forage preferences were related to vegetative type and blueberry willow, interior willow (*S. interior*) subalpine fir (*Abies lasiocarpa*) and bitterbrush were species receiving 50 percent or more of the use observed on the specific types in which they occurred. While Harry felt that red-osier dogwood, service-berry, mountain ash, and bog birch were in danger of being eliminated from the winter range in 1954, an indication of the degree of use these species received, Houston reported that condition of red osier dogwood and interior willow plants improved from 1964 to 1966 suggesting that the winter range was less intensively browsed during his study. While individual subalpine fir trees were often browsed heavily, the average percent of browsed trees was light during Houston's studies, which may indicate differences in palatability among individual fir trees. In this area, willow conditions have varied over the 1950-1966 period, suggesting differential browsing pressure. In 1966, 3 to 5 year old blueberry willow stems were producing most of the forage and receiving most of the use for this species, older live stems being severely hedged and younger stems being unbrowsed.

Bitterbrush and chokecherry (*Prunus virginiana*) were the only two species which Chadwick (1960) observed eaten by moose on the Juniper Buttes, Idaho winter range.

Knowlton (1960) reported moose winter food habits in the Ruby River area of Montana. Early winter foods of importance were willow, subalpine fir and currant (*Ribes* spp.). Later, willows, silverberry (*Eleagnus commutata)* and thinleaf alder (*Alnus tenuifolia*) were important. Willow constitued 67 and 59 percent of the early and late winter diets, respectively. This range was being heavily browsed at that time, with willow and silverberry plants deteriorating in condition (Peek, 1963).

Browse constituted 99.8 percent of the observed diet in winter on the Red Rock Lake Refuge, Montana, with *Salix myrtillifolia*, *S. planifolia*, *S. bebbiana*, and *S. geyeriana* each constituting over 10 percent of the use (Dorn, 1970). Red osier dogwood was not important because of its scarcity. Use of low-growing species like *S. wolfii* and bog birch was limited to early winter when they were available to moose browsing close to the snow level. Use of *S. wolfii* in summer by cattle was also heavy, probably because the low growth form renders it available. In the Douglas fir type, subalpine fir received more use than Douglas fir (*Pseudotsuga menziessi*), but use was restricted to certain trees which seemed to be consistently browsed.

Smith (1962) and Stone (1971) reported moose food habits in the Rock Creek area of western Montana. Willows comprised the major share of the winter diet; *Salix discolor* and *S. lemmoni* were preferred to *S. commutata*. Plants less than 15 years old received the heaviest use. Red osier dogwood was important in March. On this range, red osier dogwood was either very heavily used or, else, was in poor condition affording only limited forage.

Stevens (1970) reported food habits studies on a mountain winter range in the Gallatin region of Montana. Timber types received 82 percent of the observed use during the study period. Willow constituted 25 percent of the diet, sub-alpine fir 16 percent, mountain maple (*Acer spicatum*) 16 percent and red osier dogwood 11 percent. This winter range was being heavily used.

Wilson (1971) reported that *Salix drummondiana* made up 92 percent and *S. geyeriana* made up 4.7 percent of the total observed winter browse use in the Uinta Mountains of Utah. River birch (*Betula occidentalis*) comprised 2 percent of the use and 7 other species were observed to be browsed.

Poelker (1972) found browsing on false box (*Pachistima myrsinities*) in early fall in the Kalispell Basin of northeastern Washington. As snow covered this species, snowbrush, Douglas maple (*Acer glabrum*) and willows were taken. In mid-winter, instances of browsing on lodgepole pine (*Pinus contorta*) and alders were noted.

Table I provides a resume of important moose winter forage species as derived from six studies reported for five areas of the intermountain west. While willows were the primary forage plant in three of the four areas, all of the studies indicated that red-osier dogwood was a more palatable forage species, although it was less abundant and therefore less important than willows. Subalpine fir was an important forage species in the spruce-fir communities. Douglas fir received only limited use in the Jackson Hole and Gallatin studies, but Smith considered it to be a palatable species. Lodgepole pine (*Pinus contorta*) received sparing utilization.

Bog birch, silverberry, snowbrush, serviceberry,chokecherry,currant,mountain ash, mountain maple, and bitterbrush are palatable browses to moose and may be important locally. *Salix discolor, S. lemmoni, S. myrtillifolia, S. pseudocordata, S. drummondiana, S. geyeriana*, and *S. interior*, all taller growing, seem to be preferred willow species.

Forbs, grasses and grasslike plants receive only sparing use by moose in winter. Harry (1957) did not record use of these forage classes, but Houston (1968) recorded use on bluegrass and bromegrass on agricultural (hayfield) situations in Jackson Hole. Green algae received use in aquatic situations. These forage classes received less than one percent of the total winter forage in Houston's studies.

Elk thistle (*Cirsium foliosum*) and niggerhead (*Rudbeckia occidentalis*) received less than one percent of the winter use in Knowlton's study. Stevens (1967) however, reported that grass and grass-like plants constituted 26 percent of the contents of 10 moose rumens taken in December and January on a winter range associated with hay fields in the Big Hole valley of Montana. Since snow depths were high enough

TABLE I

Winter food habits of shiras moose on western ranges

Reference	*Location*	*Years*	*Most important species*	*Remarks*
Houston, 1968	Jackson Hole, Wyo.	1967	*Salix pseudocordata*[1], *S. wolfi*, *S. interior*, *S. lucida*, *Abies lasiocarpa*.	Feeding site examination
Knowlton, 1959	Gravelly Range, Montana	1959	*Salix* spp., *Ribes* spp., *Abies lasiocarpa*, *Populus tremuloides*, *Eleagnus commutata*, *Alnus tenuifolia*.	Early winter ; 95% of forage late winter ; 96% forage feeding site examination
Smith, 1962	Rock Creek Montana	1959	*Salix* spp., *Cornus stolonifera*, *Populus tremuloides*, *Shepherdia canadensis*, *Physocarpus malvaceus*, *Rosa* spp., *Pinus contorta*.	Rumen analysis Feeding sites ; *Salix* 90% (*S. discolor*, *S. lemmonsi*)
Harry, 1957	Jackson Hole, Wyo.	1954-54	*Salix* spp., *Abies lasiocarpa*.	See text for additional details
Stevens, 1970	Gallatin, Montana	1966	*Prunus virginiana*, *Cornus stolonifera*, *Salix scouleriana*, *S. myrtillifolia*, *S. drummondiana*, *Ribes* spp., *Amelanchier alnifolia*.	Dec.-March feeding site examination
Dorn, 1970	Red Rock Refuge, Montana	1968-69	*Salix myrtillifolia*, *S. geyeriana*, *S. planifolia*, *S. bebbiana*, *Betula glandulosa*	Feeding site examination, Dec. 20, 1968 – March 17, 1969,

[1] Houston (1968:16) indicates that the following willow species may be synonymous in his data : *Salix myrtillifolia* and *S. pseudocordata*.

to make this forage class generally unavailable, haystacks were considered the main source of grass forage in the area. Smith (1962) reported that grasses, grass-like plants, and forbs received less than one percent of the observed winter diet on his study area, while Stone (1971) reported some use of bull thistle (*Cirsium vulgare*) and lupines.

Browse species apparently constitute increasingly greater percentages of the Shiras moose diet from early to late fall. Knowlton (1960), Houston (1968) and Smith (1962) reported that browse plants constituted from 70 to 90 percent of the fall diets. Willow, subalpine fir, currant, aspen, huckleberry (*Vaccinium scoparium*) mountain ash, serviceberry, *Ceanothus*, bitterbrush, buckthorn (*Rhamnus* sp.), honeysuckle (*Lonicera canadensis*), paper birch (*Betula papyrifera*) and red osier dogwood were important fall forage plants. Forbs and grasses comprised relatively larger percentages of the fall diets than winter diets. There was more variation in the fall diets between areas than in the winter diets, perhaps because the use of a greater number of vegetative types occurred in the fall, and there was greater chance of variation in communities between areas.

Summer food habits studies reveal even greater variation between areas. In Yellowstone National Park, McMillan (1953) recorded willow as 88.5 percent, aquatics as 9.3 percent, and grasses and forbs as 2.2 percent of the diet, based on amount of time spent feeding on each forage class. *Salix geyeriana* was used three times more frequently than *S. wolfii*. Bluegrasses and wheat grasses (*Agropyron* spp.) were the grass species utilized.

Knowlton (1960) reported that browse constituted 28.6 percent, forbs 70.6 percent, and grasses and grass-like plants 0.6 percent of the summer diet in the Gravelly Range area. Willows comprised 19.3 percent and sticky geranium (*Geranium viscosissimum*) 64.2 percent of the diet. This area is one example of a western moose range wherein aquatic vegetation is extremely limited because of the high gradient nature of streams.

Houston (1968) reported that browse constituted the greatest share of the summer moose diet in the Jackson Hole area, with willow again receiving extensive utilization. Quaking aspen (*Populus tremuloides*) menziesia, (*Menziesia ferruginea*), thimbleberry (*Rubus parviflorus*), Utah honeysuckle (*Lonicera utahensis*), and fireweed (*Epilobium* spp.) were other important items. Water crowfoot (*Ranuculus aquatilis*) and leafy pondweed (*Potomageton foliosus*) were used extensively in aquatic situations.

Dorn (1970) found that *Salix myrtillifolia, Salix geyeriana,* and *Salix planifolia* and bog birch leaves constituted 86% of the summer moose diet at Red Rock Lakes Refuge, Montana. Most leaf-stripping occurred on plants over one m tall. Use of aquatics was considered minimal.

Knowlton (1960), comparing the various summer food habit studies of moose available, felt that variations were attributable to differences in vegetation on the study areas. Subsequently, Peek (1961) reported that on the Gravelly-Snowcrest study area, browse increased in importance during summers which were drier than the 1958 summer from which Knowlton obtained data. Consequently, it appears that annual variations in food habits of moose may occur within the same area.

Western Canadian food habit studies

In British Columbia, Hatter (*fide* Hosley, 1949) considered red-osier dogwood, paper birch, willows, serviceberry, quaking aspen, mountain ash (*Sorbus scopulina*) and bog birch to be palatable winter moose forage plants. Cowan, Hoar, and Hatter (1950) added hazel (*Corylus californica*), highbush cranberry (*Viburnum pauciflorum*), and alpine fir (*Abies lasiocarpa*). Scouler and Bebb willows (*S. scouleriana, S. bebbiana*), were the important willow species. Douglas Fir (*Pseudotsuga menziesii*) was seldom eaten on their study areas. These data suggest that moose food habits in British Columbia more closely approach those of moose on more eastern ranges, as will be reported.

Ritcey (1965) recorded instances of use of forage by moose on the Wells Gray Park, British Columbia, winter range. Willow and false box (*Pachistima* sp.) comprised over 75 percent of the observed use, with paper birch, hazel and red osier dogwood also receiving use. Extensive overlap in the diets (but not the areas of use) of moose and mule deer (*Odocoileus hemionus*) was found. An experimental clear-cutting increased browse production and utilization by moose for at least four years following the cutting.

Aquatic species used by moose in summer at Bowron Lake Park, B. C., included swamp horsetail (*Equisetum fluviatile*), burreed (*Sparganium* spp.), and pondweeds (*Potomageton richardsonii, P. robinsii, P. gramineus, P. natans*, and *P. amplifolius*, in order of importance) according to Ritcey and Verbeek (1969). Aquatic plants appeared to form the bulk of the summer diet. Burreeds were considered to be the chief aquatic food in Wells Gray Park by these investigators.

Analysis of 23 moose rumen contents collected in February 1970 in Cypress Hills Provincial Park in southeastern Alberta was reported by Barrett (1972). Serviceberry comprised 56 percent of the identified material on a dry weight basis, quaking aspen 21 percent and *Prunus* spp. 12 percent. Red osier dogwood, willows, honeysuckle, *Clematis* spp. Rosa spp. and lodgepole pine contributed less than 10 percent of the identifiable material. Cypress Hills form a low plateau surrounded by treeless grass plains, an island of moose habitat. The moose population increased from a transplant of four animals in 1956 to 130-180 animals in 1970, and severe browsing was common at the time of collections. This study represents the highest proportion of serviceberry reported in the diet of moose, and Barrett considered this species to be preferred over willow.

Howard (pers. comm.) reported that browse surveys along the Saskatchewan River delta in northern Manitoba taken by J. E. Bryant in 1955, showed that red osier dogwood and willows were the main species eaten. Balsam fir, quaking aspen, *Viburnum* spp. box elder (*Acer negundo)* balsam fir, balsam-poplar (*Populus balsamifera*) and raspberry (*Rubus idaeus*) were also commonly taken. In more southerly portions of moose range in Manitoba, mountain maple, quaking aspen and hazel appeared to be important.

Eastern Canadian, Isle Royale, Maine and Minnesota food habit studies

Moose food habits have been investigated primarily in winter in eastern North America. Newfoundland studies include those of Dodds (1960), Pimlott (1953), and Bergerud and Manuel (1968).

Dodds (1960) recorded 35 species of woody plants browsed by moose based on examination of browsing intensities on woody plants within sampling plots. In an area of high moose density dominated by balsam fir, winter browse use was chiefly on balsam fir (47 percent), white birch (20 percent), and raspberry (13 percent). In a lighter moose density area dominated by uncut white spruce (*Picea glauca*) and balsam fir, balsam fir constituted 44 percent, willows 22 percent and alder 11 percent of the winter browse use. On a cutover area of high moose density, fire cherry (*Prunus pennsylvanica*) was 29 percent, white birch 25 percent, balsam fir 15 percent and quaking aspen 10 percent of the diet.

Pimlott (1953) considered balsam fir and white birch the two species of universal importance to moose in Newfoundland. White birch was the most important browse species in habitats which had been burned or logged, containing low or moderate moose densities (Pimlott, 1963). Balsam fir exceeded white birch in the diet where high density populations existed. Yew (*Taxus canadensis*) was most seriously affected by moose browsing, being highly palatable and relatively intolerant to browsing (Pimlott, 1963). Pimlott thought it possible to classify browse conditions on the basis of use of these three species. If yew was highly or moderately used, the range was below carrying capacity and many palatable browse species would be available. If white birch was available, balsam would provide a small percentage of the winter food. If fir was heavily browsed, yew would be killed out and the palatable deciduous species would be severely overbrowsed and a portion eliminated from the habitat. It should be noted that the absence or scarcity of yew may not be attributable to moose in some areas, including eastern Minnesota where this species occurs infrequently on the major moose range as well as on areas where moose and deer are scarce.

Evaluation of the ability of 12 year-old balsam fir to withstand varying amounts of browsing was determined by Bergerud and Manuel (1968). Over half of the trees from which 75% of growth was removed died two years after clipping, while only one of ninety clipped at 10-50% levels died. It was not stated whether current or total growth was removed. Balsam fir trees four-foot tall were found to withstand up to 12 years of heavy browsing without dying. A preference for balsam fir with dark green needles over chlorotic, light green colored fir was noted. Crude protein content was lower in chlorotic fir, indicating that moose were selecting the most nutritious plants. Clipping experiments resulted in some darkening of the foliage of chlorotic fir. Light browsing may improve protein content by stimulating adventitious nutrient-rich shoots.

It is significant that these investigators doubted that an equilibrium between moderate moose densities and a quantity of highly palatable diversified winter moose foods could be maintained in Newfoundland, because of inaccessibility of many moose to hunters, because foods such as yew and quaking aspen could not withstand moderate use, and also because moose tended to congregate on sites wherein sought-after species were intensively utilised. However, the diet of balsam fir and white birch was considered adequate to maintain a healthy moose population.

Summer moose food habit data from eastern ranges are scarce. Dodds (1960) stated that in Newfoundland moose fed on herbaceous materials during summer. Grasses and sedges, leaves of shrubs were commonly taken. There were few aquatic areas in Newfoundland : however, small ponds, lakes and rivers were frequented. On an aquatic area used heavily within Dodd's study area, grazing was light until late June, heavy during July and decreased in August.

Telfer (1967) reported winter range surveys in Nova Scotia. Speckled alder (*Alnus rugosa*), Canada honeysuckle (*Lonicera canadensis*), allegheny blackberry (*Rubus allegheniensis*) sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) were the five most highly preferred browse species of nine species which were used in a moose yard. Beaked hazel (*Corylus cornuta*) was ranked over balsam fir, mountain maple, Allegheny blackberry and meadow-sweet (*Spiraea latifolia*). For the entire winter range, yellow birch, red maple (*Acer rubrum*), sugar maple and mountain maple (*A. spicatum*) were important forage species.

Dyer (1948) reported browse surveys in Baxter State Park, Maine. Balsam fir, mountain maple, mountain ash, white birch and fire cherry were the five most important browse species for moose. Two types of moose yards were described in this region. On high altitude yards, near summits of mountain tops, snow depths of 2.5 to 3.2 m limited browsing to reproduction above that height. Balsam fir was stripped of lateral branches up to 1.25 cm in diameter. Low altitude yards were the most common type of yarding situation in the region. Seven species made up 99 percent of the food eaten : balsam fir, mountain maple, mountain ash, white birch, striped maple (*Acer pensylvanicum*), fire cherry and quaking aspen in that order of importance. Fir constituted 54 percent of the diet, mountain maple 23 percent. Apparently these studies were made at a time when heavy browsing by moose was occurring in the area.

DesMeules (1965) determined winter moose food habits from browse surveys in Laurentide Park, Québec. In four yards examined, balsam fir comprised most of the winter diet, while in four other yards, deciduous species dominated the diet and balsam fir was moderately used. Mountain maple, white birch and willows were the most commonly browsed deciduous species. Red-osier dogwood, willows, and mountain ash the highest palatability ratings where available. Balsam fir became more heavily utilised as snow depths increased to highs in late winter. Fire cherry bark was used more commonly than quaking aspen, mountain ash or red maple bark, but all were fed upon where palatable twigs were available and hence were considered preferred foods. No evidence of browsing on arboreal lichens was noted although they were abundant in some areas studied.

DesMeules (1965) postulated that heavy utilization of balsam fir in late winter may save energy, since fir twigs weigh eight to 13 times more than deciduous twigs of similar length and therefore require less time and efforts to consume equivalent amounts. In one late winter yard, balsam fir comprised 86 and white birch 14% of the diet. This yard was about ten acres in size and was believed capable of supporting one moose for 200 days of winter (DesMeules, 1962).

Stomach analyses of 24 Ontario moose, one Manitoba and one Québec moose, taken from October 19 to May 5 (Peterson, 1953) indicated that balsam fir occurred in 21 of 23 stomachs where the tree occurs, and white cedar (*Thuja occidentalis*) occurred in small amounts in 4 stomachs, willow in 16, white birch in 11, beaked hazel in 10, quaking aspen in nine, fire cherry in four, bog birch and red-osier dogwood in two and serviceberry and maple in one each.

Browsing investigations in Ontario on St. Ignace Island (Peterson, 1953) suggested that balsam fir constituted 27 percent of the available diet, white birch 12 percent, mountain maple and red osier nine percent each and highbush cranberry five percent. Considerable seasonal variation was found in foods eaten. Conifers were practically untouched from early spring to late fall. Quaking aspen was commonly barked on St. Ignace. Mountain maple was most consistently barked, though mature trees were very scarce.

The Isle Royale browse studies (Aldous and Krefting, 1946 ; Krefting, 1951) illustrate annual variations in winter utilization patterns of moose on the same range (Table II). The diet included 33 woody species but seven species (quaking aspen, white birch, balsam fir, mountain ash, willows, red osier dogwood, yew) contributed 80 percent of the total diet and three (quaking aspen, white birch, balsam fir) contributed 48 percent, based on three years of spring browse survey data. Changes in importance of individual species were primarily related to the heavy browsing which occured during the period (Krefting, 1951). Quaking aspen became less important in the diet after 1945 because the amount eaten up to then was in excess of production. Quaking aspen accounted for 54 percent of all trees and shrubs destroyed by moose in very heavy browsing situation. Conversely, white birch, because of its higher ability to withstand browsing, increased in importance. Krefting (1951) concluded that balsam fir could not withstand continued heavy browsing and was being replaced by black spruce on Isle Royale. Yew was considered a highly preferred moose food, and was once widely distributed across Isle Royale (Murie, 1934). By 1950, it was not considered to be a source of food on the island. Mountain maple ranked higher on the palatability lists than beaked hazel, but light utilization for both species was encountered.

Krefting (1951) reported that stomachs of moose collected in the fall of 1949 contained mountain maple, balsam fir and quaking aspen. Murie (1934) reported stomach contents analysis of six moose taken between May 20 and August 10 of the summers of 1929, 1930 and 1931. Mostly browse species were found, including quaking aspen, alder, fire cherry, yew, bush honeysuckle (*Lonicera* sp), mountain maple, raspberries, beaked hazel, and willow. Small amounts of sedge, grass, mushrooms, horsetail (*Equisetum* spp.) pondweeds and large-leaved aster (*Aster macrophyllus*) were also found. Murie (1934) reported that wood fern (*Dryopteris* sp.), and swamp horsetail (*Equisetum* sp.) sedges, marsh marigold (*Caltha palustris*), jewelweed (*Impatiens* sp.) and large-leaved aster were extensively grazed. Large yellow pond lily (*Nymphaea advena*), sweetscented white pond lily (*Castalia odorata*) and *Potamageton* sp. were reported as extensively fed upon when available but were rare due to heavy use by moose on Isle Royale (Murie, 1934).

Manweiler (1941) stated that the main winter foods of moose in Minnesota were maples, ash, dogwood, hemlock (*Tsuga* sp.) quaking aspen, balsam poplar, birches, willows, juneberry (*Amelanchier* sp.), fire cherry, chokecherry and basswood (*Tilia* sp.). The basis for this was not reported, and hemlock and basswood are rare on Minnesota moose ranges. The Red

Lake area of northwestern Minnesota consists of willow, quaking aspen and bog birch communities interspersed with small stands of spruce and jack pine (*Pinus banksiana*) (Ledin and Karns, 1963). A browse survey in that area in 1949 indicated that willow formed 58 percent of the winter food, while balsam fir, white cedar, bog birch, balsam poplar, red osier dogwood, raspberry, mountain ash, aspen and tamarack (*Larix laricina*) comprised 39 percent, while black spruce, black ash (*Fraxinus nigra*), beaked hazel, white birch, highbush cranberry and alder comprised two percent of the diet. The range was considered to be in good condition. Although there was no mention of moose-deer competition for any dominant species, one suspects that white cedar was probably used more by deer than by moose.

Peek (1971) investigated forage preferences in northeastern Minnesota on a year long basis (Fig. 1), using the feeding site examination. Willows were the most important browse, year-long, but received greatest use in September through December. Bebb and pussy willows (*Salix bebbiana, S. discolor*) were the most preferred willows. Quaking aspen was the most important browse in June, declined in value through late summer, fall, and early winter, then received increased use in mid-winter. White birch ranked third in importance year-long, and remained relatively constant throughout the year. Beaked hazel, fourth in overall importance, was most intensively used in mid-winter. Fire cherry was important primarily in summer and early fall. Red osier dogwood was used primarily in fall and though remaining important, decreased in value as the winter progressed. Virtually no use occurred until twigs reddened. June berry and mountain ash remained in the diet at low but constant levels year-long. Balsam fir, almost entirely a winter forage, received progressively more use through the winter and was an important late winter forage supply. Mountain maple was used most commonly in late summer and again during the winter, but was never a major item in the diet.

Winter severity, especially snow depth and its rapidity of accumulation (VanBallenberghe and Peek, 1971), appears to have some influence on food habits. Balsam fir and beaked hazel became important items in the diet at relatively later dates during two milder winters than during the severest winter of the study. Red osier dogwood remained important in the diet for a longer period during the mildest winter than during the others. Since movement to dense cover occurred most rapidly during the severest winter, use of forage species characteristic of communities dominated by balsam fir and the spruces also occurred earlier. Snow depths appeared to be critical in use of red osier dogwood, since many plants disappeared under one m of snow.

Except in summer, browse constituted all of the observed diet. The relative importance of forbs in summer was low, but aquatics were probably the major forage source during early summer. Yellow pond lily (*Nuphar variegatum*), wild rice (*Zizania aquatica*), pondweeds, burreed (*Sparganium* spp.) and wild calla (*Calla palustris*), were commonly used.

Table II lists the five most important browse species for ten separate surveys in six areas of eastern North America. White birch, mountain ash, mountain maple and balsam fir occurred in four of the five areas. The Nova Scotia study area (Telfer, 1967) was lightly browsed, and balsam was used only sparingly. No mountain ash or quaking aspen was reported in that study area and Rowe (1957) does not mention mountain ash as being a common species in his description of Nova Scotia area. Balsam fir served mainly as a late winter forage in northeastern Minnesota, where forage supplies were not severely browsed by moose (Peek, 1971).

Mountain maple, balsam fir, and willows were important in four areas. Quaking aspen may be important only locally in Newfoundland. With the ex-

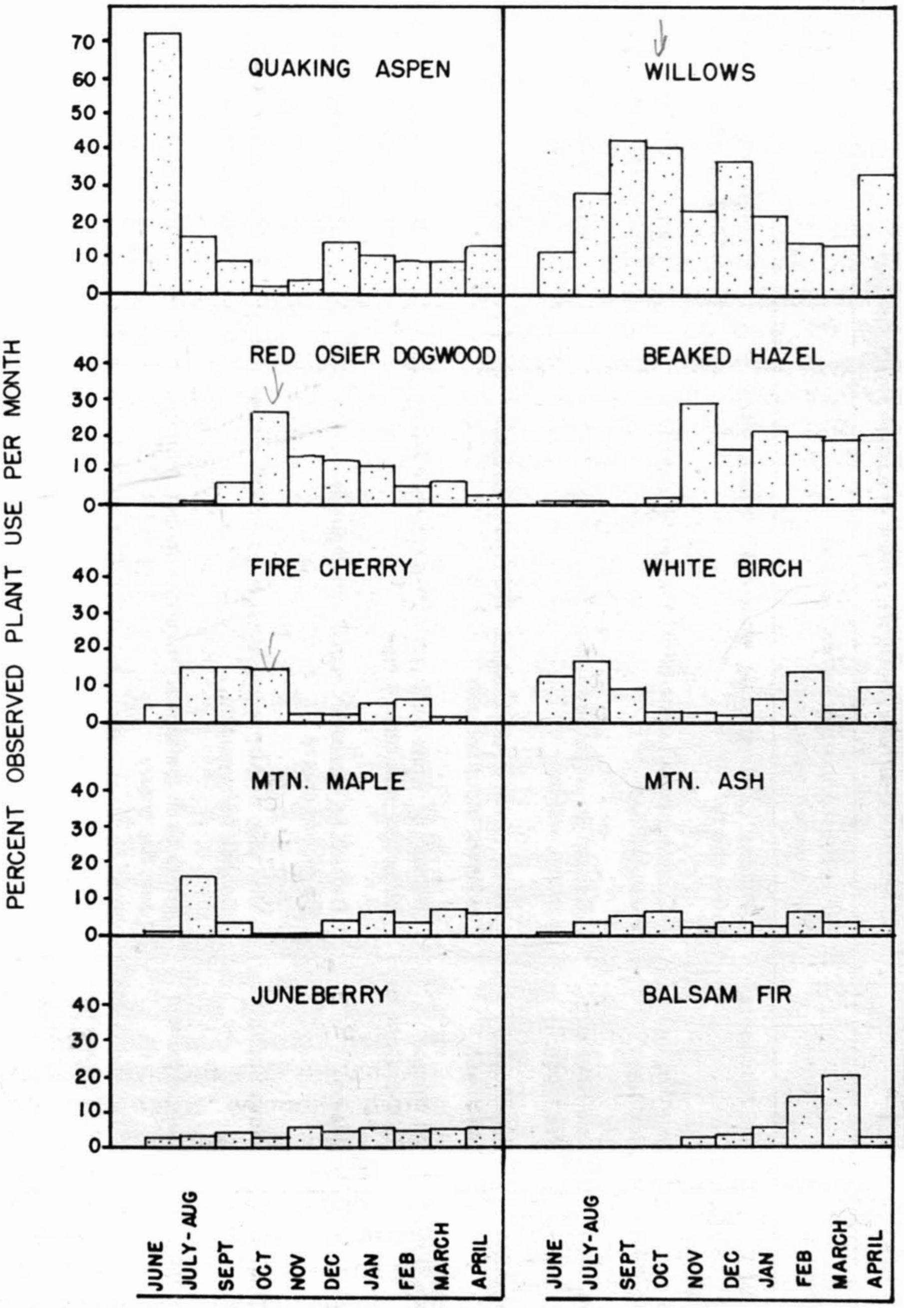

Figure I. Percentage use of ten important browse species by moose in Northeastern Minnesota as determined by feeding site examination, after Peek (1971).

TABLE II

Important browse species to moose in eastern North America

Reference	*Area*	*Five most important browse species in order or importance*	*Remarks*
Peek, 1971	NE Minnesota	Willows, quaking aspen, white birch, beaked hazel, fire cherry	Moderately high moose population Feeding site examination technique
Aldous & Krefting, 1946	Isle Royale Michigan	Quaking aspen, white birch, balsam fir, mountain ash, willows	High moose population (1945) Browse survey technique
Krefting, 1951	Isle Royale Michigan	Balsam fir, white birch, mountain ash, quaking aspen, willows	1948 higher moose population than 1945
Krefting, 1951	Isle Royale Michigan	White birch, quaking aspen, red-osier dogwood, willows, mountain ash	1950 lower moose population than 1945.
Peterson, 1953	St. Ignace Island, Ontario	Balsam fir, white birch, mountain ash, red-osier dogwood, mountain maple	1947-48. Most important species rather than most palatable
Dyer, 1948	Maine	Balsam fir, mountain maple, mountain ash, white birch, fire cherry	1940's, browse survey technique
Telfer, 1967	Nova Scotia	Mountain maple, yellow birch, sugar maple, red maple, Canada honeysuckle	1968 light browsing pressure, stem counts in spring (his Fig. 3)
Pimlott, 1953	Newfoundland	White birch, balsam fir, mountain maple, mountain ash, fire cherry	Stem count method, heavy browsing pressure
Dodds, 1960	Newfoundland	Balsam fir, white birch, raspberry, elderberry, june berries	High moose density, cutover area 1953, '56, '57. Area different from below.
Dodds, 1960	Newfoundland	Balsam fir, willows, alders, mountain maple, rhododendron	Low moose density, stem count method. Area different from above.

ception of areas in which balsam fir and white birch occur only sparingly or are absent, these two species appear to be major forages of moose on eastern North American ranges. Aldous (1952) concluded that white birch produces well under moderate to heavy use and should be used at least moderately if plant growth is to be kept within reach of deer. Bergerud and Manuel (1968) indicate that balsam fir has a strong survival tenacity.

The role of aquatics in the diet of moose

Moose are so frequently observed or photographed in water that it is easily assumed that the aquatic environment is a necessity for the species. However, major populations exist in areas across the continent, such as the Matanuska Valley of Alaska, the Gallatin Mountains of Montana, and the Cobequid Hills of Nova Scotia, where the aquatic habitats are of little significance. By contrasts, aquatics on Isle Royale have been reduced, following heavy use by moose (Murie, 1934; Krefting, 1951).

Use of aquatic areas has been attributed to escape from insect attack (Flook, 1959 ; Ritcey and Verbeek, 1969) and to the presence of palatable plants (Peterson, 1955 ; Murie, 1934 ; deVos, 1956). Use of aquatic vegetation has been correlated with the phenological state of the important forage species, yellow pond lily and wild rice, in northeastern Minnesota (Peek, 1971). Pond lily was used primarily before seed-set, and wild rice was used most before plants floated on the water surface. Use of aquatics was variable between years in that area, apparently dependent upon water levels which may control phenological development, but occurred primarily in early summer. Based on observations by DeVos (1956) and Peterson (1955) in Ontario and Peek (1971) in northeastern Minnesota, moose appeared to begin and end use of aquatics earlier further south.

Table III shows major aquatics used in ten different areas of North America. While considerable variation occurs and is to be expected, yellow pond lily, pondweeds, and horsetail appear to be preferred wherever they occur.

Discussion and conclusions

This survey has covered 41 different reports, 13 from the intermountain west, six from Alaska, and 22 from Canada, Minnesota and Maine. Since Peterson's (1955) review, at least 29 food habit studies have become available. Only nine of these studies include information on summer food habits ; only four studies contain information on yearlong food habits ; only two were longer than one year's duration.

Although the general conclusions are that willows are important to Shiras and Alaskan moose, and that balsam fir, quaking aspen, and paper birch are important to Canadian moose, local variations in forage preferences are important. This is especially relevant because habitat management should favor the locally preferred species. However, species such as red osier dogwood may be highly preferred items in the diet across the entire Canadian moose range, but may vary in abundance enough between areas to affect management considerations. Some species such as juneberry, mountain maple and beaked hazel appear to be preferred in some areas and unimportant in others. Although woody species are generally preferred, several studies suggest that forbs and aquatics may be of high local significance to moose when available and palatable.

It therefore does not appear to be very illuminating from the management standpoint to generalize about moose forage requirements, except that many preferred species appear characteristic of successional stages. Even this may be misleading because willows characteristic of riparian communities, or, of alpine tundra may be extremely long-lived, and mature balsam fir plants may be important winter forage sources.

The various forage species may respond to management practices in different ways. For instance, quaking aspen may sprout more readily and in denser stands from winter cutting than from summer cutting (Stoeckler and Macon, 1956), which in turn will affect the density of associated species, some of which may be more palatable than aspen. Response of various moose forage species to various cutting treatments and to prescribed burning should be further investigated.

Many of these studies do not give a measure of the intensity of utilization of the various species, which causes problems in comparing food habits between areas. Heavy browsing, to the point where forage preference and availability has been affected, may preclude determination of true forage preferences for an area. Food habits stu-

TABLE III

Summarization of aquatic plants preferred by moose in ten areas of North America

Location	*Major plants used*	*Reference*
Bowron Lake, B.C.	Swamp horsetail, burreed, pondweeds	Ritcey & Verbeek, 1969
Wells Gray Park, B.C.	Burreed	Ritcey & Verbeek, 1969
Little Missinaibi Lake, Ontario	Horsetail, eelgrass, pondweed, yellow pond lily, bullrush	deVos, 1958
St. Ignace, Ont.	Pondweeds	Peterson, 1955
Isle Royale	Swamp horsetail, pondweeds, sedges, yellow pond lily, sweet-scented pond lily	Murie, 1934
Algonquin Park Ontario	Yellow pond lily, watershield, sweet-scented pond lily	Peterson, 1955
Yellowstone National Park	Mud plaintain, water milfoil, bladderwort, pondweeds	McMillan, 1953
Alaska	Horsetail, rush, pondweed, burreed	Palmer (in Hosley, 1949)
Jackson Hole, Wyoming	Water crowfoot, leafy pondweed, hornwort, green algae	Houston, 1968
NE Minnesota	Yellow pond lily, wild rice, burreed	Peek, 1971

dies should include information on utilization and availability of forage species.

A related problem that involves considerations beyond moose management is demonstrated by the Newfoundland studies. Apparently a productive and relatively dense moose population can be maintained on a winter diet of paper birch and balsam fir, while other preferred, but less browsing-tolerant species are being eliminated. Since balsam fir was reproducing itself satisfactorily from the timber management standpoint, and the moose population was being maintained, by traditional criteria of wildlife management and forestry, the situation appeared to be satisfactory. However, when elimination or an important reduction occurs of other nonmerchantable species, the situation may be considered to be unduly altered from the standpoint of species diversity. If moose habitat management is to be fully integrated into other land uses, perhaps forage deterioration which does not affect moose densities or timber resources should not be considered the proper management goal. Of course, the problems of achieving adequate moose harvest to actually regulate densities, distributions and forage resources are among the practical limitations which must probably be given more immediate priority. Nevertheless, the wildlife biologist should be aware that resources other than moose or merchantable timber may be adversely affected under such conditions.

There is also a need to distinguish between the effects of natural succession and of previous over-utilization on forage preferences. For instance, balsam fir was important in the diet in an area of virgin timber supporting a low density moose population, as well as in a logged area supporting a much larger population which was intensively browsing the available forage in Newfoundland (Dodds, 1960). The high use of balsam fir in both situations appeared to be primarily related to availability, and may not be a good measure of the actual palatability of this species. Balsam fir appears to be less important when a variety of other species are present.

During the 1940's the use of balsam fir on Isle Royale was considered to be causing deterioration and elimination of the species, while the Newfoundland studies suggested that balsam fir could withstand very heavy use for as long as 12 years and survive. On Isle Royale, heavy browsing had caused quaking aspen to become less available and apparently white birch was replacing it as the most used item because of this.

Besides being influenced by species composition and intensity of grazing, forage preferences may be influenced by weather conditions, and general activity and whims of the animal (Stoddart and Smith, 1955). For instance, Peek (1971) found that increased use of alder during the rutting period in lowland types in northeastern Minnesota could be related to intensive rutting activity, wherein this highly abundant species may serve as displacement feeding source during moments of high interaction between individuals. Many of these food habit studies were made by examinations of browse in spring. The major disadvantage of this type of survey is that changes in forage preference which may occur during the winter cannot readily be determined, as these studies depict woody stem use for the whole period when woody stems are eaten. Moose may browse woody stems during the growing season, as well as during dormancy. When relating moose food habits to range condition-trend, it is important to know when a species is most intensively browsed : the physiological response of a shrub to browsing may be expected to differ according to its phenological state. Young and Payne (1948) found that summer use of four browse species by domestic sheep in northern Idaho had a more detrimental influence upon the plant than fall use.

Dodds (1960) listed several other problems with relying on this method to obtain food habits data : 1) rebrowsing of already browsed stems, 2) overlap in food habits between two or more species present on the same area, 3) early fall frosts may kill terminal shoots of same plants, including elders, which may resemble browsing. Also, this approach does not usually consider use of leaves. Yet, the major advantage of the browse examination, is that one does not have to locate individual animals, a tedious procedure in some habitat types ; moreover, adequate sample sizes may be relatively easy to obtain and only one examination of an area during the year is necessary to obtain information.

Rumen analysis is also fraught with certain problems. Several biases of this technique include : larger plant fragments, being most easily identifiable, may not be representative of the entire rumen contents because of differential digestion between plants (Bergerud and Russell, 1964). Although this may be a minor bias when only woody stems are eaten, certain shrubs such as elder and the honeysuckles may be more quickly digested than balsam fir and willows and the smaller, more delicate stems may also be digested more quickly than the coarser stems, making identification more difficult. For animals which may frequent different habitat types during a feeding period, the method does not readily determine forage preferences for each habitat type. Forage availability and feeding habits of the animals under various conditions are not considered. Ordinarily, only a small number of rumens can be obtained, and one or two samples which may reflect atypical circumstances may misrepresent the usual diet. Analysis is time consuming and often only a small portion of the rumen is identifiable.

Feeding site examinations require extensive field effort, but yield information which can be specific to a given habitat type. Problems using this technique include 1) determining what constitutes "fresh use" or use by the individual which one is following, 2) the fact that use on certain species such as willows and balsam fir may be more readily observable than on species in the herbaceous stratum, such as mushrooms, 3) the subjective determination of what constitutes a "bite" for each plant species, and 4) the problem of securing feeding sites on areas where tracks and sign are more readily observable but where the animal may only be cursorily browsing on its way to a more preferred feeding area which is less readily observable.

The use of "feeding minutes" as by McMillan (1953) in Yellowstone Park is applicable only to areas where the animals and forage species can be readily observed at close range, and when plant composition is simple enough that items in the diet can be readily identified. Also, whether semi-domesticated animals reflect forage preferences of wild conspecifics or not remains to be evaluated. In view of the problems associated with each method of obtaining food habits data, several approaches should be used whenever possible.

It must also realized that a short-term study may not provide adequate information on the forage preferences of moose for any given area. Preferences have been found to vary between years in southwestern Montana and on Isle Royale. And on areas as close together as Yellowstone Lake, the Ruby River of southwestern Montana, and Jackson Hole, Wyoming, summer food preferences appear to be quite different.

Assessment of winter forage sources alone may not provide enough information to determine whether forage supplies are a limiting factor or not; spring, summer and fall diets may have an important influence on production and survival, as indicated for deer (Klein, 1970). Most certainly a knowledge of year-long forage requirements will be important in effecting proper management involving habitat manipulation. Peek (1971) recommended logging practices that would favour creation of areas which could provide spring and fall habitats for moose as an important management procedure in northeastern Minnesota.

Food habits data are probably best interpreted when supporting information on habitat condition and trend, and population performance are also available. Until a measure of actual forage preferences of a population in a given area can be obtained through experimental procedures, habitat and population performance are meaningful ways of determining the adequacy of a diet based on field observation.

It is concluded that these studies do not depict food habits well enough to adequately compare annual, seasonal and habitat-type forage use patterns in all but a few instances. Trends in food habits according to successional sequence are inadequately reported. The influence of weather, precipitation, plant phenology and succession, as well as social behaviour, on forage use should be further investigated. A knowledge of forage requirements and preferences is prerequisite to investigations of nutritive values and digestibility of forage sources.

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NUTRITIVE VALUE OF MOOSE FORAGE

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Résumé

L'auteur passe en revue les travaux concernant la qualité des plantes dont se nourrissent les ongulés sauvages. La discussion porte tant sur l'abondance que sur la variabilité du contenu en hydrates de carbone, en lipides, en protéines de même que sur le contenu énergétique et la digestibilité des plantes impliquées. L'auteur présente les résultats de mesures *in vitro* visant à établir la disgestibilité de trois espèces d'arbustes recherchées par l'orignal (*Alces alces)* sur la péninsule de Kenai en Alaska.

Abstract

A review of evaluations of forage quality for wild ungulates is presented. The amount and variability of carbohydrates, fats, proteins, energy and digestibility of forage are discussed. Results of *in vitro* digestion of three species palatable to moose (*Alces alces)* on the Kenai Peninsula, Alaska, are presented.

Introduction

Qualitative evaluations of forage can help in habitat management and research decisions. First, a basic description of browse quality used with quantitative characteristics is important as a basic description of the range. Second, a combination of quality and quantity of forage is a valuable guide for selecting plant species to measure for long-term trend studies. Third, the combination of qualitative and quantitative measures can be used to compare different successional stages and to determine if there is a certain stage following fires or other disturbance that produces more high quality forage than other stages.

Good quality forage is highly palatable; has optimum levels of various nutrient components; has a high apparent digestibility of the nutrient components; has optimum proportions of volatile fatty acids; has adequate levels of minerals, vitamins and trace elements; and is efficiently converted into the components necessary for the animal body (Dietz, 1970). Reid *et al.* (1959) described forage quality as being dependent upon the rate at which a plant is consumed and the energy value per unit weight of the plant. Barnes (1965) considered the nutritive value of a plant, its nutrient components (including vitamins and minerals), its gross energy and its dry matter digestibility.

Nutrient components

CARBOHYDRATES

Three-fourths of plant's dry matter is carbohydrates, the chief source of energy in forage (Morrison, 1954). Carbohydrates include sugars and starches, celluloses, lignin and hemicelluloses. Most plants store reserve foods

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as starches, thus, greater amounts of sugars and starches are found in the seeds, fruits, and roots. Cellulose and hemicelluloses are more widely distributed throughout most plant tissues. They are less digestible than starches and sugars, but provide the major source of energy for ruminants who have symbiotic rumen bacteria to break them down to a more water soluble form (Dietz, 1970). Lignin forms a complex, relatively indigestible portion of cellulose that makes up the fibrous parts of stems, leaves and roots.

Carbohydrates may be measured in two fractions: nitrogen-free-extract, which contains most of the soluble carbohydrates such as sugars and starches and some of the less soluble ones such as lignin and cellulose, and crude fiber which includes relatively indigestible cellulose and lignins and is usually inversely related to quality. However, crude fiber has variable composition and digestibility and is sometimes more easily digested than nitrogen-free-extract (van Soest, 1966).

Carbohydrate content in plants varies with a number of circumstances: time of the year or season (Dietz *et al.*, 1962); precipitation which, at times, may leach the more soluble nutrients from the plant, leaving proportionately more crude fiber (Laycock and Price, 1970); position with respect to light, plants growing under a canopy or in a shaded area generally containing less carbohydrate than plants growing in full sunlight (Vallentine and Young, 1959; Laycock and Price, 1970); age of the plant, lignin generally increasing as the plant matures (Diez *et al.*, 1962; van Soest, 1966; Laycock and Price, 1970); age of the community to which the plant belongs. In the latter instance, Cowan *et al.* (1950) found that crude fiber increased in four of six moose forage species as forest age increased in British Columbia.

There are also significant differences in carbohydrate content between plant part and species. Dietz *et al.* (1962) noted that deciduous shrubs were a better source of nitrogen-free-extract than evergreen species. Short and Reagor (1970) noted that digestibility in green herbage was greater than in woody twigs, primarily because of higher lignin content in the cell walls of woody twigs. Twigs older than one year have less total available carbohydrates than younger twigs (Cowan *et al.*, 1950; McConnell and Garrison, 1966). McConnell and Garrison (1966) found that, although bitterbrush (*Purshia tridentata*) roots had high concentrations of total available carbohydrates at all seasons, the pattern of seasonal variation was the same as for tops. They felt that browsing had a consideration influence on carbohydrate content, since the plant's carbohydrate metabolism could be more easily disrupted in early spring during rapid growth than after leaf cessation. Thus, winter use of plants would probably have less effect on the growth and health of the plant than summer browsing.

FATS

Fats are distributed throughout the plant but are stored chiefly in fruits and seeds. In nutrition studies, they are presented as fats, lipids, or ether extracts. Bissell and Strong (1955) felt that plant fat was of little importance to deer because so little accumulated in the plant parts eaten. However, plants are an important source of essential fatty acids which provide approximately 2.25 times more energy than carbohydrates and protein (Morrison, 1954).

Like carbohydrate content, fat content in plants is not constant. Dietz *et al.* (1962) and Tew (1970) found that fat content in aspen (*Populus tremuloides*) increased greatly from spring to fall. Dietz *et al.* (1962), however, found no difference in fat content between two successive years in wintering shrubs. Cowan *et al.* (1950) found that fat content in willow (*Salix* spp.) and hazel (*Corylus california*) was higher in current-growth and 1-year-old stems than in older stems, and decreased as forest stand age increased. They also determined that both fat and protein content in species collected in British Columbia were different from those in the same species collected in Pennsylvania.

Dietz *et al.* (1962) determined that evergreen shrubs such as sagebrush (*Artemisia tridentata*) and juniper (*Juniperus scopulorum*) contained more fats than dedicuous shrubs which in turn contained more fats than grasses. Vallentine and Young (1959) obtained similar results with live oak (*Quercus virginiana*) and three grass species.

PROTEIN

Protein is considered the most important plant nutrient, and probably more work has been done to describe protein content in the plant and its variability than for any other nutrient. Protein provides the amino acids used by rumen micro-organisms to effectively digest carbohydrates and fats (Dietz, 1970).

Protein is particularly concentrated in the reproductive parts and active growing portions of the plant such as leaves. Thus, protein content varies considerably with location on the plant stem. Bailey (1967) found significantly higher crude protein in buds of witch hobble (*Viburnum alnifolium*) than in any other portions of the twigs. Cowan *et al.* (1970) reported similar findings with black cherry (*Prunus serotina*) and red maple (*Acer rubrum*). Bailey (1967) also found that twigs collected from the bottom portion of the plant crown had higher levels of crude protein than those in the middle or top of the crown.

Protein content in plants also varies between locations and species. Dietz *et al.* (1962) found that during the summer, plants on deer winter range had less protein than plants at higher elevations on summer range. Tew (1970) found that protein content varied greatly among eight aspen stands.

Dietz *et al.* (1962) reported deciduous shrubs were a better source of protein during the summer than were evergreen shrubs, but the situation was reversed during the winter. On the other hand, Ullrey *et al.* (1964) found that white cedar (*Thuja occidentalis*) in Michigan had lower protein content in winter than aspen.

Protein content generally decreases as the plant matures. Tew (1970) found that the protein content of aspen averaged about 17 percent in June, compared to 11.8 percent in September. Protein content in some stands was in excess of 20 percent during the early growth stages. Protein and soil moisture are positively correlated; thus, protein content is generally highest in the spring and decreases throughout the growing season. Laycock and Price (1970) and Vallentine and Young (1959) found a higher protein content of plants under a canopy than in plants in the open. Leaching also decreased protein content, particularly in mature leaves; this may explain Tew's (1970) finding that young aspen leaves contain higher levels of protein than older ones. During the non-growing season, crude protein content does not change appreciably (Bailey, 1967; Laycock and Price, 1970).

Protein content in forage increases the first year or two after a fire, but decreases thereafter (Dewitt and Derby, 1955; Lay, 1957).

Nutrient content in plants thus varies with the stage of maturity, the part of the plant, and the site upon which it grows. If exact values are needed for nutrient content, they should be obtained from the area where the study is taking place and not extrapolated from other areas. Care should be taken to collect a sample representative of normal variations within the stand. Nutrient content values reported for plants important to moose are provided in Table I.

ENERGY

The animal's requirements for energy exceeds the requirements for all nutrients combined; thus, energy is a highly significant measure of the nutritive value of feeds (Swift, 1957; Hardison, 1959; Reid, 1968). The gross energy of a plant is measured by the heat (calories) it gives off during its complete oxidation or burning. After the plant has been eaten, energy is lost in the feces, in combustible gases and in the urine. The energy remaining after these losses is called the metabolizable energy, and this is used for body maintenance, growth and nutrition of fetuses and milk production. The amount of energy lost in digestion varies with the physiological condition, species and age of the animal and composition of the forage, level of food intake and physical form of the ration. Because of such differences, a measure of gross energy provides a common basis for expressing nutritive value (Dietz, 1970). However, Swift (1957) considered metabolizable energy the most accurate and assumption-free measure of energy. He felt that the most simple and meaningful routine measure of energy was digestible energy — that derived by subtracting energy in the feces from gross energy — because it was highly correlated with metabolizable energy.

Dietz (1972) determined that evergreen and semi-evergreen shrubs and those shrubs with late leaf retention had higher gross energy than deciduous shrubs on deer range in the Black Hills. Gross energy values were greater than 4.0 kcal per gram of plant tissue for all species examined.

Digestibility

An evaluation of forage digestibility determines the amount of nutrients used. Many methods have been used: feeding trials for mule deer (*Odocoileus hemionus*: Smith, 1957; Dietz *et al.*, 1962), white-tailed deer (*O. virginianus*: Ullrey *et al.*, 1964, 1967, 1968, 1969, 1971) and domestic sheep (Crampton, 1957); grazing trials for sheep (Cook *et al.*, 1948); *in vitro* digestion for cattle (Pearson, 1970), elk (*Cervus canadensis*: Ward, 1971), white-tailed deer (Torgerson and Pfander, 1971; Short, 1971), and mule deer (Boeker *et al.*, 1972); and *in vivo* digestion for domestic sheep (Crampton *et al.*, 1960).

Comparisons of plant species digestibility should involve enough animals so that the average digestibilities can be compared statistically. Problems arise here in having enough feeding stalls to determine individual intake and to collect fecal material. Crampton (1957) used a 5 × 5 Latin square design to reduce the number of animals needed, but maintained the animals on each of 5 diets for 60 days. Such collection periods in feeding trials commonly last anywhere from 35 days to 1 year (van Dyne, 1968). Caution should be used when the feeding period is long to insure that normal physiological and behavioral changes in the animal do not influence results (McEwen *et al.*, 1957).

TABLE I

Nutritional constituents in moose forage plants

Species	*Source of Data*	*When Collected*	*Percent by dry weight*			
			Protein	*Ether Extract*	*Crude Fiber*	*Nitrogen-Free-Extract*
Abies balsamea	Bergerud and Manuel, 1968	Growing season	10.4	5.6	26.9	54.2
Abies lasiocarpa	Ullrey *et al.* 1968[1]	Winter	4.0	5.4	13.2	25.1
	Cowan *et al.* 1950	Winter	6.4	12.5	19.2	58.4
	Houston, 1968	November	5.6	7.5	20.2	50.3
Picea engelmanni	Cowan *et al.* 1950	Winter	5.4	6.6	21.6	60.8
Pinus banksiana	Ullrey *et al.* 1967[4]	Winter	3.8	4.2	15.1	22.2
Pinus contorta	Cowan *et al.* 1950	Winter	6.9	8.5	25.0	57.2
Pseudosuga menziesii	Cowan *et al.* 1950	Winter	6.5	7.8	19.9	62.7
Thuja occidentatis	Ullrey *et al.* 1964[3]	Winter	2.7	5.2	13.9	27.5
Populus angustifolia	Houston, 1968	November	6.6	4.4	24.8	50.8
Populus grandidentata	Ullrey *et al.* 1964[2]	Winter	5.0	3.4	14.8	26.6
Populus tremuloides	Cowan *et al.* 1950	Winter	7.1	7.7	28.1	53.0
Populus tremuloides	KNMR, 1963[5]	Winter average	6.8			
	Houston, 1968	November	6.9	4.8	30.0	48.6
Populus tremuloides bark	Cowan *et al.* 1950	Winter	12.7	14.2	24.2	43.1
Populus trichocarpa	Cowan *et al.* 1950	Winter	6.1	15.3	24.1	51.2
Salix spp.	KNMR, 1963[5]	Winter	6.5			
S. alaxensis	Milke, 1969	March	7.0	2.7	33.6	54.5
S. geyeriana	Houston, 1968	November	6.8	6.2	27.2	52.7
S. interior	Houston, 1968	November	5.0	3.0	40.3	40.3
	Milke, 1969	March	5.5	1.4	29.1	62.0
S. myrtillifolia	Milke, 1969	March	6.4	3.5	27.7	59.7
S. niphoclada	Milke, 1969	March	6.1	2.2	32.2	56.7
S. pseudocorda	Houston, 1968	November	6.0	4.4	31.7	56.4
S. wolfii	Houston, 1968	November	6.2	4.3	25.9	55.7
Betula glandulosa	Cowan *et al.* 1950	Winter	6.1	8.2	27.2	56.4
Betula nana	KNMR, 1963[5]	Winter average	7.1			
Betula papyrifera	KNMR, 1963[5]	Winter average	7.5			
	Cowan *et al.* 1950	Winter	7.0	8.4	29.8	52.0
Alnus stichensis	Cowan *et al.* 1950	Winter	10.0	6.6	23.7	57.0
Corylus california	Cowan *et al.* 1950	Winter	6.6	2.0	26.8	59.1
Amelanchier florida	Cowan *et al.* 1950	Winter	5.5	3.2	28.5	58.5
Acer glabra	Cowan *et al.* 1950	Winter	5.9	2.4	33.3	54.2
Acer rubrum	Torgerson, 1971	Winter	4.6	4.7	31.2	48.3
Acer sacchurum	Torgerson, 1971	Winter	5.7	2.6	31.6	44.8
Purshia tridentata	Houston, 1968	November	13.4	5.2	18.1	59.8
Purshia tridentata	Dietz *et al.* 1962	Summer	9.2	6.0	25.3	56.5
	Dietz *et al.* 1962	Early winter	7.7	5.1	28.9	56.4
	Dietz *et al.* 1962	Peak of winter	8.2	5.0	29.0	56.1
	Dietz *et al.* 1962	Late winter	11.0	13.7	18.0	53.9
Cornus stolonifera	Cowan *et al.* 1950	Winter	4.8	4.9	28.8	57.5
Vaccinium vitis-idaea	Scotter, 1965	June	6.3	2.8	15.6	72.9
	Scotter, 1965	September	7.9	2.8	20.4	66.2
	Scotter, 1965	March	6.3	3.2	17.7	70.6
Peltigera	Scotter, 1965	Year average	17.5	2.3	25.3	52.8
Cladonia	Scotter, 1965	Year average	2.6	1.3	38.4	56.8

[1] Presented as percentage of wet weight. Plant contained 50.3% moisture.

[2] Presented as percentage of wet weight. Plant contained 46.9% moisture.

[3] Presented as percentage of wet weight. Plant contained 51.8% moisture.

[4] Presented as percentage of wet weight. Plant contained 51.7% moisture.

[5] Kenai National Moose Range, 1963.

Some plant species are more digestible when eaten along with other species than when eaten alone, such as sagebrush (Hardison, 1959; Short, 1966; Nagy *et al.*, 1967). However, Forbes *et al.*, (1946, cited in van Dyne, 1968:61) reported very low variation in digestibility among 22 sheep fed a constant diet. Others have used as few as four animals to obtain mean digestibility of a ration (Dietz *et al.*, 1962). It appears that the best approach to a feeding trial is to use enough animals for each ration so that the results of a single testing period can be compared statistically.

Although there have not been many *in vitro* trials specifically for wild ruminants, this method is becoming more commonly used. *In vitro* trials involve digesting a dried, finely ground portion of plant material in a container with rumen inocula and a buffer-nutrient media under anaerobic conditions. The two-stage method of Tilley and Terry (1963) takes 4 days and the number of plant samples is limited only by space.

Morris and Kovner (1970) list three major concerns when interpreting the results of an *in vitro* trial: 1) Was the behavior of the inoculum donor the same as that of a free-ranging animal, 2) were the inoculum obtained from the donor the same as that of a free-ranging animal, and 3) were the forage samples used in the trial the same species being grazed by free-ranging animals? Tilley and Terry (1963) stress the importance of maintaining proper pH, temperature and anaerobic conditions during the first stage of their method. They also recommend taking inoculum from actively ruminating animals since inoculum from animals not recently fed, digested fiber poorly and increased the variation between digestion tubes.

Table II shows results of an *in vitro* digestion trial using moose rumen material as inoculum for digesting three forage species important to moose on the Kenai National Moose Range. Tilley and Terry's (1963) method as modified by Pearson (1970) was used. Each mean, except that of lowbush cranberry (*Vaccinium vitis-idaea*), was based on digestion coefficients obtained from five individual plants collected within close proximity of each other. While showing that willow (*Salix arbusculoides*) and lowbush cranberry were better digested, the trial also showed that there was not much variation among individual birches undergoing differing intensities of browsing.

TABLE II

Percent digestibility of three important browse species for moose, Kenai Peninsula, Alaska

	Paper Birch			*Willow*	*Lowbush Cranberry*
	Heavy use site	*Normal use site*	*Exclosure*		
February trial					
Mean	24.7^1	23.8^1	26.9^2	34.5^3	36.0^3
Std. Dev.	2.27	2.59	2.12	3.43	3.58
March trial					
Mean	24.7^4	23.6^4	25.0^4	37.3^5	37.4^5
Std. Dev.	2.14	3.02	2.34	4.10	1.58

^{1,2,3,4,5} Means superscripted by same number were not significantly different from each other, but were different from other means ($p<0.05$).

McCullough (1959) ran correlations between crude protein, crude fiber, metabolizable energy, and digestibility, using data from 70 experiments found in the literature. His conclusions were (p. 221):

> "The general lack of correlation between crude protein and metabolizable energy is not surprising since most forages are adequate in protein and the small correlation would be expected since protein content primarily affects protein digestion. The highly significant negative correlation (-0.908) between crude fiber and dry matter digestibility and (-0.932) between crude fiber and metabolizable energy represents the general decline in value due to complex carbohydrates which are not utilized by rumen micro-organisms. The increasing levels of crude fiber also represent a gradual depletion of energy nutrients since the crude fiber is replacing useable nutrients."

Quality of moose forage

Little work has been done to evaluate the quality of plants moose eat. Cowan *et al.* (1950) conducted the first comprehensive study of moose forage quality in forest stands 6, 20, and 70 years old in British Columbia. They concluded that the youngest stands in forest succession contained the largest quantities and the most nutritious forage. The importance of early successional stages to moose is well documented (Lutz, 1960; Spencer and Hakala, 1964; Geist, 1971).

The few values obtained for nutrient content of moose forage have generally been quite similar (Table I). Houston (1968) found little difference in the nutrient content among browse species in Wyoming. He noted that 18-month-old stems of blueberry willow (*Salix pseudocordata*) contained more crude fiber and less protein, ether extract, and nitrogen-free-extract than 6-month-old stems; similar to what Cowan *et al.* (1950) found with hazel and willow. Milke (1969) found that Alaskan willows had similar protein content but a lower fat content than the willows Houston (1968) examined in Wyoming. In both studies, interior willow (*Salix interior*) had a lower protein and fat content than did the other willows.

Few of the plants in Table I have a protein content as high as commercial feed supplements and many do not reach the 7 percent level Dietz *et al.* (1962) recommended as minimum for browse on good deer range. Yet moose survive quite well in areas where these "deficient" plants are the major food source. Red-osier dogwood (*Cornus stolonifera*) is a prime moose forage in northern Minnesota and is low in protein. Milke (1969) reported that three of the four willow species he examined contained less than 7 percent crude protein. Forage quality cannot be the sole characteristic in determining the quality of moose range.

Conclusions

Research in forage quality has been an important facet of the live-stock industry. In that industry, where weight gain or milk production are important, there has been extensive use of supplemental feeding and research into forage quality has played an important part in determining what makes up a high quality ration. The nutrient content in forage plants, and minimum requirements for energy, protein and the various other nutrients have been investigated but few have been able to put into practice this knowledge to improve moose range. In much of the moose range in North America, moose are not the sole occupant of the range nor is moose management the primary objective of the land manager. In fact, our opportunities to manage moose range have often come as a secondary benefit from a timber operation or fire.

Presently, more emphasis is being placed on controlled burning to improve wildlife habitats. In some parks and wildlife refuges, fire can be an important tool for wildlife management. The Kenai National Moose Range in Alaska has used tree crushers to speed the recovery of forage after a fire, and these machines can also be used to reduce in height out-of-reach forage species. When large-scale changes in the habitat are planned, the wildlife manager has the opportunity to give advice about improving moose range, and it is at this time that he has the opportunity to use the knowledge gained from browse quality research to make recommendations that may help improve the quality of the range for moose.

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REVIEW OF ENERGY REQUIREMENTS AND RUMEN FERMENTATION IN MOOSE AND OTHER RUMINANTS

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Résumé

Les auteurs dressent un bilan saisonnier des besoins énergétiques et de l'utilisation de la nourriture chez l'orignal (*Alces alces*) en le comparant à celui obtenu chez d'autres ruminants sauvages et domestiques. L'absence de mesures précises du métabolisme basal chez l'orignal et la grande variabilité de ce paramètre chez les autres ruminants domestiques et sauvages rendent très difficile l'estimation de leurs besoins énergétiques. Les auteurs posent comme hypothèse de départ que le métabolisme basal (BMR) obéit à la relation suivante:

$$\text{BMR (kcal/jour)} = 70\ W^{.75}$$

où W représente le poids corporel en kg; ils estiment en outre que le régime d'entretien nécessite 1.7 fois la quantité d'énergie requise par le métabolisme basal. Les besoins énergétiques des femelles gestantes s'accroissent soudainement en mars, en raison du développement du foetus et ces besoins vont atteindre un niveau de trois à quatre fois plus élevé que ceux qu'exige le métabolisme basal durant le mois de juin, conséquence de la lactation et de la lipogénèse.

Les auteurs décrivent les principales différences saisonnières dans le contenu du rumen et dans la consommation de nourriture. Le degré de remplissage du rumen chez la femelle atteint un maximum au début de l'hiver, un minimum à la fin du printemps et une valeur intermédiaire l'été. Le pourcentage de matières sèches dans le contenu du rumen passe par un maximum l'hiver et par un minimum l'été. Le filtrat provenant du lavage du contenu du rumen avait une teneur plus élevée en protéines brutes et plus faible en matières cellulosiques et lignine durant l'été que durant l'hiver, ce qui reflète la meilleure qualité de la nourriture consommée durant la saison chaude. Les sources bibliographiques consultées proposent des estimés fort variables de la quantité de nourriture ingérée, mais toutes semblent établir que la consommation de nourriture est plus forte durant l'été que durant l'hiver. Les auteurs considèrent que les femelles adultes consomment jusqu'à trois et même quatre fois plus de matière sèche l'été que l'hiver. Ils estiment également que l'augmentation du degré de remplissage du rumen et la diminution de la consommation de nourriture durant l'hiver sont, d'une part, le résultat d'un ralentissement dans le transit d'une nourriture de qualité inférieure et, d'autre part, d'une réduction volontaire de la consommation par l'animal.

Environ 57 pourcent de toute l'énergie digestible chez les ruminants provient des acides gras volatils (VFA) dérivés de la fermentation microbienne des hydrates de carbone et des protéines de la diète. Les auteurs ont mesuré les changements saisonniers dans la production d'acides gras volatils chez des animaux à l'état sauvage et ont établi que celle-ci est une fonction directe de la qualité de la nourriture. En hiver, la moyenne du taux de production d'acides gras volatils se situait aux environs de 18 μeq VFA/ml de liqueur du rumen par heure tandis que durant l'été, la moyenne était de 60 μeq VFA/ml par heure.

L'orignal subit des changements considérables de poids corporel durant l'année et ces changements correspondent à des changements dans la production d'énergie dérivée des acides gras volatils. L'énergie utilisable pour le métabolisme (ME), calculée d'après l'estimé de production d'acides gras volatils, passe de 7,300 kcal/jour pour une femelle, l'hiver, à 20,900 kcal/jour pour cette même femelle durant les mois d'été alors qu'elle est en lactation. Les auteurs évaluent à 6,000 kcal par jour la quantité d'énergie utilisable requise pour le métabolisme basal. Or, durant l'hiver, environ 3,900 kcal par jour doivent être obtenus du catabolisme des graisses et des protéines de réserve pour compenser l'insuffisance de l'énergie fournie par le broutement tandis que l'été, environ 7,600 kcal par jour sont mis en réserve sous forme de protéines et de graisses. Les effets de la malnutrition indiquent que toute réduction, soit de la quantité, soit de la qualité de la nourriture réduit la flore bactérienne ainsi que les taux de fermentation.

Les auteurs expriment enfin divers points de vue sur l'à propos d'utiliser l'un ou l'autre des paramètres liés à la fonction du rumen dans le but d'évaluer la condition physiologique de divers ruminants ainsi que la qualité de leur habitat.

Abstract

A review of seasonal energy requirements and utilization of food by moose, (*Alces alces*) with reference to other wild and domestic species, is presented. Energy requirements are difficult to estimate because no metabolic studies have been conducted with moose and comparative data from other wild and domestic species differ widely. It is assumed that basal metabolic rate (BMR) conforms to the empirical relationship of weight to metabolic rate, where

$$\text{BMR (kcal / day)} = 70\ W^{.75}$$

and where W = body weight, in kg and that maintenance demands approximate 1.7 × BMR. Energy requirements of female moose begin to increase significantly in March due to pregnancy and reach a peak of three to four times BMR in June, due to lactation and lipogenesis.

Major seasonal differences in rumen contents and estimates of food consumption by moose are described. Rumen fill in cow moose was greatest during early winter, lowest during late spring, and intermediate during summer. Percent dry matter was lowest during summer and highest during winter. Washed rumen contents were higher in crude protein and lower in acid detergent fiber and lignin during summer than during winter, reflecting the superior quality of summer forage. Estimates of food intake by moose vary greatly in the literature, although there is considerable evidence indicating that a greater quantity of food is consumed during summer than during winter. Dry matter consumed by adult females was estimated to be three to four times greater during summer than during winter. Increased rumen fill and decreased food intake during winter apparently result from slow passage of low quality food which restricts additional food intake, and from voluntary reduction of forage consumption.

Volatile fatty acids (VFA) produced by rumen microbes from the fermentation of dietary carbohydrates and proteins constitute approximately 57 percent of the digestible energy of ruminants. VFA production, which is directly related to food quality, was determined seasonally on free-ranging moose in interior Alaska using the "zero time rate" method. Production rates varied from a mean low of 18 μeq VFA/ml rumen liquor/hr during winter to 60 μeq VFA/ml rumen liquor/hr during summer.

Moose undergo a large seasonal change in body weight which corresponds closely to seasonal rates of VFA energy production. Metabolizable energy (ME), calculated from estimated VFA production, increased from 7,300 kcal/day in females during winter to 20,900 kcal/day in lactating moose during summer. It was estimated that approximately 6,000 kcal/day of ME was required for BMR. During winter an estimated average of 3,900 kcal/day was obtained from catabolism of fat and protein reserves to meet the energy requirements not provided by forage, while during summer 7,600 kcal/day of fat and protein were deposited.

A review of effects of malnutrition on rumen function show that decrease in food quantity or quality depresses microbial populations and rates of fermentation.

The value and practical application of using various parameters of rumen function to evaluate nutritional status of ruminants and quality of the habitat are discussed.

Introduction

As the management of wildlife species becomes more intensified, the study of wildlife nutrition becomes more critical. Food habits data were once the only food resource information considered important. However, certain deficiencies in this approach have promoted studies of greater scope to better understand relationships between wild ruminants and their food resources.

In vitro digestibility studies have been undertaken on foods of wild ruminants to rate the quality or usefulness of various forages to the animal (Short, 1971; Ward, 1971; Oldemeyer, 1974). Clinical blood chemistry techniques have recently provided a new avenue of approach to gain insight into the nutritional status of wild ungulates (LeResche and Davis, 1971; LeResche *et al.* 1974). Digestibility and maintenance requirements have been studied on wild ruminants held in pens and provide information on how the animals may utilize various diets in the wild (Ullrey *et al.* 1967, 1969, and 1971). Field studies of rumen function have enabled investigators to evaluate nutrition status and energy balance by estimating the energy wild ruminants derive from their diet (Coady and Gasaway, 1972). Wildlife nutrition must be concerned not only with availability and utilization of forage species, but also with the nutrient requirements of ruminants and their ability to convert plants to animal tissue.

The following discussion reviews seasonal energy demands for basal, maintenance and production requirements of moose, and the digestive processes which convert food into useful energy.

Energy requirements

In this review, gross energy of food consumed by an animal will be partitioned into apparent digestible and metabolizable energy. Apparent digestible energy (DE) is that portion of gross energy not excreted as feces, and it represents a first approximation of the efficiency of food digestion. Metabolizable energy (ME) is that portion of DE not excreted in urine or lost as gaseous products of rumen fermentation. ME is a measure of the energy available to or needed by an animal at a particular time for all metabolic requirements, and may be used for work, heat, and tissue synthesis.

Metabolic rate of homeotherms varies greatly within and between species, since it must meet all requirements for diverse physical and physiological activities. Basal metabolic rate (BMR) is the measure of a mammal's minimum energy demand and has been widely used for intra- and interspecies comparisons and as a base-line for computing effects of other metabolic functions. Energy requirements for maintenance (thermoregulation, activity, and specific dynamic action) and for production (i.e. body growth, gestation, milk production) are requirements above BMR and, together, these processes constitute the total energy requirements of an animal. By integrating the temporal pattern of metabolic rate, a seasonal energy budget can be calculated and the total impact of both the animal on its food supply and the environment on the animal can be evaluated.

BASAL METABOLIC RATE (BMR)

BMR is a measure of caloric requirements for minimum physiological functions. Ideally, test conditions for measuring BMR include postabsorptive state, complete inactivity, and "comfortable" microclimate (Benedict, 1938). In practice, however, these conditions may be difficult if not impossible to attain, particularly with wild species. The extent to which psychological, physiological and physical stresses on an animal can be reduced vary greatly among individuals and species. Consequently, the circumstances appropriate for measuring BMR will vary with the species, and the accuracy of measurement will largely depend upon the extent to which stresses can be minimized. While strict use of the term BMR may frequently not be applicable, it is a useful comparative concept, providing the technical difficulties of its measurement are realized.

It is well known that BMR of mammals increases as an exponential function of body weight. Brody and Proctor (1932) and Kleiber (1961) concluded from comprehensive studies that average BMR of mammals equals $70W^{.734}$ and $70W^{.75}$, respectively where BMR = kcal/day and W = body weight in kg. Differences between the two equations are strictly pedantic, although Kleiber's relationship, adopted by the Third Symposium on Energy Metabolism for Interspecies Comparisons (Blaxter and Wainman, 1964), has been more widely used in recent years.

Another useful metabolic term is fasting metabolic rate (FMR), which is greater than BMR by the amount of energy expended is standing and small postural movement during measurement (Silver *et al.*, 1969). Kleiber (1961) preferred measurement of FMR over BMR since he felt it better represented minimum energy requirements among animals unable to remain voluntarily inactive. Blaxter (1962) indicated that differences between BMR and FMR are small among domestic ruminants. However, differences may be greater among wild species due to stress imposed by captivity.

FMR of wild ungulates varies widely among species, within species measured during different seasons, and even within species measured during the same season (Table I). FMR's range from 67.8 kcal/kg$^{.75}$/day to 143.6 kcal/kg$^{.75}$/day. Silver *et al.* (1959) working with white-tailed deer (*Odocoileus virginianus*) during winter and summer, and Maloiy *et al.* (1968) working with red deer (*Cervus elaphus*) recorded metabolic rates similar to those predicted for animals of their size (Table I). However, most values for FMR range from 15 percent to 100 percent higher, and average approximately 40 percent greater than the predicted BMR. The origin of these differences is not known, although numerous factors associated with age, reproductive state, nutrition, activity, insulation, and acclimatization must be considered (Whittow, 1971).

Estimation of BMR of moose is difficult, particularly considering that metabolic data have not been reported for the species. Silver *et al.* (1969, 1971) and McEwan and Whitehead (1970) indicate major seasonal differences in BMR of white-tailed deer and resting metabolic rate of reindeer (*Rangifer tarandus*) respectively. Thus, a constant relationship between heat production and a fixed exponent of body weight may not be adequate to cover all species under all situations. For the purpose of this review and pending appropriate metabolic studies, we assume that moose under basal conditions obey Kleiber's (1961) empirical formula relating metabolims to body weight. Therefore, BMR of a 425 kg (937 lb) animal, for example, equals $70 \times 425^{.75}$ or 6,550 kcal/day. The BMR shown in Figure 1 was calcilated from Kleiber's formula and was considered to be constant throughout the year.

MAINTENANCE ENERGY

Maintenance energy is a composite of requirements for basal or fasting metabolism, thermoregulation, activity associated with obtaining food and water, and the heat increment or "specific dynamic action" of digestion and assimilation of food. It is that portion of the metabolizable energy required for existence at a minimum level of activity, where energy retention by the animal is zero. While clearly an underestimate, BMR does represent a significant portion of maintenance energy requirements.

Energy requirements by moose for thermoregulation in the cold have not been studied. Scholander *et al.* (1950) suggest that most large northern mammals do not increase their metabolic rate until temperatures are at least minus 40°C. In agreement with this hypothesis (Hart *et al.*, 1961) found no increase in metabolic rate of a 9-month old caribou (*Rangifer tarandus*) from 25°C to minus 55°C. Moen (1968) calculated that a 70 kg fasting deer standing under clear night skies with a heat production of 75.1 kcal/kg$^{.75}$/day could maintain body temperature at an ambient temperature of -40°C and wind velocity of nearly 2 mph. Fed deer could tolerate a wind velocity of over 8 mph. at -40°C without increasing their metabolic rate (Moen, 1968).

Factors such as relatively large body size, decreasing the surface to weight ratio, heat production associated with rumen fermentation, and behavioral responses assist in conserving heat and enhance cold tolerance of moose. Activity patterns observed for moose agree with this, as they may bed in open areas during very cold Alaska temperatures, rather than seeking heavy cover where a more favorable energy flux usually exists. Also, substantial movements of radio-collared moose during temperatures of -40° to -50°C have recently been recorded (Coady, 1974). Markgren (1966) noted that captive moose calves in Sweden did not appear inconvenienced by temperatures as low as −28°C and mild wind. Although high winds during very cold temperatures are unusual in most areas, these conditions could create an unfavorable energy balance for exposed moose. However, behavioral response in posture and habitat selection to cold temperature and high wind would bring the animal in a more favorable micro-

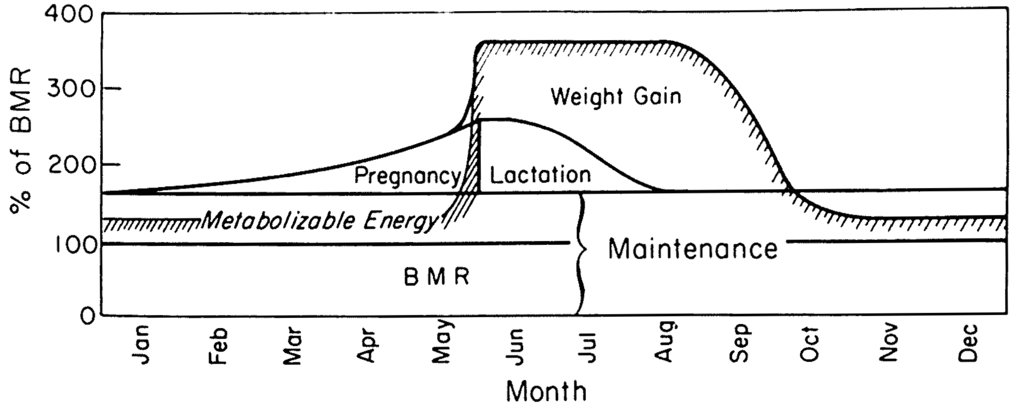

Figure 1. Seasonal energy required and metabolizable energy produced by adult female moose in interior Alaska.

climate. Therefore, it seems unlikely that metabolic thermoregulation ever constitutes a significant energy requirement for moose.

While activity patterns of moose have been studied and reviewed by numerous workers (Murie, 1934; Peterson, 1955; Denniston, 1956; Geist, 1959; 1963; Berg, 1971), duration of daily activity has rarely been determined. Restricted movements and small home range of moose during winter, particularly during periods of deep snow, have been suggested by numerous authors (cf. Coady, 1974). However, limited movement patterns do not necessarily indicate reduced activity and energy expendure. LeResche and Davis (1971) found that tame moose in Alaska fed for an average of 7.7 hours during 12 daylight hours in winter, and for 6.8 hours during 18 daylight hours during summer. No observations were made during periods of darkness. Knorre (1959) found that moose were active, primarily in feeding, 42 percent of the 24-hour day during winter and 58 percent of the 24-hour day during summer. Similar observations have been made for other ruminants. Silver (1971) recorded lowest daily activity and feed consumption for white-tailed deer during winter, and Silver *et al.* (1969) cited unpublished data indicating reduced activity and food consumption of white-tailed deer during winter.

The above studies suggest that duration of activity may be similar or somewhat less for moose during winter than during summer. Reduced activity conserves energy and may be particularly important in minimizing metabolic requirements when snow conditions hinder movement (Coady, 1974).

While maintenance energy for moose is uncertain, maintenance requirements for wild and domestic species have been estimated. Short and Golley (1968) concluded that maintenance energy demands for cattle *(Bos taurus)* in normal range activities, and perhaps for wild herbivores under usual range conditions, is 15 percent above FMR. Blaxter (1962) generalized that maintenance requirements of ruminants averaged 36 percent greater than FMR.

The above estimates appear low, especially considering that increased resting metabolic rate (RMR) of fed but quiet animals may be considerably greater than FMR (Table I). Brockway and Maloiy (1968) found an increase of 29 percent in RMR over BMR in red deer, while McEwan and Whitehead (1970) found an increase of 49 percent in RMR over BMR in reindeer during winter. Similarly, Hart *et al.* (1961) measured an increase of 49 percent in RMR of caribou during winter over BMR determined by McEwan (1970) for caribou during the same season. Energy demands by free ranging ungulates for movement would further elevate requirements above that for RMR.

Brody (1945) suggested that maintenance energy requirements for large herbivores average approximately 2 × BMR. Ullrey *et al.* (1969) calculated maintenance requirements of white-tailed deer during winter to be 1.9 times BMR, where ME = 131 kcal/day and BMR = 69 kcal/kg$^{.75}$/day. However, the excitable nature of white-tailed deer may increase maintenance re-requirements above that required for less excitable moose.

Based on partitioning available energy between BMR, maintenance, and tissue production, we estimate that maintenance requirements for moose range between 1.5 and 1.8 × BMR, and may average near 1.7 × BMR, as shown in Figure 1. Since metabolic requirements for both thermoregulation and activity are considered to remain relatively constant throughout the

TABLE I

Fasting (FMR) and resting (RMR) metabolic rate of wild ruminants

Species	*Season*	*Number of animals*	$\bar{X}$ *body wt (kg)*	*Age (yrs.)*	*Air Temp.* (°C)	*Heat Production FMR (kcal/* $W^{.75}$/day)	*RMR (kcal/* $W^{.75}$/day)	*Reference*
White-tailed Deer	Winter	2	56.8	1 ½-2	−0.4 to 3.9	67.8		Silver *et al.* 1959
White-tailed Deer	Summer	2	45.6	1 ½-2	21.2-21.5	71.2		Silver *et al.* 1959
White-tailed Deer	Winter	17	65.3	Adult	16-21.5	97.1		Silver *et al.* 1969
White-tailed Deer	Summer	9	58.6	Adult	16-21.5	143.6		Silver *et al.* 1969
White-tailed Deer	Winter	4	30.6	Fawns	16-21.5	90.2		Silver *et al.* 1969
White-tailed Deer	Summer	2	36.1	Fawns	16-21.5	130.8		Silver *et al.* 1969
White-tailed Deer	Winter	4	67.6	2.5-11.5	17.50-21.5	81.0		Silver *et al.* 1971
White-tailed Deer	Summer	2	49.0	2-11.5	17.4-19.3	139.8		Silver *et al.* 1971
Caribou	Winter	2		9 mos.	15	96.8		McEwan, 1970
Reindeer	Winter	3	74.7	Calves	15	102	157.4	McEwan & Whitehead, 1970
Reindeer	Summer	3	73.3	Calves	15		196.9	McEwan & Whitehead, 1970
Caribou	Winter	1	31.7	9 mos.	25 to -52		144.0	Hart *et al.* 1961
Reindeer		1	100	5-6	−10		132.8	Hammel, 1962
Pronghorn		4		4 mo-6 mo	21	92.8		Wesley, 1969
Red Deer		2	58	Adult	18	90.0	116.0	Brockway & Maloiy, 1968
Red Deer		1	45-50	—	—	70.0		Maloiy *et al.* 1968
Wildebeest		1	—	—	—	91.0		Rogerson, 1966
Wildebeest		1	—	—	28	104.3		Rogerson, 1968
Eland		2	—	—	28	111.2		Rogerson, 1968

year, seasonal maintenance requirements probably follow a similar pattern. Therefore, the maintenance energy requirements during both winter and summer of a 425 kg moose with a BMR of 6,550 kcl/day is estimated to be 1.7 × 6,550 or approximately 11,000 kcal/day.

REPRODUCTION

Energy requirements for pregnancy, lactation, and weight gain are major processes in adults which elevate metabolic rate above the maintenance level. A limited number of studies have been conducted to determine energy requirements among domestic ruminants for various productive processes, while few, if any, such studies have been undertaken with wild species.

Measurements of energy requirements for gestation among domestic ruminants differ widely, but generally indicate a substantial energy accumulation in fetal material and increase in maternal metabolism occurs only during the last one-third of pregnancy (Flatt and Coppeck, 1965; Flat *et al.*, 1969; Halls, 1970; Moe and Tyrrell, 1972). For example, Moe and Tyrrell (1972) found that ME requirements for cattle increased from 15 percent to 75 percent above that for the non-pregnant animal during the last one-third of pregnancy, representing an increase from 21 percent to 107 percent over BMR. Assuming a gestation period for moose of approximately 243 days (Peterson, 1955) and a parturition date of June 1, a significant increase in energy requirements for fetal development probably begins in early March.

Reid (1968) suggested that ME required for gestation can be estimated as 350 kcal/kg/day. Based on fetal growth rates of Alaskan moose (Rausch, 1959), ME for gestation increases form 875 kcal/day in March to 5,250 kcal/day at term near June I (Table II). Since weights of pregnant moose in interior Alaska range near 360 kg during spring, ME requirement per kg body weight^{75} of the female increases from 15 percent to 91 percent over BMR of the non-pregnant animal (Table II). We assume that energy requirements for gestation in moose are similar to those for cattle, and range from approximately 15-20 percent of BMR after two-thirds of the pregnancy in early March to nearly 100 percent of BMR near term, as shown in Figure 1.

Production of milk by wild ruminants has received little attention, although milk intake by moose calves (Knorre, 1959, 1961) and by reindeer and caribou calves (McEwan and Whitehead, 1971) has been studied. By weighing before and after nursing, Knorre (1959) found maximum milk

TABLE II

Fetal growth rates and energy requirements by moose for gestation in interior Alaska. Fetal growth rates from Rausch (1959)

Date	*Fetus wt (kg)*	*ME Requirement (kcal/day)*	*ME Requirement per $kg^{.75}$ of (kcal/day)*	*% Increase over BMR*
March 1	2.7	875	10.6	15
April 1	4.8	1680	20.3	29
May 1	8.8	3080	37.3	53
June 1	15.0	5250	63.5	91

consumption by moose calves in Russia to range from 1.5 to 2.0 liter per day during June, and to decrease during July to approximately 0.5 liter per day in August. Total milk consumption per calf until weaning in August or September was between 100 to 200 liter. Knorre (1961) noted that after 1.5 to 2 months of age the diet of calves consists primarily of solid foods. We have found considerable amount of herbaceous material in rumen contents of calves in Alaska towards the end of June.

To calculate metabolic requirements for lactation in moose, the gross energy of milk is required. Overman and Gaines (1933) indicated that caloric value of milk can be estimated by a formula where kcal/kg milk = 304.8 + 114.1 × F, and F = percent milk fat. Although fat content of moose milk varies among individuals and with stage of lactation, 10 percent may be considered an average value (Knorre, 1959, 1961; Cook *et al.*, 1970). Therefore, gross energy of moose milk can be calculated as 304.8 + 114.1 × 10 or 1,446 kcal/kg. It follows that maximum milk consumption of two liter/day would represent a caloric intake of about 2,900 kcal.

Knorre's studies (1959, 1961) indicate that milk consumption by moose is somewhat lower than would be predicted from studies on reindeer and caribou, and high-yielding domestic species. Using tritiated water McEwan and Whitehead (1971) calculated that average milk intake of reindeer and caribou calves during the first month of lactation ranged between 1.2 and 1.8 liter/day, or 2,760 to 4,140 kcl/day, assuming a caloric equivalent for reindeer and caribou milk of 2,300 kcal/liter. Luick and White (1971) reported that milk consumption by reindeer calves during the first two weeks of life averaged approximately 0.95 liter/day. This represented an energy intake of approximately 1,900 kcal/day.

If caloric requirements of moose calves for milk were similar to those for reindeer and caribou calves, milk consumption could be estimated. Based upon metabolic body size, if reindeer and caribou calves weighing 5 kg (5 $kg^{.75}$ = 3.34 kg) consume an average of 1,900 kcal/day in milk (Luick and White, 1971), then moose calves weighing 15 kg ($15^{.75}$ = 7.62 kg) consume 4,300 kcal/day as milk. Since caloric value of moose milk is approximately 1,446 kcal/kg, moose calves would consume approximately three liter per day.

Milk production by domestic animals is also considerably higher than that measured for moose. Payne and Wheeler (1968) suggested that milk yield in dairy cattle is represented by the equation kcal/day = 124 $W^{.75}$, where W = body weight of the female in kg. Since average weight of lactating moose in June was approximately 380 kg ($380^{.75}$ = 86.1 kg) (Table III), the calculated milk production based on dairy cattle would be 10,676 kcal/day or 7.4 (liter/day). Both estimates of mild-yield of 3 liter/day and 7.4 liter/day are considerably higher than was measured by Knorre (1961), even by intensive experimental milking.

TABLE III

Body weight and total length of lactating and non-lactating moose over two years of age during June in interior Alaska[1]

	No.	*Mean*	*Range*
Non-Lactating			
Weight (kg)	4	429	395-463
Length (cm)	4	264	242-275
Lactating			
Weight (kg)	4	380	367-390
Length (cm)	4	276	269-284

[1] Coady, unpublished.

Based largely upon the above work on reindeer and caribou, we feel that milk production by wild moose during the first few weeks after birth of a single calf is at least 3 liter/day, and may be greater.

Metabolizable energy is converted into gross milk energy with an efficiency of approximately 70 percent, although it is influenced by a number of factors such as quality of diet and stage of lactation (Reid, 1968; Blaxter, 1962). Therefore, approximately 5,600 kcal of ME are required daily to produce 3 liter of milk with a gross energy of 4,300 kcal. This amounts to 65 kcal/380 kg$^{.75}$ day, or a value almost equal to one BMR of the female during spring, as shown in Figure 1.

Metabolic costs of lactation are illustrated by lower body weights of lactating moose compared with those of dry females (Table III). Average body weight of four non-lactating adult females during late June in interior Alaska was 12 percent greater than that of lactating moose, in spite of a longer total length indicating larger average body size for the lactating animals. Lactating moose had gained approximately 20 kg while non-lactating moose had gained approximately 70 kg at the end of June over average spring weights of 360 kg. Sequential weights of individual females with and without calves at the Kenai Moose Research Center, Alaska, indicated that calf rearing "costs" were 8 to 18 percent of a cow's July-August weight (LeResche and Davis, 1971).

WEIGHT GAIN

Moose experience marked seasonal fluctuation in body weight. Average body weights for breeding female moose older than three years in interior Alaska ranged from near 360 kg in late spring to approximately 475 kg or larger in fall. These values suggest an average weight loss of approximately 115 kg or 24 percent between fall and spring. Weight gain probably occurs during approximately 125 days per year between late May and late September, when live or dead herbaceous plants and deciduous leaves are most available in interior Alaska. Thus, rate of gain is approximately 1 kg per day.

Jordan *et al.* (1970) concluded that seasonal body weight fluctuations of moose amounted to only 6.6 percent for females and 10.3 percent for males. However, Rausch (1959) and LeResche and Davis (1971) reported seasonal body weight fluctuations of 20 percent and 15-30 percent, respectively, for moose in southcentral Alaska. Verme (1970) found that a "winter-killed" bull in Michigan had lost 33 percent of his pre-winter weight.

Seasonal weight loss in moose is probably not limited to fat, but also includes substantial amounts of protein. Paquay *et al.* (1972) have demonstrated that mature cows have a capacity to store and lose up to 20-25 percent of their body protein, depending on level of feeding. Additional studies reviewed by Paquay *et al.* (1972) suggest that mobilization of reserves from liver, viscera, and especially muscle can contribute to maintenance during undernutrition in several species. Since percent protein in a carcass apparently fluctuates with level of protein intake (Paquay *et al.*, 1972) large seasonal variations in dietary protein of moose in interior Alaska suggest that labile protein reserves probably exist in the species. For purposes of this review, we assume that 25 kg or 20-25 percent of the 115 kg seasonal weight fluctuation of moose in interior Alaska is due to loss or gain of protein, while the remaining 90 kg weight fluctuation is due to loss or gain of fat.

Efficiency of fat synthesis has been measured for domestic species. Flatt and Coppeck (1965) concluded from the literature that ME is converted into body fat in the lactating animal with an efficiency of approximately 70 percent, equal to that of milk production. This efficiency averages about 58 percent in the non-lactating animal (Blaxter, 1962; Flatt and Coppeck, 1965). However, lipogenesis is closely related to diet, and the effeciency of converting ME into body fat may decrease on low quality forage (Short and Golley, 1968). Since the efficiency of protein production is uncertain, we tentatively assume that it is similar to that for lipogenesis. Differences in the efficiency of fat and protein production are probably not great and therefore should not cause significant error in estimating metabolic requirements.

Energy requirements for weight gain in moose can be calculated from rate of tissue production. Ninety kg of fat and 25 kg of protein gained during 125 summer days amount to an average weight gain of 0.72 kg of fat and 0.20 kg of protein, or 0.92 kg of tissue per day. Therefore, gross energy of tissue deposited amounts to 6,696 kcal/day of fat (9.3 kcal/g fat) and 860 kcal/day of protein (4.3 kcal/g protein), or a total of 7,556 kcal/day. Assuming 70 percent efficiency for tissue production, an average of 9,800 kcal ME/day are required to produce approximately one kg of fat and protein per day.

Summer fattening in lactating moose is probably not constant. During early summer weight gain is relatively small, while by mid-summer lactation is greatly reduced and weight gain probably occurs at a more rapid rate. Metabolizable energy shown in Figure I which is available for fat and protein production in the lactating moose probably ranges from slightly more than one time BMR during early summer to nearly two times BMR during mid -to late summer. Weight gain in the non-lactating moose is probably more uniform throughout the summer, and maximum fall weights may be somewhat greater than in the lactating animal. Rates of fattening may decline during late summer because of a reduction in quality of forage during the growing season (Oelberg, 1956).

Nutrition

Energy for maintenance, growth and reproduction is supplied through the digestion of plants. Moose, like other ruminants, rely to a great extent on microbial digestion and fermentation of plant carbohydrates and proteins in the rumen to yield useful nutritional products since they lack some of the essential digestive enzymes required to make efficient use of plant tissues. The following discussion will be directed toward the nutrient composition of moose foods, food consumption and the processes of transforming plant material into usable energy to fulfill the needs previously discussed.

NATURE OF RUMEN CONTENTS

Rumen contents include solid particles of food plants, soluble energy sources, microbial waste products, bacteria, protozoa, gases, saliva, water and many other materials. Rumen contents may be thought of as microbial culture medium maintained in relative stability by the steady input, outflow and absorption of constituents.

Dry matter in the rumen

Dry matter (DM) content varies with diet and season, and ranges from 8 to 20 percent of rumen contents in moose and most other ruminants (Short *et al.*, 1969 a, b; Church, 1969; Luick *et al.*, 1972). Dry matter content is influenced by the nature of food ingested, the time since feeding and drinking, salivary flow, passage of materials out of the rumen, and the rates of digestion and absorption (Church, 1969; Waldo *et al.*, 1965; Ingalls *et al.*, 1966). The above factors result in diurnal variations in percent DM of rumen contents. Short *et al.* (1969a), working with white-tailed deer, reported that the highest percent DM occurred early in the morning following feeding, and the lowest percent DM occurred during midday. Intermediate values were found in the late afternoon.

In moose the percent DM changes seasonally. Moose on summer range have low percent of DM in the rumen because of the high moisture content of succulent vegetation and availability of water. In winter the low moisture content of woody browse causes DM to increase to its highest value (Table IV). Moose may also reduce water intake in winter when only snow is available.

Chemical make up of rumen contents

The gross chemical compositions of rumen contents reflects the food eaten by the ruminant (Klein, 1962, 1965, 1968, 1970; Klein and Schønheyder, 1970; Klein and Standgaard, 1972; Short, 1966). Rumen contents which remain on a sieve when washed with water include primarily ingested forage and indigestible residues, and may be used to determine the approximate nutrients in the diet. Washed rumen contents probably represent a minimum estimate of protein in the forage because soluble protein and amino acids are readily digestible components. Analyses of washed rumen contents from moose in interior Alaksa indicate that dietary protein was 12 percent in summer and 6 percent in winter (Table V). LeResche (pers. comm.). also found similar protein levels (6 percent) in washed rumen contents during winter in moose from the Kenai Peninsula and southcentral Alaska (Table V). This protein content reflects a low protein diet. Protein content of winter moose browse on the Kenai Peninsula was slightly greater than that found in rumen contents. Hand picked browse samples ranged between 5 to 9 percent protein and averaged 8 percent (LeResche, pers. comm.).

Food selected by moose in winter is probably near the minimum required protein level. This value is considered to be about 7 percent for ruminants (Corbett, 1969). Murphy and Coates (1966) found that white-tailed deer fed 7 percent protein diets throughout the year were physically stunted and that does fed on low protein diets (7-11 percent) produced fewer fawns than those fed higher protein diets.

Deer in North America select browse similar in protein content to that of moose. Klein (1965) found that winter forage of black-tailed deer (*Odocoileus hemionus sitkensis*) in southeastern Alaska contained about 6 percent protein. Spring forage contained 25 percent protein and late summer forage 12.5 percent protein. Short (1969, 1971) and Torgerson and Pfander (1971) found white-tailed deer foods contained 5-8 percent protein during winter and 15-16 percent during spring.

Forage can be divided into two basic components (soluble cell contents and cell wall components) by the neutral detergent fiber (NDF) analysis of Goering and van Soest (1970). The cell contents are considered 98 percent digestible, while the cell wall component (hemicellulose, cellulose and lignin) varies in digestibility depending on lignin content. Fiber (cell wall component) is an abundant constituent of most ruminant forage and is

TABLE IV

Seasonal changes in body weight and rumen characteristics of moose collected in the Tanana Valley, Interior Alaska[1]

Season month, year	*Sex, age, reproduction status*	*Number in sample*	*Body wt (kg)*	*Rumen contents (kg wet wt)*	*% Rumen contents of body wt*	*% Dry matter in rumen contents*	*Dry matter in rumen (kg)*	*Estimated[2] digested organic matter (kg dry wt)*
Spring May 1971	Female adult pregnant	4	338	29	8.7	12.7	3.7	2.2
Summer June 1972	Female adult non-lactating	4	430	41	9.5	12.5	5.2	5.6
Summer June 1972	Female yearling non-lactating	1	227	18	8.0	11.3	2.1	2.7
Summer June 1972	Female adult lactating with calf	3	379	43	11.4	10.8	4.8	6.3
Early winter October 1972	Female adult non-lactating without calf	5	501	52	10.4	15.9	8.3	2.2
Early winter October 1972	Male adult rut	2	525	51	9.6	16.9	8.6	2.2

[1] Coady and Gasaway, unpublished.

[2] Estimate based on 8.5 moles VFA produced per kg organic matter digested (Weston & Hogan, 1968a). VFA production data is show in Table IX.

slowly digested by rumen microbes (Hungate, 1966). Goering and van Soest (1970) found that low NDF and low lignin: cellulose ratio are characteristic of more digestible forages.

Cell wall components and lignin: cellulose ratios of washed rumen contents from moose in interior Alaska were lower in summer than in winter, indicating the higher digestibility of summer forage (Table VI). We estimated digestibility of forage in June and October to be 50 and 40 percent, respectively, using the lignin ratio method and the summation equation (Goering and van Soest, 1970). High ADF and lignin values noted in Table VI for February and May are partially explainable upon the basis of technique. The rumen contents collected in these months were washed on a larger mesh sieve than those collected in June and October. The large mesh sieve retained proportionally more coarse, woody material than the sieve used for samples obtained in June and October.

Seasonal changes in rumen fill

The weight of female moose rumen contents varies with season and diet in interior Alaska, being greatest during winter and smallest during spring (Ta-

TABLE V

Seasonal variation in percent crude protein of washed rumen contents from moose and black-tailed deer in Alaska

	Percentage crude protein			
	Early winter	*Mid-winter*	*Early spring*	*Summer*
MOOSE				
Interior Alaska[1]	6	6	10	12
Kenai Peninsula[2]		6		
Southcentral Alaska[2]		6		
BLACK-TAILED DEER				
Woronkofski Island Southeast Alaska[3]			24	
Coronation Island Southeast Alaska[3]			16	

[1] Coady and Gasaway, unpubl.
[2] LeResche, pers. comm.
[3] Klein, 1965.

TABLE VI

Fiber content of washed rumen samples taken from moose in interior Alaska[1],[2]

Month	*Cell wall components (NDF)*	*Acid detergent fiber (ADF)*	*Lignin*	*Cellulose*	*Lignin/ADF*
February		67.3	26.1	41.2	0.39
May		66.3	33.2	33.1	0.50
June	51.7	40.2	11.7	28.5	0.29
October	68.9	58.9	18.5	40.4	0.31

[1] Analyses performed by WARF Institute, Inc. Madison, Wisconsin.
[2] Coady and Gasaway, unpublished.

ble IV). During winter, the greater rumen fill in moose may act to compensate in part for poorer quality forage. Microbes are provided with more substrate which leads to increased utilization of lower quality food. Rumen fill of cows was lowest prior to calving in late May, possibly because growth of the fetus occurs at the expense of rumen volume as has been demonstrated in domestic sheep and cattle (Campling, 1970). This decrease in rumen fill results in a reduction in total DE attained from the diet. Intermediate rumen fill occurs throughout the summer (Table IV). Increased digestibility and turnover of succulent food in the rumen during summer probably results in lower rumen fill in spite of greater food consumption. By contrast, rumen fill in white-tailed deer is lowest during winter (Short, 1971).

pH of rumen contents

The pH of moose rumen liquor is similar to that of other ruminants. Samples collected from freshly killed moose in interior Alaska during October and February contained rumen liquor with a pH of 6. The pH of rumen liquor in a moose killed in October was monitored for four hours following death. The pH dropped from 6 at death to 5 three hours after death. At this time fermentation had nearly stopped suggesting that pH would probably not decline further. These values were determined using pH indicator paper and are therefore only approximate. pH values are not available from moose in summer, although they may be lower than winter values because of increased fermentation rate and higher volatile fatty acid concentration. Short *et al.* (1966) found a lower pH in rumen liquor of mule deer (*Odocoileus hemionus)* during summer than during winter. Therefore, pH values may be of some use as a very general indicator of relative fermentation rates.

FOOD INTAKE, PASSAGE AND DIGESTIBILITY

Food intake, passage rates and digestibility in moose have received little consideration. However, these parameters are important to the understanding of moose nutrition and require further investigation.

Verme (1970) reported that captive moose consume 18-23 kg fresh browse per day in winter and 23-27 kg food in summer. Palmer (1944) estimated that moose required 16 kg of forage per day (air dried weight). Attempts to estimate food consumption by Alaskan moose are reported by LeResche (1970) and LeResche and Davis (1971). The utilization of winter browse was studied in pens by estimating the biomass of browse removed by known numbers of moose during the winter. Variability in estimates of food intake was high, ranging from 1.3 to 5.4 kg/animal/day (wet weight) and were considered unreliable. A second method was tried where tame moose were observed and number of bites and types of plants were recorded. Bites were then converted into pounds of food consumed. An estimate 1.7 kg/animal/day (wet weight) (1.3 kg dry wt/day) was consumed in winter and 19 kg animal/day (wet weight) during summer (Table VII). The estimate for winter was felt by LeResche and Davis (1971) to underestimate actual consumption. These same moose were capable of consuming 11 to 16 kg of pelletized commercial food per day in the previous winter.

Estimates of required digestible DM and food intake during winter can be made for moose in interior Alaska. Approximate values used in the calculation of DM consumed were the following: organic matter digested = 4,500 kcal/kg digested; metabolizable energy (ME) = 3,690 kcal/kg organic matter digested (ME = 0.82 × DE, Annison and Armstrong, 1970); digestibility of 40 percent in winter and 55 percent in summer, based on estimates made by the summation equation and lignin ratio methods discussed previously. Daily energy requirements for moose during winter are assumed to be near 1.7 × BMR.

Applying the above assumptions an estimate of the required food for moose can be calculated as follows. Cow moose in mid to late winter weigh about 400 kg and have a BMR of about 6,300 kcal/day. Metabolizable energy requirements at that time are approximately 10,700 kcal/day (6,300 kcal/day × 1.7). Body fat and protein reserves were catabolized at an average rate of 3,900 kcal/day (based on winter weight loss of 90 kg fat and 25 kg protein in 240 days). Thus, 6,800 kcal ME were supplied by the forage. It requires 1.9 kg digestible DM to supply this 6,800 kcal ME, and since DM is 40 percent digestible, 4.6 kg DM or about 6.5 kg wet weight of winter browse would be consumed (Table VII).

Dry matter digested and food consumed by moose can also be estimated from volatile fatty acid (VFA) production using the relationship described for domestic sheep by Weston and Hogan (1968a). They found a relatively constant production of VFA per unit of organic matter digested (8.5 mole VFA/kg DM). Using Weston and Hogan's relationship,

TABLE VII

Estimates of food consumption by moose are presented for several studies in kilograms per day. Note that values are in dry, air dried, and wet weights making direct comparison difficult

Summer			*Winter*	*Conditions*	*Reference*
Lactating	*Non-lactating*	*Reproductive Status Unknown*			
		23-27 wet wt.	18-23 wet wt.	Penned, hand cut browse	Verme, 1970
		16 air dried	16 air dried	Estimate for penned	Palmer, 1944
			1.3-5.4 wet wt.	Natural browse, estimated from browse removed in large pen	LeResche, 1970
	19 wet wt.		1.7 wet wt. (1.3 dry wt.)	Natural browse, estimates from bites eaten by tame moose in large pen	LeResche and Davis, 1971
			4.6 dry wt. (6.5 wet wt.)	Natural browse, estimated from energy requirements of 1.7 x basal metabolic rate	Coady and Gasaway, unpubl.
11.5 dry wt.	10.2 dry wt.		5.5 dry wt. (6.0 wet wt.)	Natural browse, estimated from digestible DM required for measured VFA production	Coady and Gasaway, unpubl.

the mean value for production of VFAs in moose feeding on winter browse in interior Alaska was equal to 2.2 kg digestible DM/day (Table IV). Therefore, DM consumed equals 5.5 kg per day with a 40 percent digestibility or about 7.9 kg/day wet weight. Caloric value of food digested is 2.2 kg × 3,690 kcal ME/kg = 8,118 kcal or 1.3 × BMR. This is less than the estimated 1.7 BMR mentioned above. However, when the additional energy (3,900 kcal/day or 0.6 × BMR) from tissue reserves is considered the total energy available equals 1.9 × BMR (12,000 kcal) which is close to the estimated requirement of 1.7 × BMR.

Similar calculations can be made for lactating moose which are in positive energy balance during summer. Estimated digested DM equals 6.3 kg (Table IV), or, assuming 55 percent digestibility for summer forage, 11.5 kg DM consumed. Caloric value of the 6.3 kg DM is equal to 23,200 kcal ME/day or 3.8 × BMR (BMR = 6,035, see Table XI).

Non-lactating cow moose during summer digested an estimated 5.6 kg DM per day equal to 20,700 kcal ME, or 3.4 × BMR (BMR = 6,100, see Table XI). This represents 10.2 kg of DM consumed or 1.3 kg less than lactating cows. Moose appear to increase food intake while lactating as do domestic cows (Campling, 1970). Corbett (1969) reported lactating dairy cows may consume as much as 50 percent more food than non-lactating cows. Dairy cattle have higher energy demands for lactation than moose since they are bred for inordinately high milk production rather than requirements of the calf.

Estimates of food consumption discussed here vary considerably according to the method by which they were calculated (Table VII). Although all food consumption estimates are approximate, they show a marked increase during the plant growing season. The increase in food consumption is reflected in rapid weight gains during the summer and the winter decrease in food intake by weight loss (see Table XI).

It is unlikely that lower food intake during the winter is a result of limited food availability. The probable cause is increased retention time of food in the rumen because of decreased digestibility. Food intake in ruminants is partially regulated by the passage rate of digesta through the gut (Weston and Hogan, 1968b; Corbett, 1969; Corbett *et al.*, 1963, and Balch, 1950).

The more rapidly the breakdown and digestion of foods in the rumen, the faster can be the rate of passage of digesta onward from the rumen to the remainder of the gastro-intestinal tract; hence the greater is the quantity of feed that must be eaten to maintain a certain degree of rumen fill. Food consumption is therefore a function of the rates of digestion in, and of passage from the rumen (Corbett, 1969). Corbett *et al.* (1963) demonstrated this relationship between digestibility and food intake in cattle. During a five week study the digestibility of grass decreased from 80 to 68 percent, and food intake fell about 20 percent. Weston and Hogan (1968b) attribute low food intake of poor quality feed to long turnover time in the rumen of domestic sheep. However, consumption increased when food was ground and pelleted because rumen turnover time was shortened.

Voluntary reductions in food intake during winter have been noted in deer fed good quality food *ad libitum* (Thompson, 1972; Wood *et al.*, 1962). This factor may also play an important role in regulating winter food consumption in moose.

The stage of maturity of pasture plants has a marked effect on rumen function parameters in domestic sheep (Hogan *et al.*, 1969). Similar effects probably occur in moose as the growing season progresses and plants mature. Hogan *et al.* (1969) found that as the grass, *Phalaria tuberosa*, matured food consumption, passage rates through the gut, digestibility and VFA production decreased and chewing activities increased. Short (1971) found that grasses and forbs utilized by white-tailed deer in Texas varied in digestibility with the stage of maturity. He sampled deer browse throughout the year and found that immature stages were more digestible than mature plants.

Since plants in immature stages of growth are most digestible and nutritious it is advantageous for ungulates to inhabit areas with diversity in habitat types, browse, topography, and long seasonal progressions of plant growth. These conditions permit selection of highly nutritious foods for the greatest length of time during the growing season. Klein (1965) found the environmental factors, altitude and topographic variation, to be primarily responsible for differences in the quality of browse and consequently for differences in growth rates of black-tailed deer in Alaska. He suggests that similar factors are of importance to Dall sheep (*Ovis dalli)* and mountain goat *(Oreamnos americanus).* These factors are no doubt important in determining the quality of moose browse and subsequent distribution and seasonal movement of moose.

While information regarding rumen turnover times or forage digestibility in moose are not available, fermentation data can be used to indicate seasonal trends. Quantity of rumen DM was greatest in moose feeding on woody browse during October in interior Alaska, while estimated DM digested was low during this time (Table IV). October forage may have a long turnover time in the rumen because of the low removal rate by digestion. By comparison, moose feeding on green plants in June apparently digested more DM per day than was present in the rumen; hence, the turnover of DM was more rapid than in winter. The only comparable study on wild ruminants of which we are aware was undertaken by Mantz and Petrides (1971) on white-tailed deer. They reported that natural browse had a greater retention time in the rumen than did a ground, pelleted, and readily digestible standard diet which might be considered equivalent to summer forage in terms of turnover. Seasonal turnover patterns described in moose and white-tailed deer are also similar to those observed in domestic ruminants.

RUMEN FERMENTATION AND UTILIZATION OF VFA

Rumen fermentation is one of the major adaptations favoring successful coexistence among ruminants and other large herbivores. The "fermentation vat" has allowed for digestion of the ubiquitous cellulose molecule and other difficult to digest polysaccharides. Over one half of the digestible DM consumed by ruminants is altered by microbial digestion and fermentation in the rumen, and from 53-62 percent of the DE goes through the rumen VFA pool alone (Gray *et al.*, 1967; Bergman *et al.*, 1965; Annison and Armstrong, 1970; Blaxter, 1962).

Rumen metabolism of carbohydrates and proteins

Carbohydrates (CHO) are the most abundant energy source for moose, making up about 60-70 percent of the diet. Carbohydrates found in plants are primarily polysaccharides, cellulose, hemicellulose, pectins, starches, and fructans. A very small portion of CHO is in the form of mono — and disaccharides such as fructose, glucose and sucrose (Church, 1969; Leng, 1970). Microbes digest and ferment much of the CHO consumed, and the ease of digestion varies with the different CHO molecules. Digestion of cellulose and hemicellulose is slower than that of starch and soluble CHO. Large, complex molecules such as cellulose, hemicellulose, and starch are first broken down by extracellular enzymes into small units. This is followed by digestion and fermentation within the microbial cell (Leng, 1970).

The general scheme of CHO metabolism is for conversion of dietary CHO into a common unit, glucose, and then to pyruvate which is metabolized to acetic, propionic, butyric and valeric acids (VFA) plus carbon dioxide and methane (Leng, 1970; Baldwin, 1965; Hungate, 1966; Hungate, 1968; Church, 1969).

Acetic acid is produced in the greatest molar quantity and is followed in order by propionic, butyric and valeric acids in moose and other ruminants (Table VIII). A schematic diagram of CHO degradation in the rumen is shown in Figure 2 (from Church, 1969 and Leng, 1970).

Dietary proteins are broken down into amino acids which are fermented to produce energy for biosynthetic processes. Amino acids may be incorporated directly into microbial cells or deaminated and fermented to produce ammonia, carbon dioxide and VFA. The proportion of VFA originating from protein is not well understood, although feeds rich in highly soluble proteins may yield substantial amounts. Branched chain VFA present in the rumen, i.e. isobutyrate and isovalerate, arise from fermentation of certain amino acids (Hungate, 1966). These branched VFA represent a small percentage of the total VFA, although they provide a relative indication of the magnitude of protein fermentation. Proteins and amino acids may escape fermentation in the rumen and pass into the lower

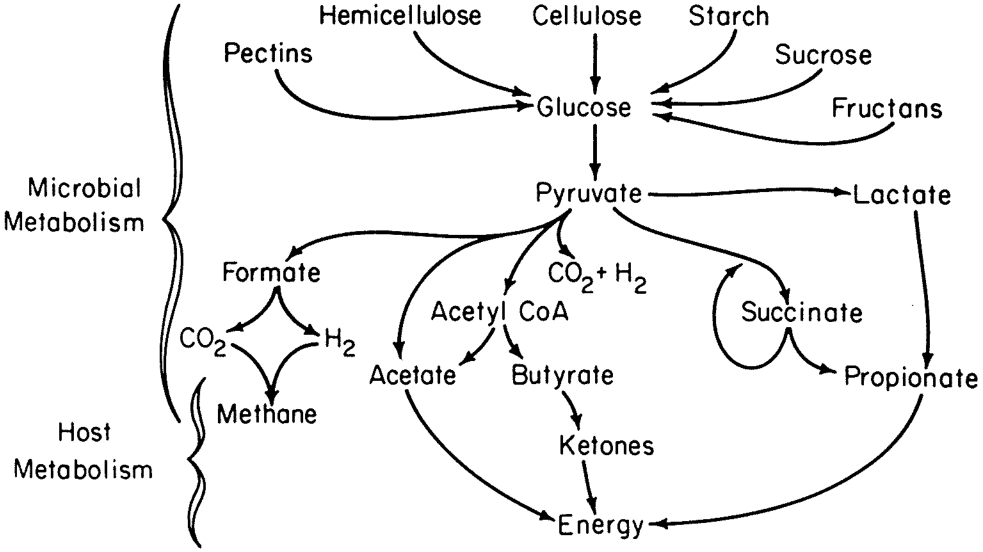

Figure 2. Carbohydrate digestion and metabolism by rumen microbes and their host (from Church, 1969 and Leng, 1970).

TABLE VIII

Comparison of initial concentration and molar percentages of VFA in rumen liquor of several species of ungulates

Species	*Diet or Season*	*Initial concentration* (μ eq/ml liquor)	*Molar percent*				*Reference*
			Acetate	*Propionate*	*Butyrate*	*Propionate*	
Moose	Spring, mixed woody browse + some green forage	65	73	18	9	4.1	Coady & Gasaway, unpubl.
	Summer, green forage	93					
	Early winter, woody browse	69					
	Mid-winter, woody browse	70	74	17	8	4.3	
Mule Deer	Winter to early spring		68	20	10	3.4	Short *et al.*, 1966
	Late spring and summer		63	22	13	2.9	
	Autumn		66	20	11	3.3	
White-tailed deer	Winter, diet largely acorns	108	59	22	15	2.9	Short *et al.*, 1969b
	Winter, diet browse and grasses	107	73	16	9	4.5	
White-tailed deer	Winter — February	97	74	19	7	4.2	Short, 1971
	May	80	72	19	9	3.9	
	July	130	59	32	9	1.9	
	November	110	54	34	12	1.6	
	February	76	62	28	10	2.2	
Domestic sheep	Early growth, low fiber	104	66	20	12	3.3	Hogan *et al.*, 1969
	Intermediate maturity	100	68	20	10	3.4	
	Mature, high fiber	76	71	18	10	3.9	
Domestic sheep	Dry season	118	65	20	16	3.3	Weller *et al.*, 1969
	Wet growing season	117	58	25	17	2.3	
	Dry season	100	68	20	12	4.0	

digestive tract where they are absorbed by the host ruminant (Hungate, 1966; Leng, 1970; Nolan and Leng, 1972; Tillman and Sidhu, 1969; Mangan, 1972). However, the major source of protein for ruminants is of microbial origin (Hungate, 1966; Nolan and Leng, 1972).

Ammonia formed by deamination of amino acids is utilized by the microbes as a nitrogen source for protein synthesis. The host ruminant also absorbs ammonia from the rumen. It is converted into urea and recycled into the rumen via salivary secretion and secretion through the rumen wall. Nitrogen in urea is converted to ammonia in the rumen and used in microbial syntheses (Hungate, 1966; Nolan and Leng, 1972; Weston and Hogan, 1967; Church, 1969). Recycling of nitrogen is an important process which presumably allows all ruminants including moose to effectively utilize low protein diets.

VFA production

More VFA is produced in the rumen from forages containing high levels of soluble CHO and protein than from foods high in fiber and insoluble components. Thus, immature stages of plants generally result in high VFA production rates whereas plants consumed in the winter or dormant period are generally difficult to digest and yield low VFA production rates (Weston and Hogan, 1968a, b, c; Hogan *et al.*, 1969; Hogan and Weston, 1969).

VFA production in moose in interior Alaska was studied during spring, summer and winter using the zero time rate methods of Carrol and Hungate (1954) (Coady and Gasaway, unpubl.). The method was slightly modified for use in field studies. The procedure involves *in vitro* incubation of a rumen content sample under conditions approximating those in the rumen. Isolation of the sample in a polyethylene jar prevented absorption of microbial end products while allowing fermentation to continue for a period of time. Subsamples from the jar were withdrawn at approximately half hour intervals and prepared for total VFA determination by steam distillation and titration with NaOH. Total daily VFA production for moose was calculated by multiplying the *in vitro* production rates per ml of rumen liquor by the total volume of liquor present in the rumen.

VFA production rates per ml of liquor in the rumen of moose varies markedly with season and consequent changes in quality of the diet. Winter diets of woody browse are of low enough quality to limit fermentation rates to approximately one-third of the VFA production rates in summer (Table IX). Apparently, the low fermentation rates in winter result from reduced quality of browse rather than a shortage in quantity, since the moose were collected on quantitatively good winter range. In late May the diet consists of some newly emerging green vegetation mixed with wood browse. VFA production rates at this time were greater than in winter but still only half that of summer values (Table IX).

Seasonal changes in rumen fill and changes in the proportion of liquor have a pronounced effect on the calculated total rate of VFA production observed in moose. Moose in winter have greater rumen fill than in summer. This has the effect of compensating somewhat for the reduced winter VFA production rate per ml of liquor by increasing the volume of substrate exposed to fermentation at any one time. VFA production in the total rumen of moose during summer was 2.6 to 2.9 times that during winter, although the rate of VFA production per ml of liquor was over three times higher during summer than during einter. Thus, the effect of increased rumen fill was that of providing more VFA to the animal than the production rate alone would suggest. The effect of changing rumen fill on total VFA production was more pronounced in cow moose during May when the rumen fill was at its lowest level. Daily VFA production in the May sample equaled that of large rumen volumes in winter because of the increased production rate per ml of rumen liquor due to the recent emergence of green plants. Lactating cow moose during summer had greater total VFA production than did non-lactating cows in spite of the similar VFA production rates. This was due to a greater rumen fill and a higher proprotion of rumen liquor in the rumen contents of lactating moose (Table IX).

Recently, many investigators have measured the VFA production in domestic animals, but few studies of VFA production in wild animals have been undertaken (Table X). To compare animals of different body size, VFA production rates were expressed with respect to metabolic body size (kg^{75}) in Table X. Wide variations in the production rates exist among species depending on the forage fed on and probably the technique used to estimate VAF production. Moose on an annual basis encompass the extreme variation seen in the other species.

Seasonal variations in total VFA production are illustrated in only three studies in Table X. Two studies were carried out on grazing domestic sheep in Australia (Weller *et al.*, 1969, and Weston and Hogan, 1968a) and the other study was on moose in Alaska (Coady and Gasaway, unpubl.). Moose showed greater seasonal extremes in total VFA production than did sheep on their respective high and low quality ranges which are a result of wet and dry seasons. This may be expected since moose have only a short summer period to replenish depleted protein and fat reserves in preparation for a winter of eight months in length. During winter, only low quality food is available and a negative energy balance persists.

VFA concentration in rumen liquor has been used as a seasonal indicator of VFA production for comparing forage quality in wild ruminants (Prins and

TABLE IX

VFA production in moose collected in the Tanana Valley, Alaska[1]

Season, Month	*Sex, Age*	*Number in sample*	*Reproductive status*	*VPA Initial concentration (µ eq/ml)*	*VFA Production rate (µ eq/hr. ml*	*Total VFA production (moles/day)*
Spring May	Female adult	4	Pregnant	65	31	18.81
Summer June	Female adult	4	Non-lactating	98	58	47.75
Summer June	Female adult	3	Lactating	89	61	53.20
Early winter October	Female adult	5	Non-lactating without calf	69	18	18.40

[1] Coady and Gasaway, unpublished.

Geelen, 1971; Short, 1963, 1971; Short *et al.*, 1969a, Short *et al.*, 1969b; Ullrey *et al.*, 1964, 1967, 1968, 1969, 1970; Bruggemann *et al.*, 1968). The correlation of VFA concentration and VFA production described by Leng (1966), Leng and Brett (1966), Leng *et al.* (1968) and Weston and Hogan (1968a, indicates VFA production can be estimated from the concentration once the relationship is established for the species. However, variation in the relationship between VFA production and concentration is considerable. Over a small range of VFA concentration, variability is likely to obscure changes in production. Therefore, in wild game studies we feel VFA concentration can be used only as an approximate indicator of fermentation rates rather than a tool to estimate actual VFA production.

Molar percentages to VFA present in the rumen is related to the gross chemical nature of the diet and fermentation patterns. Generally, forages rich in easily fermented material result in increased propionate relative to acetate. Forages high in fiber result in increased proportion of acetate (Hungate, 1966; Weller *et al.*, 1969; Hogan *et al.*, 1969). Specific incidents in closely controlled studies of domestic animals have revealed exceptions to the generalization cited above (Weston and Hogan, 1968a). Therefore, great significance should not be placed on this parameter as an indicator of food composition and quality, particularly if the investigator has relatively few samples. Table VIII summarizes VFA molar proportions in several species of ungulates. Acetate: propionate ratios show an increase during the winter or dry season which indicates a diet low in soluble CHO and proteins.

Energy value of VFA

The importance of VFA as an energy source in ruminants is well established. The energy contained in the VFA is equivalent to about 57 percent of the DE and about 70 percent of the ME for ruminants assuming that ME is about 82 percent of DE (Annison and Armstrong, 1970). Estimated VFA energy extends our understanding of moose nutrition and energy requirements because ME of free ranging animals may then be estimated.

Metabolizable energy of VFA produced in the rumen of moose which is equal to gross energy of VFA was calculated by multiplying the total moles produced per day by the molar percentage of indivudal VFA. This gave an estimated production of each acid. The number of moles of each VFA times its respective heat of combustion (kcal/mole) equals kcal of ME per day available from each VFA through oxidation. Moles produced per day (Table IX) were converted to kcal of ME as shown in Table XI. Calculated BMR was used as the standard energy unit for moose to which VFA energy was compared. Energy available from VFA in moose feeding on woody winter browse in October was calculated at 69 percent of the BMR (Table XI). This is probably a low estimate because the moose were very fat in this early winter period. Lipid deposits in these moose are approximately 100 kg and adipose tissue is metabolically less active than most other tissues. Correcting for this less active body mass would lower the theoretical BMR and increase the percentage of energy supplied by VFA. The BMR for lean body weight for these moose was about 6,300 kcal per day and VFA energy supplied 81 percent of this amount (Table XI). We suspect VFA production remains relatively constant through a "normal" winter while dormant plant parts are browsed, thus VFA energy contribution

TABLE X

A comparison of rumen VFA production based on body weight in several species of ungulates

Species Sex, Age, No. in Sample	*Conditions Season*	*Diet*	*Body Wt (kg)*	*(Body wt)$^{0.75}$*	*mMoles/ References*	*mMoles/ day/kg$^{0.75}$*	*Reference*
Moose Cow Adult n = 4	Free ranging Spring, May pregnant	Winter browse + some new green forage	338	79.0	56	238	Coady & Gasaway, unpubl.
Moose Cow Adult n = 4	Free ranging Summer, June Non-lactating	Green forage	430	94.4	111	506	Coady & Gasaway, unpubl.
Moose Cow Adult n = 3	Free ranging Summer, June lactating	Green forage	379	86.0	140	619	Coady & Gasaway, unpubl.
Moose Cow adult n = 5	early winter non-lactating without calf			105.7	37	174	Coady & Gasaway, unpubl.
Eland (*Taurotragus*) n = 1	Free ranging		520	108.9	37	176	Hungate *et al.* 1959
Zebu (*Bos indicus*) n = 1	Free ranging	Grass pasture	241	61.1	52	207	Hungate *et al.* 1959
Grant's Gazelle (*Gazella sp.*) n = 1	Free ranging		49	18.5	34	98	Hungate *et al.* 1959
Thompson's Gazelle (*Gazella sp.*) n = 1	Free ranging		24	10.5	34	98	Hungate *et al.* 1959

Suni n = 1	Free ranging		3.7	2.7	105	146	Hungate *et al.* 1959
Reindeer n = 4	Penned winter	Commercial pellets	52.8	19.5	53	143	Luick *et al.* 1972
n = 2	Penned winter	Commercial pellets + lichens + straw	105	32.8	83	267	Luick *et al.* 1972
n = 4	Penned winter	Lichens	59	21.3	66	183	Luick *et al.* 1972
Domestic sheep, ewes, adult n = 15	Penned	Early stage ryegrass (27 % prot)	43	16.8	128	329	Weston & Hogan, 1968a
		Intermediate ryegrass (12% prot)	43	16.8	125	319	Weston & Hogan, 1968a
		Mature ryegrass (6% prot)	43	16.8	79	202	Weston & Hogan 1968a
Domestic sheep, ewes, adult n = 6	Penned	Lucerne chaff	43	16.8	125	319	Leng & Leonard 1965
Domestic, sheep ewes, adult n = 4	Grazing	Wet season	53	19.6	94	255	Weller *et al.* 1969
	Grazing	Dry season	63	22.4	64	179	Weller *et al.* 1969

[1] The weight not given by authors and was estimated to be 43 kg for purposes of calculations in table.

TABLE XI

Estimates of VFA and metabolizable energy with respect to the basal metabolic rate in moose, sheep and reindeer

Species, Sex, Age	*Body Wt (kg)*	*Season*	*Diet*	*Conditions*	*Energy Derived from VFA (kcal/day)*	*Theoretical BMR (kcal/day)*	*VFA energy (% of BMR)*	*ME (% of BMR)*	*Reference*
Moose adult cows pregnant n = 4	338	May (1971) Spring	Mixed winter woody browse & new green forage	Free Ranging	5,320	5,505	98	140	Coady & Gasaway, unpubl.
Moose adult cows non-lactating n = 4	430	June (1972) Summer	Green forage	Free Ranging	13,160	6,585 (6,100)	198 (218)	283 (311)	Coady & Gasaway, unpubl.
Moose adult cow lactating n = 3	379	June (1972) Summer	Green forage	Free Ranging	14,660	6,035	243	347	Coady & Gasaway, unpubl.
Moose adult cows non-lactating n = 5	501	October (1972) Early	Woody winter browse	Free Ranging	5,080	7,410 (6,300)	69 (81)	99 (115)	Coady & Gasaway, unpubl.

Domestic sheep ewes n = 6	40		Lucerne Chaff 900 g/day	Penned	1,490	1,110	133	191	Leng & Leonard, 1965
Domestic sheep ewes n = 10	35.5	Growing Season	Grasses	Grazing	1,900	1,020	186	266	Corbett, Leng & Young, 1970
Domestic sheep ewes n = 6	40		Grass Early Stages (high quality)	Penned	1,845	1,110	166	237	Hogan, Weston & Lindsay, 1969
	40		Intermediate		1,525	1,110	137	196	Hogan, Weston & Lindsay, 1969
	40		Mature (poor quality)		855	1,110	77	110	Hogan, Weston & Lindsay, 1969
Domestic sheep ewes n = 9	37.5		Grasses Varying Stages of Maturity	Grazing	1,140	1,06	107	153	Leng, Corbett & Brett, 1968
					990	1,065	93	133	Leng, Corbett & Brett, 1968
Domestic reindeer n = 4	59		Lichens Simulated Winter Diet	Penned	1,075	1,490	72	103	Luick *et al.* 1972
n = 4	53		Commercial Pellets	Penned	765	1,37	56	80	Luick *et al.* 1972
n = 2	105		Commercial Pellets + Straw + Lichens	Penned	2,415	2,295	105	150	Luick *et al.* 1972

[1] Numbers in ( ) are calculated using the estimated lean body weight.

may increase slightly relative to the decreasing lean body weight and BMR.

It may appear that the estimated VFA energy production is insufficient and that maintenance of moose through winter is energetically impossible. However, moose in October derived and estimated 7,300 kcal/day ME from the diet, and an estimated additional 3,900 kcal/day was derived from catabolism of body tissue stores. Therefore, total ME available per day was approximately 11,200 kcal (7,300 + 3,900) or 1.8 × BMR when using the calculated BMR of 6,300 kcal/day. This value, 11,200 kcal, compares closely with the 12,000 kcal ME/day estimate, based on the conversion of VFA into kcal of digestible organic matter using Weston and Hogan's (1968a) data, discussed previously.

The spring greenup appears rapidly during late May in interior Alaska. Within a week, the region where studies by Coady and Gasaway were conducted, turns from a drab brown to a sprakling green and the moose change from a diet of wood forage to lush green foods which are digested more easily. Calories are abundant on the new diet and depleted stores of fat, carbohydrate and protein are rapidly replenished.

Moose collected in May (during the spring transition) in the Tanana Flats were near their annual low body weight. VFA energy at this time amounted to about 98 percent of the BMR, and total VFA production was similar to that during early winter (Table XI). Energy demands at this time were high because of pregnancy which left the cows in a negative energy balance and necessitated a high dependence on catabolism of stored tissues.

By late June, lactating cow moose had gained about 20 kg and VFA energy had increased to 14,700 kcal/day (Table XI). This VFA energy exceeded the BMR (calculated to be 6,035 kcal/day) by about 240 percent (Table XI). Estimated ME is 20,900 kcal/day or 3.5 X BMR, putting the moose into a highly positive caloric balance. The period of weight gain each year was approximately 125 days, and during this time an average of 7,600 kcal per day were put into stored tissue energy.

In late June, non-lactating cow moose were approximately 50 kg heavier than lactating cows, indicating that the cost of pregnancy and lactation is high in terms of potential weight gain. The energy in VFA's produced amounted to about 13,200 kcal/day; thus ME would be approximately 18,800 kcal/day. The lean body mass of non lactating cows is probably slightly greater than that of lactating cows because most of the weight gain is fat. To establish a value for calculation of BMR for nonlactating moose, 15 kg was arbitrarily added to the mean weight of lactating moose. The BMR was then calculated to be 6,100 kcal and VFA energy was 2.2 × BMR and ME was 3.0 × BMR. These values would be less if BMR were calculated using actual body weight, but adjusted weights were considered more representative of energy requirements. Table XI gives values based on actual weights.

Domestic ruminants on open range generally undergo less dramatic changes in seasonal energy balance than some wild ruminants like moose (Table XI. Sheep (*Ovis aries*) did not reach the extremes of negative or positive energy balance seen in moose even when fed very high and low quality forage. Energy balance of free ranging reindeer is probably more like that of moose, but captive reindeer used by luick *et al.* (1972) were in negative balance on all diets tested. These studies were conducted in the winter when intake is lowered which may account for these low energy values. For moose in interior Alaska the seasonal energy picture appears to be feast or famine with little in between.

EFFECTS OF UNDERNUTRITION ON RUMEN FUNCTION

Undernutrition will be considered as reduced caloric intake leading to less than optimal weight gain or weight loss. This definition is broad enough to apply to "normal" winter weight loss, starvation, or even inadequate summer range resulting in reduced fat deposition prior to winter.

During winter, the food intake of moose undergoes a normal decrease, but under certain circumstances intake may be reduced still further. Abnormally deep snow or particularly cold temperatures (−50° C or colder) may decrease food availability by restricting moose mobility.

Decreased food intake lengthens turnover time of rumen contents and decreases rumen fill (Hungate, 1966). Numbers of rumen microorganisms decline as food intake is reduced (Church, 1971) and may drop to very low numbers if inanition is prolonged (Hungate, 1966). Sheep deprived of food for three of four days show marked changes in the composition of bacterial and protozoan populations in the rumen and have reduced digestive capability (Church, 1971). Recent studies by Swope (1972) indicate that starvation in mule deer does not reduce the viability of rumen microbes. Rumen liquor from starved mule deer digested forages about as well as deer on normal rations, and counts of bacteria showed no significant declines during starvation. These results contradict earlier studies on domestic sheep and indicate all species of ruminants may not respond to starvation in similar manners. Hungate (1966) suggests that bacterial populations can remain high in the rumen of starved animals because of reduced saliva flow which cause an increase in rumen turnover time. Bacteria do not leave the rumen as fast and the population remains high. Because the available nutrients in the forage contained in the rumen will eventually become too low to sustain the microbial populations this condition is temporary. The mule deer in Swope's study were starved from 7 to 47 days, which seems too long to sustain normal numbers of viable bacteria yet numbers of bacteria were reported to remain high.

Moose that die from undernutrition in interior Alaska generally have substantial amounts of forage in the rumen. This is a result of consumption of less palatable and digestible browse as well as lengthened turnover time in the rumen. The fact that the digesta found in starving ruminants is large makes the diagnosis of starvation difficult (Hungate, 1966). Hungate suggests the use of VFA concentrations and production rates as indicators of undernutrition. Rumen VFA concentrations are of value only when samples are taken immediately after death. This usually requires that the investigator kill the animal. Although VFA concentrations and production rates are expensive and time consuming to measure, they are relatively conclusive indicators of the animal's nutritional balance at that time.

Summary and conclusions

Seasonal energy requirements of adult moose and ME available for meeting those requirements can be estimated from data presented in Figure 1. Energy required for diverse physiological functions can be described as percent of BMR, where BMR equals $70W^{.75}$ kcal/day. Maintenance energy requirements were considered to remain relatively constant, near 70 percent of BMR, throughout the year. Metabolizable energy requirements for gestation begin to significantly increase in March and reach approximately 100 percent of BMR at term in early June. Metabolizable energy requirements for lactation shortly after birth were approximately 100 percent of BMR. Milk production remains high for a relatively short time, and by August represents a relatively small energy demand. Weight gain by moose in Alaska occurs between late May and late September. Energy available for lactation and weight gain probably averages about 200 percent of BMR throughout the first half of the summer, and then declines as forage quality decreases. However, lactation during early summer significantly reduces the energy available for weight gain.

The quality of foods available to and selected by moose is superior during summer to that consumed in winter based on chemical analysis and rumen fermentation rates. Food consumption data from several studies indicate greater food intake during the plant growing season than during winter. Estimates of food intake that supply the required energy during winter and summer are 4.5 — 5.5 kg and 10 — 12 kg dry weight, respectively. The reduction in winter food consumption results from slower rates of digestion and passage through the gut and probably from a voluntary decrease in food intake as has been observed in other wild ruminants.

Microbial fermentation of plant CHO and protein in the rumen yields VFA. The ME energy in VFA represents about 70 percent of the total ME derived from the diet. Plants in the growing season, particularly immature stages, yielded the highest fermentation rates in the rumen whereas dormant plants and woody browse, being lower in digestible nutrients, resulted in lowest fermentation rates during winter. The total VFA production in moose during summer is nearly three times that of production in winter. Moose undergo greater seasonal variation in the quality of the forage and fermentation rates than do domestic ruminants which have been studied in this manner. The energy derived from rumen fermentation in moose was about 80 percent of the BMR in winter and increased to nearly 250 percent of BMR in summer. Estimated metabolizable energy obtained from forage by moose during winter was only 115 percent of the BMR, where as in summer moose produced up to 350 percent of basal requirements. In late summer and fall the quality of the forage declines until the winter values of fermentation are attained. Lipid and protein stores supply the energy required in winter which is not provided from the dietary sources, thus making ample lipid storage in summer a necessary requirement .of annual production.

The quantity or quality of winter browse is occasionally restricted by weather conditions. The effect of reduced intake on rumen function is to lengthen turnover time of rumen contents and decrease rumen fill. Numbers of microorganisms may decline to low numbers if intake remains low for an extended period of time causing a marked reduction in the fermentation rate.

Rumen function studies on wild cervids and bovids will provide comparative information on their seasonal energy balance and status. Ruminants, whether in the tropics, temperate or arctic zone characteristically are exposed to seasonal variation in forage quality. Energy is generally stored as fat and protein during the portion of the year when forage quality is high. Stored fat and protein is catabolized during the remainder of the year when ME is below the maintenance level, and moose are in negative energy balance. The estimated caloric value of VFA produced in the rumen while feeding on the various seasonal diets and subsequent estimates of ME allows for direct comparison of the animals' ability to utilize the forage and derive energy. This provides a clearer understanding of the temporal relationship of the animal to its food resource. Biologists can then recognize the importance of a particular season in relation to others, determine the importance of various foods and determine the duration of seasons based on food utilization and available energy.

Range evaluation techniques can be very time consuming, expensive and often result in information which is difficult to interpret in a usable form. Therefore, the animal utilizing the range may be an alternate evaluator and provide a more direct and sensitive indicator of range quality provided techniques can be developed to measure physiological changes in the animal. While digestive performance of moose on summer and winter range show striking differences, only subtle differences may exist among moose ranges when compared during the same season. A system using digestive information to compare various ranges could include estimates of VFA production rates, energy derived from fermentation and ME, food consumption, digestibility of forage and chemical and botanical composition of rumen contents. Data obtained from this method, especially when used in conjunction with other techniques, may provide a useful means of comparing ranges and the nutritional status of the animals.

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A REVIEW OF BLOOD CHEMISTRY OF MOOSE AND OTHER CERVIDAE WITH EMPHASIS ON NUTRITIONAL ASSESSMENT

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Résumé

Cet article passe en revue des études de caractère clinique concernant l'hématologie, la chimie du sang, le polymorphisme des protéines ainsi que l'endocrinologie des Cervidae. L'objectif ultime de telles études est de permettre de diagnostiquer l'état de santé du cheptel et les conditions du milieu et on met donc l'accent sur cet aspect de l'analyse. Les données recueillies à ce jour indiquent clairement que les facteurs tels que l'âge, le sexe, la saison, les conditions de reproduction de l'animal et la façon dont il a été traité avant les prélèvements, doivent être retenus avant de tirer de telles analyses des interprétations pouvant influencer les politiques d'aménagement de l'habitat. Or, même en tenant compte de ces effets divers, il ressort clairement de certaines études expérimentales que les paramètres hématologiques peuvent être sous l'influence des conditions de nutrition et de l'état pathologique de l'animal et ce, chez *Alces alces* tout comme chez *Odocoileus* spp. C'est ainsi que le contenu azoté (sous forme d'urée) du sérum sanguin varie en relation directe avec l'état de nutrition. Cependant, ni l'albumine du sérum ni l'hémoglobine ne peuvent servir d'indicateurs valables dans la détection de carences alimentaires quoique le niveau de ces substances dans le sang s'abaisse remarquablement dans le cas de carences sérieuses. Chez le Cerf de Virginie (*Odocoileus virginianus*), une carence nutritive s'accompagne d'une diminution dans l'abondance de thyroxine dans le sérum. Cette hormone diminue dans le sérum de l'orignal en Alaska à mesure que l'hiver progresse. Des échanges métaboliques se produisent dans des cas de sous-alimentation ou de famine et affectent ordinairement les acides gras non-estérifiés du plasma, les acides aminés, les cétones et les acides gras à chaînes courtes; mais de tels phénomènes n'ont jamais été étudiés chez les cervidés. Or, il se peut qu'ils constituent des moyens beaucoup plus raffinés d'évaluer la condition métabolique d'un animal. On a décrit des cas de polymorphisme protéinique dans le cas de la transférine chez *Rangifer* et *Odocoileus* et, dans le cas de l'hémoglobine, chez *Odocoileus virginianus*. De tels polymorphismes n'ont pas été mis en évidence chez *Alces*. L'étude des séquences fibrinopeptidiques permet de conclure que les genres *Alces*, *Rangifer* et *Odocoileus* sont très voisins l'un de l'autre.

Abstract

Clinically oriented studies of hematology, blood chemistry, protein polymorphisms and endocrinology of the Cervidae are reviewed. These studies have been directed at evaluation of herd and range conditions, so possible analyses of data in terms of diagnostic patterns are emphasized. The available data demonstrate that before such management-related interpretations can be made, the effects of age, sex, season, reproductive condition, and methods of handling must be considered. Given these boundary conditions, experimental studies have demonstrated effects of nutritional level and disease on blood values in species of *Odocoileus* and *Alces alces*. Serum urea nitrogen levels (BUN) appear to be directly related to nutritional status in several cervid species. Measurements of serum albumin and hemoglobin are not sensitive indicators although they decline with severe deficiencies. A decline in serum thyroxine with nutritional restriction has been reported in *Odocoileus virginianus*. This hormone declines over winter in Alaskan moose. The metabolic shifts occurring in malnutrition and starvation as reflected in plasma nonesterified fatty acids, amino acids, ketones, and short-chain fatty acids await study in the cervids. They offer the possibility of more sensitive indicators of metabolic status. Protein polymorphisms have been described for transferrin in *Rangifer* and *Odocoileus*, and for hemoglobin in *Odocoileus virginianus*. Studies of *Alces* have shown no polymorphisms. Fibrinopeptide sequences have suggested that *Alces*, *Rangifer*, and *Odocoileus* are closely related genera.

Introduction

Management of moose (*Alces alces*) has historically relied upon assessments of habitat carrying capacity. These assessments have involved food habits studies (Peek, 1974), range productivity (Seemel, 1969) and utilization (Milke, 1968; Telfer, 1968) studies, and estimates of general population size and trend (Spencer and Chatelain, 1953; Spencer and Hakala, 1964; Rausch and Bratlie, 1965). Secondary indicators of habitat's carrying capacity, as reflected in moose population characteristics, have also been relied upon. Population composition, natality and recruitment rates have been employed extensively to indicate populations' relationships with their habitat (Bishop and Rausch, 1974; Pimlott, 1959; Simkin, 1965).

These secondary indicators in effect summarize the manifestations of nutritional, behavioral, environmental and genetic forces acting upon a population. They have been proven inadequate in situations where delicate control of moose populations is necessary. Such indicators are of little use as predictors and of even less value in understanding specific ecological relationships. Therefore, the trend in research since Peterson (1955) last summarized knowledge of moose has been toward analyses of individual primary factors rather than of their collective manifestations. This review concerns methods of measuring nutritional status of wild moose populations and presents details of recent studies of moose blood chemistry as they relate to nutrition.

Methods of nutritional assessment

Nutritional status of individual wild animals can be assessed grossly or finely and acutely or chronically. All body tissues reflect nutritional status and history to a greater or lesser extent, and possibilities for their analyses are as numerous as the tissues themselves. Hypothetically, the ideal method for assessing nutritional status of moose populations would have several characteristics: 1) It would be sensitive to subclinical changes in nutritional status. 2) It would be specific in its indications, i.e. capable of indicating energy, mineral, protein, etc. balance. 3) It would be able to detect reasonably acute (e.g., seasonal) changes in nutritional status. 4) It would involve tissues easily collected from both live (to allow serial collections from individuals) and dead (to allow use of hunter-killed and accident-killed specimens) moose and would be little affected by the stress of collection. 5) It would involve tissues which are easy for untrained personnel to collect and preserve and which can be processed by standard inexpensive methods.

The broad spectrum of methods for nutritional assessment has been outlined by Jelliffe (1966). Potential methods for use on moose include body weight and morphometry (LeResche and Davis, 1971), analyses of urine (Blaxter *et al.*, 1966), epithelial tissue (Squires, 1963; Nutrition Reviews, 1970), saliva (Murphy and Connell, 1970), hair and nails (Sims, 1968; Crounse *et al.*, 1970a, 1970b; Strain *et al.*, 1972; Robson and El-Tahawi, 1971), rumen volatile fatty acid (VFA) production (Gasaway and Coady, 1974) and blood constituents.

Blood analyses — methods and patterns

Mammalian blood contains liquid (serum) and solid (cellular) fractions. Blood studies involve analyses of the chemical and physical properties of both the liquid and cellular fractions. Both types of analyses may be related to nutrition.

Chemical assays of serum are commonly employed in screening procedures for human patients. These tests have been assembled to detect and discriminate between disease processes common in human populations. Interpretation of test results depends upon the magnitude of a sample's deviation from normal values, and upon the pattern of results from all tests performed. Table I illustrates this concept by tabulating patterns obtained in humans during infection, malnutrition, tissue necrosis and various organ-specific diseases.

The most commonly measured parameters used in screening are those twelve measured by the "SMA-12" Technicon auto-analyzer. Patterns demonstrated in human and veterinary medicine presented here follow Coles (1967) and Davidsohn and Henry (1969).

ELECTROLYTES

Calcium

Blood calcium may increase in hyperproteinemia, hyperparathyroidism, extreme neoplasia and other abnormal conditions. Decreased calcium may result from hypoparathyroidism, vitamin D deficiency, acute or chronic renal failure, starvation associated with hypoproteinemia, parturient paresis (milk fever) and other causes. Thus, calcium depression during winter months may be related to reduced nutrition and possible hypoproteinemia and decreased vitamin D during this period. Similarly, depressed Ca may be indicative of range deterioration in certain instances.

Inorganic phosphorus

Similarly to Ca, phosphorous is elevated in hypoparathyroidism, renal failure and excessive vitamin D. Decreased inorganic phosphorus often results from simple lack of phosphorus intake, and as such can reflect dietary deficiencies.

SACCHARIDES

Glucose

Alterations in blood glucose level may be associated with pancreatic abnormalities (diabetes or insulin poisoning). Hypoglycemia may be an indication of extreme starvation, although gluconeogenesis can maintain blood glucose at high enough levels to sustain life even in severe starvation if it persists only a short while. For this reason, glucose level is not a sensitive indicator. Ketosis may be accompanied by hypoglycemia,

TABLE I

Test patterns associated with various pathological conditions in humans, applying probably generally to mammals. Constructed from data *in* Reece and Hobbie (1972 a, 1972b), Searcie (1969) and Hobbie and Reece (1972). The symbol + indicates an elevation while − indicates a depression of the condition

Assay	*Disease State*							
	Infection	*Malnutrition*	*Necrosis*	*Rapid Weight Loss*	*Renal insufficiency*	*Hepatic disease*	*Pseudohypo-parathyroidism*	*Hypo-thyroidism*
Cholesterol		−			−	+		
Calcium		−			−		−	
Phosphorus		−	+		+	+	+	
T. bilirubin			+	+		+		
Total protein	+	−			−	−,+		+
Albumin		−			−	−		
Uric acid	+	−	+	+	+			
BUN		−				−		
Glucose		−,+		+	+			−
LDH			+		+	+		+
Alkaline phosphatase			+		+	+	+	
SGOT			+	+	+	+		+

resulting from assorted digestive or nutritional disorders (including carbohydrate deficiency).

UREA COMPOUNDS

Urea nitrogen (BUN).

BUN level directly reflects dietary protein intake and protein absorption, and is thus a good indicator of protein energy balance. In addition, BUN may be pathologically elevated in cases of excess catabolism of body protein or in renal failure.

Uric Acid

Uric acid is a product of purine metabolism and, as such, may be increased in starvation for three reasons: 1) increased tissue protein turnover, 2) decreased renal excretion of the chemical due to acidosis, and 3) gluconeogenesis, with uric acid as a waste product.

STEROL

Cholesterol

Cholesterol level reflects diet, dietary changes and the state of rumen metabolism. It is elevated when diets high in saturated fatty acids are consumed. Consequently, starvation conditions may result in hypocholesterolemia. Pathological conditions that may alter cholesterol levels include thyroid and hepatic disorders and nephrosis.

PROTEINS

Total protein

Total protein is a rather insensitive indicator of nutritional status, for it is maintained at near-normal levels except in extreme distress. In sub-clinical cases of undernutrition, albumin is a better indicator. Most commonly, hypoprotenemia is the result of trauma (wound, burns) or renal disease. Occasionally, however, it can result from gluconeogenesis and, as such, can reflect dietary insufficiencies. In cases of chronic protein starvation total protein may decrease noticeably.

Albumin

Albumin is the smallest of the major serum proteins and forms 40-60 percent by weight of the total protein. Depressed albumin may indicate deficient protein intake or excessive protein breakdown. Decreased albumin is present in malnutrition and starvation.

PIGMENT

Bilirubin

Bilirubin is a pigment liberated in the reticuloendothelial system (RES) by breakdown of hemoglobin. Bilirubin measurement is commonly a test of liver function, and is also symptomatic of hemolytic diseases. Other conditions elevating serum bilirubin include jaundice, cardiac insufficiency and gangrenous pneumonia. Coles (1967) suggests, however, that bilirubin is elevated only slightly in severe hepatic disease in bovids, ovids and caprids.

ENZYMES

Alkaline phosphatase

Alkaline phosphatase hydrolyzes organic phosphate esters and is concentrated intracellularly in osteoblasts, renal tubules and the intestinal mucosa. In humans, altered concentrations of this enzyme are diagnostic of bone abnormalities and liver disease. Levels normally are elevated during periods of growth and pregnancy, due to increased osteoblast activity and the enzyme's production in the placenta. Lowered levels can indicate malnutrition.

Lactic dehydrogenase (LDH)

LDH catalyzes the lactic acid-pyruvic acid conversion, occurring in most tissues. In humans, elevated LDH levels are indicative of several pathological conditions (e.g., pulmonary or myocardial infarction, hepatis, cirrhosis, leukemia and carcinomas).

Glutamic oxalacetic transaminase (SGOT)

SGOT is elevated in cases of necrosis involving the tissues rich in the enzyme. Its concentration is especially high in the heart, liver and skeletal muscle and thus elevation is a sensitive indicator of myocardial infarction, and hepatic and muscular necrosis and stress. In cattle, SGOT elevation has been noted during starvation.

BLOOD PROTEINS

Electrophoretic fractionation of blood proteins is another common analytic technique using widely available instrumentation. This procedure separates total protein into albumin and four globulin fractions (*alpha*$_1$, *alpha*$_2$, *beta*, and *gamma* globulins) and allows calculation of albumin/globulin ratio (A/G). Changes in these values generally are indicative of the following conditions:

Alpha globulins: Serum *alpha*-globulins are elevated during infection, trauma, hypoproteinemia and acute cellular necrosis (especially alpha -2).

Beta globulins: *Beta*-globulin levels are elevated in pregnancy and sometimes during iron-deficient states. They may be depressed during severe infection and hepatic disorders.

Gamma globulins: The "gamma" fraction defined by electrophoresis is in reality a complex of proteins with many pathological correlations. Most generally, these immunoglobulins are elevated in many infectious diseases and organ disorders.

A/G ratio: A/G ratio reflects relative change in albumin and total globulin fractions and is therefore depressed in protein malnutrition and starvation. It may be elevated in cases of infection or other disorders during periods of adequate protein nutrition.

HORMONES

Thyroxine

Serum thyroxine (T_4) level reflects thyroid activity and thus is correlated directly with fasting metabolic rate and food intake. This hormone may be analyzed by the competitive protein binding method of Nobel and Barnhart (1969).

OTHER ENZYMES

Creatine phosphokinase (CPK)

This enzyme, similarly to SGOT, is elevated in tissue breakdown, including muscle injury and vigorous exercise (Rose *et al.*, 1970). It is present in skeletal muscle, heart and brain. The source may be identified by electrophoretic separation of isoenzymes. It is an indicator of physical or mental stress as well as of trauma and perhaps nutritional stress. This enzyme can be measured by the method of Nuttall and Wedin (1966).

Changes in serum levels of other enzymes indicate presence of various disease processes and their possible locations. Use of enzymes in differential diagnosis depends upon the magnitude of elevation, the time course, the type of disease process (inflammation, necrosis, trauma, etc.) and the tissue affected. Identification of the tissue source is possible by assaying for enzymes of defined localization (Table II). Such assays are being developed very rapidly in humans and offer great promise. Their application to moose will require direct confirmation and establishment of baseline norms, since variations between mammalian species have been documented (Zimmerman *et al.*, 1965).

Another potential use of enzyme measurements involves tissues as well as serum and may allow detection of changes in control systems (*e.g.*: adrenocortical activity). This might provide a more reliable index than gland weights of the functional changes in adrenal activity that are postulated to occur in response to "stress", however produced. At present, the available data on serum constituents do not provide such a correlation.

HEMATOLOGY

The basic battery of hematological values includes packed cell volume (PCV), hemoglobin concentration, leucocyte count (WBC), erythrocyte count (RBC), and differential count of leucocytes. In general, PCV, RBC and hemoglobin levels reflect oxygen-carrying capacity and homeostasis. Nutritional deficiencies can produce many anemias and anemia complexes that are reflected in these values. PCV reflects proportion of erythrocytes in whole blood and, similarly, is correlated with nutritional state. Interrelationships among all these parameters are very complex.

WBC and differential counts ar useful in diagnosing various infections, intoxications and neoplasms. Changes in absolute numbers and relative proportions of the several leukocytic cell types, when considered with other symptoms, can help differentiate among various disorders. No direct, nutritionally related

TABLE II

Serum enzyme tests: tissue specificity. From Wilkinson (1970)

Enzyme	*Tissue sources*
A. *High specificity*	
Acid phosphatase	Prostate, Erythrocytes
Alanine transaminase	Liver
Arginase	Liver
Sorbitol DH	Liver
Alcohol DH	Liver
5' Nucleotidase	Hepatobiliary tract
Glutamic DH	Liver
Amylase	Pancreas, salivary glands
Lipase	Pancreas
y-glutamyl transpeptidase	Liver
B. *Moderate Specificity*	
Aspartate transaminase (SGOT)	Liver, heart, skeletal muscle
Isocitrate DH	Liver, heart
Creatine phosphokinase (CPK)	Skeletal muscle, heart, brain
C. *Low Specificity*	
Alkaline phosphatase	Bone, liver, intestinal mucosa, placenta, kidney
Lactic dehydrogenase (LDH)	All tissues (some isoenzyme specificity)
D. *Within Cell Specificity*	
Aspartic transaminase	Mitochondria form, cell sap form
Alanine transaminase	Cell sap only

TABLE III

Possible artifactual patterns of test results. After Reece and Hobbie (1972a, 1972b), Searcy (1969) and Hobbie and Reece (1972). The symbol + indicates an elevation while – indicates a depression of the condition

	Physiological or handling condition								
Assay	*Recent meal*	*High-Protein meal*	*Lipemic serum*	*Old or on clot serum*	*High bilirubin*	*Convulsions*	*Detergent contaminated tubes*	*Hemolysis*	*Specimen dehydration*
Cholesterol		+(±)			+			+	+
Calcium			+				+		+
Phosphorus	–		–	+					+
T. bilirubin									+
Total protein			+	+	+		+	+	+
Albumin	+	+	+		+		+		+
Uric acid		+	+					+	+
BUN	+	+	+					+	+
Glucose	+(±)	+	+	–					+
LDH			+	+		+		+	+
Alkaline phophatase	+		+	+					+
SGOT			+	+		+		+	+

changes in WBC or differential counts have been established firmly, but such information can prove of value in discovering pathology resulting from nutritional deprivation.

The patterns described occur in humans and in domestic species. Many may be expected to apply to other mammals as well. However, direct confirmation by empirical or experimental data is necessary to draw firm conclusions regarding patterns in moose. Some possible sources of artifically altered test results are indicated in Table III. Some of these sources of artifact are peculiar to the Technicon SMA 12 systems which are sensitive to any changes altering the optical properties of serum, including lipemia (important for many carnivores, but not commonly seen in cervids), hemolysis, and high bilirubin level.

In addition, the SMA 12 analyses system gives incorrect (low) values for serum albumin in moose blood, due to dye binding capacities. Therefore, electrophoresis is used to determine this value.

The problem of stress

Severe artifacts may result from the animal's acute physiological state when the blood is collected. These are related to recent food intake and to handling stress. The former variables are uncontrollable in wild animals and the latter are controllable only to the extent that they can be standardized in all animals handled. Usually this extent is slight, for individuals differ in response to drugs, traps and handling. Thus, handling effects have been reported in every study to date. The very substantial effects of one method of handling an animal to obtain the samples are documented in Table IV: it is clear that many results depend upon whether the animal was drugged, or manually restrained. These

TABLE IV

Acute, effects of phencyclidine and promazine administration on hematology and blood chemistry of eight pregnant adult does (data of Seal *et al.*, (1972a). Studies were performed in April 1969. The animals were guided through runways into restraint boxes and restrained manually. Blood samples were taken and then, each animal was given 1 mg/kg of phencyclidine and 0.5 mg/kg of promazine by intramuscular injection. A second set of samples was taken 45 minutes later. The data are recorded as means ± standard deviation. Statistical analysis was done using a t-test for paired variates

Assay (units)	*Restraint*	*Post drugs*	*t*	*P*
Hemoglobin (gm/100 ml)	18.6 ± 2.5	15.8 ± 2.7	4.48	.005
Red blood cells (10^6/mm^3)	13.3 ± 1.7	11.3 ± 1.7	3.22	.02
Hematocrit (vol. %)	49 ± 6	42 ± 7	4.02	.01
Mean corpuscular volume (MCV) (μ^3)	37 ± 4	37 ± 3	0.29	NS
Mean corpuscular hemoglobin concentration (MCHC) (%)	37 ± 1	37 ± 1	0.36	NS
White blood cells (10^3/mm^3)	2120 ± 700	1500 ± 470	4.47	.005
Fibrinogen (mg/100 ml)	230 ± 35	192 ± 33	10.82	.001
Serum Protein (gm/100 ml)	5.7 ± 0.7	4.9 ± 0.4	5.24	.002
SGOT (Korman units)	128 ± 26	142 ± 32	2.63	.05
CPK (International units)	50 ± 19	101 ± 36	5.09	.005
Sodium (mEq/L)	144 ± 6	142 ± 3	0.64	NS
Potassium (mEq/L)	4.3 ± 0.3	4.6 ± 0.5	1.32	NS
Calcium (mg/100 ml)	9.8 ± 0.5	9.7 ± 0.7	1.19	NS
Phosphorus (mg/100 ml)	6.7 ± 1.0	4.9 ± 0.9	4.50	.005
Cholesterol (mg/100 ml)	66 ± 7	58 ± 5	4.33	.005

variables are, at least, known. More importantly, the marked effects of restraint 24 hours previously suggest that not only can short-term serial studies be seriously compromised, but that it is possible that levels in immediately obtained samples from wild animals may reflect the previous several days' activities (Fig. 1).

A system to classify individual excitability states based on heart rate, respiratory rate and rectal temperature has been developed for bighorn sheep (Franzmann, 1972). Each individual was classified into one of five classes of excitability (not excited, slightly excited, moderately excited, excited, and highly excited). It was concluded that classes of excitability could be established and would aid in interpreting blood values. At present, we are accumulating data based on this study to establish excitability classes for moose.

Evaluating and subsequently classifying stress states in animals may also be approached through analyses of intracellular enzymes such as LDH, SGOT and CPK, which escape into the circulatory system when cells are injured (Coles, 1967). Tissue breakdown and subsequent release of these enzymes have been examined in pathologic conditions in domestic animals (Blinko and Dye, 1958; Whanger *et al.*, 1969). The influence of handling excitability on SGOT values in bighorn sheep was de-

Figure 1. Seasonal changes in certain blood components levels. BUN stands for blood urea nitrogen.

monstrated, but no correlation with degree of excitability was noted (Franzmann and Thorne, 1970). Another potentially useful index of handling is a combination of CPK and LDH levels which show a different time course of elevation and decline after handling and tissue damage (Seal *et al.*, 1972a).

Immobilizing drugs have potentially contradictory effects on blood values. Many of these drugs calm the individuals being handled, decreasing excitability and stress. In addition, however, drugs may have other more discrete physiological affects due to their pharmacologic action (Table IV; Harthoorn, 1965; Fujita, 1970). These must be experimentally determined for each species studied.

Since obtaining blood from sufficiently large samples of wild animals is difficult by any means, standardization of procedures is often extremely difficult. Nevertheless, it is extremely important to standardize methods as much as possible, and to realize that some measured values may be more plastic under stress (*e.g.*: LDH, CPK, SGOT, glucose) than others (*e.g.*: BUN, uric acid, cholesterol, proteins). With these relationships in mind, it is possible to use the more plastic assays as stress indicators, while examining nutritional status using those values little affected by handling. In any event, it should be recognized at the outset that even well-documented "norms" for a wildlife population are not strictly comparable to resting normals for human or domestic species. Instead, the "normal" values are resting normals modified by the variable stress of the standardized animal handling procedure. For this reason, blood studies of wildlife are concerned with trends, and often require large sample sizes in order to document differences between populations.

Blood studies in wild populations — strategy and design

The multitude of stress-related variables, the difficulty of standardization, the need for confirmation of relationships for each species, and the lack of baseline "normal" values complicate blood studies of moose and other cervids. In essence, we may begin at the current level of knowledge and technology of human blood-nutrition relationships, but must reconfirm relationships and ascertain normal values, within the restrictions of hard-to-standardize procedures.

Until recently, blood studies of moose and other cervids were few and superficial and only sometimes related to nutrition. A systematic effort to use blood analyses to evaluate the condition of wild cervids was first reported by Rosen and Bishoff (1952). Braend (1962) considered blood groups in moose, Nadler *et al.* (1967) studied serum proteins and transferrins, and Houston (1969) analyzed several serum parameters from 13 moose. Dieterich (1970) reported hematology of six moose and several other arctic mammals. More thorough nutrition-related studies have been carried out on other cervidae. Herin (1968) reported 14 blood parameters for 39 elk (*Cervus canadensis*). Weber and Bliss (1972) measured 13 parameters in wild and captive elk. Kitts *et al.* (1956) related age and nutrition to hematological values in black-tailed deer (*Odocoileus hemionus c.*). Seal and Erickson (1969) and Seal *et al.* (1972a,b) have reported on extensive studies involving nutrition — stress — blood constituent relationships in white-tailed deer (*Odocoileus virginianus*).

These studies have indeed demonstrated that blood assays in these cervids are subject to more sources of normal variation than are encountered in human studies. This has substantially increased the complexity of interpretation and has made the establishment of baseline normal values difficult. Identified variables include age, sex, reproductive status, season and method of handling the animal. Evaluation of an animal's or a herd's condition, a primary motivation for these studies, has been confounded by these multiple sources of variation intermingled with other sources of variations in wild animals such as nutritional history, disease, and parasitism. The advent of experimental studies on animals of known condition and history (*e.g.*: Seal's group on *Odocoileus;* Alaskan studies on penned moose) now offers the promise of unraveling these variables and yielding the necessary information for the interpretation of results from field studies.

Establishing nutrition-blood parameter correlations in moose populations involves: (a) determining boundary conditions, or those characteristics of an individual animal that must be known before blood values may be interpreted;

TABLE V

Demonstrated boundary conditions in Cervidae. The genera covered include *Odocoileus, Alces, Rangifer* and *Cervus*. Exclusive of fetal, neonatal and first one month of life data since many differences have been documented for these periods in every mammalian species studied. The symbol + indicates that significant differences have been reported while a "0" indicates that information is lacking or inadequate. The initial condition is that animals be in good health and nutrition.

Assay	*Species*	*Sex*	*Age*	*Season*	*Reproductive status*	*Handling method*	*Fasting or fed*
Hematology							
Hemoglobin	+	+		+	+	+	0
Red blood cells	+	+		+	+	+	0
Hematocrit	+	+		+	+	+	0
MCHC	0	0	0		0	0	0
MCV	+	0	0		0	0	0
WBC	+					+	
Differential	+						
Chemistry							
Cholesterol	+		+	+	+	+	
Calcium			+	+			
Phosphorus		0	+	+		+	+
Bilirubin		0	+	+	+		
Uric acid	+			+	+		
Total protein		+	+	+	+	+	
Albumin			+	+			0
Gamma globulin	+		+	+		+	0
Glucose	+	0	+	+	+	+	+
BUN	+	+		+			+
LDH	+		+	+			
SGOT	+		+	+		+	
Alkaline phosphatase			+	+	+	+	0
CPK	+					+	0
Hormones							
Thyroxine	+			+	+	+	
Cortisol	+			+			
Insulin							
Testosterone		+	+	+	+		

(b) establishing normal values within these boundary conditions using standardized handling and collecting procedures; and (c) determining the nature and magnitude of changes wrought in blood values by known changes in food intake, nutrition, or related parameters.

Boundary conditions which have been identified in cervid species are tabulated in Table V. Those demonstrated to date for moose are listed in Table VI. Species differences have become apparent in most measurements. More critically for interpretation of literature data are the many seasonal changes and the impact of handling methods. Both of these involve effects of sufficient magnitude to invalidate uncontrolled comparisons. The effect of time of day (circadian rhythms) has not been examined for any cervid species, but has been shown to be important in other mammalian species. Other conditions of possible importance include posture at time of sampling (standing or recumbent), geographic location (latitude, elevation and climate), and perhaps genetically based intraspecies population differences.

The only data available concerning the latter conditions are those gathered in protein polymorphism studies, primarily designed to delineate subspecies and specific relationships. No polymorphisms in hemoglobin or serum protein patterns have been observed in several sub-species of moose (Table VII). This is in contrast to reindeer (transferrins) and white-tailed deer (transferrins and hemoglobins). There have been no reports on serum (or tissue) enzyme polymorphisms. In contrast, the polymorphisms of white-tailed deer hemoglobin are sufficient to apply to studies of subspecies relationships, selection effects, population differences, isolates, and geographic clines. The fibrinopeptides A (19 amino acids) and B (17 amino acids) are the most rapidly evolving peptides known at present and, hence, are most likely to provide information on phylogenetic

Table VI

Demonstrated boundary conditions in Alaskan moose. The "0" indicates that no effects of the specified condition were observed upon the assay. The "+" indicates the occurence of significant changes or significant differences and thus, that the establishment of norms requires inclusion of this condition in formulating the data base. The effects of season are probably complicated by seasonal reproductive and nutritional factors

Assay	*Sex*	*Age*	*Pregnancy*	*Season*
Calcium	0	+	0	+
Phosphorus	0	+	0	+
Glucose	0	+	+	+
BUN	+	0	0	+
Uric acid	0	0	+	+
Cholesterol	+	+	0	+
Total protein	+	+	+	+
Bilirubin	0	+	+	+
Alkaline phosphâtase	0	+	+	+
Lactic dehydrogenase	0	+	0	+
SGOT	0	+	0	+
Hemoglobin	0		+	+
Hematocrit	0		+	+
WBC	0	+	+	

relationships of closely related species and genera. Data on the sequences of fibrinopeptides A and B from moose and six other cervids (Tables VIII and IX) permit inferences concerning phylogenetic relationships among these cervids. Notably, they indicate the very close affinities of *Rangifer*, *Alces* and *Odocoileus*, with no sequence differences between the reindeer and moose and only one difference from the mule deer. Also, the three species of *Cervus* exhibited only one sequence difference, in the Sika deer. These peptides are clearly not useful for species and subspecies studies, but may allow grouping of genera at the sub-family level.

Seasonal boundary conditions in moose are especially interesting in view of seasonal changes in energy balance (Gasaway and Coady, 1974). If other conditions (sex, age, reproductive status, handling method) are kept constant, alterations in blood values caused by known seasonal changes in nutrition may be good indicators of blood-nutrition relationships. The relationships are not clear, for climatological stresses and endocrine relationships (Seal *et al.*, 1972b) also change seasonally. Nevertheless results, described below, are encouraging.

Baseline normals

It is impractical to attempt to develop baseline normal values for moose similar to those existing for humans and some domestic species. The number of individuals which must be sampled to meet boundary conditions for all population segments is prohibitive. Nevertheless, most studies of other wild cervids have presented lumped data with little or no regard to boundary conditons. Existing lumped data of moose blood values, including our own data, are presented in Table X. It is evident that moose blood values fall in the same

TABLE VII

Transferrin[1] polymorphisms in the Cervidae

Species	*Location (and subspecies)*	*Number animals*	*Observed phenotypes*	*Postulated alleles*
Rangifer tarandus (0 band in homozygotes, 0 band in heterozygotes)				
1. Gahne and Rendel (1961)	Sweden	64	6	3
2. Braend (1964a)	Norway	132	15	6
3. Braend (1964b)	Norway	829	27	8
4. Nadler *et al.* (1967)	Alaska	37	Multiple	?
Odocoileus virginianus (2 bands in homozygotes, 3 bands in heterozygotes)				
1. Miller *et al.* (1965)	Iowa	150	3	2
2. Seal and Erickson (1969)	Minnesota	100	1	
3. Seal and Verme (unpubl.)	Michigan	40	3	2
Alces alces (2 bands)				
1. Braend (1962)	Norway (*alces*)	27	1	1
2. Nadler *et al.* (1967)	Alaska (*gigas*)	7	1	
3. Nadler (1968)	Canada (*andersoni*)	1	1	
4. Seal and Karns (unpubl.)	Minnesota (*shirasi*)	150	1	1

[1] All phenotypes had at least 2 bands on electrophoresis.

TABLE VIII

Fibrinopeptide-A Sequences. From tabulation D-95 of Dayhoff, 1972). A dot indicates that the amino acid is identical with that of the reindeer in that position. A blank space indicates that the identity of the amino acid was not established.

Species	*Sequence*																		
Reindeer	Ala	Asp	Gly	Ser	Asp	Pro	Ala	Gly	Gly	Glu	Phe	Leu	Ala	Glu	Gly	Gly	Gly	Val	Arg
Moose	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mule Deer				.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Muntjak	.	.	.	.	.	.	.	Ser	.	.	.	.	Thr	.	.	.	.	.	.
Sika Deer	.	.	.	.	.	.	.	Ser	Ser	.	.	.	.	.	.	.	.	.	.
Red Deer	.	.	.	.	.	.	.	Ser	Ser	Asp	.	.	.	.	.	.	.	.	.
American Elk	.	.	.	.	.	.	.	Ser	Ser	Asp	.	.	.	.	.	.	.	.	.

TABLE IX

Fibrinopeptide-B Sequences. Taken from tabulation D-96 of Dayhoff (1972). A dot indicates that the amino acid is identical with that of the reindeer in that position

Species	*Sequence*																				
Reindeer	Gly	His	Leu	Ala	Asp	Tyr	Asp	Glu	Val	Glu	Asp	Asp	Arg	Ala	Lys	Leu	His	Leu	Asp	Ala	Arg
Moose	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mule Deer	.	.	.	.	.	.	.	.	.	Asp	.	.	.	.	.	.	.	.	.	.	.
Muntjak	.	.	Ser	Thr	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sika Deer	.	.	Ser	Thr	.	.	.	.	Glu	.	Glu	.	.	.	.	.	.	.	.	.	.
Red Deer	.	.	Ser	Thr	.	.	.	.	Glu	.	Glu	.	.	.	.	.	.	.	.	.	.
American Elk	.	.	Ser	Thr	.	.	.	.	Glu	.	Glu	.	.	.	.	.	.	.	.	.	.

TABLE X

Blood data in moose (*Alces alces*). Y = yearling ; M = male ; F = female

	A. a. gigas	*A. a. shirasi*	*A. a. andersoni*[C]	*A. a. gigas*	
Reference	Dieterich (1970)	Houston (1969)	Karns & Seal (Unpubl.)	LeResche (Unpubl.)	
Location	Alaska	Wyoming	Minnesota	Alaska	
Number of animals	2 (3X)	13	*ca* 91	*ca* 520	
Type	Captive	Wild	Wild	Wild, pen	
Ages	4 mos.	10A, 3Y	Adult	Mixed	
Sex	M	4M, 9F	65M	Mixed	
Season	Summer	Winter	Oct.-Dec.	Year-round (some serially sampled)	
Drugs	Restraint	Succinylcholine	Shot	Shot, succinylcholine, M-99, other	
Assay	$\bar{X} \pm SD$	$\bar{X} \pm SD$	$\bar{X} \pm SE$	$\bar{X} \pm SD$	± SE
Hemoglobin (gm/100 ml)	13.5 ± 0.4	—	13.3 ± 1.3	14.9 ± 4.7	0.5
Red Blood Cells ($10^6/mm^3$)	5.25 ± 0.43	—	6,2 ± 1.2	—	
Packed Cell Vol. (Vol. cells/100 ml blood)	38 ± 3	—	41 ± 5.8	40.4 ± 11.8	1.5
MCHC (gm/100 ml)	36 ± 2	—	35 ± 1.4	37 ± 4	0.4
MCV (μ^3)	72 ± 7	—	59 ± 5.6	—	
Sedimentation rate (mm/hr)	27 ± 13	—	—	—	
White Blood Cells ($10^3/mm^3$)	5.87 ± 1.13	—	—	4.19 ± 2.52	0.24
Neutrophils ($10^3/mm^3$)	2.46 ± 0.88	—	—	1.37 ± 0.75	0.16
Lymphocytes ($10^3/mm^3$)	3.10 ± 1.11	—	—	2.60 ± 0.80	0.16
Eosinophils ($10^3/mm^3$)	0.23 ± 0.17	—	—	—	
Cholesterol (mg/100 ml)	—	—	54 ± 10	87 ± 21	0.9
Calcium (mg/100 ml)	—	—	9.7 ± 1.3	10.6 ± 1.1	0.05
Phosphorus (mg/100 ml)	—	—	6.4 ± 1.3	5.6 ± 1.9	0.08
Bilirubin (mg/100 ml)	—	—	0.5 ± 0.1	0.4 ± 0.2	0.01
Uric acid (mg/100 ml)	—	—	0.7 ± 0.1	0.6 ± 0.6	0.03
BUN (mg/100 ml)	—	13 ± 3[A], 5 ± 1.8[B]	8.5 ±3.2	13 ± 12	0.5
Glucose (mg/100 ml)	—	63 ± 5.7	79 ± 8	121 ± 54	2.4
Total Protein (gm/100 ml)	—	6.4 ± 0.9	6.9 ± 0.7	6.9 ± 0.9	0.04
Albumin (gm/100 ml)	—	4.5 ± 1.4	3.3 ± 0.4	3.9 ± 0.7	0.03
Gamma Globulin (gm/100 ml)	—	—	1.6 ± 0.6	—	
Alk. Phosphatase (mU/ml)	—	—	80 ± 11	81 ± 71	3.1
LDH (mU/ml)	—	—	142 ± 15	339 ± 136	6.0
SGOT (mU/ml)	—	—	59 ± 6	159 ± 59	2.6
Thyroxine (T_4) (μg/100 ml)				5.4 ± 2.3	0.15

[A] Seven animals in July-September

[B] Five animals in October-February

[C] Sex, season and area differences found in this study ; only data on males here.

general range as those reported for other cervids. Little more can be said at this time, given the great variety of individuals tested and the methods used to secure samples. However, interesting apparent differences between groups of moose exist for mean corpuscular volume (MCV), cholesterol, glucose, BUN, albumin and serum enzymes (Table X). Further analyses of data from Minnesota and Alaska, applying the appropriate boundary conditions, may elucidate these differences if they are real.

Blood-nutrition relationships in moose

Two major continuing studies of moose blood patterns are under way in North America: those of LeResche and Franzmann in Alaska, and of Karns and Seal in Minnesota. Preliminary data from both are discussed here.

The Alaska study was designed to develop practical methods for assessing population/habitat relationships on different ranges throughout the state. It has used three primary sources of materials: (1) moose contained in four 2.6 km^2 enclosures at the Kenai Moose Research Center[1], and trapped, immobilized, bled, weighed and measured periodically; (2) unenclosed moose immobilized on the Kenai Peninsula for marking, which were then bled, measured and released; and (3) moose killed by hunters or collected for rumen volatile fatty acids (VFA) studies from several areas of the state.

The Minnesota study has thus far utilized hunter-killed specimens from two areas of the state, taken at two different times of year. Its objectives include testing regional differences in nutrition. In addition blood profiles are being used as indicators of the effects of parasitism, primarily by *Fascioloides magna*.

SEASONAL VARIATION

Natural seasonal changes in diet and food intake, coupled with seasonally varying demands of pregnancy, lactation and breeding, provide an opportunity to study blood-nutrition relationships on a pseudo-experimental basis. That is, animals sampled during winter months are analogous to experimental animals on sub-maintenance diets, and those sampled during summer are analogous to animals fed high-quality rations. Seasonal energy budgets of moose calculated from weight change, food intake and value, rumen VFA production, and theoretical considerations show profits roughly from May through September and deficits from October through April (Gasaway and Coady, 1974; Fig. 2). Although compounded by changes in photoperiod and resulting endocrine relationships (Silver *et al.*, 1969), pregnancy, prior dietary history and disease, certain blood values do reflect seasonal changes in energy balance in predictable ways (Tables XI and XII).

Urea nitrogen (BUN) varies directly in correlation with energy balance in Alaska moose (Table XI; Fig. 2), reaching highest levels during seasons of positive energy balance. Similarly, October levels in 14 males from northwest Minnesota (8.5 mg/100 ml) were significantly ($P<0.005$) higher than December levels (5.7 mg/100 ml) in seven males. BUN has been repeatedly correlated with dietary protein and protein utilization balance in cervids (Houston, 1969; Seal *et al.*, 1972b) and appears to be one of the best correlates, being relatively stable and unaffected by boundary conditions.

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[1] A joint project of the Alaska Department of Fish and Game and U.S. Bureau of Sport Fisheries and Wildlife (Kenai National Moose Range).

TABLE XI

Seasonal variation in selected blood values in adult female Alaskan moose (Data of LeResche)[1]

Assay	*Months*				
	May-June *n = 80*	*July-Aug* *n = 30*	*Sept-Oct* *n = 24*	*Nov-Feb* *n = 109*	*Mar-Apr* *n = 30*
Calcium (mg/100ml)	10.47 ± 0.62	10.61 ± 0.89	11.28 ± 0.80	10.8 ± 1.32	11.1 ± 0.58
BUN(mg/100ml)	(a) 13.0 ± 14.2 (a)	32.0 ± 7.5 (a)	21.3 ± 11.8 (a)	6.9 ± 4.8 (a)	4.0 ± 2.8 (a)
Glucose (mg/100ml)	(a) 118.6 ± 29.2 (a)	134.9 ± 41.0	134.4 ± 49.4 (a)	115.4 ± 67.7 (a)	90.8 ± 31.6 (a)
Bilirubin (mg/100ml)	0.4 ± 0.2	0.7 ± 0.3	0.8 ± 0.3	0.4 ± 0.3	0.33 ± 0.05
Cholesterol (mg/100ml)	82.5 ± 21.8 (a)	97.9 ± 17.2 (a)	109.4 ± 32.9 (a)	83.0 ± 13.9	86.8 ± 12.5
SGOT mU/ml	(a) 108.1 ± 36.0 (a)	153.9 ± 44.9	158.1 ± 36.7 (a)	212.1 ± 46.5 (a)	121.0 ± 28.7 (a)
LDH mU/ml	(a) 222.9 ± 88.3 (a)	333.7 ± 180.0	345.8 ± 81.4 (a)	389.7 ± 138.8(a)	291.0 ± 60.8 (a)
Total Protein (g/100ml)	6.9 ± 0.5 (a)	8.1 ± 0.7	8.2 ± 0.5 (a)	6.7 ± 0.7	6.8 ± 0.5
Albumin (g/100ml)	4.0 ± 0.5	4.7 ± 0.8	5.2 ±0.5 (a)	3.8 ± 0.5	3.5 ± 0.4
A/G (ratio)	1.47 ± 0.38	1 54 ± 0.53	1.72 ± 0.34	1.35 ± 0.30	1.09 ± 0.28
n	n = 92	n = 53	n = 46	n = 49	no data
Thyroxine (T_4) μg/100ml	5.8 ± 3.2	5.7 ± 1.7	5.2 ± 1.6 (c)	4.5 ± 1.4 (b)	

[1] All data are given as mean ± standard deviation. The statistical comparisons were made with the « t » test.

(a) Difference between groups of months preceding and group of months following significant at $P \leq 0.001$

(b) Difference between groups of months preceding and group of months following significant at $P \leq 0.025$

(c) Difference between groups of months preceding and group of months following significant at $P \leq 0.05$

Glucose levels are also correlated with seasonal energy balance in Alaska. This is somewhat surprising in view of rapid elevation of blood glucose in handling stress. The fact that trends in glucose levels follow seasonal energy changes suggests that collection procedures can be at least reasonably standardized, however stress-producing they might be.

Cholesterol was elevated during summer months in Alaska, suggesting a seasonal increase in dietary fatty acids. No change occurred in blood cholesterol level between October and December in northwest Minnesota. Cholesterol levels in Minnesota were significantly lower (49-56 mg/100 ml) than in Alaska (82-109 mg/100 ml), suggesting interesting differences in diet and rumen function (Peek, 1974).

Total protein levels in Alaska were elevated in summer and depressed in winter, probably reflecting changes in dietary protein. The significant decline in serum albumin levels between September-October and November-February further suggests a dietary influence, although no significant change in A/G ratio occurred. Total protein levels did not change significantly between October and December in Minnesota (Table XII).

SGOT and LDH levels in Alaska both peaked during winter months, suggesting generalized tissue breakdown during this period of negative energy balance. Annual lows are reached in May and June, when forage quality suddenly improves. These lows, however, are somewhat surprising, since near-term pregnancy and early lactation increase physical stress during this time. Volume expansion and water retention may be involved. The LDH pattern in Minnesota is similar, with December levels significantly lower (204 mU/ml) than October levels (222 mU/ml). However, SGOT levels in Minnesota declined significantly from 151 mU/ml to 85 mU/ml between October and December. Serum concentrations of both

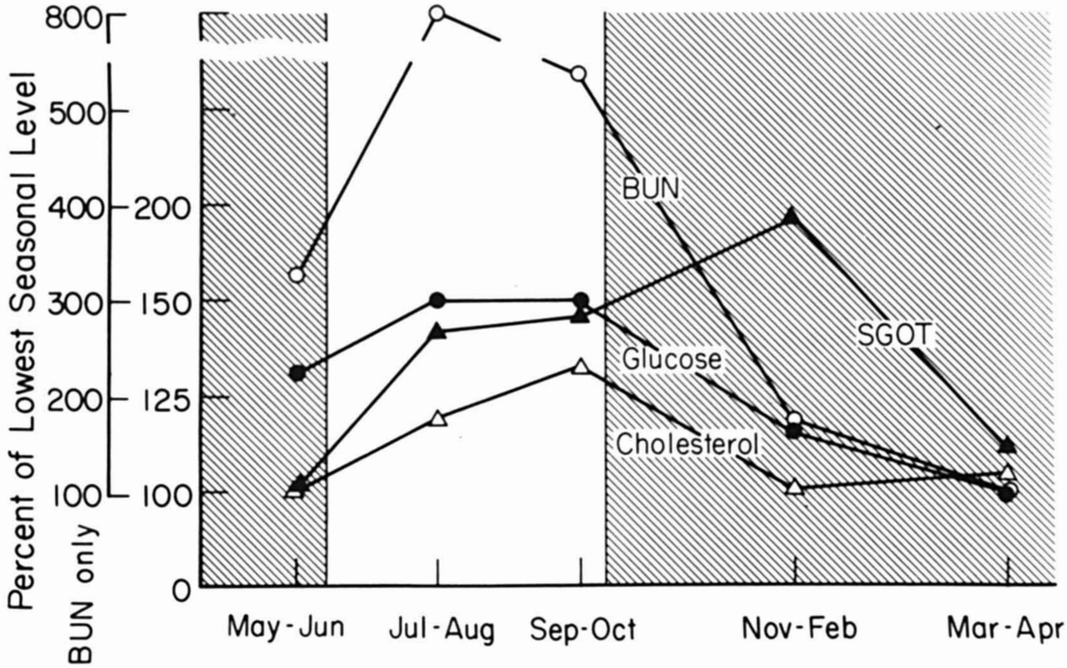

Figure 2. Blood sampling in moose, Kenai Moose Range, Alaska.

enzymes were higher in Alaska than in Minnesota, perhaps due to differences in animal handling procedures. These seemingly contradictory results deserve further exploration.

Serum thyroxine (T_4) levels in Alaska (Table XI) followed the pattern described by Seal's group for white-tail does, which involved a significant decline in serum thyroxine with reduced nutrition over a three-year period in experimental animals (Seal *et al.*, 1972b). Their studies of wild populations also yielded very low values in herds whose condition is considered poor and whose range is depleted. These studies also suggested reduced T_4 levels were due not only to low nutrition but also reflected naturally reduced metabolism and food intake in winter. Our results presented here are the first empirical evidence of such a mechanism in moose.

Hematological patterns vary seasonally in Minnesota (Table XIII), with a significant decline in erythrocyte numbers and hemoglobin concentration in males from October to December. These changes are consistent with moderate normocytic anemias, which may result from protein deficiency, or with parasitic infestation aggravated by normal seasonal decline in dietary protein. Northwest Minnesota moose do carry a very heavy liver parasite load. This condition is also reflected in significantly elevated *gamma* globulin and depressed albumin levels, relative to those found in northeast Minnesota (Table XII).

PHYSIOLOGICAL COSTS OF REPRODUCTION

Energy costs of pregnancy and lactation may approach 40-55 percent of maintenance levels in moose (Gasaway and Coady, 1974). These costs are reflected in weight deficits of 15-20 percent in late July and 6-8 percent in October-December (LeResche and Davis, 1971; LeResche, unpubl.). Tables XIV and XV illustrate how these physiological costs of reproduction may be reflected in blood values of Alaska moose.

Early-term pregnancy (October through January) resulted in a significant increase in glucose and a significant decline in cholesterol levels, by comparison with non-pregnant adult cows (Table XIV). Cows in late-term pregnancy had slightly elevated glucose levels and greatly elevated levels of SGOT, alkaline phosphatase and LDH, compared to nonpregnant cows. These

TABLE XII

Serum protein electrophoresis of Minnesota adult male moose samples. All data are expressed as means ± standard deviation. The statistical comparisons were made using the 't-test'. The Northeast-October samples were compared to the Northwest-October group to provide place or, range comparison. The Northwest-October group was compared to the Northwest-December group to provide a time or season comparison on the same range. (Data of Karns and Seal)

Area	*N*	*Total protein gm/100ml*	*Albumin gm/100ml*	*Gamma globulin gm/100ml*	*A/G*
Northwest					
October	16	6.9 ± 0.7	3.3 ± 0.4	1.6 ± 0.6	0.93 ± 0.23
December	8	7.3 ± 0.7	3.3 ± 0.4	2.4 ± 0.7 *	0.84 ± 0.15
Northeast					
October	14	6.5 ± 0.6	3.7 ± 0.4*	1.1 ± 0.4*	1.34 ± 0.26**

* $p \leq 0.01$
** $p \leq 0.001$

TABLE XIII

Hematology of adult moose from northern Minnesota (Data of Karns and Seal)

Month *Area*	*Hemoglobin (gm/100ml)*		RBC ($10^6/mm^3$		*Hematocrit (%)*		*MCV (μ^3)*		*MCHC (%)*	
	N	$\bar{X} \pm$ *S.E.*	*N*	$\bar{X} \pm$ S.E.	*N*	$\bar{X} \pm$ S.E.	*N*	$\bar{X} \pm$ S.E.	*N*	$\bar{X} \pm$ S.E.
MALES										
Northwest										
October	40	13.3 ± 1.3^{a}	41	$6.2 \pm 1.2^{c,k}$	29	41.3 ± 5.8^{e}	38	59.2 ± 5.6^{g}	37	34.6 ± 1.4^{h}
December	8	$11.1 \pm 1.2^{a,b,j}$	6	$5.0 \pm 0.6^{c,d}$		$30.7 \pm 2.7^{e,f,m}$	5	59.9 ± 4.8	7	$36.6 \pm 1.1^{h,i}$
Northeast										
October	17	13.5 ± 2.1^{b}	22	$6.6 \pm 0.3^{d,n}$	15	39.5 ± 5.3^{f}	19	62.3 ± 4.1^{g}	12	$33.7 \pm 1.5^{i,p}$
FEMALES										
Northwest										
October	8	11.6 ± 2.8	7	5.4 ± 0.7^{k}	6	33.5 ± 7.4	9	58.5 ± 7.0	9	35.7 ± 2.4
December	10	13.2 ± 1.8^{j}	9	5.7 ± 0.8	8	36.6 ± 4.3^{m}	9	59.8 ± 6.9	9	37.0 ± 2.5
Northeast										
October	8	12.3 ± 2.3	7	5.7 ± 0.8^{n}	5	37.8 ± 3.8	6	59.2 ± 3.6	7	36.0 ± 1.6^{p}

g, k, n — Difference between means statistically significant at $P < 0.05$

j, m, p — Difference between means statistically significant at $P < 0.025$

a, b, c, f, h, i — Difference between means statistically significant at $P < 0.005$

d, e — Difference between means statistically significant at $P < 0.001$

levels of SGOT and LDH suggest greatly accelerated tissue leakage in late-term, perhaps reflecting the combined effects of increased fetal demands and very low-nutrition forage. Alternately, these elevations might indicate fetal or placental injury during handling or increased cellular turnover at this time. In normal well-nourished humans, alkaline phosphatase is elevated in late-term pregnancy; whereas, SGOT is unchanged or slightly depressed.

Glucose elevations in pregnant animals are difficult to explain, but likely represents accomodation to fetal demands rather than enhanced energy reserves in pregnancy. Decreased cholesterol during early pregnancy might result from lipid uptake by rapidly-growing fetal myelin structure. Endocrine relationships might further be involved.

Blood values differ significantly between adult cows with no calves, those with one calf and those with twins (Table XV). These differences perhaps reflect some of the nutritional costs of rearing young. Cows with one calf tested in Table XV weighed a mean 368 kg, significantly less than those with no calves (392 kg), in September-December. The significant increase in BUN levels from cows with no calves to those with one and those with twins is perplexing. Perhaps a hidden seasonal bias in the sample is operating, for data from all year are lumped and progressive calf loss may have resulted in cows with calves being sampled more heavily in summer months, when BUN levels are high. Alternately, the values might reflect increased protein catabolism required for lactation. Relationships are unclear.

Glucose is highest in cows with no calves, lower in those with one calf, and lower in those with two calves (Table XV). This most likely represents the cost of lactation, which may involve glycogen stores. SGOT and LDH are significantly elevated in cows with calves, perhaps signifying, again, greater catabolism of body tissues in lactating animals. Since lactation ceases in October or November, however, this year-round elevation is difficult to explain fully.

Present applications — Need for future research

It is abundantly clear that the full potential uses of blood analyses have not been reached. Stress of handling remains a problem but results from Alaska indicate that sometimes trends might over-ride these variables if methods are standardized. The problem of handling stress is insoluble in wild animals using presently available techniques, but may be minimized using tame moose and remotely-activated devices (Farrell *et al.*, 1970).

Seasonal patterns of BUN, glucose, cholesterol, proteins and enzymes suggest that these values may be useful as indicators of nutritional status. Relationships need experimental confirmation, but eventually such indicators will allow discrimination between ranges of different qualities. Data are currently being gathered from different ranges in both Alaska and Minnesota.

The preliminary results of thyroxine assays reported here are very promising, and endocrine studies should be further pursued. We have shown that thyroxine levels vary seasonally, but we do not know whether this variation is greater on lower-quality ranges, nor what the relationships between pregnancy, fetal health and thyroid function are. Studies with animals at high and low nutritional planes, in either experimental or natural conditions, are indicated.

The only reported studies on cortisol metabolism are in the reindeer by You-

TABLE XIV

Selected blood values in pregnant and non-pregnant adult cow moose, during two seasons of the year in Alaska. (Data of LeResche)

Assay	*October-January*				*February-April*				*P*[1]
	Pregnant		*Not pregnant*		*Pregnant*		*Not pregnant*		
	n	$\bar{X}$ ± *S.D.*	*n*	$\bar{X}$ ± *S.D.*	*n*	$\bar{X}$ ± *S.D.*	*n*	$\bar{X}$ ± *S.D.*	
Calcium (mg/100ml)	26	10.7 ± 0.9	44	10.7 ± 1.1	35	11.3 ± 1.8	42	11.0 ± 0.7	0
BUN (mg/100ml)	27	5.8 ± 3.7	43	7.8 ± 5.3	35	6.1 ± 4.1	42	5.9 ± 5.1	0
Glucose (mg/100ml)	27	134.1 ± 92.2	47	107.9 ± 59.5	36	111.4 ± 55.8	43	104.3 ± 42.6	0
Bilirubin (mg/100ml)	27	0.35 ± 0.08	47	0.45 ± 0.35	36	0.35 ± 0.09	43	0.38 ± 0.19	0
Cholesterol (mg/100ml)	27	75.7 ± 16.9	47	90.4 ± 13.5	36	82.8 ± 10.6	43	85.2 ± 12.9	1
SGOT (mU/ml)	27	193.2 ± 55.6	46	200.0 ± 46.7	36	224.3 ± 38.8	43	153.1 ± 59.0	3
Alkaline Phosphatase (mU/ml)	27	50.9 ± 26.4	47	49.1 ± 48.1	36	90.7 ± 47.8	43	54.2 ± 45.9	3
LDH (mU/ml)	27	369.3 ± 151.0	47	362.3 ± 112.0	36	413.9 ± 143.7	43	331.9 ± 115.5	3
Total Protein (g/100ml)	12	6.3 ± 0.8	41	6.8 ± 0.7		No data	35	6.8 ± 0.5	0
Albumin (g/100ml)	12	3.7 ± 0.6	41	3.9 ± 0.6		No data	35	3.6 ± 0.5	0
A/G ratio	12	1.5 ± 0.3	41	1.4 ± 0.3		No data	35	1.1 ± 0.3	0

[1] Values for pregnant moose were compared with those for non-pregnant moose during each of the two time periods using the "t" test. Probabilities of differences were:

0 — No statistical difference during either time period. ($P \geq .05$)
1 — Pregnant vs. non-pregnant difference significant ($P < .001$) during October-January.
2 — Pregnant vs. non-pregnant difference significant ($P < .05$) during October-January.
3 — Pregnant vs. non-pregnant difference significant ($P < .001$) during February-April.
4 — Pregnant vs. non-pregnant difference significant ($P < .05$) during February-April.

TABLE XV

Selected blood values of adult cow moose leading and not leading calves (year-round values, Alaska). Data of LeResche. Values for cows with no calf, one calf and two calves were compared with one another using the "t" test. Probabilities of differences were:(a), (b): different at P < .001, (c): different at < .01.

Assay	With no calf		*With one calf*		*With two calves*	
	N	$\bar{X} \pm$ *S.D. P*	*N*	$\bar{X} \pm$ *S. D. P*	*N*	$\bar{X} \pm$ *S. D. P*
Calcium (mg/100ml)	125	10.5 ± 0.7	50	10.9 ± 0.8	5	10.3 ± 0.9
BUN mg/100ml)	129	12.8 ± 11.5 (a)	49	20.5 ± 12.7 (a)	5	36.0 ± 33.1 (a)
Glucose (mg/100ml)	130	122.6 ± 39.7	51	120.8 ± 38.2	5	11.4 ± 63.8
Bilirubin (mg/100ml)	130	0.45 ± 0.23	51	0.59 ± 0.28	5	0.82 ± 0.63
Cholesterol (mg/100ml)	128	86.2 ± 21.6 (a) (b)	50	101.7 ± 26.9 (a)	5	110.4 ± 15.4 (b)
SGOT (mU/ml)	128	121.9 ± 42.0 (a) (b)	50	147.7 ± 42.7 (a)	5	148.4 ± 58.2
Alkaline Phosphatase (mU/ml)	130	85.0 ± 82.5 (a)	51	37.2 ± 15.2 (a) (b)	5	86.0 ± 135.9
LDH (mU/ml)	128	261.5 ± 99.5 (a)	50	318.8 ± 88.2 (a)	5	396.2 ± 121.9 (a)
Total Protein (g/100ml)	123	7.1 ± 0.7	45	7.6 ± 0.9	5	7.6 ± 0.7
Albumin (g/100ml)	123	4.1 ± 0.6	46	4.3 ± 0.9	5	4.0 ± 0.2
A/G (ratio)	123	1.41 ± 0.43	46	1.40 ± 0.42	5	1.08 ± 0.11

sef *et al.*, (1971). They conclude that winter acclimatization is accompanied by a decrease in half life and an increase in estimated secretion rate. No comparable data exist for other cervids. Confirmation of these results would be desirable since their method for measurement of cortisol can be influenced by increases in ketone bodies which may occur in the winter metabolic state. Simple measurement of serum cortisol is almost certainly of little value since the levels of binding proteins are low, the turnover is rapid, and levels can fluctuate rapidly.

Measurements of other plasma hormone levels are not presently available. Seal's group do have data on insulin, glucagon, and thyroid stimulating hormone (TSH) levels in the white-tailed deer which will be published shortly.

An area as yet barely touched is fat metabolism. Cholesterol assays show some promise, while triglycerides probably do not. The levels of both are low in cervids. Direct measurements of long-chain fatty acids, ketone bodies, pyruvate, lactate, acetate, an proprionate, especially in conjunction with rumen VFA studies, will probably provide a more direct assessment of the animal's dependence upon its fat reserves for energy.

Protein assays performed to date have been promising, but too crude to indicate precise metabolic relationships. Measurements of serum and red blood celle amino acids — especially alanine, glycine, leucine, and isoleucine — might provide valuable information on the status of protein used for gluconeogenesis. Creatine-hydroxyproline relationships have yet to be investigated in moose. Albumin-globulin relationships have successfully detected severe liver parasitism in Minnesota, and these assays will continue to have such applications.

Serum enzyme patterns have suggested seasonal changes in tissue destruction rates. Further studies might employ enzymes of higher tissue specificity in order to explain these patterns more fully.

Thus, the data currently available and the studies in progress with cervids hold considerable promise of providing the concepts and tools for evaluating condition of wild cervids and the condition of their range relative to their needs. It also appears possible to begin unraveling influences of such factors as density and social stress, separately from nutrition, upon a given population in terms of physiological response. The ability to quantitatively describe metabolic status and its endocrine regulation has increased dramatically in the past five years as the result of new exquisitely sensitive radio-immunoassay techniques. As a result, we may soon achieve the precise formulations of these mechanisms that we need in order to measure ecological and behavioral relationships of individuals and populations.

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MINERAL COMPOSITION OF BROWSE PLANTS FOR MOOSE

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Résumé

L'habitat de l'orignal présente un bon éventail de plantes indigènes, depuis les plantes aquatiques jusqu'aux graminées, plantes herbacées et ligneuses. En été, l'abondance de ressources alimentaires coïncide pour une grande part avec l'accessibilité d'un bon assortiment de plantes et les variations dans l'ingestion d'éléments minéraux chez l'orignal peuvent donc suivre les variations dans l'abondance de la nourriture. Afin de jeter un peu de lumière sur la qualité des régimes alimentaires de l'orignal, l'auteur présente, pour un certain nombre de plantes, des données sur la teneur en éléments minéraux : éléments majeurs (P, S, Ca, Mg, K, N) et oligo-éléments (Co, Cu, Mo, Se, Zn, Mn). A l'aide des normes établies pour l'alimentation du bétail, l'auteur évalue dans quelle mesure les besoins en éléments minéraux sont satisfaits. Durant les mois d'hiver, alors que la diète est surtout composée de ramilles d'arbustes, la quantité est tout juste satisfaisante. D'autre part les plantes indigènes fournissent des quantités relativement élevées de Zn et Mn, mais à des niveaux apparemment plus bas que le niveau reconnu toxique pour les ruminants.

Abstract

The habitat of moose offers a wide range of native feed plants, ranging from aquatics to grasses, herbaceous plants and shrubs. Abundance of feed in summer largely coincides with availability of different kinds of plants. A seasonal pattern of mineral intake by moose may follow a pattern of feed abundance. Summaries of the mineral composition of groups of plants are presented to provide some insight into dietary intake of mineral elements by moose when they eat different kinds of plants and parts of plants. The presentation includes summaries of the macronutrients (P, S, Ca, Mg, K and N) and the micronutrients (Co, Cu, Mo, Se, Zn and Mn). The levels of mineral elements are evaluated for their adequacy using recognised levels for cattle, a large ruminant. An overview of the mineral composition of plants indicate that Ca, P and Se may be marginally adequate during the winter months, when the diet of moose consists principally of woody twigs. Native plants provide relatively large amounts of Zn and Mn but the amounts present appear to be below toxics levels for ruminants that eat the plants.

Introduction

Native browse plants are the principal source of feed for moose, and, except for naturally occurring salt deposits, are the primary source of mineral elements. This review presents the mineral composition of some important feed plants for moose and factors that affect their levels in the plants.

The mineral composition of plants provides a measure of the level and adequacy of nutrient elements for animals that eat the plants. It also reflects the ability of different plants to absorb nutrient elements. The mineral requirements and tolerances differ among species of plants, and levels of nutrients that meet the needs of the plants may or may not satisfy the needs of the animals that eat the plants. Different plants absorb a wide range of mineral elements, some of which have no essential role in their growth. Selenium and cobalt are examples of elements that are essential for animals but not for most plants.

Rocks and soil parent materials

The source of mineral elements for most terrestrial plants is the rock from which soils are formed. The incorporation of the different elements into rocks is outlined by Goldschmidt (1954) and Rankama and Sahama (1950). A direct relation of the mineral composition of plants to rocks is often obscure because most plants grow on soils that are formed from weathering of rock materials. Broad areas that support plant growth are underlain by unconsolidated geologic materials from mixed sources of rocks of which glacial drift, loess, alluvium and coastal plain deposits are the most important.

Soil development and weathering

The weathering of geologic deposits results in soil development and the release of the nutrient elements. These elements may then enter the animal food chain. The fate of a nutrient element released by weathering varies with its chemical properties, the intensity and direction of soil development, and its subsequent chemical reactions with products of soil weathering like clay and iron oxides.

Some broad changes in nutrient elements due to weathering are evident from studies of their vertical distribution within a soil profile. The distribution pattern of specific nutrient elements often varies widely among soils as does the actual amount present. Various chemical extractants are used to obtain estimates of probable forms of nutrient elements in soils and their availability to plants. Nutrient elements like nitrate-nitrogen that are easily extractable with water are leachable from soils. When present within rooting depths of plants, they are available for absorption by the plants. Portions that are leached beyond rooting depth of plants may end up in bodies of water and become sources of nutrient elements for aquatic plants.

Other elements released by weathering, however, may be largely unavailable or only slowly available to plants. These are elements that upon release from the rocks may become rapidly fixed in unavailable forms to plants, either through adsorption, chemical precipitation or both. Elements trapped in silicate clay or occluded in hydrous iron oxides, produced under intense soil weathering, often are not readily available to plants. The availability of many elements is pH-dependent and thus elements like Fe are generally more available to plants grown on acid soils than on alkaline soils.

Knowledge of soils and their distribution pattern provides a means to study the relationship between the mineral composition of plants and kinds of soils. Patterns of soil distribution on landscapes evolve because soil formation results from the impact of climate and vegetation on geologic deposits, as it is conditioned by slope and duration of weathering.

Most browse plants of moose grow on acid soils. Low temperatures and the presence of frozen subsoil or bedrock may restrict the rooting depth of plants in many places.

Species of plants

Cultivated plants often exhibit marked species effects in their growth and absorption of mineral elements (Beeson, 1941; Chapman, 1966). While differences in mineral composition among native plants are less well defined, some are recognized as accumulators of trace elements (Peterson, 1971). The relatively slow rate of growth of native plants grown on relatively infertile soils, under adverse climatic conditions, may affect the concentration of some nutrient elements.

Leaves generally have a higher concentration of mineral elements than do stems in improved grasses and similar differences between parts of plant might be expected among native grasses. Decreases in mineral concentration of grasses with season have been reported by Lazar and Beeson (1956) but the magnitude of the decreases was relatively small compared to differences among species of plants.

Relatively little is known about the distribution of mineral elements in various parts of woody plants browsed by moose. The process of mineral absorption by woody plants is also not well defined. Mycorrhiza, an association of woody roots with specific fungi, is present on root surfaces of some woody plants. Its presence on roots of shrubs browsed by moose remains undetermined, but a possible mechanism of mineral absorption by these plants other than from direct root absorption is indicated (Parr, 1968).

Absorption of mineral elements through the surface of leaves may also be a pathway by which mineral elements enter browse plants. The accumulation of trace elements by mosses in Sweden and the decreases in concentration with increasing distance from point sources have been observed (Rühling and Tyler, 1971). A similar pathway may be important in the mineral absorption by lichens in a moose habitat. Increases in trace elements following applications of dust and spray also suggest entry of mineral elements from leaf surfaces (Arkley *et al.*, 1960). Thorough washing and rinsing of plant materials failed to completely remove the trace elements applied. The deposition of soil particles on leaf surfaces in parts of a moose habitat may be expected where sources of loess and volcanic ash occur.

Mineral composition of plants

When tied to mineral requirements of animals established through feeding trials, studies of the mineral composition of plants provide a means to evaluate their adequacy to meet the dietary needs of animals that eat the plants. Differences in the mineral requirements among different animals are recognized as are periods when animal susceptibility to mineral deficiencies, toxicities or imbalances is high. The recognition of critical levels of deficiencies and toxicities for a number of trace elements have provided useful information in the evaluation of the mineral composition of plants. For elements like Ca and P, an imbalance appears to be more important than presence of absolute amounts. While considerable information is available, complete mineral analyses are rarely available even for some common forage plants, as the numbers and kinds of mineral elements determined have varied widely with objectives and interests of the investigators as well as with availability of analytical tools. Summaries of the mineral composition of cereal grains and forages (NAS-NRC, 1958; Chapman, 1966) provide one basis to make comparative evaluations of the mineral composition of browse plants generally and especially of the grasses.

Compared with common forage plants, appreciably less is known about the mineral composition of aquatic and woody plants that moose also eat. Some comparative data are available (Kubota *et al.*, 1970) but much of the information stems from studies of native plants undertaken for purposes other than to evaluate the nutritional quality of plants for moose (Gerloff *et al.*, 1964; Likens and Bormann, 1970; Stone, 1968).

The assessment of dietary mineral intake by moose is difficult to make with precision because the moose derives its minerals from a mixed plant source. Seasonal differences in mineral intake with seasonal changes in availability of plant species and parts of plants is a factor.

Summaries are presented by groups of plants and kinds of mineral elements — macro and micro — for the evaluation of plant sources of mineral elements. Findings from studies conducted in different geographic areas are identified and presented separately wherever possible to provide some estimate of similarities and differences in the mineral composition of plants grown in different areas habited by moose.

Information about the number of sites for which observations were available is given to provide some indication of the observations presently available from published and unpublished sources. The number of sites is indicative of numbers of plant samples taken in a number of cases, but they also include observations where more than one sample of a plant was taken and analyzed separately. When compared with the wide range of plants that moose eat, the kinds of soils on which they grow and the vast area that the moose habitate, the observations are relatively meagre.

Some evaluations to identify good and poor plant sources of mineral elements, however, seem possible using recognized levels for a large domestic ruminant like cattle (Underwood, 1966, 1971). While data summarized from different sources of information include variability due to differences in sampling techniques and analytical methods and do not readily lend themselves to statistical evaluations, they do permit directing attention to those values that appear to be consistently in the low or high concentration ranges of possible nutritional significance to moose.

MACRONUTRIENTS

The levels of the macronutrients in native grasses and sedges are not high and do not differ appreciably among samples from various parts of Alaska (Table I). There is also good agreement in macronutrient levels of the Alaska plants and of native grasses of Wisconsin. The concentration of these macronutrients in bluejoint reedgrass (*Calamogrostis canadensis*) did not differ among sites on loess, volcanic ash, colluvium and peat (Table II).

Willows (*Salix* sp.) and aspen (*Populus tremuloides*) are usually ranked high among woody plants preferred by moose. Terminal stems representing current season's growth provide a year-round source of feed. Together with leaves that are seasonally available, they are a major source of nutrient elements for moose. A summary of P, S, Ca, Mg and K concentrations in current year's growth of woody plants is presented for samples from Alaska, Minnesota and Wisconsin (Table III). Data given for Minnesota are for terminal stems after leaf fall and do not include leaves.

An effect of species differences is indicated by higher concentrations of P, S, Ca, and K in willow than in dwarf birch (*Betula* spp.). Willows of Alaska have slightly less P, S, Ca, and K than do willows of Wisconsin, but the reason for these differences is not clearly evident.

Leaves of woody plants are better sources of P, S, Ca, and K than are

Table I

Nutrient composition of grasses and sedges in Alaska and Wisconsin

Plant	*No. of sites*	*Macronutrients (%)*						*No. of sites*	*Micronutrients (ppm)*				
		N	*P*	*S*	*Ca*	*Mg*	*K*		*Co*	*Mo*	*Cu*	*Zn*	*Mn*
— Kenai moose range — Kodiak Island[1] *—*													
Bluejoint reedgrass	10		0.13	0.12	0.13		1.18	40*	0.14	1.21	3.6	30	368
Cottongrass	2		0.09	0.20	0.16		0.89	6	0.15	0.58	4.4	34	322
—Aleutians, Kodiak Is., Kenai penin.[2]													
Grasses and sedges, undifferentiated	29	1.45	0.17		0.25								
— Wisconsin[3] *—*													
Native grasses	13	0.91	0.16	0.10	0.31	0.23	1.11	17		0.22	3.4	30	81

[1] Kubota, Rieger and Lazar (1970).

[2] Kellogg and Nygard (1951).

[3] Gerloff *et al.* (1964).

* Mo and Mn values presented for bluejoint are a mean of seven field sites and for cottongrass, two sites.

Table II

Phosphorus, S, Ca, and K concentration of bluejoint reedgrass (*Calamagrostis canadensis*) grown on 10 widely different soils of Alaska

Soil drainage	*Soil parent material*	%			
		P	*S*	*Ca*	*K*
— Kenai Peninsula including the Moose Range					
Good	loess and volcanic ash	0.21	0.13	0.07	1.69
	volcanic ash	0.13	0.14	0.16	1.40
	loess	0.17	0.12	0.16	1.15
Poor	colluvium	0.14	0.10	0.13	0.79
	colluvium	0.12	0.13	0.09	1.80
Very poor	peat	0.15	0.12	0.06	1.22
	peat	0.03	0.11	0.18	0.55
— Kodiak Island					
Good	volcanic ash	0.14	0.12	0.14	1.02
Somewhat poor	volcanic ash	0.21	0.16	0.17	1.44
Very poor	peat	0.01	0.09	0.08	0.72
	Number of sites				10
	Mean	0.13	0.12	0.13	1.18
	SD	0.06	0.02	0.05	0.41

current growth of their twigs (Table IV). The P and S concentrations are uniformly low in twigs and judging by the needs of cattle appear marginally adequate for moose. The Ca concentrations are well within the low range determined in leaves of coniferous and deciduous trees of northeastern United States. A range from 0.44 to 3.69 percent of Ca was determined in leaves from 27 tree species (Chandler, 1939). Values reported for leaves include petioles and leaf blades. In a study of sycamore (*Acer pseudoplatanus*) and horsechestnut trees (*Aesculus hippocastanum*), Guha and Mitchell (1965) found that amounts of macronutrients in the petiole and in the leaf blade may vary among species of plants and with mineral elements. Concentrations of Ca, Mg, K, Na, and P did not differ among leaves sampled from the bottom, middle and top portions of the tree.

Increases in Ca concentrations with leaf maturity have been observed in leaves of trembling aspen (*Populus tremuloides*) in New York (Chandler, 1939). Leaves sampled in May had 1.2 percent Ca and gradually increased to 2.4 percent by October. Calcium content also increased with leaf maturity in sycamore and horsechestnut but the increases in Ca paralleled corresponding decreases in K and P contents (Guha and Mitchell, 1965). No changes in Na and Mg concentrations were evident. Likens and Bormann (1970), however, have observed that changes in Ca, Mg, K and K concentrations with leaf maturity may be species-dependent. Data on leaf composition presented in Table IV

Table III

Nutrient concentrations in current seasons growth (leaves and stems) of woody plants in Alaska, Minnesota, and Wisconsin.

	Macronutrients (%)					*Micronutrients (ppm)*				
	P	*S*	*Ca*	*Mg*	*K*	*Co*	*Mo*	*Cu*	*Zn*	*Mn*
— *Kenai Peninsula and Kodiak Island*[1] —										
Willow (*Salix* spp.)	0.23	0.14	0.67		0.93	1.18	0.16	5.4	84	309
Quaking aspen (*Populus tremuloides)*	0.16	0.10	0.62		0.94	0.74	0.05	6.6	71	61
Paper birch (*Betula papyrifera)*	0.17	0.10	0.43		0.65	0.35	0.09	5.0	155	788
Dwarf birch *(Betula glandulosa)*	0.07	0.07	0.34		0.35	0.46	0.17	4.8	117	796
Alder (*Alnus crispa)*	0.12	0.11	0.48		0.72					
— *Minnesota*[2] —										
Willow (*Salix* spp.)	0.28		1.35	0.15	0.71			37.3	202	118
Quaking aspen *(Populus tremuloides)*	0.34		1.43	0.22	1.14			34.8	179	.85
Beaked hazel (*Corylus cornuta)*	0.27		2.06	0.26	0.37			27.4	88	224
— *Wisconsin*[3] —										
Willow (*Salix* spp.)	0.24	0.33	1.00	0.52	1.38		0.16	7.3	148	562
Cottonwood (*Populus deltoides*)	0.22	0.32	1.04	0.54	1.31		0.11	7.5	161	84

[1] Kubota, Rieger and Lazar (1970). The number of samples determined varied widely with species of plants and the mineral element. For the macronutrients, willows from 25 sites were determined; aspens from 6 sites; paper birch from at least 8 sites; dwarf birch from at least 5 sites, and alder from 3 sites. For the micronutrients, Co and Cu was determined in willows from as many as 43 sites to as few as 14 sites for aspen. Mo on willow from as many as 16 sites to as few as 6 sites of paper birch.

[2] J. Peek (1972) unpublished (terminal stems after leaf fall). Data are given for samples from the Superior National Forest in northeastern Minnesota.

[3] Gerloff, Moore and Curtis (1964). Data are given for two samples of willow from one field site and for three samples of cottonwood from three sites.

represent samples collected in July and August. Concentration changes between sampling dates are small.

Any decreases in P, S, Ca, and K concentrations in twigs from summer to winter thus may be nutritionally important, since twigs are the major winter forage source for moose. Comparisons of twigs sampled in summer and winter indicate that the concentrations of P, S, Ca, and K are essentially similar (Table V). These comparisons are based on samples collected from three sites fairly accessible from paved roads in winter. Trees sampled in winter, however, were not the same as those sampled in summer.

Effects of soil differences generally are not evident in the concentration of P, S, K, and Ca of woody plants browsed by moose. The differences in P, S, Ca, and K concentrations are small (Table VI) in leaves of willow grown on soils of good and poor drainage and formed in a wide range of soil parent materials. Chandler (1939) has observed that Ca concentration in leaves does not differ markedly if trees are grown on soils having base saturation of 50 percent or more.

Some of the first green feed plants available to moose following spring breakup of ice in ponds, muskegs and rivers are submerged and emergent aquatic plants. Growth of these plants and their mineral composition have been studied largely because of their prolific growth in eutrophic lakes (Boyd, 1968). Relatively little, however, is known about their growth in the subarctic habitat of moose.

One sample of pond lily (*Nuphar* sp.) collected from a shallow lake in Alaska indicates this species to be a good nutrient source for moose (Table VII). Leaves have more N and P than do

Table IV

Comparison of nutrient concentrations in leaves and stems (current season's growth) of four browse plants of Alaska, including samples from the Kenai Moose Range. (From Kubota *et al.*, 1970)

Plant	*Macronutrients (%)*				*Micronutrients* [1](ppm)				
	P	S	Ca	K	Co	Ma	Cu	Zn	Mn
— *Leaves* —									
Willow	0.34	0.23	0.84	1.41	1.80	0.22	5.6	86	436
Quaking aspen	0.22	0.16	0.68	1.50	1.13	0.06	6.7	84	80
Paper birch	0.25	0.15	0.65	0.96	0.40	0.11	5.4	176	265
Bog birch	0.12	0.11	0.44	0.53	0.51	0.16	5.1	102	1117
No. sites	44	46	46	46	—	—	—	—	—
Mean	0.28	0.19	0.73	1.24	1.15	0.16	5.6	105	512
SD	0.16	0.08	0.24	0.44	1.18	0.17	1.9	60	570
— *Twigs* —									
Willow	0.12	0.06	0.53	0.50	0.55	0.10	5.1	81	183
Quaking aspen	0.10	0.06	0.58	0.56	0.35	0.05	6.5	68	42
Paper birch	0.09	0.05	0.25	0.40	0.30	0.07	4.5	135	1310
Bog birch	0.03	0.05	0.26	0.22	0.42	0.19	4.6	133	400
No. sites	44	56	56	56	—	—	—	—	—
Mean	0.10	0.05	0.44	0.45	0.44	0.10	5.1	101	386
SD	0.06	0.02	0.21	0.25	0.35	0.12	1.6	49	538

[1] Micronutrients in willow were determined on samples from 43 sites; aspen, 14 sites; paper birch, 6 sites and bog birch, 33 sites. Means of Mo and Mn presented for willow represent values determined on samples from nine field sites.

stems, and K concentration is high, especially in relation to amounts of Ca. Some aquatic plants have large amounts of Ca as carbonate coatings (Boyd, 1968) and these coatings have been removed by acid rinses prior to their analysis (Gerloff and Krombholz, 1966). The relatively low amounts of Ca in the lily analyzed may be a reflection of relatively low carbonate levels of the lakewater in which the plant was grown. Pondweeds (*Potamogeton* sp.), another food source for moose, also has similar N and P levels (Table VIII) as pond lily.

Solution culture studies with wild celery (*Vallisneria americana*) have been made by Gerloff and Krombholz (1966). Their results suggest that tissue concentrations of about 1.3 percent N and 0.13 percent P may be indicative of deficiency levels for the growth of this aquatic plant. Similar levels have not been determined for the pondweeds, but tissue concentrations of N and P suggest that probably neither N or P is limiting in the growth of this submerged plant in the infertile Wisconsin lakes studied.

Herbaceous plants and low-growing shrubs such as lingonberry (*Vaccinium vitis-idaea*), like the grasses and woody browse plants, are mostly available as feed plants during the short summer months. Fireweed (*Epilobium angustifolium*) and lupines (*Lupinus* sp.) have more P than do most other plants in moose habitat (Table IX). Together with horsetails (*Equisetum* sp.) they appear to be good sources of Ca and K. The amounts in lingonberry are comparable to amounts of P, Ca, and K in leaves and stems of woody plants (Table III).

Lichens are an important ground cover in most areas that are not seasonally or permanently flooded. Although they are a source of feed in early spring on depleted ranges (Oldemeyer, pers. comm.), the low biologic availability of

Table V

Nutrient concentrations in twigs, representative of summer and winter feed, as reflected by samples from selected sites in Alaska

Field location	*Macronutrients (%)*								*† Micronutrients (%)*					
	Summer				*Winter*				*Summer*			*Winter*		
	P	*S*	*Ca*	*K*	*P*	*S*	*Ca*	*K*	*Se*	*Co*	*Cu*	*Se*	*Co*	*Cu*
— Willow —														
7	0.15	0.03	0.53	0.49	0.13	0.09	0.38	0.33	<0.01	0.49	4.9	0.02	0.80	6.1
8	0.09	0.03	0.48	0.58	0.13	0.08	0.39	0.29	<0.01	0.54	3.9	0.01	1.37	6.3
18									<0.01	0.32	4.3	0.01	0.52	12.6
— Quaking aspen —														
3	0.11	0.06	0.29	0.77	0.15	0.09	0.49	0.36	0.07	0.23	7.4	0.08	0.43	7.6
7	0.08	0.04	0.47	0.64	0.19	0.08	0.57	0.48	0.09	0.51	4.9	<0.01	0.72	6.2
8	0.06	0.03	0.43	0.45	0.11	0.05	0.55	0.46	0.01	0.30	4.7	0.14	0.78	5.1
— Bog birch —														
3	0.05	0.05	0.20	0.23	0.11	0.06	0.22	0.21	0.02	0.22	2.8	0.02	0.05	5.3
7	0.05	0.04	0.18	0.29	0.07	0.06	0.23	0.24	0.01	0.42	6.6	<0.01	1.27	6.0
8	0.26	0.06	0.26	0.26	0.11	0.08	0.14	0.25	0.03	0.32	3.8	0.20	0.73	6.3
18									0.01	0.12	4.2	<0.01	0.30	6.2
Median	0.09	0.04	0.36	0.47	0.12	0.08	0.39	0.35	0.01	0.34*	4.8*	0.01	0.74	6.2

* Median value for samples from two summers' collection are presented.

† Essentially the same amounts of Co and Cu were in twigs sampled the following summer.

Table VI

Nutrient concentrations in leaves of willow from well drained and poorly drained soils of Alaska

Element		Soil drainage	
		Good	Poor
Macronutrients (%)[1]			
P	mean and SD	0.41 ± 0.13	0.25 ± 0.18
	range	0.24 – 0.65	0.10 – 0.76
S	mean and SD	0.24 ± 0.08	0.26 ± 0.17
	range	0.14 – 0.45	0.12 – 0.76
Ca	mean and SD	0.82 ± 0.21	0.75 ± 0.33
	range	0.51 – 1.22	0.31 – 1.47
K	mean and SD	1.45 ± 0.33	1.36 ± 0.43
	range	0.95 – 2.09	0.69 – 2.16
Micronutrients (ppm)[2]			
Co	mean and SD	1.62 ± 1.18	2.04 ± 1.67
	range	0.27 – 4.91	0.13 – 5.75
Mo	mean and SD	0.08 ± 0.07	0.32 ± 0.24
	range	0.01 – 0.20	0.03 – 0.70
Cu	mean and SD	6.0 ± 2.1	4.9 ± 1.9
	range	2.9 – 11.2	1.2 – 9.6
Mn	mean and SD	109.6 ± 58.3	762.5 ± 341.8
	range	38 – 219	289 – 1259
Zn	mean and SD	80.2 ± 45.2	92.4 ± 59.8
	range	19 – 217	35 – 240

[1] Means are presented for willow samples from at least 14 sites of soils with good soil drainage and ll from sites with poor soil drainage.

[2] Means for Mo are presented for samples from 7 sites with good soil drainage and from 6 with poor soil drainage; for Zn, samples from at least 17 sites of each are represented; for Mn, 8 from each; for Co, samples from 24 sites with good soil drainage and 19 sites with poor soil drainage.

Table VII

Nutrient composition of pond lily (*Nuphar* sp.), leaves and stems *

Element	Leaves	Stems
Macronutrient (%)		
N	3.57	1.43
P	0.31	0.19
Ca	0.63	0.74
Mg	0.15	0.25
K	3.93	2.64
Na	0.01	0.01
Micronutrient (ppm)		
Co	0.86	1.02
Mo	0.05	0.08
Cu	4	4
Zn	24	24
Mn	432	204
Fe	210	66

* Sample collected for this review by J. L. Oldemeyer from a shallow lake in Alaska during 1972.

the mineral elements they have may limit their nutritional importance (Peek, pers. comm.). The levels of N, P, and the major cations in two species of lichens from two sites are presented in Table X.

MICRONUTRIENTS

Although trace element deficiencies and toxicities are recognized nutritional problems of domestic animals in the United States (Kubota and Allaway, 1972) and in other parts of the world (Underwood, 1971), specific nutritional trace element problems in moose remain undetermined. General levels of the common trace elements in browse plants that moose eat compared with the requirements of domestic animals suggest that trace element nutrition is of possible importance. A summary of Co, Mo, Cu, Zn, and Mn is presented for grasses and sedges in Table I, for current growth of woody plants in Tables III and IV for selected herbaceous plants and lingonberry in Table IX, for pond lily in Table VII, and for lichens in Table X.

The amounts of Co with very few exceptions are above minimum levels (0.04 to 0.07 ppm) in plants required by cattle. Current growth of willows (1.18 ppm — Table III) and horsetails (1.22 ppm — Table IX) have appreciable amounts of Co. These levels are high, compared with amounts in common forage plants (Kubota, 1968), but appear to be well below toxic levels Underwood, 1971).

The Mo concentration is low in browse plants compared with Mo levels (10 to 20 ppm or more) associated with incidences of Mo toxicities in cattle (Kubota

TABLE VIII

Total N and P concentration in pondweeds (*Potamogeton* spp.) from relatively fertile and infertile lakes of Wisconsin*

Species	*No. lakes*	*No. samples*	*N (%)*	*P (%)*
Relatively infertile lakes				
P. amplifolius	1	3	3.0	0.19
P. epihydrus	1	4	2.8	0.28
P. richardsonii	2	8	2.1	0.17
P. robinsii	1	3	2.2	0.15
Relatively fertile lakes				
P. richardsonii	1	3	3.2	0.33
P. zosteriformis	1	4	3.6	0.45
Mean — all samples			2.7	0.25
SD			0.13	0.02

* Data generalized from Gerloff and Krombholz, 1966.

TABLE IX

Nutrient concentrations in herbaceous plants, horsetails and lingonberry of Alaska

Plant Samples	*Macronutritients (%)*				*Micronutritients (%)*			
	P	*Ca*	*K*	*Co*	*Mo*	*Cu*	*Zn*	*Mn*
Fireweed (*Epilobium angustifolium*)	0.39	0.95	1.82	0.14	0.44	6.2	36	114
Lupine (*Lupinus spp.*)	0.33	0.93	1.69	0.12	—	6.3	—	—
No. sites	12	12	12	35	6	35	24	6
Mean	0.39	0.95	1.80	0.14	0.44	6.2	36	114
SD	0.11	0.17	0.68	0.19	0.13	1.6	19	39
Horsetails (*Equisetum sp.*)								
No. sites	4	4	4	24	6	24	19	6
Mean	—	1.20	3.44	1.22	0.57	4.8	35	208
SD	—	0.23	0.93	1.27	0.50	3.0	21	68
Lingonbery (*Vaccinium vitis-idaea*)								
No. sites	3	3	3	3	3	3	3	3
Mean	0.12	0.43	0.51	0.11	0.10	4.7	25	1020
SD	0.02	0.17	0.12	0.04	0.07	3.1	14	—

and Allaway, 1972). Available data indicate that woody plants generally do not have large amounts of Mo. Of importance to moose, however, is the fact that most plants correspondingly have low (3 to 5 ppm) amounts of Cu, and differences among species of plants are not large. The concentrations of Cu noted in woody plants of Alaska and Wisconsin are well within the range of Cu reported in foliage for a wide range of trees (Stone, 1968). The high concentration of Cu in twigs from Minnesota (Table III), probably reflects the growth of the trees in a geologically anomalous area of high Cu (Peek, pers. comm.). Available information does not suggest an existence of nutritional problems in moose due to imbalances of Mo and Cu in feed plants.

The concentration of Zn is relatively uniform (25 to 35 ppm) in nonwoody plants and is similar to that reported for common forage plants of the eastern United States (Hodgson, *et al.*, 1971). Woody plants have more Zn, with appreciable differences among species (Table III). The amounts and differences among species of woody plants noted have been earlier observed by Stone (1968) as has been a tendency of willows, aspens and birches to accumulate Zn. Leaves and twigs have similar amounts of Zn (Table IV).

Increases in Zn with leaf maturity have been observed in leaves of gray birch (*Betula populifolia*) grown on mine tailings, but similar increases are not evident in the woody plants of Alaska. Guha and Mitchell (1965) suggest that changes in Zn with leaf maturity is species-dependent and may also vary between leaves and petioles.

The Mn concentration of most browse plants is high, (100 to 800 ppm), with lingonberry (1,020 ppm) having the most (Table IX). Quaking aspen was the only plant having less than 100 ppm of Mn (Table III). The levels in the browse plants appear to be well above any suggested minimum for cattle and below reported toxic levels for most mammals (Underwood, 1971).

Manganese concentrations of 432 ppm in leaves and 204 ppm in stems

TABLE X

Nutrient composition of foliose (*Nephroma arcticum)* and fructose *(Cladonia* sp.) lichens of Alaska

Mineral element	*Lichens*			
	Foliose[1]	*Fructose*[1]	*Mean*[2]	*SD*
Macronutrient *(%)*				
N	1.98	2.19	2.08	1.18
P	0.13	0.20	0.16	0.10
Ca	0.25	0.38	0.31	0.22
Mg	0.09	0.10	0.09	0.04
K	0.57	1.41	0.99	1.12
Na	0.02	0.01	0.01	<0.01
Micronutrient (ppm)				
Co	0.40	0.44	0.42	0.18
Mo	0.13	0.11	0.12	0.05
Cu	3	4	3.3	2.2
Zn	17	27	22	19
Mn	249	77	163	136

[1] Means are given samples from two sites.

[2] Means and SD for samples from four sites.

of the ponds lily (Table VII) are higher than in terrestrial plants, but these figures appear to be low generally for aquatic plants. A summary of aquatic plants by Boyd (1968) shows that 10 of 18 plants studied had from 1,600 to as much as 5,130 ppm of Mn.

Soil effects are small but evident in the concentration of Co, Mo, and Mn in willow leaves sampled from well drained and poorly drained soils (Table VI). Similar increases in Co and Mo concentrations with soil wetness have been observed in alsike clover (*Trifolium hybridum*) (Kubota *et al.*, 1963), and larger amounts of Mn might reasonably be expected in plants grown on wet soils.

Although better known as a toxic element, Se is now widely recognized as a trace element essential to livestock (Muth, 1967). A minimum Se requirement for the prevention of White Muscle disease, a Se-responsive disease, is currently set at about 0.05 ppm in feed plants; and the toxic level at about 4 to 5 ppm. The essentiality of Se for plant growth, however, remains unresolved except possibly for some plants that accumulate Se.

Limited data are presented in Table XI to give some indication of plant sources of Se for moose. The low amounts in grasses (0.02 ppm) are consistent with amounts present in forage plants grown on acid soils. Leaves of browse plants and herbaceous plants appear to be a better source of Se than the grasses. The plants examined do not appear to have toxic levels of this trace element.

Nutrient losses in twigs from summer to winter may be of nutritional importance. But twigs collected in winter have essentially the same amount of Se as do twigs collected in summer, and neither are good plant sources of Se (Table V). Of nutritional significance is the fact that Se content of winter twigs is low during a period when the supply of vitamin E is also low. Fresh green plants have more vitamin E than do dried plants, and Se requirements of livestock decrease somewhat with higher intake of this vitamin.

A possible Se source during the winter months are lichens. Four samples of lichens studied were found to have 0.06 ± 0.03 ppm of Se and, if eaten, may be a Se source for moose during

TABLE XI

Selenium concentration of selected native plants of Alaska

Plant	*No. sites*	*Selenium (ppm)*	
		median	*range*
Grasses and sedges	3	0.02	0.01 to 0.02
Browse plants			
leaves	11	0.08	<0.01 to 0.20
twigs	21	0.02	<0.01 to 0.20
Herbaceous plants			
Fireweed	6	0.07	0.01 to 0.66
Lupine	1	0.13	
Horsetail	2	—	0.02 to 0.24
Pond lily			
leaves	1	0.02	— —
stems	1	0.02	— —
Lichens (foliose and fructose)	4	0.06	0.03 to 0.09

the winter months. Unlike Se, winter twigs provide an adequate source of Co. The Cu concentrations are low but may be adequate in the presence of relatively small amounts of Mo.

General discussion

An evaluation of the mineral composition of browse plants of Alaska, Minnesota and Wisconsin suggests that the mineral intake of moose is higher in summer than in winter. A higher feed consumption during periods of abundant feed may magnify the seasonal differences. The biological availability of minerals may also differ with seasonally available species of plants and plant parts. The adaptability of moose to its habitat may reflect its ability to utilize mineral elements from different feed plants. Body reserves of certain mineral elements built up during periods of abundant feed may sustain the moose during periods of limited feed supply.

General observations suggest that levels of P and S are low, and the level of N might be low also. The fact that Ca concentrations tend to be low may favor the utilization of the correspondingly low P. Possible marginal adequacies of P were suggested by studies of browse plants for deer in North Carolina (Smith *et al.*, 1956). Improved growth rate of deer with P supplementation has been obtained in Pennsylvania (French *et al.*, 1955), and its need was recognized in the preparation of feed supplements for deer wintered in New York (Maynard *et al.*, 1935). Supplementation of P is also a universal practice wherever cattle are raised. Comparative data of both N and S are limited, but the importance of N/S ratio in feeds has been emphasized by Allaway and Thompson (1966).

The establishment of minimum requirements and tolerances would provide a firmer basis for evaluating the significance of mineral composition of feed plants for moose. Controlled feeding experiments with rapidly growing calves or with pregnant or lactating cows may define some of these critical levels.

Remaining largely unresolved are differences that may exist among moose ranges and their carrying capacity in different parts of North America. Significant local or regional differences among moose ranges may become apparent as more information becomes available about the mineral composition of feed plants. One possible source of information may be studies of native plants undertaken to establish some background levels of mineral cycling in the environment. Another may be studies directed towards understanding the adaptability of native plants to grow on relatively infertile soils without heavy fertilization. Mineral composition of plants is usually determined in these kinds of studies. A possible source of information about aquatic plants may be studies of their growth in streams, ponds and lakes. While the focus of these studies may be on growth of plants in eutrophic lakes, reports of these studies usually include some comparative values about plants grown in infertile waters. Uses of data from these sources necessarily entail an evaluation of analytical methods employed. The present review suggests that variations from this source may be relatively small.

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A REVIEW OF RUTTING BEHAVIOR IN MOOSE

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Résumé

La durée du rut chez l'orignal (*Alces alces*) est ordinairement brève puisque tant en Amérique du Nord qu'en Eurasie, quatre-vingt pourcent des veaux sont conçus durant une période de deux à trois semaines. Cette période coïncide normalement avec la fin de septembre et le début d'octobre.

L'auteur décrit les principaux éléments de la parade : l'approche latérale par le mâle, le *flehmen*, le contact génital, le contact avec le menton (« chinning ») et le croassement (« croaking »). Le répertoire des vocalisations utilisées durant le rut est complexe et encore incomplètement interprété. Les femelles produisent une espèce de gémissement et, dans des conditions idéales, cet appel est audible à une distance égale ou supérieure à un mille. Des différences géographiques semblent exister entre les types de vocalisations caractérisant les animaux d'Amérique du Nord d'une part et ceux d'Europe d'autre part, de même qu'entre ceux de Scandinavie d'une part et ceux d'URSS d'autre part.

Plus que chez tout autre cervidé, les femelles chez l'orignal prennent généralement une part active dans les interactions sociales associées à l'accouplement. Leurs déplacements ne sont pas coordonnés par les mâles et on a souvent vu des femelles se comporter de façon agressive envers d'autres femelles. Mâles et femelles se souillent dans des trous terreux (« wallows ») en adoptant un comportement stéréotypé. Le transfert mutuel de stimulus olfactifs semble être la fonction principale de ce comportement. On connaît mal la durée du lien qui s'établit entre les mâles d'une part et les femelles en oestrus d'autre part. Il semble bien que d'authentiques harems ne se constituent jamais chez l'orignal. La chasse provoque des changements dans la structure d'âge des mâles et dans la proportion des sexes mais sans avoir de conséquences sur la natalité, du moins dans les populations nord-américaines : tel n'est pas le cas en Scandinavie. Les causes de cette différence manifeste ne sont pas connues.

Abstract

Moose (*Alces alces*) are characterized by a concise rutting period, with 80 percent or more of calves conceived in a two- to three-week period in both North America and Eurasia. This period normally falls in late September to early October.

Motor patterns associated with courtship are described, including the male "lateral approach," *Flehmen*, genital testing, chinning and "croaking." Moose employ a complex and still poorly understood repertoire of vocalizations during the rutting season. Females make a long drawn-out moan call, audible at distances of a mile or more under ideal conditions. Geographic differences in the types of vocalizations appear to exist between North America and Europe and between Scandinavia and the U.S.S.R.

In general, females play a more active role in rutting interactions than in other cervids. Their movements tend to be relatively independent of male influences and they frequently display agonistic behavior toward other females. Both males and females participate in wallowing behavior. Mutual olfactory labeling appears to be one function of wallow use. There is still little information on the duration of bonds formed between bulls and females in estrus. True harem formation is believed not to occur in moose. Altered sex ratios and male age composition, as a result of hunting, has had little influence on natality in North American moose populations : this is not true in Scandinavia. Reasons for this apparent difference are still not clear.

Introduction

When I accepted the task of organizing the behavior section for this symposium, I soon discovered there was no one willing to review the subject of rutting behavior in moose. The only one I could persuade to do it was myself. As I got further into the task, I realized why no one else was foolhardy enough to attempt it. The relevant published literature consists primarily of observations made incidental to other goals or generalized remarks and conclusions with little supporting data of a quantitative nature. This remark is intended as a statement of fact and not as a criticism of anyone. Since this paper is based to a great extent on a review of the published literature, it is necessarily rather generalized and in many places equivocal, posing many questions that remain unanswered. Most of these questions will remain unanswered until long-term studies are undertaken during the rutting season using marked, identifiable animals.

The present paper and the one by Stringham (1974) include citations to almost all published literature on moose social behavior appearing since Peterson (1955) reviewed the subject. No attempt has been made to review social behavior during the winter months because of the paucity of information available.

My own experience with rutting moose (*Alces alces gigas*) is limited primarily to short trips over the past three years to the Kenai National Moose Range. The major goals of these trips were to record vocalizations and gain an understanding of the role of vocalizations in moose rutting behavior. Recordings obtained during these trips and presented in this review were made with a Nagra IV tape recorder at 7.5 i.p.s. and a Sennheiser MKH 805 microphone. Analyses were done on a Kay Audio Spectrum Analyzer at narrow (45 Hz) band width.

Rutting habitat

Peek (1962) mentions that most moose remained on the summer range until after the rut. Edwards and Ritcey (1958) note that the location of rutting groups is variable, dependent upon the timing of early snowfall. Hosley (1949) cites Palmer's conclusion (with regard to Kenai Peninsula moose) that rutting moose are almost always in or near clumps of spruce or alder — rarely out in the more open willow or aspen stands.

By and large, it appears that a large variety of habitat types are suitable or usable during the rut. Most of my observations on the Kenai Peninsula have been made of groups in or on the fringes of small clearings or bogs. In the Cassiar Mountains of British Columbia (V. Geist, pers. comm.) and in the Alaska Range, moose are frequently observed at or even above timberline during the rut, although there is a tendency for lone males to predominate at the higher elevations. Houston (1968) indicates that moose did not move to winter range until after the rut was completed. However, males were more mobile during the rut than females. Between September 15 and October 31, the average for observed movements of tagged males was more than 2.5 miles from the center of their summer range. Females usually moved 1.0 mile or less. Other observers, especially in Alaska, have reported greater mobility on the part of females than did Houston (Lent, unpubl.; LeResche, 1974 and pers. comm.).

Murie (1934), in regard to Isle Royale moose, believed that licks which were heavily frequented by moose in the summer also acted as focal points for rutting activity. Bouchard (1970) also describes interactions occurring at licks, including defense of lick areas, during July and August.

Timing of the rut

References to the timing of breeding activity in moose are compiled in Table I. Because actual copulation has been so rarely observed, these are based on indirect evidence, either of a behavioral nature, such as the frequency of occurrence of male vocalizations or agonistic behavior, or on extrapolations from measurements of embryos or from observations of neonatal calves.

Clearly the method used to derive the dates in Table I influences how each author views the length of the rut. Extrapolation from birth dates tends to suggest a rather limited period during which the majority of conceptions occur; this being about two weeks (Edwards and Ritcey, 1958; Peek, 1962; Knorre, 1959, 1961). Edwards and Ritcey provide the most specific data utilizing this technique. They report that 89 percent of moose embryos examined were conceived during a two-week period. Yazan (1964) reports that 84 percent of the calves are conceived before the end of September. Attempts to determine breeding season from behavioral manifestations normally result in reporting of a longer period. Such attempts are necessarily based primarily on observations of male behavior. As I discuss elsewhere, the rutting behavior of males is almost always more evident throughout the rutting period, but particularly so in the early stages of rut or pre-rut, presumably manifesting itself in many males before any females actually come into estrus. This is a common behavioral feature of northern and temperate zone ungulates (Fraser, 1968).

In spite of the differences in techniques used to derive rutting dates, there is considerable similarity among the dates, considering the wide geographic distribution covered by the papers summarized in Table I. Almost every author places the peak of the rut as falling in the latter part of September and the early part of October. In addition, most authors report considerable similarity from year to year in the same area. Markgren (1969), for example, reports remarkable similarity in conception dates, as evidenced by observations of neonates, over a period of seven years in his study area in Sweden. Almost all

TABLE I

Timing of rutting activities in moose

First rutting behavior	*Peak of rut*		*End of rutting behavior*	*Location*	*Author*
	Start	*End*			
Mid-August	Sept. 9			Newfoundland	Dodds, 1958
Early Sept.	late Sept.	early Oct.	late Nov.	British Columbia	Edwards & Ritcey, 1968
	late Sept.	early Oct.		Montana	Peek, 1962
	end of Sept.	mid-Oct.		Central Alaska	Rausch, 1959
	Sept. 1	Oct. 15		Pechora, USSR	Knorre, 1959
End of Aug.	early Sept.	mid-Oct.	early Nov.	Pechora, USSR	Yazan, 1961
	— September —			Kaluzhkoi, Ob., USSR	Rykovskii, 1964
Early Sept.	end of Sept.	late Oct.		Sweden	Markgren, 1969

observed neonates were born between May 25 and June 2. On the other hand, Kozhukov (1961) suggests that considerable annual variation (as much as two weeks in the Pechora Reserve) occurs with regard to the start of the rut. This was confirmed by a much lower average weight of embryos collected in December of the year with a late rut compared with December of the early-rut year. Both Markgren (1969) and Knorre (1959, 1961) state that late births are more common in the northern limits of Eurasian moose distribution. It is not clear whether these late births represent a general time shift in breeding activity at higher latitudes or a higher proportion of cows that are not impregnated in their first or possibly even their second estrus period. The latter alternative seems to best fit the described events. It could result from relatively low population densities and more fragmented habitat at these high latitudes. The relationship between time of breeding and population composition will be considered elsewhere. It should also be emphasized that very late births have been reported from moose populations at lower latitudes as well (Peterson, 1955; Moisan, 1956). There seems to be general agreement that the interval between estrus periods in an individual female is approximately 20 to 22 days (Edwards and Ritcey, 1958; Knorre, 1959; Kozhukov, 1961; Yazan, 1964). Markgren (1969) also states the belief of many Swedish hunters and woodsmen that dry summers and poor nutritional state may delay the rut in moose. In such cases, it is presumably the first estrus that is delayed.

Although in general, the overall timing of the rut seems to vary little from year to year in most localities, there is evidence that the level of overt activities, particularly vocalizations, associated with the rut can vary from day to day, depending upon weather conditions. I have observed the greatest number of vocalizing males on cold, clear days, especially in the evenings. Merrill (1916) made a similar generalization. Rykovskii (1964) presents data suggesting something slightly different: greatest rutting activity occurred with weather changes, either clear to cloudy or the reverse.

In connection with timing of rutting activities, the "strategies" employed by the two sexes clearly differ. Males, in order to produce maximum number of progeny, must optimize level and duration of sexual activities so that they are available as potential sires whenever an estrus female may be available, while at the same time maintaining physical condition at some level from which they can recover successfully and survive the winter. Females, on the other hand, can make themselves available for a relatively short period of time and still maximize reproductive potential for that year. If successful conception does not occur in one estrus, successive periods are possible. We do not know what the differential survival rates are for calves conceived in different estrus periods. There is considerable evidence from the genus *Rangifer* that survival is highest for offspring born near or at the peak (Baskin, 1970; Nowosad, 1974). Perhaps, the survival of late-born moose calves is also lower. However, there are evolutionary advantages in a concise breeding period quite aside from those relating to post-natal survival of offspring. For females, the advantages to themselves and their fetuses in keeping energy expenditures low is clear. Knorre (1961) has calculated that males lose 20 percent body weight during the rut, whereas females never lose more than 5 percent. A short period of disturbance of the mother-infant relationship would also be advantageous to minimize the calf's exposure to predation and prevent premature disruption of the bond. Additionally, a short breeding season permits early winter dispersal into habitats not used during the rut.

Courtship behavior

The courtship activities of male moose basically resemble those of other cervids. For the sake of discussion, I have broken down this courtship behavior into six reasonably discrete activity patterns.

THE LATERAL APPROACH

This approach, together with its accompanying display aspects, is apparently an analogue of the "sexual approach" referred to by Struhsaker (1967) in reference to elk behavior. Altmann (1959) refers to the same activities in moose as "driving." However, in reference to elk, Struhsaker and Geist (1966) distinguish between the extended head posture, used when the bull is driving or herding cows and the posture associated with the sexual approach. In moose I have not observed the extended head posture directed towards cows. Normally the male holds the head with the muzzle level with the ground or slightly downward and the neck not noticeably extended or stretched outward. The bull moves on one side of the cow and may pass in front, momentarily blocking or diverting her movement (Fig. 1). While walking, he frequently uses a swaying gait, reminiscent of that used by bulls in agonistic encounters. Altmann (1959: 422) states that bulls will "stand for hours, usually sideways three to five yards from the cow." I have not myself seen such long periods of motionless behavior in moose, but caribou (*Rangifer* sp.) will pose in the so-called "bush-gazing" or "attitude of dejection" posture for long periods of time (Dugmore, 1913; Lent, 1965). It was Altmann's impression, and it is mine also that this activity has little influence on the direction or rate of travel of the female. The term "driving" is best reserved for rutting behavior in ungulate spe-

Figure 1. A bull performing lateral approach, Kenai Peninsula, Alaska, September 1971.

cies for which this effect can be demonstrated.

GENITAL TESTING AND "FLEHMEN"

These activities normally occur together, although occasionally, either one occurs without the other. Both these patterns occur frequently before or between bouts of the lateral approach. The approach with stiff stretched posture illustrated by Geist (1963: 397) was seen by me only as a part of an approach from the rear, preceeding genital testing and not as a part of the lateral approach.

The zone of white hairs surrounding the female genitalia become much more obvious as estrus approaches (Knorre, 1959) in conjunction with swelling of the genitalia (labiae) (Fig. 2). These visual signals can be assumed to act in concert with the olfactory stimuli.

On two occasions, I have observed a cow urinating immediately before or during the genital smelling, but this does not seem to be the rule. I have not observed actual licking of the genitalia, although Geist (1963) indicates this is a common occurrence. *Flehmen* usually follows genital testing. In those events I have observed, the bull raised his neck and directed the muzzle upward. Though I have not seen this performed under good light conditions, I have the impression that actually curling of the lips is not pronounced (Heptner and Nasimovitch, 1967: Fig. 38). This seems to be true of *Flehmen* in some cervid species (Struhsaker, 1967; Halder and Schenkel, 1972).

Figure 2. Mature cow during the rut showing white borders around ano-genital area. Kenai Peninsula, September 1971.

CHINNING

Occasionally a bull will rest or rub his chin on some part of the female. Dodds (1958) describes this and I have observed it on a few occasions. This is done either on the forequarters or the hindquarters. In reference to elk, Struhsaker (1967) refers to this as "placing throat over back." It may be a dominance gesture derived from the primitive ungulate neck fight (Geist, 1971; Walther, 1973) or an incipient mounting motion. It may also function to transfer scent between individuals.

"CROAKING"

During courtship activities, bulls vocalize either sporadically or continually. The characteristic vocalization used during the courtship has been referred to most frequently as a "grunt" (Peterson, 1955; Altmann, 1959). Cows sometimes indicate awareness of the sounds through ear movements, but no other female response could be related specifically to these vocalizations in my own experience. Thompson (1949) describes an event in which a departing cow stopped when a bull, who was at a wallow, vocalized. The vocalizations will be described in greater detail below.

WALLOWING AND THRASHING

The above four groups of behavior patterns which, in the courtship context, are overtly directed towards the cow, are occasionally interrupted by bouts of wallowing or brush thrashing. This has been observed by Altmann (1959). To what extent these are communicative aspects of courtship behavior is of course unknown. A more detailed description of wallow-use follows later.

COITION

I have observed only a few attempted mountings and have never seen successful coitus in this species. Therefore I am entirely dependent upon the scanty descriptions in the literature. Skuncke (1949) states that copulation lasts a few seconds; Knorre (1959) says 2 to 3 seconds. Skuncke, Knorre, and Heptner and Nasimovitch (1967) all agree that females will have intercourse several times during the day or two of estrus. Altmann (1959) says nothing at all on the subject. Denniston (1956) describes a mounting lasting three minutes. This is amazing and is considerably longer than anything recorded for other cervid species to my knowledge (Dewsbury, 1972). There has never been any evidence to support the suggestion by Tanton (1920) that moose lie in wallows during intercourse.

Females occasionally perform what appear to be male-like acts during courtship. These include smelling of the male's ano-genital area and prodding and pushing the muzzle against the male's neck or flanks. One might also include wallowing here, as this is primarily a male activity. Several authors have reported females wallowing, although not always in the context of courtship behavior (see below). Geist (1971: 223) reviews the subject of the exhibition of male-like behavior by female ruminants. He suggests that such reversals of sexual behavior occur when the female is actually in estrus. Blows with the front hooves are occasionally directed at males by females, particularly in connection with interactions at wallows. These blows represent a very real danger to males and thus would seem to promote caution on the part of the bulls under such circumstances.

Agonistic behavior

Skuncke (1949) describes the swelling of the neck, shoulders and chest which occurs in bulls as the rut progresses. He also mentions swelling around the eyes and bloodshot eyes, all of which give the bull a "threatening" appearance. Knorre (1959) advances the idea that not only do bulls show swelling, but the skin of the shoulders actually thickens at the beginning of the rut. This functions to protect those body areas most prone to injury during fighting, as well as increasing the apparent size of the animal.

Altmann (1959) describes, non quantitatively, the basic behavior patterns performed by bulls during agonistic rutting encounters with other bulls. These include, as preliminaries, the "challenger gait" (swaying gait), in which one male moves to the other side or circles the other, or both circle one another; brush thrashing, and "displacement feeding." Geist (1963: 393) refers to "circling" which apparently involves the same activities subsumed by Altmann's terms, the "challenger gait," or the "buildup." Activity of this nature is apparently most likely to occur and be most prolonged when the contestants are reasonably "well matched." The same may be true of other preliminaries. Essentially it is an "impressing" and "size up" procedure which provides contestants with reciprocal information on antlers, size and condition of the opponent and perhaps information through other stimuli, including certainly olfactory (Fig. 3). Numerous authors (Murie, 1934; Peterson, 1955; Markgren, 1969) have mentioned that the majority of male-male encounters end with only such preliminaries. Either one or both of the agonists loses interest, so to speak, and separates or moves off to follow a female; or one simply leaves the field to the other. Peterson (1955) and Markgren (1969) cite numerous references, however, to violent and even fatal fights. Geist (1971) adds additional references. Knorre (1959) describes in detail a fight ending in the death of an old bull due to puncture of the abdominal cavity. Dodds (1958) mentions a fight which lasted for twenty minutes, but provides no details. Most actual fights seem to involve the gradual bringing of antlers into contact followed by pushing, as Altmann (1959) describes. Although I have never witnessed it, occasionally bulls will charge head-on from a distance, crashing antlers together. Such an encounter is described by Seton (1929: 208).

It is still not clear to what extent hierarchies or status positions are established among interacting bulls during a pre-rutting phase as Dodds (1958) suggests. Certainly many observers have

Figure 3. Two bulls in an aggressive encounter, Mount McKinley National Park, Alaska (Photo by W. Gasaway).

reported most violent fighting at the peak of the rut rather than before. Knorre (1959), Heptner and Nasimovitch (1967) and Pielowski (1969) all agree that the intensity of fighting and frequency of male injuries during the rut is directly related to the density of males.

In groups containing more than one cow during the rut, agonistic behavior between females is frequently observed. On three occasions, I have observed females use head-high threats. I agree with Geist's (1963) contention that this is essentially an intention movement related to striking with the foreleg, which itself has been observed in these cow-cow interactions. However, on one occasion, I observed the head of one cow actually strike against the opponent, rather reminiscent of the neck fighting of zebras (*Equus* spp.; Klingel, 1967). I have also observed the head-high threat performed frequently by a captive female yearling being dominated by a male yearling at a feeding trough. A head-low threat with head held below the line of the body does not seem to be a significant component of female rutting behavior.

It is noteworthy that females may be seen moving together during the rut, even occasionally when no male is present, and yet they display aggression towards one another but are attracted each individually to specific locations. That is, there seem to be desirable or traditional locations for rutting activity, as I have mentioned elsewhere. Bubenik (unpubl.) has observed highly agressive females, apparently in estrus, preventing other cows from approaching male consorts.

Vocalizations during the rut

Adult females, at least in North America, produce a long, more or less quavering, moan during the breeding season. An accurate description of this call was given by Merrill (1916: 124): "The call is a low quavering tone, a long drawn out *'mwar'* or *'Oo-oo-aw'*. It begins on a high key and gradually descends an octave or two. The sound can be plainly heard two or three miles away." The last statement may be questioned by some, but I can substantiate that it is little or no exaggeration. I have personally heard cows at a distance of approximately two miles.

I do not believe that cows make these vocalizations only during estrus. I have seen such vocalizing females attract bulls but then act in a non-receptive fashion to their courtship endeavors. The moans or wailing tend to be produced with less volume (amplitude) but more frequently when the cow is accompanied by a bull. A captive yearling female under sporadic observation during the rut, moaned less frequently and intensively than adult females, even though she was kept with two yearling males and successfully gave birth the following summer. This female did not achieve estrus until November.

Sonograms have been produced of 14 moans (Fig. 4). The mean duration of these calls is 1.9 sec (range 0.6 to 7.5). The call is monosyllabic. The fundamental frequencies vary from 240 to 1100 Hz. Most commonly, the fundamental starts at 700 to 800 Hz and remains constant or drops down 100 to 200 Hz during emission. Minor energy bands usually occur in the 1.1 to 1.5 Hz range. In two cases, the "fundamental" is not the lowest energy band.

I have already mentioned that the common male vocalization has been most frequently referred to as a "grunt" (Altmann, 1959; de Vos *et al.*, 1967). However, I prefer to use the term «croak» to refer to this male vocalization to distinguish it from the simple grunt emitted by cows, as when communicating with their calves. The male's rutting sound (the croak) usually has two components: a deep resonant syllable followed, or perhaps sometimes, preceeded by a non-vocal sound which seems to be produced mainly or entirely by lip and jaw movement, a popping noise which suggests suction. This element is presumably homologous with the smacking sound made by rutting reindeer (Espmark, 1964) and the "clucking" (Murie, 1951) or "popping" (Struhsaker, 1967) sounds made by elk. It may occasionally occur alone. Struhsaker states that in elk the mouth remains open during a series of these sounds, but in moose it seems to be alternately open and closed for each two-syllable unit. This sound may be produced by lone males while moving in search of females or by males in the presence of females. I have also twice heard it produced repetitively by one male approaching another, although these events might have represented cases of mistaken sex recognition.

The croaking sound had an average duration of 0.18 sec in eight recordings. One phase ranges from 50 Hz or so to 1500; the other is from over 500 Hz to 1800 with clicks peaking to 3000 Hz or more (Fig. 5).

From my own limited observations, it appears that the "croak" may attract either males or females towards the emitter and stimulates males to similarly vocalize.

There is a range of other sounds resembling croaks (Fig. 6) and produced only by males which, for the present, I must lump under the name of "barks." The function and context of use of these is not clear. I can only associate their occurrence with large aggregations and active fights or chases.

When threatened, young subordinate males will produce a whine of appeasement used by both sexes. Apparently this vocalization is not produced after the second year.

The "roar" (Geist, 1963) (Fig. 7) is apparently rarely used during the rut. I have heard this vocalization only twice, once by a cow with a young calf and the second time by an unidentified individual during the rutting season. On both occasions, the emitters had been

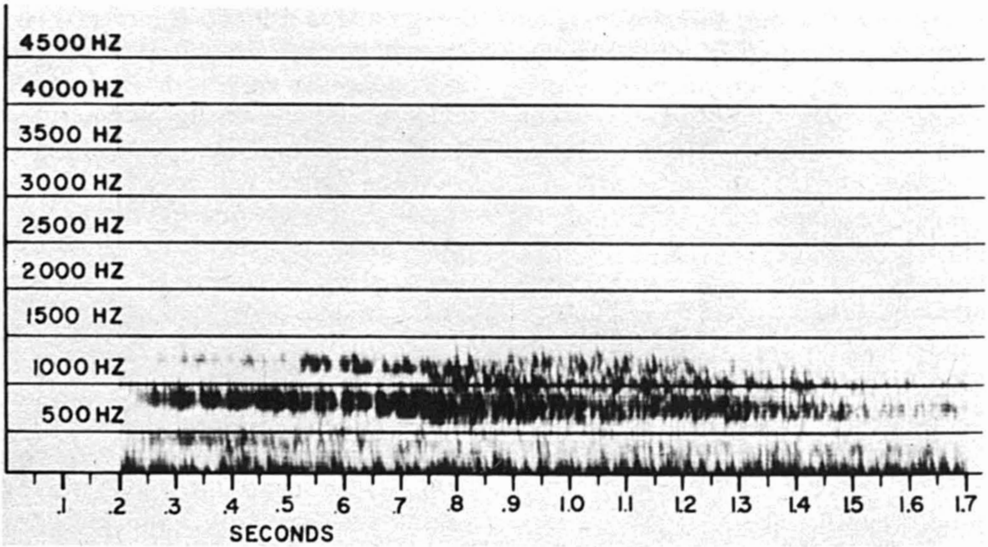

Figure 4. Sonogram of a moan emitted by a resting cow being courted by a bull, Kenai Peninsula, Alaska, September 1971.

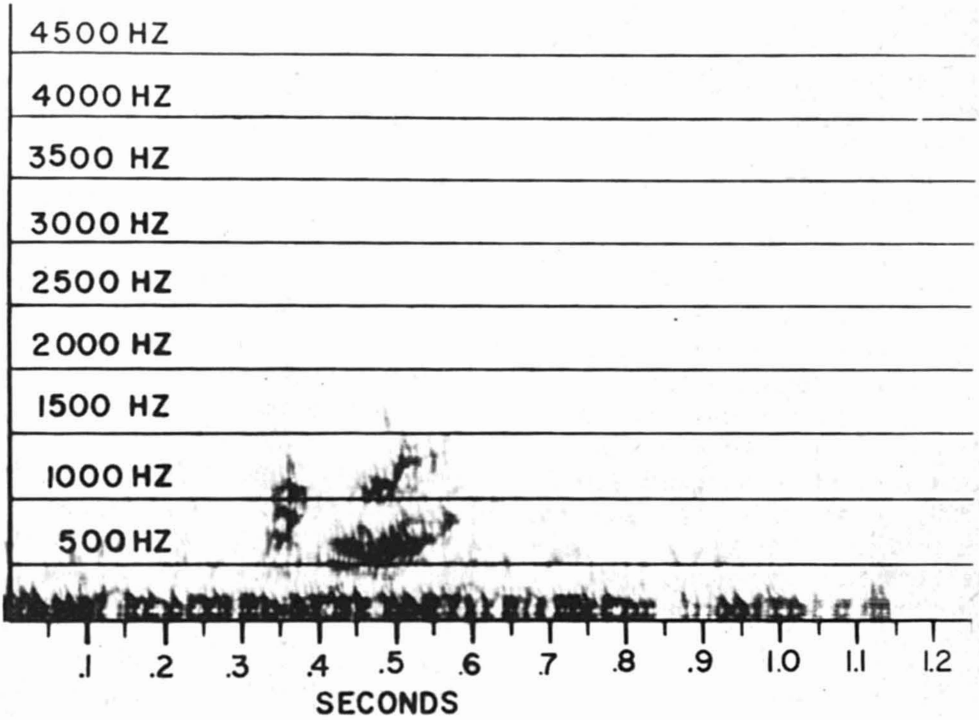

Figure 5. Sonogram of a croak produced by rutting bull and showing two phases, Kenai Peninsula, Alaska, fall 1971.

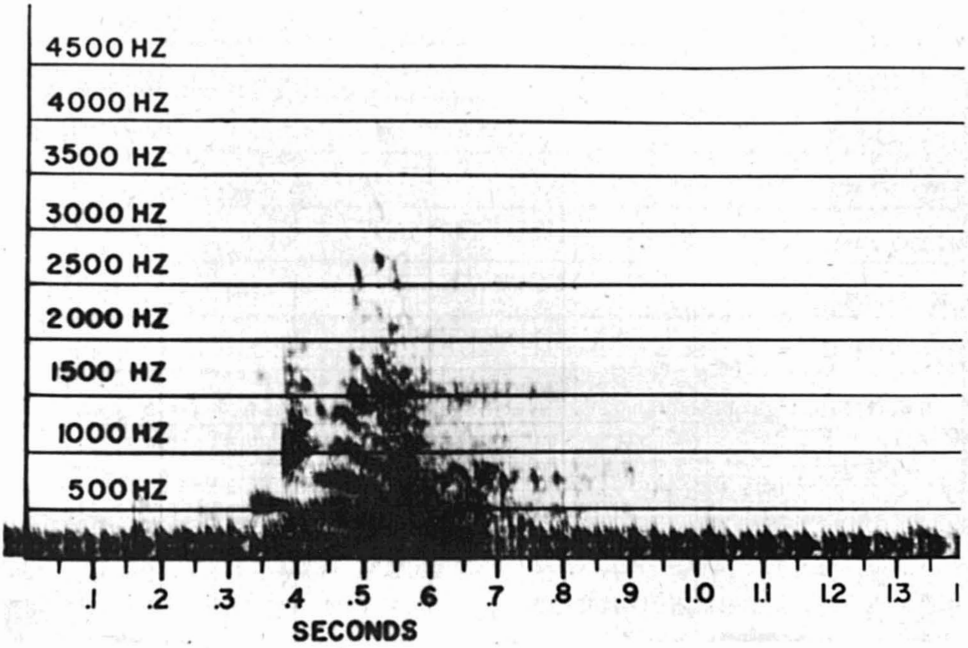

Figure 6. Sonogram of a bark produced by a mature male, Kenai Peninsula, Alaska, fall 1971.

surprised at short range, one by another moose, one by me.

There is still much to be learned regarding functional aspects of rutting vocalizations in moose. It seems clear, however, that moose have one of the most complex acoustic repertoires associated with rutting behavior, perhaps comparable to that of red deer (*Cervus elaphus*).

One aspect of moose vocalizations that intrigues me and is worthy of further investigation is that of their geographical variation. Skuncke (1949) first alluded to this by suggesting that in general, moose in Europe were not as vocal as their North American counterparts. Further, he suggested that a cline existed in Europe from the most vocal moose in Prussia to the least vocal in northernmost Sweden.

It has also become evident that the common vocalization of the male moose in the U.S.S.R. is different from that in North America and perhaps from Sweden. The names given to this vocalization in Russian ("Rëv") or German ("Rohrend") are translated as bellowing or roaring in English. Such descriptors hardly seem appropriate in North America and to my knowledge have not been used. Scunke (1949) also mentions that the Swedish word "Bröl," used in reference to red deer vocalizations, is not suitable in reference to vocalizations of bulls in Sweden. In addition to this difference, I have been struck by the lack of reference to female vocalizations in the Russian literature. The article by Rykovskii (1964) for example, deals with male vocalization in detail but makes no mention of female. Markgren (1973) states that female moose in Sweden are not so intensively vocal as they are in North America.

Non-vocal acoustic signals have already been mentioned. The most important of these are antler-produced, either during brush thrashing or during fights. These sounds are highly attractive to males. I have no observations of females being so attracted.

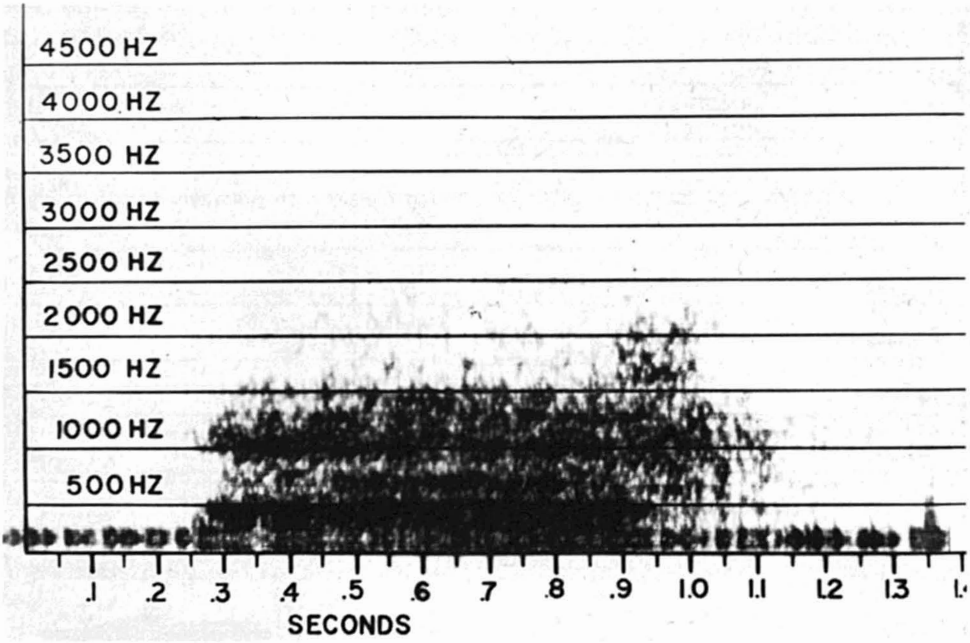

Figure 7. Sonogram of a roar produced by a cow captured in a live trap, Kenai Peninsula, Alaska, fall 1971.

Wallows

The formation and use of wallows or rutting pits seems to be universal among both North American and Eurasian moose populations. There is no concrete suggestion of behavioral differences in this regard among the various subspecies.

Wallows are initially formed by bulls pawing with their front feet. Geist (1963) presents some details on this process. Small depressions of another type are frequently found either near major wallows or by themselves. The marks associated with these scrapes suggest that they are made by antler action incidental to the activity of brush thrashing. Whether there is any tendency for such scrapes to serve as focal points for the formation of true wallows is not clear.

Many observers have noted that males tend to dig wallows at locations where females (presumably those in or entering into estrus) have urinated. It is unlikely that this is always the case however. Wallow formation by males is one of the earliest manifestations of the onset of the rut, and these early wallows are frequently at previously unused sites. Markgren (1969) has made similar observations in Sweden. On the Kenai alpine site in 1971, almost all observed male-female interactions occurred in two open marsh areas over 200 m from the nearest rutting pits, which were all in much drier substrate.

Nevertheless, many wallows do serve as focal points for intensive male-female interactions. The descriptions of Skuncke (1949), Thompson (1949) Altmann (1959) and Geist (1963) of bulls and cows interacting at wallows suggest that one function of wallowing is mutual olfactory labelling. Knorre (1959) believes that a common sequence of events is as follows: a bull forms a wallow at a place where an estrus female has urinated and he himself urinates there. Both individuals, but particularly the female, will then wallow, rubbing the mixture onto their hides. The sharp, even unpleasant odor associated with wallows and their users is said to originate from the male's urine, not the female's.

Skuncke (1949) describes similar interactions as part of post-copulatory behavior, emphasizing that the cow will repeatedly paw the pit and lie and rub in it. Bubenik (unpubl.) describes how cows are attracted to urinating bulls by both olfactory and acoustic cues.

Rutting associations

Associations of adult moose during the rut can range anywhere from the basic bisexual pair up to ten or even twenty adults in loose association. Such large groupings seem to inevitably have two or more competing or satellite males.

The size of the rutting group is influenced most strongly by the nature of the habitat and apparently less so by population composition or sex ratio. Bubenik (unpubl.) independently reached a similar conclusion. Large aggregations are found in open tundra-type terrains, particularly in alpine areas. This is true of both the alpine areas at treeline on the Kenai Peninsula and in Mt. McKinley National Park, even though the latter, being unhunted, has a greater proportion of males in the population. Large groups occasionally occur in open, old-burn areas (LeResche, pers. comm.). Most descriptions of rutting behavior from the U.S.S.R. have dealt with lowland populations in relatively heavy cover. Under such circumstances, it is rare for more than one or two adult females to occur in proximity to a prime bull simultaneously. All this suggests that simple visibility is critical to inducing aggregation among moose. In addition, acoustic signals, both vocal and antler-produced, are audible at greater distances in alpine habitat.

I view these rutting groups as aggregations induced by mutual attractions or by individual propensities to specific location and not as harems. That is, as I have discussed earlier, the prime-age males do not bring together or significantly control the movements of females. Bubenik (unpubl.) has proposed that such groups be termed "loose harems." However, it seems preferable to me to reserve the term "harem" for the "classic" type as seen in red deer, elk (*Cervus canadensis*), or muskoxen (*Ovibos moschatus*) in which the male is able to exercise some degree of control over females' movements and egress. In species with harem organizations, mate selection is in part accomplished "for the females" through the process whereby males are mutually attracted and contest with one another for possession of harems. As Darling (1937) clearly pointed out, such harems occur only where males are able to capitalize on the existing sociality of female groups. Such is not the case with moose. In addition, it has been observed in some unhunted populations that males may actually predominate in the adult age class (Markgren, 1973). Markgren has renewed the discussion of monogamy versus polygamy (polygyny) in moose. He points out that bulls are not seasonally monogamous, that is, they will seek to mate with more than one female in the course of one breeding season. He believes the ability of the bull to do so is dependent primarily upon population density and therefore agrees with Heptner and Nasimovitch (1967) who refer to the moose as being "conditionally polygamous."

Markgren believes that the series of events leading up to and following successful coition involves several days. Altmann (1959) stated a similar conclusion but suggested that bulls might interrupt one such affair for a brief consorting with another mate. This is all very vague and the need for close observations of marked animals is apparent. Certainly in natural enclosures, one bull has been known to impregnate seven females in one season (Knorre, 1959). It remains to be demonstrated that a bond of several days is necessary for successful impregnation. Circumstantial evidence related below suggests it may not be.

Effects of hunting on the rut

The effects of hunting on rutting behavior may be direct in nature, if the hunting occurs during the rut or pre-rut period, or indirect. Among the indirect effects, those of greatest interest are the effects of altered sex ratio and male age structure due to selective hunting pressures. To my knowledge, there have been no thorough studies aimed specifically at assessing these effects.

In the U.S.S.R., some consideration has been given to the effects of hunting during the rut itself, this apparently being commonly permitted. Rykovskii (1964) believes that the use of acoustic lures imitating male vocalizations can be a useful harvesting technique. During the early phase of the rut, prime bulls are said to be most likely to respond and approach such lures. This is then the best time for trophy hunting. However, for purposes of removing weaker or younger bulls, he suggests employing lures at the peak of the rut. At this time, the prime males are paired with females and will not move far from them to respond to lures. Other writers, such as Yazan (1964) deplore the use of such lures during the rut for cooperative harvest efforts because they believe it tends to remove too many of the best, dominant bulls from the population.

Markgren (1973) has commented that reproduction in Eurasian moose is more easily affected by altered sex ratios than in North American populations. He relates this difference to generally lower densities of moose in Eurasia and the stronger expression of polygynous tendencies in North America.

In certain areas of Alaska, such as the Matanuska River Valley, bulls of two years and older have been reduced in number until, for example, in 1961 there were only 28 per 100 cows, even counting yearlings, and in limited areas, the ratio was as extreme as 6:100 (Atwell, *et al.* 1963; Bishop and Rausch, 1974). Under such extreme conditions, there are indications that the period of conception is prolonged (Rausch, 1967 and unpubl.). For example, estimated conception dates for 71 embryos conceived in 1961 after several years of bulls-only hunting, were spread over a 48-day period (approximately two estrus cycles). In 1964, after three years of cow hunting, all embryos in a sample of 50 were conceived within 17 days, even though females still predominated in the population. Effects on recruitment of such extreme sex ratios are not easily separable from effects of winter snow conditions, etc. Nor has any appreciable effect on conception rate among females two years and older been detectable during these periods of extremely skewed sex ratios in Alaska.

Conclusions

In North America, the striking feature of moose rutting organization is the relatively active and independent role of the female in contrast to other cervid species. Three aspects of this have been mentioned: the lack of male control over female activities, the unusual development of vocal signals by females and, under certain conditions, the great mobility of females.

The importance of vocalizations in the reproductive behavior of moose for both long range and short range communication is clear. This stress on vocal communication relates both to the forested habitats in which moose are found and the type of social organization which they have evolved to exploit these habitats. Brereton (1971) has suggested in reference to birds that the greatest development of vocal communication and signal diversity will occur not in territorial species or in highly gregarious species but in those that show intermediate forms of social organization, which he designates as "interspersive". Moose would seem to fit well in this category. The importance of vocal signals in forested habitat is well established. Low frequency signals have greater "penetrance" in wooded habitats than do those of higher frequency (Altmann, 1967). Finally, it may be conjectured that cow moose and their offspring are less vulnerable to predators attracted by rutting vocalizations than would be many other cervid species.

According to traditional concepts of natural selection, it is most important for the female, having the greatest parental investment, to mate with the best possible individual at the best possible time. The "active" role of females becomes most critical in rutting habitat that is fragmented or linear in nature, as along river courses.

Because of habitat fragmentation and the continued dispersal of individuals into new habitat, it can be surmized that moose have evolved in a state in which at any given time, populations are divided into temporarily isolated subpopulations of greatly varying size and composition. This diversity undoubtedly requires considerable plasticity in behavior. A high degree of female mobility also appears to be associated with a sex ratio favoring females (Houston, 1968; Lent, unpubl.).

The species has adapted to rapid expansion into large areas of temporarily favorable habitat (burns) (Geist, 1971). Such rapid expansions normally involve the younger age classes of both sexes. These age classes are particularly opportunistic and will participate in breeding whenever possibilities exist because of removal of social controls.

Because of its behavioral plasticity, the species is able to reproduce adequately in spite of relatively severe alteration of social environment. This is not a matter for complacency, however, and our understanding is currently not adequate to detect more subtle influences on long-term mental health and reproduction.

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MOTHER-INFANT RELATIONS IN MOOSE

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Résumé

L'auteur passe en revue la littérature pertinente et présente des observations personnelles concernant les sites de mise bas, la mise bas proprement dite et les comportements qui y sont reliés, la protection apportée au nouveau-né et son allaitement, de même que le sevrage et l'interruption du lien unissant la mère et le veau. Les femelles sur le point de mettre bas tendent à s'isoler et fréquentent alors le couvert forestier dense. Le lèchement du nouveau-né par la mère ainsi que l'échange mutuel de stimulus dès la mise bas jouent un rôle primordial dans l'expression du comportement maternel et dans le développement d'un lien stable entre la mère et le veau. Au tout début, le jeune passe presque tout son temps à l'état de repos. Mais, dès la cinquième semaine, il est devenu presque aussi actif que sa mère. La durée moyenne de l'intervalle consacré au repos et de celui consacré aux activités diverses était de 1.5 heure chez les femelles ayant mis bas, tandis que ces valeurs étaient respectivement de 2 et de 1 heure chez les veaux. Il arrive rarement qu'un jeune soit actif quand sa mère se repose tout près et, si cela arrive, l'activité est de courte durée. Ordinairement le jeune se dresse en même temps que sa mère ou peu après et se couche un peu avant ou en même temps qu'elle. Les exceptions à cette règle semblent être plus communes chez des animaux âgés de moins d'une semaine ou de plus de six semaines. Face aux tentatives des prédateurs, les cervidés protègent leurs jeunes selon trois méthodes différentes : la dissimulation, la fuite et la défense. L'importance relative de ces trois comportements varie d'une espèce à l'autre et en fonction de l'âge du veau. Presque tous les cervidés cachent leurs jeunes dans le but de les protéger (type «*ablieger*»). Renne et caribou ont tendance principalement à adopter un comportement de fuite en présence de prédateurs (type «*nachfolger*»). Chez l'orignal, la mère défend son ou ses jeunes; cet animal appartient donc au type «*verteidiger*». Cependant, l'orignal utilise la dissimulation du veau mais la perfection de ce comportement semble moins grande que chez les cervidés de type *ablieger.* L'orignal ne présente pas un comportement caractéristique des animaux de ce dernier type qui consiste à maintenir une certaine distance entre la mère et le jeune ou entre les jeunes eux-mêmes durant les périodes de repos. Bien au contraire, le jeune orignal se dissimule encore moins quand il est seul que quand il accompagne sa mère.

La mise bas de même que le premier allaitement se font en position couchée chez l'orignal. Dès le deuxième jour, le veau peut réussir à s'allaiter pourvu que sa mère soit accroupie et, à compter du quatrième jour, il s'allaite même si celle-ci est debout. Le jeune va s'allaiter en position latérale à l'exception de la première semaine, durant laquelle il va (parfois) s'allaiter par l'arrière, entre les pattes de la femelle. Il semble bien que la silhouette ventrale de la mère, du reste accentuée par la coloration du pelage, serve à orienter les tentatives d'allaitement du jeune au moment où elle est debout ou accroupie. Quand, par contre, elle est en position couchée, la coloration des mamelons, du pis ou encore du pelage avoisinant remplit cette fonction. Le veau sollicite l'allaitement en utilisant des vocalisations, des bruits de langue et de bouche imitant les bruits pro-

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duits durant l'allaitement, en exposant en gestes vifs la coloration rosée de la langue et des gencives et en poussant la femelle de son museau. Quand l'allaitement se fait en position couchée, c'est toujours le jeune qui y met fin. Quand l'allaitement se fait en position debout, c'est toujours la femelle, du moins une fois la première semaine passée. La mère met fin à l'allaitement en avançant et en forçant le veau à lâcher le mamelon. Dès que ce dernier a atteint la troisième semaine, ce comportement se double de grognements dont le ton est modérément agressif. Les observations chez deux veaux révèlent qu'entre la première et la neuvième semaine, le temps total consacré à l'allaitement diminue dans une proportion d'environ 100 à 1. Cette baisse semble due à une amélioration du comportement d'allaitement, à une interruption des pseudo-allaitements et à une diminution de la production de lait. Il existe beaucoup de ressemblance entre les postures adoptées par la mère quand elle se tient aux aguets, d'une part, et quand elle tente d'inciter le jeune à boire, d'autre part, ce qui nécessite une grande attention chez celui-ci de façon à ne pas être pris au dépourvu en cas d'alarme. Le veau commence à brouter dès la troisième semaine et est sevré vers le cinquième mois. Le maintien du lien entre la mère et le veau accentue les chances de survie de celui-ci durant son premier hiver. La rupture de ce lien prend place ordinairement à la mise bas d'un autre veau par la mère au printemps suivant. À l'occasion, le veau peut rester associé à sa mère jusqu'à la saison du rut. En un tel cas, l'attitude de la mère (ou celle du mâle qui la poursuit sexuellement) à l'endroit d'un tel jeune (lequel est alors âgé d'un peu plus d'un an) est la même que celle adoptée à l'endroit d'un rival sexuel.

Abstract

The literature is reviewed and results of the investigator's own observations are presented on birth sites, parturition, activity patterns, protection of infants, nursing, weaning and breakdown of the cow-calf bond. Cows tend to seclude themselves prior to giving birth, often in dense cover. Licking and other reciprocal stimulation following birth is essential for eliciting activity of the neonate, arousing maternal behavior and establishing the mother-infant bond. Infants initially rest most of the time; but by the fifth week they are active almost as much as their dams. Cervids utilize three fundamental strategies to protect their infants from predators: concealment, flight and defense. The relative importance of each varies with the age of the young and from one species to the next. Nearly all cervids depend primarily upon concealment to protect infants (hiders/*Ablieger Typ*). Caribou/reindeer depend primarily on flight (followers/*Nachfolger Typ*). Moose depend mostly on defense by the dams. They are called "defenders" *(Verteidiger Typ)*. Although moose also utilize concealment, they are not as thoroughly adapted for it as hider cervids.

Moose give birth lying down and first nurse their young in that position. A calf can suckle when its dam squats by the second day, and when she stands by the fourth. Suckling between the hindlegs occurs only during the first week. Thereafter, all suckling is from a flank. A cow's ventral outline, which is accentuated by her color-shading patterns, probably releases and orients suckling attempts while she is squatting or standing. When she is recumbent, the color-shading pattern of her teats, udder, and surrounding pelage may serve this function. Calves solicit nursing by vocalizing, tongue-flicking, making sucking mouth-movements that produce sucking sounds and expose the bright pink gums and tongue in flashes, and by nuzzling the mother. When cow-calf pairs nurse lying down, the calves terminate all bouts. When they nurse standing up, the mother does so in all instances after the first week. Between their first and ninth weeks of life, two calves decreased total time nursing more than 100-fold. This was due presumably to increased sucking and letdown efficiencies, and decreases in non-sucking teat-contact, as well as to decreased milk production by the cow. Calves browse by the third week and are weaned by the fifth month. Continued association with the dam increases the calf's chances of surviving the first winter. Disassociation usually occurs in the following spring when the new sibling is born. But it may be delayed until the next rut: at that time, the yearling will be treated as a sexual rival by the dam or her suitor.

Introduction

Infant moose (*Alces alces* ssp.) are dependent upon their mothers for protection and avoidance of predators and other dangers, and from premature social contact. It is primarily the mother who insures that her calf will be in favorable conditions at appropriate periods of its development to obtain the nutrition, experience and exercise of its faculties necessary for survival and eventual reproduction. Therefore, the study of mother-infant relations is crucial to our understanding of the social behavior, ecology and management of moose.

There has been relatively little published on this topic. Altmann (1955, 1956, 1957a, 1957b, 1958, 1959, 1960, 1961, 1963) dealt with maternal care, social integration of calves and group dynamics during the rutting season. These papers are primarily summaries of her findings. Knorre studied wild and domesticated moose over a period of 40 years; his major papers (1959, 1961) deal primarily with the moose domestication project in the U.S.S.R. These papers provide some information on mother-infant relations and on milk consumption. Information on wild calves has also been published by Denniston (1956), Espmark (1969), Dodds (1955), Geist (1959, 1963, 1966, 1971), Hatter (1945), Lent (1973), LeResche (1966, 1968), Markgren (1966, 1969), McMillan (1954), Mech (1966, 1970), Merrill (1916), Peterson (1955), Seton (1929), Skuncke (1949), and a variety of others. Several workers have described tame calves, including Bierwirth (1954), Dodds (1959), Hediger (1955, 1964), Kellum (1941), Kramer (1963), Krott (1956), and Markgren (1966). Markgren's account is the most detailed.

The most comprehensive integration of the literature on mother-infant relations in ungulates is by Lent (1973). I have emphasized some of the same aspects of behavior which he did in order to allow comparison between moose and other species on as many points as possible. Among the topics which have been excluded are: maternal aggressiveness and social distance, communication, the following response and imprinting. Altmann (1958, 1963) presents some information on these subjects.

Study area

I conducted field work from mid-May through late August 1970 and mid-May to early August 1971 at the Moose Research Center on the Kenai Peninsula Alaska. The Center is operated jointly by the U.S. Bureau of Sport Fisheries and Wildlife (BSFW) and by the Alaska Department of Fish and Game (ADF&G). It is located on that portion of the peninsula which was burned extensively in 1947. The four one-mile-square enclosures contain representative vegetation, including both remnant stands of mixed birch *Betula papyrifera*, white spruce *Picea glauca*, and aspen *Populus tremuloides*, and regenerative stands of mixed birch and spruce. They also encompass some marshland that is frequented by moose during summer, surrounded by hillocks where the moose feed during winter (LeResche and Davis, 1971). The vegetation of this pen is discussed and mapped in LeResche *et al.* (1974).

Most of my observations were made in the eastern half of Pen 4. This area and the contiguous region outside the pen are covered with dense stands of new growth and mature birch, spruce, and aspen, except for a few small bog-meadows and one large one. The large bog-meadow lies in the southeastern corner of the enclosure and extends several hundred meters eastward beyond the fence. Inside the enclosure, the meadow is interspersed with burnt and new growth spruce *(P. mariana* and *P. glauca)* and some birch which provides a moderate amount of cover. Outside the fence, the meadow offers little cover for moose. The enclosure contains one small lake and a few ponds. Free-ranging moose were also observed along timberline near Timberline Lake on the Kenai Peninsula from September 16 to 27, 1971.

Most of the adults in Pens 2 and 4 had been tagged previously by ADF&G personnel, and their ages had been determined by tooth section analysis. Few yearlings and no calves were tagged during the study period. Calves were rarely identifiable except when seen with their tagged mothers. Yearlings changed appearance so rapidly that only those seen fairly often could be reliably identified. Particularly prior to mid-July 1971, the rate of change in natural markings (face structure pelage, size, shape and coloration of the vulval patch and bell) in each of the three female yearlings was too great to permit individual recognition from one semi-weekly observation period to the next.

Data on the populations in Pens 2 and 4 are provided in Table I. Further details are given by LeResche and Davis (1971). During the investigation, each moose was referred to by a letter-number code. However, these designations are easily confused by one not familiar with them; so, for the purposes of presentation, the moose have been given names. The letter-number designations, names and personal history information are given in Table II.

Attention was focused on the cows Mary Ann and Amazon and their calves in Pen 4 during May through August, 1970 and 1971. Prudence, Olga and their calves were watched occasionally. Observations were also carried out on Carie, Wanda and Suzanna in Pen 2, during the first two weeks after each gave birth in 1971. Suzanna had twins; all of the others had singlets. Considerable time was also spent with the two calves I reared, Boltar and Taunga. Boltar was less than 24 hours old when deserted by his mother due to human disturbance. When he died four weeks later, he showed signs of malnutrition (LeResche, pers. comm.) and had been scouring badly since he was a few days old. Taunga also scoured, but, once I began boiling his milk, this ceased. Taunga was probably less than two weeks old when captured on June

TABLE I

Populations of moose within the 2.6 km ^{2} (1 mi ^{2}) study enclosures

Date	*Pen No.*	*Bulls*	*Yearlings*	*Cows*	*Calves*	*Total*
VI/14/71	2	4	3	9	9	25
II/1/70	4	2	0	11	5	18
VI/14/71	4	3	3 ♀♀ 2 ♂♂	8	6	22

(after: LeResche and Davis, 1971.)

8, 1970 (estimated by LeResche, pers. comm.). He died the following December, apparently due to malnutrition; the marrow of his femur was red and jelly-like.

Procedures

Observation technique was largely determined by the type of habitat that the moose were using. Both inside and outside the enclosures, the vegetation was sufficiently dense that moose were rarely visible from distances greater than 50 to 100 m. Long distance observations were possible only when the moose were traveling along the fences or were in the large bog-meadow or the birch-spruce regrowth patches immediately surrounding it. In 1970 the cow-calf pairs I was observing avoided open areas (at least during the day), forcing me to follow at close range. To minimize adverse effects, I usually discontinued following whenever the moose became disturbed. Thus, during 1970, observer influences were often a problem, and observation could rarely be maintained for more than 4 hr at a time. However, during summer 1971, the moose could be found in relatively open areas far more often, allowing me to make the bulk of my observations unnoticed from 50 to 250 m. Observer influences were rarely a problem and observations could be maintained for much longer periods than in 1970. Moose could usually be followed from time of sighting until dusk. On a few occasions they were followed during the hours of darkness. When possible, their activities were monitored for several days in succession; but problems in visibility hampered attempts to keep continuous records of many types of behavior, such as suckling and elimination.

As they became increasingly accustomed to me, my proximity disturbed them less and less. This also facilitated observations. For instance, in spring

TABLE II

Individual identification and life-history data

Pen No.	Name and ADFG ID No. of cow	Age of cow in 1971 (years)	Name and sex of calf	Date of birth of calf
2	Carie R-70-7 (04245)	8	Twister ?	May 28-29 1971
	Suzanna untagged	4(?)	Darkness ? Lightning ?	May 21-22 1971
	Wanda # 52 cow	4	Willey ?	June 4-7 1971
	Belta R-70-4	4	Boltar* ♂	May 23 1970
4	Mary Ann R-70-1 (08742)	7	Roxy ♀	May 26-28 1970
			Rolly ♂	June 1-3 1971
	Amazon R-70-3 (09515)	3	Arnold ♂	May 21-22 1970
			Alfe ♀	May 31 1971
	Olga # 22 cow (08746)	6	Olivia ♀	Before Aug. 1969
			Oliver ♂	May 17-19 1971
	Prudence #36 cow (09869)	8	Prucilla ♀	1970
	free untagged	?	Taunga* ♂	May 24 to June 1 1970

* Hand reared (data on cows from ADF & G records; LeResche *et al.*, 1971).

1970, the cows had usually fled with their infants if they detected me even 100 m away. On two occasions, I was attacked when I came within 20 m of cows with newborn calves. But in spring 1971, I was often able to watch very young infants and their mothers from within 30 to 50 m without eliciting flight or attack.

As is typical in field studies of animal behavior, my assessment of when a moose was disturbed was largely intuitive. Nevertheless, there was an obvious need to attempt to establish what facets of moose behavior gave rise to my impressions. To the extent that it was possible to analyse this within the time available and without making extensive film records, this basis is discussed below. It is, of course; only a first step.

If a moose continued feeding or resting as I approached it and did not look up towards me or swivel its ears in my direction, I assumed that I had not been detected. The reliability of this judgement was supported by their behavior if I broke a branch, yelled, or attracted their attention in some other way. They usually looked up abruptly and often ran at least a few paces before stopping and looking back at me. As the moose became increasingly habituated to me, their responses became more subtle. As an undisturbed moose fed, it usually seemed to wander aimlessly in an area several bodylenghts in radius, for up to an hour or more. After I had been detected, especially if I attempted to move closer, the moose still seemed to wander aimlessly; but instead of remaining in a small area, it drifted away from me. If I persisted in trying to follow, an increasing proportion of its time was spent moving away from me, and less on movements towards or tangential to me. Furthermore, it moved faster, took fewer bites between steps, and defecated, urinated and performed "comfort activities" (see Geist, 1963) more often. (It was uncommon to see an undisturbed moose defecate or urinate more than once per hour — usually less often. But on one occasion when I followed Amazon for over an hour, during the last half-hour or so, she defecated three times. She also showed the other manifestations of disturbance described.) In addition, the movements of the moose being followed became more abrupt, and it seemed more sensitive to other sources disturbance. When I nevertheless continued to follow, flight became more accentuated and feeding more intermittent. Eventually, if I persisted, the moose ceased feeding and walked or trotted away. The more subtle responses, which one might call manifestations of *mild disturbance*, were strongly reminiscent of "nervous" behavior by humans. More intense responses were often reminiscent of "anxiety" or "fright".

Social interactions between the moose frenquently occurred so rapidly and lasted so briefly that without filming them, it was not possible to analyse more than a few characteristics of the events. Because of the need to concentrate on particular facets, such as ear orientations, head height and vocalizations, I was faced with the choice of either saying nothing about other features, or merely giving my overall impression of them. In most instances I said nothing, because the overall pattern was not familiar, and hence could not be named. But on those occasions that I recognized the pattern, I indicated this by use of the corresponding term. There are obvious dangers in using words like "nervous" "frightened", "threat", "submissive" and "dominant", without describing the exact patterns of behavior which they refer to. Yet, under those circumstances, these dangers were outweighed by the advantages of the more complete record which they allowed. Granted, this kind of description is vague, since the field of behavior lacks film records of "type specimens" to standardize usage, and I have no films of moose to serve as standards for my usage. However, the behaviors themselves are so distinctive and so similar to the corresponding patterns of human behavior, that there should be no danger of confusion.

During 1970 field observations were made on an irregular schedule; but in 1971 Mary Ann and Amazon were observed semi-weekly, beginning with the first week postpartum. Observations were made with binoculars and a 20X spotting-scope. Data was recorded by 35-mm SLR and 16-mm cine cameras and a pocket tape-recorder.

Parturition and related behavior

MATERNAL SECLUSION

The tendency of expectant mothers to seclude themselves is widespread among mammals (Ewer, 1968), including moose. In Wyoming, moose cows become increasingly aggressive even towards their own yearlings as parturition approaches. About 10 to 15 days before the new calves are born, cows chase their yearlings to a distance of up to 100 yards (90 m) (Altmann, 1958, 1960, 1963). After its new sibling is born, the yearling may or may not rejoin its dam (see below).

In considering maternal seclusion, a distinction should be made between association of a cow and her yearling or other moose, and simple physical proximity of individuals. Two moose are "associated" when they travel, feed, and rest together; synchrony in their activities is typical. Amazon was last seen associated with (four) other moose 12 days before she bore Alfe; but she was seen feeding within 50 m of four different individuals 4 days before calving. Mary Ann was last seen associated with her yearling Roxy 6 to 8 days before bearing Rolly. Suzanna was last seen in association with her yearling 2 days before Lightning and Darkness were born. Since observations were sporadic, however, interactions may have occurred even closer to parturition.

BIRTH SITES

Altmann (1958, 1963) mentioned three characteristics which were typical of birth sites in Wyoming: secluded shelter, available browse, and proximity to a source of water. Markgren (1968) found no indication that the sites themselves had to offer water and forage. The 15 (inferred) sites he examined did not all feature shelter, forage, and water. The most consistent feature was seclusion (screening?) from the surrounding terrain; this was found at 10 (67%) of the sites.

Peterson (1955) pointed out that many cows give birth on peninsulas and islands in lakes and rivers; he suggested that these sites may be preferred for the seclusion they offer. He based this on his own observations and those of Seton (1929), Clarke (1936), and Cowan (1946). Klein (pers. comm.) has pointed out that on the Kenai Peninsula many cows give birth on islands, spots seldom frequented by wolves, bear, or other predators. Knorre (1961) reported that cows give birth on river margins where they can drink without venturing far from their calves.

Eight of the 10 birth sites that I found were in at least moderately dense cover; the other 2 were located along enclosure fences and were probably abnormal, as I shall discuss below. Identification of birth sites was inferential in all cases, based on the very limited locomotory capabilities of the neonates and the fact that none was seen to have moved more than 5 m from where first spotted until at least a few days postpartum. Thus, by "birth site" I am referring to the area up to 5 m in radius around the spot where each neonate was first seen. In 5 of the 10 instances, the calves were still very unsteady on their feet when found, and in two of these cases, the coat was still moist from birth fluids. They had great difficulty walking and went only a few meters in any direction except when prompted to flee by their mothers in response to disturbance by the observer. The cows did this by vocalizing and leading their calves or by nudging them from behind.

In 1970 Mary Ann and an untagged cow in Pen 3 both gave birth in extremely dense stands of immature birch. When bedded down, they were not visible from 3 m away. The same was true of Mary Ann and Wanda in 1971 (Table III). In contrast, in 1971 Amazon calved in a stand of mature birch and aspen where windfall and sparse bushes provided moderately dense screening (Fig. 1). She could be seen without binoculars from over 50 m away due to her brightly colored ear flags and collar. Cover and screening at other birth sites were intermediate between these densities. In all eight of these cases, the cows fed on plants available at the immediate site. In none of the 10 cases did I find water within 75 m, though there may have been small snow-melt puddles hidden in the brush.

TABLE III

Cover density at birth sites

Fig. No.	*Cover density*	*Cow*	*Year*
	Extremely Dense	Mary Ann untagged (Pen 3) Wanda	1970, 1971 1970 1971
	Dense	Amazon Carie Suzanna	1970 1971 1971
1	Moderately Dense	Amazon	1971
	Sparse	—	—
2	Bare	untagged (wild) untagged (wild)	1970 1970

The two non-screened sites were located in the 5-m wide cleared margins flanking the enclosure fences (Fig. 2). I suspect that birth at these sites resulted from the typical reactions of Kenai moose when confronted with a fence. They will walk back and forth along several hundred meters of fence for hours, occasionally pushing against it with the head, in essentialy the same manner I often saw them push against the fence-walls of traps while trying to escape. Likewise, pushing against the fence was probably an indication that they wanted to enter areas on the other side. Moose within the enclosure pace this way even after more than 2 years of captivity. In each of these two cases, the cows calved just *outside* Pen 4. The fences around this area had been erected the previous summer (1969). Perhaps in preceding years these cows gave birth in areas now within the enclosure. There does seem to be some preference for calving areas. In 1971, Mary Ann and Amazon both calved within 100 m of their 1970 calving sites. Markgren (1969) reported a general belief among Scandinavian hunters that a cow will return to the same spot to calve several years in succession. Although pointing out the problem of proving that it is the same cow year after year, he stated that some of his observations also suggested repeated use of birth sites by individual cows.

PARTURITION

I saw no births. Knorre (1959) observed calving among domesticated moose in Russia. His findings have been summarized by Markgren (1966, p. 194): "A couple of hours before parturition the teats begin to lactate. The duration of the whole process of birth is fairly short. It takes about one and a half hour from the start of the first contractions till the birth is over. The total duration of the contractions is about 30 minutes, and the actual delivery of the calf proceeds in about 15 minutes. At first the cow stands upright, but she will lie down when the contractions become more intense. In case of twin birth there is a short

Figure 1. Birth site in moderately dense cover: Amazon with Alfe on the day of his birth, 1971.

pause in the contractions after the first calf is born. The cow will usually lick the calf during this pause. Then the contractions recommence and the second calf is born in another 15 minutes. The umbilical cord is torn off by the cow. After the delivery the cow will usually rest for one or two hours and at this time the after-birth is normally expelled. During this rest the new born calf sucks in a laying position." Skunke (1949) observed at least one birth at the Skansen Zoo in Stockholm. He reported that during labor, cows alternately bed down and arise, stretching in between. Strainings are obvious. Delivery takes 3 to 10 minutes. According to Fraser (1968), alternate standing and lying, and strainings have also been reported for other ungulates; acute restlessness is considered to be an indication of pain. Skuncke and Knorre have both indicated that cows seldom consume the afterbirth, but Markgren (1969) reported many observations of consumption.

POSTPARTUM INTERACTIONS

Calves are licked immediately after they are born (Skuncke, 1949; Knorre,

Figure 2. Birth site with essentially no immediate cover: untagged cow outside Pen 4, 1970.

1959; Altmann, 1958, 1963). Licking may cover the head, neck, shoulders, flanks, and rump of calves judging from lick marks on four that I saw while they were only a few hours old (age inferred from presence of lick marks, moistness of coat in two cases and limited locomotory capabilities). The intense reciprocal stimulation at this state is probably essential for eliciting and orienting the neonates' activities including arising, suckling, and voiding (Altmann, 1958, 1963), arousing maternal behavior and establishing the reciprocal bond between mother and infant (Lent, 1973). There is no precise indication of how long this intensive interaction continues before beginning to taper off. Lent suggested that intensity is markedly diminished by the time mother or infant ungulate first leaves the birth site. Calves that I observed were left alone by their mothers for short periods when no more than two days old — and possibly less than one day old. Altmann (1958, 1963) stated that in Wyoming, cows and calves spent the first three days after parturition at the birth site and then left together on the fourth day.

Activity patterns

Numerous studies have been conducted on the activity patterns of ungulates, especially with regard to relationships between activity and rest versus time of day. This same emphasis characterizes the literature on moose (McMillan, 1954; LeResche, 1966). Almost nothing has been published on the related topics I deal with here.

PROPORTION OF TIME SPENT ACTIVE

As was mentioned earlier, during the first few days postpartum, both calves and their mothers were bedded almost constantly; but by the end of the first week the cows spent over half of their time active; by the fifth week Rolly and Alfe did so too (Fig. 3). Considering all data on Mary Ann, Amazon and their calves, the young were active only about three-fourths as much of the time as their mothers were. During nearly 16,000 min of observation, the cows were active 59% of the time; during approximately 14,500 min of observation, their calves were active 43% of the time.

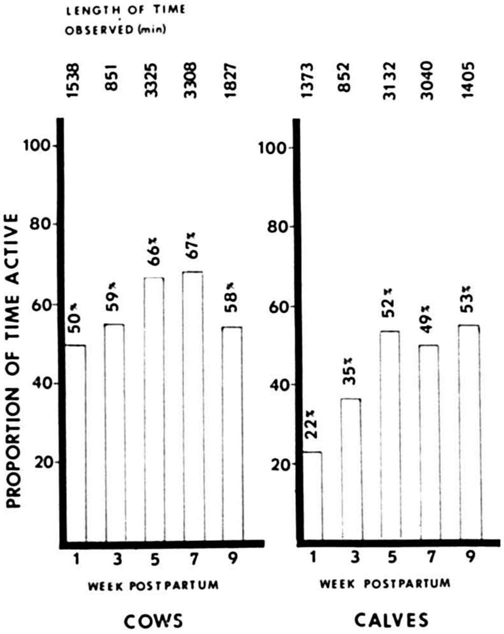

Figure 3. Proportion of time spent active as a function of calf age: Mary Ann and Amazon *vs.* Rolly and Alfe, 1971.

SYNCHRONOUS INITIATION OF REST AND ACTIVITY PERIODS

Kenai calves frequently began rest and activity periods at the same time their mothers did. There were also many occasions when a calf bedded down long before or arose long after its dam. But the reverse was rare. In only three instances (6%) did a calf bed down more than *3* min after its mother; and in only three (7%) did one get up more than *1* min before (Table IV). All but one of these exceptions were by calves at least six weeks old; that one case was by a neonate. This suggests that the frequency of exceptions is age-dependent.

According to LeResche (1966, p. 64), when cows in the Matanuska Valley utilized lakes or open meadows in the summertime, their infants: "most often left hiding after their dams had fed for 3-4 minutes, and bedded down while the females remained feeding. In about half the cases observed, the calf reappeared momentarily one or more times to approach the cow or feed while the cow continued feeding and then returned to hiding on its own. In other cases, the calf re-emerged only to greet the cow as she entered the brush, or was not seen again after bedding down." In contrast, Geist (1959) reported that during the winter calves usually fed and rested with their dams and implied that they frequently got up and bedded down at the same time the cows did.

Since Geist did not present further details or quantitative data on synchrony, more exact comparison of our findings is not possible. LeResche's statements, quoted above, suggest that Matanuska cow-calf pairs showed considerably less synchrony than Kenai pairs. This may have been due to the fact that, while Kenai calves usually fed with their mothers, Matanuska calves usually remained in cover at a distance from their dams while the cows fed in water or open meadows.

INTERRUPTIONS OF REST PERIODS VERSUS ACTIVITY PERIODS

Undisturbed cows usually remained recumbent throughout rest periods, but their calves occasionally arose "spontaneously" for a few minutes, during which they stretched, wandered around, or fed. There were also many short interruptions elicited by environmental events such as vocalizations from the dam, a low-flying plane, or a branch

TABLE IV

Cow-calf synchrony in the initiation of rest and activity periods (for Mary Ann, Amazon and their calves). In the upper part of the table, the initiation lag relative to whether cow or calf bedded down or arose first; in the lower part, the absolute value of the initiation lag

Initiation lag cow versus calf	*Rest periods (bedding down)*				*Activity periods (getting up)*			
	Mean lag (min)	*(SD) (min)*	*N*	*%*	*Mean lag (min)*	*(SD) (min)*	*N*	*%*
Lag≤ 1 min								
(simultaneous initiation)	1	—	20	38	1	—	29	64
Lag > 1 min								
calf after cow	5	(5)	8	15	29	(37)	13	29
cow after calf	1	(31)	24	46	23	(19)	3	7
Total joint periods			52				45	
Initiation lag (min)								
lag≤ 1			20	38			29	64
1< lag≤ 10			15	29			9	20
10< lag≤ 100			15	29			6	13
100< lag			2	4			1	2
Total joint periods			52				45	

breaking in the wind (When an interruption was elicited by an environmental event obvious to the observer it was labeled: "disturbed". All others were labeled: "spontaneous").

The occurrence of interruptions is illustrated in Figure 4. On August 6, 1970 Amazon and Arnold rested together nearly 4.5 hr, from 07:23 to 11:58. During this span of time Amazon arose twice to nurse her calf, dividing the 265-min rest period into three fragments (rest bouts; interruptions were excluded from calculations of rest period duration). The two interruptions averaged 7.5 min. During that same time span, Arnold arose six times, dividing his 258-min rest period into seven fragments (rest bouts). These interruptions averaged 3 min.

In general, as in this example, interruptions were distinguished from activity periods by their brevity and by the behavioral contexts in which they occurred. From the majority of instances where identification of an interruption as such was intuitively obvious, several rules were formulated for dealing with cases where judgement was more difficult. Because of their length, only two of the rules are presented below.

1) When a cow bedded down, she was either beginning or resuming a rest period. Given the additional fact that a calf was rarely active for more than a few minutes while its mother was resting, this led deductively to two corollaries: a) Whenever a cow and calf were bedded together, the calf was also engaged in a rest period. b) Whenever a calf arose, then lay down again, while its mother remained bedded, this was an interruption.

2) Whenever a cow and calf arose just long enough for nursing and perhaps brief feeding, then lay down, that was an interruption for both of them. Furthermore, whenever a calf arose just to suckle and perhaps to forage or wander around for a few minutes before lying down again this, too, was an interruption, whether or not its dam was recumbent when nursing occurred, and whether or not she had been active before nursing or remained active afterwards.

In lieu of a biological criterion for determining when an interruption had "seriously" increased or decreased the length of the rest period in which it occurred, any period interrupted by disturbance for more than 10 min and for more than 10% of its total length was omitted from calculations of mean rest period duration. Rest periods truncated by disturbance and the activity periods thereby initiated were also omitted. They were classed as "seriously disturbed". Fifteen rest periods and 5 activity periods by Mary Ann and Amazon were thus discarded as were 8 rest periods and 2 activity periods by their calves. So too, all periods seen only in part were omitted from calculations of mean duration. On those occasions when a restless cow got up leisurely within a minute or two after mild disturbance, the rest period was not considered to have been truncated.

REST AND ACTIVITY PERIOD DURATIONS

Mary Ann and Amazon averaged over 1.5 hr for both rest and activity periods. Their calves averaged nearly 2 hr per rest period and 1 hr per activity period (Table V).

There is no comparable data in the literature. LeResche (1966) presented information on feeding bouts ($\bar{x}$ = 1 hr for dams and 0.5 hr for calves), but did not relate them to activity period durations. Other investigators have not separated data on cow-calf pairs from that for other classes. Nor did they indicate whether they interpreted brief activity bouts as interruptions, and thus

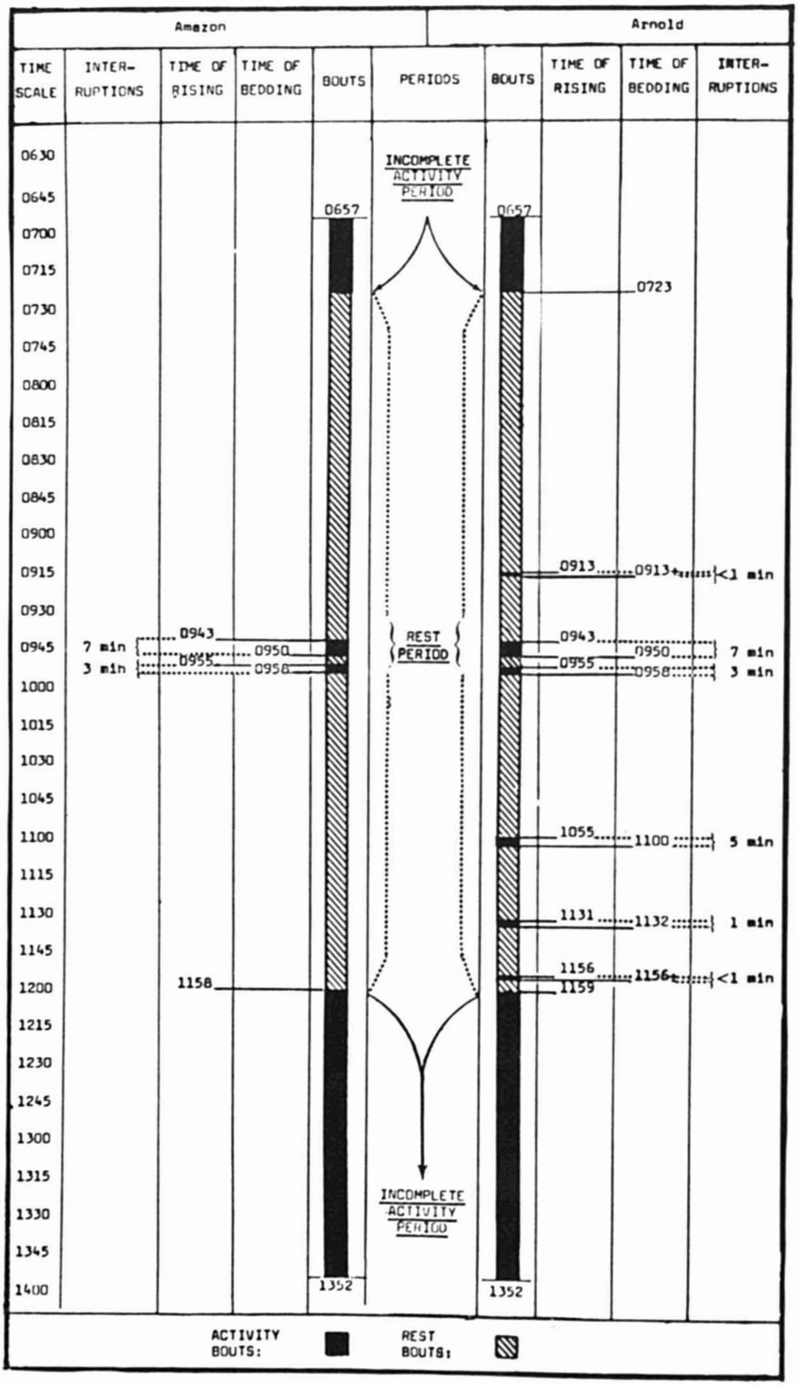

Figure 4. Typical joint rest and activity periods for a cow and calf. Amazon and Arnold, 1971. Note the differences between interruptions of the rest period *vs.* activity periods, and between periods *vs.* bouts.

whether their use of "period" is comparable to mine. Nor do they provide enough information to allow one to test whether the differences in our findings are statistically significant. McMillan (1954) observed Shiras moose during summers; these averaged 3 hr per "rest period" during the daylight hours (Table VI). British Columbian moose watched by Geist (1963) during May and June averaged about 2.5 hr per "rest period" and 0.5 hr per "activity period". Summer observations by Phillips and Berg (1972) in Minnesota revealed "periods" averaging 2 hr for rest and 1.5 hr for activity.

SPONTANEOUS INTERRUPTIONS OF REST PERIODS

Mary Ann and Amazon interrupted rest on only 23 occasions during 89 rest periods (Table VII). Eighteen of these interruptions were elicited by disturbance: 2 by aircraft, 12 by the observer, and 4 by natural events. Three of the spontaneous interruptions occurred when one of the cows arose to nurse her calf. The two instances

TABLE V

Rest and activity periods durations for Mary Ann, Amazon, and their calves

	Cows			Calves		
Rest periods	*Mean (min)*	*(SD) (min)*	*No. of obs.*	*Mean (min)*	*(SD) (min)*	*No. of obs.*
Periods disturbed mildly or not at all	103	(58)	40	113	(65)	40
"Seriously Disturbed" Periods	47	(39)	15	48	(53)	8
Total complete rest periods			55			48
Total incomplete rest periods			34			41
Total rest periods			89			89
Activity periods						
Periods initiated spontaneously	99	(54)	30	67	(40)	35
Periods initiated by disturbance	66	(64)	5	20	(0)	2
Total complete activity periods			35			37
Total incomplete activity periods			87			56
Total activity periods			122			93

TABLE VI

Summertime rest and activity period durations: cumulative data for all classes of moose

Observers	*"Rest Periods"*		*"Activity Periods"*	
	Mean (min)	*Range (min)*	*Mean (min)*	*Range (min)*
McMillan (1954)	180	25-390	—	—
Geist (1959, 1963)	150	20-280	33	10-100
Phillips and Berg (1972)	126	—	102	—

by Amazon (Fig. 4) occurred in August and are unusual for that time of the year. The only stage of calf development during which spontaneous interruptions by cows were typical was during the first several days postpartum. A cow may invite nursing by getting up and standing in place with her head elevated, so that her neck is at an angle above horizontal and her eyes at least as high as her back. (I call this the *nursing-invitation-stance)* Suzanna and Carie, the only two cows that I could watch regularly at this stage, did this frequently.

In the nine other instances that a calf of Mary Ann or Amazon interrupted rest to suckle, then bedded down again, the dam was already active before nursing and/or remained active afterwards. In two cases, the calf arose again in a few minutes and joined its mother. The longest nursing interruption was 13 min, by a three-day old calf.

The calves of Mary Ann and Amazon also interrupted rest periods on 50 other occasions. Thirty of these interruptions were elicited by disturbance: 2 by aircraft, 18 by the observer, and 10 by natural events (see later). The other 20 were spontaneous. Eighty per cent of the spontaneous interruptions occurred while the dams were resting. But only six were more than 1 min long, and only one was over 5 min in duration.

Mary Ann and Amazon usually bedded down within several meters of their young and vice versa. So on three occasions when a calf arose, wandered closer to its mother, then bedded down, this took no more than a minute or two. But on one instance, when Mary Ann bedded about 50 m from Roxy, the trip took 15 min. In all of these four cases, the primary motivation for arising may have been to move closer to the dam. On another occasion, one of the cows bedded while her calf was in a playful mood. It joined her, but arose shortly thereafter and romped again for a few minutes. During the remaining 15 spontaneous interruptions, the calf did nothing but wander around briefly, perhaps perform a few comfort activities or, in three instances, feed.

I suspect that some or all of these latter interruptions might themselves be classified as "comfort activities". Calves were much more restless than

TABLE VII

Interruptions of rest periods

Interruptions	*Cows*			*Calves*		
	Mean (min)	*(SD) (min)*	*No. of obs.*	*Mean (min)*	*(SD) (min)*	*No. of obs.*
Interruptions initiated by manmade disturbances	9	(6)	14	7	(6)	20
Interruptions initiated by natural disturbances	12	(6)	4	9	(8)	10
Spontaneous interruptions	4	(2)	5	2	(3)	20
Interruptions for nursing elicited by the dams	—	(—)	—	5	(4)	12
Total interruptions			23			62

their mothers (yearlings were intermediate). They shifted position (figited), stretched, scratched, shook, or yawned far more often. During seven seemingly typical minutes while bedded, calves performed 42 comfort activities, not counting ear twitches. Brief bouts of activity may relieve the monotony of long periods of rest.

Actually, spontaneous interruptions by calves were more prevalent during the first two weeks postpartum than these figures indicate. These figures are only for Roxy, Rolly, Arnold and Alfe — none of whom could be observed extensively during this stage. Lightning, Darkness, and Twister arose briefly at least once or twice during each period of "isolation" from their mothers, as well as occasionally while the mother was bedded alongside.

INTERRUPTION AND TRUNCATION OF REST PERIODS BY DISTURBANCE

Whether bedded moose arose upon being disturbed, the abruptness with which they got up and the length of time they remained active afterwards, all seemed to be associated with the duration and severity of the disturbance. Severity, in turn, was a function of both the disturbing event and the prior psycho-physiological condition of the moose.

On many occasions when I disturbed a cow resting with her neonate, she became motionless (i.e., "froze") except for movements of her ears and eyes. She arose only if approached closely. The cow would stand, oriented in my direction for as much as half an hour or longer, even if I had sneaked away through the brush shortly after the cow got up. Also, a few days before Mary Ann bore Rolly, she remained standing like this after spotting me from a distance of about 100 m. She had been acting strangely, and I suspect that she was in labor.

When calves were at least a week or two old, they and their mothers usually arose immediately if disturbed while resting. After calming down, which normally took no more than 10 min, they frequently bedded down at the same time; but the dams were somewhat more likely to begin activity periods rather than resume resting.

Once cow-calf pairs had become accustomed to me, they often bedded down when I was within 15m. I could sit down too and arrange my equipment (adjusting the hollow-legged camera tripod was very noisy) without eliciting even a glance in my direction. But as the rest period progressed, sensitivity to my activities increased as a function of both how noisy I had been meanwhile, and how long the moose had been bedded.

If I had remained perfectly quiet for over half an hour or so, any loud or sharp noise, such as sneezing or bumping the tripod, elicited immediate arising. On occasion, the response was explosive and followed by flight for at least a few paces. There were also instances when a moose happened to glance in my direction during a period of observer-stillness and acted startled when it saw me. One wonders whether awareness of my proximity lulled while I sat quietly, and whether this in turn lowered the threshold for later disturbance.

Response to disturbance wasn't always so extreme, however, especially if the stimulus was mild. Early in a rest period I could speak into my recorder or rustle leaves while shifting sitting position without arousing the moose. They just tenced and glanced toward me or turned their ears in my direction. Sometimes, they made no response that I could detect. But after an hour or so even slight noises got them up. This was particularly common if the cow had become restless (calves were always restless while bedded).

McMillan (1954) noted that when a bedded Shiras moose began stretching, this was an indication that it would soon get up. During the beginning and middle of a rest period, Kenai cows typically stretched, scratched themselves, shifted position slightly, yawned, or performed other "comfort activities" only a few times per hour. But during the last 10 to 15 min before they arose, comfort movements were usually much more frequent. If a cow began feeding while bedded, this was a reliable sign that she would arise within no more than 10 min, and probably sooner. Geist (1963) found that active moose performed most comfort activities just after arising or just before lying down; but he did not indicate how comfort movements were distributed through rest periods.

Thus, one is led to the hypothesis that the longer a moose rested, the greater its endogenous motivation to arise became, and thus the less exogenous stimulation was necessary to elicit this response. Early in a rest period habituated moose were aroused only by intense or unexpected disturbances. But as the period proceded, even very mild stimuli caused them to get up.

Protection of the young

Cervids utilize three fundamental strategies in protecting their infants from predators: flight, defense and concealment. The relative importance of each varies with the age of the fawn, and from one species to the next. One of the most complex and important mechanisms employed by many species in the concealment of their infants is periodic, prolonged isolation between the does and fawns. This has been named "Abliegen" by Walther (1964, 1965) and may be translated as "lying-apart". (A fawn does not necessarily remain lying at all times while its mother is away.) Does leave their fawns in hiding and feed and rest at a distance from them throughout the day and perhaps throughout the night. Nursing and grooming occur during the brief, infrequent contact periods. For example, white-tailed deer (*Odocoileus virginianus*) mothers may venture up to one mile from their young (White *et al.*, 1972) and visit them only two or three times during the 24-hr day (Jackson *et al.*, 1972). This pattern of separations, and thus the "hiding phase" (by definition), begins when the mother or infant first leaves the birth site and ends when the fawn regularly accompanies her during her daily activity (Lent, 1973). Among white-tailed deer the hiding phase may last up to several weeks (Severinghaus and Cheatum, 1956). Exposure is also minimized by the fact that mothers and young normally do not communicate while separated (communication becomes more common towards the end of the hiding phase) (Lent, 1973)).

Those ungulate species exhibiting lying-apart have been called "Ablieger Typ" by Walther (1964, 1965) and "hiders" by Lent (1973). Most of those which do not, have been called "Nachfolger Typ" or "followers"; young of these species begin accompanying their mothers regularly as soon as they leave the birth site. Prolonged separations are unusual. Thus, Lent characterized the hider vs. follower dichotomy by contrasting the normal spacing between mothers and infants of the two types, during the first weeks postpartum. In general, it has been possible to distinguish whether a given species is hider or follower on the basis of this spacing.

SPACING BETWEEN INFANT MOOSE AND THEIR DAMS

I never saw a cow venture more than 5 m from her calf on the first day or two postpartum. During the next week or so, they continued to remain within about 10 m most of the time, but they were occasionally separated from the young by 40 m or more for over an hour (Table VIII). These wider separations occurred after the calves had bedded down. They are termed "periods of isolation", to distinguish them from instances when a cow and calf were briefly separated by more than a few meters while still interacting with one another. For instance, a cow often walked several meters from her calf after interrupting nursing. Her calf sometimes followed her and tried to resume suckling. When, on the other hand, the calf bedded down, and the cow continued moving away from it as she fed, this was the beginning of a "period of isolation". "Isolation" ended when the dam returned to her calf and aroused it, or when she came near and it approached her. When the calves were a few days old, they followed or approached their mothers when seperated by up to 5 or 10 m; by age one week they did so when separated by up to 20 m. Beyond those distances they did not approach even when they obviously desired contact, as manifested by their bleating. I have observed this vocalization on well over a hundred other occasions when its function likewise seemed to be to elicit care and/or approach by or to the mother. Bleating is the juvenile form of grunting, which also solicits approach. After separations, Kenai cows rejoined their infants at or near the resting sites and nursed, groomed, and rested with them there. LeResche (1966) also saw direct reunions.

During the first two weeks of development, Kenai calves usually bedded down within a meter or two, and never over 5 m, from where their mothers were resting or had last rested with them. The one pair of twins observed, Lightning and Darkness, likewise rested within a few meters of one another. Not only did mothers and young usually rest at the birth sites for several days, but in some cases they repeatedly bedded at other sites for longer than one day. Twice, on different days, Olga and Oliver returned to a spot (probably the birth site) after fleeing over 100 m

TABLE VIII

Cow-calf spacing as a function of the calf's age, during the first two weeks postpartum

Cows	*Carie,*	*Mary Ann,*			*Suzanna,*			
Calves	*Twister*	*Rolly*			*Lightning and Darkness*			
Day of life	1	2 or 3	3 or 4	2	5	8	10	13
Maximum spacing seen (meters)	5	40	40	5	75-100	75	40	80
No. hours of observation	12.5	11.5	16	0.75	14.5	8.5	5	5
% of time cow and young were "Isolated" from each other	0	5	28	0	10	17	10	45
No. of times "Isolated"	0	1	2	0	3	2	1	1
Ratio: (times isolated)* (hours of observation)	0	0.1	0.1	0	0.2	0.2	0.2	0.2

* Note the constant ratio for Suzanna and her calves for longer than one week.

from it in response to disturbance by the observer.

All Kenai calves more than two weeks old left the bed site when obviously desiring contact rather than waiting until their dams returned. When a calf of this age was resting, its mother usually remained within 30 to 50 m, but sometimes ventured 100 to 200 m away, and rarely went over 400 m for as long as 4 hr. The calf usually joined its mother soon after arising. On two occasions, I saw a calf approach its mother from over 75 m away, although she could not have been visible to it. When a cow bedded down, it was usually within several meters of her infant. (Matanuska Valley cows also normally rested with their young, although they occasionally bedded in the open, 10 to 20 m from the calves; LeResche, 1966). When a Kenai cow and calf were both active, they usually ranged within 10 to 20 m of one another, only rarely going over 50 m apart.

Seton (1929) and Peterson (1955) have also reported separations between cows and calves less than two weeks old. Dodds (1955), LeResche (1966) and Dunn (pers. comm.) have reported them for older calves. But it is debatable whether these or the separations I observed were instances of lying-apart. Altmann (1958, 1963), Geist (1966), Espmark (1969 and pers. comm.) and Peek (pers. comm.) have found no evidence of lying-apart by moose in Wyoming, British Columbia, Sweden or Montana, respectively.

The mere fact that a mother and her young are not together at all times can not be construed as evidence of lying-apart. Theoretically, lying-apart should be distinguishable by the facts that "isolation" is maintained for long periods by the behavior of both mothers and infants, and that this isolation helps to conceal the infants. Even after hider young regularly accompany their dams during the day, separations may occur — albeit for much shorter periods, in general. Even if a dam gets up before her fawn does, and moves away from it as she feeds, it may arise and join her on its own initiative. Only during the hiding phase is concealment the major determinant of spacing between hider mothers and young (Lent, pers. comm.). Seton, Peterson and Dodds do not provide sufficient information to allow one to distinguish the nature of the separations they observed between infant moose and their mothers. LeResche and Dunn do, however.

The prolonged separations observed by LeResche (1966) in the Matanuska Valley of Alaska and by Dunn (pers. comm.) in Baxter Park, Maine, were for calves more than a week or two old (LeResche did not begin observations until mid-June; most calves in Alaska are born in late May or early June). These separations occurred when the cows fed in lakes or large open meadows. They apparently resulted from the differences in response to clearings and to deep water by cows versus their young.

In the Matanuska Valley, moose of all ages tend to avoid open areas much of the time. When they approach or pass lakes or open meadows, they move along or just within the perimeter of brush and trees. Avoidance is most pronounced for cows with calves and for lone calves (LeResche, 1966). It seems to be greatest for neonates and to decrease with maturation. During their first two weeks of life, Lightning and Darkness did not approach their mother when she was in clearings (Lent, 1973); yet I saw older calves enter equivalent areas on their own initiative without obvious hesitation. When cows feed in lakes, their infants usually remain on shore, hidden in or near cover (Altmann.

1963). This is supported by the observations of Denniston (1956), LeResche (1966), and Geist (pers. comm.). The calves seen by LeResche also remained in cover when their mothers fed in large open meadows. When a Matanuska cow left cover to feed in a lake or in the open bog-meadow encompassing it, her calf sometimes accompanied her for a few minutes before returning to cover and bedding down. Calves sometimes arose and fed before their mothers rejoined them and periodically, but briefly, visited the dams in the open. Visits became more frequent as the calves matured. By late August, they occurred at least once per half hour. Although calves sometimes tried to suckle during the visits, they were unsuccessful. Matanuska cows permitted suckling and rested with their calves only after rejoining them in cover. Similar observations have been made by Dunn (pers. comm.) in Baxter State Park. Calves were occasionally seen along the shore or in the shallows of a 60-acre (24-ha) pond as early as mid-June. By early July, they too visited their mothers in deep water for several minutes at a time before returning to the shallows or to shore.

According to Altmann (1958, 1963), these are the only circumstances under which Shiras cows were isolated from their young. In cover, Shiras calves normally accompanied the dams, as was also true of the Kenai young. (Since there were no large lakes or open meadows in Pen 4, I have no data on behavior in these habitats.) One would assume that accompanyment in cover was typical for the Matanuska Valley and Baxter Park cow-calf pairs too, although neither LeResche (1966) nor Dunn (pers. comm.) have data on this. The Matanuska moose were not visible to LeResche when deep in cover and Dunn did not collect this sort of information on the Baxter Park animals. The fact that calves do not accompany their mothers feeding in lakes is probably due to their preference for cover and aversion to deep water. The spacing thus maintained between mothers and young is definitely not lying-apart.

I have shown that separations between Kenai cows and their young occur at all stages of calf development. But there is no indication that they significantly helped to conceal the young at any stage. The only phase when calves did not join their mothers whenever they obviously desired contact, was during the first two weeks postpartum. This is the only phase when one might say that "isolation" was maintained. The reason for this maintenance is unknown. Two hypotheses are offered: The observations suggest that this may have been related to the distance separating mothers and young. Lent (1973) proposed that motivation to approach may be distance-dependent for the infants of most ungulate species. On the other hand, inhibition of approach by the calves, beyond these observed distances, may have been due to inability to see the mother in the distance because of intervening foliage. The apparent distance-dependency may have been an artifact of the small number of observations. Further investigation is necessary before conclusions can be drawn.

Although during this stage, Kenai calves remained at rest sites until rejoined by their dams, their behavior differed from the typical hider pattern in a number of respects. Cows always rested with their infants and usually fed nearby. Periods of isolation were relatively short and infrequent. When the cows did leave, their infants often bleated for them, which would have revealed the locations of the infants to any predator in the vicinity. White *et al.* (1972) stated that when white-tailed deer fawns were being tagged, their bleating attracted coyotes. (After age two weeks, Kenai calves normally accompanied their mothers feeding and frequently initiated reunions on those occasions that their mothers wandered away grazing while they rested).

Thus, although separations do occur between moose cows and their infants, there is no evidence that these are products of a mechanism for concealing them. Rather, in some instances, separation may increase exposure, instead of minimizing it. This small body of observations is not sufficient to justify concluding that moose, as a species, does not exhibit lying-apart. But the burden of proof is on whoever proposes that they do. Ideally, he should show that infant are less susceptible to predation when separated from their dams, than when associating with them.

PROTECTION OF CALVES THAT ARE ASSOCIATED WITH THEIR MOTHERS

According to Mech (1966, 1970), once a moose calf is discovered by a wolf *(Canis lupus)*, it is essentially helpless unless it is defended by its mother, regardless of whether it flees. He has seen 12 encounters between wolves and cows with calves. In four instances, the cow-calf pair stood at bay when they discovered the wolves nearby. The cow stood behind her calf, protecting it from the rear, the usual point of attack. None of these calves was killed. On a few occasions I have seen a calf stand under its mother, or try to, while she was threatening me with her head low, ears back and mane erected. In each case, the calf was aware of me and acted "frightened". Murie (1944) described how a cow in Mount McKinley National Park successfully defended her newborn calf against two huskies. In the eight other wolf encounters that Mech observed, the cow-calf pairs fled. During flight too, a cow usually remained behind her calf. So long as the calf was with its mother, it was relatively safe; but, if it became separated from her, as happened in three instances, it quickly fell prey. During my own observations calves usually followed their mothers when they fled from me or from aircraft. On those occasions that they ran ahead of their mothers, they seemed to be especially frightened and perhaps were panic-stricken. In these instances, the calves typically became separated from their mothers by more than 10 m. If a calf reacted in that same way to wolves, it would probably be killed, judging from what Mech reported.

Moose cows are also able to defend their infants against black bear *(Ursus americanus)* and sometimes against grizzlies *(U. arctos)*. Conley (1956) reported a case where a cow moose attacked a black bear that was carrying off her calf and wounded it before an observer shot the predator. Geist (1963) also described an encounter with a black bear. LeResche (1966) concluded that, although predation by bears does occur in the Matanuska Valley of Alaska, it is: "probably an important mortality factor only in very young calves. Calves more than a month old seem capable of escaping bears under ordinary circumstances [at least when accompanied by their mothers], and probably fall prey only in unusual situations of surprise or harsh environmental conditions... The demonstrated ability of a brown bear to take a young calf even though it is closely protected, as well as the much greater fear shown by moose at the presence of a brown bear, suggests that they are a more important predator on moose than the black bear, although the latter are much more numerous."

PROTECTION OF LONE CALVES

Thus, when a calf is alone, its primary safeguard against predators must be concealment. The accentuated tendency of young to avoid open areas has already been mentioned. Another mechanism for minimizing exposure is the "prone response" (term coined by Lent, 1973). When Alaskan infants are pursued by humans during tagging activities, they sometimes drop to the ground and lay motionless (LeResche, pers. comm.). However, this appears to be much less common for moose than for typical hiders. During many years of tagging, Wyoming Game Commission biologist Jim Straley saw only one instance: "The youngster had traveled a long ways and was obviously very tired" (van Wormer, 1972, p. 56).

It is a common notion that the coloration of fawns of some hider species serves to camouflage them from predators. But it is uncertain whether this is also true for moose. So far as I know moose infants are greyish-, or reddish-brown in color throughout the range of the species. Under the conditions that I observed them and in color and black-and-white protographs I took, this did not appear to my eyes to provide better camouflage than the coloration of adults. James Peek (pers. comm.) reports that both cows and calves are highly conspicuous in the open sagebrush habitat of Montana.

Some hider species protect their infants from olfactory detection through maternal consumption of the afterbirth and the neonate's feces and urine; furthermore, the infants are so nearly odorless that predators cannot detect them by scent alone (Lent, 1973). In contrast, although some moose cows do consume their afterbirth, this is not typical (see earlier). Markgren (1969 and pers. comm.) has found both afterbirth and neonatal feces at birth sites. Although I watched carefully on many occasions, I saw no indication that cows consumed either faces or urine. Since cow-calf pairs normally remain at the birth site for at least a few days (Altmann, 1958, 1963; see earlier), odors must accumulate there. Moose calves are commonly thought to be odorless (Mech, 1970), but I know of no evidence to support this. Boltar and Taunga both had a mild odor which, to me, resembled a blend of the odor of milk and of the scent that was typical of adults and yearlings that I encountered at close range. But this was milder than the scent of the older moose; I could detect it only when within about half a meter of them (On the few occasions that I was within 10 or 15 m of an infant, I was too concerned about its dam's reaction to notice whether I could smell it). Furthermore, Markgren (1966) reported that calves he reared had an odor reminiscent of formic acid associated with a greasy secretion which apparently came from sebaceous glands in the skin; this odor diminished as the calves matured. It is debatable whether the grooming that wild calves receive from their mothers could reduce these odors below detectability by predators (see Pinter, 1964 and Raesfeld *et al.*, 1965). It is also questionable whether hand-rearing could have induced such odors and that they would not develop for wild calves.

Considering that moose dams usually feed and rest near their infants, that the infants may habitually rest within a few meters of one another at the birth site or at some other location, the tendency of the young to vocalize when separated from their mothers, their lack of cryptic coloration, the poor development of the prone response (at least in Wyoming), and the fact that odors are not minimized: it seems that they are much less well adapted for concealment than are typical hider young. In view of the defenselessness of calves when alone, one must also conclude that they are not well adapted for isolation from their dams, which further argues against the occurrence of lying-apart. Moose definitely are not "hiders"; nor can they be judged as "followers" since separations do occur between cows and infants, and because they do not depend primarily on flight for protection. Rather, they fall into a third class which I will call "defenders" or "Verteidiger Typ".

SELECTIVE ADVANTAGES OF INTENSIVE CONTACT

Because of the greater ability of moose to defend their young, there would have been less selective pressure on them than on most cervids to develop means of infant concealment. Just how effective defense has been historically and currently, and thus how little pressure there has been towards minimizing infant exposure, we do not know. Nevertheless, one might wonder why moose infants are not better concealed when separations do occur.

One might also wonder whether predation losses — however extensive they may be — might not be further reduced by augmenting defense with some form of lying-apart. Presumably, a cow could remain close enough to rescue her calf if it was endangered by predators, yet far enough away — perhaps 30 to 50 m or so — to avoid revealing its location, thereby reducing the likelihood that she would have to defend it. This would seemingly minimize the danger to both mother and infant. That such a pattern is lacking suggests that the advantages of closer mother-infant association outweigh whatever predation losses occur. Perhaps the mother is more intensely motivated to protect her infant when she is with it. Perhaps the first week or so of life constitute a sensitive period for types of learning that are promoted by maternal contact and guidance (see Cow-Yearling Relationships). This is a problem that should be explored further.

ACTIVITY PATTERNS AS ADAPTATIONS FOR CONCEALMENT

Another possibility to consider is that moose have developed mechanisms of infant concealment that depend upon mother-infant association, rather than isolation — in contrast to hider species. The function of maternal "freezing" during disturbance is assuredly concealment of the neonates (see earlier). It is an appealing speculation that the reason calves are rarely active while their dams rest is because maternal recumbency inhibits activity, and that this too is a mechanism for concealment. If that is true, one would expect activity inhibition to be greatest during the first week or two, and to decrease once calves attain the capacity to flee with their mothers (around age five weeks, judging from LeResche, 1966). In particular, one would expect activity inhibition to be greatest when a dam is "freezing".

All but one case of a calf remaining up after its dam bedded or of getting up first, were by calves at least six weeks old — in accord with the above hypothesis. But, contrary to the hypothesis, most "spontaneous" interruptions while with a resting dam were by calves no more than two weeks old. In one instance when Mary Ann "froze" in response to disturbance by the observer, her neonate Roxy arose and wandered around for a few minutes, up to 3 m from her mother.

If calves actually are inhibited from activity when their dams are resting, it is presumably via their awareness of the dam's behavior. So far, we have no evidence that a neonate distinguishes and reacts selectively to the subtle differences between alarmed vs. relaxed maternal recumbency. Certainly, the neonates I observed did not seem capable of making this distinction. Not only did they seem "oblivious" to their general surroundings (including the observer), but they paid only intermittent attention to the dam. This was in striking contrast to the behavior of older calves who watched me or their mother intently when disturbed (see later) (According to Knorre, 1961, calves do not exhibit fear until at least a few days old). We can not conclude that the instance when Roxy arose while her dam was "frozen" was unrelated to the occasions when she or other calves arose when the dam was more mildly alarmed, or when the dam was relaxed. If activity inhibition during maternal recumbency was operative at this age, it was not apparent. Furthermore, this raises doubt as to the existence of inhibition at any age. Granted, calves two to six weeks old were rarely and only briefly active while their dams rested. But why would inhibition be more important at that stage than initially after birth, especially on occasions when the dam "freezes"?

Newborn roe deer *Capreolus c.* fawns may be active while their dams rest nearby. But once they are several hours old, they depend on isolation from the dam for concealment; normally they do not rest together (Espmark, 1969). So, the problem of inhibiting activity during contact periods does not arise. Espmark also noted that during periods of isolation from the mother, a roe fawn might arise occasionally for several minutes. This has also been reported for other hider species. Thus, so long as a fawn confines its activity to relatively dense cover and to occasions when it has not been disturbed, occasional "spontaneous" interruptions of rest may not significantly increase its exposure to predators.

Thus, we are faced with the following questions with regard to moose:

1) Is activity by calves inhibited when their mothers are bedded with them? Do calves remain active more of the time or interrupt rest periods more often and for longer intervals when alone than while associated with their mothers?

2) At what ages and under what conditions are "interruptions" most common?

3) If inhibition does occur and if it is a mechanism for concealment, why might it be more important between the second and sixth weeks than earlier in life? What factors (*e.g.*, neurosensory development) might prevent it from being more influential earlier?

4) If activity inhibition is not a mechanism for concealment, what functions does it serve?

Nursing

By "nursing" I refer to the transfer of milk from mother to infant, or to the mother's role in this transfer. The calf's activity is called "suckling". In the following discussion I provide various quantitative data on nursing postures, duration of nursing bouts, and other events for Kenai moose. It should be kept in mind that figures for the first two weeks postpartum are based on sporadic observations; except where specified otherwise, they represent lumped data for all calves (Table II). All quantitative data beyond that age are solely for Rolly and Alfe, based on systematic biweekly observations. Other descriptive material for calves more than two weeks old are primarily for Roxy, Rolly, Arnold, and Alfe — the offspring of Mary Ann and Amazon.

RECUMBENT NURSING

The manner of nursing changes as calves mature. They first suckle before they are 1.5 hr old, while the calf and its mother are bedded (Skuncke, 1949; Speidel, *in* Peterson, 1955; Knorre, 1959 Fig. 7, 1961). Hediger (1955), Altmann (1963) and Lent (1973) have also reported recumbent nursing. On the Kenai Peninsula, most nursing during the first day was in this position (Fig. 5). In all cases, the calf rested with its head by the udder and its rump near its mother's shoulder. This orientation was also used when they were standing. Lent calls it the "reverse parallel" position. A calf initiated recumbent suckling by kneeling on its carpal joints, bunting the udder solidly a few times, and lying down to suckle. Contact with the udder while kneeling seemed to position the calf so that it could reach the udder while bedded. Bunting may have also been easier while kneeling. When the calf was already bedded by the udder, it arose to a kneeling position and bunted the udder before lying down again and sucking. While recumbent, the calf did not bunt the udder but intermittently massaged it with its muzzle at a rate of up to once per second.

The initial hard bunts probably served to stimulate milk letdown (Fraser, 1968). Ejection depends upon muscle contractions which are controlled by oxytocin released from the posterior pituitary upon stimulation of the udder. Letdown may also be stimulated by "visual factors" (Fraser; p. 146) including, presumably, sight of the young.

During the first few days of life, Kenai calves seemed to suckle at will. Their mothers were available almost continuously. If a cow was feeding nearby, she usually returned when her calf bleated. She assumed the nursing stance, legs fully extended and head typically elevated so that her eyes were higher than her rump. When her calf tried to suckle, she bedded down, usually with her udder exposed towards the calf. Cows also initiated bouts. When resting by her calf, a cow simply arose and assumed the nursing stance. Typically, her calf arose too, even if it had been resting by her udder before she got up. If the calf remained bedded, the cow aroused it by nudging. When it tried to suckle, she lay down, enabling it to reach the udder.

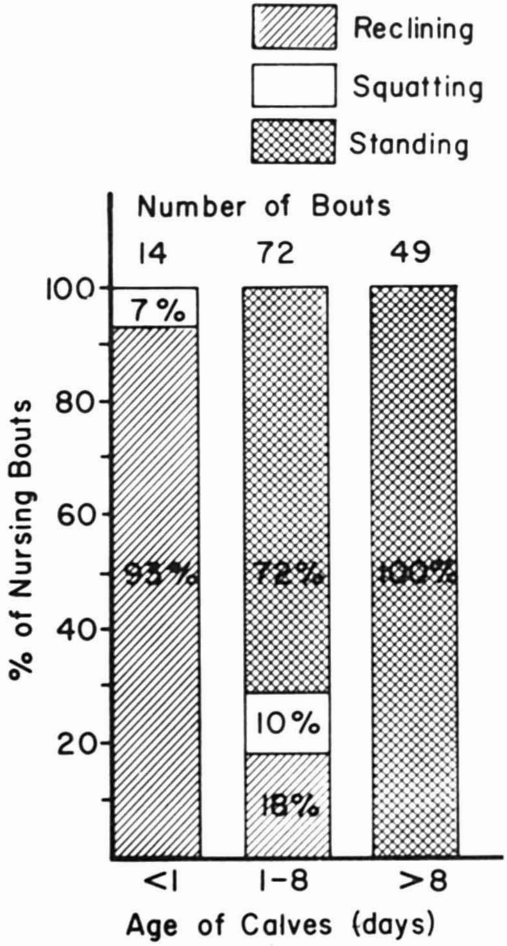

Figure 5. Posture of the cow while nursing her calf as a function of the age of the calf.

STANDING NURSING

Kenai calves only a few hours old attempted to suckle while their dams were standing; but they were not tall enough because their hind legs were extended so far out behind them that the tibiae were nearly parallel with the ground, and their fetlocks almost touched the ground instead of being nearly vertical as they are for older calves. As they grew stronger and could stand more normally (Fig. 6), they could sometimes reach the udder if the dam squatted. In one instance, Carie lowered her udder an estimated 10 to 20 cm in this manner. The nursing squat is identical to that used for urination (see Geist, 1963).

Figure 6. Boltar, a few days old.

Calves suckled from between their dam's hind legs in 17% of the bouts (n = 60) seen during their first 8 days. After that, they always suckled in the reverse-parallel position. Calves older than 8 days also tried to suckle from the rear, but none was successful. They rubbed the muzzle against the udder, perhaps bunted it a few times, then gave up and moved around to a flank to suckle. Altmann (1963) stated that Wyoming calves never suckle from the rear and suggested that the teats might not be accessible from that position. Fig. 7 shows the posteriorly accessible udder and an exposed teat of one of the Kenai cows.

Figure 7. Rear view of an udder and teat.

During the first week or so, bunting was relatively gentle. It involved mainly head and neck movements. However, by age 2.5 to 3 weeks, bunting was so vigorous that the calves' ears flopped wildly. Thrusting was performed using the whole body, especially the head, neck, and forequarters, at a continuous rhythm of about twice per second throughout each bout. The two calves reared by Markgren (1966) bunted mildly when only a few days old, but very vigorously by the second month.

STIMULI THAT ELICIT SUCKLING BEHAVIOR

I have already indicated that a calf will usually attempt suckling when its dam stands with her head elevated high enough that her neck is above horizontal. This is what I call the "nursing-invitation-stance". Further insight is provided by observations of the objects towards which Boltar, the hand-reared calf directed suckling attempts.

He was abandoned by his mother when no more than six hours old due to human disturbance. After 17 hours of abandonment, she had not returned and he was taken to camp. Boltar anxiously explored my clothing with his lips, especially around my groin, bunting weakly. When I knelt down, he knelt too, shoved his nose into my groin, and bunted upwards with considerable force. He made similar thrusts into my armpits when I held my arms a few inches from my sides. He seemed to search for a semi-enclosed area and finding one, would begin bunting. He also directed suckling attempts against the undersides of moderately large objects with space beneath them such as a table, bench, and bed, (each of which was set against the wall of a building). He approached our truck, explored its surfaces with his lips ("lip-exploration"), and bunted upwards under the running board, fenders, and the open door, in spite of the fact that it was apparently painful for him to do so, judging both from his vocalizations and the sounds of his muzzle hitting the truck. When I prepared Boltar's bottle, he became very excited; he bunted against me and explored the furniture with his lips. He seemed to bunt most forcibly against me and possibly against the underside of the table on which I was mixing the milk. Markgren (1966) stated that when he approached hand-reared calves with their milk bottles, they bunted into the air and against the fence separating him from them.

A dam's vocalizations also seemed to elicit suckling attempts. In cases where a cow assumed the nursing-invitation-stance but her calf did not look up, grunting attracted its attention. Furthermore, grunting apparently released approach in conflict situations. Calves were sometimes rebuffed when they tried to suckle (see below). Consequently, they often approached hesitantly or did not approach at all. However, upon hearing its mother's grunt a calf would run to her and begin suckling immediately. In no case was a calf rebuffed or avoided after this combination of signals.

LeResche (1966) reported that Matanuska cows initiated reunions by grunting; their calves responded by bleating and approaching them; the young stopped vocalizing only when they began to suckle. Knorre (1961) and Lent (1973) have also reported vocal nursing solicitation among moose. Lent noted that it is common in ungulates. Markgren (1966) reported that the calves he reared responded to his "food whistle" by running to him, licking their muzzles.

Kenai calves usually tried to suckle when their mothers assumed the nursing-invitation-stance or, frequently, the alert-stance. This suggests that common visible aspects of the stances were releasers.

Although elevation of the dam's head seemed to be crucial once calves were a few weeks old, this was not apparent during the first week or so. Neonates frequently tried to suckle when their mother's heads were below rump level. But I never saw an older calf attempt suckling except when the dam's neck was above horizontal. Thus, other aspects of the nursing stance must have been more important initially postpartum.

Fraser (1968) stated that a neonatal foal quickly focuses teat-seeking in the angles between his mother's limbs and body. This has also been reported for goats *Capra hircus* (Blauvelt, 1956), llamas *Lama glama* (Kraft, 1957), giraffes *Giraffe camelopardalis* (Lang, 1955; cited by Thomas, 1956) and domestic cattle (Adler *et al.*, 1958), according to Majoribanks-Egerton (1962).

Fraser (1968) also proposed that among some equidae, the dam's lower outline with shaded area beneath may release and orient suckling. Boltar's choice of objects towards which he directed suckling behavior (especially bunting) suggest that this is also true for moose. These objects included the observer, a bench, a bed, a table, and the running board, fenders, and open door of a truck. All were large or moderately large, and had open space beneath them.

Precisely what aspects of the dam's lower outline might release suckling are unknown. But it may be the dark/light interface. If so, this might explain the ventral-lateral color-shading pattern of cows (Fig. 8). Essentially all cows that I have seen, live or in photographs, have been blond on ther backs and upper flanks, rump and shoulders; their chests, lower flanks and lower rump were darker and often black; the legs are typically much lighter in color, being whitish or blondish. (However, they may be almost uniformly dark just after shedding in early or mid summer; their backs turn blond as the season advances, perhaps through sun-bleaching.) This pattern

Figure 8. Mary Ann: note the color-shading pattern of her pelage, particularly the dark chest and ventral flanks.

of color-shades would accentuate the lower outline, especially its shaded aspect.

Young bulls are also colorshaded in this way, but it is my impression that mature bulls tend to be much darker. All of the moose that I have seen that were almost completely black (except for their legs) were mature bulls. The similarity in color-shading between females and young-males is not surprising considering the widespread sexual automimicry of this type, morphological and behavioral, among mammals (e.g. Geist, 1966, 1971).

Fraser (1968) emphasized the fact that not only is suckling behavior in horses apparently released by the mare's lower outline, but mounting (by a stallion) is released by an almost identical "image", the "Torbogen". Whether a close similarity between suckling and mounting releasers also exists for moose is uncertain. I found no information on a cow's posture just prior to being mounted. But Geist (1963, p. 197) illustrates the posture of a cow moose being naso-genitally "tested" by a bull. The nursing-invitation-stance differs only in the position of the ears.

So far, we have considered release of suckling only while the dam is standing. How does a neonate find the udder when its mother is recumbent? When 6hr old Boltar was freed 5m behind his mother, where she lay while the tranquilizer (M-99) wore off, he walked directly to her, knelt and shoved his muzzle under her rump, behind one hind leg, and tried unsuccessfully to suckle. He probably had never suckled while his dam was on her feet. Perhaps some visible similarity between the angle of the dam's leg while recumbent, and my crotch while I was kneeling account for the fact that Boltar bunted my crotch more strongly in this posture than when I was standing. Furthermore, while a cow is recumbent her udder and adjacent underbelly are exposed in a rough semi-circle surrounded by the dark pelage of her chest, flank and hindleg. The teats are grey or pink (Fig. 9). This pattern of contrasting shades may also help neonates find the udder. For one thing, the blond-surrounded-by-dark may mimic light comming between the dam's hindlegs when she is standing or when she is lying with one of the hindlegs partially raised.

Figure 9. Ventral view of an udder and surrounding areas.

NURSING SOLICITATION BY CALVES

Majoribanks-Egerton (1962) reported that newborn bison calves *(Bison bison)* made sucking mouth-movements even before they could stand and suckle. When a neonatal Kenai moose approached its mother to suckle it too "phantom-sucked", as well as flicking its tongue, bleating and nuzzling the dam around her udder. However, by the time a mother-reared calf was a week or so old, it had ceased "phantom-sucking"; a week later it had also ceased nuzzling its dam prior to suckling. But, even calves eight or nine weeks old continued to vocalize and flick their tongues occasionally. Markgren (1966) also reported tongue-flicking by his calves as they approached him for milk.

"Phantom-sucking" is an exaggeration of the mouth and tongue actions used in actual sucking. The designation "phantom" refers to the fact that actual sucking does not occur, and the mouth actions are usually performed without contact with any object. It may be directed towards the dam or caretaker from at least 30 m away as the calf approaches to suckle. However, a calf may "phantom-suck" while its lips explore surfaces such as the dam's flank. These characteristics were determined primarily by watching Boltar. I could hear his "phantom-sucking" over 5 m away. During "phantom-sucking", the gums were sometimes exposed, producing highly visible flashes of color. Tongue-flicking (alternate extension and retraction of the tongue during which the muzzle sometimes appears to be licked) also produced flashes (Fig. 10). Both gums and tongue are bright pink.

Sucking sounds and flashing of gums were rhythmical and were performed about once to twice a second, roughly the same rate at which calves uttered bleats. "Phantom-sucking" and bleating sometimes occurred simultaneously and might be interspersed with tongue-flicking. These activities may be displays which help induce the mothers to permit suckling.

Figure 10. Boltar flicking his tongue and "phantom-sucking" as he approached me to bottle-suckle, 1 day old.

Nuzzling, lip-exploration, tongue-flicking and bunting all virtually ceased after Boltar was fed, then reappeared a few hours later, becoming progressively more frequent and, in the case of bunting, more intense. They might be interpreted as manifestations of hunger. Bleating also became more frequent and intense on these occasions. Likewise, Boltar's "phantom-sucking" increased until he was fed, then virtually ceased afterwards.

"Phantom-sucking" also appeared when Boltar was bedded, whether alert, drowsy, or apparently sleeping. Under these conditions, "phantom-sucking" did not indicate hunger. He did not attempt to suckle when I held the bottle near his muzzle; nor did he bunt, explore the bottle or me with his lips, or tongue-flick.

By the time Boltar was three weeks old, recumbent "phantom-sucking" had gradually been transformed into "phantom-chewing". His jaw movements had become progressively more lateral. Grinding of the molars was audible, in addition to sucking sounds, but he had not yet begun to ruminate. When he died one week later, autopsy revealed no more than a few millimeters of chewed vegetation in his digestive tract. Markgren (1966) likewise saw "phantom-chewing" in calves he reared. He interpreted this as incipient cud-chewing. That interpretation might also be applied to Boltar. However, Dieterich (pers. comm.) has reported that domestic cattle calves that were scouring badly, sometimes make grinding sounds with their teeth; most of them died. Since Boltar had been scouring badly for over two weeks, and died shortly after "phantom-chewing" appeared, the trait may have been a symptom of his poor condition.

INTERRUPTION AND TERMINATION OF NURSING

During their first eight days of life, Kenai calves frequently interrupted nursing bouts temporarily; their mothers occasionally did so too, as they stepped forward to feed. Interruptions rarely (5%; n = 66) lasted over 30 sec. After two weeks of age, interruptions were almost never more than 1 sec long, occurring mainly when calves switched teats. Interruptions were longest in cases where calves bunted the udder a few times before regrasping a teat. On the few occasions that I was close enough to see, it was noticed that cows began terminating after the fourth switch, presumably when a calf began suckling from one of the teats a second time. In contrast, beef calves may change teats many times during nursing bouts, leaving each quarter of the udder even before it is emptied and returning again later; switches and bunting become more frequent as the nursing bout nears its end (Hafez *et al.*, 1968). Bunting by moose calves also seemed to become more vigorous towards the end of a bout, perhaps due to the dwindling flow of milk.

During the first day, while cows and calves were recumbent for nursing, calves apparently terminated all bouts. They suckled at will and quit on their own initiative. Once they began to suckle standing, sometime on the first or second day, their mothers also ended many bouts: 51% during the first eight days (n = 86) and 100% thereafter. Espmark (1969) reported that in a small group of roe deer the fawns terminated all bouts on the first day, and the does terminated all bouts after the seventeenth day.

A calf terminated nursing simply by releasing the teat; it usually remained with the mother for a short while, nuzzling or licking her and being licked by her, before it moved away. A cow terminated nursing by stepping forward, usually lifting her adjacent hind leg over the calf, if it was nursing from her flank. Frequently the leg bumped the calf, sometimes making it stumble or fall. Since calves usually held on to the teat and were often dragged momentarily, this may have helped to detach them. As early as the seventeenth day, stepping forward was accompanied by a moan-like vocalization from the cow. Although moaning soon became typical, it did not occur in all instances even as late as the ninth week postpartum. Moaning often began before a cow stepped forward and sometimes continued several seconds after the calf was loose. Cows also moaned when discouraging attempts by their calves to suckle or play-fight. Calves responded by withdrawing.

MILK CONSUMPTION

The duration and frequency of nursing bouts decreased rapidly with age. Bout duration indicates the amount of time that a calf appeared to have its mouth on a teat. Detectable interruptions are not included. Data for the calves Rolly and Alfe are shown in Figures 11 and 12. They could not be observed at night, nor could they be followed continuously throughout the day. Data are most complete for the 12-hr interval from 10:00 to 22:00 (Alaska daylight time) (Fig. 13); the values given are for that time span only. Total sucking was estimated using the cumulative data for the given semiweekly period by the following formula:

$$\frac{\text{(Total sec of nursing observed)} \quad \text{(12 hr)} \; \text{10:00-22:00 hr}}{\text{(total hr of observation 10:00-22:00)}} = \text{(estimated sec of nursing) 10:00-22:00 hr}$$

For instance, during the first week postpartum, 6,630 sec of nursing were seen during 17.6 hr of observation on Rolly and Alfe between the hours of 10:00 and 22:00. If one assumes that nursing bouts during the rest of the day and night were equivalent in frequency and duration, 24-hr estimates are obtained by doubling the 12-hr values.

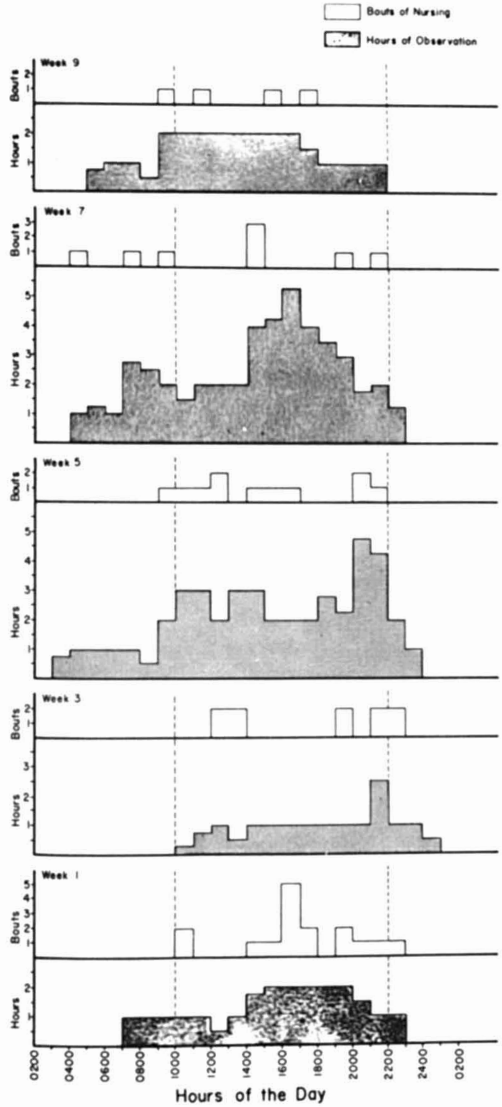

Figure 11. Number of nursing bouts and number of hours of observation of Rolly and Alfe for each 1-hour interval of the 24-hour day, for each semi-weekly observation period in 1971.

Mean duration of nursing bouts for Rolly and Alfe decreased more than 20-fold from about 400 sec each during the first week postpartum to about 20 sec each by the ninth week (Fig. 11). This was accompanied by nearly a 5-fold decrease in frequency from about 10x/12 hr, and more than a 100-fold decrease in total time nursing (Fig. 12).

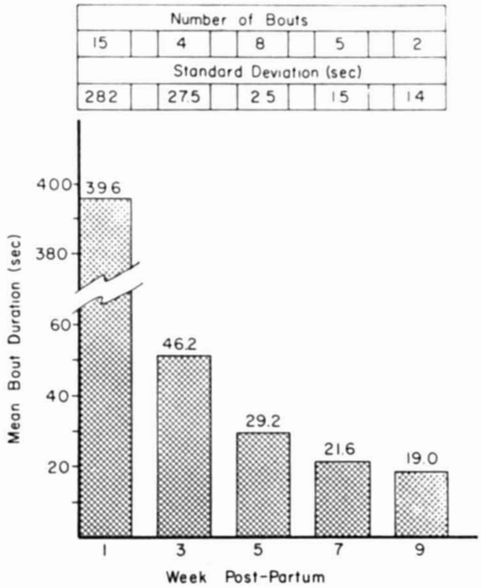

Figure 12. Mean durations of nursing bouts between 10:00 and 22:00 hr (ADT) as a function of calf age (Rolly and Alfe 1971). (*Note:* some of the bouts shown in Fig. 11 could not be timed).

During their first week of life, Rolly and Alfe suckled for an average of about 4500 sec per day during the 12-hr interval between 10:00 and 22:00 hr, which suggests a value of 9,000 sec per day. This is about twice as high as the values for roe deer *Capreolus capreolus* (4,100 sec) and reindeer *Rangifer tarandus* (4,500 sec) which may be calculated from the data on duration and frequency of suckling in Espmark (1969, Figs. 5,6; and 1971, Figs. 12, 13).

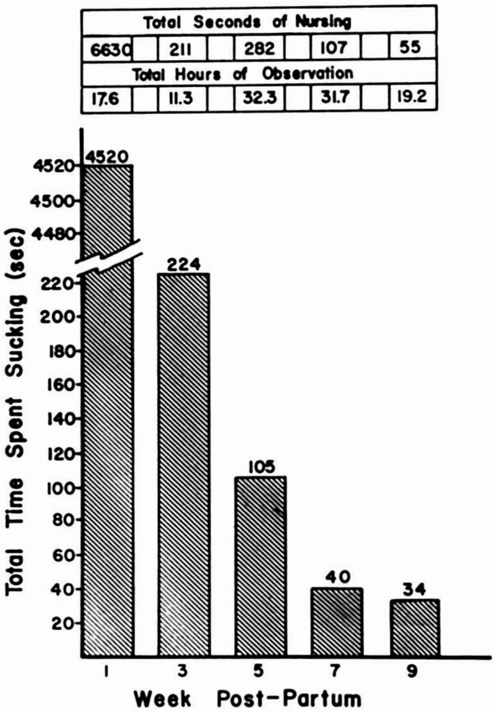

Figure 13. Total time nursing between the hours of 10:00 and 22:00 (ADT) as a function of calf age (Rolly and Alfe, 1971).

Munro (1956; cited by Hafez *et al.*, 1969, Fig. 45) observed approximately 1900 sec of suckling by a three-day old domestic lamb *Ovis aries* during the 10-hr interval between 09:00 and 19:00 hr. Extrapolation suggests a value of 4,560 sec per 24-hr. New Forest ponies observed by Tyler (1972, Fig. 21) suckled for an average of 300 sec per hour during their first week of life. If one assumes that this average is based on data for all hours of the day and night, a 24-hr value of 7,200 sec is obtained. Although it is possible that suckling by Rolly and Alfe was concentrated during hours between 10:00 and 22:00, it is more likely that they suckled equally long during the rest of the day.

Under the conditions of observation, there was no way to determine how much of the time during a suckling period that Rolly or Alfe was obtaining milk. One must expect a lag to have occurred between initial stimulation of the udder and letdown (see above) at least during the early part of the lactation term. In some cases, it can be from 45 to 90 seconds long for cattle calves. However, letdown can also be stimulated by sights and sounds that a cattle cow has learned to associate with being milked (Davis, 1962). One would expect a cow to respond similarly to the sights and sounds of her calf, and for the lag to decrease as she gains experience during the lactation period as well as with each calf born to her. Furthermore, infants may retain teat contact even after letdown has ceased. Prolonged teat contact after milk flow stopped might have occurred when both cow and infant were recumbent but would seem unlikely when the cow was standing or squatting. That would demand considerable effort by the infant to stretch so high for an extended period. If prolonged contact did occur only while both cow and infant were lying down, one would expect recumbent bouts to have been significantly longer than bouts when cow and infant were on their feet. That was not the case. Considering all calves observed during the first two weeks, recumbent bouts averaged 342 seconds (n = 21, SD = 364); standing and squatting bouts together averaged 318 seconds (n = 50, SD = 324). However, calves did sometimes hold onto a teat for a second or two as the mother was terminating the bout.

As the calves matured the rate of milk flow probably increased, due both to changes in letdown from the udder and to increased sucking efficiency. We have no data on rate of letdown for moose and no information on sucking except for bottle-feeding Boltar. His rate increased nearly 12-fold between his third day and his eighteenth. Initially he sucked on a bottle for 20 min without consumming more than I pint (½ liter).

On the other hand, the enormous amount of time that Rolly and Alfe apparently spent suckling during their first week of life, relative to later weeks, and relative to what has been reported for roe deer, reindeer, sheep and ponies, may in part be an artifact. If a neonate rested its muzzle on or near the udder or nuzzled it part of the time, that could not always be distinguished from suckling. Bunting was very mild and sporadic at that stage, and the moose were usually screened from view by vegetation. By the third week, however, there was little likelihood of such error. Bunting was vigorous enough and the cow-calf pairs visible enough that teat contact was readily distinguishable. At this age, these two calves suckled for an average of about 500 sec per day. Roe fawns and reindeer fawns both suckled over 1000 sec per day. This might suggest that moose calves actually suckled less than roe and reindeer fawns during their first week. But, it may merely indicate that the moose calves were being weaned more rapidly. By the ninth week these calves suckled an estimated 70 sec per day; roe fawns 40 to 59 days old averaged about 120 sec per day; reindeer fawns averaged roughly 250 sec per day during their eighth week, and 184 sec per day during their eleventh (Espmark, 1969, 1971).

Considering the probable decreases in non-sucking teat contact, increases in milk flow, and the possibility of systematic error during the first week, there is no reason to think that the observed 100-fold decrease in total time «nursing» was accompanied by a proportional decrease in total milk consumption during the first nine weeks of life.

Knorre (1961) indicated that the stomach (abomasum?) capacity of newborn moose calves was only about 1.5 liters. By weighing tame calves before and after suckling from their mothers, he determined that consumption varied from 0.1 to 0.5 liters of milk per nursing, according to the age of the calf. He claimed that on each of their first days of life calves ingested 0.5 to 1.0 liters/24 hr and that when consumption was greatest (about age 5 to 6 weeks), they sucked 1.5 to 2.0 liters/24 hr. Bubenik (pers. comm.) has pointed out that 0.5 to 1.0 liters/24 hr is much lower that one would expect for an infant the size of a moose calf. Calculations by Gasaway and Coady (1974) based on reindeer data support Bubenik's criticism. They estimated that a moose calf would need 3 to 4 liters/24 hr. during the first week of life. Yazan and Knorre (1964) have stated that by improving milking techniques, the daily yield of domesticated moose was increased from 2 to 6 liters, over a period of years. Thus, one must wonder whether cows gave full yield to their infants under the test conditions that Knorre used to arrive at the figure of a maximum of 2 liters per day, and whether it was possible to weigh calves accurately enough to detect an addition of only 0.1 to 0.5 liters (0.1 to 0.5 kg).

According to Knorre, during the entire suckling period pluriparous cows produced a total of 100 to 200 liters of milk, depending upon inherant capability, nutritional state, and age. Primiparous cows produced only 50 to 75 liters per season. Knorre concluded that, on the average, wild cows in the Pechora region of Russia produce about 150 liters. He states that domesticated calves achieved optimum nourishment when given milk five times per day. Furthermore, milk production by cows was also greatest when they were milked five times per day. Three cows cumulatively produced at least one-third again as much at that frequency as when milked only two to three times per 24 hr. Yazan and Knorre (1964) indicated that by improving milking techniques, the average yield of cows was increased from a maximum of 150 liters per season to 430 liters. Knorre's domesticated calves suckled eight to ten times per 24 hr when a few days old; my data suggest frequencies about twice that for Rolly and Alfe (Figs. 11, 12 and 13).

FORAGING

Bierwirth (1949, cited by Markgren, 1966) told of one calf that began chewing on foliage when it was only three days old. Kenai calves began mouthing and later chewing on leaves before they were one week old; but most did not start foraging regularly until at least two or three weeks postpartum. This agrees with the observations of Markgren (1966) in Scandinavia and Altmann (1963) in Wyoming. A calf reared by Dodds (1959) did not begin until one month of age.

The one exception to the norm among Kenai moose was Twister; he was browsing regularly when only five days old, probably because he was not obtaining enough milk to satisfy his hunger. His head and neck were twisted to one side, presumably due to an injury. I saw no evidence of this problem on his first day of life. The handicap prevented him from suckling while his dam was standing. Whenever he stretched towards the udder, he fell down. Although his mother may have continued to bed down to let him nurse, as she had done on his first day, I never saw her do so. In fact, she seemed to ignore his almost constant bleating when he tried to follow her through dense brush and windfall. He may have begun subsisting on foliage when just a few days old. When Twister was again seen in late July, only a vestige of the twist remained. He appeared to be as large and vigorous as other calves in the enclosures.

The fact that Carie apparently did not modify her behavior so as to regularly permit Twister to suckle, inspite of his handicap, cannot be explained by lack of maternal experience or by immaturity. She had already raised at least one calf successfully, in 1969.

SELECTIVE ADVANTAGES OF DELAYED WEANING

Suckling phases several months long are typical for ungulates; in some cases the young are not weaned until the following spring when they are a year old (Lent, 1973). Ewer (1968) has expressed doubt that it takes so long for rumen digestion to become fully established and has suggested that the function of prolonged lactation is to keep the infant under its mother's vigilant care. The extended nursing phase does appear to play an important role in the protection of moose calves.

For instance, the similarity between alert-stance and nursing-invitation-stance may be essential for the young to learn maternal alarm signals and other reactions which vary according to the kind of danger, etc. The alert-stance differs from the nursing-invitation-stance only in that the head is usually held higher and the ears cocked forward in the direction the animal is facing (Geist, 1963, Fig. 53); in nursing, the ears are usually directed sideways, although sometimes during nursing-invitation, the cow looks towards her calf, in which case her ears are also directed forward, toward it. The similarity between these stances frequently led to mistakes by calves. When a cow lifted her head in alarm, her calf was likely to attempt to suckle. Cows normally avoided such attempts by stepping forward or discouraging them with a moan. Nevertheless, even calves three months old still reacted to alarm-stances by trying to suckle. (In no case did a calf attempt to suckle when it was obviously disturbed.) A cow could seldom lift her head to look at something or stand in place with her head elevated without her calf watching her intently and perhaps even approaching. It is presumably the desire to suckle that keeps the moose calf so keenly attentive of its mother. Lent (1973) stated that "Such use of generalized attention-getting cues is of obvious value, particularly when the mother can more easily communicate further information after close contact is established with her offspring". Infant moose usually watch their mothers during disturbance, occasionally glancing towards the source of disturbance, but seldom staring at it. As they mature, however, they orient more towards the source of disturbance but are obviously still highly aware of what their mothers do and are quick to follow in case of flight or charging. The similarity between the nursing-invitation-stance and alert-stance may be adaptive beyond the simple fact that desire to suckle motivates attention to the cow. It maintains this attentiveness and alerts the calf in case of disturbance without frightening it unnecessarily and, thus, without producing undue emotional stress.

WEANING

When a moose cow moans to her calf, this appears to be a mild threat which is probably reinforced whenever it is bumped by her leg during nursing termination. In no case did a cow visibly threaten her calf. However, that may occur during the final stages of weaning. Lent (1973) noted that vigorous bunting appears to be painful to the mothers in many ungulate species. In some, the mothers terminate nursing or discourage suckling attempts with agonistic behavior including threats, biting and blows with head or horns. It is probably also painful when a calf holds only its mother's teat with its incisors. This may explain the "agonized" quality, anthropomorphically speaking, which characterizes nursing-termination moans. When cows discouraged suckling or play-fighting, their moans were usually more whiny, shorter and quieter.

Lent (1973) considers that for ungulates the complex of these events during nursing is associated with weaning. As the infant matures, its suckling efficiency increases, and its mother's milk supply decreases. The infant seeks more milk by bunting harder or, perhaps, by holding onto the teat after letdown has ceased even when the cow steps forward, which is painful to her. This increases her reluctance to nurse the calf on future occasions and reinforces her tendency to react aggressively when the calf attempts to suckle.

Knorre (1961) stated that in the U.S.S.R. most wild calves are weaned by mid-September, when their dams come into heat. Those cows that he found lactating in January as a rule did not have embryos in their uteri. In one case a tame cow weaned her twins when they were two months old. They continued developing normally and reproduced. Denniston (1956) reported that weaning occurred in early September for Wyoming moose, but Altmann (1958) indicated that calves continued suckling through the rutting period and were not weaned until the onset of winter. Dodds (1955) stated that he knew of no confirmed instances of suckling after September 10 in Newfoundland, but that the natives reported seeing instances in late winter. Johnson (pers. comm.) saw one case of suckling in January (1973) at the Moose Research Center. Cooney (1943) reported that weaning begins in December. Hosley (1949) believed that calves are not weaned until the next infant is born.

DEPENDENCE OF CALVES ON THEIR MOTHERS AFTER WEANING

Kenai calves became increasingly independent through their first summer. Whether this change continues during the winter is unknown. Johnson (pers. comm.) has occasionally seen calves widely separated from their mothers for more than a day in Pen 4, during the past two winters (1971/72 and 1972/73).

Numerous observers attest to the fact that the bond between cow and calf continues after weaning and that the calf continues to be dependent upon its mother at least until the following spring (Brown and Simon, 1947; Daniels, 1953, cited by Altmann, 1963; Denniston, 1956; Altmann, 1958, 1963). This problem is currently under study by Mr. David Johnson of the Cooperative Wildlife Research Unit, University of Alaska, at the Moose Research Center. Although many orphaned calves survive (LeResche, pers. comm.), some that loose their mothers even as late as November (age seven to eight months) may succumb to exposure and malnutrition. To account for this mortality, Denniston (1956) has proposed two hypotheses: 1) "...the cow initiates movements from one locale to another. In the crucial winter period an inexperienced calf is likely to stay in an area of deep snow and poor browse until too weak to escape it". 2) "A calf shares the social rank of the cow: intra-specifically and inter-specifically. A lone calf is on the bottom of the peck order and unable to compete."

Denniston's first hypothesis is supported by Altmann's (1963) observations. She agreed that maternal guidance was essential through the winter. By "guidance" she meant "choice of feeding and shelter places, safety and flight decisions, and later the selection and timing of winter groupings in the river drainages. [...] The winter group in moose does not take care of an orphan". However, calves may follow other adults (Bubenik, pers. comm.). It is not clearly established that maternal guidance *per se* is more advantageous to a calf.

Denniston's second hypothesis is supported by the observations of Houston (1973). He noted that cow-calf pairs rarely associated with other moose during the winter and attributed this largely to the cow's aggressiveness. Since adequate winter range was very limited, "better established and/or more aggressive females might be comparatively more successful than others in bringing calves through the winter". However, on the Kenai Peninsula, cow-calf pairs associate substantially with other moose during winter (LeResche, pers. comm.).

My observations are consistent with the idea that a calf shares the rank of its mother. During 1971, there were five cow-calf pairs in Pen 4. A sixth cow, probably Prudence, was accompanied by a calf on June 3 but was never seen with it again. These five cows displayed a linear hierarchy which was stable through the summer of 1971, from the time I first saw interactions in mid-June through early August when my field work ended. Furthermore, cows with calves always displaced those without calves as well as yearlings. They usually, but not always, displaced the two young bulls. I saw no interactions between the one mature bull and any of the cow-calf pairs. However, Geist (1963) indicated that cows with calves may even dominate adult males. In all agonistic encounters between two pairs at the Moose Research Center, the dominant pair was predictable from knowledge of previous encounters. Calves shared the status of their mothers in the sense that, when calves accompanying their mothers interacted, the calf of the dominant cow was usually dominant. That seemed to be associated with the fact that when a subordinate cow retreated, both calves remained near the dominant cow. The calf of the dominant cow thus had its mother for back-up. The dominant cow usually threatened the alien calf, as was typical of all cows with calves when approached by alien calves. If the mother's threat included a short charge, her calf was likely to run with her and continue chasing the alien calf when it ran. As calves matured, they became increasingly more likely to join their mothers in threatening and chasing subordinates. However, when alone, these same calves were themselves subordinate to low-ranking older individuals and to cow-calf pairs. Altmann (1963) and Geist (pers. comm.) have also seen this. It must be remembered, of course, that the fact that the Kenai moose were penned may have produced a more stable and clearly defined hierarchy than would exist among free-ranging moose.

Yearling-cow relationships

According to Denniston (1956), in Wyoming most yearlings were seen in the company of adult cows during their second summer; but, as he pointed out, he had no proof that these yearlings were with their mothers. Altmann (1958, 1959, 1960, 1963) provided a more detailed picture. She relied primarily on natural markings (antlers, bell and pelage) for recognizing individuals. She stated that most yearlings continued following their mothers closely until chased away prior to the birth of new siblings. Some became fully independent at that time. In most cases, however, a yearling continued to feed and rest in synchrony with its dam, remaining at the margin of her postpartum social distance ("life on the margin"), which was up to 90m (100 yards) in radius at its peak. As summer advanced, some yearlings were allowed to rejoin their mothers; but, when rut began, all but the most immature and submissive were treated as rivals and driven away by either the cow or her suitor, depending upon the sex of the yearling. Juvenile males frequently tried to court their mothers. Most yearlings became fully independent at this time. Geist (1963) has seen yearling bulls chased by cows.

LeResche (1966) provides quantitative data on cow-yearling disassociation in the Matanuska Valley of Alaska. He first saw new calves in late May. Thereafter, he observed only one instance (on June 1) of a yearling (loosely) accompanying a cow with a new calf, and only three cases (June 21 to June 23) where the relationship between a yearling and a lone cow was of an "offspring-maternal nature" Thirty-one percent of 70 yearlings sighted before June 24 accompanied a cow without a calf; between June 24 and August 21, this was true of only 25% of 73 yearlings seen. Whether these cows were their mothers is unknown. In many cases, there was no discernable interaction between them. When interpreting this data, it should be kept in mind that some yearlings may have been counted repeatedly (LeResche, pers. comm.).

In Pen 4, there were a variety of cow-yearling relationships. There is reason to believe that all cows with calves of the year associated only with their own yearlings. The evidence is circumstantial since individual juveniles could not be positively indentified from one semiweekly observation period to the next. Each of these cows tolerated only one yearling at a time near her; any other that approached was driven away. When an association could be observed over a period of several days, it was always the same yearling with the same cow. In 1971, the yearling with a cow was always the same sex as her calf of the previous year. Furthermore, all cows associated only with their own calves; they threatened and often chased alien calves.

I saw no instances of "life on the margin." Mary Ann tolerated her yearling Roxy within 10 m of Rolly when he was only 2 to 3 days old. Roxy was frequently associated with them for the next few weeks, but progressively less so thereafter. Mary Ann was seldom aggressive towards Roxy even during the first week after Rolly was born. Associations between other cow-infant pairs and yearlings were occasional, especially in the case of the two male yearlings. The cows were not obviously more aggressive towards the males, however.

The closest cow-yearling association was between Olga and Olivia in 1970, a year in which Olga was not seen with an infant. Olivia was especially immature physically and perhaps behaviorally. She followed Olga more consistently and synchronized activities with her more closely than the calf Rolly did with Mary Ann at 2.5 months of age. During summer 1971, Roxy and the two other female yearlings were often associated with one another and sometimes with Prudence (who did not have a calf), singly or as a group, for up to several hours at a time. One of these females may have been Prudence's daughter Prucilla. The two male yearlings were frequently seen together.

A yearling sometimes drifted from association with a cow-infant pair to the company of other yearlings, usually of its own sex, to following a lone adult, all in a single day. Yearlings also spent much of their time alone.

COW-YEARLING ASSOCIATION VERSUS COW-INFANT ASSOCIATION

It is interesting to note the parallels between the amount of cow-yearling versus cow-infant association in various parts of North America. In Wyoming, it was rare for a calf to be separated from its mother, and then only when the dam fed in water (Altmann, 1958, 1963). Furthermore cows were commonly accompanied by yearlings. In contrast, Matanuska calves were regularly separated from their dams for most of the day, while the cows fed in lakes or large open meadows. These cows were seldom accompanied by yearlings, and then rarely with a calf-like degree of activity/rest synchronization. This parallel also holds for Kenai cow-calf pairs. Cows did leave their infants, now and then, even during the first few days postpartum; cows associated with their own yearlings, at least occasionally, and in two cases, frequently. For Kenai moose, however, yearling-cow association was probably heightened by captivity, which prevented the juveniles from dispersing, had they been so inclined. If such parallels are confirmed by future investigation, it would be worth considering how greater dam-infant contact might influence the duration of their reciprocal bond as the young mature. As was discussed earlier, greater contact during early infancy may promote certain kinds of learning. This may include imprinting.

Summary

These observations, tentative generalizations and hypotheses are the products of investigation by a variety of workers.

Infant moose are dependent upon their mothers for protection and avoidance of predators and other dangers and from premature social contact. It is primarily the mother who insures that her calf will be in favorable conditions at appropriate periods of its development to obtain the nutrition, experience and exercise of its faculties necessary for survival and eventual reproduction.

1) Cows tend to seclude themselves from other moose and from predators prior to giving birth. Although they frequently choose sites in dense cover, many young are born in more exposed sites. Maximum distance from which infants were visible at birth sites on the Kenai Peninsula varied from 3m to 50m, according to cover density.

2) Following birth while the cow is bedded, the calf is licked intensively. This and other reciprocal stimulation is essential for eliciting and orienting the neonate's activities, including arising, suckling and voiding, for arousing maternal behavior, and for establishing the mother-infant bond.

3) During the first few days postpartum, both a calf and its mother are bedded almost constantly. But by the end of the first week, two Kenai cows were active over half the time — a level not obtained by their offspring until the fifth week. Over the first two months, the young were active only about three-quarters as much as their dams: about 45 percent of the time, against 65 percent for the dams. The cows averaged over 1.5 hr for both rest and activity periods. Their calves averaged nearly 2 hr per rest period and 1 hr per activity period.

4) A calf is rarely and briefly active while its mother rests nearby. It arises when or after she does, and beds down again before or at the same time as the mother. Most exceptions occurred during the first week of life of after the sixth. Although calves may be inhibited from activity while their dams rest, evidence is equivocal.

5) The longer a moose rested, the greater its endogenous motivation to arise became, and thus the less exogenous stimulation was necessary to cause it to get up. Early in a rest period habituated moose were aroused only by intense or unexpected observer-disturbances. But as the period proceeded, even very mild stimuli caused them to arise.

6) When non-habituated moose were disturbed while resting, they typically arose, prepared for flight and defense. However, cows with neonates usually "froze" into motionlessness instead; they got up, extremely agitated, only if approached closely. "Freezing" is probably a mechanism for concealing the young.

7) Cervids utilize three fundamental strategies in protecting their infants from predators: concealment, flight and defense. The relative importance of each varies with the age of the young and from one species to the next. Nearly all cervids, except caribou/reindeer and moose depend primarily upon concealment during the early weeks postpartum. They are called "hiders" (*Ablieger Typ*). A fundamental tactic employed is the postpartum "hiding phase" of periodic isolation (lying apart/abliegen) between infants and their siblings and mothers. Association periods are infrequent and short. In contrast, caribou/reindeer depend primarily on flight. They are called "followers" (*Nachfolger Typ*). Association between mother and young is continuous from birth onwards during infancy. Thus, it is possible to distinguish typical hiders from typical

followers by the amount of mother-infant association and the average spacing between them during the first weeks of life.

Moose, however, do not fit this dichotomization. Amount of association and average spacing are intermediate. Like hiders, moose infants are safeguarded by concealment, although not as thoroughly. For instance they are more, rather than less, exposed during isolation than during association with their mothers. Cows do leave their infants occasionally for up to an hour or so, but close contact is typical. Nor are the young well adapted for flight from danger. Instead, their safety is largely dependent upon the capability of their mothers to defend them from predators by combat and intimidation. Thus, they are called "defenders" (*Verteidiger Typ*).

Two major questions remain: (a) Why is defense not more thoroughly augmented by concealment — reducing the likelihood of combat with predators? (b) Why do moose not exhibit lying-apart? Is mother-infant isolation disadvantageous? Have moose evolved a different tactic, depending upon mother-infant association to conceal the young — such as perhaps inhibition of calf activity while the dam is resting? Is the mother more intensely motivated to protect her infant when she is with it? Dœs the first week or so of life constitute a sensitive period for types of learning that are promoted by maternal contact and guidance — such as perhaps, development of the mother-infant bond?

8) Moose give birth lying down and first nurse their calves in that posture. Within 1 or 2 days, however, the calves can suckle if their mothers squat. In a few days they can suckle when their dams stand. Suckling from between the mother's hindlegs occurs only during the first week. Thereafter, all suckling is from a flank.

9) Certain visible characteristics of the dam's nursing-invitation-stance release and orient suckling attempts, including her ventral outline and her color-shading patterns. The blond udder area and pink teats contrast markedly with surrounding areas of the body and legs.

10) Calves solicit nursing by vocalizing, tongue-flicking, making sucking mouth movements which produce sucking sounds and expose the bright pink gums and tongue in flashes, and by nuzzling the mother.

11) When cow-calf pairs nurse lying down, the calves terminate all bouts. When they nurse standing up, the mother does so in all instances after the first week. A cow terminates nursing by stepping forward, pulling her teat from the calf's mouth. Beginning in the third week, this is often accompanied by loud moan-like vocalizations which are mildly threatening to the calf.

12) During its first week of life, a Kenai calf was apparently in contact with the udder for at least 4,500 sec between the hours of 10:00 and 22:00 (ADT) each day. By the ninth week, this had dropped to about 34 sec per day during the same 12-hr period. This decrease of more than 100-fold in apparent nursing time does not reflect a proportionate decrease in milk consumption. Increases in flow rate, due to increased efficiency of sucking and letdown and decreases in non-sucking teat contact probably account for a significant proportion of the change, especially between the first and third weeks. Furthermore, the figures for the first week may have been exaggerated due to the difficulties of observing nursing while cow and calf were screened by vegetation.

13) The calf's desire to suckle and the similarities between the nursing-invitation-stance and alert-stance of its dam keep it highly attentive to her and pre-

pared to receive appropriate information in case of disturbance.

14) Calves may begin browsing and grazing as early as the first week postpartum but usually not until the second or third. They may be weaned as early as the second month or as late as the twelfth, but the fourth or fifth is more common. Some investigators feel that continued association with the mother through the first winter greatly increases the calf's chances of survival; this problem is under investigation in Alaska.

15) Disassociation between mothers and their calves may occur as early as the first winter, but usually not until the following spring or summer. The yearling is driven away when the new infant is born. Some become fully independent at this time. Others are allowed to reassociate with the dam and infant sibling after a few days or weeks, and may not reach independence until the following rut, when they are treated as sexual rivals by adults.

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CHANGES IN THE BEHAVIOR OF MOOSE WITH AGE AND DURING THE PROCESS OF DOMESTICATION

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Note de l'éditeur adjoint

E. P. Knorre et ses collègues ont entrepris leurs travaux sur la domestication de l'orignal *(Alces alces)* en URSS il y a presque 25 ans. Si on fait exception d'un bref compte rendu publié dans le périodique *Oryx* il y a quelques années (Yazan et Knorre, 1964), le fruit de ces travaux n'a jamais fait l'objet de publications en langue anglaise. Monsieur Knorre n'a pu prendre part aux assises du symposium, mais dans le texte qu'il nous a fait parvenir, il fait état brièvement de quelques-unes des expériences vécues durant les nombreuses années qu'il a consacrées à l'orignal. Le lecteur désireux d'obtenir plus de détails sur ces travaux ferait bien de consulter les deux volumineuses publications citées ci-dessous. Monsieur Knorre a pris sa retraite il y a quelques années, mais les recherches sur la domestication de l'orignal se poursuivent à la station de Pechora-Ilych sous la direction de M. V. Kozhukhov. En outre, Messieurs V. M. Dzhurovich et A. P. Mikhailov dirigent présentement des recherches intensives sur l'élevage de l'orignal en captivité à la Station agricole expérimentale Kostroma, URSS.

P. C. LENT

Note by Co-Editor

Work on the domestication of moose (*Alces alces*) has been carried out in the U.S.S.R. for nearly 25 years by E. P. Knorre and others. Very little information on this undertaking has appeared in English, aside from a brief article in *Oryx* some years ago (Yazan and Knorre, 1964). In his contribution to this symposium, Mr. Knorre relates briefly some of his findings from many years of work with moose. For further details, the interested reader may wish to refer to the publications cited below. Since the retirement of Mr. Knorre, the work at the Pechora-Ilych Preserve has continued under the direction of M. V. Kozhukhov. In addition, a second moose farm has been established at Kostroma Agricultural Experiment Station where an intensive breeding program is conducted and research is being carried out by V. M. Dzhurovich and A. P. Mikhailov.

P. C. LENT

Introduction

In this paper, I present material on changes in the behavior of moose which I have collected over 40 years, during the course of my observations of wild moose and my experimental work on moose domestication at the nature preserve «Buzulukskiy Bor» and in the Pechora-Ilych Nature Preserve. In both of these preserves, I also gained experience with wild moose which had markedly different behavior in comparison with that of moose on contemporary cultivated forest landscapes of the

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[1] Retired.

European part of the USSR. In cultivated forests, the wild moose has become a synanthropic animal during the past few decades and is well accustomed to its changed conditions of existence. These moose are no longer afraid of man because they now share common ground with him. During experimental work on moose domestication in the Pechora-Ilych Nature Preserve, I was able to come into contact with wild taiga moose which had not had the slightest contact with any of man's domestic activities.

Domestication of calves

Wild moose of all ages, as well as moose domesticated within four generations, were the animals investigated. During more than thirty years of the present century, 12 wild moose calves have been raised under domestic circumstances in the nature preserve Buzulukskiy Bor. On the experimental moose farm of the Pechora-Ilych Nature Preserve, 174 calves (61 captured from the wild and 113 from domesticated mothers) have been raised under domestic circumstances between 1949 and 1969.

The capture of wild moose of various ages has shown that there existed large differences in the behavior observed. Therefore, it is necessary to first examine behavioral changes with age in wild moose.

Up to the age of three days, a newborn wild moose calf displays no wildness and is not afraid of man. When its mother is out of sight, having run away from an approaching person, the young calf goes up to the person and begins to follow him as if he were its mother. This greatly simplified the capturing of calves in the taiga near the moose farm, since without any coercion they themselves followed quietly after a person, occasionally stopping to rest.

After a brief rest at the moose farm the newly captured calf was paired up, or given warmed cow milk in a nippled bottle from which it immediately began to drink greedily. After their first handling, calves are definitely as accustomed to being fed by a person as by their own mother. This associative training does not weaken with age and is one of the major stimuli causing grown domesticated moose to remain near the moose farm once they are turned out to browse in the taiga.

Moose calves captured from the wild at one week of age, already showed clear signs of being wild. They attempted to run behind their mother when she was running from an approaching person, and once captured, they would struggle to escape. To get them to the moose farm and to make them drink requires forcing, and only after repeated handling did the calf begin to drink cow milk more or less normally from a nippled bottle. Evidently, something in the behavior of the mother has been transferred to and has strenghtened in the week-old calf so that it behaves differently towards people, shunning them.

A two-week old calf is already so wild that it is difficult to capture and to feed with milk, and domesticating such a calf will require far more time. Month- and two-month old calves can be captured only while they are swimming across large rivers or with the help of special tracking dogs. We did not succeed in making them drink cow milk from a nippled bottle or out of a small bucket and they grew up only on green feed which is not good for their general physical development. It is never possible to domesticate them as well as calves captured from the wild in their first or second week of life.

Domestication of yearlings and adults

Domestication of yearling, two-year old and especially adult moose has been, in general, impossible, since they, as a rule die during capture from rupture of the cardiac mitral valve caused by nervous shock. The following incident illustrates this.

In the 1930's, I was charged with selecting a moose with large, handsome antlers for the Moscow Zoo from among those at Buzuluskiy Bor. At the time, we were retaining eight wild moose in a 100-hectare enclosure so as to use the newborn calves they produced in our domestication researches. Among them was a bull with peddle-shaped 7-pointed antlers, and we decided to capture him. Accordingly, a small 5-hectare corral was constructed beside the large enclosure, and within it along one of the outside fences a «trap» was built with a wide entrance and an narrow exit which connected to the door of a transporting pen. The entrance from the large enclosure into the small corral was left open all summer. During this season of the year, bull moose are solitary and when the desired bull wandered into the corral, he was isolated and the entrance was fenced off. A road upon which people drove and walked ran along one of the corral outside fences. This was done in order that the captured moose might begin to accustom himself to people while in the corral, so that he would be more calm during shipping. The moose was not driven into the trap, but was allowed to wander into it at will, and a man was assigned to close the entrance when he did so. At the beginning of August, one of our workers succeeded in doing this. However, when enclosed in the narrow trap with people standing by the fence, the moose's behavior changed remarkably. Contrary to our expectations, the moose made no attempt to escape through the exit. Instead, he stood in one spot, unmoving but shivering all over and breathing heavily while a thick, white froth ran out of this mouth. Since it was evident that the moose was on the brink of a nervous collapse, all the people around the trap were sent away and only I remained in a concealed place to observe the animal's final actions. No more external disturbances occurred after the people left. The moose's breathing became increasingly labored, and the froth from his mouth became first pink, then red in color. After 15 — 20 minutes, he began to sway and suddenly fell on his side, twitched his legs a little and became quiet. When I approached him he was already dead, with no heartbeat. A special committee consisting of a veterinarian and two veterinary officers performed an autopsy on the dead moose and concluded that he had died of a ruptured mitral valve caused by nervous shock.

In our experience, there are analagous cases which corroborate the impossibility not only of domesticating adult moose but also of even capturing them, since they usually die during capture.

Thus, the wildest behavior is evident in the adult, while the newborn of even a wild moose lacks any indication of wildness and in its behavior is no different from a newborn domestic animal (a calf, foal, etc.). Therefore, for domestication and successful use in agriculture (meat and milk production, work) the newborn moose calf aged three to five days is most suitable. To rear such a wild animal under domestic conditions also calls for the least amount of effort.

Behavior of domesticated animals

The behavior of domesticated adult moose raised under domestic conditions since taken as calves from the wild reflects entirely the training and regimen under which they are used to being kept. Breeding under wild taiga conditions was the most simple and inexpensive method even for the domesticated stock and the training of wild moose calves was first directed toward possible year-round free pasturing (without a herdsman). Conditioned reflexes can be developed in domesticated moose by directing their training and definite holding regimen (from the first days of life), for example their tendency toward spring and autumn movements (under natural conditions in the northern taiga). This allowed us to keep our entire 30-head herd of domesticated moose in free-ranging forest-pasture year-round without any risk that the animals would revert to the wild and leave the moose farm area when wild moose in the region began their spring and autumn movements. During the cold part of the year, when most valuable green feed is absent, the free-ranging domesticated moose remained in the moose farm area and a minimal amount of moist feed (fodder root-crops and potatoes) was given to them in the yard of the moose farm daily or periodically. They came to the yard from the free forest pasture of their own volition at the established feeding time. This same feeding impelled the domesticated moose to return to the moose farm in the autumn after they had been in free pasture during the summer. The moose intended for meat production had their calves on the moose farm and were retained with their calves for ten days so that they became accustomed to people and then were released to free pasture in the taiga for the entire summer season. In the autumn, when green forage had disappeared, these moose and their half-grown calves were brought to the moose farm where they were given supplemental feed while their calves were trained to free pasture with the herd close to the moose farm.

To determine the possible domestic uses of moose on a farm, the domesticated moose were divided into three groups of productive animals: meat producers, milk producers (Fig. 1) and work animals (Fig. 2 and 3). The moose in each group were held under different regimens and given different kinds of training, so that their behavior also differed.

Figure 1. Milking a domesticated moose at the Pechora-Ilych Game Preserve.

The holding regimen for milk moose on the farm differed the most from the pattern for domestic animals, since they were closely associated with people and domestic surroundings every day. From the first months of life, a reflex of submission to man began to develop. For this, they were disciplined to the touch of human hands during drinking and feeding, they were rubbed and their nipples were pulled, and later they were trained to the halter, to stand in stalls and to walk on a lead. During their lactation period, milk moose were pastured close to the farm in the taiga, or adjacent to the farm, in a large corral. At the established times, the milk moose would of their own volition

Figure 2. Moose being used as a pack-animal in USSR.

come from free pasture to the farm, where they were fed moist and mineral feeds and where they could find refuge in the barns from the horse and warble flies *(Tabanidae)*. The milk moose adapted to this holding regimen very well and a few finally became so accustomed to it that they were very easy to handle.

The birth of a calf to a milkmoose occurred in the barn or in the yard of the moose farm. The newborn calf was taken from its mother immediately after birth and was bottle fed using its mother's milk. As a result of this change in the mother-calf relationship, after ten days the mother lost her innate instinct and did not allow the calf near her eventually refusing to nurse it. Evidently, the maternal instinct of the milk moose is transferred to the person who milks her: she becomes very attached to the latter so that at the established milking hours, she will of her own accord, come in from free pasture to the farm in order to be milked as if she were giving milk to her own calf. The following incident illustrates this situation.

Figure 3 Moose used as a cart-animal for hauling logs in USSR.

When the third calf of the domesticated milk moose «Maika» was born, it was decided to leave the calf with its mother for the filming of several scenes for an art film entitled «Story of the forest giant». However, after calving, Maika did not behave normally toward her calf: she did not begin to lick it, did not try to feed it, did not pay any attention to it and pushed it away and walked off from it to stand in the opposite corner of the pen which had been specially constructed for the film production. When the somewhat dried and strengthened calf managed with effort to approach its mother and moved as if to nurse, Maika suddenly began to strike at it with her front feet. The moose farm workers who were present rushed into the pen and carried the calf out, but Maika had struck the calf seriously and after several hours it died. After this, the woman who had been assigned to milk Maika the previous year approached the pen and the moose immediately ran to her with soft cries and tried to lick her face and arms through the fence. Then the woman entered the pen and began to milk Maika, who was continuing to express her maternal tenderness and attachment to her. It is still suprising, however, how quickly and completely the established reflex of innate maternal instinct was elicited with the aid of a human being.

Domesticated moose used as work animals have a particular character as a result of specialized training which has developed their reflex for submission to people and also conditioned the heart and entire nervous system of the animals for work. The behavior of these animals during transportation work is very significant: calm and obedient animals are always better workers than nervous and capricious ones. Therefore, the most calm animals were selected for work training. In this connection, it is of great importance for increased productive capacity that the male moose be castrated. In our work with moose as pack animals and in cart harness, the castrated males were always the most gentle and obedient as well as enduring and able workers.

Moose can easily become good farm draught animals for transportation work and their behavior in sleigh harness or as saddle animals in no way differs from that of a horse. In some cases, working moose proved even less easily frightened than horses and more obedient. This is substantiated by many years of practical experience on the moose farm in testing the working qualities of moose. We found, for example, that our best working moose Buyan and Ural were not, in contrast to horses, afraid to approach airplanes or machines, but calmly walked right up to them.

Despite all the positive changes occurring in moose behavior during the domestication process, there remains a negative aspect: the loss of their innate fear of predators, which is evidently a result of their daily contact with dogs. Domesticated moose become susceptible to attack by canine predators in the taiga because they allow them to approach and so, can be killed by them. This seems an inevitable consequence for all domesticated ungulates.

Conclusion

Thus, the possibility of directed changes in the behavior of moose means that this valuable inhabitant of our forests can be put to a much greater use for man than in the wild state. This opens broad new perspectives for the development of moose husbandry in the forest zones of the USSR a natural food base for our herbivorous domestic animals is not present.

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SEASONAL MOVEMENTS OF MOOSE IN EUROPE[1]

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Résumé

La distribution tant historique que contemporaine de l'orignal (*Alces alces*) de même que les mouvements de cet ongulé en Europe ont été reconstitués par une analyse de toute l'information publiée sur le sujet. On a ainsi documenté une récente extension de l'aire de l'orignal en Europe, en particulier vers le nord et vers le sud. Il semble, en définitive, que le mode de dispersion et les particularités historiques de la distribution, de même que la répartition fort irrégulière des aires offrant des conditions d'hivernage adéquates, soient les principaux facteurs expliquant l'existence de migrations saisonnières (sur de longs parcours) chez l'orignal.

Abstract

The history, present distribution and different movement patterns of the moose (*Alces alces*) in Europe were studied, mainly on the basis of the literature available. The moose has recently widened its range in Europe, especially to the north and south. The dispersal mechanism and distribution history, together with the uneven distribution of the winter food reserves available are concluded to be primarily responsible for the formation of the (long-distance) seasonal migrations of the moose.

Introduction

For centuries, the moose (*Alces alces* L.) has been of great economic importance for the human population in all parts of its range in Europe. Man has had the benefit of its flesh and hide. Its use as a draught animal, a milk producer, etc., has also been examined (Knorre, 1961; Krott, 1964). Especially during human famines, moose populations have been nearly or entirely extirpated in many areas, whereas in better times man has tried to reintroduce it into these same areas.

The present paper is a review of the history and movement patterns of the moose in Europe. It also contains previously unpublished data, especially from Finland.

History of moose in Europe

Since the last glaciation (Weichsel), the range of the moose has, at its widest, covered almost the whole of Europe excluding the Mediterranean area (Kurtén, 1968). The species was exterminated in the southern, western, and central parts of Europe, so that in the 13th century the southwestern boundary of its range lay in Prussia, Poland, and Hungary (Mela, 1900).

Mela (1900) reviewed the occurrence of the moose in eastern Europe in the 19th century on the basis of Russian re-

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[1] Report No. 37 from the Värriö Subarctic Research Station.

ports, mainly the account of Fr. Th. Köppen. Mela (1900) stated that in about 1850, the range of the species was at its minimum up to that date in the European part of Russia (Fig. 1). The only area where the moose population was said to be abundant was the eastern part of the administrative district of Novgorod. At the same time the species was very rare in Fennoscandia (Collett, 1911-12; Kujala, 1931; Sainio, 1956). Small populations survived, however, both on the Scandinavian peninsula (Collett, 1911-12) and in eastern Fennoscandia (Kujala, 1931).

In the 1860's and 1870's, moose populations began to increase. Protective measures and the decrease in the populations of its most important predator besides man, the wolf (*Canis lupus*), (Pulliainen, 1965), were said to be mainly responsible for this trend (Mela, 1900; Kujala, 1931; Sainio, 1956). In Finland, for instance, moose was protected by law in 1868. The Russian moose populations widened their range in all directions, but especially to the north and northwest. Finland received moose from Russia via the Karelian Isthmus and around the northern shore of lake Ladoga. Finland also received moose from Sweden in the north, across the river Tornionjoki; this expansion was made possible by the increase in the Scandinavian moose population at the same time (Collett, 1911-12).

At the beginning of the 20th century, the Finnish moose population again decreased (Kujala, 1931; Marvin, 1959). Small populations survived in the south-

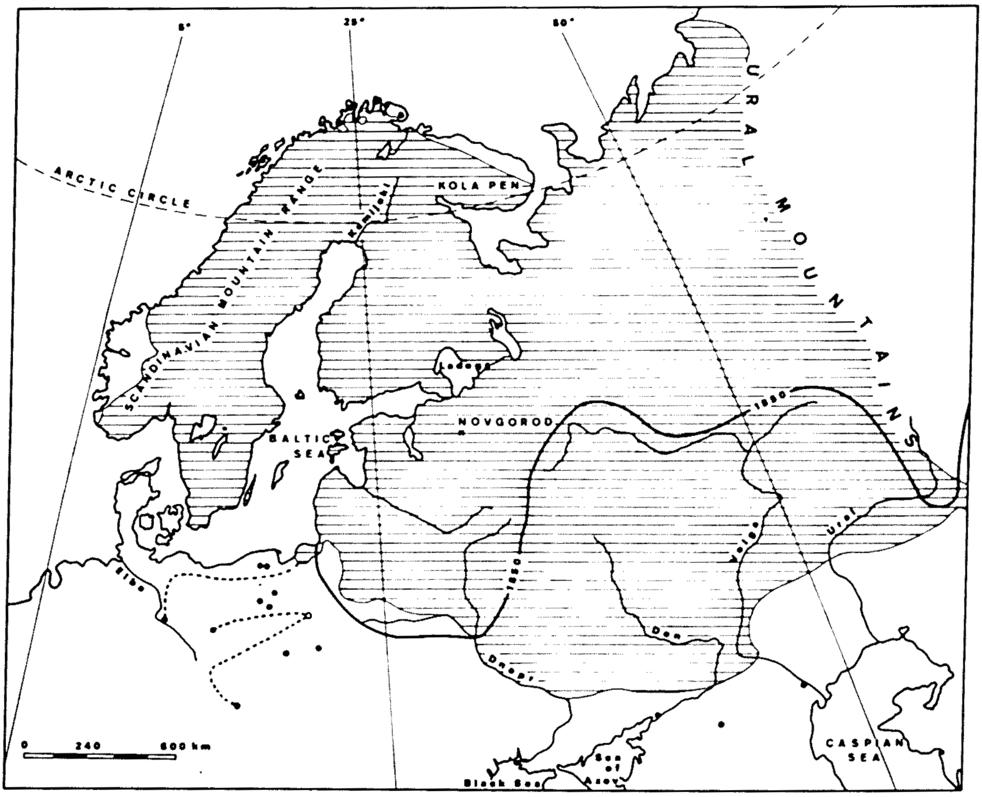

Figure 1. The present distribution (shaded) of moose in Europe, according to reports by Siivonen (1967), van den Brink (1968), Zhirnov (1969), Pielowski (1969) and Myrberget (1971) and the southern boundary of its range in about 1850. Open circle = Kampinos National Park in Poland, where moose have been reintroduced. Black circles = observation localities of wandering moose.

western and northeastern parts of the country (Sainio, 1956). The hunting which had begun in 1898 was stopped and, in 1923, the species was again protected. Petsamo, in the northeastern corner of Lapland, was the only area where licences could be obtained for shooting moose.

In the 1920's and 1930's, both the southwestern and the northeastern Finnish moose populations increased to some extent in number (Kujala, 1931; Sainio, 1956). In 1933, hunting of moose based on licences was begun, and has continued until now. Nowadays, the range of the species covers the whole country.

Since the Second World War, moose has widened its range in all directions in Europe. Figure 1 shows the present distribution of the species on this continent.

In Fennoscandia, the moose is absent only in rather small areas of southwestern Norway (Siivonen, 1967) and in the narrow coastal zone in the north (Siivonen, 1967; Myrberget, 1971). The species has recently shown a vigorous expansion to the north in the latter area (Myrberget, 1971).

In the northern part of the European U.S.S.R., the expansion of the moose to the north has led to the formation of a "tundra population" (Zhirnov, 1969). During the last 120 years, moose has widened its range in the southern parts of the European U.S.S.R. Nowadays it extends down to the forest steppe and steppe (Fig. 1). The species inhabits areas where only a few percent of the area is covered by forests (Zhirnov, 1969). Lone individuals have wandered in the neighbourhood of the Caspian Sea (Nasimovitch, 1961) and the Sea of Azov (Zhirnov, 1969). Some moose have even been observed in the northern Caucasus (Zhirnov, 1969).

Moose has also shown a tendency to widen its range to the west (Fig. 1). Lone individuals have been observed in Eastern and Western Germany, Czechoslovakia, and Austria (Heydenreich, 1961; Briedermann, 1971). An expansion of the moose population introduced near Warsaw, Poland, has increased the number of wandering individuals in both Poland and the above-mentioned countries (Heydenreich, 1961; Haber, 1964; Pielowski, 1969; Briedermann, 1971).

Movement patterns of moose

Buturlin (1934) stated that "moose is a naturally nomadic animal". My observations support this general statement. However, it might be reasonable to distinguish between the long-distance seasonal migrations on the one hand, and the wanderings of lone individuals and small groups of moose outside the continuous range of the species, and the more or less irregular local movements of the species on the other. The term seasonal migration is used to describe a phenomenon when at least dozens of moose move fairly regularly in the autumn (or early winter) along certain migration routes in a definite direction and towards a definite overwintering area which is at least 15-20 km away from the summer range. These then return in the spring, in the opposite direction along the same migration routes to the summer range.

In the following chapters the movement patterns of moose in Scandinavia, eastern Fennoscandia, and eastern Europe will be dealt with separately.

SCANDINAVIA

As far as I know, no reports have been published on the seasonal migrations of moose on the Scandinavian peninsula. Markgren (1972) has recently published data on the markings (103 individuals) and recoveries (19 individuals) of Swedish moose. Distances between the localities of marking and recovery generally varied between 0.6 and 22 km with one exception (a female calf travelled 118 km), indicating that moose tend to return to their original summer range.

Dr. Gunnar Markgren has kindly placed at my disposal the following observations on the movement patterns of the moose in Scandinavia: "It seems that in winter moose perform rather regular seasonal migrations from the highlands of the mountains down to the lowlands, to valleys and even to the coast of the Gulf of Bothnia. This can be seen very clearly in the mountains. In January and February, there are no moose at high altitudes in the mountains. Sometimes the moose gather in great herds in the valleys. The same phenomenon is very typical of the Norwegian moose populations. The behaviour of the moose population depends on the prevailing snow conditions. In winter 1965/66, when snow conditions were very severe, there were no moose in the Boda area (61°30′N, 17°00′ E) in the mountains, while a large number of moose was found on the ice of the sea and in the archipelago. In the valley of the river Ljusnans a total of 30 moose was found. On the other hand, if there is very little or no snow on the ground, moose stay at high altitudes in the mountains throughout the winter. In the 1960's, this was verified twice. In normal cases the winter movements of moose are characterized by gradual movement, at most 5-6 km without rest, from one place to another. The maximum distance between the autumn and winter quarters of moose on the coast is 30 km."

EASTERN FENNOSCANDIA

Vesterinen (1940) reported that moose of northeastern Finnish Lapland migrate seasonally. Since then, the behaviour of this moose population has been studied by the present author and his collaborators (Pulliainen and Loisa, 1967). Semenov-Tian-Shanskii (1948) studied the migrations of the species in the adjacent Lapland Game Reserve, Kola Peninsula.

Northeastern Finnish Lapland

In 1966-1972, I studied the movement patterns of moose in northeastern Finnish Lapland. Because only the preliminary results of these studies (Pulliainen and Loisa, 1967; Loisa and Pulliainen, 1968; Pulliainen, Loisa and Pohjalainen, 1968) have been published so far, some detailed data are given here.

The study area in northeastern Finnish Lapland is surrounded to the north and east by the frontier between Finland and the U.S.S.R. The border guards have made daily records of the crossings and other movements of moose in the neighbourhood of the frontier.

In the autumn of 1966, the movements of known moose groups were observed daily. During the last days of October, moose started to migrate northwards. The observations of migrating moose made by the skiing patrols on November 1, 2 and 9 are shown in Figure 3. On the observation lines III-VIII, the bulk (30 individuals) of moose were migrating northwards or northwestwards, only three moose moving to the south, while on observation lines IX-XI, 14 moose were going northwards and 12 southwards. The real migration direction of each moose which had crossed the observation line was checked by tracking it 1-2 km. At the beginning of November, the depth of the snow varied between 3 and 14 cm at observation stations I-VI, and between 25 and 38 cm at observation stations VIII-XI. Thus the bulk of moose were migrating towards areas with greater snow depth.

In the autumn of 1966, moose were also tracked individually. The observators skied along the tracks of the moose without disturbing them. The tracks were selected at random. The trails of the moose examined are shown in Figure 4. In observation areas I-II, two moose had gone east; in this area many moose crossed the frontier while moving eastwards. In observation areas III-VIII, some moose had gone rather directly northwards, while some had made a lot of curves in their movements. In observation areas IX-XI, moose had moved in many different directions.

In the autumn of 1967, the moose migration began in late October, as in the previous autumn, but the melting of the snow in early November prolonged the migration so that the last individuals were observed migrating northwards in February.

In the autumns of 1968-1972, the timing of the autumn migration of moose was studied at the Kotala observation station (Fig. 4). The observation line (1.3 km long) lies in the east-west direction on the northern shore of the river Kuolajoki. Moose can also be seen from a high tower which is situated at the east end of this line. The results are presented in Table I. The slow freezing of the river may sometimes retard the migration of moose to the north, as the animals cross the river over the ice. The earliest dates in the autumn when migrating moose were observed to cross the observation

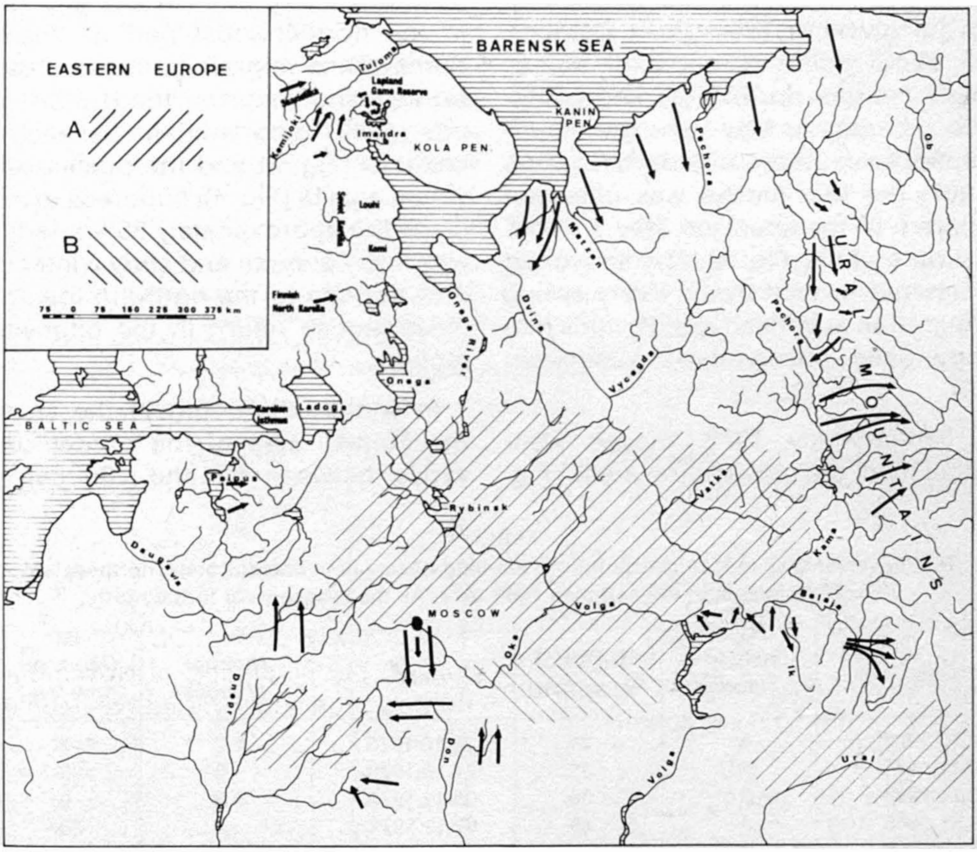

Figure 2. The directions and theoretical maximum length of the autumn migrations of moose in eastern Europe. Shaded area A: area where no seasonal (long-distance) migrations of moose were known in the 1960's (according to Zhirnov, 1969); Shaded area B: area where man's disturbing activities resulted in remarkable movement of moose in the autumn during the 1960's (according to Zhirnov, 1969).

line varied between October 5 (1969) and November 20 (1972) in the different years. Snow depth varied correspondingly between 3 and 38 cm. On October 12, 1969, five moose were seen moving northwards on the snowless ground. It is noteworthy that in the autumns of 1966-1972 no moose were observed to cross this observation line when moving southwards.

In 1968-1972, the crossings of a six kilometre-long observation line by moose were recorded every Sunday during the snowy season of the year (October to the beginning of June) in the Värriötunturi fell area and the neighbouring forests (Fig. 4). The total numbers of moose and moose groups observed to have crossed this line (in the east-west direction) are given in Table II. In October-April, about equal numbers of moose crossed the line northwards and southwards, whereas in May-June the majority of moose moved south. In the spring of 1967, the first moose was observed to migrate to the south on May 3 in observation area IX (Fig. 4). The snow had then started to melt away. Every spring the migration advanced rapidly; this had already been observed by Vesterinen (1940).

In January-May 1972, moose were counted in all the observation areas (Fig. 4) from a helicopter, an aircraft, snowscooters and during skiing trips. In observation areas IX-XI, a total of 80 moose was observed (density about 0.05 moose/km²), while in observation areas I-VIII, only 24 moose (density about 0.01 moose/km²) could be found. In October-December 1972, 74 moose were observed in the first area. The largest herd consisted of 24 moose. The true density of the moose populations is believed to be higher than the census figures mentioned. However, it is believed that the relative winter densities of the moose populations in these two areas are truly represented by the above figures.

The main wintering area of the moose of northeastern Finnish Lapland is thus in the northernmost part of this area. Some of the migrating moose cross the frontier and winter in the U.S.S.R. Zhirnov (1969) reported that between lake Imandra (Fig. 2) and the present observation area IX (Fig. 4), hundreds of moose cross the approximately 35 km long railway every autumn and early winter when they migrate to the north. In the spring, these moose return in the opposite direction.

In winter, the depth of the snow on the Finnish side of the border usually varies between 60 and 100 cm. Pine

TABLE I

The movements of moose across the 1.3 km long observation line at Kotala, northeastern Finnish Lapland, in the autumns 1968-1972. All the moose went to the north

Date	*Number of moose*	*Depth of snow (cm)*	*Date*	*Number of moose*	*Depth of snow (cm)*
28.10.1968	4	21	22.10.1970	2	3
06.11.1968	2	35	24.10.1970	3	3
08.11.1968	3	36	05.11.1970	3	6
21.11.1968	4	40	02.11.1971	4	20
05.10.1969	3	2	06.11.1971	3	22
12.10.1969	5	0	20.11.1972	8	38
30.10.1969	1	5	22.-23.11.1972	5	38
02.11.1969	2	5	03.12.1972	1	38
13.11.1969	3	12			

(*Pinus silvestris* 47%), juniper (*Juniperus communis* 24%), and birch (*Betula* spp., 22%) are the main winter food items of moose in this area (Pulliainen, Loisa and Pohjalainen, 1968).

Some moose in northeastern Finnish Lapland do not migrate to the northern wintering area. Because moose have not been individually marked and followed, we do not know the history of their movements. However, in some cases, we felt sure that the same individuals inhabited a certain area throughout the year. For instance, in 1966-1967, two moose inhabited the same locality in observation area V (Fig. 4). Willow shoots (*Salix* spp.) comprised half of the food consumed by these moose (Loisa and Pulliainen, 1968).

The present observations agree very well with the findings of Vesterinen (1940), which means that the general characteristics of the movement patterns of the moose in northeastern Lapland have remained unchanged during the past 35 years.

Other parts of Finland

The moose which spend the summer in northwestern Finnish Lapland are known to ford the Muonionjoki river (68°00′N, 23°40′E) in the autumn, on their way to Sweden to winter, and to return the same way in the spring (Mr. Arto Tolonen, pers. comm.). Unfortunately, however, no exact data on the length nor on the timing of these movements are available.

Sainio (1956) and Pulliainen, Loisa and Pohjalainen (1968) reported that the moose of western Lapland migrate to the east and northeast, to winter in the Saariselkä fell area (68°-69°N, 27°-29°E). In the late 1960's, an artificial lake was built on some of the migration routes of these moose. During the period 25 Octo-

TABLE II

The movements of moose across the 6 km long observation line in the Värriötunturi fell terrain, northeastern Finnish Lapland, in October-June 1968-1972. The recordings were performed every Sunday on the basis of the tracks in the snow

Month	*Number of units consisting of single specimens and groups which moved to*		*Total numbers of moose which had moved to*	
	the north	*the south*	*the north*	*the south*
X	14	16	23	22
XI	12	11	22	22
XII	3	4	5	6
I	9	7	20	15
II	9	7	14	10
III	4	5	6	6
IV	2	4	3	7
V	2	12	2	16
VI	0	1	0	2

ber to 2 November 1972, two female and two male moose, which had come from the southwest and were probably travelling to the Saariselkä fell area, went through the ice and were drowned in the same area (Pahtavaara; 68°05′N, 27°15′E). We lack more exact knowledge of the timing of these movements. Moose overwinter in the valleys and on the slopes of fells, often feeding in pine stands (Pulliainen, Loisa and Pohjalainen, 1968).

Sainio (1956) reported that moose which spend the summer in northern Karelia (62°30′-63°30′N, 30°-31°30′E) migrate about 100 km eastwards to their winter quarters in the autumn. Marvin (1959) reported that the directions of the autumn movements of moose in different parts of the Soviet Karelia (62°-66°N, 30°-36°E) are as follows: in Louhi (66°N, 33°E) to the east, and in Kemi (65°N, 34°E) to the west.

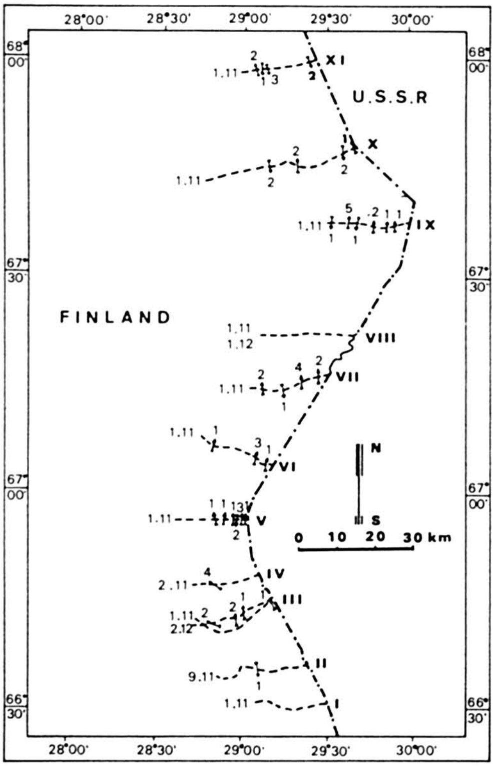

Figure 3. The observation lines I-XI in northeastern Finnish Lapland and the crossings of these lines by moose in late October and early November, 1966. Arrows indicate the directions of movements and figures, numbers of moose observed.

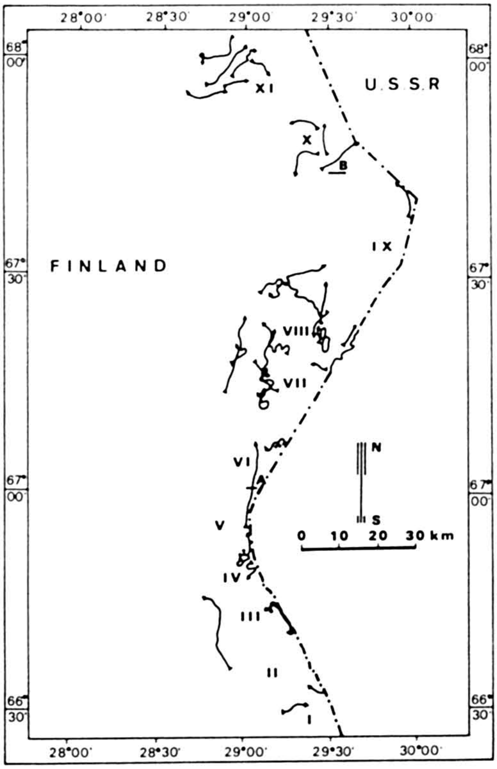

Figure 4. The observation areas I-XI in northeastern Finnish Lapland and the trails of moose tracked in this area in the autumn of 1966. A = observation line at Kotala. B = observation line in the Värriötunturi fell area and its neighbouring forests.

Twenty to thirty moose spend the summer on the four square kilometer island of Halsö, off the coast of western Finland (62°50′N, 21°15′E). In October-December, moose swim from this island to the mainland. The length of the swimming trip varies from dozens of metres to hundreds of metres. Moose winter 10-15 km inland from the lakeshore. The depth of the snow is the same on the island and on the mainland. In May, when the ice has melted, the moose swim back to the island where, in some years, a number of moose have wintered.

Sainio (1956) mentions that in other parts of the western coast of Finland the length of the autumn and spring migrations of moose varies between 10 and 60 km.

In the archipelago off the southern coast of Finland (*e.g.* on the Isle of Pettu, 60°05'N, 22°55'E), moose move between the islands and the mainland in the summer and from one island to another in the winter (Mr. Kaarlo Nygrén, pers. comm.). In the summer, cows with calves seem to be more stationary than bull moose.

In eastern Fennoscandia, moose prefer the shores of brooks, rivers, ponds and lakes and other moist places with abundant and rich vegetation as their summer habitats (Sainio, 1956; Marvin, 1959). They also feed on aquatic plants. In the autumn, moose move to harder ground. Stands of pine saplings, willow thickets, forest edge, meadows and fields are their favourite winter feeding habitats (Kangas, 1949; Yli-Vakkuri, 1956; Sainio, 1956). Thus there is a clear change of habitat both in the autumn and in the spring; that, of course, means movements from one place to another. The distances travelled and the directions of the movements seem to vary a great deal from area to area and from year to year.

Lapland Game Reserve

The following review on the moose migrations of the Russian Lapland game reserve (67°40'-68°05'N, 31°40'-32°40'E) is based on the report of Semenov-Tian-Shanskii (1948). A map which shows the places mentioned is to be found in the original paper by Semenov-Tian-Shanskii (1948).

The bulk of moose in the Kisloretsk area migrate to the southwestern part of the game reserve every autumn, only a small part of the population spending the whole winter in the valley of lake Vite. The moose use two routes during their migrations (see Fig. 2), some of them going straight over the ridge of the Tshuna tundra (about 15 km), and the others going around the southeastern edge of this mountain (about 30 km). The moose leave their summer habitats in November and December, and return in May. Very deep snow in the summer habitats (Kisloretsk) is regarded as the main cause of these migrations, although the lack of winter food in this area may also play its part. However, the timing of the migration cannot be regarded as solely dependent on snow depth. Some moose start to migrate when the first snow covers the ground, while others wait in the summer habitats until the snow depth has reached 60-70 cm. Moose return to their summer habitats when the snow is melting away and when there are already snowless places on the ground.

In the southwestern part of the game reserve, the migration of moose takes place in the same way as in the southeastern part of this area, i.e. moose start to migrate from the slopes of the Nävka mountain to the south in November-December. A small number remain and winter in the valley of the Kupes river. The moose of lake Nävka migrate westwards to the Vuva river (Fig. 2).

EASTERN EUROPE

The following review of the movement patterns of the moose in eastern Europe is based on the reports of Nasimovitch (1955), Yazan (1961) and Zhirnov (1969). Figure 2 shows the directions and theoretical maximum lengths of the autumn migrations of moose, and the areas where no seasonal migrations of the species have been reported so far. It must be emphasized that, as far as I know, markings and long-distance trackings of moose have not been carried out in great numbers in eastern Europe. I therefore speak of the theoretical maximum length of the migrations.

In the summer, in the northernmost part of eastern Europe, moose inhabit the tundra of the seashore, even as far as the Kanin peninsula. Moose may also move along the shore line in the summer. This area does not offer enough food for moose in the winter. The only logical direction of autumn migrations in this case is south (or southeast and southwest). The migrations are best known in the area of the Metzen river. They began in the 1950's when the so-called "tundra population" of the moose was formed as a result of the expansion of the animal to the north. In general, the diameter of the migration area is about 100 to 120 km. The longest migrations in the northeastern part of this area extend over 200 to 300 km.

The movements of the moose in the area of the river Pechora and its tributaries are very well known (see the review by Yazan, 1961). In the 1920's and 1930's, when the density of the moose population was very low, the seasonal migrations of the species ceased. Since 1945, when the moose population reached extraordinarily high figures, the migrations were resumed again.

The sooner the snowfall and the earlier the river freeze-up, the earlier the autumn-winter migration occurs, enabling the animals to cross the stream. The sooner the snow cover reaches the critical depth of 70 cm, the sooner ceases the moose migration. Thus, the beginning of the autumn-winter migration depends on the timing of the freeze-up and its cessation is correlated with critical snow depth. Yazan (1961) stated that the autumn migrations of the moose in this area occur as long as the carrying capacity of the winter pastures remains considerably greater than that of the summer pastures. Moose direct their migration not to an area with a low snow cover, but in the first place to an area where more food is available. In some areas both of these factors are present. The migrations of moose are noted for their uniformity as far as the routes they select in their translocation are concerned; year after year, the animals follow the same path.

Within the area of the Pechora river moose migrate in the autumn in two directions: 1) from north to south, and 2) from west to east. The former group of moose spends the winter in the pine forests of the middle and southern subzones of the taiga, where there are abundant pine-birch second growth stems which form the main staple winter food for the animals. The latter group spends the winter in the coniferous forests in the foothills and in the mountains (the western approaches of the Ural mountain range) where food plants [Siberian fir (*Abies sibirica*), mountain ash (*Sorbus aucuparia*), etc.] are abundant, provide high quality food, and are within reach of moose in spite of the high (up to two metres) snow cover.

According to Yazan (1961), the fact that moose migrate in different directions is apparently due to the peculiarities associated with the availability of winter food. The moose migrating in the coniferous forest region were accustomed to feed mainly on the pine-birch second growth in winter, whereas the moose from the foothills and mountain areas became accustomed to feeding on Siberian fir and mountain ash secondary growth. Nevertheless, while having different winter feeding grounds, the moose from the coniferous forest and foothill regions make use of common pastures in summertime.

Usually the spring migration occurs from the end of April or the beginning of May to the end of May. As soon as the snow has settled to a depth of 50-

60 cm, moose at once begin their movements northwards and westwards, to the location where they fatten up during the summer and mate in the autumn. Bulls, the strongest animals, with great endurance, are the first to begin this migration, whereas pregnant moose and cows with newly-born calves and yearlings are the last to complete such a migration. In contrast, during the autumn-winter migration the first animals to start moving are cows with their calves, whereas the last to complete the migration are the large bulls and moose cows without calves. Moreover, if in the autumn, during the first phase of the migration, moose move singly or in small groups, and towards the end of the migration only in groups of several heads each and along beaten tracks, then in the spring the opposite picture is observed: moose first move in large herds along beaten paths, and towards the end of the migration, after the snow has melted, in small groups or singly.

In the spring moose move throughout the day and night, as long as air temperature remains above freezing point, along the same routes as they do during the autumn-winter period, but in the opposite direction. The spring migration lasts 10 to 20 days, while the autumn-winter migration lasts 40 to 80 days.

Seasonal migrations of moose also occur in the middle and southern parts of the Ural mountain range between 53° and 61°N.

Moose which spend summer on the western slopes of the mountains regularly migrate east to winter on the eastern slopes and low lands of the Ural, where snow cover is not as thick as it is on the western slopes of these mountains. Moose cross the mountains along the valleys. The length of the migrations vary between 50 and 150 km. The migrations usually take place in November and December and, in winters with little snow, they may be interrupted until February. Moose cease to migrate when snow-depth reaches 50 to 60 cm. Migrating moose cross streams in certain places and use the same migration routes from year to year.

It is noteworthy that Zhirnov (1969), in his recent review of the migrations of the moose in the European U.S.S.R., does not confirm the statement of Koslovskii (1960) that the lengths of the migrations of the moose of the Ural mountains exceed 1000 km.

Moose which spend the summer in the neighbourhood of the city of Moscow migrate southwards to the other side of the Oka river. Along the upper courses of the Oka and Don rivers there are autumnal migrations of moose, both westwards and northwards. In the area east of the bend of the Volga river (in the areas of the Vatka, Kama and Ik rivers), moose migrate to the south, north and northwest in the autumn.

Seasonal migrations occur around the upper courses of the Dnepr and Daugava rivers. Moose which spend summer in the neighbourhood of the eastern shore of Peipus lake migrate eastwards in the autumn.

In the southern part of the range in eastern Europe, in the districts of Tambova, Lipetsk, Kursk, Kuibychev, Saratov, Rostov and Ukraina, moose spend the winter in the forests and in summer inhabit small forests, the edges of bogs and even corn fields on the open steppe.

In the districts of Rjasan, Mordova, and Kuibychev, man's disturbing activities have affected large-scale movements of moose from one area to another, especially during the fall hunting season (Figure 2, Area B).

In the districts of Brjansk, White Russia, and Tatar, and in the Baltic countries, the exhaustion of food reserves has been accompanied by mass emigrations from the winter quarters.

Discussion

Several theories concerning the primary causes of the seasonal migrations of moose have already been put forward. Semenov-Tian-Shanskii (1948), Nasimovitch (1955), and Heptner and Nasimovitch (1967) attribute the extensive migrations of moose to a variable snow gradient, the animals moving to regions with thinner snow during the winter. Marvin (1959) mentioned that some of the following factors are responsible for the seasonal movements of moose: 1) uneven distribution of food plants during the different seasons; 2) depth of snow (especially in late winter); and 3) shelter (against harmful insects in summer, cold and strong winds in winter, etc.). Yazan (1961) stated that the migrations of moose in the basin of the Pechora river are brought about not so much by the depth of snow covering the ground but rather by the state of the feeding base, i.e. the amount of food available per unit area. However, he verified that in some areas both a low snow cover and a lot of food are present, and yet, moose movements are observed. I believe that besides the depth of the snow and the availability of winter food, the historical background and the population dynamics of moose populations must be taken into account when discussing the possible causes of their seasonal migrations.

In the 19th century, moose was exterminated over vast areas of Europe, only a few population nuclei surviving. The present moose populations of this continent are offspring of these moose. During the past 120 years, the animal has reinvaded most of its former range in the northern and eastern parts of Europe. Population pressure, which takes the form of an increase in fighting during the rutting season and an increased tendency to emigrate (Pielowski, 1969), and/or lack of food during the critical season have probably promoted the expansion of moose to "new" areas. Dispersion of the moose has in principle taken place in all possible directions. It is, however, possible that the "new" areas inhabited in this way offer the moose living conditions only during a certain part of the year. Moose have then had to move to areas where they can find enough food during the rest of the year. Markgren (1972) has recently shown that moose tend to return to their original (summer) home range. Thus, it is likely that moose returned to the starting area along the same route that they used during the expansion phase of their movements. Following its mother, the calf does learn the traditional migration route. The transmission from one generation to the next of such a traditional movement is further enhanced by the long life-span of *Alces*. In northeastern Finnish Lapland, Dr. Ilkka Koivisto (pers. comm.) recorded a maximum age of 16 years.

The migration system of moose from a given area can be expected to be maintained so long as the offspring of the moose which formed this system are alive. If this population is destroyed, the secondary formation of a similar migration system is naturally possible, provided the natural conditions of the area have remained unchanged.

It is noteworthy that in many areas of Europe the summer and winter habitats favoured by moose are side by side. Moose can thus find suitable summer or winter habitats by moving as little as from some hundred meters to a mere few kilometers. In many cases, these seasonal movements are unnoticeable in nature. The use of certain definite routes in such cases would hardly be of survival value for the moose population, whereas when the summer and winter habitats are located a long distance (up to 300 km) away from each other the use of traditional migration routes by moose must be of great survival value.

The experiences gained so far in the different parts of Europe and described above seem to support rather well the above-mentioned theory on the development of the seasonal migration system in moose. Usually, both migratory and resident moose occur in the same population. During the expansion phase of a population, some animals usually remain stationary. In the autumn, moose from the same summer habitats outside the tundra zone migrate in more than one direction. All possible compass directions are represented among the migration bearings. The winter quarters of moose are characterized by their sufficient food reserves, but not necessarily by low depth of snow. With a considerable decrease in the moose population (Pechora), migrations gradually ceased, and when the population density increased, migrations were resumed again. In many areas of eastern Europe the seasonal migrations of moose were first observed when the density of moose populations reached a critical threshold in the 1950's.

The wanderings of moose to the tundra and steppe, their use of alpine and subalpine heaths on the fells as migration routes, and their occurrence at high altitudes on the mountains in summer (e.g. in the northern Ural, Yazan, 1961) show that the species has an effective dispersal mechanism. Actually, moose has very succesfully reinvaded vast areas of Europe which it had lost during the first half of the 19th century, although man has thoroughly changed the structure of the landscape in many areas, especially since the Second World War.

The diameter of the migration area of moose may be as much as 300 km. Thousands of moose may take part in the seasonal migrations along certain routes. Although the breadth of the movements of moose are usually smaller than those mentioned above, we must take them into consideration when planning measures for both active and passive moose management. For these and other purposes the movement patterns of moose must be examined throughout the range of the species by individual markings and trackings (e.g. by radiotelemetry; see van Ballenberghe and Peek, 1971), and censuses. We also need this information for sylvicultural purposes. Russian scientists especially (e.g. Kochetkov, 1960; Koslovskii, 1960; Zabolotskaia, 1961; Kaletskaia, 1961; Koriakin, 1961; Nikso-Nikochiu, 1962) have studied the resistance of pine plantations to moose damage which can naturally be caused by both migratory and resident individuals.

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MOOSE MIGRATIONS IN NORTH AMERICA

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Résumé

L'auteur passe en revue la documentation décrivant les migrations, les mouvements locaux et les modes de dispersion de l'orignal (*Alces alces*) en Amérique du Nord. Le domaine vital saisonnier typique est de faible superficie (5-10 km^2) et les mêmes superficies sont occupées d'une année à l'autre par les mêmes individus. Les mâles d'un an et les mâles en rut peuvent, dans certaines régions, occuper un domaine vital moins rigoureusement défini et plus vaste. Les déplacements d'un domaine vital saisonnier à un autre (migrations) comprennent trois types principaux : le type A (les déplacements de ce type se font sur de courtes distances et sans changement d'altitude), le type B (les déplacements permettant de relier deux domaines vitaux saisonniers sur des distances longues ou modérées et impliquant le passage de quartiers d'été et d'automne en altitude à des quartiers d'hiver à faible altitude sont de ce type) et le type C (les mouvements couvrent des distances modérées ou longues reliant trois domaines vitaux saisonniers distincts et impliquant des changements considérables d'altitude). On peut observer plus d'un type de mouvement en une même localité, ce qui peut donner lieu à des regroupements ou à des fractionnements de certaines populations. Les migrations se font ordinairement en empruntant des tracés traditionnels mais le moment de la migration peut varier quelque peu. Les conditions d'enneigement, la qualité des ressources alimentaires ainsi que certains stimulus internes influencent ces déplacements saisonniers. En général, les migrations de faible amplitude sont contenues à l'intérieur d'un habitat sans relief et sans grande diversité biotopique, mais la distance tant physique qu'écologique entre les quartiers saisonniers reste variable. En Amérique du Nord, les migrations régulières décrites s'étendent sur des distances allant de 1 à 170 km. Il arrive que l'orignal envahisse de nouveaux milieux mais un traditionalisme prononcé dans le choix du domaine vital et des routes de migration contrecarre cette tendance. Dans bien des cas, des mouvements de dispersion observés sur une petite échelle peuvent n'avoir été que le résultat d'un accroissement numérique de la population locale. Les migrations de l'orignal lui permettent de se maintenir, en toutes saisons, dans un environnement optimum tant aux points de vue physique, biotique que social. Il faudrait tenir compte de ces migrations avant de prendre des décisions affectant l'utilisation du territoire ou l'aménagement de la faune.

Abstract

Migrations, local movements and dispersals of moose (*Alces alces*) in North America are reviewed. Seasonal home ranges are typically small (5-10 km^2), and the same home ranges are occupied annually by individual moose. Yearlings and rutting bulls in some areas have larger and less fixed home ranges. Movements between seasonal home ranges (migrations) may be classified along a continuum including Type A (short distance movements between two seasonal ranges with little change in elevation), Type B (medium to long distance movements between only two seasonal ranges with significant differences in elevation between higher summer-fall ranges and lower winter ranges), and Type C (medium to long distance movements between three distinct seasonal ranges with significant changes in elevation). Several types of movements may occur in one area, resulting in aggregations and segregations of population segments. Migrations follow traditional routes, although timing may vary annually. Snow, forage and internal stimuli mediate seasonal movements. Physical and environmental distances between seasonal ranges vary, but generally the shortest migrations occur in flat habitat with little environmental gradient. Regular migrations of from one km to 179 km are reported from North America. Moose do disperse into new habitat, but traditions of home ranges and of movement patterns impede this dispersal. Many "dispersals" reported may in fact have been local population increases. Moose migrations provide optimal physical, biotic and social environments on a seasonal basis. Movement patterns should be considered prominently in decisions regarding land use and wildlife management.

Moose migrations in North America

Movements of moose (*Alces alces ssp.*) have long fascinated North American naturalists and scientists, but have been poorly understood until recently. Some early naturalists believed changes in abundance were actually mass migrations to and from large areas (e.g. Merrill, 1916; Heape, 1931). Others, perhaps correctly, believed that moose they observed remained life-long in one very small area (Seton, 1909, 1929; Bailey, 1930). Still others, unable to discern a pattern in recorded observations, concluded that moose were nomadic, their movements being without pattern during most of the year (Heape, 1931). Some observers recognized patterns of movement, and saw cause and effect relationships between movements and snow, rainfall, food quantity, food quality or even feces-tainted range (Heape, 1931; Hosley, 1949; Peterson, 1955). Only recently have more definitive studies in British Columbia (Edwards and Ritcey, 1956), Montana (Knowlton, 1960), Minnesota (Berg, 1971; van Ballenberghe and Peek, 1971), Wyoming (Houston, 1968), Ontario (Goddard, 1970), and Alaska (LeResche, 1972) revealed the true complexity of the migration phenomenon in moose.

Moose populations in North America vary from the extremes of sedentary to truly migratory. Every degree of migratory behavior in between the extremes seems represented on the continent. Differences in behavioral patterns are certainly correlated with habitat and terrain occupied, but may also be related to taxonomic form, annual variations in weather, and population structure. The central questions with regard to moose migrations are these: 1) How is migratory behavior, or lack of it, related to habitat, terrain and taxonomy? 2) What are the mediating causes of migratory behavior: snow, forage, internal stimuli? 3) What role does tradition play in movement patterns of individuals and populations? 4) What is the adaptive value of migratory behavior where it exists, and why is it absent from some populations?

This review considers migration in North American moose in light of these questions. Migratory behavior is defined as movement between separate seasonal home ranges, regardless of distance travelled. Local movements (within a home range) and dispersals into new areas and newly-created habitat are also discussed.

Local movements

The common denominator of an individual's use of space is its "home range", considered in this review to be the area in which the individual accomplishes its normal activities during a given period of time. "Home range" and related concepts of localized activity have been defined and redefined as often as any terms in animal ecology and behavior (Burt, 1940; Godfrey, 1954; Kaufman, 1962; Jewell, 1966; Mohr and Stumpf, 1966). My present definition ignores the fine points but allows comparisons between reported moose studies. Local movements occur within the home range. Home range may shift seasonally, and individuals may occupy more than one home range in a year. Territories, or defended areas, have never been reported for North American moose (Geist, 1963) with the possible exception of cows with calves (Altmann, 1958; LeResche, 1966).

SIZE OF HOME RANGES

Seasonal home ranges of moose are consistently small throughout North America. Casual observations and formal studies all have concluded that, regardless of how far moose habitually move between seasons, home range during a given season seldom exceeds 5-10 km^2. This is true in areas where moose migrate and where they are primarily sedentary; and in all habitats studied.

Peterson (1955) felt that moose in Ontario (*A. a. americana*) frequently passed a lifetime in an area of 32-800 km^2 (a radius of 2-10 mi). DeVos (1956) reported summer home range was about 6.0 km^2 for a cow with a calf occupying lowlands in Ontario, and Goddard (1970) characterized moose in similar Ontario habitat as having "relatively small" winter and summer home ranges.

Telemetry studies in Minnesota habitat characterized by low relief and mixed deciduous and deciduous-coniferous forests have confirmed very small home ranges in both winter and summer (*A. a. andersoni*): Berg (1971) and van Ballenberghe and Peek (1971) reported summer home ranges averaging 4.6-14.3 km^2 (the latter made 75% of their relocations within 2.6 km^2) and winter home ranges averaging 2.0 km^2. Van Ballenberghe and Peek (1971) observed an adult female that remained in a 2.4 ha area for 25 days in January and February. They concluded that "winter home ranges consisted of a series of (very small) high use areas connected by wanderings of various distances".

Moose (*A. a. shirasi*) in more mountainous areas of the western United States, similarly, have small home ranges. Houston (1968) and Knowlton (1960) studied seasonally migratory populations in Wyoming and Montana, respectively. In Wyoming, 24 of 25 moose studied had summer home ranges less than 3.8 km^2, and 35 of 39 had winter ranges this small. In Montana, summer home ranges varied between 2 and 8 km^2. Stevens (1970) also felt that moose he studied in another area of Montana were "relatively sedentary" in winter.

Alces alces gigas in Alaska have seasonal home ranges similar in size to those of other subspecies. Murie (1944) described an adult cow that spent most of her time throught the year in an area of 8 km^2 near a road. LeResche (1966) estimated summer home ranges of 4-5 km^2 for females with calves in one migratory population. Another migratory population had summer-fall above timberline home ranges of less than 32 km^2, and an apparently resident lowland population occupied home ranges year-round of less than 20 km^2 (LeResche, 1972 and unpubl. data).

SEX, AGE AND HOME RANGE SIZE

Collectively, studies to date indicate that calves and their attending cows have smaller home ranges for a short time following parturition than do other moose, and that yearlings have larger home ranges than other moose. Home ranges during rut seem to vary with the sex structure of the population.

Summer home ranges of cows with calves in various areas are summarized in Table I. Altmann (1958), McMillan (1954), LeResche (1966), LeResche and Davis (1971), and Berg (1971) documented extremely small home ranges of cows and new-born calves in Wyoming, Alaska and Minnesota. These home ranges seem to increase beginning when the calf is one to three weeks old (Berg, 1971; LeResche and Davis, 1971), until summer, summer-fall and winter home ranges are equivalent to those of cows and bulls. Houston (1968) and Saunders and Williamson (1972) could show no differences between size of seasonal home ranges of cows and bulls in Wyoming and Ontario. McMillan (1954), Peek (1962) and Berg (1971) found no differences between eventual summer home ranges of cows with calves and cows without calves. LeResche (1966) did note such a difference, but this was likely due to the fact that cows without calves began their fall migration during his observations. Knowlton (1960) suggested from scant evidence that bulls' summer home ranges were about four times as large as those of cows with calves.

Knowlton (1960), Houston (1968), Berg (1971) and LeResche and Davis (1971) showed that, during rut, bulls' movements on summer-fall range became erratic, and home range increased accordingly. This change is more properly considered a transition into another area of activity (i.e.: "rutting home range") than a true change in summer home range. Rutting home range of females may be a function of their abundance in the population relative to bulls (Houston, 1968). This idea is substantiated by my observations in areas of Alaska with very few bulls (circa 10-20 bulls: 100 cows): cows in these areas become much more active and mobile during rut than those described by Houston in Wyoming, where bull:cow proportions approached 81:100.

Data on yearling home ranges are limited and contradictory, but do suggest they may be larger than those of older moose. Seton (1909) believed young bulls wandered erratically over a wider area than mature animals. Houston (1968) maintained yearling moose in Wyoming had no "established" home ranges and moved further and more erratically than older animals. Pimlott (1959) and Simkin (1965) showed that, in Newfoundland and Ontario, yearlings were more vulnerable to hunting than other moose, and suggested larger home ranges might be a contributing factor. However, Saunders and Williamson (1972), in Ontario, found no significant difference related to age in linear movements of tagged moose.

Especially in light of the contrast between individual constancy of home ranges in adult moose and the species' tendency to disperse and explore (below), it seems logical that young moose

TABLE I

Homes ranges of moose cows with calves — Modified from Berg, 1971 —

Locality	*Time interval*	*Home range area (km²)*	*Reference*
Montana	6 July-23 Sept.	2.2	Knowlton, 1960
Wyoming	6 June-15 Sept.	5.1	McMillan, 1954
Ontario	15 Aug.-31 Oct.	6.0	DeVos, 1956
Minnesota	11 June-22 Aug.	5.9	van Ballenberghe & Peek, 1971
Minnesota	15 May-1 Oct.	15.4	Berg, 1971
Minnesota	15 May-1 Oct.	16.9	Berg, 1971
Alaska	6 June-31 Oct.	8.4	LeResche, 1966

should have larger home ranges (or broader local movements) than older animals. This remains to be confirmed by more precise studies, however.

TRADITION AND HOME RANGES

Moose in all areas of North America tend to return to the same individual home ranges year after year. Since Seton (1909) spoke of moose's "judgement founded on their memory of the country", study after study has confirmed traditional use of the same areas by the same individuals, and suggested that patterns persist over several generations.

DeVos (1956) observed a tagged calf returning as a yearling to the area of its birth after a winter's absence. Knowlton (1960) noted that the same concentration areas were used each winter in mountainous areas of Montana. Geist (1963) recognized that individual moose returned each year to their "accustomed summer range" in British Columbia.

Houston (1968) confirmed strong individual tradition among Wyoming moose. His study included both Type B and Type A populations (see below for definition of these categories) and demonstrated that marked individuals from the Type A group returned year after year to permanent summer home ranges. He believed that the Type B group, similarly, had permanent summer ranges. Specific winter home ranges were used annually by members of the Type A population. Type B animals were apparently less attached to specific winter ranges, although still traditional to a great extent. Twenty of 33 (61%) marked animals returned to established home ranges for at least two consecutive years. Five others (15%) returned only in alternate winters and the remaining 24% had not returned within one or two winters. Houston felt that the severity of winters influenced the return of the Type B group. Berg (1971) conclusively demonstrated that radio-marked moose in Minnesota lowlands returned to their established summer-fall and winter home ranges for at least two consecutive years: each marked individual (males and females were included) migrated annually between two established home ranges.

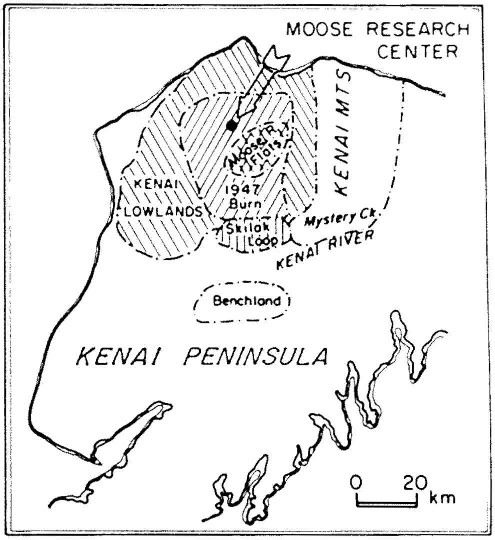

Figure 1. Locations of seasonal ranges on the Kenai Peninsula, Alaska.

Studies in Alaska since 1963 have confirmed strong traditionality in many areas by following marked calves and adults (Bishop, 1969a, 1969b; LeResche and Davis, 1971; LeResche, 1972). This traditional use is demonstrated both by populations (Fig. 1, 2) and by individuals (Fig. 3). Figure 2 shows seasonal locations over a 2.5 year period of collared moose from groups marked at various times of year in different areas of the Kenai Peninsula (Fig. 1). The figure includes moose from three migratory groups (a, b, c) and a predominately resident population (d). Each group concentrated annually in the area they were marked. At other times of the year, some groups were widely dispersed. Groups a, b and c represent animals with traditional autumn (rutting), winter and early summer (calving) ranges, respectively.

Individuals of each group had fixed spring, summer and autumn ranges (Fig. 3). These respective ranges were occupied at rather constant time intervals for the period of the study (LeResche, 1972).

Movements between seasonal home ranges

"Migration" is most commonly taken to mean regular annual movements of some distance, involving return to at least one common area during each annual cycle. The many regular shifts between seasonal home ranges reported for moose populations in North America are true migrations in this sense. Much confusion has arisen because not all populations are migratory, and because migratory and resident groups not infrequently occupy common areas during part of the annual cycle, and sometimes during rut. The interactions between migratory populations (or population segments) and resident populations (or segments) lead to seasonal aggregations and segregations, and therefore affect habitat relationships and population dynamics. Any consideration of the significance of migrations to moose populations must consider these factors.

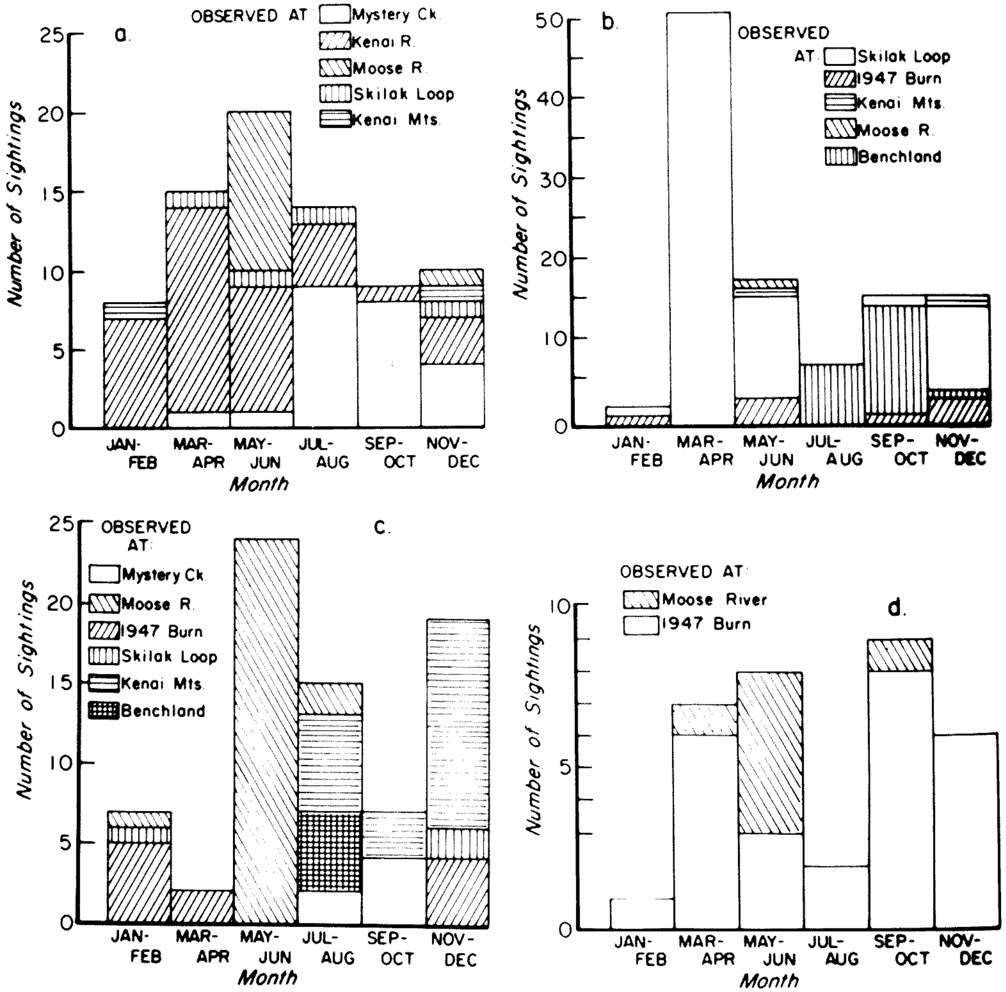

Figure 2. Bimonthly locations of groups of moose tagged at four locations on the Kenai Peninsula, Alaska: (a) marked at Mystery Creek in October, (b) marked at Skilak Loop in March, (c) marked at Moose River in May and June, (d) marked at 1947 burn in all months. (From LeResche 1972).

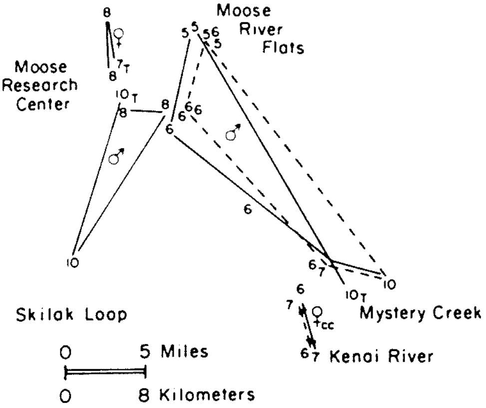

Figure 3. Migration patterns of two male and two female moose over a two-year period on the Kenai Peninsula, Alaska. "T" is tagging site, digits are month resighted (1=January, 12=December), "cc" indicates two calves present. (From LeResche, 1972).

All seasonal movement patterns reported for moose in North America represent one of three general types (Fig. 4): *Type A*, short distance movements between two seasonal ranges with little change in elevation; *Type B*, medium to long distance movements between two seasonal ranges with significant differences in elevation between high summer-fall ranges and lower winter ranges, and; *Type C*, medium to long distance movements between three distinct seasonal ranges with significant differences in elevation between high summer-fall ranges and lower winter and spring ranges. These types do not represent absolutely distinct patterns, but rather form a continuum (Table II). These patterns differ in timing and regularity, distance traveled, change in elevation involved, and number of seasonal home ranges visited annually. All represent seasonal oscillations between at least two areas or habitats, however.

TIMING AND REGULARITY OF MOVEMENTS

Timing varies between individual populations, and probably reflects differences in general seasonal climatic changes and habitats. In addition, timing varies year-to-year in some populations, perhaps reflecting annual climatic differences.

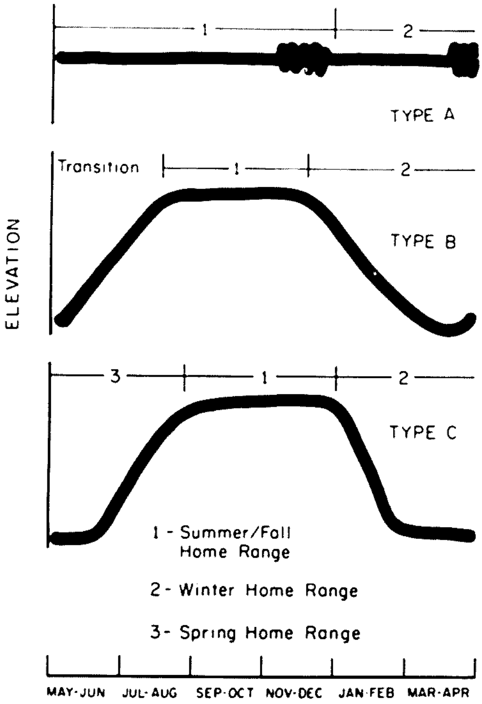

Figure 4. Types of moose migration patterns reported from North America. Broken line in Type A representation indicates periods of movement. "Transition" period in Type B may be longer or shorter than shown, and represents winter home range habitat.

Localized (Type A) populations in northwest Minnesota moved 2-6 km from summer-fall to winter ranges in late November, and all returned within a 10-day period in April in one spring (Berg, 1971). In similar habitat in northeast Minnesota, moose occupy a series of high-use winter areas beginning in January, and wander short distances between these areas until May-June when they become localized on summer ranges (van Ballenberghe and Peek, 1971). Wyoming moose, representing both Type A and Type B groups, move onto winter ranges from mid-December to mid-January, then return to spring-summer ranges from late March to mid-April (Houston, 1968). Type B groups have left this range by mid-June. More northerly groups with Type A movements (Kenai, Alaska: LeResche, 1972; and Tanana Flats, Alaska: Bishop, 1969) follow roughly the same schedule in their local movements.

Timing varies considerably annually and regionally among Type B and Type C groups. Moose in mountainous British Columbia move rapidly from late winter range to summer range in April (Edwards and Ritcey, 1956). Upward movement towards the summer range normally continues through July although a lull in movement (attributed to cold weather) sometimes occurs. In contrast, movement from upland summer ranges to lower wintering areas is normally a gradual process in this population, occurring from mid-September until abrupt upward movement begins again in April. Progression of the migration varies between years, perhaps due to differences in snow accumulation.

In Montana, moose from a Type B group first arrived at lowland winter concentrations between mid-December and mid-January and continued to drift slowly onto winter ranges as late a March (Knowlton, 1960). Return to summer range is more rapid, occurring mostly in May and June.

Two Type C populations in Alaska return to summer-fall ranges later than moose in Montana and British Columbia and remain on them for a shorter time. Movement to upland summer-fall ranges is gradual, in contrast to that in Montana and is not complete until the rut, in late September and October. Conversely, movement from upland ranges to winter ranges is sudden, and may occur as early as mid-November. This, too, contrasts with the slow winter-long descents described in Montana and British Columbia.

Movements in Interior Alaska (Tanana Flats) are similar in all respects to those at Kenai, except that ascent to summer-fall areas may not be detectable until as late as early September. In both locations in Alaska, timing of the precipitous autumn downward migration varies year-to-year, apparently depending upon snowfall. In at least one instance at Kenai, major downward movement was delayed until January.

ENVIRONMENTAL AND PHYSICAL DISTANCES BETWEEN SEASONAL RANGES

Distances between seasonal ranges can be considered as horizontal distances, elevational distances, or environmental distances. To be adaptive, movements must involve a change in environment, or travel an "ecological distance" from one environment to another. As suggested by Edwards and Ritcey (1956), a change in elevation accomplished by a relatively short horizontal movement may result in environmental changes similar to those resulting from extremely long latitudinal migrations. In regions where juxtaposition of disparate habitats in extreme, only short horizontal movements may be necessary to realize the maximum environmental changes practicable. In vast flat areas of homogeneous habitat, no reasonable migration can achieve a significant environmental change.

Seasonal migrations reported in North America involve horizontal movements of from one to more than 170 km, and include examples of all distances in between. No distinct relationship — direct or inverse — is evident between elevational shift and horizontal movement. Rather, the horizontal and elevational distances traveled are linked to environmental differences achieved at each location studied.

The shortest horizontal and elevational distances traveled occur, by definition, in Type A populations. In low-relief Minnesota habitats distances between summer and winter home ranges are only 0-10 km, although definite and regular seasonal movements do occur (van Ballenberghe and Peek, 1971; Berg, 1971). Of the 11 winter home ranges documented by Berg, three were adjacent to and two were included within summer-fall home ranges of the same individuals. No obvious advantage accrued to the moose that moved these short distances, for habitat was similar (though not equivalent) on both ends of the movements.

Type A movements in other areas, although covering only short horizontal and elevational distances, may involve large ecological changes. Resident moose both at Kenai and at Tanana Flats, Alaska, redistribute seasonally on lowland ranges, moving only a few kilometers. In so doing, however, they move from open bogs to mature hardwood forests, dense seral shrub ranges, or riparian willow habitats (LeResche *et al.*, 1974).

The two northernmost populations listed in Table II (Northwest Territories and Arctic North Slope, Alaska) both spend summer on tundra and intertidal ranges near the Arctic Ocean. Both groups undergo medium to long distance horizontal movements along river courses. These movements have small elevational components, but involve major ecological change, from exposed areas where survival in winter might be difficult (Miller *et al.*, 1972), to riparian willow habitat which offers more available forage in winter and protection from weather. These movement patterns are considered as intermediate between Types A and B.

Type B movements, which involve a change in elevation and nearly always a rather major ecological change, may involve as little as a 2 km horizontal movement (Table II). These movements are characteristic in mountainous terrain, and typically proceed between high subalpine or upland forests (summer-fall range) and low seral shrub or riparian habitat (winter range). The longest horizontal movements, in British Columbia and Wyoming, are 60 km and 40 km and also involve the greatest change in elevation (Edwards and Ritcey, 1956; Harry, 1957; Houston, 1968). The British Columbia population moves from subalpine forests 1500-2200 m elevation to lowland burns 600-1000 m elevation. Migratory moose in Jackson Hole, Wyoming, move from upland forests as high as 3300 m to flood plain willow communities 2200-2300 m elevation. Similar ecological movements are accomplished with shorter horizontal and elevational movements by moose in Montana and Alaska (Knowlton, 1960; LeResche, unpubl.). In the Gravelly Mountains, Montana, moose move between subalpine meadows and upland willows at 3000 m and riparian willow about 1000 m lower, while traversing only 2-7 km horizontally in the steep terrain. In the Kenai Peninsula "benchland", a group of moose moves from subalpine willows and alpine tundra at 1000 m elevation to riparian willow communities at 500-800 m, traversing only 2-20 km horizontally. This group sometimes oscillates between the habitats (depending upon whether bare ridges exist above timberline) several times in winter, in a manner similar to that described by McDowell and Moy (1942) in Montana.

Both Type C populations, in Alaska, move elevationally 500-800 m and horizontally 30-50 km between summer-fall and winter ranges; and 0-300 m and 20 km between winter and spring ranges. These movements are important environmentally in terms of habitat (Table II) and climatological variables Coady, 1974).

TABLE II

Summary of seasonal movements of moose in North America. Because methods of study and reporting results vary, designation of migration type is necessarily arbitrary. Designations are made to help structure consideration of the many separate situations represented

Location (study)	*Summer/Fall range (elevation, m)*	*Distance between (km)*	*Winter range (elevation, m)*	*Distance between (km)*	*Spring (calving) range (elevation, m)*	*Distance between (km)*	*Migration type*	*Remarks*
N.E. Minnesota (van Ballenberghe and Peek, 1971)	coniferous-deciduous mosaic (500-700)	local (2-6 km)	coniferous-deciduous mosaic (500-700)	local (2-6 km)			A	Local shifts in winter home range depending upon weather
N.W. Minnesota (Berg, 1971)	open willow	2-10 km	mature willow/ hardwoods	2-10 km			A	Definite, rapid but short-range seasonal shifts-no vertical component
Wyoming (Houston, 1968)	floodplain willow (2200-2300)	8-16 km	floodplain willow (2200)	8-16 km			A	Share winter-spring range with larger Type B group (below)
British Columbia (Edwards & Ritcey, 1956)	subalpine forests (1500-2200)	?	subalpine forests (1500-1800)	?			A	Both groups represent small resident segments of a much larger Type B population
British Columbia (Edwards & Ritcey, 1956)	lowland burns (600-1000)	local	lowland burns (600-1000)	local			A	See above
Tanana Flats, Alaska (Bishop, 1969)	lowland mosaic (200-250)	local ?	lowland burns (200-250)	local ?			A	Share spring-summer & some winter range with Type C population
Kenai, Alaska (LeResche, 1973)	lowland mosaic (75-100)	local 0-16 km	lowland burns (75-100)	local (0-16 km)	same as summer-fall		A	Share spring & some winter range with Type C population (below)

TABLE II (continued)

Location (study)	*Summer/Fall range (elevation, m)*	*Distance between (km)*	*Winter range (elevation, m)*	*Distance between (km)*	*Spring (calving range (elevation, m)*	*Distance between (km)*	*Migration type*	*Remarks*
Northwest Territories (Barry, 1961)	tundra (o±)	to 170 km	riparian willow ?	to 170 km			A-B	Move along rivers long distances, with little change in elevation
Arctic North Slope, Alaska (Alaska Dept. Fish & Game, 1973)	riparian willow & tundra (100-200)	0-75 km	riparian willow (200-600)	0-75 km			A-B	Move along rivers long distances, with little change in elevation; some cross crest of Brooks Range through high passes
British Columbia (Edwards & Ritcey, 1956)	subalpine forests (1500-2200)	20-60 km	lowland burns (600-1000)	20-60 km			B	Share winter & spring-summer ranges with two Type A populations (above)
Montana (Knowlton, 1960)	subalpine meadows & upland willows (3000)	2-7 km	riparian willow (2000)	1-7 km			B	Very short movement; but great elevational difference
Kenai, Alaska (LeResche, unpubl.) (benchland residents)	alpine tundra & upland willows 1000 ±	2-20 km	riparian willow (500-800)	2-20 km			B	Share spring-summer range with much larger Type C group (below)
Wyoming (Harry, 1957; Houston, 1968)	upland forest (3300)	15-40 km	floodplain willow (2200-2300)	15-40 km			B	Type A in some years, depending upon snow. Share winter range with smaller Type A group (above)
Kenai, Alaska (LeResche, 1973)	upland willows (600-750)	30-40 km	lowland burns (80-100)	20 ± km	lowland bogs (80 ±)	13-20 km	C	Share ranges with groups of Types A & A-B (above)
Tanana Flats, Alaska (Bishop, 1969)	upland willows (1000)	30-50 km	lowland burns 200-500)	20 ± km	lowland bogs (200-300)	15 km	C	Share ranges with Type A group (above)

TRADITIONAL ROUTES OF TRAVEL

Because specific home ranges are used repeatedly by individuals, we might expect routes of travel to be similarly traditional. The scant data available suggest this is the case. Knowlton (1960) described the following of drainage patterns and Houston (1968) diagrammed routes repeatedly used which also followed topographic features. Edwards and Ritcey (1956) believed that migrations retained the same essential elements year after year.

Berg (1971) and LeResche (1972) present evidence that individual moose repeatedly use the same routes of travel between seasonal ranges. In Minnesota, Berg radio-tracked a cow and a bull and found that each followed the same routes during spring and fall movements. LeResche's information from Alaska is partially included in Figure 3, which illustrates movements of three individuals over 2½ years. The individual moose were observed often enough during seasonal movements to suggest that routes they followed were at least very similar from one year to the next.

SEGREGATIONS, AGGREGATIONS AND SEASONAL MOVEMENTS

Seasonal movements of moose alter the spatial relationship between individuals and groups, and redistribute moose in relation to their habitats. When animals of different ages, sexes, and reproductive conditions move differentially, migrations cause a reordering of group make up. When migratory and "resident" groups converge or diverge, aggregations and segregations occur. The social and demographic changes resulting from such interactions are often overlooked when causes of migrations are sought.

Population segments may differ in timing and extent of seasonal movements, or in whether they migrate at all. Many studies have shown that "migratory" and "resident" populations may share the same ranges at any time of the year. Houston (1968) studied a "resident" (i.e. remaining in his study area year-round) Type A group and a "migratory" (i.e. visiting the study area only in winter) Type B group in Wyoming. These moose were aggregated during most winters, but extent of ingress by the Type B group was related to snow conditions. Type B moose were about twice as numerous as resident individuals. Edwards and Ritcey (1956) described migrations of a vast majority of moose they studied in British Columbia, but noted "a few" moose were year-round residents on this group's summer and winter ranges. A similar situation is present in the Tanana Flats, Alaska (Bishop, 1969b), where one Type A group remains in lowlands all year (but redistributes seasonally), and a larger Type C group moves between various upland ranges and the lowlands. Both groups aggregate on lowland spring calving ranges. Another small segment of the population remains in upland areas throughout the year, redistributing seasonally and mixing with Type C groups in autumn.

"Resident" and migratory groups interact in a complex manner on the Kenai Peninsula (Fig. 2). The "resident" (Type A) lowland group intermingles with the Type C migratory groups on winter and spring areas. The Type C groups, in addition, congregate with upland "residents" (Type B) in summer and fall, on upland ranges. Probably 40-50 percent of the moose involved undertake Type C movements; about 40 percent are Type A lowland "residents", and the remaining 10-20 percent have Type B movement patterns.

Segregations and aggregations assume greater social importance when they involve distinct age and/or sex classes of the population. Definite segregations by sex, age, and reproductive status have not been reported in Type A populations although redistribution of bulls during rut and of yearlings has been suggested above. Seasonal movements in these populations seem to involve all classes of animals equally.

Social segregation is common in some Type B and Type C moose populations. Peterson (1955) noted that cows, calves and yearlings tended to move to upland ranges later in the spring than bulls in Montana and British Columbia. Moose summering in upland ranges in British Columbia had higher twinning rates and perhaps higher pregnancy rates, than those resident in the lowlands (Edwards and Ritcey, 1958). This suggests a differential movement pattern between females of different reproductive capacities.

Figure 5 illustrates progression of seasonal movements by bulls and cows of a Type C population studied on the Kenai Peninsula, Alaska (LeResche, 1972). Bulls leave lowland spring ranges beginning in May and June, and all reach upland ranges by early July. Cows without calves are delayed in comparison to bulls, but precede cows with calves to upland ranges. Many cows with calves do not leave lowland home ranges until August, and many never travel as far into the hills as bulls. Rutting occurs after the bulls drift slightly downward, to elevations where cows are concentrated. Sexual segregation reoccurs after rut, when many cows begin downward movement to winter home ranges and most bulls return to the highest upland ranges. Full intermixing is not reestablished until all animals congregate on winter ranges, usually by January.

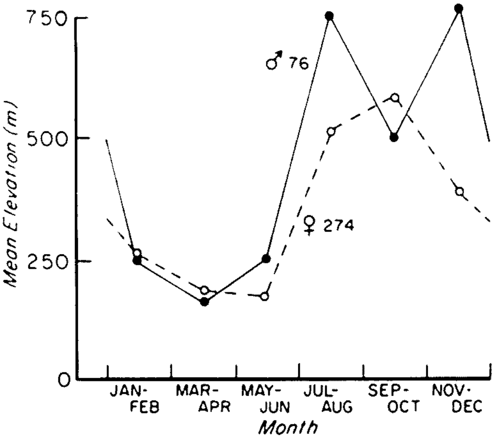

Figure 5. Mean bimonthly elevations where bulls and cows were sighted in a study of a Type C moose population on the Kenai Peninsula, Alaska. (From LeResche, 1972).

During spring, summer and early winter, this migratory population is largely segregated from the Type A group of almost equal size, which remains in the lowlands. There are significant differences in sex, age and reproductive success between the Type C and Type A groups. Bull:cow ratio may approach 60-80 in the Type C groups; whereas, it is 20-40 in the "resident" group. Type C animals are significantly older (LeResche, 1970), and calf:cow ratios are significantly lower in the Type C groups. These differences result from the more intense hunting that occurs on the lowlands, but may also reflect changes in movement patterns with age.

Type C groups on the Kenai segregate from other Type C groups as well as from lowland residents. Because individuals return annually to traditional summer-fall ranges, in specific upland drainages, breeding groups tend to retain separate identities year after year. Many of these groups contain 100-500 moose, and are largely the same individuals each autumn. During other times of the year, individuals may be widely scattered (LeResche, 1972).

MEDIATING FACTORS IN SEASONAL MOVEMENTS

Almost all descriptions of seasonal movements by moose have noted correlations with one climatological or habitat-related factor or another. Such presumptive data show that primary mediating factors differ between situations. There is recent evidence that internal time cues are also involved.

Weather and particularly snow conditions, is the most often reported mediating factor in moose migrations. Formozov (1946) and Nasimovitch (1955) have reviewed the influence of snow on distribution and movements of boreal mammals, including moose. Snow depth and characteristics definitely affect local movements and habitat selection by moose throughout North America and cause "yarding" in many instances (Seton, 1909; Heape, 1931; Peterson, 1955; Edwards, 1956; Harry, 1957; van Ballenberghe and Peek, 1971). Snow-moose relationships vary according to many factors, which are discussed in depth by Coady (1974). In general, snow causes or restricts movements by altering the energy cost of traveling or living in a habitat and by altering the availability of forage.

"Rigor of the winter" alters location of winter range of a Type B moose group in Wyoming (Houston, 1968). The migratory group only wintered in Houston's lowland study area during more severe winters. Knowlton (1960) believed that winter snow depths in Montana initiate movements downward from upland summer ranges. Edwards and Ritcey (1956) concluded that temperature is the "basic factor" mediating Type B movements in British Columbia, but that snow depth alters the effects of temperature. Spring movements halt when temperature drops in this region and resume with a rise in temperature. However, no upward movement occurs during warm periods in winter because snow depths prevent it.

Peek (1962) felt that precipitation affects summer distribution of moose in Montana, where greater use of upland habitats occurs in dry summers.

Abundance and quality of available forage change with snow conditons and with habitat. Hosley (1949:15) concluded that "depth of snow and the resulting effect on food availability...determine the locations of moose in winter". Stevens (1970) described yarding of Montana moose due to snow conditions and movements from the yards after available forage was exhausted.

Springtime movements from winter ranges may be mediated by disappearance of snow or by phenology of growing plants. Probably both factors are important. The abrupt shift from downward drift to rapid upward migration in spring described for Type B populations in British Columbia (Edwards and Ritcey, 1956) and Montana (Knowlton, 1960) suggests a sudden release by disappearance of snow rather than a movement initiated by new plant growth. Knowlton, nevertheless, concludes that "greening up" of forage initiates spring movements. In contrast, Type C Kenai Peninsula groups move from winter range onto spring concentration areas in April and May and then disperse slowly to upland summer-fall ranges beginning in June. Most snow disappears from upland ranges in May, so this movement is more likely related to plant phenology.

It is impossible to know whether seasonal movements would occur without proximate climatological and phenological stimuli. However, there is some evidence of internally mediated migratory behavior in moose. Sexual stimuli cause movements of bulls preceding and during rut. Houston (1968) postulated that the extent of movements of cows might be similarly affected, being perhaps "a function of the density of breeding males".

My studies of moose enclosed in four one mi^2 (2.6 km^2) pens near Kenai, Alaska indicate that these moose have migratory tendencies consistent with actual movements of unenclosed moose. Most individuals were born outside the pens and now are enclosed on the Kenai lowlands near the interface between a major spring range (where Type A and Type C populations aggregate), and an extensive lowland wintering area (Fig. 1). Animals enclosed in the pens are from both Type A and Type C populations. The movements of unenclosed moose are described above and by LeResche (1972). Sightings of enclosed moose along fencelines over a 34 month period were analyzed for directional tendency (i.e.: a moose sighted along the north fenceline of a pen had a northward tendency, etc.). Frequency of sightings of moose along north, east, south and west fencelines differed significantly by time of year (Table III), and directional tendency was consistent with known migrations of unenclosed moose.

During seasons of most significant migrations by unenclosed moose (e.g.: movement to calving concentration areas in March and April and migration to upland summer and rutting areas in July-August), locations of enclosed moose differed most from those predicted by χ^2 expectations under a null hypothesis of no seasonal change in distribution (Table IV). During February-April, within pen locations were weighted north and west (the direction of movement from wintering to calving areas) to contribute 44 percent to the χ^2 value. In July and August, when unenclosed moose were migrating east and south to upland summer-rutting ranges, enclosed moose were seen more often than expected along east and south fencelines. This deviation from expected values contributed 27 percent to the total χ^2 value. Similary, a westerly trend within the pen contributed 18 percent to χ^2 during the months (November — January) when unenclosed moose were gradually moving westward from rutting to wintering areas.

During pre-calving, calving and post calving periods (May–June) and during pre-rut and rut (September–October) unenclosed moose are essentially resident in calving and rutting areas. During these periods enclosed moose differed but little from expected distri-

TABLE III

Proportions of 757 observations of moose along enclosure fencelines by season and compass direction. Kenai Moose Research Center. May 1969 — March 1972[1]

Season	Fenceline				Number of observations
	North	East	South	West	
Nov. - Jan.	.21	.18	.43	.18	112
Feb. - Apr.	.36	.20	.24	.20	80
May - June	.15	.33	.31	.11	150
July - Aug.	.07	.38	.49	.06	175
Sept. - Oct.	.18	.33	.43	.07	240
Total					757

[1] Proportions of animals along each fenceline differ significantly by season ($P < .001$; $\chi^2 = 70.43$, 12 df).

bution patterns, thereby suggesting no migratory tendency (Table IV).

Enclosed moose are, of course, influenced by the external stimuli of day length, temperature, plant phenology, etc. Nevertheless, the directional tendencies they exhibit are appropriate only in light of patterns (probably learned) cued by internal timing mechanisms. For example, in autumn, the penned moose are already present on winter range, and are not affected by snow or vegetation on upland ranges. Still, their directional tendency is in the direction necessary to move from upland ranges to winter ranges.

Dispersals

There can be little doubt that moose have evolved as an opportunistic species, adapted to dispersing into subclimax habitats periodically created by fires and other disturbances (Geist, 1971). This ability is manifest in prehistoric and more recent extensions of moose distribution throughout North America (cf: Anderson, 1924; Peterson, 1955; Mercer and Kitchen, 1968; LeResche *et al.*, 1974; Krefting, 1974; Dodds, 1974; Kelsall and Telfer, 1974). It is further suggested by the countless instances of increases and declines in areas of subclimax forests (e.g. Leopold and Darling, 1953; Peterson, 1955; Lutz, 1960; Spencer and Hakala, 1964).

In fact, actual extensions of range have sometimes been more apparent than real in recent centuries (cf: Lutz, 1960; Barry, 1961; LeResche *et al.*, 1974). Instead, supposed "dispersals" have in reality been only increases in previously low-density populations. Nevertheless, true range extensions certainly have occurred, sometimes with the aid of transplants, in Western and Southeastern Alaska (Alaska Department of Fish and Game, 1973; LeResche *et al.*, 1974) and parts of Canada.

TABLE IV

Seasonal directional tendencies of enclosed and unenclosed moose. Kenai Peninsula, Alaska, 1969-72[1]

Season	*Enclosed moose*		*Activity of unenclosed moose*
	Movement relative to statistical expectation	*% contribution to χ^2*	
Nov. - Jan.	West	18%	Slow westward migration to wintering areas
Feb. - Apr.	North/West	44%	Northwestward migration to calving areas
May - June	None	4%	Occupation of calving areas
July - Aug.	South/East	27%	Eastward migration to summer and rutting areas
Sept. - Oct.	East	7%	Rutting

[1] "Statistical expectation" is the expected chi-square value with null hypothesis of no directional variation by season and relative movement is included only when observed frequently exceeds expected by more than 20 percent.

It is perhaps a moot point what proportion of large increases in moose numbers is due to immigration and what proportion results from increased productivity of resident moose. However, some recent studies indicate there is at least a short period of delay before apparent "immigration" occurs into an area of vacated habitat. The basis for this delay is likely the traditionality of movement patterns discussed here.

Goddard (1970) concluded from an eight-year study of marked moose in Ontario that there was no net movement of moose into heavily hunted areas. He felt that sustained harvest from the heavily hunted area depended upon enhanced production rather than immigration. We observed a similar pattern during early years of state management of moose in Alaska. Intensive hunting along road systems (especially in the Matanuska Valley and near Kasilof, Kenai Peninsula) significantly decreased roadside resident (Type A) populations. Late winter densities remained high due to an influx of Type C moose, but in summer and autumn, when Type C groups were away, populations were depressed from previous levels. There was no evidence of a significant influx of outside moose into the Type A populations.

Both these examples suggest a delay in filling hunter-created niches in Type A populations.

The rate at which newly-created habitat is colonized by moose is poorly known. Spencer and Chatelain (1953) and Spencer and Hakala (1964) document increase in moose numbers on the 128,000 ha Kenai (1947) burn area. Spencer and Chatelain (1953) believe that increase was probably about fourfold from 1950-1953, and it occurred "largely as a result of diversion of moose from other wintering areas". Spencer and Hakala (1964) estimate an increase from 2,000 moose in 1949 to 4,500 in 1955, which represents an increment of 9 to 21 percent annually. Whichever of these estimated increases is most accurate, it is entirely possible that reproduction by previously resident moose on the areas in question accounted for the entire increase in numbers. Neither publication reports a concurrent decrease of moose numbers in nearby areas, from which they feel immigrants originated.

The best information on moose dispersals comes from Labrador (Mercer and Kitchen, 1968). Animals introduced in southeast Labrador in 1953 have since expanded into an area of about 4,400 km^2, at a rate of about 10 km per year. Simultaneously, moose occurring naturally in southwest Labrador spread northeast at the rate of 13-24 km per year. Rate of dispersal depends on quality and quantity of habitat available, of course, as well as on intensity of other limiting factors, such as disease, hunting and climate. It is interesting to note, however, that true dispersals (as opposed to increases in density) are often relatively slow.

Management considerations

Moose migration patterns have significant influence on designation of special use lands (e.g. wilderness areas, recreational areas, highway routes) and development of hunting seasons and limits. Annual movements are especially important when they involve travel from inaccessible areas to roadside areas. Segregation of localized traditional breeding groups and the slowness of dispersal into social niches further complicates hunter management. The root of most migration-related management problems lies in management of land areas rather than moose populations. Their solutions lie in learning the nature and timing of movement patterns and the geographical origins of the groups and population segments involved.

Management problems are unique to each situation, but several general examples will illustrate their nature. Traditionality of seasonal home ranges and slowness of dispersal into vacated home ranges greatly influences hunter management along road systems where there are "resident" populations and in upland drainages where the same individuals breed repeatedly. In such situations, these groups must be considered as isolated populations rather than as portions of larger reservoirs of animals and must be harvested only within their limited annual increments.

When lands are designated for special uses — to protect certain moose "herds" or to provide for trophy hunting of large bulls, for example — it is essential to understand seasonal movement patterns of all segments of the group in question. Whithout such understanding, critical habitats (e.g. winter range, calving areas) outside the designated area might be destroyed, thereby affecting any moose from the "protected" area that might use them seasonally. Similarly, "trophy" areas near "maximum sustained yield" areas are futile if trophy animals migrate to the latter areas during hunting seasons. Conversely, maximum sustained harvest management will fail in situations where moose are not present in accessible areas when hunting is allowed. Benefits from intensive habitat manipulation for production of moose to be harvested may be minimal if lands important to the same moose at other times of the year are not also appropriately manipulated or protected.

Finally, knowledge of moose movements is critical to planning compatible human developments. Construction of a single highway or pipeline barrier across a major migration route could affect moose over tens of thousands of square kilometres. Misuse of a very small critical seasonal range for only a month each year could result in serious interference in the life cycle of thousands of moose over a vast area. These possibilities are not hypothetical, but very real in some areas (cf: LeResche, 1972). Where migrations do occur, managers must realize that free movement is of major importance to healthy moose populations.

Summary

MIGRATORY BEHAVIOR RELATED TO HABITAT, TERRAIN AND TAXONOMY

No precise relationships are evident, for often several general movement patterns are present in a single population of moose occurring in one habitat. In general, however, the most complex movement patterns occur in areas with the greatest compression of disparate habitats and climates. This situation almost always involves hilly or mountainous terrain, where different climates and biota are very close to one another. Only local movements (Type A) have been reported from the flattest terrain studied, in Minnesota and Ontario. An exception occurs in the arctic, where long migrations occur in relatively flat areas. Here, however, summer habitats are probably absolutely uninhabitable in winter. In Ontario and Minnesota travel over great distances would achieve little change in climate or habitat. This pattern is confused, however, by resident (Type A) populations occurring in almost all areas studied — including those areas where more complex movement patterns (Type B & C) occur.

There is no evidence that any of the four subspecies of North American moose has consistently different migratory behavior than any other.

MEDIATING CAUSES OF MIGRATORY BEHAVIOR

Seasonal movements are mediated by snow conditions, available forage and a combination of both. There is some evidence for internally mediated migratory tendency. Autumn movements from summer-fall to winter ranges are most often attributed to snow accumulation; whereas, reverse spring movements are associated with disappearance of snow and "greening up" of forage. Weather changes during migration periods sometimes alter the speed and progress of movements.

TRADITION AND MIGRATORY PATTERNS

Tradition is strong in movement patterns of individual moose. Movement patterns of populations change over time, but similarly contain strong elements of tradition. Specific home ranges and specific routes of travel are used on an annual basis by individuals in all areas studied. Overall annual movement patterns of populations and population segments change little year-to-year during periods when habitat relationships remain relatively stable. The extent and timing of movements varies with climatological and phenological events, but the pattern remains constant.

The rates and mechanisms of establishing migration patterns in newly-created habitats are obscure. It is probable that several years pass before traditional patterns are changed and new patterns established. Young moose and rutting bulls move most erratically. These animals might thus be the pioneers of new movement patterns.

THE ADAPTIVE VALUE OF MIGRATORY BEHAVIOR

The result of migrations is alteration of individuals' environments. Movements change physical (climatic), biotic (forage and interspecific) and social (intraspecific) relationships. It is within these relationships that we must search for the ultimate benefits accrued from migratory behavior. Relationships changing seasonally are responsible for annual movement patterns; those changing over decades or centuries are ultimately responsible for dispersals. In the final analysis, species seek the environmental relationship in which they have the greatest reproductive potential. Movement patterns will thus be selected for if they have reproductive value (MacArthur, 1972). Basic to reproduction is survival, and basic to survival is energy balance. Movement patterns will thus be selected for if they place individuals in a favorable energy balance (cf: West, 1960; Cox, 1961, 1968). The influences of forage quantity and quality and climatic variables on energy balance of moose are extremely complicated but are now at least partially understood (Gasaway and Coady, 1974, Oldemeyer, 1974, Coady, 1974).

In the grossest terms, the energy advantages achieved by a moose migrating from deep snow to less deep snow, from non-available forage to available forage, or from less nutritious forage to more nutritious forage are obvious. We can expect more thorough accounting of these relationships once energy costs and benefits of seasonal environments are measured precisely.

Social factors are even less well understood than physical and extraspecific biotic factors of migrations. Their consideration is clouded by the fact that movements achieving overwhelmingly beneficial climatic or forage relationships might result in decreasing social benefits. The converse — social benefits being important enough to over-ride unfavorable climatic or biotic relationships — might also occur. Social benefits are presently difficult to measure, but may be sought in aggregations and segregations that occur as the result of movement patterns. The most generally apparent aggregations are breeding aggregations and winter concentrations; the most obvious segregations are post-parturition segregations of cows with calves and segregation of populations during breeding.

Aggregation for breeding is necessary to reproduction, and all movement patterns must result in this one aggregation. The larger "herd", which might be intermixed on calving or wintering areas, often splits into many localized rutting populations. These populations are segregated from one another during breeding. This results in significant pre-rut movements by some segregated population segments. Several parameters, such as summer distribution of population segments and bull: cow proportions, influence these "gametic migrations," but in all cases their adaptiveness is obvious. Less obvious are the benefits derived from segregation of small populations year after year in traditional breeding ranges. Perhaps such distributions insure best use of "spotty" habitats (upland riparian willow stands, for example). In addition, regular return to traditional breeding grounds by the same individuals insures contact during the rutting season, and perhaps allows efficient social patterns to develop and persist.

In some reported cases, upland Type A populations aggregate with Type B or Type C populations, which have migrated from the lowlands, for rut. These groups might interact for only the late summer-fall period each year. In contrast, lowland Type A populations are generally isolated during rut, in lowland areas that Type B and C groups have left. Perhaps this segregation preserves genetic tendencies for both localized (Type A) and long-distance (Types B & C) migratory behavior in the same large area. Localized behavior may be adaptive only when a substantial portion of a population leaves during part of the year. It may be especially adaptive to reproducing females; whereas, the benefits of migration might be greatest to other individuals. Thus, both types of behavior are retained in the same area.

It is difficult to ascribe social adaptiveness to movements that result in aggregations on winter range; probably selection pressure for these patterns originates largely in climatic and forage advantages. Nevertheless, aggregations do occur in late winter (cf: Peek *et al.* 1974) in large expanses of good habitat where clumping is probably not required by snow or forage conditions. Social advantages of these groupings might perhaps be sought in predator-prey relationships or socialization of short yearlings before their rejection by cows.

Summer segregation of some migratory populations by sex and reproductive status might have social advantages. Part of the adaptiveness of this pattern certainly derives from localization of cows in relatively "predator-safe" habitats at a time when travel is difficult for new calves; contrasted with the forage (energy balance) advantages of upland habitats to animals unencumbered with young. Perhaps social advantage also derives from minimizing contact between young calves and moose other than their dams, at the time when their first socialization occurs.

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INFLUENCE OF SNOW ON BEHAVIOR OF MOOSE

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Résumé

L'auteur passe en revue les adaptations morphologiques et éthologiques de l'orignal à la neige, les propriétés pertinentes de la neige à cet égard (épaisseur, densité et dureté) et les méthodes de mesure appropriées. L'épaisseur refère à la couche non-portante que l'animal doit écarter en se déplaçant; la densité, déterminée en pesant un volume donné de neige, permet d'évaluer la friction exercée sur les pattes ou sur le corps; la dureté, sans doute la propriété la plus importante, détermine la force que l'animal doit appliquer pour se déplacer et la capacité portante de la neige. La dureté peut être évaluée au moyen d'un gabarit à ressort ou d'une sonde de type «Rammsonde».

Chez l'orignal, on peut considérer que la longueur des pattes et le mode de répartition du poids reflètent en quelque sorte un ajustement morphologique à la neige. Si la neige au sol dépasse le tarse, les mouvements ne sont pas gênés. Mais si la neige atteint les deux-tiers de la hauteur comprise entre le sabot et le poitrail, les mouvements sont partiellement restreints; ils le sont presque complètement, quand la neige atteint ou dépasse le poitrail. L'auteur interprète certaines différences dans la longueur des pattes comme une adaptation aux différences régionales observées quant à l'épaisseur de la neige. La répartition, entre les quatre membres, du poids par unité de surface permet d'évaluer la dureté requise pour assurer le support de l'animal.

Les mouvements graduels de l'habitat d'été à l'habitat d'hiver prennent place entre octobre et mars, en réponse à diverses conditions de neige. Cependant on assiste fréquemment à une migration accélérée vers les quartiers d'hiver, à la suite d'une accumulation hâtive de neige. En Alaska, la dureté de la neige dans les quartiers d'été peut également influencer les déplacements de l'orignal. Ces déplacements sont ordinairement rapides et coincident avec la fonte de la neige et la réapparition du sol. Par contre, les déplacements durant l'hiver sont généralement limités, particulièrement dans les périodes marquées par une forte accumulation de neige au sol.

La neige, sans être la cause des migrations, en influence la date et l'amplitude. Elle peut intervenir dans le bilan énergétique, en augmentant les besoins métaboliques et en restreignant l'accès aux ressources alimentaires. Elle peut également jouer un rôle majeur en suscitant des déplacements vers des quartiers d'hivernage dans lesquels la qualité, la quantité et la disponibilité de la nourriture sont meilleures.

Abstract

Properties of snow influencing moose, methods of measuring those properties and morphological and behavioral adaptations of moose to snow are reviewed. To moose, snow depth, density and hardness are probably the most important characteristics. Depth indicates the thickness of the medium through which an animal must move if not supported by the snow; density, measured by weighing a known volume of snow, inhibits locomotion by increasing drag on legs or body; hardness is perhaps the most important property of snow to moose since it determines the force which must be exerted to move through the snow and the capacity of snow to support the animal. Hardness can be measured with either a spring loaded hardness gauge or with a Rammsonde penetrometer.

Morphological adaptations of moose to snow may be related to leg length and to foot load. Snow depths below tarsus height provide little or no hindrance to moose; depths approaching two-thirds of the chest height partially restrict movement, and depths equal to or greater than the chest height severely restrict movement. Differences in leg length of moose between two areas in Alaska suggest a possible adaptation of leg length to regional differences in snow depth. Foot loads reflect the weight per unit areas of all four feet, and theoretically indicate the hardness of snow required to support a moose.

Gradual movement of moose from summer to winter range generally occurs between October and March in response to a wide range of snow conditions. However, abrupt migrations to winter range in response to early and deep snow frequently occur. Hardness of snow on summer range (Rammsonde values) may be related to altitudinal movements of moose in Alaska. Movements to summer range in April or May are generally rapid and coincide with snow melt and the appearance of bare ground. Local movement and activity of moose during winter are generally limited, particularly during periods of deep snow.

While snow does not cause moose migrations, it does influence the timing and magnitude of movement. Snow may alter the energy balance of moose by increasing metabolic requirements for locomotion and decreasing accessible energy reserves by limiting food availability. Migration to regions and habitats where food quantity, quality and availability are grestest depend largely on snow conditions and result in the most favorable energy balance to the animal.

Introduction

The circumboreal distribution of moose (*Alces alces*) throughout regions characterized by a seasonal snow cover illustrates the successful adaptation of the species to the nival environment. Adaptation of moose to snow can be explained, in part, on the basis of physical and behavioral characteristics. Long legs, which increase tolerance to deep snow, and movement to the most favorable habitat when snow conditions make travel laborious and food difficult to obtain are important factors facilitating winter survival.

In the following review, properties of snow important to moose and methods of measuring those properties, and physical and behavioral adaptations of moose to snow will be discussed. Needs for future research to better understand and predict the influence of snow on moose will be indicated.

Properties of snow and methods of measurement

The structural, physical, and mechanical properties of a snow cover vary greatly, depending on conditions of deposition and subsequent metamorphism. Seasonal snow covers behave in an extremely dynamic fashion, and the only completely predictable phenomenon is change itself. Metamorphic processes which take place within a seasonal snow pack have been described by numerous workers (Bader *et al.*, 1939; Formozov, 1946; Gold, 1958; Kingery, 1960; Benson, 1967, 1969; Trabant, 1970). While wind action is a major factor affecting snow as it precipitates (Sommerfeld, 1969), diagenetic processes resulting from temperature, time and settling (Keeler, 1969) begin immediately after deposition. All features of a snow pack reflect post-depositional changes as much or more than they reflect the character of snow at the time of deposition. High temperature relative to the melting point of snow and steep temperature gradients are effective in promoting vapor transport, a major cause of metamorphism. Constant fluctuations in air temperature and accumulation rate of snow cause continual changes in both thermal and gravitational forces which are perceptible within days or, sometimes, even hours.

The properties of snow can be divided into fundamental and derived characteristics. A discussion of fundamental properties, which include size, shape, orientation, and packing of particles, is beyond the scope of this review. While fundamental properties of a snow cover bear a relationship to mechanical properties and are important for a complete understanding of snow metamorphism, they are probably of minor significance in ungulate snow ecology (Pruitt, 1971a).

Derived properties of snow are those which depend on fundamental properties for their magnitude and rate of change (Keeler, 1969). Generally, they are more easily measured than fundamental properties, and are useful indices to the nature of snow. Although derived properties are numerous and diverse, relatively few are generally measured to characterize a snow cover. The most commonly measured derived properties used in biological work are depth, temperature, density and hardness.

Methods of measuring derived properties have been described by several authors (Klein *et al.*, 1950; Benson, 1962; Keeler, 1969; Test Lab, 1970a, 1970b; and others). Two similar sets of instruments, a National Research Council of Canada (NRC) kit and a USA Cold Regions Research and Engineering Laboratory (USACRREL) kit have been used to measure temperature, density, and hardness of a snow cover. However, modified snow study kits have also been used (Richens and Madden, 1973). These measurements are generally obtained in "pit" studies, in which a trench is dug in the snow to ground level. Thickness, temperature, density, hardness, and usually crystal type and size are recorded for each of the major strata. Snow samples or measurements are generally taken in a horizontal plane, although vertical as well as horizontal hardness measurements should be made (Pruitt, 1971a). The International Workshop on *Rangifer* Winter Ecology (Pruitt, 1971a) has recommended measuring the thinnest distinct strata which a given instrument size will allow.

Depth of snow cover is probably the most common and important measurement obtained in studying snow ecology of moose. Snow depth data are easily obtained and provide a measure of the thickness of the medium through which an animal must move if not supported by the snow. Depth of snow or thickness of strata can be measured with any conveniently calibrated probe. In addition, in interior Alaska, 5 cm diameter stakes, clearly calibrated at 30.5 cm (12 in) intervals, have been permanently located by the author in remote or inaccessible areas to measure snow depth from fixed wing aircraft. Depth can consistently be estimated within 3 to 5 cm of the actual snow depth, although this method has the disadvantages of limiting measurements to the number of stakes at a study site, and limiting study sites to relatively open areas where the aircraft may be flown near ground level. Snow depths relative to anatomical features of moose also provide a useful and reasonably accurate estimate of snow depth from the air.

Snow temperatures of each strata or at intervals on the pit wall, beginning at ground level or in the subnivian space and ending within 2 cm of the surface, may be measured. The importance of temperature to diagenetic processes in a snow cover was noted above. The International Workshop on *Rangifer* Winter Ecology (Pruitt, 1971a) has questioned the significance of measuring snow temperature in *Rangifer* research, and has recommended limiting measurements to ground level and air temperatures. However, a relationship between snow temperature and moose behavior has been alluded to by DesMeules (1964). The ease and speed of temperature measurement in pit studies and its possible significance to moose behavior probably merit its continued measurement. Measurements may be made with either an alcohol or bimetallic thermometer.

Density, determined by weighing a known volume of snow, is probably the most widely used index of snow type, and under certain snow conditions it may be correlated with hardness (Keeler and Weeks, 1967; Bilello *et al.*, 1970). Increased density presumably causes increased drag on legs or body of ungulates during movement, and thereby inhibits locomotion. Several snow cutters for obtaining snow density samples are available. The NRC kit employs two 250 ml snow cutters, one for soft and one for hard snow, while the USACRREL kit uses 500 ml sampling tubes. Swedish workers use a Swedish Army density "box" which reportedly gives reliable results because of its large 1,000 cm^3 volume (Pruitt, 1971a). In Interior Alaska, a 650 cm^3 plastic cylinder has been used by the writer with satisfactory results.

Snow hardness reflects the degree of bonding between crystals and in most types of snow increases as density increases and/or snow temperature decreases (Gold, 1956). In addition to snow depth, hardness is probably the most critical parameter of a snow cover to ungulates since it reflects the force which must be exerted to move legs or body through the snow, and the ability of the snow to partially or fully support the animal. NRC and USACRREL snow hardness gauges are similar, and consist of a spring loaded push rod with provision for mounting discs of different areas on one end and a calibrated gauge on the other end. The disc is pressed against a snow surface and the maximum stress associated with the initial collapse of the snow structure is noted on the gauge. By using a high and low range gauge and different sized discs, hardnesses of 0 to 100,000 g/cm^2 can be measured. Useful modifications to the instrument developed by O. Eriksson in Sweden and now used by Pruitt (pers. comm.) include a ratchet which retains the calibrated gauge at the extended position reached at the instant of snow collapse, thereby providing more accurate measurements.

Snow hardness may also be measured with a cone penetrometer, commonly referred to as a Swiss Rammsonde. The instrument and its use have been described by several workers (Bader *et al.*, 1939; Benson, 1962, Keeler,1969; Test Lab, 1970a, 1970b; and others). Basically, it consists of a hollow steel shaft with a 60° conical tip 4 cm in diameter and 3.5 cm high. A solid rod mounted on top of the steel shaft guides a hammer which is dropped from a measured height. The height of the drop, weight of the entire instrument, and depth of penetration may be related to the resistance of snow to penetration by the cone using the following formula:

$$R = \frac{Whn}{x} + W + Q,$$

where R = ram hardness number or resistance to penetration, W = weight (kg) of the dropped hammer, h = height (cm) of dropped hammer, n = number of hammer blows, x = penetration (cm) after n blows, and Q = weight (kg) of penetrometer.

This equation ignores friction between the cone and snow and elasticity in the penetrometer. However, the error is small, especially for snow of relatively low hardness (Keeler, 1969; Benson, pers. comm.).

The ram hardness number, R, indicates the resistance (kg) of a layer of snow to penetration by the cone of the penetrometer. In practice it may be useful to determine the ram hardness value for the total snow depth. To do this an integrated ram hardness number, Ri (kg-cm), is calculated by multiplying each depth increment (i) (cm) times its ram hardness number, R (kg), and summing the values from the snow surface to ground level or to any given depth. The integration indicates the work done by the penetrometer as it moves through the snow to a given depth.

The Rammsonde can be used in several ways. It can rapidly distinguish different strata and provide a ram hardness profile or an integrated ram hardness value of the total snow cover without digging a pit. Rammsonde measurements are less subject to operator error than are NRC or USACRREL snow hardness values (Benson, 1962). Limitations to the procedure include lack of resolution at low ram hardness. However, a modified 120° cone, 10 cm in diameter, has been satisfactorily used by Abele (1968) in soft snow. The hardness number obtained with the large cone is divided by a factor of 10 to obtain the approximate ram hardness value of the standard cone (Test Lab, 1970a).

Rammsonde hardness numbers can be correlated with other derived snow measurements under most temperature and snow conditions, and with the support capacity of snow. Bull (1956) and Keeler (1969) have correlated ram values to compression strength or hardness. Abele *et al.* (1965, 1968), Wuori (1962, 1963) and others have related ram hardness to vehicle support capacity of snow roads and runways.

While the Rammsonde penetrometer has been extensively used to study mechanical properties of a snow pack, it has rarely been used in biological applications. Other than Lent and Knutson (1971) working with muskox *(Ovibos moschatus)*, Coady (unpubl.) working with moose, and some investigators in Canada and Scandinavia working with *Rangifer* (c.f. Pruitt, 1971b), the instrument has not been widely used in studies of ungulate snow ecology. Additional measurements and experience are certainly required to evaluate the usefulness of the Rammsonde penetrometer in biological studies. Ease, speed, and consistency of identifying stratigraphic horizons and measuring hardness of a snow cover make the Rammsonde a potentially valuable instrument for assessing the resistance to movement through or the support capacity of snow.

Vertical hardness of snow in relation to animal support capacity has also been determined using other instruments. Pruitt (1959) experimented with measuring the resistance of snow to penetration of an artificial caribou foot to actual foot depth. He proposed measuring the penetration depth of the instrument under foot loads approximating those of caribou. Verme (1968) developed a 1.36 kg "compaction gauge" consisting of a 60 cm long rod with a cross section area of 6.45 cm^2 (210 g/cm^2). The gauge is lowered to the snow surface and released, and the depth of penetration represents the relative support factor of snow. Both Verme (1968) and Ozoga (1968) used the instrument to provide a "snow hazard" rating for white-tailed deer (*Odocoileus virginianus*).

Severity of winter weather for wild ruminants has been evaluated by several workers. Verme (1968) and Verme and Ozoga (1971) used a "chillometer" in addition to the compaction gauge noted above to develop an index of weather severity. The "chillometer" is a calorimetric device which integrates both temperature and wind to provide a relative measure of "air chill." Both "air chill" and "snow hazard" are summed to compute a severity index. Picton and Knight (1971) computed an index to winter weather conditions for big game based on weather bureau measurements. Basically, daily snow depths on ground are multiplied by the maximum daily degrees below 0°C, and the daily points are summed to provide a cumulative winter index.

Coady (1973) has examined trends in snow severity for moose in Alaska by plotting U.S. National Weather Service records of snow depth on the ground versus month throughout the winter and measuring the area under the curve with a planimeter (cf. Bishop and Rausch, 1974). A similar procedure could be used to evaluate temperature severity. While such weather records may not indicate actual conditions on winter moose range, they probably reflect relative differences between years and long term trends.

Adaptation of moose to snow

Major physical characteristics of moose influencing their mobility in snow are chest height of the animal and weight load on the feet. When moose sink into snow to depths approaching chest height and are forced to "plow" or bound through the snow, energy required for movement is greatly increased. However, snow depths below chest height may hinder movement by increasing resistance to movement of the legs. Weight load on the feet is a measure of the weight per unit area on the feet and reflects the extent to which a moose may be supported by a substrate. Under situations in which snow will partially or fully support a moose, resistance to and energy required for movement may be reduced.

Procedures for measuring chest heights and foot loads have recently been described in detail. Kelsall (1969) measured chest heights from the tip of the thoracic limb, with leg extended perpendicular to the body, diagonally to the sternum. The measurement may slightly overestimate actual chest height since the leg may be less extended on a standing than a decumbent animal. In some studies (Kelsall, 1969) hoof load, or weight on hooves alone, has been used to measure the bearing surface of the legs. However, Kelsall and Telfer (1971) and Telfer and Kelsall (1971) indicated that the entire foot from the tip of the hoof to the dew claws supports an ungulate in soft snow, and described a procedure for measuring foot areas and calculating foot loads. Foot loads measured by the previous technique are certainly minimal since the measurement does not allow for spreading of hooves and angular placement of legs in snow. However, the actual foot load is probably somewhat greater since only when standing is weight supported on all four feet. In addition, Kelsall (1969) thought that as much as three-fifths of the weight of a standing ungulate is distributed on its forefeet.

The significance of chest heights and foot loads of moose reflecting adaptation to snow were first studied in Russia and later, in North America. Nasimovitch (1955) reported that chest height of adults averaged 105 cm or greater. Kelsall (1969) found that average chest height of male moose in eastern Canada increased from 81.9 cm for calves, to 98.2 cm for yearlings, and 104.7 cm for animals older than four years. Kelsall and Telfer (1971) measured average chest heights of 106 cm for male moose older than four years in western Canada. Similar chest heights of 84, 96, and 104 cm for 60 calves, yearlings, and moose older than two years, respectively, have been found by Coady (unpubl.) in interior Alaska.

Nasimovitch (1955) noted that moose on the Kola Peninsula in Russia were unaffected by snow depths of 40 to 50 cm, while movement was definitely impeded by depths of 60-70 cm. At 60-70 cm calves frequently followed in the trail of adults. Nasimovitch (1955) concluded from the Russian literature that snow depths of 90 to 100 cm may be considered critical to moose, since at that depth winter mortality substantially increased. Kelsall (1969) reported similar observations from eastern Canada noting that movement was unrestricted by depths of 44 cm and severely restricted by depths of 70-99 cm. Snow depths greater than 90-100 cm were critical for moose unless of very short duration. Ritcey (1967) and Prescott (1968, cited in Telfer, 1970) found that depths of 60-70 cm restricted mobility of moose in British Columbia and Nova Scotia, respectively. In Alaska, substantial winter mortality has occurred in several areas of the state when snow depths exceeded 90 cm for several months (Coady, 1973).

The above data suggest that snow depths up to 40 cm, or depths approximately equal to the carpus or tarsus height, cause little or no hindrance to movement. From 40 to 60-70 cm, or depths approaching two-thirds of the chest height, movement is only slightly restricted. At depths greater than 70 cm movement is definitely impeded, while depths greater than 90 cm, or approximately equal to or slightly less than the chest height of standing moose, movement is greatly restricted to the extent that adequate food intake may become impossible. Calves, because of their shorter legs, may be restricted by snow depths somewhat less than those affecting adults, while large males may be least affected by deep snow. Differential movement of sex and age groups during winter reported by several workers (LeResche, 1974; Pulliainen, 1974) may reflect, in part, the relative ability of the different groups to move in deep snow.

Height of moose from interior Alaska and the Kenai Peninsula have been compared to illustrate that leg length in moose may be adaptive to snow conditions. In interior Alaska snow depths of 70 cm or more, persisting for several months in winter moose habitat are the rule, and depths in excess of 90 cm are not unusual. On the Kenai Peninsula, however, depths in winter moose habitat range near 40 cm for short periods, and seldom reach 60 cm. Since chest heights of moose from the Kenai Peninsula were not available, a ratio of shoulder height to total length was used to reflect relative differences in leg length and presumably in chest height of moose from the two areas. The average ratio from 31 fully grown moose from the interior was .68, while that from 64 similar animals from the Kenai Peninsula was .59 ($t = 6.13$, $P < 0.001$). Similar ratios of 18 calves 6 to 12 months of age from the Interior, and 50 calves from the Kenai Peninsula yielded averages of .72 and .70, respectively ($t = 1.82$, $P<0.1$). Absolute differences in average shoulder height of moose from the Interior and from the Kenai Peninsula were 182 cm and 172 cm for adults, and 148 cm and 141 cm for calves, respectively. Thus, both relative and absolute height of moose is lower, particularly among adults, from the Kenai Peninsula than from interior Alaska.

Variations in body size of animals may be due to genetic or nutritional differences. Since data from the Kenai Peninsula were obtained from moose on relatively poor range (LeResche and Davis, 1971) and data from the Interior from moose on relatively good range (Coady, 1973), possible nutritional differences in skeletal dimensions of animals from the two areas is possible.

While differences in skeletal growth related to nutrition do occur (Klein, 1964), there is little reason to expect that poor range on the Kenai Peninsula is responsible for preferential growth of body length over foreleg length. Thus, while nutritional deficiencies may account for smaller absolute shoulder height of Kenai Peninsula moose, it is likely not responsible for reduced height of animals relative to length.

While long legs *per se* are not necessarily an adaptation to deep snow (e.g., height facilitates the browsing habit), the selective advantage to moose of increased leg length in regions of deep snow is obvious. Therefore, observed differences in relative height of moose between the Kenai Peninsula and the Interior in Alaska are probably of genetic origin and may be related to differences in snow conditions between the two areas. Nasimovitch (1955) noted that reindeer from the taiga zone where deep, soft snow is common have longer legs than those animals from tundra areas. Nevertheless, additional studies would be useful.

Nasimovitch (1955) reported that the average "track load" of "several moose" in Russia was 420 g/cm². This value presumably represents the total foot load, and not just hoof load, of the animal. Kelsall and Telfer (1971) measured average foot loads of approximately 710 g/cm² for male moose four years and older during December in western Canada. Higher average hoof loads of 789 to 922 g/cm² were found by Kelsall (1969) for male moose of similar age from two areas of eastern Canada. The higher hoof loads from eastern Canada were measured before the rut using the area of the hoof alone. However, the lower foot loads from western Canada were determined following the rut, presumably after some weight loss, and by using the area of the entire foot.

Foot loads of moose in interior Alaska (Coady, unpubl.) are not uniform but vary with age of animal and with season. Average foot load decreased from 593 g/cm² ±94 for 8 adult cows in October to 432 g/cm² ±63 for 19 adult cows between April and June. Thus, as winter progresses and snow depth and hardness increase, foot loads of adults decrease due to seasonal loss of body weight. Foot loads of 9 calves between April and June averaged 317 g/cm² ±28, over 100 g/cm² less than adults during the same season. Thus, the shorter legs of calves may in part be compensated for by lower foot loads. No seasonal change in hoof size was noted for Alaskan moose, as Pruitt (1959) reported for caribou.

Snow density has been related to track depth of moose. Kelsall (1971) concluded from his observations that snow densities of 0.10 to 0.19 g/cm³ do not support moose, densities of 0.20 to 0.29 g/cm³ provide some support, and densities of 0.30 to 0.39 g/cm³ limit foot penetration to approximately 50 percent of the snow depth. Nasimovitch (1955) reported that snow densities of 0.20 to 0.22 g/cm³ provide little support to a running moose, while densities of 0.24 to 0.26 g/cm³ limit foot penetration to two-thirds of the total snow depth. However, under these conditions, moose experience difficulty lifting legs from holes in the snow.

Kelsall (1969) and Kelsall and Prescott (1971) were unsatisfied with attempts to relate ungulate support to snow hardness. Theoretically, a standing moose should be supported by a vertical snow hardness equal to or greater than its foot load (Kelsall, 1969; Kelsall and Prescott, 1971). However, the support capacity of snow is extremely variable, depending on presence or absence of surface crusts and the hardness of underlying snow layers. Both white-tailed deer and moose frequently broke through crusts that should easily have supported the animal. Moose, with maximum track loads of 1,000 g/cm^2, broke through crusts of 8,000 g/cm^2 at the surface, 10,000 g/cm^2 at 15 cm, and 90,000 g/cm^2 at 34 cm. Moose also broke through crusts of 10,000, 20,000, 30,000, 40,000 and 25,000 g/cm^2 to ground level at a depth of 73 cm. On other occasions moose were supported by surface crusts of 2,000 to 30,000 g/cm^2. Peek (1971b) noted that surface crusts of 7,500 g/cm^2 supported moose in Minnesota. In interior Alaska such extremely hard crusts are unusual, although I observed that an adult moose walking on a trail penetrated 20 cm in 30 cm deep snow when the hardness was 2,000 to 4,000 g/cm^2. On another occasion both a cow and calf walking on a trail penetrated 39 cm in 90 cm deep snow when the hardness was, 1,000-2,000 g/cm^2.

Preliminary attempts to use the Rammsonde penetrometer to quantify the support capacity of snow for moose have been attempted by Coady (unpubl.). The integrated ram hardness (R_i) was calculated for the total ram hardness of the snow to foot penetration depth (Table I). Average R_i ranged from 188 to 570 kg/cm for penetration depths of 22 and 42 cm, respectively. Although it is not immediately evident from the limited data above, further study may reveal a predictable relationship between R_i and depth of foot penetration in or resistance to movement through snow.

TABLE I

Integrated Rammsonde resistance of snow (R_i) to depth penetrated by adult moose in interior Alaska

Snow depth (cm)	*Track depth (cm)*	*$X\ R_i$ (kg-cm)*	*Range R_i (kg-cm)*
50	22	188	167-211
85	19	340	140-540
80	12	409	326-525
90	42	570	535-632

Throughout most of the circumboreal range of moose and within favorable habitat, snow conditions that provide support are apparently seldom extensive or persistent enough to significantly benefit moose. Even on the tundra of Alaska where snow density and hardness are very great, the snow cover in winter riparian habitat provides little or no support to moose. In other areas supporting crusts are usually extremely localized, and are apparently rarely consistent enough to facilitate travel. Murie (1944), Nasimovitch (1955), Kelsall and Prescott (1971), Peek (1971a), and others indicated that snow conditions which only partially support moose may make movement more difficult and hazardous because of the resistance to movement of legs caused by the dense snow and/or the danger of abrasion from hard crusts. Snow conditions in which depth of penetration is variable may require an animal to expend more energy recovering from breaking through crusts and climbing onto crusts than would be required to move through deep snow offering no support. However, dense, hard snow offering uniform support, such as ski or snow machine trails, may be extensively used.

Comparison of foot loads of moose from different regions may indicate adaptation to varying snow conditions. Kelsall and Telfer (1971) in western Canada measured average foot loads of 710 g/cm^2 for adult moose during December, whereas I reported foot loads of 593 for adults during October (see above). Normal snow conditions at the collection site in western Canada were not given, but presumably snow depth and hardness are at least as great as those in Interior Alaska. Although I followed procedures described by Kelsall and Telfer (1971) possible differences in measuring foot area must be considered.

Movement of moose in response to snow

The influence of snow on seasonal movements of moose has been reported by several workers, although quantitative observations are relatively limited. The greatest effort to document and review relationships between snow and moose migrations has occurred in the USSR (Formozov, 1946; Nasimovitch, 1955; Knorre, 1959, 1961; Egorov, 1965; Heptner and Nasimovitch, 1967 in van Ballenberghe and Peek, 1971). However, significant contributions have also been made in Europe (Pulliainen, 1974), and in North America (Edwards and Ritcey, 1956; Ritcey, 1967; Knowlton, 1960; Houston, 1968; Kelsall and Prescott, 1971).

Nasimovitch (1955) drew several conclusions from the copious Russian literature regarding the influence of snow on moose migrations in both mountains and flatlands of the USSR. Basically, in regions where maximum snow depth averages less than 50 cm and deep snows are of short duration, extensive seasonal migrations are uncommon, although local movements may occur. However, in areas where maximum snow depths in excess of 70 cm persist for long periods, seasonal movements occur from areas of deep to less deep snow. The longest migrations, ranging from 150 to 300 km, occur among animals living on flat terrain, although migrations of 100 to 150 km are common across divides or to lower elevations in mountainous regions. Gradual movements generally occur between October and January, and may coincide either with the first lasting snow cover, or with snow depths of 25 to 45 cm. However, some animals migrate before snowfall while others remain in summer habitat until snow depth reaches 60 to 70 cm.

Pulliainen (1974) reviewed the literature describing relationships between snow and moose migrations in Scandinavia. Movements in most areas are closely correlated with prevailing snow conditions. Gradual movements from high to low elevations usually begin in November or December, although they may be delayed or may not occur during years of little snow. Some animals, particularly cows with calves, begin migrating at first snowfall, while others, particularly bulls and cows without calves, remain at high elevations until snow depth reaches 60 to 70 cm. However, formation of icy crusts may initiate downward migration of almost all animals (Krafft, 1964). Return to summer range is usually abrupt, and occurs during May after snow melt has exposed patches of ground.

In North America several early workers, including Murie (1934) on Isle Royale, Hosley (1949) in Maine, Bauman (1941, cited in Hosley, 1949) in Yellowstone Park, Murie (1944) in Alaska, and Hatter (1946, cited in Hosley, 1949) have commented on snow depth and moose movements. However, Edwards and Ritcey (1956) in British Columbia were the first to present detailed observations on the relationships between moose migrations and snow conditions. They found that a gradual altitudinal movement from 1525-2135 m to 760-1220 m during fall and winter coincided with a gradual increase in snow depth on summer range. A rapid return to higher elevations during spring coincided with a rapid snow melt. Separation of winter and summer range was not complete, although most animals departed higher elevations by the time snow depth reached 75 cm. Upward movement to summer range was initiated when melting reduced snow depths to 30 to 45 cm. Cold temperatures appeared to alter the effect of snow by speeding movement downward in the fall and retarding movement upward in the spring.

Ritcey (1967), also in British Columbia, noted that deep snows at high elevations were responsible for the fall and winter movement to elevations below 1050 m. Arrival on winter range generally began in November when snow depth was less than 15 cm and continued throughout the winter. Departure from winter range began in late February or early March, while snow depth was as great as 125 cm but declining.

Kelsall and Prescott (1971) and Telfer (1967a, b) in the Canadian Maritime Provinces, studied winter segregation of white-tailed deer and moose in relation to moose sickness induced by the meningeal worm, *Parelaphostrongylus tenuis*. Although segregation was not complete, deer generally wintered at elevations below 200 m, while moose remained at elevations above 200 m. Snow depths of 85-90 cm above 200 m did not initiate downward migration of moose even though snow depths were more favorable and browse more abundant at lower elevations. However, relatively high snow density and hard crusts due to winter thaws and rains may have provided some support to moose, thereby reducing the effective snow depth (Telfer, pers. comm.).

Knowlton (1960) and Stevens (1970) reported that in Montana, deep snow on summer range above 1830-2135 m initiated movements to lower elevations. Movements were gradual, and frequently lasted from December to March. Harry (1957) reported that in Wyoming, increasing snow depth at high elevations resulted in a gradual downward movement and concentration of moose in mountain valleys by December. Snow conditions associated with these studies in Montana and Wyoming were not reported. However, Houston (1968) in Jackson Hole, Wyoming, found that downward movements from 2190 m to winter range at lower elevations began in late December in response to snow depth of about 80 cm on the summer range. Movement to spring and summer range began in late March in response to a snow crust formation capable of supporting moose and in response to disappearance of snow from south and east facing slopes. Moose densities on winter range were 10 moose/km^2 in Montana (Stevens, 1967:7 cited after Stevens, 1970) and 19 moose/km^2 in Jackson Hole (Houston, 1968).

Seasonal movements of moose in response to snow in Alaska have been noted by some workers. Rausch (1958) reported that an early snowfall in 1956 at high elevations in southcentral Alaska caused an early migration in November to lowland areas; he concluded from his extensive observations that snow influences but dœs not cause seasonal movements of moose.

Fall migrations in hills and moutains of interior Alaska generally occur as a gradual downward movement between December and March (LeResche, 1974). The extent, time, and composition of the migrating animals appear to be closely related to snow conditions. In late November and early December, 1970, snow depth of 90 cm (55 cm above average) at elevations of

600 to 915 m in hills near Fairbanks apparently caused an abrupt downward migration of moose to elevations below 300 m. Over 1,200 animals were seen on, or moving toward low elevation riparian habitat during 23 hours of Alaska Department of Fish and Game aerial surveys in early December. Almost no animals were found on the usual upland fall and early winter range. Snow depths of 110 to 120 cm persisted until early April and moose remained along rivers until mid-March when they apparently dispersed into adjacent timbered areas. Similar observations during 1970 were reported by Bishop (1971) for western Interior Alaska, where snow depth of 60 m during the end of November apparently precipitated an early movement of moose from upland areas to lower elevation riparian habitat, where they remained until late March. I have studied the response of moose to winter weather factors in Interior Alaska since 1971. For example, relationships between moose movement and snow conditions during 1971-1972 were examined on a study area near Fairbanks. In Figure 1, "Tracks-Valley" indicates the 7-day total of fresh moose tracks crossing a one-half mile long transect in a valley. The valley is located at 245 m elevation, and represents typical winter riparian moose habitat. "Moose-Hills" indicates the number of moose counted during frequent intensive aerial surveys in a 75 km^2 drainage above the valley transect. The upland site ranges from 550 to 670 m elevation, and consists of mixed conifer and deciduous trees and shrubs which characteristically support modest numbers of moose during summer and fall in interior Alaska. While neither "Tracks-Valley" nor "Moose-Hills" indicates actual number of animals, they are throught to reflect the trend of animal abundance on each site. Snow depths and integrated Rammsonde resistance on the total snow cover (R_i) in shrub communities on the two sites are also noted.

A decrease in the number of moose observed at high elevations and an increase in the number of fresh tracks at low elevations occurred during late December and early January (Fig. 1). The decrease in fresh tracks in the valley during mid-January may have been related to reduced activity during extremely cold temperatures (–40° to –50° C) during that period, while the decrease in tracks after late February may have resulted from a dispersal of animals away from the riparian habitat where the transect was located. After January the number of moose in the hills remained low throughout the winter.

Snow depth at high elevations gradually increased to about 80 cm at the time of movement in late December. While lowland snow depths throughout January and early February ranged from 15 to 25 cm below that in the hills, depth at the two sites remained nearly identical during the rest of winter. The R_i of the snow cover sharply increased during December preceding movement of animals. The increase resulted from both an increase in total snow depth and an increase in ram hardness of given depth increments. The dispersal of moose from lowland riparian habitat to adjacent areas during March may have been influenced by the declining R_i making travel less difficult. Dispersal from riparian habitat in March may also have been related to the lower snow depth, density and hardness in deciduous and coniferous tree communities during that time (Coady, unpubl.). The range for snow density of settled snow at the upland shrub site increased from 0.16 – 0.24 g/cm^3 in late November to 0.20 –

0.31 g/cm³ in late December, while the range of NRC snow hardness for settled snow increased from 10-50 g/cm² to 50 – 500 g/cm² during the same period.

Conclusions regarding the significance between integrated Rammsonde resistance and movement of moose would be highly premature at this time. However, based upon the above data and upon similar correlations between R_i and moose behavior in other study areas during both 1971-1972 and 1972-1973 (Coady, unpubl.), further studies using the Rammsonde penetrometer appear justified.

Movement of moose onto lowland habitat during the 1971-1972 winter was studied on two sites located 90 km from the above study area, and each approximately 1.5 km² in size. Land clearing 10 to 15 years ago has resulted in a dense regrowth of shrubs and low trees in both the non-riparian (site no. 1) and riparian (site no. 2) habitats. Moose movement onto both sites began in late December and paralleled each other very closely until early March when nearly all animals had dispersed from the sites, apparently into more densely vegetated areas. Snow depths on both sites averaged about 70 cm in late December when animals began to appear, and remained near 80 to 90 cm until late April. The maximum number of animals was 11 (density 7/km²) on site 1 in mid-January. During the preceding winter, snow depth on the sites averaged 115 cm in January and the maximum number of animals during that time was 36 (density 24/km²) (Fig. 2).

Seasonal migrations of moose in Interior Alaska are not always influenced

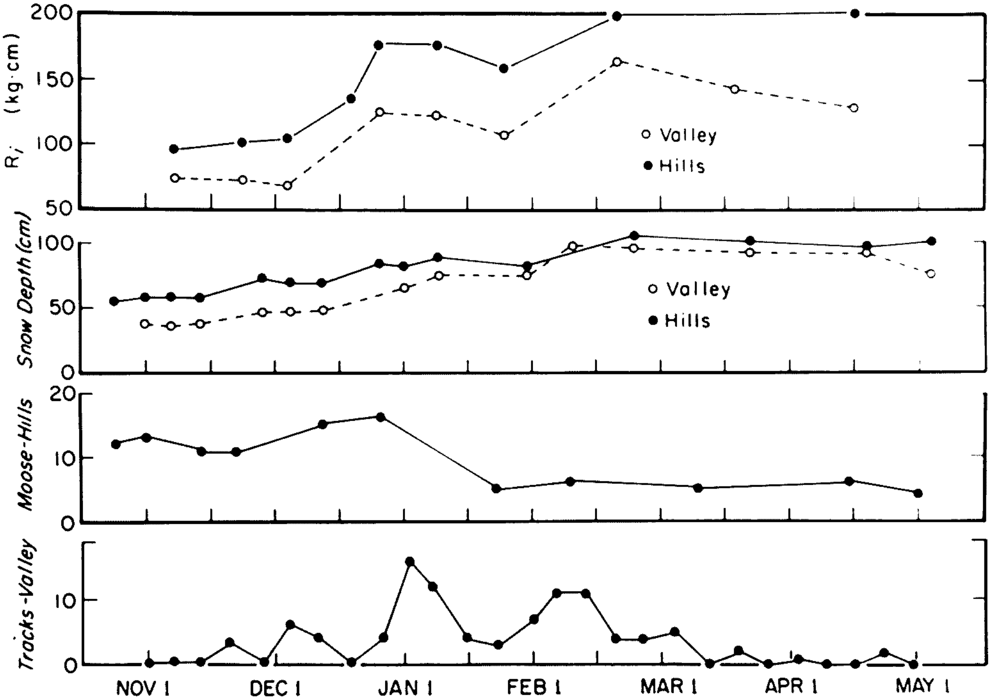

Figure 1. Movement of moose, snow depth, and integrated Ram hardness (R_i) of the snow cover at high and low elevations during winter 1971-72 near Fairbanks, Alaska. Ordinate values for the two lower curves represent the number of animals (Moose Hills) observed during aerial surveys and the seven day total of fresh tracks (Tracks Valley) crossing a one-half mile transect in a valley.

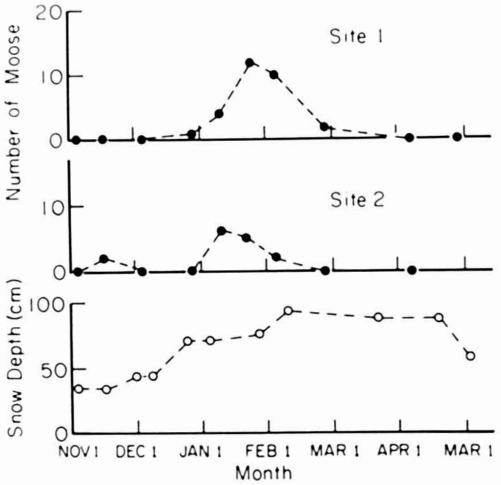

Figure 2. Movement of moose and snow depth on two sites characterized by dense deciduous regrowth during winter 1971-72 near Fairbanks, Alaska. Snow depths were similar on both sites.

by snow conditions. Movement of some animals from lowland summer range to either upland or riparian shrub habitat may begin in August, well before snowfall occurs, and continue throughout the winter. However, while initial movements may be related to factors other than snow, the speed and extent of migration is apparently influenced by snow. During winters of early or deep snow, movement of most animals from lowland summer range may occur sooner and to a greater extent than during winters of late or little snow. Availability of browse as affected by snow depth may be particularly important in influencing movements over flat terrain where local differences in snow conditions are not great. For example, late snowfall may have accounted for exceptionally heavy and extensive use of some low (40 to 60 cm high) willow (*Salix pulchra*) communities on the Tanana Flats near Fairbanks during fall and early winter, 1972.

Movement to summer range in interior Alaska apparently occurs during a relatively short period after snow melt has exposed patches of bare ground. Observations of animals and tracks suggest that when snow cover persists into mid - to late - May, substantial movement of animals does not occur until that time. However, an early thaw results in an early movement to summer range during April and early May. Advanced snow melt during spring 1973 resulted in a 70 km migration between April 10 and April 20 of a radio-collared moose from winter to summer range (Coady, 1973).

Although the above data are preliminary and highly limited in scope, they illustrate an approach to studying moose-snow relationships which may prove useful in other areas. Detailed observations of moose distribution and movements, snow parameters and temperature and wind conditions in several areas of Interior Alaska over three years will be reported in a future publication.

Habitat selection and movement on winter range in relation to snow conditions have been reported in several excellent studies (Nasimovitch, 1955; DesMeules, 1964; Telfer, 1970; Berg, 1971; Peek, 1971a, b; vanBallenberg and Peek, 1971) and reviews in this volume (Berg and Phillips, 1974; Brassard *et al.*, 1974; Peek, 1974; Peterson and Allen, 1974) and will therefore not be further considered here. Most of these studies suggest an increased use of dense cover with an increase in snow depth, density, or hardness, and a relatively small winter home range, although actual snow conditions causing a change in habitat selection or home range size are variable.

Activity of moose in response to snow

Restricted movement and small home range of moose during winter have been reported by numerous workers. Studies indicate that movements are most limited during periods of deep snow. Knorre (1959) in Russia found that the average winter home range of moose decreased from 225 ha during mild winters to 97 ha during average winters, to 5 ha during severe winters (Table II). A decrease in home range size with increasing snow depth has also been reported in Russia by Nasimovitch (1965). Knorre (1959) found that a single moose occupied only 0.1 ha during a 48-hour period of heavy snowfall, while van Ballenberghe and Peek (1971) noted that a cow in Minnesota occupied a 2.4 ha balsam fir (*Abies balsamea)* stand during 25 days of rapid snow accumulation.

TABLE II

Size of winter range in relation to snow conditions in Russia (from Knorre, 1959)

Type of winter	*Average depth of snow in March (cm)*	*Crust*	*Number of moose*	*Size of range (hectare)*	
				$\bar{X}$	*Range*
Mild	62	No	23	225	40-700
Average	98	Yes	68	97	2-500
Severe	127	Yes	96	5	0.1-20

Berg (1971) found that winter home range of radio-collared mose in Minnesota averaged 233 ha (compared to 1,400 ha during summer), although from early March to mid-April movement was generally confined to areas less than 41 ha (Phillips and Berg, 1971). Berg (1971) also determined that daily movements during winter averaged less than 0.4 km per day, while during summer they averaged 1 km per day. LeResche and Davis (1971) reported that distances moved by penned radio-collared moose on the Kenai Peninsula, Alaska, were smaller during January and February than during November and December. Coady (1973) found that movements of four radio-collared moose in interior Alaska occurred within 25 to 75 km^2 areas in upland shrub habitat during December when snow depths were 35 cm. However, movements were limited to 1.3 km^2 areas in upland shrub and lowland riparian habitat for three to five weeks in January and February when snow depths had increased to 65 cm in both areas. During late winter and particularly in spring when snow was crusted, Timofeeva (1967) found that moose in Russia remained in very limited areas for several days. However, Timofeeva (1965) also noted that the distance traveled daily by some moose may be greater during mid — to late winter than during early winter. Confinement during periods of deep snow has also been reported to occur in riparian habitat by Nasimovitch (1955), Denniston (1956), Harry (1957), Knowlton (1960), and Stevens (1970), and in non-riparian habitat by Peterson (1955), DesMeules (1962), Pivovarova (1965), and Telfer (1967a, 1970).

While activity patterns of moose have been recorded by several workers (Murie, 1934; Peterson, 1965; Denniston, 1956; Geist, 1963; Berg, 1971), the influence of snow conditions on daily activity has not been widely studied. Both Timofeeva (1967) and Nasimovitch (1965) noted that daily activity of moose in Russia decreased with increasing snow depth. Knorre (1959) found that moose were active for a total of 11 hours per day in November and December when snow depth was low, and for 10 hours per day in February and March when snow depth was high. Animals were active for 14 hours per day during the summer. Most of the active time during both winter and summer was spent feeding. Timofeeva (1967) observed an adult moose to average four steps and consume six shoots of browse per minute when the snow was 45 cm deep. The moose averaged 0.9 steps but still consumed six shoots of browse per minute when the snow was 57 cm deep. She noted that during deep snow, moose consume all available browse within reach before moving. However, Timofeeva (1967) concluded that the rate of movement in deep snow depends largely upon the availability of forage. In areas with scattered browse, moose may be forced to move further to feed than in areas of more available food.

The duration and frequency of active and resting periods is apparently influenced by season and snow conditions. Timofeeva (1965, 1967) found that during early winter when snow depths were 50-60 cm, moose rest three to eight times and average five rest periods per day. Between January and March when snow depths reach 70 cm or greater, moose rest six to fifteen times and average eight rest periods per day. However, Geist (1963) in British Columbia found that the duration of both active and resting periods was greater in winter than in summer, indicating that fewer rest and active periods per day may occur during winter than during summer. Timofeeva (1967) calculated for moose that approximately 3.9 rest periods are associated with a 1 km movement through 50 cm deep snow, 4.7 rest periods through 60-65 cm deep snow, and 6.7 rest periods through snow depths greater than 70 cm.

Conclusions

The most important and commonly measured properties of a snow cover influencing the distribution and behavior of moose are depth, density, and hardness. The integrated effect of these properties is to increase the effort required for movement. Long legs are perhaps the greatest physical adaptation to movement in snow, and selection for long legs in deep snow areas may occur. Relatively large trackloads of moose tend to decrease throughout the winter due to seasonal weight loss, thereby decreasing trackloads.

Behavioral response of moose to snow are represented by movement to areas of greatest food accessibility and by reduced activity. Increasing snow depth during fall and early winter generally results in a gradual movement from summer to winter range. The timing and magnitude of movement is closely related to the timing and rate of accumulation of snow. Although there are exceptions, early and deep snow may result in an abrupt migration of most animals from summer to winter range, while winters of little snow may result in a more gradual and delayed movement of fewer animals. Spring movements from winter to summer range generally occur after thawing has exposed patches of bare ground. Local movements and duration of activity are usually restricted during periods of deep snow and during late winter.

Factors influencing moose migrations have been reviewed by LeResche (1974) and Pulliainen (1974). While few, if any workers conclude that snow is the ultimate cause of seasonal movements, most reports indicate that it is an important factor influencing movements. Perhaps the major effect of snow is to alter the energy balance of moose by either increasing metabolic requirements for movement or decreasing access to energy sources by limiting food intake. Deep or hard snow may restrict movement to the extent that considerably more energy is expanded in moving to feed than is assimilated from ingested food. Deep or hard snow may also cover low growing browse species, thereby reducing their availability and requiring more extensive activity to feed.

Energy requirements for moose are somewhat greater than energy metabolized from food during winter (Gasaway and Coady, 1974), and therefore factors which add to energy requirements or decrease energy availability further magnify the negative energy balance and weight loss of the animal. Movements of moose to areas where food quantity, quality, and accessibility are greatest, depending on snow conditions, minimize metabolic requirements and enhance energy intake for winter existence.

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AN OVERVIEW OF MOOSE COACTIONS WITH OTHER ANIMALS

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Résumé

L'auteur passe en revue les interactions que l'orignal (*Alces alces*) peut avoir avec les autres animaux. La prédation par plusieurs grands carnivores a déjà été décrite, mais le loup (*Canis lupus*) constitue le seul prédateur efficace. Quand il existe une sélection marquée en faveur des veaux, la prédation par le loup est probablement un agent important du contrôle numérique des populations d'orignaux concernés. La prédation par l'ours (*Ursus* spp.), le cougouar (*Felis concolor*) et le coyote (*Canis latrans*) est d'importance géographique et démographique limitée. Les interactions entre l'orignal d'une part, et la chèvre des montagnes (*Ovis* spp.) ou le bison (*Bison bison*) d'autre part, sont de caractère neutre puisque ces espèces recherchent des habitats et des diètes différentes. Localement, il peut exister une certaine compétition pour la nourriture entre le bétail domestique et l'orignal. Les activités du castor (*Castor canadensis*) ont une action bénéfique sur l'orignal en ce qu'elles retardent la succession forestière et stimulent la regénération d'espèces broutées (*Populus* spp. et *Salix* spp.). Parmi les interactions de l'orignal avec des mammifères herbivores plus petits, celles mettant en cause les lièvres (*Lepus* spp.) des forêts boréales sont les plus importantes. La correspondance des diètes de ces deux animaux a été étudiée, mais les effets de la compétition qui en résulte varient localement en fonction des densités des populations, de l'épaisseur de neige au sol et de la diversité végétale. Les porcs-épics (*Erethizon dorsatum*) et d'autres petits rongeurs peuvent favoriser l'orignal localement en arrêtant ou en pertubant la succession des forêts conifériennes. Bien que peu étudiés, des rapports de compétition entre l'orignal et les tétraonidés semblent exister. Pendant l'été, les diptères piqueurs peuvent influencer le comportement de l'orignal. La tique d'hiver (*Dermacentor albipictus*) est un des ectoparasites importants de l'orignal, mais son impact sur la démographie de celui-ci reste à déterminer. Les pertes (à court terme) de nourriture et de couvert hivernaux, résultant des dommages causés au sapin baumier (*Abies balsamea*) par la tordeuse du bourgeon de l'épinette (*Choristoneura fumiferana*), sont largement compensées par les effets à long terme de ces dommages sur l'habitat de l'orignal, surtout en perturbant les stades climaciques et en stimulant la regénération d'espèces recherchées par l'orignal. En conclusion, l'auteur est d'opinion que l'aménagement de l'orignal doit se faire en tenant compte du rôle spécifique de ces différentes interactions, vues dans un contexte local.

Abstract

Moose (*Alces alces*) interactions with other animals are reviewed. Predation by several large carnivores has been described, but the wolf (*Canis lupus*) is the only effective moose predator. Where there is marked selectivity for calves, wolf predation is probably important in the regulation of moose numbers. Bear (*Ursus* spp.), cougar (*Felis concolor*) and coyote (*Canis latrans*) predation appears to be of limited geographic and demographic importance. Moose coactions with mountain sheep (*Ovis* spp.) and bison (*Bison bison*) are largely neutralistic due to differential dietary or habitat preferences. Domestic livestock compete with moose for food, primarily on a local basis. Beaver (*Castor* spp.) activities benefit moose, mainly by setting back forest succession and stimulating regeneration of browse species (*Populus* spp. and *Salix* spp.). Of moose coactions with a variety of smaller mammalian herbi-

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vores, those with the boreal hares (*Lepus* spp.) are most significant. Dietary overlap has been documented, but the effects of competition vary locally with respect to population densities, snow depth and plant diversity. Porcupines (*Erethizon dorsatum*) and other smaller rodents may benefit moose locally by arresting or setting back coniferous forest succession. Although little investigated, some competitive interactions between moose and various tetraonids exist. In summer biting insects apparently influence moose behavior. The winter tick (*Dermacentor albipictus*) also constitutes an important moose ectoparasite, but its exact demographic significance remains undetermined. Short-term losses in winter browse and shelter resulting from damage to balsam fir (*Abies balsamea*) by the spruce budworm (*Choristoneura fumiferana*) are largely offset by the long-term beneficial effects of such damage on moose habitat, namely opening up climax vegetation and stimulating the regeneration of seral browse species. It is concluded that moose management should consider the specific role of coactions within the context of local conditions.

Introduction

Contemporary ecology stresses the community or holistic approach. Any comprehensive discussion of moose (*Alces alces*) ecology must include the species' interactions with a variety of faunal components of the biotic communities within which moose occur. The objectives of this paper are twofold: (1) to provide a synthetic framework that integrates the contributions of this chapter; and (2) to review current knowledge on moose relationships with animals not covered by other contributors to this chapter. Viewed in whole, moose relationships with other animals undoubtedly embrace the gamut of positive and negative coactions as enumerated by Odum (1971). Important moose parasites are dealt with in Anderson and Lankester (1974); the relationships discussed here will thus be of a predatory, competitive, commensalistic, amensalistic, or mutualistic nature.

Predation

WOLVES

Group hunting tactics distinguish the wolf *(Canis lupus)* as the most effective natural moose predator. Commensurately, moose-wolf coactions have attracted considerable attention from ecologists (Murie, 1944; Cowan, 1947; Mech, 1966, 1970; Jordan *et al.*, 1967, 1971; Wolfe and Allen, 1973). Various aspects of these interactions are also dealt with specifically in two other papers in this symposium (Frenzel, 1974; Peterson and Allen, 1974). Only a few synoptic comments will be made here.

The question as to whether wolves constitute an effective regulating factor on their prey populations is central to the subject of moose-wolf coactions. Various investigators (Murie, 1944; Pimlott, 1967; Schaller, 1972) have noted the importance of the age distribution of a predator's kill relative to its regulatory potential on the prey population. In the case of wolves, it has been well documented (Mech, 1966; Jordan *et al.*, 1971) that juvenile and senile moose bear the brunt of predation. Logically, predation of the very old, because of their relative scarcity, effects mainly a "sanitation" or culling of the population, and is of little consequence in population limitation. However, where wolf predation is markedly selective for calves and is non-compensatory in nature, wolves probably constitute a major factor in the limitation of moose numbers, by effectively reducing recruitment to the reproductive segment of the population. The question of whether wolf predation is a density-dependent process, increasing with moose density in the manner of population-regulating mechanisms (Solomon, 1964) has not been adequately answered and merits additional investigation. Pimlott (1967) concluded that the question of population regulation remains only partially answered. He cited the difficulty of obtaining accurate data on population levels and trends of both the wolf and its principal prey species as major problems.

COYOTE

The wolf's smaller nearctic congener, the coyote (*Canis latrans*) is generally recognized as an ineffective moose predator. Studies by Cowan (1944) and Hatter (1945) in the national parks of western Canada revealed that the incidence of calf remains — largely carrion — in summer coyote scats ranged from 5 to 10 percent. Hatter considered drowned calves as the source of carrion, but Cowan conceded the possibility of some coyote predation on neonate calves, that were left by their dams for extended periods. Hosley (1949) reported little or no effect of coyotes on moose in Alaska and Montana. Observations on Isle Royale support this conclusion. Krefting (1969) found moose remains in 55 and 53 percent, respectively, of winter-spring and summer-fall coyote scats collected on the island between 1948 and 1952. Earlier, however, Hickie (1943) had noted the inability of coyotes to kill even calf moose in deep snow. Krefting and other Isle Royale investigators (Mech, 1966; Wolfe and Allen, 1973) have linked the disappearance of the coyote on Isle Royale with the advent of the timber wolf. Prior to the wolf's arrival in the late 1940's (Hakala, 1954) coyotes probably scavenged extensively on the natural turnover of old, sick or starving moose. The culling process of wolf predation, which removed these very animals from the herd, eliminated an important food source for the coyote.

Murie (1934) suggested that coyotes may benefit moose by holding snowshoe hare (*Lepus americanus*) populations in check, thus preventing overutilization of moose browse by the hares.

BEARS

Both the holarctic brown bear (*Ursus arctos*) and the nearctic black bear (*U. americanus*) have been implicated as serious predators of calf and occasionally adult moose (Hosley, 1949; Peterson, 1955; Yazan, 1963). Brown bear predation is treated by Haglund (1974); my discussion then centers primarily on the role of the black bear as a moose predator.

On the Kenai Peninsula in Alaska, Sarber (1944) linked poor calf survival with bear predation; the reported ratio was 10 black to 1 brown. However, even brown bears killed few adult moose. Dufresne (1942) also noted bears as significant calf predators in the Yukon Flats. Chatelain (1950) reported that the occurrence of calf remains in 250 scats from Kenai bears rose steadily from 1.5 percent in the latter part of May to a peak of 26.3 percent in late July and early August and then declined to zero in late August. No attempt was made in that study to differentiate between black and brown bear droppings. Moreover, no inference was given as to what extent the bears consumed — as carrion — calves that had perished of other causes.

Recent Alaskan studies contradict these findings. LeResche (1968) noted greater than 50 percent spring-fall calf mortality, but documented the occurrence of calf hair in only two (5.7 percent) of 35 black bear scats examined. Both scats were from the same bear and it was suggested that the hair may have been the result of scavenging. He also observed that three moose-brown bear encounters all elicited precipitous flight by the moose, while five encounters of moose with black bears produced either no or very low intensity fear response by the moose. In British Columbia, Geist (1960) observed that moose retreated in three of five moose-black bear interactions. However, in none of these instances was a «precipitous» flight inferred. The single confrontation between a black bear and a cow with a calf did elicit a fear response by the calf, its dam assuming a defensive posture when approached by the bear.

Hatler (1972) noted the occurrence of moose remains in only 8 percent (2.5 percent by volume) of 23 black bear stomachs from interior Alaska. The only large volume of moose flesh found harbored hundreds of maggots, which attested to its carrion origin.

Although high black bear population levels may inflict losses locally, they are not the serious decimators of moose calves throughout their range as was once thought. Conceivably, human perturbation has «artificially» juxtaposed moose and black bears, resulting in a greater incidence of black bear predation in some places than would have occurred under primitive conditions. Schorger (1949) rated the timber wolf as the black bear's chief natural enemy. Rausch (1961) reported a widespread belief in Alaska that grizzlies prey on black bears and suggested that the latter evolved as a forest animal to avoid grizzly predation. Likewise, Jonkel and Cowan (1971) suggest that the two species are compatible in dense forests, but that the black bear is less abundant in open country because predation by grizzlies on black bears is inversely related to forest density. The decimation of wolves and grizzlies by man over much of their former range may have brought about an increase in black bear numbers in more open country, where moose are more abundant (see Scotter, 1964; Kelsall, 1972). Concomitantly, fires and clearing of extensive tracts of boreal forest have probably further augmented this interaction.

FELID PREDATORS

Moose predation by cougar (*Felis concolor*) is limited and largely opportunistic. Peterson (1955) surmised that these cats may have been more important moose predators in eastern North America during pristine times. Likewise, Wright (1965) inferred some cougar predation on moose in New Brunswick during the 19th century. However, an extensive review of the subject by Young and Goldman (1946) included only one alleged record. In south-central British Columbia an examination of 132 cougar stomachs (Spalding and Lesowski, 1971) revealed mule deer (*Odocoileus hemionus*) as the predominant food item, but moose remains occurred in 11 percent of 37 stomachs from one of the two study areas. Spalding (pers. comm.) confirmed one of the animals killed as an 8-month old female; the others were classified as «young».

Hornocker (1970) found no instances of cougar predation on moose in the Idaho Primitive Area. Although moose were stated to occur in low numbers, they did not winter on the study area proper.

Information is lacking on cougar predation as a factor in early calf losses. Spalding and Lesowski (1971) concluded that there is a noticeable element of chance involved, and that in areas of abundance, cougars will prey upon moose when opportunity affords. Given the cougar's current limited numbers throughout most areas of present moose range, however, its overall impact as a moose predator is probably insignificant (see Hosley, 1949).

Other felid species occasionally kill moose. Heptner and Nasimovitch (1967) reported that moose may comprise as much as 10 percent of the tiger's (*Panthera tigris*) prey in the Sikhote-Alin Mountains of northeastern Asia. Predation by the European lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) on moose is treated by Haglund (1974).

Relations with other herbivores

Moose are commonly associated with a variety of other herbivores. My discussion will focus primarily on moose relationships with the native ungulates, domestic livestock and smaller mammalian and avian species that are not covered by other papers in this chapter.

NATIVE UNGULATES

Mountain sheep (*Ovis* spp.) and bison (*Bison bison*) are sometimes sympatric with moose in western North America. Competition, however, is probably negligible or, at most, limited due to spatial separation of preferred habitat types and different diets (see Cowan, 1950 ; Oldemeyer *et al.,* 1971 ; Flook, 1964). Indeed, complementarity may even exist whereby the impact of foraging by one ungulate species on the plant community benefits another herbivore. An example of such an effect was reported by Holsworth (1960) for Elk Island National Park, Alberta. Heavy moose and elk (*Cervus canadensis*) browsing on seral deciduous regeneration (*Populus* spp., *Salix* spp. and *Corylus* spp.) arrested forest succession and maintained grassy openings, which provided food for bison.

Moose and the diminutive roe deer (*Capreolus capreolus*) are sympatric in parts of Eurasia. Lykke and Cowan (1968) stated that, although some competition for food occurs, there is no evidence that it is serious. Markgren (pers. comm.) also discounted competition between the two and noted a parallel increase of both species in Scandinavia during the 20th century. Corroborating the findings of other investigators (Krieg, 1936 ; Rieck, 1956), he rated roe deer as «poor browsers», which feed primarily in the «field» layer. In deep snow, they are forced into dense spruce (*Picea* spp.) stands to seek out arboreal lichens and dwarf shrubs under covering branches. This habitat type is not frequented by moose. Markgren observed coincident spring feeding on early herbaceous vegetation in open fields, but noted that the two cervids appeared oblivious of each other's presence.

DOMESTIC LIVESTOCK

In many areas of western North America, the Shiras moose (*Alces a. shirasi)* shares its range seasonally with domestic livestock (cattle and sheep). Likewise, in Fennoscandia and parts of eastern Europe, cattle and other domestic animals are pastured, although far less extensively than in past centuries, in woodland, heath and meadow tracts that are also frequented by moose.

Ahlen (1965) attributed the increase of moose as well as roe and red deer (*Cervus elaphus*) during the past century in Scandinavia, largely to the decline of extensive domestic livestock pasturage, concomitant with the development of modern forestry. He provides an excellent overview of the phytosociological responses of several habitat types to grazing by cattle, horses, sheep and swine, and the implications for native herbivores.

Lykke and Cowan (1968) also described the implications of decreasing domestic livestock numbers and changing patterns of livestock husbandry practices during the past 50 years for Norwegian moose. With respect to dietary overlap, they rated goats as most competitive. However, by virtue of their numbers, sheep and cattle competition was considered more severe. Bjor and Graffer (1963) demonstrated reductions of 44 and 15 percent in hardwood regeneration on plots in clearcuts with «normal» stocking of sheep and cattle, respectively. Mean height of the surviving moose browse species was reduced by 76 and 55 percent, respectively, over those on control plots.

Several American investigators have described moose coactions with cattle and sheep. Knowlton (1960) suggested that extensive summer use of forbs by moose in the Gravelly Mountains of Montana could result in competition with sheep and elk that grazed the area during summer. In the same general area Peek (1963) found that the four major moose browse species, on both high and low ranges, were overbrowsed and in poor condition. Peek concluded that, although other browsing animals including cattle and sheep utilized the area, moose had the most significant influence on the browse species examined. Heavy utilization of aspen (*Populus tremuloides*) regeneration by sheep and cattle was recorded in some localized summer range areas. Cattle browsing of willow was negligible above 2000 meters even when the grass-sedge understory had been utilized extensively. The winter concentration area was also subject to cattle grazing each June, but Peek found less than 5 percent utilization of willow after cattle left the area and before moose returned.

Dorn (1970) investigated moose and cattle food habits on the Red Rock Lakes Wildlife Reguge in southwestern Montana. He considered forage competition insignificant. Wolf's willow *(Salix Wolfii)* accounted for 50.2 percent of all cattle browse, but was rarely taken by moose except in early winter. This third most abundant willow species on the study area served as a buffer to reduce cattle use of preferred moose species, namely *S. myrtillifolia, S. Bebbiana* and *S. Geyeriana*. Dorn also observed that cattle browsing did not become significant until the more palatable grasses, sedges and forbs had been largely utilized. Even then, most browsing was below 1.5 metre in height. Since Wolf's willow rarely attained this height and cattle browsing of other willows was confined to lower and lateral shoots, removal of the cattle could not be expected to substantially increase the amount of available moose browse above the snow. "Disturbance competition" noted by Denniston (1955), whereby moose display a behavioral intolerance to cattle, was not observed in Dorn's study.

The possibility of greater forage competition was conceded by Dorn (1970). This might result: (1) from increased trampling with heavier cattle stocking than the one animal per 2.0 hectares for 82 days on his study area; (2) in areas with a scarcity or absence of *S. Wolfii*; or (3) in situations where moose are forced to feed on this species due to the absence of more palatable willows. The second alternative apparently prevailed in the Jackson Hole area of Wyoming, where Houston (1968) reported direct competition between moose and cattle, resulting from autumn utilization of *S. myrtillifolia by* cattle.

Observations by Wilson (1971) on the north slopes of the Uinta Mountains (Utah and Wyoming) were similar to those of Dorn (1970). Cattle fed only on Wolf's willow, which was frequently browsed to a moderate degree. However, no occurrences of moose feeding on Wolf's willow were recorded; *S. Drummondiana* and *S. Geyeriana* accounted for 92.0 and 5.0 percent, respectively, of all winter moose browsing observations.

Recent studies by Ritchie (pers. comm.) in southeastern Idaho, however, suggested a negative impact of cattle on moose. Snow depths and winter moose occupancy of this predominantly willow area range from 120 to 150 centimeters and from 5 to 6 months, respectively. Most of the area was subjected to heavy summer cattle grazing, but approximately 4 hectares was fenced and received no cattle use. Aside from substantial vegetal differences (Fig. 1), fecal pellet counts revealed a significantly higher winter moose utilization of the area, which Ritchie attributed to greater forage availability. The willow species and actual stocking rate for cattle were not given.

A related facet of moose-cattle relationships is the practice of herbicidal treatment of riparian willow areas to encourage growth of livestock-preferred grasses and related plants. Such programs may significantly reduce the amount of available winter moose forage in some localities.

Moose may serve as potential reservoirs for the transmission of infectious diseases and parasites to domestic livestock. Diesch *et al.* (in press) found a higher incidence of leptospirosis in moose from northwestern Minnesota than in those from the northeastern sector of the state. The former area is characterized by higher cattle and swine populations. Karns (pers. comm.) also reported that liver flukes *(Fascioloides magna)* occurred in moose primarily in the northwest range in association with domestic livestock.

BEAVER

Coactions between moose and beaver *(Castor* spp.*)* comprise two major aspects. One, which is commensalistic,

Figure 1. Willow habitat in southeastern Idaho, showing differences in willow cover between an area heavily grazed by cattle on left and a lightly grazed area on right (photo by B. W. Ritchie).

involves the ecological effects of beaver colonization and abandonment, while the second, which is competitive (or ammensalistic), centers around dietary overlap between the two.

Ecological implications of beaver activities

Moose derive unilateral benefit directly and secondarily from tree cutting and dam construction activities of beavers. Shelton (1966) noted that Isle Royale moose frequently browsed the tops of felled trees before beavers utilized them. This feeding was not of ecological importance, however, since the amount of food involved was small in comparison with the total requirements of the moose herd. The loss of beaver food was also insignificant, since moose did not consume the bark. Similar observations have been reported by Ritcey (pers. comm.) in British Columbia and Lavsund (pers. comm.) in Sweden.

Of greater significance is the vigorous sprout growth stimulated by beaver cutting of mature trees, especially aspen (Hodgdon and Hunt, 1953; Shelton, 1966. Heavy cropping by moose prevents the sprouts from attaining a size large enough to produce much beaver food, but perpetuates regeneration of moose browse.

Inundation as the result of beaver activity kills almost all terrestrial vegetation which may include some moose food plants. These losses are likely offset in the long run by the creation of an aquatic ecosystem and its associated flora of submergent, floating and emergent aquatics. The seasonal affinity of moose for a variety of these plants when available is widely recognized. Some of the more preferred food species include the watershield *(Brasenia Schreberi)*, water lilies (*Nuphar* spp. and *Nymphaea* spp.), and pondweeds *(Potamogeton* spp.*)*. Shelton (1966) noted that production of aquatics was greatest in beaver ponds that were several years old, so that the benefit to moose need not be instantaneous.

Drained ponds, resulting from beaver abandonment, are usually invaded and soon dominated by various sedges, rushes and grasses, including several species of *Carex*, *Juncus* and *Scirpus* (Wilde *et al.*, 1950 ; Neff, 1957). Shelton (1966) listed bluejoint *(Calamagrostis* sp.) as a common grass colonizer of abandoned Isle Royale ponds. From this semi-aquatic association, plant succession proceeds slowly towards climax or subclimax vegetation. The time required for encroachment of seral woody species important to moose is a function of several factors. Knudsen (1962) observed that ponds in Wisconsin did not begin to develop woody vegetation for about 10 years. In an earlier Wisconsin study, Wilde *et al.* (1950) identified the underlying substrata as the major determinant in the persistence of marsh plants. On coarse, sandy-textured soils the sedge-rush-grass associations maintained possession for only a few years, to be replaced by aspen and paper birch *(Betula papyrifera)*. On peat or muck soils, however, the pioneer communities may effectively retard the reinvasion of woody species for several decades. A slow encroachment of willow, tag alder *(Alnus incana)*, dogwood *(Cornus stolonifera)* and other hydrophytic shrubs usually preceded the reestablishment of the original swamp hardwood and coniferous association on these sites.

Thus, it appears that the utility of drained beaver ponds to moose is limited. Shelton (1966) suggested that competition from alders, grasses and sedges, coupled with moose browsing, probably precluded regeneration of aspen in drained ponds. Direct invasion by late-successional species such as white spruce *(Picea glauca)* and balsam fir *(Abies balsamea)* would be more likely. In Colorado Neff (1957) observed that willow growth was greater around the margins of occupied ponds than on abandoned and drained sites.

The coexistence of moose and beaver may benefit moose in yet another way; beaver may serve as an alternate or, buffer prey species for wolves. Whether or not this actually effects a reduction in the frequency of wolf predation on moose has not been determined. Indeed, the relationship appears conditional and largely one of seasonal availability. Several studies (Mech, 1966; Pimlott *et al.*, 1969; Frenzel, 1974) have documented relatively high occurrences of beaver remains in spring and summer wolf scats. This coincides with the time of year when 2-year old beavers are traveling overland to establish new colonies and are particularly vulnerable. It is not implied, however, that a high incidence of beaver predation by wolves might not serve to reduce the predator's impact on young moose calves.

Moose-beaver competition

Virtual unanimity prevails among beaver ecologists with respect to the singular preference of beaver for aspen and other *Populus* species, whenever available. Willows and white birch constitute the most common second choices in western and eastern North America respectively (Shelton, 1966). The overlap in preferred food species is obvious, although this does not denote competition *a priori*. The list of food plants common to the diet of both herbivores is considerably longer, but the others are of less significance because they do not comprise a major portion of both animals' diets.

Several authors (Bassett, 1951; Semyonoff, 1951; Rudersdorf, 1952; Shelton, 1966) have considered various aspects of moose beaver competition, but quantitative data are few. It appears, however, that competition — if present — will usually operate to the detriment of the beaver. Shelton (1966) idenfified moose browsing of regenerating aspen shoots as one of the main reasons for the failure of the shoots to attain a size large enough to produce much beaver food. Similar effects in response to deer and elk browsing on aspen and willow in Colorado were hypothesized by Rutherford (1964). Rudersdorf (1952) found that neither beaver nor moose in the Jackson Hole area ate alder or lodgepole pine *(Pinus contorta)* if willow and aspen were present. Where the latter species had been removed, both animals were subsisting on alder. He also concluded that depletion of preferred food species would have greater adverse consequences on beaver.

A good example of the impact of a large herbivore on beavers is in Yellowstone National Park, where chronic high elk densities have contributed to the elimination of beaver in some areas. An investigation of the status of beaver in the 1950's (Jonas, 1955) revealed no sign of the animals in one locality where an estimated 200 had lived three decades earlier (Warren, 1926). Barmore (1967) attributed the decline to the two-fold effect of beaver cutting the mature overstory aspen, while heavy elk browsing of the regenerating shoots prevented normal reestablishment of aspen stands along the streams. An analogous joint beaver-moose impact on the vegetation in some areas is conceivable.

Dorn (1969) stated that moose-beaver competition in the Red Rock Lakes area of Montana was greater than moose-cattle competition. He noted damage to willows from cutting and inundation in several areas. Although Dorn did not consider such damage to be significant, he concluded that it could become so with a slight increase in the beaver population. Since most aspen proximal to suitable watercourses on the area had been eliminated, beaver were utilizing willow as their primary food and construction material.

Bergerud and Manuel (1968) quantified the adverse effects of excessive moose browsing on white birch *(Betula papyrifera)*, which is an important food plant for Newfoundland beaver. Aerial beaver censuses in two comparable areas of high and low moose density yielded 0.04 and 0.46 colonies per square kilometer respectively.

OTHER RODENTS

Where abundant, porcupine *(Erethizon dorsatum)* damage to coniferous trees may play a role in opening up the climax forest association. This in turn stimulates regeneration and growth of shade-intolerant browse species to the benefit of moose. Telfer (pers. comm.) observed such a complementary relationship in the Maritime provinces of Canada. He noted that many small openings in forest stands on moose wintering grounds were the result of current, or past porcupine damage. Various authors (Reeks, 1942 ; Krefting, 1965 ; Brander and Stearns, 1963) have cited several climax and subclimax conifers and hardwoods as preferred porcupine food species.

Krefting (pers. comm.) submitted that porcupine densities are often too low to be of significance in this respect. In the Lake States, however, Krefting *et al.* (1962) cited densities as high as 0.4 animals per hectare in concentration areas. Normal densities ranged from 0.08 to 0.13 animals per hectare. Decortification of conifers and hardwoods resulted in a reduction of growth rate and occasional tree mortality. Damage was rated as medium to heavy on 214,000 hectares of National Forest land in the Lake States (Krefting *et al.*, 1962).

Another commensalistic aspect of moose-porcupine association has been noted by Brander (pers. comm.). Bark is the main source of winter porcupine food, while herbaceous growth predominates in spring and summer diets (Reeks, 1942). Brander observed porcupines clipping the smaller branches of hemlock *(Tsuga canadensis)* to get at the bark of larger branches. Moose did not occur in the area (northern Michigan), but white-tailed deer *(Odocoileus virginianus)* fed extensively on the fallen clippings. It was estimated that a single porcupine dropped 1.6 kilograms of clippings per week. Other investigators, especially Curtis and Kozicky (1944) and Telfer (pers. comm.), have commented on this commensal behavior. Telfer estimated that porcupines of the densities reported by Krefting *et al.* (1962) could drop enough browse to maintain 0.3 to 1.1 moose per km^2.

Heptner *et al.* (1966) stated that muskrats *(Ondatra zibethica)*, at high densities, may be serious moose competitors. Nowhere in the North American literature have I encountered evidence substantiating this contention. Indeed, muskrats may compete with moose in summer for some aquatic food species (Fitzgerald, pers. comm.) but this does not appear critical ; in fact, as indicated by several studies (Butler, 1940 ; Takos, 1947 ; Bellrose, 1950 ; Bednarik, 1953), muskrats feed primarily on some of the coarser aquatic emergents such as cattails *(Typha* spp.*)* and bulrushes *(Scirpus* spp.*)*, which have low preference ratings for moose.

The nature of moose coactions with smaller rodent species is poorly documented. In Wells Gray Park, British Columbia, Webb (1952) suggested that the small rodent species, of which deer mouse *(Peromyscus maniculatus)* was most important, could suppress regeneration of conifers by direct damage to young plants, cone crop destruction and seed consumption. Webb concluded that moose winter yards in the park could have sustained the animals for a longer period, than had the rodents not been present. Analogous effects of small rodent populations might be extrapolated to other areas of moose range. In Norway, however, Lykke and Cowan (1968) noted that mice (especially *Clethrionomys* sp.) may be of some importance as competitors. Decortification of browse-producing species, during years of dense rodent populations, may cause a high percentage of mortality in these plants.

HARES

Throughout much of the northern hemisphere, moose occurrence coincides with that of the boreal hares. Despite this spatial and at least partial dietary overlap, considerable controversy exists as to the gravity of competition between these herbivores. Quantitative studies on the subject are few and the findings are by no means unanimous.

Reports of early Alaskan observers («An Alaskan» 1923; Dufresne, 1942) condemned snowshoe hares *(Lepus americanus)* as severe moose competitors for willow, birch and alder. Coady (pers. comm.) reported that these and other deciduous shrub species such as aspen and cottonwood *(Populus balsamifera)* are preferred by moose and also used extensively by hares in interior Alaska. Coniferous species, larch *(Larix laricina)*, black spruce *(Picea mariana)*, and white spruce, are used extensively by hares but rarely if ever by moose. Coady noted that the portions of those species browsed by both animals differed, depending largely on snow depth. Based on his experience in interior Alaska, O'Farrell (pers. comm.) doubted the existence of serious moose-snowshoe hare competition, because the many species of willows and other shrubs constitute a «3-dimensional array», which could supply both consumers at different levels. Heptner *et al.* (1966) reached similar conclusions with respect to competition between moose and *L. timidus* in Russia.

Oldemeyer (pers. comm.) provided quantitative data on hare and moose utilization of marked birch plants on the Kenai Moose Range. During the winter of 1971-72 the hares, which were at, or approaching a population peak, browsed approximately 25 percent of the 984 marked plants. On one plot in a moose exclosure, the hares browsed 92 percent of the 24 marked plants to some degree and completely removed current annual growth from six of the plants. Oldemeyer observed that hares did more damage to plants less than a metre high by browsing the main stem rather than the lateral branches as they would have on taller plants. Whether this browsing pattern actually competes with moose was unknown, since the smaller plants produce less forage. Lateral branches clipped by the hares appeared to be in a location less readily reached by moose, as leaders in the upper portions of the crown.

In Newfoundland, Dodds (1960) found definite similarities in the feeding patterns of both herbivores, characterized by: (1) utilization of herbaceous material during summer and woody plants in winter ; (2) browsing primarily of smaller and younger stems ; and (3) the tendency to browse individual plants heavily. Of the 30 woody species on the study area, 27 were browsed to some degree by both moose and hare. Heavy moose utilization of balsam fir regeneration reduced winter cover for hares, thus precluding their habitation of cutover areas for several years. Competition for birch — the most important species for hares and the most important hardwood species for moose — increased only from the time hares began to inhabit cutovers. As the cutovers progressed towards climax conditions, total use of birch, and thus competition, declined significantly due mainly to decreased moose utilization. Dodds concluded that extensive competition for food occurred only in cutover areas with predominant fir regeneration. Areas with a spruce canopy and ericaceous understory probably provided hares with palatable foods, which were not readily taken by moose. He suggested, however, that in cutover areas moose browsing could moderate hare population fluctuations (see Keith, 1963) by maintaining near static low densities for 10 years or more. Similarly, Bergerud and Manuel (1968) believed that moose damage to birch stems and coniferous cover had reduced snowshoe hare densities in central Newfoundland.

Mercer (pers. comm.) stated that moose in Newfoundland are strongly competitive with both snowshoe and arctic hares *(L. arcticus)*. Preferred winter foods for the arctic hares are white birch and other hardwoods. Mercer attributed the scarcity of hares in some areas to declines — and even local eradication — of white birch browse available to hares, quite possibly as the result of overbrowsing by moose.

In northeastern Nova Scotia, Prescott (1968) emphasized the potential negative impact of snowshoe hares on moose. While only «slight» actual competition was observed, he noted direct dietary overlap. Of the 26 woody species recorded on the study area, 20 were browsed by both moose and hare. More importantly, most species browsed by moose were also utilized heavily by hares. Prescott pointed out that deep snow could substantially increase the degree of competition. Fifty percent of the total stems of all species tallied were in the 0 to 0.6 metre height class. This class accounted for 57.6 percent of all hare-browsed stems, as compared to 16.4 percent of moose-browsed stems. Deep snow cover would have a two-fold effect by reducing the total forage availability for both species and by forcing hares to feed on taller stems, which comprised the bulk of moose browse.

The effects of high snowshoe hare populations on forest vegetation in New Brunswick were investigated by Munroe (1969). Hare populations on the study area were believed representative of densities elsewhere in the province, but moose and deer were present only in limited numbers. Browsing by hares and ungulates on regenerating shoots — especially balsam fir — was greater in clear cutovers than in partial cutovers. Hares accounted for 78 and 49 percent of the total browsing on the two types of cutovers, respectively. Browsing on all species was most severe in the 1 to 2 meter height class. Browsed balsam fir showed a 35 percent reduction in growth over those not currently browsed. Munroe suggested that repeated browsing might allow spruce to replace fir as the dominant species in the forest association.

Ritcey (1965) reported that the browse preferences of snowshoe hares, moderately abundant on moose winter range in Wells Gray Park, differed from those of moose. The most productive moose range supported few hares, competition being important only on marginal range. The immediate impact of hare competition was outweighed by the long-term beneficial effect of selective hare browsing, which retarded coniferous forest succession. Ritcey (pers. comm.) also inferred a locally and minor beneficial effect of moose browsing on hares, the latter species feeding on willow and aspen branches broken down by moose.

Generalization as to the severity of moose-hare competition is difficult. Given, however, the lagomorph's propensity for periodic high population densities, at least localized competition for food undoubtedly occurs, contingent upon snow conditions and the availability of alternate food species. In this context, Telfer (1972) reported a high degree of adaptation by hares to utilization of available browse species. The potential for serious competition would appear to be greater in the simpler, more northern ecosystems with inherently lower plant diversity.

Where significant competition does exist, those predators which prey extensively on the lagomorphs may be beneficial to moose. The question of whether this predation functions as a true population depressant, when hare numbers are at peak densities, is not within the scope of this discussion. The role of the coyote in this respect was noted above (Murie, 1934). The importance of the snowshoe hare in the diet of the lynx *(Lynx canadensis)* is well documented (see Saunders, 1963; Nellis, Wetmore and Keith, 1972). A variety of other terrestrial and avian predators may play a similar role, if any.

TETRAONIDS

Little is known about possible competitive relationships between moose and various Eurasian and North American tetraonids. Circumstantially, dietary overlap and spatial association would suggest the potential for such competition.

The importance of willow and birch in the winter diet of the holarctic ptarmigan *(Lagopus* spp.*)* is well documented (Peters, 1958; Weeden, 1967; Rajala, 1966; Pulliainen, 1970; May and Braun, 1972). Weeden (pers. comm.) stated that moose-ptarmigan competition on willow probably occurs in Alaska, its severity being determined locally by the availability of alternate food species such as alder for the ptarmigan. In Newfoundland, Mercer (pers. comm.) reported competition for winter food between moose and both willow *(L. lagopus)* and rock *(L. mutus)* ptarmigan. These birds utilize forests adjacent to barren grounds in winter, their preferred food species being white birch. The impact of moose browsing on the birch appeared more severe on the rock ptarmigan, since this species is more restricted to the barren grounds and immediately contiguous forest in winter, whereas the willow ptarmigan may migrate considerable distances from their spring-to-fall barren ground habitat. Pulliainen (1970, 1972, and pers. comm.) submitted that moose-ptarmigan competition also occurs in Finland, but the exact nature of the relationships has not yet been quantified. Moreover, it is difficult to divorce the confounding influence of differential local hare densities in these situations (Loisa and Pulliainen, 1968).

Cases can be made for moose competition with other tetraonids. Bergerud and Manuel (1968) inferred that heavy moose utilization of white birch in central Newfoundland may have had a negative effect on the recently introduced ruffed grouse *(Bonasa umbellus)*, which also utilized birch. Similarly, Lykke and Cowan (1968) stated that some competition for food undoubtedly exists with black grouse *(Lyurus tetrix)* and capercaillie *(Tetrao urogallus)*. Whether it is of significance has yet to be documented. Catkins of *Betula tortuosa* and *B. nana* represent an important food item for black grouse in northern Europe (Pulliainen, 1970). Moose may also browse the twigs of these species heavily.

Some invertebrate coactions

My review has emphasized moose relationships with other mammalian and avian species. However, some of the more important invertebrate coactions merit cursory treatment. Of primary significance are those with arthropod pests and phytophagous forest insects.

ARTHROPOD PESTS

Moose are plagued by a variety of dipteran pests, of which the tabanids are most important in influencing their behavior. Peterson (1955) rated the moose fly *(Lyperosiops alcis)* as the most serious pest in Ontario. However, more recent and detailed accounts of moose behavior (Denniston, 1956; De Vos, 1958; Geist, 1960) include little or no mention of moose behavior in response to biting insects. Heptner and Nasimovitch (1967) noted that some members of the Tabanidae serve as vectors in the transmission of anthrax. Other biting insects, such as deer flies *(Chrysops* spp.*)* and blackflies *(Simulium* spp.*)* have been suggested as of possible importance to moose, but there exists some concensus that these species are of relatively minor or at best of secondary significance (Olsen and Fenstermacher, 1942; Mech, 1966; Heptner and Nasimovitch, 1967).

Accounts of moose natural history frequently report that they actively seek out water as a refuge from biting insects. Murie (1934), Peterson (1955) and De Vos (1958) noted the dearth of observations validating this behavior and submitted that moose enter water primarily to cross it or feed on aquatic vegetation. Flook (1959), however, suggested that the use of water to escape pests may be common in some situations. He observed several moose standing in deep and swift-flowing water, where aquatic plants were not present, apparently seeking refuge from blackflies. Müller-Using and Schloeth (1967) maintained that moose do not bathe in mud as suggested by earlier investigators (see Peterson, 1955), but that they do seek relief from insects in water or extensive reed *(Phragmites* sp.*)* beds. In East Prussia, Kramer (1963) observed a bull moose which spent at least 2 hours in a pond with only its head above water, while two small rafts of ducks swam around the animal picking horseflies from its nose. On Isle Royale Jordan (pers. comm.) has observed that moose frequenting beaver ponds often pick up leeches *(Hirudo* sp.*)* on lesions and abraded areas.

Another hypothesis for moose utilization of water has been advanced by Kelsall and Telfer (1974), namely that moose are poorly adapted to hot temperatures and may enter water in summer to cool off. Whether this is the case, or whether they actually retreat to water for protection from insects, it would appear that the cooler air currents of higher elevation habitats would reduce their reliance on water for either reason.

Botflies *(Cephenomyia* spp.*)* have been reported as occasional moose parasites in North America (Cowan, 1951 ; Peterson, 1955). However, Heptner and Nasimovitch (1967) rated them as the most important dipteran parasite throughout the moose's range in Russia. They noted that younger animals may occasionally — although most infrequently — succumb to inanition as an indirect result of heavy infestation by the larval stages of these flies.

Probably the most significant moose ectoparasite is the winter tick *(Dermacentor albipictus)*. Its life history has been reviewed by Hatter (1950), Cowan (1951) and Peterson (1955). Whether the ticks constitute a primary cause of moose mortality is subject to some controversy, although there appears to be some positive correlation between the degree of infestation and weak, emaciated or dead animals (see Mech, 1966). In British Columbia, Hatter (1950) observed high moose mortality as the result of a tick-malnutrition complex. However, Ritcey and Edwards (1958) concluded that a heavy infestation of ticks alone does not seriously weaken moose. They also observed considerable annual variation in the extent and severity of infection.

PHYTOPHAGOUS INSECTS

Defoliation by various forest insects may affect moose primarily in two ways: (1) in reducing food as the result of extensive damage and mortality in important browse species ; and (2) in altering species composition and/or successional patterns in the plant community struck by the insect epidemic. An example of the latter effect is given by Blais (1961), who cited an approximate 75 percent increase in the volume of balsam fir in forests of the Gaspé Peninsula over a 30-year period, due primarily to the destruction of white spruce by the European spruce sawfly *(Diprion hercyniae)*. This vegetational change has probably been beneficial to moose. Extensive mortality in forest stands as the result of insect epidemics may often predispose them to a greater risk of severe fire and its associated synecological consequences.

Throughout the boreal forest zone of North America, the spruce budworm *(Choristoneura fumiferana)* rates as the most widespread and destructive forest insect. The spruce budworm literature is voluminous and has been effectively reviewed by Morris (1963),Schoenike (1965) and Strand (1972). However, as is the case with other phytophagous insects, most works deal primarily with the autecology and population dynamics of the insect and the effects of epidemics on host species of economic significance. The synecological implications of spruce budworm attacks have received little attention.

The significance of spruce budworm to moose is greatest in the eastern area of their association, where balsam fir — the principal host species and a major component of the climax forest — is an important moose food. In areas of heavy infestation, successive defoliation often results in extensive balsam fir mortality. Peterson (1955) emphasized the reduction in winter moose browse resulting from spruce budworm damage to balsam fir in Ontario. He did, however, note some « compensations », namely that such areas frequently display a rapid regeneration of young balsam fir, the speed of this regeneration depending on local conditions. It is generally accepted that older stands (40 years and older) are both more vulnerable to budworm outbreaks and more seriously damaged by defoliation than younger stands. The overstory mortality often releases the frequently abundant advanced reproduction of balsam fir. In Ontario, Ghent *et al.* (1957) observed an increase of formerly less abundant small perennials and shrub species following spruce budworm attacks. Raspberry *(Rubus idaeus)* and mountain maple *(Acer spicatum)* generally showed the highest frequency of occurrence, but several more palatable moose-browse species became moderately abundant. These included white birch, aspen, sand-cherry *(Prunus pensylvanica)*, beaked hazelnut *(Corylus cornuta)* and bush honeysuckle *(Diervilla lonicera)*. Balsam fir regeneration was also present, which would in time succeed and shade out these mid-successional species.

In New Brunswick, Telfer (pers. comm.) described a vegetational pattern consisting of essentially two age classes, produced by recurrent budworm outbreaks. One age class was approximately 70 to 80 years of age, while the other (40 year-old stands) originated after the previous attack. The new outbreak usually killed much of the older stands and large patches in the 40 year-old stands. Thick stands of seral brush species such as those described above soon invaded the openings produced by the budworm attack.

As inferred above, fire may follow spruce budworm attacks, in which case plant succession may be set back even further. The long-term consequences of these perturbations are probably beneficial to moose. For example, on Isle Royale, the 1936 burn, which destroyed climax vegetation on about one third of the island's surface area, was preceded by a severe budworm outbreak. The invasion of aspen, paper birch and other seral species in this area essentially «rejuvenated» moose habitat.

In summary, it appears that the opening up of climax forest stands and the subsequent successional consequences, brought about by budworm epidemics, generally compensate and even outweigh the short-term reductions in food supply resulting from the death of mature trees.

Conclusion

One generalization that can be drawn from the foregoing discussion is perhaps platitudinous, but valid nonetheless. Moose coactions with other members of the biotic communities in which it occurs often vary in effect from one locality to another. The severity of predatory and competitive interactions are subject to a complex milieu of physical and biological modifiers, of which nival conditions, population densities of the animals involved, and overall plant and faunal diversity are perhaps most important. With respect to the latter, the various animal coactions appear more clearly defined and of greater consequence in relatively simple ecosystems that are characterized by often harsh climatic factors, less biotic diversity and generally lower community homeostasis. It is imperative, therefore, that moose ecologists and managers consider the specific role of coactions within the context of local conditions.

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MOOSE RELATIONS WITH PREDATORS IN SWEDEN, WITH SPECIAL REFERENCE TO BEAR AND WOLVERINE

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Résumé

Les relations prédateur-proie entre l'orignal (*Alces alces*) et quatre grands carnivores de Suède sont passées en revue. Les résultats d'études effectuées dans d'autres régions sont aussi rapportés. A la suite de l'extermination presque totale du loup (*Canis lupus*) en Scandinavie, l'ours brun (*Ursus arctos*) y est le seul prédateur potentiel sérieux de l'orignal. La prédation se produit surtout au début du printemps et à l'automne. Les pertes des mois d'avril et mai sont reliées aux conditions de neige qui accroissent la vulnérabilité des orignaux. Ceux-ci, lorsque blessés par les chasseurs constituent des proies faciles pour les ours pendant l'automne. Quelques veaux sont aussi prélevés pendant l'été. Les études de dépistage ont révélé que les ours qui attaquent les orignaux sont habituellement de gros animaux dont le pied arrière a une longueur d'au moins 24 centimètres. La densité peu importante des populations d'ours de même que la faible fréquence de la prédation amènent l'auteur à conclure à l'impact minime de celle-ci sur la dynamique des populations d'orignaux en Suède. Le glouton (*Gulo gulo*) est aussi capable de tuer un orignal, mais une telle forme de prédation n'est pas fréquente. Les attaques d'orignaux adultes par le lynx (*Lynx lynx*) sont rares et aucun cas de succès de cette forme de prédation n'est rapporté pour la Suède. Le lynx, présentement en expansion numérique en Scandinavie, peut cependant être responsable de la perte de quelques jeunes veaux.

Abstract

Predatory relationships between moose (*Alces alces*) and four large carnivores in Sweden are reported. Results of studies in other areas are also reviewed. Due to virtual extermination of the wolf (*Canis lupus*) in present-day Scandinavia, the brown bear (*Ursus arctos*) constitutes the only potentially serious moose predator. Losses to bears do not exceed a few percent of the annual moose harvest. Predation occurs primarily early spring and autumn. April-May losses are linked to snow conditions which increase moose vulnerability. Moose crippled by hunters provide easy prey for bears in the fall. Some young calves are taken during the summer months. Tracking investigations have revealed that bears attacking moose are usually large animals with a hind-foot lenght of at least 24 centimetres. The low number of bears and relative infrequence of predation indicate minimal demographic impact on moose in Sweden. Wolverines (*Gulo gulo*) are capable of killing moose, but such predation is infrequent. Attacks on adult moose by lynx (*Lynx lynx*) are rare and no cases of successful predation have been verified in Sweden. The lynx, which is currently increasing in Scandinavia, may be responsible for some losses in young calves.

Introduction

Predators no longer play a major role in the ecology of moose (*Alces alces*) in Sweden and Norway. Formerly, large carnivores, especially the wolf (*Canis lupus*), were probably of considerable demographic significance. Hagen (1960) noted the coincidence of a protracted period of relative moose scarcity in Norway during the 18th and first part of the 19th centuries with several "wolf periods". Man's persistent efforts to eradicate this predator (see Pulliainen, 1965) have drastically reduced its numbers over much of northern Eurasia. Presently, the brown bear (*Ursus arctos*) remains as the only potentially consequential moose predator in Sweden.

Moose occur throughout Sweden with their total numbers estimated at between 100,000 and 150,000 animals. The current annual harvest lies between 35,000 and 40,000. In the northern area, where most of the large predators are found, normal late winter moose densities range from 0.2 to 0.3 animals per km^2 but vary considerably according to local food conditions. Population densities are higher and generally more stable in the southern provinces, where 0.6 to 0.8 animals per km^2 is a common figure.

This paper discusses the ecological and behavioral aspects of bear and wolverine (*Gulo gulo*) predation on moose, particularly with respect to the situation in Sweden. Consideration is also given to the possible roles of the wolf and European lynx (*Lynx lynx*) as moose predators.

Information on the habits of the four large predators in Sweden is based primarily on information collected from 1960 to 1964 by the author.

Methods

The methods employed have been described by Haglund (1965, 1968). Basically, the procedure involved winter tracking of bear, wolf, lynx and wolverine by two-man ski patrols. These patrols searched at random for the tracks of one of these predators and followed the first set of tracks encountered, as far as possible without alarming the animal. The observers also collected specimens from reindeer (*Rangifer tarandus*), roe deer (*Capreolus capreolus*), and moose killed by the predators. The specimens included mandibles, radio-ulna and metacarpal bones, heart and the entire head where possible. In some cases, predator fecal material was also collected.

Results and discussion

BROWN BEAR

Moose predation by brown bears is well documented in both European and North American literature. There appears to be, however, considerable disagreement among individual investigators as to the significance of such predation relative to the moose populations involved.

Lykke and Cowan (1968) submit that the brown bear can kill moose of any sex and age class. In Russia, Nasimovitch and Semenov-Tian-Sanskii (1951) recorded the loss of 20 moose to bears in the Lapland Nature Preserve from 1930 to 1940. Of the animals killed 54 percent were adults. Knorre (1959) reported five cases of moose predation by bears in the Pechora Nature Preserve from 1938 to 1949. Three (60 percent) of these were calves. In the same area, Yazan (1961) noted that 17 of 25 moose whose deaths were attributable to predators between 1955 to 1960, had been killed by bears. Of these 14 (84 percent) were adults.

In the North American literature, Cowan (1944) concluded that the grizzly bear was a more significant summer predator of moose in the Rocky Mountains national parks of western Canada than was the wolf. Sarber (1944) and Chatelain (1950) likewise implicated brown bears as serious predators of moose calves in Alaska. More recently, LeResche (1968) observed a brown bear killing two young sibling calves and their dam. However, LeResche concluded that calves more than a month old appeared capable of escaping bears under normal circumstances. Craighead and Craighead (1972) observed grizzlies killing full-grown moose, wapiti (*Cervus canadensis)* and even bison (*Bison bison)* in Yellowstone National Park. The authors noted, however, that in most cases the animals were attacked in deep snow, while crossing rivers, or when otherwise physically incapacitated. Some were so near death from inanition that they did not resist attack. The Craigheads assessed the grizzly's role as a carnivore prior to and immediately following hibernation as: "first a scavenger, second a predator on small prey species — especially when these are at high densities, and last a killer of large prey animals" (Craighead and Craighead, 1972, p.33).

Bears and moose in Sweden

The total Swedish bear population is estimated to be between 250 and 400 animals distributed primarily in the northern two-thirds of the country (i.e. above 62° N latitude). These figures alone suggest that bear predation has a relatively insignificant impact on the population dynamics of Swedish moose.

The Scandinavian bear is basically omnivorous. Plant material predominates in the diet and the animal component comprises largely ants and other insects. However, many accounts of bears killing moose are narrated, related in newspapers, and verified in some cases. There is no doubt that a full-grown bear, under "favorable" conditions, can kill even a full-grown moose twice its own weight. Hellgren (1967) reviewed an incident from Frostviken in which a single bear killed nine moose (one bull, four cows and four short-yearlings) during a 10-day period in April 1967.

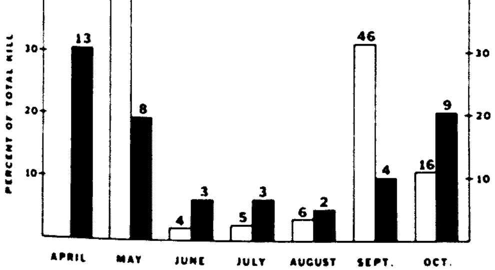

Fig. 1. Monthly distribution of bear kills of 141 reindeers and 42 moose in Sweden, 1960-1964. Numbers denote sample sizes by month.

Comparison of bear predation on moose and reindeer

Bear predation on reindeer is concentrated in May and September, while moose kills commence somewhat earlier in spring and continue later in autumn. Bears kill few moose or reindeer during the months of June through August (Fig. 1).

Bears in Sweden normally commence hibernation from mid-October to mid-November and emerge between 10 April and 10 May each year. The hibernation period is 15-30 days longer in the north. Following emergence bears can kill moose more easily due to weather conditions that produce on the snow a frozen crust which is sufficient to support the predator but not moose. This happens most commonly when the weight differential between the animals is great and is thus less frequent with reindeer which may weigh less than large bears. Heptner and Nasimovitch (1967) noted that bear predation on moose in taiga areas of Russia is most severe in years characterized by mid-winter thaws which produce such crusting conditions. They point out that the taiga offers no alternate food sources for bears that temporarily emerge from hibernation during warm spells.

Calf drop in Swedish reindeer herds occurs in mid-May when the bears can be found at relatively high elevations in mountainous areas close to the calving grounds. Calf losses from bears can be quite severe.

The peak of the reindeer rut occurs in mid-September. Reindeer herders often maintain that bulls are easy prey for bears after the rut. The percentage of adult males (36 percent) among bear kills is higher than the comparable fraction (25 percent) of reindeer killed by other large predators. By contrast, the moose rut peaks a couple of weeks later and seems to contribute little to the total number of moose killed by bears. However, Yazan (1961) maintained that the rutting period of moose in the Pechora Nature Preserve coincided with a higher incidence of bear predation because moose were less cautious at that time of year.

Another potential factor in increased predation on moose is the hunting season which takes place in September and the first weeks of October in Sweden. Some animals are inevitably crippled and these afford easy prey for bears, or they may be found dead by bears and consumed as carrion. Such circumstances can result in inflated reports of actual bear kills.

Predator and prey behavior

The normal hunting technique for the bears is to stalk their prey as closely as possible and then attack in a short rush. If the prey animal is lying down its vulnerability is greater. In its attack, a bear attempts to reach the moose's back and neck region, striking blows with the paws and biting at the neck. The kill itself is generally accomplished with the jaws. Moose are difficult for bears to stalk and kill because moose have excellent auditory and olfactory senses and good espace speed.

Some details of bear hunting behavior are of interest. In the afore-mentioned instance of a medium-sized bear killing nine moose in less than a forthnight, prior to this extremely carnivorous behavior the same bear had lived primarily on ants and plant materials. Another case was observed in which a large male chased two young moose for appropriately eleven kilometres. After giving up the chase, it dug up 18 anthills within 3.2 kilometres. In one precisely documented case, a party of four bears killed a cow moose by driving her to an ambush. Similarly, Crainghead and Crainghead (1972) noted instances of two or more grizzlies pursuing and killing elk and bison in well coordinated attacks. I know of one case in which a cow protected her 2-month old calf by chasing the bear away.

As indicated above, bear attacks on moose are usually of brief duration after which — in the event of a failure — the bear leaves the trail and looses interest in its prey. In such cases, it is usual for the moose to relax and begin feeding; sometimes, it returns to the site of the attack. After fairly long chases, moose may flee considerable distances (up to 6 to 8 kilometres). Undoubtedly, moose sometimes are severely frightened by the chase or even by the presence of a bear. Occasionally, the mere scent of a bear precipitates a sustained flight reaction just as human scent may elicit a greater fear response than visual or auditory perception of human presence.

Impact of bear predation

Bear predation on adult moose in Sweden appears quite localized and sporadic. It is virtually unknown over large areas of moose habitat even where bears are relatively numerous. In other areas, it occurs occasionally and even with some frequency, mostly due to highly predatory individuals, usually mature males. Bears were tracked in snow for 563 kilometres on 106 different days. Moose were observed on 52 of theses days, but only eight attacks were made on moose, all of which were unsuccessful. However, bears made 22 visits to old moose and reindeer carcasses.

Individual bears in Sweden differ distinctly in food habits. My observations tend to substantiate the contention that bears which pursue and kill moose are fullgrown individuals.

Moose is a large prey species even for a bear. In seven (88 percent) of eight observations where bears have chased moose, the predators had a hind-foot length of 24 centimetres or more (Fig. 2), indicating that the bears involved were full-grown and probably males.

The belief that smaller and younger bears do not prey on ungulates is unfounded, however, as small bears kill sheep and chase reindeer. The results of my tracking investigations revealed a significant difference in size (as indicated by mean hind foot length) between these bears and those hunting moose. The values were 19.7 and 25.9 centimeters respectively.

Of 42 verified cases that I know of moose killed by bears, 20 (48 percent) were attributable to "favorable" snow crusting conditions. In five other cases (12 percent), the moose had been previously wounded, probably by hunters. Eight (19 percent) appeared to be the result of occasional summer predation. The other nine cases (21 percent) all occured during September and October. It is probable that even some of these were indirectly due to ill-aimed hunters' bullets.

Sex and relative age were determined for 18 bear-killed moose. Six (33 percent) were adult bulls, two of which were large full-grown animals. Another seven (44 percent) were adult cows. Two (11 percent) were short-yearlings (11 months) and the remaining two (11 percent) were young calves (1-2 months). Nasimovitch and Semenov-Tian-Sanskii (1951) reported a preponderance of males (2:1) over females among moose killed by bears in the Lapland Nature Preserve in Russia.

The bear is an opportunistic predator that takes large prey under favorable circumstances. On the other hand, bears may often find that moose is more than a match because of its size, or that it is unapproachable because of its sharp senses. The dearth of alternate food sources in the spring when the bears emerge from their dens, and the need for high protein food in early autumn preparatory to hibernation, may explain the higher incidence of predation in the spring and autumn than during the summer.

The low numbers of bears in Sweden and the even lower numbers of large bears suggest that they nowhere si-

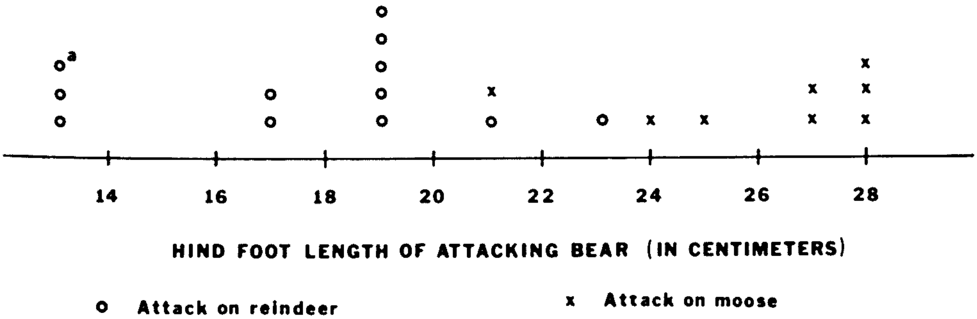

Fig. 2. Distribution of bear attacks on 11 reindeers and 8 moose in Sweden according to the hind foot length (in centimeters) of attacking bear. a = attack by two young bears (approximately 15 months) together with a larger one. Mean hind foot length of bears attacking reindeer = 19.7 centimeters; mean hind foot length of bears attacking moose = 25.9 centimeters.

gnificantly influence the moose population by killing adult moose. Of greater significance is neonatal predation on calves during the last weeks of May and in June. Calves are very vulnerable at this time if their dams cannot sucessfully chase the predator. There are indications of calf losses due to bear predation in parts of Sweden, but quantitative data have not yet been collected. Very few remnants of such kills are left for identification and they are easily overlooked. However, qualitative observations in certain areas where bears are most abundant or where an especially carnivorous bear is roaming indicate lower annual calf production than in bear-free areas. Similar conclusions have been suggested by earlier North American investigators (Sarber, 1944; Chatelain, 1950).

It has also been reported in Sweden that local moose populations move out of areas where bears are hunting them. In several cases, however, moose and bear coexist and both increase their numbers.

In summary, bears do not seem to be making serious inroads on the moose population anywhere in Sweden. Losses to bears probably do not exceed a few hundred animals annually and might be considerably lower. At the same time, the yearly harvest by man in areas where bears occur is approximately 12,000 animals. Thus the estimated losses to bears do not constitute more than 1-2 percent of the legal harvest, and there are no valid reasons for reducing the number of bears in order to protect moose populations.

MOOSE RELATIONS WITH OTHER PREDATORS

Wolverine

Moose predation by wolverines is an interesting example of how some predators may occasionnaly kill prey animals with a weight 10-20 times greater than their own. The larger felids normally do not kill animals larger than three to four times their own weight (see Hornocker, 1970 and Schaller, 1972). The bear has difficulties with a moose twice its own weight. Wolves commonly kill large ungulates, but this is almost always the result of group hunting tactics. In the mustelid family, however, one finds cases where solitary animals — by a combination of voraciousness, swiftness in their attack and specialized killing tactics — can kill animals more than 10 times their own weight. In Sweden, a case of a marten (*Martes sp.)* killing a full-grown roebuck has been documented; the ermine (*Mustela erminea)* kills hares (*Lepus* spp.) and large capercaillie (*Tetrao urogallus)* cocks; and the wolverine (10-20 kilograms) has been known to kill adult moose weighing from 200 to 300 kilograms or more.

Attacks on moose by wolverines are, however, most infrequent. In 960 kilometres of tracking wolverines in areas where moose were very common, no attacks were observed and wolverines displayed no interest in moose or moose tracks. Conversely, moose seldom showed any fear reaction to wolverines or their tracks. However, after completion of theses studies, one case was substantiated. That attack occured in the last week of April and involved a large cow moose — in apparently good condition — and her two 11-month calves. The cow succeeded in ridding the predator from her back by rolling in the snow. She was found dead the following day, however, from external and internal injuries inflicted by the wolverine bites and clawings. I know of seven such cases reported and verified in Sweden during the last three to four decades.

The role of the wolverine as a moose predator is the subject of some controversy. Krott (1959) termed him the "hyena of the North" and pointed out that carrion was the major component of both winter and summer diets. Likewise, Heptner and Nasimovitch (1967) characterized the role of the wolverine as more of a scavenger than a true moose predator. The same conclusion was reached by Yazan (1961).

The wolverine's large "snowshoe-like" paws endow it with a locomotory advantage in the deep and often crusted late winter snow over large ungulates which may offer the only source of food at this time of year (Krott, 1959). It has been shown (Haglund, 1966) that in certain snow conditions the wolverine is able to move much better than a fox (*Vulpes vulpes)* which sinks in the snow much deeper than the larger predator. Teplov (1955) calculated the wolverine's weight-load-on-track at a mere 22 grams/cm^2. Under certain conditions, the wolverine can kill moose and other large ungulates, especially those in an alreagy weakened condition. Cowan (1944) documented a case of a wolverine killing a bull moose in deep snow in Jasper National Park.

Rausch and Pearson (1972) found moose remains in 14 percent of 193 wolverine digestive tracts from Alaska and the Yukon Territory. Concurrent field observations by these investigators revealed a high incidence of wolverines feeding on moose and caribou that had been killed by wolves and hunters as well as on some that had apparently succumbed from natural non-predatory cuuses. They concluded that wolverines are capable of killing large ungulates if the latter are under "unusual environmental stress". However, wolverines used carrion extensively whenever available, and the impact of their occasional predation on large ungulates was probably not significant.

In Sweden, Haglund (1966) found that of 59 visits to carcasses by wolverines 50 involved reindeer — many killed by lynx. Another was a bear and three were moose. The remainder involved smaller animals. It was also found that 26 reindeer had been killed by wolverine.

In Finland, Pulliainen (1963) reported that reindeer comprised the principal winter food of northern wolverines. He classed the wolverine as the most important former reindeer predator.

Records of wolverine predation on moose stem primarily from the Russian literature. Makridin (1964) stated that ungulates are an important part of the wolverine diet and that they successfully attack moose. More detailed accounts are given by other investigators. Teplov (1955) described the winter food habits of wolverine in the Pechora Nature Preserve. Moose and wild reindeer comprised 36.7 and 36.1 percent, respectively, of the diet during the winter of 1937-38. He noted that most of the moose and reindeer actually killed had been previously wounded, and many were eaten as carrion.

Knorre (1959) documented 13 cases of wolverine predation on moose in the same area from 1938 to 1939. Five animals were less than one year old (one of which was lame); seven (2 bulls and 5 cows) were in their second year of life. The only large bull killed had previously been shot poachers and then chased by a lynx for some time. Most kills occured in February and March. Ambush tactics as well as coursing attacks were observed.

Yazan (1961) described one case in the Pechora where a wolverine pursued an adult bull in deep snow (February 1958) and jumped upon it. The moose ran approximately 150 metres with the predator on its neck and then collapsed. When found, the moose was still alive but paralyzed. Its neck was ripped open and the spinal cord apparently injured. As indicated by the examination of 30 reindeer carcasses that had been killed by wolverines, this is the typical killing technique of wolverines in Sweden. The wolverine bites into its victim's back and neck, injuring the muscles and nerves around the spinal cord.

Finally, Teplov (1960) reported three cases in which pregnant cows aborted their foetuses, when chased by wolverines. The foetuses were consumed by the predators.

Wolf

As mentioned previously, the wolf has been virtually exterminated in Sweden. A few individuals still range in the northern mountains, where reindeer are common. Only two cases of actual predation (where a big lone wolf killed two moose calves in winter) have been documented during the past decade. Some unsuccessful and "half-hearted" attacks on moose have also been observed.

Lynx

The lynx of the northern Europe is big and powerful; large males may weigh up to 30 kilograms or slightly more. They easily kill reindeer three times their own weight. There are no known cases in Sweden in which lynx have killed adult moose, but one record from Norway might be authenticated. During the tracking studies, one case was tracked, in which an attacking lynx was up on the back of a moose at three consecutive times. This occurred in February and involved a single moose (sex undetermined) at least 20 months old. There were no indications that the moose was badly hurt, but it had lost much hair in each attack from the predator's claws.

Lynx may prey upon newborn moose calves. While this has not been verified in Sweden, Bergerud (1971) reported high neonatal losses among Newfoundland caribou as the direct or indirect result of predation by the smaller North American lynx (*Lynx canadensis*). Knorre (1959) noted that moose predation by lynx in the Soviet Union was rare, but a high percentage of the few kills that did occur were calves.

The lynx is increasing in Fennoscandia (Haglund, 1968; Lykke and Cowan, 1968; Pulliainen, 1964). The increase in lynx numbers in Sweden could conceivably bring with it some cases of predation on moose calves.

In another Newfoundland study, Saunders (1963) stated that moose provided food for lynx as carrion resulting from the fall hunting season, from late winter poaching, or possibly as the result of predation. The percent occurrence of moose remains in lynx digestive tracts and scats was as follows: spring, 18; summer, 3; fall, 42; and winter, 13. Circumstantially, the low occurrence of moose in summer, and the fact that all moose remains in the material analyzed derived from adult animals suggest little or no lynx predation on moose calves in that area. It should be reiterated that the North American lynx is considerably smaller than its European counterpart. Burt and Grassenheider (1952) give 6.8-13.6 kilograms as the range of body weights for *Lynx canadensis*, while comparable figures for *L. lynx*, as cited by van den Brink (1957), range from 18 to 38 kilograms.

Conclusion

As a whole, the large predators effect at best a very limited impact on the population dynamics of Swedish moose. Presently, only the brown bear may, under particular circumstances and in localized instances, affect the density and distribution of specific subpopulations. One factor contributing to the minor impact of predation may be that the large stocks of "tame" reindeer (semidomesticated and more or less free-ranging) of approximately 200,00 head in northern Sweden serve as a buffer between the predators and moose. Even if the bears do not kill many reindeer themselves, carcasses from the heavy winter predation on reindeer by wolverine and lynx offer them a ready source of food in the spring. For all the predators involved, the moose represents a stronger and more difficult prey species, and not without risks for the attacker.

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OCCURENCE OF MOOSE IN FOOD OF WOLVES AS REVEALED BY SCAT ANALYSES: A REVIEW OF NORTH AMERICAN STUDIES[1]

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Résumé

Dans les régions où les deux espèces sont sympatriques, l'orignal (*Alces alces*) constitue la proie naturelle du loup (*Canis lupus*). L'étude des fumées déposées par le loup sert à évaluer l'effet de la prédation tout en fournissant des données sur l'abondance relative des proies, leur disponibilité saisonnière et l'utilisation différentielle des différentes classes d'âge, de même que sur l'effet des conditions du milieu sur la prédation. L'article passe en revue les principaux travaux d'auteurs américains faisant usage de la technique d'analyse des fumées portant sur les deux mammifères mentionnés. L'orignal et les ongulés en général constituent les proies principales du loup, tandis que le castor (*Castor canadensis*), le lièvre (*Lepus americanus*) et d'autres petits mammifères constituent des proies d'importance secondaire pour ce prédateur. Ces dernières peuvent cependant constituer une partie importante de la diète durant certaines saisons comme, par exemple, la saison de confinement au terrier ou encore la saison d'activité autour des sites de rendez-vous. Il est utile de connaître l'abondance relative d'une proie dans le milieu, mais ce renseignement ne permet pas de prédire l'importance qu'elle aura dans la diète du prédateur. L'importance d'une proie donnée dépendra de sa disponibilité, c'est-à-dire de sa vulnérabilité ou encore de la sélection active dont elle fera l'objet de la part du prédateur. Les cerfs (*Odocoileus* spp.) occupent ordinairement une place plus importante que celle occupée par les autres espèces d'ongulés, ce qui peut être l'indice d'une disponibilité plus élevée et non pas d'une abondance plus grande. Certaines études ont du reste établi qu'une utilisation estivale accrue des faons et des jeunes orignaux par le loup s'expliquait par une disponibilité accrue de ces proies. Les résultats d'une étude menée durant une série d'hivers rigoureux révèlent que les animaux et tout particulièrement les veaux, autant chez les cerfs que chez l'orignal, affaiblis par les dures conditions hivernales, connaissent un taux de prédation accru de la part du loup. L'examen des fumées ne permet pas de distinguer les activités du loup comme vidangeur (la proie était déjà morte) ou comme prédateur (le loup a abattu la proie); pour cette raison, il est possible que cette méthode d'analyse surestime légèrement la mortalité imputable à la prédation. Les chercheurs considèrent de plus qu'il est nécessaire de recueillir simultanément des données sur d'autres facteurs susceptibles d'influencer l'activité du prédateur. Presque toutes les études révèlent que le prédateur ne peut agir comme facteur limitant les populations d'orignaux. Certaines d'entre elles suggèrent que la prédation puisse exercer un certain contrôle sur les nombres lesquels sont eux-mêmes affectés par de nombreux facteurs du milieu, y compris l'homme et ses façons d'utiliser le territoire. Le fait que le loup choisisse des animaux plus jeunes et plus vieux que la moyenne d'âge de la population semble abondamment documenté. Pour mieux comprendre le rôle que joue la prédation par le loup, il serait important de mettre au point des moyens de discerner entre l'action du loup comme vidangeur et son action comme prédateur, en particulier dans le cas des faons et des jeunes orignaux.

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Abstract

Moose *(Alces alces)* serve as food for wolves (*Canis lupus*) where they co-exist. Scat analysis provides prey availability, seasonal importance and age class use data and, with related environmental data, is useful in evaluating predation biology. Scat analysis literature is reviewed and North American moose-wolf studies are summarized. Moose and other large ungulates are primary wolf prey, with beaver (*Castor canadensis*), hare (*Lepus americanus*) and small mammals secondary but seasonally important, particularly during wolf denning and rendez-vous site activities. Relative prey abundance provides information but is not necessarily related to food item importance *per se*. Prey availability in terms of vulnerability or selection may also influence food item importance. Greater wolf food importance values are often found for deer (*Odocoileus* spp.) than for other associated ungulates, possibly reflecting availability rather than abundance. Various studies indicated increased deer fawn and moose calf summer use, apparently related to availability and not local abundance. Data from one study involving successive, harsh Minnesota winters suggested herd debilitation from winter stress related to increased wolf predation on moose and deer, particularly calves and fawns. Carrion feeding versus direct predation is indistinguishable by means of scat analysis. Scat content then may over estimate predation mortality. Supportive field data on other factors influencing predator food intake are thus important. Most studies indicate that wolf predation is not limiting moose populations. Some suggest that wolves control moose numbers, but this is affected by numerous environmental factors including man and land use practices. Predation selectivity by wolves on moose and other ungulates for younger and older animals is well documented. Differentiation between predation and carrion feeding, especially use of calves and fawns, would enhance understanding of wolf predation ecology.

Introduction

This paper reviews North American wolf food habits studies accomplished specifically by analyses of scats (fecal droppings) of wolves associated with moose. Published work from Alaska, Canada and the northern contiguous United States is summarized as well as information from two independently conducted studies in northeastern Minnesota not yet reported in the conventional literature.

Field and laboratory methods

Early techniques for documentation of food habits of predatory mammals were based largely on direct observations and crude stomach and scat analyses. During the past 50 years, publications describing gross and microscopic identification of hair and skeletal fragments (Hausman, 1920; Mathiak, 1938; Dearborn, 1939; Williamson, 1951; Mayer, 1952; Stains, 1958; and Adorjan and Kolenosky, 1969) have facilitated scat analysis procedures. A hair impression method (Williamson, 1951) increased reliability of microscopic identification and made age and seasonal classifications possible. Adorjan and Kolenosky (1969) produced an excellent pictorial guide to hair identification using similar procedures. These methods have been used extensively, after modification, by Halverson (1969), Pimlott *et al.* (1969), and Byman (1972).

Scat collection methods have varied among investigations as to season and site, and with respect to the size of study area. In most cases, an opportunistic approach was employed with likely wolf haunts such as trails, dens, rendez-vous sites, logging and other roads being searched. Scats are often deposited in clearings and on rock outcrops (Fig. 1). Kolenosky and Johnston (1967) found a higher scat incidence on rock in spring and fall than in mid-

Figure 1. Photo of wolf scat as usually found on rock outcrop or trail. Labels shown were used to identify each scat collected in the Lake Isabella study area.

summer, suggesting that wolves avoided higher temperatures of such surfaces in summer. Our 1968-72 collections in northeastern Minnesota were made systematically from a selected, definite set of trails and abandoned logging roads. Collections by Mech (1966) from trail systems on Isle Royale probably approached non-random rather than random collecting.

The literature contains little mention of gross handling of scats. Our field handling of scats emphasized caution to minimize the possibility of personnel contacting potential parasites. Scats also were autoclaved adequately prior to handling in the laboratory.

North American studies

The following summaries include only those studies which provide information on moose-wolf relationships obtained from analysis of moose content in wolf scats.

ALASKAN STUDIES

Murie (1944) pioneered quantitative work on wolf food habits using direct and indirect field methods in Mt. McKinley National Park, Alaska. Of 1174 scats from Dall sheep (*Ovis dalli*) and caribou (*Rangifer tarandus*) ranges, nine contained moose (0.67 percent frequency occurence of total food items). Estimated wolf density for the 5180 km ^{2} park area was reported as one wolf per 130 km ^{2}. Murie noted local and wide wolf movements in relation to prey availability, adaptation to other prey species, incidence of young prey in the diet, and occurrence of non-ungulate summer food items as important in understanding wolf biology.

Some aspects of Alaskan wolf population ecology were presented by Rausch (1967) from data obtained from 4470 wolf carcasses and field observations. Ungulate prey densities were given for parts of four Alaskan game management units, and in all of these, moose occurred in the wolf diet. Evidence of wolf cannibalism was noted from scat analyses.

Other publications on wolf biology which treat direct observation of food habits of Alaskan wolves include Burkholder (1959) and Merriam (1964).

CANADIAN STUDIES

Scat data were used in two investigations of wolf-moose relationships in western Canada. Cowan's (1947) work is recognized as an important contribution to quantitative interpretation of wolf predation. Cowan's 1943-46 studies over the 18,130 km ^{2} Rocky Mountain National Park of Canada showed 358 ungulate occurrences in wolves' annual diet (80 percent occurrence in total diet). Elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*) and moose had percentage occurrences of 47, 15 and 7 percent, respectively. Occurrences in scats approximated their local relative abundance (33, 11 and 4 percent), and corresponded to percentages of 118 big game hunter kills (54, 23 and 12 percent). Thus, moose was the third item of importance among big game followed by bighorn (*Ovis canadensis*), caribou, and mountain goat (*Oreamnos americanus*). Cowan noted that contribution to the annual diet was not strictly related to prey abundance but also to factors affecting ease or necessity of capture. Cowan also compared moose populations in wolf-inhabited and wolf-free areas and concluded that their predation was not important to calf survival to yearling age, although all moose in summer scats collected were calves. Eighteen percent of the wolves' annual diet was smaller mammals, with hares (*Lepus americanus*) and beaver (*Castor canadensis*) important. Summer diet had a higher content in rodents. He stressed difficulty in obtaining unbiased and representative samples, especially in summer.

Saskatchewan timber wolves were studied by Banfield (1951) in Prince Albert National Park during the winters of 1947, 1949, and 1951. A small sample of winter scats from the area's southern elk range contained elk, moose, snowshoe hare, mule and white-tailed deer (*Odocoileus virginianus*) in order of prevalence. After re-establishment in 1923, park wolf numbers had increased due to big game availability. Estimates of abundance were not given for moose; numbers were low in 1932 due to epidemic and heavy tick infestations, but increased in 1942-43 following fires which provided new range. Moose increases continued through 1951.

Several investigations were conducted in the central and eastern boreal forests of Canada. Peterson (1955) cited scat collections on St. Ignace Island in Lake Michigan where moose far outnumbered deer. However, moose occurred in but 36 percent of the scats with deer in 57 percent. He related this to deer being the easier prey, which possibly diverted predation pressure from moose. He considered wolves probably the most serious natural moose predator, but discounted wolf predation in summer as being significant. Kolenosky and Johnston (1967) noted summer wolf food habits and habitat use in an Ontario radio-tracking study, where wolves subsisted largely on beaver and occasionally on other small mammals.

The ecology of the timber wolf in Algonquin Park, Ontario, was studied by Pimlott *et al.* (1969). They summarized wolf food habits based on 1435 wolf scats collected from 1958 through 1962, essentially under ice-free conditions except for a 1962 winter scat collection. Wolf density in a 2,590 km^2 area approached four per 100 km^2, while that for deer, moose and active beaver colonies approached 600, 20, and 40 per 100 km^2, respectively. Summer droppings showed deer, moose, and beaver percentage frequency occurrences as 80, 8, and 7 percent, respectively. Deer was more important in winter. Data collected in 1960 from one out-lying area (Parkesley) showed that percentage frequency of occurrence in 206 scats approached 27, 1, 59, 3, and 9 percent for deer, moose, beaver, hare and "other", respectively. In another area (Marten River) percentage frequency of occurrence approximated 42, 17, 37, 0.5, and 3 percent for the same prey species in 226 scats. These researchers considered percentage frequency of occurrence of a food item as representative of the importance of that prey species in the diet. Summer scat collections provided prey age class distributions. Fawns and calves occurred in 71 and 88 percent, respectively, of deer and moose occurrences.

UNITED STATES STUDIES

Intensive wolf-moose studies in Isle Royale National Park, Michigan, in northern Lake Superior (Allen and Mech, 1963; Mech, 1966; Jordan *et al.*, 1967; Johnson *et al.*, 1968; and Peterson and Allen, 1972) constitute: "... the most detailed and longest-termed study of large predators which has ever been undertaken" (Pimlott *et al.*, 1969).

Of 438 summer scats collected on Isle Royale by Mech (1966) from 1958-60, moose contributed 76 percent of 516 items, while beaver comprised 11 percent. Adult-calf percentage occurrences were 15.8 and 48.2 percent, respectively, for "fresh" or summer scats; and a near reversal, 47.9 and 15.5 percent, respectively, for "old" or autumn and winter scats. Unidentified moose percentage frequency of occurrence was 12.2 percent in all wolf scats. Mech considered the greater predation pressure on calves in summer due to greater vulnerability as compared to winter when the pressure switched to adults.

Jordan *et al.* (1967) published 1961-66 Isle Royale wolf observations with interpretations of Mech's (1966) earlier estimates. Major wolf food was moose with beaver secondary, based on 85 and 10 percent frequency of occurrence, respectively, in over 900 scats collected. Moose total density was given as 800-1000, or 145-185 per 100 km^2. The estimated fall beaver population approximated 900.

The first of several Minnesota wolf studies was that of Olson (1938), who excluded ungulates from the major portion of wolf summer foods. This finding is not supported by other studies except in that beaver and smaller animals supplement large ungulates in summer, particularly during denning and rendez-vous site stages of activity (Murie, 1944; Cowan, 1947; Thompson, 1952; Tener, 1954; Mech, 1966, 1970; Jordan *et al.*, 1967; Pimlott *et al.*, 1969; Halverson, 1969; Byman, 1972). Graphic representation of summer occurrence of ungulates (Fig. 2) demonstrates their importance in the summer wolf diet.

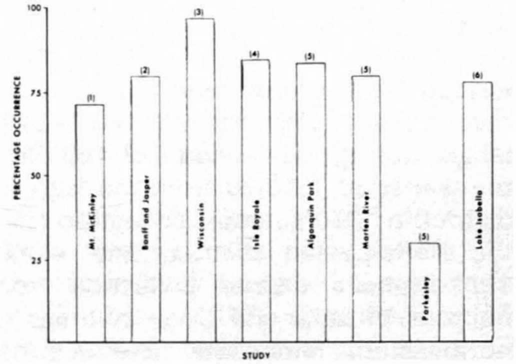

Figure 2. Occurrence of ungulates in summer diet of wolves in North America. (1) Alaska: Murie, 1944; (2) Alberta: Cowan, 1947; (3) Wisconsin: Thompson, 1952; (4) Michigan: Mech, 1966; (5) Ontario: Pimlott *et al.*, 1969; (6) Minnesota: this study (modified from Pimlott *et al.*, 1969).

Stenlund (1955) made the first comprehensive ecological studies of Minnesota wolves; he indicated moose as a minor wolf prey species based on extensive field knowledge and examination of 67 wolf stomachs and a small scat sample from areas of the Superior National Forest.

A project to study wolf-prey relationships in northeastern Minnesota was initiated in the winter of 1966-67 and continued through May, 1969, as reported by Mech and Frenzel (1971). I began seasonal wolf scat food habits work with several students in 1967 on a definite set of logging roads and trails designated as "The Lake Isabella Study Area" on the Superior Forest, in a selected area of the study region used by Mech and Frenzel (1971). Halverson (1969) analyzed results of work completed in 1967-1968; these will be treated with results of data I obtained in 1969, 1970, and 1972.

In June 1969, however, Byman (1972) began work on wolf food habits and internal parasites. These studies dealt with "exploited" wolf populations outside but immediately adjacent to and east of where Halverson (1969) and I worked, and extended farther east to the shore of Lake Superior. Byman (1972) analyzed wolf scats collected during the summer of 1969 and the winter of 1969-70 from the Isabella district, a 1970 summer collection from the Tofte-Lutsen district, and a fall 1970 Isabella district collection from portions of Lake and Cook counties of northeastern Minnesota. Byman's data (exclusive of 1970 home site collections) are presented in Table I. The fall 1970 sample was thought to underestimate young animals due to molt changes. Other scat food items pointed to greater summer use of small mammals and plant materials but emphasized the importance of deer and the fact that beaver surpassed moose in over-all use. Fawn use in summer was also considered important. Year-to-year differences in summer wolf food habits due to differential use of moose and beaver (and hares) were compared, as were seasonal collections on the Isabella district and food habits at four rendez-vous sites.

Lake Isabella area study

These investigations were supportive to predation studies of Mech and Frenzel (1971). Specific year to year qualitative and quantitative information on wolf food habits was considered important in several ways: (1) for comparison with prey harvest data (as in Mech and Frenzel, 1971); (2) to obtain needed baseline information in the event of either predator or prey population changes; (3) for information on predicted future wolf management needs; (4) to determine the time when fawns come into the wolf diet; and (5)

TABLE I

Food habits of timber wolves in northeastern Minnesota with reference to deer, moose, and beaver (from Byman, 1972)

Sample	*No. of scats*	*Food item percentage frequency of occurrence*				
		Deer		*Moose*		*Beaver*
		Adult	*Fawn*	*Adult*	*Calf*	
Summer 1969 (Isabella)	164	32.0	19.1	16.5	11.3	4.6
Winter 1969-70 (Isabella)	69	66.2	—	21.1	—	1.4
Summer 1970 (Tofte-Lutsen)	124	31.8	12.9	3.5	3.0	13.5
Fall 1970 (Isabella)	36	48.7[a]	15.4[a]	5.1	2.6[a]	17.9
All Samples[b]	547	43.7		12.4		15.7

[a] Fawns and calves probably underestimated due to fall molt.

[b] Including Tofte-Lutsen homesite collections (278 scats) in summer, 1970.

to establish, realistic interpretation criteria of scat classification categories as to: "old", "recent", or "fresh."

The study area for this work was an approximate 194 km² parcel of several townships just north of Isabella Lake in Lake County, Minnesota, in the southern central portion of the Boundary Waters Canoe Area of the Superior National Forest (Fig. 3 and 4). Here, a definite complex of trails and roads were designated from which scats were collected seasonally during snow-free periods in 1967-1970 and 1972.

Collections made throughout the first study season (1967) were from June until mid-July and were random. The advantage of non-random sampling over this set of trails was then recognized and later samplings were planned for spring, early summer, late summer and fall over the same trails. In this way seasonal changes in area use by wolves and seasonal changes in food habits could be determined.

In 1968 the same road-trail system was sampled as follows: (1) early May, representing winter and/or early spring wolf activities; (2) early summer; (3) late summer; and (4) late fall. Trails were left scat-free after each collection. Systematic collections following this pattern were conducted in 1969 and 1970, were omitted in 1971, and in 1972 were made only in late summer and early fall. Scats collected were treated and analyzed using

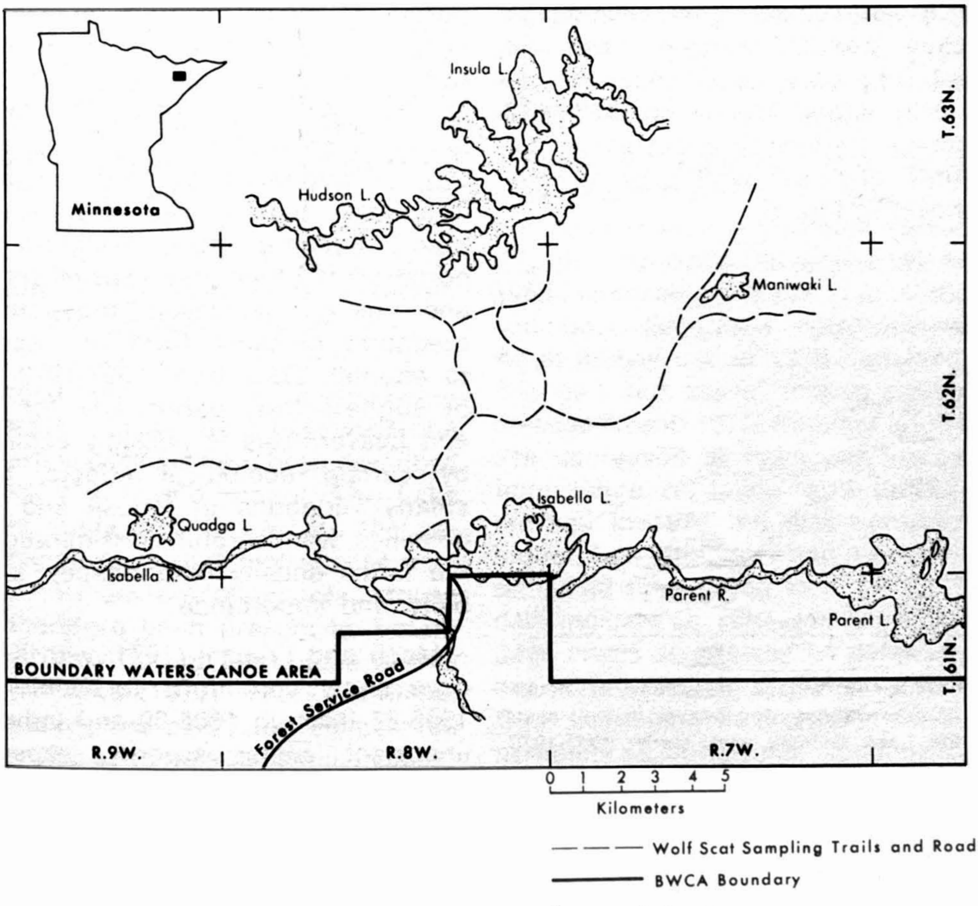

Figure 3. Sketch map of Lake Isabella study area, Lake County, Minnesota.

Figure 4. Typical habitat in Isabella Lake study area.

a modified hair impression method mentioned earlier (Halverson, 1969). Table II summarizes data relating to collection periods, sample size, and percent frequency occurrences of various prey items. Trends in 1967-1972 percentage frequency occurrences for the three principal wolf prey species are shown in Fig. 5.

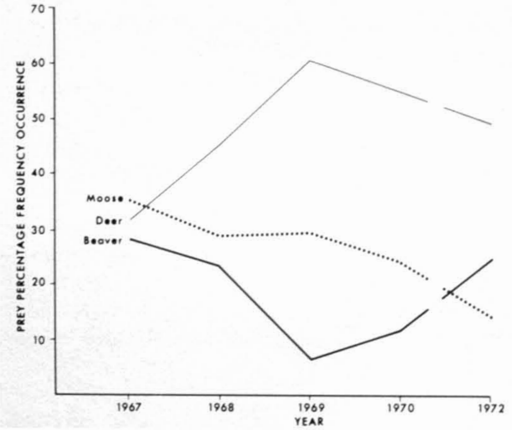

Figure 5. Percentage frequency of occurrence of deer, moose, and beaver in wolf scats from the Lake Isabella area study, 1967-1970, 1972.

Deer and moose importance as wolf food varied somewhat indirectly with one another throughout 1967-69. As deer importance increased there appeared to be a decrease in moose importance, at least until 1970 when importance values for both moose and deer declined. Beaver importance varied indirectly as compared with that of deer. As deer and moose importances decreased from 1970 to 1972, beaver importance as food increased. It appears that as one prey species (deer) became more available, importance of other prey species (moose and beaver) decreased, thus shifting predation pressure from one species to another. Data from 1967-1972 (Fig. 5) suggest this, particularly for deer and beaver. This is possibly explained by certain ecological effects, particularly variations in moose and deer densities with careful consideration of the terms density (abundance), availability, and importance.

Mech and Frenzel (1971, with Karns) gave snow conditions for winters of 1966-67 through 1968-69 and indicated important winter severity, especially for 1968-69. Generally winters since 1966 through 1971-72 have been harsh with deep snow and low temperatures, particularly in the Lake Isabella area. Likewise, Peterson and Allen (1974) presented similar winter severity conditions for these periods in their Isle Royale moose-wolf studies.

Van Ballenberghe (1972) related severity of winters and forest over-maturity to observed deer decreases since 1968 in northeastern Minnesota. Moreover, summer deer/moose track ratios have decreased from a value aproaching 1.0 in 1969 to 0.06 (1 deer/ 18 moose) in 1972, based on several track counts I made on segments of abandoned, rock-raked road in the study area. Mech (pers. comm.) considered deer to have become more sparse in the Lake Isabella area after 1968. Further, he has indications of reduced deer numbers there from radio-tagged local wolf packs moving back and forth to distant areas where deer are more plentiful. Thus, independent field observations suggest a decrease in deer density beginning probably in 1968. It appears that possible debilitation of the area's deer herd due to successive harsh winters, and certainly since the severe 1968-69 winter, has combined with long-term and more subtle deteriorating range conditions (Wetzel, 1972) to reduce deer numbers.

General increases in northeastern Minnesota moose densities over the past several decades have been described by Peek (1971) and others. The Lake Isabella study area lies within the general region of relative high moose density in northeastern Minnesota. Moose have therefore been present as potential wolf prey during the course of this study. Peek (1971) has estimated moose densities of 90 to 190 per 100 km^2 for this specific area since 1968.

Estimated beaver densities for the region during 1968-1972 probably approach 1.0 colony per 10 km^2 of stream area (Van Ballenberghe, 1973).

Knowing the utilization pressure of prey species involved as well as their relative abundance during the 1967-1972 period, it is possible to interpret predator response to prey availability. Deer importance (Table II) increased from 1967 to 1968 and through 1969 with total percentage frequency of occurrence of about 32, 46, and 61 percent, respectively, for those years. This may reflect increased deer vulnerability to wolf predation from lowered physical vigor as a result of winter stress despite a decrease in deer numbers. Adult deer carrion from winter kills, and particularly from extensive spring and early summer fawn mortality, could have further contributed to increased deer use by wolves. This is indicated by higher fawn use during this period, particularly during summers. Relative deer occurrence in scats — or the percentages of scats containing deer — for 1967-1970, and 1972 is given in Table II, in which increases in total deer as well as fawn and summer fawn use are shown.

Fawn and adult deer importance increased with that of moose calves in 1968, but adult moose importance decreased (Fig. 6). Deer-fawn and moose-calf use in 1969 increased while use of adult moose and deer decreased commensurately. Adult moose use in 1970 remained unchanged and use of moose calves decreased little in 1970. Summer adult deer use decreased as fawn use increased. Importance of fawns and calves decreased in 1972 but was considerably higher than adult deer and moose which remained unchanged from 1970. These data indicate an increased availability of deer fawns regardless of decreases in over-all abundance of that prey species. Carrion feeding or increased fawn vulnerability to wolves may account for increased fawn use. Karns (pers. comm.) states that recent Minnesota Department of Natural Resource fawning studies in this same area showed a high (perhaps reaching 75 percent of all births!) inci-

TABLE II

Summary data of wolf scat content from Lake Isabella study area, Superior National Forest, Minnesota, 1967-1970, 1972

Year	Season	No. of scats	*Food item percentage frequency of occurrence*										*Total food items*
			Deer			*Moose*			*Beaver*	*Hare*	*Small mammals*	*Other*	
			Adult	*Fawn*	*Total*	*Adult*	*Calf*	*Total*					
1967	Summer	348	23.0	9.4	32.4	30.0	6.8	36.8	29.2	0.0	0.0	1.6	370
1968	Spring	77	54.7	—	54.7	26.6	—	26.6	16.0	0.0	0.0	2.7	75
	Summer	90	26.0	15.6	41.6	19.8	12.5	32.3	26.1	0.0	0.0	0.0	96
	Fall	23	34.6		34.6	23.1		23.1	38.5	0.0	0.0	3.9	26
	Total	190	45.6	—	45.6	28.9	—	28.9	23.8	0.0	0.0	1.7	197
1969	Spring	61	54.5	—	54.5	38.2	—	38.2	5.9	1.4	0.0	0.0	68
	Summer	120	12.4	50.3	62.7	2.1	25.5	27.6	6.9	0.0	<3.0	0.0	145
	Fall	9	80.0	—	80.0	10.0	—	10.0	10.0	0.0	0.0	0.0	10
	Total	190	61.0	—	61.0	30.1	—	30.1	6.7	0.4	1.8	0.0	223
1970	Spring	32	57.9	—	57.9	23.7	—	23.7	15.8	2.6	0.0	0.0	38
	Summer	77	3.2	52.1	55.3	2.1	22.3	24.4	8.5	5.3	5.3	1.2	94
	Fall	3	33.3	—	33.3	0.0	0.0	0.0	66.7	0.0	0.0	0.0	3
	Total	112	55.5	—	55.5	23.7	—	23.7	11.9	4.4	3.7	0.7	135
1972	Summer	45	2.0	36.0	56.0[a]	1.4	12.5	13.9	20.0	2.0	4.0	0.0	50
	Fall	17	31.8	—	31.8	4.5	—	4.5	36.4	22.7	4.5	0.0	22
	Total	62	48.6	—	48.6	13.9	—	13.9	25.0	8.3	4.2	0.0	72
Total		902	45.7	—	45.7	30.3	—	30.3	20.5	1.3	1.2	1.0	997

[a] Included 18.0% frequency of occurrence of deer not known by age class.

dence of stillborn fawns. This, combined with poor survival of those born alive, could account for the exceptionally high fawn percentage frequency occurrences found in this study. Winter stress appears to be the principal ecological factor involved.

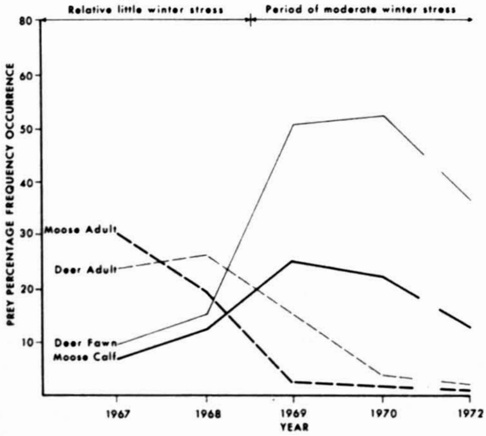

Figure 6. Percentage frequency of occurrence of adult deer, deer fawns, adult moose, and moose calves in wolf scats from the Lake Isabella study area during summer periods, 1967-1970, 1972.

Moose occurrence (Table II and Fig. 5) showed a general decrease in importance, throughout 1967-1970, 1972, commensurate with the increase in deer importance values just described for that period. A possible interpretation of this phenomenon is the shift in predation pressure from one species to the other as a function of vulnerability. Adult moose appear less vulnerable to wolf predation than deer; however, moose calves, like deer fawns, show greater vulnerability. Increased summer use of calves by wolves occured from 1968 trhough 1970.

Peek (1971, pers. comm.) conducted intensive moose studies in this same area (Maniwaki Lake) and in December censuses estimated the mean number of moose per 100 km^2 as follows: 115 in 1968, 192 in 1969, 135 in 1970, 88 in 1972. Moose populations appear to have first increased, then decreased since 1968. His observed 1969 increase corresponds to our observed increase in wolf use of calves in 1969 as compared to 1968. Again this may reflect vulnerability of calves due to their weakened condition as a result of winter stress, or to a decreased efficiency of protection by cows for this same reason. Peek (pers. comm.) considers this a real possibility. Thus, increased calf losses from winter stress and with consequent carrion feeding could contribute to the indicated increased calf use by wolves. Peek (1971) considers wolf predation to be an important mortality factor for moose.

Peek (pers. comm.) has also observed an increase in the moose twinning rate in the Maniwaki Lake area from 13 to 22 percent between 1971 and 1972. This could represent a compensatory relationship following higher moose use by wolves prior to 1971 and influence of wolves on moose population numbers through calf predation, as discussed by Jordan *et al.* (1967), Pimlott *et al.* (1969), and Mech (1970). Mech and Frenzel (1971) reported only six winter moose carcasses used by wolves between January 1967 and spring 1969. Mech (pers. comm.) has not observed any apparent increased incidence of winter moose use by wolves from 1969 to the present. However, in the 1972-73 winter, Mech observed a decrease in wolf pack size and starvation in wolf pups on the study area, suggesting a decreased potential for wolf predation on moose. This would agree with indications of decreased wolf use of the area or an actual decline in wolf numbers suggested by decreased scat incidence from over 300 in 1967 to 112 in 1970 for comparable collecting periods (Table II).

Conclusion

Some predator-prey relationships suggested by the 1967-1972 Lake Isabella area data have important field implications. Prolonged, accumulative winter stress on moose and deer appears to increase predation rates on these prey. Predation pressure apparently shifts seasonally from living old in winter and spring to living young in summer, due to increased vulnerability of the latter prey age class. Increase in prey use as revealed by scat content can be independent of prey abundance. That is, a prey species can show higher importance as a food item (percentage frequency of occurrence) without actually occurring in higher numbers in the population. Second, carrion feeding on moose and deer can result in misleading predation data when based on scat content alone. Scat analysis does not provide information concerning status or condition of live prey which might have contributed to predation involvement, or more importantly, distinguish between carrion feeding and actual predation (Pimlott, 1967). Therefore, interpretations of predation biology based on scat analyses must be made with the fullest possible understanding of particular field situations which might influence percentage frequency of occurrence of food items.

Acknowledgements

The detailed and productive work of contributors reviewed here is acknowledged with apology to those inadvertently overlooked or carelessly missed. Support and cooperation given my field work by agencies or individuals is appreciated and include Macalester College, the New York Zoological Society, University of Minnesota, Minnesota Department of Natural Resources, Bureau of Sport Fisheries and Wildlife, and the U.S. Forest Service. Special appreciation is extended to past students Brian Buss, Steve Fagerlie, Paul Halverson, and Dick Shank, for valuable help, and to Dr. L. David Mech, Bureau of Sport Fisheries and Wildlife, for his advice and assistance. Unpublished information provided by Dr. Mech, Dr. James Peek, University of Idaho, and by Mr. Pat Karns of the Minnesota Department of Natural Resources is also acknowledged.

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SNOW CONDITIONS AS A PARAMETER IN MOOSE-WOLF RELATIONSHIPS[1]

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Résumé

Une augmentation de l'épaisseur de la neige au sol durant les derniers hivers à l'Isle Royale a accentué l'importance de l'influence des conditions d'enneigement sur les relations orignal-loup (*Alces alces* — *Canis lupus*). Malgré la faible pression relative exercée par leurs pattes, les loups sont gênés dans leurs mouvements par une couche de neige épaisse et molle. Toutefois, ils tirent souvent profit d'une augmentation de la densité de la neige et de la «croûte» découlant de son vieillissement. La pression exercée par les sabots des orignaux est beaucoup plus grande, mais leurs pattes plus longues les aident à se déplacer sur la neige. Sur l'Isle Royale, l'augmentation de la neige au sol a entraîné une concentration des orignaux sous les peuplements de conifères bordant les lacs, lesquels constituent les principaux axes de déplacement des loups. La diminution de la nourriture disponible pour les orignaux, subséquente à une mobilité moindre, entraîne une augmentation des cas de déficiences alimentaires, principalement chez les veaux, ce qui a pour effet d'augmenter leur vulnérabilité à la prédation par le loup. Durant les années d'accumulation exceptionnelle de neige au sol, les loups ont généralement augmenté la proportion de veaux et de «jeunes adultes» dans leur récolte. Les renseignements recueillis jusqu'à maintenant révèlent que les veaux ayant survécu à un hiver rigoureux semblent plus vulnérables que la normale par la suite.

Abstract

Increased snow depths on Isle Royale in recent years have emphasized the important influence of snow conditions on moose-wolf (*Alces alces* — *Canis lupus*) relationships. In spite of a relatively light weight-load-on-track, wolves are hampered by deep snow of low density. However, they often benefit from increased density and crusting conditions associated with mature snow. Moose have a much greater weight-load-on-track, but are aided in snow by their long legs. On Isle Royale, increased snow depths resulted in a concentration of moose in conifer cover along lakeshores, which are primary travel routes for wolves. Reduced availability of forage, a result of lowered mobility in deep snow, brought about a higher incidence of malnutrition, especially in calves, resulting in greater vulnerability to wolf predation. In years of deep snow, wolves have generally increased their kill rate of calves and "prime-age" moose. Information to date suggests that calves surviving a severe winter show greater than normal vulnerability as young adults.

Introduction

It has long been recognized by residents of Hudsonian and montane areas of North America that depth and condition of snow on the ground vitally affect wildlife. This is particularly true of ungulates such as deer (*Odocoileus virginianus*) and moose (*Alces alces*).

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[1] Journal paper No. 5016 of the Purdue University Agricultural Experiment Station.

Adaptations beneficial in deep snow are seen in the splay-toed foot structure of the caribou (*Rangifer tarandus*) and the long legs of moose.

This paper investigates the effect of snow conditions on moose and wolves and the resultant changes in the nature of wolf predation on moose. In the last decade much new knowledge has been gained concerning moose-snow interaction. Building on the pioneering works of Formosov (1946) and Nasimovitch (1955), DesMeules (1964) and Telfer (1970) documented the important effect of snow depth on moose distribution and behavior. Peek (1971) and Kelsall and Prescott (1971) presented quantitative data on snow density and hardness in addition to depth, and related these to moose habitat selection and mobility. Kelsall (1969) and Kelsall and Telfer (1971), working on several species of ungulates, have shown that chest height and weight load vary significantly according to sex and age and can affect an animal's performance in deep snow. The effect of snow on wolves and wolf predation was dealt with by Formosov (1946) and Nasimovitch (1955) in the Soviet Union, and more recently by Mech *et al.* (1971) in Minnesota. Present interpretations relative to moose and wolves are based on observations covering 14 annual winter study periods since 1958 in Isle Royale National Park, Michigan.

Study area and methods

Isle Royale is a roadless island of 544 km^2, 24 to 29 km from the Ontario shore of Lake Superior. Some 72 km in length and up to 14 km in width, it is a series of basaltic and conglomerate ridges covered with seral stages of conifer and hardwood forests (Linn, 1957). Much of the forest has been logged and/or burned in historic times. The fauna lacks numerous vertebrate species common on the mainland, notably white-tailed deer, black bear (*Ursus americanus*), porcupines (*Erethizon dorsatum*), racoons (*Procyon lotor*), skunks (*Mephitis mephitis*), and several kinds of small rodents (*Tamias spp.*, *Microtus spp.*, *Clethrionomys spp.*) and insectivores (*Blarina spp.*, *Condylura spp.*, *Sorex spp.*). Moose reached the island, probably by swimming, before 1910. The population irrupted and severely depleted its food supply during the 1920's and underwent a major natural reduction during the 1930's. Wolves immigrated to Isle Royale, no doubt by way of winter ice, during the late 1940's. The wolf population, preying on moose and beaver (*Castor canadensis*), has varied from approximately 17 to 30, and moose numbers in midwinter have been approximately 1000 (2 per km^2) for most of the period of these studies (Jordan *et al.*, 1967; Wolfe and Allen, 1973).

The winter study period on Isle Royale commonly began in late January, and extended to mid-March. Observations of moose and wolves, which included extensive tracking, were made from an Aeronca Champion aircraft.

Snow studies utilized a modification of the compaction gauge developed by Verme (1968) in upper Michigan deer studies. Mech *et al.* (1971) have also used this device in northern Minnesota. The compaction gauge (cross-sectional area: 1.98 cm^2 could be loaded with lead weights to simulate and load up to 650 g/cm^2. Our general procedure was to begin at 100 g/cm^2, and increase the weight-load until the instrument reached the ground when dropped from the snow surface. Because of the great variability in snow cover, 10 or more readings were taken for each weight-load, at increments of 50 g/cm^2. These tests were carried out in several different canopy types approximately on a weekly basis. In addition, physical characteristics of the snow profile were measured at two-week intervals in an open area near camp headquarters according to the method of Klein *et al.* (1950). Non-systematic depth readings were taken at remote sites where conditions permitted the aircraft to land.

Results

In the 9 years prior to 1968, we considered snow depths of about 60 cm to be "normal," the common range of variability being between 50 and 76 cm. This period did not produce the extremes that have obviously changed moose distribution, foraging and vulnerability to wolf predation since 1968. The winters of 1968 and 1969 were characterized by minimum and maximum snow depths respectively, and introduced a phase of the study in which it became evident that critical analysis of snow conditions was essential to an appraisal of long-term moose-wolf relationships.

In the winter of 1968, with only 23 to 36 cm of snow on the ground, both moose and wolves were generally more active in all habitats than had been observed in other years. In particular, they made exceptional use of a burn of 130 km^2 dating from 1936. In 1968, the lake edges were not traveled or utilized to the usual extent. It became evident in the following years that the use of shorelines and adjacent thick stands of conifers increased in direct proportion to snow depth. This was an outstanding feature of moose activity in the winters of heaviest snow, 1969, 1971, and 1972.

After severe winters, there has been a marked reduction in the twinning rate, regarded by Pimlott (1959) as a sensitive indicator of productivity. Based on summer observations, the twinning rate for Isle Royale moose from 1958 through 1963 was 32 percent (for 188 cows with calves) (Shelton, 1966). After the hard winters of 1969, 1971, and 1972, only 9.5 percent of 63 cows with calves were accompanied by twins. The intervening year, 1970 (in the "normal" snow-depth range), showed a twinning rate of 20 percent for 25 cows with calves.

In addition to effects on habitat utilization and moose productivity, unusually deep snow brought about several changes in moose-wolf relationships. Some of these are evident in Table I, which summarizes basic information for the winters since 1967.

In order to reappraise the more general effects of snow conditions, past snow depth records were compiled from field notes and annual project reports. In most cases depth readings had been taken in open or nearly open woods at the southwest end of the island. Due to the variation in manner and frequency of measurement, and the fact that snowfall is not always uniform over the entire island, these records were used to assign one of three broad categories of snow depth (low = less than 51 cm; medium = 51-76 cm; high = over 76 cm) to any time period. All wolf-killed moose for which we knew an approximate date of death were assigned to one of these snow-depth categories. The yearly distribution of kills according to this classification is shown in Figure 1, which provides a general picture of relative snow depths since 1959.

Observations on Isle Royale indicate that above-average snow depths during several recent winter study pe-

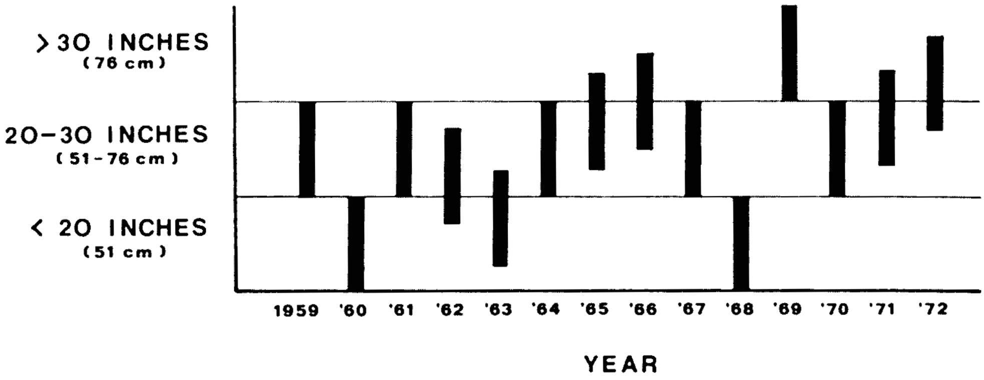

Figure 1. Distribution of Isle Royale moose kills by gross snow depth categories, 1959-72. The position of the bar (total bar length is 100 percent) indicates the proportion of the total kill in categories represented during the 7-week winter study period.

riods are in marked contrast to snow depths in early years of the project. U.S. Weather Bureau records for Grand Marais, Minnesota, located in the north shore of Lake Superior 80 km west of Isle Royale, show an average yearly increase for January-March snowfall of 5.89 cm for the last 14 years (Fig. 2). The only major departure from this trend was in 1968, when snowfall was far below normal.

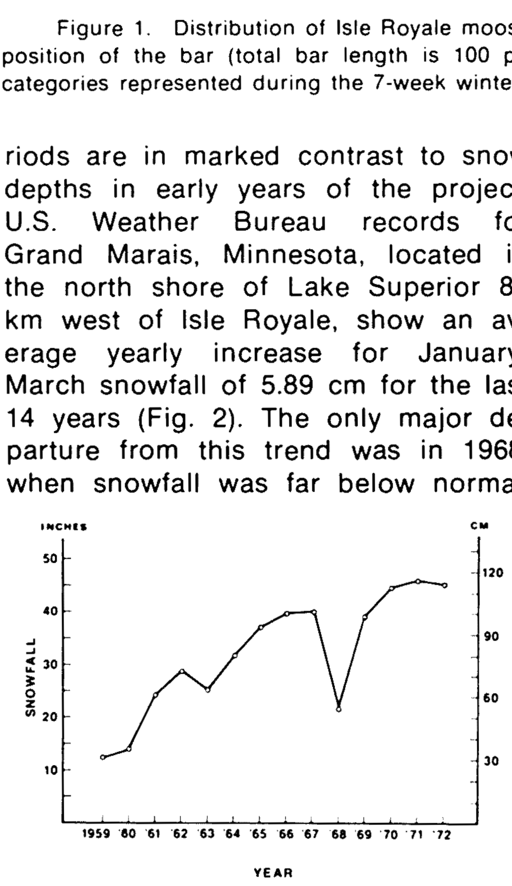

Figure 2. January-through-March snowfall for Grand Marais, Minnesota (U. S. Weather Bureau).

PHYSICAL CHARACTERISTICS OF SNOW

It is generally simpler to measure the physical characteristics of snow than it is to assess their relationships to wildlife. Of the snow measurements recommended by the National Research Council of Canada (Klein *et al.*, 1950), depth, density, and hardness (the force-per-unit-area necessary to collapse the snow structure) are believed to have the most significant effect on moose and wolf mobility.

In a given location these physical parameters are continuously changing due to the gradual process of snow maturation (firnification) as described by Klein *et al.*, (1950). Newly fallen snow is often light and fluffy, with a reported density of 0.03 to 0.19 g/cm^3 (Klein *et al.*, 1950; Moen and Evans, 1971; Kelsall and Prescott, 1971). Through the action of wind, insolation, and gravity, a layer of new snow begins to settle and compact. Individual snow crystals lose their delicate shape and often become bound to one another, either by direct sublimation or melting and refreezing. Wind, especially when accompanied by high relative humidity, facilitates bonding between snow grains. This may result in a "wind crust," as often seen on frozen waterways and other exposed areas. As snow ages, its depth will decrease and the density will increase, with old, dry snow often showing densities of 0.30 to 0.35 g/cm^3. Thaws accompanying rising temperatures and rains bring about a rapid decrease in depth and an increase in density to 0.40

and 0.50 g/cm^3. Crusts often appear in the snow profile and can be of primary importance to wildlife.

A coniferous canopy has a pronounced effect on the snow profile beneath by its interception of falling snow and its influence on the maturation process (Pruitt, 1958). Lesser snow depths beneath coniferous cover have been noted by DesMeules (1964), Peek (1971), and Kelsall and Prescott (1971). On Isle Royale, a tract with a heavy conifer canopy averaged 29 percent (range: 23-33 percent) less snow than a nearby opening in 1972. An adjacent area, with a sparse deciduous canopy and exposed to prevailing winds, showed 15 percent (range: 9-19 percent) less snow than the open area over the 7-week period (Fig. 3).

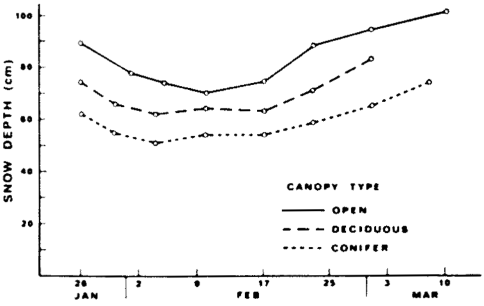

Figure 3. Snow depth at three sites on Isle Royale, 1972, illustrating the effect of overhead canopy.

Microclimate is significantly altered by the presence of an overhead canopy. Besides shielding the surface below from the direct effects of wind and solar radiation, a snow-retaining canopy serves as a thermal insulator, reducing the amount of upward infrared radiation at night (Ozoga, 1968; Moen and Evans, 1971). The net effect is to retard maturation of the snow cover, generally resulting in softer, fluffier snow in areas with a heavy canopy. Crusts are less well developed, and thus vertical hardness is almost always lower in canopied areas (Kelsall and Prescott, 1971). These conditions on Isle Royale were reflected on compaction gauge data for three stations differing in canopy coverage (Fig. 4). Beneath conifer cover, penetration (at 100 g/cm^2 averaged 30 percent greater (range: 17 to 50 percent) than at a nearby open station.

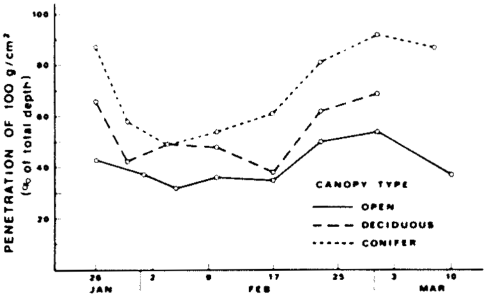

Figure 4. Penetrability (determined by compaction gauge) of snow at three sites on Isle Royale, 1972. Stations correspond to those in Figure 3.

EFFECTS OF SNOW CONDITIONS ON MOOSE AND WOLF MOBILITY

In order to compare the relative effects of deep snow on moose and wolves, we may consider body weights of the two species in relation to their respective track areas. Reported weight-loads for moose vary from 420 g/cm^2 to over 1000 g/cm^2 (Nasimovitch, 1955; Kelsall, 1969; Kelsall and Telfer, 1971). On Isle Royale we measured a total of 220 fresh tracks of 17 moose, and calculated an average track depth for each set of tracks. Compaction tests were then conducted nearby to determine the weight load that best simulated track depth. The average value was 230 g/cm^2 (s.d. = 43), considerably less than the static foot-load measurements of moose previously mentioned. This suggests that as a moose's hoof penetrates the snow profile, progressive packing of the snow beneath the hoof greatly increases the support provided. In addition moose may receive support from that portion of the leg immediately above the hoof and dew claws. Coady (1974) presents a comprehensive discussion of the effect of snow on moose mobility.

Wolves differ considerably from moose in their ability to travel in specific snow conditions, due to a lesser weight-load-on-track and relatively short legs. Measurements by Nasimovitch (1955) in the Soviet Union yielded standing weight-load figures of 89 to 114 g/cm^2 for five wolves. Preliminary compaction gauge tests of wolf tracks on Isle Royale indicated that a weight-load of approximately 100 g/cm^2 best simulates wolf track depths. Nasimovitch (1955) pointed out that in spite of a small weight-load-on-track, a wolf sinks to its chest in light snow (density$\approx$0.21 g/cm^3). Thus with more than 40 cm of snow (of low density), it became more difficult for wolves to pursue roe deer (*Capreolus capreolus*) and sika deer (*Cervus nippon*), and with 50 to 60 cm, pursuit through untracked snow was almost impossible. A density of 0.33 to 0.35 g/cm^3 in the upper part of the snow profile is sufficient to support a wolf, according to Nasimovitch (1955), and strong crusts within the profile can work to the advantage of the wolf if the prey is breaking through. For example, wolves appeared to be aided considerably on Isle Royale in February, 1972, by a crust located about 20 cm beneath the surface of the snow. At times, this crust even supported trotting wolves, through moose calves broke through it. Similarly, wolves were supported by a surface crust that formed after a rain during the winter of 1966, enabling them to make extensive use of inland areas.

TABLE I

Recent snow depth and kill data, Isle Royale National Park

Year	Winter study dates	General snow description	Snow depth range	Total kills examined[1]	Calves killed	
					No.	Percent
1967	2 Feb. – 17 Mar.	"normal" depths, low density	58-79 cm (23-31 inches)	12	2	16.7
1968	30 Jan. – 14 Mar.	winter of least snow	23-36 cm (9-14 inches)	12	2	16.7
1969	31 Jan. – 14 Mar.	winter of most snow	81-112 cm (32-44 inches)	29	14	48.3
1970	29 Jan. – 14 Mar.	"normal" snow depths	56-58 cm (22-23 inches)	14	7	50.0
1971	26 Jan. – 11 Mar.	deep snow, low density	51-91 cm (20-36 inches)[2]	32	19	59.4
1972	23 Jan. – 10 Mar.	deep snow of longest duration	71-102 cm (28-40 inches)	35	17	48.5
			Average 1959-72	20.4	6.9	29.6

[1] In some years, all of the known wolf kills could not be examined.

[2] Snow depths were above 76 cm (30 inches) for most of the 1971 study period.

In contrast, Mech (1966) detailed several hunts when wolves were hampered considerably by a light surface crust that did not support them.

MOOSE AND WOLF RESPONSE TO SNOW CONDITIONS

In addition to its influence on moose and wolf mobility, the effect of snow on behavior and distribution is central to a proper understanding of moose-wolf relationships. Adaptive responses allow these animals to inhabit regions where snow depths show a wide range of variability. The relationship between snow conditions and habitat selection by moose is well documented (see Coady, 1974) and will not be considered further in this paper.

Wolves, by nature extensive travelers, often avoid deep snow by using such features as frozen waterways, ridges, and game trails for long distance movements (Mech, 1970). The shoreline of Isle Royale and the long, narrow inland lakes have always been primary travel routes in winter. When traveling overland through deep snow, wolves move in single file, thus packing a good trail. Some of these are used repeatedly and become habitual pathways. The long, windblown ridges of Isle Royale also are travel routes for wolves. These are likewise used by moose, which occasionally lean out over a cliff to reach untouched browse. The winter of 1971 provided an interesting example of the common use of ridgetop areas, when we recorded five cases of moose falling over cliffs varying in height from 4 to 12 m when attacked by wolves.

WINTER MOOSE DISTRIBUTION

The distribution of vegetation types on Isle Royale largely explains moose distribution (a typical distribution pattern appears in Jordan *et al.*, 1967). Linn (1957) described the two primary forest associations on the island, the white spruce (*Picea glauca*) — balsam fir (*Abies balsamea*) forest and the sugar maple (*Acer saccharum*) — yellow birch (*Betula alleghaniensis*) forest. Only the spruce-fir climax type is found along the periphery of the island, where atmospheric moisture is higher and temperatures during the growing season are lower.

Midwinter use of burns appears to be greatly affected by snow depths. In 1960, with snow depths ranging from 30 to 41 cm, Mech (1966) found considerable numbers of moose in Isle Royale burns. Likewise, with the record low snow depths of 1968 (less than 36 cm), moose again moved into these burn areas.

The highest moose densities in midwinter normally occur in either the spruce-fir forest or successional types with ample conifer reproduction, especially along gently sloping, south-facing, shorelines. These shoreline areas comprise about 15 percent of the island, and commonly show densities exceeding 4.0 moose/km^2. By way of contrast, in 1972 we estimated a moose density of less than 0.4/km^2 for 57 percent of the island, primarily the interior regions and the 1936 burn. Due to the concentration of moose along lakeshores, these habitats have traditionnally been over-browsed, a situation aggravated by the deep snow conditions of 1969, 1971, and 1972.

The locations of wolf-killed moose illustrate the effect of snow conditions, reflecting both moose distribution and wolf travel routes (Table II). Snow depth has a highly significant effect on the frequency of kills adjacent to shorelines and a significant effect on the occurence of kills in burns (99 percent and 95 percent confidence intervals for the differences between per-

TABLE II

Effects of snow depth on location of wolf-killed moose

Snow depth	*Kills within 805 m^2 of a lakeshore* (%)	*Kills in burn areas* (%)
Less than 51 cm (n = 47)	49	32
Greater than 51 cm (n = 227)	81	14

[1] 805 m = 0.5 mile.

centage figures in the former and latter cases are 0.32 ± 0.21 and 0.18 ± 0.14, respectively, according to Wonnacott and Wonnacott, 1969).

EFFECT OF SNOW ON WOLF PREDATION

Since wolves and moose differ in their ability to cope with specific snow conditions, we might expect that an unusual snow cover would result in changes in this predator-prey relationship. Mech (1966) details several hunting accounts in which snow conditions interfered with the ability of wolves to maintain pursuit of a moose. On the other hand, Formosov (1946) and Nasimovitch (1955) refer to wolves tacking a heavier toll of certain hoofed animals in late winter. When the process of snow maturation is well advanced, or when crusts form, wolves may be supported better than their prey. Thus wolves increased their kill of white-tailed deer in northeastern Minnesota in February and March, 1969, after very deep snow began to settle and compact (Mech *et al.*, 1971). Kolenosky (1972) believed that the kill rate of deer by wolves in east-central Ontario was increased by deep snow in 1969.

Of the moose killed by wolves in winter on Isle Royale since 1959, an approximate date of death was available for 275 animals. To each of these a snow-depth category, as described previously, was assigned. Because of the unprecise nature of available information, the classification system is necessarily general.

Kill rate

The number of carcasses located from the air each winter provided a gross indication of the kill rate of the Isle Royale wolves. This index was only approximate, since the amount of time spent following wolves and searching for kills varied considerably at different periods of the study.

Nevertheless, unusually deep snow contributed to an obviously increased rate of predation on moose in some situations. In 1969, 1971, and 1972 (the years most severe for moose), known wolf kills numbered 30, 34 and 36, respectively. The average number for all other years was 18.

Less than complete utilization of many moose carcasses by wolves, first noted in 1969, was also evident in 1971 and 1972. Frequently the hide was pulled off and the carcass largely cleaned of meat on one side, with the skleton left articulated. Sometimes, legs were removed and the hide partially eaten. This was in marked contrast to earlier years, when it was usual for the entire skeleton, including legs, to be disarticulated and the cartilaginous parts eaten.

During periods of deep snow, when both moose and wolves use shorelines extensively, there are more frequent contacts between the two species. The escape and defense capabilities of moose may be severely restricted by snow conditions, although wolves may also be handicapped. This and the state of malnourishment of some of the moose appear to explain, at least in part, the increased kill rate. Evidence of nutritional hardship was especially evident in the spring of 1972, when we recovered 10 carcasses of moose that appeared to have died of malnutrition during the previous winter. All but one were less than 0.8 km (0.5 mile) from a shoreline. The bone marrow of these animals was either partially or totally depleted of fat. Three moose in this condition were found after the severe winter of 1971, but in previous years such records were rare.

These observations parallel those of Mech *et al.* (1971), who noted that white-tailed deer also increase their use of lake edges under conditions of deep snow. They, too, pointed out that deep snow can increase the kill by wolves through effects on the health and defensive behavior of deer.

Mortality among adult moose on Isle Royale occurs primarily during mid- or late-winter (January through April), as shown by the lack of antler development in 72 percent ($n = 148$) of adult male remains found randomly during summer field work. Thus, snow conditions can have a significant effect on annual adult mortality of moose.

Predation on calves

Snow depth also has an important effect on calf vulnerability to wolf predation. When snow depths on Isle Royale exceeded 76 cm, the percentage of calves in the kill increased. Of 193 moose killed when snow depths were less than 76 cm, 59 (31 percent) were calves. When snow depth exceeded 76 cm, 37 of 76 kills (49 percent) were calves (95 percent confidence interval is 0.18 ± 0.13 for the difference between the percentages, according to Wonnacott and Wonnacott 1969).

According to Kelsall (1969), the chest height of 6-month-old calf is about 82 cm. In deep snow a calf finds it easiest to follow in the tracks of its mother. But, when defending their young, cows invariably move to the rear of their calves, providing protection for the area most vulnerable to wolf attack. While this is a highly adaptive behavior under normal circumstances, when snow is deep, the calf must break trail under a great handicap. This slows the movements of the pair when wolves approach. In 1972, wolves supported by a crust were observed trotting easily beside a calf that was struggling to move through the deep snow, protected from behind by its mother. In another case, wolves surprised a cow and calf who were browsing a short distance from one another. They wounded the calf before the mother could come to its aid. In 1971 we recorded two cases of calves probably abandoned on lake edges by their mothers, who may have gone inland to feed. One of these was killed by a wolf. Another calf that was widely separated from its mother was injured (perhaps mortally) by a wolf before the cow could drive off the wolf. Deep snow can be critical in such situations.

The vigor of calves can be strikingly reduced by malnutrition during long periods of severe snow conditions, and calf vulnerability is increased accordingly. Routine examination of bone marrow from calves has shown a greater incidence of fat-depleted marrow in recent years: of twenty-one 8- to 10-month-old calves examined from 1959 through 1964, 19 (90 percent) had undepleted fat reserves in the long leg bones. All of these calves died when snow depths were either medium or low. Since 1965 we have examined 33 calves of a similar age, and only 7 (21 percent) had undepleted fat reserves (99 percent confidence interval is 0.69 ± 0.28 for the difference between the percentages, according to Wonnacott and Wonnacott, 1969). The majority (79 percent) of these calves died during the severe winters of 1969, 1971, and 1972.

The selection process

Data on moose mortality from Isle Royale indicate that wolf predation is highly selective for calves and old animals, generally 7 or more years of age, which often show debilitating conditions of various kinds (Mech, 1966; unpublished data). However, of 42 adult moose killed by wolves during the severe winters of 1969, 1971, and 1972, 38 percent were from 1+ to 3+ years of age. This contrasts sharply with all other years, when kills in this age group accounted for only 12 percent of 113 kills. Table III shows the age distribution of moose killed by wolves under varying snow depths. A 5 × 3 contingency test comparing age at death with approximate snow depth did not indicate a statistically significant interaction ($\chi^2 = 11.43$; d.f. = 8; $p<0.18$), although variation in the 1+ to 3+ year age group accounted for 48 percent of the χ^2 value obtained. In the deepest snow category, we see that the frequency of kills in the young age groups equals or slightly exceeds that of the old age groups. However, even in this case wolf predation is selective for older animals, which are considerably less numerous than the younger age groups.

It is evident that long-term changes in the age distribution of the moose herd or the vulnerability of certain age groups might affect the age distribution of the kill, independent of snow conditions. To test this possibility, we examined the age distribution of adult moose killed under conditions of medium snow depths for the periods 1959-62, 1963-66, and 1967-72. The only consistent trend in this comparison was a general increase in the frequency of moose kills in the 1+ to 3+-year-old group. The percentage of the total kill included in this group for each time period was 2, 19, and 34 percent, respectively. Most of the increase during the last period may be attributed to the effect of snow conditions, since 6 of the 10 animals in the 1- to 3-year-old category in this sample died when snow depths temporarily dropped below 76 cm in 1971 and 1972, winters generally regarded as severe for moose. Three other moose in this group were killed as yearlings early in 1970. It is noteworthy that these animals were calves during the severe winter of 1969, suggesting a continuing vulnerability in that cohort.

TABLE III

Age distribution of 159 adult Isle Royale moose, killed by wolves in winter under varying snow depths

Age (Years)	Snow depth					
	Less than 51 cm		51 – 76 cm		More than 76 cm	
	No.	Percent	No.	Percent	No.	Percent
1+ – 3+	2	5.9	16	18.2	11	29.7
4+ – 6+	3	8.8	9	10.2	5	13.5
7+ – 9+	13	38.2	22	25.0	10	27.0
10+ – 12+	12	35.3	27	30.7	5	13.6
13+ – 16+	4	11.8	14	15.9	6	16.2
Total	34	100.0	88	100.0	37	100.0

Relative to the latter point, long-term effects of a severe winter may be subtle and difficult to assess. A major nutritional handicap in the first winter of life may affect calf development and increase the vulnerability of young moose in the years when "normally" they are practically immune to wolf predation. This is further suggested by kill records on Isle Royale for the winter of 1972, when 8 of 17 adult moose killed by wolves were either yearlings or 2+ years old. It was observed particularly in the winter of 1971 that some calves were underdeveloped, even stunted and bone measurements confirmed this. Kill records indicate that at least some calves in the winter of 1970 also were physically handicapped and more vulnerable to wolves. Of 14 known kills, 7 were calves (Table I), and of the four whose bone marrow was examined all were found to be fat-depleted. These were kills of the first half of February, and snow depth obviously did not explain their vulnerability. It is evident that the ecological picture is not complete. Beginning in 1969, three out of four winters were characterized by heavy snow cover, which provides opportunity for further studies of residual effects in the years immediately ahead.

Conclusions

Depth and other characteristics of snow of the ground commonly mediate the vulnerability of moose to wolf predation. The mobility of both species is affected, as are moose distribution and wolf travel patterns. Deep snow impairs the defense capabilities of moose, increases moose-wolf contacts on heavily traveled shorelines, localizes moose in long-overbrowsed habitats, and leads to malnutrition of calves and some adults. Calves and "prime age" adults comprise a large share of the population, and an increase in the vulnerability of these age groups results in a proportionate increase in the number of moose that can be killed by wolves. A series of severe winters could depress the moose population through effects on adult mortality and calf production and survival, although this has not been demonstrated on Isle Royale.

Acknowledgements

Studies of the wolf and its two prey species, moose and beaver, have been in progress on Isle Royale since 1958. Organized and directed by Durward L. Allen, Professor of Wildlife Ecology, the program was the primary research of doctoral candidates L. David Mech and Philip C. Shelton and post-doctoral associates Peter A. Jordan and Michael L. Wolfe. Rolf O. Peterson began his doctoral research in 1970.

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INTERRELATIONSHIPS OF MOOSE AND DEER OF THE GENUS *ODOCOILEUS*

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Résumé

L'auteur examine la nature des relations de l'orignal (*Alces alces*) avec, d'une part, le cerf de Virginie (*Odocoileus virginianus*) et d'autre part, le cerf mulet (*Odocoileus hemionus*) en ce qui a trait à la distribution, au comportement, au choix de l'habitat hivernal, aux préférences alimentaires, à la maladie, à la résistance aux prédateurs et à la productivité, partout où ces ongulés sont sympatriques. Normalement, les conditions d'accumulation de neige n'influencent pas l'orignal durant l'hiver et celui-ci est assez régulièrement dispersé à cette saison. Au contraire, les cerfs se rassemblent en grands nombres dans des régions favorables, à mesure que la couche de neige au sol s'épaissit. Quand l'orignal se rassemble dans des quartiers d'hivernage, il semble choisir des aires offrant tant des ressources alimentaires convenables que des conditions d'accumulation de neige limitant au minimum les mouvements. Par contre, les cerfs semblent choisir des quartiers d'hivernage plus en fonction de la qualité du couvert qu'on y trouve qu'en fonction des ressources alimentaires présentes. Il arrive que les deux occupent les mêmes aires d'hivernage quand l'accumulation de neige au sol est considérable. Orignal et cerf font usage des mêmes plantes durant l'hiver, et il est vraisemblable que la concentration de grands nombres de ces animaux dans le même habitat entraîne une compétition directe pour les ressources alimentaires disponibles. Dans de telles circonstances, le cerf aurait sans doute l'avantage sur l'orignal, en raison de son potentiel reproducteur plus élevé. L'aptitude qu'a le cerf de Virginie à coexister auprès de l'homme et de ses exploitations agricoles lui permet de survivre et même d'envahir des aires que l'orignal et le cerf mulet avaient été forcés d'abandonner. Par contre, l'orignal réagit mieux aux perturbations du milieu forestier que constituent les feux ou les exploitations commerciales de la forêt. Généralement, tout agent entraînant la disparition du couvert forestier sur de vastes superficies ne favorise pas les cerfs. Quand leurs populations sont à haute densité, orignal et cerfs peuvent interférer mutuellement les uns avec les autres en réduisant la qualité et la quantité de nourriture. Le vers des méninges, *Parelaphostrongylus tenuis*, dont l'hôte normal est le cerf de Virginie, a probablement constitué le plus important de tous les facteurs affectant les populations d'orignaux. Si le cerf mulet peut aussi héberger ce parasite et permettre sa transmission à l'orignal, il faudrait s'attendre à ce que les populations d'orignaux de l'ouest du continent soient sérieusement affectées.

Abstract

Relationships between moose (*Alces alces*) white-tailed deer (*Odocoileus virginianus*) as well as mule deer (*Odocoileus hemionus*), are evaluated on the basis of distribution, behavior, winter habitat and food preference, disease, predator and productivity considerations within sympatric ranges. Moose normally are not restricted by average winter snow depths and tend to be more dispersed in winter, while deer concentrate in favorable areas in large numbers with increasing snow depths. When moose do concentrate they tend to seek out areas of favorable food and snow depth. Deer normally seek areas which provide shelter, food being of secondary importance. In deep snow both may occupy similar areas.

Moose and deer generally use the same plant species as winter food and utilization of the same habitat in large numbers will likely lead to direct competition for available food. Deer, with greater reproductive potential than moose, would appear to have an advantage. The ability of white-tailed deer to adapt to settlement and agriculture has allowed them to persist in or invade areas where moose and mule deer were forced out. Moose appear better able to cope with habitat perturbations such as fires or lumbering. Any factor that reduces large areas of cover is usually detrimental to deer. Both moose and deer at high densities may adversely affect one another by reducing the quality and quantity of available food. The meningeal worm *Parelaphostrongylus tenuis*, which is carried by white-tailed deer has probably had more effect on eastern North American moose populations than any other single factor. The apparent spread of this nematode into the west could have serious effects on western moose populations if mule deer can also serve as hosts.

Introduction

The geographic ranges of moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*) overlap in a broad band along the southern edge of the boreal forest in North America (Fig. 1). This, together with general similarities in local distribution, habitat, and food habits would appear to present opportunities for interspecific conflict within the sympatric range. However, few studies have been concerned with interspecific relationships. The recent discovery of *Parelaphostrongylus tenuis* as the causative agent of moose disease (*cerebrospinal nematodiasis*) has focused some attention on interrelationships of moose and white-tailed deer in the east, but little has been done in the west where distributions of all three species overlap. This

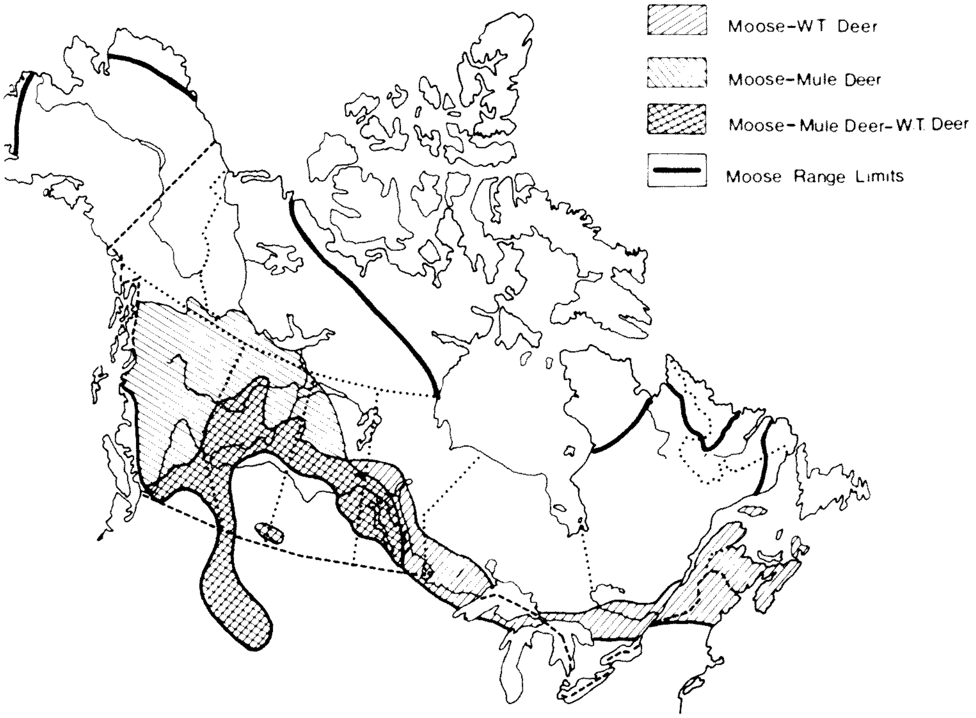

Figure 1. The overlapping moose-deer ranges across North America shown were defined by combining data from many sources. This review refers mainly to published studies carried out in these overlapping ranges.

report summarizes available information on major environmental requirements of the three species, particularly winter food habits and habitat selection, and assesses possible coactions and associated demographic implications among the three ungulates.

The present southern limit of moose distribution has changed little since 1875 (Peterson, 1955) with the exception of the mountainous and intermountainous regions of British Columbia, Wyoming and Utah (Houston, 1968; Wilson, 1971) and Newfoundland (Pimlott, 1955), which have subsequently been occupied. On the other hand both white-tailed deer and mule deer have extended their ranges into boreal forest regions to the north in the last century, invading almost all of the southern half of moose range.

In the east, white-tailed deer rapidly spread northward well into the boreal forest biome, except in Québec where excessive snow depths apparently stopped them. In the west, their progress has been slower.

Mule deer, commonly thought of as an open grassland-parkland type, has also expanded rapidly northward and is still slowly extending its range (Webb, 1967). Much of their more southerly range is apparently being slowly encroached upon by the white-tailed deer (Soper, 1964).

Habitat relationships

Habitats utilized by moose and deer differ considerably from one area to another. This seems to be due largely to the variations in available habitat but may also be influenced by climate, land-use practices and the activities of other animals. Therefore, for the most part, interrelationships probably can only be, or should be, evaluated on a local area or range basis rather than over broader geographic areas.

The moose is generally classified as a boreal-coniferous-forest species, the white-tailed deer as a deciduous brush-forest inhabitant and the mule deer as an occupant of more open range. Thus, the sympatric ranges may represent marginal habitat for all three ungulates.

That moose and deer generally have different geographical ranges and somewhat dissimilar local distributions suggests broad differences in ecological adaptions and tolerance of environmental conditions. The northern and altitudinal limits of deer are evidently set by winter characteristics (Krämer, 1972). Since mule deer generally range further north and higher in elevation than white-tailed deer (Soper, 1964), they apparently can tolerate longer and more severe winters (Krämer, 1972). Moose seem to be limited primarily by the availability of browse plant species during the winter, though the excessive snow depths of parts of Québec (Potter, 1965) may exceed their physical tolerance level (Formosov, 1946; Kelsall, 1969) and could be limiting.

Telfer, from studies of relations between moose and white-tailed deer in central New Brunswick (1968, 1970a) and in Nova Scotia (1967a), concluded that although moose and deer used similar shelter-providing habitat types under deep snow conditions, they rarely used the same areas. Moose tended to remain near the more favorable feeding areas even when restricted by snow depths. In general, the habitat chosen by moose was composed of a mosaic of small forest patches of varying ages and species composition that averaged between 0.4 and 0.8 hectares (Telfer, 1970 b), while the habitat most utilized by white-tailed deer was a dense, continuous coniferous type with few openings (Telfer, 1967a).

In the Maritimes-Maine region there is evidence for at least two broadly different patterns of winter habitat selection by moose and white-tailed deer which also tends to reduce spatial overlap in local distribution. In the upland areas, moose typically choose the upper third of a south or southwest facing slope, frequently preferring the edge between the upper deciduous forests and the coniferous stands of the valleys (Telfer, 1965; Prescott, 1968). Most wintering areas are over 180 metres in elevation (Prescott, 1968; Kelsall and Prescott, 1971). White-tailed deer, on the other hand, prefer the lower third of slopes facing south and south-west. Most were found under 180 metres in elevation (Telfer, 1967b; Nowosad, 1968; Kelsall and Prescott, 1971). In the lowlands deer "yards" occurred primarily on the middle or lower portions of south or west facing slopes or along river valleys. Moose tended to use north and east exposures more, but most of their late winter range also had south or west exposures (Telfer, 1968).

In the western Canadian provinces where moose, white-tailed deer and mule deer are sympatric, a different situation occurs. The mule deer has recently extended its range northward from the open grassland-parkland into the coniferous forest. The white-tailed deer has remained closely associated with agriculture and the broad fertile floodplains of the larger rivers (Soper, 1964). In northern Alberta, the occurrence of white-tailed deer seems to be associated with the availability of nutritious winter foods, such as nitrogen and carbohydrate-rich agricultural crops and micro-habitats that moderate the effects of cold and snow. Woodlots, ridges or the edges of water courses with mature spruce canopies seem necessary for survival in deep snow winters (Webb, 1967). Moose appear to prefer mixed upland forests with frequent open and burned areas, while mule deer may be found in either situation.

Moose and white-tailed deer appear to be even more segregated in the northwest, especially in the mountainous areas (Fig. 2), though mule deer are still found within the range of both (Wishart, personal communication). In most areas there is almost complete winter segregation of moose and white-tailed deer. Moose and mule deer both utilize the subalpine zone. Only moose wintering in the alpine zone seem to be above deer winter range. Of three broad community types described by Stelfox and Taber (1969), only one, the mountain foothill grasslands, is commonly used by white-tailed deer. The mixed coniferous forests occurring between homogeneous coniferous forests and grasslands provide year-long habitat for both white-tailed and mule deer; while the upper subalpine zone provides summer range for moose and mule deer. The third, comprised of wet bottomlands covered with willow (*Salix* spp.), dwarf birch (*Betula glandulosa*) and sedge-grass vegetation, supports moose year-long and mule deer during the winter. Some coniferous forests are mo-

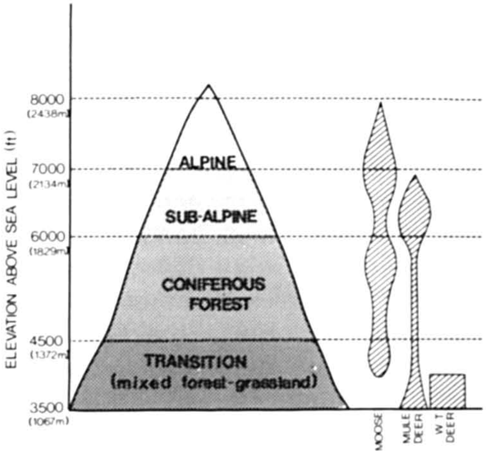

Figure 2. Midwinter distribution of moose and deer in the Rocky Mountain National Parks (from Stelfox and Taber, 1969).

derately productive of moose and, to a lesser extent, mule deer. The more southerly coniferous forests of northwestern Montana, northern Idaho and northeastern Washington are quite productive of white-tailed deer as well (Mackie, pers. comm.).

Moose are no longer common except on the margins of the aspen parkland biome, but where they occur, they utilize semi-open aspen areas, open shrub meadows and the transition zones between them in winter (Holsworth, 1960). In this area white-tailed deer are confined to brushy or wooded river flats and coulees, aspen grove parklands, and mixed wood forests (Soper, 1964). Mule deer are found along the forest edges where they thrive on the seral stages of forest succession (Webb, 1959).

Behavioral relationships

Behavioral responses of moose and deer, particularly during winter, may have important bearings on interspecific relations. Studies pertinent to an understanding of the winter behavior of moose are those of Edwards and Ritcey (1956), DesMeules (1964), Telfer (1967a), Kelsall (1969), Peek (1962), Kelsall and Prescott (1971), Coady (1974), Peterson and Allen (1974).

The reactions of deer in snow are documented by Edwards and Ritcey (1956), Telfer (1967b), Ozoga (1968), Gilbert *et al.* (1970) and others.

Moose are only occasionally restricted by snow depths over most of the overlapping moose-deer range. In Laurentides Provincial Park, Québec, DesMeules (1964) found that moose shifted from cutover areas to closed canopy areas with small to medium openings when snow depth reached 76-86 centimetres. As snow depth increased, the moose became more and more confined to coniferous cover. He suggested that, in winter, moose selected habitat providing the preferred snow depth, between 60 and 100 centimetres. On this basis he described moose as *Chionophiles* — "animals that possess definite morphological or behavioral adaptions enabling them to live in snowy regions, and that are limited in their distribution to snowy regions" (Pruitt, 1959).

Moose seldom occur in large groups (Houston, 1971). DesMeules (1964) found that with increasing snow depth, the number of animals in each group decreased, averaging less than two in mid-winter. This widespread distribution of a wintering moose population tends to spread out browsing pressure on the habitat. Houston (1971) suggested that within the boreat forest biome an evolutionary premium may have been set on small group sizes. Single moose or small groups could more successfully find and utilize scattered winter forage under deep snow conditions. The quasi-solitary nature of moose also tends to lessen association of large numbers of moose and deer in similar wintering areas (Telfer, 1968).

Deer habitat requirements undergo a definite change with changing snow depths (Day, 1963). Throughout the northern portion of their range, deer tend to concentrate, sometimes in large numbers, in areas with favorable climatic and shelter conditions. These are generally lower topographic locations. In the east, dense coniferous cover, as occurs along river channels, is commonly used. In the mountainous areas of the west, downward altitudinal migrations in winter are common. Mule deer frequently remain at higher elevations than white-tailed deer, although they still tend to concentrate.

With persistent deep snow, moose may be forced into areas similar to those used by yarded deer. Should the same areas be utilized, direct competition for food probably occurs (Peterson, 1955). In the western mountains a combination of topographical features, climate, and restricted favorable habitat forces moose to concentrate in some winters (Ritcey, 1967); and in winters of deep snow, moose may heavily utilize areas where deer concentrate.

There is no evidence of agonistic behavior between moose and deer. Peterson (1955) found moose and deer utilizing the same mineral licks without conflict. Moose have also been observed in deer wintering areas without apparent conflict other than possible competition for food (Peterson, 1955; Ritcey, 1967; and others).

Food relationships

Although food habits of the individual species have been widely studied (see: Peterson, 1955; Hosley, 1956; Hill, 1956), comparative data are scarce and not available from many areas of overlapping range.

In the Maritimes-Maine region, considerable dietary overlap occurs between moose and white-tailed deer. In Nova Scotia, six species — mountain maple (*Acer spicatum*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), balsam fir (*Abies balsamea*), red maple (*Acer rubrum*), and beaked hazelnut (*Corylus cornuta*) — comprized over 90 percent of the moose diet (Prescott, 1968). All except hazelnut were among the eight most important browse species for deer in the same province (Nowosad, 1968). Striped maple (*Acer pensyivanicum*), white birch (*Betula papyrifera*), and beech (*Fagus grandifolia*) were the others. Dodds (1960) found that all these species plus witherod (*Viburnum cassinoides*) were important deer foods.

On Anticosti Island, where white-tailed deer and moose were both introduced around the turn of the century (Cameron, 1958), deer, apparently as a consequence of over-browsing on white birch, quaking aspen (*Populus tremuloides*), mountain ash (*Sorbus americana*), fire cherry (*Prunus pensylvanica*) and hazelnut are largely restricted to feeding on balsam fir (Cameron, 1958; Pimlott, 1963): in 1955, balsam fir was being reduced and even white spruce was being heavily browsed (Pimlott, 1963). No data were available for moose on Anticosti Island; however, in Newfoundland, which has similar floristic characteristics and where only moose are present, white birch and balsam fir provided more of the food taken than all the other species combined (Pimlott, 1955; Dodds, 1960).

Gill (1957) listed white cedar (*Thuja occidentalis*) as the most important winter browse species for white-tailed deer in Maine with red maple, big-toothed aspen (*Populus grandidentata*), striped maple, mountain maple, red osier dogwood (*Cornus stolonifera*), witherod and willow receiving high use. Only occasionally was balsam fir utilized extensively. Moose utilize all these species in Maine (Hodgdon, 1961). Wright (1956) listed 12 browse species as receiving heavy use by both moose and white-tailed deer in New Brunswick; but some differences were evident. Browse lines on cedar were common in heavily used deer yards while browse lines on balsam fir were evident in moose wintering areas.

In Québec, balsam fir and white birch were the only species browsed in a temporarily used moose wintering area in Laurentides Provincial Park (DesMeules, 1962): but recent studies indicate that mountain maple and beaked hazelnut are certainly as important as balsam fir in most areas and, at any rate, more important than white birch throughout the range in the province (Brassard *et* *al.*, 1974). As to white-tailed deer in Québec, it appears that the main browse species are: beaked hazelnut, mountain maple, sugar maple, red maple, red osier dogwood and balsam fir in the range west of Montréal; north and east of this city, red maple, chokecherry, sugar maple and balsam fir are the main browse species. The browse plants most sought after by white-tailed deer are white cedar, red maple, moose wood *(Viburnum alnifolium)* and sumach (*Rhus typhina*) (Huot, 1973). Pimlott *et al.* (1968) had noted white cedar, hemlock (*Taxus canadensis*) and yellow birch as the main browse plants for white-tailed deer north and west of Montréal: but their summary was based on the results of a few short visits in a few deer yards. Recent investigations indicate that there is a definite overlap between the present diet of both moose and deer in Québec; there may also be an overlap between the food preferences of the two animals since, in the case of deer at least, preferences and actual diet appear to be two different things. However, only occasionally are moose and deer observed together on the same wintering areas (Huot, pers. comm.).

Peterson (1955) noted a definite overlap between moose and white-tailed deer food habits in the central portion of the range with only white cedar and balsam fir, respectively, excluded from preferred diets of deer and moose. Also, four (red osier dogwood, mountain maple, juneberry (*Amelanchier* spp.) and mountain ash) of eight species heavily used by moose in northern Minnesota (van Ballenberghe and Peek, 1971) are preferred white-tailed deer foods (Erickson *et al.*, 1961). The other four (white birch, willow, quaking aspen, and balsam fir) are moderately preferred deer foods.

Virtually no comparative or comparable food studies are available for the western Canadian moose range. Nor is directly comparable information available on moose-deer food habits within the range of the Shiras moose (*A. a. shirasi*), although several studies have been conducted on the individual species. Western serviceberry (*Amelanchier alnifolia*), Oregon grape (*Mahonia repens*), Rocky Mountain maple (*Acer glabrum*), Ponderosa pine (*Pinus ponderosa*) and quaking aspen are important food species: (Martinka, 1968; Kamps, 1969; Hildebrand, 1971) for white-tailed deer in Montana with most of these as well as creeping juniper (*Juniper horizontalis*) and common juniper (*J. communis*) important to mule deer (Lovaas, 1958). All these species were used by moose of this region (Denniston, 1956; Harry, 1957; Knowlton, 1960; Peek, 1962; Stevens, 1970; Schladweiler, 1971). Willow was the most important winter moose browse species recorded in almost all areas with Douglas fir (*Pseudotsuga taxifolia*), western serviceberry, chokecherry (*Prunus virginiana*) and red osier dogwood also heavily utilized.

In Wells Gray Provincial Park, British Columbia, a broad overlap in food preferences occurs between moose and mule deer (Ritcey, 1967). Both preferred false box (*Pachistima canbyi*), willow, paper birch, and red osier dogwood. Moose also used quaking aspen, hazel and Douglas fir. Cowan and Guiguet (1965) listed all these species except false box and Douglas fir plus serviceberry and high-bush cranberry (*Viburnum trilobum*) as browse species preferred by moose province-wide. Overlap was noted in the case of quaking aspen, willow, red osier dogwood and serviceberry, which are most favored by mule deer. Douglas fir may also be utilized by mule deer.

All of these data suggest that moose and deer frequently, if not generally, use similar plant species as winter food on sympatric ranges. Utilization of the same habitat in large numbers could result in direct competition for available food supplies at least during winter. Data on food habits during other seasons are generally insufficient to evaluate overlap and possible conflict in any one area.

It is important to point out that both moose and deer food habits vary extremely between and, often locally, within habitat types so that possible conflicts can only be evaluated on a local area basis.

Other relationships

Disease

The discovery of the nematode *Parelaphostrongylus tenuis* as the causative agent of "moose disease" (Anderson, 1964) and its life cycle has placed an entirely new light on moose-deer interrelationships, at least in eastern North America. Anderson (1972) reviewed relationships between this meningeal worm and native cervids in North America (see also Anderson and Lankester, 1974).

The white-tailed deer is the normal primary host and carrier of the meningeal worm which apparently is pathogenic in moose, inflicting a fatal neurological disorder called parelaphostrongylosis (Anderson and Lankester, 1974).

This "moose disease" has been associated with the marked declines in moose populations in Nova Scotia and New Brunswick and may have been responsible for similar declines in Maine and Minnesota (Anderson, 1972). It is also common in southwest Ontario (Anderson, 1964). The parasite has been found in the aspen parkland of Manitoba (Bindernagel and Anderson, 1972) and may be slowly moving westward in the white-tailed deer population.

There is some question as to the effects of the nematode on mule deer (Anderson, 1972). Should mule deer become a carrier, their close association with moose in the west may bring about a situation similar to that in the east.

Predators

Wolves (*Canis lupus*) are the only major predators common to moose and deer but deer appear to bear the brunt of wolf predation in areas of sympatric occurrence. Moose are also taken, but not in proportion to their number in the local ungulate population (Pimlott *et al.*, 1969; Frenzel, 1974).

Productivity

Deer have a greater reproductive potential than moose. This would appear to give deer the advantage in situations of mutual initial invasions of new habitats or in rebounding after catastrophes such as severe winters or fires. This factor may have been involved on Anticosti Island where moose and deer were both introduced around 1900 (Cameron, 1958). In 1952, Cameron (1958) estimated the deer population at not less than 350,000 and the moose population at 250.

Human settlement

Settlement and agricultural land-clearing are factors that have consistently favored white-tailed deer both in the east and west (Hosley, 1956; Krämer, 1972), although intensive agriculture discourages them (Bird, 1961). The ability of white-tailed deer to adapt to settlement has been an important factor in their present widespread distribution. The reduction of favorable habitat and increased hunting pressures that come with settlement are important factors that have contributed to reductions in moose (Peterson, 1955) and mule deer populations (Krämer, 1972). Grazing by domestic livestock in the west has also adversely affected moose depending on stocking rates and the diversity and abundance of forage species (Wolfe, 1974). Although white-tailed deer are similarly affected, there is some evidence that overgrazing by cattle has allowed mule deer to spread and increase their numbers (Krämer, 1972).

Interspecific competition

"Competition becomes important when two organisms strive for something that is not in adequate supply for both of them" (Odum, 1963:93). Peterson (1955) noted: "The most important ecological relationship between white-tailed deer and moose seems to be one of competition for food. Perhaps in a theoretically balanced population, these two species could occupy the same habitat without serious competition. In areas where either moose or white-tailed deer become abundant, there is little doubt that direct competition for available food takes place, especially during the winter months". Yet, the literature makes no reference to any area where deer or moose directly influenced the other through competition for available habitat or food supplies. Anticosti Island may have been one exception but competition, if it did occur, was not documented (Pimlott, 1954, 1963). The possibility of competition was also raised in several other studies but never documented (Peterson, 1955; Benson, 1958; Dodds, 1963; Ritcey, 1967 and others).

Competition of moose and deer with other big game species is also only inadequately documented and subject to speculation. For example, under somewhat artificial circumstances in Elk Island National Park (Holsworth, 1960), elk and moose have been able to maintain high populations in areas of sympatry. White-tailed deer are present only where elk numbers are low. When elk are forced to depend heavily on browse, large herds invading a deer yard may seriously affect the deer since they utilize a greater variety of foods and can out-reach deer. Moose are rarely confined because of their longer legs (Kelsall and Telfer, 1971) and would not be forced to compete with elk under these circumstances. Webb (1967) speculated that a combination of elk, bison and moose on the aspen-parkland prior to settlement successfully precluded large deer numbers.

Conclusions

Moose, because of their greater physical stature and behavioral and physiological adaptations to colder climate and deeper snows, should be able to compete successfully with deer on an individual to individual basis within their sympatric range.

With the general overlap in distribution and food habits, any evidence of habitat-use overlap presents the opportunity for severe competition, even though not well, if at all, documented. Because of wide variations in food habits, range use habits, and climatic conditions, any generalization with respect to competition must be made with extreme caution. Such interpretation is possible only on a local area to area basis with full knowledge of habitats and habitat use in that area and of the population consequences of the interactions.

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ROCKY MOUNTAIN ELK — SHIRAS MOOSE RANGE RELATIONSHIPS

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Résumé

L'aire de distribution de l'orignal (*Alces alces*) appartenant à la sous-espèce *shirasi* se superpose presque en totalité à l'aire de distribution du wapiti (*Cervus canadensis*) appartenant à la sous-espèce *nelsoni*. L'auteur dresse une comparaison du mode d'utilisation de l'habitat dans le but de vérifier si la compétition existe et d'établir la nature exacte des relations entre les deux espèces. L'orignal passe ordinairement l'hiver dans les plaines alluviales ou dans les forêts alpines, se nourrissant alors principalement de broutilles ligneuses, tandis que le wapiti fréquente à cette saison les habitats ouverts dans lesquels l'accumulation de neige est moindre et où il peut obtenir les graminées qui constituent la fraction principale de sa diète. Au printemps, l'orignal peut fréquenter ces milieux ouverts et y consommer une certaine quantité de plantes herbacées (forbs) tandis que le wapiti occupe encore les portions les plus élevées de ses quartiers d'hiver où il recherche les nouvelles pousses de graminées. À l'été, au moment où l'orignal regagne les alpages, graminées et broutilles constituent les principaux éléments de sa diète alors que le wapiti, de son côté, utilise principalement les herbacées. À l'automne, au moment où l'orignal regagne ses quartiers d'hiver, les broutilles prennent de nouveau une importance accrue alors que les graminées constituent encore la principale ressources alimentaire du wapiti. Presque tous les travaux révèlent que le saule (*Salix* spp.) constitue la base de l'alimentation de l'orignal et ce, à tout moment de l'année. Les modes d'utilisation de l'habitat, les habitudes alimentaires, la morphologie et l'organisation sociale permettent de définir pour ces deux espèces des niches écologiques bien distinctes. Cependant, quand les conditions climatiques sont particulièrement défavorables ou quand les ressources alimentaires sont faibles, un certain degré de compétition interspécifique peut apparaître entre les deux ongulés.

Abstract

Over most of its range the Shiras moose (*Alces alces shirasi*) occurs sympatrically with the Rocky Mountain elk (*Cervus canadensis nelsoni*). Range use habits of both species are compared to provide insight into interspecific relationships and possible competition. Moose generally winter in bottom areas and upland forests, foraging largely on browse, while elk feed in more open types with less snow, where grass forms the major portion of the diet. In spring, moose may utilize more forbs in open types, while elk generally utilize green grass on the upper portion of their winter range. In summer, browse and forbs are important to moose as they migrate to higher elevations, while elk utilize primarily forbs. As moose return to the winter range in fall, a higher percentage of browse occurs in the diet, while elk subsist primarily on grasses. In almost all cases, willow *(Salix* spp.*)* is the key species for moose on a year around basis. Under normal conditions, the two species appear to fill two discrete ecological niches with respect to range use, food habits, physical characteristics, and social organization. Interspecific competition, which maintains the species in their respective ecological niches, appears important only where forage resources have been depleted or weather conditions are especially severe.

Introduction

Over most of its range in the Rocky Mountains the Shiras moose (*Alces alces shirasi*) occurs sympatrically with the Rocky Mountain elk or wapiti (*Cervus canadensis nelsoni*). Relationships between the two have evolved over many years with records of both species side by side dating back to the Pleistocene. While numerous studies have been conducted on the range use and food habits of each species, interspecific relationships have not been thoroughly investigated. Some authors, including Cowan (1950), Murie (1951), McMillan (1953b), Peterson (1955), Denniston (1956), Holsworth (1958), Knowlton (1960), Houston (1968), and Cole (1969) recognized the association and commented on the possibility of competition. This paper reviews range use characteristics and discusses interspecific relationships.

Criteria presented by Cole (1958) to assess competition between big game and livestock may be of value in understanding possible conflict between two ungulate species. These criteria are: (1) both species use the same range areas; (2) both species use the same forage plants; (3) forage plants used in common are important forage for either species; and (4) the forage plants are in limited supply or deteriorating in production as a result of use. In order to apply these criteria to the Shiras moose and elk, I reviewed a number of studies on range use and food habits of both species made within the present moose distribution (primarily in Montana, Wyoming, and Idaho). Close spatial association of the two species on the study areas was not considered a prerequisite to determine habitat and forage preferences, since the number of ranges where habits of both species have been studied simultaneously is limited.

Range use and food habits

WINTER

Moose generally move to lower elevation flood plain areas where deciduous browse, especially willow (*Salix* spp.), is abundant. These ranges may comprise extensive willow bottoms as in Jackson Hole, Wyoming (Houston, 1968) or Red Rock Lakes, Montana (Dorn, 1970). They may be smaller, gallery, willow-aspen (*Populus tremuloides*) — cottonwood (*Populus* spp.) types along stream courses as in the Gravelly Mountains (Knowlton, 1960) or Rock Creek, Montana (Smith, 1962). In still other areas, aspen stands may be the key winter range (Stevens, 1970).

Food habit studies (Table I) on these ranges indicate the importance of browse to moose. Knowlton (1960) reported 98 percent of the winter diet in the Gravelly Mountains was browse, the primary species being willow (63 percent), and silverberry (*Elaeagnus commutata*). In Jackson Hole, browse formed 99 percent of the winter diet (Houston, 1968). Blueberry willow (*Salix pseudocordata*), interior willow (*S. interior*), subalpine fir (*Abies lasiocarpa*), red osier dogwood (*Cornus stolonifera*), narrow leafed cottonwood (*Populus angustifolia*), and bitterbrush (*Purshia tridentata*) were the most important species on the more commonly used vegetation types. Dorn (1970) found willow formed 99 percent of the moose diet at Red Rock Lakes, Montana. In the Gallatin Mountains, Stevens (1970) reported browse to be 99 percent of the winter diet with the primary species being willow, serviceberry (*Amelanchier alnifolia*), dogwood, and chokecherry (*Prunus virginiana*).

In contrast to the use of deciduous types, other investigators including Jonkel (1963), Stevens (1967) and Houston (1968) have reported lower density moose populations utilizing coniferous forest types in winter. They often remain scattered throughout the higher elevations, utilizing temporary "yards" to overcome deep snow. In the Gallatin-Madison area, Montana, Engelmann spruce (*Picea engelmanni*) — subalpine fir and Douglas fir (*Pseudotsuga menziesii*) — lodgepole pine (*Pinus contorta*) vegetation types were used heavily (Stevens, 1967). Food habit studies on these higher elevation conifer ranges revealed extensive use of subalpine fir. Jonkel (1963) also reported heavy use of subalpine fir in Northwest Montana.

The adaptability of the Shiras moose to available forage was shown by examination of 10 rumens collected in January in the Bighole Valley, Montana (Stevens, 1967). On this heavily used willow range, 26 percent of the diet was grasses and grass-like plants, a portion of which came from haystacks, since snow depths made native grasses generally unavailable.

Elk appear to be broader spectrum feeders and able to occupy more varied winter habitat types. On most of the ranges, however, grass or sagebrush

TABLE I

Summary of winter food habits of Shiras moose and elk on all vegetation types

Area	*Reference*	*Forage class (%)*			*Key species*
		Grass	*Forbs*	*Browse*	
MOOSE					
Jackson Hole, Wyoming	(Houston, 1968)	Tr	Tr	99	willow
Gravelly Mtns., Montana	(Knowlton, 1960)	Tr	2	98	willow, silverberry
Upper Gallatin, Montana	(Stevens, 1966b)	1	Tr	99	willow, Douglas-fir
Lower Gallatin, Montana	(Stevens, 1970)	0	1	99	willow, chokecherry, serviceberry
Bighole, Montana	(Stevens, 1967)	26	Tr	74	willow, *Cyperaceae*
Red Rock Lakes, Montana	(Dorn, 1970)	0	Tr	99	willow
ELK					
Jackson Hole, Wyoming	(Cole, 1969)[1]	72	2	26	sedges, willow, wheatgrass, bluegrass
Gravelly Mtns., Montana	(Rouse, 1957)	90	3	7	three-tipped sage
Upper Gallatin, Montana	(Wilkins, 1958)	43	4	52	conifer, willow, grasses
Upper Gallatin, Montana	(Lovaas, 1963)	40	Tr	60	big sagebrush
Sun River, Montana	(Knight, 1970)[2]	77	16	7	wheatgrass, fescue
Crow Creek, Montana	(Gordan, 1968)	72	26	2	wheatgrass, fescue
Flathead, Montana	(Rognrud and Janson, 1971)	10-40	Tr	60-90	mountain maple, willow, fescue
Bitterroot-Selway, Idaho	(Rognrud and Janson, 1971)	65	Tr	25	serviceberry, chokecherry, wheatgrass, fescue

[1] Interpolated from author's data weighted to vegetation types.

[2] Grassland vegetation type (74 percent of use).

(*Artemisia* spp.) vegetation types, usually on south exposures and ridge tops, seem to be preferred when available.

In the Sun River drainage of Montana, Knight (1970) found elk utilizing grassland 59 to 90 percent of the time, depending on weather conditions. Gordan (1968) observed 98 percent of the elk on Crow Creek, Montana, on grassland or sagebrush types in winter; no use was recorded on the aspen-willow type. Rouse (1957) reported 99 percent of his elk observations in the Gravelly Mountains were on sagebrush or grassland areas.

Food habits (Table I) on these areas reflected elk habitat preferences. On the Sun River, grass comprised 85 percent of the elk diet on the grassland type and 70 percent in the bottom areas (Knight, 1970). Gordan (1968) found grass to comprise 72 percent of the winter diet on Crow Creek, with browse contributing only 2 percent. In the Gravelly Mountain area, rumen analyses indicated grass, forbs, and sagebrush comprised 90, 3, and 7 percent, respectively, of the elk diet (Rouse, 1957). In December, in Jackson Hole, Cole (1969) reported elk using meadow and grassland types prior to annual movement to the refuge. Grass or grass-like plants constituted 72 percent of the elk diet on these areas.

Elk use of browse ranges has, however, also been observed in western Montana (Rognrud and Janson, 1971) and northern Idaho (Young and Robinette, 1939). Gaffney (1941) rated browse, primarily mountain maple (*Acer glabrum*) and willow, as the major forage class in the elk diet in the Flathead drainage, Montana, which he attributed to availability. Browse was also important winter elk forage in Elk Island National Park, Alberta (Holsworth, 1960) and Riding Mountain Park, Manitoba (Blood, 1966). Aspen, willow, and serviceberry were the key species. In the Gallatin drainage, noted for chronic overuse by elk (Lovaas, 1965), studies by Wilkins (1958) indicated that browse, primarily big sagebrush, constituted 52 percent of the elk diet although most of the winter range is grassland. Rognrud and Janson (1971:40) noted: "elk prefer native bunch grasses for winter food. However, they are very adaptable and will feed on other grasses, sedges, forbs, and browse."

SPRING

Moose generally continue to feed largely on browse in the spring, but increased use of forbs has been noted in some areas (Table II). These changes come with movement out of the bottoms to more open, upland vegetation types. In Jackson Hole, Houston (1968) made 57 percent of his spring moose observations in the willow type and 18 percent in upland forests. Food habits studies showed that browse constituted 68 and 45 percent of the diet on willow and forest types, respectively. Key species were willow, silverberry, aspen, serviceberry, sticky geranium (*Geranium viscosissimum*),. and valerian (*Valeriana* spp.). In the Upper Gallatin drainage, Stevens (1966b) reported most moose using upland forests, herbaceous parks, and aspen stands in spring. Browse was most important in the diet in all but the parks where forbs made up 55 percent of the diet. Primary species were willow, currant (*Ribes* spp.), serviceberry and sticky geranium. On the lower Gallatin drainage, Stevens (1970) showed that browse formed 94 percent of the diet, of which 32 percent was willow. Denniston (1956) reported moose feeding on grass and sagebrush in the spring.

Elk generally change to a diet of green grass as soon as it becomes available in the spring. Knight (1970) found elk still using the winter grassland areas in April, but moving into coniferous forest types during the spring period. Grass use declined from 99 percent of the diet in April to 35 percent in June on grassland types. Forb use increased with little browse use in either month. In Crow Creek, Montana, Stevens (1966a) reported that most of the elk were still on grassland or sagebrush types in April, but by June, feeding was primarily in park forests at higher elevations. Food habits showed grasses and forbs constituted 77 percent and 23 percent of the diet, respectively. In Jackson, Hole, Cole (1969) found that most elk fed on bunchgrass and sagebrush types during the spring period, and that grass formed 75 and 60 percent of the diet for each type, respectively. Browse was only important in the coniferous forest type where spirea (*Spirea betulifolia*) and pachystima (*Pachystima myrsinites*) were used. Rouse (1957) rated grass most important in the elk diet on the sagebrush type, where most of the elk in the Gravelly Mountains were feeding at that time.

SUMMER

In summer, browse areas, particularly willow sites, continue to be used by moose, although often at higher elevations. Browse is most important in the diet except when forbs or aquatic plants are particularly available (Table III). Summer habitat use by moose in Jackson Hole changed little from other seasons with 63 and 20 percent of the observations in willow types and upland forest, respectively (Houston, 1968). Food habits studies showed browse to be most important on all types, although forbs comprised 24 percent of the diet in the upland forest type. Willow remained the most important species. In the Gravelly Mountains, Knowlton (1960) reported 54 percent of the moose observations on the meadow type and 31

TABLE II

Summary of spring food habits of Shiras moose and elk on all vegetation types

Area	References	*Forage class (%)*			Key species
		Grass	*Forbs*	*Browse*	
MOOSE					
Jackson Hole, Wyoming	(Houston, 1968)	11	34	55	willow, bitterbrush, sticky geranium
Upper Gallatin, Montana	(Stevens, 1966b)	7	24	70	willow, sticky geranium
Lower Gallatin, Montana	(Stevens, 1970)	Tr	6	94	willow, currant, serviceberry
ELK					
Jackson Hole, Wyoming	(Cole, 1969)[1]	63	29	8	wheatgrass, bluegrass
Gravelly Mtns., Montana	(Rouse, 1957)[2]	90	6	3	
Sun River, Montana	(Knight, 1970)[1]	61	38	Tr	fescue, dandelion
Crow Creek, Montana	(Gordan, 1968)	73	28	0	fescue
Crow Creek, Montana	(Stevens, 1966a)	77	23	Tr	Idaho fescue

[1] Interpolated from author's data and weighted to vegetation types for seasonal total.
[2] Rumen analysis.

percent on willow bottoms. Forbs were most important forage class in the diet (71 percent). Peek (1963) suggested that this high use of forbs by moose on that area may have been related to the high precipitation in 1958. He observed greater use of willow in the same area the two following years, which were drier. In Yellowstone National Park, McMillan (1953b) found that two willow species made up 75 percent of the summer moose diet. In that study, aquatic plants were more important than has been shown for the Shiras moose over most of its range. He also noted that moose used Geyer's willow (*Salix geyeriana*) more than Wolf's willow (*Salix wolfii*) (55 and 20 percent of the diet, respectively), but elk in the area preferred the latter. Dorn (1970) made 84 percent of his summer moose observations in the willow vegetation type. Browse formed 98 percent of the diet with three willow species and bog birch (*Betula glandulosa*) most important. He concluded that availability was paramount in determining dietary composition, followed by adaptation and palatability.

Some variability also appears in elk summer range use and food habits. They are generally found in alpine meadows and subalpine herbaceous parks where forbs contribute the major portion of the diet. Martinka (1969) reported elk in the valley areas of Jackson Hole using the bunchgrass-sagebrush vegetation type extensively in summer. The elk diet in this type was mostly forbs (83 percent) and grasses (17 percent). Only in willow and coniferous forest types did browse constitute a significant part of the diet, while on the

TABLE III

Summary of summer food habits of Shiras moose and elk on all vegetation types

Area	*Reference*	*Forage class (%)*			*Key species*
		Grass	*Forbs*	*Browse*	
MOOSE					
Jackson Hole, Wyoming	(Houston, 1968)	4	17	79	willow
Gravelly Mtns., Montana	(Knowlton, 1960)	Tr	71	29	willow, sticky geranium
Yellowstone Park, Wyo.	(McMillan, 1953b)	8	17 (aquatics)	75	willow, aquatic plants
Red Rock Lakes, Montana	(Dorn, 1970)	Tr	2	98	willow, bog birch
ELK					
Jackson Hole, Wyoming	(Martinka, 1969)	65	26	9	bluegrass, aster, clover, dandelion
Gravelly Mtns., Montana	(Rouse, 1957)	3	95	2	forget-me-not
Sun River, Montana	(Knight, 1970)	46	54	—	alpine bluegrass, buttercups
Crow Creek, Montana	(Stevens, 1966a)	16	76	6	dandelion, clover
Selway Game Pres., Idaho	(Young and Robinette, 1939)*	45	18	37	maple, serviceberry, chokecherry, willow

* Interpolated from data presented by authors.

forest type various browse species comprised 60 percent. In the Gravelly Mountains elk used higher elevation open vegetation types in summer (Rouse, 1957); forbs comprised 91 to 95 percent of the diet. In the Crow Creek drainage, Stevens (1966a) found most of the elk in the summer using herbaceous parks at higher elevations. Seventy-six percent of the diet was forbs, while willow formed only 7 percent. Knight (1970) noted greater use of grass in the summer with 46 percent compared to 54 percent for forbs. Recent studies by the author in Rocky Mountain National Park, in areas not presently inhabited by moose, indicate that willow may form a substantial part of the elk summer diet. Young and Robinette (1939) also indicated heavy use of browse when it was available. Mountain maple, serviceberry, bittercherry (*Prunus emarginata*) and willow furnished the major portion of the summer forage.

FALL

In fall, moose generally return to an almost pure browse diet (Table IV) but on somewhat more widely distributed ranges than in winter. In Jackson Hole they were still using willow types, although less than for other seasons. Willow was the most important browse species (Houston, 1968). Knowlton (1960) reported increased use of willow types

TABLE IV

Summary of fall food habits of Shiras moose and elk on all vegetation types

Area	*Reference*	*Forage class (%)*			*Key species*
		Grass	*Forbs*	*Browse*	
MOOSE					
Jackson Hole, Wyoming	(Houston, 1968)	2	5	93	willow, ceanothus, serviceberry
Gravelly Mtns., Montana	(Knowlton, 1960)	2	7	91	willow, subalpine fir
Upper Gallatin, Montana	(Stevens, 1967)	1	5	94	willow, huckleberry
Lower Gallatin, Montana	(Stevens, 1970)	Tr	11	88	subalpine fir, willow, huckleberry
Red Rock Lakes, Montana	(Dorn, 1959)	1	4	95	willow
ELK					
Jackson Hole, Wyoming	(Cole, 1969)[1]	79	16	5	bluegrass, sedges
Gravelly Mtns., Montana	(Rouse, 1957)[2]	80	14	3	
Sun River, Montana	(Knight, 1970)[2]	66	20	14	needle-and-thread, blue-grass, aster, bog birch
Gallatin, Montana	(Greer, 1958)[2]	69	8	23	conifer, willow, grasses
Selway Game Pres., Idaho	(Young and Robinette, 1939)	40	20	40	

[1] Interpolated from author's data and weighted to vegetative types for seasonal total.
[2] Rumen content analysis.

with reduced use of subalpine meadows. Browse comprised 91 percent of the diet with willow, subalpine fir, currant and aspen the most important species. Stevens (1967) found heavy use of subalpine forest, upland forests and park types in the upper Gallatin drainage. Willow and low huckleberry (*Vaccinium scoparium*) were the most important species in the fall moose diet, which was 94 percent browse. Dorn (1969) reported browse to make up 95 percent of the moose diet at Red Rock Lakes. Willow was most important, with 85 percent of the use, but in the upland forest areas, aspen was also important.

With their return to lower elevation winter ranges, grass again becomes the primary item in the elk diet. In Jackson Hole, elk use of bunchgrass types increases in fall with some increase in the use of meadows (Cole, 1969). Grass became the most important forage except on herblands where forbs remained important. Knight (1970) also reported a progressive increase in the use of grassland although elk continued to frequent timber types as well. Grass was important in the diet, as indicated by rumen analyses, comprising 66 and 65 percent respectively in October and November. On two elk feeding sites examined in a lodgepole pine-aspen type in December, however, 71 percent of the use was browse, mostly bog birch, aspen, and huckleberry. In the Gravelly Mountains, Rouse (1957) reported grass to be most important in the fall elk diet, constituting 80 percent of the rumen samples examined. Analysis of rumen samples from the Gallatin drainage showed that grasses formed 69 percent of the diet and browse (mostly conifer and willow) 23 percent (Greer, 1958). Fall was the only period that Kufeld (1973) rated willow to be "highly valuable" as elk forage as indicated by 48 different studies.

Discussion

Winter is usually the critical period for large cervids in the Rocky Mountains. Snow accumulations restrict the size of ranges occupied and the potential for conflicting habits increases. Most studies suggest that high density moose populations are supported on lower elevation flood plain areas where deciduous browse, especially willow, is abundant. Almost the total diet is composed of browse. Other, lower density moose populations are supported by coniferous forests at higher elevations. Relatively deep snow accumulations are characteristic of both ranges. Elk do not appear to utilize either of these areas under normal conditions although open meadow bottom lands may provide a major forage source. They will, however, invade lower elevation, primary moose habitat, when the forage on upland sagebrush and grass ranges is depleted or when snow accumulations preclude foraging on the low vegetation. This is often a temporary condition as a result of a particularly severe winter or following a storm. Gaffney (1941) stated that in the Flathead drainage 76 cm of snow was sufficient to cause elk to feed largely on browse. In Jackson Hole, Murie (1951) noted that although both were browsers and fond of willow, elk had not invaded the deep snow, brushy areas that moose used as winter range.

Range use and food habits of the two species do not appear to overlap to any great extent on winter range as long as normal elk habitat remains available (Fig. 1).

In northern Europe, similar relationships appear to exist between moose (*Alces alces*) and red deer (*Cervus elaphus*) on the winter range. Ahlén (1965) reported differences in habitat use, food preferences, and methods of feeding from studies in Sweden and

Norway. Browse was the major winter forage class for moose in all studies with common juniper (*Juniperus communis*), birch (*Betula* spp.), Scotch pine (*Pinus sylvestris*) and willow being important species. Moose derived most of their food from clearings and open forest types, utilizing the shrub layer forage. Red deer fed in the dense spruce thickets utilizing the "field layer" for forage where snow was normally not so deep.

Continued use of browse by moose in summer and use of forbs by elk would generally indicate little dietary overlap on the summer range (Fig. 1). The general quantity and availability of all forage and habitat types when snow is not a factor tends to support this. However, McMillan (1953a) noted that increased use of willow types by elk was resulting in damage which could seriously affect moose populations in Yellowstone Park. Both Martinka (1969) and Houston (1968) indicated that summer elk use on limited areas in Jackson Hole could affect moose winter forage supplies. Flook (1964), reporting findings of Mair (1952), discussed the indirect effect that elk browsing on aspen had on moose populations. Elk browsing on regeneration apparently retarded the growth of aspen on which beaver (*Castor canadensis*) depend for food. Without food, the beaver abandoned the colonies and allowed the water levels to drop, which reduced the aquatic habitat preferred by moose. It should be noted, however, that natural succession would normally also proceed in this direction with similar consequences, although over a longer time span.

Factors other than range use and food habits may also affect range relationships of the two species. Houston (1968) commented on the survival value of the quasi-solitary social organization of the Shiras moose. The ability to exist at low densities gives it a competitive edge over a herding species such as elk in the climax subalpine forests. Widely distributed moose populations can more efficiently utilize the scattered winter forage available in these forest types. The elk is generally linked to open areas, where large amounts of forage required by a herding species are concentrated.

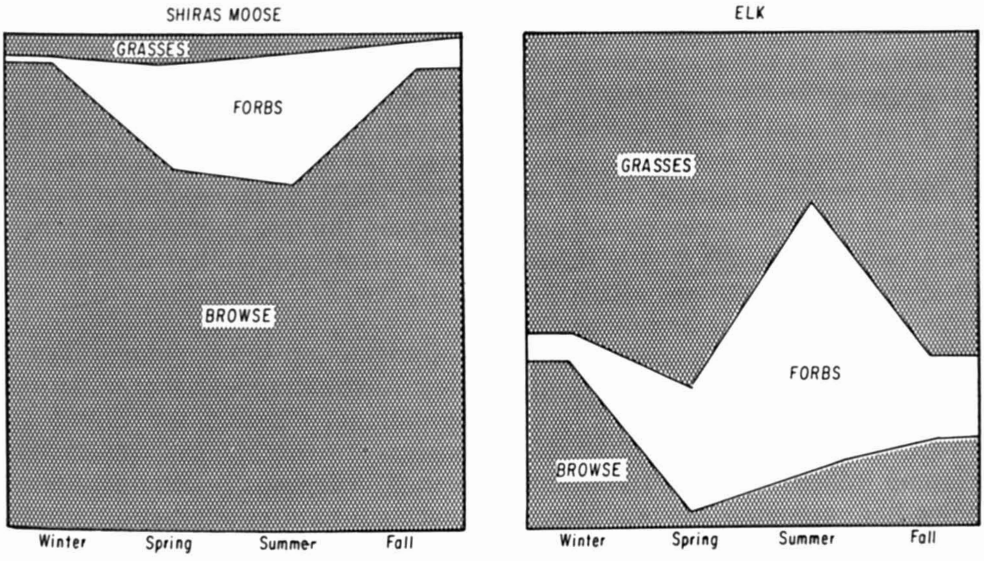

Figure 1. Comparison of year-long food habits for Shiras moose and elk in the Rocky Mountains based on 19 studies referred to in Tables I-IV.

Ahlen (1965) noted that the moose was anatomically, physiologically, and ethologically adapated to the taiga biome. The short neck and long legs are a body contruction suitable for browsing and walking in deep snow. Kelsall (1969) reported that snow depths of over 70 cm impeded moose (average chest height = 99-105 cm) movements. Red deer with chest heights of 57 to 89 cm were restricted by snow depths 50 to 70 cm (Nasimovitch, 1955). Rocky Mountain elk measured by Kelsall and Telfer (1971) had average chest heights of 88 and 82 cm for males and females, respectively. Flook (1964) also stated that moose tolerate greater snow depths than other cervids. Cole (1969) noted that deep snow (61 cm or more) appeared to allow moose to "out-compete" and ultimately preclude elk from using significant portions of the main willow food sources for moose. Lesser snow depths, however, permitted elk to utilize willow in conjunction with herbaceous food sources and ultimately "out-compete" moose. These differences in tolerance of snow depth may be the significant factor influencing distribution of the two species.

Interspecific antagonism and resulting dominance of elk over moose was noted by Brown and Simon (1947) under the artificial situation of a winter feed ground in Jackson Hole. Holsworth (1958) also commented that there was indication of elk dominance over moose but the relationship was nearly neutral in Elk Island National Park, Alberta. If this occurs, such aggression would affect the success of one species over another in close association such as on a winter range.

In some cases, higher reproductive capacity can enhance the success of one species in competition with another (Wilson and Bossert, 1971). Investigators appear to agree that twins and yearling female breeding may occur more commonly in moose populations than in elk. These differences could give the moose a slightly higher reproductive potential but wide variation occurs between areas in both species, making general comparisons of actual productivity between species difficult.

Interspecific competition is generally difficult to assess or demonstrate under field conditions. This is true for moose and elk. Using the criteria for competition proposed above, we can see that under certain circumstances, interspecific competition will occur. The two cervids may use the same range areas and forage plants. The forage plants may be important to one or both species. The ranges can be depleted, often under circumstances that may be related to livestock grazing or human disturbance of natural balances (Lovaas, 1970). Cowan (1950) and Flook (1964) suggested that decreased moose populations in parts of the Canadian Rockies were related to increasing populations of reintroduced elk. Cole (1969), however, believed that differences in food habits and environmental conditions influenced distribution and prevented biologically significant competition whereby one species could progressively displace the other. Murie (1951) also concluded that little direct competition existed between elk and moose. Holsworth (1958) observed spatial separation between the two species and concluded that direct competition was of little importance.

Considering the ecology of both species, it would appear that under normal conditions, elk and the Shiras moose occupy two fairly discrete ecological niches. Interspecific competition, however, is a natural interaction among native herbivores which is necessary to maintain their respective niches. One species may be able to exploit the habitat of another in the absence of that species. Each species, however, is successful to varying degrees in "exclusion" competition on portions ot the range. The moose has been able to expand its range in the face of well established elk populations as in Jackson Hole, Wyoming (Houston, 1968). The elk, on the other hand, when reintroduced into the Canadian Parks was able to displace the moose on the lower snow depth ranges.

Owing to the versatility and adaptability of both species, especially the elk, the determination of competition and its significance must be made by specific studies and related to management objectives for each individual range.

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REPRODUCTION AND PRODUCTIVITY OF MOOSE

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Résumé

Depuis 1955, des recherches démontrent que l'orignal (*Alces alces*) est une espèce dont le potentiel reproducteur est beaucoup plus élevé qu'on ne le croyait. Ce taux de reproduction élevé permet donc de prélever au moment de la chasse une récolte plus importante, avec le résultat que l'orignal devient, parmi le gibier, l'une des espèces les plus intéressantes. Le taux de reproduction peut être estimé précisément à partir des taux d'ovulation, de grossesse et de fécondation; ainsi, la compilation des données recueillies dans diverses régions de l'aire de reproduction révèle une remarquable homogénéité. Seule la catégorie des animaux d'un an peut faire varier la production au sein du cheptel. Le taux d'accroissement varie de 31 à 36 pourcent et la productivité brute de 24 à 26; ces deux paramètres sont très semblables dans les populations d'Amérique du Nord et de Suède. L'auteur passe en revue les nombreuses méthodes de calcul de la productivité nette et compare les résultats obtenus dans diverses régions. Chez les populations d'orignaux occupant un habitat de qualité, la productivité nette est toujours évaluée à 20-25 pourcent. L'auteur termine en mentionnant les domaines de recherches les plus profitables pour l'avenir.

Abstract

Since 1955, research has shown that the moose (*Alces alces*) is a much more productive species than formerly believed. This has resulted in a significant increase in the importance of moose as a game species owing to the increase in allowable harvest which the higher reproductive rates indicate to be permissible. Keys to reproductive performance are ovulation rates, pregnancy rates and fertilization rates: data for various areas are compiled and show a rather remarkable similarity. The largest variations occur in the yearling class which is the youngest productive class in any moose herd. Rates of increase and gross productivity for North American and Swedish moose are summarized and found to be remarkably similar, ranging from 31-36 percent and 24-26 percent respectively.

The several methods used in calculation of net productivity are reported and results compared for various study areas. From studies of moose on good range, net productivity consistently is determined to be in the range of 20 to 25 percent. Several areas are recommended as the most productive avenues for intensified future research.

Introduction

Among the most important parameters for which information must be obtained to plan a sound management program for any species are measures of reproductive rates and production. Moose are no exception to this rule. In recognition of this need, moose managers and researchers have devoted considerable time and effort to produce estimates of these parameters for their management programs.

The findings in this area, with the possible exception of the development of more reliable census methods, have probably had a greater influence on moose management in the last 15 years than the results from any other research area.

Up until 1955, adequate information about moose productivity on which to base an efficient moose management program was not available. Peterson (1955) thoroughly reviewed the available information prior to 1955 and was forced to come to the conclusion that the moose was a relatively slow reproducing species even among the Cervidae. That these conclusions were based on methods which could only under the most favourable or circumstances produce valid observations was amply shown by Pimlott (1959) and Markgren (1969).

It was Pimlott in his important 1959 publication who disproved the validity of field observation of calf percentages as a reliable index to productivity. In the course of his review of all of the previously available information on moose reproductive rates he laid to rest the "barren-cow" concept that had dominated earlier literature dealing with moose reproduction. Also, he logically examined the factors which likely gave rise to observational biases against accurate cow-calf ratios. These included: "(1) the secretive behaviour of the cow when accompanied by a calf, particularly a young calf; (2) the tendency of a cow to be observed without a calf, and (3) the incorrect identification of yearlings" an age class which does not contribute to calf production but which, because of their size, can be confused, especially by inexperienced observers, with older sexually mature cows.

By 1965, as a result of the work published by Pimlott (1959) Edwards and Ritcey (1958), Simkin (1965) and reported by Rausch (1959), North American moose managers recognized that the moose could stand a much higher level of utilization than previously suspected. As a result of this, its importance as a game animal increased considerably. Primarily because of these findings, intensity of moose management at least in North America, has increased in the intervening years to the extent that in Ontario, for example, as many moose are harvested annually as we thought we had in the days when Peterson was carrying out his pioneering studies.

I wish to divide this review into two separate sections. The first will deal with various facets of reproduction physiology, the second will deal with productivity.

Reproduction

OVULATION RATES

An excellent key to the reproductive rate of a population is the ovulation rate. This is obtained by determining the number of ovulations per breeding season per 100 cows.

In studies conducted to date, ovulation rates have been determined by counting the number of primary *corpora lutea* in pairs of ovaries collected after the breeding season has ended or at least after the peak of rutting activity has ceased. Perhaps the two most valuable figures to be gained from studies giving ovulation rates are the proportion of the youngest age group which ovulates and the number of multiple ovulations occurring in the adult segment.

Prior to Pimlott's study, it was generally conceded that moose did not breed until they were at least two and one half years old. However, subsequent studies based on examination of reproductive tracts (uteri and/or ovaries) have shown that there is a great deal of variation in the age at which cows ovulate for the first time, with many reaching sexual maturity at 18 months.

Table I shows yearling ovulation data reported for different study areas. The ovulation rate for yearlings in Alaska could not be determined from the published data but it would be at least 33 percent. Similarly, there is considerable variation from area to area in ovulation rates of cows two and one half years old and older as shown in Table II.

PREGNANCY RATES

Although ovulation rates may be a good index to the condition of animals on a certain range, not all ovulations result in pregnancy. A more refined estimate of reproductive performance can be gained by determining the pregnancy rate. This is the number of conceptions in a year per 100 cows.

Where it is possible to collect specimens sufficiently long after conception for foeti to be macroscopically visible, that is about 20 days after conception according to Markgren (1969), use of this technique is ideal. Edwards and Ritcey (1958), Pimlott (1959), and Rajakoski and Koivesta (1966) were able to obtain large enough samples of specimens at this time of year to use this technique.

TABLE I

Yearling ovulation rates in moose

Location	*Number of yearlings*	*% Ovulating*	*Ovulation/100 yearling cows*	*source*
Newfoundland	69	48	54	Pimlott (1959)
Ontario	68	35	38	Simkin (1965)
Montana	2	0	0	Peek (1962)
Alaska	6	33	NA*	Rausch (1958)+
Sweden	73	41	NA*	Markgren (1964)
Sweden				
— Inland	37	8	8	Markgren (1969)
— Coastal	77	53	57	Markgren (1969)
Finland	88	82	89	Rajakoski and Koivisto (1966)

* Not available.

\+ From Rajakoski and Koivesta (1964).

TABLE II

Ovulation rates of moose 2.5 years of age and older

Location	*Number of moose*	*Number of corpora lutea*				*% Ovulating*	*Ovulations/ 100 moose*	*Source*
		0	*1*	*2*	*3*			
Newfoundland	188	28	123	37		85	105	Pimlott (1959)
Ontario	140	19	67	51	3	86	127	Simkin (1965)
Montana	14	4	10			71	71	Peek (1962)
Sweden								
— Inland	128	11	91	26		91	126	Markgren (1969)
— Coastal	140	7	49	75	4	95	150	Markgren (1969)

In Ontario, although the hunting season opens around October 1st and extends to at least mid-December, most of the harvesting usually takes place in the first few weeks which is too soon after the main rutting period of late September to provide specimens where foeti or embryos can be readily identified. Consequently, a new technique was developed (Simkin, 1965) using *corpora albicantia* from the previous breeding season as an indicator of pregnancy rates.

This technique gave results similar to those obtained in other studies where foeti counts were made with animals having similar ovulation rates. Furthermore, the technique, which involves histological examination of *corpora albicantia* shows promise of providing a method whereby the complete reproductive history (i.e. number of pregnancies) of a cow could be determined. This is indicated in Figure 1 by the observed linear relationship between the number of pigmented *corpora albicantia* or scars, and age. Markgren (1969) also found the same linear relationship between the number of scars and age although he did not attempt to break the ages of his sample of moose into as many categories as was the case in the Ontario sample.

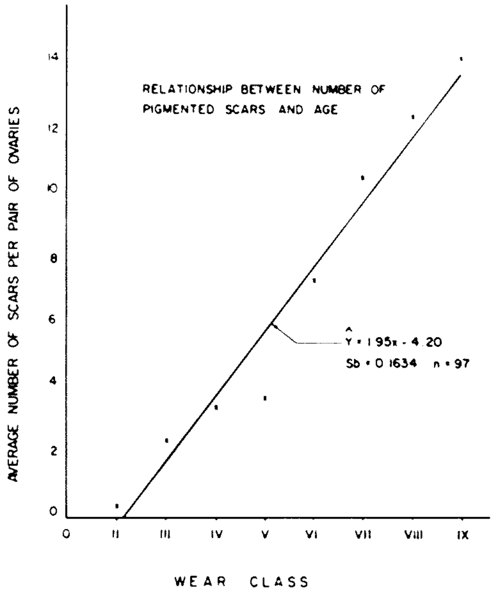

Figure 1. Relationship between age of the cow and the number of ovarian scars in moose.

There are considerable differences in the reported pregnancy rates between areas (Table III). The most dramatic differences being in the yearling age class.

Various authors have discussed the reasons for such observed differences in wild and domestic animals and a substantial volume of literature has been produced documenting the relationship between reproductive performance (ovulation rates and pregnancy rates)

TABLE III

Pregnancy rates in moose

Location	*Age when bred*	*N*	*% Pregnant*	*Pregnancies/ 100 cows*
Newfoundland	*18 mo.	78	46	47
—	30 mo. and older	239	81	100
Ontario	**18 mo.	12	17	17
	30 mo. and older	87	87	113
British Columbia	*18 mo.	15	0	0
	30 mo. and older	169	76	120

* Adapted from Pimlott (1959).
** From Simkin (1965).

and levels of nutrition. For white-tailed deer (*Odocoileus virginianus*) populations, Morton and Cheatum (1946) were among the first to document significant differences in ovulation rates and pregnancy rates between areas with different quantities and qualities of food. They found that in good habitat, 36% of the fawns bred while only 4% bred on poor range. Results of more stringently controlled experiments carried out with domestic animals have provided further proof of this relationship between food quality and reproductive performance.

Reid *et al.* (1957) and Sorensen *et al.* (1959) working with domestic cattle at Cornell University, selected trios of female calves at an early age and placed them on either a high, medium or low nutritive level diet for at least 80 weeks. Heifers on the high quality diet came into heat at 37.4 weeks, those on medium diet at 49.1 weeks and those on low diet at 72 weeks. Lutwak-Mann (1962) reported essentially the same phenomenon. She stated: "the initiation of the first oestrus and the age at which an animal first ovulates is markedly influenced by the nutritional level. The first oestrus occurs in low plane heifers at 18 months. Whereas in animals on a medium or high plane of nutrition it takes 12 and 9 months respectively".

Pimlott explained the great variation in yearling breeding performance between his Newfoundland study areas on the basis of differences in range quality, (67 percent of the yearlings on the better range were ovulating as opposed to 29 percent on the poorer range).

FERTILIZATION RATES

It is of importance to know what proportion of the eggs shed become fertilized. In order to convert from ovulation rate to pregnancy rate one must calculate the fertilization rate. This is determined by comparing the number of ovulations per 100 cows with the number of pregnancies per 100 cows.

Data are available from the Newfoundland and the Ontario studies which permit calculation of this rate (Table IV). In addition, Swedish moose fertilization rates have been estimated at 85 percent and 75 percent for adults and yearlings respectively (Markgren, 1969).

In other cervids, Robinette (1956) reported a fertilization rate of 90 percent for Utah mule deer (*Odocoileus hemionus*), and Cheatum and Severinghaus (1950) showed a fertilization rate of 91 percent for white-tailed deer on the better New York state range. It appears that for cervids on good range, fertilization rates are high and consistently around 90 percent, at least within the adult age classes.

TABLE IV

Fertilization rates of moose

Location	Age of animal	Ovulations per 100 cows	Pregnancies per 100 cows	Fertilization rate
Newfoundland*	Yearling	54	47	87
	Adult	103	95	92
Ontario**	Yearling	37	17	46
	Adult	127	113	89

* From Pimlott (1959).

** From Simkin (1965).

SILENT HEAT PERIOD

If one is going to use ovarian analysis to obtain information on reproductive performance, consideration must be given to the presence or absence of a silent heat period; that is, an estrus cycle which occurs prior to the main rutting period in which ovulations occur without the usual manifestations of rutting estrus and subsequent fertilization. This was first reported for North American moose by Simkin (1965) where he showed that 33 percent of the Ontario specimens had undergone a silent heat cycle. Bäckström (1952) had reported earlier that for Swedish moose a silent heat period is the rule rather than the exception; however, in 1969 Markgren, also reporting on Swedish moose, indicated evidence of silent heat cycles but suggested that it was not as common a phenomenon as reported by Bäckström (1952).

In domestic animals silent heat periods have frequently been recorded. Grant (1934) referring to domestic sheep stated: "the first heat period of the breeding season tends to be shorter than the succeeding ones" ... and "the first heat period is produced by one or more cycles of ovulation which are unaccompanied by heat" ... then "it may be supposed that at the beginning of the breeding season the amount of hormone produced is insufficient to produce the mating propensity although enough is produced to cause the typical vaginal changes".

Hafez (1954) writing on studies conducted with the domestic buffalo in Egypt reported silent heat periods in 36 percent of the animals studied. He suggested that this phenomenon is perhaps due to the failure of secreted estrogens to reach the threshold required for estrus or to the intervention of a nervous block due to secretion in excess of the critical level.

Productivity

Three terms which are most frequently used when comparing the reproductive characteristics of game animals, big game in particular, are: 1) rate of increase, 2) gross productivity and 3) net productivity. Pimlott (1959) and Simkin (1965) both calculated rates for these factors in their studies and compared them with rates obtainable from other studies.

Definitions, methods and calculations are as follows:

RATE OF INCREASE

This is the number of calves which a population of one hundred moose with given sex ratios and given pregnancy rates would produce. Thus, as reported in Simkin (1965), a herd of 100 moose with 25 calves, 18 yearlings and 57 adults with a sex ratio of 100♂♂: 100♀♀ and reproductive rates for yearling ♀♀ of 20 calves/100 and of 113 calves per 100 adult ♀♀'s would produce 34 calves. The rate of increase for this herd would be 34 percent.

Rates of increase calculated for populations reported in the literature are shown in Table V.

The area where necessary valid data are most frequently lacking, to calculate rate of increase, is the adult sex ratio. Sex ratios in the kill are frequently biased to bulls. Observational data are usually biased to cows. The vulvar patch method described by Mitchell *et al.* (1964) is probably the best method to use to obtain sex ratio information for use in rate of increase calculations.

GROSS PRODUCTIVITY

This is the percentage of the population that could be removed annually on a sustained yield basis if all of the young which were conceived were success-

TABLE V

Rates of increase in four moose populations from Simkin (1963)

Location	*Adult sex ratio*	*Reproductive rates*		*Population composition*			*Rate of increase*
		Yearling	*Adults*	*Calves*	*Yearlings*	*Adults*	
Newfoundland	52:48	0.46	0.95	22	18	60	32
Ontario	50:50	0.20	1.13	25	18	57	34
British Columbia	50:50		1.02	22	18	60	31
Sweden	44:56		1.30	29	21	50	36

fully borne and survived to the hunting season.

The same basic information needed for calculation of rate of increase is needed here.

As stated earlier, two different methods have been used to obtain reproductive rates — namely, those based on foeti or embryo counts and those based on information obtained from *corpora albicantia.*

Gross productivity rates obtained for areas where necessary data have been published are included in Table VI.

TABLE VI

Gross productivity for four moose populations from Simkin (1963)

Location	*Gross productivity %*
Newfoundland	24
Ontario	25
British Columbia	24
Sweden	26

NET PRODUCTIVITY

This is the percentage of a stable population that can be removed on a sustained yield basis after mortality from causes other than hunting has been deducted.

Net productivity has been calculated in different ways in the past and Pimlott (1959) adequately reviewed most of these, pointing out the attributes of each method.

Briefly, the methods are:

(a) *occurrence of calves in the population* immediately prior to the opening of the hunting season $\frac{C}{c + y + a} \times 100$
where c = calves, y = yearlings and a = adults.

(b) *occurrence of yearlings in the population*

or

$$\frac{y}{c + y + a} \qquad \frac{y}{a} \qquad \frac{y}{y + a} \times 100$$

Following the points raised by Pimlott, the most common method used is the last shown, i.e. net productivity equals:

$$\frac{y}{y + a} \times 100$$

As shown by Pimlott and by Simkin, the direct use of yearling percentages collected from the hunt kill statistics is usually not valid and a conversion factor which takes into consideration that yearlings are more vulnerable than older moose must be applied. This so called "vulnerability factor" has been shown to vary for different populations and for different times of the year. Generally, for early seasons in heavily hunted areas, it falls somewhere between 1.3 and 1.8 (Pimlott, 1959; Simkin, 1965).

Estimates of net productivity have been calculated for several moose populations using the different methods referred to above and have been published in papers already referred to. These are shown in Table VII.

The similarity between estimates of gross and net productivity must be commented on. Two possible reasons for the slight differences are:

(a) moose, at least in the areas where published studies have been done, suffer very low *in utero* mortality and calves produced are little affected by predation or other incidental causes of mortality, diseases, accidental losses, etc., and

(b) the parameters used to calculate gross productivity, particularly the adult sex ratio, may have erred on the conservative side. That is, there likely are more cows in the population than used in the calculations. (The sex ratio at six months of age is 100: 100; adult bulls are consistently over-represented in the harvest, 120-150: 100 cows; and there is no other known mortality factor which affects one sex more than another).

TABLE VII

Estimates of net productivity for moose in various areas

Location	*Net productivity %*	*Method**	*Source*
Newfoundland	20-25	$\frac{y}{y+a} \times$ Vulnerability factor	Pimlott (1959)
Ontario	24	Yearling percentage calculated from regression analysis	Simkin (1965)
Alaska	17	$\frac{c}{c+y+a}$	Spencer and Chatelain (1953)
Kenai Pen., Alaska	10	$\frac{c}{c+y+a}$	Spencer and Chatelain (1953)
Susitna Valley, Alaska	23	$\frac{c}{c+y+a}$	Spencer and Chatelain (1953)
North America	16-17	y/a	Peterson (1955)
Sweden	25	$\frac{c}{c+y+a}$	Sckunke (from Pimlott, 1959)

* where y = yearling, c = calf and a = adult.

Discussion

It is safe to conclude that most of the large gaps in our knowledge about moose reproduction and productivity have been filled, particularly since 1955. To carry out a moose management program it is essential that this knowledge be used and that continued studies be conducted to keep it up to date.

Several areas for future research are easy to identify:

1) collection of ovaries from moose of known reproductive history to be used to determine if indeed the complete reproductive history of

a cow can be determined from a detailed ovarian analysis;

2) further studies on the incidence of silent heat periods and a definitive explanation of their function and significance;
3) further studies on the histology of *corpora albicantia* of oestrus and pregnancy to allow for identification of easier methods to differentiate between the two and to age scars of previous breeding seasons;
4) detailed studies of reproduction and productivity related to specific habitat types of varying quality;
5) development of methods which provide at low cost, accurate estimates of sex ratios of moose populations;
6) collection of reproduction information on populations with different vital statistics and at different levels of density.

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ON THE EVOLUTION OF REPRODUCTIVE POTENTIAL IN MOOSE

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Résumé

L'auteur propose une théorie selon laquelle le potentiel reproducteur des ongulés serait fonction de l'ensemble des variables écologiques auxquelles chacune des espèces de ce groupe est exposée. Or l'orignal échappe à la règle générale selon laquelle les gros ongulés ne donnent naissance qu'à un seul jeune. Le potentiel reproducteur de l'orignal semble influencé, d'une part, par la disponibilité de parcelles d'habitat créées quand le feu effectue des trouées dans la forêt climacique et, d'autre part, par l'utilisation d'un habitat stable constitué par la forêt climacique elle-même chaque fois que le premier type d'habitat n'est pas disponible. Dans l'habitat forestier créé par le feu, un milieu particulièrement favorable à l'alimentation de l'orignal, les femelles ne portant qu'un seul jeune seront défavorisées puisque l'embryon risque d'atteindre des proportions trop grandes pour une mise bas normale ; aussi, celles qui mettent bas des jumeaux ou des triplets seront-elles favorisées. Quand les processus normaux de succession font disparaître cet habitat temporaire, que les conifères réapparaissent et que la capacité de support du milieu vis-à-vis l'orignal diminue, les femelles ne mettant bas qu'un seul jeune seront avantagées puisque elles vont concentrer les ressources limitées du milieu dans un seul embryon bien développé ; dans les mêmes circonstances, les femelles multipares risquent davantage de produire plusieurs jeunes insuffisamment développés et moins viables. Cette interprétation, quand on l'applique à un autre ongulé nordique, le caribou, nous permet de comprendre comment il se fait que la multiparité soit à peu près inconnue chez cette espèce.

Abstract

A theory is presented according to which the reproductive potential of ungulates would be a function of the ecological variables individual species are adapted to. It is shown that the moose is a special case in that it departs from the general rule that large bodied ungulates give birth to single young. The reproductive potential of moose is shown to be a function of the rapidly expanding but slowly contracting habitats moose colonize after forest fires remove climax forests and after these are replaced by a deciduous flora favourable to moose ; it is also shown to be a function of the small areas of stable habitat moose find within climax forest where they can survive in the absence of burn-habitat. In the burn-habitat, selection works against females that conceive single young since when forage is abundant such young are likely to grow too large to permit normal birth ; cows conceiving twins or even triplets are favoured. When burn-habitat is reinvaded by conifers and the carrying capacity for moose declines, cows conceiving singles are favoured since they can concentrate limited resources to bear a single, well-developed young ; cows conceiving twins are likely to bear two ill-developed, non-viable young. It is shown that the same ecological events described for moose, but applied to the biology of caribou, explain the virtual lack of multiple births for that species.

Introduction

The evolution of reproductive characteristics in moose *(Alces alces)* deviates considerably from that of other ungulates. Unfortunately there is no published theory of the evolution of reproductive characteristics in ungulates and it is, therefore, necessary to present the outlines of such a theory before proceeding to discuss the special case of the moose. As a rule ungulates — excepting the Suidae — bear only one young at a time (Krumbiegel, 1954), while multiple births are confined largely to a few species from the temperate regions. It is probably for this reason that ungulates have received so little attention from students of the relation between ecology and reproductive traits in animals.

Evolution of reproductive characteristics in ungulates

One can recognize three major ecological variables which affect reproductive characteristics in ungulates. These are effective temperature or chill at the time of birth, predation pressure, and periodic superabundance of food. In addition, one can superimpose a bioenergetic principle, namely that females will maximize the energy available to them for reproduction and growth (Geist, 1971).

The recognition that effective temperature is an important ecological variable in the evolution of ungulates is based primarily on the superb work of Australian agricultural scientists on the neonatal mortality of domestic sheep (Purser and Young, 1959; Safford and Hoversland, 1960; Alexander, 1960, 1061; Alexander *et al.*, 1959, 1962; Alexander and Peterson, 1961; Watson and Elder, 1961; Gunn and Robinson, 1963; Robinson *et al.*, 1961; Wallace, 1948; Schinkel and Short, 1961). I have reviewed their work elsewhere (Geist, 1971) and have shown there why it is relevant to an understanding of the biology of wild ungulates. For this reason I shall only outline the theoretical considerations below: if the young of an ungulate is born into low ambient temperatures and/or subjected to winds that significantly increase chill, the young must first have a relatively large body size to decrease the surface-to-mass ratio in order to reduce the rate of cooling relative to its rate of metabolism; and, second, it must have a store of metabolizable energy (fat) to sustain a high metabolic rate lest it become hypothermic. The lower the ambient temperature and the higher the convective heat loss at birth, the larger must be the young.

The size of an ungulate at birth is obviously a function of its genetic constitution as well as of the energy and nutrients available to the pregnant female in excess of her maintenance requirements. In general, birth weight is directly related to nutrition in late pregnancy (Wallace, 1948; Robinson *et al.*, 1961; Preobrazhenskii, 1961). For every given habitat and season there is, hence, a minimum body size at birth below which the young will succumb to hypothermia.

Furthermore, below a specific minimum birth weight a young will succumb regardless of the temperature in which it is born due to inadequate physical development (see Wallace, 1948). Conversely, above a given body weight a young is unlikely to survive for it may be deformed passing the relatively small birth canal (dystocia), or die while getting stuck in the birth canal, or cause so much pain at birth as to be deserted by its mother. Since phenotypic birth weight is a function of forage quality and quantity available to the female during gestation, clearly there can be danger to the female and foetus from excessive feeding as well as from insufficient feeding (see Geist, 1971, p. 284-93).

If we apply the above reasoning to the biology of wild ungulates, we can predict that species bearing small young must find ways and means to guard their neonates from hypothermia. This could be done if the species bore its young relatively later in the year when ambient temperatures are higher. A comparison of calving seasons of small-bodied ungulates with large-bodied ones in Siberia, as described by Heptner *et al.*, (1961), indicates that such forms as roe deer *(Capreolus capreolus)*, and musk deer (*Moschus moschiferus*) have somewhat later fawning seasons than do large-bodied forms such as red deer *(Cervus elaphus)* or moose *(Alces alces)*. That this method does result in increased neonatal survival was demonstrated by the experiment of Watson and Elder (1961) in which the lambing of domestic sheep was delayed in order that it could take place at a warmer season.

A second method to avoid hypothermia of the young is to construct a nest for them in a sheltered locality and brood them. Among ungulates this method is found in wild boar (*Sus scrofa)* which bear very small young compared to other ungulates (Frädrich, 1967). In addition, the piglets huddle in one mass, effectively reducing their surface area to heat loss (Frädrich, 1967; Gundlach, 1968); this behaviour occurs most frequently at low ambient temperatures. It is these adaptations that probably free wild pigs in temperate climate to farrow at any time of the year, even in winter, and thus permit them to bear twice a year provided there is mast (Oloff, 1951).

In addition to delaying birth to a warmer season, and building shelters for the young, one can identify several mechanisms which would reduce the chances of hypothermy to the young. Excepting the suids and camelids (Krumbiegel, 1954; Frädrich, 1967), ungulates clean the fur neonates of birth fluids, thereby drying the coat, and stimulating circulation and metabolism in the young. Herscher *et al.* (1963) note that some lambs not licked by their dam died soon after birth without rising. Hiding during parturition would secondarily place the young into shelter from wind thereby reducing chill. It is probable that some northern ungulates which bear relatively small young will select microclimates most favourable to the young at birth such as sunbaked soil or the warmest parts of the day.

The second part of the theory deals with predation pressure and its selection for birth number, birth weight, and maternal adaptations. We can identify three adaptive syndromes, the first two of which, however, merge into each other and are difficult to separate. The essence of these adaptive syndromes were recognized by Gosling (1969).

(a) At birth, the young is large, highly developed, and can soon escape predators by running, although its survival is augmented by maternal protection during the neonate stage. This adaptive syndrome appears to be common to gregarious species from open landscapes. The birth of a single large calf is mandatory to maximize the calf's ability to run shortly after birth; to permit post-natal growth to start from a relatively large body, shortening the time between birth and the time the calf is large enough to outrun predators; and, to channel all the available milk supply into one, rather than two calves, to permit maximum growth rate. Cryptic colouration would not be necessary since the calf does not hide, or does so only exceptionally. Moreover, it is born in open areas with little cover for hiding. Twinning would be selected against under the heavy predation pressure since it maximizes the critical vulnerable period when the youngsters are susceptible to predators. The extent of this predation is exemplified by the work of Kruuk (1972) on hyenas in relation to wildebeest. About three quarters of the calves born in the Ngorongoro crater fall victim to predators each year, most of them in their first week of life.

A further means to reduce predation on calves in some species with this syndrome is to mass females into large, dense herds and synchronize calving. This shortens the birth season and saturates a relatively small area with calves, swamping the predators (Gosling, 1969 ; Kruuk, 1972). In addition, wildebeest bear young primarily in the early morning when predators are least active (Estes, 1966). It is likely that the large calving herds of barren-ground caribou *(Rangifer tarandus)* have the same function as do the large herds of saiga antelope *(Saiga tatarica)* at calving time (Bannikov *et al.*, 1961).

(b) Although all ungulate species that have been observed were found to defend their young against predators, provided the predator was relatively small, maternal defence becomes obviously more effective the larger the female. In large-bodied gregarious ungulates, defence of the young by its mother or an organized group of conspecifics becomes increasingly more common. Nevertheless, flight is still the preferred means of avoiding predators, even in such formidable species as the gaur *(Bibos gaurus)* (Schaller, 1967). Species in which adults commonly defend their young are the buffalo *(Syncaffer, Bubalus)* (Sinclair, 1973 ; Eisenberg and Lockhart, 1972): the rhino (*Discornis* spp.) (Kruuk, 1972 ; Schaller, 1972) ; the elephant (*Loxodonta* spp.) (Eisenberg and Lockhart, 1972 ; Sikes, 1971) ; the muskox *(Ovibos moschatus)* (Pedersen, 1958) ; and the zebra *(Equus burchelli)* (Kruuk, 1972). This behaviour was probably also a significant factor in the biology of such species as the horse *(Equus caballus)* and the camel *(Camelus)*. Despite the increased potency of maternal defence, the young are still forced to run in the species indicated above, and selection should still favour one large young which quickly outgrows the vulnerable neonatal age. The syndromes (a) and (b) form the "follower type" syndrome as defined by Walther (1961) and elaborated on by Lent (1973).

(c) A third adaptive syndrome is characterized by hiding behaviour in the young. As in the previous syndromes, it reduces the contact with predators per unit time, but does so quite differently. The young escape detection rather than capture. Synchronization of births would be selected against where the species exist year round in high density, since this would concentrate the number of calves per unit area, per unit time. This, in turn, would permit predators to concentrate their activities temporarily on the hidden but relatively abundant youngsters, leading to greater predation loss through chance alone. A relatively low number of prey per unit area would also foil the development of a search image by the predator (see Hinde, 1970). In African bovids with the hiding syndrome, we often find that births are distributed over much of the year (Ansell, 1960) ; the same is found in subtropical cervids in India (Schaller, 1967).

Cryptic colouration is apparently selected for as is hiding behaviour, on the part of the young. The young are born in habitats where hiding is possible. Twinning is permitted here since the young are in concealment during the critical early stages of life ; from the prevalence of the hiding syndrome, we may assume that it is an effective means of escaping predators. Although at the time of birth females tend to hide and disperse, the opposite may also occur, as indicated for the saiga above. Here, calving herds gather in areas far from watercourses, apparently to minimize contact with wolves. On the whole, the hiding syndrome is confined to small-bodied species, be they from plains or forests. For a more detailed description of the "hiding syndrome," I refer to Lent (1973).

The third part of the theory deals with periodic superabundance of forage during late gestation and lactation. It is puzzling why twinning in ruminants is confined largely to temperate cervids and bovids, while close relatives from tropical and subtropical regions bear only one young. This is most noticeable in gazelles where such northern species as goitered gazelle *(Gazella subgutterosa)*, Tibetan gazelle *(Procapra picticaudata)*, Mongolian gazelle *(P. gutterosa)* and saiga often or regularly twin (Heptner *et al.*, 1961 ; Walther, 1968) in contrast to their African cousins *(G. thomsoni, G. granti, Antidorcas marsupialis)* (Walker, 1964 ; Walther, 1968). A condition favouring twinning is a seasonal superabundance of forage, and this, the boom-bust economy (summer-winter) of the temperate regions does provide. In temperate regions, plant production is concentrated into the summer months, while in the tropics, plant production is spread much more evenly throughout the year. Secondly, snow cover restricts availability of forage, making the snow season a time of relative scarcity. Decreased plant productivity and plant dormancy as well as restrictions imposed by the snow regime in winter, as compared with the great plant productivity of summer, create the boom and bust economy of the north. Warm deserts with sporadic rainfall also create a boom and bust economy. We find in correlation that some African desert gazelles do twin. Furthermore, in addition to the seasonal superabundance, the long daylight hours in the north during summer permit carbohydrate accumulation as discussed by Klein (1970), which is probably the reason why the caloric density of plant tissues increases from the equator to the pole (see Jordan, 1971). These factors should permit a greater rate of milk production for northern than for southern forms — a concept that remains to be verified. Third, in the absence of periodic growing seasons, plant tissues containing a high level of protein may be scarce and thus limit milk production. Tropical forages may well be protein deficient. This would select for single over twin births. The manner in which twinning is selected will be discussed for moose below.

The foregoing outlined the role played by the major ecological variables affecting reproductive characteristics in ungulates. It did not touch mountain bovids which can be considered a special case (Geist, 1971), nor did it treat the special case of the moose. It is best, now, in the following discussion not to treat the moose in isolation but to contrast it against the caribou, in which twinning is almost non-existent (Krumbiegel, 1954; Zhigunov, 1961 ; Kelsall, 1968).

Evolution of reproductive characteristics in moose

As pointed out earlier (Geist, 1967, 1971), the maternal behaviour of moose, their social system and anti-predator strategies can be explained as functions of snow conditions moose encounter, and the habitat they inhabit which — due to periodic forest fires — is rapidly and greatly expanded, throwing moose populations relatively often into the expanding phase (Geist, 1967; 1971, p. 106-107, 121-124). This argument is equally crucial to the understanding of multiple births in moose, while its converse explains the absence of multiple births in caribou.

To moose living in areas of relatively stable habitat (alluvial soils with deciduous, woody vegetation ; dwarf birch and willow flats above timberline), forest fires in adjacent conifer climax forests permit a population to expand. During the expanding phase, cow moose are confronted by abundant forage ; once carrying capacity is reached they are confronted by less forage and higher costs in procuring it. The abundance of forage to moose invading "burn habitat" and its scarcity at carrying capacity when climax forests encroach, are the key elements in the following hypothesis. It in no way denies the complex vegetation/moose relationships especially in the mountains (Houston, 1968).

Let us look first at the situation when forage is relatively scarce, that is, when the female must expend much energy in procuring forage of relatively low quality. This situation will probably exist on old burns that are beginning to be reinvaded by conifers, in which the deciduous trees have grown rather tall, thus reducing the available forage per unit area. During the course of the winter, the snow accumulates and hardens (Telfer, 1967 ; Kelsall and Prescott, 1971) and the moose are soon forced to reduce their daily radius of activity, and to search out areas with low snow or soft snow such as steep moraine slopes or dense conifer forests (Edwards and Ritcey 1956 ; Heptner *et al.*, 1961; Heptner and Nasimovitch, 1968; DesMeules, 1964; Kelsall and Prescott, 1971 ; Houston, 1968 ; and personal observations). Simultaneously, it has been noted that moose reduced their total activity, increased the intensity of browsing on individual bushes, and increasingly fed on forage species they preferred least in early winter such as pine and birch (Heptner *et al.*, 1961 ; Heptner and Nasimovitch, 1968). The implication of these observations is that, as the snowblanket increases in height and density, the cost of living goes up for moose and the return on energy expended goes down.

It is noteworthy, though, that moose need not search out the shallowest snow as Telfer (1967) and Kelsall and Prescott (1971) showed for moose in Nova Scotia. The most strenuous of times, judging from the data of Heptner and Nasimovitch (1968), comes in late winter at a time when the embryo begins its rapid growth towards full-term development. Clearly, it is advantageous, therefore, for moose to bear the smallest possible young that can still keep up with its dam shortly after birth if many or large predators force the female to flee (see Le Resche, 1966). In short a small, single young is adaptive when resources are marginal in part due to the cost of living imposed by a high, dense snowblanket in late winter. This would explain the relatively low birth weight of moose calves which is on the average 9–11 kg (Heptner and Nasimovitch, 1968), as compared to the high birth weight of wisent *(Bison bonasus)*, an ungulate of body weight comparable to that of the moose: wisent calves weigh twice as much as moose calves on average (Heptner *et al.*, 1961). Under conditions of low forage availability and quality, twins — in contrast to single calves — are not likely to reach survivable size at birth (about 7 kg ; Heptner and Nasimovitch, 1968). Second, if udder development in moose is a function of the gestating females' forage regime, as it is in domestic sheep (Wallace, 1948), then the female is not likely to produce enough milk for twins to reach survivable size in fall. The same milk supply will probably permit a single calf to grow adequately. Hence, under the postulated forage conditions there will be selection against cows that twin regularly, and for cows that bear single young.

Let us now conceive of a cow which has moved to a former burn on which there is an abundance of forage. Let us assume the cow ovulates only one egg and grows only one young in her uterus. Since forage is readily available, even in late winter, we can expect the calf to grow well. This means that under very good forage conditions the cow will carry an exceptionally large calf, considerably larger than the average of 9-11 kg. In fact, since cow moose can potentially grow *two* calves 9-11 kg each, for a foetal mass of 18-22 kg, a cow with only one calf in the uterus may grow a calf well in excess of 16 kg. At calving time it can be predicted that the cow, or her calf, and more likely both of them will be in severe trouble. The calf chances dystocia ; the female, a stuck calf and death thereafter. Even if the calf is born, it may cause so much pain that the female may desert it as is known from domestic stock (see Geist, 1971). That such tragedies do occur we know from Bergerud (pers. comm.) who found caribou cows in the field with young protruding that they where unable to bear. In fact Bergerud (1971) regards mortality from abnormal births to be the most important factor in female mortality in Newfoundland caribou. He also notes that in Newfoundland caribou calves are heavier than those born on the barren grounds. This would be an evident reason for dystocia. Therefore, under conditions of highly favourable forage availability and quality it can be expected that natural selection will act against cow moose bearing single calves.

Conversely, cows that ovulate two eggs and convert the available energy and nutrients into two normal calves will have uncomplicated births. Moreover, the large udder development of the female and the forage availability lead to the growth of large calves prior to winter. Hence, we should have here selection for females that twin.

It can be validly asked why moose should not evolve still greater fecundity by bearing triplets. The foetal mass a cow moose can bear is close to 23 kg, about the same as a female bison or wisent of similar body weight. Taking this as a constant, then, triplets would weigh at birth about 7.7 kg, and quadruplets about 5.7 kg. From experience gained by Russian workers, we know that calf moose weighing 7 to 8 kg at birth, or less, are so weak that they normally die apparently even if granted care and attention by experienced personnel (Heptner and Nasimovitch, 1968). This suggests that, even under optimum forage conditions, triplets (let alone quadruplets) are likely to be born too small and weak to be viable. In addition, triplets would strain the female severely during lactation and still fail to reach survivable size in fall. Moreover, lactation may place so great a burden on the female that she may fail to come into heat the following rutting season. This is suggested by work done with Siberian reindeer (Preobrazhenskii, 1961).

This suggests that moose are exposed to conflicting selection pressures on refuge habitats versus early seral plant communities on former burns, or if exploiting burns, during the expanding versus the contracting population phase. The conflicting selection for single or multiple births has evidently produced a mechanism that ties ovulation rate to the nutritional regime of the female. The nature of this mechanism remains to be discovered. Granted such a mechanism together with the mandatory selection for high reproductive rates in expanding populations allows one to predict that where moose exploit mainly stable plant communities in a large geographic area (where there are no forests to burn) and where the snow levels do not fluctuate greatly, there will be a preponderance of selection for cows of long life expectancies producing single calves ; conversely, in taiga areas with little permanent habitat for moose to exploit, and reasonably frequent forest fires, there will be selection mainly for cows with low life expectancies producing multiple births. In addition, where large predators, such as brown and grizzly bears, are common on moose calving grounds, we can expect selection to shift in favour of large, single young ; such a situation could be expected in southern Alaska judging from the work of Le Resche (1966). The foregoing predictions have not been verified and may ultimately serve as tests of the present hypothesis.

Forest fires also affect caribou, but in a manner quite different from moose. Forest fires rob caribou *suddenly* of forage, be it in the mountains of British Columbia (Edwards, 1954), or in the taiga adjacent to the tundra (Scotter, 1964). The following hypothesis is invalid unless the assumption is made that forest fires rob caribou of forage suddenly, and decrease the carrying capacity of the area for caribou till the forest has returned to the climax stage. Since climax forests return very slowly, caribou populations in essence are always at carrying capacity, but suddenly *exceed* carrying capacity due to forest fires. This statement is still valid, even if the burns provide some winter forage for caribou several years after a forest fire, in the form of browse, provided the carrying capacity of the burn does not exceed that of the climax forest. Since at carrying capacity we can expect no selection for twins (since caribou calves must be born large to escape hypothermy and predators, the caribou cow being too small to defend the calf against large predators), and since caribou — granted the above proposition — are periodically confronted in their evolutionary history by scarcity of forage, we cannot expect selection for anything but single births. Twins would be selected for if habitat and forage availability fluctuated dramatically and if predation pressure were so low as to permit a reduced birth weight of about 3 1/2 kg. Clearly, theoretical considerations suggest that caribou live almost permanently at carrying capacity. It is generally acknowledged that twinning is a most exceptional event in the genus *Rangifer* (Kelsall, 1968 ; Bergerud, 1971).

Summary

(1) A general theory of the evolution of reproductive characteristics is presented for ungulates with which the unusual reproductive traits of the moose are compared.

(2) Three major ecological variables affect reproductive characteristics in ungulates : effective temperature at time of birth, predation pressure, and periodic superabundance of food.

(3) Adaptations in ungulates to avoid hypothermy of neonates are a reduction of the surface-to-mass ratio by increasing birth size, shifting parturition to time periods of low heat loss, constructing nests and brooding young, hudling by young, removal of water from the birth coat of the young, seeking out shelter for parturition, and stimulating increased metabolism of young by licking it.

(4) We can identify two basic adaptive syndromes in ungulates which minimize contact between the neonate and its predators :

(a) In the first adaptive syndrome, common to many ungulates from open plains, the young maximizes its chances to avoid predators by outrunning them. This requires exceptionally high development at birth, a rapid growth rate, and channelling all available milk into one — rather than two — young to maximize growth rate. A massing of parturient females plus synchronization of births in a few species swamps the predators with neonates in a few relatively small areas. In large-bodied ungulates maternal and/or group defence reduce the threat of predation to the young in its vulnerable early age.

(b) In the second adaptive syndrome, common to ungulates of usually small body size inhabiting forests and savannahs, the young minimizes contact with predators by hiding. This requires

appropriate colouration and hiding behaviour on the part of the young. Twinning is permitted in this syndrome.

(5) Seasonal superabundance of forage in temperate climates, coupled with the high caloric density of that forage, and relatively great availability of high-protein forage during the spring and early summer, predict thereotically a greater milk production for north-temperate ungulate species than for tropical forms. Hence, twinning is permitted where seasonal superabundance of forage exceeds the populations' capacity to consume it.

(6) Ecological variables affecting the reproductive biology of moose appear to be, first, the high cost of life under conditions of deep and hard snow in late winter which selects for a minimum size calf under conditions of generally low forage availability and poor forage quality, and, second, the periodic availability of good habitat due to forest fires, which selects for twins.

(7) There must be a mandatory selection for high reproductive rates in expanding populations of moose, favouring the evolution of twinning.

(8) It can be predicted that in stable habitats with relatively stable climates selection will favour long-lived cow moose bearing single young ; in areas with many forest fires selection will favour short-lived cows producing multiple births ; in regions with many large predators selection will shift in favour of single, large calves.

(9) The evolution of birth number in caribou is discussed. It is shown how forest fires affect birth number in caribou in a manner diametrically opposed to that in moose.

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ANNUAL YIELD, SEX AND AGE OF MOOSE IN ONTARIO AS INDICES TO THE EFFECTS OF HUNTING

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Résumé

Une chasse à l'orignal (*Alces alces*) délibérément abusive pratiquée dans le sud de l'Ontario a permis de démontrer que les indices les plus révélateurs d'une surexploitation étaient une diminution graduelle de la récolte annuelle et une baisse ininterrompue dans la proportion des mâles abattus. Une proportion élevée d'animaux âgés de 1.5 an peut faire craindre une augmentation de la pression de chasse, sans nécessairement signifier une surexploitation. Dans le sud de l'Ontario, le cheptel a retrouvé son équilibre rapidement, après l'interrruption de la chasse.

L'analyse des données obtenues pendant 20 ans dans 14 districts et 5 stations d'enregistrement n'ont fourni que très peu d'indices de surexploitation dans le nord de l'Ontario. Seul le district de Kenora a présenté simultanément les trois indices au cours des quatre dernières années. Il y eut diminution de la récolte dans deux autres districts, tandis qu'on notait, pour une des stations d'enregistrement, diminution de récolte et déséquilibre passager dans la proportion des sexes.

Il faut considérer la surexploitation par la chasse comme l'échec d'une politique de rendement soutenu, puisque trop d'animaux ont été prélevés par les chasseurs. Selon les faits observés en Ontario, il semble qu'on puisse se fier aux indicateurs d'exploitation. Puisqu'une population surexploitée peut vraisemblablement rétablir rapidement ses effectifs, on peut donc, sans risque, établir les quotas de chasse de façon à prélever le surplus annuel dans sa totalité.

Abstract

Deliberate over-harvest of moose (*Alces alces*) in southern Ontario revealed that decreasing annual yields and consecutive low proportions of bulls in the harvest are the best indicators of over-hunting. High percentages of yearlings in the harvest may warn of increased hunting pressure but not necessarily of over-hunting. In southern Ontario, the moose herd recovered quickly when hunting was prohibited for two years.

In northern Ontario, relatively little evidence of over-hunting was found in 20 years' data from 14 districts and additional information from 5 checking stations. Only Kenora District has shown all three of the above indicators of heavy hunting or over-hunting during the past four years. Two other districts have shown decreased yields and one checking station showed a decreased yield and a brief change in sex ratios, all within the last five years.

Over-hunting is seen as failure to maintain optimum annual yields because too many animals have been removed by hunters. Consideration of the evidence from Ontario suggests that the criteria for detecting over-hunting are reasonably trustworthy; since recovery from over-hunting is likely to be quite rapid, moose can be harvested close to their annual surplus with confidence.

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Introduction

Leopold (1933) emphasized the need for data on annual yield, sex and age of wildlife to provide a sound basis for wildlife management and this view has become widely accepted (e.g. Wing, 1951; Mosby, 1963). In the management of moose (*Alces alces*), annual yields have been examined for evidence of over-hunting in Europe (e.g. Skuncke, 1949; Markgren, 1974) but have been used relatively little in North America (Pimlott, 1959). Sex and age data have provided much information about moose biology (e.g. Edwards and Ritcey, 1958; Pimlott, 1959; Simkin, 1965; Timmerman, 1972) but considerably less about the effects of hunting (Pimlott, 1959; Bergerud and Manuel, 1962; Simkin, 1964). This paper describes the use of annual yields and the sex and age ratios of harvested animals as indices to the effects of increased hunting pressure on moose in Ontario, and especially as indicators of over-harvest.

Data collection and aging methods

Three major changes in method have affected the collection of data in Ontario. The first involved reports from hunters. Since 1953 hunters in Ontario have been asked to report the numbers, sex and age of moose they shot. At first, nearly 90 percent of the hunters returned questionnaires attached to hunting licences, but the rate of return fell as numbers of hunters increased. In 1959 systematic sampling was introduced, using strata composed of the forest districts (Fig. 1) and aiming for 90 percent returns. Sample size was adjusted to obtain reports on 400 moose from each district where that many were shot, in order to provide 95 percent binomial confidence limits within 10 percent of the mean for ratios near 50:50 (Mainland, 1952). In practice, confidence limits were always wider due to deviation from 50:50 and a necessary further breakdown between moose harvested by residents many of whom hunt for meat and those harvested by non-residents who are more inclined to hunt for trophies. This method continued until 1968 when the survey was centralized and a computer used to help handle the mailing and the analysis of results. Difficulties in procedure resulted in only 60 percent returns for residents and non-residents during the first year, and 64 percent for residents, 83 percent for non-residents during 1969. In 1970 the return rate increased to 84 percent for residents and declined only slightly to 81 percent for non-residents. In order to reduce costs in 1971 and 1972, much smaller samples were drawn systematically from all licence holders of the province without stratification. The percentage of returns in 1971 was 86 percent for residents and 92 percent for non-residents; in 1972 it was 85 percent for residents and 93 percent for non-residents.

The second change in methods involved the collection of moose jaws for aging. Passmore, Peterson and Cringan (*in* Peterson, 1955) began the collection of jaws and developed the wear-class method of aging moose. Following their study, officials in some districts began asking hunters to bring in moose jaws on a routine basis. Appeals followed in widely circulated news releases but still relatively few jaws were collected. Checking stations provided good collections from specific locations where single roads gave entry to good moose hunting areas, but collections from other areas remained sparse. Then in 1967 an attractive cloth crest was provided for hunters bringing in a moose jaw (Fig. 2). The jaw collection increased by 72 percent in the first year with the greatest increases in districts where adequate samples had never previously been collected. Jaw collections have continued to grow since that time. Now some districts collect jaws from 50 to 60 percent of the moose that are shot and in some cases, district totals exceed 1,000 jaws.

The third major change was in aging techniques. In early years, only the wear-class method was available. This method can provide consistent results when all jaws are collected into one place and carefully sorted into piles for different wear classes, but considerable skill and practice are required. To provide quality control of the data, courses in aging moose were introduced at convenient centres throughout northern Ontario during the mid-1950's and were repeated annually until 1971. Each course was followed by an examination and only those who had passed were allowed to age moose. Still, much variability remained and there was no way of detecting instances when the recommended procedures were not followed. The variations in reliability of data re-

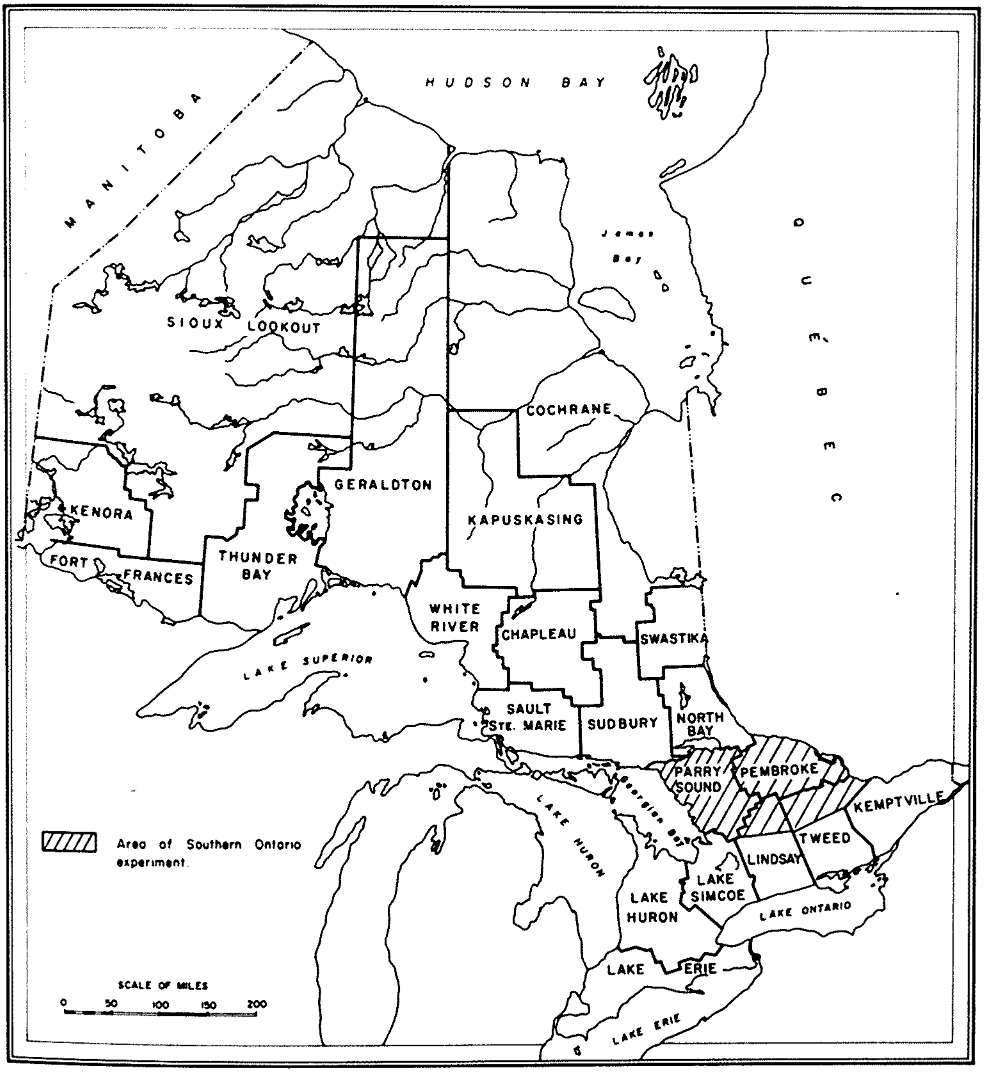

Figure 1. Map of Ontario showing forest districts which constituted the basic management units for moose. All management units north of Parry Sound and Pembroke are collectively referred to as "Northern Ontario".

Figure. 2 Successful Moose Hunter crests for hunters bringing in moose jaws (or, since 1971, incisors) have greatly increased the size of samples collected from moose harvested in Ontario.

sulting from individual differences in using the wear-class method make interpretation of results difficult.

In 1959, Sergeant and Pimlott discovered that cementum layers in sectioned incisors gave more reliable estimates of age and could be counted in a more objective manner. This method was tried as early as 1960 but it was not until Simkin (1967) compared the wear class and cementum aging methods that the latter was recommended for field use. Several districts used both methods from 1968 to 1970 and by 1971 the incisor sectioning method was adopted as standard.

In addition to improving the accuracy of aging older animals (Simkin, 1967), the change to aging by incisors also facilitated collection of larger samples from hunters since incisors could be removed more easily than whole jaws.

The southern Ontario experiment in over-hunting moose

In 1960, H. G. Lumsden, Supervisor of Game Management, proposed a deliberate over-harvest of moose. Southern Ontario was the obvious place for such an experiment since moose were relatively few, access was good, and hunters, lured by deer (*Odocoileus virginianus*), were numerous. The immediate question for moose management was, "Can moose in southern Ontario sustain an annual hunt under current conditions of unlimited licence purchase and a season of two weeks?" Two general questions also seemed important: 1) What are the best indicators of over-hunting? 2) Will an over-hunted moose herd recover when hunting is discontinued, and if so how rapidly?

Study area

The area included all occupied moose range south of the French and Mattawa Rivers (Fig. 1). This is an area of mixed forest, which was heavily cut for conifers in past years, and has now regenerated largely to pole-sized hardwoods. Moose were very scarce there from about 1930 to 1950 and no moose hunting had been permitted from 1933 to 1956. In spite of this closure, densities remained noticeably lower than in northern Ontario. Moose seasons were re-introduced in 1965 but only in alternate years. A special $26 deer/moose licence was required until 1961. These restrictions seemed necessary because approximately 150,000 deer hunters used the many roads to penetrate nearly every part of the woods and establish camps from which organized groups of five to fifteen men hunted. Presumably, many of these men were also potential moose hunters.

Methods

To find the effect of over-harvest, an open season for hunting moose in southern Ontario was recommended for the first two weeks of November during four consecutive years (1960-63) and the special $26 licence was discontinued so that any resident of Ontario could hunt moose using the regular $10 moose licence. After four years, intermittent seasons were again recommended. Mailed surveys brought returns from over 95% of the hunters in most districts. Jaws were collected and aged by the wear-class method.

Results

EVIDENCE OF OVER-HUNTING

Harvests began to decline after 1961 (Table I). By 1963 it was obvious that moose could not sustain an annual hunt under these conditions. The reversion to an intermittent type of season produced no apparent benefit in 1965 when harvests reached their lowest levels. By 1968, after two additional years' closure, the harvest rose again to pre-1961 levels. Similar harvest levels have been maintained since that time with seasons every second year. Aerial counts showed corresponding decreases and increases (unpublished data) and thus confirmed that these figures reflected actual changes in the moose population.

SEX RATIOS AS INDICATORS OF OVER-HUNTING

During 1956 and 1958 all southern districts reported sex ratios heavily weighted to bulls (Table II), but from 1960 onward sex ratios in Parry Sound and Tweed Districts began to favour cows. In 1961 this change occurred in Lindsay District and by 1963 in Pembroke District. Parry Sound and Lindsay Districts showed a reversal of the trend after 1968. In Pembroke District, where an additional moose season was permitted in 1966, sex ratios of moose only approached a one-to-one ratio, until 1972 when a preponderance of bulls was again reported. Tweed District on the southern fringe of the moose range and with a high density of big game hunters has continued to report more cows than bulls. Thus the change from more bulls to more cows in the harvest coincided with the initiation of over-hunting and more bulls were again recorded, immediately in two districts and later in a third, when the moose herd began to recover.

AGE RATIOS AND OVER-HUNTING

Changes in age ratios related to over-hunting were more difficult to find. The proportion of calves among the moose reported shot by hunters fluctuated erratically (Table II). In the jaw collection (Table III), the only significant changes in percentage between years were in wear class V+ ($\chi^2 = 17.02$, $P < 0.05$) and these bore no relation to the period of over-hunting (1962-65). Although the changes in percentage of yearlings were not significant over-all ($\chi^2 = 12.06$, $P < 0.10$), the percentage of yearlings shot prior to 1962 was significantly higher than the percentage shot afterward ($\chi^2 = 5.25$, $P < 0.025$). But no increase in the percentage of yearlings occurred after hunting was again reduced (1956-61 averaged 32.5% yearlings; 1962-5 averaged 26.1% yearlings; and 1968-72 averaged 26.0% yearlings); therefore, the meaning of this significant difference remains obscure. The only change which seemed of any real interest was an apparent increase in the percentage of yearlings as hunting intensity increased. If it occurred regularly, such a change might provide warning of increased hunting pressure. This idea was supported by Simkin (1964) who found high percentages of yearlings among heavily hunted moose in northern Ontario.

CONCLUSIONS

1. The moose herd in southern Ontario was over-hunted with an-

TABLE I

Numbers of moose hunters and harvest in southern Ontario. Harvest data indicate over-hunting in each district between 1961-1965

Year	*Parry Sound*		*Pembroke*		*Lindsay*		*Tweed*		*Total*	
	Licenced hunters	*Harvest*	*Licenced hunters*	*Harvest*	*Licenced hunters*	*Harvest*	*Licenced hunters*	*Harvest*	*Licenced hunters*	*Harvest*
1956	463	200	136	48	198	74	71	30	868	352
1958	661	330	108	55	255	123	116	41	1140	549
1960	899	400	144	95	321	155	116	52	1480	702
1961	1783*	483	373*	119	690*	219	254*	62	3100*	883
1962	1655	437	448	172	575	143	172	33	2850	785
1963	1393	272	389	100	455	79	132	10	2369	461
1965	1376	216	371	73	352	50	117	28	2216	367
1966			314	76						
1968	1854**	442	490**	142	419**	140	241**	21	3004**	745
1970	1740	289	584	90	358	69	152	33	2834	481
1972	1899	246	1119	246	508	126	206	42	3732	660

* First use of regular moose licence.

**First use of centralized survey (most previous surveys brought over 95 percent returns).

TABLE II

Sex and age ratios of moose shot in southern Ontario

Year	*Parry Sound*			*Pembroke*			*Lindsay*			*Tweed*			*Total*		
	Animals reptd.	*♂♂ /100 ♀♀*	*cc*/100 ♀♀*	*Animals reptd.*	*♂♂ /100 ♀♀*	*cc/100 ♀♀*	*Animals reptd.*	*♂♂ /100 ♀♀*	*cc/100 ♀♀*	*Animals reptd*	*♂♂ /100 ♀♀*	*cc/100 ♀♀*	*Animals reptd*	*♂♂ /100 ♀♀*	*cc/100 ♀♀*
1956	184	135	57	39	131	69	74	107	48	30	140	60	327	128	57
1958	365	121	46	54	108	17	123	108	48	41	146	69	533	118	44
1960	391	78	41	62	141	41	146	107	49	52	70	22	647	88	41
1961	483	118	66	120	142	92	219	87	57	62	76	72	884	108	67
1962	430	99	70	77	106	34	119	74	64	31	29	53	657	90	63
1963	213	115	48	66	86	41	73	69	83	8	20	40	360	97	53
1965	183	86	46	49	88	8	45	82	82	17	133	33	294	88	43
1966				41	119	38									
1968	164	110	63	47	95	29	58	182	59	13	67	33	282	116	55
1970	101	111	55	47	91	50	49	153	73	21	69	10	218	112	45
1972	35	155	64	35	114	20	18	114	6	6	52	0	94	118	29

*cc–calves

TABLE III

Variations in moose ages in Parry Sound District, southern Ontario. Only three representative age classes (based on wear-classes of Passmore, Peterson and Cringan, 1955) are presented. Data represent percentages of the kill according to age class

Age (wear)-class	*1956*	*1958*	*1960*	*1961*	*1962*	*1963*	*1965*	*1968*	*1970*	*1972*
I	31.4	31.5	32.0	34.6	27.0	32.3	17.5	24.6	28.9	23.4
II	12.8	12.1	19.0	16.5	13.9	13.5	23.7	18.3	14.0	12.5
IV +	24.4	34.9	17.0	25.2	27.0	29.2	23.7	22.5	24.0	14.4
Sample size	86	149	100	127	115	96	80	142	121	64

nual hunting seasons of two weeks in November and hunting open to any resident who wished to buy a moose licence.
2. The best indicator of over-hunting from the harvest statistics was a decreasing annual harvest per unit area in the absence of other explanation for such a decline.
3. The second most important evidence of over-hunting was a change of sex ratios in the harvest from a ratio favouring bulls to one favouring cows.
4. Age ratios seemed of relatively little importance in detecting over-hunting, although the increasing percentage of yearlings suggested that this parameter might be worth examining further.
5. The moose responded relatively quickly to a closed season, following over-hunting, with substantial increases in herd size.
6. Since the experiment, satisfactory moose harvests have been maintained in this area by a system of intermittent open seasons, possibly with resulting increased yields as suggested by Walters and Bandy (1972).

Monitoring moose hunting in northern Ontario

The early motive for gathering statistics on moose hunting in northern Ontario was simply to obtain the data necessary for sound management (Leopold, 1933 and others). Then the evidence demonstrating over-hunting in southern Ontario raised the question "Is there any similar evidence of over-hunting in northern Ontario?" The data were examined at two levels: 1) the forest districts which comprised the basic management units and 2) special study areas with limited access where substantial numbers of moose could be examined at checking stations.

THE AREA

The northern Ontario moose range is primarily boreal forest with vast expanses of solid conifer and many other areas where conifers are mixed with intolerant hardwoods. Cutting for wood pulp continues to produce improved moose range but fire suppression has greatly reduced production of improved range through burning. Other major differences from southern Ontario include denser moose populations, fewer humans, poorer access, and much longer hunting seasons (in some areas from mid-September to mid-December).

Monitoring the harvest in districts

Annual estimates of numbers of moose killed in each district (Table IV) provide a first means of examining the effects of hunting. All districts showed increasing harvests up to about 1961. Thereafter, the harvests fluctuated independently in each district except for 1965 and 1966 when many districts reported exceptionally high harvests for reasons that are not clear. No evidence of decreasing yields occurred until 1968 when Kapuskasing reported a sharply reduced harvest. In that district the harvest has continued at this lower level except for 1970. In 1969 Cochrane and Kenora also showed reduced harvests which have not recovered to former levels except for 1971 in Cochrane.

Exceptionally rainy weather complicated the picture during 1968 and 1969, but this fact probably does not explain all of the decreases observed for those years. No similar circumstance affected the hunt in 1971 or 1972; therefore, it seems at least possible that the observed decreases were the result of over-hunting.

TABLE IV

Total number of moose harvested by district in northern Ontario between 1953 and 1972

District	*1953*	*1954*	*1955*	*1956*	*1957*	*1958*	*1959*	*1960*	*1961*	*1962*	*1963*	*1964*	*1965*	*1966*	*1967*	*1968*	*1969*	*1970*	*1971*	*1972*
Kenora	250	208	192	247	400	357	598	1284	1557	1648	1352	1173	1497	1614	1303	1332	1104	978	1071	904
Sioux Lookout	223	372	602	828	925	990	1157	1112	1648	1578	1669	1336	2284	1823	1410	1493	1429	1534	2200	2013
Fort Frances					15	56	144	159	256	344	268	358	240	284	267	282	352	258	242	294
Thunder Bay	51	83	245	354	360	538	837	1099	1071	1656	1915	1907	2428	2309	2281	1591	1990	1617	1728	1947
Geraldton	96	187	321	323	991	1086	1160	1348	1427	1450	1338	1221	1823	1790	1608	1376	1266	1088	1237	1319
Total, N.W. Ontario	**620**	**850**	**1360**	**1752**	**2691**	**3027**	**3896**	**5002**	**5959**	**6676**	**6542**	**5995**	**8272**	**7820**	**6869**	**6074**	**6141**	**5475**	**6473**	**6477**
Kapuskasing	148	226	494	587	826	775	1121	996	1025	1040	1316	1191	1344	1141	1036	839	976	1103	824	951
Cochrane	148	222	285	505	474	511	485	640	511	761	887	803	866	1102	838	946	739	754	822	691
White River	34	108	115	165	252	245	303	482	650	663	735	678	763	891	661	757	715	717	714	706
Chapleau	30	66	90	202	280	294	359	463	595	363	594	430	571	683	438	620	722	608	879	827
Gogama	50	83	157	214	250	330	392	441	639	475	485	392	440	518	480*					
Swastika	62	80	128	320	347	412	470	511	559	646	868	751	748	712	929	872	838	938	749	712
Total, N.E. Ontario	**472**	**785**	**1269**	**1993**	**2429**	**2567**	**3130**	**3533**	**3979**	**3948**	**4885**	**4245**	**4732**	**5047**	**4382**	**4034**	**3990**	**4120**	**3988**	**3887**
S.S. Marie	29	22	140	365	370	413	696	594	799	663	806	783	829	661	709	520	689	562	612	678
Sudbury	11	75	39	310	269	612	855	493	654	581	535	426	415	494	669	944	869	920	1011	1093
North Bay		49	59	120	184	168	348	426	439	279	345	475	362	495	578	478	643	841	949	979
Total, N. Central Ontario	**364**	**146**	**238**	**795**	**823**	**1193**	**1899**	**1513**	**1892**	**1523**	**1686**	**1684**	**1606**	**1650**	**1956**	**1942**	**2201**	**2323**	**2606**	**2750**
Total for all districts in northern Ontario	**1456**	**1781**	**2867**	**4540**	**5943**	**6787**	**8925**	**10,048**	**11,830**	**12,147**	**13,113**	**11,924**	**14,610**	**14,517**	**13,207**	**12,050**	**12,332**	**11,918**	**13,072**	**13,114**

* Gogoma District was divided among Sudbury, Chapleau and Swastika Districts after 1967.

TABLE V

Bulls per 100 adult cows for resident hunters in Ontario by district

District		*1955*	*1956*	*1957*	*1958*	*1959*	*1960*	*1961*	*1962*	*1963*	*1964*	*1965*	*1966*	*1967*	*1968*	*1969*	*1970*	*1971*	*1972*
Kenora	♂♂/100 ♀♀	174	133	115	140	129	110	147	113	130	83	107	113	120	202	100	101	109	117
	Sample Size	**137**	**147**	**211**	**185**	**53**	**208**	**242**	**166**	**138**	**148**	**157**	**228**	**123**	**124**	**150**	**142**	**48**	**50**
Sioux Lookout	♂♂/100 ♀♀	136	177	115	120	154	133	140	123	169	111	93	127	97	132	127	121	100	114
	Sample Size	**184**	**202**	**204**	**216**	**49**	**267**	**222**	**145**	**167**	**133**	**172**	**177**	**126**	**102**	**136**	**207**	**58**	**94**
Fort Frances	♂♂/100 ♀♀			100	100	86	204	160	144	129	196	162	128	167	150	153	81	300	162
	Sample Size			**14**	**29**	**24**	**92**	**94**	**78**	**80**	**148**	**89**	**114**	**96**	**60**	**124**	**94**	**16**	**34**
PA/Thunder Bay	♂♂/100 ♀♀	132	168	137	143	110	168	102	147	130	105	130	148	131	135	120	165	107	110
	Sample Size	**160**	**303**	**249**	**342**	**120**	**143**	**70**	**106**	**124**	**119**	**136**	**134**	**127**	**61**	**132**	**140**	**95**	**143**
Geraldton	♂♂/100 ♀♀	141	116	93	140	154	123	104	117	121	132	128	153	93	247	116	115	92	130
	Sample Size	**229**	**212**	**747**	**608**	**162**	**186**	**223**	**213**	**259**	**188**	**267**	**238**	**208**	**111**	**151**	**124**	**77**	**101**
Kapuskasing	♂♂/100 ♀♀	147	144	179	165	215	156	215	139	175	157	120	117	154	213	158	110	124	118
	Sample Size	**242**	**290**	**343**	**450**	**126**	**134**	**167**	**167**	**195**	**195**	**220**	**150**	**132**	**72**	**134**	**121**	**65**	**109**
Cochrane	♂♂/100 ♀♀	144	283	153	129	144	152	134	129	175	134	117	176	137	181	181	106	126	186
	Sample Size	**139**	**368**	**304**	**351**	**57**	**88**	**75**	**117**	**132**	**136**	**143**	**91**	**71**	**59**	**87**	**77**	**70**	**80**
White River	♂♂/100 ♀♀	94	82	110	129	244	148	122	143	143	106	102	164	165	119	131	152	95	129
	Sample Size	**64**	**102**	**149**	**144**	**44**	**121**	**99**	**90**	**119**	**101**	**85**	**95**	**61**	**81**	**83**	**83**	**37**	**48**
Chapleau	♂♂/100 ♀♀	154	124	184	145	85	256	168	142	133	94	89	168	181	248	139	200	121	126
	Sample Size	**71**	**132**	**176**	**181**	**35**	**24**	**37**	**143**	**119**	**101**	**117**	**169**	**90**	**73**	**98**	**115**	**42**	**79**
Gogama	♂♂/100 ♀♀	113	165	189	204	174	170	280	176	137	109	118	262	195*					
	Sample Size	**113**	**138**	**162**	**237**	**51**	**161**	**152**	**138**	**152**	**140**	**133**	**145**	**109**					
Swastika	♂♂/100 ♀♀	168	130	85	122	119	111	99	140	212	173	136	157	158	176	152	128	205	107
	Sample Size	**118**	**237**	**230**	**197**	**92**	**81**	**87**	**115**	**162**	**139**	**139**	**90**	**129**	**69**	**63**	**82**	**58**	**85**
S. S. Marie	♂♂/100 ♀♀	250	102	141	112	103	134	169	161	124	114	164	110	110	121	122	154	282	131
	Sample Size	**108**	**252**	**181**	**256**	**81**	**78**	**104**	**47**	**56**	**47**	**58**	**86**	**42**	**53**	**51**	**41**	**42**	**67**
Sudbury	♂♂/100 ♀♀	343	151	110	133	91	164	154	205	150	325	131	130	113	194	188	196	216	132
	Sample Size	**31**	**103**	**162**	**377**	**103**	**58**	**59**	**58**	**50**	**68**	**67**	**46**	**64**	**94**	**72**	**85**	**79**	**130**
North Bay	♂♂/100 ♀♀		129	93	130	144	66	82	128	173	161	97	116	211	116	152	98	131	166
	Sample Size		**87**	**145**	**115**	**54**	**107**	**74**	**41**	**41**	**81**	**61**	**54**	**56**	**41**	**53**	**66**	**67**	**117**

* Gogama District was divided among Sudbury, Chapleau and Swastika Districts after 1967

The sex-ratios for these districts provide another line of evidence. Only sex ratios of moose shot by resident hunters are included (Table V) because nonresidents nearly always shoot a higher proportion of bulls. Yet, in nearly all districts during most years, the sex ratios among moose shot by residents also strongly favoured bulls. Some temporary reversals occurred in some districts such as Chapleau in 1964 and 1965 and Sioux Lookout in 1965, but these apparently resulted from sampling error only, since the sex ratios strongly favoured bulls again afterward. There is no evidence of reversed sex ratios in Kapuskasing or Cochrane Districts such as one would expect from their decreased annual yields. Although the sex ratios did not reverse in Kenora District, they did remain nearly equal from 1969 to 1971 and increased relatively little in 1972. This appears to be the only instance where sex ratios have shown a change which might be attributed to heavy hunting.

The percentage of yearlings is shown only for areas accessible by roads and waterways as these areas are the most heavily hunted. Table VI shows little evidence of increased percentages of yearlings due to heavy hunting, even in these easily accessible areas. A major exception is Kenora District where the percentage of yearlings has remained high for many years. This was not true in the less accessible parts of Kenora District. Thus again Kenora District is the only one to show evidence that hunting may be producing changes in the moose herd.

Monitoring the harvest at checking stations

The first checking station and the one which has provided the longest run of data was located on Highway 105 which links a major highway with the remote village of Red Lake. Sex and age data are nearly continuous for sixteen years. Despite fears of over-hunting as early as the mid-1950's, the numbers of moose checked at this station have continually increased (Table VII). Furthermore, there has been no consistent decrease over a number of years in the ratio of bulls to cows, even in the more accessible areas. Bulls never comprise

TABLE VI

Percentage of yearlings (1 yr) among moose 1 yr and older harvested by hunters from heavily hunted areas accessible by road and water in selected districts of Ontario

District		*1964*	*1965*	*1966*	*1967*	*1968*	*1969*	*1970*
Kenora	% Yearlings	40.4	44.3	34.7	37.5	31.3	45.5	43.9
	Sample size	121	129	171	110	164	307	351
Sioux Lookout	% Yearlings	23.7	45.6	37.7	26.5		30.3	22.5
	Sample size	172	107	92	200		146	127
Thunder Bay	% Yearlings	22.3	22.6		23.7	29.4	22.4	33.0
	Sample size	190	224		800	691	740	752
Geraldton	% Yearlings	31.5	21.7	20.9	27.9	26.7	22.9	26.4
	Sample size	107	155	164	223	283	304	405
Cochrane	% Yearlings	26.2	36.8	35.4	20.3	24.3		
	Sample size	45	78	48	210	177		
Gogama	% Yearlings	34.4	31.6	29.6	30.1			
	Sample size	135	149	170	165			
White River	% Yearlings	20.0	28.6	38.5		22.6	29.2	30.2
	Sample size	58	28	70		207	194	220

as high a proportion of the harvest in more accessible areas as in less accessible areas, probably because hunters can afford to be more selective for trophy bulls in the latter (Simkin, 1964). The percentage of yearlings has been high for many years in the more accessible areas, but it is not increasing. In fact there have been fewer very high percentages of yearlings in recent years than in the mid-1960's. The reason for this slight decrease in percentages of yearlings is not known.

Saunders, Williamson and Addison (pers. comm.) suggested that the annual count of moose at the Red Lake Road Checking Station might not reflect decreased harvests in traditional hunting areas because any decreases there would be masked by the high success of hunters expanding into new grounds each year. However, Simkin (pers. comm.) obtained data which suggested this was not the case at least up to 1966: the figures he reported (Table VIII) showed no downward trend in the annual yield even though the numbers of hunters in the area increased nearly three times. More recent figures have not yet been analysed in this way.

Simkin (1964) showed that the many hunters along the Red Lake Road who hunted in areas which were accessible by roads and waterways killed higher percentages of yearlings than the relatively few hunters in more remote areas where aircraft were needed for access. This difference has continued for ten years (Table VII) and probably also represents hunter selection for large bulls in remote areas. Still, there is some indication of the difference narrowing due to the slightly decreasing percentages of yearlings in more accessible areas and an increase in percentages of yearlings in remote areas. The reason for this second trend is also unknown. Perhaps hunters flying to the same lakes

TABLE VII

Sex ratio and percentage of yearlings in moose harvested in Sioux Lookout District and checked at the Red Lake Road Check Station between 1957 and 1972

	Accessible areas				*Less accessible areas*			
Year	♂♂ / *100* ♀♀	*Sample size*	% *Yearlings*	*Sample size*	♂♂ / *100* ♀♀	*Sample size*	% *Yearlings*	*Sample size*
1957	117	226	44.1	93				
1958	128	230	31.2	138				
1959	165	254	40.1	137				
1960	79	500	45.5	334				
1961	161	370	42.9	219	154	99	35.1	37
1962	178	317	35.7	129				
1963	143	250	33.3	129	174	134	20.0	50
1964	88	175	34.0	100	148	151	22.9	48
1965	123	286	45.5	156	131	187	32.9	70
1966	119	265	42.4	132	193	223	29.4	51
1967	188	187	34.2	79	153	192	19.0	63
1968	156	159	25.5	98	187	155	20.0	85
1969	104	286	35.3	150	148	134	25.4	134
1970	127	332	42.3	137	158	178	30.3	185
*1971**	118	363	31.7	312	173	172	31.4	156
*1972**	102	318	39.2	288	109	247	27.3	194

* Aged by incisor method.

each year are creating small heavily hunted areas in the remote country and thus are less able to select larger animals.

Attempts at examining similar differences in other districts were not very successful. Some districts, notably Geraldton, showed differences between percentages of yearlings in more and less accessible areas. But in most districts the distinction between more and less accessible areas became blurred by changes in access patterns and means of travel so that no consistent differences can be seen.

The Black Sturgeon Road near Thunder Bay (Thunder Bay District) has also played an important part in providing evidence that moose were not being over-hunted despite heavy hunting pressure. In recent years, its usefulness has diminished due to alternate access routes which make complete checks of hunters using the area impossible but no evidence of over-hunting has been detected. Similarly, no evidence of over-hunting has appeared in figures from the Shabotik checking station near White River (White River District) and the Aubinadong checking station near Sault Ste. Marie (Sault Ste. Marie District). In the latter instance, the evidence from harvest statistics showing moose herd stability despite heavy hunting was supported by aerial inventories (Mantle, 1972).

The checking station near Englehart in northeastern Ontario (Swastika District), unlike the other checking stations, showed a sharply decreased harvest in 1970 (Table IX). In addition, the sex ratio showed some indication of fewer bulls. Although the percentage of yearlings had increased for two years, it then decreased again. These observations raised suspicions that over-hunting might be occurring. Unfortunately, interpretations was complicated by (1) increasing road access which allowed more hunters each year to bypass the checking station and eventually rendered it useless and (2) a shorter period of operation during 1970, which, however, still encompassed the period when 80-90 percent of the moose were usually checked. Hunting continues in the area but apparently at a lower level of intensity than previously. This appears to be the first checking station in northern Ontario to show some suggestion of over-hunting.

Discussion

WHAT IS OVER-HUNTING?

These results cannot be discussed without considering what constitutes over-hunting. Over-hunting is a term with strong emotional connotations that render loose usage unwise. Yet, I have never seen it defined. To some, shooting any animal would constitute over-hunting. To others, there is no over-

TABLE VIII

Moose harvest for the English River hunting region of the Red Lake Road study area. Data from Simkin (pers. comm.)

Year	*1957*	*1958*	*1959*	*1960*	*1961*	*1962*	*1963*	*1964*	*1965*	*1966*
Total harvest English River	73	68	72	133	106	73	79	62	87	80
Index to no. of hunters checked on Red Lake Road (1958,1.0)	nil	1.00	1.13	1.92	1.52	2.02	2.04	1.74	2.24	2.70

hunting as long as one animal remains alive. Probably any definition of over-hunting will arise from one's objectives in managing moose. Management to produce maximum current numbers would lead to a view of over-hunting different from management to produce a continuing supply of large healthy animals. Management aimed at resource production might lead to a different view of over-hunting from management aimed at recreational benefits for people (see Cumming, 1974). Perhaps Leopold's (1933) definition of game management will provide some common ground: "Game management is the art of making land produce sustained annual crops of wild game for recreational use."

If we accept this statement, then in my view the concept of over-hunting should be related to that of sustained yield. When an optimum yield is no longer sustained because too many animals have been removed by hunters, over-hunting has occurred. This remains true whether the yield is in numbers of animals, pounds of meat or recreational user days of specified quality. The qualification that the sustained yield must be optimum is important. A yield might be reduced deliberately from a situation of overpopulation without this action being construed as over-hunting. On the other hand, even a constant annual yield might constitute over-hunting if it held the population much below the carrying capacity of the range.

The problem of determining the optimum yield relative to the carrying capacity of a given range is a difficult one requiring detailed knowledge of the animal, its requirements and the capacity of the land to produce these requirements. It is a problem which we, in Ontario, have only recently begun investigating (e.g. Houser, 1972) and it has not yet played a large part in determining the objectives of moose management. Starting as we did from a situation of little or no hunting, it seemed satisfactory to accept as an approximation of the optimum yield, the highest yield that could be sustained as hunting pressure increased.

EVIDENCE OF OVER-HUNTING

These considerations provide a framework for examining evidence of over-hunting moose in Ontario.

Evidence of over-hunting from decreasing annual yields

The suggested definition makes it almost axiomatic that decreasing yields should provide the first line of evidence concerning over-hunting. We deduced that over-hunting had occurred in southern Ontario from the following facts: 1) Evidence of range deterioration never appeared before or during the experiment; therefore there was no decrease in numbers of moose from this cause, nor was there any overpopulation of moose requiring a reduction in numbers. 2) Major alternate sources of mortality were unknown. 3) Neither the numbers of hunters nor their effort decreased greatly. 4) Moose harvests decreased rapidly and consistently in all district after 1961.

Thus decreasing annual yields resulted from the intentional over-harvest of moose in southern Ontario. Similar evidence of over-hunting moose in Scandinavia was reported by Markgren (1974). Gulland (1972) presented data showing decreased yields of whales (*Balaena* spp.) as evidence that they were being over-exploited. If one accepts the above views concerning what constitutes over-hunting, then a decreasing yield without alternative explanation is the best evidence of its occurrence.

Relatively little evidence of decreasing annual yields was found in the data from northern Ontario. Only three districts and one checking station showed any indication of decreasing yields. Although the data were affected by mild rainy weather during two of these years and, in the case of the checking station, alternate access routes may have influenced results, still the evidence cannot be entirely discounted. Over-hunting may have occurred in at least some of these instances. But despite the forty-fold increase in numbers of hunters since 1951 (Cumming, 1972), over-hunting in northern Ontario seems a rare occurrence.

Evidence of over-hunting from changing sex ratios

Theoretical considerations suggest that a harvest heavily biased to bulls must show some change in the sex ratio as exploitation increases. Assuming with Simkin (1965) that (1) nearly equal numbers of each sex are born and (2) nearly equal numbers of each sex occur in the population, then if the harvest constitutes a major mortality factor, a bias toward bulls will inevitably decrease the male component of the population more quickly than the female component. Even though the vulnerability of bulls remains greater than that of cows, their decreasing availability will eventually reduce their occurrence in the harvest and sex ratios will shift toward ratios favouring cows.

Apparently, this was what happened in southern Ontario. Early harvests were heavily biased toward bulls. When over-hunting occurred, more cows than bulls were taken. Then, after some closed seasons, the ratios again changed to favour bulls. Thus a change from more bulls to more cows in the harvest appears to be the second most important evidence of over-hunting.

Few suggestions of such a change were found in hunter statistics from northern Ontario. The Englehart checking station reported a higher proportion of cows than bulls at a time of suspected over-hunting (Table IX), thus increasing the suspicions raised by rather weak evidence of a decreased yield. In Kenora District, sex ratios approached equality and this change occurred along with stronger evidence of over-hunting from decreasing yields. Perhaps, when bulls are very much more vulnerable than cows, equal sex ratios should be considered evidence of possible over-hunting. Since these were the only reported instances of such changes, the evidence from sex ratios in the harvest supports the conclusion that there has been little over-hunting in northern Ontario.

Evidence of heavy hunting from age ratios

Although the southern Ontario experiment produced no convincing evidence that age ratios could be used as indicators of over-hunting, there was a suggestion that they could be used to detect increased hunting pressure. This idea was supported by evidence from the Red Lake Road checking station where the heavy hunting in readily accessible areas produced higher percentages of yearlings in the harvest than the lighter hunting in less accessible areas. Furthermore, high percentages of yearlings were recorded in Kenora District along with decreasing yields and equal ratios of bulls and cows. Thus, high percentages of yearlings in the harvest may warn of increased hunting pressure but they cannot in themselves be considered evidence that over-hunting has occurred. When other lines of evidence indicate that there is no over-hunting, a high percentage of yearlings in the harvest probably indicates near optimum use of the resource.

Some of the recorded percentages of yearlings are higher than the theoretical reproductive potential derived from ovarian analysis (Simkin, 1965). This could be due to 1) yearlings being more vulnerable to hunters than older age classes as suggested by Pimlott (1959) and Simkin (1965) or 2) yearlings moving more readily into areas where the population was reduced through heavy hunting. Such movement of young animals has been described for moose in Wyoming (Houston, 1968) and for many other species (e.g. roe deer, *Capreolus capreolus*, Cumming, 1966). However, preliminary results from tagged moose in Ontario do not support this idea (Saunders and Williamson, 1972).

RELIABILITY OF EVIDENCE

Evidence of over-hunting is important because management decisions based on such evidence are likely to reduce opportunities for hunting and decrease the use of the resource. When these decisions are based on inadequate evidence, wasteful non-use may result. The preceding considerations suggest that decreasing annual yields with no alternative explanation and preponderance of females in the harvest provide sufficiently reliable evidence for management action. Increasing percentages of yearlings provide somewhat less reliable early warning. Certainty is never possible because of the many influences affecting data collected under field conditions. For example, the qualification "in the absence of alternative explanation" is sometimes difficult to assess when considering decreasing yields. The range may have deteriorated, or subtle influences such as decreasing ability of the hunters may have affected results. Therefore, all evidence should be examined, including if possible, estimates of population size. However, because of the many sources of error involved in aerial surveys (LeResche, 1970), I consider such estimates to be supporting rather than primary evidence. Presumably in some instances, population estimates could de-

TABLE IX

Sex and age data from Englehart checking station, Swastika district, Ontario

	1964	*1965*	*1966*	*1967*	*1968*	*1969*	*1970**
Total number of moose recorded at the checking station	105	122	90	110	104	100	59
Yearlings as a % of all moose older than calves	20.0	27.1	25.0	29.9	34.5	38.6	23.8
Sample size of aged moose	60	59	48	67	58	57	42
Adult ♂♂/100 adult ♀♀	112	148	175	131	77	142	110
Sample size of sexed moose	91	109	77	110	104	75	56

* Check station operated only during first 16 days of the season, not on subsequent weekends, but 80-90 percent of the moose are usually checked during that period.

crease markedly without any corresponding decline in the number of moose harvested. Such a decrease in population estimates might lead to investigation of the possibility of disease or some other problem, but as long as the annual yields remained stable, it would not constitute evidence of over-hunting.

The last statement assumes not only that the described evidence is reliable for detecting over-hunting but that its absence is sufficient ground for concluding that no over-hunting has occurred. This could be an even more serious matter. Erroneous conclusions of no over-harvest could conceivably result in a greatly reduced moose herd. The evidence from the southern Ontario experiment indicates that any such reduction is not as disastrous as many people fear. The moose population there recovered within a few years when the hunting season was closed and it seems reasonable to expect a similar response elsewhere. Still, it is a situation to be avoided, and one wonders whether the mere absence of evidence of over-hunting, of the type found in southern Ontario, is sufficient ground for concluding that over-harvest is not occurring? Several possible loop-holes come to mind:

1) The yield may be sustained through immigration of moose from surrounding inaccessible areas to accessible areas where they are being over-hunted. An answer to this objection must involve the purpose of game management. If the objective of management were to produce from every acre of land the maximum number of moose that the range would support or perhaps to maintain the resource at some specified level, such a situation would indeed constitute undetected over-hunting. But if the objective is to maintain optimum annual yields, as I think it should be, then there seems little difference whether the moose come from areas immediately adjacent to access roads or from areas more remote, so long as the annual yield is maintained. Such a situation merely extends utilization of the resource into areas where moose would otherwise be unused. Under conditions of limited access, small accessible areas may have to be harvested beyond their annual surplus to achieve an adequate harvest from the area as a whole. Of course, if access increased and the heavily hunted areas became large, the proposition would no longer hold: then each area would have to be treated as a separate unit from which a sustained yield was to be maintained. Such a situation may have existed in northern Ontario at the Englehart management unit where new roads eventually opened to hunters nearly all of a 500 mi^2 area. Under these conditions, more flexible regulations are required to limit the harvest in such areas to levels below the annual surplus.

2) A similar objection to the use of decreasing yields as indicators of over-hunting, concerns the possibility that hunters may maintain the harvest level by moving into new areas each year after shooting more than the annual surplus in older areas, as has been suggested for the Red Lake Road study area. But again, as long as the annual yield is maintained, it makes little difference if the harvest comes from different areas. If the time should come when all areas were hunted beyond their annual surplus, the yield would inevitably decrease, and, on the evidence of the southern Ontario experiment, that would be the time to reduce hunting pressure to allow the moose population to recover.

The real fear probably is of a sudden decrease. If the local removals could be arranged to rotate in a manner similar to tree harvesting, there would be no problem. But if the hunters were systematically working their way through an area, might they not reach the end and then bring about a sudden and sharp decline in harvest for the whole area? To this I would answer that such a situation has yet to be demonstrated. Even if it were shown to occur, this would not mean that declining yield was an unreliable indicator of over-hunting. It would only mean that this indicator, though reliable, did not provide early enough indication of over-hunting for the wildlife manager to take appropriate action. The results of the southern Ontario experiment suggest that such a sudden turn of events is unlikely. Even with twice as many licenced hunters as available moose, and harvest rates as high as 37 percent of the estimated fall population, there has been no decrease so sudden that corrective action could not be taken. Furthermore, when action was taken, positive response of the moose herd was quite rapid.

3) Perhaps a more serious objection is that decreased yields might be offset by the increased effort of hunters. But as Leopold (1933) first pointed out, the law of diminishing returns will dissuade hunters from hunting areas with low populations long before the animals are eliminated. In fact, the chances seem slim that hunters would severely reduce the moose herd through increased effort without the evidence showing as decreased yields. Any undetected over-hunting would be very short-term. Certainly, the mere observation of increasing hunter effort is no evidence of over-hunting. When moose hunting was first allowed in northern Ontario in 1951 after two years of complete closure, many residents were able to shoot moose while both hunter and animal were standing beside a road. The fact that this is no longer common may be related to decreased moose densities near roads or changes in moose behaviour, but it does not provide evidence that moose are over-hunted.

4) Decreasing yields may be thought unreliable indicators of over-hunting because of the possibility that statistics from large areas may not show decreased yield although numbers of moose have been reduced in some sectors. An example is provided by the regional totals for northern Ontario (Table IV) where the decreases in Kapuskasing and Cochrane Districts were sufficient to depress the total harvest for northeastern Ontario, but the decreased harvests in Kenora District would not have been detected in the totals for northwestern Ontario. However, masking of local decreases is not important as long as the areas involved are small. If they are large, the fault lies with the data gathering system, rather than with the concept that decreasing yields are the best indicators of over-hunting. The solution lies in improving the former rather than rejecting the latter.

Absence of a change in sex ratios is probably good evidence of the absence of over-hunting in most cases, but it may not be entirely dependable. For one thing, the data from southern Ontario were for a November hunt. Evidence from northern Ontario indicates that bulls are relatively more vulnerable in October than in November and December (Table X). Similar evidence was presented for moose in Newfoundland by Pimlott (1959). This being the case, it is possible that the number of bulls in the population could be reduced to very low levels in early October before any change in sex ratios of the harvests occurred. Furthermore, the number of cows could be reduced below optimum levels without a change in sex ratios, under the exceptional circumstance that the vulnerability of the bulls prevented a reversal of sex ratios before the cows

TABLE X

Seasonal evolution of the sex ratio in the moose harvest in Ontario

		1970		*1971*		*1972*	
	Week	*Calculated number of moose shot*	*Calculated ♂♂/100 ♀♀*	*Calculated number of moose shot*	*Calculated ♂♂/100 ♀♀*	*Calculated number of moose shot*	*Calculated ♂♂/100 ♀♀*
(Sept. 15)	38	146	96	7	600	3	200
	39	124	162	8	250	14	160
	40	1774	219	125	231	108	220
(Oct.)	41	5237	168	415	197	622	160
	42	2010	96	158	133	276	91
	43	982	88	112	95	145	98
	44	587	97	63	110	81	68
(Nov.)	45	800	97	37	67	48	153
	46	417	54	31	118	94	139
	47	231	49	24	125	43	79
	48	169	87	13	67	18	33
(Dec.)	49	403	75	33	92	26	120
	50	417	78	47	94	25	83
(Dec. 15)	51	210	128	27	77	38	127

were over-harvested. This would require rather fine balancing which seems unlikely. All this assumes, of course, that unbalanced sex ratios will not produce social ill health as suggested by Bubenik (1972).

The absence to date of intensive regulatory management of the moose herd in northern Ontario is largely due to reliance on these indicators to detect over-hunting. There has been little evidence of need for such intensive management and since intensive management is costly, it is not good management when it is not necessary. However, the recent indications of over-hunting in some areas suggest that preparations for more intensive management should begin. These preparations, including such measures as the formation of smaller management units, are now underway.

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MOOSE POPULATION FLUCTUATIONS IN ALASKA, 1950-1972

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Résumé

A partir de données recueillies à l'aide d'inventaires aériens et par d'autres méthodes, les auteurs décrivent l'état des populations d'orignal, les variations de la productivité des cheptels et les indices d'abondance et de survie de l'orignal dans quatre régions de l'Alaska durant la période 1950-1972. Entre 1950 et 1960, les populations étaient élevées ou en expansion dans toutes les régions étudiées, grâce aux facteurs suivants: des feux de forêt étendus et fréquents durant les années 40 et 50, de bonnes conditions d'enneigement au cours des années 50, le contrôle des prédateurs au cours de la même période et, enfin, un règlement limitant la chasse aux mâles seulement jusqu'en 1960. Entre 1960 et 1970, plusieurs hivers furent marqués par des conditions d'enneigement très défavorables, ce qui eut pour effet de provoquer une mortalité hivernale modérée ou élevée chez l'orignal; cette mortalité semblait déterminée surtout par l'épaisseur et la persistance de la couche de neige au sol, mais elle variait selon la densité du cheptel et les conditions de l'habitat. La mortalité affectait principalement les veaux et, dans une moindre mesure, les vieux sujets. Les mâles semblaient plus susceptibles que les femelles. Dans les cas les plus extrêmes, toutes les classes d'âge étaient atteintes et la mortalité frappait 50 pour cent et plus de la population. Les inventaires aériens permettent de dresser la structure d'âge et de sexe du cheptel; cela permet de détecter les changements imputables à la mortalité hivernale et à des agents de mortalité sélectifs comme, par exemple, la chasse aux mâles.

A la suite d'une forte mortalité hivernale, chaque population semblait maintenir, durant la phase de récupération, une composition qui lui était caractéristique et qui était apparemment déterminée par une combinaison particulière de facteurs du milieu. Dans un cas (Nelsina Basin), la prédation par une forte population de loups a probablement ralenti considérablement l'accroissement d'une population réduite d'orignal. L'accroissement annuel a atteint 25 à 30 pour cent durant les périodes favorables à l'augmentation de la population et dans les régions caractérisées par des hivers cléments, une faible abondance relative de prédateurs et une forte récolte par la chasse; de tels taux ne se maintenaient pas quand les conditions du milieu se détérioraient. On peut s'attendre à des variations considérables dans la production et la survie des populations d'orignal dans les régions où les modifications exercées par l'homme sur l'habitat ou sur les populations elles-mêmes sont insignifiantes; il est nécessaire de tenir compte de cette réalité au moment de formuler des programmes d'aménagement.

Abstract

Moose population status, and trends in productivity, survival and abundance monitored by aerial surveys and other means in four Alaskan study areas during 1950-1972 are reviewed. Moose numbers were high or increasing from 1950 to 1960 in all areas studied due to extensive and repeated wildfire in the 1940's and 1950's, moderate snow severity in the 1950's, predator control in the 1950's, and the restriction of hunting to bulls only prior to 1960. During the 1960's, several winters of severe snow conditions precipitated moderate to high winter moose mortality, mainly in response to varying depth and duration of snow cover, but modified by moose population levels and habitat condition. Mortality primarily affected calves and secondarily affected old moose. Males appeared more susceptible than females. In the most severe cases all age classes were affected, and losses equalled 50 percent or more. Aerial sex and age composition survey data reflected major changes in population structure resulting from winter mortality and from selective mortality such as hunting of bulls.

Population composition during recovery following extensive winter mortality was not consistent among study areas, and varied in response to the particular combination of ecological factors prevailing at the time. In one area (Nelchina Basin) a high wolf population probably played a major role in retarding growth of a reduced moose population. Annual increments of 25 to 30 percent occurred during periods favorable to population increase and in areas with mild winters, few predators, and intensive hunting, but did not persist under less favorable circumstances. The potentially great variation in moose production and survival in areas where population and habitat manipulation are minimal should be recognized in formulating management programs.

Introduction

Early historical records, accounts of older residents, subsistence use patterns of Athabascan residents, and the probabilities of development and successional change within plant communities all indicate moose (*Alces alces gigas* Miller) have been distributed throughout most of Alaska for some time (LeResche *et al.*, 1974). The same sources indicate recent range extensions in northwestern Alaska and southeastern Alaska and dramatic, usually positive, changes in population densities in many areas within the last 50 to 75 years. Factors contributing to moose increases included: widespread creation of seral range through increased incidence of natural and man-caused fires (Hardy and Franks, 1963), homesteading and construction; decline in market hunting and a shift to restrictive regulations; climatic changes resulting in improved growth of browse in marginal areas; and a period of intensive predator control in several areas. Of these, fire was most important (LeResche *et al.*, 1974).

During the late 1940's and 1950's, these factors, combined with series of relatively mild winters, resulted in nearly optimal conditions for moose population growth.

None of the factors contributing to moose increases are permanent, or temporally consistent. Populations which increase during periods of favorable circumstances are subject to readjustment of numbers in the face of changing conditions. In Alaska these readjustments have often been dramatic "crashes", triggered by unusually severe winter conditions. In other cases readjustments of numbers or in composition have been more subtle. Change in population structure has also occurred in response to hunting pressure in certain areas.

We review recent population changes in four areas where long-term studies have been done: the Matanuska Valley, the Nelchina Basin, the Tanana Flats, and the Kenai Peninsula (Fig. 1). Moose populations in all of these areas have in common a pattern of relatively rapid population growth with ensuing stabilization or decline in recent years depending upon local circumstances.

Unwritten accounts and some data indicate moose numbers in other parts of Alaska have also fluctuated widely. Interactions of factors mentioned above probably account for these fluctuations, but aside from the study areas discussed here, data are usually insufficient to demonstrate cause and effect. A notable exception exists at Yakutat, in southeastern Alaska, where natural invasion of moose from Canada 40 to 50 years ago (Klein, 1965) resulted in a very recent (1970-71) population peak and subsequent decline.

Study areas

The four study areas differ considerably in physiography, climate, habitat, history of use since arrival of western culture, and contemporary accessibility, all of which have a bearing on present moose populations.

TANANA FLATS

The Tanana Flats comprise a broad lowland (elevation 400 to 1000 ft or 130 to 328 m) within Warhaftig's (1965) Tanana-Kuskokwim Lowland physiographic section. Plant communities ranging from herbaceous bog to white spruce (*Picea glauca*) stands, plus aquatic communities in open, standing water occur in a complex mosaic (see LeResche *et al.*, 1974). The climate is typically continental, with warm summers, cold winters and low precipitation (Table I). Snow regularly reaches two ft. (60 cm), (Table I) in depth, and is usually light and soft (Coady, 1974). Lightning-caused wildfire is common in interior Alaska, and much of the Tanana Flats has burned at some time with rather variable effects on later succession (LeResche *et al.*, 1974). The extensive bogs have discouraged permanent human occupancy of the Tanana Flats, but trappers and hunters have seasonally used the area for years. Major and minor winter trails have been made and used at various times since white settlement.

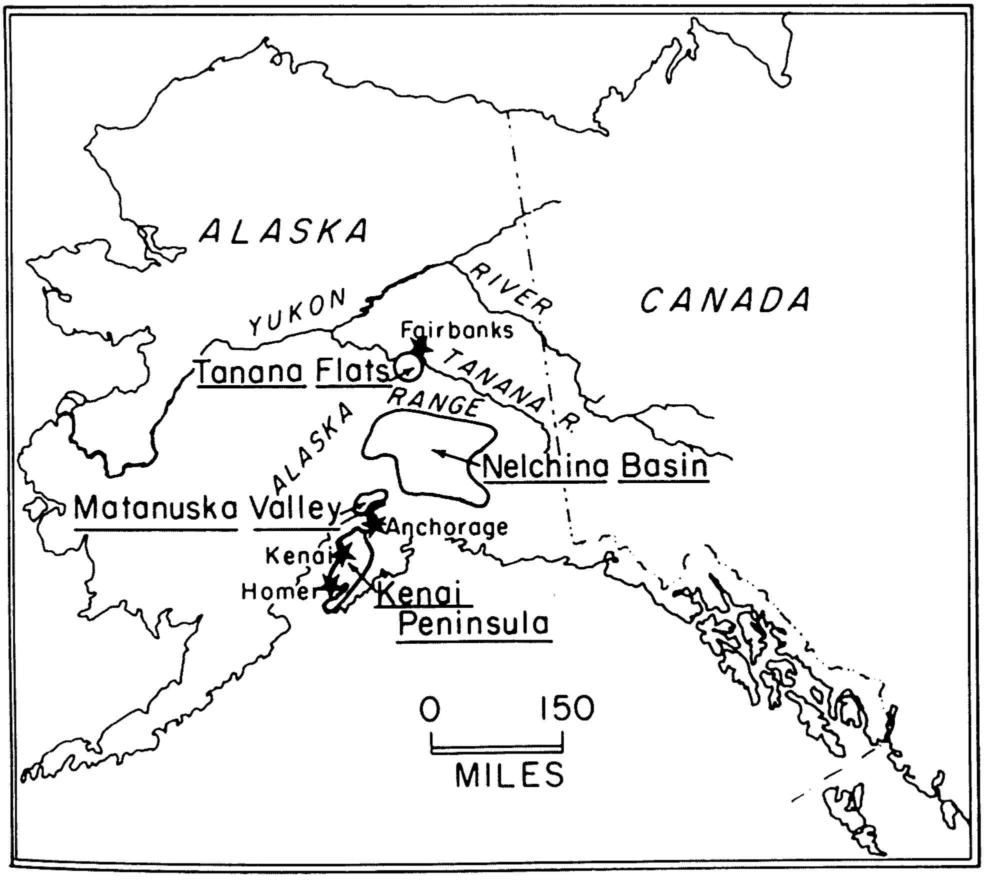

Figure 1. Moose study areas, Alaska.

With the decline of prospecting, gold mining, and associated market hunting and trapping prior to World War II (1941), use of the area declined. The entire area was subsequently made a military reservation and civilian access was prohibited (but still occurred) from 1943 until 1961 when it was reopened. During summer, the area is largely inaccessible, but the advent of snowmachines has made much of the area accessible to winter recreationists. Military activity in the area has also increased. In spite of access difficulties, the Tanana Flats has become an important recreation area. Because the Flats abut the outskirts of Fairbanks, a population center, their importance will surely increase. The Flats are the largest known moose calving grounds in central Alaska.

NELCHINA BASIN

In contrast to the Tanana Flats, the Nelchina Basin is largely a plateau (elevation approximately 1200 to 4000 ft, about 400-1300 m), dissected by tributaries of the Susitna, Copper and Nenana Rivers, and essentially surrounded by mountains. It lies within Warhaftig's (1965) Coastal Trough physiographic province.

The climate is essentially continental, but tends to be less extreme than in interior Alaska (Table I). Naturally caused wildfires are less frequent and smaller than in interior Alaska because of less flammable vegetation and slightly greater precipitation (Hardy and Franks, 1963; Skoog, 1968). Winter temperatures and snow depth tend to be less severe than in interior Alaska (Table I). Because of considerable open terrain, areas of higher elevation may either be blown free of snow or have hardpacked or drifted snow.

Skoog (1968) felt that in most years snow depth was not a serious problem

TABLE I

Examples of general climatic data in Alaska moose study areas, 1971, and snow depth, January 1971 and January 1972

Climatic data 1971	*Study area*				
	Tanana Flats (Fairbanks)[2]	*Nelchina Basin (Gulkana)*	*Matanuska Valley (Agric. Station)*	*Kenai Peninsula*	
				(Kenai)	*(Homer)*
July mean temp (F°)[1]	61.0	56.8	56.8	53.2	51.6
Dec. mean temp (F°)[1]	-5.8	-5.7	12.5	14.1	23.0
Annual mean temp (F°)[1]	23.8	24.2	32.0	30.6	33.0
Annual precip. (in)	12.31	13.54	17.33	18.80	22.29
Snow depth[3]					
Jan. 31, 1971	35(89)	9(28)	0(0)	3(8.5)	1(2.5)
Jan. 31, 1972	28(71)	40(100)	6(15.5)	15(38)	9(23)

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[1] U.S. ESSA (Environmental Science Services Administration) records. Monthly and annual means are means of daily means.

[2] Weather stations of record. Not strictly representative of entire study area.

[3] Figures without parentheses in inches; with parentheses in cm.

for caribou (*Rangifer tarandus*) because critical depth (20 in or 50 cm) generally occurred late in December if at all, and was halved by April. Therefore, in most winters snow depth is not a serious hindrance to moose, but exceptions have occurred.

Caribou range studies begun in 1954 by Hanson (1958) and amplified by Skoog (1968) provide a general understanding of physiography and vegetation in the Nelchina Basin. Of the 17,500 mi² (45,000 km²) studied by Skoog (1968), only 45 percent (7,910 mi² or 20,490 km²) lies below 3000 ft (915 m) elevation. About 42 percent of the area lies between 3000 and 5000 feet (915 to 1525 m); the balance is above 5000 feet (1525 m). Because the upper limit of suitable moose habitat is usually found at about 3000 feet (915 m) and occasionally reaches 4000 feet (1220 m) (Alaska Department of Fish and Game, 1973), physiography of the Nelchina Basin restricts the potential for seral range.

Skoog (1968) developed an aerial transect sampling system to estimate distribution and quantity of major vegetation types in the Nelchina Basin. In brief, he found that spruce (*Picea* spp.) forest covered 31 percent of the area, dwarf birch (*Betula nana*), dwarf heath (*Cassiope* sp.) and sedge meadow types covered about 36 percent, 18 percent of the area supported essentially no vegetative cover, and the willow type, including *Salix alaxensis, S. barclayi, S. glauca, S. pulchra* and *S. richardsonii* covered 5.4 percent of the area. He noted that willows were found to some extent in various other range types as well. The balance of the area (10%) supported various vegetation types of limited distribution and quantity. Skoog estimated that 38 percent of the spruce type had burned at some time, probably since 1930, and commented that he had found no evidence of fire above timberline.

Although development by people has not been extensive, considerably more human activity has occurred in the Nelchina Basin than on the Tanana Flats. Various early trails and roads traversed the area. The Copper River Valley was a major pre-historic and historic access route to the interior, as was the Susitna River Valley and the Matanuska River (Skoog, 1968). Prospectors ranged widely over the area from the early 1900's through about 1940. For the most part, however, these early activities had little effect on the area.

Various trails subsequently became roads, and major roads now provide access to all quarters of the Basin. Substantial areas are still not accessible by highway vehicles, but increasing availability and use of offroad vehicles has eased access to such areas. Access by light aircraft is reasonably good in several parts of the Nelchina Basin. With increased ease of surface access from Anchorage and Fairbanks and a growing human population, a rapid increase in recreational use of the Nelchina Basin is expected, with a consequent rise in hunting pressure.

MATANUSKA VALLEY

What has come to be known as the Matanuska Valley study area includes the lower portions of the Susitna and Matanuska River Valleys, all of which lie in Warhaftig's (1965) Coastal Trough physiographic province. The lowland area is physiographically fairly uniform, and is primarily a "glaciated lowland containing areas of ground moraine and stagnant ice topography, drumlin fields, eskers, and outwash plains..." (Warhaftig, 1965, p. 65). Elevations in the Valley proper range from sea level on the south to 2000 feet (600 m) in the extreme eastern valley, but most of the

Valley lies between 50 to 600 feet (15 to 180 m) elevation. Foothills adjacent to the Valley on the north and east support important sub-alpine summer and fall habitat to elevations of 3000 to 4000 feet (910 to 1200 m), (Alaska Department of Fish and Game, 1973).

Valley vegetation originally was open, low growing spruce forest with closed spruce-hardwood forest in elevated, better drained areas (Viereck and Little, 1972). Land clearing has altered plant cover substantially in the more level, central portion of the Valley, but in the peripheral areas original vegetative types predominate. Extensive wet bogs similar to those on the Tanana Flats (LeResche *et al.*, 1974) occur in the western portion of the study area. These are important calving areas for moose.

Climatic conditions in the Matanuska Valley are relatively mild compared to the Nelchina Basin and the Tanana Flats (Table I). Snow usually does not persist until November and brief thaws usually associated with high winds may eliminate most of the snow cover during any month of the year. Snow depth comparable to the other study areas seldom persists.

In the earliest stages of white settlement, most of the Matanuska Valley was not inhabited to any great extent. As transportation corridors developed from points south, beginning about 1916, development proceeded rapidly. The mild climate and relatively level, well-drained (though largely infertile) land encouraged homesteading as did the Alaska Railroad, completed in 1922. An immigration of government-sponsored homesteaders from 1935 to 1940 had a massive positive impact on future moose numbers through ensuing extensive land clearing and fires. Much of the cleared land was destined to become seral range in later years. Portions of these lands now support maturing even-aged stands of quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*), with a greatly diminished capacity for moose.

Disposal of relatively small parcels of land to private ownership for recreational sites is becoming the most important land use trend. The proximity of the growing Anchorage population center assures a continued demand for this purpose. With little impetus for land clearing, this development will probably be unfavorable for moose.

Access by road to various parts of the Matanuska Valley is well developed compared to most important Alaska moose ranges. Seral succession of willows along new roads has replaced, to a limited extent, browse lost through succession on older ranges.

KENAI PENINSULA

The Kenai Peninsula consists of two major physiographic sections: (1) the Kenai Mountains, in the eastern portion of the Peninsula, and (2) the foothills and Kenai lowlands, in the west (Warhaftig, 1965). The western portion has been of greatest importance to moose; it includes the Kenai National Moose Range, and has been the scene of continuing moose studies by the Alaska Department of Fish and Game and the U.S. Fish and Wildlife Service since the 1940's. Warhaftig (1965) described the western Kenai Peninsula as part of the Cook Inlet-Susitna lowlands. In general terms it is similar to the Matanuska Valley. The northern portion consists of a broad lowland from which the Kenai Mountains rise rather abruptly. To the south, rolling foothills extend progressively farther west from the mountains and reach the sea at Kachemak Bay near the Peninsula's south end.

Climate on the Kenai Peninsula is moderated by Cook Inlet, but the maritime influence diminishes rapidly with increasing distance from the coast (Table I). Near Kachemak Bay, at Homer, temperatures are much more moderate, precipitation is greater, and snow cover, while it may be as deep or deeper than inland, is usually less persistent than on the northern lowland.

The difference in climate is reflected in patterns of dominant vegetation types. Coastal spruce-hemlock (*Tsuga heterophylla*) and interior white spruce-paper birch forests meet near Homer (Viereck and Little, 1972). Coastal and southern areas are not susceptible to wildfire and stands of spruce tend to dominate except in disturbed areas. The foothills support considerable areas of sub-alpine and alpine communities which are extremely important summer, fall and early winter moose habitat. In contrast, the northern lowlands, where spruce-birch forests are dominant, have sustained numerous fires which have resulted in large quantities of seral range and many moose (Hakala *et al.*, 1971; Spencer and Chatelain, 1953; LeResche *et al.*, 1974).

The western Kenai Peninsula was one of the earliest areas to be settled by Caucasians and has had some degree of settlement since the late 1700's. Causcasians were largely transient except in coastal areas, however. Extensive settlement and road systems did not develop until after World War II. Presently a major road traverses the western Peninsula from east to west and extends south along the coast to Homer. A few secondary roads exist, but most of the area remains inaccessible by road. Light aircraft with pontoons formerly landed in the many lakes of the northern lowlands but are now restricted by regulation. In the south, all-terrain vehicles and horses have been used extensively for hunting and other recreation.

Methods

Several study methods were common to all areas, but for various reasons, additional investigations were done at different times in some of the study areas.

AERIAL SEX AND AGE COMPOSITION SURVEYS

The most important data for evaluating trends in production, survival, sex ratios and relative abundance have resulted from systematic aerial surveys. Several procedures for aerial surveys have been tried, but those described here have proved to be most effective and have been used most consistently since 1960.

Fall surveys were made in specified geographic areas after complete snow cover occurred (October to December), but before most bulls shed antlers (mid-December). In areas of moderate terrain the flight pattern consisted of parallel transects approximately 0.5 mile (0.8 km) apart at an altitude of 300 to 500 feet (90 to 150 m). In rugged terrain, contours of the land were followed, and altitude varied. Transect lines were briefly deviated from when necessary to adequately examine moose. The attempt was made to count and classify all moose as to sex and age (adult bulls, yearling bulls, cows and calves). The attempt to record all moose was primarily a criterion of sampling procedure, since we recognize that many moose will be missed even with excellent survey conditions (LeResche and Rausch, 1973).

Spring surveys were done similarly, but usually in different geographic areas than fall counts due to movements of moose to calving areas. Two variations of spring surveys were used: (1) preparturition surveys from late April to mid-May were used when the main objective was to assess survival of the previous year's calves, because that age group seems more difficult to find and identify at parturition time; (2) parturition surveys from mid-May to mid-June were done when progression of parturition and natality rates were of prime interest (Rausch and Bratlie, 1965). Estimates of over-winter calf survival have been based on the latter surveys in most years, however.

High performance aircraft such as the Piper PA-18 Supercub are used almost exclusively for aerial sex and age composition surveys.

Fall composition surveys have been done annually with few exceptions in the study areas considered here. Spring surveys have been done in most years since 1960 in the Matanuska Valley and Tanana Flats, and in some years on the Kenai Peninsula.

CENSUSES AND POPULATION ESTIMATES

A stratified random square mile census similar to that of Siniff and Skoog (1964), and Evans *et al.* (1966) was used in the Matanuska Valley in 1966 and 1967. This technique also has been used by the U.S. Fish and Wildlife Service on the Kenai National Moose Range in 1965, 1967, 1971, and 1973. The technique has not been used on the Tanana Flats nor in the Nelchina Basin.

Rough population estimates have been made for the various study areas from time to time based on general knowledge of moose numbers, relative abundance reflected by aerial composition survey data, and harvest levels.

HARVEST

Hunters have been required to use a moose harvest report since 1963 (Rausch *et al.*, 1966). Kill data obtained have been used in evaluating impact of hunting on sex and age composition and number of moose.

Age composition of the kill by hunters has been monitored through collection of lower jaws or teeth. Age determination was done by counting cementum layers (Sergeant and Pimlott, 1959), and by eruption and wear patterns (Passmore *et al.*, 1955) in earlier years.

REPRODUCTION

Although the data will be only briefly referred to, large collections of female reproductive tracts have been made in various years when antlerless moose hunting seasons occurred in the Matanuska Valley and Kenai Peninsula. Small numbers of reproductive tracts have been collected from hunters and from accidentally killed moose on the Tanana Flats and adjacent areas. The larger collections have usually been made a sufficient time after the rut to allow assessment of conception rates by macroscopic examination of the reproductive tracts.

TAGGING PROGRAMS

Data from calf tagging programs in the Matanuska Valley and Tanana Flats and adult tagging on the Kenai Peninsula will be referred to only briefly in this paper as they relate to population considerations.

DEFINITION OF TERMS

Two terms used extensively herein are ambiguous unless defined. "Production" is the percentage of calves in the total population in fall. It is the same as Pimlott's (1959) net productivity of calves. "Survival" as used herein means the percentage of yearlings (about 1.5 yr. old) in the total population in fall and corresponds to one definition of net productivity of yearlings cited by Pimlott (1959), but was not his preferred definition. Where we refer to data from spring surveys we qualify our remarks.

"Natality" means the incidence of live births in spring.

The number of yearlings in fall was estimated by doubling the number of yearling bulls seen. Yearling bulls can usually be identified by antler size, but yearling cows cannot be reliably identified. Except where hunting is a factor, mortality for males and females is assumed (but not proven) to be the same through at least 1.5 years of age. Klein (1970) noted that on poor quality range young deer (*Odocoileus virginianus* and *O. hemionus*) suffer differential mortality which favors females. A similar phenomenon may occur among moose, but is undocumented. Where heavy harvests of yearling bulls occur this technique can lead to erroneous conclusions, which will be discussed below.

Results

EARLY POPULATION TRENDS, 1950-1960

We noted that in general, optimal conditions existed for moose population growth in the study areas by the late 1940's. In most of these areas, systematic efforts to assess moose population trends and characteristics did not commence until 1954-1955. Thereafter, field work was intensified, and by the early 1960's characteristics of moose populations considered here were reasonably well documented, although attendant biological implications perhaps were not fully appreciated because little basis for comparisons existed.

Inferences regarding the status of moose populations drew heavily from aerial sex and age composition survey data, supplemented by range evaluations and limited harvest data. A brief review of comments and conclusions from this earlier period is necessary for an appreciation of later events. Where a continuum of data exists from the earlier period to the present, data are tabulated together to facilitate review.

TANANA FLATS

Aerial moose composition surveys were begun on the Tanana Flats in 1956 and continued through 1959 (Olson, 1959). Surveys were not strictly comparable to those performed after 1960, but they are included because the relatively high proportions of calves and yearlings lend support to Olson's contention that moose numbers were increasing during that time.

Most other interior Alaska work during this period was not directly related to the Tanana Flats study area, but a census attempt in March 1956 (Olson, 1956) should be mentioned. The census covered 7,000 mi^2 (18,130 km^2) of the Tanana Valley, including the Tanana Flats study area (about 925 mi^2, or 2,396 km^2). Moose were counted along randomly selected portions of transects. The resulting estimate was 2,240 moose (1,570 to 2,910, $P < .05$), a density of 0.32 moose/mi^2 (.22-.42, $P < .05$), or about 0.12/km^2. This estimate was undoubtedly low, and the causes were most likely application of random sampling to non-random distribution of moose, as Olson (1956) suggested, and overestimation of visibility of moose (LeResche and Rausch, 1974).

NELCHINA BASIN

Moose study efforts were begun in the Nelchina Basin in fall, 1952 (Alaska Game Commission, 1953). As in the Tanana Flats study area, the main emphasis through 1959 was on aerial composition surveys in fall. In 1955 efforts to establish well defined geographic areas where subsequent comparable annual surveys could be made were intensified and emphasis was placed on assessing the nature and importance of sexual segregation to population sampling (Scott, 1956). Much more emphasis was given to interpretation of sex and age ratio data, as well. Survey areas established in the Nelchina Basin and the Matanuska Valley by Scott (1956) have been used since, with additions and refinements. By 1958, most survey areas presently used were established and efforts to better assess hunter harvest and age composition of the kill were begun (Rausch, 1959a).

In 1952, moose numbers in the Nelchina Basin were considered to be increasing (Alaska Game Commission, 1953; Spencer and Chatelain, 1953). Calf production (proportion of calves five to six months old) indicated by count data suggested an increasing population. Some of the productivity data are improbable, however, e.g. 90 calves: 100 cows in 1953, and are probably the result of sampling error (Rausch, 1959a). A relatively high proportion of bulls existed in this early period, but ratios exceeding 80 to 85 bulls: 100 cows are generally the result of biased sampling. We have found that bulls are somewhat less abundant than cows under unhunted conditions where we believe samples were representative.

The consensus that moose numbers were increasing and that sex and age ratios were affected only slightly by hunting in this early period is supported by the composition survey data. Exceptions to this generalization were known to occur in local, more accessible areas, but these were of limited importance.

MATANUSKA VALLEY

Moose population investigations in the Matanuska Valley developed similarly to those of the Nelchina Basin, but commenced in 1949 (Alaska Game Commission, 1950) and were intensified more rapidly (cf. Scott, 1956; Rausch, 1958, 1959b). Early work emphasized winter distribution, winter range conditions, and winter range density estimates. Spencer and Chatelain (1953) indicated browse condition was deteriorating in the lower Susitna-Matanuska Valley and presented winter moose density figures of 5.1 moose/mi^2 for the Lower Susitna Valley, and 11.4 moose/mi^2 (2 and 4.4 moose/km^2 respectively) for the Matanuska Valley wintering areas. Extreme values ranged from 0.14 to 57.5 moose/mi^2. (0.05 to 22.0 moose/km^2).

Later moose study efforts emphasized population identity, seasonal altitudinal movements, differential movement patterns in relation to sex and age, and the relationship of sex and age ratios to harvest patterns (Scott, 1956; Rausch, 1958, 1959a, 1959b). In brief, these studies demonstrated that: (1) there were at least two distinct breeding populations wintering together in the Matanuska Valley; (2) moose along the Susitna River Valley immediately north of the Matanuska Valley were of a distinct population from Matanuska populations; (3) cows, cows with calves and yearlings comprised a higher proportion of moose found in lowland areas, compared to those found in adjacent uplands; (4) trends in bull:cow ratios were sensitive indicators of hunting pressure; and (5) trends in proportions of calves and yearlings found in fall surveys appeared sensitive to factors affecting production (proportion of calves five to six months old), and survival (to 1.5 years of age) (Rausch, 1958; 1959a, 1959b). Associated studies (Rausch, 1959b) showed that 94 percent of adult cows bred successfully. This information was of primary importance in interpreting population data from not only the Matanuska Valley but from other areas as well.

KENAI PENINSULA

Spencer and Chatelain (1953) and

Spencer and Hakala (1964) summarized early work on range, food habits, populations and effects of fire on the Kenai National Moose Range. Fall aerial composition surveys date from 1950, while spring survival and parturition counts were done from 1957 to 1963 and in several years since.

Spencer and Hakala (1964) noted that high moose numbers occurred in 1913, 1916, 1922-23, 1936, 1945, and 1960, and suggested the causes of subsequent declines were overpopulation and severe winters. Their estimates of moose numbers ranged from 2000 in 1950, to nearly 6000 in 1958-59 followed by a slight decline in 1959 to 1961. They concluded that the vast 1947 burn reversed the downward population trend by providing quantities of new seral range.

SYNTHESIS WITH RECENT INVESTIGATIONS (1960-1972)

TANANA FLATS

Analyses of moose population trends in the Tanana Flats have been based almost entirely on aerial composition surveys done in fall and spring (Table II). Moose harvests have been monitored since 1963 through a mandatory harvest report system, but the dispersed nature of hunting has made collection of specimens from the kill inefficient and unfruitful. Analyses of small collections of female reproductive tracts suggest that conception rates among adult cows are similar to those in other areas of the state; i.e. 85 to 95 percent (Rausch, 1959a, 1965).

Data on calves tagged on the Tanana Flats (1966, 1968, 1969, 1970) have provided some indications of seasonal dis-

TABLE II

Indices to moose production and survival, Tanana Flats, Alaska, 1956-1972

Year	*Spring*			*Fall*					
	% Yearlings[a]	*Yearlings: 100 Cows*	*Sample size*	*% Male Yearlings*[a]	*% All Yearlings*[b]	*Calves: 100 Cows*	*% Calves*[a]	*Males: 100 Cows*	*Sample size*
1956				7	14	48	21	84	221
1957				4	8	37	20	44	74
1958				11	22	43	22	53	194
1959				7	14	49	22	70	180
1960				10.6	21.2	47.0	19.8	83.0	1015
1961	14.7	48.7	3129[c]						
1962	8.2	23.3	1903[c]	4.3	8.6	41.5	22.1	43.2	891
1963				5.5	11.0	49.0	22.4	69.0	1041
1964				5.6	11.2	45.3	21.2	67.0	1240
1965	10.3	17.6	1274[c]	5.0	10.0	26.0	16.0	40.0	989
1966	5.3	7.6	816	2.0	4.0	26.0	14.9	42.0	832
1967	4.5	11.0	848	3.8	7.6	25.4	14.4	50.8	528
1968	6.4	15.7	984	5.6	11.2	38.8	20.1	47.1	897
1969	9.8	26.4	447	9.2	18.4	43.5	23.4	41.3	752
1970	18.4	34.3	521	5.4	10.8	32.1	19.8	28.9	500
1971	4.4	5.6	499	0.9	1.8	31.2	18.0	42.2	567
1972	11.0	16.9	611	5.9	11.8	38.2	20.6	46.8	644

[a] Percentages are percentages of age class in the sample.

[b] Percent all yearlings in the fall is obtained by doubling the percentage of yearling males.

[c] Ratios derived from cumulative total of moose obtained on replicate counts.

tribution (Bishop, 1969 and unpublished data). We view the Flats data as indicative of general trends of moose production and survival in this portion of interior Alaska.

Moose numbers on the Flats appear to have experienced a classic population build-up, "crash", and subsequent recovery twice since Olson's (1956) first report that moose numbers were increasing. Aerial composition survey data which are the primary means for assessing these fluctuations are reviewed here.

Olson's (1959) assumption that moose numbers were high in 1959 seems well founded on the basis of his observations, and ours beginning in 1960 (Table II, Fig. 2). Production of calves and survival of yearlings were both high and production of calves continued at a high level through 1964. We believe the population was at least maintaining about the same level during this period, but growth may well have ceased, because the proportion of yearlings in fall dropped.

In fall 1965 it was clear that calf production had dropped considerably (Table II), and virtually no twins were seen. Moose were still very abundant, and large aggregations were common on certain seral ranges (unpublished survey data). Snow depth the previous winter was minimal (Table III). It seems most likely that moose numbers had exceeded a critical balance with food supply, and reproduction was adversely affected.

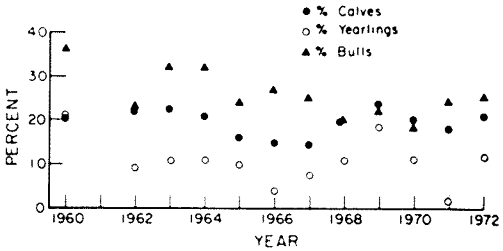

Figure 2. Moose population indices, Tanana Flats, Alaska, 1960-1972.

TABLE III

Snow depth and total snowfall, Fairbanks, Alaska, 1955-1972. From ESSA records

Date	*Dec.*			*Jan.*			*Feb.*			*Mar.*			*April*			*Total snowfall (in)*
	1	10	20	1	10	20	1	10	20	1	10	20	1	10	20	
1971-72	8	8	25	25	23	21	29	28	24	23	24	25	24	23	21	—
1970-71	37	24	35	34	36	36	35	38	37	41	42	37	36	32	17	145.7[1]
1969-70				5	5	5	10	9	1	10	8	8	3	1	T	—
1968-69	7	7	24	19	21	21	22	21	20	19	19	19	22	15	T	—
1967-68	8	10	17	17	18	17	31	27	25	24	21	20	19	18	18	72.2
1966-67	28	23	19	17	17	17	22	23	23	22	25	24	37	25	23	102.7[2]
1965-66	14	13	14	35	31	26	19	20	45	36	34	32	22	12	7	123.9[1]
1964-65	13	18	17	23	22	16	15	14	16	17	10	9	3	T	0	55.3
1963-64	4	9	9	8	9	7	10	9	10	15	16	15	13	9	6	56.7
1962-63	2	4	5	6	6	10	17	14	14	14	19	18	30	25	29	70.3
1961-62	13	16	18	17	19	20	22	31	35	29	31	25	17	15	14	97.8
1960-61	12	7	7	8	15	11	7	14	14	13	12	11	10	6	6	41.0
1959-60	10	12	13	20	33	29	27	21	16	17	12	12	7	6	6	69.8
1958-59	10	9	9	17	21	19	18	34	36	35	28	24	17	14	10	61.0
1957-58	4	5	6	5	8	10	12	14	14	13	10	8	5	3	T	38.9
1956-57	9	11	12	12	21	29	24	31	31	27	21	16	11	8	4	64.4
1955-56	8	8	18	28	27	22	25	27	31	38	35	28	22	21	10	84.0

[1] Years of known high moose winter mortality.

[2] Year of known moderate moose mortality.

These circumstances were followed by two successive years of severe snow conditions; 1965-66, and 1966-67. Reduced proportions of calves and yearlings were reflected in both fall and spring 1966 survey data. Direct evidence of mortality in spring, 1966, consisted of 23 adult and yearling carcasses attributed to winter mortality, and seven calves, which were either stillborn or died soon after birth. One sick calf was recovered but died soon after capture of pneumonia and anemia. Observations of stillborn calves was unprecedented during intensive calf tagging efforts done for five years in the Matanuska-Susitna Valley (Bishop, 1970).

As much as 50 percent of the Tanana Flats and adjacent moose populations may have died in winter, 1965-66.

The following winter (1966-67) was less severe, but snow depths of 24 to 37 in (60-93 cm) (Table III) persisted from mid-March to mid-April, a period of greatly increased energy demands for pregnant cows (Gasaway and Coady, 1974). Survival to the fall yearling stage improved, but calf production did not.

Improved production and survival became evident in 1968 and continued through 1969. By fall 1969 calves represented about 23 percent of the population, a level comparable to that observed in the late 1950's and early 1960's when the population was approaching or perhaps had reached its peak. Survival to yearling age followed a similar pattern.

Based on spring data, 1970 promised to be an excellent year. However, a record snowfall occurred in winter, 1970-71. Snow depth approached 40 in. (100 cm) inches by December 10 when aerial surveys on the Flats were completed; the first dead calf was reported at the end of November and a dead adult was seen December 10 (M. Buchholtz, unpublished data).

Data from fall, 1970, on calf production, yearling survival, and bull:cow ratios do not fit the anticipated trend (Table II). Aside from very difficult working conditions (temperatures were already reaching −40°F during the time of surveys) there are two possible explanations for observed declines in production and survival: 1) mortality, especially among calves was already occurring — the early death of a calf suggests this, as does the one dead adult and the high number of natural and accidental deaths reported in December; 2) moose distribution was probably substantially altered by the rapid, early increase in snow depths. Moose movements to riparian and prime seral range normally occur later in winter as snow depths increase (Rausch, 1958; Coady, 1974).

The reduced proportion of bulls observed may be related to distribution changes and to antler loss in December when a substantial part of the counts were done. There is no good estimate of winter mortality in 1970-71, but we suspect it again approached 50 percent of the population.

By the fall of 1971, yearlings were virtually non-existent. That the proportion of calves remained as high as it did (18 percent) is surprising, but suggests that a substantial proportion of cows surviving the winter were pregnant and that losses in other age groups, especially yearlings, were severe.

Calf production and yearling survival improved again in 1971-72. Fall 1972 indices indicate calf production was about 20 percent, but the proportion of yearlings remained low. It is unlikely that the adult population will have increased by fall 1973, but with this winter's relatively mild conditions a substantial increase in calf survival rates is expected.

Aerial composition survey data from the Tanana Flats seem to portray the classic situation of population increase and abrupt decline in response to a climatic crisis. However, other factors obviously affect moose numbers and related data, and their role must be considered.

Variability in survey data

Aerial surveys have several potentially serious shortcomings as a sampling technique, including variations in the skill of observer and pilot, weather, lighting, snow conditions, activity of moose, visibility of moose and differential movements of sex and age classes at various times of the year (LeResche and Rausch, 1974; Bergerud and Manuel, 1969; Rausch, 1959a; LeResche and Davis, 1971). By standardizing sample areas, seasonal timing of surveys, survey patterns and experience level of personnel, year-to-year variations can be reduced, but not eliminated.

Inconsistencies such as wide variations in bull: cow ratios occur, perhaps in response to differences in weather conditions or survey techniques. Other indices therefore may be suspect. However, other data usually support aerial survey data. For example, a comparison of 1970 and 1971 survey data indicates a pronounced decline in the proportion of yearlings in 1971. Data compiled by John Coady on moose mortality near Fairbanks, in the winter of 1970-71, show that about 63 percent of moose which definitely died of malnutrition were calves, and 27 percent of those that died from accidents, etc. were calves (Fig. 3). Because moose used roads, trails, and yards when snow became very deep, many moose that eventually would have starved undoubtedly died from accidents or removal. Of 163 observed moose mortalities in the winter of 1970-71, 73 (45 percent) were calves. These data support the 1971 fall aerial survey data wherein yearlings are virtually absent.

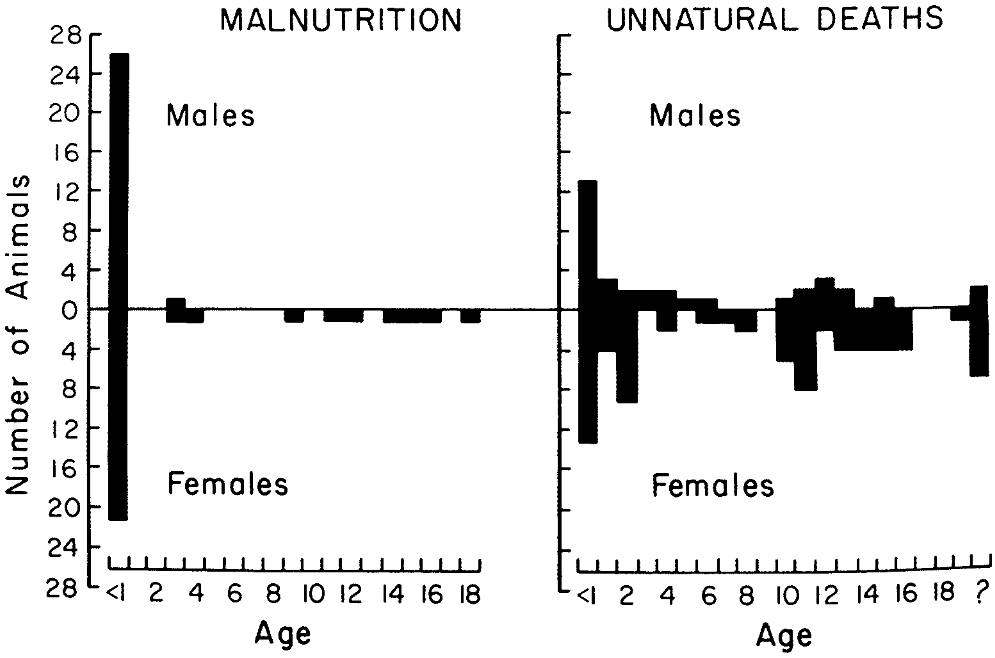

Figure 3. Age-specific sex ratios of moose winter mortality 1970-1971, Fairbanks, Alaska.

Hunter harvest

Although harvests from Game Management Unit 20A (the administrative area immediately south of the city of Fairbanks which includes the Tanana Flats) increased from 206 in 1963 to 350 in 1972, the number of moose taken from the Flats regularly ranged from 90 to 150 annually (Bishop, 1970; Buchholtz, 1973). The increased harvest draws on the Tanana Flats population to some extent because some moose move from the Flats to the adjacent foothills in late summer and fall (Bishop, 1969 and unpublished data).

Moose numbers in Management Unit 20A may have dropped to 3000 to 4000 following the "crash" of 1965-66 (Alaska Department of Fish and Game, 1973) but a review of 1966 survey data suggests 5000 to 6000 survived. Population growth was not rapid until 1969, and the following year another severe decline occurred.

If the proportion of yearlings seldom exceeds 15 percent in relatively "stable" populations as past data suggest (Rausch and Bishop, 1968), then it appears likely that proportions of up to 10 percent yearlings may be no more than maintenance level annual increments, except in areas where mortality factors such as deep snow or predation are of minimal importance.

Thus, moose numbers of the Tanana Flats and adjacent areas probably increased little over the period 1965-66 to 1973. If an estimate of 4000 for Game Management Unit 20A is correct, the 1972 harvest approached the annual increment (the number of yearlings entering the breeding population). Assuming the population to be as high as 6000, hunting would claim about 60 percent of the annual increment under present conditions.

It is likely that the situation on the Tanana Flats is analagous to that in the larger area; if no more than 33 percent of moose present were observed during composition surveys in 1971, the population would have been (3)547 + hunter kill of about 120 = 1761, and the harvest would have equalled about seven percent of the population. If 50 percent of moose present were seen, the kill would have equalled about 10 percent of the population, essentially the annual increment. Hunter harvest appears to be a potentially significant factor in growth of this population but it is unlikely to have contributed to major declines, nor has it produced a precipitous decline in the proportion of bulls.

Yearling recruitment may be somewhat greater than our data indicate. Estimation of yearlings in fall tends to be conservative, because it relies on recognizing yearling bulls by their antler development. Yearling antler development ranges from "spikes" to well developed small palms. Spikes can be overlooked under poor counting conditions, and well developed palms may cause the observer to call the animal an adult (2 years old or more). The latter error may be compensated to some extent by 2.5-year-old moose with underdeveloped antlers.

Predation

The impact of wolves (*Canis lupus*) on the Tanana Flats moose is unknown. Predator control activities occurred in the general area from the late 1940's through 1959-60, and aerial wolf hunting occurred there regularly until 1972-73, but numbers killed on the Tanana Flats and adjacent areas are difficult to determine. However, wolves persisted. During the 1960's several active wolf dens existed on the Flats for various periods. In general, wolf numbers in central Alaska were increasing during the early 1960's, the same period when moose numbers seemed to have peaked, and in 1971-72. Reduction of wolves from the combined efforts of predator control and aerial hunters during the 1950's may have materially aided moose increase in the late 1950's and early 1960's.

Habitat

Coady (LeResche *et al.*, 1974) studied moose habitat on the Tanana Flats. He noted that in general the Flats are good summer habitat, but are of only moderate value as winter range. Tall shrub communities, which are of most value to moose in winter, occur on about 10 percent of the Flats. Substantial quantities of willows are decadent. Browse species occur in several other types as well, but winter range is quite limited. During years of high moose numbers the quantity of browse is probably marginally sufficient.

Snow depth and duration

We have implicated deep snow in poor survival of moose, but it should be emphasized that depth and duration must be considered. Coady (unpublished data) graphically represented winter severity at Fairbanks in terms of snow depth and duration. Official records on snow depth on the last day of each month were plotted, and the area under the curve (Fig. 4) was measured using a planimeter. The numbers derived (Fig. 4, Table IV) are relative. Winters of heavy moose mortality (1965-66, 1970-71) are immediately apparent, even though depths recorded at the weather station tend to be conservative (Coady, pers. comm.) Duration of considerable snow depth in 1966-67 was relatively brief, but our earlier comment that timing (March-April) with respect to energy demand was critical becomes apparent in Figure 4.

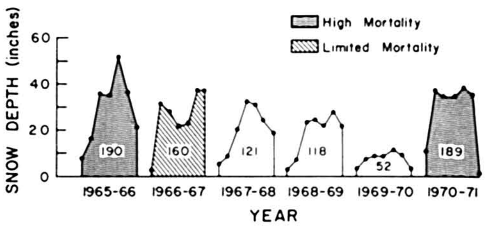

Figure 4. Winter severity as reflected by snow depth and duration. The figures enclosed represent arbitrary units of winter severity obtained by integrating the area under the curve.

Coady (unpublished data) also reviewed snow severity for various periods since 1950 and found that average snow severity based on depth and duration was greatest for the period 1966-1972 (Table IV) when two major moose declines occurred and lowest during 1952 to 1958, when moose were increasing.

TABLE IV

Average relative snow severity for various periods based on depth and duration of snow cover, Fairbanks, Alaska. Compiled from ESSA records by John Coady

Year ending	*Snow severity*
1950-1972	113.2
1950-1960	110.3
1952-1958	96.1
1959-1965	101.1
1961-1972	115.9
1966-1972	132.3

Migration and population mixing

Moose are attracted to the Tanana Flats in spring from a broad but poorly defined area. The Flats are a prime calving and early summer feeding area (Bishop, 1969; LeResche *et al.*, 1974). Moose tagged as calves on the Flats have been observed at various later dates as far as 30 to 50 (50 to 80 km) miles both northeast and south of the Flats, but most observations and recoveries of tagged moose occurred on the Flats, where surveillance has been most consistent (Rausch, 1971). However, surveillance has been sufficient in the Alaska Range south of the Flats to suggest that the majority of cows with tagged calves are found on the Flats (or perhaps return there) through early winter. Bull movements seem to resemble those described by LeResche and Davis (1971) on the Kenai Peninsula, where some remain in lowlands while others leave the lowlands earlier than cows and return later. Variations in such movements of bulls probably account for the occasional unexpected proportions of bulls seen on the Flats.

We believe trends in production and survival observed on the Tanana Flats are valid for the central Tanana Valley because (a) there is probably good consistency in population identify on the Flats from year to year, and (b) to a considerable extent winter conditions affecting moose observed on the Tanana Flats affect adjacent moose populations similarly, particularly in severe winters when most moose concentrate in a relatively small area with rather similar habitat and snow conditions.

In summary, following a period of increase, a substantial decline in moose numbers on the Tanana Flats was precipitated by extreme snow severity in 1965-66. Production and survival subsequently rose progressively through 1969. In 1970-71 declines in production, survival and numbers of moose again occurred in response to high snow severity. Production and survival rose again in 1972, more sharply than before.

Although prolonged, deep snow cover precipitated these declines, it seems clear that moose densities and food supply in combination with snow severity determined the magnitude of these declines, and other variables such as hunting and predation were of limited importance on the Tanana Flats.

NELCHINA BASIN

We noted earlier that the Nelchina Basin is of great size and diversity. To discuss trends in moose population characteristics for the entire Basin as a unit can be misleading, but because population trends are similar troughout most of the area we feel it is justified.

We also noted that moose numbers in the Nelchina Basin were considered to be increasing during the late 1940's and early 1950's (Spencer and Chatelain, 1953). Subsequent aerial composition survey data confirmed this impression (Scott, 1956; Rausch, 1959), although the severe winter of 1955-56 reduced production and survival (Rausch, 1958; and Table V).

Moose probably reached maximum numbers about 1960 (Rausch, 1967). Production of calves and survival as measured by fall composition surveys were consistently good up to 1961 (Table V, Fig. 5), with the exception of 1956.

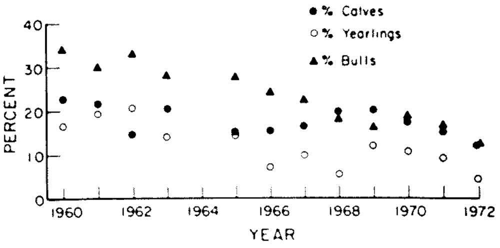

Figure 5. Moose population indices, Nelchina Basin, Alaska, 1960-1972.

The winter of 1961-62 proved to be quite severe in terms of snow depth (Table VI) and moose mortality was known to be extensive (Rausch, 1969). Fall composition surveys in 1962 reflected the decline in calf production, but survival to yearling age remained surprisingly high.

Small gains in production and survival have been made in some years since 1961-62, but the general trend in both indicates has been downward for the

TABLE V

Indices to moose production and survival, Nelchina Basin, Alaska, 1952-1972

Date	*Total ♂♂ per 100 ♀♀*	*% Male yearlings*[a]	*% All Yearlings*[b]	*Calves per 100 ♀♀*	*Calf % in herd*	*Total sample*
1952	60.9	6.7	13.4	40.0	19.9	683
1953	107.4	12.4	24.8	89.8	28.8	1100
1954	109.0	9.9	19.8	78.7	27.3	1700
1955	92.0	11.6	23.2	54.4	22.0	2200
1956	63.6	6.6	13.2	26.3	13.8	1099
1957	69.3	7.7	15.4	41.6	19.7	2295
1958	66.2	5.5	11.0	37.6	18.5	3490
1959[c]						
1960	84.1	8.3	16.6	56.1	22.7	1367
1961	63.5	9.7	19.4	45.9	21.9	2977
1962	64.0	10.5	21.0	28.1	14.6	2357
1963	54.5	7.0	14.0	40.1	20.6	2061
1964[d]						
1965	46.3	7.2	14.4	26.5	15.3	5933
1966	40.5	3.8	7.6	26.6	15.9	4534
1967	37.7	5.1	10.2	27.7	16.7	5338
1968	29.9	2.9	5.8	32.8	20.2	3042
1969	26.7	6.3	12.6	32.7	20.4	4098
1970	30.0	5.7	11.4	29.6	18.0	4549
1971	24.5	4.9	9.8	23.4	15.8	5256
1972	17.6	2.7	5.4	17.7	13.0	3994

[a] Percentages are percentages of age class in sample.
[b] Percent all yearlings in fall is obtained by doubling the percentage of yearling males.
[c] No data.
[d] Late count, sex composition not usable.

TABLE VI

Snow depths in years of high moose mortality and in contrasting years, Nelchina Basin[a], Alaska

Year	*Snow depth (in) on selected dates*															*Mortality*
	Dec.			*Jan.*			*Feb.*			*Mar.*			*Apr.*			
	1	10	20	1	10	20	1	10	20	1	10	20	1	10	20	
1971-72	19	24	23	34	36	38	40	42	39	38	38	54	45	45	42	High
1970-71	11	9	9	11	8	8	9	7	9	9	8	7	5	3	2	
1966-67	13	13	13	16	25	25	25	30	34	35	27	10	9	3	1	
1965-66	26	26	28	28	28	31	31	31	33	34	34	36	26	19	8	Moderate
1964-65				13	13	21	21	21	28	32	14	11	T	T	T[b]	
1961-62	7	9	14	18	26	30	35	35	34	32	32	36	31	7	4	High

[a] Snow depths measured at Gulkana. Not strictly representative of the entire Basin.
[b] Trace.

Nelchina Basin as a whole. A surprising corollary is a similar general trend in the proportion of bulls (Table V).

Another somewhat severe winter occurred in 1965-66, but its effects are poorly known. However, the drop in proportion of yearlings in fall, 1966 suggests substantial mortality within that cohort.

Finally, the winter of 1971-72 produced a record snowfall in the Nelchina Basin, and moose calves began dying in December 1971 (Johnson, 1973). Production and survival indices reached a new low in fall, 1972 (Table III, Fig. 5).

From this brief summary, some parallels between population fluctuations on the Tanana Flats and in the Nelchina Basin are apparent. Moose numbers in both areas apparently increased and peaked, or stabilized, in the early 1960's. Major declines occurred in different years but in close chronological proximity and apparently in response to critical changes in the same factor — snow severity.

Subsequently levels of production and survival were similar but it appears that the Nelchina populations did not respond to improved conditions for production and survival as did the Tanana Flats moose. Additionally, the proportion of bulls declined steadily in the Nelchina Basin, but remained relatively constant on the Tanana Flats.

The same factors potentially affect moose numbers and survey data in the Nelchina Basin as in the Tanana Flats, but there appear to be differences in their impact.

Variability in survey data

Little can be added to the discussion of this factor presented earlier. One important point that will be discussed under harvest is that the high proportion of yearling males in the hunter harvest creates an underestimate of survival to the yearling stage, because in most years the bulk of the harvest occurs before aerial surveys are done.

Hunter harvest

The number of bulls killed by hunters has declined very gradually since 1963 (Table VII). Harvest of cows has fluctuated in response to regulatory changes.

Age composition of the bull harvest has changed dramatically since 1966 (Fig. 6). In 1966 yearlings comprised about 15 percent of jaws collected from hunters, whereas in 1971 this proportion rose to 32.5 per cent. If these samples are representative of the entire kill, about 200 yearling bulls were taken in 1966 compared to 366 in 1971.

The proportion of bulls observed on aerial surveys in the Nelchina Basin has declined rapidly since 1962, while the bull harvest has declined very slowly. Through increased use of off-road vehicles and aircraft, hunters have become more efficient in reaching many areas where formerly hunting effort was light (unpublished data, Alaska Department of Fish and Game). Thus, it appears that through increased hunting efficiency, the harvest has remained almost constant during a period when survey data indicate a decrease in moose numbers.

The percentage of yearling males observed on fall aerial surveys is doubled to provide an estimate of percentage of all yearlings, on the assumption that mortality rates are similar for males and females during their first 1.5 to 2 years of life. Thus, if yearling male harvests are great, estimates of yearlings from survey data will be lowered. Unfortunately, spring aerial surveys have not been done in the Nelchina Basin to

TABLE VII

Moose harvests in the Nelchina Basin[a] 1963 to 1971

Year	Season	Male	Female	Unknown	Total	Hunters	Percent success
1963	Total	1385	343	7	1735		
1964	Total	1213	394	0	1607		
1965	Total	1318	3	10	1331		
1966	Total	1336	181	36	1553	4163	27
1967	1st	1009	319				
	2nd	112	0				
	Total	1217[b]	319	16	1552	4027	39
1968	1st	1013	243				
	2nd	171	0				
	Total	1240[b]	243	29	1512	4476	34
1969	1st	817	0				
	2nd	87	7	8			
	Total	1204[b]	7	8	1219	3381	36
1970	1st	746	56	14			
	2nd	271	58	8			
	Total	1141[bd]	158[c]	30[b]	1329	3585	37.6
1971	1st	703	333				
	2nd	205	338				
	Total	1126[b]	671[e]	18	1815	4881	36

[a] Game Management Unit 13.

[b] Date unknown kills are included.

[c] 220 antlerless moose were known killed.

[d] Adult, antlerless bulls killed during late antlerless season included.

[e] Data from antlerless permit returns.

provide comparative data on yearlings prior to hunting season.

Production in the Nelchina, while good in a few areas, has been poor overall since 1962, even following normal winters. Hunter harvest of calves has increased somewhat, but not enough to account for lowered production (Fig. 6). In addition to severe snow conditions, two factors may be related to poor production and survival: predation, and food supply, or habitat.

Predation

Rausch (1969) documented wolf control activities and studies conducted in the Nelchina Basin from 1948 to 1969. Wolf numbers increased from 12 in 1953 to about 400 to 450 in 1965, and declined to an estimated 300 in 1967. Because trapping and hunting have increased in recent years it is unlikely the wolf population now exceeds 300. The maximum numbers of wolves seen by aerial observation in 1971-72 was 176 (Stephenson and Johnson, 1973).

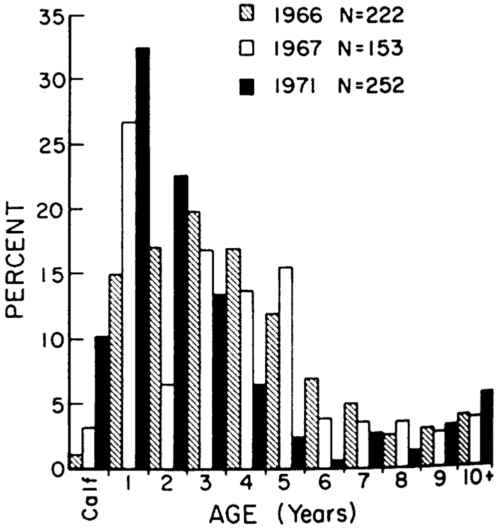

Figure 6. Age distribution of male moose harvest, Nelchina Basin, Alaska, in 1966, 1967, and 1971.

The inverse relationship of wolf numbers with moose production and survival in the 1950's and early 1960's, the present low production of moose concomitant with at least a moderate wolf population, and the high incidence of moose as prey (Stephenson and Johnson, 1972; Rausch, 1969) suggest wolves may presently have a significant impact on moose production and survival.

The effects of combined predation by man and wolf probably have had the capacity to preclude moose population growth in the Nelchina after hard winters reduced the numbers of moose, and may contribute to further declines of moose.

Habitat

The quantity and quality of range in the Nelchina Basin is poorly known. We noted earlier that much of the Nelchina Basin lies at timberline or above; therefore seral range quantity is definitely limited. Beyond that, few fires have succeeded in burning an appreciable area in the last 20 to 25 years (Johnson, 1973). A high snowshoe hare (*Lepus americanus*) population in 1964 caused considerable browse mortality in portions of the Nelchina Basin (Alaska Department of Fish and Game, 1973); Rausch (1969) notes that some ranges were heavily used by moose through the early 1960's, with up to 50 percent dead stems occurring in some stands. However, it is unlikely that food limitations, except through interaction with severe snow conditions, would precipitate a "crash" or sustain a decline in the Nelchina Basin.

Snow depth and duration

Snow severity can be a critical mortality factor in the Nelchina Basin as it is on the Tanana Flats. Although annual snow depths are generally less than those on the Flats, during the period considered in this study, frequency, severity and chronology of severe snow years in the Nelchina closely paralleled those of the Tanana Flats, with similar results among moose.

Perhaps the most significant consideration with respect to Nelchina Basin moose is that, with present use levels by man and predators, it is unlikely that moose numbers can recover to former levels. Rausch (1969) estimated there were 25,000 to 30,000 moose in the Nelchina Basin in 1965. If this number dropped 30 to 50 percent since then as a result of minimal production, harvest and predation and the severe winter of 1971-72, the current annual harvest level plus predation and other natural mortality could exceed a 10 to 15 percent annual increment and further depress moose numbers. Regulatory measures are already being taken to reduce harvests.

MATANUSKA VALLEY

High moose numbers in the Matanuska and lower Susitna Valleys in the early 1950's prompted Chatelain (1951, 1953) to strongly recommend more liberal hunting seasons as a means of preventing severe range overuse. By 1955 it was clear from aerial surveys that the proportion of male moose in the population was very low, and that if substantial numbers of moose were to be harvested, they would have to be females. However, cows were protected by Federal law until 1959 (Rausch *et al.*, 1974).

Aerial survey data for the Matanuska Valley moose show rather consistent patterns for several population indices, in contrast to the situations in the Nelchina Basin and Tanana Flats (Table VIII, Fig. 7).

The proportion of bulls has been depressed at least since the early 1950's

TABLE VIII

Indices to moose production and survival, Matanuska Valley, Alaska, 1955-1972

Date	Total ♂♂ per 100 ♀♀	% yearling males [a]	% All Yearlings [b]	Calves per 100 ♀♀	Calf % in herd	Total sample
1955	9.2	2.7	5.4	40.6	27.1	1450
1956	9.9	2.6	5.2	53.2	32.6	460
1957	7.6	3.0	6.0	50.0	31.7	662
1958	6.2	1.9	3.8	47.1	30.7	1338
1959	6.4	1.6	3.2	47.9	31.0	793
1960	12.8	8.0	16.0	26.0	18.5	373
1961	5.8	2.2	4.4	44.4	29.6	363
1962	4.1	1.8	3.6	44.7	30.1	326
1963	*No Survey*					
1964	9.1	4.0	8.0	47.2	29.3	1156
1965	20.2	8.0	16.0	51.3	29.7	1084
1966	13.4	7.0	14.0	47.1	29.3	744
1967	14.5	6.6	13.2	51.9	31.0	1420
1968	17.0	4.6	9.2	53.0	31.0	1179
1969	*No Survey*					
1970	9.0	3.6	7.2	42.2	27.7	1154
1971	10.2	4.8	9.6	42.4	27.6	1329
1972	8.0	3.9	7.8	31.4	22.3	772

[a] Percentages are of age classes in the sample.

[b] Percentage all yearlings in fall is obtained by doubling percentage yearling males.

by intensive hunting. Although proportions of bulls have varied from 4 to 20 per 100 cows, pregnancy rates for adult cows have consistently been about 90 percent (Rausch and Bratlie, 1965; Rausch, 1967).

The very low proportion of bulls found in 1962 prompted elimination of the August-September hunting season in 1964 and 1965, which produced the desired increase in bulls. Proportions of bulls remained relatively constant from 1966 to 1968 and possibly 1969. A downward trend appears in progress now.

Variations in the proportion of yearlings as shown in Figure 7 parallel those of bulls, in large measure because the high harvest of bulls strongly affects the calculated proportion of yearlings (Rausch and Bishop, 1968; Didrickson, 1973). Spring surveys (Table IX) indicate that the true proportion of yearlings is about 25 percent. Yearling mortality between spring and fall is probably minimal, therefore the data represented in Figure 7 may underestimate the pre-hunting proportion of yearlings by 50 percent or more.

Throughout the period reviewed calf production has remained remarkably consistent in spite of marked changes in bull: cow ratios and relatively severe winters in 1954-55, 1961-62, 1965-66 and

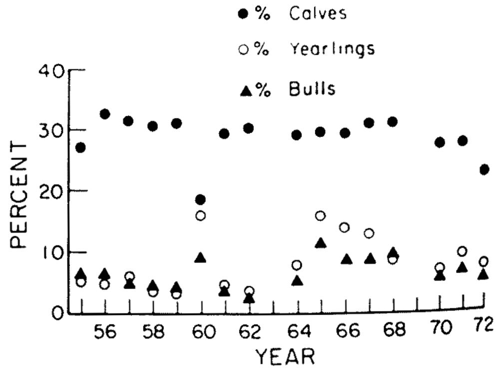

Figure 7. Moose population indices, Matanuska Valley, Alaska, 1955-1972.

1970-71. Survival as measured in spring has also been consistently good.

The recent decline in calf production, however, is probably symptomatic of a change in trend, and will be discussed below.

TABLE IX

Proportion of yearlings in the Matanuska Valley moose population in May and June, from aerial survey data

Year	% *Yearlings*	*Sample size*
1961	25	717*
1962	24	1099*
1965	18	212
1966	26	245*
1968	24	244

* Percent yearlings computed from cumulative totals of repeated counts.

Variability in data

The major potential source of error in Matanuska Valley survey data is in assessing survival on the basis of yearling bulls observed in late fall, as discussed above. A second potential problem is that Matanuska Valley moose exhibit seasonal migrations similar to those described for the Kenai Peninsula (Rausch, 1958; LeResche and Davis, 1971; LeResche, 1972). Early fall surveys may produce a further bias against bulls, which tend to be more abundant in upland areas. Because adequate surveys depend on snow cover and increasing snow cover stimulates movement to the Valley (Rausch, 1959), errors related to population identity and to differential movements of bulls and cows are probably small. Fall surveys have been very consistent with regard to area covered and personnel, and reasonably consistent with regard to timing.

Hunter harvest

Within the limits of range capacity, hunter harvest is the most important factor regulating sex and age composition of moose in the Matanuska Valley, and potentially, numbers as well.

Prior to 1960, when only bulls could be killed, harvests were estimated at 275 to 300 annually (Rausch, 1967), and were sufficient to maintain low proportions of bulls but did not affect production (Table VII, Fig. 7). With elimination of the early bull season in 1964 and 1965, the proportion of bulls increased greatly. Resumption of the August-September season resulted in another decline in the proportion of bulls. Unfortunately, the early bull season is a tradition preferred by the public and sought by them in regulatory deliberations even though biologically a late October – November season would insure that the maximum number of bulls would be available for breeding.

We pointed out earlier that succession on seral range and change in land development patterns continue to reduce available winter range in the Matanuska Valley. Bratlie (1968) suggested that had not moose numbers been reduced by implementing antlerless moose seasons in 1960, production and survival would have deteriorated rapidly in response to these encroaching range problems.

The large kill of cows in 1962 (Table X) resulted from public demand for a reduction of local Valley moose populations which were causing damage to farms and gardens. The effort was successful. By 1965, substantial numbers of cows had been taken and in that year, heavy, early snow precipitated an influx of moose to the Valley floor. The result was a hunting kill of about 1000 moose on one day, and about 1200 for the entire season. A census similar to that of Evans *et al.* (1966) conducted in February 1966 indicated a moose population of 2,953 ± 466 (p. 10) in an area of 407 mi^2 (1054 km^2).

TABLE X

Moose harvests in the Matanuska Valley, Alaska, 1960-1972

Year	Harvest	
	Male	*Female*
1960	300*	300
1961	300*	300
1962	350*	1000
1963	350	300
1964	250	275
1965	580	660
1966	200	75
1967	159	0
1968	366	0
1969	343	120
1970	269	0
1971	431	378

* Estimated.

Subsequent antlerless moose harvests were reduced or eliminated in response to public opinion. The harvest of bulls resumed its previous pattern, but with a shortened season which reduced the harvest in 1966 and 1967.

The Matanuska Valley population was considered growing through 1970 and 1971, although production had declined slightly. In 1972 the number of moose observed on composition surveys dropped drastically. Predators are relatively scarce in the Matanuska Valley. While snow severity is generally low, severe winters in 1961-62, 1965-66 and 1970-71 affected much of the Matanuska Valley, and probably contributed to reduced populations. However, successional change on large areas of important browse species, the legal kill and the combined mortality due to accidents and illegal hunting may well be most important as determinants of this population's long-term welfare.

Reasons for the current decline in production are not clear. It may be that the relationship between moose numbers and food supply has deteriorated to the point that production has been adversely affected.

Production may also have suffered as a result of increasing bull harvests in recent years. Excessive bull harvests may depress production either by reducing conception rates or by prolonging the conception period of the population, which could result in late-born calves less able to contend with rigors of the following winter. Conception rates of moose in the Matanuska Valley and elsewhere in Alaska do not seem to have suffered from reduced bull:cow ratios, but a wide range of fetus size was found on the northern Kenai Peninsula (Unit 15A) in 1965, where bull: cow ratios were generally low, and may have been extremely low in local areas (Rausch, 1967). The proportion of bulls in the Matanuska Valley population is presently very low, and production has declined. It is possible that the low bull: cow ratio may be a significant contributing factor to low production, particularly if moose rutting populations are as traditional as recent evidence indicates (LeResche, 1972).

KENAI PENINSULA

Spencer and Hakala (1964) concluded that moose numbers on the Kenai National Moose Range (the northern two thirds of the Kenai Peninsula) reached a peak in 1960, but from later censuses and aerial composition survey data it appears the populations continued to grow, or at least were stable, through 1971 (Table XI).

As with the other study areas we have discussed, the presence of more than one population complicates consideration of trends among Kenai moose. LeResche (1972) identified four populations on the northern Kenai Peninsula, outlined their movements and suggested the presence of several others that mixed to some degree on lowland wintering grounds.

Because these population elements are all affected to some degree by in-

TABLE XI

Moose population estimates, Kenai National Moose Range, Alaska,* 1965-1971

Year	*Estimate and confidence interval* (P. 10)	*Moose/mi²* (*Moose/km²*)
1965	7432 ± 1560	3.8 (9.8)
1966	7152 ± 1262	3.7 (9.6)
1967	6732 ± 1413	3.5 (9.1)
1971	7904 ± 1461	4.1 (10.6)
1973	5692 ± 1348	2.9 (7.5)

* Data from U.S. Bureau of Sport Fisheries and Wildlife, Kenai National Moose Range. Population estimation method follows Evans *et al.* (1966). Moose wintering areas censused are mainly in Game Management Unit 15A, but include portions of Unit 15B.

teractions of moose densities, quality of winter habitat and winter weather conditions, we will discuss their fate in general as portrayed by fall aerial composition survey data and other information from the northern Kenai. Most of the area lies in Game Management Unit 15A, but much of the discussion applies to Game Management Unit 15B, the adjacent administrative area to the south.

The southern Kenai (GMU 15C) is a very different situation involving different moose populations which we will briefly discuss later.

Aerial composition surveys have been conducted on the Kenai National Moose Range since 1950 (Table XII). We will not discuss data from the 1950's except to note that for the northern Kenai in general the proportion of bulls has shown a steady decline; production and survival dropped in the mid-fifties but rose again in the early 1960's at the time Spencer and Hakala (1964) suggested the population had peaked.

Increasing browse production in the 1947 burn (LeResche *et al.*, 1974; Spencer and Hakala, 1964) and moderate winters were the major factors contributing to the rising moose numbers noted by 1960. Increasing harvests continued to reduce bulls (Alaska Department of Fish and Game, unpublished data), an increased proportion of cows resulted, which in turn promoted greater production.

TABLE XII

Indices to moose production and survival, Kenai National Moose Range, Alaska, 1950-1964. Fall aerial survey data from Kenai National Moose Range headquarters

Year	*Total* ♂♂ *per 100* ♀♀	% *males*	% *Yearling males*[a]	% *all yearlings*[b]	*Calves per 100* ♀♀	% *calf in herd*	*Total*
1950						6.6	1158
1951	69.0		7.0	14.0	23.0	12.0	1513
1952	50.0		10.0	20.0	21.0	12.0	1136
1953	62.0		4.0	8.0	26.0	14.0	2901
1954	84.0		6.0	12.0	27.0	12.0	2048
1955	50.0		4.0	8.0	19.0	13.0	3109
1956	51.0		4.0	8.0	24.0	14.0	3777
1957	43.0		4.0	8.0	35.0	20.0	3155
1958	44.0		5.0	10.0	42.0	23.0	3373
1959	40.0		6.0	12.0	39.0	21.0	4736
1960	34.0		4.6	9.2	49.1	26.0	3482
1961	36.5		4.6	11.4	34.6	20.0	2314
1962	29.8		4.0	8.0	41.0	23.9	3506
1963	no counts						
1964	25.2		2.9	5.8	27.1	17.8	4128

[a] Percentages are percentages of age classes in sample.

[b] Percent all yearlings in fall obtained by doubling percent yearling males.

Data from 1962 to present have been rearranged into northern Kenai (GMU 15A), middle Kenai (GMU 15B), and lower Kenai (GMU 15C) groups to correspond more closely to known distinctions between moose populations and to management considerations such as hunting pressure. These data are the basis for much of our discussion.

Aerial composition survey data for the northern Kenai are given in Table XIII. In 1962, the proportion of bulls was already considerably depressed. Production was good, but indicated survival to the yearling age was poor (Fig. 8). Here, as in the Nelchina Basin and the Matanuska Valley, the estimates of yearling proportions were depressed due to disproportionate removal of yearling bulls by hunting. This portion of the Kenai was relatively accessible and hunting pressure was high.

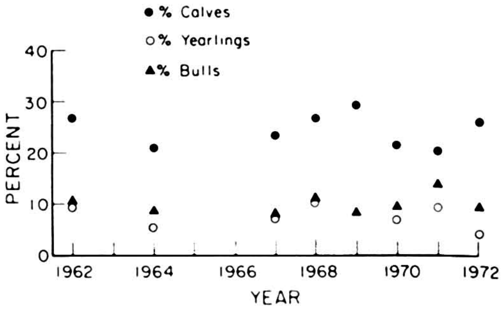

Figure 8. Moose population indices, northern Kenai Peninsula, Alaska, 1962-1972.

This general situation of fair to good production but poor to fair survival persisted during the period 1962-1972 with indices varying from year-to-year (Fig. 8). Indices have risen in certain years. In some years, particularly between 1962 and 1969, gains in these indices probably represent real gains in the population. Aerial quadrat censuses conducted by the Kenai Moose Range staff suggested a growing, or at least stable, population through 1971 (Table XI). However, production of calves had definitely declined in 1970 and 1971 and yearling survival was poor.

LeResche and Davis (1973) noted extensive use of low-growing nonbrowse plants particularly *Vaccinium vitis-idaea* and *Peltigira* sp. in 1970-71. Shallow snow depth left the former exposed in winter, and early spring melting exposed the latter. Use was particularly heavy on depleted range in one moose enclosure. They postulated that mild

TABLE XIII

Indices to moose production and survival, Northern Kenai Peninsula*, 1962-1972, fall aerial survey data **

Year	*Total ♂♂ per 100 ♀♀*	*% males*[a]	*% Yearling males*[a]	*% all yearlings*[b]	*Calves per 100 ♀♀*	*% calf in herd*	*Total*
1962	16.7	10.3	4.8	9.6	43.8	27.0	1568
1964	12.0	8.5	2.7	5.4	29.9	21.0	2471
1967	11.7	8.0	3.3	6.6	34.3	23.5	575
1968	20.0	10.3	5.1	10.2	46.9	26.7	2661
1969	17.4	8.1			42.8	29.7	705
1970	14.1	9.1	3.6	7.2	32.1	21.9	1586
1971	2.14	14.0	4.8	9.6	31.5	20.6	2027
1972	15.6	9.9	2.0	4.0	41.2	26.3	1723

a Percentages are percentages of age classes in sample.

b Percent all yearlings obtained by doubling percent yearling males.

* Game Management Unit 15A.

**Data primarily from Kenai Moose Range, regrouped for management unit.

winters contributed to the high carrying capacity of the 1947 burn by allowing access to nonbrowse foods.

Their hypothesis is supported by almost total mortality of calves in the 1947 burn in 1971-72 when snow depths of up to 30 inches persisted from mid-December to late February, and moderate to high mortality in 1972-73 when relatively deep snow persisted in local areas. Other age classes, however, have suffered little. Similar mortality patterns occurred in limited areas as early as 1967-68 (unpublished data).

Loss of most of the 1971-72 calf crop is demonstrated by the low percentage of yearlings in the 1972 data (4 percent). Another manifestation of the loss is the apparent increase in proportion of calves. Lack of yearling cows and absence of yearlings in general inflates the calf proportion estimate by reducing either base (cows or total moose) to which calves are compared. Results of the 1973 aerial quadrat census seem to confirm losses due to two harsh winters since 1971 (Table XI). The 1973 census results are equivocal, however, because many moose wintered in adjacent foothills (James Davis, pers. comm.).

The declining proportion of calves, loss of two calf crops under conditions that generally do not produce such high losses in other areas, e.g. Tanana Flats and Nelchina Basin, the high use of non-browse plants noted by LeResche and Davis (1973) and the near elimination of willow and aspen from the 1947 burn (LeResche and Davis, 1973) all indicate the northern Kenai moose populations are in precarious balance with their winter range, and relatively minor increases in winter severity can precipitate substantial losses of calves.

Moose from the middle Kenai Peninsula (Unit 15B) have experienced similar but less pronounced changes in proportions of bulls, in production and in survival (Table XIV). Hunting intensity is lower because many of these moose are in foothill areas during hunting season and are relatively unavailable (LeResche, 1972).

Production and survival are both generally lower than among northern Kenai lowland moose, even though both groups of moose share lowland wintering areas to some extent. These differences are consistent with most "highland-lowland" comparisons of moose population characteristics in Alaska (Rausch, 1959, 1967, 1969).

On the southern Kenai (GMU 15C), moose subsist primarily on riparian wil-

TABLE XIV

Indices to moose production and survival, Middle Kenai Peninsula*, 1962-1971, fall aerial survey data **

Year	*Total ♂♂ per 100 ♀♀*	*% males*[a]	*% Yearling males*[a]	*% all yearlings*[b]	*Calves per 100 ♀♀*	*% calf in herd*	*Total*
1962	43.0	23.9	3.3	6.6	36.9	20.4	1832
1964	44.2	26.7	3.2	6.4	21.6	13.0	1437
1967	28.8		2.4	4.8	15.8	10.9	457
1970	37.8	24.6	2.1	4.2	14.5	9.4	817
1972	30.9	19.6	1.3	2.6	26.8	17.0	1093

[a] Percentages are percentages of age classes in sample.

[b] Percent all yearlings obtained by doubling percent yearling males.

* Game Management Unit 15 B.

** Data from portions of Kenai National Moose Range, regrouped to fit management unit.

lows in winter, and become very concentrated in such areas during winters of deep snow. Hunting has depressed bull populations (Table XV) but production has been good. Survival, however, has been marginal. These moose populations have received less study than those in Units 15A and 15B, but casual field observations indicate winter range has deteriorated rather consistently over the last 15 to 20 years in many formerly important areas (Spencer and Chatelain, 1953), at least partly due to overuse. It is very likely that this trend will continue. Winter losses in 1970-71 and 1971-72 were high as the result of snow 3 to 4 ft. (1-1.3 m) deep that persisted for 1.5 month in 1970-71 and for 2 to 2.5 months in 1971-72.

Consideration of major influences and their effects on Kenai moose populations provides some unique contrasts with factors affecting moose in the other study areas. Because these influences are best known for the northern Kenai, our remarks relate primarily to that area.

Hunting has greatly depressed bull: cow ratios on the northern Kenai (Table XII), but those populations frequenting more remote sub-alpine areas in fall have been affected least (LeResche, 1972 and Table XIV). The same data indicate the inverse for productivity.

Predation has been minimal in comparison to the other areas as a result of the apparently complete disappearance of wolves in the early 1900's and their recent return about 1968. It is unlikely that brown/grizzly (*Ursus arctos*) and black bears (*Ursus americanus*) could have substantially compensated for this loss. We concluded earlier that wolves probably were important in controlling moose numbers in the Nelchina area following a moose decline. Kenai moose were free of this influence for about 60 years.

Wildfire has produced extensive habitat for moose periodically during the same time (Spencer and Hakala, 1964; Hakala *et al.* 1971). Major fires may in fact have "rehabilitated" a greater proportion of several populations' winter ranges more frequently than has occurred anywhere else in the state.

The final consideration is the characteristically mild winters in terms of snow depth and duration compared to other areas reviewed, excepting the

TABLE XV

Indices to moose production and survival, Lower Kenai Peninsula*, 1964-1971, fall aerial survey data

Year	*Total ♂♂ per 100 ♀♀*	*% males*[a]	*% Yearling males*[a]	*% all yearlings*[b]	*Calves per 100 ♀♀*	*% calf in herd*	*Total*
1964	22.4	8.1	2.8	5.6	24.3	19.5	1848
1965	32.6	19.9	5.9	11.8	31.2	19.0	1889
1966	16.9	11.5	4.3	8.6	30.7	20.8	794
1967	21.0	13.3	4.2	8.4	40.0	25.6	3038
1968	20.5	12.8	3.8	7.6	40.1	25.0	1883
1969	13.9	9.5	4.5	9.0	27.9	19.1	1636
1970	20.4	14.1	2.3	4.6	24.3	16.8	1992
1971	26.0	17.8	5.3	10.6	18.7	12.8	1436
1972	9.8	7.2	0.6	1.2	25.4	18.8	2073

[a] Percentages are percentages of age classes in sample.

[b] Percent all yearlings in fall obtained by doubling percent yearling males.

*Game Management Unit 15C.

Matanuska Valley. The combination of factors affecting moose numbers on the northern Kenai has thus been uniquely favorable to moose population growth and to maintaining very high population levels.

The climatic crises which have occurred in recent years, and most dramatically in 1971-72 and 1972-73 as a result of moderate snow depths, probably would not have occurred if the range in general had not previously been overused for many years. It is likely that even at lower population levels than presently exist on the northern Kenai, similar mortality on a lesser scale may occur because of chronically deficient range. This is essentially what happened during the 1960's when the populations were still growing. Given moderately severe winters, substantial calf mortality will undoubtedly occur again even though the population has declined as a result of recent winter die-offs, because there has been no substantial range improvement. To what extent regrowth on a 1969 burn of 86,000 acres (34,400 ha) may alleviate winter range problems remains to be seen. Because this burn occurred largely to the west of present major winter ranges, its benefit may be minimal.

Welfare of moose populations in the middle Kenai (GMU 15B) are affected similarly by most of the considerations discussed above because of overlapping winter ranges and climatic conditions. Because a greater proportion of moose in Unit 15B seasonally use foothill areas, however, their circumstances are somewhat different (LeResche, 1972). We noted that differences in effects of hunting and that alternatives to wintering in the 1947 burn do exist, at least in milder years. Under present management plans lower hunting pressure will be maintained. Major improvement of winter range conditions will depend on implementation of range improvement efforts or on wildfire.

Conditions on the southern Kenai, though less well understood, appear chronically poor. Limited and chronically overused browse, heavy hunting pressure on bulls, difficulty in establishing effective cow seasons, loss of some habitat to agriculture and occasional very severe winters promise to sustain a basically unsatisfactory management situation, with little relief in view for moose populations. Should logging become economically feasible, some improvement of habitat may ensue.

Summary and discussion

We presented data and general accounts that indicate moose numbers increased throughout most of Alaska between 1940 and the early 1960's. The technique most widely used for assessing moose welfare during that period (and to date) was aerial sex and age composition counts, repeated annually between October and December, usually in the same geographic areas. Aerial counts showed consistently high productivity and survival in the study areas considered during this early period; moose numbers were increasing in general. The four study areas differ considerably with respect to physiography, vegetation and climate, yet moose increases were relatively well synchronized. The most probable causes for moose increases in order of importance were: 1) extensive and repeated wildfire for many years, and especially in the 1940's and 1950's; 2) a period of relatively mild winters in terms of snow depth, primarily in the 1950's; 3) low wolf numbers, at least partly due to predator control directed at wolves, primarily in the 1950's; 4) restrictive hunting regulations and generally low hunting pressure from 1925 through 1959.

Stabilization or decline occurred in the 1960's and early 1970's in all study areas in response to varying influences of snow severity, habitat changes, predation and hunting.

Moose numbers on the Tanana Flats stabilized in the early 1960's, production and survival declined, and the population crashed in winter 1965-66 in response to prolonged deep snow. Winter 1966-67 was moderately severe and precluded population gain. Moose productivity, survival and numbers subsequently rose until winter 1970-71, when record snow depths again produced major mortality. Predation, hunting and habitat considerations appeared not to have contributed to these declines nor did they substantially inhibit subsequent population growth. Availability of winter browse is affected by snow depth and is therefore involved in the extent of winter mortality. As a result of overall population declines and increased hunting pressure, hunting is now a potentially limiting factor on population growth.

In the Nelchina Basin moose numbers probably peaked in 1960. Extensive winter mortality in response to unusually severe snow conditions occurred in 1961-62, at a time when wolf numbers and hunting pressure both were beginning to increase rapidly, and when high hare numbers may have caused reduction of available browse. Severe winters in terms of snow depths recurred in 1965-66 and in 1971-72.

General trends in population numbers, productivity, and survival were downward after winter, 1961-62. The proportion of bulls found in fall surveys declined rapidly while harvest of bulls declined slowly, and a marked shift to a younger bull age structure in the harvest occurred. Harvest of bulls exceeded production of bulls. Based on experience elsewhere in Alaska, increased production could have been expected, but did not occur. Although habitat deficiencies remain a possible contributing factor, increasing wolf numbers were probably most important in causing substantially reduced productivity and survival. Although wolf numbers seemed to have declined in recent years, the winter of 1971-72 effectively eliminated any gain that may have accrued to this moose population. While deep snow was clearly the factor precipitating population decline in the Nelchina, predation and hunting appear to have impeded population recovery, in contrast to the Tanana Flats.

In contrast to both the Tanana Flats and the Nelchina Basin, the Matanuska Valley had a long history of relatively mild winter conditions, good access, land clearing and associated fires, and intensive bulls-only moose hunting. Few wolves inhabited the area. Moose numbers were at high level by the mid-1950's, and continued to be high through the 1960's. Substantial harvests of antlerless moose were provided for in the early 1960's to take advantage of the highly productive population and (in 1962) to reduce moose damage to agricultural products. Although the proportion of bulls in the population continued to be quite low and these bulls were mainly yearlings, productivity remained relatively high through the late 1960's. A declining trend in production has ensued since 1969. Fall 1972 survey data suggest a continuing decline in numbers and in productivity. Factors contributing to this decline have been loss of winter habitat through normal vegetative succession and winter losses in 1961-62, 1965-66, and 1970-71. Currently, hunter harvest and non-hunting mortality (poaching, collisons with cars, etc.) are important mortality factors. The low bull:cow ratio may be partly responsible for low productivity.

On the northern Kenai Peninsula moose numbers have fluctuated dramatically over the last 70 years, primarily in response to creation of seral range by wildfire and its subsequent maturation. During the period 1960-1972, moose numbers rose to reach an apparent peak by 1971, then declined when calves were essentially eliminated in response to greater than normal snow depth in 1971-72. Substantial calf mortality also occurred in 1972-73. Older age classes were little affected. Similar but less extensive mortality occurred in the 1960's. In the main wintering area (1947 burn) willow and aspen have virtually been eliminated, and moose have been observed to use nonbrowse plants extensively in winters of normal snow depth. These considerations strongly suggest that moose numbers are sufficiently high to be in critical balance with an extensive, but qualitatively marginal range. Small increases in winter (snow) severity are sufficient to cause extensive losses of calf moose, but have limited effect on adults.

Predation and hunting appear to have little effect on moose numbers, although the latter has strongly affected sex and age ratios. Wolves were absent from the Kenai between about 1900 and 1968.

Moose on the southern Kenai also experienced extensive mortality in 1970-71 and 1971-72 in response to extremely deep, persistent snow (3 to 4 ft. (1 to 1.3 m)). Prior to these winters moose were relatively abundant, with good productivity but a strongly distorted sex ratio in favor of cows.

Fire-caused seral range is practically non-existent on the southern Kenai because the moist climate discourages fire. Moose heavily depend upon subalpine and riparian range and large areas of the latter, which constitute most of the winter range, are decadent. A major readjustment of moose numbers or an active range rehabilitation program appears necessary to alter moose-range relations on what seems to be a chronically overstocked range. Recent winter mortality may have effected such a readjustment in moose numbers.

Fluctuation in moose numbers is hardly a recently discovered phenomenon. Historical accounts from Alaska alone reflect numerous changes in abundance and distribution (LeResche *et al.*, 1974). Moose increased rapidly in many parts of North America around the turn of the century and most authors attributed these increases to vegetation change following fires, logging, or other disturbances (Peterson, 1955). In some cases, moose numbers grew rapidly following natural expansion or transplants into previously unoccupied areas. Peterson (1955) noted that in certain areas moose numbers had declined following a period of rapid increase.

Fluctuations in moose numbers will continue in response to ecological and management changes. On wild and semi-wild lands such as comprise much of Alaska, northern Canada, and portions of the U.S.S.R., such fluctuations depend largely on natural events, and therefore may be dramatic increases or decreases. In contrast, population changes are likely to proceed by small increments on the more closely managed lands of Scandinavia.

In the Alaskan studies considered here, wildfire with subsequent seral succession has had the major positive influence on moose numbers, while unusually great snow depth has been the major mortality factor. However, the influence of snow has varied, depending on depth and duration of snow cover, moose density and availability and quality of habitat.

In Interior Alaska, where winters are cold and snow persists, moose mortality in years of extreme snow depth has included substantial numbers of adult moose in addition to nearly total loss of calves. Widespread mortality of this sort has been characteristic of the Tanana Flats and Nelchina Basin, other parts of Interior Alaska not discussed in this paper, and coastal areas in years of unusually deep, persistent snow.

Winter mortality may also affect bulls more strongly than cows. Pitcher (unpubl. data) found heavy mortality of adults in addition to calves in the coastal-facing, heavy snow area of the Susitna River Valley, adjacent to the Matanuska Valley. Mortality was heavier among bulls (94 of 161 dead moose examined), and included bulls of all ages except those four and five years old. Bulls comprised 24 percent of adult moose observed in fall surveys and 65 percent of observed adult winter mortality. Cows apparently were less susceptible to winter mortality. All dead cows (n = 67) examined were either less than four years or more than 11 years old.

In general, winter mortality in Alaskan areas where deep, persistent snow is a regular phenomenon seemed to affect a broad range of age classes, and it seemed to have operated somewhat independently of moose densities and quantitative or qualitative characteristics of range. Further, bulls seemed more susceptible than cows.

Winter mortality in more temperate Alaskan areas, such as the Matanuska Valley and the Kenai Peninsula has generally been less spectacular. Although winter mortality has surely had some effect on moose in the Matanuska Valley in certain years, it has been much less dramatic than in Interior Alaska. At present it may well be that moose mortality in the Matanuska Valley caused by collisions with automobiles and trains, poaching and miscellaneous factors compensates to a considerable extent for winter mortality. About 200 moose were killed by means other than hunting and natural mortality in 1971 (Didrickson, 1973).

Mortality patterns on the northern Kenai Peninsula show further variation. Winter mortality has commenced at lower snow depths and/or after shorter duration of deep snow than in Interior Alaska. Further, known winter mortality has been much more selective for calves than in other areas studied. In that area, fire has promoted extensive seral succession, and moose populations have become very high. The characteristically mild winters apparently have encouraged persistence of moose densities capable of altering plant composition by eliminating willows and aspens on a large part of the winter range.

Although adult moose on the northern Kenai apparently have suffered little mortality as a result of winter snow conditions, other evidence suggests the security of large moose numbers is tenuous. Production of calves has been only fair to moderate and it appears that cows grow more slowly than on the Tanana Flats (Coady, unpubl. data). LeResche and Davis (1973) noted extensive use of non-browse plants by moose in winters of normal snow depth and persistence. These observations plus the characteristics of winter mortality already mentioned, indicate that more moose exist on the northern Kenai moose ranges than can be supported in winter by the traditional browse available, and that the balance is easily upset by small variations in other ecological factors such as snow conditions.

To summarize, in contrast to Interior Alaska, the extent and specific nature of moose winter mortality in the milder Matanuska and Kenai areas seems much more susceptible to variations related to moose density, habitat characteristics and other mortality factors.

Edwards (1956) reviewed weather records, reports of snow conditions, and reports of ungulate abundance in British Columbia from about 1900 to 1950. He concluded that deep snow caused declines of wild ungulates and that years of deep snow occurred in groups rather than randomly. In a very cogent discussion, he noted that: food and cover can modify the effect of snow conditions, deep snow periods may be somewhat predictable because they tend to group; normal differences in snow depth between different winter ranges may considerably influence usability of a similar range resource; and finally, that a comprehensive view of ungulate-range-snow interactions is needed to avoid errors in interpreting variations in ungulate abundance, range use and effects of hunting or other management methods. Edwards' ideas encompassed virtually the entire scope of this paper. However, he did not mention predation as a potentially important factor in population fluctuations.

Some final comments regarding productivity of moose are necessary. Pimlott (1959) concluded that a net productivity (yearlings expressed as a percentage of yearlings plus adults) of 25 percent could be expected on good range. Simkin (1965) obtained a similar estimate for moose in north-western Ontario. In the present study, moose approached this level of productivity on a regular basis only in the Matanuska Valley, and, for certain periods, on the northern Kenai Peninsula. In other areas, where various ecological factors usually presented greater resistance to moose population growth, high productivity was reached only during periods of moose population expansion, when range, predation and winter conditions were optimally favorable for moose. Similar situations have been observed elsewhere. For example, Knorre (1959) showed a pronounced decline in percentage of calves in years of deep snow on the Pechora-Ilych State Nature Preserve, U.S.S.R. Mercer and Kitchen (1968) found only nine percent calves in Labrador, where they concluded that snow depth limited moose distribution.

Thus, high productivity cannot be assumed for moose when considering management alternatives. Edwards (1956) noted that management efforts tended to assume stable game populations, while in fact populations continued to fluctuate in spite of management efforts.

With increasing resource use by humans, it is doubly important to anticipate and compensate for game population fluctuations.

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MOOSE OF THE ASIATIC PART OF THE U.S.S.R.

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Résumé

Si l'on fait exception de petites populations en Mongolie et en Chine, la distribution de l'orignal en Asie est entièrement limitée à l'intérieur des frontières de l'U.R.S.S. Les populations asiatiques de l'orignal sont sans doute les plus connues de l'hémisphère. Dès le 17ème siècle, des chasses abusives entamèrent les populations dont les effectifs diminuèrent sans arrêt jusqu'au niveau le plus bas atteint vers le milieu du 19ème siècle. Les principaux facteurs ayant contribué à ce déclin sont d'abord la chasse abusive—surtout celle exercée durant les hivers où les conditions de neige sont très défavorables—et ensuite, les épizooties transmises à l'orignal par le bétail domestique. A compter de 1919, la population commença à récupérer à la suite de l'adoption de règlements de chasse prohibant la capture d'animaux durant la période où la neige entrave leurs libres déplacements et n'autorisant la chasse que durant les mois de novembre et décembre seulement. En outre, l'orignal a bénéficié de l'exode massif des habitants de la taiga vers les villages et les villes. Enfin, l'augmentation des exploitations forestières a également joué un rôle dans l'accroissement des populations d'orignal en augmentant la quantité d'habitats de qualité.

Abstract

In Asia, moose are almost entirely confined to the USSR the exception being small populations in China and Mongolia. Less is known about the moose of Asiatic USSR than about any other population of moose. Early reductions began in the 17th century as a result of intensive hunting pressure and the decline continued until moose populations reached their lowest ebb in the middle of the 19th century. Important factors which have caused decreases in moose numbers over the years are over-hunting, especially in winters of adverse snow conditions and infection with various cattle diseases. By 1919, the population began to recover as a result of the passing of hunting laws which, for instance, provided for only a November-December season and for the prohibition of hunting during the period when snow conditions restricted moose mobility. In addition, moose also benefited from the mass movement of people from the vast taiga areas into towns and cities. Another factor which is of considerable importance is the increased logging activity which has greatly enlarged the amount of good moose range.

Range changes and population dynamics of the moose in the 17-20th centuries

The distribution of moose in Asia is almost entirely confined to the USSR — mainly in Siberia and in the Far East with a very limited number in northern Kazakhstan (Fig. 1). Outside of the USSR a small population exists only in China and Mongolia.

In west Siberia and in the Altai there is a European subspecies of moose (*Alces alces alces* L.), in east Siberia and Yakutia — an east-Siberian one (*Alces alces pfizenmayeri* Zuk.), in the south of the far east — an Ussuri one (*Alces

alces cameloides Milne-Edw.). Recently (Yegorov, 1972), the moose of the Kolyma and Indigirka River Basins has been classed as *Alces alces gigas* Miller. The Asiatic moose has not been well studied: as a whole, it is undoubtedly the less well known subspecies of moose in the world. For instance, the investigation of their ecology has hardly begun and there is not a single review of the distribution and numbers of moose in Siberia and the far east. As a result, the total volume of scientific information, on these moose is 15-20 times less than for the moose of the European part of the USSR.

There are also few data on the range, history and population dynamics of the moose in northern Asia. The first general information on the subject dates from the 17th century, the time of the beginning of the large-scale penetration of Russian settlers into Siberia. At that time, the moose were numerous and widely distributed in the taiga zone of northern Asia, from the forest-tundra up to the forest-steppe and the insular forests of southern Siberia.

The reduction of range and numbers of moose in northern Asia started in the Trans-Urals at the beginning, and in western Siberia about the middle of the 17th century. This process coincided with the reduction of saiga numbers (*Saiga tatarica*) which was also connected with the period of intensive hunting in the western part of Siberia. During the 18th century, range and numbers of moose continued to decline. From the beginning to the middle of the 19th century, moose numbers were at their lowest in this area and the northern range limit in western Siberia extended further south than in the European part of the USSR (Fig. 1). Later on, when there was a reduced demand for moose skins for export and clothing for the Russian army, a significant rise in moose numbers took place. During the civil war the moose population was reduced again.

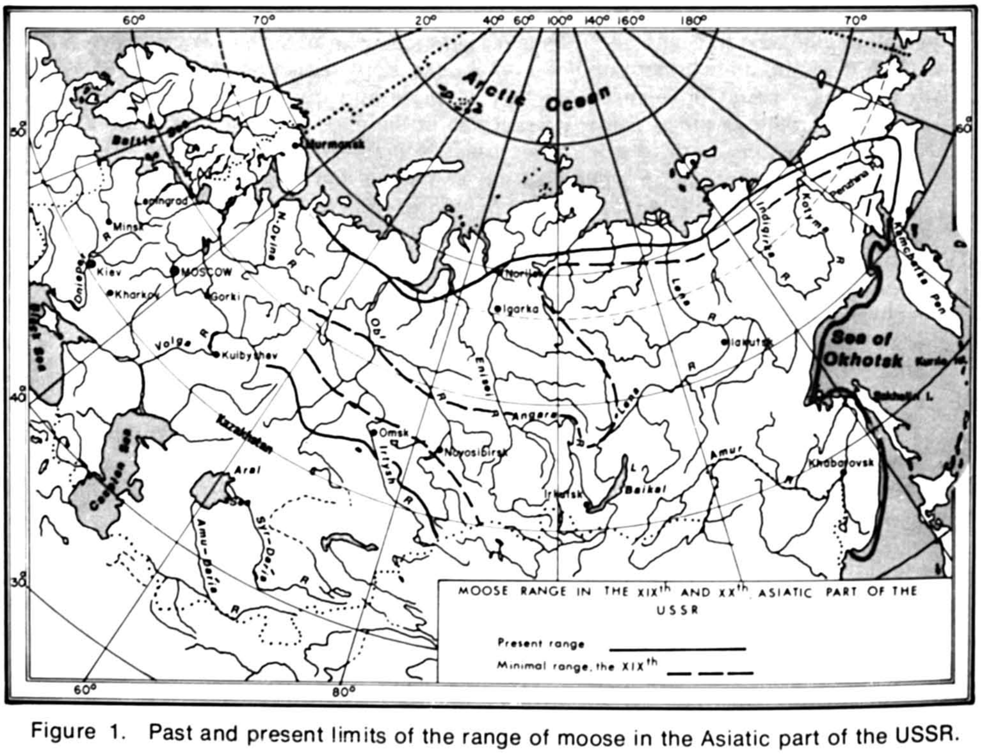

Figure 1. Past and present limits of the range of moose in the Asiatic part of the USSR.

Generally, the chronology of the reduction of moose densities and range is very similar between the European part of the USSR and western Siberia. In Siberia, the reduction of moose populations occurred some decades later. Repopulation was also delayed by about 10-15 years.

Eastwards from the Enisei river, because of the scarcity of data, it is hard to retrace the moose population dynamics. In central Siberia (up to the Lena River), range reductions similar to those occurring in the European USSR and Siberia took place. In eastern Siberia (eastwards from the Lena River) moose numbers and distribution remained fairly static, except for the extreme northeast where there was a considerable westward reduction in occupied moose range in the 19th century with subsequent recovery in the 20th century (see Kistchinski, 1974).

The proportion of habitat utilized was not so severely reduced as were the total numbers throughout Siberia. Best estimates suggest that about 20-30% of the present range was occupied (Fig. 1) while total moose numbers were ten times lower than at present. Areas most affected were in Enisei, Siberia, in the southern taiga and the forest-steppe regions of Siberia.

We consider that the main cause of the moose decline was over-harvesting. The regions where many alien fur trappers settled became the most damaged, particularly those where the mean annual maximum depth of snow on the ground was 70-90 cm. In such places, the moose was quickly exterminated (when the snow is deep and covered by a hard ice crust for a one or two-week period, which is typical for the continental climate of Siberia, the moose has great difficulty in escaping hunters).

The last large void in the moose range remained until about 1946-1950 as an immense dip of its northern limit towards the south, in the Enisei-Taz-Siberia, i.e. in the region with the highest snow depth among the flat territories of the USSR. Such a distribution of the moose range suggested to Formozov (1946) the idea that moose cannot survive in areas with snow depth in excess of 90-100 cm. This hypothesis proved to be wrong. At present, the moose inhabits the Enisei basin north in Siberia to the northern edge of the forest-tundra. Unfortunately, the wrong outline of the northern limit of moose range in Siberia — with a dip to the south almost to the Angara — still can be found in our latest monographs and reviews (Bobrinskii *et al.*, 1965).

A supposition of Kirikov (1966) that the moose in the 17th, 18th and 19th centuries was exterminated by hunters and infectious cattle diseases is probably correct only for the European part of the country and part of southern Siberia. In the other parts of Siberia the moose did not come in contact with cattle to any extent.

The restoration of moose numbers in the Asiatic part of the USSR began later than that in the European part where increases began after 1919 as a result of the resolution of the Council of Peoples' Commissars on the hunting seasons and the adoption of other hunting regulations. For instance, throughout the European part of the USSR, moose and roe-deer (*C. capreolus*) hunting was forbidden. In Siberia, moose hunting was only permitted during November and December, and hunting during the snow-crust period was strictly forbidden. A number of other measures were taken to ensure the protection of moose.

An increase in moose numbers and range took place in the European part of the country between 1930-35. In most parts of Siberia the increase occurred later. For instance, in the Krasnoiarsk territory, on the Angara and on the upper and middle Ob' River significant increases in the moose population occurred only after 1950.

By 1972, the restocking of moose range in the Asiatic part of the USSR was nearly completed. In only a few remaining small areas in the northeast of the country (e.g. Chukotka), is the process of re-establishment continuing. Furthermore, moose numbers are increasing in Kamchatka, an area where moose never became permanently established (Kistchinski, pers. comm.).

The main reason for the increasing numbers of moose is the effective system of protective measures. Also of great importance are the changes in the distribution of hunters which have occurred. During recent years, the population has become more concentrated in towns and big settlements, thus leaving vast taiga areas, especially in northern Siberia, with a much smaller resident population. In addition, logging, which has increased in the southern taiga, has produced range much more favourable to moose than that which formerly existed.

Present moose range

The present distribution of moose range in northern Asia is similar to that of the 16th and 17th centuries. However, it differs in some details from that described by Heptner *et al.* (1961) in the last monograph for the middle of the fifties.

The northern limit of year-long moose range extends right to the tree line. In western Siberia, near the Ob' River, the limit is a little further north than the Arctic circle. Eastwards it diverges to the north and from the Pur and the Taz estuaries reaches Dudinka on the Enisei. Then, the limit goes along the northern boundary of the typical forest-tundra, along the lower reaches of the Khatanga, the Lena, the lana and the Kolyma rivers including also the Anadyr basin.

In the summer, the moose often visit the open tundra. Following the shrub bordered river valleys, they can reach the Arctic tundra zone (for Taimyr, 72-73°N.)

During recent years the most interesting fact about the northeastern areas is the penetration of moose into the northern part of Kamchatka region, in the Penzhina river basin (Fil and Demianiuk, 1971). At present, moose are found all over the Penzhina basin where, according to the last aerial census data (1970) the population numbers about 1,000.

As formerly, there are no moose on most of the Kamchatka Peninsula and on Sakhalin, Kuril and Shantar islands. These areas are characterized by a very deep snow cover (up to 90-100 cm and even more). However, in our opinion, the physiogeographical conditions by themselves, in the absence of hunting pressure, cannot prevent moose from occupying these areas (at least Kamchatka and Sakhalin). In the southern part of the far east, moose are absent in the southern part of Primor'e territory (to the south from Khanka Lake).

Along the southern boundray of the USSR, westwards to Kazakhstan, moose are found practically everywhere. Small territories of Transbaikalian steppes, not included by Heptner *et al.* (1961) in the moose range, are now frequently visited by these animals. Sometimes, moose live there permanently along the rivers, in the valley forests.

Present population dynamics of moose

Ground censuses of moose for the vast territories of the Asiatic part of the USSR cannot provide comprehensive population information; hence, the estimate of total moose numbers is very inadequate, especially for the 1940's and 1950's. Wide use of aerial censuses has been made in the Asiatic part of the range only since the sixties by the Russian Soviet Federated Socialist Republic (RSFSR) Department of Wildlife Management and Reserves (Glavokhota RSFSR). These data are objective, but still only provide indices to actual densities because of the comparative smallness of the areas sampled and the lack of a completely satisfactory census method.

The total numbers of moose in the Asiatic part of the USSR was estimated in 1971 as 220,000 animals (Table II). Nearly all the moose are concentrated on the RSFSR territory. (In Kazakhstan, there were only 1000-1200 moose in 1971). As compared with the European part (estimated in 1971 at about 400,000), the Asiatic population is not large. In 1970, in the USSR as a whole, there were nearly 700,000 moose (RSFSR, 600,000; Ukraine, 13,000; Byelorussia, 23,000; Estonia, 10,000; Latvia, 17,000; Lithuania, 7,000; Kazakhstan, 1,000 animals).

Presumably, moose in the Asiatic part of the USSR are still well below carrying capacity. Although it is quite probable that population estimates are low, the main cause of the comparatively low number of moose lies in the fact that the northern Asiatic portion of the USSR is as a whole, poorer habitat for moose than the European part of the USSR.

In the Asiatic part, the moose population is densest in the southern regions (southern taiga and forest-steppe regions) and in the plains with a well developed network of rivers and bogs. These are the southern part of western Siberia and Priamur'e, as well as plains and intermountain areas of southern Siberia.

As stated earlier, the depth of snow itself does not limit moose numbers and there are many densely populated

TABLE I

Estimates of moose populations in vast natural areas of the Asiatic part of the USSR 1965-71

Areas	*1965*	*1966*	*1967*	*1968*	*1969*	*1970*	*1971*
West Siberia	45,400	38,100	38,000	34,700	36,900	42,200	38,750
Central Siberia	21,000	20,600	20,600	20,700	19,400	20,300	19,100
Iakutia	37,000	37,000	37,000	47,500	48,000	48,000	47,000
North-East of the USSR	No valid estimates available				7,500	9,200	10,500
South of the Far East	40,000	34,500	32,600	29,950	29,350	29,500	30,000
Mountain regions of South Siberia	44,700	46,700	49,700	40,700	46,000	49,000	53,500
Total	188,100	176,900	177,900	173,550	187,150	198,200	198,850

areas which are characterized by deep snow. Among vast natural areas, the following have the densest moose populations: West Siberia, South of the Far East, mountain regions of South Siberia and Iakutia (Fig. 2 and Table I).

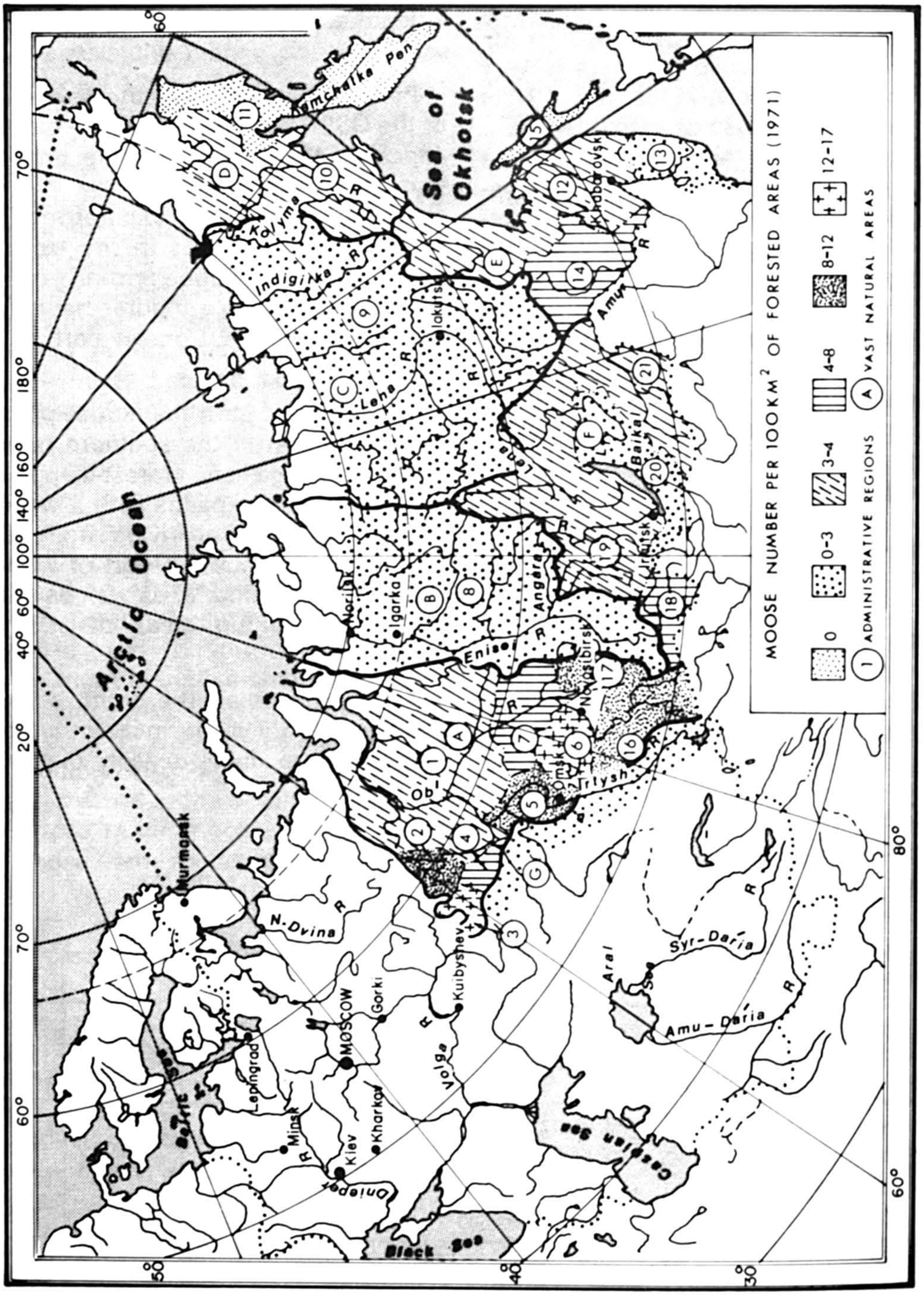

Figure 2. Moose densities in the Asiatic part of the USSR, 1971. Vast natural areas are identified by a letter as follows: A — West Siberia; B — Central Siberia; C — Iakutia; D — Northeastern USSR; E — South of the Far East; F — Mountain region of Southern Siberia. (Continued next page)

TABLE II

Moose numbers in the Asiatic part of the USSR, 1971

Areas	*Number*	*Forested areas (km^2)*	*Mean number per 100 km^2 of forested areas*
West Siberia (with Zaural'e regions)	55,510	887,420	6.25
Tiumen region	15,000	458,120	3.26
Sverdlovsk region	11,500	119,430	9.64
Cheliabinsk region	4,200	25,760	16.29
Kurgan region	1,060	15,490	6.84
Omsk region	3,550	36,090	9.86
Novosibirsk region	6,000	37,680	16.01
Tomsk region	14,200	194,850	7.23
Central Siberia (Krasnoiarsk territory)	19,100	1,234,110	1.55
Iakutia (Iakutia Autonomous Republic)	47,000	1,839,820	2.56
Northeast of the USSR	10,500	408,410	2.46
Magadan region	9,500	287,860	3.30
Kamchatka region (northwestern part of Penzhina district only)	1,000	30,550	3.33
South of the far east	30,000	996,970	3.00
Khabarovsk territory	17,000	562,400	3.02
Primor'e territory	1,900	124,180	1.53
Amur region	11,100	244,390	4.45
Sakhalin region	—	—	—
Mountain regions of south Siberia	53,500	1,352,880	3.94
Altai territory	8,000	74,690	10.72
Kemerovo region	6,500	56,440	11.55
Tuva Autonomous region	4,000	88,020	4.55
Irkutsk region	21,000	664,030	3.16
Buriatia Autonomous Republic	5,000	201,830	2.48
Chita region	9,000	267,870	3.36
Total	215,610	6,719,610	3.20

Administrative regions are numbered as follows: 1 — Tiumen region; 2 — Sverdlovsk region; 3 — Cheliabinsk region; 4 — Kurgan region; 5 — Omsk region; 6 — Novosibirsk region; 7 — Tomsk region; 8 — Krasnoiarsk territory; 9 — Iakutian ASSR; 10 — Magadan region; 11 — Kamchatka region; 12 — Khabarovsk region; 13 — Primor'e territory; 14 — Amur region; 15 — Sakhalin region; 16 — Altai territory; 17 — Kemerovo region; 18 — Tuva Autonomous region; 19 — Irkutsk region; 20 — Buriatia ASSR; 21 — Chita region.

More than 50 percent of the moose of the Asiatic part of the USSR is located in the smaller southwestern part of the territory south of 60-62°N.

There is no doubt that the moose numbers in central Siberia are higher than current estimates but an adequate moose census has not been carried out there yet. According to the preliminary data, the moose population in central Siberia seems to be not less than in Iakutia (47,000) where estimates are based on the results of thorough aerial censuses.

The highest moose numbers occur in the boggy southern taiga of western Siberia and Amur Basin (50-70, sometimes 100 animals per 100 km^2). In some small areas — insular and belt forests of the Ob' forest-steppe (Altai territory) within this region — densities of 100-200 moose per 100 km^2 are known.

Northwards, in the middle taiga, the moose densities decline and reach only 30-40 animals per 100 km^2 in the best forests of river valleys, while outside of river valleys, 10 moose per 100 km^2 is an average density. In the northern taiga, the moose densities do not exceed 10 per 100 km^2 in river valleys and 2-3 per 100 km^2 in other habitats. In the forest-tundra, the densities are low, ranging from 5 to less than 1 animal per 100 km^2.

Such densities are characteristic of specific moose habitats within these broad forest zones. When one considers the whole forested area, density figures become considerably lower, and in the richest regions of West Siberia, do not exceed 11-16 animals per 100 km^2 (Cheliabinsk, Novosibirsk, Kemerovo regions, Altai territory). Northwards, the mean moose density is very low (2.5-3.5, rarely reaching 7 animals per 100 km^2 of forested areas).

As stated earlier, the population dynamics of moose in the Asiatic part of the USSR have not been studied extensively and more or less reliable data on the moose numbers exist only for the period after 1950. Furthermore, the data for 1950-1960 are also less accurate and based upon methods incomparable to those used in subsequent years.

In spite of these restrictions, it can be concluded that: 1) there are no appreciable annual fluctuations of moose numbers throughout the vast territories; 2) the former range has been nearly all re-occupied but the moose densities are still far below carrying capacity; 3) there is no rapid growth of moose numbers in the Asiatic part of the USSR in contrast to what is occurring in the European part; during recent years a stabilization of numbers has taken place, and in some regions (Buriatia, Amur region), there has been even a decrease in the moose population.

We are convinced that the main factor deterring the subsequent growth of moose numbers in the Asiatic part of the USSR is illegal harvesting. In the European part, a more effective protection program has produced very positive results and in reserves with special protection, the moose density is 5-14 times greater than in adjacent territories (Bannikov and Teplov, 1964).

The forecast for moose numbers in the Asiatic part of the country is favourable provided protection measures are implemented. Another reason for optimism is the development of clear cutting as a forest harvesting method, which is converting vast continuous stands of virgin taiga into habitat considerably more favourable for moose.

Management of moose resources

Data on the licensed kill of moose in the Asiatic part of the USSR are presented in Table III. It reaches 6-8.7 percent of the population in only a few regions (Amur region, Sverdlovsk region, Novosibirsk region). In most cases, the kill does not exceed 2.5-4 percent of the total population, and, on the average is established at 3.21 percent.

The total moose kill in the Asiatic part of the USSR is all but impossible to estimate. However, it is known that the local people kill a considerable number of moose for their personal needs. Moose hunting by natives, all of whom receive free permits, is practically uncontrolled. At present, the estimated total moose kill seems to be at least three times more than that given in Table III. Therefore, in some regions, the total kill can reach 20-30 percent of the population. In most cases, it seems to average 10-15 percent.

TABLE III

Licenced kill of moose in the Asiatic part of the USSR, 1946-1971

Areas	*1946*	*1950*	*1960*	*1965*	*1970*	*1971*	*% of total population 1971*
West Siberia (with Zaural'e regions)	1845	180	1982	2071	2163	2427	4.39
Tiumen region	1000	109	611	288	538	458	3.05
Sverdlovsk region	365	55	543	534	523	749	6.51
Cheliabinsk region	—	—	18	—	17	96	2.29
Kurgan region	—	—	40	—	49	47	4.43
Omsk region	210	—	—	81	64	84	2.37
Novosibirsk region	170	16	306	504	500	519	8.66
Tomsk region	100	—	464	664	472	474	3.33
Central Siberia (Krasnoiarsk territory)	200	71	587	276	429	492	2.59
Iakutia (Iakutia Autonomous Republic)	700	1120	1247	1974	1932	1885	4.01
Northeast of the USSR	—	—	23	104	104	140	1.35
Magadan region	—	—	23	104	104	140	1.48
South of the far east	300	598	1816	1914	1834	1616	5.40
Khabarovsk territory	300	500	1078	665	963	866	5.09
Primor'e territory	—	—	18	82	55	61	3.21
Amur region	—	98	720	1167	816	689	6.22
Mountain regions of South Siberia	1729	278	921	1240	1586	1627	3.04
Altai territory	—	—	99	200	357	306	3.83
Kemerovo region	—	—	71	168	223	232	3.57
Tuva Autonomous Republic	250	—	111	106	61	74	1.85
Irkutsk region	329	171	185	183	518	618	2.94
Buriatia Autonomous Republic	150	81	128	293	210	225	4.50
Chita region	1000	26	327	290	217	172	1.91
Total	4774	2247	6576	7579	8048	8190	3.21

Because of the severe natural conditions of northern Asia, the quotas for moose hunters must be low. The allowable moose kill, in the opinion of Bannikov (1964), should not exceed 10 percent of total population for habitats with densities no greater than 10 animals per 100 km^2. Such densities are characteristic of nearly all the regions of the Asiatic part.

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DYNAMICS OF MOOSE POPULATIONS IN THE FOREST ZONE OF THE EUROPEAN PART OF THE USSR AND IN THE URALS

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Résumé

Après avoir atteint un seuil extrêmement bas au début du 20ème siècle, les populations d'orignal du secteur européen de l'URSS augmentèrent graduellement durant les quelques quarante ou cinquante années qui suivirent. Dans certaines régions, la population s'accrut à un rythme plus rapide que dans d'autres: de telles explosions démographiques entraînaient des migrations vers les régions périphériques et provoquaient une expansion de l'aire de distribution. En conséquence, l'orignal vint à occuper des habitats que l'on avait jusqu'alors considérés comme peu propices à cet animal. L'expansion de l'aire de distribution dans les directions nord et sud se fit en plusieurs étapes: un influx soudain d'immigrants précédait l'occupation d'une nouvelle région; un tel influx avait d'abord l'apparence d'une migration saisonnière de caractère temporaire pour ensuite faire place à l'établissement de populations permanentes d'orignaux dans ces habitats nouvellement envahis. Des études plus approfondies de la dynamique des populations d'orignal dans le secteur européen du pays devraient conduire à l'établissement d'un taux d'exploitation par la chasse qui soit généralement plus élevé et ce, dans les diverses régions.

Abstract

Moose numbers in the European part of the USSR, after reaching low levels at the beginning of the 20th century, gradually increased for the last 40-50 years. In some regions, population density increased more rapidly than in others: such local outbreaks led to emigration into peripheric areas and to a subsequent expansion of the range. As a result, moose spread into habitats which, until recently, had been considered unfavourable. Range expansion to the north and south took place by stages: moose occupation of new areas was preceded by waves of immigrants; the latter took the character of temporary seasonal migrations which, later on, gave way to the establishement of permanent moose populations in these newly invaded habitats. Further studies on moose population dynamics in the European part of the country should allow for an increase in the rate of exploitation of moose by hunters in the various regions.

Introduction

The study of moose (*Alces alces*) biology began in the Soviet Union long ago and at the present time it is one of the major objects of zoological research in our country. In 1962, a special laboratory which studied the principles and methods of moose exploitation and moose reproduction was founded. The laboratory was headed by Professors A. G. Bannikov and U. P. Teplov. As a result of its rather short activity, the laboratory published three issues of the Proceedings under the title "The biology and hunting of the European elk" (1964, 1965, 1967).

At present, the Central laboratory of wildlife management and reserves is engaged in the study of the ungulates of the Russian Federation and is studying the ecology and management of moose in particular.

Early history

Information on former moose distribution and numbers is very scarce and scattered in different, hard to obtain historical documents. Thus, to get a general idea of moose population dynamics for the past centuries, one should take into consideration the data on historical changes of moose range. Range expansion and reduction was reflected in the abundance of this species. All these data are summarized in works by Heptner *et al.* (1961), Kirikov (1959, 1960) Sokolov (1959) and others.

Up to the 16th century moose were widely distributed and ranged throughout the European part of the country which included almost the whole forest and forest-steppe zones and perhaps in some parts, the steppe zone of the European part of the country as well. Evidently, between the Danube and the Don rivers the boundaries of its range reached the shores of the Black and the Azov Seas. Its northern limit might have spread to the southern boundaries of the tundra.

In the 17th and 18th centuries the southern border of moose range evidently spread to the northern part of the steppe zone. By the middle of the 19th century an almost catastrophic decrease of moose numbers took place and the range shrunk from the steppe zone far into the north, in some places for 450 and even 1000 km, particularly in the area of the Middle Russian Highland. About the middle of the 1850's moose numbers began to increase and they reappeared in many territories of the central regions of European USSR. Also, a new southward expansion of the moose range took place — up to 100-200 km in the east and west and 500-600 km in the central part.

By 1880, moose were widely distributed and in good numbers in the forest zone again: this status was maintained until about 1910 when it began to decrease again. World War I and the Civil War favoured the growth of poaching that adversely affected moose in a number of regions. For a short period of time, moose became almost extinct in many places. Thus, at the beginning of the 20th century, there were about 3,000 moose in Latvia and Estonia and by the end of the World War I it was estimated there were only 20 left. At the end of the 1920's in the centre of European USSR, moose density amounted to only a few individuals per 100 km^2 of forest area.

Recent population dynamics

In the early 1930's, moose numbers began to increase markedly due to government measures that had been taken to protect the species. The occupied range began to expand both north and south. The following rate of increase speaks for itself: in Byelorussia in 1927, the number of moose was approximately 150; in 1936, 380; in Lithuania in 1939, about 300; in Smolensk region in 1937 there were about 500 moose. During that decade, moose spread all over the forest zone, having reached rather high densities in some places. Unfortunately, detailed data on moose numbers at that time is lacking as a regular census of moose in the majority of regions of the European part of the Union did not begin until the end of the 1940's and the beginning of the 1950's.

During the 1940's, moose numbers continued to increase. This species inhabited the forest-steppe zone and, in some places, it spread into the steppe zone. In some regions the range expansion amounted to 100, 200 and even 500 km farther south than in 1928. Occupied range increased in the north also and reached as far as 65° N in the Urals.

In the second half of the 1940's, the average moose density (in animals/ 1000 ha of forest) in the central regions of the European part of the Union with predominantly mixed and coniferous forests varied from 0.8 to 1.0, in the northern coniferous forest from 0.6 to 0.7 and in the southern deciduous forest from 0.3 to 0.4 (Danilov, 1949). During this period, intensive moose movements to the southwest and south took place and moose appeared in the territories of eight regions of North Ukraine.

In the 1950's moose spread more widely in the forest-steppe zone. By 1952 they spread in the upper Dnieper and middle and lower reaches of the Volga rivers as well as in the Urals, where they moved well into the south and dispersed into the mountainous regions and the valley of the Ural river up to 55°E. (Heptner *et al.*, 1961). In the north, the limit of moose distribution evidently reached the forest tundra. At the same time, moose numbers increased in the western regions: in Byelorussia in 1952, the population amounted to 600-800 moose (Serzhanin, 1961). Numbers increased in the Baltic Republics too; for instance, in Estonia in 1950 a 52 percent increase over the previous year was reported (Ling, 1959).

The increase of numbers on vast areas along the southern edge of the range resulted in overpopulation of the moose habitat and the expansion of its year-round range still further south. They appeared beyond the previously established range limits more frequently and in a number of regions, their movements assumed the character of regular seasonal migrations. As a result of this, moose appeared in five areas, mainly in the steppes of the Ukraine, and in Volgograd and Rostov regions.

In comparison with the late twenties, moose numbers in some regions increased 20-50 times and they amounted to thousands of animals. Among others, the regions of Leningrad, Moscow and Kalinin are locations where this situation occurred. At the end of the 1950's, a further increase took place in most regions of the forest zone except the north taiga (Arkhangelsk Region, Karelia and Komi Autonomous Socialist Republics). It gave rise to a new immigration wave which was most pronounced in the eastern part of the steppe zone. Thus, moose appeared on the coast of the Azov sea. In the north, moose inhabited a strip of forest-tundra and then came out into the open tundra and reached the shores of the Barents and the Kara seas.

The average density in that decade was 0.4-1.7 moose/1000 ha in the northern taiga; 3.2 in the subzone of mixed forests and 5.1 near its southern limit. At the same time, densities fluctuated in the Urals from 1.2 in the southern mountain-forest part to 1.0 in the central part; in the eastern foothills of the southern Urals it was the least — about 0.3. In the northeastern steppe regions, densities in some places reached 0.4 per 1000 hectares of forest (Fig. 1).

In the early 1960's, in a number of regions of the forest zone, densities reached a peak. Overpopulation took place in all favourable habitats and a decline began because of still more intensive moose immigration into adjacents regions. It was particularly noticeable in the forest-steppe areas bordering on the steppes and in some parts of the central part of the forest zone. In the north and northeastern sectors of the forest zone, moose numbers increased simultaneously, with greatest increases in the latter.

In southern and central Urals a gradual rise in moose numbers was observed from 1960 to 1966; this was followed by a slight decrease but since

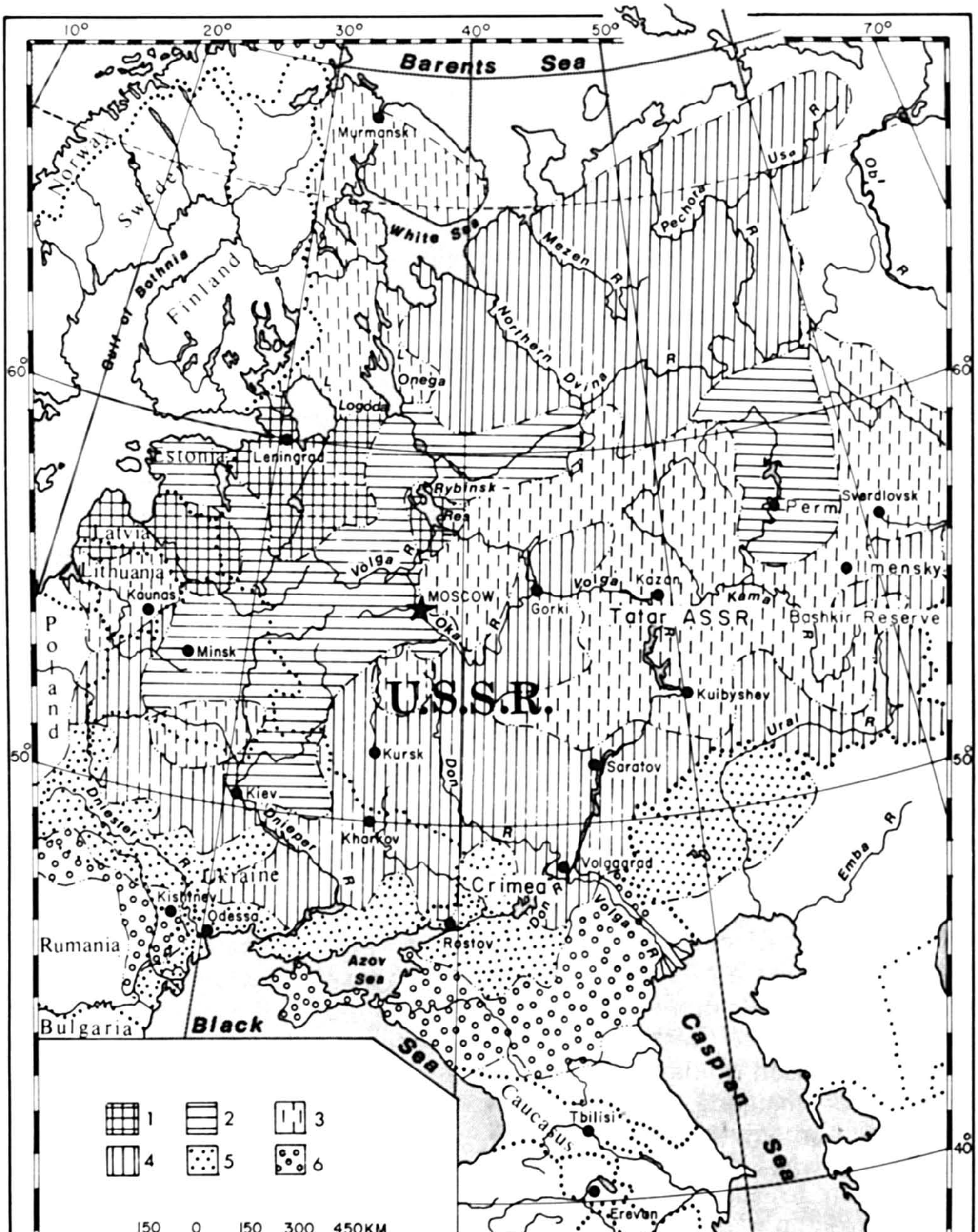

Figure 1. Average density (in number/1000 ha) during the period 1952-1961 in the European part of the USSR. Density code is: 1- more than 4.0, 2- between 3.1 and 4.0, 3- between 2.1 and 3.0, 4- between 1.1 and 2.0, 5- between 0.0 and 1.0, 6- presence of regular immigrants.

1970 the stock has begun to increase again. In the southern Urals, moose spread into the eastern foothills, e.g. forest-steppe and steppe areas bordering on Kazakhstan.

Maximum moose numbers in the Russian Soviet Federated Socialist Republic was recorded in 1962 and after that, there was a decline which lasted till 1968. At the same time an intensive spreading of moose into the steppe zone went on. Moose appeared in northwestern foothills of the Caucasus having moved over 300-400 km of steppe habitat. This wave of immigration swept seven other regions of the Ukraine and densities in some of them at present have reached carrying capacity. At the end of the last decade moose have turned up regularly in Stavropol Territory. In the west of Byelorussia and in the Baltic republics, moose numbers are still on the increase.

Average moose density for this decade fluctuated in the northern taiga forests from 0.6 to 1.8, in the northwestern part of the forest zone from 1.8 to 6.7; in the central area of the forest zone from 1.3 to 4.9; in the Urals, depending upon the geographic region, it varied from 0.5 to 1.8 (in animals/ 1000 ha of forest). In the southern part of the forest-steppe and north of the steppe itself, moose densities reached high numbers: in the eastern steppe zone they varied from 2.0 to 4.2 and in the west from 0.1 to 6.3 individuals per 1000 hectares of forest (Fig. 2).

In the early 1970's densities began to increase almost everywhere but they have not yet reached their former maximum level. Most likely this can be accounted for by the continuation of range expansion. The species is now found in quite new sectors of the European part of the country; in the Carpathians, in northern Moldavia, in the steppes of Crimea, and in the dry steppes and semi-deserts of Kalmykia, in flood-land forests of the Asktakhan region. The regions of maximum moose density in comparison with those of former decades are farther to the southwest and west of the forest zone.

Thus, in the early 1970's, the limits of moose range have reached, and in some places even extended further, those of historic times (Heptner *et al.*, 1961).

The causes of changes in moose numbers

Poaching and predation were the most important reported factors reducing moose populations. However, some known increases in moose numbers, for example, in the middle of the 19th century and in the 1940's, took place at a time when wolf *(Canis lupus)* numbers were high and when poaching was no less than ever. Thus, there is good reason to believe that the importance of predation and poaching may refer to those distant historic times when the stock of this species decreased or increased. In subsequent fluctuations of moose numbers both factors most likely contributed to declines caused by some other factors. When moose numbers increased, these negative factors (poaching and predation) could slow down the rate of growth, particularly in the early stages, but most likely they could not affect the overall trend.

The changes in forest vegetation as a result of forest fires or timber harvesting on vast areas were also considered a factor that influenced changes in moose numbers and densities. Thus, it is considered that large scale destruction of coniferous forests and their replacement by young, deciduous forests caused an increase in moose in the second half of the 19th century. Some scientists attribute the increase in moose numbers in the 20th century to the same factor.

The next increase in moose numbers that began at the end of the 1920's and the beginning of the 1930's took place under extremely favourable conditions. First and foremost, it was closely related to strict state controlled moose protection measures, active destruction of predators, wolves in particular, and good food resources on vast areas because of wood-cutting as well as fires in conif-

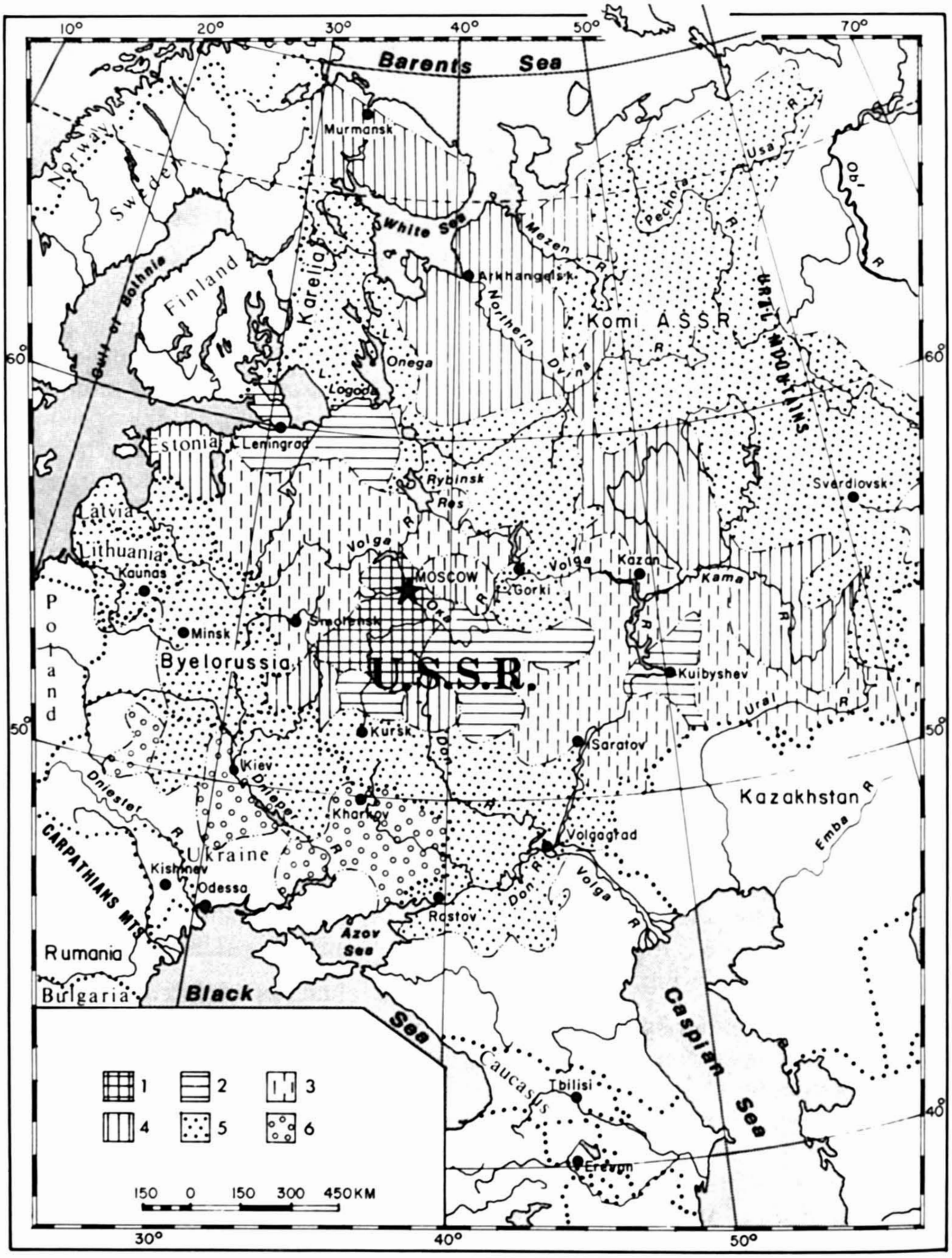

Figure 2. Average moose density (in numbers/1000 ha) during the period 1962-1971 in the European part of the USSR. Code as in Figure 1.

erous forests. The hunting ban at the beginning and underkill of moose in subsequent years favoured the progressive increase in moose numbers.

Nature reserves played a very important and positive part in moose conservation. At present, more than 30 reserves are established in the European part of the Union. Most of them are located in the forest zone. When moose numbers were low, these protected territories became the places of moose concentration. Moose density in reserves was always 5-15 times higher than in the adjacent areas.

In favourable habitats with low moose densities, numbers increased first and foremost because of an increase in fecundity and a reduction in the number of barren females. This all happened in a very short period of time of about 12 to 15 years.

The subsequent population increase, to an overpopulation level, worsened habitat conditions. As a result, reproductive rates fell while at the same time the tendency of populations to migrate was strengthened.

Moose from the Pechora basin may serve as an example of the points mentioned above (Shubin and Yazan, 1958; Knorre, 1959; Yazan, 1961). In 1949-1954 the average fecundity was 1.47 embryos per pregnant female; in 1955-56, 1.37; in 1957, 1.20; in 1958 and 1959, 0.96. This decrease in reproductive performance was accompanied by an observed increased tendency of moose to disperse to new ranges (in 1946/47, 100 moose crossed a 10 km strip of land during census and in 1956/57 — more than 1,000 were known to have done the same).

Females with two calves can be used as an indicator of fecundity as well. Observations on this factor were made in a number of local breeding grounds with increased moose density. For example, in Oksky reserve the number of females with two calves in overpopulated areas was reduced to 20 percent in 1962, although in previous years it had reached 86 percent (Zykova, 1964). Yurgenson (1964) observed a high percentage of females with twins in areas of rapid population increase (in Ulianovsk Region — 88.9 percent, Riazan'Region — 66.6 percent, Tatar Autonomous Socialist Republic — 51,7 percent). At the same time in places where the moose had possibly reached carrying capacity, the percent of twins was decreasing: in Mordovia to 13.3 percent, in Tula Region to 23.8 percent. As a rule, the proportion of barren females in such populations increased. In the basin of the Pechora River prior to 1955, barren females were not found among the killed animals while in 1957 they comprised 10 percent, and in 1959 — 30 percent. Evidently, in all these cases of moose overpopulation, intraspecific mechanisms regulating fecundity began to act.

Migrations

In many forested and non-forested areas, particularly in the regions bordering on areas of high moose concentration, the increases were explained mainly on the basis of migration. These were caused by changes in the life conditions of the animal: overpopulation, worsening of food resources and uneven distribution of snow cover. During the last 10-15 years, moose migrations have been noted in many regions of the forest and forest-steppe zones.

Intensive and regular moose migrations connected with snow depth and availability of food in different seasons were registered in the Urals (Knorre, 1959). Most of the moose inhabiting the right bank of the Pechora river migrate to the south and southwest from their summer habitats in the autumn-winter period. In winter, moose concentrate mainly in the watersheds of the Pechora, Kama and Vychegda rivers and in the northern Perm Region.

In the 1950's, a more intensive stream of migrants moved across the Pechora river in a section 150 km wide and the distance between the extreme points reached 300 km. In the autumns of 1956, 1957 and 1958, 1500-2000 moose crossed a 15 kilometre broad section here. In the 1960's, the scale of these seasonal movements was reduced and the most likely reason for this reduction was the overutilization of food supplies.

In the Perm Region (of central Urals), intensive seasonal moose movements as long as 150 km took place from the basin of the Vishera River to the east beyond the limits of the main Urals range across the mountain, Denezhkin Kamen'. In the 1940's, a few thousand moose migrated from the Perm Region beyond the Urals. At present in the north of the Sverdlovsk Region, at least four large wintering grounds for moose coming from Perm Region are known. In the southern Urals, moose make regular movements into the region of Bashkir reserve and Il'mensky reserve. In the former, during the autumn-winter period, moose move from the western foothills of the Urals across the Belaia river to the eastern part of the Urals range. The migration front reaches 50-60 km and its length is 150-160 km. As a result of these migrations moose density in Bashkir Reserve in winter time increases 15-20 times over that at other times of the year

In the northeastern part of the southern Urals, seasonal moose shifts are not so pronounced but have another character. That is, in the spring, moose migrate from the Urals to the east over the Il'mensky range and in autumn before the beginning of the rut they return.

Quite a different type of movement was noted in the 1950's on the border of the forest and forest-steppe zones and later in the forest-steppe and steppe zones. In some cases strict seasonality was observed after moose returned to their former grounds (from the steppe regions). As was shown in subsequent years, it was an important stage for the next immigration to unusual habitats — the steppe zone in particular.

Moose resources and their exploitation

Total moose numbers in the regions of the European part of the Russian Soviet Federated Socialist Republic (RSFSR) fluctuated approximately from 120-125,000 individuals in 1952 to 360,000 in 1962, but by 1971 they declined to 320,000. For the last 12-15 years, large numbers of moose have immigrated beyond the limits of the RSFSR to other republics. Thus, if we take into account numbers in the Ukraine, Byelorussia and Baltic republics, the total population in the whole European part of the Union in 1971 comprised about 380-390,000.

The average annual increase of moose in the RSFSR for the period 1952-1972 was equal to 5.8 ± 3.3 percent, varying from 10 percent between 1952 and 1961 to 2.5 percent between 1962 and 1971. The maximum increases were registered in 1957 (28 percent) and in 1962 (22 percent). Minimum increase was recorded in 1958 (0.4 percent). After 1962 the average annual increase has been insignificant and during the last decade population decreases have been recorded six times, varying from 2.3 percent in 1971 to 14.4 percent in 1965.

The reduction in average annual increase in the forest zone took place first and foremost in the areas of highest moose density. In the north-eastern part of the forest zone which has been occupied at maximum density since 1962, there was pratically no increase for the last 10 years (0.4 percent on average instead of 18.0 percent in the previous decade).

At the same time, in the regions of intensive moose immigration, an extremely high annual increase of moose stock was noted recently: in the western part of the forest zone, between 1966 and 1971, it averaged 20 percent per year with a maximum in 1967 of 54.5 percent over 1966; in the Ukrainian woodlands it averaged 10 percent with a maximum in 1967 of 16.7 percent and finally in the western part of the steppe zone it averaged 25 percent between 1966 and 1971 and in 1970, 58.8 percent over the preceding year. In the Urals in Perm Region only, the average annual increase rose from 1.7 percent between 1953 and 1961 to 5.8 percent between 1962 and 1971.

Among the factors affecting moose populations, hunting should be mentioned first of all. The effect of predators has been reduced in the last 15-20 years because of low densities of wolves. The bear's (*Ursus arctos)* influence is rather local.

Although annual legal moose shooting began at the end of the 1940's, too few moose are harvested to prevent an overall increase in moose numbers. In 1955 in the European part of the RSFSR, 2.3 percent of the total moose stock were shot. In subsequent years the moose kill fluctuated from 5.8 percent in 1961 to 7.0 percent in 1955. There is reason to believe that approximately the same quantity of moose perishes from other reasons.

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MOOSE INVENTORY METHODS: A REVIEW

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Résumé

Les techniques permettant d'estimer la densité des populations d'orignal (*Alces alces)* comprennent: le dénombrement des tas de crottins, l'analyse des âges et des sexes dans la population, les décomptes révélant les tendances saisonnières et les dénombrements aériens.

Les méthodes d'inventaires aériens font appel soit à des recensements complets sur toute une superficie donnée ou sur des places-échantillons établies au préalable, le long de transects, ou encore à des techniques photographiques conventionnelles ou sur émulsions sensibles à l'infra-rouge. En dépit des contraintes imposées par le type d'appareil, l'expérience du pilote et des observateurs, les conditions météorologiques et le moment du dénombrement, l'inventaire aérien reste néanmoins supérieur à l'inventaire terrestre en ce qu'un petit nombre de personnes est en mesure de couvrir de grandes superficies en peu de temps. Récemment, on a mis au point et on a éprouvé des techniques d'inventaires spéciales en Alaska, à Terre-neuve et en Ontario: l'auteur passe en revue ces techniques et compare leurs qualités et leurs défauts respectifs.

Abstract

Methods for estimating moose (*Alces alces)* population densities include fecal pellet counts, sex and age structure data, seasonal trend counts and aerial enumeration. Aerial census methods involve attempts to visually count moose on entire areas, on preselected plots, along transect lines and experiments with airborne conventional photography as well as infrared thermal imagery. Although the aerial survey has severe limitations including type of aircraft, experience of pilot and observers, weather conditions and time of survey, it nervertheless is superior to ground surveys in the short time in which a small number of observers are able to cover large areas. Recently, specific techniques have been designed and tested in Alaska, Newfoundland and Ontario: these techniques are reviewed and their strengths and weaknesses discussed.

Introduction

According to Geis (1971), sound game management and research require reliable estimates of animal population levels and their harvest composition. A completely satisfactory census method has not yet been devised for moose (*Alces alces).* Sample area counts on representative areas of habitat or range is presently the most commonly used tool. Due to moose behavioural habits and the type of forested habitat they prefer, accurate population numbers are extremely difficult to obtain. Moose do not yard or congregate in large numbers as do white-tailed deer (*Odocoileus virginianus),* but do tend to form aggregations in early winter. The size of the moose population, especially in accessible range is reflected in part by the size of the hunting kill and the frequency by which animals are viewed.

This paper reviews past and present moose inventory methods and some of their associated problems.

Ground surveys

PELLET GROUP COUNTS

Counting big game animal faeces to estimate population levels were first developed for deer in the late 1930's (Bennett *et al.*, 1940). Pellet group counts estimate either the actual or relative numbers of big game animals, or their days of use in a given area (Neff, 1968). According to Riney (1957), such counts can provide an objective measure of substantial population fluctuations, help determine preferred habitat types and seasonal use patterns. Neff (1968) provides a thorough review of the technique for big game trend, census, and distribution information and discusses its shortcomings and problems.

The primary use of pellet group counts for moose appears to be to obtain information on relative moose densities between areas or years. These indices can be used, along with aerial surveys and harvest statistics, to estimate trends in population levels. The underlying assumption is that the number of pellet groups counted in an area is closely related to the time an animal spent in the area (Neff, 1968).

In northern latitudes, pellet group surveys are usually conducted in early spring (April and May) immediately after snow melt and before full emergence of leaves. At this time the previous winter's pellet groups are lying on top of the autumnal leaf drop and are relatively easy to see.

Fecal material is classified as "winter" (pellets) or "summer" (non-pelletized). A subjective judgement is made by survey crews regarding "new" groups deposited the preceding winter or "old" groups deposited previous to that. (LeResche, 1970). Most survey plots are circles or rectangles and are distributed in some form of random or systematic design. Krefting and Shine (1960) developed a multiple — random — start systematic sampling technique for making deer pellet group counts in northern Minnesota. Krefting (pers. comm.) has subsequently used this system for moose pellet studies on Isle Royale. Pellet groups are usually deposited in a clumped rather than random pattern in preferred winter habitat (DesMeules, 1965; Neff, 1968). In such areas sampling has frequently been carried out along with browse or habitat surveys (Bergerud and Manuel, 1968; Simkin, 1961) on winter concentration areas or on permanently marked plots which are periodically cleared (Neff, 1968). Stratified random sampling as described for Michigan deer by Eberhardt (1960) is considered desirable whenever possible.

Problems associated with the pellet group technique include, observer bias and fatigue in counting groups, the small area actually sampled, rapid loss of pellets through insect attack and rain, decreased visibility of groups as vegetation advances, size of plot and type of surface terrain. Another problem is the determination of daily deposition rates. Human error, or observer bias is considered by Neff (1968) the thorniest problem. Careful standardization of procedure and rigorous adherence to standards are necessary to minimize this.

The average daily defecation rate has been a subject of considerable discussion since Edwards (1956) first suggested 14.9 groups per moose per 24 hours for animals in Wells Gray Park, British Columbia. Simkin (1959, 1961) and Macfie (1958a) used this rate in determining winter moose densities in Northern Ontario. Vozeh and Cumming (1960) revised the rate to 13.0 based on personal communications between Edwards and Cumming. This rate (13.0) has been widely used in Ontario (Close, 1968; Hall, 1964, 1965; Gibson, 1964a, 1971; and Armstrong, 1965) as well as by Ritchie in Idaho (pers. comm.). DesMeules (1968) reported an average rate of 21.5 depositions per day for two moose (11.9 by a cow and 9.6 by a calf) for a period of 11.3 days in Laurentides Provincial Park Québec. He suggested the use of an average of 10.7 depositions per moose per day based on these findings. LeResche (1970) estimated average daily rates to be 10.3 groups using Alaska's estimates of new groups in penned animals. A year later, LeResche and Davis (1971) revised the estimate to 32.2 groups per day from cleared plots in a 2.6 km^2 pen. Jordan (pers. comm.) indicated that his data on Isle Royale, when compared to aerial survey work, suggested a rate of 15.8 groups per moose per day. DesMeules (1965) found 14.9 depositions per moose per day in another winter yard in Laurentides Provincial Park. Gibson (1964b) suggested a rate higher than 13.0 to account for the unrealistic estimates of population obtained on Shakespeare Island, Lake Nipigon, Ontario.

The discrepancy in daily rates may be attributable in part to sampling error due to incorrect pellet aging (Gibson, 1964b; LeResche and Davis, 1971; and Simkin, 1959). DesMeules (1968) suggested differential defecation rates between cows with calves versus lone cows. Gibson (1964b) noted that diet may affect deposition rate. Smith (1964) has documented this for mule deer (*Odocoileus hemionus).*

In Ontario, pellet group counts have been used since 1958 as a standard technique for investigating winter moose concentration areas. Their use however has generally declined since 1967 due to many problems inherent in the methods which make interpretation difficult. The most important of these was the lack of any useful information on deposition rates (Cumming, pers. comm). Counts were usually conducted in conjunction with a standard browse survey using a modified survey method as described by Passmore and Hepburn (1955). Browse survey areas were normally determined from annual aerial inventories conducted during January and February.

Although it remains to be proven that pellet group counts provide reliable population estimates it is generally conceded that they do provide a good basis to compare relative densities between areas and from year to year on a single area.

DIRECT OBSERVATIONS

Experienced observers have carried out ground sightings of moose in various parts of North America. Pimlott (1959) reported that field staff in Newfoundland gathered 9,881 observations of moose (8,610 of which were identified by sex) in a six year period between 1950 and 1955 using record cards. Several other Provinces including Ontario (Peterson, 1955), Québec (Moisan, 1952), New Brunswick (Wright, 1956) and Nova Scotia (Dodds, 1963) have also used record cards. The major problem according to Pimlott was related to the ability of observers to segregate calves, bulls and cows. Minnesota used a postcard record which was filled out and mailed by field co-operators in the early 1960's (Karns, pers. comm.). Karns feels contrary to Pimlott that the data obtained was extremely worth while and collection may be continued in the future. Fire-tower men observed and tabulated the sex of animals sighted in Maine during the summers of 1965 to 1969 (Dunn, 1966; 1969). In Ontario, during the period 1949-1955, numbers of moose were estimated from trappers reports compiled annually for each Provincial administrative area (Reynolds, 1953; Cumming, pers. comm.).

The main weakness in ground counts is the difficulty in seeing moose in dense vegetation. In Alaska, LeResche (1972) reported that eight men spent 312 man-hours counting browsed twigs over a two week period in a moose enclosure but recorded only 21 moose mostly along cleared fencelines. Known densities in each pen averaged 46.1 per 10 km^2 (12 per mi^2).

Direct ground observations of moose in general does not provide reliable data on absolute population levels. Such data however can be useful in determining population trends and herd composition.

HUNTER HARVEST STATISTICS

Information on relative population levels of moose can be obtained from hunter harvest data. Hunter checking stations represent an excellent source of information on some management areas. Both Ontario (Timmermann, 1967; Hagan and Saunders, 1970) and Saskatchewan (Quinn and Runge, 1970; Quinn and Wiltse, 1971) have employed results of such check stations. Manitoba has recently used check stations, Conservation Officers records and a telephone questionnaire for local hunters (Hahn, pers comm.). Krefting, (pers. comm.) indicates that kill statistics work quite well as a population trend determinator in Norway and Sweden. Saskatchewan (Balez, 1969) and Ontario (Barbowski, 1972) both use a mail questionnaire survey based on a sample of licenced hunters.

Harvest quotas for Montana are determined in part by range conditions, age structure of the harvest and past hunting success (Schladweiler, pers. comm.). Lykke and Cowan (1968) feel that total kill is only broadly indicative of population, and gives no indication of the fluctuations in effort that went into the success achieved. The length of the hunting season as well as licence fee increases can have a very marked effect on harvest statistics. Both Peterson (1955) and Pimlott (1961) felt data in most parts of North America where hunting pressure is uneven and access to vast areas of moose range is difficult to be little better than rough trend indicators.

Another, and perhaps quite sensitive indicator of the relative size of the population is to be found in the percentage of bulls in the hunters take (Lykke and Cowan, 1968): "In Norway, a high bull percentage indicates a good moose population in relation to hunting pressure, the reverse occurs during a population decline." The Norweigan bull proportion has averaged 55.5 percent with fluctuations from 50 to 60 percent in normal years. However, Sweden has maintained a mean bull fraction of 54.5 percent despite the rapid increase in total kill.

In future, there may be a potential for indirect population estimation of moose based on survival and reproduction or by the change in ratio method developed for Michigan deer by Eberhardt (1960). This type of comparison to estimates of absolute populations obtained by other means can be made by using an index or relative measure of population trend.

Aerial surveys

DIRECT ENUMERATION

One of the first attempts at counting moose from the air was by Bowman

(1955) in Ontario during July 1949. Although Bowman was able to see moose mainly along water courses, much work was necessary before an acceptable field technique could be developed and applied.

Transects

The transect or strip method of censusing moose usually involves parallel flights along preselected azimuths at a constant altitude over snow covered ground. Banfield *et al*. (1955) have summarized the strip census method generally used. In Ontario, the transect method was originally conducted in a 4-seater DeHavilland piston Beaver aircraft. A crew of four men consisting of pilot, a navigator, and two observers was used (Trotter, 1958). Flight lines running north and south were laid out on a map of the area to be surveyed. The desired degree of coverage dictated distance between transects. Flying was done at an altitude of 250 m (800 feet) at an air speed of 140 km (90 mi) per hour. Moose were spotted by the two observers. The navigator's duty was to see that the aircraft followed the flight line and to record the location of the moose observed.

One of the basic problems in using the transect method is in the determination of the width of coverage. Moose are usually counted in a strip 0.2 km (0.125 mi.) wide on either side of the aircraft (Saugstad, 1942; de Vos and Armstrong, 1954 and Rausch and Bratlie, 1965). In Maine, Dunn (1966) used a total strip width of 0.5 km (0.3 mi.) to compute the total area covered. The angle of sight is used to determine transect width (Saugstad, 1942; Edwards, 1952). In this method, the observations are limited to a definite field, the outer margin of which is marked by guides — one on the window and the other on the strut of the aircraft (Banfield *et al.*, 1955). Transect width is calculated from the tangent of the fixed angle and a fixed altitude.

Aldous and Krefting (1946) made the first estimates of moose numbers based on transect lines on Isle Royale, Michigan. Population estimates were based on the percentage of the total range sampled. Mech (1966) employed a similar method in a later count. Similiar use of transect lines and the problems associated with their use have been reported for British Columbia (Edwards, 1952, 1954; Martin, 1952), Alaska (Spencer and Chatelain, 1953; Bentley, 1961), Ontario (deVos and Armstrong, 1954; Peterson, 1955; Trotter, 1958; Fowle and Lumsden, 1958), Maine (Dunn, 1966), Saskatchewan (Quinn, 1971; Hope, 1972) and Alberta (Lynch, 1971).

The transect method was discontinued in Manitoba in 1971 according to Jahn (pers. comm.) because the results obtained lacked the necessary accuracy needed to provide information of use for management. Ontario reached the same conclusion (Fowle and Lumsden, 1958) due to variable results obtained on the Province's relatively closed forest cover and discontinued its use in favour of the intensive search method (Trotter, 1958).

Aerial transects have also been used as a method of obtaining indices of density for different areas. This procedure was used to stratify areas prior to random quadrat sampling in northern Minnesota (Karns, 1967), northwestern Ontario (Addison, 1971), central Alberta (Lynch, 1971) and Alaska (Evans *et al.*, 1966). The State of Maine has used line transects since 1965 to define relative population levels of moose as a basis for establishing a legal season (Dunn, 1971).

Complete counts of selected plots

Aerial surveys of randomly selected plots were first introduced by Ontario in 1958 (Cumming, 1957; Lumsden, 1959). Population estimates were based on the number of moose actually observed plus those estimated to have been present but not seen on each 65 km^2 (25 mi^2) plot. This technique of counting commonly referred to as the intensive search or orbiting method described by Trotter (1958) formed the basis for the first province-wide survey of moose in Ontario (Lumsden, 1959). Recently Lynch (1971) in Alberta, Evans *et al.* (1966), in Alaska, Bergerud and Manuel (1969) in Newfoundland and Mantle (1972) in Ontario have used intensive search on randomized quadrats or blocks 2.6 km^2 in size. Quadrat or block sampling generally tends to give higher estimates than obtained by flying transects or linear strips Lynch (1971) reported that in Alberta only 67 per cent of the moose observed on block surveys were spotted during straight line counts. Evans *et al.* (1966) in Alaska estimated only one-fourth as many moose were seen in a given area surveyed using linear strips as compared to intensively searching quadrats.

The method basically consists of dividing the area to be censused into strata on the basis of population densities previously determined, gridding each stratum into sampling units of a given size, randomly selecting a number of sample plots in each stratum and intensively searching each plot.

The major problem in counting moose in forested habitat is determining the number not seen. In Alaska, LeResche and Rausch (1974) were able to quantify the accuracy and precision of aerial censusing using controlled experiments. Many factors affect this accuracy and precision when visually counting moose.

The type of aircraft used is all important. The characteristics of aircraft best suited for aerial survey work include maneuverability and slow flight capabilities. Adequate horsepower and weight to minimize the effects of wind is also desirable. A speed range of 104-144 kilometres per hour (65-90 mi per hr.) at an altitude range of 60-240 m (200-800 feet) is considered ideal. In North America, the Supercub aircraft seems to best fit these specifications (Evans *et al.*, 1966, and Bergerud and Manuel, 1969). Larger aircraft including the Cessna 180 and both the piston and turbine powered DeHavilland Beaver are regarded to be too fast and heavy for intensive searching (Bergerud and Manuel, 1969). Helicopters have the advantages of low speed, low cruising height, excellent visibility, and ease of handling. However they have a limited range and are much more expensive to charter than fixed wing aircraft. The pilot's abilities are virtually as important as the type of aircraft employed.

Confidence intervals on the estimate of moose actually seen depends on the variability in numbers between plots and the number of plots surveyed (Addison, 1970). Plot size can affect total counts. Both Bergerud and Manuel (1969) and Evans *et al.* (1966) favour smaller plots of 2.6 km^2 because of less observer fatigue and their precision in boundary determination. Larger plots however may reduce the bias of edge effect. The variance about the mean number of moose per plot tends to decrease with larger plot size. Smaller plot size conversely should tend to increase the variance (Addison, pers. comm.) "For any given sampling effort there should be an optimum solution to the selection of plot size and plot numbers.

Census plots should be large enough to represent cross sections of micro-habitats or be stratified" (Addison, pers. comm.) Evans *et al.* (1966) felt that stratification of range into high to low density strata would help account for variance found in a heterogeneous distribution pattern. This could reduce the variance and thus reduce confidence intervals. Bergerud and Manuel (1969) pointed out that plots should not include so many animals that accuracy is lost and should not produce too many zero plots. Broad confidence intervals obtained from a high number of zero plots are usually due to the fact that moose distribution is generally contagious rather than random. Addison (1970) submitted that samples are seldom sufficiently large to reduce the confidence interval to less than ± 30 percent. This large spread in population estimate, which may account for only a fraction of the actual number of moose is caused by the inability to see all the animals persent.

In Newfoundland, Bergerud and Manuel (1969) estimated the number of present but uncounted animals on each plot by multiplying the number of areas with tracks by the mean observed aggregation size. Their goal was to combine track and animal counts into the overall population estimate. They accomplished this by justifying the inclusion of a mean size of aggregation. "However their result is simply en estimate of the mean number of moose per plot (or per square mile) without any measure of the confidence limits" (Addison, pers. comm.). Broad confidence limits if calculated still apply to this type of estimate. Calculations by this method for data from the Shabotik study area in the White River district of Ontario showed an increase of the mean by 20 percent. "This was not a significant increase ($P < .05$) over the mean calculated without the inclusion of tracks" (Addison, pers. comm.)

The observers ability to see animals is extremely important in serial censuses. In the past many workers have attempted to estimate the proportion of moose seen. In areas of dense forest cover, visibility may be as low as 40 percent (Addison, 1970) while in more open areas it may approach 70 to 80 percent (Pimlott, 1961; Edwards, 1954). Under ideal weather conditions in Alaska, 49 observers flew 74 replicate counts over four fenced 2.6 km^2 moose enclosures (LeResche and Rausch, 1974). They noted that experienced and inexperienced observers flying 15 minutes over each enclosure saw 68 and 43 percent, respectively of the moose present.

Many factors affect visibility. These include past and recent observer experience, number of observers, weather conditions, habitat and terrain, time of day, and relative moose densities. LeResche and Rausch (1974), discuss each factor in relation to the accuracy of counts derived from a known number of penned animals in representative habitat and conclude that census conditions must be ideal and as nearly constant from year to year to obtain counts which are valid trend indicators.

After much trial and error the following criteria have been identified as important to obtaining a reliable census: 1) Counts should be made within a short period of fresh snowfall (5 days), 2) Clear or lightly overcast days are preferred, 3) Wind speeds less than 10 knots, 4) Counting periods should be restricted to short periods of 2-3 hours during midday (10:00 to 14:00 hours), 5) Only currently experienced observers and pilots should be used, 6) Sufficient time should be allotted to fully search each plot (e.g. a minimum of 15 minutes per 2.6 km²), 7) Accuracy can be increased by using more than one observer and including animals tallied by the pilot, 8) Maximum counts in most forested habitats can only be secured in late December, January and February before moose shift into heavier cover (Vozeh and Cumming, 1960; DesMeules, 1964; Bergerud and Manuel, 1969).

Complete counts of selected plots invariably underestimate the actual population. The use of an expansion factor to account for animals not seen may be misleading. Variability in successive counts of the same area over a winter period has been well documented (Vozeh and Cumming, 1960; Addison, 1970; and LeResche and Rausch, 1974). Table I demonstrates the variability in counts that can occur during repeated surveys of the same sample area (Addison, 1970).

In summary, there is no doubt that counting moose from aircraft while moose are on their winter range is presently the most practical way to estimate moose numbers in most North American ranges. There are, however, many variables which affect accuracy and precision, most of which are not easily quantifiable. Population data thus obtained are best treated as trend indicators and not as absolute numbers. Allowable harvest levels should not be set on the basis of aerial census data alone.

AERIAL SURVEYS VERSUS PELLET GROUP COUNTS

Pellet group counts have been used in conjunction with aerial surveys to indicate moose population trends in many North American moose ranges. Krefting (pers. com.) has made periodic pellet group counts on Isle Royale from 1948 to 1970 and finds them a valuable tool in determining population trends as well as patterns of winter habitat use. Pellet counts have been used on a limited basis in the Superior National Forest in northern Minnesota during the mid 1960's on plots which have been flown the previous winter (Karns, pers. com.). Results generally agreed with aerial observations when using a deposition rate of 13.0 per day. Jordan *et al.* (1972) have used pellet counts in conjunction with aerial surveys to study the herbivore-vegetation and predator-prey relationships on Isle Royale. Heavy clumping around blown down trees which moose stripped of bark has resulted in estimates in excess of 3.8 animals per 1.0 km² (10 per mi²) on some areas.

Even under ideal conditions, aerial estimates tend to be conservative when compared to pellet group counts. Sim-

TABLE I

Seasonal variations in the Moose count on the Englehart Management Unit, in the Swastika District of Ontario

Year (winter)	*Month*	Number of moose		*Total*
		N. Sector	*S. Sector*	
1964-65	Dec.	32	34	66
" "	Jan.	14	14	28
" "	Feb.	14	12	26
" "	Mar.	8	10	18
1967-68	Feb.	60	50	110
1968-69	Feb.	—	—	59

kin (1959) estimated nearly twice the density of moose in one study area using pellet group counts as obtained by aerial survey methods. He concluded that pellet group counts collected in a similar manner in different areas provide a useful index to moose numbers rather than an absolute population estimate. Gibson (1971) compared both pellet group counts and aerial counts on Shakespeare Island, Lake Nipigon (Ontario), before and five years after hunting had been permitted. Pellet counts indicated a 96.4 percent decline in moose while aerial counts indicated a 95.8 percent decline.

A comparison between mean estimates of a moose pellet group survey and an aerial survey in the Kenora Forest District (Ontario) in 1970 suggests that 50-59 percent more moose were estimated by the pellet group survey. In a more dense forest cover area of the district a range of 300-400 percent as many moose were estimated by pellet group counts when compared to aerial census surveys (Gustin, 1973).

Vozeh and Cumming (1960) recommended that a series of aerial counts be taken and averaged if a true comparison of the pellet group count is desired. It is suggested that the large differences which can be obtained are due to the fact that, usually, a single aerial count was compared with the calculated average winter population obtained from pellet counts. They illustrated their point by showing that the mean count from 12 winter aerial surveys was well within the 95 percent confidence limits obtained from pellet group counts on the same area.

Gustin (1973) has recently used the pellet group technique to estimate population densities of moose on a land area of 16,900 km^2 of suitable moose habitat in the Kenora Forest District of Northwestern Ontario. He estimated the total population of moose to lie between 11,440 and 13,520 at the 95 percent confidence interval (6.8-8.0 moose per 10 km^2). Aerial survey estimates for the entire district (31,650 km^2 or 12,173 mi^2) indicated a range of 0 to 25,685 with a mean of 7,182 (0-8.1 per km^2). Table II demonstrates the variability in estimates that can occur.

INDIRECT ENUMERATION

Track counts

Winter census of moose by counting tracks on transects has been used extensively over large areas of the Soviet

TABLE II

A comparison between aerial surveys and pellet group counts results in various moose censuses

Location	*Population estimate (moose per 10 km^2)*		*Comparison factor*
	Aerial survey	*Pellet groups counts*	
Idaho[a]	23.1-28.8	38.4	1.0-1.3, 1.7
Ontario[b]	5.3	36.1	1.0-6.8
Ontario[c]	3.8	43.5-63.8	1.0-11.4, 16.8
Ontario[d]	12.7	25-51.5	1.0-2.0, 4.1
Ontario[e]	7.7-30.8	15	1.0-2.0, 0.5

[a] Ritchie (pers. comm.)
[b] Close (1968)
[c] Hall (1964 and 1965)
[d] Gibson (1964a)
[e] Macfie (1958b)

Union (Semyonoff, 1956 and Priklonskiy, 1968). Tracks of animals such as moose can be clearly seen from low flying aircraft. Fresh tracks are usually clear-cut with sharply defined shadows while old tracks have indistinct outlines and soft shadows (Bentley, 1961).

Track counts have been used to estimate the number of moose missed by direct observation. Bentley (1961) in Alaska, estimated from fresh tracks that for every moose seen, three or more were missed. It is usually assumed that areas of daily activity of groups or single animals are distinct and only occasionally do groups of tracks overlap. This of course depends largely on how soon after a major snowfall the survey is carried out.

In Ontario, Gawley and Dawson (1965) found little correlation between track indices and actual numbers of moose observed. They concluded that although the system might be valid under optimum weather conditions with 10 to 15 cm (4-6 in) of new snow and absolutely clear weather; these conditions are infrequently encountered and the continued use of the track index technique to determine relative moose densities was not recomended. A similar survey in Alaska in 1962 was abandoned due to difficulty in estimating the area of daily activity and interpreting the data (Evans *et al.*, 1966). Minnesota used track counts to determine moose distribution.

Perhaps the best use for track counts is the determination relative density levels for stratifying range, prior to direct counting.

Aerial photography

Aerial photography has witnessed many advances during the past 20 years. Smaller cameras, which use a variety of colour and black and white emulsions have received increased attention as a practical and economical remote sensing technique.

In Ontario, Passmore (1963) submitted that winter aerial photography held promise as a moose census tool. He indentified the chief requirements as: 1) photographs be of a scale of 48m to one cm (400 feet to the inch) and 2) they should be taken 36 hours after snowfall on bright days in March between 10:00 and 14:00 hours.

These conditions are difficult to obtain. Moose become more difficult to observe either to the eye or with the camera as they frequent coniferous cover in late winter (Banfield *et al.*, 1955; Vozeh and Cumming, 1960; DesMeules, 1964; and Bergerud and Manuel, 1969). Passmore's ideas are generally not accepted as a census technique due to such problems as: 1) accurate determination of scale and strip width; 2) unfavourable light and atmospheric conditions; 3) lack of knowledge on daily activity patterns of moose in various habitats; 4) photo interpretation and 5) difficulty in replicating the survey flight path.

The advantages of aerial photography include a permanent record of animals censused, moderate cost of film using modern miniature cameras and the large area of range which can be covered in a relatively short time period.

Infrared thermal imagery

Infrared scanning equipment which detects and records heat rather than visible light holds great promise as a big game censusing technique. Croon *et al.* (1968) demonstrated the first actual success in censusing white-tailed deer in Michigan on a snow covered 5.2 km^2 (2 mi^2) area of very open deciduous habitat. Graves *et al.* (1972) in Pennsylvania found that for deer, limitations of the equipment used made large scale aerial surveys using infrared detection equipment impractical unless the census area is flat and relatively free of obstructing vegetation. McCullough *et al.* (1969) summarized the progress made in large animal census by thermal mapping and discussed problems and limitations of the system. The salient points were: 1) Foliage presents a barrier to infrared; 2) Infrared is presently more applicable to open range lands, tundra, low brushy areas or defoliated deciduous forests; 3) Variations in weather conditions, apparent temperature of animals and the variability in temperature of inanimate objects in the background affect performance; 4) A pilot, an aircraft the size of a Cessna 180 or larger, an equipment engineer and a skilled interpreter are required; 5) The equipment is very expensive.

In Ontario, infrared thermal imagery was tested as a fire detection device during the late 1960's. It was hoped that high equipment costs could partially be offset by using the scanner as a big game census tool during the winter months. Addison (1970) used an infrared line scanner in an attempt to census moose in Northwestern Ontario. Cold temperatures in the cabin of the aircraft caused malfunctions in the electrical equipment. "Moose were included in some of the imagery, but at a point just prior to scanner failure as the critical temperature of -10°C (14°F) was reached" (Addison, 1970). LeResche (pers. comm.) has tried an infrared scanning device and found it entirely unsuccessful for counting moose in Alaska.

Many problems are inherent in the use of infrared thermal imagery for moose censusing. Infrared radiation does not readily penetrate green foliage so, evergreens present an effective barrier, (McCullough *et al.*, 1969; Addison, 1972; Croon *et al.*, 1968 and Graves *et al.*, 1972). This problem can partially be overcome by censusing in the winter months when deciduous foliage is absent and moose are mainly in less dense coniferous and deciduous forest habitat.

Addison (1972) maintained that increased knowledge of moose behaviour and seasonal habitat preferences are necessary prerequisites to the use of infrared imagery in the estimation. Weather conditions including wind velocity, humidity, amount of solar radiation, and background temperature all influence the differential amounts of heat emitted by the animals and their background. Addison (1972) suggested that a manual gain control system would allow the enhancement of the animals image to make identification possible in open canopy. Interpretations of imagery can be difficult as objects of similar temperatures to moose are indistinguishable from the animal (Addison, 1971). The system, however, has the advantage of being consistent and can be adapted to the strip census. Further, its permits coverage of larger areas than is possible using visual methods during the same time period.

Continued improvement in infrared technology is certain in the future and the results to date suggest cautious optimism toward air-borne thermal infrared systems as a censusing technique for big game.

Discussion

Overton and Davis (1969) state that the goals of population estimation should be two-fold. The first should be to derive the best estimate possible, commensurate with the study objectives, while the second should to examine the precision of the estimate — how well the assumptions are met and the effect of sampling error. The diversity of moose ranges across North America in itself suggests that methods of census should be designed to fit the situation.

In summary, I suggest that no single source of information should be used to assess population trends. All sources available should be carefully weighed to obtain a composite picture of population levels. Depending on the amount and accuracy of such information, there will probably be areas showing decreasing population trends and others showing static or increasing trends. Management policies and programs to meet the various objectives will then have to be tailored accordingly.

In the future, more intensive management will require more accurate estimates of moose numbers. Methods must be more refined and accurate in order to more precisely predict the influence of increasing human activity on the resource. Ecological impact studies will become increasingly important and inventory surveys will have to provide information upon which to base intelligent resource decisions. The orbiting method of aerial census, when properly carried out, is probably the best available technique. We should however work towards some uniformity in application of this census technique. Moose range should be stratified into types with real differences in carrying capacity. Separate aerial surveys should be conducted in various parts of the range to obtain calf-adult ratios and sex ratios of adults as soon as sufficient snow for counting is available.

The future challenge lies in improving and perfecting more accurate methods of population inventory and using such information as a basis of a management program designed to ensure an optimally used and healthy moose population.

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MOOSE HARVESTING PROGRAMS IN CANADA

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Résumé

Les statistiques de chasse révèlent que le nombre d'orignaux (*Alces alces*) récoltés par les chasseurs au Canada a augmenté entre 1951 et la fin des années '60. Elles révèlent la présence d'une forte hausse dès l'élargissement de la réglementation restreignant la chasse aux mâles seulement; mais, même au Yukon et dans les Territoires du Nord-Ouest où la chasse est encore limitée aux mâles, le rendement n'a cessé de croître. On assiste maintenant à un plafonnement et, dans certaines provinces, à une légère diminution du rendement. Les moyens utilisés pour influencer le niveau de la récolte sont les suivants: durée de la saison de chasse, périodes distinctes pour la poursuite des mâles et des femelles, interdiction complète de la chasse et contingentement des chasseurs. Trois critères aidaient à déterminer dans quelle mesure on s'approchait du rendement maximum potentiel: stabilité dans le rendement de la chasse d'une année à l'autre, égalité du rapport des sexes et proportion élevée de jeunes animaux (veaux et animaux de 1.5 an) dans la récolte. La réglementation actuelle semble convenable s'il s'agit de maintenir le rendement près de l'optimum, mais on souhaiterait pouvoir atténuer les fluctuations dans la récolte d'une année à l'autre et augmenter la proportion de veaux abattus. Dans les provinces où les deux sexes font l'objet de la chasse, les mâles sont généralement un peu plus abondants que les femelles dans le produit de la chasse. L'établissement de saisons de chasse distinctes pour les mâles et pour les femelles a favorisé une augmentation des possibilités récréatives offertes au public. L'auteur remarque que les programmes d'aménagement semblent mettre peu l'accent sur la qualité de la viande et souhaite que le public prenne une part plus active dans l'énoncé des objectifs d'aménagement.

Abstract

A survey of moose (*Alces alces)* hunting statistics showed that there was an upward trend in Canadian moose harvests from 1951 to the late 1960's. Harvests showed large increases when either sex seasons replaced bulls only seasons but in the Yukon and Northwest Territories, harvests rose even though they continued to harvest only males. There has been a recent levelling or downward trend in the harvests from some provinces. Methods used to control harvests are season length, different seasons for male and female moose, closed seasons, and restrictions on the number of licences issued. Three criteria were used to determine whether maximum sustained yield was being attained: small yearly fluctuations in the harvest, equal sex ratios in the kill and a harvest containing a high proportion of calves and yearlings. Present regulations appear adequate to achieve harvests which are generally compatible with a maximum yield objective but a better control of fluctuations in the kill and an increased harvest of calves is needed. Sex ratios in the kill have been only slightly skewed towards males in most provinces where both sexes are hunted. Different seasons for males and females have been chiefly instrumental in increasing the amount of recreation. There has been little consideration to obtaining quality meat in the harvest. There is a need for more public involvement in formulating objectives.

Introduction

Harvest regulation has been the chief management function of Canadian moose biologists. They have accomplished little in the way of habitat protection or improvement for they have seldom been in a position to control the use of forested lands which produce moose.

The harvest regulatory function is vitally important because it influences the quality and quantity of both recreational experiences and harvested animals. Canadians annually obtain approximately 1.5 million days of hunting recreation (extrapolated from Pearse-Bowden, 1972) from the moose resource and the harvest represents nearly 30 million pounds of meat.

This paper compares results of harvest management procedures across the country through a survey of kill statistics, hunter success records, and current hunting regulations. I hope that the survey will provide managers with an insight into the implications of following various alternative patterns of regulatory management.

Tradition is important in determining hunting methods, season opening dates and attitudes towards harvesting antlerless animals and because of this, management is often less rational than would otherwise be expected. In this paper I have ignored the possible influence of tradition and political pressures in directing programs, concentrating instead on the results of these programs.

RECENT HISTORY

Moose populations in Canada during the 1940's were considered to be low from the Maritime provinces to Alberta (Hatter, 1949; Peterson, 1955). Most provinces had closed seasons on moose or restricted hunting to bulls only (Table I). Populations were probably much higher than believed for later estimates were increased with better knowledge of moose densities (Cumming, 1974). In 1964, British Columbia estimated its moose population at 300,000 (Robinson, 1964) and in Alberta, Pattison (1970) reported a population of 63,000 in Zone I in the northern part of the province. These two estimates exceed that for all of Canada reported by Peterson (1955).

Over-hunting probably had occurred in acessible areas but the figures for harvests do not suggest that legal hunting could have depressed moose numbers over all of Canada. No ecological reason has been advanced which would explain the low population status re-

TABLE I

Recent moose hunting seasons in Canada

Region	*Years of closed seasons*	*Season re-opened on females*
Alberta	1950-1951; 1953-1954	1959
British Columbia	none	1952
Manitoba	1945	1953
New Brunswick	1936-1959	1966
Newfoundland	to 1945	1952
Northwest Territories	none	not open
Nova Scotia	1938-1962; 1964	1965
Ontario	1949-1950	1955
Québec	none	1964
Saskatchewan	1942-1945; 1947-1952	1953
Yukon	none	not open

ported by Hatter (1949) for most of the country.

By the 1950's, it became evident that the mere protection of populations was no longer a valid objective. Therefore, most of the major moose producing provinces re-opened hunting seasons (Table I), while those with open seasons modified them to allow the hunting of both sexes rather than restricting the harvest to males.

NEW OBJECTIVE

A new objective emerged in the 1950's, that of "maximum sustained yield." The objective is inappropriate for the regulation of harvests from local populations as it implies stability of yields: moose are most abundant in early stages of forest succession and therefore, numbers will fluctuate locally with time. For moose populations dependent on areas approaching an unsuitable stage of succession, a planned depreciation of the yield would be the correct harvest management. Stability of yields can only be achieved if early successional stages are constantly being replaced. Therefore in this discussion, I will use the term 'maximum yield' to infer that yields are maximized over a period of time. The maximum yield objective was also deficient because it did not specify the sex, age or condition of the harvested animals. In spite of these deficiences, the objective was embraced by most game managers of the era.

A solid theoretical background for maximum yields was made available by Scott (1954) who reviewed the major studies of population growth and the theory of yields from fish populations, pointing out their application to the management of ungulate populations. The example of Scandinavian managers (Skuncke, 1949), was probably a major factor in bringing about a change from harvesting only bull moose to hunting both sexes in Canada.

HARVEST INCREASE

Harvests more than doubled in 4 provinces in the 1950's after the hunting of antlerless moose was permitted, and rose rapidly until the late 1960's, when a levelling trend became apparent (Fig. 1). In the Yukon, where antlerles seasons were not introduced, harvests rose almost as rapidly.

In some provinces, Newfoundland for example, logging was responsible for producing more moose (Pimlott, 1953; Bergerud and Manuel, 1968). In others, increased harvests were due to better access, more hunters, and the introduction of antlerless seasons.

Harvests in British Columbia rose steadily in the 1950's, while populations were declining over much of the province. Regenerating forests on large burns of the south central interior which had produced much of the harvest were aging beyond their peak of ability to sustain moose (Hatter, 1949). New burns did not occur because most of the fire susceptible areas had already been burned and because fire suppression techniques were improved. The area burnt annually in the south declined about 50 percent between 1936 and 1970. In the north, control was not effected until about 1960.

Harvests increased on a provincial basis because hunting seasons were gradually liberalized while access to populations in central and northern regions was improved. Data from British Columbia hunter sample shows that in 1950, over half of the moose kill occurred in the area south of Quesnel (in the southern 1/3 of the province) but by 1969, less than 1/4 of the harvest occurred there. Similar pioneering' probably took place in the prairie

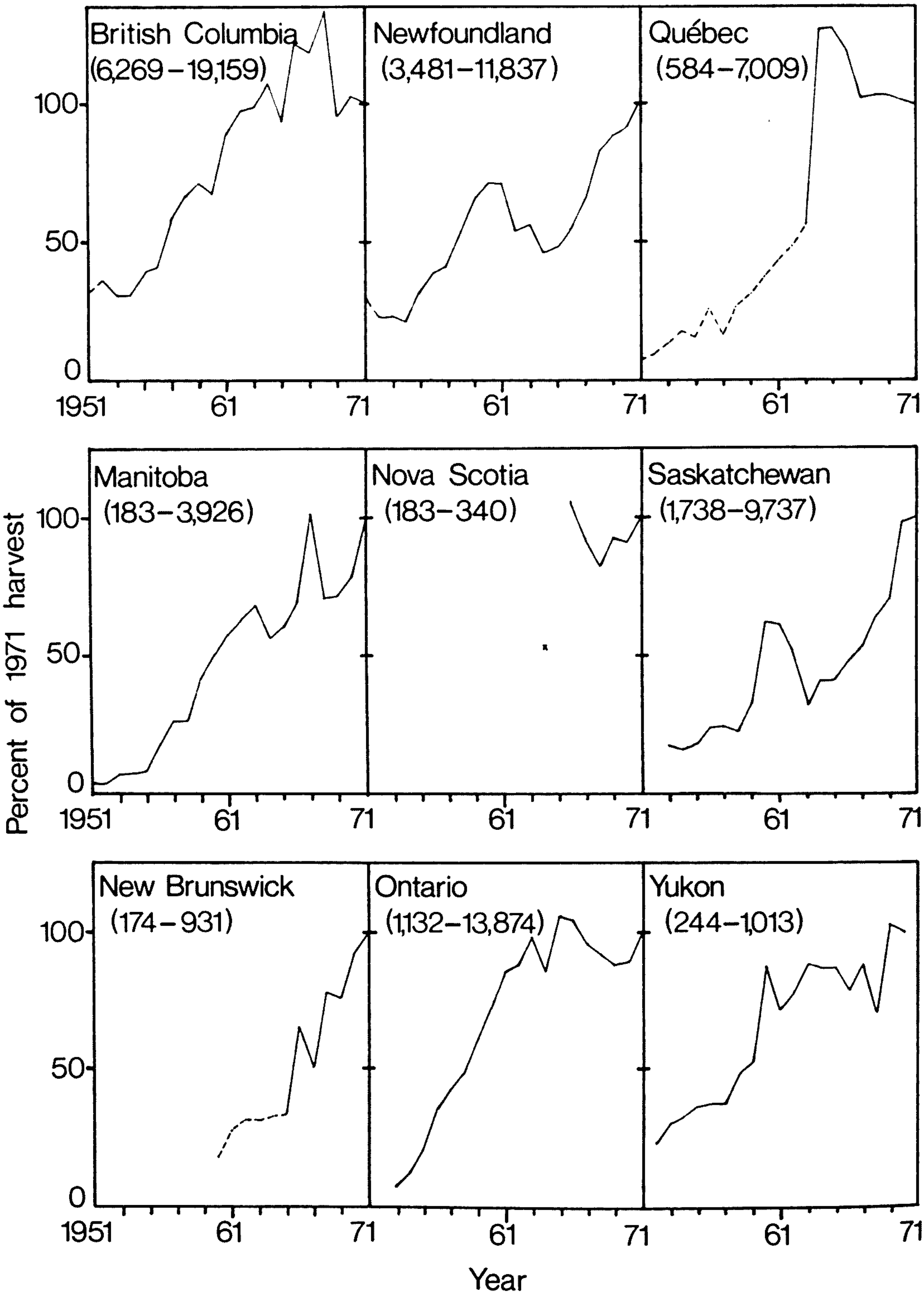

Figure 1. Provincial moose harvests between 1951 and 1971. Broken lines indicate periods of bull only regulations.

provinces where increased exploitation of the boreal forest was responsible for better access (Telfer, 1972).

In New Brunswick and Québec, antlerless seasons were not introduced until the 1960's. Hunters had already been provided better access so there were more dramatic increases in harvests with the change from bulls only to any moose seasons.

Managers then had markedly increased harvests through the introduction of seasons on antlerless moose. To offset the threat of overhunting, provinces and territories were subdivided into a number of management units, protecting accessible areas with restricted seasons while allowing liberal seasons in the hinterlands. Some provinces attempted to control harvests by varying season lengths, while others, Ontario in particular (Cumming, 1974), favoured closing the season completely for times or areas of scarcity. In the west, managers sought to manipulate the sex ratio of the kill as well as the total harvest imposing long seasons on bulls and only short seasons on antlerless moose. Harvest control by limiting the number of licences issued has been a later innovation although Newfoundland used this method as early as 1935.

Conditions for maximum yield

Because maximum yield was the apparent objective of most administrations for the period 1960-1971, I attempted to use kill statistics to judge whether this was being realized. It was assumed that three conditions must exist if maximum yield is being attained:

1. Harvests should show small yearly fluctuations.
2. The sex ratio in the kill should approach 1 : 1.
3. The proportion of calves and yearlings in the harvest should be high in relation to the potential productivity for the species.

HARVEST FLUCTUATIONS

The first condition was chosen because climatic or other ecological changes are seldom drastic enough to induce severe year to year variations in net productivity, the parameter on which yields are based (Gross, 1969). Exceptions to this generalization should occur mainly on the edges of the moose's geographic distribution. Sudden increases or decreases in the kill usually indicate previous underharvests or over harvests due to inappropriate regulations.

In a recent paper, Walters and Bandy (1972) suggests that properly regulated periodic harvests rather than annual harvests would increase big game yields. However, if true, this would only change desired harvest stability from a one year basis to a two year basis as shown in their computer model simulation.

The harvest statistics (Table II) show that kills in most provinces have exhibited fairly large year to year variations, but the greatest year to year change was recorded in the transition from bulls only to any moose season in Québec (Fig. 1). Even excluding this change there was an increase in the harvest of more than 45 percent between two seasons in Manitoba and a decrease of more than 25 percent for a comparable period in British Columbia. However, recent provincial harvests are much more stable than in the years preceding the closed seasons of the 1940's (see, Fig. 60 *in* Peterson, 1955). The Canadian harvest (Fig. 2) rose rapidly between 1954 and 1960 at a slower rate to 1965, and has since continued erratically upward.

TABLE II

Variations in annual moose harvests and in annual hunter success

Region	*Period*	*Mean annual harvest*	*Coefficient of variation in harvest*	*Mean annual success*	Coefficient of *variation in success*
British Columbia	(1960-1971)	19,575*	17 %	42 %	7 %
Manitoba	(1964-1971)	2,997*	20 %	46 %	16 %
New Brunswick	(1960-1972)	538**	54 %	52 %	43 %
Newfoundland	(1960-1971)	8,079**	26 %	51 %	4 %
Nova Scotia	(1964-1971)	301**	19 %	36 %	20 %
Ontario	(1960-1971)	12,675*	9 %	26 %	5 %
Québec	(1960-1972)	6,229**	36 %	16 %***	20 %***
Saskatchewan	(1960-1971)	5,896*	35 %	48 %	21 %
Yukon	(1960-1970)	916**	16 %		

* Estimated kill;
** Recorded kill;
*** For years 1955-1968.

The reason for the wide harvest fluctuations may be that seasonal hunter success tends to vary less than the kill (Table II).

Hunters will apparently increase their effort to maintain individual success when they must compete for moose with more hunters, or when there are fewer moose. Regulation of harvests on the basis of anticipated hunter success will fail because more people hunt when moose are readily available and because residual hunters increase their efforts when moose are scarce. Where seasons are short, harvest stability may be achieved under certain conditions because the amount of individual hunter effort cannot vary so much. The most stable provincial kill figures are from Québec in the period 1967 to 1972 when the kill varied from 7,135 to 7,009 and showed a maximum year to year variation of less than 2 percent. Seasons in this province are relatively short (2 to 3 weeks) and co-incide with the rut.

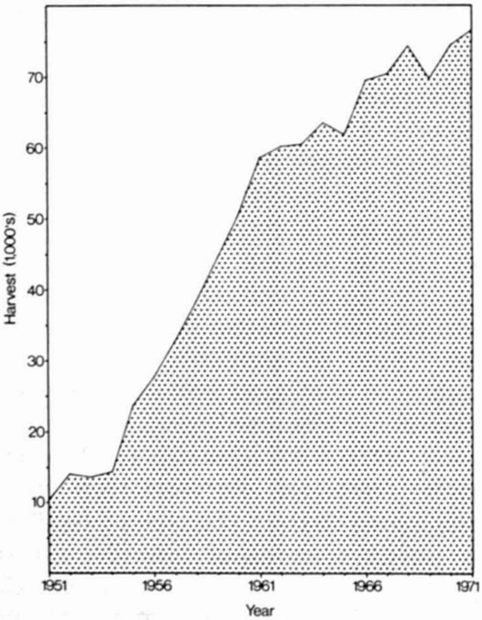

Figure 2. Canadian moose harvest. Estimates for Nortwest Territories and Alberta included for all years by extropolation, only discontinuous data being available for these jurisdictions.

Provinces such as New Brunswick and Nova Scotia which controlled hunter numbers by limiting the issuance of licences have exerted even less control over harvest and success variation than other administrations.

Ideal harvest control would require a limit on the numbers of hunters and that the season remain open until a specified quota of moose had been killed. Aside from a few situations, like controlled slaughter of surplus animals in

National Parks, such 'open ended' moose seasons are not held in Canada.

SEX RATIO IN THE KILL

The second condition should apply because the adult sex ratio is nearly equal in moose (Peterson, 1955) and there is little difference in longevity of the sexes. If hunter harvest is to replace natural mortality, the kill must be approximately equally divided between the sexes. The farther that sex ratios in the kill depart from 1:1, the farther the harvest will depart from maximum yield.

Western provinces have long used sex differential seasons to avoid overharvesting females. Where strong skewing towards males occurs in the kill over a period of years, it is obvious that legal hunting is not controlling the population. But except in Manitoba, imbalances in the sex ratios of harvested moose have not been great on a province wide basis (Table III) despite the prevalence of long bull seasons in relation to antlerless seasons (Table IV). In fact, in British Columbia, where the ratio of the length of the bull season to the length of the cow season varied from 1.4: 1.0 in 1964 to 3.0:1.0 in 1971, bulls made up 58 percent of the total harvest for the 8 year period — less than in Nova Scotia where regulations did not differentiate between sexes. However, cutbacks in the length of antlerless seasons in several British Columbia management areas in 1971 resulted in bulls making up 67 percent of the provincial harvest in that year.

It is puzzling that Alberta has been reducing the ratio of the male to female season — 3.3:1 in 1965 to 1.5:1 in 1972 at the same time British Columbia was increasing its ratio. Both provinces have been experiencing increased hunting pressure and better access to hunting areas with construction of roads used in resource exploration and exploitation.

PROPORTION OF CALVES AND YEARLINGS IN A HARVEST

Because hunters select larger moose in preference to calves, maximum yields are probably not approached in any of the provincial harvests. The highest reported calf yield in Canada was 18 percent of the total resident kill in Ontario (1967). This is well below calf yields in Seden — 24 percent average in Cälveborg (Markgren, 1969) and a peak of 49 percent in Vastmanland (Lykke, 1974).

Selection against calves is strongest where moose are abundant and is less so in heavily hunted areas. Calf: cow ratios in the kill (36: 100) during the period 1964-1970 were not significantly different from those (38: 100) in post season aerial surveys in heavily hunted Management Area 14, British Columbia. But in lightly hunted Management

TABLE III

Sex and age ratios in recent moose harvests

Region	Period	*Ratio %* *Bulls: cows: calves*	*Ratio: 100 cows* *Bulls: cows: calves*
British Columbia	(1964-1971)	58:33: 9	176:100:27
Manitoba	(1964-1971)	69:26: 5	265:100:19
Nova Scotia	(1964-1971)	59:31:10	190:100:32
Ontario	(1964-1971)	50:36:14	139:100:41
Québec	(1964-1972)	55:37: 8	149:100:22

TABLE IV

Characteristics of moose hunting seasons in Canada, 1972

Region	*Num. moose mgmt. areas*	*Restriction on number of licences*	*Maximum days in season*	*Average ratio of length of bull season to cow season*
Alberta	11	no	107	1.5:1
British Columbia	24	no	108	3.0:1
Manitoba	31	no	97	1.4:1
New Brunswick	2	yes	?	1:1
Newfoundland	19	yes***	88	1:1 **
Northwest Territories	12	—	93	1:0
Nova Scotia	2	yes	10	1:1
Ontario	6	no	92	1:1
Québec	23	no*	24	1:1
Saskatchewan	15	yes***	84	1:1
Yukon	1	no	129	1:0

* Except in special park hunts;
** 2 zones have short bulls only season;
*** In certain areas only.

Area 28, the ratios in the kill (33: 100) were significantly less than the (55: 100) observed in post season flights.

Pimlott (1959) explored the possibility of using the yearling fraction of the kill to measure productivity but concluded that because yearlings are more vulnerable to hunting that adults, their occurrence in the harvest is not a true reflection of their occurrence in the population.

However, data from British Columbia (Fig. 4) suggests that during the rut, yearling males are no more vulnerable that adults although they are much more vulnerable in the pre-rut period. Similar B.C. data from female moose also suggests that female yearlings are no more vulnerable than female adults during or after the rut although pre-rut samples of female moose are too small to indicate their vulnerability during that time. A yearling fraction determined from moose collected in a hunting season confined to the rut may then be a good indication of the productivity of the population.

In Nova Scotia, 26.6 percent of the moose other than calves in the kill from 1964 to 1971 were yearlings (Nova Scotia, 1971). This is near the theoretical maximum for moose and may be truly representative of the herd's productivity because the hunting season Oct. 1-12) coincides with the rut.

CARCASS QUALITY

Since moose are primarily harvested for meat, managers should ensure that the hunt is carried out when the animals will yield the heaviest carcasses of the highest quality. The fall weight of moose varies with the presence or absence of fat deposits in adults or of growth attained in calves and is a useful indication of quality as well as quantity of meat.

Fall weight curves (Fig. 3) were constructed from weights obtained from a captive bull and female calf moose as well as from hunter killed moose in Wells Gray Park, British Columbia and from weights of moose in Nova Scotia (Nova Scotia, 1971; in Alberta, Blood *et al.*, 1967). The pattern will vary slightly from area to area depending on range conditions and the timing of the rut.

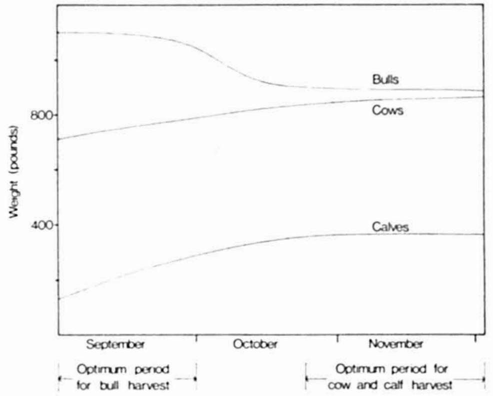

Figure 3. Patterns of fall weight in moose. Based in part on data from captive animals.

These data show that the best time for converting bull moose to moose meat is from early to mid-September — a fact recognized by Caton (1877): «The proper season for hunting the moose is at the commencement of the rut, say in September... Then it is that he is in the best condition and the venison is the choicest». Although rutting bull moose do not acquire a strong flavour and odour to the degree observed in male caribou, elk and mule deer, they lose some palatability during the rut. McGillis (1972) concluded that bull moose in Elk Island National Park in Alberta do not recover any fat lost during the rut before the onset of winter. My observations of bull moose killed in Wells Gray Park, British Columbia, agree with this. The optimum harvest period for cows and calves is mid to late November or possibly later where good range conditions exist and winters are not severe.

In most provinces, hunting is most intensive during the rut in late September and early October so bulls are shot after their peak of condition while cows and calves killed during this period have not yet reached maximum fall weights. If it is at all possible, cows and calves should be harvested after calves are weaned. Judging from lactation in harvested cows (Well Gray Park, B.C.), this may not be until early October. The attainment of a larger size would also enhance overwinter survival of orphaned calves.

There are estimated increments in dressed meat of 23 to 50 kg (50 to 120 lb) for bulls, 18 to 36 kg (40-80 lb) for cows and 5 to 14 kg (10 to 30 lb) for calves available through choosing the correct harvest period.

MAXIMIZING RECREATION

A more recent objective than maximum yield is that of obtaining the maximum amount of recreation from the resource. To achieve this, seasons should be regulated so that hunting takes place when moose are least vulnerable to hunting especially where demand for hunting is high in relation to the supply of animals. The general pattern of fall behaviour may be described from hunter success patterns documented at Cache Creek and Wells Gray Park, B.C., from unpublished field observations and from Altmann (1956). In early September, moose of both sexes are moderately vulnerable where they are associated with aquatic habitats. However, in the western mountains they are often widely dispersed in alpine and sub-alpine habitats at this time of year and are difficult to hunt successfully. Moose of both sexes travel little until the tempo of pre-rut activity of the bulls increases in mid-September. The vulnerability of all moose increases with the peak of the rut in late September and in early October but bulls are more easily hunted than cows in this period. Adult bulls are more vulnerable during the rut than yearling bulls (Fig. 4). After the rut, there is a period during which all moose, and especially adult bulls, appear to feed intensively, travel little and during which hunters have difficulty in finding them. As moose move to their winter ranges, they again become vulnerable, espe-

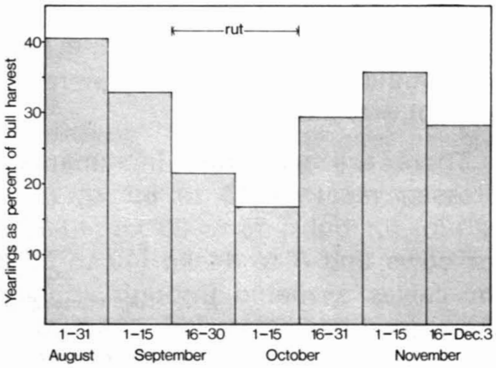

Figure 4. Vulnerability of yearling males expressed by % occurence in the bull harvest. Data from Cache Creek Checking Station, B.C., base on 5,751 aged bulls. Data from Low (1966-1969).

cially in the mountains where migration brings heavy winter concentrations of moose to valley bottoms in December and January.

Where hunting seasons for both sexes of moose open at the beginning of the rut, the harvest can be taken very quickly. This appears to be wasteful in that more hunting could be sustained from a population with earlier openings.

Sex differential seasons (Table IV) are the most effective means of spreading the hunt over a longer period of time. The increased amount of recreation produced from such seasons is more important than any gain made in total yields. The danger of overharvesting is also decreased in sex differential seasons but there is no empirical evidence to prove that killing a disproportionate number of males can increase the yield from a moose population.

Harvest distribution for moose over a long open season in British Columbia (Fig. 5) shows that hunting can be sustained over a long time with little harvest prior to the rut, and that a large percentage of the harvest is taken during the rut. No province in Canada protects moose during the rut when they are most vulnerable. Saskatchewan, in fact, has an early season which appears to be designed to coincide with the rut, and a late season when the animals are easily hunted on their winter range.

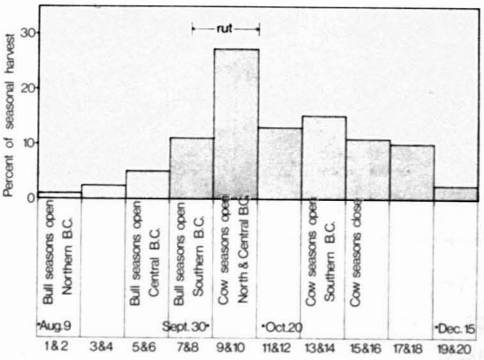

Figure 5. Moose harvest in bi-weekly periods over a long hunting season in British Columbia.

SETTING MANAGEMENT OBJECTIVES

This discussion has illustrated some of the ways in which regulatory management may influence the attainment of several credible objectives such as producing a maximum yield of moose, producing quality meat, and maximizing recreation. I have not yet attempted to describe the compromises which would have to be made to obtain the greatest total benefits and have not tried to judge the validity of existing objectives.

Basic information on what people want from the resource is needed so that valid management objectives can be formulated. For example, if the growing demand of non-hunters to see wildlife is to be met, existing objectives will have to change. Pearse-Bowden (1972) showed that overcrowding of hunting areas in another area of major concern which may require a revision of traditional objectives.

The problem of managing resources in a manner appropriate to meet public demands has been explored by Chapman (1972). Many of his ideas including the need for presenting alternatives to the public, and for public preference surveys are applicable to the problem of regulating moose hunting.

Summary and conclusions

Moose seasons were closed in several provinces for varying periods of time during the 1940's and early 1950's. After the seasons were reopened, managers gradually liberalized hunting regulations to increase harvests. There has been a general upward trend in the kill for all provinces that reopened moose hunting. Québec and British Columbia have had lower harvests in recent years.

The increased harvests were due to a variety of factors including hunting either sex of moose instead of males only, better access for hunters, and increased numbers of hunters. Increased moose populations were also responsible for higher harvests in some areas but in British Columbia harvests rose while populations were declining over much of the province.

Present regulations appear adequate to achieve harvests which are compatible with a maximum yield objective except that hunters select against calves and a better control of fluctuations in the kill is needed.

Sex ratios in the kill have been only slightly skewed towards males even where season lengths for bull moose are much longer than for antlerless moose. Sex differential seasons have been more effective in increasing the amount of hunting recreation by spreading out the hunting period.

There appears to have been little consideration to providing quality meat in the harvest. Bulls are usually shot after their peak of condition while cows and calves are often shot before they have attained their maximum fall weight.

There is a need for better measurement and consideration of public demand in formulating objectives.

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MOOSE MANAGEMENT IN THE CONIFEROUS-DECIDUOUS ECOTONE OF NORTH AMERICA

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Résumé

L'aire méridionale de distribution de l'orignal dans l'est de l'Amérique du nord recoupe la zone de transition — l'écotone — entre les forêts conifériennne et décidue. C'est dans cet écotone que l'activité humaine et les percées de l'urbanisation ont le plus fait sentir leurs effets sur l'abondance et l'habitat de l'orignal. Après une période de 20 à 40 ans de prohibition de la chasse, l'abondance du cheptel a permis une récolte rigoureusement surveillée au Nouveau-Brunswick, en Nouvelle-Écosse, au Minnesota et au Maine.

Dans les régions où l'orignal est devenu plus abondant, on a observé une diminution du Cerf de Virginie. Sauf au Maine, où l'interdiction de la chasse à l'orignal fut maintenue, la chasse contrôlée s'est avérée un excellent outil d'aménagement des populations. Quant à l'aménagement de l'habitat lui-même, il est en grande partie subordonné à l'exploitation industrielle des résineux.

Les statistiques tendent à montrer que l'ouverture récente de certains territoires à la chasse a permis un rajeunissement du cheptel et favorisé sa production.

Abstract

The southern range of moose in eastern North America is contained in the coniferous-deciduous ecotone. It is within this ecotone that the activities of man associated with advancing civilization have reduced moose populations and habitat most drastically. Following two to four decades of closure, moose have become sufficiently numerous to warrant controlled harvests in new Brunswick, Nova Scotia, Minnesota and Maine. Decreases in white-tailed deer populations have been noted in areas of rising moose numbers. With the exception of Maine, where moose hunting is still not allowed, controlled harvests have been used as the primary management tool. For the most part, habitat management is dependent upon commercial pulpwood cutting operations. Successive moose harvests in areas recently opened to hunting have generally resulted in younger and more productive herds.

Introduction

The southern range of moose (*Alces alces*) from Nova Scotia west to Minnesota (Fig. 1) occurs in what Pitelka (1941, *in* Odum, 1953) refers to as the "coniferous-deciduous forest ecotone" (Fig. 2). It is within this area that man's

Figure 1. 1973 Moose distribution in Minnesota, Maine, New Brunswick and Nova Scotia

activities have had the most drastic effects on moose populations. Early settlers were dependent upon moose in these areas as a source of meat; moose meat and hides were items of trade, and regulations were put into effect at an early date to protect the animals (Dodds, 1974). In this ecotone, moose were extirpated from Pennsylvania in 1790, Massachusetts by the beginning of the 19th century, New York in the 1860's, and about 1900 in Vermont (Peterson, 1955). Current populations of less than 100 moose occur in Michigan and Wisconsin (Karns, 1964) and Vermont (Day, pers. comm.) and 220 are reported in New Hampshire (Anon. 1971).

The demise of moose was largely due to the effects of logging and settlements which brought about more intensive hunting and changed the habitat. This habitat change, while not wholly unfavorable to moose, allowed existing white-tailed deer (*Odocoileus virginianus*) populations to expand or inhabit areas north of their original range. This population increase and range expansion

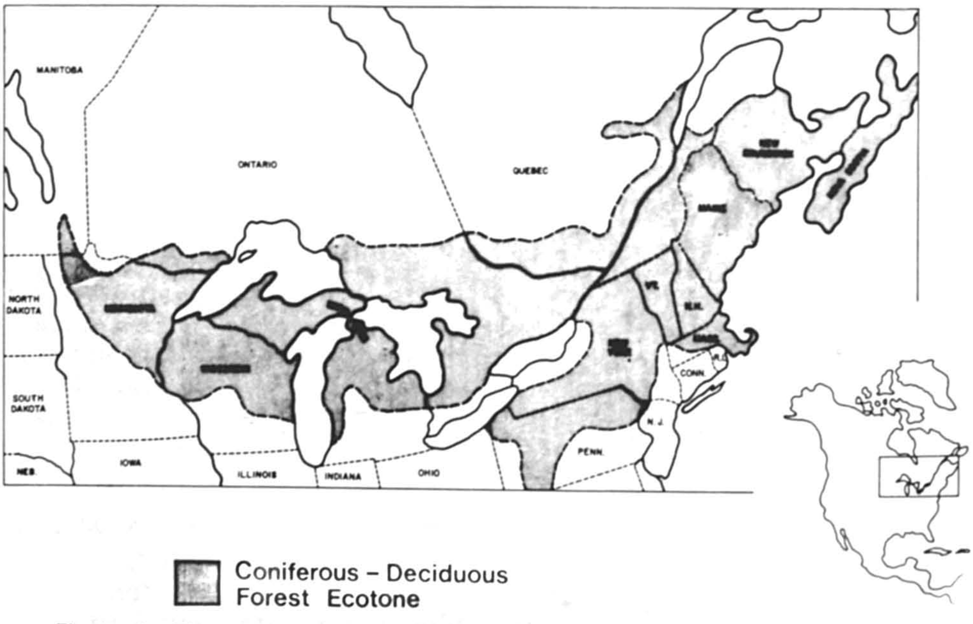

Figure 2. The coniferous-deciduous forest ecotone as described by Pitelka (1941)

of white-tailed deer brought with it the meningeal worm, *Parelaphostrongylus tenuis*, the etiological agent of moose disease (Anderson, 1963). *P. tenuis* infection in moose elicits a central nervous system syndrome and generally provokes the death of the host animal. *P. tenuis* may reach epidemic status in moose resulting in, or contributing to, considerable mortality.

Moose habitat and distribution

Moose in the coniferous-deciduous ecotone occupy a spruce-fir-aspen-birch forest type that is commercially exploited for the production of pulpwood. The area of occupied moose habitat varies from 16,830 km^2 in Nova Scotia, representing approximately 36 percent of the total area of the province, to 77,670 km^2, or approximately 95 percent of the total area of Maine (Table I). The distribution of moose in this area is presented in Figure 1. Moose densities for Maine and Minnesota are given in Figures 3 and 4. Lack of current census data for New Brunswick and Nova Scotia precludes any finer definition of population densities.

The maintenance of suitable moose habitat is largely dependent upon pulp cutting operations. Cutting patterns vary, but are principally clear-cuts. In New Brunswick, Nova Scotia, and Maine, clear-cutting of spruce-fir has resulted in large areas of sapling hardwoods conducive to moose and detrimental to deer in that the critical winter cover is removed.

TABLE I

Area of occupied moose range in the coniferous-deciduous ecotone.

Area	*Approximate moose range (km^2)*	*Total area (km^2)*
New Brunswick	62,140	72,490
Nova Scotia	16,830	54,370
Maine	77,670	85,950
Minnesota	38,830	217,480

The only specific moose habitat management that occurs throughout this area is in northwestern Minnesota. In this area, willow and aspen stands are being bulldozed and/or burned to maintain them in the seral stage of succession (Berg and Phillips, 1974).

The dependency of moose habitat on the operations of commercial logging is evident when one considers that most of the moose range in Nova Scotia, New Brunswick and Maine is under control of private paper companies, either through lease from the government or direct ownership.

Recent history

Since 1900, moose populations have fluctuated drastically in this portion of the range. Benson (1957), reviewing the status of moose in Nova Scotia from 1908 to 1937, based on hunter-kill records, noted a series of ups and downs in the population which was thought to be due to hunting. As a consequence, season lengths and bag limits were reduced. Hunters demanded shortened seasons after the record kill of 1927 because the increasing number of hunters and reduced hunter success led them to believe that protection was needed to increase the populations. It was obvious by 1937 that moose populations were lower than those of the previous decade and the season was closed with the objective of increasing the populations. Following the closure of the season, the herd experienced a temporary increase prior to the population crash in late 1940's and early 1950's (Benson, 1957; Dodds, 1963).

Moose were considered rare in western Nova Scotia throughout the 1950's and are only recently showing signs of small increases in numbers in this area. This is an area of relatively low snow cover from mid-December to early April. Deer and moose wintering habitats generally coincide, which accounts for a high prevalence of *P. tenuis* in moose.

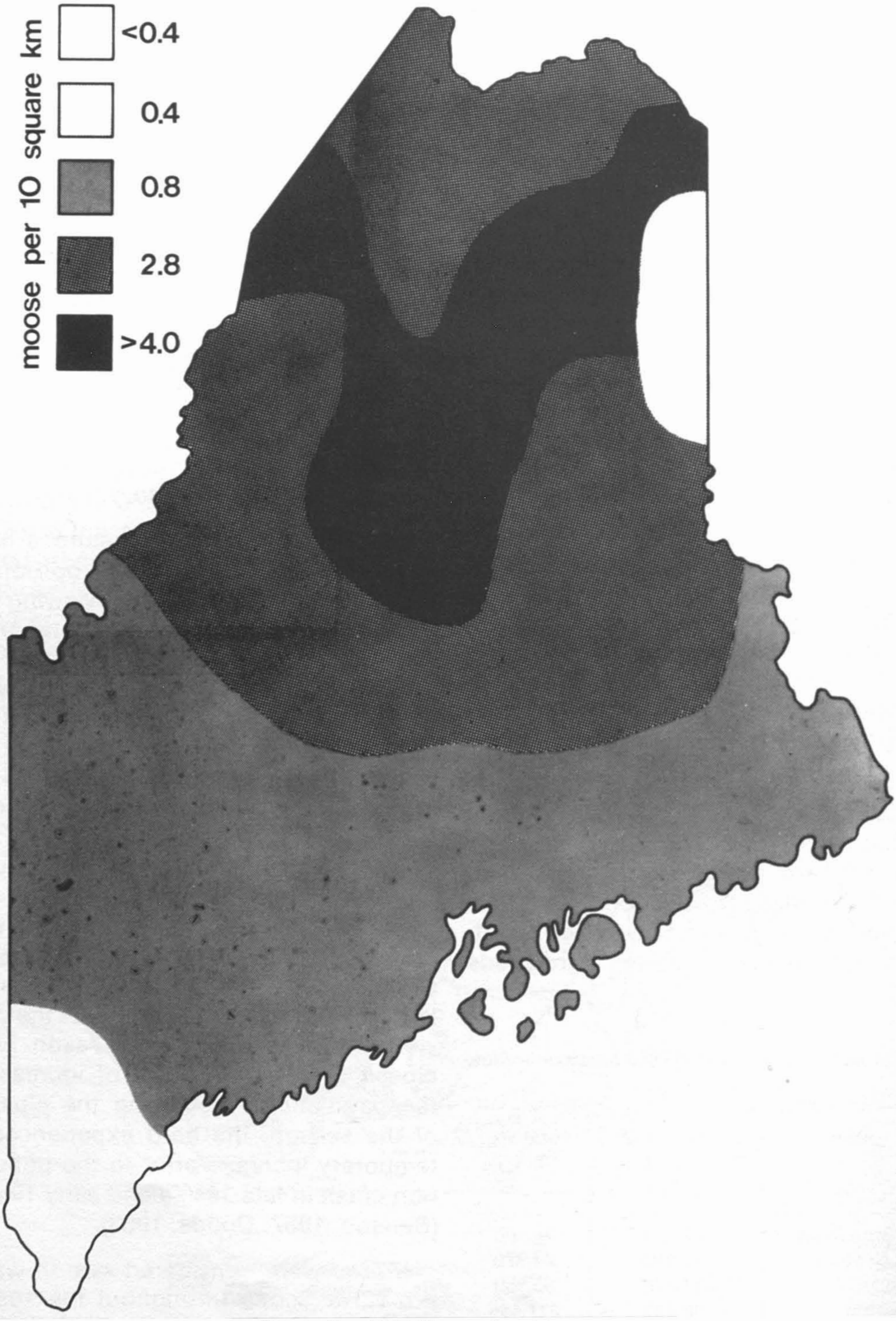

Figure 3. 1973 Moose densities in Maine

In the four counties of the northeast mainland of Nova Scotia, a mountain ridge results in a separation of the deer and moose winter range. Telfer (1965) noted that deer wintered below 122 meters elevation while moose remained on the high plateau most of the year. In this highland area, moose populations have not fluctuated as dramatically as in the rest of the province. Benson (1956) indicated that the 1956 moose densities in the highland area were comparable to those of 1930-37. Aerial surveys of this area in 1963 indicated densities of 0.6 moose per km^2 (Telfer, 1965). Based on this and other data, a limited

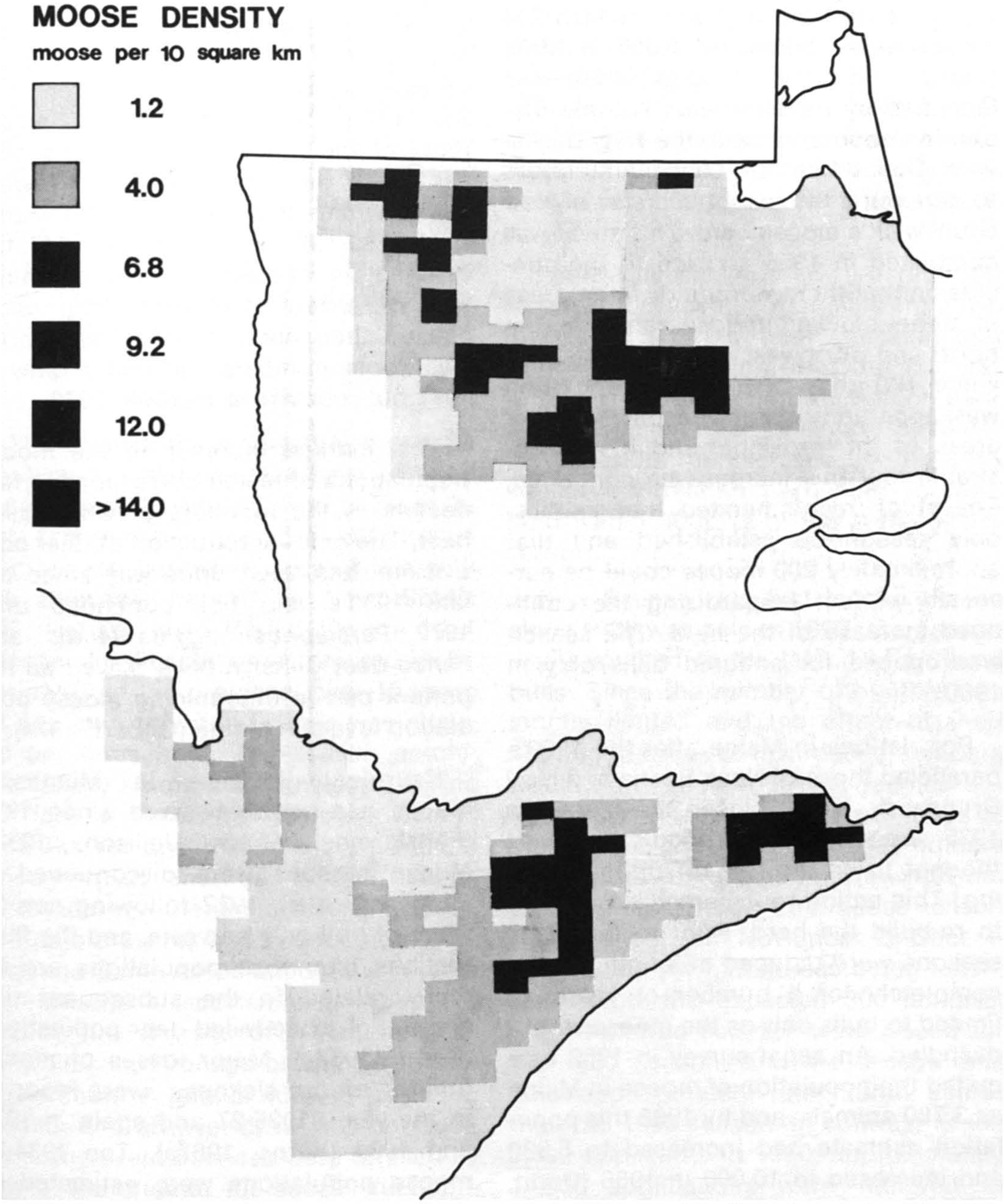

Figure 4. 1973 Moose densities in the major moose range of northwestern and northeastern Minnesota

harvest of moose in the highlands area was recommended by the Wildlife Division of the Department of Lands and Forests. In 1964 a limited moose season was established.

The recent history of moose in New Brunswick is somewhat similar to that for Nova Scotia. New Brunswick held its last open season in 1936, in which 205 moose were taken by 2,397 hunters (Carter, 1961). In 1950 a study was launched by the Northeast Wildlife Station in cooperation with the New Brunswick Department of Lands and Mines to determine the extent and size of New Brunswick's moose herd. This study was completed in 1956 and led to the conclusion that there were fairly large areas of under-stocked moose range in the north and northwest portion of the province (Wright, 1956). The population was apparently rising steadily in other areas of the province, and it was desirable that this increase be continued. The study recommended that a bulls-only season be established and that approximately 200 moose could be harvested without jeopardizing the continued increase of the herd. The season was opened for antlered bulls only in 1960.

Populations in Maine after the 1900's paralleled those of Nova Scotia and New Brunswick. Maine closed the season in 1935 because the population was thought to be too low to support hunting. This action represented an attempt to re-build the herd. Prior to this time, seasons were reduced in length, closed completely for a number of years, or limited to bulls only as the moose stocks dwindled. An aerial survey in 1952 estimated the population of moose in Maine as 3,780 animals, and by 1965 this population estimate had increased to 6,830 and increased to 10,000 in 1966 (Dunn, 1966). Improvement in census techniques accounted for a portion of this increased population estimate. In 1971 the census estimated the moose population as 13,220 moose (Dunn, 1972). The population increased annually until the unusually severe winter of 1970-71 which was marked by heavy mortality in both deer and moose. During this winter the minimum temperatures ranged to -45° C through central and northern Maine. Snow began to accumulate in December, and average depths reached over 127 centimeters on March 15 in the central portion of the state where most of the moose mortality was concentrated. January snow depths were 79-89 centimeters, February and March depths 89-102 centimeters and 117-125 centimeters, respectively. The combination of severe cold and deep snow caused direct and indirect moose mortality. Moose numbers declined slightly in 1971 but rebounded again in 1972.

This marked increase in the moose populations of Maine corresponded to a decline in the numbers of white-tailed deer. The gradual reduction of deer populations has been underway since the late 1950's and has continued until 1972. *Parelaphostrongylus tenuis,* and hence deer density, have played an important part in determining moose population levels in Maine (Gilbert, 1974).

Neurologic disease in Minnesota moose has been observed since 1912 (Fenstermacher and Jellison, 1933). Moose seasons were discontinued in Minnesota after 1922 following several years of bull-only harvests, and the fluctuations of moose populations are directly related to the subsequent rise and fall of white-tailed deer populations (Karns, 1967a). Major losses of moose due to "moose sickness" were reported in the years 1925-27 and again in 1933 and 1934 (Karns, 1967a). The 1934-35 moose populations were estimated as 0.07-0.12 moose per km^2 (Olson, H. F., pers. comm.) in central Lake County of northeastern Minnesota. The 1965 population in this same area was estimated at 0.7 moose per km^2 (Karns and Magnus, 1965). Aerial censuses of moose in Minnesota have indicated a population increase from 1959 to 1965 at which time the herd became static and reductions in productivity were noted (Karns, 1967b).

Recent efforts to obtain a moose season in Minnesota commenced in 1959 with bills being introduced in all of the successive biennial legislative sessions. Authority was granted in 1971 to conduct a limited moose hunt in 1971 or 1972. A proposal to hunt moose is currently being considered by the legislature in the State of Maine. Under this plan, 1,000 permits would be issued to state residents.

Moose seasons

The regulations adopted in the three political jurisdictions that have adopted moose seasons are tailored to meet local preferences, and the number of hunters are limited in accordance with the allowable harvest. In Nova Scotia 400 licenses were issued for the 1964 season. Applicants were required to be residents of the province, over 18 years of age and only one license was allowed per household. The season permitted taking animals of either sex during 10 days in September which coincided with the rut and placed the season far enough in advance of the deer season to discourage the illegal taking of deer. A public drawing was conducted by the Fish and Game Association (now Wildlife Fereration), a sportsmen's group, to reduce the charges of giving licenses for political patronage on the part of the government. A total of 400 licenses were issued, and an over-draw was conducted in the event licenses were refused by any of the original 400 successful applicants. This system has worked well, and has continued for all of the successive seasons. In succeeding years no person was permitted to apply for a license for one year after having been selected.

Moose hunting was continued in Nova Scotia with the exception of 1965 when a legal technicality prevented opening the season. The number of permits was increased to 800 in 1966 and to 1,000 in 1967 and subsequent years. Over 14,000 applications have been received each year for the available permits. In 1971 a mandatory hunter safety and gun handling test was initiated. This test must be passed by every successful applicant before a license is issued.

The successful hunters are required to present the whole mandible from the moose to a Department checking station within 24 hours after the kill and to supply additional information on their hunting activity and the moose taken. Unsuccessful hunters are required to submit information pertaining to their hunt within 30 days of the close of the season.

New Brunswick's first moose season since 1936 was held in 1960. The season was restricted to the taking of antlered bulls. Since the number of hunters was strictly limited and the effect of their hunting in areas of low moose numbers would be negligible, it was deemed unnecessary to restrict hunting to areas of high moose population. The 400 hunters were chosen in a random drawing from the 8,231 applicants. The moose season was opened from November 28-December 2, with 174 bull moose being taken, well below the expected 300 animals. Eight hundred licenses were issued for the 1961 season, and the season was held approximately one month earlier than the 1960 season. In contrast to the 8,000 applicants in 1960, approximately 17,000 applications were received in 1961 from which 800 licenses were selected in a public drawing. The overall hunter success rate dropped from 46 percent in 1960 to 36 percent in 1961 when a total of 264 antlered moose were shot. It appeared that moose were more wary in the second season and were much harder to shoot. Any-moose hunting was initiated in 1966, and annual seasons have been held since that time.

Minnesota's long sought moose season became a reality in the fall of 1971. In an effort to distribute the hunting to as many individuals as possible, four hunters were permitted on a single permit to take one moose. Applications were accepted only from parties of four which applied to hunt one of the six zones. Licenses were allotted on the basis of a drawing. A total of 9,264 parties applied for the 400 permits. Licenses cost $100, and the season was split with the first half occurring from 2-14 October and the second half from 4-19 December. This split season allowed hunters to take advantage of a variety of hunting conditions including calling and the use of water routes in the early season and tracking and snowmobiles in the later season. Hunting success for individual zones varied from 84 to 100 percent with the average being 93 percent. Hunting was allowed for moose of either sex and any age.

In Minnesota, all moose taken during the season had to be registered at one of seven registration stations. Information regarding the hunt and biological specimens (incisor teeth, thyroid glands, and brains) were collected from the moose at these registration stations. Kill sites were located and a detailed examination was made of the viscera for parasites and reproductive tracts were collected from the cows (Karns, 1972). Hunters made blood collections using a specially prepared kit for hematology, blood chemistry, bacterial and virus isolations (LeResche *et al.*, 1974; Diesch *et al.*, 1972; Johnson *et al.*, 1972).

Recreation

Moose seasons in eastern Canada and in Minnesota have provided recreation to a rather small segment of the hunting public. Nova Scotia has made an effort to determine the amount of recreation and expenditures connected with the moose hunt. Since reopening of the Nova Scotia moose season in 1964, it has provided nearly 200,000 hours of recreational hunting for license holders and at least many additional hours for non-license holders who accompany hunters. Economically, moose licenses provide $15,000 annually to provincial revenue. Check station data have revealed that approximately $50 is spent per license holder for expenses connected with the hunt in addition to the license, and represents some $50,000 in total expeditures per year on the part of hunters up to the point of registering the kill. This does not include such expenses as meat cutting, freezing, taxidermy fees, etc.

Enforcement

Enforcement problems are a part of any season and the moose seasons are no exception. One of the difficulties in hunting such a large animal as the moose by an individual is transporting the carcass out of the woods. Minnesota handled this by licensing four hunters in a party to shoot a single moose. In Nova Scotia problems developed when successful hunters gave a portion of the meat to non-licensed individuals. This lead to illegal possession of moose meat by non-hunters. This has been partially corrected by issuing permits after the close of the season for the possession of moose meat. There was some apprehension under Minnesota's system about parties taking more than one moose, but this occurred only rarely.

Non-hunting mortality

Poaching and collisions with vehicles, including trains, accounts for the highest percentage of reported non-hunting mortality in moose throughout this area as revealed by figures for 1970 (Table II). In most instances moose mortality is compiled from reports submitted by law enforcement personnel, which may account for a bias towards poaching and road-kills.

In Maine, the number of mortalities has increased from 84 in 1968 to 216 in 1970. This increase of mortality is another reflection of the moose population increase in that state. The magnitude of reported moose mortality in Minnesota is erratic, varying from 30-60 animals annually. Non-hunting mortality in New Brunswick and Nova Scotia has been relatively stable over the past few years.

Predation

Other than disease, a potential natural limiting factor to moose populations would be predation. The only area in which large predators may exert an influence on moose populations is northeastern Minnesota where a resident population of timber wolves (*Canis lupus*) exists (Stenlund, 1955; Mech and Frenzel, 1971; Byman, 1972; Frenzel, 1974). The only other large animal that may be capable of preying on moose in the coniferous-deciduous ecotone is the black bear (*Ursus americanus*), but its effectiveness as a predator on moose is deemed to be negligible.

In northeastern Minnesota, Stenlund (1955) reported that moose population increases occurring during the early 1950's may have been halted by wolf predation. More recent studies in this area (Byman, 1972) showed that about one-fourth of the summer diet of timber wolves consists of moose, with a high proportion of calves occurring in the diet in June and July. Karns (1972) reported that *in utero* production of moose was similar in both areas of Minnesota, but there is considerable difference in net productivity. Net productivity, as measured by winter aerial census and classification counts, is generally between 20-35 percent in northwestern Minnesota, an area of low timber wolf density, and 10-15 percent in northeastern Minnesota (Karns, unpubl. data)

TABLE II

Reported non-hunting mortality of moose for calendar year 1970 in New Brunswick, Nova Scotia, Maine and Minnesota

Cause of mortality	*Area*							
	Maine		*Minnesota*		*New Brunswick*		*Nova Scotia*	
	N	%	N	%	N	%	N	%
Vehicles, including trains	75	34.7	17	54.8	85	45.4	3	13.0
Poaching	96	44.4	9	29.0	69	36.9	3	13.0
Disease	15	6.9	1	3.2[1]			8	34.8
Accidental					24	12.8		
Unknown	30	13.9	4	12.9	9	4.8	9	39.1
TOTAL	216		31		187		23	

[1] Does not include diseased animals handled by Section of Game personnel.

where the current wolf population is about 3.9 wolves per 100 km^2 (Mech and Frenzel, 1971; vanBallenberghe, 1972). It is apparent from the data that predation on moose by wolves does occur. It cannot, at this time be considered as a serious limiting factor to the moose population of northeastern Minnesota where observed population densities of over 3.9 moose per km^2 have been recorded (Karns, 1967c).

Age structure of harvests

The purpose in examining the age structure of the animals is to gain insight into the population dynamics of the herd. In any such attempt it is realized that biases occur, and the data presented here offer no exception. The fact that moose hunters select for larger animals is apparent by the low number of calves in the harvest from those areas open to the taking of moose of any age. The timing of the season in relation to the rut alters the age and sex ratio of the harvest, with adult bulls being more vulnerable to the hunter during the rut period of late September and early October. Hunter selection for sex of the animal he takes may also alter the sex ratio of the harvest.

Ages of the animals harvested may not necessarily reflect the age structure of the herd, particularly when only a small proportion of the population is removed by hunting (Anderson, 1953; Karns and Shepperd, 1968). Despite these limitations, it is possible to make valid judgements regarding some aspects of population dynamics.

Moose ages were determined by wear class (Passmore *et al.*, 1955) in New Brunswick, Nova Scotia, and Ontario (Cumming, 1974). Ages of moose in Minnesota were determined using the dental cementum technique of Sergeant and Pimlott (1959). Appropriate age groups were combined so the Minnesota data would conform to the wear class analysis.

Data from northwestern Ontario (Simkin, 1965) for the years 1957-61 are included to offer a comparison between this herd with its long history of hunting and the herds recently opened to hunting, as in Nova Scotia, New Brunswick and Minnesota.

Comparison of the age structures of moose harvested in Minnesota, New Brunswick and Nova Scotia were made by calculating the mean wear class, survival rate (Eberhardt, 1969), and survivorship curve technique of Deevey (1947).

The mean wear class of male moose taken in New Brunswick has decreased with 12 successive hunting seasons from 3.60 and 3.43 in 1960 and 1961, respectively, to 2.23 in 1971 (Table III). Harvest was limited to antlered bulls in New Brunswick from 1960 to 1965. During this period the mean wear class of bulls declined from 3.60 in 1960 to 2.58 in 1965.

With New Brunswick's first any-age, either-sex season in 1966, the mean wear class for all moose was 2.20. By sex, the mean wear class was 2.31 for bulls and 2.03 for cows. In 1971 the mean wear class for all moose was 2.25. In comparing the mean wear class from 1966 to 1971, it is evident that any changes in the age structure were very slight. Survivorship data (Table IV) indicate no significant change ($\chi^2_{7df} =$ 10.05, NS) in the age distribution of the total moose harvest from 1965 to 1971 in New Brunswick.

Relatively little change was noted in the mean wear class of moose in Nova Scotia from 1964 to 1970, nor did much change occur in the calculated survivorship (Table IV).

Data from Minnesota indicate mean wear class for moose in the northwestern zone of 3.90 and 4.96 in the northeastern zone. This difference in age structure is due to higher moose mortality occurring in the younger age classes of moose in northwestern Minnesota as a result of parasitic infections, primarily *Fascioloides magna*, the liver fluke, and *P. tenuis*, the meningeal worm (Karns, 1972). The range in northwestern Minnesota is the only area covered by this discussion in which *F. magna* is considered to be an important moose pathogen.

Upon inspection, the survivorship data (Table IV) and calculated rate of survival (Table V) again indicate a decrease in age of the herd as hunting

TABLE III

Mean age class of moose harvested in selected years for areas in the coniferous-deciduous ecotone of North America and compared to northwestern Ontario

Area	*Year*				
	1960	*1961*	*1965*	*1966*	*1971*
New Brunswick	3.60 ♂	3.43 ♂	2.58 ♂	2.20[1] ♂ ♀ 2.31 ♂ 2.03 ♀	2.25 ♂ ♀ 2.23 ♂ 2.28 ♀
Nova Scotia				2.83[2] ♂ ♀	2.63[3] ♂ ♀
Northwestern Minnesota					3.90 ♂ ♀
Northeastern Minnesota					4.96 ♂ ♀
Ontario (pooled data from 1957-1961)	2.41[4] ♂ ♀				

[1] First any-age either-sex season in New Brunswick
[2] 1964 and 1966 data combined, no season in 1965
[3] 1970 and 1971 data combined
[4] Simkin, 1965

TABLE IV

Calculated survivorship of moose

Area	*Minnesota*	*New Brunswick*						*Nova Scotia*		*NW Ontario*[1]
Wear class	*1971* ♂ ♀	*1960* ♂	*1961* ♂	*1966* ♂ ♀	*1971* ♂	*1971* ♀	*1971* ♂ ♀	*1964-66* ♂ ♀	*1970-71* ♂ ♀	*1957-61* ♂ ♀
C	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000
I	975	987	963	870	932	848	903	895	886	804
II	922	904	836	623	674	606	650	687	628	504
III	830	737	639	366	329	391	351	443	434	391
IV	685	461	397	158	137	212	163	298	301	297
V	549	288	251	77	73	106	84	208	152	224
VI	296	90	100	32	39	23	34	124	77	156
VII	148	64	73	14	14	10	13	80	51	95
VIII	0	38	27	0	3	7	5	38	30	46

[1] Simkin, 1965

TABLE V

Chapman-Robson survival values for all moose of wear class II and older

Area	Year			
	1960	*1961*	*1965*	*1971*
New Brunswick	0.74	0.74		0.67
Nova Scotia			0.73	0.73
Minnesota				0.79
Northwest				0.79
Northeast				0.80
Ontario[1]	0.78			

[1] Simkin, 1965

is carried out over a number of years. The decrease of older animals in the herd brought about by hunting is desirable as it has reduced the number of low producing, older cows and thus allowed an increase in herd productivity. A case in point is in the southeastern portion of New Brunswick where prior to being opened for moose hunting it was an area of low moose productivity. With a controlled harvest, the average age of the herd was reduced and a noticeable increase in calf production occurred.

Productivity

Recognizing that hunters select for moose larger than calves, the proportion of yearlings in the harvest has been used as a measure of net productivity by Pimlott (1959) and Simkin (1965). Both workers applied further mathematical corrections to the yearling data to compensate for varying vulnerability of yearlings to hunting.

The most prominent in our data is wear class II. This suggests that our hunters are selecting for animals larger than yearlings. This would be particularly true for seasons in New Brunswick prior to 1966 which were limited to antlered bulls, and in Minnesota's month-long season. In the case of Minnesota, hunters had an opportunity to observe several animals during the course of their hunt. In contrast to this, wear class I is the most prominent age class in the Ontario data.

Although net productivity estimates based on the yearling age cohort may be biased in the case of the earlier New Brunswick and the Minnesota data (Table VI), later estimates from seasons in which any moose are legal may provide trend information, and means to strengthen these observations should be sought.

TABLE VI

Net productivity of moose as based on number of yearlings in the harvest

Area	*1960*	*1961*	*1965*	*1966*	*1971*
New Brunswick	8.4	13.3	27.4	28.4[1]	27.9
Nova Scotia				23.2	28.6
Minnesota					5.8
Ontario	38.6[2]				

[1] First any-moose season in New Brunswick; [2] Simkin, 1965

Summary

1. Hunting seasons for the taking of moose were closed in the 1920's and 30's in response to low moose populations in Minnesota, Maine, New Brunswick, and Nova Scotia.
2. Hunting, alteration of habitat and the white-tailed deer-meningeal worm association were responsible for the reduced moose population.
3. Increases in moose populations generally began in the late 1940's-early 1950's and has been accompanied by reduced white-tailed deer populations.
4. Moose hunting is now established as the major management tool in Nova Scotia, New Brunswick, and Minnesota after closures lasting between 24 and 49 years.
5. A shift of moose populations to younger, more productive age classes has accompanied successive moose harvests on areas recently opened to moose hunting.

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SOME ASPECTS OF MOOSE MANAGEMENT IN NEWFOUNDLAND

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Résumé

Depuis son introduction à Terre-Neuve en 1904, l'orignal n'a cessé de s'accroître jusqu'à 1960. Entre 1960 et 1972, la population a subi un déclin général dont les causes vraisemblables étaient la chasse excessive des populations facilement accessibles et la détérioration que faisaient subir à leur habitat, par broutement excessif, les populations vivant dans les régions reculées.

En 1973, on estimait à 50,000 tant le nombre d'individus dans la population que la capacité de support de l'habitat forestier: mais selon l'accessibilité, des portions de ce milieu forestier étaient surpeuplées tandis que d'autres étaient sous-occupées.

Presque tous les efforts d'aménagement ont eu pour objectif d'obtenir une répartition plus adéquate de la pression de chasse. Aussi, a-t-on institué, dès 1953, un système de zonage du territoire. On doubla ce zonage d'une limitation au nombre de permis émis en accord avec des quotas pré-établis, et, dès 1972, ce système régissait toute chasse à l'orignal dans environ 30 pourcent du territoire de la province. En 1973, le système fut élargi à la province toute entière. Les quotas sont établis à l'aide d'une formule incorporant les informations suivantes: la population totale d'orignal, la productivité du cheptel, les pertes dues à la chasse illégale, la mortalité naturelle, le taux d'accroissement recherché ainsi qu'une prédiction quant au succès de la chasse. Il faut des estimations récentes et précises de la population avant de pouvoir appliquer la formule avec succès.

La chasse légale a permis la récolte de 160,000 orignaux entre 1904 et 1973. Durant la période 1960-1972, la récolte annuelle variait, selon le district, de un orignal par 3.6 mi^2 (9.3 km^2) à un orignal par 8.0 m^2 (20.7 km^2) et représentait une proportion allant de 12 à 22 pourcent de la population totale.

Abstract

Newfoundland moose increased rapidly from their introduction in 1904 until 1960. There was a general population decline from 1960 to 1972 attributed to overhunting of accessible areas and to range deterioration through overbrowsing where access was poor.

Estimates of 50,000 moose were obtained both for the total population and range carrying capacity in 1973 but there were underpopulated and overpopulated areas depending on accessibility.

Management was largely directed towards properly distributing the harvest. This first involved a zoning system starting in 1953. A licence-quota system was added in 1964 and 30 percent of the island had a quota system by 1972. In 1973 all Newfoundland was placed in the quota system. Quotas are set by a formula using total moose population, productivity, poaching loss, natural mortality, desired increase, and predicted hunting success. Accurate current population data is necessary for applying the formula.

About 160,000 moose were legally harvested between 1904 and 1973. Annual harvest rates varied from one moose per 3.6 mi^2 (9.3 km^2) to one moose per 8.0 mi^2 (20.7 km^2) and from 12 to 22 percent of the population in the period 1960-1972

Introduction

Since moose were first introduced into Newfoundland in 1878 and 1904 (Pimlott, 1953) the population increased virtually unchecked except for human exploitation until about 1960. Thus, Newfoundland's moose management situation was somewhat different than most areas of North America owing to the recency of the moose population, Newfoundland's insular nature, the fact that no other important large browsing herbivore existed (20,000 caribou are also present on the island) and the uniqueness of various aspects of its vegetation.

Various aspects of moose management in Newfoundland to 1962 have been reported on by Pimlott (1953, 1959a, 1959b) and Bergerud (1962). Since then, there has been no report dealing with the total moose management situation in Newfoundland. In this paper we examine population fluctuations, the hunter harvest, and methods used to distribute hunting pressure according to moose densities, productivity, and range carrying capacity primarily in the period 1960-1973.

Methods

POPULATION DENSITY ESTIMATES

Moose were censured prior to 1964 using aerial strip-census surveys in mid-winter. From 1964 until 1971 we used the quadrat-census technique (Bergerud and Manuel, 1969) with stratified random sampling and fixed-wing aircraft. Counts were usually made immediately following snowfalls and always with 100 percent snow cover and experienced observers. In 1972-73 we used helicopters (mainly Bell 206 aircraft) and 4 km^2 quadrats (1.544 mi^2). In 1973 we flew over 500 hours in an attempt to obtain 8-12 percent ground coverage of about one-half insular Newfoundland. We feel that with good weather conditions and using helicopters we obtain accurate results over most Newfoundland terrain.

POPULATION TREND DATA

Kill data were obtained from licence returns which hunters were required by law to submit to the Wildlife Service within seven days of the date of kill or within seven days of the end of the season if no kill was made. Although the law was not enforced, returns averaged 82 percent of the licence holders (Table I). These returns indicated the hunter's name and address, where he hunted, date and sex of kill, number of antler points, length of time hunted, the number and sex of moose and caribou seen and whether animals were adults or calves. From 1965 to 1971 a $5.00 rebate was paid to all hunters submitting a return but we realized only a 5.9 percent increase in returns (Table I). However, when the rebate was abolished, licence returns dropped from 71 percent in 1971 to 56 percent in 1972.

NET PRODUCTIVITY ESTIMATE

During 1953-56 and 1963-73 lower jawbones were collected for aging at check stations on logging roads augmented by small samples mailed from other areas. Estimates of productivity and sex ratios were also obtained from aerial classification of calves, adult bulls and cows during fall and winter.

Hunting regulations

From 1945-52 and in 1954 bull-only hunting existed over most of the island. In 1953 and 1955-63 an island-wide either-sex season existed. During 1964-66 non-residents were restricted to bull-only hunting in relatively accessible regions and either-sex hunting in the inaccessible south coast-Northern Peninsula areas which were overbrowsed (Fig. 1). Bull-only resident and non-resident seasons existed during 1964-66 on the Avalon Peninsula, 1964-69 and 1972 on the Burin Peninsula and 1967-72 on the Baie Verte Peninsula.

The northern one-third of the Great Northern Peninsula was closed during 1960-64, 1967-70 and 1972. It had a bull-only season during 1965, 1966 and 1971 due mainly to political pressure. The Burin Peninsula had a closed season 1960-62. The Avalon Peninsula was open for the first time in 1964. All other parts of the island have had an open season since 1945. Season length has remained fairly constant at about 3.5 months, September-December, in inaccessible areas and management areas and usually about one month in relatively accessible areas (Fig. 1).

The zoning system introduced in 1953 was designed primarily to regulate harvests according to moose population density, carrying capacities of land and hunter accessibility. Depending mainly on changes in the above three criteria,

TABLE I

Newfoundland moose kill 1945-1972

Hunting season	*Licences issued*	*Per cent returns*	*Total* kill*	*Hunting* success*
1945	2,475	99	753	30
1946	3,845	90+	1,213+	32+
1947	5,048	90+	1,476+	29+
1948	6,021	87	2,239	37
1949	5,931	75	2,264	38
1950	7,240	94	2,736	38
1951	8,660	92	3,481	40
1952	6,523	92	2,723	42
1953	5,196	95	2,757	53
1954	5,754	90	2,497	43
1955	6,624	94	3,795	57
1956	8,654	89	4,692	54
1957	8,797	87	4,910	56
1958	10,206	80	6,361	62
1959	13,381	51	7,767	58
1960	15,386	58	8,400	55
1961	14,507	86	8,370	58
1962	11,970	83	6,459	54
1963	12,721	79	6,560	50
1964	11,207	77	5,482	48
1965	12,116	77	5,670	46
1966	12,698	84	6,484	50
1967	15,226	84	7,747	50
1968	17,508	81	9,790	54
1969	20,091	83	10,484	51
1970	21,955	75	10,850	48
1971	24,760	71	11,837	46
1972	24,000±	50	10,126	42
Total and means	318,500	82	157,923	50

* Adjusted for non-reporters.

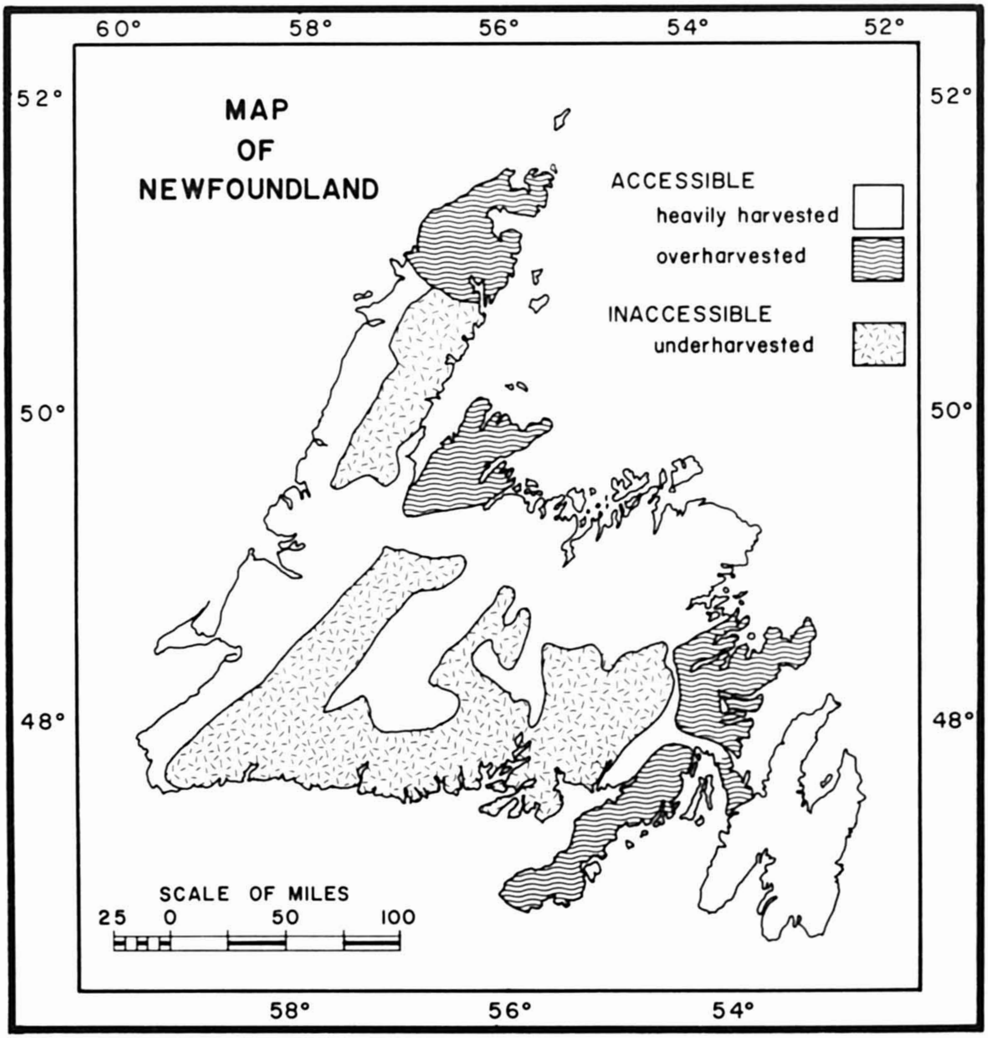

Figure 1. Accessible and inaccessible areas in relation to moose hunting pressure.

zones were added or deleted and boundaries changed from year to year.

In 1964, an area incorporating the Rattling Brook logging-road system (Fig. 2) was zoned for a limited number of licences to be issued on a first-come-first-served basis. In 1965, this quota system was applied to three other logging areas: Millertown, Badger-Exploits and Terra Nova. Thus in 1965 there were 3,600 mi^2 (9000 km^2) with the quota system (termed « Moose Management Areas » as distinguished from general-season areas termed « Moose Zones »). These areas remained relatively unchanged until 1969 when the Anguille Mountains and Glenwood Areas were incorporated and Terra Nova dropped due to inaccessibility (total of 3,300 mi^2 (8550 km^2) or 8 percent of the total island area). In 1972, five other areas were added (Fig. 2) thus placing 30 percent of Newfoundland in "Management Areas".

In 1972, with the exception of the Baie d'Espoir area, the quota was calculated according to the formula:

$$\text{Licence sale} = \frac{(P \times NP) - (PL + NM + DI) \times 100}{S}$$

where P = total population, NP = percent net productivity, PL = poaching loss, NM = natural mortality, DI = desired increase and S = predicted hunting success.

However, until 1972 the formula: Licence sale = (P × NP) × 100/S was applied in some areas usually resulting in a decrease in moose populations in those areas.

In 1973, all moose hunting in Newfoundland was on a quota basis with 36 moose management areas (Fig. 3).

The quota system is probably the best moose management method for present Newfoundland conditions since greater precision is exercized in controlling the legal kill, and hence, regulating densities at or near the carrying capacity of the range. Of course, the quota system can provide a maximum allowable sustained kill on an area basis only when precise estimates of moose densities, carrying capacity, and harvests are available.

Figure 2. Moose management areas in Newfoundland in 1964-1972 having a fixed quota on the number of licences issued. Ratling Brook (RB); Millertown (MT); Badger-Exploits (BE); Terra Nova (TN); Anguille Mountains (AM); Glenwood-Gambo (GG); Baie d'Espoir (BD); Avalon Peninsula (AP); Corner Brook (CB); Taylor's Brook (TB).

Potential moose population under present forest management

During the period 1966-70 a land capability inventory for moose and caribou was conducted in Newfoundland under the Canada Land Inventory (Anon., 1965 and Perret, 1969). Basically a phytosociological plant community classification was rated for moose and caribou based on vegetation-productivity estimates and animal use of plant communities (Mercer *et al.*, 1970). High, moderate, and low moose capability areas accounted for 20, 16 and 64 percent respectively of the total land area of insular Newfoundland (Fig. 4). Based on observed moose densities and vegetation-productivity measurements, we estimate that under present management the three habitat ratings can sustain 4, 2 and 0.4 moose per mi^2 (1.5, 0.8 and 0.15 per km^2) respectively. Thus, Newfoundland can sustain a population in excess of 50,000 moose.

Moose population trends

Although moose harvest statistics and licence sales are not always correlated with moose populations they can give an indication of the order of magnitude of the population size.

Newfoundland had its first moose season in 1946 when 80 licences were permitted. This quota was gradually increased to 300 licences in 1944 and an unrestricted licence sale in 1945 (Pimlott, 1953). With the exception of a small percentage of the total area of Newfoundland, the licence sale was unrestricted from 1945 to 1972. Since 1945 when 2,475 licences were sold, annual licence sales increased at almost constant rates for the periods 1945-71 except for the periods 1951-53 and 1960-64 when sales declined (Table I and Fig. 5). These decreases may be explained by major decreases in season length (Pimlott, 1953 and Fig. 6). Minor changes in season lenth appear to have been relatively ineffective (Table II). A change in non-resident licence fees from $35.00 to $75.00 in 1964 may have been mainly responsible for the decrease in that year (Table III).

The annual legal kill increased from 750 animals in 1945 to 11,600 in 1971. Trends in the kill data were highly correlated with licence sales since seasonal success rates did not vary greatly, ranging from 29 to 40 percent from 1945 to 1951 and from 42 to 62 percent thereafter (Table I).

Indices of population change were obtained from the hunter-report statistics (Fig. 7): moose seen per hunter day, 2) percent successful hunters, 3) days hunted per successful hunter, 4) percent success per day hunted and, 5) sex ratio of the kill. Perhaps the best data to indicate population changes, (those with the fewest biases), are success rate per unit effort and the number of moose seen per day. Daily success declined 52 percent and moose seen per day decreased by 53 percent between 1960 and 1972.

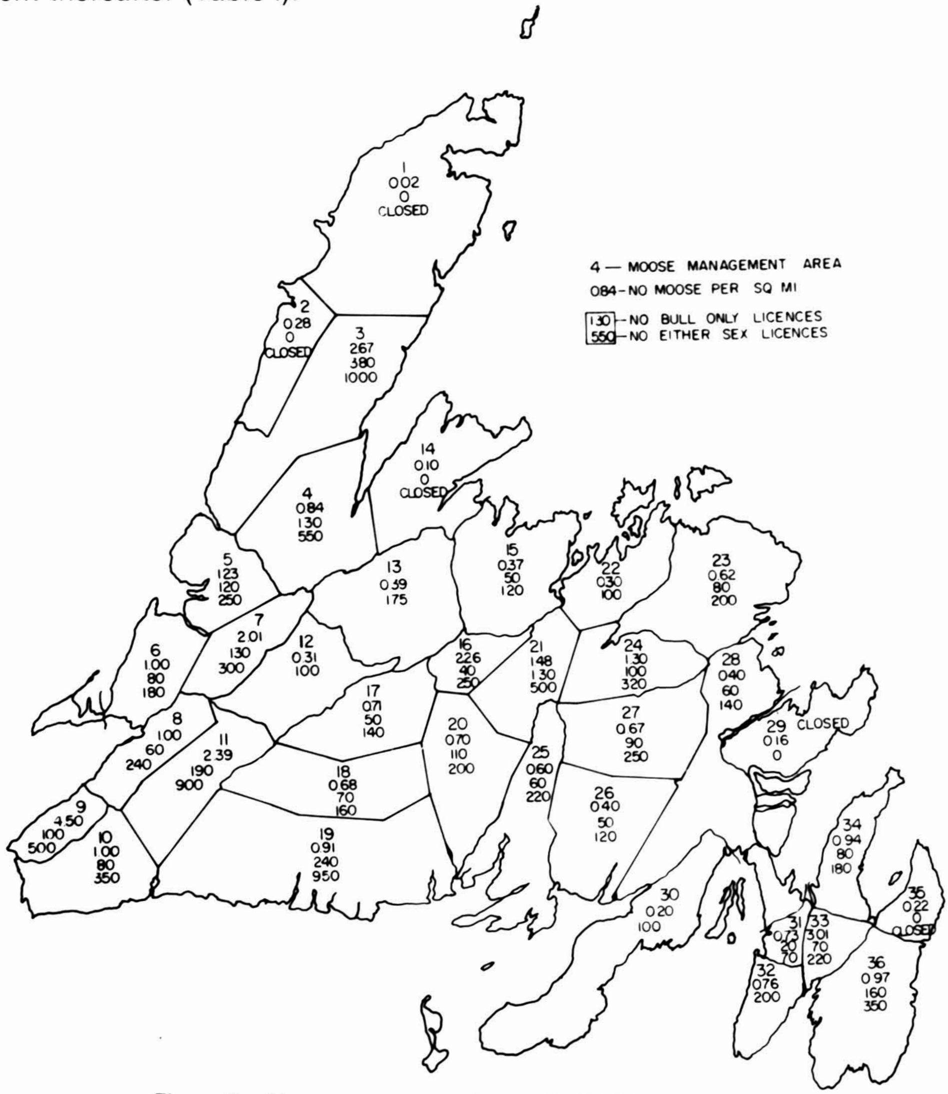

Figure 3. Moose management areas in 1973 in Newfoundland.

Although annual kills (Fig. 5) are probably positively correlated with population trends between 1945 and 1960, there is no such relationship apparent after that from the above indices (Fig. 7).

A population decline was also indicated by quadrat censuses which showed decreases in densities in some management areas after 1965. For example, decreases of 76 percent, 60 percent and 33 percent occurred between 1964-72 in Rattling Brook, Millertown and Terra Nova respectively (Table IV).

A decrease also was evident in the White Bear River country where 2.2 moose per mi^2 (0.8 per km^2) were counted in August 1967 using a strip census and a Cessna 180 aircraft versus one moose per square mile in March 1973 using a block census and helicopter. The decrease in Millertown must have been much greater between 1960, when 13 moose per mi^2 (5.0 per km^2) were shot near roads during the hunting season (Bergerud *et al.* 1968) and 1973 when 0.7 moose per mi^2 (0.3 per km^2) were counted in the area.

Based on the above data we believe that the moose population in Newfoundland increased rapidly until about 1960 after which it declined. The decline was partially due to overharvesting in accessible forested areas owing to a conscious effort by the Wildlife Service to curb excessive overbrowsing but having very little population data upon which to base management. Perhaps just as important was low moose productivity in inaccessible overbrowsed areas. Observed percent calves ranged from 10 percent in inaccessible areas to 20-40 percent in accessible areas.

Harvests and densities

Almost 160,000 moose have been legally harvested in Newfoundland

TABLE II

Moose kill statistics and season length, 1956-72, for three selected kill zones in Newfoundland

Year	*Area 8*[2]			*Area 13*[2]			*Area 26*[2]		
	Total kill	*Success ratio*	*Length season (days)*	*Total kill*	*Success ratio*	*Length season (days)*	*Total kill*	*Success ratio*	*Length season (days*
1956	311	52	31	27	93	122	347	57	31
1957	303	52	30	—	—	121	406	51	30
1959	640	57	109	30	61	109	706	60	109
1960	1,261	57	61	22	71	132	472	79	79[1]
1961	916	57	82[1]	16	62	111	573	69	82[1]
1962	1,064	51	76[1]	22	81	106	285	54	31
1963	993	52	78[1]	22	65	107	202	54	16
1964	879	52	79[1]	16	84	79[1]	163	52	13
1965	936	55	79[1]	22	58	103[1]	212	49	13
1966	1,023	60	75[1]	—	—	104	226	51	20
1967	1,273	66	75[1]	19	73	104	369	43	27
1968	1,255	62	75[1]	69	68	111	523	62	27
1969	1,208	57	72[1]	129	61	113	501	50	36
1970	1,341	58	65[1]	117	49	113	443	44	28
1971	1,253	53	65[1]	232	57	65[1]	490	44	29
1972	1,352	52	61[1]	293	52	48	404	39	20

[1] Split Season.

[2] See Fig. 8 for location.

since the first season was declared in 1936 (Table I). Probably well over 250,000 moose have been harvested legally and illegally since moose were introduced to Newfoundland in 1878 and 1904 (Pimlott, 1953 and 1959a).

The area (island-wide) required to support a yearly harvest of one moose between 1960-71 was 3.6-8.0 mi^2 (9.3-20.7 km^2). The range between kill zones in 1971 was 0.7 to 143 mi^2 (1.8 to 370 km^2) (Figure 8). When one considers that about one-half of Newfoundland consists of productive and scrub forest (Table V) these harvests are probably comparable with those of Scandinavia and probably higher than those for most other areas in North America (Lykke and Cowan, 1968). A high kill per unit area has been maintained in kill-zone 8 since about 1960 (Table VI). Population density estimates there in the winter of 1972 indicated 4.5 moose per mi^2 (1.7 per km^2).

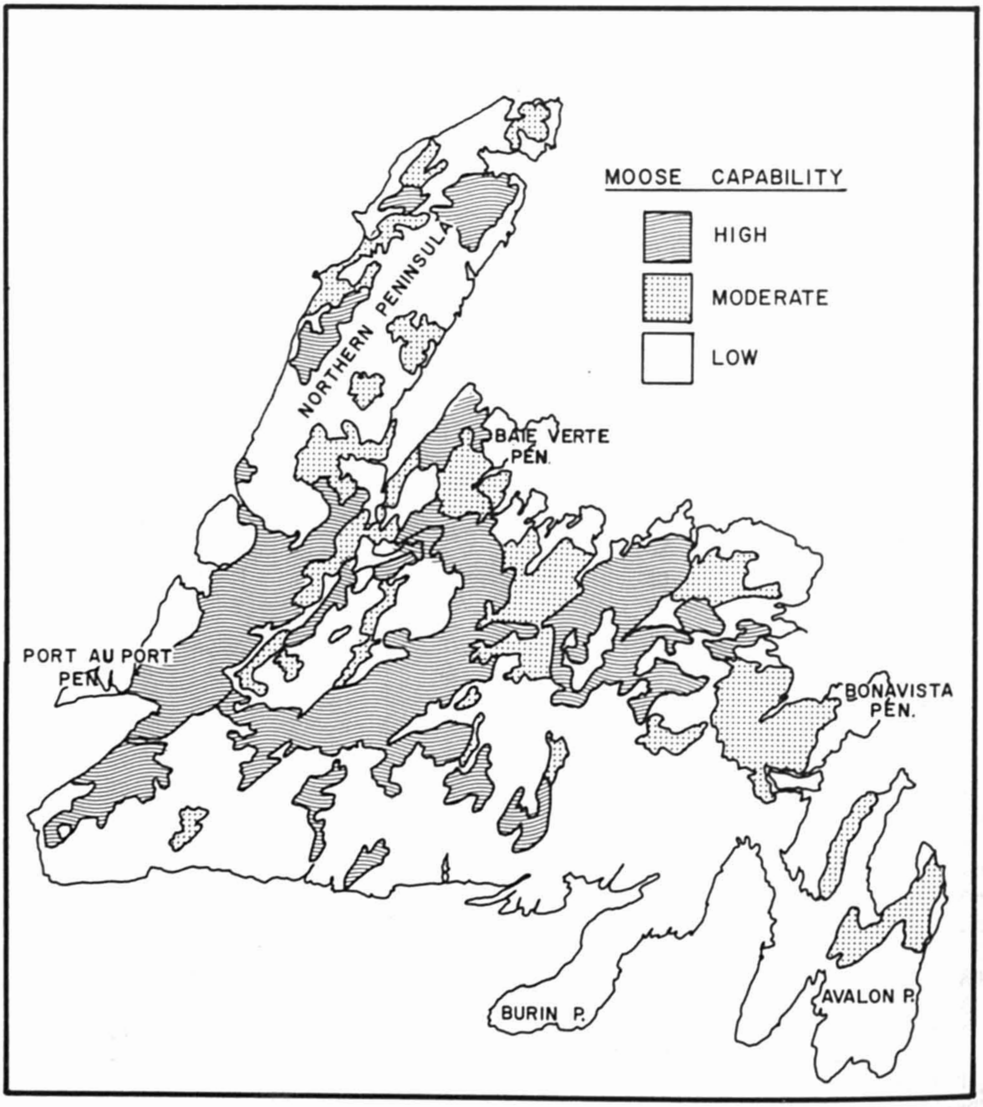

Figure 4. High, moderate and low moose capability range in Newfoundland based on the Ungulate Capability, Canada Land Inventory (CLI) Survey. The three classes represent CLI classes 1-3, 4 and 5-6 respectively.

TABLE III

Resident and non-resident moose licence sales in Newfoundland from 1953 to 1971

Year	*Resident*	*No. licence sales non-resident*	*Total*	*Per cent non-residents*
1953	4,969	206	5,175	3.9
1954	5,510	220	5,730	3.8
1955	6,389	287	6,676	4.3
1958	9,818	388	10,206	3.8
1959	12,725	718	13,443	5.3
1960	13,880	1,294	15,174	8.5
1961	12,929	1,578	14,507	10.8
1962	9,418	2,552	11,970	21.3
1963	9,642	3,079	12,721	24.2
1964*	9,883	1,324	11,207	11.8
1965	10,857	1,259	12,116	10.3
1966	11,240	1,458	12,698	11.4
1967	13,344	1,879	15,223	12.3
1968	15,087	2,474	17,561	14.0
1969	16,976	3,115	20,091	15.5
1970	18,605	3,350	21,955	15.2
1971	21,140	3,734	24,874	15.0
Total	202,412	28,915	231,527	12.4

* Non-Resident Licence Fee Increased from \$35 to \$75.

Thus there were probably six moose per mi^2 (2.3 per km^2) prior to the fall hunt which removed 23 percent of the animals.

Population density estimates for various regions of the province are shown in Fig. 3. The total moose population in 1973 is probably in excess of 50,000 whereas in 1960, based on hunter reports, Bergerud *et al.* (1968), and personal interviews, it must have been well in excess of 100,000.

TABLE IV

Changes in moose densities in four management areas, 1964-72

Area	*Moose per* mi^2		
	1964	*1972*	*Change* %
Rattling Brook	4.7(46)[1]	1.8 (50)[1]	−76
Millertown	2.0 (45)	0.8(108)	−60
Terra Nova	1.2 (19)	0.9 (70)	−33
Gambo	1.1 (36)	1.5 (70)	+36

[1] Number of quadrats flown in parenthesis.

Management problems

THE QUOTA SYSTEM

When the demand for moose in Newfoundland became greater than the supply, it became obvious that general season zones, which regulated only the sex of the kill and season length, were inadequate controls of the moose kill. Hence, in 1964 the quota system was first at-

TABLE V

Land classes of Newfoundland (from Gogos and Roth, 1971)

Land class	*Total area (Acres)*	*Per cent*
Forested	9,355,857	33.9
Softwood Scrub	5,966,959	21.6
Hardwood Scrub	71,337	0.3
Soil Barren	4,272,307	15.5
Bog	3,942,042	14.3
Water	2,781,040	10.0
Rock Barren	928,466	3.4
Cleared Land	203,907	0.7
Agriculture Land	15,661	0.1
Total	27,537,596	99.8

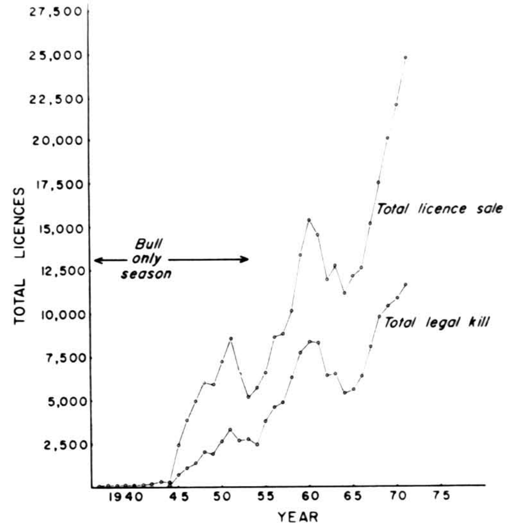

Figure 5. Licence sales and estimated legal kill in Newfoundland between 1936 and 1972.

tempted in "moose management areas". Since then, it has become apparent that unless populations are closely monitored it is difficult to maintain densities at desired levels. For example, the Rattling Brook management area was not counted during the period 1966-72 and the decrease from 6 to 1.5 moose per mi^2 (2.3 to 0.6 km^2) was considered undesirable; the population there could be maintained at densities in excess of three animals per mi^2 (1.2 per km^2) rather than the present 1.5 (0.6). A similar situation existed in Millertown and Rattling Brook. However, generally, the use of the quota system has worked well in other management areas. For example, in Glenwood-Gambo and the Anguille Mountains areas, populations appear to be increasing or stable since 1964 and 1968, respectively, the years when accurate censusing began. Also, population fluctuations appear to have been smaller in management areas than in areas with a general season.

In practically all accessible areas other than management areas, moose populations are below carrying capacity. Some areas have been seriously overhunted. We are convinced that the best method to curb this lack of precision is the use of a quota system. This method of regulating kills should

TABLE VI

Annual legal kill for kill-zone 8 (Anguille Mountains area)

Year	*Total reported kill*	*Per cent success*	*Per cent returns received* [1]	*Total adjusted kill*	*Kill per Sq. mi.*
1956	292	55	84	320	0.34
1957	282	56	82	313	0.34
1959	433	76	51	641	0.70
1960	926	72	59	1,087	1.18
1961	847	62	80	954	1.04
1962	966	56	82	1,072	1.16
1963	876	58	79	993	1.08
1964	766	58	77	880	0.96
1965	815	62	71	939	1.02
1966	933	65	84	1,022	1.11
1967	1,161	71	84	1,272	1.38
1968	1,121	69	81	1,253	1.36
1969	1,096	62	83	1,208	1.31
1970	1,146	67	75	1,338	1.45
1971	1,040	62	71	1,252	1.36
1972	729	52	50	1,093	1.19
Total and means	13,429	61	75	15,635	1.06

[1] Per cent returns for the total island.

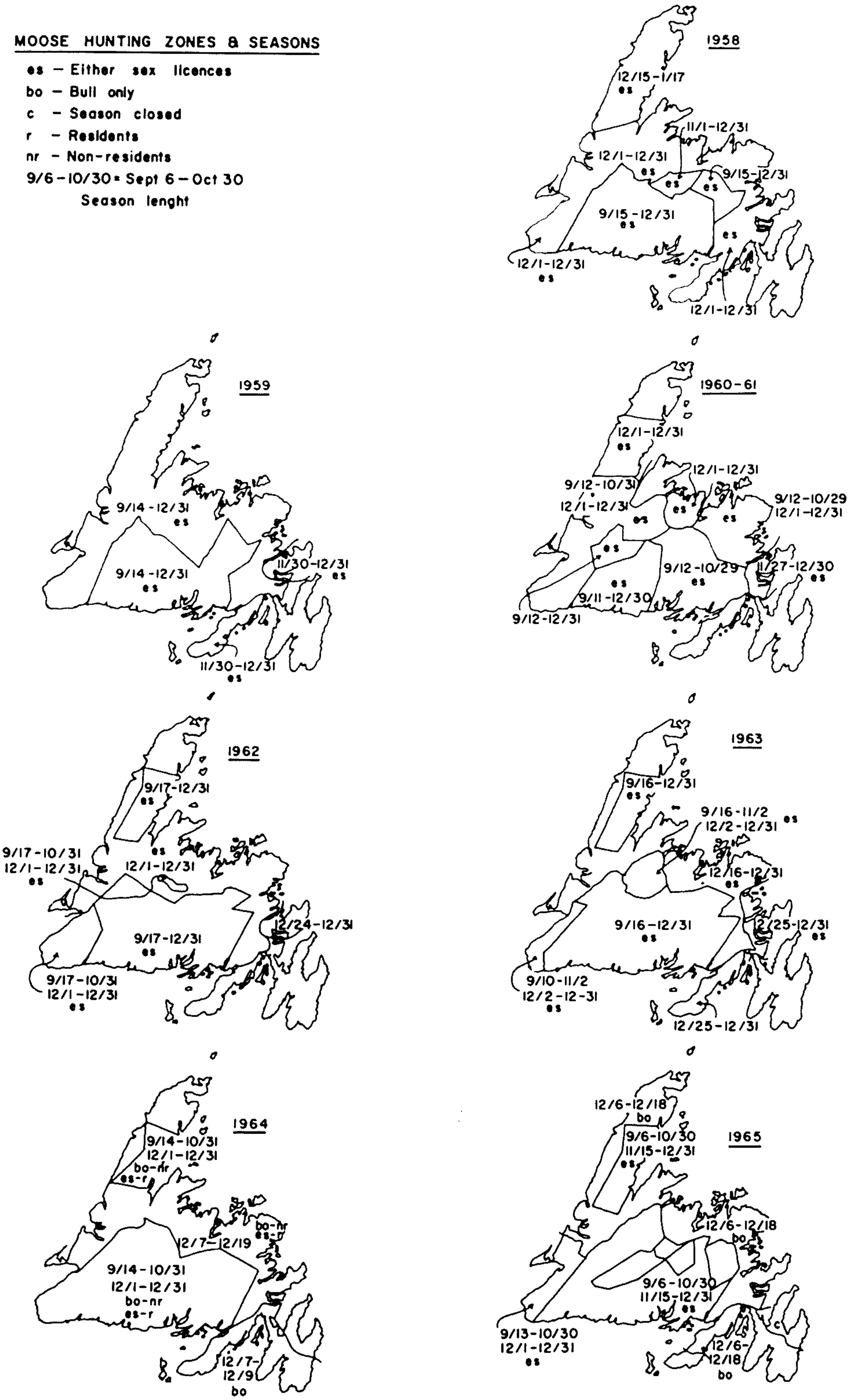

Figure 6. Zones and seasons in Newfoundland during the period 1958-1965.

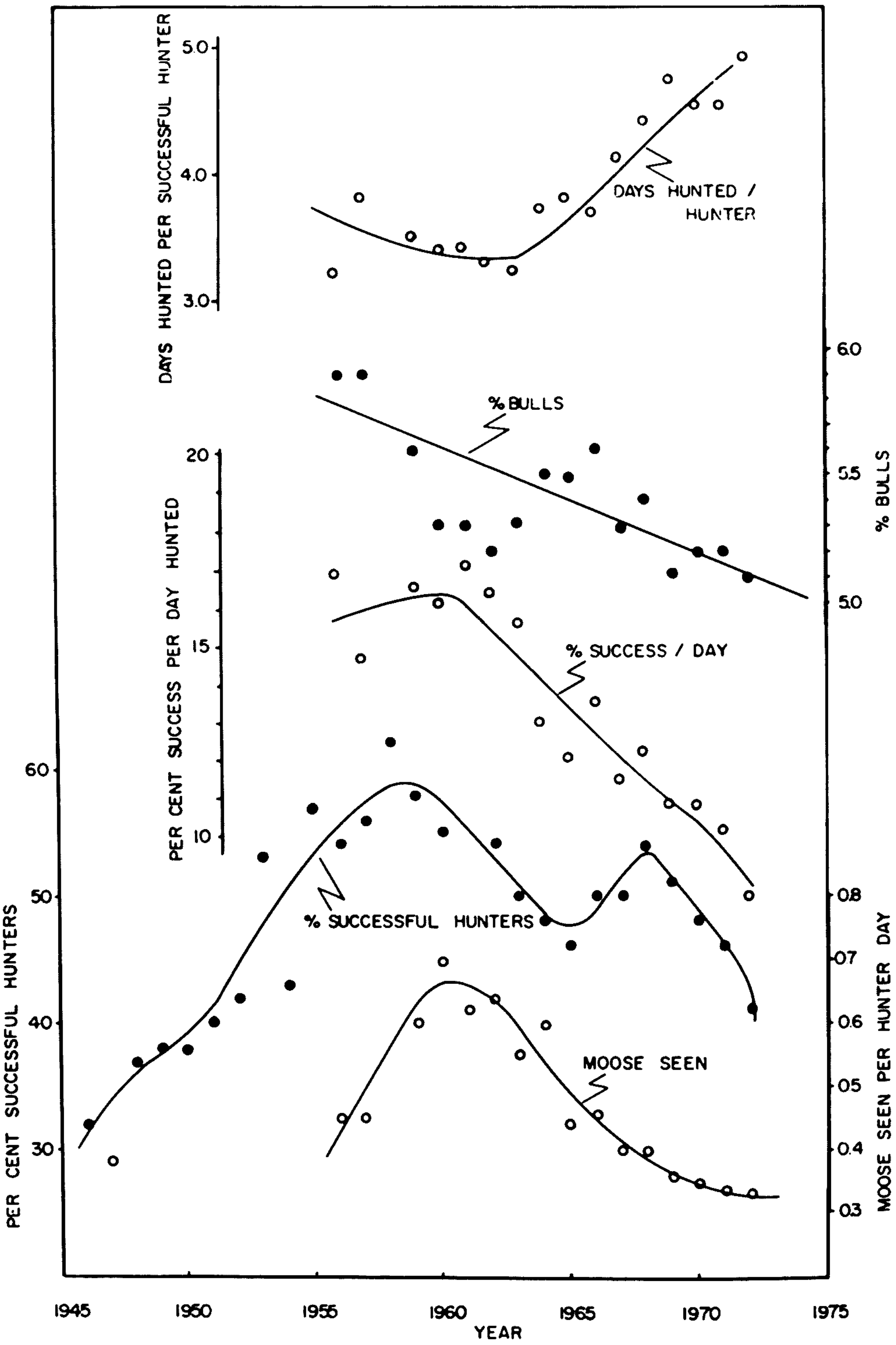

Figure 7. Indices of population derived from the hunter-report statistics in Newfoundland between 1945 and 1972. A definite downward trend in the moose population begins about 1960.

theoretically be more precise than general seasons if one has accurate information regarding moose populations and carrying capacity of the land. The system has also been applied successfully in Scandinavia (Lykke and Cowan, 1968) and Nova Scotia (Patton, 1968).

THE PROBLEM OF INACCESSIBILITY

On the south coast of Newfoundland the moose population exceeds the carrying capacity of the winter habitat on which the dominant species is balsam fir (*Abies balsamea*). This species occurs in timbered river valleys, in isolated stands in sheltered hillside situations, and in more exposed areas as low prostate communities. Overall, the range is submarginal moose habitat but densities in excess of five moose per mi^2 (1.9 per km^2) probably existed there at the peak population years around 1960. Accurate censuses

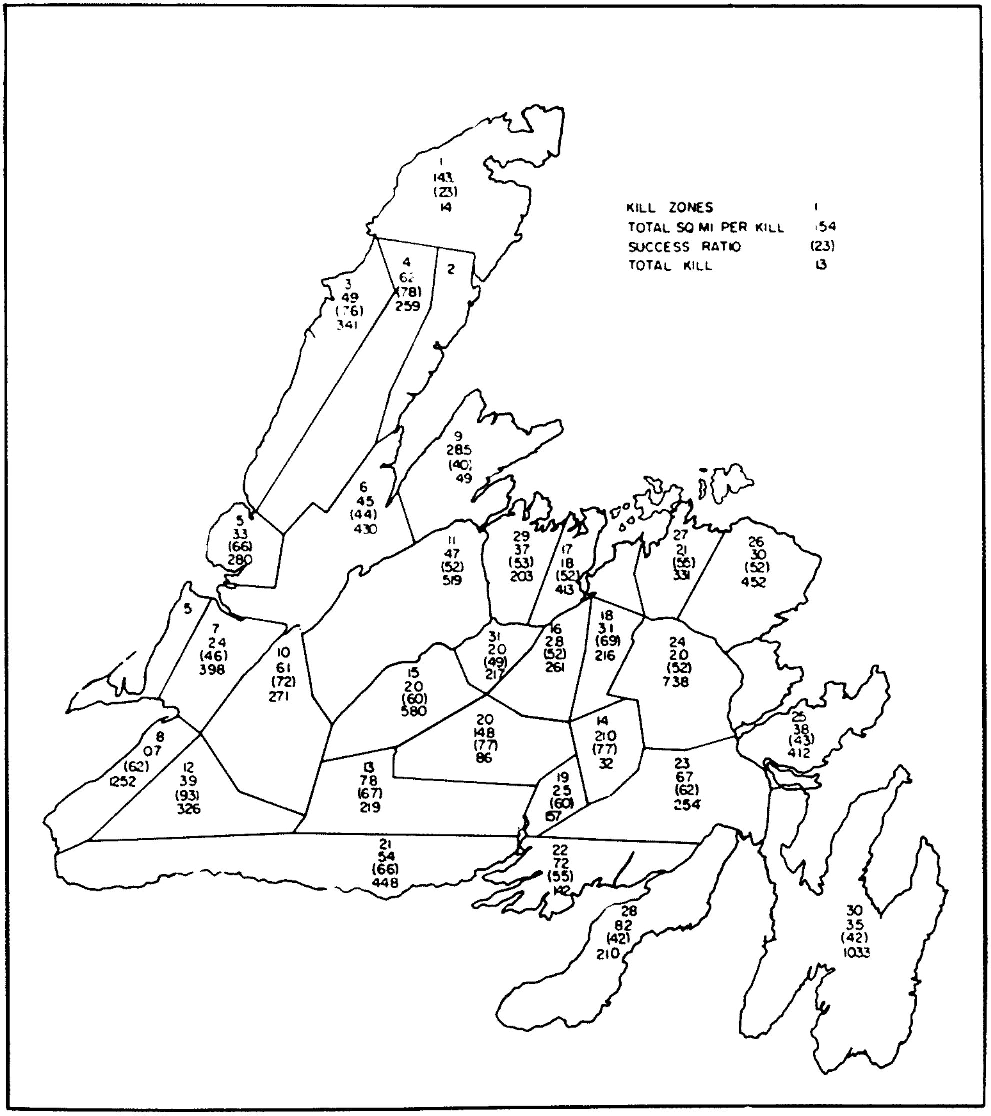

Figure 8. Kill zones in analyzing hunter returns (71% of the total licence sale) showing total kill, success ratio, and number of square miles per moose kill in 1971. The data is adjusted for non-reporters.

in 1973 placed densities at less than one animal per mi^2 (0.4 per km^2). Only virgin territory could produce densities of this magnitude in this subalpine situations, since less than 20 percent of the total area contains suitable moose winter habitat, the remainder being maritime barrens. Also, there are no roads and woodcutting in this area is insignificant, less than 6 percent of the area being in commercial forests (Gogos and Roth, 1971).

Prior to the introduction of moose into Newfoundland, the southern forests had a different composition, particularly a more abundant shrub flora. With low hunting pressure moose increased for about 56 years resulting in removal of most of the shrub component. Moose reproduction declined and the population decreased. Now, in many areas of Newfoundland, forest composition is changing to a higher percentage of spruce since moose have effectively eliminated balsam fir and white birch (*Betula papyrifera*) regeneration.

Throughout Newfoundland the comparative lack of roads has resulted in an uneven moose harvest, but in recent years more hunters, particularly non-residents, are getting into wilderness areas by chartered aircraft.

MOVEMENT

Movement could be an important unknown in moose management in Newfoundland. Seasonal moose migrations could play havoc with any management program if it were not accounted for when computing licence quotas on an area basis. For example, if in winter, moose move north from the southern maritime barrens region into the commercial forested area of Central Newfoundland, then, fall licence quotas for the latter area, based on winter census estimates would be much too high and overhunting would occur.

We know that there is a considerable 'fall shuffle' that is initiated by the onset of a snow-cover in November and this has been the main reason for split seasons. The animals shift to areas where food is more plentiful above the snow. We do not know what distances are involved, but monthly aerial censuses indicate that on some areas they may be considerable. Substantial migrations occur in Alaska (Le Resche, 1974), and Minnesota (Berg and Phillips, 1972).

Resighting of 30 moose tagged in Grey River in a 90 mi^2 (233 km^2) study area during 1963-64 did not indicate any large scale migrations. Movements in excess of 5 miles (8 km) were probably exceptional. However, the Grey River study area is 20 miles (32 km) from the nearest commercially logged forests. Movement studies are now being conducted in the commercial forests north of the subalpine barrens area. Presently, in setting seasons we assume negligible movement.

MORTALITY ESTIMATES

We believe that practically all adult mortality can be accounted for by human predation, both legal and illegal. Since the wolf (*Canis lupus*) became extinct in Newfoundland around 1911, the only wild carnivores in Newfoundland capable of killing moose are bears (*Ursus americanus*) and lynx (*Lynx canadensis*); there is no evidence of significant predation on moose by either of these animals. Based on mortality estimates from survivorship curves, estimates of kill mortality from hunter licence returns, and population estimates, we believe that natural mortality, crippling loss and poaching probably total less than 15 percent of the total population in the more accessible areas in Newfoundland. In southern inaccessible areas it is probably higher.

Natural adult mortality was probably less than ten percent in accessible areas and included mainly accidents involving automobiles and trains, falling through the ice, and becoming mired in bog pools. Crippling loss estimated from hunter reports appears to be very low. Also a survey done in 1960, when 250 mi^2 (647 km^2) were scanned in high density areas that were heavily hunted, indicated negligible crippling loss.

Poaching probably removed at least 5 percent of populations annually in accessible areas during the entire period prior to 1970. In recent years, Newfoundland law enforcement has not kept pace with poaching which in 1972 and 1973 probably reached 10 percent.

Acknowledgements

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MOOSE MANAGEMENT IN ONTARIO FROM 1948 to 1973

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Résumé

Les politiques d'aménagement de l'orignal (*Alces alces*) en Ontario ont eu successivement les objectifs suivants : protection absolue ; degré d'utilisation modérée ; incitation à une utilisation accrue ; utilisation maximale compatible avec un rendement soutenu ; développement d'une source de récréation et de revenus pour les citoyens de la province. La mise en oeuvre de ces politiques d'aménagement a consisté surtout à apporter des solutions aux problèmes du moment, ce qui ne diffère guère de tout programme d'aménagement de la faune. Les problèmes relatifs à la biologie de l'orignal et aux conséquences de la chasse ont été résolus de façon satisfaisante. Il reste encore beaucoup à accomplir en ce qui concerne les problèmes relatifs à son habitat et à son aménagement. Récemment, on a reconnu que la planification à long terme et l'éducation du public devaient constituer des éléments importants de toute politique d'aménagement et la réalisation de ces objectifs représente un défi pour l'avenir.

Abstract

Objectives of moose management in Ontario have envolved from simple protection, through permitting some use, to encouraging increased use, maintaining sustained yield and providing recreational and economic benefits for people. Management practice has consisted largely of solving problems, the major activity of any wildlife management program. Problems concerning moose biology and the effects of hunting have been adequately handled. Those involving moose range and how to manage it need further attention. Recently, long range planning and public education have become recognized as important requirements and they present a challenge for the future.

Introduction

Moose (*Alces alces*) management in Ontario began with R. L. Peterson's investigations during 1949-51 which provided the basis for early management policy and the starting point for all subsequent investigations. From that beginning moose management gradually evolved through changing purposes and increasing knowledge of moose into a relatively large operation. Moose hunting now provides some 460,000 user-days of outdoor recreation annually for the people of Ontario, an annual income of over $2 million in licence fees ($1.4 million from outside the province), an additional income from outside the province of nearly $3 million in general expenditures and a redistribution of over $8 million within the province. Obviously the moose herd constitutes a resource worth managing. This paper presents the changes of purpose, the problems faced and the efforts to solve these problems which have comprised moose management in Ontario.

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Changing objectives of moose management in Ontario

Early objectives of moose management were never stated and can only be deduced from records of events. Statements of purpose concerning wildlife management, which were published later, can be assumed to include moose. Finally, explicit statements of moose management objectives were included. Additional information on objectives came from unpublished papers, personal communications of other employees and from memory.

Prior to 1946, the whole emphasis of the Department of Game and Fish was on law enforcement. Presumably the objective was to protect wildlife, including moose, by enforcing the regulations made under The Game and Fish Act. In 1946 amalgamation with the Department of Lands and Forests brought Dr. J. F. K. Harkness to the head of the new Division of Fish and Wildlife and inaugurated the use of biological data to establish programs of game management. At that time it was generally held that numbers of moose were declining throughout Ontario and that increased hunting was a real threat to their continued well-being (Ont. Dep. Lands and Forests, 1947; Peterson, 1948, 1949). As a result, the hunting season for moose was closed for the entire province in 1949. The objectives of this closure seemed to be: 1) to build up the moose herd to huntable densities; and 2) to ensure that moose were not overexploited before enough was learned about them to permit adequate management (Lumsden, pers. comm.). This second objective was supported by hiring R. L. Peterson to carry out a province-wide investigation of moose from 1949 to 1951 (Peterson, 1955).

When the moose season was re-opened in 1951, there was a determination to supervise all hunting closely. In accord with Peterson's (1951) recommendations, the season was limited to the extreme north of Ontario and was for bulls only. The objective of the season was to harvest about 700 bull moose (Peterson, 1951). There seemed to be much doubt whether enough moose would be left for a season again the following year.

By the time I moved to northern Ontario in 1954, the situation had changed considerably. There was no longer any question about the ability of the moose herd to support annual seasons. Hunting for moose of either sex had been introduced in some areas during 1953. With estimates of moose numbers increasing each year (unpublished data), the objective became one of obtaining more use from an underdeveloped resource. About that time, a decision was made in head office to adopt the principle of "any moose seasons only" and by 1957 all bull seasons were eliminated. A determination grew to close the entire hunting season if necessary before returning to a bulls only season (Lumsden, pers. comm.) and this policy continues to the present time. This new position appeared to follow a change of mind by Peterson concerning the desirability of bull seasons, resulting from his study of European literature (Peterson, 1955: 217).

In 1956, the movement toward more liberal seasons was given additional impetus by the discovery of new methods of counting and sampling the moose herd (Fowle and Lumsden, 1958; Cumming, 1958). These methods were employed during the winter of 1958-59 for the first province-wide aerial inventory of moose. When the estimate of 125,000 moose in Ontario was compared with the annual harvest of less than 9,000 moose, seasons were again liberalized and an effort was made to rationalize and simplify them by eliminating differences in starting dates and season lengths which had no biological justification.

In 1958 the first of a series of statements of purpose by the Fish and Wildlife Division or Branch was published in the Annual Report of the Minister of Lands and Forests (Table I). These statements provide a good gauge of the changing emphases in moose managment in Ontario. The Minister's Annual Report for 1958 stressed sustained yield, maximum production and compatibility with other uses of the land and water. In 1959, the importance of habitat management was first recognized, along with the need for sharing limited resources. Within the Fish and Wildlife Branch a policy statement was circulated in 1960 proclaiming four principles: 1) sustained yield, which implied that the harvest should be regulated to avoid reducing the standing stock; 2) full use, which indicated that the resource was to be used, not merely preserved; 3) multiple use, which recognized competing demands on the land; and 4) public use, which emphasized the public ownership of the resource and recognized an obligation to make its use as widely available as possible. Some of the same themes were expressed in the Minister's Annual Report for that year (Table I).

Little further development occurred before 1965 when there was a surprising return to a statement of purpose similar to that of 1958. Then in 1966 came the first indication of a major change in emphasis. Rather than stressing the management of a resource, the statement proclaimed the need for providing recreational and economic benefits for people. The statements of 1967 and 1968 marked a transitional stage with both benefits to people and management of a resource included in the statement of purpose.

Finally, by 1969 the change was complete. A new goal statement for the entire Department provided the framework:

> "To encourage on private lands and waters, and to provide from Crown lands and waters, a continuing combination of renewable resource production and outdoor recreational opportunities most consistent with the social and economic wellbeing of the people of Ontario."

In accord with this goal, the objectives of Outdoor Recreation were:

> a) "to provide opportunities for a wide variety of outdoor-recreation experiences, oriented to day use, accessible to, and for the benefit of, all the people of Ontario;"
> b) "to provide on an economically sound basis, opportunities for the enjoyment of outdoor-recreation experiences on an overnight or extended use basis;"
> c) "to provide continuing outdoor-recreation opportunities for tourism to benefit the economy of Ontario and its communities." (Ont. Dept. Lands and Forests, 1969).

In 1967 I was asked to prepare for the Minister's Annual Report a statement of purpose specifically for moose management (Table I). It reflected current Department thinking by including the idea of viewing as well as hunting but it still implied an orientation toward managing a resource. A new statement in 1969 continued with similar views. Then in 1970 the change in outlook of the Department was incorporated into a goal statement for moose management, which was to provide recreational opportunities and economic benefits from the moose herd (Table I).

Thus, the objectives of moose management in Ontario went through a progression: 1) protection from suspected over-exploitation; 2) development of some use; 3) increased use of an under-developed resource; 4) sustained yield and optimum use of a resource product; 5) recreational and economic benefits to the people of Ontario.

Problems and solutions in Ontario moose management

Moose management in Ontario has progressed through solving problems related to the scientific basis for management and the means of achieving the most benefits. This section considers these problems and their solutions, or our progress toward solving them.

PROBLEM 1

Are there enough moose for hunting?

The first Annual Report of the Minister of Lands and Forests to include a Division of Fish and Wildlife (1947:42) stated: "Our moose have shown a distinct tendency to go downhill". In 1948, R. L. Peterson, then a university student, indicated in a confidential report to the Department of Lands and Forests (Peterson, 1948) that he had found corroborating evidence in results from questionnaires collected for ten years by the Royal Ontario Museum of Zoology. A high percentage of cooperators had

TABLE I

Statements of management purpose in Ontario from Annual Reports of the Minister of Lands and Forests (1958-1970) (Ontario Dept. Lands and Forests, 1958-1970)

A.	*Statements of purpose concerning wildlife management* *1958* "The purpose of the Fish and Wildlife Division is to manage the fisheries and wildlife resources of Ontario on a sustained yield basis, with the maximum production of all forms compatible with other uses of land and water." "It is our duty to use the resources of science for a constant improvement of our procedures and results, to consider all varieties of public interest in fisheries and wildlife, and to render an intelligent accounting to the public." *1959* "The objective of the Fish and Wildlife Division is to manage the public land and water areas of Ontario and the fish and wildlife resources which they supply so as to give the maximum possible yield and to assure its equitable distribution among those who wish to use it." *1960* "One of the aims of the Fish and Wildlife Branch is to provide full utilization of fisheries and wildlife resources now available to the public with due regard for future generations." *1966* "The Branch and its field staff have continued in directing its programmes towards permitting the people of Ontario the maximum recreational and economic benefits of the fish and wildlife resources." *1967* "To manage the lands and waters of the Province to ensure that (a) the maximum recreational and economic benefits are gained from the wildlife and fish species while keeping management practices compatible with other land and water uses; and to (b) permit the full harvest of the annual natural increases of fish and game species on a sustained yield basis."
B.	*Statements of purpose concerning moose management* *1967* "The objective of moose management in Ontario is to provide the most hunting and viewing of moose which can be sustained without interfering with other interests." *1969* "To provide: 1) a moose population as large as can be reconciled with timber production and forest management in general, and 2) as much hunting and viewing as the population will sustain." *1970* "The purpose of moose management in Ontario is to provide recreational opportunities and economic benefits from this resource."

expressed the opinion that moose were decreasing. With no independent evidence to permit evaluation of these reports, Peterson had little choice but to accept them. Without reliable estimates, he could only guess that there might be 20,000 moose in Ontario. From observations of moose in the field he estimated an annual increase of 15 to 20 percent, or less than 10 percent for the male segment. Calculating that 3,000 hunters would harvest 30 percent of the male segment, he concluded, "This then has resulted in a systematic depletion of moose in accessible areas"; therefore, "Ontario can never again afford unlimited moose hunting" (Peterson, *loc. cit.*).

In further calculations, Peterson (1949) assumed an average population density of one moose per ten square miles over some 300,000 square miles of moose range and concluded that there must be about 30,000 moose in Ontario. Again comparing the calculated kill of 3,000 moose with an assumed low rate of increase of only 8.5 percent for bulls, he asked: "How can the moose population hold its own when a higher percent is being removed than can be replaced?" He concluded: "Continuation of the present trend of increase in moose hunters can mean nothing short of suicide for moose hunting as either a sport or an industry" (*loc. cit.*). He stated that there was no question of moose becoming extinct, but that "in only a few years the moose population would become so low that moose hunting would not again be possible within the lifetime of the present generation regardless of any protective measure". In the absence of any contrary evidence, these conclusions were widely accepted. The moose season was closed for 1949 and 1950 and when it re-opened in 1951, there was a very real question whether Ontario's moose herd could sustain annual sport hunting.

SOLUTION: *Hunt records plus surveys*

The answer to this question was obtained in two ways. The first approach was to keep accurate records of the numbers of hunters and of moose harvested. These harvest statistics showed increasing annual yields from 1951 until recent years (Cumming, 1974) and thus, helped to dispel doubts about the capability of the Ontario moose herd to sustain annual hunting.

The second approach was to try improving on Peterson's estimates of moose numbers. Early estimates from trappers' reports showed no evidence of decreased numbers of moose after hunting was permitted again but, rather, increased estimates each year. Thus, the population estimates confirmed the conclusion from hunter statistics that the moose herd could support annual harvests. The 1958-59 aerial inventory which estimated 125,000 moose in Ontario (Lumsden, 1959) put this conclusion beyond doubt and went further, revealing that the moose were, in fact, greatly under-utilized. A similar problem arose in southern Ontario when moose hunting was re-opened in 1956 following closure since 1933 and it was solved in a similar way (Cumming, 1974).

PROBLEM 2
Can over-hunting be detected? What happens if too many moose are shot?

From the late 1940's, there was always concern by some members of the public and frequently by members of the Department's professional staff, that liberal regulations might allow too many moose to be shot. Would a moose population that had been reduced below a certain level recover? Might such a moose herd, as Peterson (1949) had suggested, take many years to increase again to huntable densities? Could overhunting be detected in time to prevent such a catastrophe? The people responsible for managing wildlife remained vulnerable to criticism while these questions went unanswered.

SOLUTION: *The southern Ontario experiment*

It had become evident by the late 1950's that the numbers of hunters then pursuing moose could not over-hunt them in the major northern Ontario moose range. Hence, it was decided to liberalize hunting, as an experiment, for the relatively small moose herd in southern Ontario. The requirement of a special licence was removed and open seasons were declared annually from 1960 to 1963. The experiment, described in detail by Cumming (1974) revealed that a continual decrease in numbers of harvested moose in the absence of alternative explanations, provides the best evidence of over-hunting. A change in the sex ratio of harvested moose from more bulls to more cows was a further consequence of over-hunting, and an increasing percentage of yearlings indicated that the annual harvest was approaching the annual surplus. These were statistics easily collected elsewhere in Ontario and this knowledge provided some assurance that over-hunting could be detected.

The data from southern Ontario at first seemed to support Peterson's early (1949) prediction that an over-hunted moose herd would require a long time to recover. Although the season in southern Ontario was closed entirely in 1964, even fewer moose were harvested in 1965 than in 1963. But then, after two more years without hunting, the harvest returned to more acceptable levels. Aerial counts confirmed that the herd had recovered to near pre-experiment densities. Thus, the moose herd recovered quickly from over-hunting, once hunting was removed.

The answers to these questions allowed substantial increases in the lengths of moose seasons throughout northern Ontario with confidence that any resulting over-hunting could be detected and quickly remedied.

PROBLEM 3

How far will moose move to fill heavily harvested areas?

Although the statistics demonstrated that moose were being underharvested in northern Ontario as a whole, some areas were exploited more heavily than others. Those places where the harest was heaviest (e.g. the Red Lake Road) continued to surprise everyone by showing little evidence of over-hunting. Even when the number of hunters more than doubled, the number of harvested moose remained nearly the same (Simkin, pers. comm.). The only apparent explanation seemed to be that although hunters would shoot most of the available moose each year (or a constantly available proportion within easy travelling distance of the roads and waterways) they would be replaced by immigrating moose during the following year. Supporting this idea was the fact that, on these areas, yearlings at times comprised over 40 percent of the harvested moose older than calves. These observations raised the question, how large an area does a road-water system exploit when surrounding areas are lightly hunted? Without the answer to this question there was no way of determining what proportion of the herd was being harvested since the area from which they were drawn was unknown. A similar question became even more important as additional roads were built near existing ones and power toboggans began to allow hunters to reach farther from access points; how far will moose move into areas where they are heavily harvested, or perhaps even shot out, each year?

PROGRESS: *Tagging moose from helicopters*

The answer to these questions obviously required tagging and the key was provided by Simkin (1963) when he found he could tag moose from a helicopter. Tagging was carried out at four locations in northern Ontario but only in the Geraldton and Sioux Lookout areas were enough moose tagged to provide usable data. These two studies provided impressively close results (Goddard, 1970; Saunders and Williamson, 1972). The average distance of six miles between location of tagging and location of shooting gives some indication of the distance moose might travel to replenish heavily hunted areas. But, obviously, many questions remained to be answered. Moose tagged during June and July and recovered by hunters during October — December provided only two locations on a map. Where were the moose during the interval? Where did they go during the remainder of the year? When did movement into an area occur? Moose might move into depleted areas between January and June, perhaps at calving time, without being detected until the next hunting season.

Radio telemetry seemed a suitable way of obtaining answers to these questions; therefore, in 1969, materials were assembled for a first attempt. Six transmitters placed on moose produced some useful results but all were silent by mid-winter. Problems with equipment prevented any useful radio monitoring in 1970 and 1971. By 1972 a new transmitter design developed by the Research Branch had proved more satisfactory and enabled the initiation of a full scale telemetry project. Results from this project are still being compiled.

Thus, some progress has been made toward finding out how far moose will move, but the question is far from answered.

PROBLEM 4
Can we change hunter distribution?

As far back as 1948 it was obvious that the distribution of moose hunters in Ontario was very uneven (Peterson, 1948). Many would crowd into a few accessible areas, leaving others lightly hunted. This uneven distribution presented problems in potential overharvest of accessible areas and known under-harvest of inaccessible areas. It also resulted in complaints of crowding by hunters and suspected reduction in hunter success due to the noise and commotion which seemed to frighten moose away from the most crowded areas. The question was what to do about it.

PROGRESS: *Long seasons, road maintenance, technology*

One way of reducing hunter congestion was to spread the hunting over longer seasons. As improved estimates revealed more moose, it was possible to lengthen the hunting season until at maximum it extended in some parts of Ontario from September 15th to January 8th. Unfortunately, about 80 percent of the hunting still occurred during the first two weeks of October, following the opening of hunting in the major moose producing areas. As a result much of the crowding remained.

It was observed that logging roads provided good access for moose hunters while woods operations were continuing and for some time afterwards, but eventually bridges would begin to collapse and roads would fall into disrepair. In 1969, 1970 about $50,000 was provided to districts for maintenance of these logging roads. Unfortunately, major repairs were sometimes required and the program was eventually discontinued. Some maintenance has been carried on afterward as part of the general roads programs of the districts.

Another possibility was to take advantage of modern technology. After preliminary trials in 1961 and 1962 (Armstrong, 1963), hunters were allowed to search for moose by aircraft in two specified areas in 1963. The hunter was required to turn in his regular hunting licence for a special one, and to return this special licence to the issuer before the fifth day after expiry. He was also expected to bring his moose for inspection, and fill in the report attached to the licence. This method of reporting was very effective. In 1962 only 12 of 421 hunters failed to report and in 1963 all 236 hunters in one area reported (Armstrong, 1963). Also in 1965, only 3 of 298 permittees failed to report (Hagan, 1965). Success of the hunters who used aircraft to search for moose was a phenomenal 79 percent in 1962, 87 percent in 1963 and 89 percent in 1965. Numbers of hunters participating increased each year. As Hagan (1965) reported, the system was successful in promoting hunting in remote areas, but the three hundred or so hunters taking part did little to reduce congestion among the thousands of hunters in more accessible areas. Then, despite the careful control, reports of hunters using aircraft to spot moose outside the prescribed areas increased, and in 1967 the special licence was revoked. Still, the impetus had been given and, encouraged by consistent advice by Department personnel, increasing numbers of hunters turned to aircraft to reach more remote hunting grounds. At first these were mostly non-residents, but in recent years more residents have also been flying to remote areas. Unfortunately, spotting moose from aircraft presents enforcement problems that seem insoluble. Furthermore, the practice is considered unsporting by some hunters who do not use aircraft themselves and, perhaps more importantly, by some members of the general public. Thus the advantages for distributing hunters more widely are accompanied by other disadvantages and the future usefulness of this method seems questionable.

The invention and rapidly gained popularity of snowmobiles provided another assist in distributing hunters. With these machines, hunters could travel farther from roadways into areas not accessible by automobile. More hunters were also attracted to late season hunting. But again, abuses threaten the continued use of these vehicles in connection with moose hunting. Possibly some actual cases, and many imagined ones, of hunters using convoys of snowmobiles to herd moose into circles to be "slaughtered" have done much to give these machines a poor public image. Although statistics show that relatively few moose are taken during the period when snowmobiles can operate, many complaints that their use leads to overshooting may force enactment of further restrictions. A few reports of hunters combining aircraft and snowmobiles using two-way radio communication have added to the unpopularity of both.

Altogether, progress in redistributing hunters has been limited and this remains a major problem.

PROBLEM 5

What proportion of a moose herd can be harvested safely?

Peterson (1955) concluded from his own studies and those of others, that less than half of the adult cows (two years old and older) produce calves each year. Most of the evidence came from observations of cows with calves in the wild and although Peterson knew the data to be shaky (1955, p. 60) he had no alternative but to accept them. These data led him to conclude (*ibid.*, p. 216) that the average annual increment was about 16 percent, ranging between 12 percent and 25 percent.

He reasoned that if bulls only were to be taken by hunters, the safe kill must remain between 6 and 12 percent of the total adult population in order to maintain breeding stock. However, Peterson himself was the first to point out that a more reliable measure of the average rate of reproduction was highly desirable for management (*ibid.*, p. 216).

SOLUTION: *Collection of ovaries and ages of harvested moose*

In view of the urgent requirement for more precise data on moose reproductive rates, Simkin began in 1957 to collect ovaries from cow moose in addition to the lower jaws and hunter statistics normally collected at the checking station on the Red Lake Road of northwestern Ontario (Simkin, 1965). The study was given added impetus by reports from British Columbia (Edwards and Ritcey, 1958) and Newfoundland (Pimlott, 1959) that suggested higher reproductive rates than those calculated by Peterson (1955). Simkin's study showed that barren cows were quite rare, contrary to Peterson's evidence, making up no more than 10 percent of the cows over two years old. He calculated the rate of increase as 34 percent rather than 16 percent suggested by Peterson (1955). The twinning rate was about 25 percent confirming Peterson's (1955) figure for this parameter.

Simkin went on to compare the gross productivity, calculated from ovarian analysis, with net productivity, calculated from the ages of moose harvested by hunters. He found that in Ontario, as in Newfoundland and Sweden (Pimlott, 1959), the differences between these parameters were slight. Loss of calves appeared small and thus, nearly the whole gross production of the herd was available for harvest.

Simkin's study was particularly important since it allowed for doubling the theoretical harvest rate for any particular moose herd. It had been doubled already by including cows in the harvest; therefore, the calculated allowable harvest became nearly four times what Peterson had recommended. More work remains to be done in establishing reproductive rates for other parts of Ontario and in finding rates of loss among calves, but the original question was answered.

PROBLEM 6

Will moose destroy their range? What do they eat?

With the examples of white-tailed deer (*Odocoileus virginianus*) in many parts of North America before him (e.g. Leopold *et al.*, 1947) and with reports of damage to vegetation by moose from Sweden (Hamilton, 1947), Finland (Kangas, 1949), Isle Royale (Aldous, 1946) and Alaska (Spencer and Chatelain, 1953), Peterson (1955) was conservative in suggesting that moose might change the composition of the forest when their densities were high. The increasing estimates of moose numbers in Ontario throughout the 1950's raised the spectre of another over-browsed range similar to the famous Kaibab (Rasmussen, 1941), but involving an animal capable of causing much greater damage. Would moose ruin the forests of northern Ontario? Would they increase to the point where they eliminated their food supply and crash to even lower levels than in 1949 when the season had to be closed? The whole future of sustained yield management of moose in Ontario hung on the answer to this question.

SOLUTION: *Browse surveys*

Beginning in 1956 browse surveys were carried out across northern Ontario. Some were aimed at comparing rates of browsing in different habitat types such as burned areas, cut areas and insect killed areas, but most, especially from 1960-70, were aimed at finding the extent of browsing in areas where aerial counts of moose in winter had revealed the highest densities.

The results were reassuring. Even in places where moose were most numerous, browsing was seldom found on more than 50 percent of the available stems of suitable browse species. In a few cases, browsing was more intensive on favoured species but never to the extent that the survival of these plants was threatened over large areas. No evidence was discovered of moose densities so great that the available food might be completely used and the animals faced with starvation. The pre-eminence of mountain maple (*Acer spicatum*), mountain ash (*Sorbus americana*), red-osier dogwood (*Cornus stolonifera*), balsam fir (*Abies balsamea*) and beaked hazelnut (*Corylus cornuta*) as food plants was established, along with some idea of regional differences in food habits of moose.

PROBLEM 7

How does forest management affect moose range?

With most of the early problems solved or being investigated, by 1968 problems of range began to emerge. White-tailed deer in Ontario were in serious trouble because of severe winters and deteriorated range conditions resulting from changes in forest cutting practices. Forest practices were changing in northern Ontario too. How would the changes affect moose?

PROGRESS:

Beginning in 1968, crews of students investigated the effects of forest practices on moose browse during each spring and summer (summarized by Henderson, 1973). Some practices such as scarifying (Fig. 1) and aerial spraying reduced available browse temporarily but all disturbances produced more browse over a longer term. Young browse plants remained available to moose in one area for at least 20 years. At the same time new problems appeared. Several efforts to find the effects of removing escape cover by clear cutting large areas (Fig. 1) were inconclusive. The very long term effects of changes in forest rotation were questioned but not answered. These problems are still important for the future of moose management.

PROBLEM 8

What direct action can be taken to improve moose range?

Even if the range requirements of moose and the effects of forest management become better known, the feasibility of action to improve that range remains uncertain. Management of white-tailed deer range in eastern Ontario has achieved heightened impact by concentrating efforts on places where great concentrations of deer gather during winter. But moose, in Ontario, do not concentrate in special areas during winter to the same degree. Therefore, to improve moose range to a similar extent would require the treatment of major portions of northern Ontario. Few areas are so valuable for moose production that they justify spending money directly to improve the range, unless very low cost methods such as burning can be employed. Prescribed burning is a possibility in some localities but it can hardly be used throughout northern Ontario where valuable pulp and timber crops are also grown. The question of how to improve moose range over such vast areas is an important one for the future.

PROGRESS: *Imput to forest management plans*

One solution to the problem is to provide an input to forest management plans so that the requirements of moose are considered along with the requirements of regeneration. District biologists in Ontario are now familiarizing themselves with the mechanisms of planning for forest management so they can provide inputs at the right stages. Unfortunately, most biologists to date have entered the planning process at an advanced stage. When licences are signed and cutting plans approved, it is too late to ask for consideration of moose. The requirements of moose must be included in the planning from the beginning.

Still, some progress has been made. One side-benefit derived from this participation of wildlife managers in forest management planning is that foresters often become interested in the problems of wildlife management, and begin planning for wildlife themselves. This benefit has been evident in white-tailed deer range management which has gone on for a longer time and it is now beginning to appear in moose range management. Such interest by foresters promises well for the future.

A second benefit from biologists attempting to contribute to forest management plans is that this process quickly identifies the gaps in our knowledge of moose requirements. In fact, these gaps are so evident that some biologists are reluctant to make any suggestions at all. But to wait until the result of every suggested change in forest management can be accurately predicted is to opt out altogether. Many people will continue changing the forest in ways which completely ignore the requirements of moose. Unless those concerned with moose management make recommendations on the basis of present knowledge, any benefits to moose from these changes will be entirely due to chance.

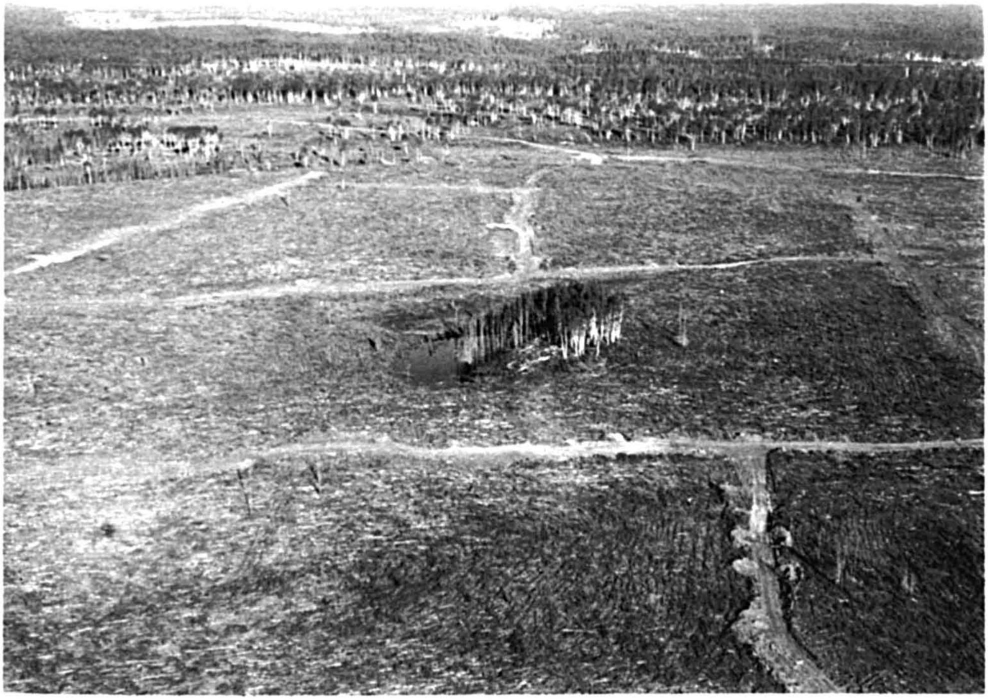

Figure 1. An example of clear cutting followed by scarification to expose mineral soil, one of the common silvicultural practices used to promote regeneration which must also affect moose range for better or for worse. More information concerning these effects is required. Dog River Area, Thunder Bay District, Ontario (Photograph, H. R. Timmermann).

One example of the kind of input which can be provided is contained in a new manual to guide foresters in more aesthetically pleasing forest practices (Ont. Min. Natural Resources, 1973). During preparation of this document wildlife biologists successfully argued that wildlife constitutes an important element of forest aesthetics and, therefore, should be considered of equal importance with a pleasant view. The suggestions for moose range management included in the guide can undoubtedly be improved in future years, but at the very least they should produce forest conditions less hostile to moose than those arising through chance.

Discussion

This review provides an opportunity for re-examining some of the basic tenets of wildlife management. One wonders, for example, how important policy statements really are. The value of clearly thought out management policies seems unquestionable. For example, the longer moose seasons which followed some of the early policy changes in Ontario demonstrated clearly the effect of policy on management practice. But these policies were unstated. Is anything more required? Unstated policies work well in relatively small organizations that have good internal communication and plenty of experienced staff. But as these organizations grow, taking on new employees and as the emphasis shifts from problem solving to planning for the future, the need for stated policy increases. It is probably for this reason that policy statements for moose management in Ontario appeared relatively late in its history. Yet the newer changes in policy have not resulted in substantial alterations in moose management practices. Perhaps the shifts were too subtle. Or perhaps they were too recent. Maybe policy statements take longer to affect complex organizations. However, it seems likely that as planning for future management progresses, these policy statements will play a major role in determining the direction it takes.

Another question concerns the content of policy statements. Conservation implies wise use, but this leaves open the question of what is wise. The answer, of course, will change with the changing needs of people. During an earlier period, wise use might have included taking moose as food for pioneers, but this would hardly be wise use in the modern world. Decisions concerning what is wise are also affected by the changing ideas of managers, concerning what is involved in wildlife management. To some, it might mean protecting a species from unfair exploitation. Perhaps such a notion lay behind the early emphasis on law enforcement. To others, it involves managing a resource. As Trippensee (1948:v) stated, "Fundamentally, it is the process of making land and water produce sustained crops of wild animals", or as Wing (1951:1) proclaimed, "Wildlife management is the branch of conservation that handles wildlife as an attribute of the land". These ideas probably formed the basis for the period of increasing use in Ontario.

Perhaps many wildlife managers would still stand by these definitions. If that is so, it raises questions about the wisdom of the newer Ontario statements. I suspect that many wildlife managers would object that our primary responsibility is to the resource and that people must come second. With this position, I must agree. Perhaps responsibility to the animals has not been emphasized enough in Ontario. We have witnessed the destruction of too many plants, animals and ecosystems by people whose sole concern is economic gain and who hold totally irresponsible attitudes toward the heritage with which they were entrusted, to ignore this vital consideration.

On the other hand, statements concerning benefits to people still imply the continued existence of a healthy viable moose population. Certainly the resource must be protected, but the question then becomes, what should be done with it? The current policy statement in Ontario goes beyond most such statements in specifying that the moose will be used for the recreation of residents and for the economic returns to be derived from providing recreation for both residents and non-residents. In these respects, it comes close to the statement by Leopold (1948:3), "Game management is the art of making land produce sustained annual crops of wild game for recreational use".

But wildlife management involves more than forming policies. Information gathering remains an important aspect. In some cases, it may be sufficient merely to collect the kind of information which has been useful elsewhere. But a more profitable approach is to collect information which will help in solving problems. For the most part, this has been our aim in Ontario. Although we were not entirely successful, this problem-oriented approach has been one of the strengths of Ontario's moose management program; for despite the importance of other aspects such as planning, the essence of day to day wildlife management practice is the careful identification of problems and collection of the facts required to solve them. Again this idea is not far from one expressed by Leopold (1948:39), "Game management consists largely of 'spotting' the limiting factor and controlling it". The last point, of course, is important. Having found the problem and collected the facts, we must be willing to take the necessary steps to assure a suitable solution. But this requirement, in turn, becomes only one more problem which the wildlife manager must solve.

In Ontario we have managed to solve satisfactorily most of the problems that concern moose population management. We have found that we have plenty of moose for hunting. We can detect overhunting and know that moose recover quickly from it when given respite. We have obtained useful knowledge of the extent of moose movements but not enough and work is continuing. On the other hand, poor hunter distribution remains a difficult problem that may force us to adopt new measures such as regulating numbers of hunters on management units. Some problems will always remain.

Progress toward solving the problems of range management has been less satisfactory. We have obtained a working knowledge of the range requirements and food habits of moose but more remains to be learned. We know that moose do not threaten their range in northern Ontario, but we do not know why. We are developing ways of maintaining and providing for good moose range through forest management plans, though much more remains to be done along this line. We have as yet found no way of taking direct action to improve moose range.

This is not to imply that all problems have been investigated and all aspects of management implemented. We know little about the behaviour of moose. We wonder, for example, how disturbance by hunters affects the mating behaviour of moose; how an unbalanced sex ratio may interfere with "social well being" (Bubenik, 1972); how social behaviour is related to such important observations as the movement of moose from lightly hunted to heavily hunted areas; and whether social behaviour may be at least partially responsible for the relatively static moose population in northern Ontario. These questions all need answering in order that management may be based on a full understanding of moose biology.

Lack of planning has been a major weakness in our management program to date. Although the solving of problems is the major work of a wildlife manager, he is in error if he emphasizes this aspect of management to the exclusion of all others. Planning is all too easily neglected in the heat of solving current problems. We need to progress from the stage where problems are solved as they arise to the stage where they are foreseen and provided for in plans which lead toward clearly stated goals.

Perhaps an even more important weakness has been our use of relatively ineffective methods for disseminating information to people. It is most important to solve the problem of how to lead people to accept sound management policies. I avoid the terms "people management" and "people manipulation" because they suggest control over people, even during their leisure hours. Our job is not to manage people but to manage resources for the benefit of people. Yet sometimes through ignorance or misunderstanding, people deprive themselves of benefits which could be theirs. One wonders in retrospect whether the closure of the moose season in 1949 was really justified on the basis of low and declining moose numbers or whether the real problem was not ignorance about moose? Looking back, it appears, that ignorance was at least the greater problem. The increase in our knowledge of moose and their requirements since that time has put wildlife managers in a position where management in ignorance should never again be necessary. But unless the general populace are aware of this knowledge and can fully trust those in charge of moose management, they might again demand reduced or closed seasons in mistaken concern for the welfare of the moose. Two of the biggest problems facing moose managers in Ontario in the near future, particularly in view of the increased awareness of ecological problems and concern about misuse of our resources, are how to communicate to people the essential facts and principles of moose management and how to minimize the credibility gap which always exists between a people and their elected and hired servants.

These are the strengths and weaknesses of moose management in Ontario. It is by maintaining the strengths and improving on the weaknesses that future moose management must progress.

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CHASSE CONTRÔLÉE À L'ORIGNAL DANS LES PARCS ET RÉSERVES DU QUÉBEC (1962-1972)

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Résumé

La chasse contrôlée à l'orignal (*Alces alces*) a d'abord été organisée dans le parc des Laurentides à compter de 1962 et ce mode d'exploitation existe maintenant dans sept parcs et réserves du Québec. Dans la réserve de Matane, le parc des Laurentides et le parc de la Vérendrye, tout groupe de deux chasseurs doit se faire accompagner d'un guide et le succès de la chasse est présentement d'environ 85, 60 et 55 pourcent respectivement. Par contre, dans les divers parcs et réserves où les chasseurs ne sont pas accompagnés d'un guide, le succès de chasse varie de 0 à 42 pourcent. Dans les parcs et réserves pour lesquels on dispose de données s'étendant sur au moins cinq ans, les effets de la chasse contrôlée sont les suivants: rajeunissement de la population, augmentation de la proportion de jeunes animaux (veaux et animaux de 1.5 an) dans la récolte, accroissement de la proportion des mâles dans cette récolte et apparition d'indices suggérant une augmentation de la productivité des cheptels exploités.

Abstract

Controlled moose hunts were first organized in Laurentides provincial park in 1962 and have since been introduced in seven other parks or fish and game reserves throughout the Québec. In Matane fish and game reserve, Laurentides and La Vérendrye provincial parks, the party of two hunters must further be accompanied by a licensed guide and hunting success therein now stands at 85, 60 and 50 percent respectively. In other parks and reserves, hunters may operate on their own and hunting success there varies between 0 and 42 percent. In areas that have now been hunted for at least five years, the effects of the hunt upon moose populations have begun to appear: a lowering of the mean age, an increase in the proportion of young animals (calves and yearlings) in the harvest, an increase in the male/female ratio and signs of rising productivity in the exploited herds.

Historique

Le programme de chasse contrôlée à l'orignal (*Alces alces*) dans les parcs et réserves a débuté au Québec en 1962 dans le parc des Laurentides où toute chasse était prohibée depuis 1928 (DesMeules, 1967). Les principaux objectifs visés par cette chasse étaient d'ouvrir de nouveaux territoires aux chasseurs et de rajeunir une population inexploitée depuis longtemps. Par ricochet, cette exploitation devait nous permettre d'obtenir des données scientifiques concernant l'effet de la chasse sur ces populations d'ongulés.

La réponse enthousiaste des chasseurs à cette innovation et les renseignements utiles obtenus ont incité le

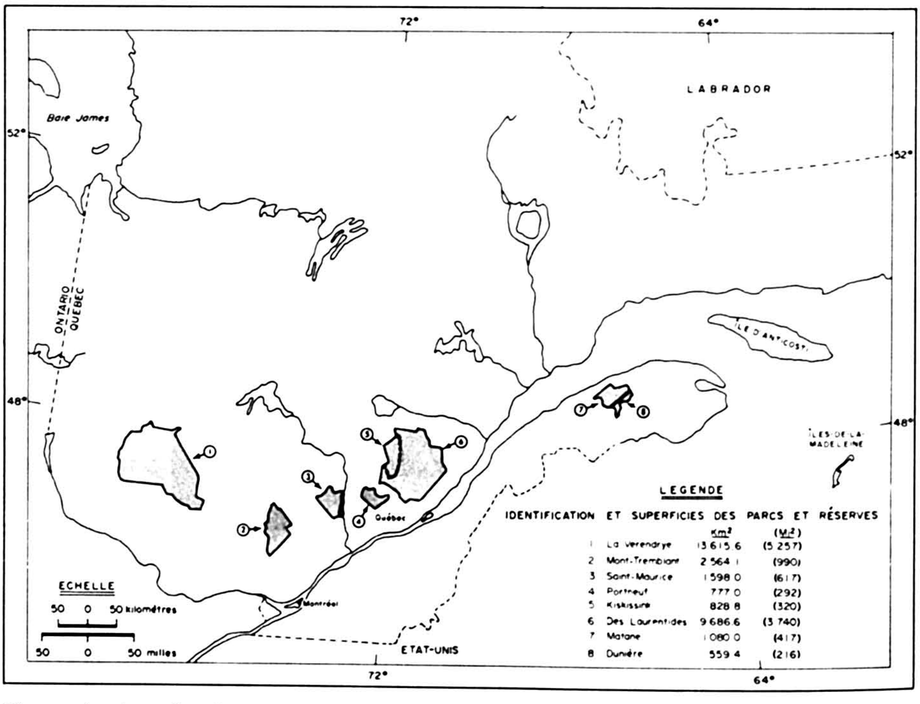
Ministère du tourisme, de la chasse et de la pêche à étendre ce genre de chasse à d'autres secteurs. Ainsi, la chasse contrôlée a été entreprise dans le parc de La Vérendrye et la réserve de Matane en 1964, la réserve du St-Maurice en 1967, la réserve de Portneuf en 1969, la section nord-ouest du parc des Laurentides (Kiskissink) en 1970, la réserve de Dunière et le parc du Mont-Tremblant en 1972 (fig. 1). Les résultats de chasse de 1962 à 1965 (DesMeules, 1966) et ceux recueillis depuis 1966 sur la dynamique de nos populations d'orignaux devraient nous permettre de planifier une chasse plus rationnelle dans l'avenir, tant à l'intérieur qu'à l'extérieur des parcs et réserves.

Nous tenterons d'abord d'exposer le mécanisme opérationnel de ces chasses contrôlées avant d'exposer et d'analyser ensuite les résultats obtenus.

Organisation de la chasse contrôlée

PLAN DE CHASSE

La première étape consiste à établir le plan de chasse, la récolte permise étant fixée après évaluation de l'abondance de l'orignal, de son taux de productivité nette et de l'accessibilité du territoire. Avant l'ouverture d'un territoire à la chasse contrôlée, un inventaire aérien permet de déterminer la densité moyenne de l'orignal. Ensuite, une mise à jour des routes primaires et secondaires s'impose pour déterminer la superficie accessible du territoire. En se basant sur le taux de productivité nette et sur les principaux facteurs décimants de la population de même que sur les données disponibles dans la littérature (Pimlott, 1959), DesMeules (1966) a suggéré un taux d'exploitation hypothétique de 20 pourcent. La récolte permise ainsi établie, on peut ensuite déterminer le nombre de chas-



LEGENDE

IDENTIFICATION ET SUPERFICIES DES PARCS ET RÉSERVES

		Km²	(M²)
1	La Verendrye	13 615.6	(5 257)
2	Mont-Tremblant	2 564.1	(990)
3	Saint-Maurice	1 598.0	(617)
4	Portneuf	777.0	(292)
5	Kiskissink	828.8	(320)
6	Des Laurentides	9 686.6	(3 740)
7	Matane	1 080.0	(417)
8	Dunière	559.4	(216)

Figure 1. Localisation des parcs et réserves où s'organisent des chasses contrôlées à l'orignal au Québec.

seurs qui seront admis, chaque groupe de deux chasseurs ayant la possibilité d'abattre un seul animal. Lorsque le plan de chasse est établi, il ne reste qu'à répartir les chasseurs sur le territoire de façon équitable.

MODE D'OPÉRATION

D'une façon générale, le mode d'opération de la chasse contrôlée (décrit par DesMeules, 1966) n'a pas tellement changé depuis 1962. Cependant, certaines améliorations suggérées par les chasseurs et par le personnel ont été incorporées au mode d'opération.

SÉLECTION DES CHASSEURS

Les individus désireux de participer à la chasse doivent soumettre une demande à cette fin, six mois avant l'ouverture de la saison de chasse. Le candidat doit, déjà à ce moment, verser un montant de $30.00. Cette somme lui sera créditée si son nom figure parmi la liste des chasseurs élus ou retournée si le sort ne le favorise pas. Durant les premières années, les chasseurs pouvaient soumettre leur inscription en équipes de deux ou quatre chasseurs, chacun des membres du groupe devant être identifiée sur le formulaire; en 1971, l'essai a également été fait avec des groupes de trois. Depuis 1972, seuls les groupes de deux chasseurs peuvent soumettre une demande et celle-ci est produite au nom d'un des deux partenaires. Les groupes sont ensuite désignés par le sort, grâce à un ordinateur. La liste des chasseurs perdants est également dressée et c'est en tête de cette liste qu'on choisit les groupes qui seront invités à remplacer un groupe de chasseur gagnant incapable de prendre part à la chasse.

GUIDES ET TAUX

Dans les réserves du St-Maurice, de Portneuf et de Dunière, les services d'un guide ne sont pas requis. Ailleurs, chaque groupe de chasseur doit obligatoirement se faire accompagner d'un guide.

Le tarif exigé est de $76.00 par chasseur pour droit de chasse et service du guide. Là où le service du guide n'est pas requis, le prix est de $37.50 par chasseur.

PÉRIODES DE CHASSE

Chaque groupe de chasseurs peut chasser durant quatre jours consécutifs. La période de séjour est cependant de cinq jours dans les réserves où les services d'un guide ne sont pas requis.

La saison de chasse débute vers la fin de septembre pour une durée approximative d'un mois. De 1962 à 1971, l'entrée des chasseurs se faisait régulièrement à chaque jour. En 1972, à l'exception du parc de La Vérendrye, les dates d'entrée des chasseurs étaient à intervalle de cinq jours, de sorte que le nombre de groupes admis était fonction du nombre total de groupes de chasseurs divisé par le nombre de dates d'entrée.

TERRITOIRES DE CHASSE

Les territoires de chasse sont délimités en fonction de l'accessibilité. En général, le groupe de deux chasseurs a le privilège exclusif de chasse sur un territoire variant de 15 à 80 km^2 (6 à 30 mi^2). De 1962 à 1971, le chasseur devait, dès son arrivée, choisir au hasard son territoire. En 1972, on a utilisé ce procédé dans le seul parc de la Vérendrye. Ailleurs, l'attribution des zones a été faite par ordinateur en même temps que la sélection des chasseurs, de sorte que tout l'ensemble du territoire était occupé simultanément par les chasseurs.

STATIONS DE VÉRIFICATION

À la fin de son séjour, le chasseur doit se présenter aux stations de vérification pour permettre aux représentants du Service de la faune de prélever certaines pièces anatomiques et de recueillir les informations essentielles: on y détermine le sexe de l'animal abattu, son âge et la présence de lait chez la femelle. Le cœur, les poumons, le foie, les reins, la langue et la peau sont soigneusement examinés afin d'y déceler la présence possible de parasites. Certaines données connexes à la chasse telles, le nombre d'heures de chasse, telles le nombre d'heures de par groupe de chasseurs, sont également obtenues lors de l'entrevue.

Résultats

La chasse contrôlée est présentement en opération dans sept parcs et réserves, couvrant une superficie totale de 29,738 km^2 (11,482 mi^2). Le tableau I regroupe les variables permettant d'élaborer le plan de chasse dans chacun de ces territoires. La densité moyenne de l'orignal y varie de 0.3 à 0.8 au km^2 (0.7 à 2.1 au mi^2).

Le nombre de chasseurs posant leur candidature pour cette chasse a augmenté graduellement, passant de 700 en 1962 à 4,326 en 1972 (fig. 2). Depuis le début du programme des chasses contrôlées, 11,757 chasseurs ont été admis sur un total de 20,526 demandes.

Les résultats de la chasse apparaissent au tableau II. Les données comparées du nombre d'orignaux abattus et du succès de chasse font ressortir le point suivant: dans les parcs et réserves où le guide doit accompagner les chasseurs, le succès de chasse moyen des cinq dernières années est de l'ordre de 60 pourcent dans les parcs des Laurentides et La Vérendrye et au-delà de 80 pourcent dans la réserve Matane. Par contre dans les réserves où le service d'un guide n'est pas requis le succès a fluctué entre zéro et 42.5 pourcent.

Le tableau III donne la moyenne du nombre d'orignaux aperçus par les chasseurs de même que l'effort fourni

TABLEAU I

Données préliminaires au calcul du plan de chasse [*] à l'orignal dans les parcs et réserves du Québec

Endroit	*Superficie*		*Densité de l'orignal par*		*Estimé de la population totale*	*Superficie accessible*		*Éstimation de la population accessible*	*Récolte permise* [***]
	Km^2	Mi^2	Km^2	*Mi^2*		*Km^2*	*Mi^2*		
La Vérendrye	13,615.6	5,257	0.4	1.0	5,257	3,172.7	1,225	1,225	300
Mont-Tremblant	2,564.1	990	0.5	1.3	1,287	901.3	348	452	40
St-Maurice	1,598.0	617	0.3	0.9	555	310.8	120	108	20
Portneuf	774.1	299	0.5	1.3	388	388.5	150	195	40
Kiskissink	828.8	320	0.4	1.0	320	621.6	240	240	48
Laurentides [**]	8,743.8	3,376	0.3	0.9	3,038	4,623.1	1,785	1,606	192
Matane	1,080.0	417	0.8	2.1	876	766.6	296	622	140
Dunière	5,533.5	206	—	—	—	429.9	166	—	77
Total	29,737.7	11,482	—	—	11,721	11,214.5	4,330	4,448	857

[*] Le plan de chasse est ajusté en fonction de certains paramètres: il voisine 20 pour 100 de la population accessible et les variations sont expliquées dans le texte.

[**] Laurentides, à l'exclusion de Kiskissink.

[***] Le plan de chasse et, par conséquent, la récolte permise ont pu varier d'une année à l'autre dans certains parcs: voir le tableau II.

pour abattre un orignal (mesuré en heures de chasse/groupe de chasseurs). Le nombre d'orignaux aperçus par groupe de chasseurs passe d'environ 2.5 en 1962 à 1.3 en 1972 dans les parcs des Laurentides et de La Vérendrye, alors que dans la réserve de Matane, il y a diminution de 7.0 en 1964 à 2.0 en 1972. Le nombre moyen d'heures nécessaires à un groupe de chasseurs pour abattre un orignal est variable selon l'endroit. Dans le parc des Laurentides et la réserve de Matane, l'effort de chasse est passé respectivement de 24 heures en 1962 à 42 heures en 1972 et de huit heures en 1964 à 17 heures en 1972 alors que dans le parc La Vérendrye, il a fluctué entre 13 et 17 heures. Bien que nous n'ayons pas inclu dans le tableau les résultats des autres secteurs, il importe de souligner que dans les réserves où l'on préconise une chasse sans guide, le nombre moyen d'animaux

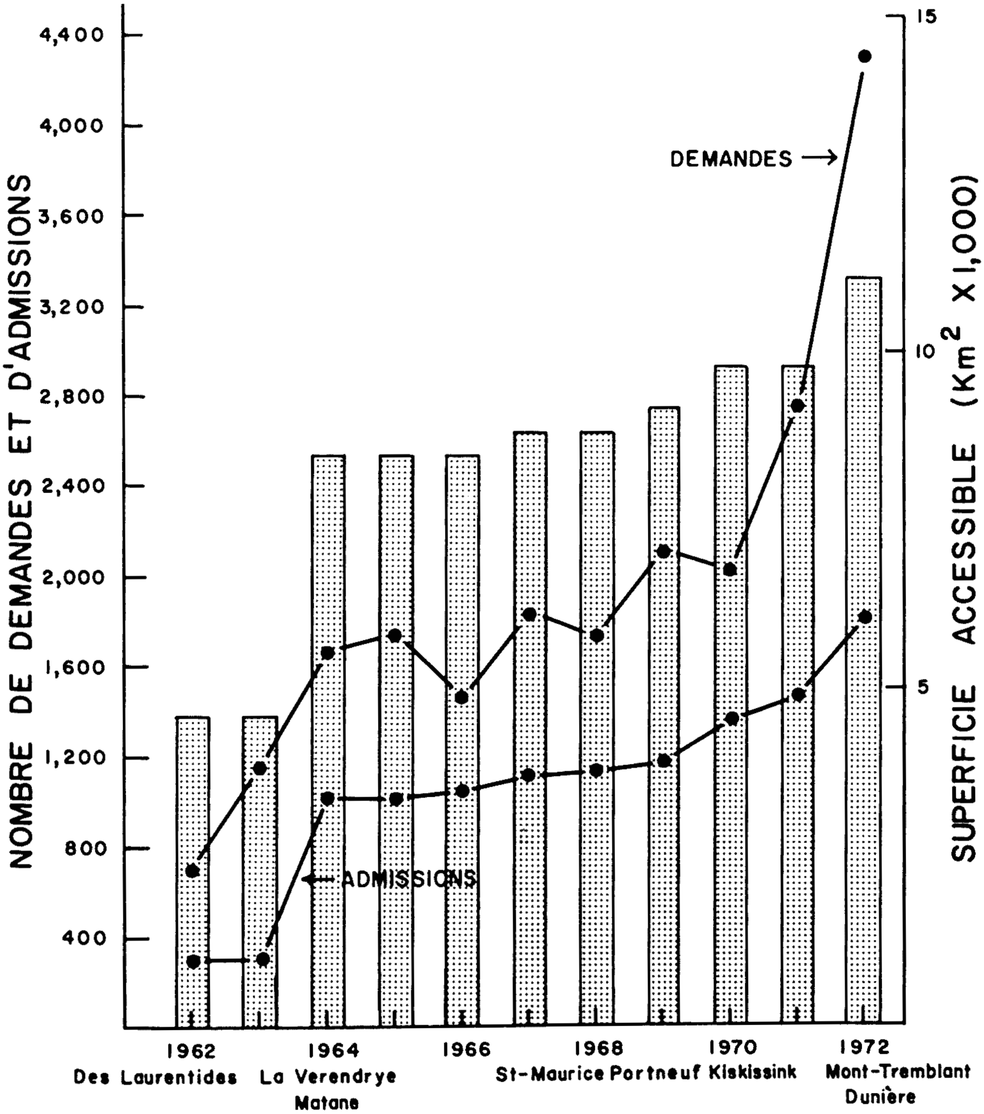


Figure 2. Progression du nombre de demandes, du nombre d'admissions et de la superficie accessible aux chasseurs dans le cadre des programmes de chasse controlée à l'orignal depuis 1962.

TABLEAU II

Résultats bruts de la chasse contrôlée à l'orignal dans les parcs et réserves du Québec[1] (1962-1972)

Endroits	*Années*	*Nombre d'orignaux tués (a)* / *Récolte permise (b)*[2] (a/b)	*Orignaux blessés* (c)	*Récolte probable* (a + c)	*Succès de la chasse* % (a/b × 100)
La Vérendrye	1964	237/300(296)	—	—	80.0
	1965	243/300	45	298	81.0
	1966	212/300(295)	57	269	71.9
	1967	185/300(292)	49	234	63.3
	1968	192/300(306)	78	270	62.7
	1969	192/300(313)	60	252	61.3
	1970	183/300(299)	46	229	61.2
	1971	170/300	58	228	56.6
	1972	156/300(299)	52	208	52.2
Mont-Tremblant	1972	32/40	3	35	80.0
St-Maurice	1967	12/42 (41)	0	12	29.2
	1968	15/30	18	33	50.0
	1969	19/30	19	38	63.3
	1970	5/30	4	9	16.7
	1971	0/30 (31)	2	2	0.0
	1972	7/20 (19)	0	7	36.8
Portneuf	1969	14/40	2	16	35.0
	1970	10/40	4	14	25.0
	1971	15/40	4	19	37.5
	1972	34/80	2	36	42.5
Kiskissink	1970	21/32 (26)	9	30	80.7
	1971	28/40 (37)	7	35	75.7
	1972	30/48	13	43	62.5
Laurentides	1962	127/150(152)	25	152	83.5
	1963	113/150(152)	54	167	74.3
	1964	107/150(146)	59	166	73.3
	1965	113/150(148)	—	—	76.3
	1966	104/150	15	119	69.3
	1967	91/150	—	—	60.7
	1968	92/150	14	106	61.3
	1969	102/150	22	124	68.0
	1970	121/192	32	153	63.0
	1971	115/192	24	139	59.9
	1972	102/192	21	123	53.1
Matane	1964	45/50 (46)	—	—	97.8
	1965	58/60	9	67	96.6
	1966	72/75	12	84	96.0
	1967	63/70	7	70	90.0
	1968	85/90	13	98	94.4
	1969	62/72	11	73	86.1
	1970	75/85 (84)	15	90	89.3
	1971	118/140	23	141	84.3
	1972	117/140	21	138	83.5
Dunière	1972	20/77 (71)	9	29	28.1

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[1] Les données pour les parcs des Laurentides, de la Vérendrye et la réserve de Matane sont exprimées sous forme graphique dans la figure 3.

[2] Quand le nombre de groupes de chasseurs qui ont effectivement pris part à la chasse diffère du nombre prévu (récolte permise), ce nombre apparait entre parenthèses.

observés fluctue entre 0.4 et 0.8, alors que l'effort de chasse varie entre 54 et 96 heures.

Le tableau IV groupe les valeurs disponibles sur la répartition des sexes dans la récolte (ce qui peut évidemment différer de la proportion des sexes existant dans la population). Dans tous les endroits pour lesquels nous disposons de longues séries de données

TABLEAU III

Moyenne du nombre d'orignaux aperçus par groupe de chasseurs et du nombre d'heures par animal tué

Année	*Parc de la Vérendrye*		*Parc des Laurentides*		*Réserve de Matane*	
	Nombre d'orignaux	*Nombre d'heures**	*Nombre d'orignaux*	*Nombre d'heures ***	*Nombre d'orignaux*	*Nombre d'heures ***
1962			2.5	24.0		
1963			2.0	21.0		
1974	2.3	17.0	2.3	24.0	7.0	8.1
1965	2.1	20.0	1.9	24.0	5.1	8.6
1966	1.8	13.0	1.7	27.0	5.5	11.6
1967	2.3	16.0	1.8	32.0	4.8	13.0
1968	1.7	14.5	1.4	21.0	3.9	11.8
1969	1.5	14.3	1.8	22.0	4.1	10.6
1970	1.6	14.2	2.3	18.0	3.7	13.9
1971	1.5	13.4	1.6	38.0	2.9	15.9
1972	1.4	19.4	1.3	42.2	2.0	17.6

* Calculé uniquement à partir des groupes de chasseurs ayant tué un orignal.

**Calculé à partir de tous les groupes de chasseurs.

TABLEAU IV

Sexe des orignaux tués durant la chasse contrôlée dans les parcs du Québec (1962-1972)

Parc (durée de la chasse)	*Orignaux tués*	*Mâles*		*Femelles*		♂♂/♀♀
		N	*Pourcentage*	*N*	*Pourcentage*	
La Vérendrye (1964-1972)	1,754	980	55.9	774	44.1	1.27 [a]
Mont-Tremblant (1972)	34	14	41.2	20	58.8	0.70
St-Maurice (1967-1972)	58	27	46.6	31	53.4	0.87
Portneuf (1969-1972)	69	34	49.3	35	50.7	0.97
Kiskissink (1970-1972)	79	51	64.6	28	35.4	1.82 [a]
Laurentides (1962-1972)	1,184	708	59.8	476	40.2	1.49 [a]
Matane (1964-1972)	694	389	56.1	305	43.9	1.28 [a]
Dunière (1972)	20	9	45.0	11	55.0	0.82
TOUS LES PARCS	**3,892**	**2,212**	**56.8**	**1,680**	**43.2**	**1.32** [a]

[a] Test de χ^2, P <0.01

(parc de la Vérendrye, parc des Laurentides et réserve de Matane, de même que dans Kiskissink), les mâles sont plus abondants que les femelles. Par contre dans les réserves de Portneuf, de St-Maurice, de Dunière et dans le parc du Mont-Tremblant, les femelles sont plus abondantes que les mâles dans l'échantillon prélevé par les chasseurs; toutefois les différences trouvées n'ont aucune valeur statistique. Cependant, quand on cumule les données pour tous les parcs, la prépondérance des mâles dans la récolte reste manifeste et statistiquement significative.

La figure 3 donne un aperçu de l'âge moyen du segment de population récoltée dans le parc de La Vérendrye, la réserve de Matane et le parc des Laurentides. Dans ce dernier, il est possible de discerner un rajeunissement évident de la population se produisant à un rythme de 0.34 an/ par année ($P < .01$). Dans le parc de La Vérendrye et la réserve de Matane, il est plus

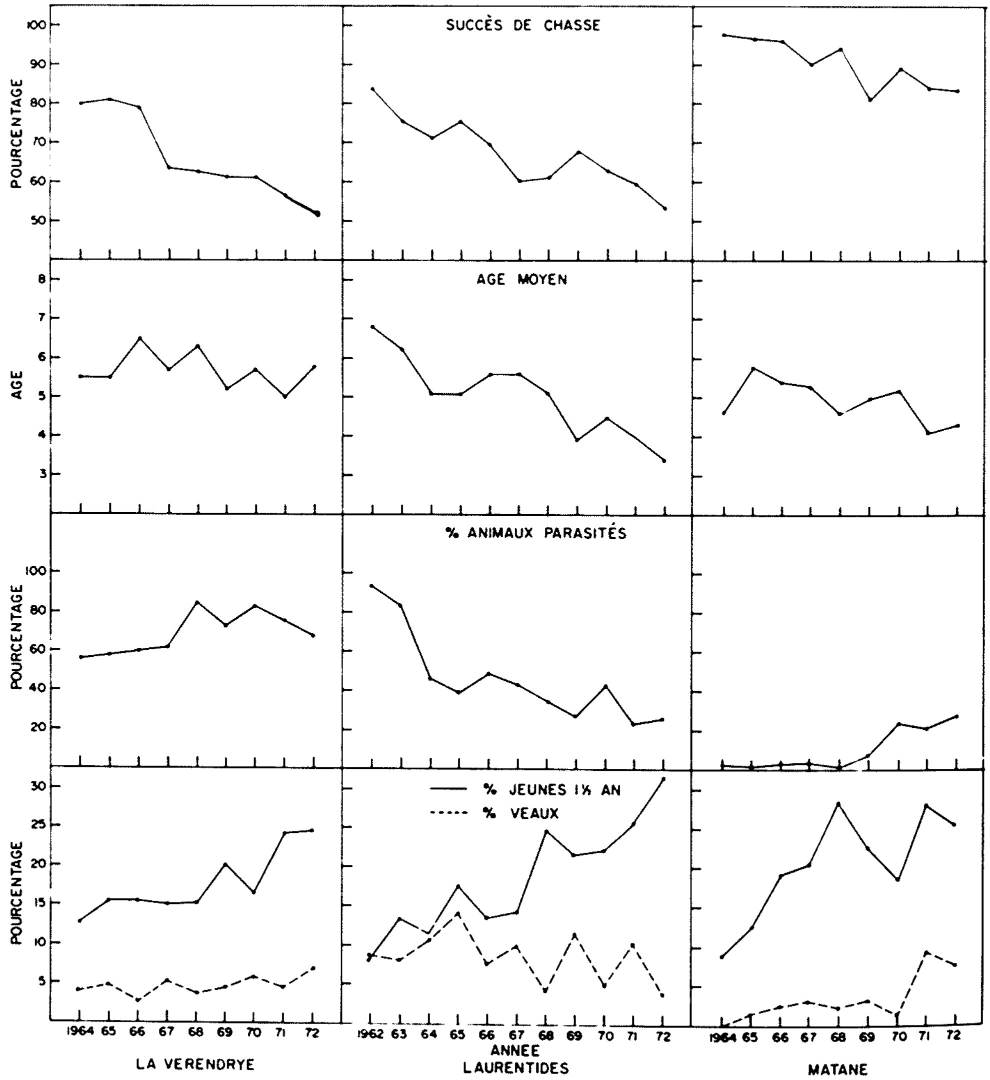

Figure 3. Variations imputables à la chasse sur certains des paramètres mesurés.

audacieux d'interpréter le changement d'âge moyen de la même façon.

Le pourcentage d'animaux parasités apparaît sur la figure 3. Les principaux parasites observés furent *Echinococcus granulosus*, *Taenia krabbei* et *Taenia hydatigena*. Dans le cas du parc des Laurentides, on note une diminution remarquable dans la fréquence du parasitisme : après 11 ans d'exploitation soutenue, seulement un orignal sur quatre environ semble porter des parasites externes ou internes facilement détectables à l'examen visuel direct. Par contre, l'échantillon prélevé dans le parc de la Vérendrye reste fortement parasité tandis que celui de la réserve de Matane donne des indices d'augmentation du taux de parasitisme.

Le tableau V montre la fréquence de jeunes (1.5 an) dans la récolte en excluant les veaux. La moyenne des cinq dernières années est respectivement de 27.6, 21.3 et 25.9 pour dans le parc des Laurentides, le parc de La Vérendrye et la réserve de Matane. Si l'on applique le facteur de conversion découlant de la vulnérabilité différentielle de ces jeunes (1.6), tel que défini par Pimlott (1959) et Simkin (1965), ces pourcentages seraient respectivement de 17.0, 13.3 et 15.4 pour la même période dans la population.

Afin de déceler un changement de densité dans la population du parc des Laurentides, nous avons utilisé les résultats d'inventaires de DesMeules et Brassard (1963), de même que des résultats d'inventaires routiniers effectués par le Service de la faune en 1966, 1967, 1969 et 1970. Le tableau VI montre les densités d'orignaux calculées et la population estimée au cours des inventaires de 1962 à 1970.

Nous avons illustré dans la figure 3 certaines informations déjà exposées dans l'un ou l'autre des tableaux du texte de façon à pouvoir visualiser plus rapidement les importants changements dans l'un ou l'autre des paramètres mesurés consécutivement à l'exploitation.

TABLEAU V

Fréquence des jeunes (y) de 1.5 an dans la population adulte (a). La fréquence est exprimée en pourcentage ($\frac{y}{y+a}$) × 100 et en fréquence pondérée pour éliminer l'effet de la vulnérabilité accrue des jeunes.

Années	*Parc de la Vérendrye*			*Parc des Laurentides*			*Réserve de Matane*		
	N Total	*Fré-quence*	*Fréquence pondérée*	*N Total*	*Fréquence*	*Fréquence pondérée*	*N Total*	*Fré-quence*	*Fréquence pondérée**
1962				116	10.4	6.5			
1963				104	14.5	9.1			
1964	228	13.2	8.2	93	11.8	7.4	45	8.9	5.6
1965	231	16.4	10.2	97	20.6	12.9	55	12.7	7.9
1966	206	16.0	10.0	95	14.8	9.2	71	19.7	12.3
1967	175	**	—	82	15.9	9.9	61	21.3	13.3
1968	185	15.7	9.8	88	26.4	16.5	83	28.9	18.1
1969	168	22.0	13.7	90	24.5	15.3	60	23.4	14.6
1970	172	17.4	10.8	115	23.5	14.7	74	18.9	11.8
1971	162	25.3	15.8	52	28.8	18.0	69	30.6	18.1
1972	145	26.2	16.4	98	34.7	21.7	73	27.7	14.5

* Facteur de pondération utilisé 1.6 (Pimlott, 1959; Simkin, 1965).

** Données non disponibles.

TABLEAU VI

Résultats des inventaires aériens dans le parc des Laurentides (1962-1970)

Années	*Densité de l'orignal*		*Population estimée***
	/Km ^{2}	*/Mi ^{2}*	
1962	0.27 ± 0.11	0.72 ± 0.29**	1,080
1966	0.37 non disp.	0.96	1,440
1967	0.28 non disp.	0.74	1,110
1969	0.37 non disp.	0.95	1,425
1970	0.34 ± 0.04	0.88 ± 0.11**	1,320

* La population a été estimée pour une superficie accessible de 3,900 km ^{2} (1,500 mi ^{2}).

**$P < 0.05$.

Discussion

Le mode de chasse institué dans les parcs du Québec semble très apprécié. Cette préférence vient probablement de ce que le chasseur trouve dans les parcs ainsi aménagés : 1) l'avantage d'être le seul à utiliser un territoire pendant quatre jours ; 2) une sécurité accrue ; 3) d'excellentes chances de succès, surtout dans les parcs et réserves où la présence d'un guide est obligatoire.

GROUPEMENT DES CHASSEURS

A l'origine, on permettait aux chasseurs de se présenter en groupe de deux ou quatre individus. Or, il s'est avéré que d'après les commentaires recueillis, les chances de succès et aussi l'harmonie au sein du groupe étaient passablement entravées. Les principales difficultés rencontrées étaient les suivantes : 1) problème de substitution d'un groupe de quatre chasseurs créé par le désistement d'un chasseur du groupe ; 2) la cohabitation des quatre chasseurs et des deux guides permettait de comparer la compétence de ces derniers, il en résultait assez souvent une perte de confiance envers celui qui semblait le moins doué ; 3) lorsqu'une partie du groupe avait la chance d'abattre un orignal, le comportement des chasseurs chanceux nuisait alors à la préparation mentale des autres chasseurs pour la chasse du lendemain.

L'essai des groupes de trois avec restriction d'un orignal pour le groupe a été tenté dans la réserve du St-Maurice en 1971. Le peu d'enthousiasme des chasseurs manifesté par un nombre de demandes très restreint nous a incité à discontinuer cette modalité. Conséquemment, le groupe de deux chasseurs avec un guide est probablement le groupement idéal, puisqu'il élimine les problèmes signalés plus hauts et permet à tous les participants de faire une chasse plus active.

INSCRIPTION DES CHASSEURS

Depuis 1972, seul le chef du groupe s'inscrit et ceci donne plus de souplesse au système en réduisant le nombre de désistements de chasseurs choisis au moment du tirage au sort. Les chasseurs ont réagi favorablement à ce changement par une participation accrue au moment de l'inscription. En l'espace d'un an le nombre de candidats aux chasses contrôlées est passé de 2,744 (1971) à 4,326 (1972). Cette augmentation ne peut être attribuable à l'addition de nouveaux territoires, puisque seulement 258 chasseurs en ont fait la demande (fig. 2).

RECRUTEMENT DES GUIDES

La pénurie de guides compétents est un problème persistant, les meilleurs guides étant vite recrutés par les pourvoyeurs. Face à cette pénurie et aussi afin de permettre une chasse à un coût moindre, une chasse contrôlée sans guide se pratique dans les réserves de Portneuf, du St-Maurice et de Dunière. Le succès moyen de chasse y est cependant inférieur à celui obtenu dans les parcs et réserves où l'on utilise les services d'un guide. (tableau II). Ce fait laisse supposer que si l'on veut perpétuer une chasse de qualité avec un succès élevé, on devra considérer la présence du guide comme essentielle. Le recrutement des guides devrait être facilité dans l'avenir, puisque notre système d'éducation technique offre maintenant un programme de formation des guides de chasse et de pêche.

SUPERFICIE DES ZONES DE CHASSE

La superficie des zones de chasse a également subi des modifications au cours des années. Les chasseurs qui n'avaient que des zones de quelques kilomètres carrés en 1962 ont maintenant à leur disposition des territoires de 26 à 78 km^2 (10 à 30 mi^2). Cependant, si les zones de faibles superficies peuvent diminuer les chances de réussite des chasseurs, les zones de grande superficie peuvent occasionnellement donner un résultat similaire. D'après certains guides, il semble que le chasseur perd beaucoup de temps à explorer le territoire qui lui est assigné et plus celui-ci est grand, plus le chasseur dispersera son effort de chasse. La superficie qui semble davantage répondre aux normes de l'efficacité pourrait se situer entre 20 et 26 km^2 (8 et 10 mi^2).

L'ADJUDICATION DES ZONES DE CHASSE

De 1962 à 1971, l'adjudication des zones de chasse en présence des chasseurs et des responsables dans les différents parcs donnait souvent lieu à des critiques. En 1972, le Ministère a décidé d'assigner à l'avance, par ordinateur, les territoires de chasse. Cette mesure devait permettre une distribution plus uniforme de la récolte, un rendement accru des guides, lesquels ont alors le temps de se reposer entre deux périodes de chasse et finalement une diminution des critiques du chasseur. Dans son ensemble, ce changement de modalité a donné des résultats encourageants, mais il a rendu le système plus rigide, de sorte qu'il est maintenant plus difficile, en cas d'imprévu, d'apporter des changements de zones sans s'attirer les critiques des chasseurs. Les guides compétents qui aidaient à l'abattage de huit à douze orignaux par saison sont maintenant limités à une possibilité de six bêtes alors que les guides moins compétents ne semblent pas avoir obtenu des succès supérieurs aux années antérieures.

L'ensemble des modifications apportées au système depuis 1962 et une publicité améliorée ont certainement contribué à augmenter l'intérêt du public envers la chasse contrôlée. La progression presque constante du nombre de demandes au cours des années (fig. 2) semble indiquer une approbation des chasseurs aux améliorations apportées. En plus de ces modifications, l'ouverture de nouveaux secteurs est un autre facteur qui a accentué cette progression.

ANALYSE DES RÉSULTATS DE LA CHASSE

Dans le tableau de chasse (tableau II) on note que la récolte permise n'est pas toujours liée à un prélèvement de 20 pourcent. Cette récolte dans la plupart des parcs et réserves est ajustée en fonction du succès de chasse attendu, du nombre de zones disponibles, de la popularité du parc auprès du public et de certaines contraintes politiques. Dans le même tableau, on constate que le prélèvement est probablement plus élevé que ne le laisse supposer le tableau de chasse officiel. En ajoutant les animaux blessés, on obtient un nombre qui, dans certains parcs et pour certaines années, ou bien se rapprochera du plan de chasse ou bien le surpassera. Les orignaux touchés ne sont cependant pas tous blessés mortellement ni tous rapportés, de sorte que ces valeurs ne servent que d'indices. Pour vérifier l'importance de cette variable dans le parc des Laurentides, la récolte probable des cinq dernières années montre un taux moyen de prélèvement de 17 pourcent, soit un taux comparable à celui des autres parcs. D'autre part, la baisse progressive du succès de chasse dans les parcs avec guide obligatoire est normale puisque ces populations n'avaient pas subi de pression de chasse avant l'avènement des chasses contrôlées. Le succès de chasse, qui varie de 50 à 65 pourcent depuis les cinq dernières années dans les parcs des Laurentides et de La Vérendrye laisse supposer qu'un succès de cet ordre correspond à ce qu'on peut attendre dans des territoires où la densité moyenne de l'orignal varie de 0.3 à 0.4 au km^2 (0.7 à 1.0 au mi^2). Cependant, pour maintenir un succès supérieur à 60 pourcent nous devrons reévaluer notre plan de chasse et, si nécessaire, élaborer un programme de restauration des populations. Dans le cas de la réserve de Matane, le succès de chasse qui se maintient toujours à un taux supérieur à 80 pourcent peut être attribuable à une densité plus élevée d'orignaux. Les parcs et réserves où l'exploitation est récente devraient présenter une inflexion semblable dans les courbes décrivant le succès de chasse.

Ailleurs, dans les réserves où les services d'un guide ne sont pas requis, on note que le succès moyen est de l'ordre de 25 pourcent. Bien que ces résultats soient nettement inférieurs à ceux des secteurs où le guide est obligatoire, ils dépassent néamoins les succès enregistrés sur les territoires libres où le succès global varie entre 10 et 15 pourcent.

EFFORT DE CHASSE

Le prélèvement soutenu d'une récolte annuelle a également eu des répercussions sur le nombre d'orignaux observés par groupe de chasseur de même que sur le nombre d'heures nécessaires pour tuer un orignal (tableau III). La baisse progressive du nombre moyen d'orignaux observés ne semble pas être une conséquence de la diminution du cheptel. Cette baisse semble plutôt attribuable à l'élimination progressive des orignaux en bordure des routes ou encore à une adaptation du comportement de l'orignal face à son insécurité pendant la saison de chasse. Le nombre moyen d'heures de chasse nécessaire pour tuer un orignal a augmenté avec les années et ce changement peut être attribuable aux mêmes facteurs. Contrairement au parc des Laurentides et à la réserve Matane, l'effort de chasse déployé dans le parc de La Vérendrye a été calculé à partir des groupes de chasseurs chanceux de sorte qu'on peut supposer que l'effort fourni est plus grand que ne le démontrent les résultats.

Dans les territoires où la chasse est récente, on devrait observer à l'avenir les mêmes tendances dans l'allure des courbes que celles observées dans les parcs et réserves exploités depuis 1962 et 1964.

EFFET DE LA CHASSE CONTRÔLÉE SUR LES POPULATIONS

Dans l'ensemble, les données incluses dans les tableaux IV et V et dans la figure 3, permettent de déceler certains effets de la chasse contrôlée sur nos populations d'orignaux. Ces résultats sont partout apparents dans les parcs et réserves où ce genre de chasse se pratique depuis au moins cinq ans. Notre analyse traitera donc des parcs de La Vérendrye, des Laurentides et de la réserve de Matane où les résultats de la chasse montrent que les changements dans la population se manifestent par une légère modification du rapport des sexes, par un rajeunissement des populations et par une augmentation de la productivité nette.

RAPPORT DES SEXES

Dans les parcs et réserves, pour lesquels nous disposons d'un échantillonnage substantiel (parc de La Vérendrye, parc des Laurentides et réserve de Matane), de même que dans le secteur Kiskissink, la répartition des sexes dans la récolte est significativement en faveur des mâles ($P<.01$) (tableau IV). Cette prépondérance des mâles, qui se manifeste également quand on totalise le tableau de chasse des parcs et réserves, s'explique vraisemblablement par une plus grande vulnérabilité du mâle pendant la saison de chasse, laquelle coïncide avec la période du rut et aussi, par le choix délibéré que les chasseurs font des mâles. Dans ce dernier, cas, il se peut que le choix du chasseur soit facilité par la compétence de son guide ou encore, dans des cas bien spécifiques (accessibilité à de nouvelles zones), par une plus grande disponibilité d'orignaux.

Pour ces raisons nous ne croyons pas que la proportion mâles : femelles observées dans la chasse représente la proportion réelle des sexes existant dans la population.

RAJEUNISSEMENT DE LA POPULATION ET PARASITISME

Un autre effet de la chasse est de rajeunir les populations. Ce rajeunissement s'est surtout manifesté par une baisse progressive de l'âge moyen et par des modifications survenues dans la structure d'âge des populations, notamment une augmentation des pourcentages de veaux et des jeunes (1.5 an) dans la récolte.

Ce phénomène est plus évident dans le parc des Laurentides (fig. 3). Les courbes semblent montrer que les véritables signes de rajeunissement de la population se sont manifestés après six saisons de chasse, soit après 1968. En plus d'une baisse plus rapide de l'âge moyen, on constate qu'à partir de cette même année, le pourcentage de jeunes (1.5 an) dans la récolte s'est élevé au-delà de 20 pourcent. Une conséquence de ce rajeunissement semble être la diminution du taux de parasitisme, qui était de 93 pourcent au début et se stabilisa autour de 25 pourcent après 1968.

Dans le parc de La Vérendrye, les signes de rajeunissement de la population sont plus lents à se manifester. L'âge moyen suit une fluctuation en escalier (fig. 3) à décroissance très lente et le pourcentage de jeunes (1.5 an) dans la récolte n'est supérieur à 20 pourcent que depuis 1971. Quant au pourcentage d'animaux parasités, il se maintient autour de 70 pourcent (fig. 3). Nonobstant certains changements qui se dégagent des résultats de chasse de 1971 et 1972, ces indices tendent à démontrer que le cheptel serait sous-exploité. Il apparaît évident que la nature physique du territoire avec sa multitude de nappes d'eau et la très grande étendue des zones de chasse ne permettent pas de répartir la pression de chasse de façon aussi efficace que dans les autres parcs.

Par opposition aux deux autres parcs, la réserve de Matane occupe une superficie restreinte. La population d'orignaux était exploitée intensivement sur toute la périphérie depuis longtemps de sorte qu'au départ nous avions une population plus jeune et en meilleur état de santé que dans les autres parcs. La lente diminution de l'âge moyen et l'accroissement relativement modéré de la proportion des jeunes dans la récolte peuvent être attribuables aux facteurs suivants : 1) avec une densité d'orignaux supérieure aux autres parcs et un territoire facilement accessible à la chasse, le chasseur semble exercer un choix plus prononcé qu'ailleurs pour les mâles et les femelles adultes; 2) à l'inverse des autres parcs, le plan de chasse a été remanié à tous les ans.

Même si l'âge moyen se maintient à un palier supérieur à quatre ans, il ne semble pas y avoir de recrudescence du taux de parasitisme comme le laisse supposer la figure 3. Nous considérons que la hausse enregistrée depuis 1970 est due à la présence à la station d'enregistrement, d'un vétérinaire qui fait le décompte des individus parasités. Par comparaison à la situation générale, ces quelques individus (de 20 à 25 pourcent des animaux abattus) sont en outre très faiblement parasités car l'autopsie n'a permis de déceler plus de trois parasites que chez sept pourcent d'entre eux (Gonthier, 1972). Ce faible taux de parasitisme dans la réserve de Matane pourrait s'expliquer par l'absence du loup (*Canis lupus)* principal vecteur *d'Echinococcus granulosus.*

PRODUCTIVITÉ

Bien que possédant peu d'informations permettant de mesurer le taux de productivité, nous avons tout de même essayé de déceler l'effet du rajeunissement sur cette variable. Dans le parc des Laurentides, deux types de données nous permettent de constater que le rajeunissement de la population a produit un accroissement du cheptel et de sa productivité.

1) Exception faite de 1967, où les conditions de neige au sol ont rendu presque impossible le dénombrement des aires d'hivernement, les résultats de l'inventaire aérien suggèrent un accroissement de la population (tableau VI).

2) La productivité nette calculée à partir du pourcentage de jeunes dans la récolte, $\frac{y}{y+a}$ et corrigée, selon le taux de vulnérabilité (Pimlott, 1959; Simkin, 1965), s'est accrue depuis 1968 (tableau V).

La moyenne des pourcentages pondérés de jeunes (1.5 an) dans la récolte des cinq dernières années (17.2 pourcent) diffère significativement de la moyenne des pourcentages obtenus au cours des six premières années suivant l'ouverture de la chasse contrôlée (9.1 pourcent) ($t = 4.94$, $P < 0.05$).

Lors d'un dénombrement partiel effectué dans le parc des Laurentides en mars 1972, le pourcentage de jeunes dans la population était de 16 pourcent ($N = 77$). L'analogie qui existe entre la moyenne de la productivité nette des 5 dernières années de chasse mesurée dans le tableau de chasse (17 pourcent) et le pourcentage de jeunes dénombrés par l'inventaire aérien de mars 1972 (16 pourcent) laisse supposer que la productivité nette du parc des Laurentides serait de l'ordre de 16 à 17 pourcent. On note cependant une augmentation brusque du pourcentage d'animaux de 1.5 an en 1971 et 1972. Le pourcentage pondéré est passé de 14.7 en 1970 à 21.7 pourcent en 1972 de sorte qu'il se rapproche des moyennes de 23.6 obtenue en Ontario de 1956 à 1965 (Simkin, 1965) et de 23.0 à Terre-Neuve de 1953 à 1956 (Pimlott, 1959).

Dans le parc de La Vérendrye et la réserve de Matane, l'absence de données comparables sur les densités d'orignaux par unité de surface de même que le manque de données sur la proportion des jeunes par rapport aux adultes à la fin de l'hiver nous limitent aux seules données du pourcentage pondéré des jeunes (1.5 an) dans la récolte. La différence entre la récolte de jeunes des quatre dernières années du parc de La Vérendrye et celles des quatre premières est faiblement significative (t = 3.44, P < 0.05), ce qui laisse supposer que le rajeunissement lent de la population a permis un accroissement modéré de la productivité nette. Bien que le pourcentage des deux dernières années semble supérieur à celui des autres saisons de chasse, une interprétation de cet accroissement ne peut se faire qu'avec prudence.

La fluctuation des pourcentages de productivité nette obtenus dans la réserve de Matane peut être attribuable, d'une part, à la modification du plan de chasse d'une année à l'autre et, d'autre part, au choix du chasseur en faveur des adultes, mâles et femelles. Dans ce dernier cas, le choix pouvait être influencé par le pourcentage de succès des années antérieures et par les guides, conscients du potentiel de leur territoire de chasse et de la réserve en général. Tous ces faits, interprétés en regard d'une densité plus élevée qu'ailleurs (tableau I) et du maintien du succès de chasse au dessus de 80 pourcent depuis le début du programme tendent à démontrer que la pression de chasse a été insuffisante : aussi, on peut difficilement considérer que le pourcentage de jeunes dans la récolte jusqu'en 1970 est un juste reflet de la productivité nette de la population. Il est probable que le facteur de conversion utilisé pour tenir compte de la vulnérabilité différentielle des jeunes (1.6) est trop élevé dans les circonstances.

Conclusion

Il semble que la chasse contrôlée dans les parcs et réserves du Québec se révèle un excellent outil d'aménagement de l'orignal. Elle fournit en outre plusieurs milliers de jours de récréation de haute qualité au public chasseur. Nous estimons que depuis le début du programme, cette chasse contrôlée a fourni environ 50,000 jours de récréation aux chasseurs, et que ceux-ci ont dépensé deux millions et demi de dollars pour pratiquer leur sport. Un rajeunissement des populations semble se traduire par un accroissement de la productivité nette. Là où le taux de récolte semble devoir se rapprocher du taux de productivité nette, comme dans le parc des Laurentides, en même temps que le succès de chasse diminue, il faudra prévoir un réajustement du plan de chasse probablement par la fermeture en rotation de certaines zones de chasse. Nos efforts à l'avenir devront se concentrer sur les moyens de mesurer la productivité à divers niveaux avec une plus grande précision.

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MOOSE MANAGEMENT IN ALASKA

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Résumé

Un examen des voies suivies en Alaska pour établir des programmes de chasse à l'orignal révèle un asservissement à l'opinion publique—fréquemment teintée d'émotivité — et aux pressions politiques exercées sur les trois principaux fonctionnaires en charge. Ces influences interviennent même quand tous les indices biologiques prescrivent clairement un changement de réglementation pour assurer tant la conservation de l'animal que l'intérêt public.

Certains programmes furent affectés dans leur réalisation, parce qu'en les formulant on avait tenté de tenir compte de tous les désirs du public, ou encore de mettre sur pied des politiques valables autant pour la recherche que pour l'aménagement.

Quand, en 1971 et en 1972, on étendit de nouveau la chasse à tous les animaux, on eut d'abondantes récoltes, à une époque où les populations étaient en diminution par suite apparemment d'une détérioration de leur habitat. Malheureusement, plusieurs hivers rigoureux coïncidèrent avec cet élargissement et certaines populations furent décimées dans une proportion de 90%. De plus, on nota certains cas de prédation très forte par les loups. Dans l'esprit de ceux qui veulent une chasse restreinte aux mâles, c'est seulement à l'élargissement de la chasse, et non à la combinaison de tous ces facteurs, que sera attribuée la diminution du cheptel. D'où, possibilité de nouveaux affrontements.

Les programmes d'aménagement sont presque toujours fondés sur un petit nombre d'indices sur la condition du cheptel ou sur une analyse incomplète des données. Mais, quand il est possible à l'aménagiste de faire une analyse approfondie de tous les indices disponibles, les techniques d'aménagement peuvent sans aucun doute jouer leur rôle convenablement.

Les programmes qui font appel à des politiques généralement bien reçues du public ont plus de chance d'être bien accueillis. Aussi, afin d'assurer un peu de continuité aux programmes d'aménagement dans le cadre des structures administratives actuelles, y a-t-il lieu de les fonder sur des politiques d'aménagement de chacune des espèces, des plans régionaux par espèce et des programmes coopératifs de gestion des terres.

Abstract

An examination of the processes used in Alaska to formulate moose hunting regulations strongly suggests that public opinion, often wholly based upon emotion, and political pressure on the three appointive levels of the Department were paramount in determining the fate of some moose hunting seasons. This occured even when sound biological information indicated an alternate course would provide more benefits to the resource and to the people.

Staff regulatory proposals contributed to the instability of the program in some areas by attempting to establish regulations to satisfy every public objection or regulations that would simultaneously accomplish management and research objectives.

When antlerless seasons were successfully reinstituted in 1971 and 1972, relatively large harvests coincided with a time when certain moose populations were declining, apparently because of deteriorating range. Unfortunately several catastrophic winters also coincided with the reinstated antlerless seasons and in some instances, local moose populations may have been lowered by 90 percent. Finally some moose populations were subjected to intense predation by wolves. The combination of natural events and renewed antlerless seasons are separable in the minds of those who oppose anterless hunts — they will isolate the antlerless seasons as the single factor responsible for decreased hunting opportunity and the entire confrontation may be repeated.

In most instances, management practices still are based upon relatively few indices to moose population status or upon incompletely analysed data; when the manager can base his decisions on the fully analyzed information from the available indices, present techniques are adequate.

Management plans based upon generally accepted policies offer the most likely opportunity for obtaining public support of management practices. To that end, species management policies, areal species plans, interagency cooperative management plans and land use planning and agreements will form the basis for formulating a program that may achieve continuity under the existing administrative structure.

Introduction

Moose *(Alces alces gigas)* have been an important component of the Alaska fauna for many centuries (LeResche *et al.*, 1974). Their abundance and distribution has been directly linked to the dynamics of the glacial epochs. In contemporary time, early successional stages of vegetation resulting from lightning and man caused wildfire, volcanic eruptions, river flooding, bank-cutting and the retreat of glaciers has strongly influenced both numbers and distribution of moose. Moose were an important source of food, clothing and implements for Alaska's earliest inhabitants. Later, in the 19th and early 20th centuries, those who came to exploit the area's gold and fur resources also depended upon moose meat for a part of their sustenance. Moose meat continues to be common table fare in rural and metropolitan Alaska but the ungainly beast's recreational and aesthetic benefits are now equally important assets.

The subject of this paper is management of moose during the contemporary period. Management problems have persisted or recurred throughout the past four or five decades. These problems have taken the form of periodic die-offs, winter-time invasions of metropolitan areas, moose being eaten by wolves *(Canis lupus)*, moose damaging farm crops, moose use of railroad and highway rights-of-way, and conflict of public vs. Department management philosophies. Moose have been too abundant, too scarce (often at the same time, depending on viewpoint) and too controversial. We will end this paper by opening a perspective on the future of moose management in the state.

Present basis for management

LEGAL BASIS

The legal basis for management of moose in Alaska stems from the commonly accepted principle that resident (indigenous) game species are held in trust by the several states for the common use of their citizens. Recent federal legislation has raised many large questions about future federal-state wildlife management relationships, but that problem is beyond the scope of this review. In Alaska, the right of the state to manage all fish and wildlife is further buttressed by the specific mention in the Statehood Act that the fish and game residing in Alaska are the responsibility of the state. Again, recent federal acts tend to degrade this portion of the Statehood Act and raise grave questions about jurisdiction that perhaps only can be solved by Congress or the courts. We are referring to the Marine Mammals Protection Act of 1972, the Rare and Endangered Species Act of 1964 and to the 1971 act banning the use of aircraft in taking game (Public Law 92-159).

The Alaska Constitution, Article VIII, establishes a basis for regulating all natural resources. Several sections pertinent to the management discussions follow:

> "Section 3. Wherever occurring in their natural state, fish, wildlife, and waters are reserved to the people for common use."
>
> "Section 4. Fish, forests, wildlife, grasslands and all other replenishable resources belong to the State and shall be utilized, developed, and maintained on the sustained yield principle, subject to preferences among beneficial uses."

The passage pertaining to sustained yield, subject to preferences among the beneficial uses, has caused considerable controversy in interpretation (Weeden, 1973). Some believe this section refers to perpetuating the resource through careful allocation of beneficial uses while others, more attuned to commercial activities, translate sustained use into maximum yield. While the intent of the writers never may be clarified, the constitution does provide the legislature with considerable latitude in structuring resource management agencies.

The first state legislature (1959) provided for a Department of Fish and Game and a Board of Fish and Game to act as the rule making body of the department (Alaska Statutes, 1959). The board does not possess budgetary or administrative authority and its rule making authority is limited in several important ways. Among the board's powers are the following: 1) While the board has statute authority to designate game areas, the Department of Natural Resources has overlapping and superior authority on state lands. Any single purpose wildlife area over 640 acres (250 ha) requires legislative approval. 2) Establishing open seasons and closed seasons. 3) Establishing methods and means for taking fish and game. 4) Setting quotas and bag limits.

The commissioner of the Department of Fish and Game has the authority to alter board-established seasons and area designations by field announcements. Hence, seasons and/or hunt areas can be set to coincide with the abundance or availability of a particular stock or population of game. In addition, the commissioner may declare an emergency and alter bag limits in accordance with Title 44 SLA 1972. The field announcement and emergency powers granted to the commissioner are unusually broad and useful devices in aid of achieving management goals.

The board has an additional responsibility for establishing local advisory committees whose function is to relay public opinion to the board about management problems in specific localities. These boards have no rule making authority but they often have proven to be powerful forces once the members understand the political processes of state administration.

The structure of the Department of Fish and Game is significant to the management discussions that follow in subsequent sections. Of considerable moment is the fact that the board, the commissioner, deputy commissioners and division directors are all appointed by the governor and serve at his pleasure! Board and commissioner nominations must be approved by a majority of the legislature sitting in joint session.

Alaska Constitution, "Article III, Section 25. The head of each principal department shall be a single executive unless otherwise provided by law. He shall be appointed by the Governor, subject to confirmation by a majority of the members of the legislature in joint session, and shall serve at the pleasure of the Governor, except as otherwise provided in this article with respect to the Secretary of State. The heads of all principal departments shall be citizens of the United States."

This structure is hardly a basis for program continuity in a politically oriented society.

Regulations promulgated by the board provide for public participation in nominating season openings and closures, season length, bag limits, methods and means, closed areas and types of animals to be hunted. This extremely democratic process has led to increased staff work, prolonged board meetings, and it has provided a platform for some truly nonsensical regulation proposals. At some sessions over 200 proposals have been considered by the board (Alaska Board of Fish and Game, 1960-1973). Nevertheless it has stimulated public participation in wildlife matters. Some modification of the system designating that only certain titles of the code will be open for modification could reduce the undesirable aspects of the process.

TECHNIQUES

Data acquisition for management purposes has alternately emphasized range condition and the animal as a reflection of the range. Acquisition techniques have varied accordingly. Early studies by Chatelain (1951) and Spencer and Chatelain (1953) emphasized range conditions. Later studies by Scott (1956), Rausch (1957) and Rausch and Bratlie (1965) concentrated on the animal. In the past few years, range-moose interrelationships have received renewed attention (Bishop, 1969; Seemel, 1969; LeResche, 1968). Management decisions, however, rely heavily upon information obtained from a few basic data gathering techniques focusing on moose population characteristics as a kind of instantaneous summary of recent habitat conditions. The aircraft is the most important data gathering tool as it is used to make sex and age composition counts and censuses. Indices from those counts provide the backbone of the decision making matrix. Details of aircraft use and other standard techniques are discussed by Bishop and Rausch (1974).

Harvest size is determined through the use of a mandatory harvest ticket in combination with permit and registration hunts. This procedure provides a precise estimate of harvest in most game management units.

In some areas where a precise knowledge of total numbers is required, censuses are made using the random stratified square technique (Siniff and Skoog, 1964; Evans *et al.*, 1966).

Recently a study was conducted to evaluate the efficiency of total counts (LeResche and Rausch, 1974). Under the conditions tested, moderately dense to open spruce-birch regrowth and mature forests, experienced observers saw approximately 70 percent of the known moose population contained in four, one-square-mile enclosures.

Aerial counts of calves (10-12 months old) have been used in selected areas to evaluate recruitment. This technique appears superior to all other techniques for estimating overwinter survival of calves, providing an adequate sample can be obtained.

Age information has been collected on a statewide basis but the results seldom have been applied.

Pregnancy and fertility rates have been determined on many ranges either by direct examination of materials collected during hunting seasons or through palpatation when marking and tagging moose. Marking and tagging using drugs to immobilize adult animals and direct capture techniques to obtain newborn calves have been used to identify discrete populations.

Management procedures

Regulations governing the take of a species are perhaps among the oldest forms of game management. In Alaska during the "modern era", regulations have been designed with the goal of optimizing the harvest in terms of yield or recreational and economical benefits. To do this, the state has divided the land mass into 26 game management units, each representing a somewhat distinct physiographic entity (Fig. 1). Tagging and marking (Rausch, 1965; LeResche, 1974) provide data on individual population and on this basis, some game management units are partitioned into subunits or some similar designation.

The annual regulations recognized traditional use patterns where these were compatible with the welfare of the resource. This has not been simple. Not only has knowledge been scanty about the effect of traditional hunting on moose numbers, but the "traditions" themselves have changed often and significantly with advent of new hunting tools (riverboats, snowmobiles, etc.) and in response to socio-economic acculturation.

Management procedures included measuring hunting pressure, annual harvests (Rausch *et al.* 1966) and the impact of harvests upon moose populations; evaluating herd productivity and measuring the influence of environmental forces (predation, range conditions

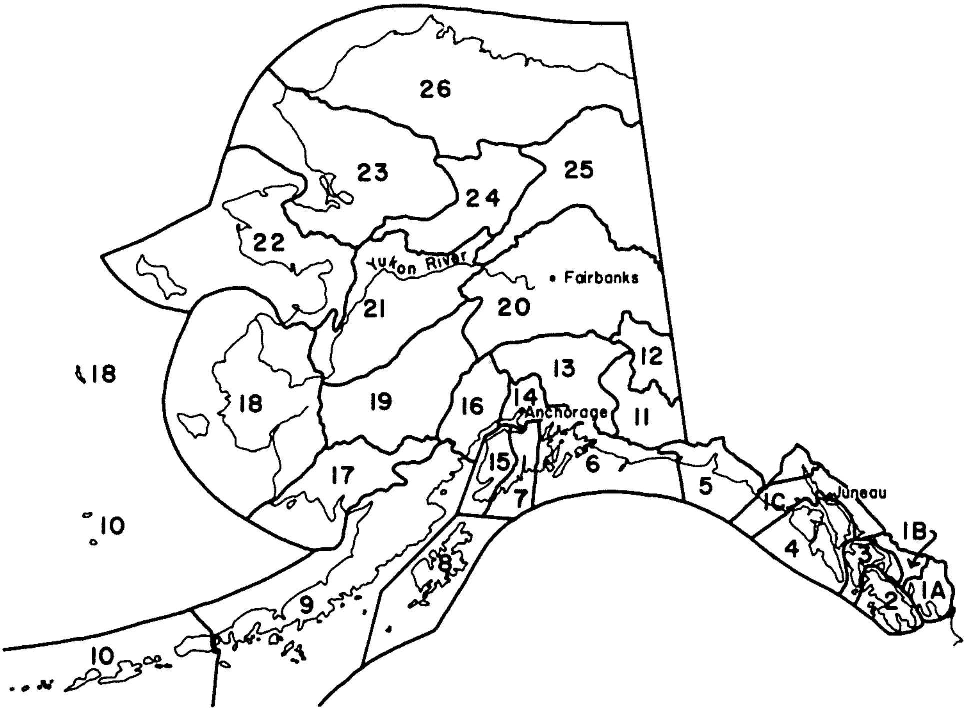

Figure 1. Moose management units in Alaska.

and weather). The dynamics of the populations are reported by Bishop and Rausch (1974).

Prior to 1963 when a mandatory harvest ticket system was introduced (Rausch *et al.* 1966), the size of harvests was estimated from check stations and other indices. Annual harvests from 1963 through 1971 are presented in Table I and Fig. 2. The annual kill by hunters is small compared to the estimated total moose population of 130,000 — 160,000 animals. The small kill reflects poor distribution of hunters caused by extremely limited or costly access, human population centers located a great distance from some of the larger concentrations of moose, conservative hunting regulations and restrictions on access to certain large federal reservations.

Most of the harvest comes from the southcentral portion of the state where a network of roads traverse several areas supporting large numbers of moose and where most of the citizens reside. In interior Alaska, near Fairbanks, hunting along the major rivers and from roads accounts for a substantial proportion of the annual kill. There is an annual unreported harvest of several thousand moose in the outlying "bush" communities.

Although the annual yield is much below the potential, a few small areas have produced substantial portions of the harvest, especially those areas where all components of the moose population are subject to hunting. The yield of approximately 0.3 moose per km^2 (1963-1971) from a portion of the Matanuska Valley (Table II) of approximately 1950 km^2 compares favorably with published accounts of yield from intensively managed Scandinavian moose populations (Lykke, 1974). Unfortunately the seasons were held irregularly due to design, climatic phenomena and to political interference. The large harvest in 1962 was designed to reduce the portion of the population that resided on the valley floor which had inflicted considerable damage upon farm crops (Table II). The high 1965 kill is attributed to unseasonally heavy snowfall in November causing early migration of the alpine population segments into the lowlands. A harvest of approximately 1,000 animals occurred in one day when some 5,000 to 6,000 vehicles with 10,000 to 15,000 hunters entered the valley on opening day of the hunting season. Subsequent to the hunt a stratified random aerial census provided an estimate of 3,000 animals (Rausch, 1965). In recent surveys there is some indication that the population has decreased. Calf production to fall decreased in 1971 and 1972 (Alaska Department of Fish and Game, 1973). The reason for the decreased proportion of calves is not clear but it may be related to the effects of lowering the mean age of cow moose through hunting.

Historically and today in much of the state, hunting seasons are designed to place most of the harvest pressure on males. Hunting restricted to antlered males has contributed to low yield, reduced recreational opportunity, overuse of winter ranges and possibly reduced herd productivity. Aerial sex and age ratio counts of selected moose populations show dramatic decreases in the proportion of antlered males concurrent with increased license sales, better aircraft and A.T.V.'s. In some portions of Game Management Unit 13 the ratio of males to females dropped from 1:1 to 0.1:1 in less than 10 years during the 1960's and early 1970's. In the readily accessible Matanuska Valley post hunting season ratios of 10 males per 100 females had been achieved by the early 1950's (Spencer and Chatelain, 1953).

Theoretically, removal of most of the adult males could lead to a reduced production of calves if the remaining males cannot breed all of the females. This problem has apparently had little influence on the welfare of moose populations under study (Rausch, 1959; Rausch and Bratlie, 1965). In the Matanuska Valley it appeared that the period of conception was lengthened, i.e., some cows were conceiving on the second estrus cycle, when the bull: cow ratio was below 10 males (16 months of age and older) per 100 cows of similar ages. Closing the season on males until after the breeding season resulted in a higher incidence of conception at first estrus, and, of course, increased the proportion of bulls in the population (Rausch, 1965.)

Potential net yield (number of moose harvestable per 100 moose alive) available to the hunter may be lower over much of Alaska than in Scandinavia because predation and periodic severe winters are major factors over much of Alaska.

Environmental controls

Predator control to benefit big game ungulates has been practiced in Alaska to some degree since earliest recorded times (Lensink, 1959). The first territorial legislature established a bounty on wolves in 1915 and it continued in some form over parts of the state through 1972. It is still permitted in three Southeast game management units but no funds were appropriated for fiscal year 1973. In 1968, the Board of Fish and Game was given the authority to establish wolf bounty units and they subsequently abolished the bounty in all units where moose are important game animals.

Control of wolves by governmental agencies was formally organized on an intensive area-wide basis by the Predator and Rodent Control Branch of the Bureau of Sport Fisheries and Wildlife in 1948. Their efforts included widespread use of strychnine and cyanide, aerial shooting, and trapping (Lensink, 1959; Rausch, 1961 and 1964). This program continued until the state assumed wildlife management responsibility in January 1960. Liberal hunting and trapping seasons persist and only this year did aerial hunting terminate.

Predator control activities, particularly the use of poison and in some areas aerial shooting, did lower wolf populations. Other factors, however, including disease and intrinsic factors may have contributed to the generally low wolf populations during the 1950's and early 1960's. By mid-1960 wolves were generally abundant with local exceptions and recently they have reached historic peaks of abundance.

The relationship of wolves and moose is complex and generalizations are futile. A long-term study in the Nelchina Basin revealed no significant competition for moose between man and wolves when the moose population was extremely high, the wolf population increasing and hunting pressure varying from high to negligible (Rausch, 1969). Earlier studies in other areas, notably on Isle Royale (Mech, 1966) strongly suggest wolves can limit or stabilize moose population size even when hunting is not a factor. Pimlott (1967) postulated that under special conditions wolves may play a major role in limiting moose populations. In Alaska in some instances, wolves apparently prefer moose even when other big game is numerically more abundant (Rausch, 1969). Moose calves are an important component of the wolf's diet in the summer and winter (year-round). At some

TABLE I

Moose harvest data in Alaska between 1963 and 1971 from harvest ticket data

Game management unit	*1963*				*1964*				*1965*				*1966*				*1967*			
	♂♂	♀♀	†	*Total*	♂♂	♀♀	†	*Total*	♂♂	♀♀	†	*Total*	♂♂	♀♀	†	*Total*	♂♂	♀♀	†	*Total*
1	149	1		150	158	65		223	128	35	4	167	168	60	2	230	174	48	2	224
2	2			2				0				0				0				0
3	4			4				0				0				0				0
4	1	2		3				0				0				0				0
5	189	111	2	302	154	111		265	153	125	4	282	116	90	6	212	154	108	1	263
6	15	2		17	15			15	24			24	23	1		24	37			37
7	251	174	2	427	163	206		369	60	1		61	112	1		113	123	1	1	125
8				0				0				0	2			2				0
9	179	46	2	227	185	64		249	213	68	4	285	240	75	8	323	301	68	9	378
10	1			1				0				0				0				0
11	86	37		123	89	38		127	116	70	2	188	89	69	5	163	108	70	2	180
12	138	22	1	161	145	16		161	151	33	6	190	156	19	7	182	136	42	4	182
13	1385	343	7	1735	1213	394		1607	1318	3	10	1331	1336	181	36	1553	1217	319	16	1552
14	925	557	4	1486	795	525		1320	1127	1125	10	2262	565	202	9	776	482	4	9	495
15	1021	417	2	1440	1212	858		2070	841	731	12	1584	819	307	18	1144	641		6	647
16	344	27	2	373	262	61		323	333	52	7	392	393	144	18	555	281		1	282
17	61			61	31	1		32	41	1		42	25	1		26	37		1	38
18	75	3		78	39			39	28		2	30	31	1	1	33	19	4	1	24
19	144	24		168	96	33		129	121	28	1	150	136	43	4	183	93	40	5	138
20	1324	131	2	1457	1034	242		1276	1050	140	33	1223	814	157	23	994	658	187	11	856
21	168	72	7	247	137	49		186	96	31	1	128	114	50	2	166	111	42	2	155
22	68	1		69	57			57	55	3	2	60	52	1	1	54	56		1	57
23	76	1		77	73			73	44		1	45	68		1	69	65	10		75
24	92	4		96	84	18		102	66	14	4	84	52	17	3	72	61	21		82
25	77	2		79	55	2		57	52	1		53	70	12	1	83	38	15	1	54
26	13			13	13			13			1	1	12			12	5			5
UNK.	59	4	1	64	6	1	70	77	32	9		41	57	13	9	79	59	13		72
TOTAL BY SEX	6847	1981	32		6016	2684	70		6049	2469	105		5450	1444	154		4856	993	73	
TOTAL BY YEAR				8,860				8,770				8,623				7,048				5,922
TICKETS ISSUED				32,412				29,904				32,924				31,549				31,941
UNSUCCESSFUL				16,287				12,365				22,244				14,741				14,160
DIDN'T HUNT				5,415				6,380								5,915				7,539
NO INFORMATION																456				300
COULD NOT CONTACT												862				637				947
NO REPLY				1,849				2,173				1,198				2,702*				2,894*
LOST TICKETS																257				179

Game management unit	1968				1969				1970				1971			
	♂♂	♀♀	†	*Total*	♂♂	♀♀	†	*Total*	♂♂	♀♀	†	*Total*	♂♂	♀♀	†	*Total*
1	157	62	4	223	120	29	0	151	99	37	1	137	119	54	1	174
2				0												
3				0												
4				0												
5	177	133	3	313	163	161		324	141	140	7	288	104	124	2	230
6	45	9	0	54	53	13	2	68	42	35	4	81	38	54	1	93
7	160	1	3	164	174	4	1	179	152	11	2	165	153	14	2	169
8				0												
9	366	72	5	443	317	70	6	393	266	84	2	352	317	116	7	440
10	1			1												
11	99	34	8	141	101	59	2	162	126	115	1	242	90	89	2	181
12	132	30	2	164	125	29	4	158	110	26	3	139	107	45		152
13	1240	243	29	1512	1204	7	8	1219	1141	158	30	1329	1126	614	18	1758
14	680	38	5	723	709	203	11	923	559	8	19	586	787	706	18	1511
15	855	27	13	895	877	139	8	1024	716	338	21	1075	788	617	14	1419
16	432	46	9	487	615	167	7	789	598	212	15	825	585	235	16	836
17	45	0	1	46	11	1	3	15	23		2	25	36		1	37
18	15	2	1	18	13		1	14	7			7	10	1	1	12
19	111	29	3	1433	117	30	5	152	135	33	5	173	152	33	4	189
20	818	177	12	1007	890	224	5	1119	883	224	27	1139	846	206	20	1072
21	125	40	3	168	135	26		161	100	31	6	137	127	57		184
22	33	1	1	35	69	1	2	72	70		1	71	59		1	60
23	30	4	0	34	53	13	1	67	36	24	1	61	50	13	1	64
24	39	4	1	44	59	12		71	45	7	4	56	62	15	2	79
25	50	21	1	72	77	31		108	39	15	1	55	52	21		73
26	15	4	1	20	25	6	1	32	16	7	2	35	33	3	2	38
UNK.	67	14	3	84	128	16	7	151	107	13	14	134	80	21	11	112
TOTAL BY SEX	5692	991	108		6035	1241	76	7352	5426	1518	168	7112	5721	3038	124	8883
TOTAL BY YEAR				6,791				7,352				7,112				8,883
TICKETS ISSUED				35,705				51,060				45,919				49,048
UNSUCCESSFULL				15,624				13,954				13,645				17,435
DIDN'T HUNT				9,449				4,174				4,340				11,826
NO INFORMATION				346				1,679				507				302
COULD NOT CONTACT																
NO REPLY				3,273				15,602**				11,986				10,459***
LOST TICKETS				222				526				117				362

† Sex unknown.

* One only reminder letter sent.

** Packets initiated.

*** Back to single species ticket.

TABLE II

Moose harvest, Matanuska Valley from Premier Mine to Willow, 1954-1971[1]

Year	*Male*	*Antlerless*
1954	275	0
1955	275	0
1956	275	0
1957	275	0
1958	300	0
1959	300	0
1960	300	150
1961	300	300
1962[2]	350	1000
1963[3]	350	300
1964[3]	250	275
1965[3]	580	660
1966[3]	200	75
1967[3]	159	0
1968[3]	366	0
1969[3]	343	120
1970[3]	269	0
1971[3]	431	378

[1] Harvest figures have been adjusted and "rounded" because harvest units have not been consistent from year to year.

[2] Registration hunt.

[3] Harvest tickets.

wolf dens, moose calf remains comprised 95 percent of the identifiable material in wolf scats (Rausch and Bishop, 1968) and winter kills are predominantly of calves (Burkholder, 1959; Alaska Department of Fish and Game, 1973). Major reduction in the calf cohort has serious implication upon productivity. Calf moose remains in wolf scats and around wolf dens during early summer do not rule out the possibility that wolves scavenged calves, as moose calves die from a variety of causes (LeResche, 1968).

In a recent extremely severe winter, 56 percent of 57 wolf kills were calves while the balance of the sample appeared representative of the sex and age composition known to be present on the range (Stephenson and Johnson, 1973). The condition — as revealed by marrow fat (Neiland, 1970) — of the wolf-killed moose was superior to that of specimens from moose that died from other causes (Stevenson and Johnson, 1973).

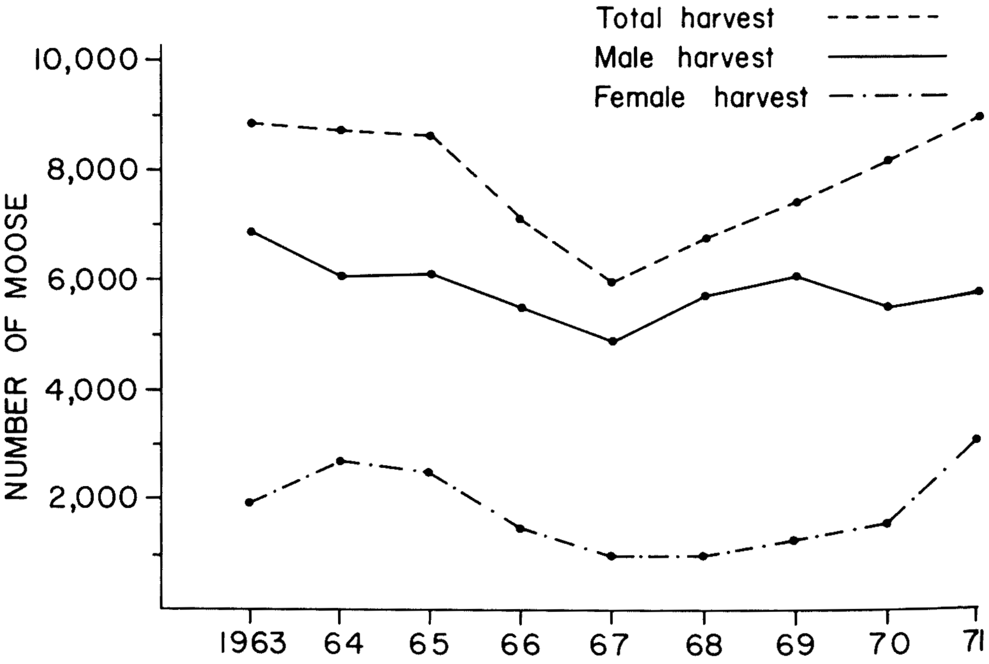

Figure 2. Moose harvest in Alaska, 1963-1971.

The relationship of wolves to moose populations certainly is not clear at this time but in situations where severe winters result in moose population decreases, wolf populations may accelerate this decrease through intense use of the youngest age classes. Their use of older age classes appears to be random. On ranges where hunting pressure is sufficient to use the annual surpluses wolves are directly competing for the resource. Management solutions under present laws and preservationist activities do not appear available short of eliminating hunting for ungulates.

Black bear *(Ursus americanus)* prey upon moose calves and in spring both species tend to concentrate on marshy areas to feed on newly emergent vegetation. Chatelain (1950) concluded that on the Kenai Peninsula a large black bear population was responsible for substantial calf mortality but that its relevance to the welfare of the moose population was unknown.

Brown bears *(Ursus arctos)* kill moose of all ages whenever the opportunity occurs. The relative scarcity of bears suggests that seldom is their use of moose of importance to the herd. Local exceptions may occur on the Alaska Peninsula where bears are abundant and seemingly occupy spring ranges with calving moose. Calves and adults are taken. Nevertheless, the moose population established and increased after the bear population was well established and it is doubtful that at this time predation by brown bears has an unfavorable impact on the moose population.

Public response to management procedures

The research and management investigations by Chatelain (1951), Spencer and Chatelain (1953) and Scott (1956) did not culminate in changed management procedures because federal law did not allow hunting of cows and yearlings. In addition the long period of conservatism that followed market hunting and exploitation concurrent to the gold mining era had conditioned many long-time residents in their resistance to change. The long period of conservatism plus parochial attitudes of residents combined to set the stage for a major confrontation between the new state administration and elements of the public when the Department of Fish and Game Board authorized the first antlerless seasons for the fall of 1960.

The first seasons were carefully controlled and of extremely limited magnitude. To a considerable extent they were designed to evaluate population status (Rausch, 1965). Initially, public opposition was local and largely based on emotionally charged issues. A considerable amount of public support for scientific management existed and the department generally considered the first seasons successful though they were so limited that few benefits accrued to the habitat. The Department rapidly expanded the seasons and number of antlerless animals available to hunters.

In the Matanuska Valley, in Game Management Unit 14, a long-standing feud between farmers and moose was resolved in 1962 by having a 40-day any moose season during which approximately 1200 moose were killed (Table II). The results did benefit farmers but they also generated fear among some hunters and conservationists that moose would be eliminated. Statewide harvests of cows increased dramatically (Fig. 2). As hunting seasons were extended, antlerless moose became legal over more of the state and, in some cases, the bag limits were increased allowing two moose per person per year (Table I). In southcentral

Alaska in 1964 and 1965, unusually heavy snowfall just before antlerless season opened concentrated thousands of moose along highways. The resultant slaughter (1000 moose were killed in a small portion of the Matanuska Valley in one day) polarized public opposition to antlerless moose seasons. At least one sportsman's organization was formed for the purpose of eliminating cow moose seasons. As the opposition grew, the Department was attacked by political opportunists who realized its structural weaknesses.

Public meetings were held at which department employees were verbally attacked and subjected to other techniques designed to discredit the Department. Eventually petitions and raw political power were employed and meaningful antlerless seasons gradually disappeared from much of southcentral Alaska, particularly in 1966, 1967, 1968, 1969 and 1972 (Tables I and II).

In 1968, a petition containing over 7,000 names was used by politicians to obtain an investigation of the moose situation by the legislative council. Eventually, the commissioner, not a biologist, cancelled the antlerless seasons in the Matanuska Valley. In 1971, a group attempted to obtain a court injunction against certain scheduled antlerless seasons. At the hearing they attempted to show that moose populations were depressed, browse abundant and that antlerless seasons were causing all moose management problems. After two days of trial they dropped the case primarily because none of their witnesses were accepted as experts and their prospects for obtaining an injuction were very dim.

The repeal of antlerless seasons by commissioner's announcement and the attempted injunction represent the apogee of public criticism. The legislature was involved in the dispute through the legislative council and through the legislative process. Annually several legislators introduce legislation to nullify specific antlerless seasons or to permanently close the season on cow moose. None of the attempts have succeeded; primarily because there is a deep-seated public resentment toward legislative interference in regulatory matters pertaining to fish and wildlife.

Measuring the extent of public dissatisfaction with the department's programs is particularly frustrating because, when anti-cow hunters were most strident, up to 15,000± people were applying for and using antlerless hunting permits. In a further attempt to evaluate public attitude toward cow moose seasons, the president of the state Senate in 1972, Mr. Jay Hammond, analyzed the responses of local advisory committees to a legislative resolution requesting elimination of antlerless seasons until December 31, 1974.

None of the advisory committees that responded favored the legislative action and most favored some form of antlerless moose seasons. It seems then that a large number, perhaps a majority of the people, were tacitly supporting progressive management so long as they did not have to publicly defend the Department.

The Department has undertaken a self examination and as a result it has launched a program designed to establish policies, plans and priorities for managing moose populations and for preserving moose habitat (the ultimate key to retaining management options).

This planned approach did allow reestablishment of many antlerless moose harvests in Southcentral Alaska in 1971 when very large harvests were achieved in portions of Game Management Units 13, 14, and 15 (Table I). Unfortunately, these harvests coincided with a major decline in certain moose populations brought about by the interaction of severe winters, depleted ranges and predation. In 1972, a number of antlerless seasons again were cancelled and reestablishing public confidence in the department will require new approaches, plus time.

Future management plans

Future management plans will be designed to fulfill our responsibilities to the resource while establishing a basis for meaningful interchange with the public we serve. The first step in such a move entails establishing a coordinated plan accepted by staff and public. An attempt toward this goal was made in 1973 when the Game Division completed a set of management policies (Alaska Department of Fish and Game, 1973). The broad guidelines present the probable options available to managers responsible for guiding resource use. This resource use policy states:

"*Moose management policy:* To many people, the moose *(Alces alces)* symbolizes Alaska. The largest state seems a fitting home for this largest member of the deer family, but Alaska does not have a monopoly on moose. They range across Canada, the northern states, and throughout northern Eurasia. Although moose are often considered animals of the forest, they also occupy drainages on the treeless tundra, and use sub-alpine areas. (...)"

"Moose in Alaska, from the scattered populations in Southeastern to those on the fringes of the tundra, represent a tremendous resource of recreation and food. Their adaptability to a variety of natural conditions and to the various activities of man allows a wide range of management possibilities.

"The broad spectrum of needs and desires of an increasing human population in Alaska must be considered in formulating moose management programs."

"*Moose policy statement:* The Alaska Department of Fish and Game recognizes the Constitutional mandate of the State of Alaska to manage moose on the sustained yield principle for the benefit of the resource and the people of the state, and also recognizes that national interests must be considered.

The Department recognizes the singular importance of maintaining suitable habitat for moose, and advocates the development and implementation of comprehensive resource use planning.

The Department recognizes that there are many uses of moose, the present priorities may not be the priorities of the future, and that management plans must consider all uses.

The Department recognizes that responsible moose management must be based on scientific knowledge.

In many areas of the state, recreation is the most important use of moose. Recreational uses include: Sport hunting in its various forms; observation, both incidental to other activities and as the primary objectives; and wilderness experience, which includes the aesthetic rewards of being aware of or observing moose in natural interactions with their environment. The Department recognizes its responsibility to provide for all these uses in its management plans, and holds that they are generally compatible.

Sport hunting with the gathering of meat as an important consideration has traditionally been the dominant use of moose in Alaska. This use will be encouraged in most areas, and salvaging of all edible meat will remain a condition of taking moose.

In most areas, moose will be managed to provide maximum recreational opportunity. This concept recognizes the value of the opportunity to be selective in hunting, to enjoy uncrowded hunting conditions, to make use of remote areas, and to enjoy various other experiences which enhance wild-life-oriented activities.

In selected areas with highly developed access and intensive hunter use, or where the human population is partially dependent upon moose for food, moose will be managed for the maximum sustained yield of animals. Management techniques may include harvest of moose of all sexes and ages, liberal seasons and bag limits, access improvement, and habitat manipulation.

Certain areas of the state will be managed to provide hunting opportunities of the highest aesthetic quality. Management techniques may include, but are not limited to, regulation of access, regulation of sex, age, and antler size and conformation of animals taken, and population manipulation.

The Department will encourage recreational observation of moose through public information and education, and will provide for such activities in its management plans. Although hunting is generally considered compatible with recreational observation of moose, certain areas exceptionally suited to viewing moose as the primary objective may be zoned in time or space to restrict hunting in favor of observation of moose in their most natural population and social structure.

The Department will manage moose to provide sustained yields of animals for humans and for wild carnivore populations that depend upon them for food. Whenever substantial conflicts arise between humans and predators over the use of moose, the predator population will be managed to minimize such conflicts.

A few areas may be reserved for scientific studies where moose populations and/or habitat can be manipulated.

The Department has demonstrated that transplanting moose for restocking former ranges or stocking vacant habitat can be a useful management tool. Because transplants often have unforeseen detrimental effects, importing and transplanting of moose will be generally opposed, but may be approved if substantial public benefit can be shown. Proposed transplants will be reviewed by the Department and must meet the following minimum requirements to be approved: 1) The proposed transplant site must provide sufficient and suitable habitat to support a viable population of moose as determined by comprehensive study; 2) prior study must establish that the introduction of moose will not adversely affect the numbers, health, or utilization of resident species.

Moose are one of the few still-wild species that have been domesticated with some success. However, because wildlife belongs to all the people, the domestication of moose for commercial purposes is normally not considered a wise use of the resource and usually will be discouraged by the Department.

In some nations, moose meat and by-products are important commercial commodities. In Alaska, however, recreational hunting of moose is the major use of moose, with food gathering and other recreational pursuits being additional important considerations. In remote areas, where food gathering is the primary use of moose, regulations should be sufficiently liberal to allow the taking of an adequate supply of meat. The Department, therefore, holds that commercial harvesting of moose for the sale of animal products is unjustified.

When others conduct research on moose within Alaska, the Department will request a description of proposed studies and make recommendations in the best interest of the species and the people of the state. The Department will cooperate with other agencies or individuals whose research may provide useful information on moose.

The Department may issue permits for capturing, holding, importing and exporting of moose for stocking, public education and scientific study, byt only after demonstration that suitable habitat or holding facilities are available to the permittee. Permits will not be issued unless substantial benefits which are consistent with the Department's management policies can be demonstrated.

The Department recognizes that situations may arise requiring control of moose. Controls will be implemented only after an investigation by Department personnel has determined a valid need exists. The Department will discourage undue competition with moose by human activities including agriculture and animal husbandry.

Whenever appropriate, control of moose will be effected by recreational hunting. The Department holds that it is the owner's responsibility to protect his property from damage by moose. Reasonable efforts must be made to protect life and property by means other than the destruction of moose. When control by removal of moose is necessary, humane methods will be used and meat will be salvaged.

Protection and manipulation of habitat are of foremost importance in moose management. Much of the most productive moose range is in early post-disturbance successional stages. Therefore, disturbances such as fire, logging in small blocks, and selective land clearing will be encouraged where moose production is the best use of the land. When possible, the Department will engage in habitat manipulation by the use of fire, mechanical means, or other methods.

Some moose populations depend upon climax sub-alpine, successional riparian, or marshy lowland plant communities for vital activities such as mating, calving and feeding. These critical areas will be recognized, designated and protected.

The Department recognizes the need to provide access planning for and control of moose hunters and observers. In some areas where moose are managed for maximum sustained yield and/or maximum recreational opportunity access may take the form of roads, airstrips, snow machine trails, hiking trails, canoe routes, boat landings, and horse trails. The Department may disseminate information about access. In areas managed primarily for high quality hunting and compatible uses, access may be restricted to some or all of those nonmotorized means listed above. Seasonal time and area zoning may allow for compatible uses of the resource, however, and will be encouraged." (Alaska Department of Fish and Game, 1973).

The next logical procedure is to prepare species plans for each habitat unit or definable area. This difficult task is now well underway and completion of some segments are anticipated in 1974.

Interim agreements with land owning agencies and short-term plans, five years or less, have been consumated with appropriate agencies. Examples include an agreement with the Department of Interior, Bureau of Sport Fisheries and Wildlife concerning a five-year plan for managing moose on the Kenai National Moose Range. This area of over 5,000 km^2 has presented unusual problems to managers because of the restrictive attitude toward public access and antlerless seasons prevalent at some levels of federal government. The five-year agreement lists specific areas where hunting will be allowed and quotas set. In addition, the agreement provides for data collecting for the purpose of evaluating the effects of various intensitites of exploitation.

Environmental controls will receive much more emphasis as plans are developed to implement policy and as human exploitation of natural resources increases. Maintaining adequate space for moose populations will necessitate new agreements with federal, state, borough and private landowners. In addition, manipulation of vegetation using fire and man-made devices will assist in stabilizing moose populations at high levels and provide the many benefits attendant to such populations. Because certain other species, notably caribou *(Rangifer tarandus)* and some furbearers, require climax vegetation, it is necessary to select with care areas where vegetation is manipulated.

The lands within the state are now undergoing partition among the various claimants, federal, state and native. The Native Claim Settlement Act of 1971 will ultimately transfer at least 16,000,000 ha of land into private native ownership. The act also provides the federal government opportunity to classify and perhaps obtain through congressional action some 32,000,000 ha of choice recreational and forest lands. Finally the state was allocated approximately 40,000,000 ha at statehood and the selection process is still underway. The far-reaching impact that this disposal of lands will have upon wildlife cannot be overestimated.

The act also created an advisory federal-state land use planning commission whose duties include recommending land use priorities to the Secretary of Interior and to Congress. The success of this important land planning function cannot be assessed at this time.

Environmental controls, principally maintaining vegetation in a productive stage for the benefit of moose, in all probability will be assigned high priority by the Department of Fish and Game. Techniques employed will include agreements with landowners allowing wildfire to burn unchecked, the use of controlled fires, and mechanical manipulation of vegetation in areas where fire is not a suitable device.

Acknowledgments

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MOOSE MANAGEMENT IN NORWAY AND SWEDEN

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Résumé

Entre 1900 et 1930, un total de 3,500 orignaux étaient chassés chaque année en Norvège et en Suède (soit 1.2 orignal par 100 km² ou 3.2 orignaux par 100 mi²). Certains changements écologiques ont entraîné des accroissements de la récolte annuelle qui s'élève maintenant à 40,000 têtes (soit 14.1 orignaux/100 km² ou 36.5 orignaux/100 mi², dans la partie productive de la forêt). L'aménagement est sous la responsabilité de l'Etat et des propriétaires terriens, ces derniers possédant 75-80% du territoire forestier. La Norvège exige, pour accorder un droit de chasse, une superficie minimale, déterminée en fonction de la densité des populations. En Suède, il y a deux saisons de chasse: la première est brève et non restrictive; la seconde, plus longue, est contrôlée quant au nombre et au type d'animaux abattus. On favorise une pression de chasse élevée. On vise à abattre de 50-60% de mâles et une forte proportion de jeunes animaux, veaux compris. L'un des objectifs majeurs est de protéger les femelles adultes très productives, et un nombre convenable de mâles adultes. Au moment d'émettre des permis de chasse sur leur territoire, les propriétaires établissent au préalable le rapport des sexes recherché — et parfois même la proportion des veaux; pour parvenir à cet objectif, ils font varier le prix des permis de façon appropriée.

L'aménagement de l'habitat forestier de l'orignal prend de plus en plus d'ampleur, car la valeur relative des ressources cynégétiques s'accroît rapidement. L'auteur fait état des nombreux problèmes de recherches à considérer, en signalant que les questions d'équilibre numérique sont manifestement les plus importantes.

Abstract

In the period 1900 — 1930 Norway and Sweden harvested a combined total of around 3,500 moose annually, (1.2 moose/100 km² or, 3.2 moose/100 mi² of productive forest). Several ecological changes caused populations to increase, and annual harvests are now around 40,000 (14.1 moose/100 km² or, 36.5 moose/100² of productive forest). Governments and landowners share in management; 75-80 per cent of the forest area is privately owned. Norway stipulates a minimum area requirement to harvest a moose, the area varying with moose densities. Sweden has a short general season with no bag limits, but closely regulates the kill and its composition in a later and longer special season. A high hunting pressure is preferred. The harvest should consist of 50-60 per cent bulls, and a high proportion of young moose, including calves. A major objective is to retain mature, highly productive females and a fair number of full-grown bulls. When renting out moose hunting, landowners normally predetermine sex ratio in the kill, sometimes also the calf ratio, and differential rates are often used to obtain a desired ratio of young to mature animals. Intentional moose habitat management, mainly through forest management, is increasing because of a rapid rise in hunting values related to other resources. There are many research needs listed; those concerning population balance are regarded as most important.

Introduction

Moose is the most valuable game species in Norway and Sweden. The combined annual harvest is approximately 40,000 animals, with a basic meat value of some N. kr. 75 millions ($12 millions). An even larger recreational value adds to this sum (Lundin, 1972 b). Around 200,000 people take part in the hunt. Thus the necessity of good management is clear. We have made much progress but discussions between hunters, biologists and the public will continue.

The moose population

The history and development of moose populations in Scandinavia is dealt with by Dr. Gunnar Markgren of Sweden (Markgren, 1974). There have been pronounced fluctuations (Skuncke, 1949; Lykke, 1960; Curry-Lindahl, 1961).

Harvest statistics for Norway and Sweden (Fig. 1 and 2) are useful to indicate trends in the moose population, as hunting pressure has been relatively even, all areas are easily accessible, and mortality, except for hunting, is normally low. Poaching (included in the Norwegian figures prior to 1952, and in the Swedish data prior to 1922) is a factor of unknown size. It may have been more prevalent than we usually think, especially in the period 1915-1935. However, this would not drastically alter the general trends of population curves.

In both countries there was a very rapid increase in the kill, and the populations, from the 1930's to the 1960's. This involved increased local densities as well as a range extension.

Comparisons of peak harvests with those of earlier years (Table I) are based on the productive forest land occupied by moose which totals 228, 000 km² (88,000 mi²) in Sweden and 56,000² (21,600 mi²) in Norway.

TABLE I

Moose harvests by area of productive forest in Scandinavia

Country	*1914 harvest per*		*Peak harvest* per*	
	100km²	*100 mi²*	*100km²*	*100 mi²*
Norway	2.2	5.7	14.1	36.5
Sweden	1.2	3.1	15.7	40.6 **

* 1963 in Norway, 1970 in Sweden.
** Including 27.5 per cent calves.

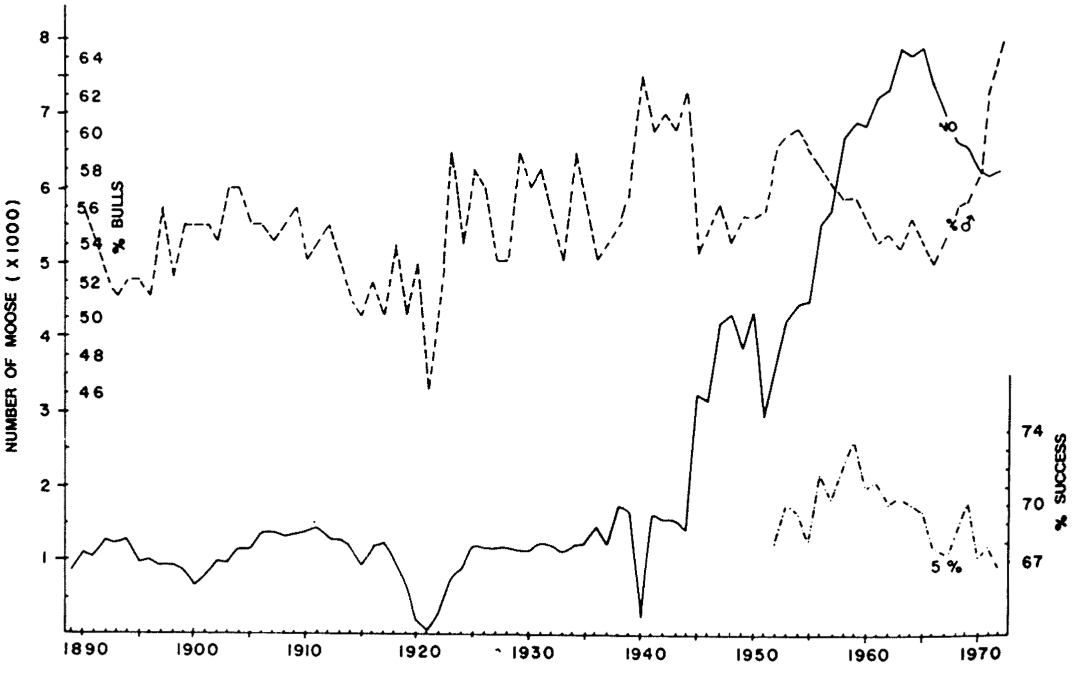

Figure I. Moose harvest in Norway between 1889 and present.

While moose densities at the beginning of this century were around 0.1 moose per km² (0.26 per mi²) in Norway and somewhat less in Sweden, both countries reached densities of about 0.8 moose per km² (2.0 per mi²) around 1960. Densities vary between districts as a result of different qualities of soils, topography, climate and other factors. Figure 3 shows harvests per unit area in Norway. In the peak population years the counties of Nord-Troendelag and Vestfold in Norway as well as Skaraborg in Sweden had an overall density of 1.5-1.6 moose per km² (4.0 per mi²). The municipality of Verdal in Nord-Troendelag had around 2.0 (5.0-5.5) and populations with greater densities could probably be found. Except for the Verdal figure, which is based on a winter moose count the densities mentioned are calculated.

Factors controlling the moose populations in Scandinavia have been subject to some investigations. An explanation of the rapid and large increase in this century has been of especial interest (Pimlott, 1959 and 1962; Ahlén, 1965; Hagen, 1968; Lykke and Cowan, 1968; Markgren, 1969; Myrberget, 1972). Of prime importance have been changes in forest management (Lykke, 1957; Delbeck, 1964; Lykke, 1964; Huse, 1965), in husbandry (Bjor and Graffer, 1963; Christensen, 1964; Borgedal, 1966 and 1967; Ahlén, 1968), climatic changes (Lykke and Cowan, 1968), and hunting (Salvesen, 1929; Olstad, 1934). Diseases and parasites (Holt, 1962), accidents (Lykke, 1952; Krafft, 1964; Hamilton, 1964 and 1969), and predators since 1850 (Schulz, 1931; Olstad, 1945; Hagen, 1960; Hellgren, 1967; Myrberget, 1969) have been of minor importance. A discussion of the factors involved is dealt with by Markgren (1974). Since 1850, moose have likely been controlled almost entirely by hunting and by the factors influencing quality and quantity of food.

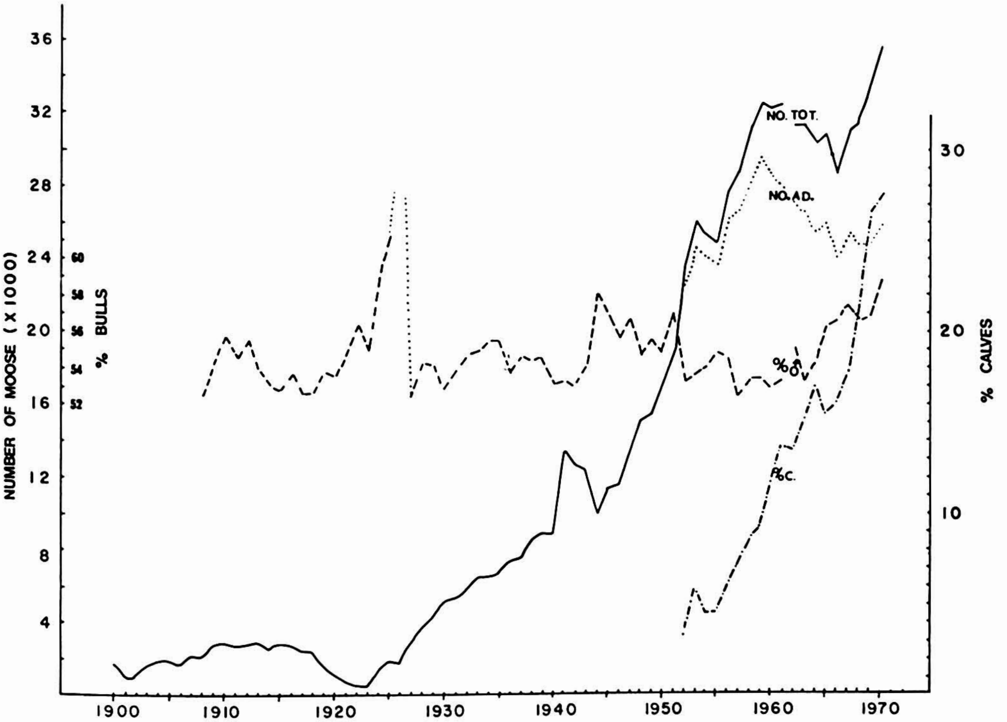

Figure 2. Moose harvest in Sweden between 1900 and present.

Moose management

In Scandinavia, hunting rights belong to the landowner and most of the land is privately owned. Approximately 80 percent of the forest area in Norway and 75 percent in Sweden is in private ownership. A few forest companies own approximately 10 percent of the Norwegian and 25 percent of

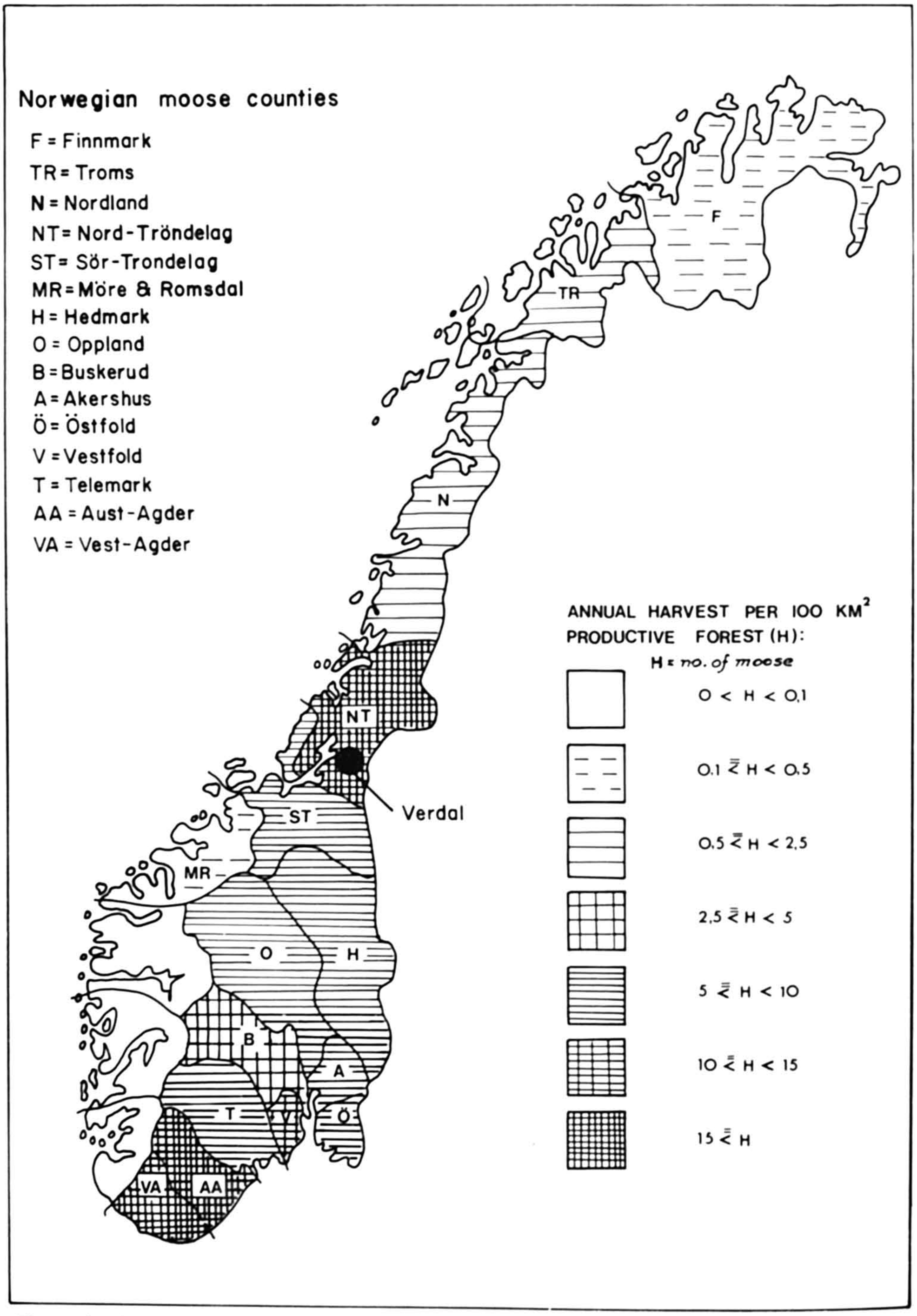

Figure 3. Yearly moose harvest per unit area in Norway averaged for the period 1945-1964.

the Swedish forest area. The other private holdings are small, with an average size of 40 hectares (100 acres) in Norway.

AIMS AND PRINCIPLES

Generally speaking the aim of Scandinavian moose management is to preserve a high quality moose population of optimal density throughout its normal range. Important parts of the aim are: to protect the moose population itself, to obtain maximum recreational and economical values on a sustained basis, and to integrate moose management with other land uses.

A high quality moose population should be a stable one, i. e., having a good ability of withstanding negative working forces: it should have high productivity and low natural mortality and be capable of producing a high economic value from hunting. An optimal density gives the highest quality moose population without interfering with other land use to intolerable degrees. Scandinavian resource management is almost exclusively based on multiple use principles (Lykke, 1971). The normal range of moose can therefore to a large extent be defined by the species itself.

These aims and definitions imply a moose population with many middle-aged, highly productive cows. Furthermore, the yearly removable number of animals should be high, the hunt should give a large quantity of meat, and the chances of seeing, and perhaps shooting a large bull should be fairly good. This requires a population kept at a somewhat under-capacity level to obtain high productivity while protecting browse resources from over-population and forests from excessive moose damage (Westman, 1958; Lykke, 1964). The judgement of moose damage has changed considerably recently, due to hunting values increasing rapidly while net incomes in forestry have been decreasing.

The aims of management and their implications are much the same throughout both countries. The principles must be adjusted to the current moose situation, which varies from district to district. It is of prime importance to have sensitive methods of management, which can be implemented quickly whenever and wherever needed.

HUNTING METHODS AND HARVEST REGULATIONS

Moose hunting is almost always carried out with the help of a dog which may be used loose or leashed (Fig. 4). Drive hunts are used to some extent, and pass hunting is often combined with the leashed dog method. Each hunter or hunting team has a specified hunting area for exclusive use. The hunters are land-owners, their professional staff, forest workers and others locals. These hunters know the area well, and the moose population fairly well, as the same areas are hunted by the same people each year.

Figure 4. The dog, a elk hound, shows signs of near presence of moose.

Since 1952, Norway has had harvest control by area. Before that, there was a long period during which one moose per year could be harvested on each property, almost regardless of size. In addition, owners of large properties had the opportunity to get permits for harvesting more animals. The hunting season is fourteen days, in September-October. In some districts it is divided in two periods, before and after the rut. The minimum area requirement for taking a moose is set by the Department of Conservation after advice from a local game committee in each municipality. The area size, depending on moose density, damage to forests, etc., may vary even within a municipality. It usually runs between 200 and 2,000 hectares (500-5,000 acres) of moose habitat. Landowners with small areas may unite to obtain a permit. The landowners apply through the game committee for permission to harvest the wanted number of moose. There are no regulations requiring a landowner to harvest moose, or that the harvest should have a specific composition. A closed season for certain sex or age groups may be used, and through agreements and information, the authorities try to orient harvest composition.

Before 1931, Sweden's moose harvest was controlled only by the length of the season. Since then Sweden has had a dual system consisting of a short general season, usually two to four days with almost no area requirements, no bag limits, nor any predetermination of the harvest composition, and a longer special season of variable length, usually around four weeks. In the latter the take of moose is specified beforehand as to numbers, sex ratio among adults, and number of calves. About half the harvest is made in the special season. There is a strong desire in Sweden to drop the general season, and use a special season only. This would be more like the Norwegian system, but with a better control of harvest composition. This has already been adopted by three counties, on an investigational basis (André, 1968; André and Lundmark, 1971; Stålfelt, 1970 and 1972).

The lack of governmental regulations as to harvest composition, especially in Norway has to some extent been compensated by private regulations imposed by individual landowners. These regulations, through directions and systems of rent, are only feasible on large properties.

CONTROLLED HARVEST — PROBLEMS, COMPROMISES AND METHODS

Harvest control is by far the most important direct moose management effort made in Norway and Sweden. Within the limits of other ecological factors, mainly food, the moose population can be regulated through hunting. The final aim is a completely controlled harvest, taking into consideration biological, economical and other aspects.

A controlled harvest must be based on a thorough knowledge of moose ecology, the particular population, its habitat and food supply, as well as the specific aims of management if it is to be meaningful. General knowledge of the species among Scandinavian hunters and landowners is fairly good, and has probably increased considerably in the last few years due to recent publications by Ahlén (1965), Lykke (1968), Markgren (1969), Myrberget (1972) and others, and to continuing public discussions of harvest systems.

Knowledge of local moose populations is established by ground counts (Lykke, 1968), aerial counts (Stålfelt, 1969; Almqvist, 1973), and by interpretations of hunting statistics and hunter observations (Haagenrud, 1972). So far, the latter source is the most important. Delivering the lower jaw (for aging) and the ovaries (for reproduction studies) together with information of the killed moose (date, place, weight, antler size, calves at heel, etc.), is becoming a more widely used practice lately in both countries. In addition, the hunter must report his daily observations of moose seen, their sex ratio and calf fraction. He also gives a general evaluation of the moose population, its size and balance with food supply. Hunting methods and the practice of hunting the same area year after year makes this information valuable. The information is compiled by the Department of Conservation.

A relatively high hunting pressure is preferred in both countries although it is regulated by different means. The Norwegian system of area requirements should theoretically give the best control, but it may not be responsive enough. In periods of rapid changes of moose densities, the needed adjustments of area requirements can lag behind. This may easily lead to underharvests during increase periods and overharvests in decrease periods and this probably happened in Norway in the years 1945-65 (Fig. 1). The Swedish general season may lead to overharvest but it represents an automatic working pressure on the herd to prevent overpopulations. This may be one of the reasons why Sweden probably has managed to stabilize its population better than Norway during the last fifteen years.

The number of moose killed is only one aspect of hunting pressure. A relatively small harvest may have a severe effect if it consists of middle-aged, highly productive moose. Sex, age and quality composition of the harvest is an important part of the control. As we normally try to manage our moose population around the inflection point in its curve of increase, productivity is high, and the harvest should include a high percentage of young animals. In the long run, the sex ratio of the kill should equal the sex ratio of net production, which is usually about 50:50, or perhaps slightly favoring males. The bull percentage usually runs around 55 in both countries, (Fig. 1 and 2). It is felt that the sex ratio in the living populations should be nearly equal to obtain adequate reproduction. Considerably fewer bulls might periodically be kept, if the moose population is very dense. Under normal densities there are dangers of overharvesting the bull fraction (Markgren, 1970).

With unregulated harvest composition in Scandinavia most of the time, hunter preference for large animals, especially bulls, has led to unwanted situations. Heavy hunting pressure, which was necessarily imposed on the Norwegian moose population in the early 1960's, resulted in the kill of most of the highly reproductive segment of the population. This left Norway with a moose population having an unsuitable age composition. The adjustment of this situation takes time and demands a controlled harvest. The example has taught us to spare mature cows and a fair number of full-grown bulls in order to obtain a stable and highly productive moose population with a high recreational value.

The harvest of moose calves has become a key object in discussions of controlled harvest (Lundin, 1964 and 1965; Stålfelt, 1966; Dahl, 1968; Korbu, 1969 and others). The debate has no doubt had educational effects, as controlled harvest has been brought into the limelight, but the topic itself may not be such a dominating factor in moose management as the discussions indicate.

The advantages of a high calf percentage in the kill are: a rapid increase in mean age of the population, if hunting pressure on middle-age moose is reduced correspondingly: the winter population can be kept at a minimum: hunters can take a large number of animals: and they harvest the age group with the largest death risk in the coming winter. It is important to have the option of harvesting calves when an increased kill is needed. The population can thus be reduced without destroying its most valuable segment. The results of a thoroughly controlled harvest (including a high calf percentage) in the two Swedish counties Västmanland and Kronoberg indicate a positive effect (Fig. 5; see also Stålfet, 1970). In both counties the aims have been to obtain a high-quality moose population. A somewhat increased density was an additional aim in Kronoberg. The number of harvested animals (including calves) and the amount of meat has increased, as well as the mean age and productivity of the moose population (Fig. 5).

As pointed out by those (mainly hunters) opposing a high percentage of calves in the kill, there are disadvantages too: natural selection should get the chance of working more than a summer, decision of sex and individual quality is difficult at the age of 4-6 months and a tendency of shooting the largest calves is a danger. The curve of body growth indicates 1 1/2 years as a better age for harvesting young moose and hunters are willing to pay more for hunting rights of yearlings. Thus the recreational value of the total moose harvest does not only stem from the number of animals shot nor of the amount of meat obtained.

The main objective in a controlled harvest is not the shooting of calves, but to spare middle-aged moose. Periodically it may be desirable to harvest many calves. The calf kill should concentrate on individuals with the least chance of surviving the coming

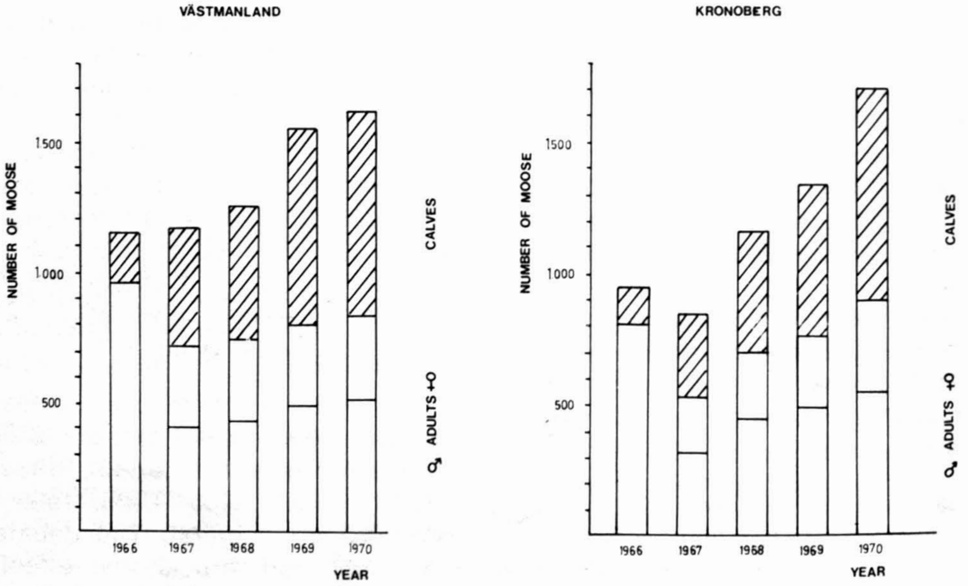

Figure 5. Controlled moose harvest in two swedish counties. Data from André and Lundmark, 1971.

winter — late born calves and the one of twins.

Moose management must be a compromise between various aims, and variation with the actual moose population situation is necessary. Stabilization, increase or decrease of densities, call for different methods. In many parts of Scandinavia it is desirable to keep densities around today's level, but to better the quality of the moose population. To achieve this, a relatively high hunting pressure is needed, and the hunt should be mainly directed towards young and small animals. Middle-aged moose should be spared, and bulls should make up 50-60 percent of the harvest. How high the calf percentage of the kill should be is open to question. Taking biological as well as economical aspects into consideration, a reasonable percentage seems to be around 20. Large departures from this value may be permitted at intervals.

To reduce moose densities in Verdal, Norway, in the 1960's , the harvest was increased as well as the percentage of cows (Lykke, 1968). For the sake of the remaining population, and because the lone calf has an uncertain future (Markgren, 1964) the percentage of calves in the kill should have been high. Increased densities, which are desirable in many parts of northern Sweden today (Stålfet, 1972) are obtained through lowered hunting pressure. Completely closed seasons are no longer regarded as a good management tool because maintaining hunting traditions and getting the yearly check-up of the population and its habitat by hunters is important.

Some new governmental regulations may be needed both in Norway and Sweden to obtain the wanted harvest control. The Norwegian system is sufficient to regulate harvest size but the Swedish one probably needs improvement. Furthermore, Norway must control harvest composition. This would require the authority to predetermine at least the sex ratio of the harvest, perhaps also the calf percentage. Approved moose management plans worked out for the large land holdings, including State Forests, may be an alternative. Small holdings are still a problem, and these will need permits specified as to harvest composition each year. An alternative, is to demand that a moose hunting area should be large enough for the harvest of at least three animals yearly. This would increase the interest in good management, and make it easier to enforce a controlled harvest.

We can probably never reach an optimal harvest through law or other official authority. The hunter take within an age/sex group will to some extent be left out, although this is very important. Larger hunting areas, education and information will hopefully lead to the interest of a best possible moose management by those having the hunting rights. Selecting the right animals demands a relatively long hunting season. The Norwegian season is too short.

Private regulations may be an effective tool in supplementing the official ones, especially on large land holdings. Many forest companies try to direct moose harvest composition through the lease contract. The rent system used is of prime interest. A quite common method some years ago was to rent out moose hunting to the highest bidder. This led to a wrong harvest composition, as hunters selected the largest possible moose. Today this system is being replaced by rent systems which direct the harvest towards selected age and sex groups. This can be done in many ways. The contract and rent system presently used at the forest company Vaerdalsbruket, Norway may be used as an example:

Here the aim is a slightly higher moose population, built up slowly, a higher mean age of both sexes, and a larger segment of mature bulls. This is made clear to the hunters, together with current harvest policy, in which the take of young and small moose is a main objective. They are also given an evaluation of the previous year's hunting results. The moose hunt is almost exclusively leased to the firm's forest workers and professional staff and other local people, who hunt the same area each year unless the contract is broken. Each hunting area gets 2-5 moose permits per year.

The main points in the contract are as follows: The harvest must conform to management policy. The number of moose is specified, including their sex ratio and the minimum number of calves to be taken. The hunters are always free to shoot calves instead of adults if they want to. Cows with calves at heel are not to be shot. The hunting team is to consist of up to three armed hunters with a dog. Lower jaws and ovaries must be delivered after the hunt, together with specified reports. Each moose is weighed by an authorized person, to whom the hunters also must show any antlers. Butcher's weight and antler size, including number of tines, is reported to the firm.

The rent consists of a basic fee, a weight-dependent fee, and an antler fee. The basic fee, N. kr 200 per moose ($36.00) is paid in advance and is not returned. The final rent is calculated after the hunt, and based upon the actual moose killed. The rent per kg of meat is found by the formula: $x = y/30 + 2.50$, where x = kr per kg, and y = butcher's weight. Each antler tine exceeding 6 is charged with kr 50 ($9.00). The basic fee is subtracted. Thus a calf of 60 kg will cost kr 4.50 per kg ($0.81) or, totally kr 270 ($48.50). A moose of butcher's weight 120 kg (for instance a relatively small 1 1/2 year old) will cost kr 6.50 per kg ($1.17) or totally kr 780 ($140.00) while a bull of 300 kg with a 20 tine antler will cost kr 14,80 per kg ($2.66) or totally kr 4,450 ($800.00). In addition there are taxes, 20 percent today, and governmental licences (Wegge, 1970).

This system leads to shooting of mostly small moose, 1 1/2 years old, small (for various reasons) older moose, and some calves. This makes the hunt more demanding and safer, as the hunters must select their animals carefully. The low basic fee also leads to a calm hunt as there is little monetary loss to unsuccessful hunters.

MANAGING HABITAT FOR MOOSE

As mentioned before, habitat modification has affected moose considerably in Scandinavia. Changes in forest management and in husbandry have resulted in more moose food produced, less competition, and thus the possibility of maintaining a larger population. The positive effect is mostly accidental though, as these habitat manipulations have not been done for the sake of the moose.

Today there is a growing tendency to apply intentional habitat management for the benefit of moose and other wildlife. Its background is the rapid increase in hunting values compared with other resources and a generally increasing concern for nature conservation.

Both in Norway and Sweden there are only general laws (for forestry, nature conservation, pollution, etc.) regulating multiple use of land. Work is being done to get more specific rules into the laws or introduce new laws with such rules. Special interest is paid to forestry practices, for recreational reasons. I believe that Scandinavian landowners will intensify application of practices beneficial for wildlife whether new law enforcements occur or not, this being in their own interest. A lot of such practices are already in use. I will, as an exemple, refer to some of the directions applied by a large company, Vaerdalsbruket, which concerns moose habitat.

The whole forest area shall be managed on a sustained yield basis. No large area should be let out of normal forest management for a long period of time. This is meant to secure a "stable" moose food production. No clearcut (sum of age classes up to approximately 30 years) shall exceed 100 hectares (250 acres). The size is usually far less. A chessboard-like system of clearcuts is preferred to produce a good mixture of food and cover, and a beneficial edge effect. Edge forest, towards mountains, swamps and water is normally left out of forest management. Cover is left along streams and unproductive hill edges to protect routes for migration and daily movement. Clearing the clear-cuts of unwanted shrubs is done very sparingly as most of them are valuable moose food, including mountain ash, willows, aspen and birch. On areas with middle or low forest values no brush removal is done at all. Herbicides are not used at present. Forest draining is kept to a minimum. Land for improved pastures is rented out to farmers in the district at a low price. Building of huts and other recreational facilites is concentrated on specific areas where wildlife will suffer least. The use of motorized vehicles outside roads is prohibited summer and winter although special permits for transportation along predetermined routes may be obtained.

These directions are not unique to the firm mentioned as other large forest companies in Scandinavia work under similar rules. In time the result will hopefully be a landscape highly beneficial for moose and other wildlife.

Research needed

The intensity of moose research in Scandinavia has been far too low in relation to recreational and economic values of the resource, especially in Norway.

The key components of intensified moose research should be the balance between population and food, indicators of this balance, and the composition and quality of populations. These indicators include reproductive patterns and animal quality especially as reflected in body weight of younger age individuals and by antler size of males. The best possible sex and age statistics of both the harvest and the living population should be obtained. Mortality, besides legal hunting, diseases, parasites and behaviour are other fields of research. Better methods for counting and classifying moose should be developed.

The moose food complex is another main field of research. Studies of browsing intensities, in relation to populations and the assessment of optimal browsing intensities for various plants and plant communities are of great importance. Quality and quantity of food produced under various conditions of successions, soils, climate, etc. need to be studied. The same is true for food and area competition, the effect of forest fertilizing and draining, and the use of pesticides. We also lack sufficient knowledge on the amount of food needed, and its variation with age, body weight and time of the year.

Research projects mentioned here do not constitute a complete survey but more intensive efforts along these lines would certainly mean an important step towards a better understanding of moose ecology, and as a result, a sounder basis for wise management.

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ORIGNAUX TUÉS SUR LA ROUTE DANS LE PARC DES LAURENTIDES, QUÉBEC, DE 1962 À 1972

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Résumé

De 1962 à 1972, 324 orignaux ont été tués sur le boulevard Talbot dans le Parc des Laurentides, Québec. Ce facteur de mortalité représente un taux d'exploitation de 15 à 20% de la population d'orignaux vivant à proximité de la route. Il y a une corrélation positive entre le nombre d'orignaux tués par année et par mois et le nombre de véhicules. Le nombre d'orignaux tués a plus que doublé pendant cette période de 11 ans. Cette augmentation s'accompagne d'une diminution de l'âge moyen des animaux tués. La mortalité chez les veaux n'est pas significativement différente selon les sexes, mais chez les adultes plus de femelles que de mâles sont tués. Considérant le rapport des sexes de la population chassée, aucune différence de vulnérabilité selon les sexes n'a été déterminée chez les veaux. Significativement plus de femelles que de mâles ont été tués de juillet à novembre, mais aucune différence n'a été observée pour la période de mai-juin. L'âge moyen des orignaux tués sur la route est significativement plus bas pour certaines années que l'âge moyen des orignaux tués à la chasse et les deux diminuent. La majeure partie des accidents surviennent entre les mois de juin et août et plus de 80% se produisent la nuit. Le nombre d'orignaux tués par véhicule enregistré dans le parc est le plus élevé en juin et juillet et réduit en août, septembre et octobre. L'intensité de la circulation et la mortalité de l'orignal suggèrent que l'orignal est actif pendant toute la nuit.

Les déplacements et la mortalité des orignaux ont été étudiés en fonction de la présence de mares situées de chaque côté de la route. La forte concentration de sodium et de calcium trouvée dans ces mares provient des épandages de sels l'hiver sur les routes. La fréquentation de ces mares par l'orignal est reliée à la concentration en sels. Très peu de relations ont pu être établies entre la mortalité et la fréquentation ou la concentration en sels de mares. Cependant, 2.3 fois plus d'orignaux sont tués où il y a des mares que là où il n'y en a pas. L'âge moyen des orignaux tués sur des secteurs avec mares est significativement plus élevé que sur les secteurs sans mare. Ceci peut indiquer une différence de vulnérabilité selon les âges pour ces deux secteurs.

Abstract

From 1962 to 1972, 324 moose road kills have been recorded in Laurentide Park, Québec. This mortality factor represents a rate of exploitation between 15 to 20% for the population of moose living adjacent to the road. There is a positive correlation between the number of moose killed by month and by year and the number of vehicules. The number of moose killed on the road has more than doubled during his period of 11 years. With this increase we also observe a decrease of the mean age of animals killed. More adult females than males are killed but we could not find any significant difference for the sex-ratio of calves. According to the sex-ratio in the hunted population the vulnerability was not different among sexes for calves. Significantly more females

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than males were killed from July through November but no difference is observed in the May-June period. The mean age of moose killed on the road is significantly lower for some years than the mean age of moose harvested by hunters, and both means are decreasing. Most road kills happen between June and August and more than 80% of the kills occur at night. The number of moose killed per vehicle registered in the park is higher in June and July, and lower in August, September and October. Traffic volume and moose mortality suggest that moose is active all night.

Moose movement and mortality have been studied in relation to ponds located on each side of the road. The high concentration of sodium and calcium found in these ponds comes from winter salt application on the road. Moose frequentation of the ponds is related to salt concentration. Very few relations have been found between moose mortality and the frequentation or salt concentration of the ponds. Twice as many moose are killed where ponds occur, as compared with sectors where there are no ponds. The mean age of moose killed in sectors with ponds is significantly higher than in sectors without ponds. This may indicate a difference in vulnerability among ages for those two sectors.

Introduction

Les accidents routiers impliquant des orignaux posent un sérieux problème dans plusieurs régions du Québec. Les collisions et les tentatives des conducteurs pour les éviter produisent les résultats suivants: des pertes de vie, des blessures et de nombreux inconvénients pour les humains; des dommages considérables aux véhicules; et la mort d'individus d'une espèce faunique importante.

Ce genre d'accident est attribuable à deux principaux groupes de facteurs: facteurs relatifs aux véhicules (nombre, vitesse) et aux routes (nombre, mode de construction et d'entretien) et facteurs relatifs aux animaux (densité et structure de la population, comportement et facteurs du milieu qui lui sont liés). Il est indispensable d'augmenter les connaissances de ces variables afin de diminuer les accidents routiers impliquant des orignaux.

A notre connaissance aucune étude n'a encore été publiée sur ce sujet. Le seul document faisant mention d'orignaux tués sur la route est celui de Thompson (1967) rapportant un total de 46 orignaux tués sur les routes de trois États américains. Nous avons fait une étude dans le Parc des Laurentides sur un certain nombre des facteurs mentionnés plus haut, soit le nombre de véhicules, l'entretien des routes par l'épandage de chlorure de sodium et de calcium, la structure de la population d'orignaux tués et un aspect du comportement de l'orignal à proximité des routes. Les buts de la présente étude sont: d'analyser les données sur les orignaux tués accidentellement sur la route dans le Parc des Laurentides de 1962 à 1972; d'évaluer l'effet de ce facteur de mortalité sur la population d'orignaux vivant aux abords des routes; d'analyser certaines causes de l'augmentation du nombre de collisions; et d'étudier l'effet des épandages de chlorure de sodium et de calcium sur le comportement et la mortalité des orignaux sur la route.

Description de l'aire à l'étude

Le Parc des Laurentides est un territoire boisé de 3,696 milles carrés (9 569 km^2) situé dans le bouclier canadien à 30 milles (48 km) au nord de la ville de Québec. Une route principale, le boulevard Talbot, le traverse du nord au sud et se scinde en deux tronçons au centre du parc pour desservir principalement deux villes situées plus au nord. Cette route est à deux voies et s'étend sur 117.4 milles (189,1 km). L'hiver, la surface de roulement est maintenue au pavage grâce à l'application de grande quantités de chlorure de sodium, soit 50 tonnes courtes/mille/année (55,5 tonnes métriques/mille/année), et de quantités moindres de chlorure de calcium, soit 0.8 tonne courte/mille/année (0,88 tonne métrique/mille/année). La vitesse maximale permise est de 60 milles (96,6 km) à l'heure. Tous les véhicules traversant le parc, au nombre d'environ 800,000 par année, sont enregistrés à l'entrée et à la sortie du parc.

Les abords de cette route ne sont pratiquement pas habités. Pour les fins de cette étude, la route fut divisée en trois sections en utilisant la jonction des deux embranchements venant du nord comme point divisionnel. Ces trois sections seront identifiées comme les sections sud (49 milles, 78,9 km), nord-est (31.5 milles, 50,7 km) et nord-ouest (37 milles, 59,5 km).

Le Parc des Laurentides fait l'objet d'une chasse contrôlée à l'orignal depuis 1962. La récolte est relativement stable et le taux d'exploitation du secteur accessible, calculé à partir des données de Bouchard (1972), se situe entre 8 et 10%.

Méthodes

Les données sur les orignaux tués ont été recueillies par les employés du Service de la faune qui remplissaient un formulaire pour chacune des carcasses examinées. Un certain nombre de cas d'accidents n'ont pas été enregistrés, l'animal blessé fuyant en forêt. Le formulaire n'a pas été le même pour toute la période considérée. Pour les années 1969 à 1972 cependant, il donnait les informations suivantes: localisation par système mercator (± .06 mille, ± 0,1 km), date et heure de l'accident, sexe et âge de l'orignal (classe d'âge, selon Passmore *et al.*, 1955).

Un inventaire des mares situées à proximité et de chaque côté de la route fut exécuté à la fin de juillet et au début d'août 1969 sur les sections sud et nord-est et sur une route secondaire ne recevant pas d'application de sel. La technique consistait à circuler lentement sur l'accotement de la route et à localiser les mares. Chaque mare était pointée sur une carte à l'échelle 1:50,000. La distance à partir de l'accotement était mesurée ainsi que les dimensions de la mare. Nous avons également évalué la fréquentation de ces mares par l'orignal. Trois classes de fréquentation ont été déterminées selon l'abondance des pistes, soit: éparse (une piste au maximum), occasionnelle (entre deux et quatre pistes) et assidue (plus de quatre pistes, souvent sentier entretenu par l'orignal).

Des échantillons d'eau provenant de 61 mares situées sur la section sud et de 20 situées sur la route secondaire, ont fait l'objet de dosages du sodium et du calcium et de déterminations de la conductivité spécifique. La conductivité spécifique fut évaluée par la méthode des cellules à conductance, tandis que la concentration des deux ions a été obtenue par la méthode d'absorption atomique.

Résultats

ORIGNAUX TUÉS SUR LA ROUTE

De 1962 à 1972, un total de 324 orignaux ont été tués et enregistrés sur les 117.4 milles (189.1 km) de route du Parc des Laurentides soit une moyenne de 29.5 orignaux par année ou un orignal tué et enregistré par année et par 4 milles (6,4 km) de route (tableau I). Le nombre d'orignaux tués a plus que doublé pendant cette période de 11 ans. Une moyenne de 38.2 orignaux tués a été enregistrée pour les cinq dernières années. Il n'y a pas de différence significative entre les nombres de veaux mâles et femelles tués (95♂ : 100♀). Le rapport des sexes des adultes (un an et plus) favorise considérablement les femelles (58 : 100).

L'âge moyen[1] des orignaux adultes (1 an et plus) tués sur la route diminue plus ou moins régulièrement depuis 1966 (fig. 1). Il est passé de 3.79 ans en 1966 à 2.17 en 1972. Cette différence est significative (P> .975). Une tendance similaire est notée dans la population chassée du Parc des Laurentides (fig. 1). L'âge moyen des individus tués à la chasse est cependant significativement plus élevé (P> .95) que celui des orignaux tués sur la route pour les années 1967, 1970 et 1971.

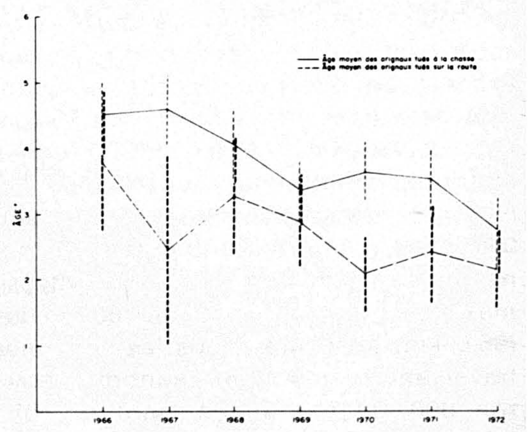

Figure 1. Âge moyen des orignaux adultes tués sur la route et à la chasse dans le Parc des Laurentides de 1966 à 1972. Les classes d'âge sont considérées comme étant l'âge réel.

La presque totalité des accidents routiers impliquant des orignaux se produisent du début de mai au milieu de novembre (fig. 2), près des trois quarts (72.4%) entre le début de juin et la fin d'août et près de la moitié (46.2%) entre le milieu de juin et la fin de juillet.

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[1] Dans les calculs d'âge moyen, nous considérons les classes d'âge (Passmore *et al.*, 1955) comme étant l'âge réel.

TABLEAU I

Mortalité annuelle des orignaux sur le boulevard Talbot dans le Parc des Laurentides, de 1962 à 1972

Année	*Mâle*		*Femelle*		*Age ou/et sexe non déterminé*	*Total*
	Veau	*Adulte*	*Veau*	*Adulte*		
1962		2			17	19
1963	3	6	3	8	3	23
1964	—	—	—	—	—	20[1]
1965	3	5	1	8	0	17
1966	1	6	3	17	2	29
1967	2	8	2	12	1	25
1968	2	9	7	13	2	33
1969	3	2	5	17	0	27
1970	5	6	4	20	0	35
1971	8	18	8	13	0	47
1972	8	14	4	22	1	49[2]
Total	35	76	37	130	26	324

[1] Données non disponibles ; estimation de 20 orignaux tués et enregistrés selon certains renseignements fragmentaires.

[2] L'enregistrement s'est terminé le 11 novembre.

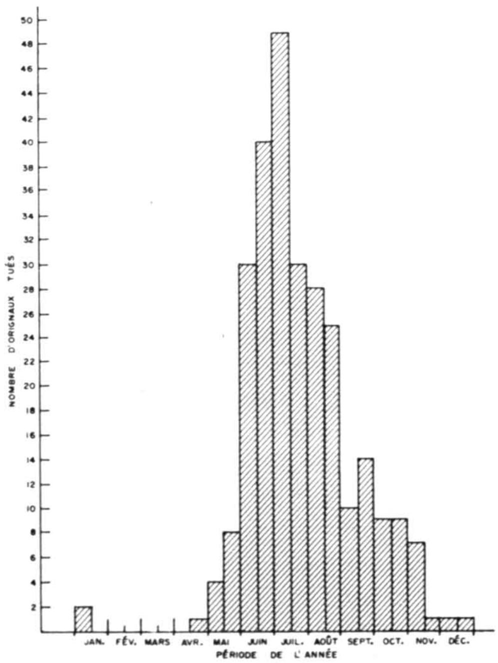

Figure 2. Période de l'année où les orignaux ont été tués accidentellement sur la route dans le Parc des Laurentides de 1963 à 1972. Les données de 1964 ne sont pas considérées. La date de mort n'a pas été notée dans six cas additionnels.

Le rapport des sexes des orignaux adultes tués sur la route a été examiné en fonction de la période de l'année, afin de déterminer si la tendance favorisant les femelles était constante pendant toute l'année. Le test du chi-carré appliqué aux valeurs cumulées des mois de mai et juin et de juillet à novembre montre une différence très significative (P> .99) du rapport des sexes pour ces deux périodes. Le tableau II montre que le rapport des sexes de mai et juin se rapproche de l'égalité (91 : 100), alors qu'il favorise considérablement les femelles (39 : 100) pour les autres mois considérés.

Les accidents routiers impliquant des orignaux se produisent presque à toute heure (fig. 3). Cependant 75.1% ont eu lieu entre 20 h et 03 h et 58.8% entre 20 h et 24 h.

Considérant la nuit comme débutant au coucher du soleil et finissant à son lever, on obtient que 83.6% des orignaux sont tués durant la nuit et 16.4% durant le jour (fig. 4).

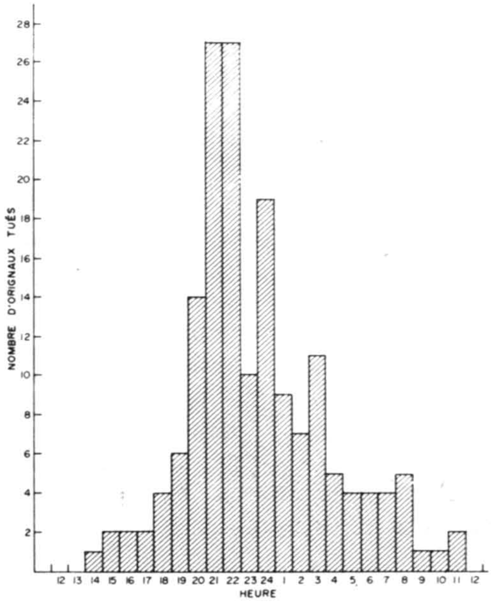

Figure 3. Fréquence horaire (heure légale de l'Est) des mortalités d'orignaux sur la route dans le Parc des Laurentides de 1967 à 1972. L'heure de la mort n'a pas été considérée dans 51 cas.

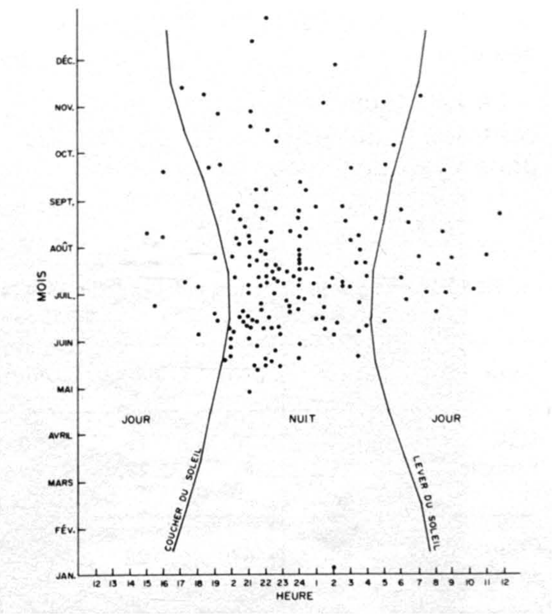

Figure 4. Distribution horaire (heure légale de l'Est) et mensuelle des orignaux tués sur la route dans le Parc des Laurentides. L'heure de la mort n'a pas été considérée dans 51 cas.

MARES SAUMÂTRES

Un total de 132 mares ont été localisées sur deux sections de la route à l'étude, soit la section sud et la section nord-est totalisant 80.5 milles de longueur (129.8 km) ce qui fait 1.64 mare par mille (1.1 mare par km). Deux types de mares ont été identifiées selon leur localisation et leur forme: les fossés (fig. 5), situés à quelques pieds de l'accotement, étroits et de longueur très variable (quelques pieds à plusieurs centaines de pieds) et les étangs, situés habituellement plus loin de l'accotement (3 à 10 pieds, 90 à 300 cm) de forme plus ou moins circulaire et de dimension très variable (20 à 25,000 pieds carrés (2 m^2 à 2,300 m^2). Parmi les 132 mares, 102 étaient des fossés et 30 des étangs.

La fréquentation par l'orignal était éparse pour 55 mares (43%), occasionnelle pour 30 mares (24%), assidue pour 42 mares (33%) et inconnue dans le cas de 5 mares. Parmi les mares à fréquentation assidue et occasionnelle 52 (72%) sont des fossés et 20 (28%) des étangs.

La conductivité spécifique et la concentration de sodium et de calcium dans l'eau des mares de la section sud et de la route secondaire sont comparées dans le tableau III. La conductivité spécifique et la concentration en sodium et en calcium sont de beaucoup supérieures dans l'eau des mares de la section sud que dans les mares de la route secondaire.

Les valeurs moyennes de conductivité spécifique et de concentration de sodium et de calcium sont mises en relation avec les classes de fréquentation des mares par l'orignal dans le tableau IV. La fréquentation augmente de façon significative avec un accroissement de la conductivité spécifique et de la concentration en sodium et en calcium de l'eau des mares. Il n'y a cependant pas de différence significative ($P > .80$) dans la conductivité spécifique et la concentration en sodium et en calcium, entre les mares à fréquentation occasionnelle et les mares à fréquentation assidue.

Parmi les 158 orignaux enregistrés sur les trois sections de route à l'étude de 1969 à 1972, 79 ont été tués sur la section sud, 40 sur la section nord-est, 34 sur la section nord-ouest et 5 cas n'ont pas été localisés. Pendant cette période la localisation des lieux d'accident était suffisamment précise pour

TABLEAU II

Rapport des sexes mensuel des orignaux adultes tués sur la route dans le Parc des Laurentides de 1963 à 1972[1, 2]

Sexe	*Mai*	*Juin*	*Juillet*	*Août*	*Septembre*	*Octobre*	*Novembre*	*Total*
Mâle	10	28	15	9	4	5	0	71
Femelle	11	31	39	24	8	9	4	126
Pourcentage de mâles	48	47	28	27	33	36	—	36

[1] Les données de 1964 n'ont pas été considérées. Dix cas additionnels pour lesquels la date ou le sexe n'étaient pas connus ont été négligés.

[2] Les mois de décembre, janvier, février, mars et avril n'ont pas été considérés vu le nombre trop restreint de données.

qu'on puisse établir une relation avec l'emplacement des mares. Nous avons considéré qu'une mare située à 0.25 mille (0,40 km) de l'emplacement de l'accident était associée à celui-ci. Sur les sections sud et nord-est, où les mares étaient inventoriées, un total de 110 orignaux ont été tués de 1969

Figure 5. Fossé le long du boulevard Talbot dans le Parc des Laurentides.

TABLEAU III

Valeurs moyennes de conductivité spécifique et de concentration en sodium et en calcium de l'eau des mares de la section sud et de la route secondaire

Paramètres analysés	*Mares de la section sud (N = 61)*	*Mares de la route secondaire (N = 20)*
Conductivité spécifique (mhos/cm)	461.44	23.19
Concentration en sodium (ppm)	64.63	0.67
Concentration en calcium (ppm)	4.10	1.31

TABLEAU IV

Valeurs moyennes de conductivité spécifique et de concentration en sodium et en calcium de l'eau des mares échantillonnées de la section sud en relation avec la fréquentation de ces mares par l'orignal

Classe de fréquentation par l'orignal	*Concentration moyenne de sodium (ppm)*	*Concentration moyenne de calcium (ppm)*	*Conductivité spécifique (mhos/cm)*	*Nombre d'échantillons*[1]
Eparse	26.6	2.16	221.5	27
Occasionnelle	86.0	5.46	603.0	14
Assidue	106.3	6.04	794.5	19

* Différence significative (P > .95).

[1] Un échantillon n'a pas été considéré parce qu'on ignorait sa classe de fréquentation par l'orignal.

à 1972 dont 87 (73.1%) à une distance de moins de .25 milles (0,40 km) d'une ou de plusieurs mares. Les mares auxquelles les accidents sont associés présentent des taux de fréquentation divers. Cet aspect est examiné dans le tableau V.

Considérant le total de 119 orignaux tués sur ces deux sections de route pendant cette période de 4 ans, 32 (27%) ont été tués dans un secteur de route où il n'y a pas de mare, 23 (19%) à proximité de mare(s) à fréquentation éparse, 61 (51%) à proximité de mare(s) à fréquentation occasionnelle ou assidue et 3 (3%) à proximité de mare(s) non classée(s) en ce qui a trait à la fréquentation par l'orignal.

TABLEAU V

Nombre d'orignaux tués sur la route, à proximité de mares diversement fréquentées sur les sections sud et nord-est du boulevard Talbot, de 1969 à 1972

Classe de fréquentation par l'orignal	*Nombre d'orignaux tués*
Eparse	23
Eparse et occasionnelle[1]	1
Eparse et assidue[1]	16
Occasionnelle	13
Occasionnelle et assidue[1]	11
Assidue	20
Non classée	3

[1] Parfois le lieu de l'accident était situé à proximité de deux mares différemment fréquentées par l'orignal.

Le tableau V ne tient pas compte de l'importance relative des mares. Cet aspect peut être abordé de deux façons, soit en considérant le nombre total de mares dans chaque classe de fréquentation, ou en attribuant à chaque mare une certaine longueur de route. Pour cette analyse, on ne peut considérer que les cas où les orignaux sont tués à proximité d'une seule mare dont on connaît la fréquentation ou de plusieurs mares de même fréquentation. Lorsque des accidents surviennent à moins d'un quart de mille (0,40 km) de deux ou plusieurs mares à fréquentation différente, il n'est pas possible de les relier à la fréquentation des mares.

Le tableau VI montre, qu'en considérant le nombre de mares en cause dans chaque classe de fréquentation, il y a près de deux fois plus d'orignaux tués aux mares à fréquentation assidue et 1.5 fois plus aux mares à fréquentation occasionnelle par rapport aux mares à fréquentation éparse. Il n'y a cependant pas de différence du nombre d'orignaux tués pour les différentes classes de fréquentation, lorsque l'on considère seulement les mares impliquées dans les accidents.

La seconde méthode, considérant la longueur de route attribuée aux mares, fournit également une autre évaluation de l'importance de chacune. Elle tient compte de la proximité des mares et permet également d'obtenir une estimation pour les orignaux tués sur des secteurs exempts de mare.

TABLEAU VI

Nombre d'orignaux tués sur la route à proximité des mares considérant leur fréquentation, Parc des Laurentides de 1969 à 1972

	Classe de fréquentation			
	Eparse	*Occasionnelle*	*Assidue*	*Non classée*
Nombre d'orignaux tués à proximité d'une seule mare ou de plusieurs mares de même fréquentation (A)	23	13	20	3
Nombre total de mares suffisamment isolées* (B)	13	5	6	2
Nombre de mares impliquées dans les accidents en (A) (C)	9	6	7	1
Indice A/B**	1.76	2.60	3.33	1.50
Indice A/C**	2.55	2.17	2.86	3.00

* Nous avons tenu compte seulement des mares distantes de plus de un quart de mille (.40 km) l'une de l'autre, car les orignaux tués près de mares trop voisines et à fréquentations différentes n'avaient pas de chance d'être considérés en (A).

**Le text de X^2 montre qu'il y a une différence significative ($P > .975$) pour les valeurs A/B entre les mares à fréquentation éparse et assidue, également entre les mares à fréquentation éparse et occasionnelle.

TABLEAU VII

Nombre d'orignaux tués par mille de route, compte tenu de la présence ou de l'absence de mares et de la fréquentation de celles-ci par l'orignal, Parc des Laurentides de 1969 à 1972

	Caractérisation de la route en fonction de la présence ou de l'absence de mares et de la fréquentation de celles-ci par l'orignal				
	Sans mare	*Avec mares à fréquentation éparse*	*Avec mares à fréquentation occasionnelle*	*Avec mares à fréquentation assidue*	*Avec mares à fréquentation inconnue*
Nombre d'orignaux tués à proximité d'une seule mare ou de plusieurs mares de même fréquentation (A)	32	23	13	20	3
Longueur de la route en mille pour les sections sud et nord-est (B)	44.7	14.7*	10.3*	10.1*	1.6
Indice A/B	.71	1.56	1.26	1.98	1.87

* Lorsque plusieurs mares étaient situées à proximité l'une de l'autre (moins de .25 mille, .40 km), une longueur égale à la moitié de l'intervalle considéré était attribuée à chacune.

TABLEAU VIII

Nombre d'orignaux tués sur la route à proximité d'une seule mare et concentration en sodium, calcium et conductivité spécifique d'un échantillon d'eau de ces mares, Parc des Laurentides de 1969 à 1972

	Concentration de sodium (ppm)			*Concentration de calcium (ppm)*			*Conductivité spécifique (mhos/cm)*		
	(0-10.0)	*(10.1-60)*	*(+60.1)*	*(0-2.0)*	*(2.1-5.0)*	*(+5.1)*	*(0-50.0)*	*(50.1-500.0)*	*(+500.1)*
Nombre d'orignaux tués à proximité d'une seule mare ayant fait l'objet d'analyse chimique (A)	7	3	7	7	5	5	7	4	6
Nombre de mares situées à proximité des lieux des accidents en (A)	4	2	5	4	4	3	4	3	4

Le tableau VII montre qu'il y a 2.3 fois plus d'orignaux tués par mille de route là où il y a des mares que là où il n'y en a pas. Le test du chi-carré appliqué à ces valeurs montre une différence très significative (P> .99). Ce même test ne montre pas de différence significative (P> .75) du nombre d'orignaux tués aux mares diversement fréquentées toutes proportions gardées tant qu'au nombre de mares dans chaque classe de fréquentation.

Le test du chi-carré appliqué aux valeurs se rapportant au nombre d'orignaux tués et au nombre de mares impliquées dans les accidents pour les trois classes de chacune des analyses chimiques (tableau VIII) ne montre aucune différence significative (P> .50). Il n'y a donc pas de relation entre le nombre d'orignaux tués et la concentration en sodium, en calcium et la conductivité spécifique de l'eau des mares.

Dans le tableu IX nous étudions le rapport des sexes des animaux tués sur les secteurs de route avec et sans mares dans le but d'attribuer la différence de distribution des sexes observée dans la population totale tuée sur la route à la présence ou l'absence de mares.

Le test du chi-carré appliqué au tableau IX montre qu'il n'y a pas de différence significative (P> .50) entre le rapport des sexes des orignaux tués sur des secteurs avec ou sans mares et ceci pour les deux classes d'âge considérées.

Il y a cependant une différence significative (P> .90) de l'âge moyen des orignaux adultes entre ceux tués à proximité d'une ou de plusieurs mares et ceux tués sur les secteurs sans mare : 2.54 ans pour les orignaux tués à proximité de mares et 1.81 an pour ceux tués sur les secteurs sans mare.

CIRCULATION ROUTIÈRE

Il existe une corrélation rectiligne significative (r = .54 ; P > .95) entre le nombre de véhicules traversant le Parc des Laurentides annuellement et le nombre d'orignaux tués sur la route de 1965 à 1972 (fig. 6). Une corrélation

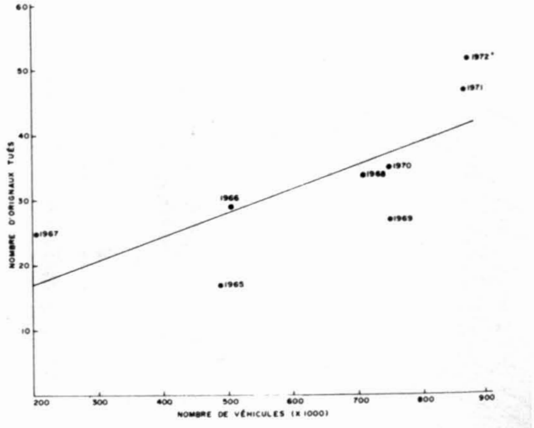

Figure 6. Nombre d'orignaux tués et circulation routière annuelle, de 1965 à 1972. Pour 1972, le nombre total d'orignaux tués pendant l'année a été estimé à 52.

TABLEAU IX

Rapport des sexes des orignaux tués sur la route dans le Parc des Laurentides de 1969 à 1972, sur des secteurs sans mare et à proximité d'une ou de plusieurs mares

Secteurs	*Mâles*		*Femelles*		*Pourcentage de mâles*	
	Veaux	*Adultes*	*Veaux*	*Adultes*	*Veaux*	*Adultes*
Sans mare	6	8	4	14	60	36
Avec mares	13	22	11	39	54	36

rectiligne très significative ($r = .77$; $P > .99$) existe également entre la circulation mensuelle des véhicules et la mortalité correspondante des orignaux sur la route (fig. 7).

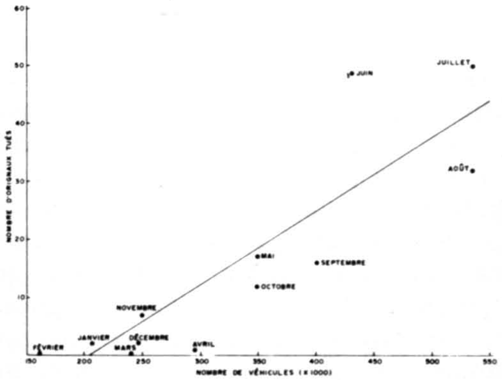

Figure 7. Nombre d'orignaux tués et circulation routière mensuelle de 1968 à 1972.

Discussion

EFFET SUR LA POPULATION

Les accidents routiers impliquant des orignaux dans le Parc des Laurentides sont un facteur de mortalité important de la population vivant près de cette voie de circulation. Nous avons déjà évalué à .88 orignal par mille carré (0,31/km^2) la densité de la population pour l'ensemble du parc (Grenier, 1970). Aucune différence de densité appréciable n'a été observée aux abords des routes; par conséquent, ce chiffre est considéré comme représentant la densité de la population à cet endroit. La présente étude démontre que .25 orignal est tué en moyenne par mille (0,16/km) de route et par année. Il est difficile d'évaluer avec précision la population d'orignaux aux abords des routes. Cependant plusieurs travaux suggèrent que l'orignal se déplace très peu en été (Murie, 1944; McMillan, 1954; DeVos et Pearson, 1955). Selon Knowlton (1960), le domaine vital des mâles est d'environ un mille (1,6 km) de rayon et celui des femelles de 1/2 (0,8 km). Houston (1968) mentionne que 95% des domaines vitaux d'été de 25 adultes avaient 1 1/2 mille carré (3,9 km^2) ou moins. Celui des jeunes individus d'un an variait de 2 1/4 milles carrés (5,8 km^2) pour 62.5% des cas observés, à 24 milles carrés (54 km^2). Considérant ces données on peut fixer grossièrement que le domaine vital des orignaux ayant des chances d'être tués par des véhicules s'étend à un mille (1,6 km) de chaque côté de la route. Ce chiffre permet d'établir un taux de mortalité par unité de surface soit 0.125 orignal tué par mille carré (0,05 km^2). Cette estimation, comparée à la densité de la population, révèle que 14.2% des orignaux vivant aux abords des routes sont tués par des véhicules. Ce pourcentage n'inclut pas les orignaux frappés et non enregistrés: un cas est rapporté en 1965, 13 en 1966, deux en 1968 et quatre en 1969. Cette information n'est pas disponible pour les autres années.

Une certaine proportion de ces animaux meurent certainement des suites de leurs blessures. Nous avons trouvé à deux endroits des carcasses d'orignaux probablement frappés sur la route quelques années auparavant.

Il semble donc que le pourcentage d'orignaux tués serait plus près de 15 à 20% si l'on considère les animaux non enregistrés. Un tel taux de mortalité implique que les accidents routiers sont sans aucun doute un facteur de mortalité très important. Pimlott (1959a) considère un taux d'exploitation de 20 à 25% comme élevé. Simkin (1965) fixe à 24% la productivité nette de l'orignal dans le nord de l'Ontario.

L'âge moyen très bas des orignaux tués sur la route semble également indiquer que la mortalité résultant des accidents routiers représente une forte exploitation des animaux vivant à proximité. La chasse contrôlée à l'orignal se faisant exclusivement sur les routes secondaires très peu d'animaux vivant aux abords du boulevard Talbot sont prélevés par ce mode d'exploitation. Simkin (1964) rapporte une forte différence de la structure d'âge de deux populations, l'une fortement chassée, l'autre légèrement exploitée. Ces données suggèrent un âge moyen plus bas pour la population fortement exploitée. Cependant, l'âge moyen des animaux tués sur la route peut représenter une plus grande vulnérabilité des jeunes orignaux aux accidents routiers.

CAUSES DE L'AUGMENTATION DE LA MORTALITÉ

L'augmentation du nombre d'orignaux tués sur la route peut être attribuable à plusieurs facteurs. Bien que nous ayions trouvé que le nombre de véhicules est un facteur important, cependant la corrélation n'explique que 54% de la variation. Une autre cause serait l'accroissement de la population d'orignaux du Parc dans l'ensemble. DesMeules (1965) rapporte une densité de .72 orignal par mille carré (0,27/km^2) et nous l'évaluons à .88 orignal par mille carré (0,34 km^2) (Grenier, 1970). Cette différence est significative ($P > .95$). Aucune donnée n'est disponible sur la modification de vitesse de la circulation routière pendant la période considérée, mais il y a lieu de croire qu'aucun changement important ne s'est produit. Il n'y a également pas eu de changements appréciables dans le mode d'entretien des routes.

L'augmentation du nombre d'orignaux tués s'accompagne d'un rajeunissement de cette population. Ce rajeunissement peut être attribué à une augmentation de la proportion d'animaux en bas âge dans la population aux abords des routes. Cette augmentation pourrait provenir soit d'un accroissement de la productivité soit d'un apport extérieur de jeunes orignaux, ou des deux. Selon Simkin (1964) une population fortement exploitée augmente son taux de productivité. Houston (1968) et Peterson (1955) mentionnent que les jeunes orignaux (jusqu'à 2 ans) sont plus mobiles et n'ont pas de domaine vital défini. Goddard (1970) montre que les mouvements des jeunes orignaux (2.4 ans et moins) peuvent être plus considérables que ceux des vieux animaux. Le même auteur mentionne cependant que les grands secteurs intensément chassés ne sont pas repeuplés par des orignaux venant de régions éloignées. Selon Pimlott (1959b), il demeure toutefois possible que si la mortalité dépasse la productivité nette près des routes d'accès une dispersion et une repopulation par l'orignal des habitats adjacents en résultent. Nous ne possédons pas de données pour l'affirmer mais il est possible que l'augmentation du nombre d'orignaux tués soit attribuable en partie à une augmentation de jeunes orignaux aux abords des routes.

PROPORTION DES SEXES

Plus de femelles que de mâles adultes (58:100) sont tués sur la route. Le rapport des sexes de la population adulte sur pied pour l'ensemble du parc a été évalué à 61:100 (Brassard et Beaumont, 1973). La différence de rapport des sexes n'étant pas significative ($P > .50$), on ne peut conclure à une vulnérabilité plus grande des femelles aux accidents routiers.

Les différences mensuelles de distribution des sexes montrent que les femelles adultes sont plus vulnérables de juillet à novembre. Bellis et Graves (1971) trouvent des résultats similaires, à l'exception du mois de novembre, pour les cerfs de Virginie (*Odocoileus virginianus*) tués sur la route en

Pennsylvanie. Jahn (1959) détermine une vulnérabilité plus grande des cerfs de Virginie mâles adultes tués sur les routes au Wisconsin. Il observe cependant que la vulnérabilité des adultes aux accidents routiers varie selon le mois.

Le rapport des sexes des veaux tués sur la route (95:100) est semblable à celui observé dans la population chassée (100:100), calculé à partir des données de Bouchard et Moisan (1974). Nous croyons que le rapport des sexes des veaux tués à la chasse est représentatif de la distribution des sexes de cette classe d'âge dans la population car les chasseurs ne font pas de choix d'un sexe pour les orignaux de cet âge et il n'y a pas de raison de croire que l'un ou l'autre des sexes soit plus vulnérable. Il n'existe donc pas de vulnérabilité plus grande aux accidents routiers pour les mâles ou les femelles de cette classe d'âge. Bellis et Graves (1971) obtiennent des résultats similaires sur une population de cerfs de Virginie tués sur la route en Pennsylvanie. Les données de Jahn (1959) cumulant dix années suggèrent cependant une vulnérabilité plus grande des cerf de Virginie mâles de cette classe d'âge.

ÂGE MOYEN

La différence de l'âge moyen des orignaux tués sur la route et à la chasse peut représenter la différence d'âge des deux populations ou une plus grande vulnérabilité des jeunes orignaux vivant aux abords des routes. Toutefois un biais considérable peut être apporté dans l'âge des animaux tués à la chasse par le choix qu'exercent les chasseurs. Il n'est donc pas possible avec ces données d'attribuer une vulnérabilité plus grande des jeunes aux accidents routiers.

VARIATIONS MENSUELLES ET HORAIRE DU NOMBRE D'ORIGNAUX TUÉS

Les données montrant la variation saisonnière du nombre total d'orignaux tués lors d'accidents routiers suggèrent que l'orignal ne fréquente pas beaucoup la route pendant l'hiver. C'est la période où ses déplacements sont limités par la neige (DesMeules, 1965).

Le nombre d'orignaux tués par rapport à l'intensité de la circulation démontre que les chances d'accidents sont particulièrement élevées en juin et juillet et réduites en août, septembre et octobre, considérant seulement la période où le comportement de l'orignal n'est pas affecté par la neige.

Les variations horaires du nombre total d'orignaux tués lors d'accidents routiers suggèrent une activité différente de l'orignal pendant la journée. Plusieurs auteurs (Denniston, 1956; DeVos, 1958; McMillan, 1954; Bouchard, 1967) mentionnent que l'activité de l'orignal serait particulièrement élevée à l'aube et au crépuscule. Geist (1963) rapporte quatre périodes d'activité principales, une à l'aube, deux pendant la journée et une au crépuscule. Nos résultats suggèrent une activité intense pendant toute la nuit avec une période d'activité maximale entre 20 h et 24 h. Ces résultats sont cependant biaisés par la variation de la circulation des véhicules et par le comportement différent de l'orignal en réaction aux véhicules et à leurs lumières pendant le jour et la nuit. Pendant le jour il est difficile, considérant les facteurs de biais, de déduire une différence horaire d'activité. Pendant la nuit il semble logique de croire que les réactions de l'orignal vis-à-vis les véhicules sont homogènes pendant toute la période. Nous ne possédons malheureusement pas les données sur la variation horaire de la circulation routière mais nous avons de bonnes raisons de croire que celle-ci diminue à partir du milieu de la nuit. Nos données suggèrent donc une activité élevée de l'orignal pendant toute la nuit. Rausch (cité par Geist, 1963) lors d'une étude en Alaska trouve que 80% des accidents entre un orignal et un train se produisent pendant la nuit. Altmann (1956) rapporte certaines activités de l'orignal pendant la nuit. Hosley (1949) mentionne que la plupart des déplacements estivaux de l'orignal se font la nuit. Le peu d'observation d'orignaux le long de la route pendant le jour et la circulation plus intense nous portent à croire que l'orignal est beaucoup plus actif la nuit que le jour aux abords des routes.

Les variations horaires du rapport des sexes montrent que l'activité des mâles et des femelles est proportionnelle pendant les diverses heures de la journée.

LE SEL ET LES ORIGNAUX TUÉS SUR LA ROUTE

Une des hypothèses à l'origine de ce travail était que les épandages de sels sur les routes amenaient une concentration élevée de sodium et de calcium dans l'eau de mares situées le long de la route. L'orignal attiré par ces sels fréquenterait davantage les endroits où les concentrations sont les plus élevées. Cette fréquentation plus intense se traduirait par une mortalité plus considérable à proximité de ces mares.

La différence considérable de concentration de calcium et de sodium entre les échantillons provenant des routes secondaires et ceux provenant de la section sud montre que l'épandage hivernal du chlorure de calcium et de sodium augmente fortement la concentration de ces sels dans les mares le long de la route. La conductivité spécifique étant représentative de la quantité d'ions dans la solution suit évidemment la même tendance que le sodium et le calcium. Une concentration équivalente de sodium (72 ppm) a été obtenue par Hutchinson (1967) pour des mares situées à une quinzaine de pieds des grandes routes dans l'État du Maine.

La fréquentation plus élevée notée aux mares à forte concentration de sodium et de calcium et à conductivité spécifique élevée montre bien le pouvoir d'attraction qu'exercent les sels minéraux sur l'orignal. La concentration très élevée du sodium suggère que cet élément est un des principaux facteurs d'attraction. Ce phénomène a déjà été mis en évidence par plusieurs auteurs. Rush (1932) trouva une forte concentration de sodium dans des sources («licks») fréquentées par du gros gibier au Parc national de Yellowstone. Honess et Frost (1942) obtinrent des résultats semblables dans 12 sources. Knight et Mudge (1967) ont déterminé que certains composés de sodium étaient les seuls à être plus abondants dans les sources que dans le milieu. Des études au Montana et en Idaho (Stockstad *et al.*, 1953) ont montré que les composés de sodium sont les minéraux recherchés dans les sources par les ruminants. Le même auteur fit une «étude cafétéria» (*cafeteria study*) où des ruminants avaient le choix de 23 composés. Les composés de sodium furent les plus consommés. Dans une étude similaire, Dalke *et al.* (1965) et Smith (1954) trouvent respectivement que le mouflon d'Amérique (*Ovis canadensis*) et le cerf de Virginie préfèrent les composés de sodium. L'utilisation du sel ordinaire par le gros gibier a été rapportée par plusieurs auteurs. Des études ont été faites par Rognrud (1955) et Dalke *et al.* (1965) sur l'utilisation du sel en aménagement. Les raisons pour lesquelles les ruminants préfèrent les composés de sodium sont trop peu comprises pour permettre plus que des conjectures à ce sujet (Knight et Mudge, 1967).

Les résultats du tableau VII montrent que les risques d'accidents sont 2.3 fois plus élevées là où il y a des mares que là ou il n'y en a pas. Les mares seraient donc des lieux particulièrement propices aux collisions impliquant des orignaux. L'augmentation des risques de collision ne semble cependant pas reliée à la fréquentation des mares par l'orignal. Ce phénomène est difficilement explicable. Il est possible que les observations relatives à la fréquentation, effectuées en juillet et août 1969, ne soient pas valables pour toute la période étudiée (1969 à 1972). Il existe certainement des cas où la fréquentation des mares s'est modifiée pendant cette période de quatre ans ; cependant, nos observations tendent à montrer une fréquentation assez constante d'année en année. Il est également peu probable que la concentration en sodium ait varié beaucoup pendant ce laps de temps, puisque les épandages de sels furent à peu près les mêmes durant toute la période. L'âge moyen plus élevé obtenu pour les orignaux tués aux mares par rapport à ceux tués sur les secteurs où il n'y a pas de mares suggère la possibilité que des animaux plus âgés donc plus expérimentés et moins vulnérables aux accidents routiers, fréquentent les mares plus que les orignaux jeunes, moins expérimentés et plus vulnérables, traversant la route au hasard. Cette hypothèse peut expliquer l'absence de relation entre la fréquentation et la mortalité des orignaux à proximité des mares. Il demeure cependant qu'une mare même très peu fréquentée est un lieu aussi propice aux accidents routiers qu'une mare assidûment fréquentée.

L'absence de différence dans le rapport des sexes des orignaux tués sur les secteurs avec et sans mares montre que ce facteur ne change pas la vulnérabilité des sexes.

Les résultats du tableau VIII suggèrent que la mortalité des orignaux sur la route n'est pas en relation avec la composition chimique de l'eau des mares. Le petit nombre d'animaux tués à proximité d'une seule mare ayant fait l'objet d'analyse chimique nous empêche toutefois de tirer des conclusions définitives à ce sujet. Cependant la composition chimique de l'eau des mares étant fortement reliée à la fréquentation, les données des tableaux VI et VII nous portent à croire qu'une augmentation de sels minéraux dans l'eau des mares le long de la route n'amène pas une augmentation parallèle du nombre d'animaux tués à proximité de ces points.

Remerciements

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AGE, GROWTH, CONDITION AND DENSITY OF RAINBOW SMELT *OSMERUS MORDAX* (MITCHILL) FROM TWO LAKES IN THE MATAMEK WATERSHED, QUÉBEC[1]

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Résumé

Une comparaison est faite entre deux populations d'éperlan, *Osmerus mordax* (Mitchill), provenant de deux lacs du bassin de drainage de la Matamek, Québec.

La capture par unité d'effort a été utilisée pour estimer la population du lac Muskrat. Pour ce lac, on estime la population à 1286 poissons de 3 ans et plus, ce qui représente une densité de 21.1 poisson à l'hectare. La population du lac Bill semble de beaucoup inférieure à celle du lac Muskrat.

La croissance individuelle moyenne de l'éperlan au lac Muskrat est plus lente au cours des âges inférieurs qu'au lac Bill. La longévité et la taille maximum sont cependant similaires pour les deux lacs.

Aucune tendance particulière ne se dessine dans le facteur condition (facteur embonpoint) pour le lac Muskrat. Cependant, pour le lac Bill, le facteur embonpoint décroît avec l'âge. Ceci peut être expliqué par haut degré de parasitisme dû au copepode *Ergasilus* sp. au niveau des branchies des individus plus âgés.

Abstract

Populations of rainbow smelt *Osmerus mordax* (Mitchill), were compared in two lakes in the Matamek watershed, Québec. Catch per unit effort was used to estimate the smelt population inhabiting Muskrat Lake. An estimate of 1286 fish only included those 3+ and older. This represented a density of 21.1 fish per hectare. The density of smelt in Bill Lake appeared to be much less than in Muskrat Lake. Growth of smelt in Muskrat Lake was slower among the lower age groups than for the same species in Bill Lake. Their longevity and maximum size was similar for both lakes. No trend was shown in the condition factors of Muskrat Lake smelt, but Bill Lake smelt decreased in condition in the older age groups. This was probably caused by the heavy parasitization with the copepod *Ergasilus* sp. on the gills of the larger smelt.

Introduction

This paper describes a study carried out on rainbow smelt in two lakes in the Matamek watershed (Fig. 1). The rainbow smelt occurs in rivers and lakes in New York State, the Maritime Provinces, Québec and Eastern Ontario. Smelt were initially introduced in Crystal Lake, Michigan, in 1912, and have sub-

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sequently spread to all of the Great Lakes. Although smelt have been increasing in importance as a commercial and sport fish, few population estimates have been made. An assessment of the smelt stock in the Miramichi River has been made by the fishing returns of the tagged and fin-clipped smelt (McKenzie, 1964). The bathymetric distribution of smelt in Lake Erie was reviewed by Ferguson (1965), but no population estimate was attempted.

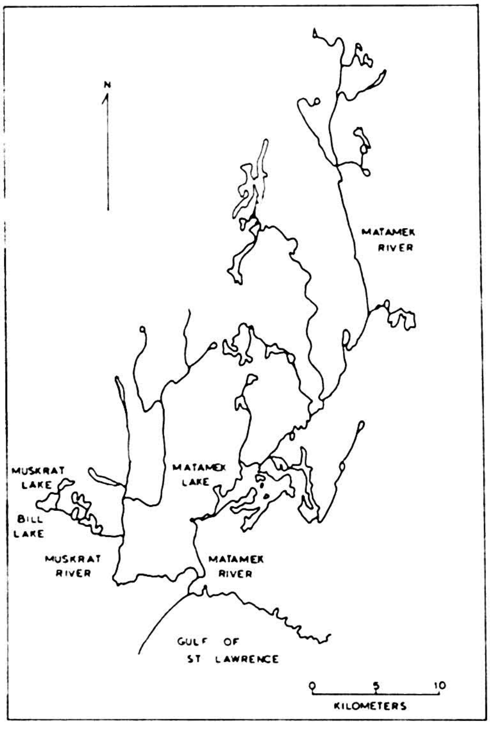

Figure 1. Matamek River, Québec.

Description of study area

The Matamek River empties into the Gulf of St. Lawrence approximately 30 km east of the city of Sept-Iles. Muskrat Lake and Bill Lake are about 13 km north-west of the mouth of Matamek River (50°19′N, 65°57′W) and have elevations of 106 m and 95 m above sea level, respectively. Both lakes lie in the Champlain Plain at the base of the Laurentian Plateau (Fig. 1).

Muskrat Lake has an area of 61 hectares and the shoreline measures 4.1 km. The maximum depth is 28 m. It contains three species of fish; rainbow smelt, *Osmerus mordax* (Mitchill); threespine stickleback, *Gasterosteus aculeatus* (Linnaeus); ninespine stickleback, *Pungitius pungitius* (Linneaus). This lake is fed by three streams, and it drains into Bill Lake via a beaver pond and an 11 m waterfall.

Bill Lake is 164 hectares and has a shoreline of 7.9 km including islands. The maximum depth is 29 m. Three sizeable streams flow into the lake, one being the outflow from Muskrat Lake. Bill Lake is drained by the Muskrat River. It contains five species of fish; brook trout, *Salvelinus fontinalis* (Mitchill); American eel, *Anguilla rostrata* (Le Sueur); threespine stickleback and ninespine stickleback. Waterfalls prevent anadromous species from reaching the lake from the Gulf of St. Lawrence.

Muskrat Lake and Bill Lake are comparable in having a narrow littoral area. The water in both lakes is dark brown in colour due to the allochthanous humic acids leached from the soil on the surrounding igneous rock. Pope (1973) gives the following chemical characteristics of the lakes.

Chemical characteristics	Bill Lake	Muskrat Lake
Conductivity (μmhos/cm, 25°C)	23.3	23.3
pH	6.5	6.5
Alkalinity (mg/l as $CaCO_3$)	5	5
Hypolimniol O_2 (mg/l)	11.5	11.5
Ca^{++} (mg/l)	0.91	1.88
Cu^{++} (mg/l)	0.008	0.008
Fe^{++} (mg/l)	0.069	0.041
Mg^{++} (mg/l)	0.415	0.039
K^{+} (mg/l)	0.280	0.148
Na^{+} (mg/l)	5.08	2.10

Materials and methods

Three trap nets with 100 feet leaders, 1 inch stretched mesh wings and trap were fished in Bill Lake for 66 days (June, July and August) in 33 different locations. At the end of this period 11-gill nets ranging in size from 0.75 to 2.0 inch stretched mesh were fished for 14 days. These gill nets were then fished in Muskrat Lake for 30 days (August, September). Scales were removed from the left side of the fish between the lateral line and the dorsal fin. These were mounted (Power, 1964) and aged by the method outlined by McKenzie (1958). All specimens were weighed to the nearest gram on an Ohaus spring scale.

The smelt population of Muskrat Lake was estimated by the Leslie method using a least-squares line (Omand, 1950). The method involves plotting catch per unit effort per day against cumulative catch removed prior to that day. The unit of effort consisted of eleven gill nets and the x-axis intercept of the line represents an estimate of the population originally present. The slope of the line fitted to the data represents catchability. Ricker (1958) outlines this method. Due to the selectivity of the gill nets and recruitment of 2+ fish to the catchable portion of the population, the estimate included only the 3 + to 8 + age groups. Confidence limits at the 95% level of probability were set for the population estimate using the method outlined by De Lury (1951).

Results

POPULATION ESTIMATE

The population estimate of 3 + and older smelt in Muskrat Lake was 1286 (Fig. 2). The 95 percent confidence limits for this estimate are 1170 and 1454. This estimate represented a population density of 21.1 fish per hectare (8.7 fish per acre).

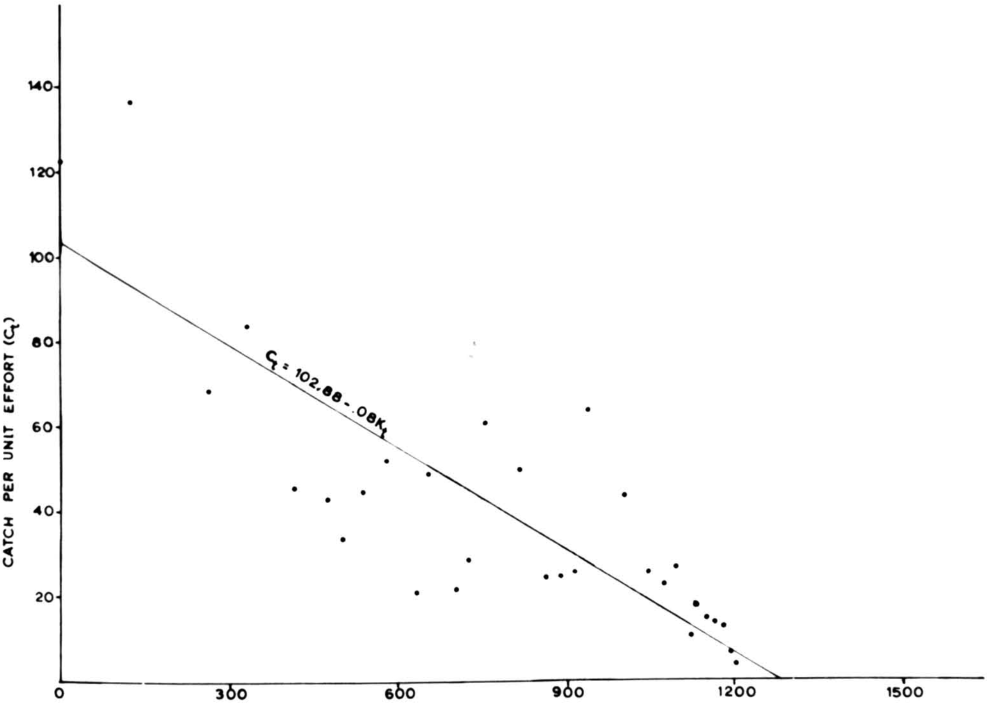

Figure 2. Leslie graph of catches of smelt in Muskrat Lake, 1970.

An attempt was made to do a mark and recapture population estimate of the smelt in Bill Lake. A number of smelt were marked and released in apparently good condition, but none were recaptured in the gill nets. Fourteen days of gill netting in Bill Lake yielded 240 smelt while 815 smelt were gill netted in Muskrat Lake in the same period of time. Both samples were taken at about the same time of year under comparable conditions, thus it appears that the density of smelt in Muskrat Lake is much greater than the density in Bill Lake. This may be due to interspecific competition in Bill Lake from the trout and eels.

GROWTH

A sample of 337 smelt from Muskrat Lake were aged for a growth study. The mean length at the time of capture and absolute growth in weight and length for each age group are shown in Table I. Figure 3 shows that the growth pattern of the Muskrat Lake smelt was almost linear.

Three hundred and seventy-two smelt from Bill Lake were aged and the mean length and absolute growth in length and weight are shown in Table II. Young smelt grew better in Bill than in Muskrat Lake but the growth decreased in the older age classes for Bill Lake smelt. Subsequently the size of the 8+ age class in Bill Lake was similar to the size of the 8 + fish in Muskrat Lake (Fig. 3).

CONDITION FACTOR

The condition factors for samples of smelt from Muskrat Lake and Bill Lake were calculated and the results are shown in Tables III and IV respectively. No trend was shown by the condition factors for Muskrat Lake smelt except for the very low condition factor (0.49) calculated for the 2 + age class. This was probably due to the severe intraspecific competition for food among this age class. Older smelt cannibalized the younger ones and the condition factors for the adults were higher. In Bill Lake, where the smelt population was not as dense, the 2 + age class had a

TABLE I

Age, length, weight and growth of smelt, Muskrat Lake, 1970

Age	No. fish	Length			Weight		
		Mean length (mm)	Absolute growth (mm/yr)	Relative growth (% increase)	Mean weight (g)	Absolute growth (g/yr)	Relative growth (% increase)
1+	1	81.0			2.0		
			22.7	28.0		3.8	190.0
2+	31	103.7			5.8		
			34.0	32.8		15.1	260.3
3+	46	137.7			20.9		
			29.8	21.6		17.0	81.3
4+	62	167.5			37.9		
			31.9	19.0		22.8	60.2
5+	113	199.4			60.7		
			22.4	11.2		23.6	38.9
6+	64	221.8			84.3		
			33.7	15.2		38.9	46.1
7+	17	255.5			123.2		
			25.2	9.9		37.5	30.4
8+	3	280.7			160.7		

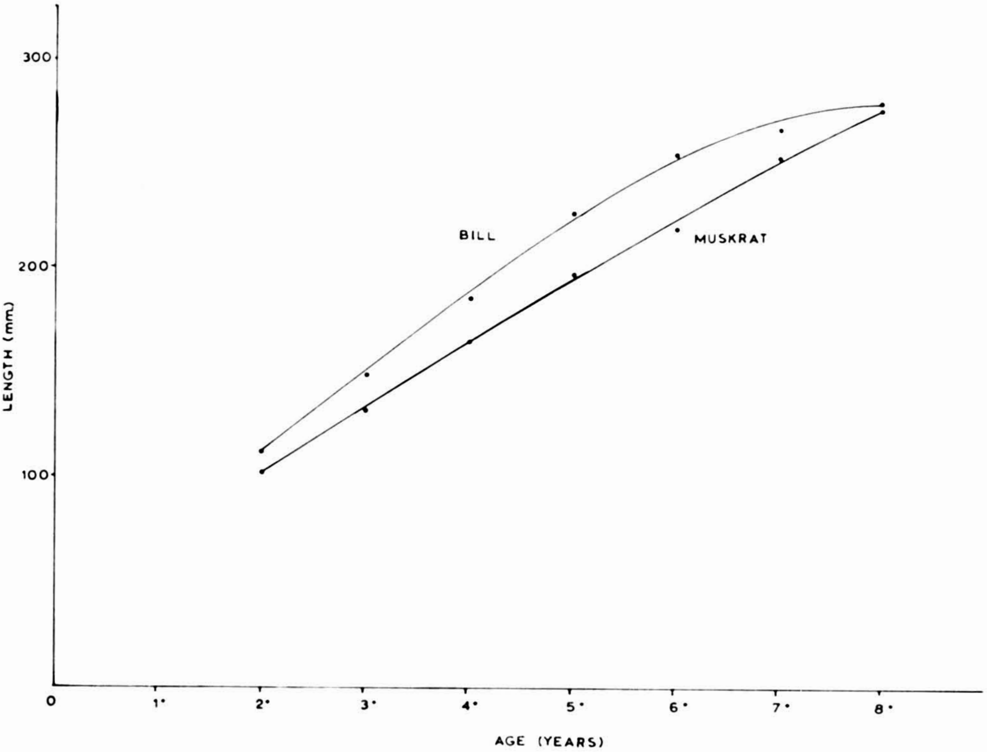

Figure 3. A growth comparison of the smelt populations from Bill Lake and Muskrat Lake, 1970.

TABLE II.

Age, length, weight and growth of smelt, Bill Lake, 1970

Age	No. fish	Length			Weight		
		Mean length (mm)	Absolute growth (mm/yr)	Relative growth (% increase)	Mean weight (g)	Absolute growth (g/yr)	Relative growth (% increase)
2+	10	113.4			12.8		
			36.0	31.7		13.5	105.5
3+	23	149.4			26.3		
			36.8	24.6		29.0	110.3
4+	37	186.2			55.3		
			42.3	22.7		41.8	75.6
5+	81	228.5			97.1		
			28.9	12.6		32.8	33.4
6+	148	257.4			129.5		
			12.2	4.7		7.6	5.9
7+	70	269.6			137.1		
			12.4	4.6		11.6	8.5
8+	3	282.0			148.7		

higher condition factor (0.80). The condition factor decreased in the older age classes of the Bill Lake smelt. This trend may be partly due to the heavy infestation by the parasitic copepod *Ergasilus* sp. on the gills of the larger smelt. This infestation was not particularly noticeable on the smelt in Muskrat Lake.

Discussion

A unique aspect of this study is that this is the first time to our knowledge that a population estimate of rainbow smelt has been completed in an inland lake. The Leslie method was used because marking was found impractical at summer temperatures. It was done in Muskrat Lake after finding that smelt would be the only species in the lake affected by this method. No effort was made to enumerate the younger age classes in the population using this method due to the selectivity of the gillnets.

The growth of smelt in Bill Lake and Muskrat Lake differed from other populations studied in the variation of the amount of annual growth shown per year class. The smelt in Matamek Lake grew much faster until age 3 + (Saunders and Power, 1970). Burbidge (1969), reported that the smelt in Gull Lake, Michigan, made their greatest annual growth during their second year. This was also true of the smelt in the Miramichi River, New Brunswick (McKenzie, 1958) and Lake Superior (Bailey, 1964). Apparently, this coincided with the attainment of sexual maturity, and the growth rate declined steadily thereafter. The growth rate of smelt in Bill Lake did not decline until age 4 +. This may be related to late maturation but due to the time of year that the sampling was carried out, fecundity and maturation was not studied in detail. The growth of smelt in Muskrat Lake stayed relatively constant for all age classes. Good

TABLE III

Condition factors of smelt taken by gillnets in Muskrat Lake during August, 1970

Age	2 +	3 +	4 +	5 +	6 +	7 +	8 +
No. of fish	22	46	50	53	50	17	3
Condition factor, K	.49	.78	.77	.80	.73	.73	.73
Range	.24-.80	.40-1.22	.58-1.11	.62-1.10	.33-.88	.55-.83	.71-.75
S.D.	.14	.18	.11	.09	.10	.08	.02
S.E.	.03	.03	.02	.01	.01	.02	.01

TABLE IV

Condition factors of smelt taken by trapnet and gillnet in Bill Lake, 1970

Age	2 +	3 +	4 +	5 +	6 +	7 +	8 +
No. of fish	11	22	36	42	37	38	3
Condition factor, K	.80	.77	.78	.78	.75	.69	.66
Range	.60-.97	.51-.92	.47-.94	.47-.97	.60-1.02	.52-.91	.61-.76
S.D.	.12	.08	.10	.10	.10	.09	.08
S.E.	.04	.02	.02	.01	.02	.01	.05

growth of the older fish can be explained by the high density of juvenile smelt in the lake and the predation upon them by the older smelt. Lack of interspecific competition in Muskrat Lake may also be a factor inducing good growth of older smelt.

Acknowledgements

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PRÉSENCE DE *SHEPHERDIA CANADENSIS* (L.) NUTT. DANS LA RÉGION DU PARC DES LAURENTIDES, QUÉBEC, AU TARDIGLACIAIRE.

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Résumé

Shepherdia canadensis est actuellement absent de la flore du Parc provincial des Laurentides, Québec. L'analyse pollinique a toutefois mis en évidence plusieurs sites fossiles pour cette région. L'aire actuelle de cette espèce au Québec montre des disjonctions liées à son caractère d'héliophyte et de basiphyte. Elle est mieux comprise lorsqu'on fait intervenir la distribution ancienne, révélée par l'analyse pollinique. Des hypothèses écologiques et biogéographiques sont proposées pour l'interprétation de l'aire actuelle.

Abstract

Shepherdia canadensis is presently absent in the Laurentide Provincial Park flora (Québec). However, pollen analysis has provided evidence for a lateglacial or early postglacial presence of the species in this area. The present distribution of *Shepherdia* in Québec shows disjunctions that are related to the autecology of the plant (heliophyte, basiphyte). The disjunctions can be better understood by examining the past distribution, through pollen analysis. Ecological and biogeographical hypothesis are put forward in an attempt to explain the present distribution of the species.

Introduction

Dans un récent article, Whitehead (1972) a montré l'apport de l'analyse pollinique à la solution des problèmes de disjonction d'aires chez les plantes. Il mentionne notamment des cas où la méthode a pu mettre en évidence un déplacement de certaines espèces (p. 128). Il émet par ailleurs des doutes quant au caractère de preuve irréfutable que peut constituer la présence de grains de pollen fossiles pour établir la distribution ancienne d'un taxon, ou suggérer les mécanismes par lesquels l'aire actuelle a pu être obtenue (p. 131). Au Québec, les travaux d'analyse pollinique n'ont en général pas été effectués à des fins de paléophytogéographie, mais plutôt en vue d'établir un cadre de référence stratigraphique pour la géologie du Quaternaire. La littérature disponible est donc grandement inadéquate et laisse entier le problème de l'apport de l'analyse pollinique à la solution de problèmes phytogéographiques, sauf pour les arbres les plus abondants.

Le présent article traite de *Shepherdia canadensis* au Québec et veut apporter des éclaircissements sur sa distribution actuelle, à la lumière de récentes données sur sa distribution tardiglaciaire et du début du post-glaciaire, telle que révélée par l'analyse pollinique.

Shepherdia canadensis (L.) Nutt.

AUTÉCOLOGIE ET DISTRIBUTION

La shépherdie est un arbuste buissonnant à floraison très printannière, dioïque, appartenant à la famille des Eléagnacées.

D'après Fernald (1950) et Marie-Victorin (1964) et tacitement chez les botanistes, l'espèce est réputée calcicole, ou au moins basiphile. Les stations québécoises connues de shépherdie sont en effet soit calcareuses, soit constituées de dépôts de plages marines riches en bases. Sur les plages au moins, la plante apparaît héliophile. Elle subsiste toutefois en sous-bois, sur substrat calcaire (station de Val Jalbert, au lac Saint-Jean) mais elle n'y fleurit pas et sa croissance est mauvaise. Ducruc (1972) a observé des individus bien développés, associés au *Ledum groenlandicum* Oeder dans un mélèzin très ouvert près de Fort-Chimo, en Ungava. Ce dernier site repose sur les roches basiques de la fosse du Labrador, et confirmerait le caractère basiphile de l'espèce. Il reste toutefois à établir cette basiphilie expérimentalement.

Shepherdia canadensis possède des nodules racinaires, provoqués par la présence d'Actinomycètes, capables de fixer l'azote atmosphérique (Stewart, 1967 *in* Ritchie and Lichti-Federovich, 1968). Ces auteurs suggèrent l'idée que ce caractère ait pu conférer à l'espèce un certain avantage dans la colonisation des milieux fraîchement libérés des glaces. M. Lalonde (comm. pers.) a même suggéré que ce caractère pouvait, dans une certaine mesure (à établir expérimentalement), induire une certaine indépendance de la plante vis-à-vis des éléments nutritifs et du pH.

Shepherdia canadensis couvre au Québec une aire de plus de treize degrés de latitude et se retrouve à basse altitude au sud. Ceci tendrait à lui conférer un caractère de relative indifférence vis-à-vis des conditions climatiques (principalement la température, et la durée de l'ensoleillement d'été), dans les limites de son aire.

La shépherdie montre une distribution générale transcanadienne qui déborde un peu au nord des États-Unis d'Amérique. Elle est un élément constant, quoique peu abondant, de la flore forestière à l'ouest du bouclier canadien (J. C. Ritchie, comm. pers.). Au Québec, la plante semble assez rare. La représentation la plus complète et la plus récente nous est fournie par le travail de C. Rousseau (1971, pages 404 et 405, et carte no 683). La figure 1 reproduit la carte de cet auteur. Son détail dépend de l'échelle ainsi que du degré d'avancement de l'inventaire floristique. Toutefois, étant donné l'autécologie probable de *Shepherdia*, la figure représente sans doute assez bien la réalité. L'espèce est très probablement exclue de la région du Parc des Laurentides qui nous intéresse particulièrement ici (confirmé par Robert Gauthier, comm. pers.). Le substrat acide qui caractérise cette dernière région, allié à une couverture végétale à caractère zonal, bien adaptée au milieu et à compétition agressive, provoque au sein de l'aire de *Shepherdia* une disjonction très nette entre les sites calcaires de la région de Québec et ceux du lac Saint-Jean, notamment (voir figures 1 et 2).

Shepherdia canadensis possède des grains de pollen dont la morphologie est distincte. Ils sont tricolporés et longiaxes. Le colpus est long et étroit, le pore, circulaire et très net. L'exine est épaisse et sa surface, nettement rugulée. Les grains ne peuvent être confondus avec ceux des autres Eléagnacées susceptibles d'être retrouvés en analyse pollinique, à savoir *Shepherdia argentea* Nutt. et *Eleagnus commutata* Bernh., ces derniers étant fortement bréviaxes.

Par ailleurs, l'espèce est entomogame; elle produit relativement peu de pollen et celui-ci tombe très près du lieu d'émission, ce qui permet d'assigner à sa découverte une valeur paléontologique comparable à celle offerte par la découverte de macrorestes. En d'autres termes, les grains de pollen n'ont pas pu être apportés de très loin par le vent.

Ritchie et Lichti-Federovich (1968) ont d'ailleurs montré que l'espèce était fortement sous-représentée polliniquement et que l'abondance de *Shepherdia* au Manitoba devait être beaucoup plus grande dans le passé.

SITES FOSSILES

La figure 1 montre la distribution géographique des sites où du pollen fossile de *Shepherdia canadensis* a été re-

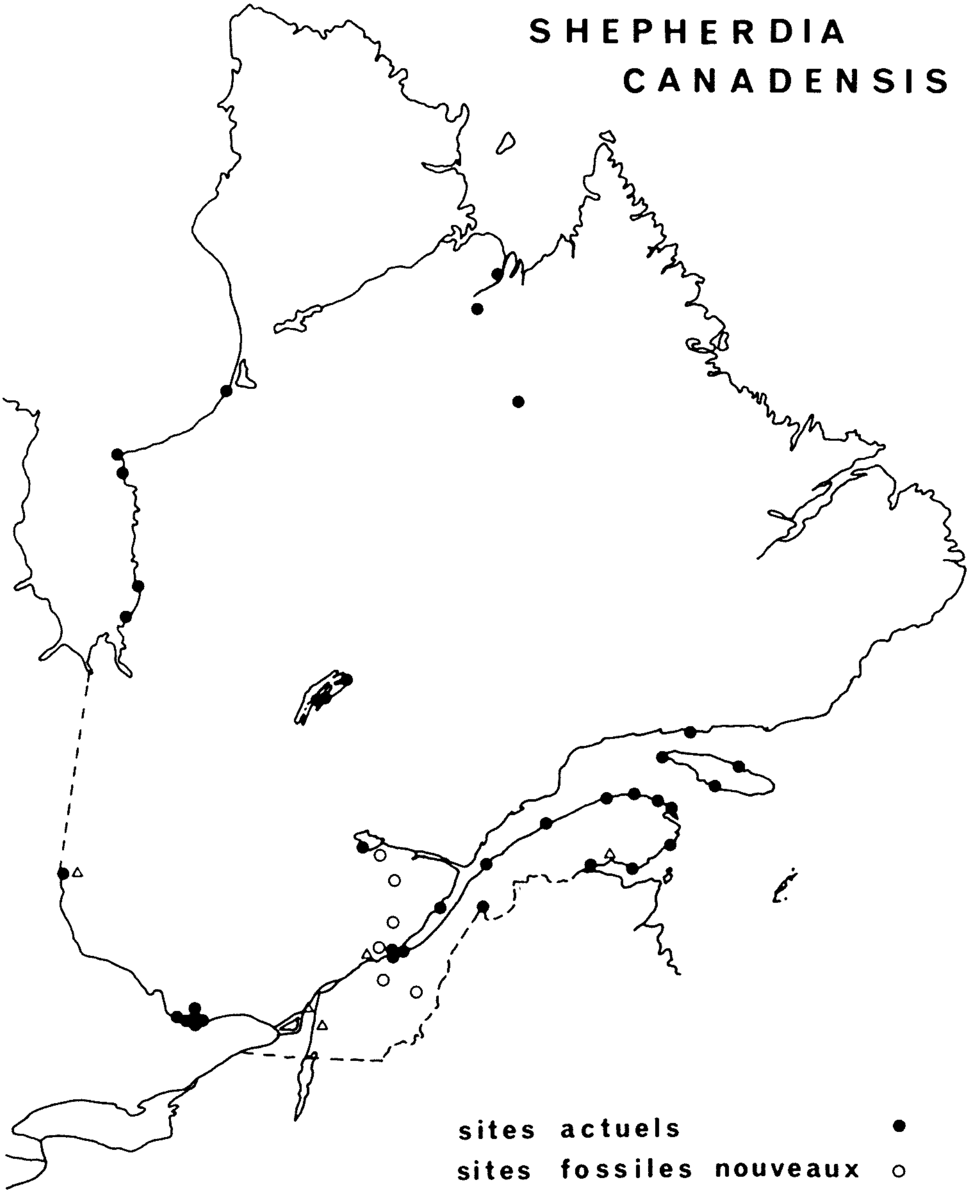

Figure 1. Distribution géographique actuelle de *Shepherdia canadensis* au Québec, d'après C. Rousseau, 1971 (points noirs), et fossile (cercles et triangles) d'après divers auteurs (voir le texte).

trouvé. Ceux représentés par des triangles résultent d'études polliniques d'auteurs divers (Terasmae, 1960; Lasalle, 1966; Vincent, 1973). Ils se caractérisent par le fait qu'ils sont situés près des stations actuelles, ou sur des sols comparables à ceux des stations actuelles. Les sites représentés par des cercles résultent de mes propres travaux, et couvrent principalement la région du Parc des Laurentides où abondent les podzols. Les roches sous-jacentes sont surtout des granites et des gneiss à l'origine des dépôts glaciaires les recouvrant.

Les grains de pollen fossiles de *Shepherdia canadensis* se trouvent associés à ceux des taxa suivants; *Saxifraga* type *oppositifolia* L., *Ambrosia, Artemisia, Dryas, Epilobium,* Caryophyllacées, Crucifères, Cyperacées, Graminées. Ce sont les herbacées les plus importantes. Elles sont accompagnées d'une proportion variable de pollen d'arbustes tels *Betula glandulosa* Michx., *Eleagnus commutata* Bernh., *Juniperus* et *Salix*. Le pourcentage des grains de pollen arboréens varie entre 50 et 70, chez les spectres associés à *Shepherdia*. Le pin (*Pinus*) et l'épinette (*Picea*) sont les arbres les mieux représentés.

L'interprétation des données polliniques permet de reconstituer le paysage végétal contemporain de *Shepherdia canadensis* (Richard, 1971, 1973a 1973b). Ce dernier a appartenu de façon constante et reproductible, d'un diagramme pollinique à l'autre, soit à la bétulaie à bouleau glanduleux, qui est une formation arbustive ouverte, soit à la pessière à épinette noire et bouleau glanduleux, également très ouverte. Ces formations succédèrent immédiatement à la toundra et représentent les premiers stades de l'afforestation. La présence du pollen de *Shepherdia* dans les diagrammes polliniques concernés couvre toujours une très courte période séparant des époques au-delà et en deçà desquelles l'espèce était virtuellement absente des diagrammes. La figure 2 donne l'âge des fossiles de *Shepherdia canadensis* à titre indicatif, d'après les articles déjà cités.

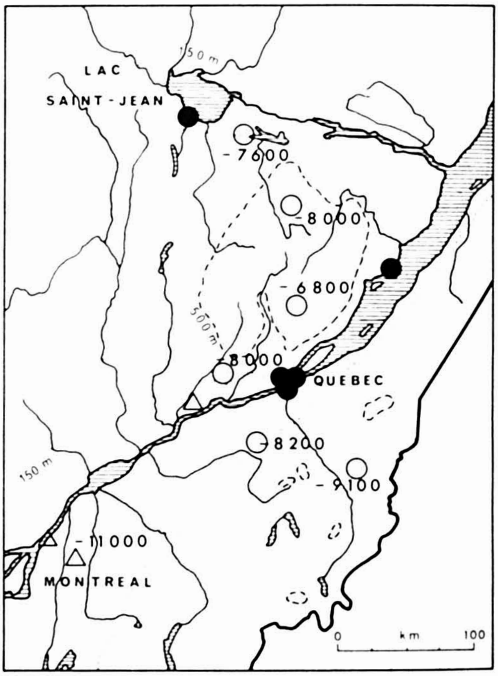

Figure 2. Détail de la distribution géographique actuelle et fossile de *Shepherdia canadensis* dans la région du Parc des Laurentides et des environs. La ligne pointillée délimite approximativement les basses-terres, et le tireté, les massifs montagneux. L'altitude est exprimée en mètres. L'âge des sites fossiles est présenté à titre indicatif.

Discussion

L'intérêt de la découverte du pollen fossile de *S. canadensis* dans le Parc des Laurentides réside dans le fait que l'espèce y est présentement absente et que le substrat y est actuellement acide. Quels ont pu être les facteurs permettant sa présence à la fin du tardiglaciaire ou au début du postglaciaire, et quels mécanismes ont pu jouer dans sa disparition? On peut faire appel à deux types d'hypothèses pour tenter de répondre à ces questions.

HYPOTHÈSES ÉCOLOGIQUES

D'une part, si l'espèce est réellement calcicole ou, du moins, basiphile, elle a pu s'installer dans le Parc des Laurentides (et sur l'ensemble du Bouclier précambrien) à une époque où, fraîchement libérés des glaces, les sols étaient plus riches en bases. En effet, les feldspaths, notamment, ont pu fournir initialement les bases nécessaires, contenues dans la «farine de roche» constitutive des dépôts morainiques. Lorsque l'éluviation et la podzolisation naissantes eurent appauvri le sol en surface par l'entraînement en profondeur des bases labiles, *Shepherdia canadensis*, ne trouvant plus les conditions nécessaires à sa survie, disparaissait progressivement du territoire, à l'exception des enclaves calcaires ou basiques (Val Jalbert, lac Mistassini, par exemple). Un phénomène identique expliquerait la richesse de la flore initiale, en marge des glaciers en régression au Groënland (professeur Iversen, comm. pers.).

D'autre part, soit indépendamment soit plus probablement en concomitance avec le phénomène précédent, *S. canadensis* (héliophyte) a eu, à l'arrivée de la flore forestière, à subir la compétition de plantes adaptées aux sols zonaux en formation, dont des arbres qui réduisaient progressivement la proportion des lieux ouverts. La plante s'est alors réfugiée sur des sols particuliers (calcaires), délaissés par la flore zonale (agressive sur substrat acide), ou sur des sols azonaux reconstituant sans cesse des conditions pionnières, c'est-à-dire les plages marines.

HYPOTHÈSE BIOGÉOGRAPHIQUE

Ce qui précède présuppose l'existence d'une zone de végétation ouverte à la marge du glacier en retrait, car *Shepherdia canadensis* est une héliophyte. Des analyses polliniques récentes (Lasalle, 1966) ont mis en évidence l'existence d'une telle zone et d'autres travaux (Richard, 1971, 1973b et 1973c) ont confirmé la présence d'une végétation de toundra au tardiglaciaire et l'ont étendue à plusieurs localités du Parc des Laurentides et du piedmont appalachien au sud de Québec. Dans l'état actuel des recherches, il est impossible d'évaluer la largeur de cette zone ni d'affirmer qu'elle formait ou non un «corridor arctique» *continu* (Rousseau, 1968) en bordure du glacier. Toutefois, chaque diagramme nouveau, situé dans des conditions physiographiques susceptibles de mettre en évidence cette zone de végétation ouverte, apporte immanquablement des preuves de son existence.

En ce qui concerne *Shepherdia*, les quelques éléments de datation disponibles semblent montrer qu'il n'y a pas eu *une époque* où cette plante possédait une aire continue, mais bien un *balayage métachronique* du territoire, lié à la retraite de l'inlandsis, par une formation végétale ouverte plus ou moins continue. C'est à la faveur de ce balayage que *Shepherdia* a pu s'installer un peu partout, et persister jusqu'à nos jours selon que les facteurs écologiques sus-mentionnés ont joué ou non.

Conclusion

La distribution géographique actuelle de *Shepherdia canadensis*, montrant des disjonctions d'aires liées à son caractère d'héliophyte et (possiblement!) de basiphyte, est éclairée d'une lumière nouvelle grâce à l'analyse pollinique qui a mis à jour une distribution tardiglaciaire (ou du tout début du postglaciaire) tout à fait inattendue.

Une zone de végétation ouverte, métachronique, a permis l'installation de l'espèce qui, très tôt, a dû subir les avatars de conditions édaphiques éphémères et d'une compétition inexorable aboutissant à la distribution actuelle.

Le cas de *Shepherdia canadensis* n'est pas unique. Les espèces arctiques-alpines, endémiques dans la région de l'estuaire du Saint-Laurent et de la Gaspésie, ont dû être isolées à peu près de la même manière, comme l'ont d'ailleurs souligné plusieurs auteurs (Wynne-Edwards, *in* Morisset, 1971; Rousseau, 1968). Seule l'accumulation des diagrammes polliniques pourra démontrer le bien fondé des hypothèses qui, comme dans le cas de *Shepherdia*, expliquent la distribution actuelle de certaines espèces à aire disjointe dans nos régions.

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LES SOUS-GENRES ET LES SECTIONS DU GENRE *PINUS*

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Résumé

L'auteur traite de la taxonomie des sous-genres et des sections du genre *Pinus*. Il fonde d'abord ses arguments sur la morphologie des cônes et le nombre de faisceaux fibro-vasculaires dans les aiguilles, aussi sur les caractères évolutifs des espèces. Il subdivise le genre *Pinus* en quatre sous-genres et onze sections délimités au moyen de clés et de descriptions.

Abstract

The author deals with the taxonomy of the subgenera and sections of the genus *Pinus*. His arguments are based primarily on the morphology of the cones, and on the number of fibro-vascular bundles inside the needles, but also on the evolutionary characters of the species. He suggests that the genus be divided into four subgenera and eleven sections, which are circumscribed by keys and descriptions.

Introduction

Le présent article, de concert partiellement avec les opinions avancées par de Ferré (1953), propose la division du genre *Pinus* en quatre sous-genres, et leur subdivision en onze sections, le tout fondé sur des critères morphologiques et évolutifs. Quoique traités séparement ci-dessous, les caractères morphologiques et évolutifs nous semblent les uns et les autres aussi importants pour une bonne compréhension des sous-genres et aussi, par la suite, des sections.

Caractères morphologiques des sous-genres

Bien que depuis Koehne (1893) on ait généralement divisé le genre *Pinus* en deux grands sous-genres fondés sur la présence d'un ou deux faisceaux libéro-ligneux dans les aiguilles (aiguilles haplostelées ou displostelées), nous considérons une telle division à la fois trop artificielle et trop simple. Nous sommes d'accord quant à la valeur certaine des faisceaux libéro-ligneux à titre de critère majeur, mais nous croyons qu'à l'intérieur de chacun des groupes délimités par Koehne résident des différences aussi importantes — et certainement plus naturelles — telles celles qui ont trait aux fruits et aux graines. Par exemple, le fait que l'umbo de l'écusson (ou apophyse) soit terminal chez une partie des Pins à feuilles displostelées et le fait que deux espèces mûrissent leurs fruits en trois saisons de croissance plutôt qu'en deux, motivent des différenciations majeures. Bref, on a depuis 1893 fondé les sous-genres de Pins surtout sur des caractères de l'appareil végétatif; on a oublié la simple règle — suivie antérieurement et avec raison par les principaux monographes du genre — que les caractères des organes de reproduction ont aussi leur importance.

À la suite de ces considérations et d'accord avec plusieurs taxonomistes du XIXème siècle (Endlicher, 1847 ; Carrière, 1855 ; Engelmann, 1880 ; Lemmon,

1895) nous restituons les Pins ayant des cônes à umbo terminal au rang de sous-genre. En outre, nous élevons au même rang le groupe de Pins qui mûrissent leurs cônes en trois saisons de croissance plutôt qu'en deux. Ces deux différenciations nous permettent de proposer la division du genre *Pinus* en quatre sous-genres décrits ci-dessous :

I. Sous-genre *Pinus*. Cônes mûrissant en deux saisons de croissance, munis d'umbos (ombilics) dorsaux simples ; aiguilles (pseudophylles) displostelées (à 2 faisceaux libéroligneux), la plupart décurrentes sur le rameau et à gaines généralement persistantes.

II. Sous-genre *Pinea*. Cônes mûrissant en trois saisons de croissance, munis d'umbos (ombilics) doubles, concentriques, dorsaux ; aiguilles comme chez le sous-genre *Pinus*.

III. Sous-genre *Ducampopinus*. Cônes mûrissant en deux saisons de croissance, munis d'umbos dorsaux, mucronés ou épineux ; aiguilles (pseudophylles) haplostelées (1 seul faisceau libéroligneux) non décurrentes sur le rameau, et à gaines généralement caduques dès la première saison de croissance.

IV Sous-genre *Strobus*. Cônes mûrs munis d'umbos terminaux, non épineux, non mucronés ; aiguilles et gaines comme chez le sous-genre *Ducampopinus*.

Caractères évolutifs des sous-genres

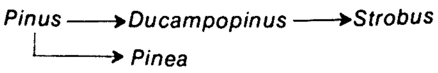
Partant du principe que « chaque organe ou système doit être considéré séparément pour que l'on puisse discuter son évolution » (Dittmer, 1964, p. 511) et que les organes ont généralement évolué de la forme indifférenciée à la forme spécialisée ; nous fondant aussi sur les opinions de Shaw (1914) et de Gaussen (1960), si nous considérons le cône femelle — qui d'ailleurs est universellement reconnu comme étant l'organe le plus caractéristique de l'ordre des Coniférales — nous pouvons désigner sans hésitation le sous-genre *Strobus* comme le plus récent. En effet les apophyses des cônes chez ce sous-genre proviennent de la croissance apicale spécialisée de chaque écaille, tandis que, chez les trois autres sous-genres, elles correspondent au principe de la croissance radiale du cône entier, caractère plus primitif. Gleason (1952) abonde dans le même sens lorsqu'il écrit : *"In certain species the upper portion of the apophysis is obsolete ; the transverse line then corresponds to the end of the cone-scale and the umbo is strictly terminal"*.

Considérant en deuxième lieu le rameau du Pin, nous constatons que les sous-genres *Strobus* et *Ducampopinus*, avec leurs rameaux à surface lisse et à section parfaitement circulaire, furent vraisemblablement formés après les deux autres sous-genres qui possèdent des pseudophylles à bases décurrentes.

Examinons ensuite l'anatomie des feuilles et, d'accord avec nos prédécesseurs, nous acceptons l'idée que les feuilles contenant deux faisceaux libéroligneux (dites diplostelées) sont plus primitives que celles qui en ont un seul. Les sous-genres *Ducampopinus* et *Strobus* seraient donc issus du sous-genres *Pinus*.

Si nous analysons le fait que les membres du sous-genre *Pinea* prennent trois saisons de croissance à mûrir leurs fruits, contrairement aux trois autres sous-genres, nous avons le choix d'affirmer que cette propriété est plus primitive que l'autre (cônes biennaux) ou, à l'inverse, plus récente. Mais vu que les fruits triennaux, avec leurs umbos doubles et concentriques, sont probablement issus de fruits biennaux, nous pouvons inférer que le sous-genre *Pinea* est plus récent que le sous-genre *Pinus*.

La synthèse de l'évolution de ces quatre organes ou systèmes permet d'arriver à un certain nombre de conclusions. Parmi celles qui nous semblent les plus plausibles, nous suggérons la suivante :



Un autre caractère qui permet de croire en la plus grande ancienneté du sous-genre *Pinus* réside dans la persistance des gaines à la base des pseudophylles. Ces gaines ne remplissent aucun rôle physiologique utile (sauf peut-être protéger des gelées printannières au moment où les toutes jeunes aiguilles sont encore tendres) et tous les membres du sous-genre *Strobus*, plus évolué, s'en débarrassent dès l'été suivant. Il en va de même avec le sous-genre *Ducampopinus* sauf pour une espèce (*P. nelsonii*), tandis que dans le sous-genre *Pinus*, contenant les deux tiers des espèces du genre, seulement *P. lumholtzii* se développe de la sorte. Cette gradation tend à confirmer généralement notre hypothèse.

Caractères évolutifs des sections

A nouveau d'accord avec les concepts de Shaw (1914) et de Gaussen (1960), nous pensons que dans chaque sous-genre les Pins à cônes persistants ou sérotineux sont plus récents que ceux à cônes caducs et déhiscents. Acceptant aussi le fait que les graines à aile articulée ont précédé les graines à aile adnée ou nulle, que les cônes petits existèrent avant les gros et que les aiguilles à section non aplatie ont vu le jour avant celles de *P. krempfii*, il nous devient facile de dresser les schémas de la filiation des sections, au sein de chaque sous-genre, bien entendu :

I. *Pinus* → *Pinaster* → *Laterales*
   └→ *Sula*
II. *Pinea* → *Leiophyllae*
III. *Balfouria* → *Parrya*
   └→ *Ducampopinus*
IV. *Strobus* → *Cembra*

Description et synonymie des sous-genres et des sections

Voici maintenant d'autres détails sur chacun des sous-genres et des sections. Nous traiterons seulement des sections, bien qu'il soit possible, mais plus ou moins souhaitable, de subdiviser les sections en sous-sections : avec les sections, le lecteur peut avoir une vue d'ensemble suffisamment claire des différents éléments dont se compose le genre, sans avoir à recourir aux critères mineurs qu'il faudrait nécessairement utiliser pour définir les sous-sections.

On trouvera dans le précieux ouvrage de Little et Critchfield (1969) une bibliographie assez complète et une étude intéressante sur les noms des divisions et subdivisions du genre *Pinus* créées par les auteurs botaniques durant la période de 1753 à 1959, c'est-à-dire pendant un peu plus de deux siècles. Cet ouvrage nous a été fort utile lors de la rédaction du présent article, et vu que rien ne sert de répéter la synonymie détaillée qu'il contient, nous nous bornerons à la compléter en énumérant seulement les synonymes publiés depuis 1960 par les auteurs suivants : Hudson (1960), Gaussen (1960), Jahrig (1962), Debazac (1964), Mirov (1967) et Little et Critchfield (1969) ; nous citerons aussi les synonymes antérieurs à 1960 qui sont nécessaires à la bonne intelligence du texte.

I. SOUS-GENRE *PINUS*

Synonymes récents :

Pinus sous-genre *Eupinus* Gaussen, H. — Les Gymnospermes actuelles et fossiles, fascicule VI, chapitre XI, p. 94-95 (1960). Publication invalide.

P. sous-genre *Diplyoxylon* Mirov, N.T. — The Genus *Pinus*, p. 521 (1967). Publication invalide. Dans les deux cas, la publication est invalide par défaut de description en latin.

Description originale *in* Endlicher, S. L. — *Synopsis Coniferarum*, p. 137-138 (1847). La description d'Endlicher était rédigée pour comprendre toutes les espèces de pins actuellement nommés comme tels. Autrement dit, son sous-genre

Pinus équivalait au genre *Pinus* actuel; la transcrire ici ne comporte donc aucun intérêt.

Description nouvelle: voir ci-dessus en français.

Descriptio: Strobili biennes; umbo dorsalis, simplex; pseudophylli fasciculis vascularibus 2, basi saepius decurrentibus et vagina plerumque persistentes.

Ce sous-genre, le plus important des quatre en ce qui concerne le nombre d'espèces, se subdivise naturellement en quatre sections qui peuvent être identifiées grâce à la clef dichotomique suivante:

A. Cônes décidus dans l'année ou dans la deuxième année qui suit leur maturité (parfois persistant plus longtemps chez certains individus exceptionnels); cônes souvent actinomorphes .... B
  B. Graines munies d'une aile articulée (attachée le long d'une fine ligne périphérique) ....section *Pinus*
  BB. Graines munies d'une aile adnée sur l'une des faces de la graine ....section *Sula*

AA. Cônes persistant plus de deux ans après leur maturité; cônes souvent obliques (zygomorphes), parfois actinomorphes C
  C. Graines munies d'une aile mince (moins de 1 mm); cônes de grosseur ordinaire ....section *Pinaster*
  CC Graines munies d'une aile épaisse (plus de 1.5 mm); cônes très gros (plus de 8cm de largeur, lorsque fermés) .. ..section *Laterales*

Avant d'aborder l'énumération des sections, la mise au point suivante s'avère nécessaire. Elle concerne Loudon (1838), qui adopta deux séries de sections, les unes supérieures aux autres. Par exemple, la section *Binae* (vol IV, p. 2152) comprend les sections *Sylvestres* (p. 2152), *Laricio* (p. 2200), *Pinaster* (p. 2213), *Halepenses* (p. 2231) et ainsi de suite. Conformément à l'opinion récente du Comité général de la nomenclature de l'Association internationale de taxonomie végétale (Voss, 1973), nous acceptons les sections primaires et rejetons les secondaires.

I.1. SECTION *Pinus*

Synonymes récents:

Pinus sections *Merkusioides*, *Taedoponderosoides (pro parte typica)*, *Khasyo-silvestroides* Gaussen, H. — Les Gymnospermes actuelles et fossiles, fascicule VI, chapitre XI, p. 95 (1960). *Nomina invalida quia desunt descriptiones latina.*

P. sections *Pinaster-Taeda* et *Pinaster-Lariciones* Hudson, R. H. — Inst. Wood Sci. J., 6:40 (1960). *Nomina invalida quia desunt descriptiones latina.*

P. sections *Pseudostroboides (pro parte)* et *Occidentaloides (pro parte typica)* Jahrig, M — Willdenowia, 2:345 (1962). *Nomina invalida quia desunt descriptiones latina.*

P. section *Sylvestris* Debazac, E.F. — Manuel des Conifères, p. 92 (1964).

P. section *Ponderosa-Banksiana (pro parte typica)* Debazac, E.F. — *loc. cit.*, p. 101 (1964). Les noms de Debazac furent invalidement publiés, eux aussi faute de description latine.

P. sous-section *Sylvestres* Loudon ex Little & Critchfield — Subdivisions of the Genus *Pinus* (Pines), p. 12 (1969). Holotype: *Pinus sylvestris* L.

P. sous-section *Australes* Loudon *ex* Little & Critchfield — *loc. cit.*, p. 14 (1969). Lectotype: *Pinus palustris* Miller.

P. sous-section *Ponderosae* Loudon *ex* Little & Critchfield — loc. cit., p. 14 (1969). Holotype: *Pinus ponderosa* Lawson.

Lectotype: *Pinus sylvestris* Linné

Description nouvelle: Pins à cônes caducs (généralement décidus moins de deux ans après leur maturité), graines munies d'une aile articulée, cônes souvent actinomorphes ou presque actinomorphes; autres caractères identiques à ceux du sous-genre *Pinus*.

Voilà une grande section, contenant trente-six espèces, c'est-à-dire plus du tiers du genre, répandues çà et là dans toute l'aire propre aux Pins, sauf l'Himalaya et une grande partie de la Chine, qu'elle n'a pas encore atteints.

Little et Critchfield (1969) incluent dans la section *Pinus* la très importante section *Pinaster* Loudon, circonscrite ci-dessous, et la section *Laterales* avec ses graines particulières. Nous différons d'opinion avec eux: les cônes mûrs rapidement caducs et souvent actinomorphes des Pins de la section *Pinus*, telle que nous la comprenons, constituent un groupe homogène et facilement identifiable, par opposition aux cônes mûrs persistant au moins trois ans et souvent obliques de la section *Pinaster* Loudon. Autrement dit, nous donnons ici au caractère de caducité des cônes autant d'importance que dans le sous-genre *Strobus* où nos sections, là aussi, sont reconnaissables d'après ce caractère.

Voici l'énumération, par ordre alphabétique, des espèces de la section *Pinus* telle que différenciée ici :

Pinus caribaea Morelet
P. cooperi Blanco
P. cubensis Grisebach
P. densiflora Siebold & Zuccarini
P. durangensis Martinez
P. elliottii Engelmann
P. engelmannii Carrière
P. glabra Walter
P. hartwegii Lindley
P. heldreichii Christ
P. herrerai Martinez
P. jeffreyi Greville & Balfour
P. leucodermis Antoine
P. luchuensis Mayr
P. lumholtzii Robinson & Fernald
P. massoniana Lambert
P. maximinoi H.E.Moore
P. merkusii Jung
P. michoacana Martinez
P. montezumae Lambert
P. mugo Turra
P. nigra Arnold
P. occidentalis Swartz
P. palustris Miller
P. ponderosa Lawson
P. pseudostrobus Lindley
P. resinosa Aiton
P. rudis Endlicher
P. sylvestris Linné
P. taeda Linné
P. taiwanensis Hayata
P. teocote Schiede & Deppe
P. thunbergiana Franco
P. tropicalis Morelet
P. uncinata Miller *ex* Mirel
P. washoensis Mason & Stockwell

Note : Certains individus de *P. densiflora* et *P. resinosa* ont parfois des cônes mûrs persistant plus de deux ans.

I.2. SECTION *Sula* Mayr

Synonymes récents :

Pinus section *Longifolia* Debazac, E.F. — Manuel des Conifères, p. 111. (1964). *Nomen invalidum quia deest descriptio latina.*

P. sous-section *Canarienses* Loudon ex Little & Critchfield — Subdivisions of the genus *Pinus* (Pines), p. 11 (1969). Holotype : *P. canariensis* C. Smith.

Holotype : *Pinus roxburghii* Sargent.

Description originale *in* Mayr, H. — Waldungen von Nordamerika, p. 428 (1890).

Description récente *in* Little & Critchfield — *loc. cit.*, p. 11 (1969). *sub. nom. Pinus* subsect. *Canarienses.*

L'aile non détachable des graines caractérise cette section. Shaw (1914) découvrit ce caractère et créa un groupe pour les deux espèces concernées. Plus tard, la plupart des monographes du genre l'ont imité.

Deux espèces, l'une africaine (endémique des îles Canaries), l'autre de l'Himalaya:

Pinus canariensis C. Smith
P. roxburghii Sargent

I.3. SECTION *Pinaster* Koch *in* Syn. Fl. Germ. Helv., 2ème éd., vol. 2, p. 766 (1844). *Emend.*

Synonymes récents :

Pinus section *Halepensoides* Gaussen, H. — Les Gymnospermes actuelles et fossiles, fasc. VI, chap XI, p. 95 (1960). Publication invalide, faute de description latine.

P. section *Banksianoides* Jahrig, M. — Willdenowia, 2 : 346 (1962). Publication invalide, faute de description latine.

P. sous-section *Sylvestres* Loudon *ex* Little & Critchfield — Subdivisions of the Genus *Pinus* (Pines), p. 12 (1969). *Pro parte, typo excluso.*

P. sous-section *Australis* Loudon *ex* Little & Critchfield — *loc. cit.*, p. 13. *Pro parte, typo excluso.*

P. sous-section *Contortae* Little & Critchfield — *loc. cit.*, p. 15.

P. sous-section *Oocarpae* Little & Critchfield — *loc. cit.*, p. 15.

Holotype : *Pinus pinaster* Aiton.

Description nouvelle : Pins à cônes nettement persistants, la plupart sur le même arbre décidus plus de deux ans après leur maturité ; cônes souvent obliques (zygomorphes) ; graines munies d'une aile mince (moins de 1.5 mm) ; autres caractères comme ceux du sous-genre *Pinus.*

Cette section ressemble beaucoup au groupe *Insignes* Shaw accepté ensuite par Rehder (1949). Elle avait auparavant été définie par Mayr (1890) qui l'appella section *Banksia* et la décrivit formellement sous ce nom. Les lois de la nomenclature nous obligent à remonter à Koch. Nous n'avons pu consulter le livre de Koch, qui est très rare. Si, par hasard, la publication de sa section *Pinaster* était invalide, le nom correct serait le même, mais par un auteur différent: section *Pinaster* Endlicher *in* Synopsis Coniferarum, p. 166 (1847).

Présente en Amérique du Nord, en Europe, au Moyen-Orient et en Extrême-Orient, elle comprend vingt-trois espèces dont certaines sont parmi les plus répandues du genre *(Pinus contorta, Pinus divaricata, Pinus kesiya, Pinus tabulaeformis,* etc.). C'est toujours facile de reconnaître les Pins appartenant à cette section parce que les cônes persistants, nombreux dans la cime des arbres, s'imposent à la vue à longueur d'année. Il suffit de ne pas le confondre avec les membres des sections *Leiophyllae, Balfouria* et *Cembra* appartenant à d'autres sous-genres.

Voici les espèces par odre alphabétiqe:

P. attenuata Lemmon
P. brutia Tenore
P. clausa (Chapman) Vasey *ex* Sargent
P. contorta Douglas *ex* Loudon
P. divaricata (Aiton) Dumont de Courset
P. echinata Miller
P. greggi Engelmann *ex* Parlatore
P. kesiya Royle *ex* Gordon
P. halepensis Miller
P. hwangshanensis Hsia
P. lawsonii Roezl *ex* Gordon
P. muricata D. Don
P. oocarpa Schiede
P. patula Schiede & Deppe
P. pinaster Aiton
P. pringlei Shaw
P. pungens Lambert
P. radiata D. Don
P. rigida Miller
P. serotina Michaux
P. tabulaeformis Carrière
P. virginiana Miller
P. yunnanensis Franchet

Note: *P. lawsonii* est intermédiaire entre cette section et la section *Pinus*; nous l'avons placé ici en raison de ses cônes obliques.

I.4. SECTION *Laterales* Lemmon, *emend.*

Synonyme récent: *Pinus* sous-section *Sabinianae* Loudon *ex* Little & Critchfield - Subdivisions of the Genus *Pinus* (Pines), p. 14 (1969).

Description originale *in* Lemmon, J.G. — Handbook of West-American Cone Bearers, 3rd ed., p. 37 (1895).

Lectotype (choisi ici): *Pinus torreyana* Parry *ex* Carrière.

Description nouvelle *in* Little et Critchfield — p. 14 (1969), *sub nom. Pinus* subsect. *Sabinianae.*

Les trois espèces composant cette section sont remarquables à plusieurs points de vue: cônes un peu obliques très larges et surtout très lourds, à écussons massifs terminés par un gros umbo long et pointu; graines munies d'une aile épaisse (environ 2mm) à la base; aiguilles longues (moyenne: ± 25 cm) et robustes, à hypoderme épais.

Leur aire naturelle de répartition se limite à la côte de la Californie (U.S.A.) et à la Baja California (Mexique).

Pinus Coulteri D. Don
Pinus sabiniana Douglas *ex* D. Don.
Pinus torreyana Parry *ex* Carrière

II. SOUS-GENRE ***PINEA*** (ENDLICHER)STAT. NOV.

Basionyme: *Pinus* section *Pinea* Endlicher — *Synopsis Coniferarum*, p. 182 (1847), *pro parte typica.*

Holotype: Pinus pinea Linné

Description *in* Endlicher — *loc. cit. (sub nom.* Sectio XI. *Pinea*): «*Squammarum apophysis pyramidata, umbone centrali Semina aptera. Folia gemina aut rarissime terna*».

Descriptio nova: Strobili triennes; umbo dorsalis duplex, concentrica; pseudophylli sicut subgenus Pinus.

Ce sous-genre comprend essentiellement les espèces de Pins dont les cônes mûrissent en trois saisons de croissance; le plus petit des quatres, il est formé de deux sections comprenant une seule espèce chacune, et dont voici la clé naturelle:

A. Cônes mûrs sub-sessibles, déhiscents et caducs à maturité, cônelets à écailles à sommet arrondi, graines munies d'une aile détachable à la base, gaines des aiguilles persistantes ....section *Pinea*

B. Cônes mûrs nettement pédonculés, sérotineux et persistants, cônelets du premier et du deuxième été à écailles à sommet mucroné, graines munies d'une aile adnée (soudée) à la base, gaines des aiguilles rapidement caduques ....section *Leiophyllae*

II.1. SECTION *Pinea*

Synonyme récent :

Pinus sous-section *Pineae* Little & Critchfield — Subdivisions of the genus *Pinus* (Pines), p. 12. (1969).

Description récente *in* Little & Critchfield, — *loc cit.*, p. 12 (1969), *sub nom. Pinus* subsect. *Pineae*.

Description nouvelle : Pin à cônes mûrs subsessiles, rapidement déhiscents à maturité, cônelets formés d'écailles à sommet arrondi, graines munies d'une courte aile détachable, gaines des aiguilles persistantes.

Descriptio: Strobili subsessiles, praecoces dehiscentes, squamis strobilorum emucronatae: seminibus ala brevi articulata; pseudophyllorum vaginis persistentibus.

Cette section comprend exclusivement *Pinus pinea* L., le célèbre Pin pinier (ou parasol) des pays tempérés bordant le nord de la Méditerranée. Il fut le premier des Pins à être mentionné dans la littérature sous le nom latin de *Pinus*; dans l'Antiquité, depuis l'Hispanie jusqu'à la Palestine on récoltait ses graines comestibles.

II.2. SECTION **Leiophyllae** (Loudon *ex* Little & Critchfield) stat. nov.

Basionyme : *Pinus* subsect. *Leiophyllae* Loudon *ex* Little & Critchfield — Subdivisions of the Genus *Pinus* (Pines), p. 11 (1969).

Description nouvelle : Cônes mûrs pédonculés, sérotineux et persistants, cônelets du premier et du deuxième été à écaille à sommet mucroné, graines munies d'une aile adnée (soudée) à la base, gaines des aiguilles rapidement caduques.

Descriptio: Strobili pedunculati, serotini et persistentes, squamis primo et secundoannis mucronatis; seminibus ala adnata; pseudophyllorum vaginis non persistentibus.

Cette section comprend exclusivement *Pinus leiophylla* Schiede & Deppe. Loudon, dès 1838, créa une «section» spécialement pour cette espèce essentiellement nord-américaine qui s'étend jusque dans l'Arizona et le New Mexico (U.S.A.). Entre autres particularités extraordinaires, elle a la faculté de se reproduire par rejets de souche (Shaw, 1914).

III. SOUS-GENRE *DUCAMPOPINUS* (A. CHEVALIER) DE FERRÉ *EX* CRITCHFIELD & LITTLE, *EMEND.*

Pinus sous-genres *Paracembrapinus (pro parte, typo excluso)* et *Ducampopinus* de Ferré, Y. — C.r. hebd. Séanc. Acad. Sci., Paris, 235:228 (1953). Publication invalide parce que contraire à l'article 33 du Code international de la nomenclature botanique.

Description originale (*Sub* nom. *Ducampopinus* gen nov.) *in* Chevalier, A. — Revue Bot. appl. Agric. trop., 24 : 30 (1944).

Validation du nom du sous-genre *in* W. B. Critchfield and E.L. Little — Geographic distribution of the pines of the world (Misc. Publs U.S. Dep. Agric., No. 991, p. 5, 1966).

Description nouvelle : pour la description en français, voir ci-dessus au début de l'article.

Descriptio nova: Strobili biennes; umbo dorsalis, mucronata vel aculeata; pseudophylli fasciculo vasculari unico, basi non decurrentes vagina plerumque caduci.

La publication des sous-genres *Paracembrapinus* et *Ducampopinus* par de Ferré (1953) resta invalide parce qu'elle ne contenait pas de diagnoses ou de descriptions latines et aussi parce qu'elle n'était pas conforme à l'article 33 du Code de la nomenclature botanique : les synonymes remplacés [«*Paracembra* Koehne» et «*Ducampopinus* (Chevalier, *pro gen.*)»] n'étaient pas accompagnés d'une référence à la publication originale.

La première, de Ferré voulut élever au rang de sous-genre la sous-section *Paracembra* de Koehne (1893). Avant Koehne, l'on rattachait *Paracembrapinus* au sous-genre *Pinus;* après lui, on en fit une section du «sous-genre

Haploxylon», c'est-à-dire le sous-genre opposé au sous-genre *Pinus*. Cette différence d'opinions provient de fait que primitivement (avant 1893), on accorde de l'importance exclusive à l'umbo central, mais qu'après 1893, la plupart des taxonomistes déclarent primordial le faisceau libéro-ligneux dans les aiguilles. Nous croyons que les caractères de l'appareil reproducteur ont priorité sur les caractères végétatifs; mais nous reconnaissons cependant que le nombre des dits faisceaux (liés à la non-décurrence des pseudophylles) importe lui aussi et dès lors nous acceptons d'emblée le point de vue publié par de Ferré. Voici d'ailleurs son raisonnement: «S'il fallait réunir ce groupe «*Paracembra*» à l'un des deux précédents: *Diplopinus* (sous-genre *Pinus)* ou *Cembra* (sous-genre *Strobus)*, ne vaudrait-il pas mieux accorder la priorité aux caractères de l'appareil reproducteur et de l'embryon, plutôt qu'aux caractères de l'appareil végétatif, par conséquent rattacher les *Paracembra* non aux *Cembra*, comme on l'a fait jusqu'à maintenant, mais aux *Diplopinus* (sous-genre *Pinus)*... ?»

Nous considérons *Pinus krempfii* comme une espèce devant être incluse dans l'ancienne sous-section *Paracembra* de Koehne. Or c'est justement le nom de sous-genre *Ducampopinus* qui fut publié et décrit validement le premier. Nous sommes donc forcé de faire disparaître le nom *Paracembra* (légitime seulement dans la catégorie des sections et des sous-sections) et d'accepter *Ducampopinus* qui à partir de maintenant devient un grand sous-genre de trois sections.

Voici la clé de ces trois sections:

A. Aiguilles linéaires-lancéolées; trachéides des ravons absentes .... section *Ducampopinus*

AA. Aiguilles aciculaires; trachéides des rayons présentes .... B

B. Graines dépourvues d'aile .... section *Parrya*

BB. Graines ailées .... section *Balfouria*

III.1 SECTION Ducampopinus

Synonymes récents:

Pinus sous-genre *Ducampopinus* Gaussen H., *sensu stricto*, et section *Krempfioides Gaussen, H. — Les Gymnospermes actuelles et* fossiles, fasc. VI, chap. XI, p. 93 (1960). *Nomina invalida qui a desunt descriptiones latina.*

P. sous-genre *Ducampopinus* (A. Chevalier) de Ferré *ex* Critchfield & Little — Geographic distribution of the pines of the world, p. 5 (1966), *sensu stricto*, tel que le taxon fut délimité par ces auteurs.

Description *in* Little, E.L. & W. B. Critchfield — Subdivisions of the Genus *Pinus* (Pines), U.S.A. Dept. Agriculture Misc. Publ. 1144: 7 (1969), *sub nom. Pinus subgen. Ducampopinus.*

Holotype: *Pinus krempfii* Lecomte.

Seule espèce appartenant à cette section, *P. krempfii* croît naturellement dans les montagnes de la région de Dalat, au Viêt-nam du Sud. Shaw (1924) fut le premier à la classer dans une catégorie: il l'inclut avec *Pinus aristata* et *P. balfouriana* dans le groupe *Balfourianae* créé par lui en 1914 (Shaw, 1914). Voici son opinion: "*Lecomte's species is* [...] a *Soft Pine (Haploxylon). The dorsal umbo of the cone-scales places it in the subsection Paracembra while the long and effective seed wing associates in with the group Balfourianae*". Nous n'avons pas cru devoir nous conformer à cette opinion conservatrice qui possède quand même beaucoup de valeur. Les aiguilles exceptionnelles de *P. krempfii*, outre l'anatomie de son bois, nous ont plutôt incité à le placer hors la section *Balfouria* Mayr. Pour résumer, nous avons adopté une solution intermédiaire entre celle des auteurs récents et celle de Shaw.

III.2. SECTION *Parrya* Mayr, *emend*

Synonyme récent:

Pinus section *Parryanoides* Gaussen, H. — Les Gymnospermes actuelles et fossiles, fasc. VI, chap. XI, p. 173 (1960). *Nomen invalidum quia deest descriptionis latina.*

Lectotype: *Pinus quadrifolia* Parlatore *ex* Sudworth.

Description originale *in* Mayr, H. — Die Waldungen von Nordamerika, p. 428 (1890).

Description récente: *in* Little & Critchfield — Subdivisions of the Genus *Pinus* (Pines) p. 10 (1969), *sub nom. Pinus* subsect. *Cembroides* Engelmann.

Cette section comprend huit espèces limitées au sud-ouest des Etats-Unis et au nord du Mexique. On leur a donné un nom collectif: «Pins pignons d'Amérique» (en anglais: *nut pines;* en espagnol: *Piñons*). Leur port, à cime basse, large, arrondie, est typique. Le *P. nelsoni* Shaw se place légèrement à part: il a des aiguilles à gaine persistante. On pourrait créer une sous-section pour lui.

Pinus cembroides Zuccarini
Pinus culminicola Andresen & Beaman
Pinus edulis Engelmann
Pinus maximartinezii Rzedowski
Pinus monophylla Torrey & Frémont
Pinus nelsoni Shaw
Pinus pinceana Gordon
Pinus quadrifolia Parlatore *ex* Sudworth

III.3. SECTION *Balfouria* Mayr, *emend.*

Synonymes récents:

Pinus section *Paracembra* Hudson, R.H. — Insf. Wood Sci., 6:40 (1960). *Nomen invalidum quia deest descriptio latina.*

P. sous-section *Gerardianae* Loudon *ex* Little & Critchfield — Subdivisions of the genus *Pinus* (Pines), p. 10 (1969).

Holotype: *Pinus balfouriana* Greville & Balfour.

Description originale *in* Mayr, H. — Die Waldungen von Nordamerika, p. 428 (1890).

Description nouvelle: Arbres à cônes mûrissant en deux saisons de croissance, munis d'umbos dorsaux, mucronés ou épineux, à graines ailées; aiguilles haplostelées et aciculaires; bois pourvu de trachéides des rayons.

La distinction effectuée par Shaw (1914) entre le groupe *Gerardinae* et le groupe *Balfourianae* est tellement peu importante (ailes des graines longues et courtes) qu'il nous semble impossible de ne pas les réunir tous les deux dans une seule section.

Récemment, on a découvert au Mexique un pin (*Pinus rzedowskii*) dont les caractères de l'appareil végétatif ne ressemblent pas beaucoup à l'un ou l'autre de ces groupes mais dont les caractères des cônes et des graines s'avèrent à peu près identiques. Nous l'incluons dans cette section qui est peut-être constituée des plus anciennes espèces de pins encore vivantes. Elle en comprend cinq: trois de l'ouest du continent nord-américain, deux de l'Asie. Fait remarquable, elles ont toutes une aire de répartition assez petite et ceci nous porte à conclure que leur vitalité diminue.

Pinus aristata Engelmann
Pinus balfouriana Greville & Balfour
Pinus bungeana Zuccarini
Pinus gerardiana Wallich
Pinus rzedowskii Madrigral & Caballero.

IV. SOUS-GENRE *STROBUS* (SPACH) LEMMON

Synonyme:

Pinus sous-genre *Haploxylon* Rehder *in* Bailey, L.H. — The Cultivated Evergreens, p. 302 (1923); lectotype (choisi ici): *Pinus cembra* Linné.

Nous avons choisi *Pinus cembra* comme lectotype de ce nom de sous-genre afin de le bien placer comme synonyme du sous-genre *Strobus*. Autrement, il pourrait être rattaché au sous-genre *Ducampopinus* tel que délimité ici et une telle action aurait pour effet de rendre invalide la publication de celui-ci.

Publication originale *in* Lemmon, J.G. — Handlook of West-American Cone-Bearers, 3rd ed., p. 20 (1895): "*Cones with the exposed part of the scales (the apophysis) usually thin, and with an apical protuberance (umbo), devoid of prickles or spines. Leaves in 5's, short, 1 1/2 to 2 inches long, their shealths loose and deciduous*".

Description nouvelle: Voir ci-dessus en français, au début de l'article.

Descriptio: Umbo terminalis, inermis, emucro-

nata; pseudophylli et vagina sicut subgenus Ducampopinus.

Comme on le voit, nous avons exactement les mêmes vues que Lemmon à ce sujet, Lemmon qui s'est inspiré partiellement ou entièrement de Endlicher (1847) et de Engelmann (1880). Ces deux auteurs du dix-neuvième siècle ont accordé une importance primordiale à la position de l'umbo sur l'apophyse (ou écusson) du cône, organe de reproduction. Il nous paraît plus rationnel que ce caractère doive passer avant la structure anatomique des aiguilles ou du bois, ou la morphologie des pseudophylles, indûment préférées depuis le début du siècle.

Ce sous-genre se subdivise en deux sections dont voici la clé naturelle:

Cônes rapidement déhiscents et caducs à maturité, à apophyses minces; graines munies d'une aile (longue ou rudimentaire) ....section *Strobus*
Cônes indéhiscents et persistants à maturité, à apophyses plus épaisses; graines dépourvues d'aile ....section *Cembra*

IV.1. SECTION *Strobus*

Synonymes récents:

Pinus sections *Armandioides, Parvifloroides, Stroboides* et *Flexiloides* Gaussen, H. — Les Gymnospermes actuelles et fossiles, fasc. VI, chap. XI, généralités, genre Pinus, p. 182 (1960). *Nomina invalida quia desunt descriptiones latina.*

P. sous-section *Strobi* Loudon *ex* Little & Critchfield — Subdivisions of the genus *Pinus* (Pines), p. 8-9 (1969).

Holotype: *Pinus strobus* L.

Description nouvelle: *in* Little & Critchfield, p. 9 (1969).

Seize espèces répandues un peu partout dans l'aire de répartition globale du genre. Deux taxonomistes, trouvant que cette section et la suivante, si différentes des autres, méritaient un classement supérieur, ont créé pour elles un nouveau genre: *Strobus* Opiz, *Leucopytis* Niewland.

Voici l'énumération alphabétique des espèces:

Pinus amamiana Koidzu
Pinus armandii Franchet
Pinus ayacahuite Ehrenberg
*Pinus chiapensis (*Martinez) Andresen
Pinus dalatensis de Ferré
Pinus fenzeliana Handel-Mazetti
Pinus flexilis James
Pinus lambertiana Douglas
Pinus monticola Douglas *ex* D. Don
Pinus morrisonicola Hayata
Pinus parviflora Siebold & Zuccarini
Pinus peuce Grisebach
Pinus strobiformis Engelmann
Pinus strobus Linné
Pinus wallichiana A.B. Jackson
Pinus wangii Hu & Chang

IV.2. SECTION *Cembra* Spach

Synonyme récent:

Pinus sous-section *Cembrae* Loudon *ex* Little & Critchfield — Subdivisions of the Genus Pinus (Pines), p. 8 (1969).

Holotype: *Pinus cembra* Linné

Description originale *in* Spach, E., Hist. Nat. vég. phanérogames, vol. II, p. 398 (1842).

Description nouvelle *in* Little & Critchfield, p. 8 (1969), *sub nom. Pinus* subsect. *Cembrae.*

Les cinq espèces appartenant à cette section ont une aire de distribution nordique et alpine. Quatre d'entre elles se trouvent en Eurasie, une seule en Amérique du Nord:

Pinus albicaulis Engelmann
Pinus cembra Linné
Pinus koraiensis Siebold & Zuccarini
Pinus pumila Regel
Pinus sibirica Du Tour

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Bernard Boivin, taxonomiste au Ministère fédéral de l'agriculture à Ottawa, nous a grandement aidé à organiser nos recherches et à sélectionner les critères utiles pour la logique de cet article. Nous l'en remercions vivement. Ce travail n'engage cependant que notre propre responsabilité.

TABLEAU STATISTIQUE

Sous-genre	Section	Espèces
I. *Pinus*	1. *Pinus*	36
	2. *Sula* Mayr	2
	3. *Pinaster* Koch	23
II. *Pinea* (Endlicher) Landry	4. *Laterales* Lemmon	3
	1. *Pinea*	1
	2. *Leiophyllae* (Loudon) Landry	1
III. *Ducampopinus* (A. Chevalier) de Ferré	1. *Ducampopinus*	1
	2. *Parrya* Mayr	8
	3. *Balfouria* Mayr	5
IV. *Strobus* (Spach) Lemmon	1. *Strobus*	16
	2. *Cembra* Spach	5
Totaux	11 sections	101 espèces

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LES FACIÈS DU PLÉISTOCÈNE MARIN DES COLLINES D'OKA, QUÉBEC

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Résumé

Le village d'Oka est situé à environ 32 km (20 milles) à l'ouest de Montréal, au pied d'un petit massif précambrien, sur la rive nord du lac des Deux-Montagnes. Les collines qui s'étendent dans un secteur NW-NE par rapport au village ont joué le rôle de pièges à sédiments lors des mouvements de glaces de la dernière glaciation.

Des masses de till ont été remaniées dans cette zone, au moment de la transgression de la mer de Champlain, entre moins 12,000 et moins 9,800 ans. En pratique la plupart des caractères sédimentaires suggèrent que les périodes majeures de mise en place des sédiments littoraux correspondent à un mouvement régressif (par étapes, saccades...?).

Les caractères pétrographiques et minéralogiques des sédiments démontrent une origine locale du matériel, surtout grenvillienne et paléozoïque.

L'étude des faunes dans une optique paléoécologique apporte des précisions fort utiles à la compréhension de l'environnement dynamique (bathymétrie...) et fournit en outre des données nouvelles sur les fluctuations de l'environnement chimique (salinité) et physicochimique (cycle des températures).

Abstract

The village of Oka is situated about 32 km (20 miles) west of Montréal at the foot of a small Precambrian body. The range of hills, immediately to the northwest and northeast of the town constituted a depositional area (acting like traps) for clastic materials, during the last ice advance.

Units of till were reworked in this region during the advance of the Champlain Sea over the St. Lawrence lowlands in the period 12,000 BP — 9,800 BP. Sedimentary features suggest that the most important phases of deposition of the littoral sediments correspond to a period of sea regression (in stages, in jerks...).

The petrographic and mineralogical features of the sediments indicate a local origin and a more significant influence of the Grenville and paleozoic materials.

Paleoecological studies of the fauna yielded detailed informations on the bathymetry (the dynamic environment) and also on variations in the chemical and physical environment (salinity and temperature).

Introduction

Un travail d'équipe a permis d'aborder l'étude des dépôts quaternaires des basses terres du Saint Laurent dans la région d'Oka, sous des aspects multiples : relations stratigraphiques, caractères sédimentologiques, pétrographiques et minéralogiques; inventaire paléontologique : paléoécologie. D'autres méthodes d'approche telles que disposition géomorphologique, datations au carbone 14, dosages de l'oxygène 18 et du carbone 13 sont menées parallèlement mais ne sont pas abordées dans la présente étude.

On sait que la mer de Champlain forma un golfe entre les Laurentides au nord et au nord-ouest, les Appalaches au sud-est et au sud et les Adirondacks vers le sud et le sud-ouest. Sur sa rive nord, plusieurs faits montrent que la mise en place du matériel marin a pu se faire au contact du front glaciaire pendant environ 1,000 ans. Dénudés ou non, les reliefs environnants influencèrent la sédimentation des rivages : apports de matériel fraîchement façonné par les glaces ; apport d'eau douce perturbant les caractères physiques et chimiques du milieu marin déjà particulier par sa configuration géographique. Or les collines d'Oka formèrent toujours, même lors du niveau le plus élevé des eaux, un petit archipel assez éloigné des rivages bordiers. On peut donc considérer que le milieu marin se présentait dans cette zone avec ses caractères les plus généraux.

D'autres reliefs de moindre importance formèrent des points hauts ou des hauts fonds, soit pendant toute la durée, soit à la fin seulement de l'épisode marin, tels les Montérégiennes et le massif de Rigaud ainsi que plusieurs crêtes d'eskers des environs de Montréal (Primauville ou Mercier, par exemple).

Le massif précambrien d'Oka affleure à quelques kilomètres à l'ouest de Montréal. Il se présente, au milieu des basses terres, comme un petit relief très découpé qui s'étend dans un secteur NW-NE par rapport au village d'Oka, sur le bord nord du lac des Deux-Montagnes. Les altitudes de ces collines s'étagent entre 100 m et 250 m. La plaine environnante vers les Laurentides est sise à quelques 30 m de hauteur tandis que le lac et le Saint-Laurent, vers le sud, ne sont qu'à 22 m d'altitude. La zone particulière décrite dans cet article est limitée par les latitudes nord 45°30'-45°35' et les longitudes ouest 74°00'-74°10' (fig. 1).

TRAVAUX ANTERIEURS

Depuis Goldthwait (1910) plusieurs auteurs se sont intéressés à la mer de Champlain. Citons parmi les travaux généraux ceux de Goldring (1922), le premier à aborder l'aspect paléoécologique (influence de la salinité sur les faunes champlainiennes), et ceux d'Elson et Elson (1959), définissant deux phases successives de la mer de Champlain (phase à *Hiatella arctica* et phase à *Mya arenaria*). Dans la région étudiée, certains affleurements ont été signalés par Elson (1969b) et Wagner (1970). Cet auteur a d'ailleurs établi un inventaire très complet des faunes de la mer de Champlain qui peut servir de base à toute étude paléoécologique. Parmi les contributions récentes visant des objectifs similaires ou connexes à la présente étude, signalons celles de David (1972), Dionne (1971, 1972), Gadd (1971), Gadd *et al.* (1972 a et b), Lasalle (1965, 1966, 1970).

Étude sédimentologique

Rappelons brièvement que les collines d'Oka et, à un degré moindre, les Montérégiennes, ont joué le rôle de pièges à sédiment lors des mouvements des glaces de l'inlandsis laurentidien lors de la dernière glaciation. Des masses de tills se sont accumulées à l'abri des éperons résistants ou sur les versants de dépressions. D'ailleurs le réseau de ces dépressions suggère une orientation préférentielle de l'érosion. Ces sédiments furent par la suite partiellement ou presque entièrement remaniés lors de la transgression champlainienne.

D'un point de vue géomorphologique, les sédiments remaniés appartiennent au type dit traditionnellement «dépôts de plage», avec des terrasses légèrement inclinées ennoyant parfois de petits reliefs du substratum (ou socle rocheux).

LES FACIÈS CARACTÉRISTIQUES

Pour des raisons de clarté nous définirons les trois grands types de faciès visibles sur le terrain, soit, par ordre décroissant de granulométrie : les rudites, les arénites, les lutites. En effet la terminologie courante (till remanié, sable et argile champlain) devrait être modifiée. Sans être parfaitement satisfaisante, la terminologie adoptée ici se réfère au moins à une échelle granulométrique internationale (fig. 2). En pratique les deux premiers faciès correspondent au matériel glaciaire remanié qui fut presque entièrement privé de la fraction fine de sa matrice (les argiles, les silts, voire les sables très fins).

Les *rudites* représentent la fraction supérieure à 2 mm. Les éléments dominant sont généralement supérieurs à 1 cm de diamètre et atteignent fréquemment plusieurs décimètres. Parfois ci-

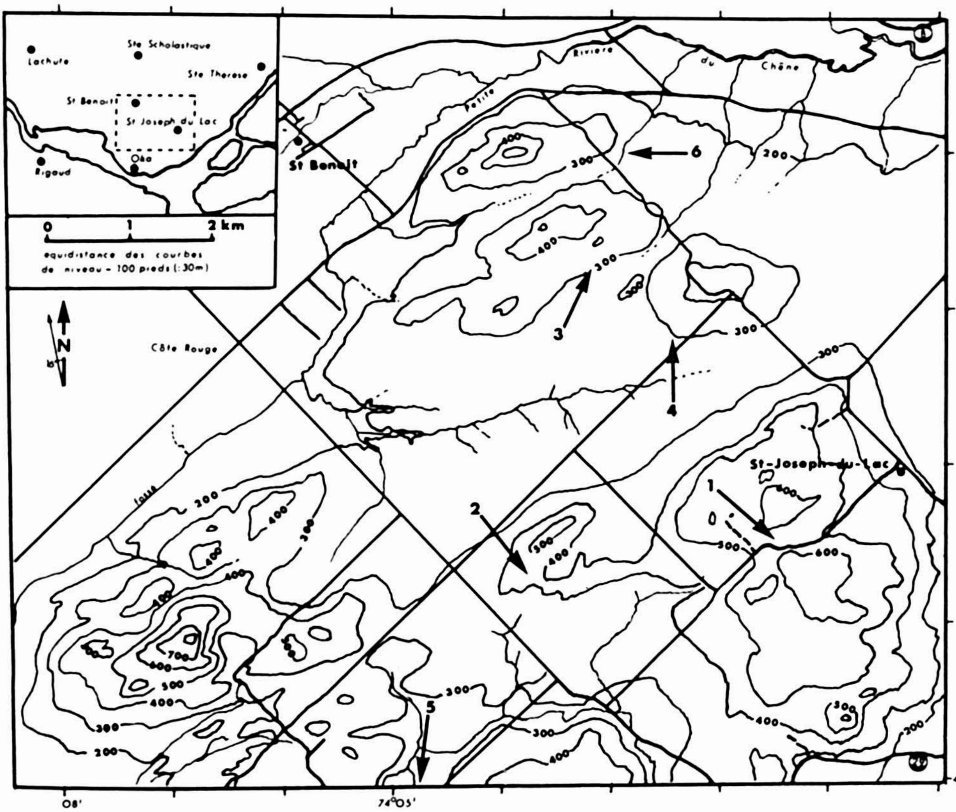
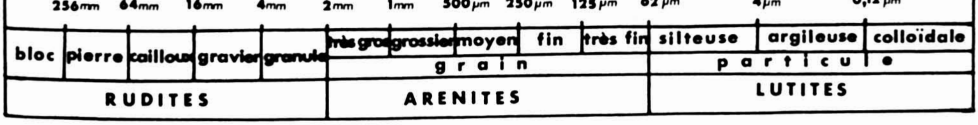


Figure 1. Localisation des affleurements : 1- Saint-Joseph-du-Lac ; 2- fermes Husereau ; 3- ferme Cataphard ; 4- rang Sainte-Germaine ; 5- ferme Binette ; 6- route de Saint-Benoit. (Extrait de la carte topographique au 1/50,000e, feuille 31G/9 E du Ministère de la défense nationale du Canada).



Roches détritiques terrigènes

256mm	64mm	16mm	4mm	2mm	1mm	500µm	250µm	125µm	62µm	4µm	0,12µm	
bloc	pierre	cailloux	gravier	granule	très gros	grossier	moyen	fin	très fin	silteuse	argileuse	colloïdale
					grain					particule		
RUDITES					ARENITES					LUTITES		

Figure 2. Echelle granulométrique adoptée (d'après « Chambre syndicale de la recherche et de la production du pétrole et du gaz naturel — Essai de nomenclature des roches sédimentaires — Technip — Paris — 1967).

mentés par des oxydes de fer ou un peu de calcite, ou encore une calcite fibreuse abondante, ces sédiments deviennent alors des conglomérats. On a pu observer ces différents types de cimentations dans d'autres sites (par exemple, au sud-est du mont Yamaska pour le cas de la calcite fibreuse).

Les *arénites*, communément appelés sables, sont comprises entre 2 mm et 0.062 mm. Ce terme recouvre les sables littoraux[1] qui sont très souvent des aréno-rudites, c'est-à-dire contenant une proportion variable de grains compris entre 2 et 10 mm environ.

Les *lutites*, communément appelées "argiles champlainiennes", peuvent inclure des faciès très proches des sables très fins (aleurite en français, *silt* en anglais). Elles comprennent tous les éléments inférieurs à 0.0612 mm.

Les caractères macroscopiques

Bien que chaque affleurement présente ses particularités, quelques traits généraux sont assez fréquents sinon permanents et méritent d'être signalés.

a) Les rudites ne présentent pas toujours de prime abord l'aspect stratifié qu'on leur connaît en maints endroits. Parfois, seul l'agencement des galets les plus aplatis permet d'identifier la stratification. Le plus souvent la matrice grossière (granules, sables grossiers) ou plus fine souligne cette stratification. Il arrive aussi que certaines accumulations de galets (Bourcart, 1941 : 2.5 à 50 cm) subarrondis à subanguleux ne présentent pas de matrice.

Parmi les caractères sédimentologiques, signalons : les très forts pendages (ou inclinaisons) sédimentaires (25°-30°-35°) ; une évolution morphoscopique relativement importante qui se traduit moins par l'émoussage des galets que par la disparition des stries sur ceux qui en possédaient (galets calcaires ou carbonatés en général) et l'incrustation des balanes tout autour de blocs presque métriques...

Si l'on établit les rapports L/I et L/E des galets de taille moyenne (méthode Wentworth, 1935) on peut mettre en évidence leur caractère glaciaire. Leur forme révèle encore parfois le fameux type «fer à repasser». On a également remarqué que 20 à 30% des galets carbonatés de 3 cm ont un indice de dissymétrie marin : AC/L compris entre 0.545 et 0.558 (méthode Cailleux *et al.*, 1959). Toutefois, cette méthode demandera des adaptations pour que l'on puisse l'appliquer de façon systématique aux sédiments littoraux grossiers de la mer de Champlain.

b) Dans les arénites les particules sont de taille moyenne à grossière (médiane = 0.250 à 0.610 mm), si l'on néglige les intercalations d'aréno-rudites. Elles sont disposées en strates d'épaisseurs variables (30 cm à moins de 10 cm). On y relève toujours des pendages sédimentaires élevés (15°-20°). De rares éléments plus grossiers (granules, graviers) témoignent de la présence très proche du matériel d'origine. Leur couleur dépend de la composition pétrographique : jaune ocre lorsque les quartz sont nettement dominants, comme c'est le cas ici, ou plus gris lorsque les carbonates sont en proportion notable. Parmi les structures internes des strates il faut signaler quelques beaux terriers de Lamellibranches et surtout la présence de petites mégarides de plages : leur longueur d'onde atteint 90 à 100 cm et leur amplitude 10 cm. De telles rides peuvent être observées au sommet des lits frontaux (*fore-* ou *front-set*).

c) Les lutites (ou argiles) occupent les parties basses des dépressions des

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[1] A ne pas confondre avec les sables marquant la phase de retrait de la mer de Champlain et qui recouvrent les terrasses inférieures (phase estuarienne).

collines et d'une façon générale la plaine des basses terres. Dans les cas favorables, au pied des strates d'arénites, des lits ou laminae d'argile verdâtre viennent s'interdigiter aux strates grossières avec d'ailleurs des accumulations importantes de coquilles en thanatocénose. Les pendages sédimentaires que l'on y relève alors (12°-18°) s'inscrivent bien dans le schéma général du passage latéral aux lits de base (*bottomset*).

AFFLEUREMENTS TYPES (fig. 1 et 3)

Trois affleurements principaux ont fait l'objet de recherches plus détaillées. Ce sont par ordre d'altitude décroissante: 1) la carrière de Saint-Joseph-du-Lac (altitude 167 à 152 m, coordonnées: 45 30'18"N, 74 00'19"0); 2) les fermes Husereau (altitude 137 à 122 m, coordonnées: 45 30'16"N, 74 00'45" O); 3) le rang Sainte-Germaine (altitude 106 à 84 m, coordonnées: 45 30'34" N, 74 00'30"O).

Les deux premiers sites montrent surtout des rudites grossières à forts pendages sédimentaires. Toutefois, aux fermes Husereau, on peut aussi voir, en quelques centaines de mètres, un passage latéral à des dépôts caillouteux et graveleux. Au rang Sainte-Germaine, par contre, on peut observer tous les faciès définis, des rudites aux lutites. Les deux premières coupes, assez monotones, ne feront l'objet que de brèves descriptions tandis que la troisième sera plus détaillée.

Coupe de Saint-Joseph-du-Lac

Il s'agit d'une carrière située à un tournant de la route qui mène du village de Saint-Joseph à celui d'Oka, en traversant l'ensemble des collines.

Une épaisse succession stratifiée (environ 50 m) de dépôts grossiers parfois riches en débris coquilliers repose en contact franc sur un petit noyau de till non remanié et dans lequel aucune structure n'a pu être relevée vu l'exiguité de l'affleurement. On retiendra les faits suivants:

- — matrice sablo-argileuse du till non remanié (à la base);
- — couche de contact, de quelques centimètres, relativement bien triée: on n'y trouve que des granules et des graviers propres, c'est-à-dire sans matrice argileuse ou sableuse;
- — niveaux riches en débris coquilliers près de la base de la partie remaniée;
- — forts pendages sédimentaires des galets stratifiés autour du noyau de till (24° à 53° vers le secteur SE à NE);
- — inclinaison générale des stratifications vers le secteur SSE-SSW de l'ordre de 22°.

Coupe des fermes Husereau

A 400 m, au nord des fermes du même nom, une ancienne exploitation de «graviers» et une plus récente offrent les indications suivantes:

- — à l'affleurement le plus haut, environ 15 m de dépôts très grossiers, très mal stratifiés mais riches en débris de coquilles, montrent de gros blocs parfois incrustés de balanes dans une matrice aréno-silteuse.
- — latéralement, 200 m au SSW, 4 m d'aréno-rudites très mal classées mais très nettement stratifiées offrent des surfaces de ravinement à pendage faible de quelques degrés. Sur l'un des fronts de taille à 1.70 m de la base, et dans le centre d'une «gouttière», on a noté un gros bloc subarrondi de 0.50 m de diamètre. D'autres blocs anguleux sont parsemés dans ces sédiments relativement fins. Des lits coquil-

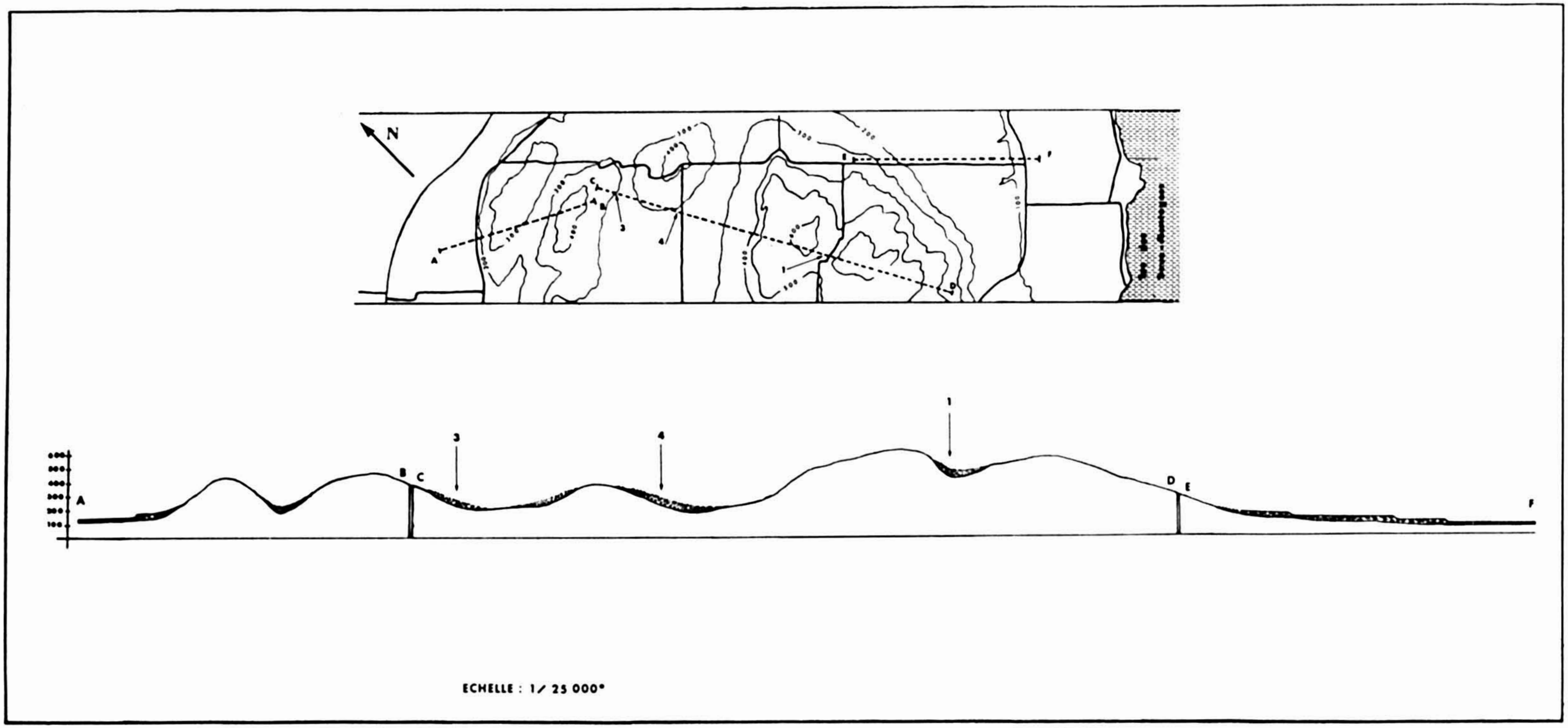

Figure 3. Coupe topographique des affleurements 1,3 et 5, déjà situés sur la figure 1.

liers, en débris ou coquilles entières, sont présents dans tout l'affleurement. Sur le front de taille E et au plancher de l'exploitation, quelques affleurements de roche en place sont visibles. D'autres pointements semblables émergent çà et là dans les prairies avoisinantes. Des relevés des pendages sédimentaires sur galets ou stratifications font apparaître une inclinaison moyenne de 6° à 10° vers le secteur SW à W. Localement on peut rencontrer des orientations divergentes des lits ou des strates: 8° vers le SE.

Rang Sainte-Germaine (fig. 4)

L'intérêt de cet affleurement est double: on peut en effet y observer d'une part une épaisseur remarquable de sédiments, pratiquement continue sur 65 m, et d'autre part la série complète des faciès, y compris les zones de passages entre ceux-ci.

La plupart des analyses de laboratoire ont été effectuées sur des échantillons provenant de cette coupe.

Sur le versant sud de la colline, qui atteint 129 m, une terrasse marine entaillée d'une carrière déjà ancienne offre la succession stratigraphique suivante, en partant de la base:

— ***Unité Ib sur la coupe:*** 33 mètres de rudites très grossières dont les pendages sédimentaires atteignent 25° à 27° vers le SSW, dans la partie occidentale de la carrière. Il s'agit de galets et blocs décimétriques à métriques richement incrustés de balanes et moules, tantôt sans matrice et laissant entre eux des vides, tantôt noyés dans une matrice d'arénite (médiane de la matrice = 0.640 mm). Il n'a pas été possible d'observer le contact avec le till non remanié à cet endroit-là. Par contre du matériel glaciaire d'origine existe à la ferme Cataphar, environ 500 m au NW, où il forme un petit relief contre le socle rocheux.

Il convient de signaler, en un point sous cet ensemble, la présence d'un horizon de 3 m d'épaisseur où l'on a relevé des niveaux argileux et sableux, très riches en débris coquilliers. Des galets de taille variable y sont présents quoique clairsemés et n'atteignant jamais les dimensions de ceux de l'unité Ib. Les lits sédimentaires ont des inclinaisons plus faibles: 13° vers le SSW. Nous l'appelons unité Ia: sa présence est intéressante sur le plan interprétatif, mais l'exiguité de l'affleurement ne permet pas pour le moment d'en faire une unité différente.

— ***Unité II:*** Au sommet de l'unité Ib des strates arénitiques apparaissent. Elles alternent sur 10 m avec des biseaux de rudites qui sont bien stratifiées.

— ***Unité III:*** Environ 15 m d'arénites succèdent aux dépôts précédents. Ces arénites montrent une évolution dans l'épaisseur des strates: 20 à 30 cm à la base, avec peu de fossiles entiers et de nombreux débris coquilliers; 5 à 7 cm au sommet, avec nombreux fossiles en place, parfois dans un long terrier vertical. Retenons quelques faits significatifs: rares galets de quelques centimètres de diamètre; présence de petites mégarides de longueur d'onde métrique et d'amplitude décimétrique; pendages sédimentaires variant de 22° à 30° vers le SE et SSE (fig. 10 a).

— ***Unité IV:*** Latéralement, au sommet stratigraphique mais au pied de la terrasse marine, on distingue des arénites identiques aux précédentes, mais où s'intercalent des argiles verdâtres en lits de 1 cm environ. Certains niveaux sont très riches en débris de coquilles. Les inclinaisons y évoluent de 18° à 12° vers le sud.

Enfin, à quelques mètres au sud, un fossé de drainage délimite la plaine argileuse cultivée.

L'étude granulométrique de cette séquence apporte des précisions aux caractères macroscopiques du matériel. Ainsi, en examinant la succession des différentes courbes de fréquence, on peut facilement reconnaître dans les rudites fossilifères une matrice sableuse «très pauvrement classée» ($\sigma = 2.09$) et sans aucun mode défini. A la base des arénites apparaît un début de tri recon-

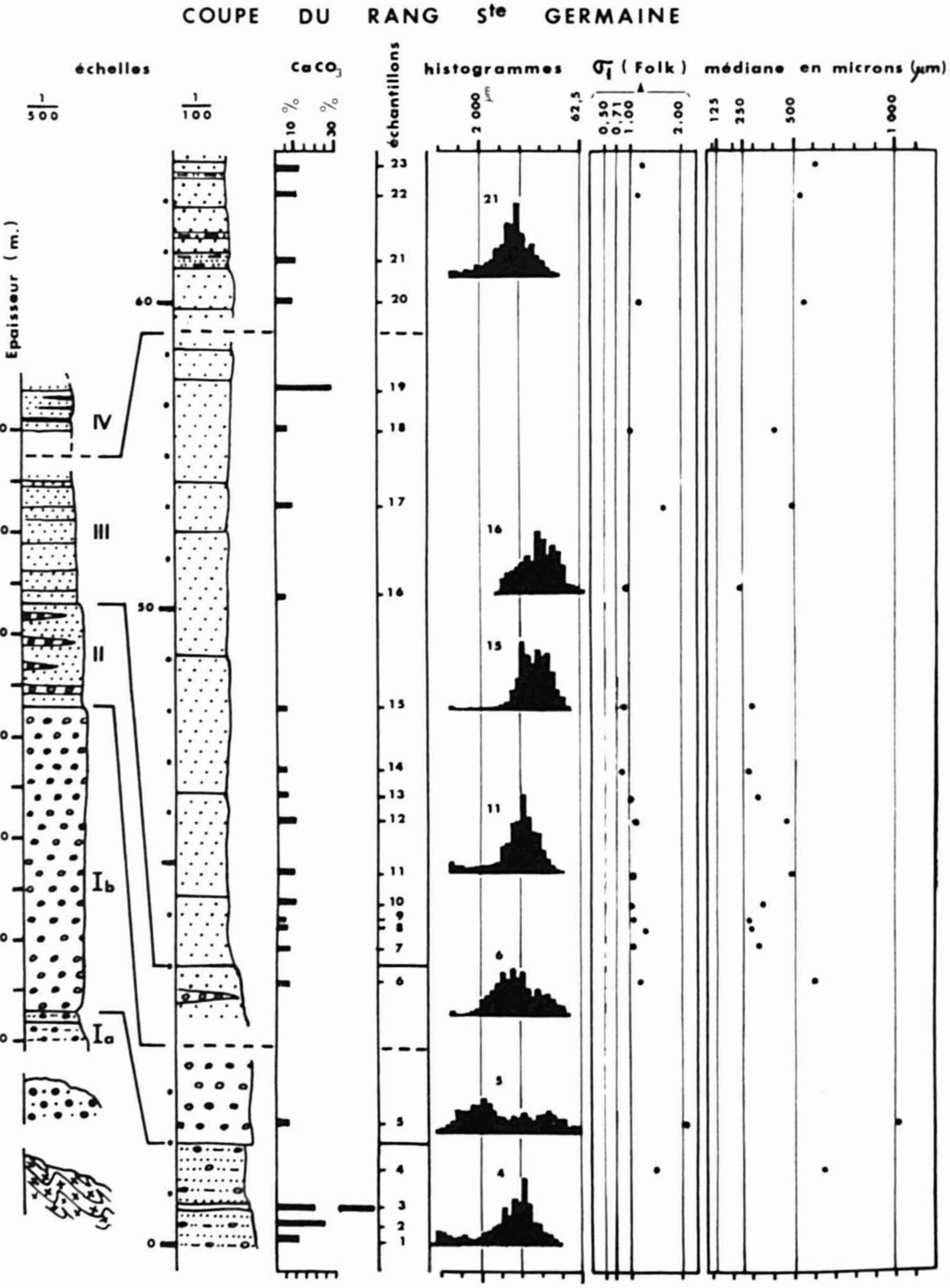

Figure 4. Coupe du rang Sainte-Germaine: lithologie (unités Ia, Ib, II, III, IV); pourcentage de calcite; échantillonnage; histogrammes des échantillons 4, 5, 6, 11, 15, 16 et 21; «déviation standard» et médiane en microns de la plupart des échantillons.

naissable à la diminution du nombre de modes ; vers le sommet de l'unité III, le sédiment passe de « très pauvrement » à « pauvrement classé » (σ = 1.18 à 0.88) et les courbes sont unimodales (fig. 4 et 5).

ORIGINE DU MATÉRIEL

Les comptages de galets dans les trois affleurements évoqués (fig. 6) mettent en évidence la double origine du matériel glaciaire : sédimentaire local (60 à 45%) et métamorphique (31 à 54%). Donc, d'un côté le matériel sédimentaire ne diffère en rien des roches présentes dans les premiers groupes stratigraphiques du paléozoïque inférieur connus immédiatement au nord des collines, tandis que de l'autre le matériel métamorphique reflète la composition du socle dans les collines. Un très faible pourcentage d'anorthosite suggère une influence allochtone mineure : ces résultats convergent apparemment avec ceux obtenus sur les tills de fond de la région de Sainte-Scholastique (Laverdière et Guimont, 1972).

La seule relation que l'on puisse faire entre la variation dans les pourcentages respectifs des deux catégories de galets

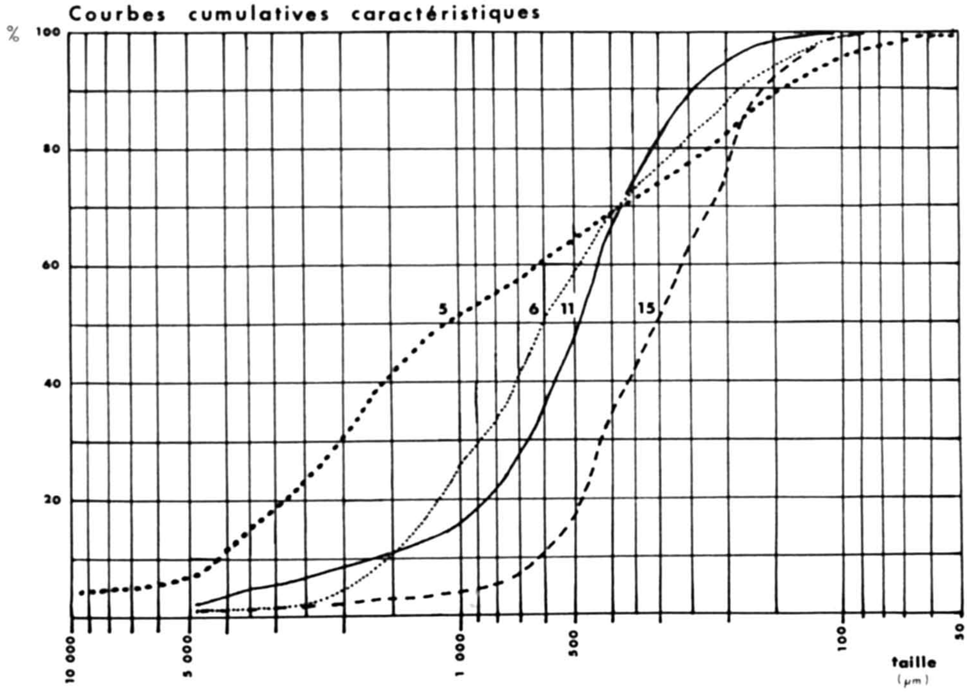

Figure 5. Granulométrie : courbes cumulatives caractéristiques des échantillons 5, 6, 11 et 15.

nature des galets et % / Sites	R. Sédimentaires					R. Métamorphiques et Ignées							Divers
	calcaire	dolomie	dolomie gréseuse	grès	Total	quartzite	gneiss	amphibolite	anorthosite	pegmatite	quartz filonien	Total	
n° 1	24	22	7	16	69	15	9	4	-	-	3	31	1
n° 2	14	23	12	11	60	15	17	7	1	2	-	42	-
n° 4	14	15	5	11	45	44	10	-	-	-	-	54	3

Figure 6. Répartition pétrographique dans les rudites.

et la localisation semble liée à l'altitude. La durée du remaniement, d'autant plus importante que l'on descend, peut expliquer la diminution du pourcentage relatif des roches les plus tendres (calcaire, dolomie, amphibolite), alors que le matériel résistant, grès-quartzitique et quartzite, se concentre à la suite de l'élimination des roches plus fragiles dans les niveaux fortement remaniés.

L'analyse minéralogique révèle qu'il s'agit de sables essentiellement quartzeux mais contenant une proportion non négligeable de débris de carbonates, de feldspaths et de minéraux lourds. Les carbonates sont représentés par des fragments de calcaires ou autres roches carbonatées du paléozoïque, et par des débris coquilliers contemporains de la sédimentation. L'analyse de quelques échantillons montre que les constituants majeurs se répartissent comme suit: 70 à 85% de quartz; 5 à 12% de carbonates; 9 à 15% de minéraux lourds; 1 à 3% de feldspaths. On a noté que les micas étaient peu abondants.

Dans la fraction lourde, on trouve, parmi les minéraux communs ou abondants: grenat, amphibole, pyroxène (hypersthène), tourmaline et minéraux opaques; et parmi les minéraux peu fréquents: épidote, sphène, zircon et pyroxène monoclinique. Les trois premiers minéraux sont certainement les plus représentatifs de la fraction lourde puisque les minéraux opaques et surtout la tourmaline, minéral très résistant et peu altérable, sont peu significatifs de l'origine et de l'évolution du matériel constitutif des sables.

Parmi les grenats on observe une très nette prédominance des grenats pourpres violacés (du type spessartine) sur les grenats rouges (du type pyrope et almandin). Les premiers sont caractéristiques des roches métamorphiques acides telles que les gneiss très quartzeux et les quartzites, tandis que les seconds sont plus fréquents dans les roches basiques ou ultrabasiques. Plusieurs comptages ont montré que le rapport grenats violacés sur grenats rouges varie de 2.7 à 4.3. Or, Dreimanis *et al.* (1957) ont fait remarquer qu'un rapport supérieur à 1.2 était caractéristique des métasédiments grenvilliens, ce qui concorde parfaitement avec l'idée présumée d'une origine locale du matériel.

Un examen morphoscopique montre que ces sables sont essentiellement composés de grains anguleux de type «non-usés» (NU). Il s'agit de grains et minéraux brisés aux arêtes vives. Ce caractère s'observe aussi bien pour les tailles inférieures que pour les dimensions supérieures à 0.5 mm. L'angulosité n'a donc pas eu le temps de disparaître au cours de la brève reprise des sédiments glaciaires par la mer de Champlain. Un émoussage très faible caractérise quelques grains des arénites moyennes; mais on ne peut parler de vrais «émoussés-luisants» (EL).

L'influence des grès et grès-quartzitiques du Potsdam et surtout ceux du membre Thérésa est clairement manifestée par la courbe de fréquence des grains dits «ronds-mats» (R.M.). Leur pourcentage atteint, avec les ronds-mats cassés, 17 à 21% dans les tailles de 0.420 à 0.590 mm. La présence de ces grains toujours dépolis souligne la brièveté du remaniement de la mer de Champlain. En effet aucun n'a pu devenir «émoussé-luisant»: Lambert (1972) obtient des résultats comparables sur 2 échantillons de la même région.

MODE DE MISE EN PLACE

Nous pouvons démontrer, en nous basant sur l'observation minutieuse de l'évolution morphoscopique des galets et blocs, que les durées relatives des remaniements vont en augmentant lorsqu'on s'adresse à des rudites mises en place à des altitudes de plus en plus basses. Donc les remaniements plus longs, alliés à des horizons à pendages sédimentaires plus faibles, traduisent des stabilisations du niveau des eaux. Certains de ces niveaux peuvent se trouver fossilisés sous les rudites à très forts pendages qui marquent la régression générale, par exemple l'unité Ia du rang Sainte-Germaine.

On peut schématiser la mise en place des rudites de la façon suivante: les amas de tills suffisamment indurés formaient des petites falaises qui furent sapées par les vagues, principalement à l'occasion de tempêtes ou violents orages comme l'ont suggéré Terasmae *et al.* (1972). Au pied de ces abrupts une plage plus ou moins inclinée permettait un remaniement variable des blocs qui finalement s'accumulaient en lits frontaux à forte inclinaison sous une profondeur d'eau de quelques mètres à quelques dizaines de mètres. Les données paléontologiques (voir paléoécologie ci-dessous) confirment cette hypothèse. La matrice sableuse ne sédimentait pas facilement, emportée par les courants et vagues qui pouvaient ébranler les blocs: ceux-ci, possédant une énergie potentielle élevée, pouvaient alors se déplacer facilement sur la pente. La vie pouvait même continuer dans les anfractuosités ménagées entre ces blocs non jointifs: le phénomène est bien connu sur les côtes abruptes et chaotiques de nos jours. Que le milieu devienne plus calme, et des vasières, où décantaient des sédiments plus fins, s'installaient au pied de la falaise ou dans les zones plus favorables. A l'occasion, des blocs hétéroclites pouvaient même y rouler.

Avec le recul des eaux le matériel grossier devenait moins accessible; tout d'abord de plus rares périodes de fortes énergies intercalaient quelques biseaux de rudites dans les arénites qui se mettaient en place sous quelques mètres d'eau. Une influence saisonnière par les glaces du rivage n'est pas exclue. Quelques galets roulaient encore ou, tels ceux qui sont plus aplatis, glissaient sur le sable: ils soulignent maintenant la stratification avec un pendage légèrement plus fort que le sédiment (phénomène classique). Les courants de houle côtiers construisaient des mégarides aux crêtes légèrement obliques ou parallèles à la côte.

Latéralement, vers le large, mais c'est surtout vers le sommet de notre séquence stratigraphique que nous avons la chance d'observer ce phénomène synchrone, les eaux plus calmes permettaient la sédimentation des argiles.

Des points restent à préciser pour expliquer l'origine du matériel arénitique quartzeux assez considérable dans certains cas (rang Sainte-Germaine); on sait toutefois que le ruissellement devait être intense, la végétation étant encore très restreinte. De plus les reliefs d'Oka formaient à ce moment-là un réseau d'îles assez complexe pour favoriser les courants côtiers qui participaient à la construction de ces accumulations. On peut identifier d'autres amas quartzeux à des altitudes comparables: ferme Binette (fig. 1).

Paléoécologie

Si l'on rencontre parfois, dans les sédiments, des niveaux très denses en fossiles, le nombre d'espèces représentées est relativement faible, très certainement à cause de la dessalure de la mer de Champlain, accentuée vers l'ouest (Goldring, 1922 a et b; Wagner, 1970). Toutefois, l'importance numérique des espèces les plus courantes permet une bonne étude paléoécologique.

Les espèces que l'on peut trouver dans les dépôts marins des collines d'Oka sont, d'après Wagner (1970, planche hors-texte):

Macoma balthica Linné
Elphidium bartletti Cushman
Hiatella arctica Linné
Mytilus edulis Linné
Heterocyprideis sp.
Ostracode indét.
Mya arenaria Linné
Balanus sp.
Globulina glacialis Ascanius
Bryozoaire indét.

liste à laquelle il faut ajouter, d'après Elson (1969):

Balanus hameri Ascanius

et, d'après la collection des auteurs:

Balanus crenatus Bruguière
Mya truncata Linné

En règle générale, la faune est représentée, à plus de 98%, par des populations de l'une ou plusieurs des espèces suivantes:

Hiatella arctica
Mytilus edulis
Macoma balthica
Mya arenaria
Balanus crenatus

Deux types de biocénoses caractérisent les dépôts étudiés: animaux fixés sur les galets des rudites (*Hiatella, Mytilus, Balanus*), animaux fouisseurs dans les arénites (*Macoma, Mya*). D'autre part, les zones de passage d'un faciès à l'autre, rudites-arénites ou arénites lutites, se marquent par des variations faunistiques importantes: superposition des deux biocénoses dans le premier cas, populations en thanatocénose dans le second.

Le rang Sainte-Germaine (fig. 7) montre le meilleur exemple de cette répartition des faunes. L'étude sera donc axée sur cet affleurement.

BIOCÉNOSE DANS LES RUDITES (UNITÉ Ib)

Dans ces dépôts grossiers, étagés de 167 à 84 m, des traces de vie marine sont toujours présentes. Il est cependant difficile, dans un tel milieu, de définir une densité de population. Les variations quantitatives de la matrice et des éléments grossiers ne permettent pas de repérer un volume de référence constant.

Dans les populations inventoriées, *Mytilus edulis*, *Hiatella arctica* et *Balanus crenatus* sont souvent dominants. Au rang Sainte-Germaine, *Mytilus edulis* se présente sous l'aspect de grappes de coquilles, entre les blocs, en parfait état de conservation: malgré leur fragilité, 77% des valves ont pu être récoltées intactes; 54% des coquilles ont d'ailleurs encore les valves gauches et droites accolées et n'ont pas été remplies de sédiment au cours de la fossilisation. La coquille elle-même a conservé sa structure initiale (couche externe de calcite, couche interne d'aragonite). Ces nombreux caractères éliminent toute idée de déplacement posthume des individus et intègrent l'espèce dans la biocénose, ce qui est confirmé par la régularité des histogrammes que l'on a pu établir dans cette population (fig. 8). L'allure bimodale de la courbe peut s'expliquer par la succession de générations d'inégale importance (mortalité larvaire élevée certaines années, en raison de conditions de vie plus difficiles).

Des histogrammes aussi réguliers (fig. 8) ont été tracés pour une population de *Hiatella arctica* de Saint-Joseph-du-lac. Il semble bien que les rudites correspondent au milieu de vie de *Hiatella*, que l'on trouve d'ailleurs souvent valves accolées, et que, par conséquent, sa présence soit normale dans cette biocénose. Si l'on se réfère au mode de vie des représentants actuels, un substratum rocheux est absolument nécessaire. Lorsque la lithologie le permet, l'espèce est lithophage, les coquilles s'installant dans un terrier creusé, de préférence dans des calcaires et, parfois, dans des grès à ciment attaquable par les acides (Hunter, 1949). Sinon on les trouve fréquemment installées à l'intérieur de coquilles d'autres Lamellibranches, comme *Mytilus* par exemple, où elles se fixent par un byssus court. Dans ce dernier cas, le rapport *Hiatella/Mytilus* est voisin de 1/50 (Hunter, 1949). Or, dans les populations fossiles étudiées, ce rapport est de l'ordre de l'unité. Il faut donc imaginer un autre mode de fixation. Entre 50 et 70% du matériel grossier (grès-quartzite, gneiss) est peu favorable au creusement des terriers. Dans quelques blocs calcareux, des perforations assez régulières ont pu être notées (fig. 10 b). Est-ce l'oeuvre des *Hiatella* ? C'est possible, mais ces quelques trous ne permettent pas d'expliquer leur densité. Il faut, par conséquent, admettre un mode de fixation entre les blocs ou à l'intérieur d'anfractuosités.

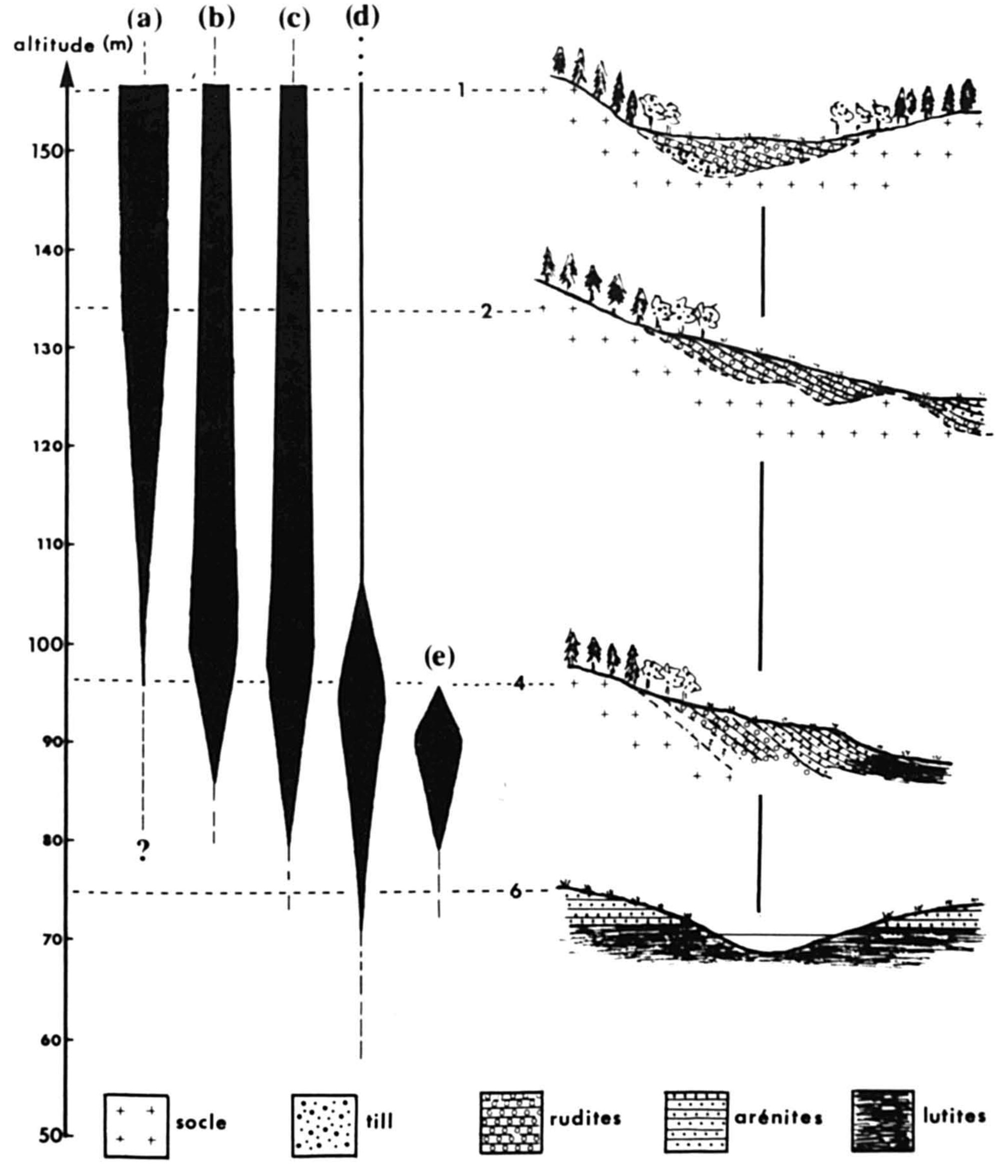

Figure 7. Distribution des espèces dominantes en fonction des altitudes. Fossiles : (a) *Hiatella arctica* (b) *Mytilus edulis* (c) *Balanus crenatus* (d) *Macoma balthica* (e) *Mya arenaria*. Affleurements : (1) Saint-Joseph-du-Lac ; (2) fermes Husereau ; (4) rang Sainte-Germaine ; (6) route de Saint-Benoit.

Les *Balanus crenatus* se présentent eux aussi sous l'aspect d'une population de la biocénose: les individus sont encore fixés sur les blocs, certains se détachant parfois de leur support au moment du prélèvement (fig. 10 c).

A partir de cette biocénose à *Mytilus*, *Hiatella* et *Balanus*, le milieu de vie peut être assez bien défini: une température moyenne supérieure à 4°C, car on sait qu'en deçà, la respiration s'interrompt chez *Mytilus* (Moore, 1958); une salinité probablement peu élevée, car même si ces espèces tolèrent une assez forte dessalure, il faut noter qu'elles ont toutes une légère tendance au nanisme, les longueurs moyennes étant assez basses (variant de 23.5 mm à St-Joseph, à 18.9 mm à la ferme Cataphard, pour *Hiatella* et, de 24.75 mm à Saint-Joseph, à 29.6 mm à Sainte-Germaine, pour *Mytilus)*, et que par conséquent, les conditions de vie n'étaient pas optimales.

Enfin, le trait essentiel de ce microhabitat est certainement le «fond rocheux» qui permet une fixation directe, ou par un byssus, de ces animaux.

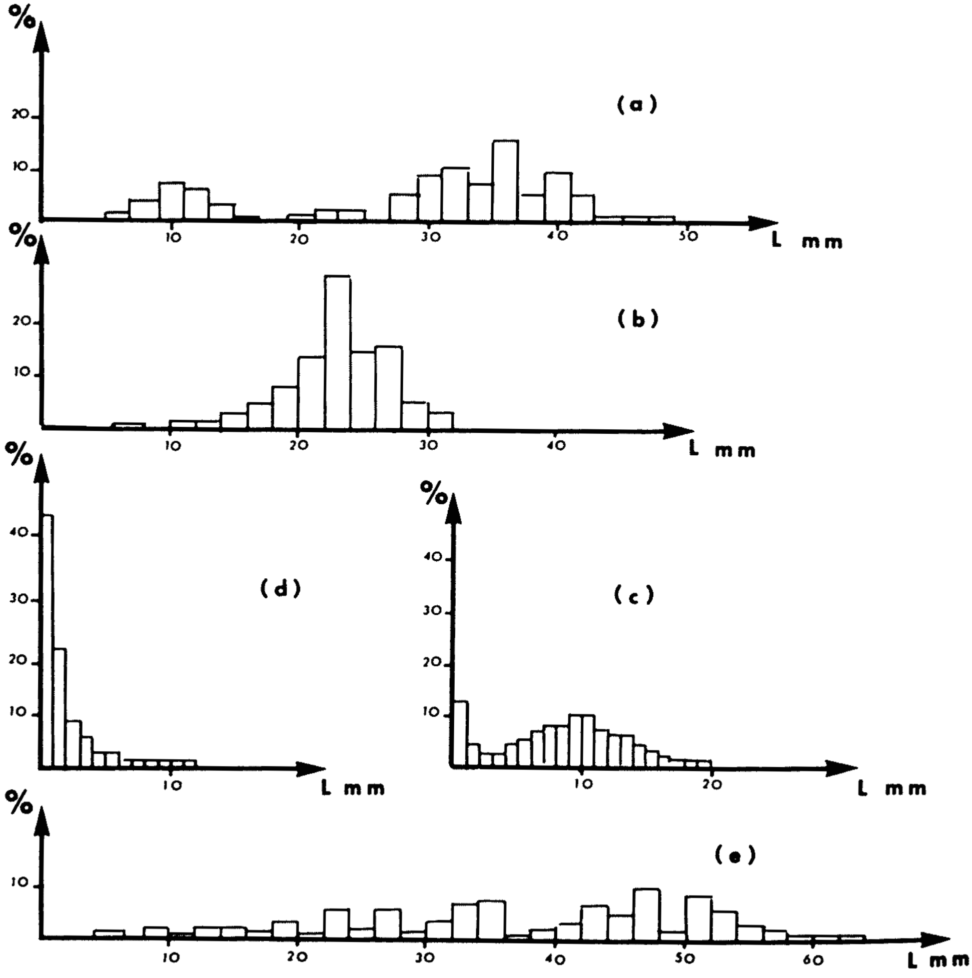

Figure 8. Histogrammes des longueurs de quelques espèces (a) *Mytilus edulis* (affleurement no 4); (b) *Hiatella arctica* (affleurement no 1); (c) *Macoma balthica* (affleurement no 4); (d) Histogramme comparatif dans une population de lamellibranches du Lutétien du Bassin de Paris; (e) *Mya arenaria* (affleurement no 4).

LA ZONE D'INTERDIGITATIONS RUDITES-ARÉNITES (UNITÉ II)

Dans cette zone qui annonce la fin de la sédimentation grossière, la matrice devient plus abondante et l'on rencontre même parfois des strates franchement sableuses (fig. 10 c). Du point de vue écologique, on voit apparaître, par exemple au rang Sainte-Germaine, une biocénose à *Macoma balthica* en position de vie verticale (fig. 10 c) associée à *Balanus*.

Cette modification dans les faunes reflète essentiellement le changement de fond et, probablement, une diminution de la profondeur qui, pour *Macoma*, ne peut excéder 15 m (Kindle et Wittaker, 1918), s'accompagnant peut-être d'une légère augmentation des températures moyennes puisque, d'après Lammens (1967), la reproduction s'arrête chez *Macoma* en deçà de 10°C.

BIOCÉNOSE DANS LES ARÉNITES (UNITÉ III)

Au rang Sainte-Germaine, on trouve comme espèces dominantes ou influentes dans les sables: *Macoma balthica*, *Mya arenaria* et *Hiatella arctica*, avec des densités de population atteignant parfois un maximum de 300 individus par dm^3 de sédiment non foissonnant dans les lits les plus fossilifères. Toutefois, ces différentes populations ne sont pas équivalentes. Les variations des espèces dominantes et du pourcentage de coquilles brisées (fig. 9) permettent de distinguer quatre populations successives et écologiquement inégales: une biocénose à *Macoma*, puis une thanatocénose à *Hiatella* suivie d'une nouvelle biocénose à *Macoma*, à laquelle se joint (au niveau «i») une population de *Mya*.

La biocénose à Macoma

Les coquilles apparaissent dans plusieurs strates de quelques cm de hauteur où plus de 80% d'entre-elles sont verticales, valves jointives, sans orientation particulière de la charnière. Il semble, d'après Brafield et Newell (1961), que l'orientation des coquilles ne puisse être reliée qu'à un phototropisme. Les histogrammes de chaque population échantillonnée montrent une même allure bimodale, se marquant par un premier pic entre 1 et 7 mm et un second entre 10 et 14 mm; l'écart entre les deux pics varie autour de 9 mm; la longueur moyenne varie de 6.79 mm (niveau «b») à 12.44 (niveau «c»). Au niveau «g», l'espèce atteint le plus brillant développement en représentant 99.98% de la faune, pour une densité maximum de 330 individus par dm^3.

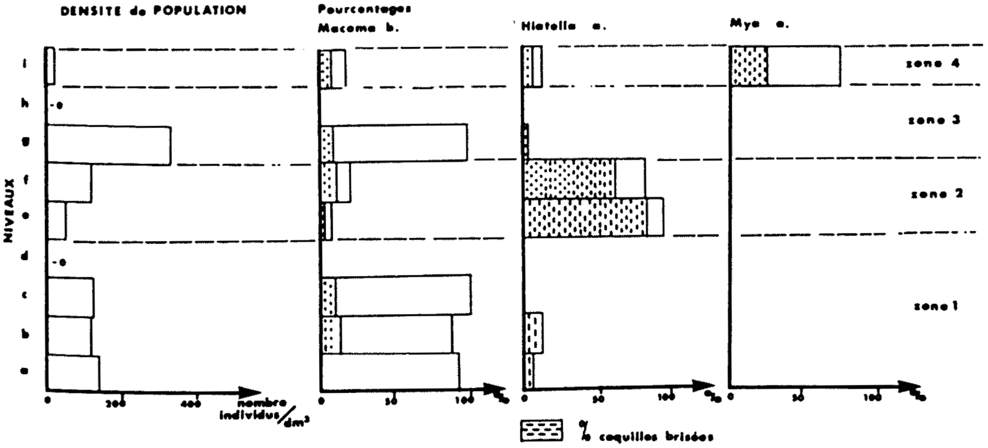

Figure 9. Variation des populations dans les arénites du rang Sainte-Germaine.

L'histogramme théorique d'un lamellibranche, dont larves et adultes partagent la même aire de vie, a une allure asymptotique (la mortalité larvaire étant très élevée), avec parfois un bombement «gaussien» vers les tailles adultes moyennes (fig. 8).

L'histogramme de cette population du niveau «g» pourrait s'en rapprocher (fig. 8). Sinon, l'allure bimodale peut s'interpréter encore comme une alternance de générations dont la survie dépend des conditions climatiques.

La biocénose à Mya

Au niveau «i», *Mya arenaria* fait son apparition. Il semble que l'espèce se superpose à la population précédente de *Macoma*, puisque cette dernière est encore présente, en position de vie, dans ce niveau.

Mya arenaria domine largement, avec un pourcentage de 75.4% suivi de *Hiatella arctica*, 14%, puis *Macoma balthica*, 9.5%. Cette population est certainement la plus spectaculaire, malgré la faible densité (25 individus au maximum par dm^3): ceci est dû à la grande taille des *Mya*. Plus de 96% des coquilles ont les deux valves encore en connexion et sont disposées verticalement avec la partie postérieure, correspondant au siphon, dirigée vers le sommet des strates (fig. 10 d).

Notons que 93% des coquilles présentent, en outre, la particularité d'être parallèles; la charnière se situe vers le haut de la pente sédimentaire, le bord ventral vers le bas, les valves s'ouvrant, en quelque sorte, vers le large: dans cette position l'animal peut ainsi ouvrir à volonté ses valves sans que le sable ne remplisse la coquille.

Les histogrammes (fig. 8) montrent une allure plurimodale assez mal mise en évidence, ici, par le fait que les classes de longueur et de largeur sont grandes. Nous verrons plus loin que des variations de températures sont certainement à l'origine de ces inégalités entre les générations.

Si l'on compare cette population à celle, actuelle, étudiée par Swan (1952a, 1952b) dans le golfe Saint-Laurent, on constate que les rapports biométriques sont identiques, au centième près, mais la dimension maximale atteinte par les représentants fossiles est moitié moindre que celle des coquilles actuelles. Une telle différence dans les tailles laisse supposer que, malgré sa belle apparence, cette population fossile est loin de traduire les conditions de vie optimales de l'espèce.

Une autre curiosité remarquable que l'on a pu noter dans cet affleurement est l'influence du fond. D'une part, l'apparition des *Mya* correspond au sables qui présentent le meilleur classement; d'autre part, dès que la granulométrie devient grossière dans le niveau, avec des éléments de l'ordre du centimètre, les *Mya* sont alors situés au coeur d'un terrier vertical de 20 cm de hauteur sur 5 cm de diamètre, rempli de sédiments plus fins et recoupant les stratifications. (fig. 10 e).

La thanatocénose à Hiatella

Le pourcentage de valves brisées de *Hiatella* varie de 75 à 83% et traduit un remaniement et un transport certain des coquilles avant la fossilisation. Nous savons d'ailleurs qu'un tel fond meuble ne permet pas leur installation. Même si les *Hiatella* ont une origine allochtone on peut supposer qu'ils sont contemporains du dépôt des sables et donc de l'installation des *Macoma* et *Mya*. L'association de ces trois espèces permet de fixer avec une assez bonne approximation les conditions de vie.

La température paraît avoir été un facteur prédominant. Si, pour *Macoma*, une température supérieure à 10°C (Lammens, 1967) semble nécessaire pour la reproduction, les véligères de *Mya* ne se développent qu'au delà de 12°C (Laursen, 1966) sauf exception, tandis que *Hiatella* demande des températures plus basses (moins de 10°C).

L'alternance, d'abord de *Macoma* et *Hiatella*, puis de *Hiatella* et *Mya*, conduit à supposer des températures moyennes favorisant, par périodes, ces trois espèces. On assisterait alors à une alternance d'années thermiquement «fastes et néfastes» pour les larves de *Macoma* et *Mya*. Les périodes défavorables se marquent par une recrudescence des *Hiatella*. En poussant plus loin le raisonnement, on peut admettre pour la base des sables des températures estivales moyennes de l'ordre de 10°C ou plus et, pour le sommet, des moyennes estivales supérieures à 12°C, donc, une augmentation progressive de la température moyenne annuelle au cours de la sédimentation des sables.

La profondeur n'excédait certainement pas quelques mètres, l'optimum pour *Macoma* et *Mya* se situant dans la zone de balancement des marées. L'aire spécifique ne déborde pas 6 mètres audessous des plus basses marées (Laursen, 1966; Kindle et Whittaker, 1918). Quant à la salinité, on peut supposer qu'elle était toujours aussi faible, sinon plus basse que pour les biocénoses à *Hiatella* ou *Mytilus*. *Macoma* et *Mya* tolèrent une dessalure pouvant atteindre près de 4‰ (Zenkevitch, 1963). Le dernier caractère marquant les biocénoses à *Macoma* et *Mya* est le fond meuble.

Que retenir de ces exemples, sinon que la biocénose typique de ce que l'on appelle couramment les «tills remaniés» voit s'associer, avec plus ou moins de régularité, *Mytilus*, *Balanus* et *Hiatella*. Elle caractériserait la première phase de la mer de Champlain, marquée par la mise en place ou le remaniement du matériel grossier laissé par les glaciers, dans des eaux froides et relativement profondes. Contrairement à l'idée souvent admise (Elson et Elson, 1959), rien ne permet d'affirmer que cette première phase ait été marquée par une salinité supérieure à 23‰. Il semble que la présence de *Portlandia arctica*, utilisé comme le «marqueur salin» type (Wagner, 1970), soit la preuve avancée pour justifier une telle salinité. Sa présence dans certaines varves scandinaves (communication orale de Nils-Axel Morner) amène certaines réserves dans l'interprétation de la salinité à partir de ce seul critère. Enfin, la biocénose dans les sables littoraux est celle de mollusques fouisseurs (*Macoma* et *Mya*). Elle n'est toutefois pas constante, puisque *Mya* montre des exigences plus grandes que *Macoma* en ce qui concerne la température et la nature du fond, mais en fait, elle caractériserait la deuxième phase de la mer de Champlain, régressive et donc moins profonde et plus chaude.

Conclusion

Cette étude n'est qu'une première approche à la stratigraphie des dépôts champlainiens. Il nous a paru utile de faire l'inventaire des faciès littoraux caractéristiques d'une grande partie de l'histoire de la mer de Champlain. Bien sûr il existe quelques preuves de niveaux marins ou de lignes de rivages plus élevées (Stanfield, 1917; Gadd, communication orale) et certainement plus basses (crête Saint-Dominique, esker de Primauville-Mercier...; Prichonnet *et al.*, 1972) mais les collines d'Oka résument l'histoire de la régression de cette mer entre 167 m et 84 m (550 à 250 pieds), soit entre moins 11,000 ans environ et moins 10,300 ans (GrN 2035) et/ou 9,900 ans (GiF 2107).

En règle générale le matériel remanié par la mer de Champlain est d'origine

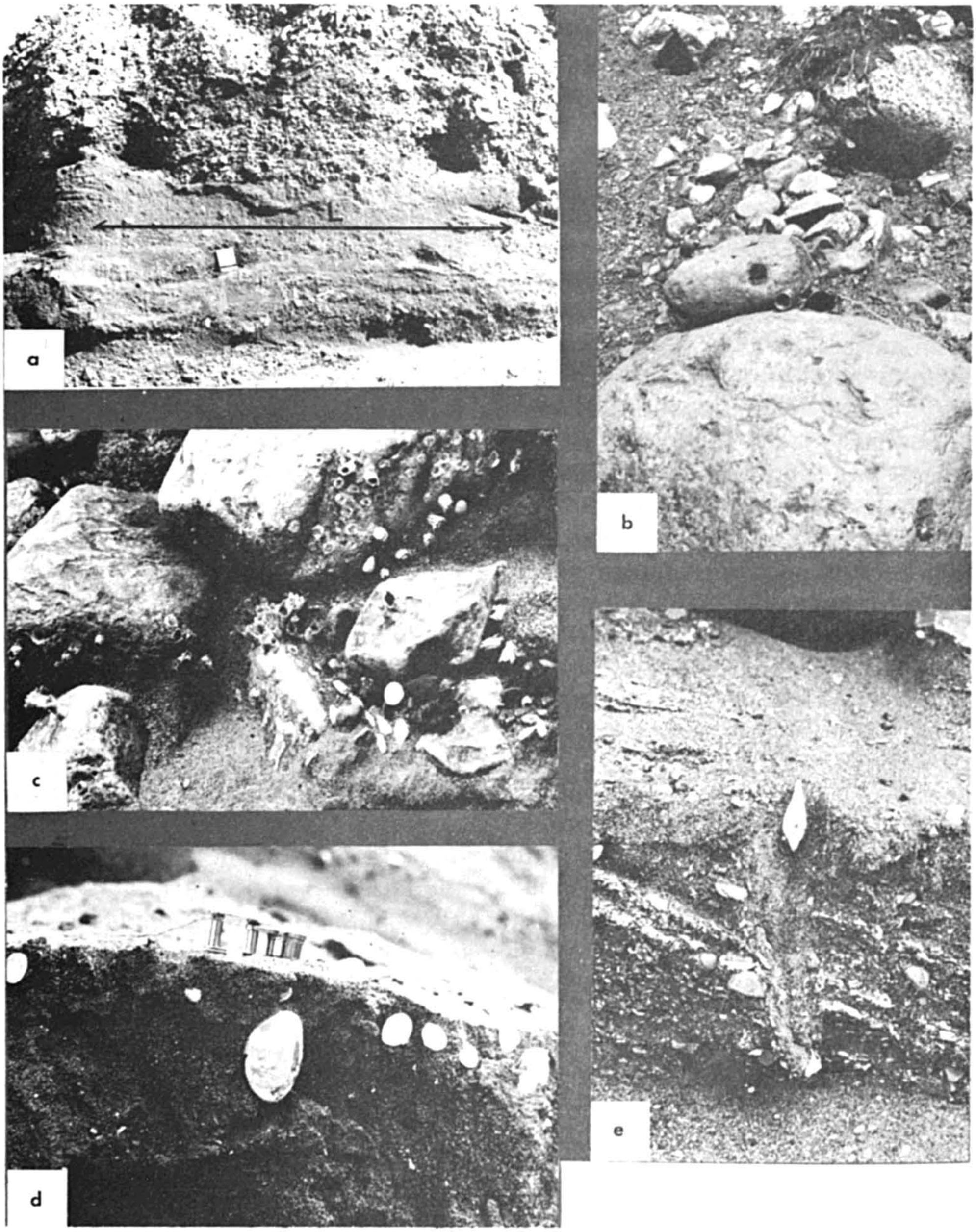

Figure 10. Photographies (a) Mégarides dans les arénites du haut de plage. (b) Type de perforations que l'on rencontre dans des galets carbonatés et qui pourraient représenter des terriers de *Hiatella arctica*. (c) Zone d'interdigitation rudites-arénites : superposition d'une population de *Macoma balthica* en position de vie verticale dans les passées sableuses, à une population de *Balanus crenatus*, fixés sur les blocs des rudites. (d) Biocénose à *Mya arenaria* et *Macoma balthica* dans les arénites du rang Sainte-Germaine. A remarquer, la position caractéristique des *Mya*, par rapport au pendage sédimentaire, tandis que les *Macoma*, plus petites, montrent une orientation quelconque de leur charnière. (e) Terriers de *Mya arenaria* recoupant la stratification, dans des zones d'arénites plus grossières (rang Sainte-Germaine).

glaciaire. Dans le cas présent, ce matériel fut emprunté au soubassement, soit local (les collines pour le cristallin), soit proximal (les basses terres limitrophes pour le sédimentaire paléozoïque).

La durée de ce remaniement fut suffisante pour supprimer, par exemple, les stries glaciaires des galets carbonatés, mais trop brève pour user les grains de quartz «non-usés» ou encore élaborer des «émoussés-luisants» à partir des «ronds-mats». En outre, l'abrasion du matériel le plus tendre et la densité des incrustations sur les éléments les plus grossiers, qui augmentent dans les sédiments d'altitude plus basse, suggèrent des stabilisations tardives du niveau des eaux.

Notons enfin que les informations paléoécologiques corroborent parfaitement les données sédimentologiques pour les affleurements cités :

— lorsque des sédiments très grossiers se mettent en place sous une tranche d'eau assez importante, par effondrements (brutaux) des falaises sapées dans les tills, les faunes sont représentées par des espèces tolérant ces profondeurs (*Hiatella* et *Balanus*) ; c'est le cas de Saint-Joseph-du-Lac, de fermes Husereau et des dépôts très grossiers de base (rudites) du rang Sainte-Germaine ;

— lorsque la profondeur diminue et que la dynamique du milieu décroît, des sédiments plus fins (arénites) succèdent aux précédents et les faunes très littorales s'installent (*Mya, Macoma...*).

Donc, parallèlement au relèvement isostatique, au retrait progressif des eaux marines et au réchauffement général de l'environnement, on voit se modifier les aires spécifiques : régression des *Hiatella* et apparition des *Mya*.

Enfin, si l'allure générale des faciès met en évidence un mouvement régressif de la mer, la construction de tels dépôts littoraux, très développés, suggère des niveaux de stabilisation. Pour R.W. Fairbridge (communication orale), une remontée eustatique et le relèvement isostatique régulier du socle peuvent, lorsque les deux mouvements se compensent, expliquer une stabilisation provisoire du niveau de la mer et permettre ainsi la construction de formations littorales plus développées (barres, terrasses, flèches). Dans la zone étudiée, il semble que l'on puisse définir au moins deux niveaux de stabilisation à des altitudes décroissantes : le premier à environ 190-170 m (dépôts de Saint-Joseph-du-Lac) ; le second à 110-90 m (dépôts du rang Sainte-Germaine).

Un point important reste à éclaircir : y a-t-il régression par saccades ou simplement enregistrement partiel d'un phénomène continu très lent, la construction de formes littorales typiques étant surtout liée aux conditions paléogéographiques locales (matériel glaciaire disponible, forme du rivage et courants côtiers...) ? Les affleurements étudiés suggèrent des stabilisations ou des «phases régressives» lentes séparées de périodes où la «régression» est plus rapide et laisse donc peu de trace.

Au delà de ces résultats partiels des questions demeurent posées, à la fois à propos de la phase transgressive de la mer de Champlain et de la période de régression générale dans les basses terres du Saint-Laurent. D'une part il faut établir des corrélations détaillées, de proche en proche, grâce aux observations recueillies dans des zones comparables aux collines d'Oka, comme les Montérégiennes, et sur les lignes bordières des rivages nord et sud de cette mer ; d'autre part l'approche géochimique devrait permettre de préciser notre connaissance des conditions physicochimiques et d'établir une solide chronologie des évènements de la fin du Pléistocène dans cette région du Québec.

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COMMUNICATIONS BRÈVES

ADDITION À LA FLORE DE TERRE-NEUVE: *LYCOPODIUM ALPINUM* L.

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Lycopodium alpinum L.

NEWFOUNDLAND. St. Barbe South District: Gros Morne (C-121); north slope of Gros Morne near summit with *Salix herbacea, Cassiope hypnoides, Phyllodoce caerulea.* Lat. 49°36' N, Long. 57° 47'W; alt. 2500 ft. July 6, 1973, *Bouchard & Hay 73-201* (CAN, MT). — St. Barbe South District: Western Brook Pond (P-140); *Scirpus cespitosus, Carex oligosperma, Sphagnum* bog with numerous flashets and exposed boulders — on felsenmeer. Lat. 49° 41'N, Long 57° 44'W; alt. 2350 ft. July 25, 1973, *Bouchard & Hay 73-305* (CAN, MT).

Ce sont les premières récoltes du *Lycopodium alpinum* L. à Terre-Neuve, trouvées sur la côte ouest de l'île. Ce lycopode habite des landes à *Cladina* et à *Empetrum* sur le haut des *Long Range Mountains*, à plus de 730 mètres d'altitude.

Espèce arctique-alpine, le *L. alpinum* L. a une distribution circomboréale (Porsild, 1964). Au Canada, il est apparemment absent de la Saskatchewan, du Manitoba, de l'Ontario et des Provinces maritimes (Boivin, 1966). En Amérique du Nord, grâce à différentes chaînes de montagnes, on le retrouve dans les localités situées au sud de l'ensemble de sa distribution. Dans l'ouest il rejoint l'Orégon, alors que dans l'est, il se retrouve jusqu'en Gaspésie (Wilce, 1965). Il n'est donc pas surprenant de le voir aussi sur le haut des *Long Range Mountains* de Terre-Neuve.

Cette nouvelle mention souligne le caractère boréal de la flore des *Long Range Moutains* et ajoute un élément de plus à nos connaissances phytogéographiques de Terre-Neuve.

Les spécimens ont été déposés dans l'Herbier du Parc National Gros Morne, Terre-Neuve, à l'Herbier National (CAN), Ottawa, et à l'Herbier Marie-Victorin de l'Université de Montréal (MT). Monsieur Roger Gauthier et Monsieur Ernest Rouleau ont eu l'amabilité de reviser le texte de cette brève communication.

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PROVANCHER ET LA NOMENCLATURE TAXONOMIQUE DU PIN BLANC

(PINUS STROBUS L.)

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Provancher (1863) publia sa *Flore canadienne* plus de cent ans après le *Species Plantarum* de Linné (1753). Il s'ensuit que dans son livre, les noms latins spécifiques se conforment au système binaire linnéen. Pourtant, il y a une exception, une seule, et c'est un trinôme appliqué au Pin blanc, *Pinus strobus* L. Il s'agit de *Pinus alba Canadensis* Prov. (p. 554), sorte d'appellation hybride, plus longue que le binôme linnéen, mais généralement plus courte que les «noms-descriptions» d'usage universel pendant le siècle qui précéda 1753.

Rousseau et Boivin (1968, p. 1511) furent les premiers à remarquer cette anomalie. Ils commentèrent succinctement que «Provancher ne justifie pas ce choix, qui n'implique d'ailleurs que la reprise d'un nom pré-linnéen.» Est-ce vraiment le cas? Et alors, quel est ce nom pré-linéen et où Provencher le prit-il? Le fait de répondre à ces questions peut nous permettre de connaître une source additionnelle du texte de la *Flore canadienne,* les autres sources livresques étant fournies par l'auteur lui-même, dans sa préface: «Pour le reste, écrivit-il, nous nous sommes servi de quelques rares articles de journaux canadiens et des ouvrages des Botanistes américains Torrey, Gray, Nuttall, Wood, Carey, Flint, Sullivant, Brown, et de la Flora Boreali Americana de sir W. Walker Hooker, de celles de Michaux, Pursh, etc.»

D'abord, dans l'espoir de trouver le trinôme de Provancher chez les auteurs mentionnés ci-dessus, nous avons consulté leurs principales oeuvres, depuis le *Flora of North America* de Torrey & Gray (1838-1840) jusqu'au *Flora Americae Septentrionalis* de Pursh (1814). Nous n'y avons noté aucun trinôme latin de *Pinus strobus* ou ses synonymes. Tout au plus les noms anglais "white pine," "Weymouth's Pine" et "Lord Weymouth's Pine" y paraissent-ils.

Ensuite, nous avons consulté la littérature scientifique, de 1553 à 1860, comprenant les ouvrages traitant du Pin blanc. Afin d'y arriver, nous avons d'abord lu les livres majeurs de Linné (1753), Gronovius (1762) et Endlicher (1847), l'étude de Marie-Victorin (1926), la bibliographie de Rehder (1949), l'*Index Kewensis,* etc.

Voici la liste complète des auteurs qui ont publié un synonyme livresque de facture pré-linnéenne du Pin blanc typique et que nous avons consultés: Belon (1553) (voir à ce sujet Hickel, 1924, p. 57), Plukenet (1696, p. 297), Tournefort (1700, p. 586 et p. 666), Plukenet (1705, p. 171), Colden (1751, p. 79), Duhamel de Monceau (1755, p. 127) et Gronovius (1762, p. 152). Nulle part n'y trouve-t-on "*Pinus alba Canadensis.*" Seul Duhamel du Monceau nous met sur la piste. Voici son texte: "*Pinus Canadensis quinquefolia, floribus albis, conis oblongis & pendulis, squamis Abieti fere similis.* Gault. Pin de Canada à cinq feuilles dont les cônes sont longs, pendants, et dont les écailles sont molles, presque comme celles du Sapin; ou Pin blanc de Canada; ou Pin de Lord Wimouth." — "Pin blanc de Canada'', c'est la traduction française de ce que nous cherchons!

Les noms de facture linnéenne ne nous éclairent pas plus! Les botanistes d'avant Provancher auraient pu utiliser un trinôme semblable à celui de *Pinus alba Canadensis*, ayant l'idée que le troisième terme soit variétal. Mais non. Seul *Pinus alba* existe, par Aiton (1789, p. 371) mais la description qui l'accompagne se rapporte à l'Épinette blanche (*Picea glauca* (Moench) Voss). Un autre *Pinus alba*, celui de von Hoffmannsegg (1824, p. 99) est un *nomen nudum* que l'on suppose traduire le Pin blanc.

Est-ce à partir de rien que Provancher a choisi ce nom? C'est possible mais nous en doutons: les hommes de science ont tendance à partir d'une base lorsqu'ils innovent. Ce ne sont pas des gens purement imaginatifs. Tout ce que l'on peut croire de fantaisiste chez Provancher c'est qu'il aimait pas l'épithète spécifique *strobus*. Il nous en informe implicitement dans un passage de sa préface que citent Rousseau et Boivin (1968, p. 1509).

A-t-il traduit un nom vernaculaire? L'expression Pin blanc du Canada n'est pourtant pas d'origine vernaculaire. Le seul nom qu'utilise couramment le peuple du Canada français est Pin blanc (le premier qui cite ce nom est Charlevoix, 1744). Dans certaines régions, entre autres dans la Gatineau, on entend parfois Pin jaune. En France, on l'appelle presque toujours Pin de Weymouth, rarement Pin du lord. Pour les noms aux États-Unis, je cite Michaux fils (1810, p. 103): «Cette espèce de pin, l'une de celles de l'Amérique septentrionale qui offre le plus d'intérêt, est connue, dans tous les États-Unis ainsi qu'en Canada, sous le seul nom de *White pine*, Pin blanc, à cause de la couleur de son bois qui est toujours très blanc au moment où il vient d'être travaillé: elle reçoit cependant encore quelquefois dans le New-Hampshire et dans le district de Maine, les dénominations secondaires de *Pumpkin pine*, Pin potiron; d'*Aple pine*, Pin pomme, et de *Sapling pine*, Pin baliveau, qui, comme nous le verrons, sont les résultats de quelques propriétés particulières.» Et je cite Sudworth (1897, p. 13): «*White Pine, Weymouth Pine, Soft Pine, Northern Pine, Spruce Pine.*» En Grande Bretagne, selon Miller (1762), il portait le nom de «Lord Weymouth's pine», ou par certains, «New-England pine». Les appellations «eastern white pine» et «american white pine», parfois utilisées aux États-Unis et au Canada, sont d'origine livresque et elles datent du XXe siècle.

A-t-il repris un nom latin ancien, du moins une portion des phrases qui composaient les noms scientifiques de forme pré-linnéenne? Or, d'après le relevé complet des auteurs énumérés ci-dessus, nous voyons que non.

Reste alors la possibilité la plus plausible: le «Pin blanc de Canada», de Duhamel du Monceau, expression trouvée *nulle part ailleurs* avant Provancher, et peut-être envoyée à Duhamel par J.-F. Gaultier, le médecin du Roi en Canada avec qui il entretenait des liens étroits de correspondance. Provancher aurait pu se contenter de choisir *Pinus alba*, s'il n'aimait pas *P. strobus*, mais dans ce cas plutôt étrange, il aurait voulu, vraisemblablement par esprit de précision, et inspiré par Duhamel, apposer le troisième nom «*Canadensis.*»

Duhamel du Monceau constituerait donc une autre source de la *Flore canadienne* de Provancher.

Remerciements

Il me fait plaisir de remercier M. Bernard Boivin qui m'a aidé à trouver la documentation prélinéenne sur le Pin blanc.

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ADDITIONS À LA FAUNE DES CARABIDAE (COLEOPTERA) DU QUÉBEC

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Une étude des collections entomologiques du Québec ainsi que des recherches personnelles sur le terrain nous ont permis d'ajouter dix nouvelles espèces à la faune des Carabidae du Québec. Il s'agit respectivement de *Acupalpus partiarius* Say, *A. testaceus* Dejean, *Anisodactylus carbonarius* Say, *Bembidion concolor* Kirby, *B. yukonum* Fall, *Carabus sylvosus* Say, *Cicindela lepida* Dejean, *Dyschirius pilosus* Leconte, *Stenolophus humidus* Hamilton et *Tachys proximus* Say. La liste des Coléoptères carabiques du Québec s'élève maintenant à 429 espèces. Pour chacune de ces additions nous indiquons le comté et la localité de capture, la date de la récolte, le nombre de spécimens récoltés, le nom du collectionneur, la collection dans laquelle la récolte entomologique est conservée[1] ainsi que le nombre de spécimens qui s'y trouvent; les données connues sur l'habitat, la dynamique et la répartition de ces espèces en Amérique du Nord sont également incluses.

Acupalpus partiarius Say, 1823, p. 90.

Distribution — ÎLE-DE-MONTRÉAL: Montréal 1 et 8-V-1938, A. Robert et J. Ouellet (4, UM); même localité 23 et 27-1V-1961, G. Robert et M. Larochelle (2, AL); même localité 2-V-1968, E.J. Kiteley (1, AL; 1, EJK). L'aire de répartition de cette espèce nord-américaine s'étend, au sud, jusqu'au Texas, et à l'ouest, jusqu'au Kansas. Au Canada, elle a été observée dans le sud de l'Ontario (Lindroth, 1968, p. 937). La mention de cette espèce pour le Québec (Chagnon, 1934, p. 153) n'avait pas encore été confirmée.

Habitat — Peu connu. Lindroth (*loc. cit.*) a capturé ce coléoptère au Lac Erié, sous des débris de rivage.

Dynamique — Un spécimen attiré à une source de lumière artificielle (E. J. Kiteley, communication personnelle).

Acupalpus testaceus Dejean, 1829, p. 460.

Distribution — ÎLE-DE-MONTRÉAL: Montréal 30-1V-1936, un spécimen récolté par A. Robert (UM). Cette espèce semble limitée à l'est des Montagnes Rocheuses; son aire de distribution s'étend, au sud, jusqu'au Texas, et au nord, jusqu'en Ontario (Lindroth, 1968, p. 938).

Habitat — Identique à celui de l'espèce précédente.

Dynamique — Ailes membraneuses complètes, sans doute fonctionnelles.

Anisodactylus carbonarius Say, 1823, p. 32.

Distribution — BERTHIER: Berthierville 5-V-1950, R. Béique (1, JPL). SAINT-MAURICE: Pointe-du-Lac 20-V-1929, 20-VII et 1-VIII-1936, F. Laliberté (4, AL; 9, MJL). Cette espèce de l'est de l'Amérique du Nord étend son aire de distribution, au sud, jusqu'au Missouri (Casey, 1914, p. 173), et à l'ouest, jusqu'au Michigan et au Colorado; au Canada, ce Carabidae a été signalé

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[1] Les abréviations employées dans le texte identifient les collections suivantes: AL — Collection André Larochelle, Rigaud; CNC — Collection Nationale Canadienne, Ottawa; EJK — Collection Eric John Kiteley, Montréal; JPL — Collection Jean-Paul Laplante, Sainte-Foy; LRF — Collection du Laboratoire de Recherches Forestières, Sainte-Foy; MJL — Collection Firmin Laliberté, Sainte Foy; SRSJ — Collection de la Station de Recherches de Saint-Jean, Saint-Jean; UL — Collection de l'Université Laval, Sainte-Foy; UM — Collection de l'Université de Montréal, Montréal.

dans le sud de l'Ontario (Lindroth, 1968, p. 849). La mention de cette espèce pour le Québec (Chagnon, 1934, p. 155) est confirmée pour la première fois.

Habitat — inconnu.

Dynamique — inconnue.

Bembidion concolor Kirby, 1837, p. 54

Distribution — BONAVENTURE: Nouvelle 14-VII-1970, A. Larochelle (2, AL); Port-Daniel 17-VII-1970, A. Larochelle (2, AL). GASPÉ-EST: Anse-à-Beaufils 30-IX-1967, J.-P. Laplante (1, LRF); Cloridorme 26-VII-1970, A. Larochelle (13, AL); Wakeham 20-VII-1970, A. Larochelle (1, AL). GASPÉ-OUEST: mont Albert 23-VII-1970, A. Larochelle (7, AL); Rivière-à-Claude 24-VII-1970, A. Larochelle (4, AL). SAGUENAY: Rivière à l'Huile 14-VII-1971, A. Larochelle (2, AL); Rivière McDonald 15-VII-1971, A. Larochelle (1, AL); Rivière Vauréal 16-VII-1971, A. Larochelle (1, AL). Cette espèce presque transaméricaine étend son aire de distribution, au sud, jusqu'au Colorado; au Canada, elle a été signalée notamment à Terre-Neuve, en Nouvelle-Écosse, au Nouveau-Brunswick et dans l'ouest de l'Ontario (Lindroth, 1963, p. 304). La mention de cette espèce pour le Québec (Chagnon, 1934, p. 105) n'avait pas encore été confirmée.

Habitat — Ce Carabidae vit sur les rives des cours d'eau rapide et froide; le sol est graveleux et humide, sans végétation.

Dynamique — Ailes membraneuses complètes, sans doute fonctionnelles.

Bembidion yukonum Fall, 1926, p. 131.

Distribution — NOUVEAU-QUÉBEC: Poste-de-la Baleine 17-V-1970, R. Audet (3, UL; 3, LRF). SAGUENAY: Sept-îles 19-VII-1971, A. Larochelle (1, AL). TERRITOIRE DE MISTASSINI: 60 milles à l'est de Fort Rupert 16-VII-1963, J.E.H. Martin (1, CNC). Cette espèce circumpolaire a été signalée au Manitoba, en Colombie britannique, dans les Territoires du Nord-Ouest, au Yukon et en Alaska (Lindroth, 1963, p. 321).

Habitat — Sur les rives argileuses des mares (Lindroth, *loco citato*). Trois spécimens récoltés par R. Audet ont été trouvés sous des pierres, les trois autres ont été récoltés sur le sol, celui-ci étant composé de terre argileuse. Le spécimen que nous avons récolté provient d'une plage argileuse de la baie de Sept-Iles.

Dynamique — Les ailes membraneuses sont dimorphes, étant soit complètes, soit réduites à leur extrémité (Lindroth, *loco citato*).

Carabus sylvosus Say, 1825, p. 75.

Distribution — HUNTINGDON: Hemmingford 6-VIII-1925, un spécimen récolté par G.H. Hammond (SRSJ). L'aire de répartition de cette espèce du sud-est de l'Amérique du Nord s'étend, à l'ouest, jusqu'à l'Iowa; au Canada, elle n'a été signalée que dans le sud de l'Ontario (Lindroth, 1961, p. 41).

Habitat — Dans les bois feuillus, en terrain humide (Lindroth, *loco citato*).

Dynamique — Ailes membraneuses très réduites, non fonctionnelles.

Cicindela lepida Dejean, 1831, p. 255.

Distribution — VAUDREUIL: Choisy 30-VII et 15-VIII-1972, trente-trois spécimens récoltés par A. Larochelle (AL). Cette espèce nord-américaine étend son aire de distribution, au sud, jusqu'au Nouveau-Mexique, (Willis, 1970, p. 4) et au nord, jusqu'en Ontario, au Manitoba et en Saskatchewan (Wallis, 1961, p. 68).

Habitat — Dans les sablières et dunes, formées de sable blanc, sec et très fin; le sol y est dépourvu de végétation ou presque.

Dynamique — L'espèce vole bien.

Dyschirius pilosus Leconte, 1857, p. 80.

Distribution — BERTHIER: Berthierville 28-V-1972, un spécimen récolté par A. Larochelle (AL). L'aire de répartition de cette espèce recouvre l'est de l'Amérique du Nord depuis le Texas jusqu'à l'Ontario et le Manitoba (Lindroth, 1961, p. 157).

Habitat — On a retrouvé cet insecte au bord d'un étang, en terrain humide, sablonneux, à végétation éparse, en compagnie des espèces suivantes: *Dyschirius montanus* Leconte, *D. pallipennis* Say et *Elaphrus fuliginosus* Say (Berthierville).

Dynamique — Inconnue.

Stenolophus humidus Hamilton, 1893, p. 305.

Distribution — VAUDREUIL: Rigaud 3-VI-1941, un spécimen récolté par J. Ouellet (UM). Cette espèce de l'est de l'Amérique du Nord étend sa distribution, au sud, jusqu'en Pennsylvanie et au New Jersey; au Canada, elle a été rapportée du sud de l'Ontario (Lindroth, 1968, p. 916).

Habitat — L'habitat est peu connu. Lindroth (*loco citato*) a capturé trois spécimens de cette espèce à Delhi, dans le sud de l'Ontario, dans un marais à quenouilles (*Typha latifolia*); le sol était sablonneux et traversé par un ruisselet.

Dynamique — Ailes membraneuses complètes, sans doute fonctionnelles.

Tachys proximus Say, 1823, p. 88.

Distribution — VERCHERES: Varennes 7, 18 et 21-VI-1971, Y. Bousquet (12, AL). L'aire de répartition de cette espèce de l'est de l'Amérique du Nord s'étend, au sud, jusqu'en Caroline du Sud, et à l'ouest, jusqu'au Nebraska; au Canada, elle n'était connue que du sud de l'Ontario (Lindroth, 1966, p. 432).

Habitat — A Varennes, sur une rive du Saint-Laurent, en terrain argileux, humide avec végétation moyenne, en compagnie de *Tachys obliquus Casey* (Y. Bousquet, communication personnelle).

Dynamique — Ailes membraneuses complètes, sans doute fonctionnelles.

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REVUE DES LIVRES

EHRLICH, P., R. EHRLICH, A.H. HOLDREN and P. JOHN, 1973. **Human ecology.** W.H. Freeman and Company, San Francisco. xii + 305 p. 15.3 x 23 cm. Broché, $4.95.

Cet ouvrage traite de l'Homme dans ses relations avec la biosphère et dans son évolution culturelle, technologique et sociale. Il se divise en deux parties. Dans la première, les auteurs présentent les problèmes que l'Homme s'est créé au cours de son évolution dans le temps et dans l'espace; dans la deuxième ils proposent des solutions possibles à ces problèmes.

Le premier chapitre constitue le sommaire de la première partie. Les auteurs y résument la situation actuelle, ou mieux, la tendance actuelle en ce qui concerne la population humaine, l'exploitation des ressources et l'environnement, et ils se posent la question: l'Homme est-il réellement dans une situation précaire?

Le deuxième chapitre porte sur la *Population humaine*. C'est une analyse des taux de natalité et de mortalité au cours des âges et surtout depuis la révolution agricole et industrielle. Cette analyse permet de suivre l'évolution des taux de croissance des populations humaines dans les pays industrialisés ou soi-disant riches et les pays sous-dévelopés, ainsi que la croissance de la population globale au cours des âges. Ensuite, dans une analyse de la structure de la population humaine et de sa répartition à la surface de notre planète, les auteurs font des projections démographiques dont le réalisme est d'une troublante évidence.

Le troisième chapitre traite de la limite de l'espace terrestre, de l'énergie, et des ressources naturelles non renouvelables. Étant donné que seulement le tiers environ de la surface des terres est cultivable, les auteurs font voir que l'expansion des villes et des réseaux routiers ainsi que les développements industriels empiètent sur les terres arables en plus d'en altérer la qualité, de sorte que la limite de leur productivité sera bientôt atteinte même dans les pays développés. Quant à l'énergie, dont la consommation monte en flèche, comme elle est d'origine fossile, elle est limitée et bientôt les réserves pétrolières seront épuisées et l'on devra retourner à l'usage plus accentué du charbon en attendant que la généralisation de l'usage de l'énergie nucléaire, avec les dangers qu'elle présente, vienne se substituer à l'énergie fossile. L'énergie hydro-électrique est déjà exploitée presque au maximum et la maîtrise de l'énergie solaire ne semble pas rentable. L'énergie utilisable par l'Homme n'est pas illimitée, loin de là.

Quant aux ressources minérales, plusieurs d'entre elles sont près de leur épuisement. Les auteurs étudient les limites de production des ressources renouvelables et en premier lieu de la nourriture. Insistant sur le fait que déjà la faim dans le monde se fait sentir à une échelle croissante, ils font voir que, même en poussant la productivité au maximum et en exploitant à la limite les ressources alimentaires marines, le problème de la faim va aller en s'accentuant, étant donné que le nombre de bouches à nourrir croît plus vite que ne peut croître la production alimentaire. Parmi les autres ressources renouvelables, l'eau se fait rare en bien des régions, et l'Europe occidentale ainsi que le continent nord-américain utilisent respectivement trois fois et deux fois plus d'eau que l'évaporation océanique ne leur en redonne, épuisant ainsi les réserves souterraines.

Abordant le problème de la pollution, les auteurs étudient la pollution de l'air et de l'eau puis ils traitent des déchets solides, des pesticides, des métaux lourds, des radiations, des produits chimiques mutagènes, de la pollution par le bruit et la mauvaise qualité du milieu urbain.

Dans le chapitre suivant, les auteurs font voir que l'Homme contribue à la perturbation, voire à la destruction des écosystèmes. Ils insistent, en particulier, sur le fait que l'Homme, par l'introduction d'engrais en agriculture, d'insecticides, de pesticides ou d'herbicides, interfère progressivement avec les cycles biochimiques et modifie, en les simplifiant, les chaînes alimentaires et, de ce fait, les rend de plus en plus fragiles. Cette influence de l'agriculture moderne se fait déjà sentir dans les océans où aboutissent finalement les eaux contaminées des continents.

Dans le septième chapitre les auteurs cherchent à déchiffrer le réseau des erreurs écologiques afin d'ébaucher des solutions. Ainsi, ils essaient d'évaluer l'impact que peut avoir sur l'environnement une consommation définie qui est, bien sûr, reliée à une production et une technologie de production définie. L'environnement, comme ses constituants biotiques, possède une certaine résistance ou autodéfense contre les facteurs qui tendent à le modifier et c'est ce qui représente l'impact sur l'environnement. En perfectionnant la technologie on peut assurer une plus grande consommation par une population croissante sans accroître sensiblement l'impact sur l'environnement, mais ceci n'est vrai que pour certaines productions et pour un temps limité. C'est pourquoi il importe de retenir que l'amélioration souhaitable de la technologie ne résoudra pas tous les problèmes, et surtout il faut admettre que dans bien des cas en supprimant des causes de pollution on en crée de nouvelles. Ainsi, si on remplaçait les moteurs à combustion interne par des moteurs électriques dans les automobiles, on augmenterait la pollution que causent les usines génératrices d'électricité. De toute façon, comme le déclarent les auteurs, la correction de divers facteurs relevant de la technologie ne suffira pas à neutraliser l'impact de la croissance démographique. Et c'est pourquoi les auteurs, dans le huitième chapitre de la deuxième partie intitulée *Solutions*, proposent la limitation de la population. Cette première solution, ils en étudient les méthodes, depuis les méthodes anticonceptionnelles diverses jusqu'à l'avortement et même la stérilisation volontaire, voire, obligatoire. Mais le hic de cette solution est le temps. En effet, avant que l'application de ces méthodes et la planification familiale se généralisent et arrêtent réellement l'explosion démographique, il s'écoulera un temps assez long et, surtout, il faudra que les individus soient sensibilisés à l'idée que l'humanité doit cesser de croître et que toutes les sociétés changent leur attitude concernant le comportement sexuel et la reproduction. Ceci semble presque utopique suivant les auteurs, mais, pour eux, ce doit être le principal objectif à atteindre.

Dans le neuvième chapitre, la seconde solution proposée, est le changement du comportement des humains à l'égard de l'environnement et aussi à l'égard de leurs frères humains. Cette solution implique des changements radicaux dans le système économique, dans l'exploitation des ressources, dans le concept d'environnement et le degré de consommation; elle implique des changements radicaux dans les systèmes sociaux et politiques et surtout dans l'éducation qui doit devenir plus réaliste. Il s'agit de tâches très considérables puisqu'elles doivent s'accomplir à l'échelle mondiale, et surtout être axées sur un nouveau mode de développement ou de progrès.

Enfin, dans le dixième et dernier chapitre, les auteurs font un résumé de la situation actuelle et font des recommandations. Bien que pessimistes dans l'exposé de la situation actuelle, les auteurs croient que les problèmes peuvent être résolus pourvu que, premièrement, le plus tôt possible on arrive à un contrôle de la population, les Etats-Unis devant donner l'exemple dans cette démarche, deuxièmement, qu'une campagne massive soit lancée pour améliorer l'environnement, ce qui veut dire ramener l'économie à un niveau compatible avec les lois de l'écologie et les ressources limitées de la planète, i.e. réduction de la consommation inutile des ressources et de l'énergie et distribution juste et universelle des biens de consommation. Il faut assimiler la terre à un vaisseau spatial dont l'équipage doit être limité et en rapport avec les réserves alimentaires et autres qu'il transporte.

L'ouvrage que nous venons de résumer est un véritable traité d'écologie à l'échelle humaine et il serait opportun qu'un tel ouvrage fût diffusé dans les milieux scolaires. En effet il s'agit d'un véritable traité d'éthique humaine.

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COLLIER, B. D., G.W. COX, A.W. JOHNSON, P.C. MILLER, 1973. **Dynamic ecology.** Prentice-Hall, Englewood Cliffs, N.J. 563 p., ill. 18 × 24 cm. Relié, prix non indiqué.

COLINVAUX, P.A., 1973. **Introduction to ecology.** John Wiley & Sons, New York. ix + 621 p., ill. 18 × 26 cm. Relié, prix non indiqué.

Deux nouveaux volumes d'écologie arrivent sur le marché. L'un, *Dynamic ecology*, examine les concepts fondamentaux de structure et de fonctionnement des écosystèmes tenant compte à la fois de l'écologie végétale et animale. Partant du niveau d'organisation individuelle, il traite de l'adaptation des êtres vivants et de leurs liens avec l'environnement physique puis, de la structure, de la limitation et de la concurrence au niveau de la population. Sont abordés ensuite les problèmes de la structure et de l'évolution des communautés d'êtres vivants et, finalement, ceux de l'intégration de la structure et de la fonction d'un écosystème. De nombreux exemples tirés des publications écologiques récentes supportent la discussion à tous les niveaux rendant le livre très intéressant à quiconque cherche un traité de base d'écologie générale moderne.

Le deuxième volume, *Introduction to ecology*, part du principe que "*ecology is a pleasant science*" (p.v.) et son auteur décide d'écrire un livre que l'on puisse non seulement consulter mais aussi lire. Il le divise en quatre parties. Dans la première, il trace l'histoire de l'évolution de l'écologie et de la notion de l'écosystème. La deuxième partie décrit l'écosystème et la place qu'y occupent les êtres vivants. Suit la troisième partie traitant de la concurrence entre êtres vivants et de la lutte entre prédateurs et la proie. Enfin, la quatrième partie est une synthèse des trois premières. Elle aboutit aux notions classiques de communauté, de succession, d'écosystème et d'équilibre. Un livre différent, sur les thèmes classiques d'écologie générale.

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MARKS, G.C. ET T.T. KOZLOWSKI, 1973. **Ectomycorrhizae, their physiology and ecology.** Academic Press, New York. xiv + 444 p., 69 fig., 35 tab. 16 × 23 cm. Relié, $28.50.

Les éditeurs de ce volume, tous deux bien connus pour leurs recherches sur la physiologie des arbres forestiers, ont su s'assurer la collaboration de ceux qui ont fait de la biologie des ectomycorrhizes un «domaine sérieux de recherche» au cours des dix dernières années. On y retrouve les contributions suivantes: Marks et Foster sur l'anatomie et la morphologie, Zak sur la classification, Meyer sur la distribution des mycorrhizes, Bowen et Theodorou sur la spermosphère, Bowen sur la nutrition minérale, Hackskaylo sur les échanges de glucides, Slankis sur les hormones, Rambelli sur la rhizosphère, Marx sur les relations avec les maladies racinaires et enfin Mikola sur les applications de toutes ces connaissances dans la pratique de la foresterie.

Pour celui qui a suivi ce domaine de recherche au cours des dix dernières années, il apparaît que les progrès dans les aspects concernant l'anatomie et la physiologie ont perdu un peu de leur élan au profit des travaux concernant la classification, la distribution écologique et les relations des ectomycorrhizes avec les organismes phytopathogènes. On se souviendra que Zak en 1964 avait ouvert la voie aux recherches de Marx qui couronnent actuellement les travaux sur les mycorrhizes. Encore une fois ici Zak fait figure de pionnier dans le difficile domaine de la classification des ectomycorrhizes. Il propose en effet un système beaucoup plus réaliste que celui de Dominik et qui est inspiré de celui couramment utilisé pour les lichens.

Meyer discute la distribution des ectomycorrhizes en forêt naturelle et en plantation. Il faut sans doute lui reprocher d'avoir reproduit trop fidèlement des informations qui ne reposent pas sur des bases solides et qui peuvent semer la confusion. Par exemple, il mentionne la présence d'ectomycorrhizes dans le genre *Acer*.

Le travail de Bowen mérite une attention particulière; il traite de l'absorption des sels minéraux. Ce chapitre devrait intéresser tous ceux qui s'occupent de la production de plants forestiers, de la fertilisation et de la fertilité en milieu naturel.

Deux chapitres concernent des aspects plus fondamentaux de la mycorrhization; ils traitent des échanges de sucres et d'hormones entre les organismes associés. Peut-être cette partie a-t-elle connu un développement excessif par rapport aux autres aspects. Pour le moment elle donne un peu l'impression de piétiner sur place.

Les deux derniers chapitres traités par Marx et Mikola contiennent tous les espoirs que les spécialistes du domaine nourrissent plus ou moins ouvertement. Comme disait Marx récemment: «Il s'agit maintenant de montrer que la mycorrhization des arbres forestiers est un processus susceptible d'applications concrètes».

Enfin, il faut craindre que le titre du volume, associé aux noms de deux chercheurs reconnus pour leurs travaux sur les arbres forestiers, ne perpétue dans l'esprit des forestiers la notion maintenant désuète voulant que les arbres ne portent que des ectomycorrhizes. Les recherches des dernières années montrent la fréquence et l'importance des endomycorrhizes phycomycétoïdes pour les arbres, surtout ceux qui viennent dans les sols à humus de type mull.

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BASSETT, I. J., 1973. **The plantains of Canada.** Monograph no 7. Ministère de l'agriculture du Canada, Division de la recherche, Ottawa. 47p., 18 pl. 15.5 × 23 cm. Broché, prix non indiqué.

Cette courte monographie, la septième de cette intéressante collection, apporte au botaniste amateur ou professionnel un outil de travail excellent et commode pour l'identification et l'étude des plantains du Canada.

Après une courte introduction et une clé de détermination des espèces (au nombre de 17) chaque taxon est repris séparément et comporte une description, une liste de synonymes, des notes sur la distribution géographique, les nombres chromosomiques, les dimensions du pollen, etc. Les belles illustrations d'Ilgvars Steins et des cartes de répartition de chaque espèce complètent le travail.

On reprochera peut-être à l'auteur la brièveté de son texte et de ses explications mais, en réalité, il nous donne beaucoup, sous forme très condensée, et cette monographie résume des travaux antérieurs auxquels on peut se référer. La question des choix taxonomiques reste, comme toujours, matière à controverse et on peut se demander, par exemple, pourquoi notre *Plantago maritima* n'est pas considéré comme une sous-espèce de la plante européenne? Il n'y a pas là de divergence entre les nombres chromosomiques, comme chez les sous-espèces de *P. elongata*, mais le processus de spéciation lente qui se trouve engagé est aussi important, à notre avis, qu'un saut brusque du degré de polyploïdie.

La présentation et la qualité de l'impression sont très satisfaisantes et nous n'avons remarqué que l'oubli de l'emploi du caractère ordinaire dans l'Index pour les noms qui ne sont pas des synonymes. Du côté des illustrations, les changements fréquents d'échelle dans les dessins des capsules et des graines ne facilitent pas les comparaisons rapides. Quoi qu'il en soit, ces peccadilles n'enlèvent rien à la valeur de ce petit traité des plantains.

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ORVIG, S., 1973. **Energy fluxes over polar surfaces.** Proccedings of the WMO Symposium, Moscow 3-5 August 1971. Organisation météorologique mondiale, Genève, note technique no 129, 299 p., nombreuses illustrations. 21 × 27.5 cm. Broché, prix non indiqué.

Un symposium consacré aux flux d'énergie au-dessus des régions polaires s'est tenu à Moscou en août 1971. Les principaux résultats sont rassemblés dans cette note technique, qui a été composée par le professeur Orvig de Montréal. Les sujets sont regroupés en cinq séries, que nous allons analyser l'une après l'autre.

1. *Les flux d'énergie au-dessus de surfaces terrestres*: Dans la première étude faite sur le glacier continental de Devon Island, Holmgren insiste sur les variations du bilan d'énergie en fonction de la situation synoptique et attribue la variabilité du bilan estival de fusion glaciaire aux fréquences différentes d'une année à l'autre des cyclones frontaux qui amènent de l'air chaud, humide et venteux, sur la surface du glacier. Kuhn détaille les composantes du bilan radiatif en courtes longueurs d'onde au-dessus du plateau antarctique oriental. L'absorption du rayonnement par l'atmosphère est assez forte mais difficile à mesurer car elle se fait dans les deux sens: au passage du rayonnement solaire vers le bas et au retour du rayonnement réfléchi par la surface dont l'albédo est de 87%. Des mesures spectrales différentielles ont montré que la seconde absorption valait près de la moitié de la première. Le problème se complique d'ailleurs à la suite des réflexions multiples entre la surface et la base des nuages. L'auteur a calculé en détail toutes les composantes du bilan de faibles longueurs d'onde et les a comparées avec celles d'une ville industrielle anglaise (Kew) et le désert du Pérou (La Joya), déjà étudiés par Lettau (1969).

La troisième étude est due à G. Wendler et porte sur des mesures de la variation journalière du bilan thermique dans l'Alaska. Par temps clair: le bilan est positif en été et l'excédent est surtout utilisé pour l'évaporation; cette dernière se réduit au tiers en automne (équinoxe) où le bilan reste légèrement positif. La perte hivernale est compensée par la condensation (59%), le flux de chaleur du sol (30%) et le flux de chaleur sensible. Par temps couvert: le bilan devient négatif en automne et les pertes hivernales sont très variables d'un type de temps à un autre.

2. *Etudes du vent et analyses détaillées du flux d'énergie*: Trois textes sont rassemblés de manière un peu superficielle dans cette partie de l'ouvrage. Radok étudie les vents katabatiques de surface sur le pourtour du plateau antarctique. Il les compare de manière ingénieuse aux vents alizés des régions tropicales et montre que dans les deux cas la température potentielle et l'humidité augmentent vers l'aval du courant. Un texte de Vinge sur les profils de température et de vent observés au-dessus de la banquise, le long d'une tour de 27 m de haut pendant un mois de janvier, permet de

préciser la faible hauteur (quelques mètres) de la couche limite et certains paramètres nécessaires aux équations de turbulence des basses couches. Enfin, Alisson étudie les flux d'énergie qui accompagnent la formation de la glace de mer en donnant en détail les équations sur lesquelles reposent les valeurs des flux.

3. *Etudes régionales des flux d'énergie:* Langleben a calculé les valeurs de l'albédo de la banquise dans les eaux de l'arctique canadien à partir des observations de vols aériens pendant l'été 1970. On peut obtenir des valeurs de l'albédo avec des pyranomètres montés sur un avion et il est possible d'évaluer la réflexion sur des photos aériennes avec la formule: $A = 10 - 1/10\ (49 - 3.2P)$. A = albedo de la surface en %; I concentration de la glace en 1/10; P = importance des eaux de fonte en surface en 1/10. Les photos couvrent des surfaces de 60km² et le radiomètre des étendues 500 fois plus grandes. L'intérêt de ces mesures est de fournir des données utilisables à l'échelle synoptique et deux vols par mois semblent suffisants. Les valeurs observées tournent autour de 35 à 50%. Orvig et Vowinkel présentent un article intéressant, mais pas toujours très clair, sur le bilan énergétique à l'échelle synoptique au-dessus des régions centrales de l'océan polaire, en mesurant, en particulier, les différences entre les surfaces englacées et celles qui sont libres de glace (effet d'oasis). Le flux de chaleur sensible est 63 fois plus grand en février au-dessus de l'eau qu'au-dessus de la glace mais les différences deviennent faibles en été. Les écarts entre les flux de chaleur latente sont également sensibles mais comme les valeurs absolues des flux sont moindres à cause des basses températures, elles pèsent moins dans les différences entre les deux milieux. L'apport de l'effet d'oasis des eaux libres sur le bilan régional total des régions arctiques est loin d'être négligeable et dépend évidemment du pourcentage d'eaux libres. Enfin, de Thompson, un texte sur le bilan thermique d'une zone libre de glace dans l'Antarctique à la station de Vanda (77° 31 lat. s.). Le bilan de rayonnement annuel est positif, contrairement au bilan négatif attendu sous ces latitudes, à cause du faible albédo (20%) estival.

4. *Etudes globales à grande échelle:* D'abord une simulation numérique de l'influence de la glace de la mer arctique sur le climat, par un groupe d'auteurs: Fletcher, Mintz, Arakawa et Fox, qui intègrent les équations de base des mouvements atmosphériques en comparant le cas où l'océan est couvert de glace avec celui où la mer est libre de glaces. Les documents comparatifs présentés concernent la température, le vent, la pression, l'évaporation, les précipitations et le bilan thermique. Borisenkov et Chernukhin, de l'Institut de recherches arctiques de Leningrad font une estimation des composantes du bilan d'énergie au nord du 50 parallèle et de la manière dont ce bilan se maintient, compte tenu du rôle des eaux océaniques. Enfin, Pogosyan s'intéresse aux relations entre stratosphère et troposphère. Les réchauffements occasionnels de la stratosphère en hiver sont causés par des advections méridiennes originaires de la troposphère.

5. *Interactions entre l'océan et l'atmosphère:* D'abord une étude des déplacements des glaces dans le golfe du St-Laurent, par Pounder, Johannessen et Wright, en fonction des vents et des courants marins. Les cartes préparées régulièrement par les services météorologiques à partir de photos aériennes donnent des informations trop qualitatives sur les mouvements des glaces d'où l'idée de suivre des glaces à la dérive et de laisser entraîner un bateau par une banquise flottante (Le Stephenville, en mars 1969). Les déformations de la banquise sont en liaison directe avec les variations locales du vent qui dépendent indirectement des processus atmosphériques à grande échelle et des échanges énergétiques plus locaux, mais ce problème reste très complexe. Dans la dernière note, Bogorodsky, Gaytskhoky et Tripolnikov discutent de méthodes de mesure par avion de l'épaisseur de la glace et en proposent un modèle photométrique approché.

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VASARI, Y., H. HYVÄRINEN et S. HICKS, (éditeurs), 1972. **Climatic changes in arctic areas during the last ten-thousand years.** A symposium held at Oulanka and Kevo, 4-10 October, 1971. *Acta Univ. Oulu,* A3, Geol. 1, 511p., 28 tab., 120 fig. 17 × 25 cm. Cartonné, prix non indiqué. Distribué par Oulu University Library, 90100 Oulu 10, Finlande.

Ce volume regroupe les 23 communications d'un symposium réunissant 26 chercheurs actifs autour du thème des changements du climat des régions arctiques durant les derniers 10,000 ans. L'idée du symposium est due au professeur Jean Malaurie, de la Sorbonne. Les participants provenaient de huit pays. Quatre d'entre eux venaient du Canada. Le symposium était placé sous l'enseigne de la multidisciplinarité. Parmi les nombreuses contributions, mentionnons une magistrale revue d'Olsson sur l'interprétation des résultats de datation au radiocarbone ainsi qu'une très intéressante communication de Blake concernant l'âge moyen des bois d'épaves retrouvés sur les plages soulevées de l'arctique canadien. L'archéologie, la dendrologie, la climatologie, la glaciologie et la malacologie sont venues appuyer la géologie quaternaire dans l'effort d'élucider l'évolution des paléoclimats arctiques. Une place de choix a été réservée à l'analyse pollinique qui fait l'objet de six articles. Toutefois, la qualité de ces derniers est assez inégale. Les travaux de Fredskild et de Ritchie, portant respectivement sur le Groëland et le delta du McKenzie, se détachent nettement des autres par leur qualité.

Un total de plus de 650 références bibliographiques listées ajoute à la valeur de ce livre qui constitue une excellente revue de littérature sur le sujet. De plus, chaque communication est accompagnée de la discussion qu'elle a provoquée ce qui, pour le spécialiste, complète l'ouvrage de façon très intéressante. Ce dernier y trouvera certaines données nouvelles, l'étudiant gradué, de bonnes sources bibliographiques. Malgré la facture assez pauvre du volume, plusieurs figures, tableaux et diagrammes sont pratiquement illisibles (p. 180, par exemple) ou ne permettent pas de réutiliser les données, on devrait le lire avant de partir en expédition dans le grand nord.

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WILLIAMSON, S.J., 1973. **Fundamentals of air pollution.** Addison-Wesley Publishing Co., Don Mills, Ontario. xv + 472 p., 162 fig., 29 tab. 24 × 16.5 cm. Relié, prix non indiqué.

Les fondements de la pollution atmosphérique à l'intention des étudiants du premier cycle, sans recours excessif à la mathématique (calcul différentiel utilisé dans un seul chapitre) et conduisant à une excellente compréhension des phénomènes de la pollution atmosphérique, voilà ce que nous offre cet excellent manuel.

Selon une approche multidisciplinaire, l'auteur puise l'essentiel de son exposé à même la météorologie, la chimie, la physique et l'ingénierie. Il traite même, dans un dernier chapitre de l'interface entre les aspects physiques et politiques. Mais l'accent porte manifestement sur la compréhension des phénomènes physiques: lois fondamentales de l'atmosphère, bilan d'énergie, mouvements atmosphériques à grande, moyenne et petite échelles, dispersion des effluents, études des smogs sulfureux et photo chimiques dans leurs sources, leurs constituants et leurs réactions, et une étude spéciale sur les aérosols. Un chapitre préliminaire fort intéressant traite des effets nocifs: l'étudiant y apprendra comment mesurer de façon objective l'effet si subjectif des odeurs sur les individus et les populations, comment saisir l'impact des polluants sur le système respiratoire, comment quantifier les effets des polluants sur la visibilité atmosphérique.

L'étudiant appréciera aussi les qualités suivantes de l'auteur: sa proximité des articles originaux (pour la plupart vieux de quelques années à peine et tirés des grandes revues scientifiques); souci constant de départager le connu de l'inconnu, le vérifié de l'hypothétique; et son excellente présentation pédagogique se signalant par une série de questions et de problèmes à la fin de chaque chapitre (pourquoi ne pas avoir fourni les réponses quantitatives aux problèmes?), la discussion en annexes de sujets plus élaborés, l'utilisation uniforme du système international d'unités MKS avec présentation, en annexe, des facteurs de conversion. Ajoutons enfin que la profondeur de champ des sujets traités est partout apparente et qu'on indique à l'étudiant des voies d'approfondissement grâce aux suggestions de lectures apparaissant à la fin de chaque chapitre. Somme toute, un excellent texte pouvant servir d'introduction à la compréhension scientifique de la pollution atmosphérique à l'étudiant qui possède déjà une bonne base collégiale en chimie, physique et mathématiques, mais n'a encore rien acquis en météorologie, ni en ingénierie.

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HADAS, A., D. SWARTZENDRUBER, P.E. RIJTEMA, M. FUCHS et B. YARON, 1973. **Physical aspects of soil water and salts in ecosystems.** *Ecological studies,* volume 4. Springer-Verlag, New York. xvi + 460 p., 65 tabl., 221 fig. 16 × 24 cm. Relié, $34.80.

Les pédologues essaient de donner une base scientifique à l'art ancien qu'est l'irrigation. Ce livre est une collection de textes présentés et discutés au symposium sur la technologie et la physique de l'eau du sol tenu en Israël en 1971. Les auteurs traitent des aspects théoriques et pratiques des phénomènes physiques associés avec l'eau du sol. Les textes sont groupés en cinq sujets.

Le mouvement de l'eau dans le sol: La première section traite en profondeur de l'infiltration, de la redistribution de l'eau dans le sol et de l'écoulement vers les racines. L'utilité des modèles mathématiques décrivant le mouvement de l'eau dans le sol est analysée. On discute des problèmes causés par l'hétérogénéité du sol et de l'applicabilité de la théorie de l'infiltration en conditions naturelles.

Les intéractions eau-sol: Dans cette section on traite de la rétention de l'eau par les sols argileux et de l'eau liquide en contact avec les particules minérales dans un sol gelé. Un des auteurs discute de la valeur du concept de la capacité au champ et des avantages de la détermination de celle-ci *in situ* plutôt qu'en laboratoire.

L'évapotranspiration: Dans le premier texte on rapporte la quantité de publications disponibles sur l'évaporation et on énumère chronologiquement les contributions les plus importantes sur le sujet. Le concept de l'évapotranspiration potentielle y est discuté. Les autres contributions portent sur l'évaporation et le régime thermique des sols nus, l'absorption de l'eau par les plantes et les facteurs qui affectent l'évaporation et la transpiration.

Les besoins en eau des plantes: Cette quatrième section traite exclusivement des problèmes pratiques d'irrigation pour satisfaire les besoins en eau des plantes.

Contrôle de la salinité: L'accumulation et le délavage des sels dans le sol sont des problèmes importants dans les régions semi-arides. Ces problèmes sont traités du point de vue théorique et pratique dans la dernière section.

Les deux premières sections sont recommandées pour le spécialiste de pointe en hydrodynamique des sols. La troisième section est très intéressante et peut-être comprise par celui qui possède des connaissances théoriques en micrométéorologie et en hydrodynamique des sols. Le langage utilisé dans la quatrième section est simple et à la portée de tout ingénieur. Enfin, la dernière section discute de problèmes peu fréquents dans nos conditions climatiques. C'est un livre que je recommanderais pour les bibliothèques scientifiques.

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BIBLIOTHÈQUE
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THE NORTH AMERICAN SPECIES OF *LEIOPHRON* NEES, 1818 AND *PERISTENUS* FOERSTER, 1862 (HYMENOPTERA: BRACONIDAE, EUPHORINAE) INCLUDING THE DESCRIPTION OF 31 NEW SPECIES

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Résumé

Les espèces nord-américaines des genres braconides *Leiophron* Nees et *Peristenus* Foerster sont revisées. Quatre espèces sont transférées de *Leiophron* à *Peristenus* faisant ainsi de nouvelles combinaisons de noms. *Euphorus spiniscapus* Muesebeck est relégué au rang de synonyme postérieur de *L. cephalicus* (Provancher). Trente-et-une nouvelles espèces sont décrites, 11 de *Leiophron* et 20 de *Peristenus*. Des clefs sont fournies pour les groupes, pour 19 espèces de *Leiophron* et 24 espèces de *Peristenus*.

Abstract

The North American species of the braconid genera *Leiophron* Nees and *Peristenus* Foerster are reviewed. Four species are transferred from *Leiophron* to *Peristenus*. *Euphorus spiniscapus* Muesebeck is suppressed as a junior synonym of *L. cephalicus* (Provancher). 31 new species are described, 11 in *Leiophron* and 20 in *Peristenus*. Keys are provided to the groups and 19 species of *Leiophron* and to 24 species of *Peristenus*.

Introduction

The North American braconid species reviewed in this paper have been classified in the genera *Leiophron* Nees (=*Euphorus* Nees) and *Euphoriana* Gahan. The genus *Peristenus* Foerster, which was considered by most previous authors a synonym of *Leiophron*, was re-established by Loan and Bilewicz-Pawińska (1973) recently. These authors defined *Peristenus* as including a group of species characterized chiefly by tergite 1 of the gaster closed beneath at its base and male genitalia with dorsal and ventral parameres subequal basally. Characters of *Peristenus* and *Leiophron* are outlined in a review of European species (Loan, 1974). In the latter paper *Euphoriana* was suppressed as a synonym of *Leiophron*.

Muesebeck (1936) dealt with seven species of *Euphorus* and one of *Euphoriana*; two species of *Leiophron* and two of *Euphoriana* were since described (Loan, 1966, 1970a, 1970b). Of the species described in these genera, or placed therein by Muesebeck, four are now transferred to *Peristenus* and eight to *Leiophron*. A total of 11 new species of *Leiophron* and 20 of *Peris-*

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tenus are described. Type specimens of both North American and European material were studied.

Peristenus is a remarkably homogeneous genus which is not at present divisible into species groups. *Leiophron*, however, contains a grouping of naturally diverse species. These are organized here into four groups to indicate relationships and to facilitate identification. The *Scitulus* species group is characterized chiefly by an open submediellan cell. The hairy median and submedian cells and impressed notaulices indicate a closer relationship to *Peristenus* than that of the other species groups of *Leiophron*. The *Occipitalis* species group shares with *Maculipennis* and *Uniformis* groups a closed submediellan cell. However, unlike the latter groups, the front wing venation of the *Occipitalis* species groups is complete. The *Maculipennis* and *Uniformis* groups appear to contain the most advanced species of *Leiophron*. They are similar except that the cubitus of the *Maculipennis* group is indicated. The wings are often infuscated and the venation of both groups is reduced; the notaulices are not or scarcely indicated.

Many of the new species were collected in the district of Belleville, Ontario, and chiefly near Fuller (latitude 44° 24′ N, longitude 77° 24′ W) by the author and D.G. Reid during a survey of parasites of the nymphs and adults of mirids (plant bugs). This paper is based on the material of the Belleville survey and the general collections of these groups in the Canadian National Collection and U.S. National Museum. Host records are given if species were reared or otherwise associated with mirid hosts.

The life-histories and incidence of parasitism of species collected at Belleville and records of mirids parasitized by braconid eggs or larvae will be given in a subsequent paper.

Holotypes are deposited as indicated for each new species. Paratypes are assigned to the Canadian National Collection (CNC) and, where material is sufficient, to the U.S. National Museum (USNM), British Museum (Natural History) (BM), and the Zoological Institute, U.S.S.R. Academy of Sciences, Leningrad (ZIL).

Biology

HOSTS AND LIFE HISTORY

The known North American species of *Peristenus* and *Leiophron* are specific parasites of plant bugs belonging to the family Miridae (Craig, 1963; Clancy and Pierce, 1966; Loan, 1965, 1966, 1970a, 1970b) while the closely related species of *Euphoriella* Ashmead so far have been reared only from Psocoptera (Muesebeck, 1956; Sommerman, 1956; Loan and New, 1972). However, associations with different host groups have been reported from other continents: in Europe *Leiophron* has been reared from Psocoptera (Broadhead and Wapshere, 1966; Richards, 1967; New, 1970) and in Africa *Euphoriella* from a mirid and *Leiophron* from a lygaeid (Nixon, 1946). There are many additional records of braconid larvae which have been found in nymphs or adults of mirids (Leston, 1959, 1961 in England). Unfortunately, because immature stages cannot yet be identified to species or genus, these records cannot be assigned with certainty to known species.

Whether the braconid is monophagous or attacks two or more mirid species is difficult to determine as rearings are interrupted by diapause or, frequently, by the dealth of the larva or adult in the cocoon. Some of the parasites for which hosts are noted in this paper appear to be species specific. Others appear to be broadly polyphagous. For example, *P. pallipes* (Curtis) attacks six species in four genera (Loan, 1965). Waloff (1967) in England reared three braconid species from a mirid complex on broom. She found that *L. heterocordyli* Richards parasitized one species only, whereas *L. apicalis* Haliday parasitized two on broom and one on gorse, and *P. orthotyli* (Richards) three mirid species, all on broom. Most, if not all of the African species described by Nixon (1946) appear to be species specific. In coexisting populations of *Lygus rugulipennis* Poppius and *Stenodema virens* (L.) in Poland it was determined that *rugulipennis* was parasitized by three species of *Peristenus*, whereas *virens* was attacked by a fourth species specific for it (Loan and Bilewicz-Pawińska, 1973).

The adult emerges from an overwintering cocoon in the soil and parasitizes first or second instar mirid nymphs. Development is solitary and supernumaries die as eggs or remain moribund as first instar larvae. There are five larval instars (Loan, 1965) but only four according to Ammah-Attoh (in Waloff, 1967). In pale-bodied hosts, such as nymphs of *Plagiognathus*, the mature larva distends and discolors the abdomen; in adult hosts, however, there is no external evidence of parasitism. Development and emergence may take place in the mirid nymph or, alternatively, in the teneral adult. Examples of the latter type are *P. pallipes* in *Lygus lineolaris* (Palisot de Beauvois) and *P. plagiognathi* (Loan) in *Plagiognathus* spp. (Loan, 1965, 1966). The mature larva ruptures the side of the mirid's abdomen and drops to the ground where it spins a tough, thick-walled cocoon within the top 2-4 cm of the soil. The larva migrates through the soil particles for a short period of time; however, if cocoon formation is not begun within a few hours following emergence the larva will die. No examples were seen by me of larvae forming their cocoons three weeks or more after emergence as noted by Waloff (1967).

In temperate and north temperate regions the life cycle is usually univoltine and controlled by a diapause which roughly synchronizes the emergence of adult parasites with the development of the mirid population. A bivoltine species is known from Poland (Loan and Bilewicz-Pawińska, 1973) and multivoltine species from Turkey (Drea *et al.*, 1973) and Uganda (Nixon, 1946). The parasite with a univoltine life cycle remains in its cocoon for the greater part of its life-time because of diapause. Larvae of *P. pallipes*, for example, emerge from *Labops hirtus* Knight in May and early June and form cocoons from which adult parasites do not emerge until the following April and May (Loan, 1965).

COLLECTING AND REARING

The presence of parasites usually can be determined from dissections of mirid nymphs. The most practical and efficient way to collect nymphs, and in some cases mirid adults, is to beat foliage of trees, shrubs, and tall herbs over a beating frame. The nymphs are more easily seen on black cloth rather than on white. It is useful to shade the cloth to protect the nymphs from the heat of the sun. The nymphs are captured by a tube-type aspirator and gently blown into ice-cream cartons containing foliage of the breeding plant. Samples are then dissected in the laboratory to determine whether or not the population is parasitized. If the parasites are chiefly first instar larvae, rearing should not be attempted until additional, later samples indicate that the larvae are mature or nearly so.

Mirid nymphs or adults parasitized by such larvae are then collected and placed on foliage over pots of soil. Emergence of the larvae is indicated by the death of the mirids or by the unsteady walk and flattened, twisted abdomens of live mirids. When the rearing has been completed the soil pots are identified by plastic tags, covered with fine, plastic mesh wired in place, and transferred without delay to a shady place outdoors. The pots are lightly covered with sphagnum moss and buried slightly below the soil surface. No further attention is required until the following spring. As soon as the snow has gone, but not later than late April, the pots are lifted and removed indoors or to an insectary. A polybag is slipped over each pot to trap emerging parasites.

Waloff (1967), Bilewicz-Pawinska (1968), Clancy and Pierce (1966) and Drea *et al.* (1973, laboratory rearing) have outlined rearing methods of mirid parasites which differ in some detail from this account. It is important to note that Bilewicz-Pawińska found that the number of emerging adult parasites decreased if the cocoons in the soil were disturbed.

Taxonomy of *Leiophron* Nees

KEY TO NORTH AMERICAN SPECIES GROUPS OF *LEIOPHRON*

1. Submediellan cell opened; median and submedian cells sparsely or abundantly hairy; notaulices indicated partly or completely or rarely absent; wings usually hyaline .... *Scitulus* species group
   Submediellan cell closed; median and submedian cells glabrous; notaulices absent in most species; wings often infuscated 2
2. Veins of front wing complete .... *Occipitalis* species group
   Veins of front wing reduced so that discocubital cell open behind, or consisting only of second abscissa of radius, basalis, discoideus, and nervulus 3
3. Cubitus indicated .... *Maculipennis* species group.
   Cubitus absent .... *Uniformis* species group.

KEYS TO NORTH AMERICAN SPECIES OF *LEIOPHRON*

Scitulus species group

1. Discoidal cell opened behind .... (1) *Leiophron tuberculatus* (Muesebeck)
   Discoidal cell closed behind 2
2. Bicolorous: head light reddish, entire thorax castaneous .... (2) *Leiophron* ***birdi*** n. sp.
   Light reddish with mesonotum somewhat darker but not castaneous 3
3. Posterior face of propodeum about 45° from the transverse; malar space unusually wide, exceeding basal width of mandible or length of flagellar article 1; face very wide, almost 2.0 times eye width (♂); head very polished, swollen at lower genae (♂) .... (3) *Leiophron* ***borealis*** n. sp.
   Posterior face of propodeum approximately vertical, dorsal face short; malar space and face width much less than described above .... (4) *Leiophron scitulus* (Cresson)

Occipitalis species group

1. Mesonotum unusually long and narrow, longer than wide .... (5) *Leiophron* ***compressus*** n. sp.
   Mesonotum typically as wide as long or wider than long 2
2. Head subcubital; frons rather flat and long; face depressed between eyes which protrude past face; eye with long axis more horizontal than vertical 3

Head rectangular; otherwise not as above 5

3\. Reddish black; front wing deeply infuscated; notaulices absent .... (6) *Leiophron* ***fuscipennis*** n. sp.

Light reddish; wings hyaline; notaulices lightly impressed 4

4\. Eye small, scarcely longer than wide (♂), and shorter than face width, long axis much less than 90° from the transverse .... (7) *Leiophron* ***grohi*** n. sp.

Eye larger, 0.7 times as long as wide, and longer than face width, long axis almost horizontal (♂) .... (8) *Leiophron cephalicus* (Provancher)

5\. Front wing lightly or moderately infuscated 6

Front wing hyaline 7

6\. Bicolorous; head light reddish, thorax castaneous; tergite 1 slightly more than 2.0 times as long as wide at apex, distinctly wider at apex than at base .... (9) *Leiophron* ***pallidipennis*** n. sp.

Light reddish; tergite 1 almost 3.0 times as long as wide at apex, sides subparallel .... (10) *Leiophron occipitalis* (Muesebeck)

7\. Black; postocellar space exceeding ocular-ocellar space; flagellum short, thickened distally (♀); nervellus as long as radial cell .... (11) *Leiophron* ***provancheri*** n. sp.

Reddish; postocellar space less than ocular-ocellar space; nervellus spurlike, not nearly as long as radial cell .... (12) *Leiophron* ***brevipetiolatus*** n. sp.

Maculipennis species group

1\. Uniformly reddish black, flagellum yellowish; frons depressed between antennal sockets .... (13) *Leiophron* ***fumipennis*** n. sp.

Reddish or reddish brown; frons not as described above 2

2\. Flagellar articles 12-13 (♀), apical articles wider than long, flagellum unusually short, 1.3 times head width; mesonotum perfectly smooth; front wing strongly infuscated .... (14) *Leiophron maculipennis* (Ashmead)

Flagellar articles exceed 13 (♀) 3

3\. Front wing infuscation not pronounced, area bordering radial cell almost hyaline; face as wide as eye; apex of clypeus not obviously truncate, protuberances at lateral margins absent (♂) .... (15) *Leiophron muesebecki* (Loan)

Front wing rather deeply infuscated; face wider than eye (1.2:1); apex of clypeus distinctly truncate with protruding lateral margins (♂) .... (16) *Leiophron* ***rufipennis*** n. sp.

Uniformis species group

1\. Occiput broadly immargined behind; slender, light yellowish species .... (17) *Leiophron uniformis* (Gahan)

Occiput margined though carina behind vertex rather thin 2

2\. Eye black; traces of notaulices indicated by short, transverse, fine striae; mesepisternum delimited posteriomedially by finely sculptured, wide depression; tergite 1 not carinate on sides; flying in the Belleville, Ontario district in late summer; parasitic on *Lygus lineolaris* .... (18) *Leiophron lygivora* (Loan)

Eye green; traces of notaulices not as evident as in *lygivora*; mesepisternum without a distinct depression as described for preceding species; tergite 1 carinate on sides; flying in the Belleville district in early summer; parasitic on *Trigonotylus coelestialium* (Kirkaldy) .... (19) *Leiophron* ***trigonotylidis*** n. sp.

***Scitulus* species group**

1. *Leiophron tuberculatus* (Muesebeck)

Euphorus tuberculatus Muesebeck, 1936: 31. Holotype: ♀, labelled "Jacksonville, Fla.; Type; *Euphorus* Type [hand-written]; Type No. 49917 USNM; *Euphorus tuberculatus*. Mues. Type Det. Muesebeck". In the U.S. National museum, Washington, D.C.

Leiophron tuberculatus: Shenefelt, 1969: 47.
Euphoriana tuberculatus: Loan, 1970: 441.

L. tuberculatus is light reddish brown and distinctive by absence of the recurrens vein. The notaulices are impressed as in the type, or not indicated (figs. 12, 31).

DISTRIBUTION: **United States.** Florida, Georgia, Kentucky, New Hampshire. (Georgia and Kentucky records from the Canadian National Collection from specimens captured in a Malaise trap).

2. *Leiophron* ***birdi*** n. sp.

Holotype: ♂ , United States. New York, Lake Placid, 2000′; 19. VII. 1962, coll. J.R. Vockeroth. In the Canadian National Collection, Ottawa. CNC 13, 140.

Paratypes: 1♂, Canton, Maine, L-2, T-2; 1♂, Wilawana, Pennsylvania, 7.1.1940, coll. R.H. Crandall (both USNM).

HOLOTYPE MALE: Length about 3.0 mm. Bicolorous. Head light reddish; flagellum dark reddish brown; legs reddish yellow with tibia III dusky; front wing hyaline, veins moderately infuscated.

Head rectangular, in profile eye directed downward rather than forward; frons polished, smooth without a medial carina; face lightly hairy, as wide as eye, 0.7 times eye length, 1.2 times as wide as apex of tergite 2; malar space not greatly extended, about 0.5 times basal width of mandible, slightly greater than POL; flagellar articles 14, article 2 about 0.5 times eye length or 2.0 times POL, 1+2 1.3 times greater than face width; occipital carina incomplete medially for a short distance. Mesonotum shiny, with sparse, fine hairs and widely-scattered, fine punctures; notaulices complete, foveolate; mesepisternum smooth, shiny. Stigma of front wing broad, 2.0 times as long as wide; radial cell about as long as parastigma; first intercubitus entering cubitus just above recurrens (fig. 32). Tibia III 0.86 mm long. Tergite 1 (fig. 6) 2.3 times as long as wide at apex, finely reticulate, 1.3 times as wide at apex as femur III.

FEMALE: Unknown.

The color, large size, complete front wing venation, open sub-mediellan cell, and impressed notaulices separate *birdi* from its Nearctic relatives.

This species is named for the Manitoba naturalist Ralph Durham Bird (1901-1972).

DISTRIBUTION: **United States.** Maine, New York, Pennsylvania.

3. *Leiophron* ***borealis*** n. sp.

Holotype: ♂, Canada, Ontario, One-sided Lake. 1-15. VII. 1960, coll. S.M. Clark. In the Canadian National Collection, Ottawa. CNC 13, 141.

HOLOTYPE MALE: Length about 2.0 mm. Light reddish brown. Head and mesonotum darkest areas of body; scape and pedicel pale yellowish contrasting with dusky flagellum; legs, tergite 1, 0.5 of gaster basally behind tergite 1 yellowish; tibia III somewhat infuscated; wing veins lightly infuscated.

Head smooth, polished, temples and genae swollen; frons smooth, impunctate, without a medial carina; face in front view apparently glabrous but with inconspicuous, thin, fine hair, unusually wide, 1.4 times as wide as length of eye, subequal to length of tergite 1; eye small, oval, 1.4 times as long as wide; malar space unusually wide, slightly wider than basal width of mandible, as wide as apex of tergite 1 or length of flagellar article 1, malar suture sclerotized; flagellar articles 15, flagellum gradually widens distally from article 1 which is 4.5 times as long as wide; OOL greatly exceeds POL, longer than malar space; occipital carina strong on sides, very weak dorsally with medial area effaced. Mesonotum smooth, impunctate, polished, notaulices impressed, foveae weak approaching area of convergence; sternaulis foveolate, complete across mesepisternum. Stigma 2.3 times as long as wide; radial cell scarcely 0.3 times as long as stigma width, metacarpus not extending distad of second abscissa of radius at wing margin; nervulus

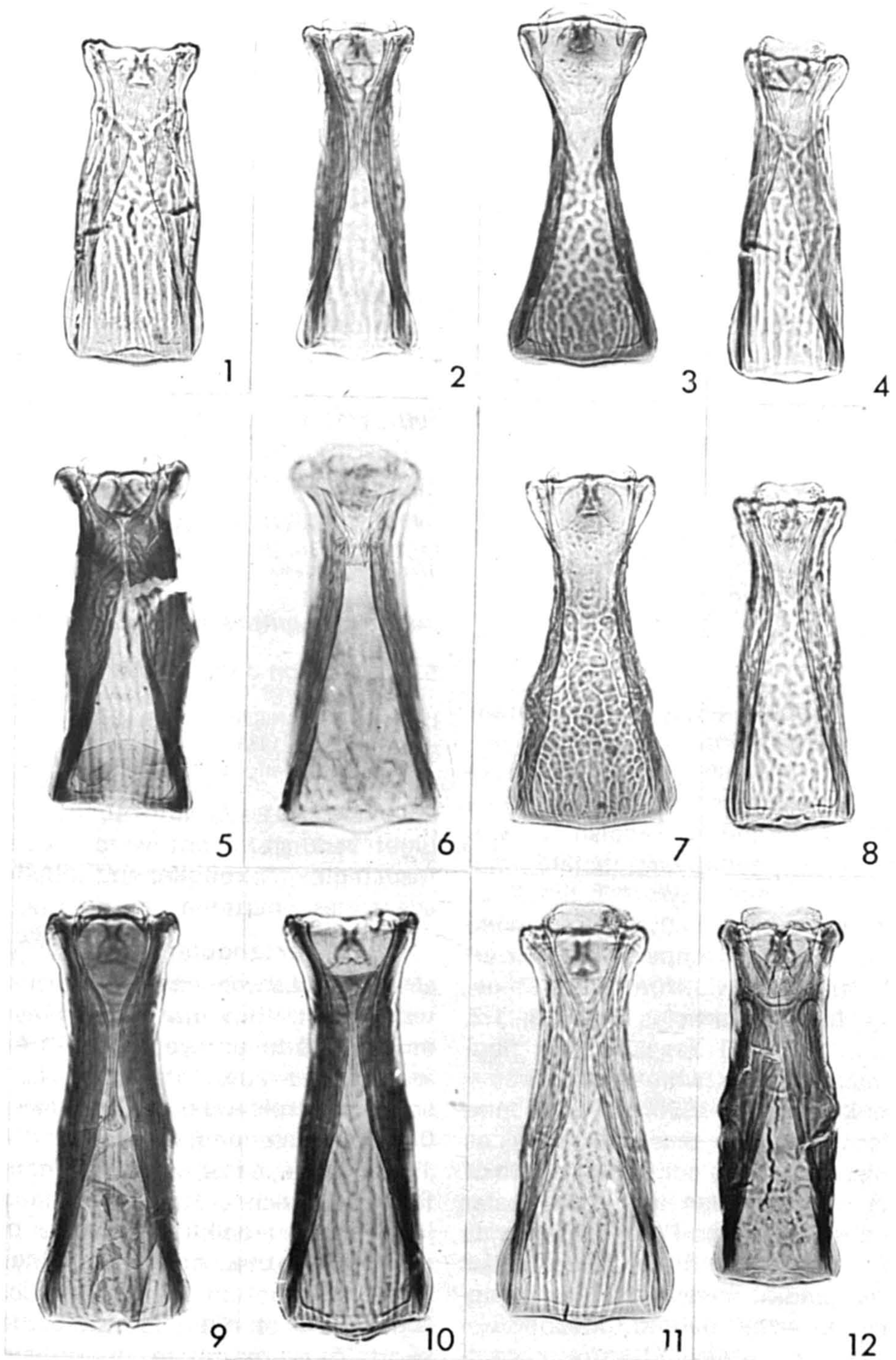


Figure 1-12. *Leiophron* species. tergite 1 ventral view. 1, *uniformis*; 2, *muesebecki*; 3, *cephalicus*; 4, *trigonotylidis*; 5, *fumipennis*; 6, *birdi*; 7, *grohi*; 8, *lygivora*; 9, *rufipennis*; 10, *occipitalis*; 11, *compressus*; 12, *tuberculatus*. X 180.

interstitial; median, submedian cells hairy (fig. 33). Propodeum exareolated. Femur III almost as wide as apex of tergite 1; tibia III 0.55 mm long. Tergite 1 2.5 times as long as wide at apex, medially marked by shallow, linear, confluent depressions, sides with 2-3 carinate striae from base to apex.

FEMALE: Unknown.

L. borealis is a distinctive species in its group. It may be recognized in the male sex by the pronounced malar space and highly polished head with an unusually wide face.

DISTRIBUTION: **Canada.** Ontario.

4. *Leiophron scitulus* (Cresson)

Euphorus scitulus Cresson, 1872: 227.

Holotype: ♂, labelled "Ill; Type No. 1774-; *Euphorus scitulus* Cr."

In the Academy of Natural Sciences, Philadelphia.

Leiophron scitulus: Shenefelt, 1969: 46.

Length about 1.8 mm. Bicolored. Head, mesepisternum, propodeum, tergite 1, legs reddish yellow; flagellum dusky; stemmaticum, mesonotum, gaster behind tergite 1 reddish brown. Frons, vertex, genae impunctate, glabrous; face hairy. Eye 1.3 times as long as wide; face 0.9 times as wide as eye or length of scape + flagellar article 1; length to width ratios of scape, pedicel, flagellar articles 1-3, 1.8, 1.2, 2.3, 1.5, 1.4: 1.0 respectively; flagellum hairy, broken (with 14 segments = articles Muesebeck 1936), 1 + 2 as long as eye; OOL 2.0 times as long as POL, about equal to combined length of pedicel and flagellar article 2; malar space about equal to POL, 0.6 times as long as basal width of madible; ocellar triangle acute at median ocellus; occipital carina weak behind. Mesonotum quite smooth, somewhat hairy; notaulices complete and rather finely impressed except distinctly wide and shallow anteriorly; mesepisternum depressed medially below, depression with fine irregular carinae; propodeum unusually short, posterior face vertical. Front wing venation complete except first abscissa of radius absent; stigma 2.2 times as long as wide; radial cell very short, about as long as parastigma, 0.2 times as long as stigma width; nervellus of hind wing absent; basella broken at its middle, marginal cilia longer than either abscissa. Femur III almost 0.7 times as wide as apex of tergite 1; tibia III 0.58 mm long. Tergite 1 granulose-rugulose, 1.8 times as long as wide at apex, base to apex width 7:12, apex not as wide as eye.

FEMALE: Unknown.

The unusually short, vertical propodeum, small size, and color are distinctive of *scitulus*.

DISTRIBUTION: **United States.** Illinois.

Occipitalis species group

5. *Leiophron* **compressus** n. sp.

Holotype: ♂, United States. California, Anaheim, 14, IV. 1948.

In the U.S. National Museum, Washington, D.C.

HOLOTYPE MALE: Length about 3.7 mm. Light reddish. Front wing weakly infuscated except cubital and radial cells; eye irridescent green.

Head rectangular; frons, vertex smooth, polished, entirely glabrous; face with short, thin hair, about as wide as eye, 0.8 times eye length, 1.4 times as wide as apex of tergite 1; malar space conspicuous, as long as POL, 0.6 times as long as flagellar article 1, 0.8 times basal width of mandible; flagellar articles 15, 1 + 2 almost as long as eye; ocelli within the posterior limits of eye; occipital carina complete. Mesonotum 1.3 times as long as wide, area of notaulices indicated by short, tranverse striae; mesepisternum smooth, polished. Stigma 2.0 times as long as wide; radial cell relatively long on wing margin, 0.4 times as long as stigma width, 1.4 times as long as parastigma; recurrens not interstitial with first intercubitus; second abscissa of cubitus not quite as long as parastigma (fig. 34); nervellus much shorter than either abscissa of basella of which the basal is longer. Tibia III 0.68 mm long. Propodeum exareolate, posterior face rather abrupt, dorsal face short. Tergite 1 striate, 2.6 times as long as wide at apex (fig. 11); femur III 0.7 times as wide as apex of tergite 1.

FEMALE: Unknown.

This species is described from a single specimen. Its narrow mesonotum appears to be a unique feature.

DISTRIBUTION: **United States.** California.

6. *Leiophron* ***fuscipennis*** n. sp.

Holotype: ♀, United States. Louisiana, Tallulah, Airpl. 4092.
In the U.S. National Museum, Washington, D.C.

HOLOTYPE FEMALE: Length about 2.7 mm. Uniformly dark reddish brown approaching black. Scape, pedicel and basal 5 flagellar articles greyish yellow; legs dark testaceous; tergite 1 not as dark as other body segments; front wing deeply infuscated with distal edge, most of radial cell, and area below parastigma hyaline.

Head massive, subquadrate, in side view eyes large, nearly horizontal, protruding forward; lower genae unusually wide, somewhat swollen, over 3.0 times as wide as eye; face flat, vertical, about as wide as eye, 0.7 times eye length or length of flagellar articles 1 + 2; eyes strongly convergent on face; malar space extruded, 1.4 times basal width of mandible, about equal to OOL; flagellum broken, article 1 long and slender, 2.0 times as long as POL; frons polished, smooth, with an obsolescent medial carina; occipital carina complete behind vertex. Mesonotum smooth, without a trace of notaulices, polished, glabrous; mesepisternum also smooth. Stigma 2.0 times as long as wide, slightly wider than length of radial cell; front wing in infuscated areas thickly covered with relatively coarse, dark setae; veins as shown (fig. 35). Tergite 1 long and slender, 4.0 times as long as wide at apex, only slightly wider at apex than base, carinate laterally, weakly striate dorsally, spiracles well behind middle.

MALE: Unknown.

This very distinctive species is described from a single specimen. Unfortunately, the legs are broken and incomplete. Distinguishing characters are its black color, deeply infuscated wings, large head and smooth genae, and large, horizontally-directed eyes.

DISTRIBUTION: **United States.** Louisiana.

7. *Leiophron* ***grohi*** n. sp.

Holotype: ♂, Canada. Ontario, Blackburn, 27. VI. 1955, coll. C.D. Miller. In the Canadian National Collection, Ottawa. CNC 13,142.

Paratypes: 1♂, data as for type; 1♂, Ottawa, Ontario, 19.VII,156, coll. W.R.M. Mason, 1♂, Rte. 2, New Hampshire and Maine Line, Maine, sweeping G. and W. [grey and white] birch, 7.VIII.1965, coll. Lipovsky.

HOLOTYPE MALE: Length about 2.8 mm. Reddish. Flagellum dusky; mesonotum, propodeum reddish brown; veins weakly infuscated; wings hyaline.

Head rectangular; eyes in profile directed more forward than downward, but not enlarged and not directed slightly upward as in *cephalicus* (Provancher); in side view, lower genae extending past the eye and, in front view, these genae wider than the eye; face 1.1 times as wide as eye length, 1.4 times apex of tergite 1; eyes small, not convergent on face, anterior and posterior width nearly the same; malar space about equal to basal width of mandible, not as long as POL (6:8); flagellar articles 18, 1 and 2 of equal length, 1 + 2 equal eye width; scape with setae but not with short, dark spines like *cephalicus;* POL not quite as long as OOL, about equal to flagellar article 1; occipital carina incomplete for a very short distance medically. Mesonotum shining, notaulices scarcely indicated, otherwise smooth and glabrous; mesepisternum indistinctly granulose. Propodeum rather short, sloping sharply behind to posterior, vertical face. Femur III 0.7 times as wide as apex of tergite 1; tibia III 0.77 mm long. Tergite 1 finely reticulate, open widely beneath from base to apex, almost 2.3 times as long as wide at apex (fig. 7).

FEMALE: Unknown.

L. grohi bears some resemblance to *cephalicus* (Provancher) but is separble chiefly by the small eye and wide face. The species is named for the Canadian botanist Herbert Groh (1883-1971).

DISTRIBUTION: **Canada.** Ontario. **United States.** Maine.

8. *Leiophron cephalicus* (Provancher)

Microctonus cephalicus Provancher, 1886: 127. Holotype: ♂, labelled "17 [on white paper]; 1118 [on yellow paper]; *Euphorus cephalicus* Prov. [written by Provancher on white paper with double red border-Provancher second collection label]". Type by monotypy, cited by Gahan and Rohwer, 1917: 399. In the Provancher collection, Université Laval, Québec, Québec.

Euphorus cephalicus: Provancher, 1888: 379; Muesebeck, 1936: 30.

Leiophron cephalicus: Shenefelt, 1969: 46.

Euphorus spiniscapus Muesebeck, 1936: 30-31. Holotype: ♀, labelled "Colo. 1329; Collection C.F. Baker; Type No. 49916 USNM: *Euphorus spiniscapus* Mues.; Type Det. Muesebeck". In the U.S. National Museum, Washington, D.C. **new synonym.**

Muesebeck (1936) described *Euphorus spiniscapus* from two females and separated it from *cephalicus* chiefly by the presence of a spinose scape. The type of *cephalicus* is a male, from the Ottawa area. I have examined a female from Ottawa in the Canadian National Collection that resembles *spiniscapus* except for absence of the spinose scape. The scape of the *cephalicus* type is not glabrous but bears spines that are not as long as those of *spiniscapus* nor as sclerotized. The tergite 1 of *cephalicus* (fig. 3) and of *spiniscapus* is similar. Since these species are similar in morphology except for the scape, it is suggested that the spinose scape is a sexual character. For this reason *spiniscapus* is suppressed as a junior synonym of *cephalicus*.

DISTRIBUTION: **Canada.** Ontario. **United States.** Colorado.

9. *Leiophron* **pallidipennis** n. sp.

Holotype: ♀, United States. Arizona, Patagonia, IV. 11. 1949, coll. Nogales, 68898, 49S 5713. In the U.S. National Museum, Washington, D.C.

HOLOTYPE FEMALE: Length about 2.2 mm. Bicolorous. Antenna, head, legs, light reddish; thorax, propodeum, gaster castaneous; wings mostly hyaline with a pale infuscation of the medial and submedial cells; cubitus, second abscissa of radius, recurrens, first intercubitus weakly infuscated.

Head in profile subquadrate with eye projected forward, its anterior margin in line with and at right angles to base of mandible; lower genae not noticeably swollen, not as wide as eye; frons smooth without a carina; face somewhat wider than eye, about 0.6 times eye length, equal to apical width of tergite 1; eyes strongly convergent on face; malar space short, 0.5 times basal width of mandible; flagellar articles 13, all longer than wide, 1 as long as 2, not much longer than pedicel (5:6); POL about equal to OOL, slightly longer than flagellar article 1; lateral ocellus somewhat behind posterior eye margin; occipital carina very fine, weak behind vertex but apparently complete. Mesonotum smooth, highly polished, glabrous, notaulices not indicated; mesepisternum shining, smooth and convex above, granulose with fine, short striae below. Stigma deep, 2.0 times as long as wide or 1.4 times as long as wide if area distad of parastigma not included; radial cell less than 0.5 times stigma width, hardly exceeding length of parastigma (fig. 36); cubitus very weak, scarcely indicated distally; nervulus interstittial; nervellus short, almost punctiform. Femur III as wide as base of tergite 1; tibia III 0.61 mm long. Tergite 1 1.7 times as long as wide at apex, base 0.7 times as wide as apex with a large dorsal depression on each side, dorsal face with closely-spaced parallel striae.

MALE: Unknown.

This species, described from a single specimen, has an unusually short tergite 1. Its distinguishing characters are indicated in the group and species keys.

DISTRIBUTION: **United States.** Arizona.

10. *Leiophron occipitalis* (Muesebeck)

Euphorus occipitalis Muesebeck, 1936: 29-30. Holotype: ♀, labelled "StaCruz Mts. Cal.; Type; *Euphorus* [hand-written]; Type 49915 USNM; *Euphorus occpitalis* Mues.: Type; Det. Muesebeck". In the U.S. National Museum, Washington, D.C.
Leiophron occipitalis: Shenefelt, 1969: 42.
Euphoriana occipitalis: Loan, 1970: 441.

L. occipitalis is light reddish. The front wings are lightly infuscated and the venation is complete. The tergite 1 is unusually long with the sides subparallel (fig. 10).

DISTRIBUTION: **United States.** California.

11. *Leiophron* **provancheri** n. sp.

Holotype: ♀, United States. Texas, Limpla Co., 5000', 30. V. 1959, coll. W.R.M. Mason. In the Canadian National Collection, Ottawa. CNC 13, 143.

HOLOTYPE FEMALE: Length about 2.4 mm. Uniformly reddish black, polished. Antenna, face yellowish; front and middle legs light testaceous, hind legs infuscated; wings hyaline, veins weakly infuscated.

Head rectangular; frons polished, entirely glabrous and impunctate; eyes large, convergent on face which is 0.7 times eye width, 0.5 times eye length, as wide as apex of tergite 1, covered with fine hair; malar space less than basal width of mandible (5:7), about equal to flagellar article 1; flagellum very short, 1.2 times head width, thickened distally, 5-13 articles quadrate or slightly wider than long, 1 about as long as 2; POL a little longer than flagellar article 1; occipital carina complete. Mesonotum impunctate, glabrous, no trace of notaulices. Propodeum very finely rugulose-reticulate. Femur III 0.7 times as wide as apex of tergite 1; tibia III 0.63 mm long. Tergite 1 2.2 times as long as wide at apex, striate, heavily sclerotized (fig. 13).

MALE: Unknown.

This species is described from a single specimen. Its color and unusually short flagellum (♀) are distinctive. *L. provancheri* can be separated from others of the *occipitalis* group, also without notaulices, by the key characters. It is named for the pre-eminent Canadian taxonomist L'Abbé Léon Provancher (1820-1892).

DISTRIBUTION: **United States.** Texas.

12. *Leiophron* **brevipetiolatus** n. sp.

Holotype: ♂, United States. Colorado, Mt. Vernon nr. Golden, 7200', 31.VII.1961, coll. C.H. Mann. In the Canadian National Collection, Ottawa. CNC 13,144.

HOLOTYPE MALE: Length about 2.4 mm. Reddish brown. Face, lower genae, antenna, legs light reddish yellow; wings hyaline, all veins weakly infuscated.

Head subquadrate, 1.2 times as long, from above frons depressed, face outlined past antennal sockets and eyes; frons, vertex polished, smooth, glabrous; face with short, fine hair not apparent in front view, as wide as eye, 0.8 times eye length; eye somewhat rectangular; malar space short, about 0.3 times basal width of mandible or flagellar article 1, 0.5 times POL; OOL exceeds POL; flagellar articles 14 (distal article(s) missing); occipital carina interrupted behind ocellar triangle. Mesonotum smooth without indication of notaulices; mesepisternum irregularly depressed, shiny; wing veins (fig. 37): stigma 2.5 times as long as wide; radial cell 0.5 times stigma width, somewhat longer than parastigma; median cell predominantly glabrous. Femur III 0.7 times as wide as apex of tergite 1; tibia III 0.68 mm long. Tergite 1. 1.9 times as long as wide at apex, finely striate, spiracles about the middle, sides quite parallel behind spiracles (fig. 14).

FEMALE: Unknown.

L. brevipetiolatus, described from a single specimen, is characterized by an unusually short tergite 1.

DISTRIBUTION: **United States.** Colorado.

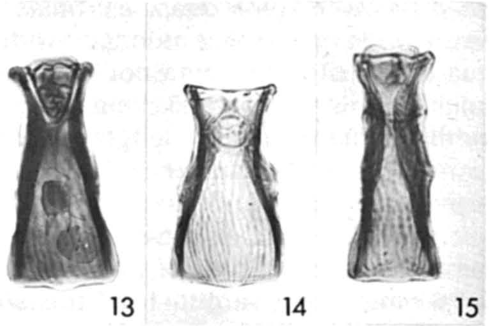
***Masculipennis* species group**

13. *Leiophron* ***fumipennis*** n. sp.

Holotype: ♂ , Canada. Québec, Old Chelsea, summit King Mt., 1150', V. 1964, coll. J.R. Vockeroth. In the Canadian National Collection, Ottawa. CNC 13,145.

HOLOTYPE MALE: Length about 2.9 mm. Dark reddish brown approaching black. Face reddish concolorous with scape and pedicel; flagellum reddish yellow; legs dark testaceous with tibia II, III infuscated, wings with light greyish maculation below parastigma and below stigma and radial cell.

Frons, vertex, genae highly polished, smooth, glabrous; face with short, thin hair, wider than eye (22:20), about 1.5 times as wide as apex of tergite 1, 0.8 times eye length; malar space about equal to flagellar article 3, not as long as 1 (7:10) which is about as long as POL or OOL; flagellar articles 15, all longer than wide though 10-14 almost subquadrate; occipital carina thin medially but apparently complete. Mesonotum polished and smooth like head without a trace of notaulices; mesepisternum with a faint suggestion of very fine striae. Stigma raised above wing margin, 2.0 times as long as wide; veins as shown (fig. 38); radial cell about equal to parastigma, 0.2 times as long as stigma; nervellus much shorter than either abscissa of basella. Femur III 0.8 times as wide as apex of tergite 1; tibia III 0.74 mm long. Tergite 1 with well-separated distinct striae, 2.3 times as long as wide at apex (fig. 5).



Figures 13-15. *Leiophron* species, tergite 1 ventral view. 13, *provancheri*; 14, *brevipetiolatus*; 15, *maculipennis*. X 180.

FEMALE: Unknown.

This species is described from a single specimen. As indicated in the species key, *fumipennis* is similar to *maculipennis*, but differs chiefly by its polished, black appearance and larger size.

DISTRIBUTION: **Canada.** Québec.

14. *Leiophron maculipennis* (Ashmead)

Sierola maculipennis Ashmead, 1887: 75.

Hologype: ♂ , labelled "Jacksonville, Fla.; Type; *Euphorus (Sierola) maculipennis* Ash. Type [written label]; Type No. 44725 USNM; *(Sierola) Euphorus maculipennis* (Ash.) Type Det. Muesebeck", In the U.S. National Museum, Washington, D.C.

Euphorus maculipennis: Muesebeck, 1936: 30.
Leiophron maculipennis: Shenefelt, 1969: 40.
Euphoriana maculipennis: Loan, 1970b: 441.

HOST: *Diaphnocoris chlorionis* (Say) breeding on *Gleditsia triacanthos* L., in the Belleville, Ontario district.

L. maculipennis (figs. 15, 48-51) is reddish brown with infuscated wings. The veins of the front wing are greatly reduced and the flagellum of the female is unusually short with 13 articles.
DISTRIBUTION: **Canada.** Ontario. **United States.** Florida.

15. *Leiophron* ***muesebecki*** (Loan) new combination

Euphoriana muesebecki Loan, 1970b: 441-442. Holotype: ♀, labelled "Belleville, Ont. C.C. Loan, 25.V.1967; reared 21°C laboratory ex *Lopidea marginalis* (Reut); host nymphs coll. 10-14.VII.1966 ex *Spirea latifolia*; *Euphoriana muesebecki* Loan CNC NO. 10739 Holotype". In the Canadian National Collection, Ottawa.

HOST: *Lopidea marginalis* (Reuter).

Leiophron muesebecki (fig. 2) is light reddish with the wings very lightly infuscated. It is most similar to *L. rufipennis* which is known only from the male.
DISTRIBUTION: **Canada.** Ontario.

16. *Leiophron* ***rufipennis*** n. sp.

Holotype: ♂, United States. Nebraska, Sutherland, 4.VI.1961, coll. W.R.M. Mason. In the Canadian National Collection, Ottawa. CNC 13, 146.
Paratype: 1♂, Simcoe, Ontario, 19.VI.1939, coll. G.S. Walley.

HOLOTYPE MALE: Length about 3.4 mm. Light reddish brown. Antenna reddish yellow; gaster dark reddish brown; front wing rather deeply infuscated below parastigma, on each side of second abscissa of radius, and below stigma and radial cell.

Frons, vertex, genae polished, completely smooth and glabrous; face rather wide, 0.9 times eye length, 1.6 times as wide as apex of tergite 1; malar space as long as flagellar article 5, about 0.6 times basal width of mandible; flagellar articles 18; POL not as wide as OOL which is about as long as flagellar article 1; occipital carina incomplete medially for a short distance. Mesonotum without a trace of notaulices, smooth and glabrous. Front wing veins (fig. 9): radial cell length equal to parastigma and 0.2 times as long as stigma. Propodeum with short, transverse striae on sides and dorsal face. Femur III about 0.9 times as wide as apex of tergite 1; tibia III 0.88 mm long. Tergite 1 long and slender, 2.7 times as long as wide at apex; dorsal face with distinct, widely-spaced striae (fig. 39).
FEMALE: Unknown.

L. rufipennis is a large, reddish brown species with reduced front wing veins and prominent infuscated areas of the front wings. It resembles mostly *muesebecki* from which it can be separated on the basis of the wing infuscation, larger size, and truncate clypeus with protruding lateral margins.
DISTRIBUTION: **Canada.** Ontario. **United States.** Nebraska.

***Uniformis* species group**

17. *Leiphron* ***uniformis*** (Gahan) new combination

Euphoriana uniformis Gahan, 1913: 433. Holotype: ♂, labelled "Hagerstown, Md., 18.Vii.1912; Webster No. 5967; Type No. 16351 USNM; *Euphoriana uniformis* ♀ Type Gahan". In the U.S. National Museum, Washington, D.C.

BIOLOGY: Clancy and Pierce (1966).
HOSTS: *Lygus hesperus* Kinght and *L. elisus* Van Duzee (in southern California and Arizona); *L. lineolaris* (in New Jersey) (Clancy and Pierce 1966).

L. uniformis (fig. 1) is a remarkably homogeneous species. It is slender with a subcubital head, immargined vertex and small ocelli. The material at the U.S. National Museum is light yellowish.
DISTRIBUTION: **Canada.** No capture records. **United States.** Widely distributed.

18. *Leiophron* **lygivora** (Loan) new combination

Euphoriana lygivora Loan, 1970a: 193-194.
Holotype: ♀, labelled "Fuller, Ont., lat. 44° 24' N, Long. 77°25'W., Em. 14, VIII. 1969 from *Lygus lineolaris*; nymphs coll. 21.VIII.-6.IX. 1968; breeding plant *Solidago canadensis*; *Euphoriana lygivora* Loan CNC 11588 Holotype". In the Canadian National Collection, Ottawa.

BIOLOGY: Loan (1970a).
HOST: *Lygus lineolaris.*
MALE: Unknown.

Leiophron lygivora (fig. 8) is reddish yellow with a dark brown propodeum. It is not as slender nor as yellowish as *uniformis*, and the occiput is clearly margined. *L. lygivora* closely resembles *trigonotylidis* new species from which it is separated by host and phenology, and the structural and color characters noted in the key to species.

DISTRIBUTION: **Canada.** Ontario.

19. *Leiophron* **trigonotylidis** n. sp.

Holotype: ♀, Canada. Ontario, VI concession Sidney Township at provincial highway No. 15, swept from red clover, *Trifolium pratense* L., and timothy, *Poa canadensis* L., 3.VI.1970. In the Canadian National Collection, Ottawa. CNC 13,147.

Paratypes: 19♀, 7♂, data as for type except 1♂ reared from *Trigonotylus coelestialium* 4.V.1971. 1♀, Foxboro, swept from grasses on railroad right-of-way 23.V.1971 (USNM, BM, ZIL).

HOST: *Trigonotylus coelestialium.*

HOLOTYPE FEMALE: Length about 2.7 mm. Light reddish. Flagellar articles 1 and 2 testaceous, succeeding articles dusky; stemmaticum not distinct, legs light testaceous; propodeum, apex of gaster reddish brown; wing area distad of basalis very lightly infuscated.

Head subquadrate; face flat in profile view, vertical with eye directed forward; frons (fig. 45) flat becoming declivous anterior to ocelli, very finely granular; face a little wider than eye, 0.7 times eye length, not as wide as length of flagellar articles 1 + 2 (16:18), 1.3 times greater than apex of tergite 1; malar space not unusually deep, 0.5 times length of flagellar article 2; OOL obviously longer than POL; flagellar articles 13, penultimate article subquadrate, all others longer than wide, flagellum thickened apically; occipital carina well-defined on side of occiput, very weak medially a distance as long as eye. Mesonotum (fig. 44) quite flat medially, notaulices not indicated, granulose and sculptured with very fine, transverse striae; prescutellar suture divided medially by a single major carina; mesepisternum as shown (fig. 46). Femur III about 0.8 times as wide as apex of tergite 1; tibia III 0.65 mm long. Tergite 1 with several distinct, lateral striae above and below spiracles, otherwise somewhat granular with short, weak confluent striae, 2.5 times as long as wide at apex (fig. 4).

The female paratypes of *L. trigonotylidis* are much alike: the propodeum is light reddish brown contrasting with the light reddish head, thorax and much of the gaster. There are 13 flagellar articles except for two specimens with 14 articles. Males differ from females as follows: eye small, about as long as width of face, as wide as apex of tergite 1; malar space almost as long as flagellar article 2; flagellar articles all longer than wide though subapical articles not much longer than wide; propodeum reddish.

DISTRIBUTION: **Canada.** Ontario.

Taxonomy of *Peristenus* Foerster

KEY TO THE NORTH AMERICAN SPECIES OF *PERISTENUS*

1. Dark reddish brown or piceous ... 2
Bicolorous or light reddish ... 21

2. Frons punctate (punctures close together or granulose-punctate or rugulose punctate) ... 3
Frons apparently impunctate or with fine setiferous punctures or other fine microsculpture ... 11

3. Mesepisternum entirely punctate or rugulose punctate; mesoscutum and sometimes vertex and upper genae punctate; tendency for interstitial nervulus to be present ... 4
Mesepisternum granulose or smooth with areas of fine microsculpture; vertex and genae usually impunctate ... 5

4. Flagellar articles mostly 21 (19-23) in ♀ and 23-24 (21-25) in ♂; flight period May to early July in eastern Canada ... (1) *Peristenus pallipes* (Curtis)
Flagellar articles mostly 19-20 (17-22) in ♀ and 22 (21-24) in ♂; flight period late July to September in eastern Canada ... (2) *Peristenus pseudopallipes* (Loan)

5. Flagellar articles 15-16 (♀) ... 6
Flagellar articles more than 16 (♀) ... 7

6. Flagellum dusky without reddish aspect; post-ocellar space about equal to length of flagellar article 1; legs III infuscated ... (3) *Peristenus* ***nixoni*** n. sp.
Flagellum yellowish, less commonly reddish or reddish dusky; post-ocellar space usually greater than length of flagellar article 1; legs III yellowish ... (4) *Peristenus* ***vitidis*** n. sp.

7. Tergite 1 entirely reticulate-rugulose; flagellar articles 24(♂), reddish with apical half reddish dusky; radial cell rather short, 0.7 times as long as stigma width; large piceous species ... (5) *Peristenus* ***pini*** n. sp.
Tergite 1 striate or rugulose striate; flagellum more or less entirely reddish dusky; radial cell about as long as or longer than stigma width ... 8

8. Mesonotum shiny, chiefly impunctate, glabrous except scutum with isolated, fine hairs; piceous species ... (6) *Peristenus* ***alni*** n. sp.
Mesonotum not obviously shiny, hairy; scutum weakly or distinctly punctate ... 9

9. Flagellum dusky red; post-ocellar space usually less than length of flagellar article 1; recurrens usually post-furcal, second abscissa of cubitus often indicated; tergite 1 up to 2.0 times as long as wide at apex ... (7) *Peristenus* ***dumestris*** n. sp.
Flagellum yellowish; other characters not as described above ... 10

10. Punctures of frons dense, in some specimens almost rugulose near ocellar triangle; flagellum thick towards apex, less than 2.0 times as long as head width ... (4) *Peristenus* ***vitidis*** n. sp.
Punctures of frons fine, more discrete, or in some specimens frons relatively impunctate; flagellum not much wider apically than basally, 2.0 times or more as long as head width ... (16) *Peristenus* ***solidaginis*** n. sp.

11. Eye pinkish grey in death; flagellum not much wider at apex than base, 17-20 articles (♀), 19-23 (♂), yellowish or reddish dusky; piceous ... (8) *Peristenus* ***brimleyi*** n. sp.
Eye blackish in death or if greyish then flagellar articles fewer than 17 (♀) ... 12

12. Frons, vertex, mesonotum smooth, polished, quite glabrous; mesepisternum also smooth; sometimes slightly punctate above and below; occipital carina complete only on sides of occiput ... (9) *Peristenus levifrons* (Muesebeck)
Not as described above ... 13

13. Radial cell 0.5-0.7 times as long as stigma width ... 14
Radial cell about as long as stigma width ... 15

14. Flagellum yellowish concolorous with legs, 17 articles (♀), apical articles quadrate; frons entirely impunctate; cubitus somewhat weak; reddish brown ... (10) *Peristenus* ***juniperoides*** n. sp.
Flagellum dusky, darker than legs, 15-16 articles (♀), 18-20 (♂), apical articles except penultimate longer than wide (♀); cubitus stronger than in *P. juniperoides* n. sp.; black ... (11) *Peristenus* ***juniperinus*** n. sp.

15. Flagellar articles 13-14 (♀); flagellum reddish dusky, unusually short; black ... (12) *Peristenus* ***reidi*** n. sp.
Flagellar articles exceed 14 ... 16

16. Flagellar articles 15-16 ( ) 17
Flagellar articles exceed 16 ( ) 18

17. Flagellum yellowish and not as dark as legs; tergite 1 2.0 times as long as wide at apex; black .... (13) *Peristenus* ***salixidis*** n. sp.
Flagellum dusky; tergite 1 short and broad, not 1.5 times as long as wide at apex; reddish brown .... (14) *Peristenus* ***chlamydatidis*** n. sp.

18. Flagellar articles 17 ( ), 12-16 chiefly longer than wide, light reddish dusky not contrasting with leg color; frons entirely smooth; tergite 1 with discrete striae more or less parallel from base to apex .... (15) *Peristenus* ***laricinae*** n. sp.
Apical flagellar articles nearly quadrate or wider than long ( ) 19

19. Frons with distinct, abundant, fine, setiferous punctures; flagellum yellowish or reddish yellow not contrasting with leg color, 17-18 articles ( ), 19-22 (♂); black .... (16) *Peristenus* ***solidaginis*** n. sp.
Frons smooth without abundant setiferous punctures 20

20. Nervulus almost interstitial; veins quite hyaline, stigma dark; first abscissa of radius usually not short; mesoscutum not as dark as lateral lobes of mesonotum; flagellar articles 18-19 ( ), 20-22 (♂), basal 1 and 2 somewhat pale with apical 14-17 or 14-18 quadrate or subquadrate and none wider than long ( ); pronotum of often light testaceous or yellowish; reddish brown .... (17) *Peristenus* ***dicyphovora*** n. sp.
Nervulus postfurcal but approaches basal vein; all veins distinctly pigmented; first abscissa of radius not as long as in *P. dicyphovora*; flagellar articles 17-18 ( ), 21 (♂), concolorous, apical articles of from approximately 10-15 quadrate, and from approximately 15-17 wider than long; black .... (18) *Peristenus* ***lonicerae*** n. sp.

21. ♂ 22
28

22. Nervulus interstitial; tergite 1 open beneath at base, unusually short and broad, 1.3-1.6 times as long as wide, apex exceeds eye length .... (19) *Peristenus* ***bicolor*** n. sp.
Nervulus postfurcal; tergite 1 not as described above 23

23. Flagellar articles 15-18 24
Flagellar articles 19-22 25

24. Flagellar articles 15; occipital carina well-developed; vertex with scattered large punctures; light reddish with head and mesonotum concolorous; small, 1.6 mm long; tibia III 0.50 mm long .... (20) *Peristenus* ***zingiberis*** n. sp.
Flagellar articles 16-18; occipital carina weak; vertex impunctate; bicolorous with castaneous mesonotum; tibia III 0.70 mm long .... (21) *Peristenus plagiognathi* (Loan)

25. Frons punctate; legs, flagellum almost concolorous, light yellowish; face, genae, and frons beside eye pale yellowish; remainder of frons, vertex piceous, concolorous with mesonotum and mesepisternum; scutum with setiferous punctures; foveae of notaulices shallow, narrow and linear; large species, tibia III 1.0 mm long .... (22) *Peristenus* ***tacamahacae*** n. sp.
Frons impunctate; color and other characters not as described above 26

26. Pronotum, face, lower genae yellowish; mesonotum and mesepisternum dark reddish brown. .... (17) *Peristenus* ***dicyphovora*** n. sp.
Not as described above 27

27. Occipital carina fine, weak behind ocellar triangle; basal flagellar articles not as dark as apical articles; mesonotum smooth except for setiferous punctures on scutum; notaulices narrow, linear, almost non-foveolate; malar space as long as flagellar article 2; stigma width not much greater than radial cell length .... (23) *Peristenus* ***clematidis*** n. sp.
Occipital carina well-developed and strong behind ocellar triangle; notaulices wide, carinae of foveae distinct; malar space not as long as flagellar article 2; radial cell 0.5-0.8 times as long as stigma width; light reddish with head not as dark as remainder of body, mesonotum dark brown or reddish; mesepisternum reddish or almost black .... (24) *Peristenus* ***wallisi*** n. sp.

28. Eyes convergent on face; eye length typical, greatly exceeding face width 29
Eyes not noticeably convergent on face; eye unusually small, its length about as wide as face or not much greater 30

29. Flagellum with 16-18 articles, apical articles quadrate or subquadrate; mesepisternum completely reddish or partly reddish brown posteriorly; occipital carina fine, rather weak medially .... (21) *Peristenus* ***plagiognathi*** (Loan)

Flagellum with 17-19 articles, all articles longer than wide; mesepisternum and mesonotum dark brown, head yellowish or light reddish; occipital carina well-developed .... (24) *Peristenus* ***wallisi*** n. sp.
30. Flagellar articles 1-6 pale, remaining articles dusky red .... (23) *Peristenus* ***clematidis*** n. sp.
Flagellar articles concolorous, dusky red .... (19) *Peristenus* ***bicolor*** n. sp.

1. *Peristenus pallipes* (Curtis)

Leiophron pallipes Curtis, 1833:476. Lectotype: . Designated by Loan (1974). In the National Museum of Victoria, Melbourne.

Microctonus barbiger Wesmael, 1835:69-71. Lectotype: . Designated by Loan (1974). In the Institut Royal des Sciences Naturelles de Belgique, Brussels.

Euphorus pallipes: Westwood, 1840:62.

Peristenus barbiger: Foerster, 1862: 251.

Euphorus mellipes Cresson, 1872: 227. Synonymized by Muesebeck (1936).

Microctonus barbiger Wesmael, 1835:69-71. Lectotype: . Designated by Loan (1974). In the Institut Royal des Sciences Naturelles de Belgique, Brussels.

Euphorus tuberculifer Marshall, 1887: 57. Synonymized by Loan (1974).

Peristenus pallipes: Loan, 1974.

BIOLOGY: Loan (1965, 1970a).
HOST: *Lygus lineolaris* (first generation), *Adelphocoris lineolatus* (Goeze), *A. rapidus* Say, *Labops hirtus* Knight, *Leptopterna dolobrata* (L.), *Capsus ater* L.

Peristenus pallipes (figs. 67-70) is characterized chiefly by a rugulose-punctate mesepisternum. It is recognized from *P. pseudopallipes* by biological characters and number of flagellar articles as noted in the key to species.
DISTRIBUTION: Holarctic.

2. *Peristenus* **pseudopallipes** (Loan) new combination

Leiophron pseudopallipes Loan, 1970a: 189. Holotype: , labelled "Fuller, Ont. Can. 3.VIII.1967, C.C. Loan; reared ex nymphs *Lygus lineolaris*; nymphs coll. 4.IX.1966 ex *Solidago canadensis*; *Leiophron pseudopallipes* Loan Holotype CNC No. 11587". In the Canadian National Collection, Ottawa.

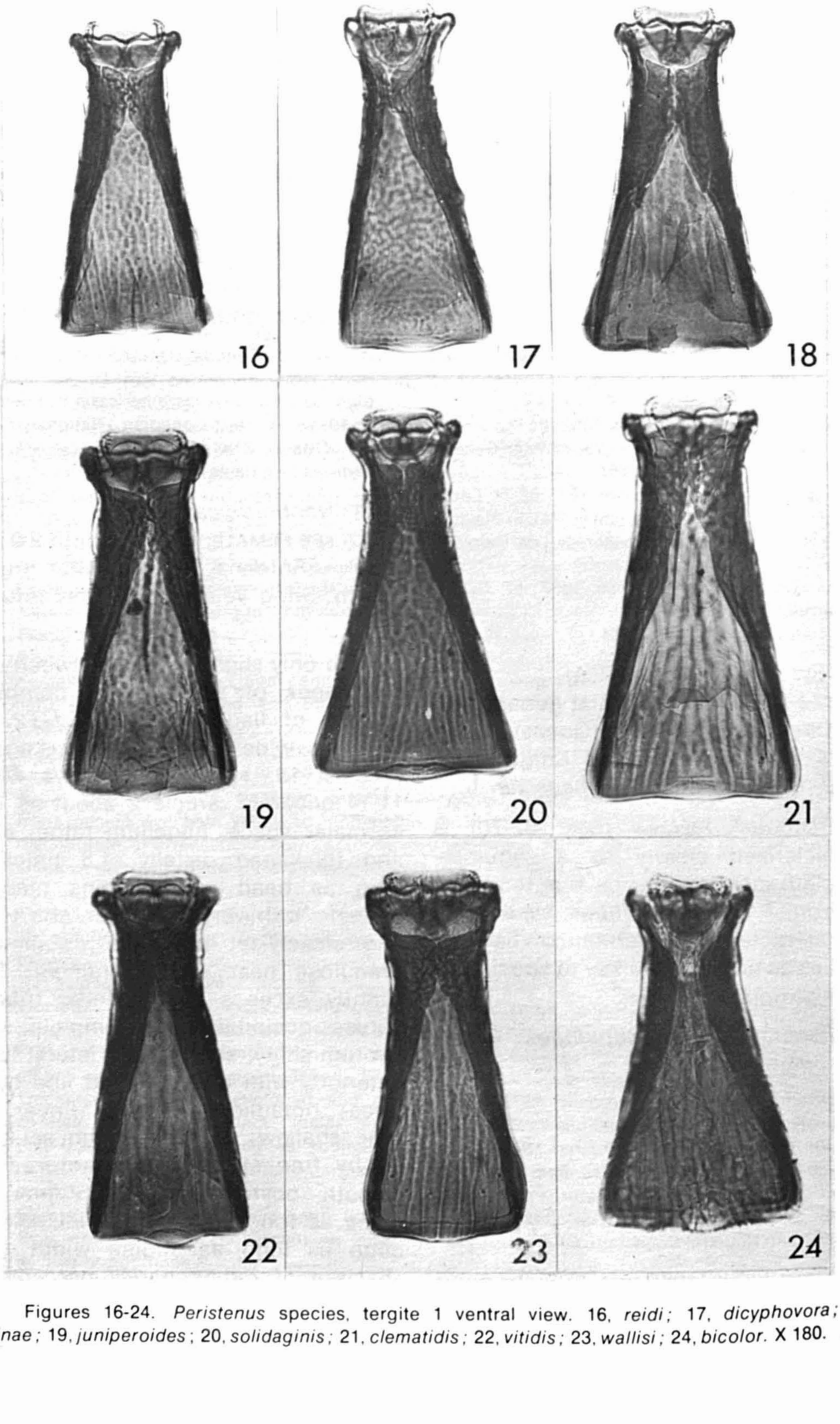
BIOLOGY: Loan (1965-late summer population noted as *pallipes*, 1970a); Streams *et al*, (1968).
HOST: *Lygus lineolaris* (second generation).
DISTRIBUTION: Northeastern North America.

3. *Peristenus* **nixoni** n. sp.

Holotype: . Canada, Ontario, Foxboro, from *Neoborus canadensis* Van Duzee, breeding plant sapling *Fraxinus americana* L. reared 27. IV.1971. In the Canadian National Collection, Ottawa. CNC 13,148.
Paratype: 1 , data as for type.

HOST: *Neoborus canadensis*
HOLOTYPE FEMALE: Length about 2.9 mm. Black. Antenna, legs light greyish brown; wing veins moderately infuscated.

Face only slightly wider between eyes than apex of tergite 1 or combined lengths of flagellar articles 1+2, 0.8 times as wide as eye length; flagellar articles, 15, 1+2 equal to eye width, 11-14 quadrate, article 2 about as long as malar space, flagellum rather short and thickened distally, 1.8 times as long as head width; frons medially carinate with very fine, thin, short hair and closely-set punctures; somewhat granulose near ocellar traingle; POL slightly exceeds OOL, ocellar triangle obtuse; occipital carina complete. Mesonotum shiny, scutum and lateral lobes anteriorly with fine hair and fine punctures; notaulices, narrow, linear, foveae shallow; mesepisternum sculptured by fine striae and punctures but smooth posteriodorsally. Stigma 2.3 times as long as wide; radial cell not quite as long as stigma width; first abscissa of radius barely perceptible; nervulus postfurcal. Femur III 0.5 times as wide as apex of tergite 1;



Figures 16-24. *Peristenus* species, tergite 1 ventral view. 16, *reidi*; 17, *dicyphovora*; 18 *laricinae*; 19, *juniperoides*; 20, *solidaginis*; 21, *clematidis*; 22, *vitidis*; 23, *wallisi*; 24, *bicolor*. X 180.

tibia III about 0.78 mm long. Tergite 1 with fine, closely-spaced striae, broad behind, apex wider than eye, 1.5 times as long as wide at apex.

MALE: Unknown.

As indicated in the species key, *P. nixoni* is most similar to *vitidis* new species. Other characters useful for separating the two species are: the mesonotum of *nixoni* is finely hairy and finely punctured, whereas in *vitidis* the mesonotum is more shiny, with sparse hair and larger and not as closely-spaced punctures.

This species is named in honor of Mr. G.E.J. Nixon, Commonwealth Institute of Entomology, London, in recognition of his many contributions to euphorine taxonomy.

DISTRIBUTION: **Canada.** Ontario.

4. *Peristenus* ***vitidis*** n. sp.

Holotype: ♀, Canada. Ontario, Fuller, from *Lygocoris viburni* (Knight) breeding on *Vitis labrusca* L., reared 3.V.1967.
In the Canadian National Collection, Ottawa. CNC 13, 149.

Paratypes: 14 ♀, 20♂, Fuller, reared from *L. viburni* 29.VI-19.V.1969; 3 ♀, 2 ♂, reared from *Taedia scrupeus* (Say) 29.IV-29.V.1967; 3 ♂, reared from *T. scrupeus* 18.V.-3.VI.1968; 7 ♀, 4 ♂, swept from *V. labrusca* 2.VI.-11.VI. 1966; 2♂, captured in soil emergence trap underneath *V. labrusca* 27.IV.1968 (USNM, BM, ZII).

HOSTS: *Lygocoris viburni, Taedia scrupeus.*

HOLOTYPE FEMALE: Length about 3.0 mm. Black. Antenna light reddish yellow; legs light testaceous; gaster behind tergite 1 somewhat reddish on sides basally; wing veins rather lightly infuscated.

Frons (fig. 59) thickly punctate, punctures not coarse but close together, fewer punctures next to ocelli; eyes large and convergent on face; face not quite as wide as eye or apex of tergite 1, equal to combined lengths of flagellar artices 1 + 2, almost 0.7 times eye length; flagellar articles 16, article 1 about as long as POL, 2 as long as malar space, 9-15 approximately quadrate; flagellum short, thickened distally, 1.7 times as long as head width; POL unusually long, distinctly longer than OOL or distance from median to lateral ocellus; occipital carina complete. Mesonotum (fig. 58) shiny, scutum with prominent, not coarse setiferous punctures, lateral lobes glabrous posteriorly; notaluices foveolate; mesepisternum finely rugulose with a small, smooth medial area. Stigma 2.7 times as long as wide, sides behind about equal, width equal to length of radial cell; first abscissa of radius obliterated; first recurrens entering radial cell, second abscissa of cubitus very short (fig. 43). Femur III almost 0.6 times as wide as apex of tergite 1; tibia III 0.81 mm long. Tergite 1 striate with some striae confluent and some medial reticulae, almost 1.7 times as long as wide at apex (figs. 22, 60).

P. vitidis is a medium-sized, piceous species with the flagellum light reddish yellow concolorous with the legs. It seems to consist of two forms attacking mirids on wild grape: one parasitic on *Lygocoris viburni* with flagellar articles 15-17 (♀) and 18-19 (♂); the other parasitic on *Taedia scrupeus* with flagellar articles 18-19 (♀) and 20-23 (♂). Distinctive species characters shared by these forms are the color of the flagellum, legs and body; and, in many specimens, a dense, uneven rugulose punctation of the frons and ocellar triangle. The post-ocellar distance is pronounced in specimens reared from *Lygocoris,* usually exceeding the length of flagellar article 1 (♀). Though the post-ocellar space is also marked in specimens reared from *T. scrupeus,* on the average it is subequal to the length of flagellar article 2 (♀). Despite these differences, for the present this material is considered to represent a single species.

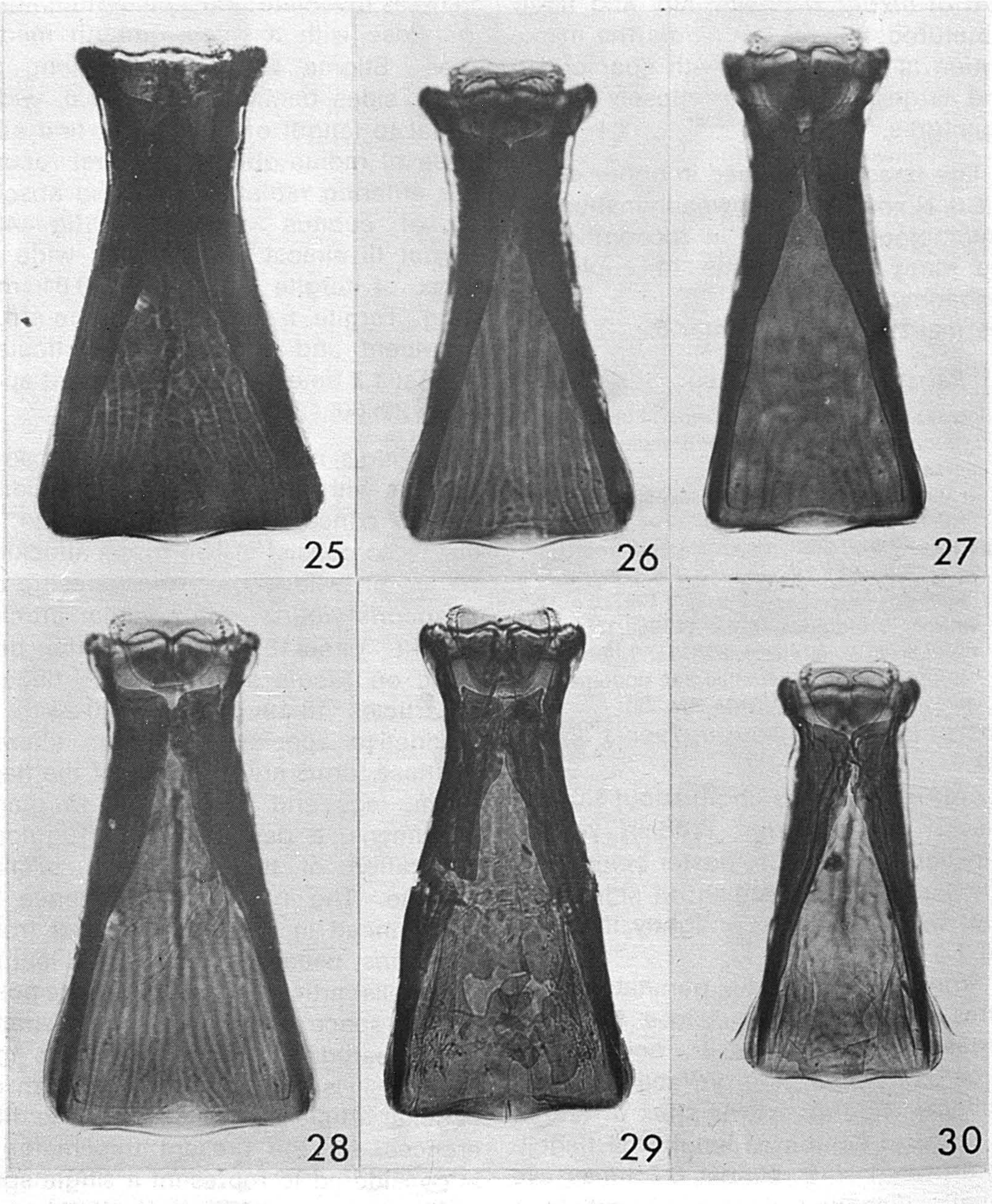
DISTRIBUTION: **Canada.** Ontario.

5. *Peristenus* ***pini*** n. sp.

Holotype: ♂, Canada. Ontario, Holloway (8 miles north of Belleville), captured in a soil emergence trap under mature *Pinus strobus* L., 27.V.1968. In the Canadian National Collection, Ottawa. CNC 13,150.

HOLOTYPE MALE: Length about 3.0 mm. Black. Flagellum dusky from article 14, other articles light reddish concolorous with scape and pedicel; legs light testaceous, leg III somewhat darker.

Face thickly hairy, 0.9 times as wide as eye length or equal to combined lengths of flagellar articles 1 + 2, 1.2 times as wide as apex of tergite 1; flagellar articles 24, basal 3 about equal



Figures 25-30. *Peristenus* species, tergite 1 ventral view. 25, *levifrons*; 26, *alni*; 27, *tacamahacae*; 28, *dumestris*; 29, *pini*; 30, *juniperinus*. X 180.

width, scape + pedicel only slightly longer than flagellar article 1; OOL about equal to POL; frons punctate, hairy, medially carinate; occipital carina complete. Mesoscutum hairy, punctures small; notaulices foveolate; mesepisternum lightly punctate with weak, indefinite foveae. Stigma 2.2 times as long as wide; radial cell 0.7 times as long as stigma width; nervulus not interstitial; basella broken about its middle, either abscissa longer than nervellus. Femur III 0.7 times as wide as apex of tergite 1; tibia III 1.0 mm long. Propodeum finely reticulate. Tergite 1 rugulose, 1.7 times as long as wide at apex (fig. 29).

FEMALE: Unknown.

This species is distinguished by its large size, short radical cell, and rugulose tergite 1.

DISTRIBUTION: **Canada.** Ontario.

6. *Peristenus* ***alni*** n. sp.

Holotype ♀, Canada. Ontario, Fuller, captured in soil emergence trap under *Alnus rugosa* var. *americana* (Regel) Fern., 5.VII.1968. In the Canadian National Collection, Ottawa. CNC 13,151.

Paratypes: 3 ♀, data as for type but captured 11-16.VII.1968.

HOLOTYPE FEMALE: Length about 3.2 mm. Black. Flagellum light reddish dusky; face, frons next to eye with reddish aspect; scape, pedicel light testaceous; legs testaceous.

Face as wide as eye, 0.7 times eye length, slightly wider than apex of tergite 1, covered with silvery hair; frons with a fine, medial carina, completely and finely punctate; OOL about equal to POL: malar space as long as flagellar article 4; flagellar articles 18, apical 4 excluding last article quadrate; occipital carina complete though weak medially. Mesonotum shiny, scutum sparsely hairy and lightly punctate; notaulices narrow and fine but foveae carinate. mesepisternum shiny, quite smooth with a rugulose-punctate area below. Stigma almost 3.0 times as long as wide; radial cell about as long as stigma width; nervulus interstitial; medial cell not as hairy as cubital or discoidal cells. Femur III almost 0.7 times as wide as apex of tergite 1; tibia III 0.88 mm long. Tergite 1, 1.8 times as long as wide at apex, striae distinct, widely separated (fig. 26).

MALE: Unknown.

P. alni is characterized by a chiefly impunctate, almost glabrous mesoscutum and a reddish tinge to the frons and face. It is also distinguisehd by the radial cell having a length about equal to the stigma width.

DISTRIBUTION: **Canada.** Ontario.

7. *Peristenus* ***dumestris*** n. sp.

Holotype: , Canada. Ontario, Belleville, reared from *Phytocoris* sp., breeding on *Cornus racemosa* Lamb., 31.III.1968. In the Canadian National Collection, Ottawa. CNC 13,152.

Paratypes: 1♂, Belleville, swept from *C. racemosa* 7.VII.1964; 2♀, 4♂, data as for type, reared 20.XII.1967 at 21°C in laboratory; 1♀, 5♂, data as for type, reared 31.III.-4.IV.1968; 1♀, swept from *C. racemosa* 1.VI.1967. 1♀, Fuller, reared III.1968 from *Phytocoris* sp., breeding on *Solidago canadensis* L.; 2♀, reared 11-19.V.1969 from *Phytocoris* sp., breeding on *C. racemosa*.

HOST: *Phytocoris* sp.

HOLOTYPE FEMALE: Length about 3.3 mm. Black. Antenna dusky red becoming darker distally; face, legs light testaceous; wing veins lightly infuscated with first intercubitus and second abscissa of radius basally darker.

Head 1.5 times as wide as long, 1.4 times as wide as thorax; frons (fig. 53) with closely-spaced, shallow, large punctures with a semi-mat finish extends to vertex, finely-hairy, medially carinate; face about as wide as combined lengths of flagellar articles 1 + 2, 0.7 times as wide as eye length, 1.1 times as wide as apex of tergite 1; flagellar articles 21, not greatly thickened distally, all longer than wide, flagellum 2.6 times as long as head width; occipital carina complete. Mesoscutum punctate and quite hairy as are lobes of mesonotum laterally and anteriorly (fig. 52); notaulices foveolate; mesepisternum medially depressed with fine punctures and fine striae. Stigma 2.3 times as long as wide; radial cell length exceeds stigma width, about 0.5 times as long as stigma; recurrens not interstitial with first intercubitus; second abscissa of cubitus short but distinct (fig. 42); first abscissa of radius absent. Femur III almost 0.7 times as wide as apex of tergite 1; tibia III 1.1 mm long. Tergite 1 striate, 1.9 times as long as wide at apex (figs. 28, 54).

This is a large, black species with a dusky red flagellum. It appears to be characterized by a rather long tergite 1 with the apical margin narrow. The males have a similar color; a single male paratype has an unusually pale face with testaceous lower genae. The flagellar articles varied in number from 18-22 for females, and 21-24 for males. As noted in the species key, flagellar article 1 exceeds the distance between the lateral ocelli (POL).

DISTRIBUTION: **Canada.** Ontario.

8. *Peristenus* ***brimleyi*** n. sp.

Holotype: ♀, Canada, B.C., Gagnon Road 6 miles west of Terrace, 24.VI.1960, coll. C.H. Mann. In the Canadian National Collection, Ottawa. CNC 13,153.

Paratypes: 3 ♀, 4 ♂, locally as for type, 8.VI.-4.VII.1960, coll. J.G. Chilcott and R. Pilfrey; 3 ♀, 1♂, Hixon, B.C., 19.V-25.VI.1966, coll. E.D.A. Dyer; 1♂, 13.V.1965, coll. E.D.A. Dyer. 1♀, Terrace, B.C., 9.VII.1960, coll. W.R. Richards. 1♀, 2♂, Spring Creek, Terrace, 11.VI.1960, coll. C.H. Mann. W.W. Moss (at 220'). 1♀, 1♂, Waterton, Alta., 8-11.VI.1962, coll. W.R.M. Mason.

HOLOTYPE FEMALE: Length about 3.0 mm. Black. Antenna yellowish; eye greyish; legs yellowish with tibia III somewhat infuscated.

Frons finely punctured; face hairy, about as wide as eye or apex of tergite 2, 0.6 times eye length; malar space as long as basal width of mandible or flagellar article 2; POL = OOL, 0.8 times as long as flagellar article 2; flagellar articles 17, sub-apical articles subquadrate, others longer than wide; flagellum 2.2 times head width; occipital carina complete medially. Mesonotum shiny, scutum with fine punctures and sparse hair; notaulices fairly deep, foveolate. Stigma 2.7 times as long as wide, somewhat wider than length of radial cell (5:7) which is prominently bowed; nervulus slightly postfurcal. Femur III 0.6 times as wide as apex of tergite 1; tibia III 0.81 mm long. Tergite 2 striate, nearly 1.7 times as long as wide at apex.

P. brimleyi is characterized by the color of the eyes, antennae and legs. Unlike the holotype specimen, most of the flagellar articles of the paratype material are longer than wide subapically. The antennae are chiefly light yellowish but in a few specimens are reddish dusky.

This species is named for J.H. Brimley, an amateur entomologist from Wellington, Ontario.

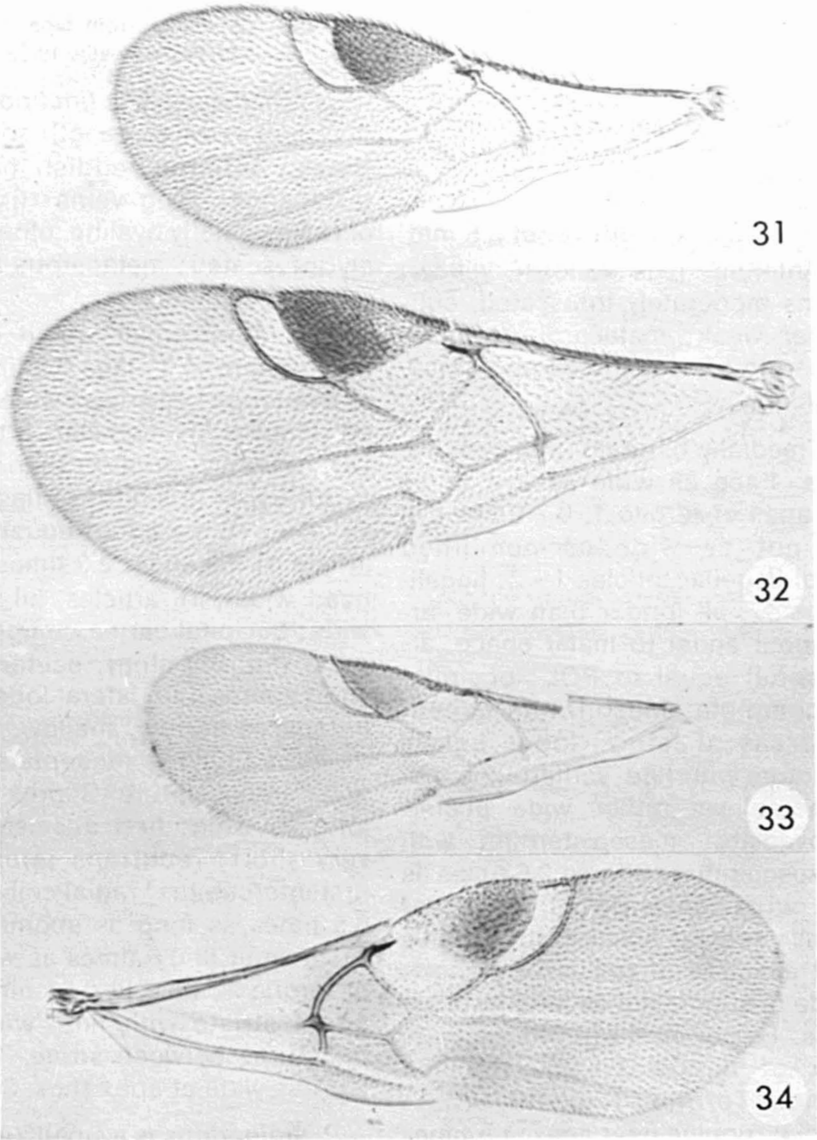
DISTRIBUTION: **Canada.** British Columbia; Alberta.

9. *Peristenus* ***levifrons*** new combination

Euphorus levifrons, Muesebeck, 1936: 32.
Holotype: , labelled "Colo. 1341; Collection C.F. Baker; Type No. 49918 U.S.N.M.; *Euphorus levifrons* Mues. Type Det. Muesebeck". In the U.S. National Museum. Washington, D.C.
Leiophron levifrons: Shenefelt, 1969: 40.

The smooth frons, mesonotum and mesepisternum distinguish *P. levifrons* (fig. 25) from other species of *Peristenus*. In addition, the occiput is widely immargined behind the vertex.

DISTRIBUTION: **United States.** Colorado.



Figures 31-34. *Leiophron* species, front wing. 31, *tuberculatus*; 32, *birdi*; 33, *borealis*; 34, *compressus* × 125.

10. *Peristenus* **juniperoides** n. sp.

Holotype: . Canada. Ontario, Fuller, reared from *Bolteria luteifrons* Knight breeding on *Juniperus communis* L., 2.IV. 1968. In the Canadian National Collection, Ottawa. CNC. 13, 154.

Paratypes: 1 . from type locality, captured in soil emergence trap under *Juniperus communis*. 24.IV.168; 2 . beaten from *J. communis* 25.IV.1967 and 12.V.1967.

Host: Bolteria luteifrons.

HOLOTYPE FEMALE: Length about 2.6 mm. Black. Antenna, legs reddish yellow; wing veins moderately infuscated, cubitus rather weak; metacarpus indicated on margin of radical cell and somewhat beyond.

Frons medially carinate, mat-like, impunctate. Face as wide as eye or as wide as apex of tergite 1, 0.7 times eye length, not as wide as combined lengths of flagellar articles 1 + 2; flagellar articles 17, all longer than wide, article 6 about equal to malar space, article 1 about equal to POL; occipital carina complete. Mesonotum except medial areas of lateral lobes lightly hairy, scutum with fine, setiferous punctures; notaulices rather wide posteriorly, foveolate; mesepisternum with fine microsculpture. Stigma 2.6 times as long as wide, as wide as length of radial cell; second abscissa of cubitus and first abscissa of radius very short; distal side of stigma not as long as proximal side. Femur III 0.6 times as wide as apex of tergite 1; tibia III 0.62 mm long. Tergite 1 finely striate with medial rugulae near apex, 1.6 times as long as wide at apex (fig. 19).

The reddish yellow flagellum and long radial cell with an infuscated metacarpus separate this species from *P. juniperinus*. The flagellar articles of the 2 males are 20 and 22; the flagellum of the ♀ paratype is incomplete.

DISTRIBUTION: **Canada.** Ontario.

11. *Peristenus* **juniperinus** n. sp.

Holotype: ♀ Canada. Ontario, Belleville, reared from *Dichrooscytus tinctipennis* Knight breeding on *Juniperus virginiana* L., 22-III. 1968. In the Canadian National Collection, Ottawa. CNC 13, 155.

Paratypes: 2 , 5 ♂ from type locally, data as for type with rearing dates 19-22.III.1968.

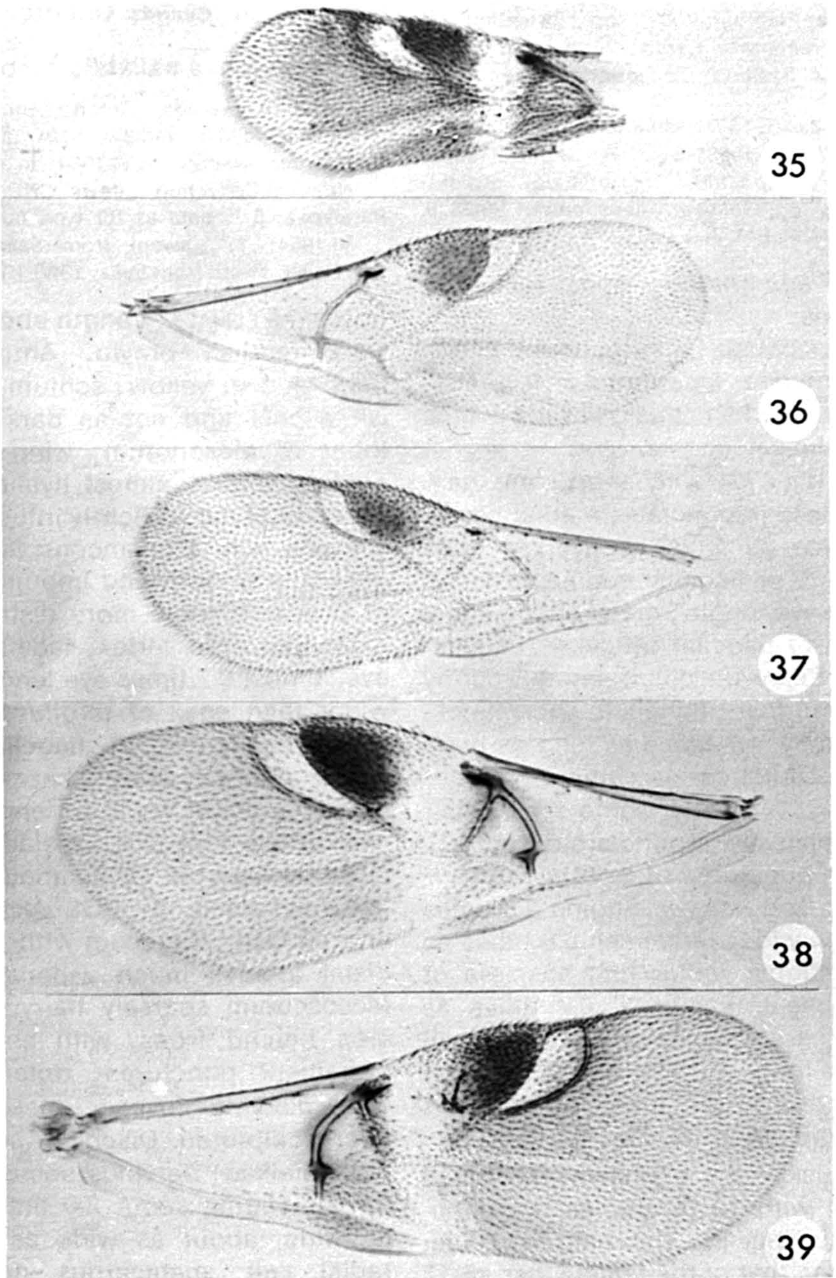
HOST: *Dichrooscytus tinctipennis*.

HOLOTYPE FEMALE: Length about 2.6 mm. Black. Antenna reddish brown; legs testaceous; wing veins: first abscissa of radius chiefly hyaline, others moderately infuscated; metacarpus not indicated.

Eye rather small, about as wide as apex of tergite 1; face 0.9 times as wide as eye length, nearly as wide as combined lengths of flagellar articles 1+2; OOL slightly greater than POL, POL about equal to length of flagellar article 1; malar space about equal to flagellar article 3; flagellum 2.3 times as long as head width, 16 articles, all longer than wide; occipital carina complete. Mesonotum (fig. 65) shiny, scutum with fine, short sparse hair, lateral lobes glabrous; notaulices narrow, shallow, fine with indistinct foveae; mesepisternum with fine microsculpture. Stigma 2.0 times as long as wide; first abscissa of radius very short; recurrens interstitial with first intercubitus; radial cell short, about 0.5 times as long as stigma width (fig. 41). Femur III 0.6 times as wide as apex of tergite 1; tibia III 0.61 mm long. Tergite 1 striate with fine, widely-spaced punctures between striae, 1.8 times as long as wide at apex (figs. 30, 64).

P. juniperinus is a small, piceous species with dusky antennae. It is distinct by a short radial cell which, in females, is about 0.5 times as long as the stigma width; the radial cell of males is somewhat longer. The wing veins are rather weakly infuscated: the metacarpus is absent or only very slightly indicated. The number of flagellar articles in the two female syntypes is 15; in the five male syntypes the number varies from 18-20.

DISTRIBUTION: **Canada.** Ontario.



Figures 35-39. *Leiophron* species, front wing. 35, *fuscipennis*; 36, *pallidipennis*; 37, *brevipetiolatus*; 38, *fumipennis*; 39, *rufipennis*. X 125.

12. *Peristenus* ***reidi*** n. sp.

Holotype: ♀, Canada, Ontario, Belleville, reared from *Plagiognathus* spp., breeding on *Cornus racemosa* Lamb., 24.III.1968. In the Canadian National Collection, Ottawa, CNC 13,156.

Paratypes: 29 ♀, 15 ♂, same data as for type but reared 1-30.III.1968. 31 ♀, 7 ♂, Fuller, reared from *Plagiognathus nigronitens* (Knight) breeding on *Solidago canadensis*, 26-28.III. 1968 (USNM, BM, ZIL).

HOSTS: *Plagiognathus* spp., including *nigronitens.*

HOLOTYPE FEMALE: Length about 2.2 mm. Black. Antenna, legs more or less concolorous, reddish dusky; wing veins weakly infuscated.

Frons (fig. 73) with short, fine hair, more or less impunctate; medial carina weak; face as wide as eye, or apex of tergite 1, or flagellar segments 1 + 2, 0.7 times eye length; malar space equal to length of flagellar article 4; flagellar articles 13, 9-12 quadrate, 1 slightly longer than POL; flagellum short, thickened distally, 1.7 times as long as head width; occipital carina complete. Mesonotum (fig. 74) shiny, some sparse hair though relatively impunctate except obsolescent punctures of scutum; notaulices deep and narrow. Stigma 2.5 times as long as wide; radial cell 0.8 times as long as stigma width; first abscissa of radius absent. Femur III 0.7 times as wide as apex of tergite 1; tibia III 0.63 mm long. Tergite 1 with uniform discrete striae, 1.7 times as long as wide at apex (figs. 16, 75).

The dusky, short, distally thickened flagellum with 13-14 articles is distinctive of this species. The male flagellum, longer than that of the female, has 16-17 articles and is yellowish. *P. reidi* is very similar to *P. salixidis* from which it differs chiefly by the number of flagellar articles and color of the female flagellum.

The name of this species recognizes the important contribution of D.G. Reid to the mirid parasite project at Belleville.

DISTRIBUTION: **Canada.** Ontario.

13. *Peristenus* **salixidis** n. sp.

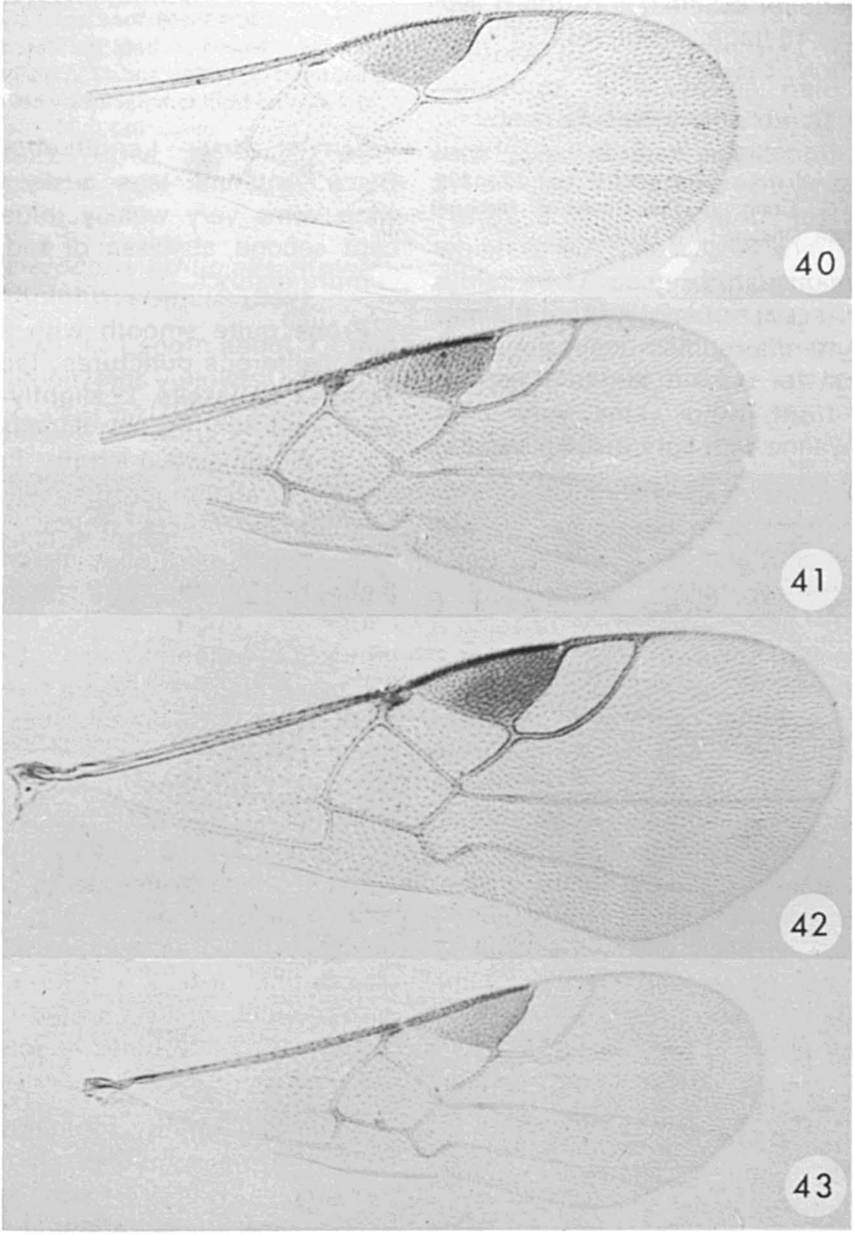
Holotype: ♀, Canada, Ontario, Belleville, swept from tree-like, female *Salix* sp., in *Salix-Populus* swamp, 10.VI.1964. In the Canadian National Collection, Ottawa. CNC 13,157.

Paratypes: 5 ♀, data as for type but swept 4-12. VI.1964; 1 ♀, swept from *Salix*, 19.V.1970. 1 ♀, Fuller, swept from *Salix*, 13.VI.1964.

HOLOTYPE FEMALE: Length about 2.2 mm. Dark reddish brown. Antenna, legs light reddish yellow; scutum with reddish aspect and not as dark as lateral lobes of mesonotum; wing veins, excepting stigma, almost hyaline, second abscissa of radius lightly infuscated.

Frons with fine, inconspicuous hair, generally smooth and impunctate; area of ocellar triangle more distinctly hairy extending onto vertex; face as wide as eye, almost 0.7 times eye length, slightly wider than apex of tergite 1, equal to combined length of flagellar articles 1 + 2, densely hairy; basal width of mandible about equal to length of flagellar article 1 or OOL; malar space not quite as long as OOL, about equal to flagellar article 2; POL slightly longer than OOL; flagellum with 15 articles, distal articles much wider than long. Mesoscutum sparsely hairy, similar to area behind frons, with shallow, not prominent punctures; notaulices fine with discrete foveae; mesepisternum microsculptured. Discoidal cell prominently stalked; nervulus somewhat postfurcal; stigma about 2.0 times as long as wide, about as wide as length of radial cell; metacarpus not distinct beyond radial cell; parastigma rather deep, prominent. Femur III a little less than 0.5 times as wide as apex of tergite 1; tibia III 0.65 mm long. Tergite 1 nearly 2.0 times as long as wide at apex, finely striate with some punctures between striae, basal 0.25 rugulose.

MALE: Unknown.



Figures 40-43. *Peristenus* species, front wing. 40, *dicyphovora*; 41, *juniperinus*; 42, *dumestris*; 43, *vitidis*. X 125.

This species is most similar to *reidi*. It differs chiefly by the number and color of the flagellar articles; 5 of the 6 syntypes have 15 flagellar articles.

DISTRIBUTION: **Canada.** Ontario.

14. *Peristenus* ***chlamydatidis*** n. sp.

Holotype: ♀, Canada. Saskatchewan, White Fox, reared from *Chlamydatus* sp., 20.I.1952, coll. H.G. Craig. In the Canadian National Collection, Ottawa. CNC 13,158.

HOST: *Chlamydatus* sp.

HOLOTYPE FEMALE: Length about 2.2 mm. Black. Antenna reddish dusky, legs yellowish; gaster behind tergite 1 reddish brown; front wing veins very pale, almost hyaline with light greyish stigma.

Head rather deep, 1.3 times as wide as long; frons with barely perceptible, very fine punctures; face hairy, 0.7 times as wide as eye length; width of face, eye, and apex of tergite 1 about equal; malar space not as long as basal width of mandible; POL 0.8 times as long as flagellar article 1; flagellar articles 15, 10-14 slightly longer than wide, flagellum thickened distally; occipital carina weak behind ocelli. Mesoscutum with fine, sparse hair and indistinct punctures, lateral lobes of mesonotum glabrous, shiny; notaulices finely foveolate; mesepisternum granulose. Stigma 2.6 times as long as wide, width equal to length of radial cell; basella interrupted above its middle, basal abscissa much longer than nervellus (5:9). Femur III 0.6 times as wide as apex of tergite 1; tibia III 0.59 mm long. Tergite 1 striate, barely 1.5 times as long as wide at apex.

MALE: Unknown.

This small, distinctive species is known from a single specimen. It was identified by Craig (1963) as *Euphorus pallipes*.

DISTRIBUTION: **Canada.** Saskatchewan.

15. *Peristenus* ***laricinae*** n. sp.

Holotype: ♀, Canada. Ontario, Holloway (8 miles north of Belleville), captured in soil emergence trap under *Larix laricina* (Du Roi) K. Koch in a tamarack/black spruce swamp, 15.V.1968. In the Canadian National Collection, Ottawa. CNC 13, 159.

Paratypes: 1 ♀, 1 ♂ data as for type except captured 30.V.1968 and 17.V.1968 respectively; 1 ♀ beaten from tamarack 22.V.1970.

HOLOTYPE FEMALE: Length about 2.2 mm. Black. Antenna, legs dusky yellowish; wing veins very weakly infuscated except second abscissa of radius which is more distinct.

Frons quite smooth with some very fine, setiferous punctures; face as wide as apex of tergite 1, slightly less than combined lengths of flagellar articles 1 + 2, 0.6 times eye length; flagellar articles 17, all longer than wide except penultimate article which is subquadrate, article 1 not quite as long as POL, 3 about as long as malar space; occipital carina fine but complete. Mesoscutum and lateral lobes of mesonotum sparsely hairy, punctures present but not prominent, posteriorly lateral lobes polished; notaulices narrow; mesepisternum indistinctly granulose with some fine, short striae, smooth posterio-medially. Stigma 2.4 times as long as wide, about as wide as length of radial cell; first abscissa of radius very short. Femur III 0.6 times as wide as apex of tergite 1, tibia III 0.77 mm long. Tergite 1 with parallel, well-separated striae from base to apex, 1.8 times as long as wide (fig. 18).

The taxonomic characters of this species are summarized in the key to the species. It is distinctive by the relatively long flagellar articles and clearly striate tergite 1.

DISTRIBUTION: **Canada.** Ontario.

16. *Peristenus* ***solidaginis*** n. sp.

Holotype: ♀, Canada. Ontario, Fuller, reared from *Slaterocoris* spp., breeding on *Solidago canadensis*, 9.V.1969. In the Canadian National Collection, Ottawa. CNC 13,160.

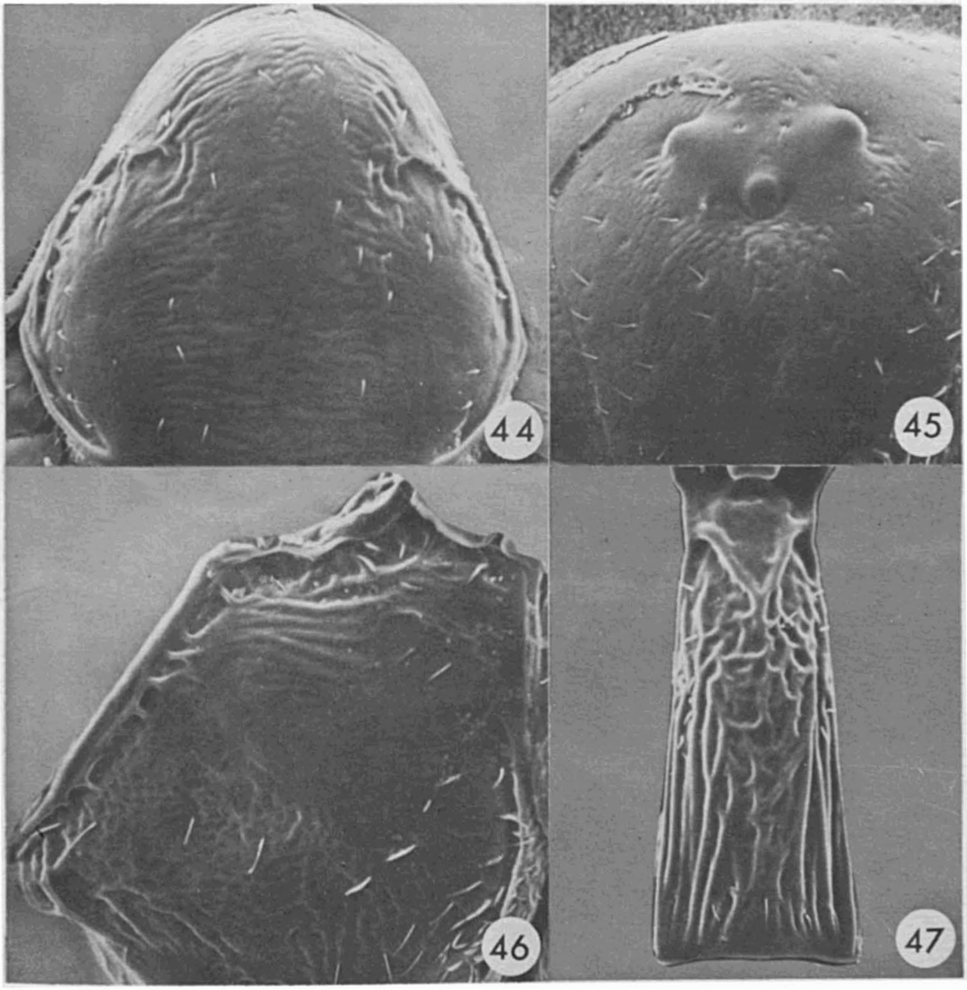
Paratypes: 2 ♀, 1 ♂, data as for type, reared

9-11.V.1968; 6♀, from type locality swept from *S. canadensis* 17.V.-9.VII.1968 and 21.V.1969; 1♀, 1♂, from type locality captured in soil emergence traps underneath *S. canadensis*, 23 V.1968 and 21-22.V.1969, respectively. 26♀, 23♂, Foxboro, swept from *S. canadensis*, 17-28.V.1968 and 18.V.-6.VI.1970. 4♀, 4♂, Foxboro at Mud-Cat Lane, swept from *S. canadensis*, 26.V.-21.VI.1970; 3♀, 6♂, reared from *Slaterocoris* nymphs 3-7.V.1971 (USNM BM, ZIL).

HOSTS: *Slaterocoris atritibialis* (Knight); *breviatus* (Knight); *stygicus* (Say).

HOLOTYPE FEMALE: Length about 2.7 mm. Black. Antenna, legs yellowish with dusky tinge; wing veins moderately infuscated with second abscissa of radius and cubitus almost hyaline.

Frons (fig. 71) with fine, setiferous punctures; face densely hairy, not as wide as eye nor as wide as apex of tergite 1, 0.6 times eye length; flagellar articles 18, article 1 exceeds POL (10:8), 3 about equal to malar space which is 0.7 times basal width of mandible, 13-17 quadrate; occipital carina complete. Mesonotum (fig. 72) shiny, scutum sparsely hairy with an impunctate aspect though there are small obs-



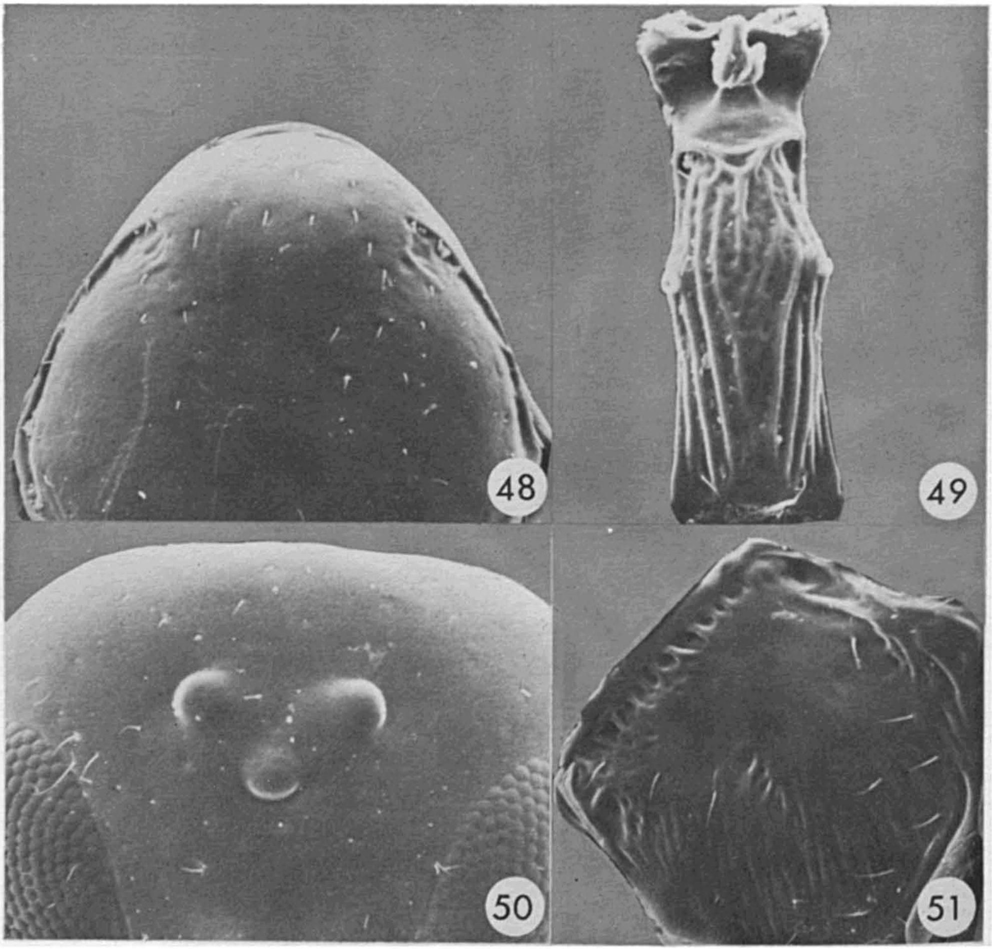
Figures 44-47. *Leiophron trigonotylidis*. 44, mesonotum; 45, frons; 46, mesepisternum; 47, tergite 1 dorsal view. Scanning electron microscope photographs 225-245 X.

cure punctures; notaulices fine, narrow, almost non-foveolate; mesepisternum finely micro-sculptured, smooth and shiny towards posterior corners. Stigma 2.7 times as long as wide, proximal side longer than distal side; first abscissa of radius distinct, about as long as stalk of discoidal cell; cubitus rather weakly defined; radial cell slightly longer than stigma width. Femur III 0.6 times as wide as apex of tergite 1; tibia III 0.72 mm long. Tergite 1 with fine, closely spaced parallel striae, 1.7 times as long as wide at apex (figs. 20, 76).

The yellowish, rather long flagellum which is not much wider apically than basally, and the fine punctures of the frons are the chief recognition characters of this species. It is most similar to *vitidis* n. sp., with which it is coupled in the species key. The extent of infuscation of the second abscissa of the radius and the cubitus is variable. The number of flagellar articles of the paratype specimens is as follows:

Sex of specimen	No. Flagellar articles					
	17	18	19	20	21	22
♀	15	12	1	0	0	0
♂	0	0	1	6	4	1

DISTRIBUTION: **Canada.** Ontario.



Figures 48-51. *Leiophron maculipennis.* 48, mesonotum; 49, tergite 1 dorsal view; 50, frons; 51, mesepisternum. Scanning electron microscope photographs 225-245 ×.

17. *Peristenus* **dicyphovora** n. sp.

Holotype: ♀, Canada. Ontario, Belleville, swept from *Rubus odoratus* L., 12.VI.1963. In the Canadian National Collection, Ottawa. CNC 13,161.

Paratypes: 2♂, data as for type. 1♀, Fuller, beaten from *R. odoratus* 8.VI.1966; remainder captured in soil emergence traps under *R. odoratus* IV.30-V.13. 1968.

HOST: Associated by dissections of nymphs and capture records with *Dicyphus agilis* (Uhler) breeding on *Rubus odoratus*, but not confirmed by rearing.

HOLOTYPE FEMALE: Length about 2.9 mm. Dark reddish brown. Antenna, face, frons next to eyes pale testaceous; legs pale yellowish; wing veins distinct but lightly infuscated.

Face lightly hairy, about as wide as apex of tergite 1, not as wide as eye, 0.6 times as wide as eye length, almost as wide as combined lengths of flagellar articles 1 + 2; malar space 0.5 times as long as flagellar article 1; flagellar articles 19, all except penultimate article longer than wide, with segments 15-17 subquadrate; flagellum long, 2.7 times as long as head width; POL slightly exceeds OOL; POL: flagellar article 1 length, 4:6; occipital carina weak the width of an ocellus behind vertex. Mesonotum smooth, scutum with a few indistinct punctures and with thin, short, not prominent hair, scutum not as dark as lateral lobes of mesonotum; notaulices fine and narrow; mesepisternum shining, medially depressed with granulose areas and fine punctures. Stigma almost 3.0 times as long as wide; radial cell about as long as stigma width; first abscissa of radius distinct; nervulus somewhat post furcal (fig. 17). Femur III rather narrow, 0.6 times as wide as apex of tergite 1; tibia III 0.86 mm long. Tergite 1 chiefly rugulose-reticulate, carinate laterally, not quite 2.0 times as long as wide at apex (fig. 40).

The number of flagellar articles in males varies from 20-22 and in females from 18-19. This species is a medium-sized, dark reddish *Peristenus*. The face of the females is quite pale and the flagellum is also light colored and distinctly long. The color of males is variable: some are entirely dark reddish brown while the pronotum of others is yellowish. The scutum is usually paler than the lateral lobes of the mesonotum. Other characters for identification are the impuctate frons, the fine, narrow notaulices and the rugulose tergite 1.

DISTRIBUTION: **Canada.** Ontario.

18. *Peristenus* **lonicerae** n. sp.

Holotype: ♀, Canada. Ontario, Kaladar (8 miles west), swept from *Lonicera* sp., 26. V.1969. In the Canadian National Collection. Ottawa. CNC 13,162.

Paratypes: 7♀, 2♂, data as for type, swept 26-28.V.1969.

HOST: Associated by dissections of nymphs and capture records with *Dicyphus agilis* breeding on *Lonicera* sp., but not confirmed by rearing.

HOLOTYPE FEMALE: Length about 2.0 mm. Black. Antenna dusky; legs light testaceous with coxae yellowish; second abscissa of radius, first intercubitus infuscated like stigma, other veins greyish yellow.

Frons with fine microsculpture, impunctate; face with fine, appressed hair, not as wide as eye (17:21) nor apex of tergite 1, 0.6 times eye length; eyes large and convergent on face; flagellar articles 18, 1 about 2.0 times as long as 2 which is not quite as long as malar space, 16-17 wider than long, 13-15 quadrate, POL not as long as 1; flagellum 1.6 times as long as head width; occipital carina complete. Mesonotum moderately hairy except lateral lobes posteriorly, not polished, scutum with obsolescent punctures; notaulices foveolate, shallow. Stigma 2.6 times as long as wide, about as wide as length of radial cell; first abscissa of radius very short, leaving stigma at its centre.

Femur III 0.5 times as wide as apex of tergite 2; tibia III 0.95 mm long. Tergite 1 striate with medial rugulae, 1.6 times as long as wide at apex.

P. lonicerae is a rather large, black species not immediately distinct from others of similar habitus. In the species key it runs to a couplet with *P. dicyphovora*, but as indicated, it is easily distinguished from that species.

DISTRIBUTION: **Canada.** Ontario.

19. *Peristenus* ***bicolor*** n. sp.

Holotype: ♀, Canada. Ontario, Foxboro, swept from *Solidago canadensis* 31.V.1970. In the Canadian National Collection, Ottawa. CNC 13,163.

Paratypes: 1 ♀, 4 ♂, data as for type, swept from *S. canadensis* 27.V.-18.VI.1968; 3 ♂, from type locality, reared from *Slaterocoris* spp., 8. V. 1968 and 8.V.1970. 8 ♀, 4 ♂, Foxboro at Mud-Cat Lane, swept from *S. canadensis* 11-13.V. 1968, 30.VI.1969, 2-5.VI.1970; 4 ♀, 1 ♂, reared from *Slaterocoris* spp., 6-7.V.1971 (USNM, BM ZIL).

HOSTS: Reared from a complex of *Slaterocoris* spp., including *stygicus, atritibialis*, and *breviatus*.

HOLOTYPE FEMALE: Length about 2.8 mm. Bicolorous. Head light reddish; legs reddish yellow; flagellum dusky; body black with gaster behind tergite 1 dark reddish brown; wing veins well infuscated.

Head in side view with relatively small eye, wide lower genae, and face rounded protruding slightly beyond the eye; frons (fig. 63) smooth with a medial carina; stemmaticum indicated; eye unusually small for a female *Peristenus*, length about equal to face width, eyes not at all convergent on face; malar space distinctly exceeding basal width of mandible, about equal to flagellar article 2; POL not as long as flagellar article 1 nor quite as long as OOL; flagellar articles 18, 1 +2 about equal to face width, all longer than wide, flagellum 2.5 times head width; occipital carina broken for a very short distance medially, not weak. Mesonotum (fig. 62) smooth, almost impunctate, scutum almost glabrous; notaulices wide, deeply foveolate; mesepisternum finely rugulose-striate above and below, smooth posterio-medially. Stigma 2.5 times as long as wide, proximal side not as long as distal side; radial cell 0.7 times as long as stigma width; first abscissa of radius very short; nervulus interstitial; nervellus not as long as either abscissa of basella. Femur III 0.5 times as wide as apex of tergite 1; tibia III 0.88 mm long. Tergite 1 with subparallel, discrete striae, tergite rather short, 1.4 times as long as wide at apex, relatively wide at base and apex, base almost 0.5 times as wide as apex, not fused or touching at base beneath (figs. 24, 61).

P. bicolor is readily recognized by its color; short and broad apically tergite 1; small eye and wide face of the female; interstitial nervulus; and, usually, an incompletely fused tergite 1 at its base beneath.

DISTRIBUTION: **Canada.** Ontario.

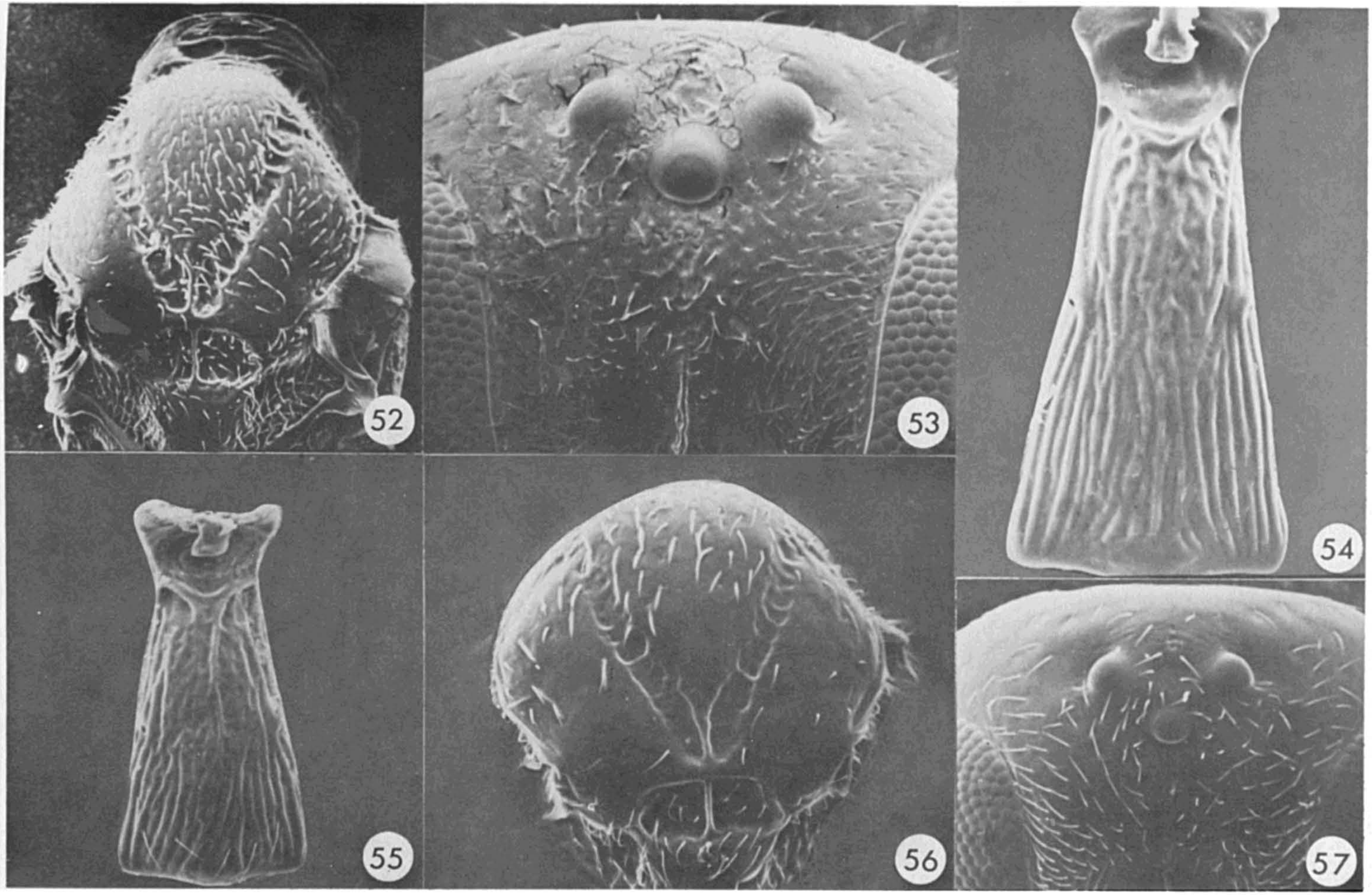
20. *Peristenus* ***zingiberis*** n. sp.

Holotype: ♂, Canada. Ontario, Kaladar (8 miles west), reared from *Macrotylus sexguttatus* (Provancher) breeding on *Asarum Canadense* L., IV. 1968. In the Canadian National Collection, Ottawa. CNC 13,164.

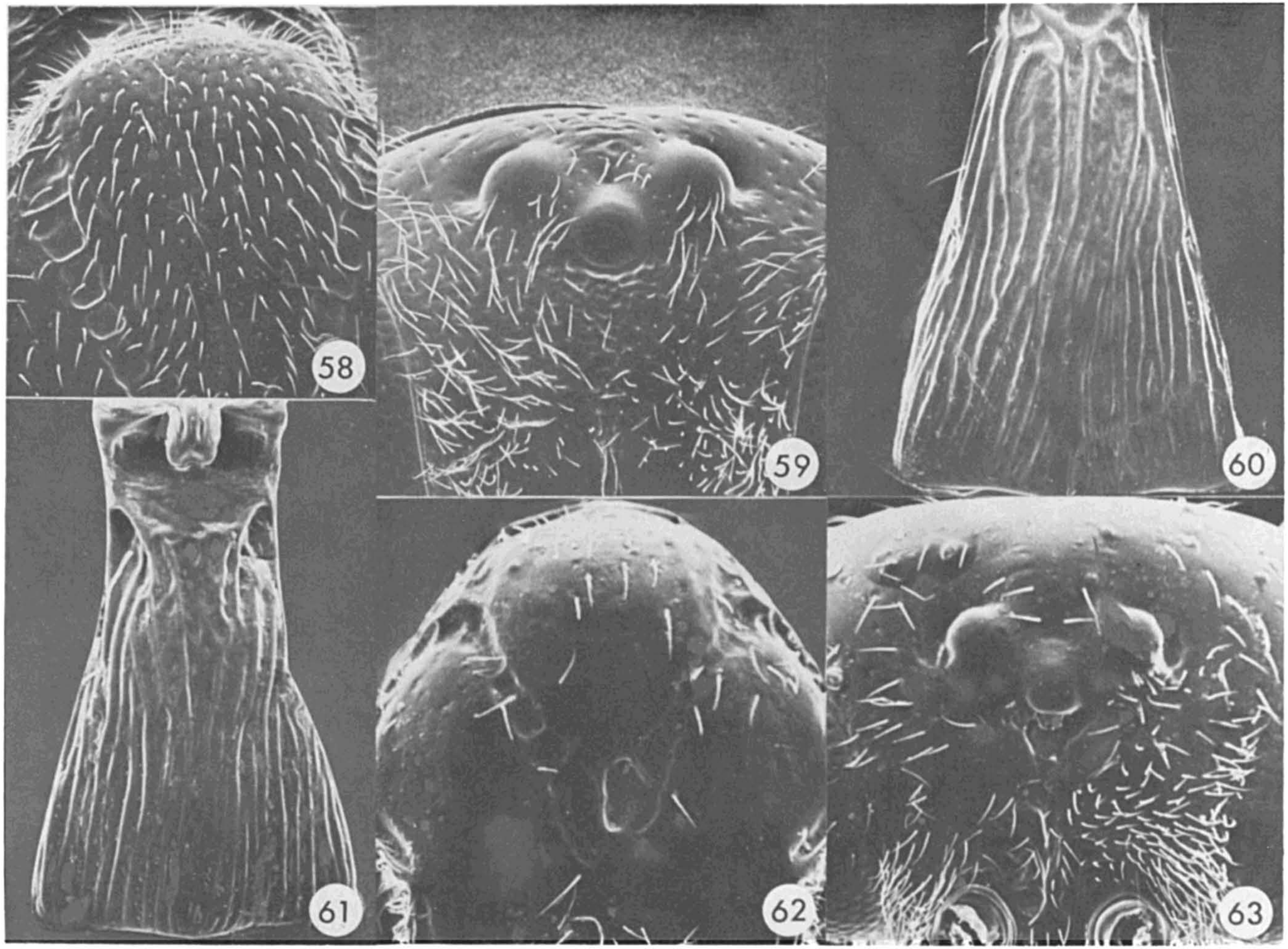
HOST: *Macrotylus sexguttatus.*

HOLOTYPE MALE: Length about 1.6 mm. Light reddish brown. Face, genae, reddish yellow; flagellum reddish brown; legs light testaceous; wing veins lightly infuscated.

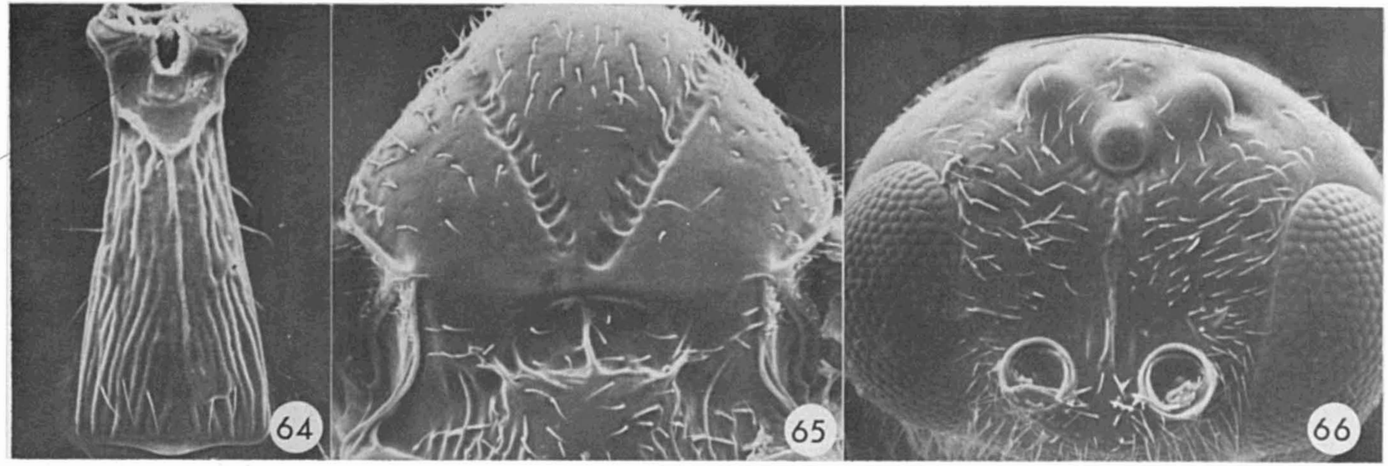
Frons with very fine, setiferous punctures and without a medial carina; face about as wide as eye length, slightly more than combined flagellar articles 1 + 2; flagellar articles 15, distinctly hairy, all longer than wide, 1 about as long as scape, 2 about equal to malar space; occipital carina complete behind. Notaulices wide, foveae indistinct, fine and shallow, completely non-carin-



Figures 52-57. *Peristenus* species, body sculpture. Figures 52-54, *Peristenus dumestris*: 52, mesonotum; 53, frons; 54, tergite 1 dorsal view. Figures 55-57, *Peristenus plagiognathi*: 55, tergite 1 dorsal view; 56, mesonotum; 57, frons. Scanning electron microscope photographs 225-245 X.



Figures 58-63. *Peristenus* species, body sculpture. Figures 58-60, *Peristenus vitidis*: 58, mesonotum; 59, frons; 60, tergite 1 dorsal view. Figures 61-63, *Peristenus bicolor*: 61, tergite 1 dorsal view; 62, mesonotum; 63, frons. Scanning electron microscope photographs 225-245 X.



Figures 64-66. *Peristenus juniperinus*. 64, tergite 1 dorsal view; 65, mesonotum; 66, frons. Scanning electron microscope photographs 225-245 X.

ate; scutum very sparsely hairy with some obsolescent, indistinct punctures; lateral lobes smooth; mesepisternum granulose with smooth areas posteriorly. Stigma 2.5 times as long as wide, about as wide as radial cell on wing margin; first abscissa of radius very short. Femur III 0.8 times as wide as apex of tergite 1; tibia III 0.51 mm long. Tergite 1 finely striate, sides nearly parallel behind spiracles which slightly protrude, apex about as wide as eye, 2.0 times as long as wide at apex.

FEMALE: Unknown.

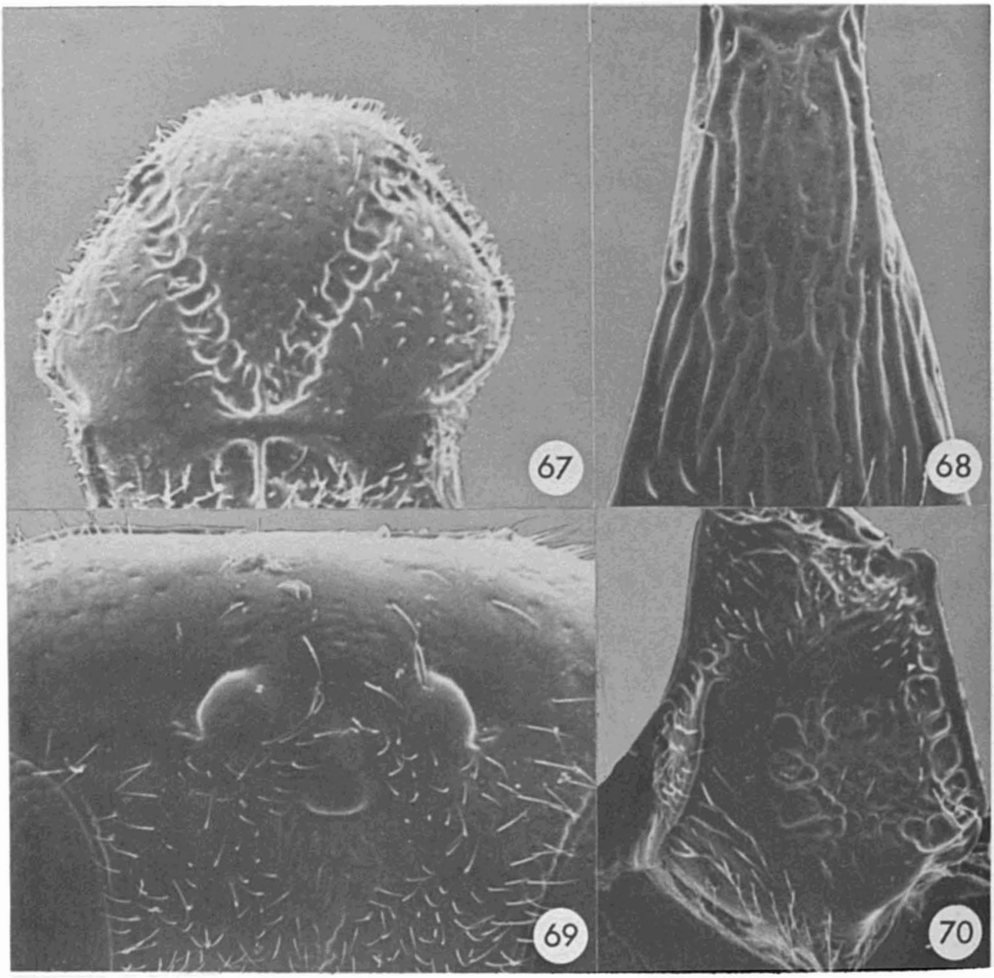
P. zingiberis is the smallest known Nearctic species of the genus. It is distinct by size and color, the pale wing veins, wide and shallow notaulices, and characters of tergite 1.

DISTRIBUTION: **Canada.** Ontario.

21. *Peristenus* **plagiognathi** (Loan) new combination

Leiophron plagiognathi Loan, 1966: 89-94.

Holotype: ♀, labelled "Belleville, Ont. 31.V. 1962. C.C. Loan; reared ex *Plagiognathus* sp ex *Spirea*; *Leiophron plagiognathi* Loan CNC No. 13, 184 Holotype". In the Canadian National Collection, Ottawa.



Figures 67-70. *Peristenus pallipes*. 67, mesonotum; 68, tergite 1 dorsal view; 69, frons; 70, mesepisternum. Scanning electron microscope photographs 225-245 X.

BIOLOGY: Loan (1966).
HOSTS: *Plagiognathus albonotatus* Knight and *P. cornicola* Knight breeding on *Spirea latifolia* L.

Among bicolorous species, *P. plagiognathi* (figs. 55-57) is recognized by a fine, rather weak occipital carina. The flagellum of the female is thickened distally with the subapical articles quadrate; that of the male has 16-18 articles.
DISTRIBUTION: **Canada.** Ontario.

22. *Peristenus* **tacamahacae** n. sp.

Holotype: ♂, Canada. Ontario, Foxboro, captured on trunk of mature *Populus balsamiferae* L., 18. VII. 1969. In the Canadian National Collection. Ottawa. CNC 13, 166.
Paratype: 1 ♂, Canada. Nova Scotia, Annapolis Royal, 15.II. 1932, No. 560, coll. F.C. Gilliatt.

HOLOTYPE MALE: Length about 3.3 mm. Bicolorous. Frons beside eye, genae, face, pronotum anteriorly, antenna, legs pale yellowish; frons medially, thorax, gaster reddish black; wing veins very weakly infuscated.

Frons finely punctured, medially carinate; face as wide as flagellar segments 1 + 2, 0.9 times as wide as eye length; eye as wide as apex of tergite 1; OOL not as long as POL which is 1.5 times longer than malar space; flagellar articles 19 (incomplete, distal segment(s) missing), 1 slightly longer than scape; occipital carina fine, complete. Mesoscutum moderately hairy, not prominently punctured; lateral lobes of mesonotum smooth, glabrous; notaulices foveolate; mesepisternum rugulose except for a narrow, smooth, medial band. Stigma 2.8 times as long as wide; radial cell about as long as stigma width. Nervulus postfurcal; recurrens interstitial with intercubitus. Femur III 0.7 times as wide as apex of tergite 1; tibia III 1.0mm long. Tergite 1, 1.8 times as long as wide at apex, dorsal face with a few lateral striae from spiracles to apex, otherwise reticulate (fig. 27).
FEMALE: Unknown.

This large, handsome species is characterized by a bicolorous frons and otherwise yellowish head contrasting with the dark thorax and gaster. Its pale wing veins and reticulate tergite 1 are also distinctive.
DISTRIBUTION: **Canada.** Ontario, Nova Scotia.

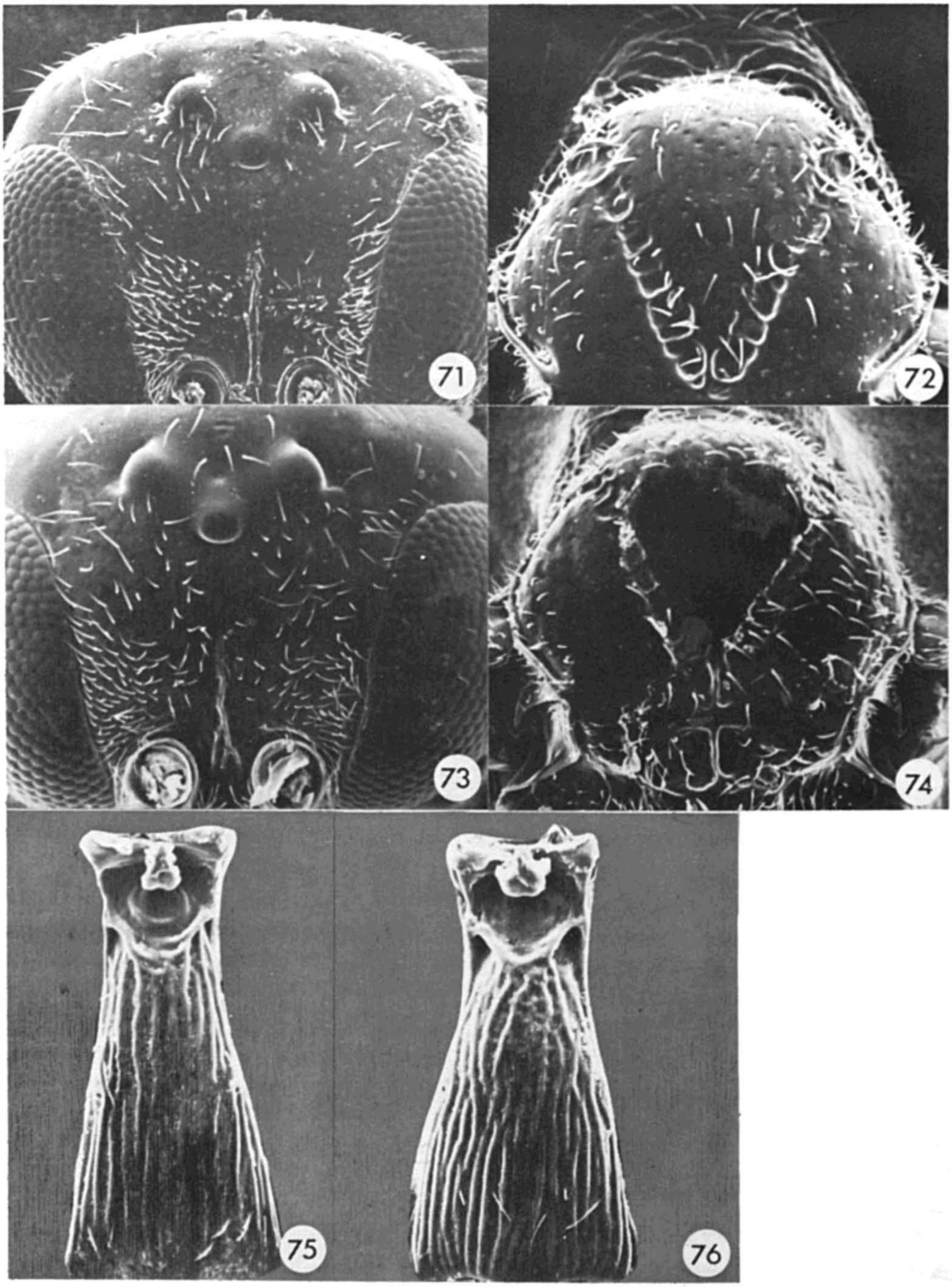
23. *Peristenus* **clematidis** n. sp.

Holotype: ♀, Canada. Ontario, Wallbridge, reared from *Halticus uhleri* (Knight) breeding on *Clematis virginiana* L., 3.IV. 1968. In the Canadian National Collection, Ottawa. CNC 13, 167.
Paratypes: 20 ♀, 3 ♂, data as for type except reared 24.III-8.IV.1968 and 1 ♀ swept from *C. virginiana* 9.VII,1968.

HOST: Reared from *Halticus uhleri*.
HOLOTYPE FEMALE: Length about 3.0 mm. Bicolorous. Similar to *P. bicolor* new species except flagellar articles 1-6 pale, and frons reddish brown; wing veins yellowish hyaline with first intercubitus and second abscissa of radius lightly infuscated.

Head, in side view, a right angle at the eye with the face vertical, frons horizontal and the eye with its long axis somewhat horizontal and protruding forward slightly past the face; eye smaller than usual, face almost 0.9 times as wide as eye length and with white, appressed hair; frons with some fine setiferous punctures and a fine medial carina: POL as long as flagellar article 1, or malar space, or basal width of mandible; flagellar articles 21, all longer than wide, 1 + 2 longer than face width; flagellum not much wider distally, 2.8 times as long as head width; occipital carina fine, not continuous medially behind ocellar triangle. Mesonotum with sparse, flat hair on scutum and anteriorly on lateral lobes, relatively smooth, not shiny except lateral lobes posteriorly; notaulices foveolate, deeper posteriorly than in front; mesepisternum without smooth areas, granulose and with very fine, interrupted striae. Stigma 2.4 times as long as wide, about as wide as length of radial cell. Tibia III 0.92 mm long. Tergite 1, 2.0 times as long as wide at apex, striate, apex about as wide as face (fig. 21).

This very distinctive species is characterized by the shape of the head and color of the flagellum, very small eye, and pronounced malar space. There is a



Figures 71-76. *Peristenus* species, body sculpture. Figures 71-72, 76, *Peristenus solidaginis*: 71, frons; 72, mesonotum; 76, tergite 1 dorsal view. Figures 73-75, *Peristenus reidi*: 73, frons; 74, mesonotum; 75, tergite 1 dorsal view. Scanning electron microscope photographs 225-245 X.

tendency for the nervulus to be interstitial. The number of flagellar articles in both males and females varied from 19-20. The sexes are unusually difficult to distinguish by secondary characters as the size of the eye and ratio of eye length to face width is similar. The flagellum of the male, however, is uniform reddish dusky rather than pale basally as in the female.

DISTRIBUTION: **Canada.** Ontario.

24. *Peristenus* **wallisi** n. sp.

Holotype: ♀, Canada. B.C., Terrace, Spring Creek, 200', captured 1.VI. 1960, coll. W.W. Moss. In the Canadian National Collection, Ottawa. CNC 13, 165.

Paratypes: 1♂, Robson, B.C., 22.V.1950, coll. H.R. Foxlee; 6♀, 4♂, as type locality and identified as Spring Creek, Terrace, or Gagnon Road 6 miles west of Terrace, coll. B. Hemming, R.J. Pilfrey, W.W. Moss, and C.H. Mann.

HOLOTYPE FEMALE: Length 3.1 mm. Bicolorous. Head reddish yellow with frons near eyes reddish brown; eye greyish; legs yellowish with tibia and tarsi of II and III infuscated; body castaneous; wing veins distinctly infuscated, stigma dark with proximal end hyaline.

Head deep, 1.3 times as wide as long; frons finely setiferous, smooth; eyes protrude forward, not noticeably convergent on face; face, eye, apex of tergite 1 approximately equal width; face hairy, 0.7 times as wide as eye length; malar space 0.7 times basal width of mandible, only slightly less than POL which is 0.6 times as long as flagellar article 1; flagellar articles 18, all longer than wide; ocelli rather large; occipital carina complete. Mesonotum quite impunctate, shiny, scutum with fine, sparse hair; notaulices well-impressed, foveolate; mesepisternum smooth medially, finely rugulose above and below. Stigma 2.5 times as long as wide as length of radial cell. Femur III 0.6 times as wide as apex of tergite 1; tibia III 0.97 mm long. Tergite 1 striate, 1.6 times as long as wide at apex (fig. 23).

P. wallisi is a medium-sized, bicolorous species. It is distinctive by a short malar space, and short radial cell on the wing margin; tergite 1 is carinate on the sides from base to apex; and the flagellar articles are all longer than wide. These characters and others listed in the species key separate it from other bicolorous species of *Peristenus.*

The species is named for the Manitoba naturalist John Braithwaite Wallis (1877-1962).

DISTRIBUTION: **Canada.** British Columbia.

Acknowledgements

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Naturaliste can., 101:861-891 (1974).

VASCULAR PLANTS OF NAHANNI NATIONAL PARK AND VICINITY, NORTHWEST TERRITORIES

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Résumé

Cet article rapporte la présence de 483 plantes vasculaires dans le parc national de Nahanni et les environs. Parmi ces plantes, *Danthonia intermedia, Carex peckii, Trifolium pratense, Pastinaca sativa, Mimulus guttatus, Salix novae-angliae* et *Viola tricolor* sont des additions à la flore du district de Mackenzie. Une nouvelle espèce est décrite: *Aster* **nahanniensis** W.J. Cody. De plus, 67 espèces sont rapportées pour la première fois des monts Mackenzie. Des extensions d'aires importantes sont signalées pour d'autres espèces, par exemple *Diapensia obovata*.

Abstract

This paper reports 483 vascular plants from Nahanni National Park and vicinity. Of those *Danthonia intermedia, Carex peckii, Trifolium pratense, Pastinaca sativa, Mimulus guttatus, Salix novae-angliae* and *Viola tricolor* are believed to be additions to the flora of the District of Mackenzie. *Aster* **nahanniensis** W.J. Cody, a new species, is described. In addition, 67 species were recorded from the Mackenzie Mountains for the first time. Other plants, such as *Diapensia obovata*, are significant range extensions.

Introduction

The writers had the opportunity to study vascular plants in the Flat and South Nahanni River areas, which are poorly known from a botanical standpoint. Cody collected at the settlement of Nahanni Butte and on the slopes of Nahanni Butte Mountain in 1961. In 1967 he continued such activities near the headwaters of the Flat River while based at Tungsten. Both field trips were sponsored by the Plant Research Institute.

Scotter collected vascular plants from the Flat and South Nahanni River areas during late June, early July, and mid-September 1970 and in mid-September of 1971. Such endeavours, however, were incidental to the major purpose of assessing the area for national park potential (Fig. 1 and 2). That study was sponsored by Parks Canada and the Canadian Wildlife Service.

The area covered extends from Nahanni Butte (61°03′N, 123°23′W) near the confluence of the South Nahanni and Liard rivers west to Tungsten (61°58′N, 128°14′W) near the Yukon and Northwest Territories boundary and in a north-

Figure 1. Virginia Falls, with water plunging to the river more than three hundred feet below, is one of the paramount features of Nahanni National Park. Photo — George W. Scotter.

Figure 2. The gate, a narrow portal guarded by Pulpit Rock, in Third Canyon, is another landmark of Nahanni National Park. Photo — George W. Scotter.

south direction from latitude 61°03′N to 62°41′W. Plants were obtained from 60 sites, ranging in elevation from 600 feet (180 m) at Nahanni Butte to 5,500 feet (1,680 m) in the Mountains near Tungsten (Fig. 3).

CLIMATE

The climate of the area is continental with short warm summers and long cold winters. Even though high temperatures have been recorded in the Flat and South Nahanni River valleys, the growing season is short and never free from the danger of frost. At Fort Simpson, there is an average frost-free season of only 70 to 75 days (Raup, 1947).

Short-term climatic data are available from only two locations within the area. At both Tungsten [elevation 4,250 feet (1,300 m)] and the Peñorroya prospect

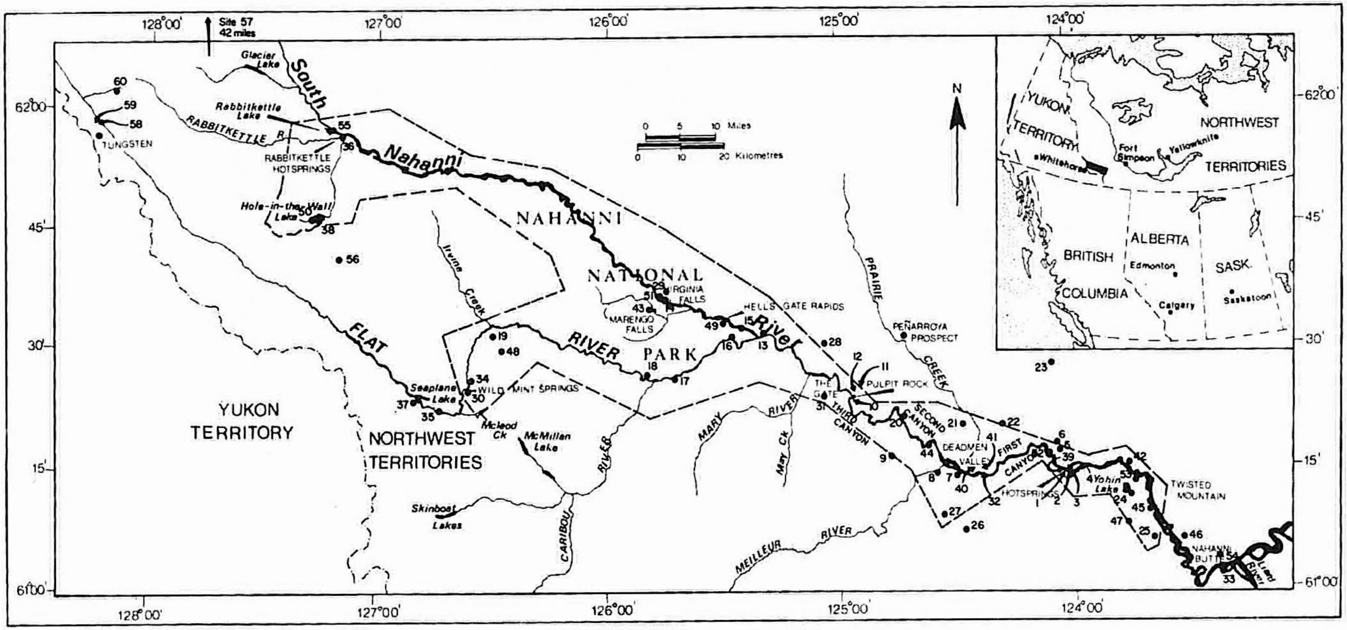

Figure 3. Map of the Flat and South Nahanni River areas, Northwest Territories, showing the sites referred to in the list of species.

site [elevation 2,850 feet (870 m)], mean daily minimum temperatures were above freezing in June through August. June and July are pleasant summer months in the South Nahanni and Flat River areas with practically no darkness and temperatures reaching into the low eighties (27°C). July is the warmest month of the year.

The coldest month of the year is January. There are only about 5 hours of sunshine daily, and temperatures have dipped as low as -55°F (-48°C). The temperature in January rarely rises above zero (-18°C).

June, July, and August are the months of greatest rainfall, with July being the wettest month. The average yearly precipitation is about 23 inches (58 cm) at the two stations, but is probably much more variable in other portions of the area.

Snow may fall over the headwaters of the Flat River during every month except June, July, and August. November is the month with the greatest snowfall. The total snowfall for the average year is about 100 inches (254 cm). Farther east the snowfall is generally less.

Small watercourses begin to freeze as early as mid-September, and ice may form on the larger streams in October. High mountain lakes freeze over by the end of October.

Although the South Nahanni River ice usually breaks up in late April, the river is not navigable until mid-May. The Flat River ice breaks up about the same time. By June, little snow remains on the mountains.

GEOLOGY AND GEOMORPHOLOGY

The mountains west of the Mackenzie River, in the Northwest Territories, are largely composed of sedimentary rocks. The Mackenzie Mountains subdivision is composed of north-trending thrust sheets, faulted folds, and broad elongated uplifts and depressions. The major thrust faults and axial planes of the large folds dip either east or west (Bostock, 1948).

The Liard Plateau subdivision is an area of broad, even-topped ranges of hills, rising to about 4,500 feet (1,370 m). The folds which form this plateau strike north. The northern part of the plateau has a higher relief than the southern part. The South Nahanni River cuts deeply into the beds which form the plateau (Bostock, 1948).

The South Nahanni River and its largest tributary, the Flat River, originate near the Yukon border, at about 3,500 feet (1,070 m) elevation. The South Nahanni River flows southeastward for 250 miles (402 km) and joins the Liard River at Nahanni Butte. Peaks along its route generally range from 4,500 to 6,000 feet (1,370 — 1,830 m) in elevation, although the Ragged Range in the northwest rises to over 9,000 feet (2,750 m).

The Mackenzie Mountains and Liard Plateau show the effects of glaciation. Glacial erosion is shown by cirques and pinnacles in the mountains and by scoured bedrock in the lower Liard Plateau (Bostock, 1948). Glacial deposition is evident by the presence of moraines and glaciofluvial deposits by kame terraces in the Flat River valley (Gabrielse, Roddick and Blusson, 1965). Remnants of glaciers are still present in the higher mountains, especially in the Ragged Range.

The last continental glaciers did not intrude far into the South Nahanni and Flat River area. The hummocky moraine in the eastern part of the area probably marks their most westerly extent. Sections of the Nahanni and Flat rivers and the Prairie Creek valley probably supported valley glaciers that produced wide but steep-sloped valleys. Near the peaks of many mountain ridges, amphitheater-like scars of cirque glaciers are evident. Ice from most of these cirque glaciers probably did not reach the main valley glaciers.

Most of the surface materials covering the bedrock were derived locally from the weathering of the bedrock, and were transported only short distances by glaciers, gravity, or running water.

Erosion by running water has produced narrow and deep, steep-walled valleys and canyons. During spring flooding rivers are especially effective agents in removing the accumulated debris from crumbling bedrock faces. Some of that debris is deposited in alluvial flats and fans, only to be carved into new channels by sudden floods in the rivers.

Figure 4. Lush vegetation surrounds the hot-springs at the mouth of First Canyon, an oasis in an otherwise harsh environment. Photo — George W. Scotter.

The texture of the alluvium deposited by flooding rivers depends upon the speed of the current at any given location. Generally, fine-grained sand interbedded with organic debris is found on the floodplains of larger rivers, although gravel bars may occur locally. Swift creeks, prone to flash floods, usually deposit much gravel and rock rubble. Fluvial deposits laid down in the beds of rivers and creeks consist of well-sorted sand and gravel materials.

Peaty organic materials accumulate on poorly-drained flats. Permafrost occurs in some peat deposits and on some lower slopes.

Bedrock is exposed in a fairly large portion of the area.

Additional information on the geology of the area is available in publications by Cameron and Warren (1938), Kingston (1951), Patton (1958), Douglas and Norris (1960), Green (1965), and Blusson (1968).

Springs

One of the most interesting features of the Flat and South Nahanni rivers area is the presence of several mineral springs whose temperatures are higher than river water temperatures. Two types of thermal springs are found in the area: normal thermal springs, where the waters are heated in passing through the earth at great depths, and anomalous thermal springs, which are probably heated by the chemical reaction of the water with minerals in the bedrock through which they pass (Brandon, 1965). The springs at Clausen Creek (Fig. 4) are a good example of normal springs, while the springs at Hole-in-the-Wall Lake are probably of the anomalous type. Most or all of the springs are saline, their salinity varying with the size and depth of their underground flow system.

Large thermal springs are located along the south bank of the South Nahanni River, upstream from Clausen Creek and below First Canyon. The flow of water from the main pool has been measured at 300 gallons (1,364 l) per minute. The temperature of the pool was measured at 95°F (35°C) (Brandon, 1965). The chief mineral constituent is sodium chloride, and the water has an odour of hydrogen sulphide.

Rabbitkettle Hotsprings (Fig. 5), near the confluence of the Rabbitkettle and South Nahanni rivers, have formed a spectacular terraced, flat-topped deposit of tufa or calcium carbonate. This circular deposit, about 225 feet (69 m) in diameter, rises 90 feet (27 m) above the Rabbitkettle River. Successive terraces from 6 inches (15 cm) to 12 feet (3.7 m) thick produce a layer-cake-like structure. The main spring comes from a pool about 12 feet (3.7 m) in diameter near the center of the top terrace. The water temperature of the spring was measured at 69°F (21°C) (Gabrielse, Roddick and Blusson, 1965).

Other warm springs are to be found near Hole-in-the-Wall Lake at the headwaters of a tributary which enters the South Nahanni near Rabbitkettle Hotsprings. This area has towering cliffs of Cretaceous granitics to the west and appears to emerge from the same Ordovician and Silurian formations as do Rabbitkettle Hotsprings, though almost no tufa deposits are present.

Several warm springs that occur near the Flat River (Fig. 6), downstream from Seaplane Lake, also emerge from Ordovician and Silurian beds. Water is warmed after passing through a geothermal gradient between the limestone and the nearby Cretaceous granitics. "Old Pots" Spring, located at 61°31′30″N, 126°30′W, gushes in great volume to fill a large pond, and several high-walled deposits

Figure 5. Rabbitkettle Hotsprings, located near the confluence of the Rabbitkettle and South Nahanni rivers, is a terraced deposit of tufa. Photo — George W. Scotter.

Figure 6. Wild Mint Springs rimmed with a profusion of flowers. A number of plants collected in such sites are reported as range extensions. Photo — N. M. Simmons.

of tufa, or "pots", are also present. The Wild Mint Springs, near McLeod Creek at 61°25′30″N, 126°35′W, have deposited dolomitic material containing both calcium and magnesium salts. Another spring near the headwaters of the Flat River at Tungsten warms an extensive meadow.

Vegetation

The vegetation of the Flat and South Nahanni River areas is poorly known. Detailed plant cover descriptions are available for only two small sections: Glacier (Brintnell) Lake (Raup, 1947) and Hole-in-the-Wall Lake (Arnold, 1961).

Jeffrey (1961, 1964) published descriptions of the forest types along the Lower Liard River. Several of those types are also found in the Flat and South Nahanni River areas.

The vegetation of the Flat and South Nahanni River area is characterized by boreal and alpine plant species. An altitudinal transition is shown from the closed forests in the lowlands to alpine tundra on the mountains. Treeline is at about 3,900 feet (1,190 m) on south- and west-facing slopes, but occurs at about 3,600 feet (1,100 m) on the north- and east-facing slopes. The influence of aspect is illustrated in the occurrence of vegetation: north- and east-facing slopes carry a vegetation that would be found at higher elevations on the south- and west-facing slopes.

Dense growth of tall trees occurs on valley bottoms especially on floodplains. White spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*) (Fig. 7 and 8) are the dominant species in undisturbed stands, often with shrub layers of alder (*Alnus incana*), squashberry (*Viburnum edule*), and wild rose *(Rosa aci-*

cularis). Even-aged stands of trembling aspen (*Populus tremuloides*) may occur in some bottomlands with only a few scattered white spruce. Alder (*Alnus crispa*) and wild rose are common in the shrub layers. Forest stands regenerating after fire usually consist of trembling aspen and white birch (*Betula papyrifera*), with some white and black spruce (*Picea mariana*). Dense, tall white spruce may grow on some alluvial flats in nearly pure stands. The forest floor is usually covered with feather mosses.

Figure 7. White spruce is a prominent forest type within the region. Photo — George W. Scotter.

Open stands of trees that reach a height of 30 to 50 feet (9 — 15 m) at maturity are common. In undisturbed stands white spruce dominates, growing with a mixture of trembling aspen and white birch. At higher altitudes, and on north-facing slopes, black spruce becomes more prominent, growing in mixture with white spruce, lodgepole pine (*Pinus contorta* var. *latifolia*), or jack pine (*Pinus banksiana)*. Alder *(Alnus* spp.) and Labrador tea *(Ledum groenlandicum)* are found in the shrub layer. Just below the treeline alpine fir (*Abies lasiocarpa*) is found growing in mixture with black and white spruce.

Figure 8. Note the distribution of conifers and hardwoods along the Flat River. The mineral lick on the south bank of the Flat River is frequented by moose, Dall sheep, and woodland caribou. Photo — N. M. Simmons.

On some dry, south- or west-facing slopes pure stands of lodgepole or jack pine may grow. Lodgepole or jack pine may regenerate on such sites after fire, although white and black spruce in mixture with white birch are also common. Alder (*Alnus crispa*) is a common shrub species in such areas.

On rocky slopes scattered white spruce and lodgepole or jack pine may grow. Lodgepole pine stands are more common in the western portion of the area and jack pine stands are found near Nahanni Butte.

Open forests of scattered, stunted trees occur in different areas because of soil-rock-water relationships. These trees seldom reach the height of 30 feet (9 m) at maturity. Open coniferous stands occur below the treeline, especially on north- and east-facing slopes. These consist mainly of stunted, scattered black spruce, alpine fir, and lodgepole or jack pine. Outcrops of solid or fractured bedrock present a poor environment for plant growth. In such places scattered white and black spruce or lodgepole and jack pine may grow. On peat deposits, black spruce trees may grow as open, stunted muskeg forests. After fires have burned these scattered, stunted forest stands, the regeneration may favour the coniferous species of black spruce or lodgepole and jack pine or a mixture of conifers with white birch.

A widely-occurring type is the open black spruce and reindeer lichen forest. The soil is generally heavy (loam to clay) and is covered by shallow peat. Permafrost usually occurs at 4 feet (1.2 m) below the surface. This condition is common on gentle north- or east-facing slopes and on other lower slopes where the gradient is less than 10 percent.

Treeless areas occur as the result of environmental factors. Some bottomlands are subject to frequent flooding and deposition of alluvial silt and sand which kill the vegetation. In such places willows and alder may grow, although some areas are completely devoid of vegetation. On steep mountain slopes bedrock outcrops and loose scree prohibit tree growth. These areas are usually devoid of vegetation, save for some grasses or dwarf shrub species (Fig. 9). Alpine tundra is found on the higher mountains, and is characterized by mountain avens (*Dryas* spp.), ericaceous shrubs, sedges, and grasses. The high water table in some wetlands prohibits the growth of trees, but supports sedges, cottongrass (*Eriophorum* spp.), and some low shrub vegetation. Vegetation associated with hotsprings is often luxuriant and of major floristic and ecological interest.

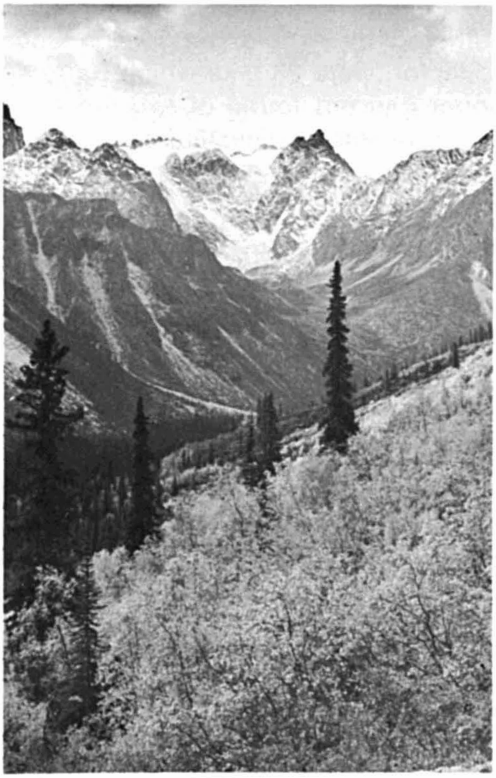

Figure 9. Dwarf birch communities dominate the vegetative cover immediately above treeline. Among the pinnacles of the saw-toothed Ragged Range are some of the highest points in the Mackenzie Mountains. Photo — George W. Scotter.

PLANT DISTRIBUTION

Plant distribution within the Mackenzie Mountains is likewise little known. The first listing of plants from these mountains was that of A. E. Porsild (1945). He reported a total of 256 taxa which he and V. C. Wynne-Edwards had collected along the now abandoned Canol Road. In this same publication, Porsild also reported 102 taxa which Wynne-Edwards had collected on Lone Mountain and Mount Nahanni, on the east flank of the Mackenzie Mountains.

Hugh M. Raup (1947), in his "Botany of Southwestern Mackenzie" recorded 283 taxa which he and J. H. Soper had collected at Glacier Lake in 1939. Porsild (1961) recorded 104 taxa which Edward W. Arnold collected in the vicinity of Hole-in-the-Wall Lake. In that paper Porsild noted that among the taxa gathered by Arnold, an inexperienced collector, were 28 taxa which Raup and Soper had not found in two months of intensive study at Glacier Lake.

Cody (1960) reported a few collections from along the Canol Road where it enters the Mackenzie Mountains. Both Cody (1963) and W. W. Jeffrey (1961) recorded a few taxa from the Liard Range and Nahanni Butte. Jeffrey (1961) also reported the collection of 15 plant species from Virginia Falls, on the South Nahanni River.

Porsild and Cody (1968) divided the Continental Northwest Territories into six floristic zones. The area treated by the present paper covers parts of two of these zones: 1 — the Mackenzie Mountains, and 6 — the lowlands which extend from the Slave River west to the Liard River and a narrow strip adjacent to the upper Mackenzie River. Porsild and Cody (1968) reported a total of 558 taxa from Zone 1.

The present paper records a total of 483 taxa which were collected by the authors from the South Nahanni and Flat River drainages. Of this number, 433 were found in Zone 1 of Porsild and Cody (1968), 140 were found in Zone 6, and 90 were common to both zones. Of the 433 taxa recorded for Zone 1, 70 are additional to those reported by Porsild and Cody (1968). *Aster nahanniensis* is described as new. In addition, four other native Canadian species are reported as new to the District of Mackenzie: *Danthonia intermedia, Carex peckii, Salix novae-angliae* and *Mimulus guttatus;* and three species, *Trifolium pratense, Viola tricolor,* and *Pastinaca sativa,* are added to the introduced flora of the District of Mackenzie.

The 433 taxa from Zone 1 were examined to ascertain their phytogeographic affinities: 157 were circumpolar in distribution; 130 had more or less wide-ranging North American ranges; 80 were Amphi-Beringian; 34 were Cordilleran; 23 were endemic to the Alaska-Yukon-western Mackenzie region; 3 were Amphi-Atlantic; 5 were introduced from the Old World; and there was one hybrid.

Approximate location of the collection sites are shown in Figure 3. Other site data are listed below:

1. Plant communities around hotsprings and stream, 61°15′N, 124°03′W, elev. 850 ft. (260 m), 26 June 1970, *Scotter 12242-12277;* 19 Sept. 1971, *Scotter 17435.*
2. Plants along trails near hotsprings, 61°15′N, 124°03′W, elev. 850 ft. (260 m), 26 June 1970, *Scotter 12278-12316.*
3. Plants in clearing around a cabin, 61°15′N, 124°03′W, elev. 850 ft. (260 m), 26 June 1970, *Scotter 12317-12341.*
4. Plants on rock ledge and surrounding white spruce forest, 61°15′N 124°03′W, elev. 875 ft. (270 m), 26 June 1970, *Scotter 12342-12357.*
5. Gravel bar on South Nahanni River, 61°16′N, 124°04′W, elev. 900 ft. (280 m), 26 June 1970, *Scotter 12358-12364.*
6. White water spring, 61°17′N, 124°05′W, elev. 950 ft. (290 m), 26 June 1970, *Scotter 12365-12375.*

7. Deadmen Valley, near cabin; white spruce and black cottonwood community, 61°15'N, 124°30'W, elev. 1,050 ft (320 m), 27 June 1970, *Scotter 12376-12400.*
8. Along Meilleur River; white spruce and black cottonwood community, 61°17'N, 124°34'W, elev. 1,100 ft. (340 m), 27 June 1970, *Scotter 12401-12430.*
9. Black spruce, feather moss and lichen community, 61°17'N, 124°47'W, elev. 1,300 ft. (400 m), 28 June 1970, *Scotter 12431-12437.*
10. White spruce community along bank of river, 61°25'N, 124°55'W, elev. 1,300 ft. (400 m), 28 June 1970, *Scotter 12438-12456.*
11. Black spruce and white spruce forest with open south-facing slopes, 61°26'N, 124°54'W, elev. 1,500 ft. (460 m), 28 June 1970, *Scotter 12457-12461.*
12. Gravel pavement near river, 61°26'N, 124°55'W elev. 1,300 ft. (400 m), 28 June 1970, *Scotter 12462.*
13. Island in South Nahanni River, 61°32'N, 125°20'W, elev. 1350 ft. (410 m), 28 June 1970, *Scotter 12463-12480.*
14. Vicinity of Virginia Falls, South Nahanni River, 61°37'N, 125°44'W., elev. 1,800 ft. (550 m), 29 June 1970, *Scotter 12481-12523.*
15. Mature spruce and feather moss community, Flat River, 61°32'N, 125°24'W, elev. 1,500 ft. (400 m), 30 June 1970, *Scotter 12524-12526.*
16. Open lodgepole pine community, Flat River, 61°31'N, 125°27'W, elev. 1,750 ft. (530 m), 30 June 1970, *Scotter 12527-12534.*
17. Mineral lick area, Flat River, 61°27'N, 125°42'W, elev. 1,800 ft. (550 m), 30 June 1970, *Scotter 12535-12549.*
18. Spruce muskeg, Flat River, 61°28'N, 125°51'W elev. 1,825 ft. (560 m), 30 June 1970, *Scotter 12550-12554.*
19. Burned-over area, Flat River, 61°33'N, 126°30'W, elev. 1,850 ft. (560 m), 30 June 1970, *Scotter 12555-12562.*
20. Burned-over area; birch, lodgepole pine, and black poplar stand, 61°21'N, 124°43'W, elev. 1,800 ft. (550 m), 30 June and 1 July 1970, *Scotter 12563-12566.*
21. Alpine community, 61°20'N, 124°28'W, elev. 5,100 ft. (1,560 m), 2 July 1970, *Scotter 12567-12594.*
22. Alpine community, 61°21'N, 124°20'W, elev. 4,800 ft. (1,460 m), 2 July 1970, *Scotter 12595-12628.*
23. Alpine community, 61°27'N, 124°05'W, elev. 3,700 ft. (1,130 m), 2 July 1970, *Scotter 12629-12642.*
24. Shore of Yohin Lake, 61°12'N, 123°46'W, elev. 712 ft. (220 m), 2 July 1970, *Scotter 12643-12656.*
25. Wind-blown sandy area, 61°07'N, 123°42'W, elev. 2,450 ft. (750 m), 14 September 1971, *Scotter 17410.*
26. Alpine community, 61°08'N, 124°27'W, elev. 4,100 ft. (1,250 m), 2 July 1970, *Scotter 12657-12680.*
27. Alpine community, 61°11'N, 124°33'W, elev. 5,050 ft. (1,540 m), 2 July 1970, *Scotter 12681-12687.*
28. Alpine community, 61°32'N, 125°03'W, elev. 4,500 ft. (1,370 m), 3 July 1970, *Scotter 12688-12705.*
29. Alpine community, Sunblood Mountain, 61°38'N, 125°44'W, elev. 5,000 ft. (1,530 m), 3 July 1970, *Scotter 12706-12713.*
30. Mineral springs, Flat River region, 61°25'N, 126°36'W, elev. 2,500 ft. (760 m), 3 July 1970, *Scotter 12714-12775, 13619b.*
31. Alpine community, 61°25'N, 125°05'W, elev. 5,200 ft. (1,590 m), 3 July 1970, *Scotter 12776-12788.*
32. Dry canyon, 61°15'N, 124°23'W, elev. 1,800 ft. (550 m), 3 July 1970, *Scotter 12789-12825.*
33. Nahanni Butte; lowland in the vicinity of the settlement, 61°03'N, 123°24'W, elev. 600 ft. (180 m), 5 and 7 Aug. 1961, *Cody & Spicer 12004-12024, 12060;* 5 July 1970, *Scotter 12826-12862;* 19 Sept. 1971, *Scotter 17438.*
34. Mineral springs region south of the Flat River, 61°25'N, 126°36'W, elev. 2,500 ft. (760 m), 12 Sept. 1970, *Scotter 12863-12874.*
35. Mineral springs region north of the Flat River, 61°23'N, 126°44'W, elev. 1,900 ft. (580 m), 12 Sept. 1970, *Scotter 12875-12887.*
36. Rabbitkettle Hotsprings, 61°56'N, 127°11'W, elev. 2,000 ft. (610 m), 12 Sept. 1970, *Scotter 12888-12891;* 16 Sept. 1971, *Scotter 17423-17424.*
37. Mature spruce forest, Seaplane Lake, 61°24'N, 126°49'W, elev. 2,400 ft. (730 m), 12 Sept. 1970, *Scotter 12892.*
38. Hole-in-the-Wall Lake, 61°46'N, 127°16'W, elev. 3,900 ft. (1,190 m), 12 Sept. 1970, *Scotter 12893-12896;* 18 Sept. 1971, *Scotter 17431-17433.*
39. Plant communities around springs, 61°16'N, 124°03'W, elev. 850 ft. (260 m), 10 Sept. 1970, *Scotter 12897-12924.*
40. Floodplain near mouth of Prairie Creek, 61°16'N, 124°26'W, elev. 1,400 ft. (430 m), 10 Sept. 1970, *Scotter 12925-12933.*
41. Dry canyon, 61°15'N, 124°23'W, elev. 1,700 ft. (520 m), 11 Sept. 1970, *Scotter 12934-12947.*
42. Low-lying area near the South Nahanni River, 61°15'N, 123°46'W, elev. 775 ft. (240 m), 9 Sept. 1970, *Scotter 12233-12234.*
43. West of Marengo Falls, 61°36'N, 125°49'W, elev. 2,000 ft., (610 m), 12 Sept. 1970, *Scotter 12235.*

44. Treeline community, 61°18'N, 124°37'W, elev. 4,200 ft. (1,280 m), 12 Sept. 1970, *Scotter 12237*.
45. Burned-over area, 61°09'N, 123°40'W, elev. 750 ft. (230 m), 13 Sept. 1970, *Scotter 12238-12239*.
46. Floodplain above the South Nahanni River, 61°06'N, 123°34'W, elev. 700 ft. (210 m), 13 Sept. 1970, *Scotter 12240*.
47. Crevice between rock blocks in the alpine area, 61°08'N, 123°45'W, elev. 3,500 ft. (1,070 m), 14 Sept. 1971, *Scotter 17411*.
48. Along stream near "Old Pots" Spring, 61°32'30"N, 126°29'W, elev. 2,500 ft. (760 m), 16 Sept. 1971, *Scotter 17412-17422*.
49. Gravel bar near Hell's Gate Rapids, 61°34'N, 125°29'W, elev. 1,400 ft. (430 m), 17 Sept. 1971, *Scotter 17425*.
50. Hotsprings near Hole-in-the-Wall Lake, 61°47'N, 127°18'W, elev. 4,200 ft. (1,280 m), 18 Sept. 1971, *Scotter 17426-17429*.
51. Small lake northwest of Virginia Falls, 61°37'N, 125°46'W, elev. 1,850 ft. (560 m), 18 Sept. 1971, *Scotter 17430*.
52. Pine forest on rock outcrop above the South Nahanni River, 61°17'N, 124°06'W, elev. 2,350 ft. (720 m), 19 Sept. 1971, *Scotter 17434*.
53. Small lake north of Yohin Lake, 61°13'N, 123°45'W, elev. 710 ft. (220 m), 19 Sept. 1971, *Scotter 17436-17437*.
54. Nahanni Butte Mountain slopes, 61°04'N, 123°23'W, elev. 600 — 2,500 ft. (180 — 760 m), 6 July 1961, *Cody & Spicer 12025-12059*.
55. Recently-burned area adjacent to Rabbitkettle Lake, 61°57'N, 127°13'W, elev. 2,050 ft. (630 m), 10 Aug. 1967, *Spicer 1759-1777, Cody & Spicer 17896-17929*.
56. Lakeshore and among and on boulders by unnamed lake 9 miles south-southeast of Hole-in-the-Wall Lake, 61°42'N, 127°10'W, elev. 4,700 ft. (1,430 m), 10 August 1967, *Spicer 1778-1792, Cody & Spicer 17930-17957*.
57. In turf on slope by "Grizzly Bear" Lake and in small wet meadow back of lakeshore, 62°41'N, 127°50'W, elev. 4,200 ft. (1,280 m), 10 Aug. 1967, *Spicer 1793-1825, Cody & Spicer 17958-18023*.
58. Valley floor and hotspring area near headwaters of Flat River, 61°58'N, 128°15'W, elev. 3,500 ft. (1,070 m), 20-22 July 1967, *Cody & Spicer 16348-16400;* 23 July thru 6 Aug. 1967, *Spicer 1501-1692;* 7 and 11 Aug. 1967, *Cody & Spicer 17676-17693, 18024-18027*.
59. East- and west-facing mountain slopes near Tungsten, 61°58'N, 128°15'W, elev. 3,500 — 5,500 ft. (1,070 — 1,680 m), 20-22 July 1967, *Cody & Spicer* (included in numbers for site 58); 23 July thru 6 Aug. 1967, *Spicer* (included in numbers for site 58).
60. 8 miles north of Tungsten in the headwaters of the Flat River: gravel terminal moraine and stream valley below glacier, 62°02'N, 128°10'W, elev. 4,500 — 5,500 ft. (1,370 — 1,680 m), 8 Aug. 1967, *Spicer 1693-1758, Cody & Spicer 17703-17828*.

Annotated list of vascular plants

In the list which follows, numbers within brackets indicate collection sites. Brief comments are included on the abundance and distribution of many of the plants within the region. New records for the District of Mackenzie or the Mackenzie Mountains are indicated.

The first set of all the collections is preserved in the herbarium of the Biosystematics Research Institute, Department of Agriculture, Ottawa (DAO). Some duplicates have been deposited in the herbaria of the Canadian Wildlife Service at Edmonton and the University of Calgary (UAC).

OPHIOGLOSSACEAE

Botrychium lunaria (L.) Sw. var. *minganense* (Vict.) Dole — 17972 [57]. Rare in turf at back of beach. In the Mackenzie Mountains it is otherwise known only from Lone Mountain in the Nahanni Range (Raup, 1947).

Botrychium virginianum (L.) Sw. var. *europaeum* Ångstr. — 16351 [58]. Hidden among thick vegetation by the hotsprings at Tungsten. Rare in Mackenzie District and thus far known from only two other sites in the Mackenzie Mountains: Lone Mountain (Raup, 1947) and Mount Flett (Cody, 1963).

POLYPODIACEAE

Athyrium filix-femina (L.) Roth spp. *cyclosorum* (Rupr.) C. Chr. — 17429 [50]; 16367 [58]. These Mackenzie Mountain sites were both adjacent to hotsprings. Porsild (1961) recorded this species from Hole-in-the-Wall Lake. The only other collection from Mackenzie District was from near Fort Liard (Jeffrey, 1961).

Cryptogramma crispa (L.) R. Br. var. *sitchensis* (Rupr.) Hultén — 1713, 17739 [60]. Rare on limestone talus slope. The only other collection of this variety in the District of Mackenzie is from Red Mountain near Glacier Lake (Raup, 1947).

Cystopteris fragilis (L.) Bernh. — 12349 [4]; 12510B [14]; 12700 [28]; 12941 [41]; 17424 [36]; 1583 [59]; 17818 [60]. Moist rock ledges and slopes.

Dryopteris austriaca (Jacq.) Woynar — 17428 [50]; 1645, 16357, 16361 [58]. Known in the District of Mackenzie from only these two localities (Cody and Porsild, 1968).

Dryopteris disjuncta (Ledeb.) Morton — 12904 [39]; 1575, 1646, 16362 [58]. Moist woods and streambanks near hotsprings.

Dryopteris fragrans (L.) Schott s. lat. — 12894, 17432 [38]; 1652 [59]; 17812 [60]. Collected on sunny, rocky slopes. Sole occurrences noted.

Dryopteris phegopteris (L.) C. Chr. — 16360 [58]. In deep moss and humus under *Dryopteris austriaca* and *Abies lasiocarpa*; this is the only site thus far recorded in the District of Mackenzie (Cody and Porsild, 1968).

Dryopteris robertiana (Hoffm.) C. Chr. — 12343 [4]; 12499 [14]. Fairly common in woods and shrubby areas. New to the Mackenzie Mountains.

Matteuccia struthiopteris (L.) Todaro var. *pensylvanica* (Willd.) Morton — 12336 [3]. Rare on the floodplains of the South Nahanni River. The only previous records from the District of Mackenzie were those by Jeffrey (1961) and Cody (1963).

Woodsia glabella R. Br. — 12342 [4]; 12510A [14]; 12613 [22]; 12798 [32]; 16400 [59]. An occasional species which seems to prefer calcareous, rocky habitats.

EQUISETACEAE

Equisetum arvense L. (incl. *E. calderi* Boivin) — 12248 [1]; 12860B [33]. Common on floodplains and in a number of other habitats.

Equisetum fluviatile L. *(E. limosum* L.) — 12260 [1]; 17683 [58]. Seen along a stream from hotsprings and on floodplains at two localities only.

Equisetum hyemale L. var. *affine* (Engelm.) A. A. Eaton *(E. prealtum* Raf.) — 12312 [2]. Commonly seen on recent floodplains and in balsam poplar forests; previously known from several sites on the Liard River, but not from the South Nahanni River drainage.

Equisetum palustre L. — 12405 [8]. Seen on mud and silt bars.

Equisetum pratense Ehrh. — 12298 [2]; 12860 [33]; 1543 [58]. A common species on floodplains and in balsam poplar and white spruce forests.

Equisetum scirpoides Michx. — 12316 [2]; 12943 [41]. Found in coniferous forests.

Equisetum sylvaticum L. var. *pauciramosum* Milde — 12675 [26]. An occasional species of depressions from lowland forest to alpine regions.

Equisetum variegatum Schleich. — 12807 [32]; 18023]57]. Only two collections from a coniferous forest and on a gravel beach.

LYCOPODIACEAE

Lycopodium alpinum L. — 17947 [56]; 1824 [57]; 1731, 17764 [60]. Alpine and subalpine situations.

Lycopodium annotinum L. s. lat. — 12552 [18]; 12659 [26]; 1815 [57]; 16359 [58]; 1805, 17755 [60]. Found from lowlands to the alpine region.

Lycopodium clavatum L. var. *monostachyon* Grev. & Hook. — 1783, 17948 [56]. Subalpine; rare in the District of Mackenzie and known from only one other site, Glacier Lake, in the Mackenzie Mountains (Raup, 1947).

Lycopodium complanatum L. s. lat. — 17433 [38]; 1784 [56]. Infrequent in shrub zone near treeline.

Lycopodium selago L. — 12638 [23]; 12686 [27]; 1735, 17760 [60]. In alpine tundra; apparently not common.

SELAGINELLACEAE

Selaginella selaginoides (L.) Link — 13619b [30]. Found on damp ground near a mineral spring. Omitted in error by Porsild and Cody (1968) from Zone 1, but previously reported from that area by Porsild (1945) and Raup (1947), as well as being known from more recent collections preserved in DAO.

PINACEAE

Abies lasiocarpa (Hook.) Nutt. — 12896 [38]; 1577, 1758 [58]; 17811 [60]. May be present near treeline throughout much of the area.

Juniperus communis L. s. lat. — 12373 [6]; 12806 [32]; 1814, 18012 [57]; 1599, 1660 [59]; 17828 [60]. Dry open slopes and in some mixed wood forests.

Juniperus horizontalis Moench — 12367 [6]; 12815 [32]; 12032 [54]. Dry and rocky slopes; previously known from the east flank of the Mackenzie Mountains (Raup, 1947), but not from the interior.

Larix laricina (DuRoi) K. Koch — 12493 [14]. A widespread but never abundant species in the area.

Picea glauca (Moench) Voss s. lat. — 12395 [7]; 12706 [29]; 1816 [57]; 1753, 1754 [58]. Widespread throughout the area, with the best development on old floodplains.

Picea mariana (Mill.) BSP. 12436 [9]; 1775 [55]. A common tree throughout the region.

Pinus contorta Dougl. var. *latifolia* Engelm. — 12231 [20]; 12232 [14]; 12236 [34]; 12233 [42]; 12235 [43]; 12237 [44]; 17434 [52]; 1627 [59], Skinboat Lakes (Flook 38). A common tree in the Flat River region and along the Liard Range (Jeffrey, 1961; Cody, 1963) with more scattered distribution along the South Nahanni River (Fig. 10).

Pinus banksiana Lamb. [*P. divaricata* (Ait.) Dumont] 12234 [42]; 12238, 12239 [45]; 12240 [46]; 12033A, 12033B [54]. Scattered in the eastern portion of the South Nahanni region. All samples showed indications of hybrid derivations.

Figure 10. Although not previously recognized, lodgepole pine is a common forest type along the Flat River, with more scattered distribution along the South Nahanni River. Photo — George W. Scotter.

TYPHACEAE

Typha latifolia L. — 12644 [24]. Seen only on the shore of Yohin Lake (Fig. 11). The nearest collection within the District of Mackenzie was at Fort Simpson (Cody, 1961).

SPARGANIACEAE

Sparganium minimum (Hartm.) Fries — 12767 [30]. First collection from the Mackenzie Mountains; found in association with hotspring pools.

POTAMOGETONACEAE

Potamogeton natans L. — 17929 [55]. In 6 feet (2m) of water at Rabbitkettle Lake. This is the only record for this species for the District of Mackenzie. It is disjunct from the nearest known site by some 700 miles (214 km) (see Cody and Porsild, 1968, p. 264).

Potamogeton pusillus L. — 1649 [58]. In warm water of hotspring pool. In the Mackenzie Mountains thus far known only from this single location.

Figure 11. Common Cattail is present along the fringes of an island in Yohin Lake. The lake, with its numerous islands, is extremely interesting from botanical and ornithological standpoints. Photo — George W. Scotter.

SCHEUCHZERIACEAE

Triglochin maritimum L. — 12656 [24]; 12722, 12742 [30]. First collections from the Mackenzie Mountains; found in association with hotspring pools and on the shore of Yohin Lake.

Triglochin palustre L. — 12275 [1]; 12540 [17]; 12911 [39]; 17687 [58]. Fairly common near hotsprings and in natural salt lick areas.

GRAMINEAE

X *Agrohordeum macounii* (Vasey) Lepage (*Agropyron trachycaulum* X *Hordeum jubatum*) — 12536 [17]; 1640 [58]. Sole occurrences noted, but to be expected wherever the parents are found together; it is known from several sites along the Liard River (Cody, 1963).

Agropyron pectiniforme R. & S. — 12832 [33]. Introduced plant, collected from Nahanni Butte.

Agropyron sericeum Hitchc. (*A. trachycaulum* sensu Porsild, 1943) — 12548 [17]; 12830 [33]. Occasional on sand bars and disturbed areas.

Agropyron trachycaulum (Link) Malte var. *glaucum* (Pease & Moore) Malte — 12054 [54]. Natural clearings and disturbed situations. First report from the Mackenzie Mountains.

Agropyron trachycaulum (Link) Malte var. *novae-angliae* (Scribn.) Fern. — 12257 [1]' 12937 [41]; 18025 [58]. Found on riverbanks and dry open sites.

Agropyron trachycaulum (Link) Malte var. *trachycaulum* — 12276 [1]; 12017 [33]; 12909 [39]. From openings near hotsprings and at the settlement of Nahanni Butte.

Agropyron violaceum (Hornem.) Lange — 12354 [4]; 12380 [7]; 12817 [32]; 12022 [33]; 1611 [59]. River bars and openings and subalpine to alpine situations.

Agrostis exarata Trin. — 12258 [1]; 17420 [48]; 1641; 17691 [58]. Occurrences noted near warm and cool springs. This species was recorded as new to the District of Mackenzie on the basis of the collections from hotspring meadows at Tungsten. Its occurrence in similar situations in the lower South Nahanni drainage is most interesting.

Agrostis scabra Willd. — 12828 [34]; 1648 [58]. Openings near hotsprings.

Alopecurus aequalis Sobol. — 12007 [33]. Recently-cleared bushland, rare.

Arctagrostis arundinacea (Trin.) Beal — 12836C [33]; 12912 [39]; 1794, 18016 [57]; 1744, 17774, 17825 [60]. Occasional near hotsprings and on floodplains.

Beckmannia syzigachne (Steud.) Fern. — 12529B [16]; 12826, 12016 [33]. Wet ground near a hotspring and near rivers. First collection from the Mackenzie Mountains; previously known from the lowlands of the Mackenzie and Liard rivers (Raup, 1947).

Bromus ciliatus L. — 12322 [3]; 12834 [33]; 12910 [39]; 17693 [58]. Infrequent in openings near hotsprings.

Bromus pumpellianus Scribn. var. *arcticus* (Shear) Porsild — 12286 [2]; 12379 [7]. From clearing near cabins; collection No. 12379 is the first collection recorded from the Mackenzie Mountains.

Calamagrostis canadensis (Michx.) Beauv. — 12255 [1]; 12836 [33]; 12895 [38]; 12918A [39]. Common throughout the area.

Calamagrostis lapponica (Wahl.) Hartm. — 12863 [34]. Openings near hotsprings.

Calamagrostis neglecta (Ehrh.) G.M. & S. — 17916 [55]. Silt bank of lake.

Calamagrostis purpurascens R. Br. — 12377 [7]. From a white spruce — balsam poplar community.

Cinna latifolia (Trev.) Griseb. — 12023 [33]. Flood terrace of river (Cody, 1963).

Danthonia intermedia Vasey — 12285A [2]. New to the District of Mackenzie; the map in Hultén (1968) indicates collection sites in south-central Yukon, northern British Columbia, and at Lake Athabasca in northern Alberta. This collection was from Zone 6.

Deschampsia brevifolia R. Br. — 1793, 17960, 17979, 18017 [57]. Turf and meadow by lakeshore.

Deschampsia caespitosa (L.) Beauv. — 12364 [5]; 12477 [13]; 12717 [30]; 12938 [41]; 17425 [49]. Occasional on floodplains and at a hotspring.

Elymus innovatus Beal — 12360 [5]; 12434 [9]; 12776 [31]; 12816 [32]; 12012 [33]; 12932, 12933 [40]; 1770, 17898 [55]; 1594 [59]. Infrequent from floodplains to alpine communities.

Elymus sibiricus L. — 12829, 11490, 12024, Nowosad 3, [33]. Infrequent at Nahanni Butte (Cody, 1963).

Festuca altaica Trin. — 12580 [21]; 1780, 17944 [56]; 18009 [57]; 1603 [59]. Alpine tundra and subalpine communities.

Festuca baffinensis Polunin — 12624B [22]. From alpine tundra; sole occurrence noted.

Festuca brachyphylla Schultes — 12893 [38]; 17814 [60]. Occasional in alpine tundra.

Glyceria striata (Lam.) Hitchc. var. *stricta* (Scribn.) Fern. — 12272 [1]; 12553 [18]; 12727 [30]; 12865 [34]; 17422 [48]; 1558, 1647, 17690 [58]. Moist soil near hotsprings and floodplains; otherwise known along the Liard River.

Hierochloe alpina (Sw.) R. & S. — 12666, 12669 [26]; 12703 [28]; 1659 [59]; 17730, 17759 [60]. Occasional in alpine tundra.

Hierochloe odorata (L.) Wahl. — 12441 [10]. Along bank of the South Nahanni River.

Hordeum jubatum L. — 12529A [16]. First collection from the Mackenzie Mountains; probably introduced here.

Muhlenbergia glomerata (Willd.) Trin. var. *cinnoi-*

des (Link) F. J. Herm. — 12045 [54]. Sole occurrence noted (Cody, 1963). This collection was recorded by Porsild and Cody (1968) as Zone 6, but should be Zone 1.

Phalaris arundinacea L. — 12833 [33]; 17421 [48]. Drainage ditch near airfield and near a hotspring. The collection from the hotsprings is the first from the Mackenzie Mountains.

Phleum pratense L. — 12827 [33]. Introduced grass at Nahanni Butte.

Phragmites communis Trin. var. *berlandieri* (Fourn.) Fern. — 17437 [53]. A single collection from the shore of a small lake near Yohin Lake. Cody (1963) first reported this species, based on a collection by G. Kraus, from the same locality, which is the only one known in the District of Mackenzie. The Kraus collection was inadvertently recorded as Zone 1 by Porsild and Cody (1968).

Poa alpigena (Fries) Lindm. f. — 12513 [14]; 17945 [56]; 17680 [58]; 17810 [60]. Gravelly sites, by hotsprings and in moss over rocks.

Poa alpina L. — 12266 [1]; 12281 [2]; 17961 [57]; 17684 [58]; 17824 [60]. Openings near hotsprings, alpine turf and wet river terrace.

Poa arctica R. Br. — 18021 [57]; 17808 [58] 17776 [60]. Streambanks and lakeshores.

Poa glauca Vahl s. lat. — 12247 [1]; 12317, 12320 [3]; 12530 [16]; 12624A [22]; 12777 [31]; 12818A [32]; 12831 [33]; 17813 [60]. A fairly common plant with wide ecological tolerance.

Poa palustris L. — 12259, 12270 [1]; 12318, 12321 [3]; 12009 [33]. Collected only at a hotspring, a nearby opening, and about the settlement at Nahanni Butte.

Poa paucispicula Scribn. & Merr. — 1693, 1748, 17715, 17722, 17745, 17801 [60]. Frequent at this site in the headwaters of the Flat River, but not noted elsewhere; Raup (1947) does however cite several collections from the Glacier Lake area.

Puccinellia borealis Swallen — 12288 [2]; 12531 [16]; 12543 [17]. About hotsprings, natural game licks and in open lodgepole pine community.

Puccinellia interior Th. Sor. — 12280 [2]; 12543 [17]; *det.* A. E. Porsild. Collection No. 12543 from a mineral lick area near the Flat River is the first report from the Mackenzie Mountains.

Schizachne purpurascens (Torr.) Swallen — 12323 [3]. Known in the Mackenzie District from Great Bear Lake, the Slave River lowlands and the Liard River.

Sphenopholis intermedia (Rydb.) Rydb. — 12287 [2]; 12319 [3]; 12835, 12836B [33]; 12864 [34]. Found in meadows, on streambanks, and near hotsprings. Collection No. 12864 is the first from the Mackenzie Mountains; other collections from District of Mackenzie have been from the Great Slave Lake lowlands and along the Liard River.

Trisetum spicatum (L.) Richt. s. lat. — 12271 [1]; 12280, 12284 [2]; 12378B [7]; 12668 [26]; 1790, 17939 [56]; 1792, 17997 [57]; 1749, 17703, 17752 [60]. A fairly common species with wide ecological tolerance.

CYPERACEAE

Carex aquatilis Wahl. — 12404 [8]; 1766 [55]; 1779A [56]; 17677 [58]. Seen in shallow water of marshes and streams.

Carex atrosquama Mack. — 1541 [58]; 1696 [60]. Terminal moraine and streambanks.

Carex canescens L. — 12402 [8]; 12479 [13]; 17954 [56]. Along streambanks and floodplains.

Carex capillaris L. — 12515 [14]; 17923 [55]; 17970 [57]. Lake and river shores.

Carex concinna R. Br. — 12378 [7]; 17911 [55]. Opening in mixed forest and in recent burn.

Carex diandra Schrank — 12724, 12726 [30]. On border of a hotspring; sole occurrence noted.

Carex eburnea Boott — 12283 [2]; 12324 [3]; 12376 [7]; 12512 [14]; 12819 [32]; 12889 [36]; 12931 [40]. Collected from various dry and rocky sites.

Carex filifolia Nutt. — 12059 [54]. Noted only on the slopes of Nahanni Butte; this is the second record for the District of Mackenzie (Cody, 1963). This collection was recorded by Porsild and Cody (1968) as Zone 6, but should be Zone 1.

Carex franklinii Boott — 12518 [14]; 17980 [57]. Sole occurrences noted; collected near Virginia Falls and at «Grizzly Bear» Lake.

Carex glacialis Mack. — 12523 [14]; 12578A [21]. Found near Virginia Falls and in an alpine tundra community.

Carex gynocrates Wormskj. — 12039 [54]. Sole occurence noted but Raup (1947) stated that it was common at Glacier Lake.

Carex interior Bailey — 12729 [3]. From hotspring ponds. This is the second record of this species for the District of Mackenzie. It was first reported by Thieret (1961) from around a marly lake at Mile 61 Enterprise — Mackenzie River Highway.

Carex lachenalii Schk. — 1779B, 17953 [56]; 17782 [60]. Sole occurences noted; apparently rare in the Mackenzie Mountains.

Carex limosa L. — 12646 [24]. Sole occurrence was noted near Yohin Lake.

Carex macloviana d'Urv. — 17431 [38]; 1504, 17676 [58]. Sole occurrences noted were on the gravelly shore of Hole-in-the-Wall Lake and adjacent to the hotsprings at Tungsten.

Carex media R. Br. — 17934 [56]; 18020 [57]. Lake banks and thickets.

Carex membranacea Hook. — 12522A [14]; 12625A [22]; 17968, 18015 [57]. Noted in wet habitats.

Carex microchaeta Holm — 12667 [26]; 1585 [59]. Wet meadows in alpine tundra.

Carex microglochin Wahl. — 18003 [57]. Wet meadow by lake; rare, known in the Mackenzie Mountains from only one other locality near Glacier Lake (Raup, 1947).

Carex misandra R. Br. — 12577B [21]; 12626 [22]; 12701 [28]. Alpine tundra habitats.

Carex nardina Fries — 12578 [21]; 12702 [28]. Dry sites in alpine tundra.

Carex peckii Howe — 12282 [2]. Dry site near clearing. First collection from the District of Mackenzie. This a North American species which is found across Canada from Québec to the Peace River country. The map in Hultén (1968) also indicates two isolated sites in Yukon and Alaska.

Carex petricosa Dewey — 12522B [14]; 12579 [21]. Collected from near Virginia Falls and in alpine tundra.

Carex podocarpa R. Br. — 17969 [57]; 1618 [59]; 1717, 17750, 17794, 17809 [60]. Subalpine meadows and tundra turf.

Carex pyrenaica Wahl. — 1707, 17707 [60]. Noted only at this site; apparently rare in the Mackenzie Mountains.

Carex rostrata Stokes — 12716 [30]; 12866 [34]; 17417 [48]; 17681 [58]. Collected from hotsprings but noted in other habitats.

Carex saxatilis L. var. *major* Olney (*C. physocarpa* Presl) — 12522A [14]; 12551 [18]; 1786 [56]. Moist habitats.

Carex scirpoidea Michx. — 12514, 12516 [14]; 12577A, 12594 [21]; 12718, 12723, 12725A [30]; 12818B, 12820 [32]; 12047 [54]; 17982 [57]; 1604 [59]. Fairly common with rather wide ecological tolerance.

Carex viridula Michx. — 12728 [30]; 12878 [35]. Associated with hotspring sites. First collections from the Mackenzie Mountains.

Eleocharis palustris (L.) R. & S. — 12478 [13]. First collection from the Mackenzie Mountains; from a muddy shore of an island in the South Nahanni River.

Eriophorum angustifolium Honck. — 12625B [22]; 12680 [26]. Alpine tundra habitats.

Eriophorum brachyantherum Trautv. & Mey. — 12521 [14]; 1529 [59]. Sole collections near Virginia Falls and in the vicinity of Tungsten.

Eriophorum scheuchzeri Hoppe — 12480 [13]; 12633 [23]; 1746, 17804 [60]. Wet habitats (Fig. 12).

Eriophorum triste (Th. Fries) Hadač & Å. Löve — 12627 [22]; 17767 [60]. Wet alpine tundra habitat.

Eriophorum vaginatum L. — 12407 [8]; 12665 [26]. Wet habitats.

Kobresia hyperborea Porsild — 12623 [22]. Rocky slopes in alpine tundra.

Kobresia simpliciuscula (Wahl.) Mack. — 17995 [57]. Noted only at this location.

Scirpus caespitosus L. ssp. *austriacus* (Pall.) Asch. & Graebn. — 12723A, 12725B [30]. Wet place at a hotspring.

Scirpus microcarpus Presl — 12252 [1]. Wet habitat near hotsprings.

Scirpus validus Vahl — 12265 [1]; 17436 [53]; 1759 [55]. Wet habitat near hotsprings and on the shores of small lakes.

LEMNACEAE

Lemna minor L. — 12649 [24]. Collected in Yohin Lake.

JUNCACEAE

Juncus albescens (Lange) Fern. — 17984 [57]. Moist turf; noted only at this site.

Juncus alpinus Vill. ssp. *nodulosus* (Wahlenb.) Lindm. — 12473 [13]; 12714, 12719A [30]; 1559 [58]. Wet habitats.

Juncus balticus Willd. var. *alaskanus* (Hultén) Porsild — 12299 [2]; 12359 [5]; 12542 [17]; 18005 [57]. Wet habitats including river flats.

Juncus balticus var. *littoralis* Engelm. — 12720 [30]. First collection from the Mackenzie Mountains; from hotspring ponds.

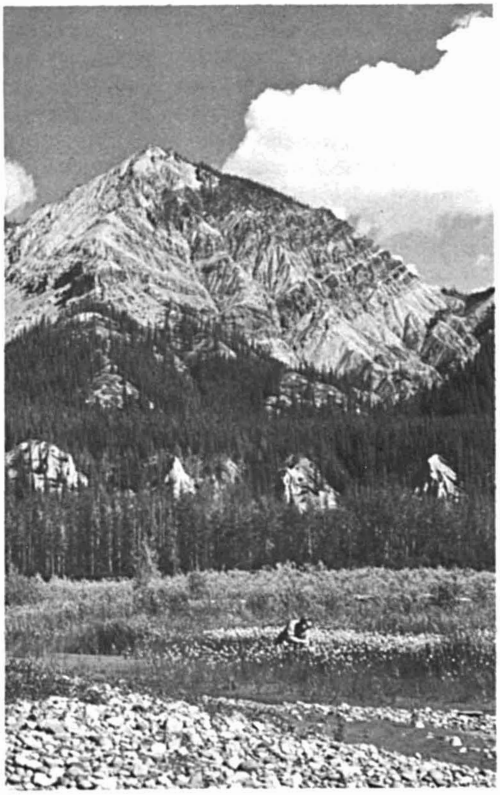

Figure 12. Cottongrass growing near the confluence of the Flat and South Nahanni rivers. Photo — George W. Scotter.

Juncus bufonius L. — 12251 [1]; 12837, 12838 [33]; 17689 [58]. Wet habitats.

Juncus castaneus Smith — 12519 [14]; 17985 [57]; 1632 [58]; 1706 [60]. Wet habitats on lakeshores and tundra turf.

Juncus nodosus L. — 12719, 12721 [30]; 12874B [34]. First collections from the Mackenzie Mountains; from hotspring ponds.

Luzula arcuata (Wahl.) Wahl. — 16393 [59]; 17705, 17800 [60]. Mountain slopes.

Luzula confusa Lindeb. — 12682, 12687 [27]; 16394 [59]. From a heath community in alpine tundra and alpine slopes.

Luzula parviflora (Ehrh.) Desv. — 1778 [56]; 17959 [57]; 1507, 1634 [58]; 1745 [60]. Borders of thickets streambanks and lakeshores.

Luzula spicata (L.) DC. — 17805 [60]. Alpine streambed; noted only at this site.

LILIACEAE

Allium schoenoprasum, L. var. *sibiricum* (L.) Hartm. — 12339 [3]; 12462 [12]. From moist meadows and gravel pavement near rivers.

Lloydia serotina (L.) Rchb. — 12622 [22]; D. Dineley 28 July 1967 [57]; 16385 [59]. Alpine tundra.

Maianthemum canadense Desf. var. *interius* Fern. — 12304 [2]. Collected from a white spruce and balsam poplar forest.

Smilacina stellata (L.) Desf. — 12242 [1]; 12771 [30]; 12052 [54]. The first two collections were from hotspring areas, the last from the steep lower slopes of Nahanni Butte.

Streptopus amplexifolius (L.) DC. var. *americanus* Schultes — 1576, 1643, 16358 [58]. Hotspring area at Tungsten; this is the third record for the District of Mackenzie and the second for the Mackenzie Mountains. E. W. Arnold collected it by a hotspring near Hole-in-the-Wall Lake (Porsild, 1961) and W. Jeffrey (1961) gathered it in the lowlands of the Liard River near the British Columbia border.

Tofieldia coccinea Richards. — 12595 [22]. Infrequent in alpine tundra.

Tofieldia glutinosa (Michx.) Pers. — 12715 [30]. Second collection from the Mackenzie Mountains; from a hotspring site. Omitted in error by Porsild and Cody (1968) from Zone 1, but previously reported from Nahanni Mountain by Porsild (1945) on the basis of a specimen collected by V.C. Wynne-Edwards.

Tofieldia pusilla (Michx.) Pers. — 12350 [4]; 12433 [9]; 12496 [14]; 12796 [32]. Infrequent in moist habitats.

Veratrum eschscholtzii Gray — 16355 [58]; 17795 [60]. Hotspring meadows and subalpine clearings in the western Mackenzie Moutains.

Zygadenus elegans Pursh — 12348 [4]; 12588 [21]; 12811 [32]; 12049 [54]; 1809, 17983 [57]; 1544 [58]; 1621 [59]. Forest openings to alpine tundra.

IRIDACEAE

Sisyrinchium montanum Greene — 12041 [54]. Steep lower slopes of Nahanni Butte. Omitted in error by Porsild and Cody (1968) from Zone 1, but previously reported from that area by Porsild (1945) and Raup (1947) on the basis of a specimen collected by V. C. Wynne-Edwards on Nahanni Mountain. The collection reported here is thus the second for the area.

ORCHIDACEAE

Corallorhiza trifida Chat. — 12459A [11]. Noted in white and black spruce forests.

Cypripedium calceolus L. var. *parviflorum* (Salisb.) Fern. — 12369B [6]; 12481 [14]. Infrequent in moist habitats.

Cypripedium guttatum Sw. — 12448 [10]. Sole occurrence noted; collected from a white spruce forest on an old floodplain (Fig. 13).

Cypripedium passerinum Richards. — 12289 [3]; 12389 [7]; 1762, 17917 [55]. Infrequent in moist white spruce and balsam poplar stands.

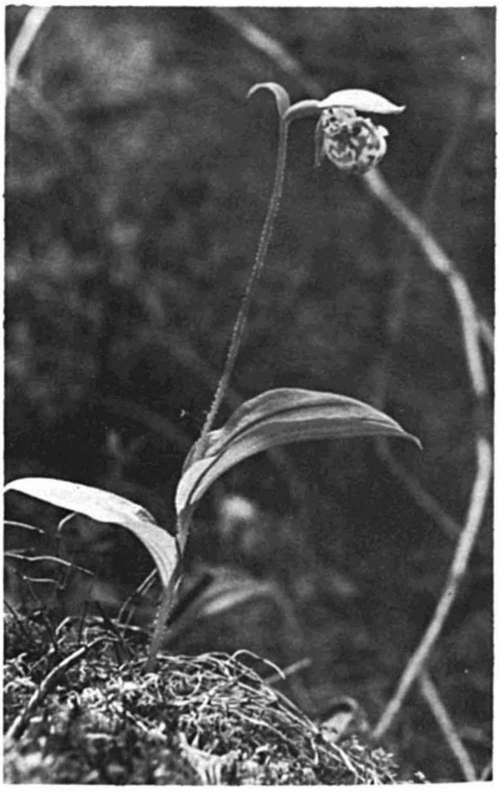

Figure 13. A Lady's Slipper *(Cypripedium guttatum)* growing under a white spruce canopy near Pulpit Rock. Photo — George W. Scotter.

Goodyera repens (L.) R. Br. — 12459B [11]; 12524 [15]. Associated with heavy moss cover in white spruce forests.

Habenaria dilatata (Pursh) Hook. — 1501 [58]. Common in the hotspring meadow at Tungsten; second record for Mackenzie District (Porsild, 1961).

Habenaria hyperborea (L.) R.Br. — 12406, 12420 [8]; 12758 [30]; 17415 [48]; 1767, 17920 [55]. Infrequent in moist habitats.

Habenaria obtusata (Pursh) Richards. — 12412 [8]; 12525 [15]. Mossy habitats in a spruce forest.

Orchis rotundifolia Banks — 12396 [7]. Moist habitat in a spruce forest; first collection from the Mackenzie Mountains.

SALICACEAE

Populus balsamifera L. — 12398 [7]; 17907 [55]; 1650 [58]. Common on juvenile soils of floodplains and terraces.

Populus tremuloides Michx. — 12564 [20]; 1773, 17908 [56]; 1500, 1542 [58]. Present in fire disturbed regions.

Salix alaxensis (Anderss.) Cov. var. *alaxensis* — 12547 [17]; 16376 [59]; 17778 [60]. From mineral lick area and mountain slopes.

Salix alaxensis (Anderss.) Cov. var. *longistylis* (Rydb.) Schneid. — 12468 [13]. Growing on juvenile soils of an island.

Salix arbusculoides Anderss. — 12393 [7]; 17912 [55]. Lowland forest sites.

Salix arctica Pall. — 12621 [22]; 12634 [23]; 1695, 1699, 1709, 17712, 17716, 17718, 17733 [60]. Fairly common on dry alpine tundra.

Salix barclayi Anderss. — 1523, 1534 [59]. Mountain slopes at Tungsten.

Salix barrattiana Hook. — 12597 [22]; 17993 [57]. In alpine meadows.

Salix bebbiana Sarg. — 12508 [14]; 12869 [34]; 17903 [55]. Fairly common from river flats to dry forest habitats.

Salix brachycarpa Nutt. ssp. *niphoclada* (Rydb.) Argus — 12511 [14]. Riverbank habitat.

Salix candida Flügge — 12753 [30]. From edge of hotspring ponds; first collection from the Mackenzie Mountains.

Salix commutata Bebb — 17999 [57]; 17768, 17773 [60]. Alpine meadows and streambanks in the western parts of the Mackenzie Mountains.

Salix glauca L. var. *acutifolia* (Anderss.) Schneider — 12374 [6]; 12487, 12501, 12502 [14]; 12635 [23]; 1537 [58]; 1624 [59]. Found in thickets along riverbanks to alpine tundra.

Salix interior Rowlee — 12465, 12466, 12467, 12472 [13]. Common colonizing shrub on new alluvium. First collection from the Mackenzie Moutains.

Salix lasiandra Benth. — 12471 [13]; 12536, 12549 [17]. Common riparian shrub on new alluvium; first collection from the Mackenzie Mountains.

Salix monticola Behh. (*S. padophylla* Rydb.) — 12393 [7]; 12890 [36]. Along rivers and streams at low elevations. New to the Mackenzie Mountains.

Salix myrtillifolia Anderss. — 12438, 12447 [10]; 12485 [14]; 12554 [18]; 17918 [55]; 17998 [57]; 1625 [59]. Moist areas in spruce forests.

Salix novae-angliae Anderss. — 12773 [30]; 1538 [58]; 17714 [60]. Collected from hotspring sites and terminal moraine. New to the Mackenzie Mountains and the District of Mackenzie.

Salix pedicellaris Pursh — 12651 [24]. Muskeg site near Yohin Lake.

Salix planifolia Pursh spp. *planifolia* — 12679 [26]. Collected from alpine tundra.

Salix planifolia Pursh ssp. *pulchra* (Cham.) Argus — 1789, 17938 [56]; 1698, 17736, 17823 [60]. Slopes, streambanks and thickets above treeline.

Salix reticulata L. — 12490 [14]; 12575 [21]; 17941 [56]; 18007 [57]; 1520, 1608 [59]. Fairly frequent in alpine tundra; also collected from Virginia Falls.

Salix richardsonii Hook. — 17914 [55]; 1791, 17936 [56]; 17822 [60]. Mountain slopes, valley bottoms and alluvial streambeds; not common in the Mackenzie Mountains.

Salix rigida Muhl. (*S. mackenzieana* Barratt) — 12469 [13]; 12541 [17].Found on an island and in a natural salt lick area; otherwise known in the District of Mackenzie from the lowlands of the Liard and Mackenzie rivers. New to the Mackenzie Mountains.

MYRICACEAE

Myrica gale L. — 12645 [24]; 12884 [35]. Fairly frequent in muskegs and in shallow water. Collection No. 12884 is the first reported from the Mackenzie Mountains.

BETULACEAE

Alnus crispa (Ait.) Pursh — 17410 [25]. Fairly common on floodplains and in mixed forests.

Alnus incana (L.) Moench — 12313 [2]; 12423 [8]. First collections from the Mackenzie Mountains. A common species of floodplains and lowlands.

Betula glandulosa Michx. — 12507 [14]; 12925 [40]; 1788, 17950 [56]; 1657 [59]; 17815 [60]. A common species at high elevations and occasional in spruce forests.

Betula papyrifera Marsh. var. *commutata* (Regel) Fern. — 12936 [41]. Seen in mixed forests and on floodplains.

Betula papyrifera var. neoalaskana (Sarg.) Raup — 12872 [34]; 17925 [55]; 1656 [59]. Seen in mixed forests, burned-over areas and on floodplains.

URTICACEAE

Urtica gracilis Ait. — 12329 [3]. From thickets near a cabin; probably introduced here.

SANTALACEAE

Geocaulon lividum (Richards.) Fern. — 12370 [6]; 17928 [55]. Infrequent on dry forest sites.

POLYGONACEAE

Oxyria digyna (L.) Hill — 1639 [58]; 1549, 1616 [59]; 1716, 17732 [60]. Moist alpine and subalpine slopes.

Polygonum viviparum L. — 12365 [6]; 12443 [10]; 12517 [14]; 12812 [32]; 1806 [57]; 1566, 1671 [58]; 1527 [59]; 1728 [60]. Fairly frequent throughout much of the area.

Rumex arcticus Trautv. — 17826 [60]. Wet meadows and river bottoms; occasional.

Rumex occidentalis S. Wats — 17413 [48]; 1565, 1755 [58]. Infrequent in moist habitats; also noted at Yohin Lake.

CHENOPODIACEAE

Chenopodium berlandieri Moq. var. *zschackei* (Murr.) Zobel — 12254 [1]; 12847 [33]; 12915 [39]. An introduced species near settlements.

Chenopodium capitatum (L.) Asch. — 12244 [1]; 12461 [11]; 12020 [33]. Seen in artificial clearings, disturbed sites and along riverbanks.

PORTULACACEAE

Claytonia tuberosa Pall. — 17990 [57]; 17806 [60]. Deep wet moss in alpine meadows.

Montia lamprosperma Cham. — 16366 [58]. In mud by hotspring pools; in the Mackenzie Mountains, known only from this locality.

CARYOPHYLLACEAE

Arenaria dawsonensis Britt. — 12793B [32]; 12877, 12879 [35]; 12048 [54]. Moist sites at low elevations.

Arenaria rossii R.Br. — 12631 [23]; 12779 [31]. Calcareous areas of the alpine zone.

Arenaria rubella (Wahlenb.) Smith — 12695B 12704 [28]; 12793A [32]; 12025 [54]. Scree slopes and dry ridges in the alpine tundra.

Arenaria uliginosa Schleich. — 12695A [28]. Sole occurrence noted in alpine tundra.

Cerastium beeringianum Cham. & Schlecht. — 12598 [22]; 1795, 17973 [57]; 1638, 16363, 17701 [58]; 1581 [59]; 1742 [60]. Occasionally noted on gravelly ridges in the alpine zone and in subalpine valleys.

Melandrium apetalum (L.) Fenzl ssp. *arcticum* (Fries) Hultén — 16399 [59]. Steep rocky slope above treeline.

Melandrium apetalum (L.) Fenzl spp. *attenuatum* (Farr) Hara — 12602 [22]. Sole occurrence noted; collected from alpine tundra.

Melandrium taylorae (Robins.) Tolm. — 12556 [19]. First collection for the Mackenzie Mountains; sole occurrence was in a recently burned-over area.

Sagina linnaei Presl — 17978 [57]. Turf at back of beach; rare in the Mackenzie Mountains.

Silene acaulis L. var. *exscapa* (All.) DC. — 12568 [21]; 12609 [22]; 12677 [26]; 1592 [59]. Fairly frequent in alpine tundra.

Stellaria calycantha (Ledeb.) Bong. — 1574, 17679 [58]; 1694, 17708 [60]. Moist situations.

Stellaria crassifolia Ehrh. — 12887 [35]; 1502 [58]. Hotspring sites.

Stellaria laeta Richards. — 12615 [22]; 12705A [28]; 12778 [31]. Occasional on alpine tundra.

Stellaria longipes Goldie — 17946 [56]; 1536 [58]. Moist situations.

Stellaria media (L.) Cyrill — 12014 [33]. Occasional in cabin clearing at Nahanni Butte; introduced.

Stellaria monantha Hultén — 12606 [22]; 12705B [28]; 17791 [60]. Occasional on stony habitats in alpine tundra.

CERATOPHYLLACEAE

Ceratophyllum demersum L. — 12643 [24]. This is only the second record for the District of Mackenzie; Thieret (1962) recorded it from Mile 38.5S of the Yellowknife Highway.

NYMPHAEACEAE

Nuphar variegatum Engelm. — 17430 [51]. Noted on a few small lakes above Virginia Falls and at Yohin Lake. This is the first collection from the Mackenzie Mountains.

RANUNCULACEAE

Aconitum delphinifolium DC. ssp. *delphinifolium* — 12608 [22]; 1801, 17964 [57]; 1606 [59]; 1722, 17781 [60]. Moist habitats in alpine tundra and meadows.

Actaea rubra (Ait.) Willd. — 12274 [1]; 12732, 12746B [30]; 1756 [58]. Noted on terraces, in mixed forest, and near hotsprings.

Anemone multifida Poir. — 12460B [11]; 1769, 17901 [55]. Collected from an open, south-facing slope and a recent burn.

Anemone narcissiflora L. — 18006 [57]; 1617 [59]; 17757 [60]. Moist alpine tundra.
Anemone parviflora Michx. — 12310 [2]; 12355 [4]; 12375 [6]; 12425 [8]; 12504 [14]; 12604 [22]; 1820, 17975 [57]; 1532, 1669, 1687 [59]. Fairly frequent in a variety of habitats.
Anemone richardsonii Hook. — 1738, 17786 [60]. Moist meadow in subalpine zone.
Aquilegia brevistyla Hook. — 12557 [19]; 12746A [30]. Noted in a recently burned-over area and in a meadow near a hotspring. Flowering July 3.
Delphinium glaucum S. Wats. — 12765 [30]; 1800, 17962 [57]; 16349 [58]. Protected lakeshores and hotspring sites.
Ranunculus abortivus L. — 17686 [58]. Hotspring meadow.
Ranunculus eschscholtzii Schlecht. — 17743 [60]. Moist tundra turf.
Ranunculus macounii Britt. — 12264 [1]. Sole occurrence noted.
Ranunculus sceleratus L. var. *multifidus* Nutt. — 12006 [33]. Recently cleared bushland.
Thalictrum alpinum L. — 12591 [21]; 17967 [57]. Infrequent in alpine meadows.
Thalictrum venulosum Trel. — 12055 [54]; 16352, 16353 [58]. Lower mountain slope at Nahanni Butte and about the hotsprings at Tungsten.

FUMARIACEAE

Corydalis aurea Willd. — 12243 [1]. Sole occurence noted.

CRUCIFERAE

Arabis drummondii Gray — 1572, 1636 [58]. Disturbed situations at Tungsten.
Arabis hirsuta (L.) Scop. ssp. *pycnocarpa* (Hopkins) Hultén — 12246 [1]; 12295 [2]; 17419 [48]. Infrequent around a small clearing, trails to a cabin, and near a hotspring. Collection No. 17419 is the first from the Mackenzie Mountain region.
Arabis lyrata L. var. *kamchatica* Fisch. — 17966 [57]; 1668 [59]. Alpine tundra and sheltered rock faces.
Barbarea orthoceras Ledeb. — 1637 [58]. Disturbed situation near Tungsten.
Brassica campestris L. (*B. rapa* L.) — 12328 [3]. An introduced weed.
Braya humilis (C. A. Mey.) Robins. — 12261, 12267 [1]; 12361 [5]; 12440 [10]; 12460A [11]; 12802, 12790 [32]; 12919, 12921 [39]; 12947 [41]. Fairly frequent in a variety of habitats.
Braya purpurascens (R. Br.) Bge. — 12781A [21]. Sole occurrence noted; from alpine tundra.
Capsella bursa-pastoris (L.) Medic. — 12268 [1]; 12327 [3]; 12011 [33]; 12901 [39]. An introduced weed.
Cardamine bellidifolia L. — 1712, 1720, 17737 [60]. Moraine and talus slope.
Cardamine umbellata Greene — 1747 [60]. Wet streambank.
Descurainia richardsonii (Sweet) O.E. Schulz — 12250 [1]. From a clearing near a cabin.
Draba alpina L. — 12600 [22]. Stony habitat in alpine tundra.
Draba cana Rydb. (*D. lanceolata* Royle) —12880, 12885 [35]; 12037 [54]. Collected from a hotspring site and from the slopes of Nahanni Butte.
Draba cinerea Adams — 12780 [31]. From a stony habitat in alpine tundra.
Draba corymbosa R.Br. (*D. bellii* Holm) — 12619 [22]; 12781B, 12788 [31]. Stony habitat in alpine tundra.
Draba fladnizensis Wulfen — 12692 [28]. From rocks and scree slopes in alpine tundra.
Draba lactea Adams — 12589 [21]; 16384 [59]. Collected from alpine tundra.
Draba lonchocarpa Rydb. — 12603 [22]; 12693, 12694 [28]; 12708, 12713 [29]; 12785 [31]; 16378 [59]. Frequent on rocks and scree slopes of alpine tundra. New to the Mackenzie Mountains.
Draba longipes Raup — 18018 [57]; 1581B [59]. Alpine tundra and rocky slopes.
Draba porsildii G.A. Mulligan — 12618 [22]. A new species presently being described by G.A. Mulligan.
Erysimum cheiranthoides L. — 12325 [3]. Collected from a clearing around a cabin.
Lepidium bourgeauanum Thell. — 12385 [7]. An introduced weed; collected near a cabin at Deadmen's Valley. New to the Mackenzie Mountains.
Lepidium densiflorum Schrad. — 12019, 12842, [33]. Introduced weed at Nahanni Butte.
Lesquerella arctica (Wormskj.) S. Wats. ssp. *arctica* — 12503 [14]; 12583 [21]. Rock faces and dry slopes.
Parrya nudicaulis (L.) Regel — 12599, 12612, 12620 [22]. Occasional in alpine tundra communities.
Rorippa islandica (Oeder) Borbás — 12528 [16]; 1651 [58]. Moist habitats near the Flat River.

DROSERACEAE

Drosera rotundifolia L. — 12653 [24]. Found in a peat bog near Yohin Lake.

CRASSULACEAE

Rhodiola integrifolia Raf. — 17931 [56]; 1822, 17958 [57]; 1613 [59]; 1725, 17756 [60]. Moist rocky tundra in the western parts of the Mackenzie Mountains.

SAXIFRAGACEAE

Mitella nuda L. — 12305 [2]; 12736 [30]. Growing near streams from hotsprings.

Parnassia fimbriata Konig — 17796 [57]; 17763 [60]; 1622 [59]. Moist tundra turf.

Parnassia kotzebuei Cham. & Schlecht. — 12491 [14]; 17974 [57]. Collected from a wet meadow near Virginia Falls and at «Grizzly Bear» Lake.

Parnassia palustris L. var. *neogaea* Fern. — 12411 [8]; 12739, 12743, 12770 [30]; 1524 [58]. Frequent at hotsprings and occasional in wet meadows and along streams.

Ribes glandulosum Grauer — 12417 [8]; 1503 [58]. Infrequent in mixed forests at low elevations.

Ribes hudsonianum Richards. — 12558 [19]; 12922 [39]. Infrequent in recent burns, mixed forests, and along streams.

Ribes lacustre (Pers.) Poir. — 12908 [39]. Along stream and in mixed forests.

Ribes oxyacanthoides L. — 12427 [8]; 12775 [30]; 12918D [39]. Occasional in mixed forests.

Ribes triste Pall. — 12918B [39]; 1642 [58]. Fairly frequent in spruce forests and along streams.

Saxifraga adscendens L. ssp. *oregonensis* (Raf.) Bacigalupi — 17702 [58]; 1581A [59]. Occasional in the western parts of the Mackenzie Mountains on alpine turf and talus slopes.

Saxifraga aizoides L. — 12439 [10]; 12890B, 17423 [36]; 16369, 16370 [58]; 1578 [59]. Along streams and on wet slopes; infrequent.

Saxifraga caespitosa L. s. lat. — 12605 [22]; 16390 [59]. Infrequent in alpine tundra habitats.

Saxifraga cernua L. — 12691 [28]; 16389 [58]; 17817 [60]. Infrequent in moist habitats.

Saxifraga lyallii Engler — 1582, 1670 [59]. Moist protected situations on steep mountainsides.

Saxifraga nivalis L. — 12697 [28]; 17784 [60]. Dry, stony slopes and rocky crevices.

Saxifraga oppositifolia L. — 12345 [4]; 12567 [21]; 12607 [22]; 12810 [32]; 12920 [39]; 16396 [59]. Rather frequent in a variety of habitats.

Saxifraga punctata L. ssp. *porsildiana* Calder & Savile — 16388 [59]; 1697, 17717 [60]. Moist moraine and steep alpine slopes.

Saxifraga rivularis L. — 16380, 16391 [59]; 17783 [60]. Steep rocky alpine slopes and crevices.

Saxifraga tricuspidata Rottb. — 12356 [4]; 12372 [6]; 12573 [21]; 12786 [31]; 12890A [36]; 1610, 16387 [59]; 1721 [60]. Frequent on rock ledges and dry ridges.

ROSACEAE

Amelanchier alnifolia Nutt. — 12296 [2]; 12034 [54]. Frequent in some balsam poplar and mixed forests.

Dryas alaskensis Porsild — 17933 [56]. In moss over rocks by lake in subalpine zone.

Dryas crenulata Juz. — 1573 [58]; 1602 [59]. Steep banks and mountainside.

Dryas drummondii Richards. — 12362 [4]; 12445 [10]. On gravel bars; abundant in limited areas (Fig. 14).

Dryas integrifolia Vahl — 12497 [14]; 12581 [21]; 12822 [32]; 1808, 18008 [57]. Frequent in alpine tundra and in other habitats.

Dryas octopetala L. — 12672 [26]. Infrequent in alpine tundra.

Fragaria virginiana Duchesne ssp. *glauca* (S. Wats.) Staudt — 12256 [1]; 12306, 12311 [2]; 12861 [33]; 17896 [55]; 1521, 18024 (58). Frequent in natural and artificial openings at Nahanni Butte and at hotsprings.

Geum aleppicum Jacq. var. *strictum* (Ait.) Fern. — 12752 [30]; 12862 [33]. No. 12752 is the first collection from the Mackenzie Mountains.

Geum macrophyllum Willd, ssp. *perincisum* (Rydb.)Hultén — 1511B, 1555 [58]. Common about the hotsprings and in disturbed gravel by the airstrip.

Luetkea pectinata (Pursh) Ktze. — 17770 [60]. Moist moss over limestone talus on steep creek bank. Rare; the only other record in the District of Mackenzie for this western North American species is from the Richardson Mountains (Porsild, 1943).

Potentilla biflora Willd. — 12630 [23]. Rocky slope in alpine tundra.

Potentilla diversifolia Lehm. ssp. *glaucophylla* (Lehm.) Lehm. — 17963 [57]. Turf and shoreline about «Grizzly Bear» Lake.

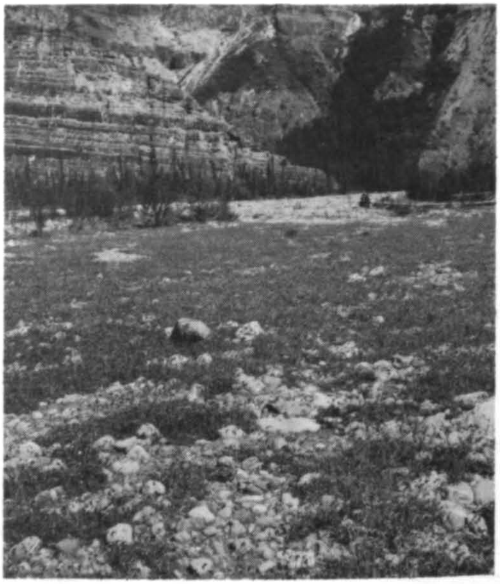

Figure 14. Yellow Dryad and other plants are common on plains which are subjected to flash flooding at frequent intervals. Photo — George W. Scotter.

Potentilla elegans Cham. & Schlecht. — 12681 [27]. Rocky slope in alpine tundra.

Potentilla fruticosa L. — 12388A [7]; 12823 [32]; 1776 [55]; 1818 [57]; 1522 [59]. A frequent species with wide ecological tolerance.

Potentilla hyparctica Malte var. *elatior* (Abrom.) Fern. — 12685 [27]; 17816 [60]. Alpine tundra and rock crevices.

Potentilla ledebouriana Porsild — 12572 [21]; 12616 [22]; 12709 [29]. Occasional in alpine tundra on scree slopes and ridges.

Potentilla nivea L. ssp. *hookeriana* (Lehm.) Hiitonen — 12030 [54]. Steep lower slope of Nahanni Butte.

Potentilla norvegica L. — 12273 [1]; 12334 [3]; 12546 [17]; 17414 [48]; 1511A, 1556 [58]. Occasional in most habitats at low elevations; frequent in disturbed situations.

Potentilla palustris (L.) Scop. — 12650 [24]; 15951 [56]; 1505 [58]. In shallow water of ponds, lake margins and streams.

Potentilla pensylvanica L. — 12535 [17]; 12848 [33]; 12029 [54]. Dry sites in disturbed areas.

Prunus pensylvanica L. f. — 12053 [54]. Steep lower slopes of Nahanni Butte; at the northern limit of its range *P. pensylvanica* is found only in sites similar to this were there is little competition. New to the Mackenzie Mountains.

Prunus virginiana L. — 12307 [2]. Common near a hotspring and hotspring stream; the only other records of this species occurring in the District of Mackenzie are those of Thieret (1961) from along the Enterprise — Mackenzie River Highway.

Rosa acicularis Lindl. — 12315 [2]; 12852 [33]; 1760, 17897 [55]; 1516 [59]. Frequent on floodplains, terraces, and mixed forests.

Rosa woodsii Lindl. — 12058 [54]. Steep lower slope of Nahanni Butte; rare in the District of Mackenzie where it is known only along the Liard and Mackenzie rivers and at the west end of Great Slave Lake.

Rubus acaulis Michx. — 12492 [14]. Seen in moist meadows and thickets.

Rubus chamaemorus L. 12663 [26]. Peat bog in alpine tundra.

Rubus pubescens Raf. — 12293 [2]. Frequent on floodplains and terraces and in mixed forests.

Rubus strigosus Michx. — 12308 [2]; 12505 [14]; 12789 [32]; 12900 [39]. Frequent on juvenile soils of floodplains and terraces.

Sibbaldia procumbens L. — 1710, 17726 [60]. Among rocks and on gravel moraine; in the District of Mackenzie found occasionally in the western parts of the Mackenzie Mountains and in the Richardson Mountains.

Sorbus scopulina Greene — 12907 [39]. Sole occurrence noted; the only other District of Mackenzie collections are from sites adjacent to the Liard River.

Spiraea beauverdiana Schneider — 12670 [26]. Bog habitat in alpine tundra.

LEGUMINOSAE

Astragalus alpinus L. — 12413 [8]; 12561 [19]. In a burned-over area and a forest opening.

Astragalus americanus (Hook.) M. E. Jones — 12768 [30]. First collection from the Mackenzie Mountains; the nearest sites to this are along the Liard River.

Astragalus canadensis L. [*A. americanus* sensu Jeffrey (1961)] — 12841, 12856 [33]; 12036 [54]. This species was reported from the steep slopes of Nahanni Butte by Cody (1963), but in error it was not listed for Zone 1 by Porsild and Cody (1968).

Astragalus eucosmus Robins. — 12399 [7]; 12449 [10]. First collection from the Mackenzie Mountains; the nearest records for this species are from Fort Simpson where it has been collected several times.

Astragalus tenellus Pursh — 12428 [8]. First collection from the Mackenzie Mountains; previously known in the District of Mackenzie from along the Slave, Hay, Mackenzie, and Liard rivers.

Astragalus umbellatus Bge. — 12632 [23]; 12710 [29]; 12783 [31]; 1800 [57]; 16382, 16401 [59]. Infrequent in alpine tundra.

Hedysarum alpinum L. var. *americanum* Michx. — 12294 [2]; 12366 [6]; 12384 [7]; 12509 [14]; 18010 [57]; 1598, 16392 [59]. Frequent in mixed forests and along riverbanks and gravel bars.

Hedysarum mackenzii Richards. — 12381, 12390 [7]; 12596 [22]; 12797, 12803 [32]. Frequent along riverbanks and in rocky areas. Flowering June 27.

Lathyrus ochroleucus Hook. — 12309 [2]. Infrequent in thickets and mixed forests.

Lupinus arcticus S. Wats. — 12409 [8]; 1774, 17902 [55]; 1551, 1620 [59]. Infrequent on moist and dry habitats on mountain slopes and along rivers and streams.

Melilotus alba Desr. — 12850 [33]. An introduced plant at Nahanni Butte.

Melilotus officinalis (L.) Lam. — 12335A [3]; 12905 [39]. An introduced plant.

Oxytropis deflexa (Pall.) DC. var. *foliolosa* (Hook.) Barneby — 12400 [7]. Along a riverbank.

Oxytropis glutinosa Porsild — 1612B, 16379 [59]. Steep rocky mountain slopes.

Oxytropis hyperborea Porsild — 12463 [13]; 12569 [21]; 12640 [23]; 1546 [58]. Seen from sandy sites on islands in the South Nahanni River to alpine tundra.

Oxytropis jordalii Porsild — 12690 [28]. Infrequent in dry habitats of alpine tundra.

Oxytropis maydelliana Trautv. — 12688 [28]; 16386 [59]. Infrequent in alpine tundra.

Oxytropis pygmaea (Pall.)Fern. — 12610 [22]; 12689 [28]; 12782 [31]. Fairly frequent in alpine communities.

Oxytropis varians (Rydb.) Hultén — 12403, 12429 [8]. Collected near Meilleur Creek; first collection from the Mackenzie Mountains.

Oxytropis viscidula (Rydb.) Tidestr. — 12383, 12387 [7]; 12450 [10]. Fairly frequent along riverbanks.

Trifolium hybridum L. — 12012 [33]. Introduced plant at Nahanni Butte.

Trifolium pratense L. — 12326 [3]. An introduced plant collected from near a cabin site in Zone 6; first collection for the District of Mackenzie.

Vicia americana Muhl. — 12416 [8]. Collected from a streambank; first collection from the Mackenzie Mountains.

GERANIACEAE

Geranium richardsonii Fisch. & Trautv. — 16350 [58]. Hotspring meadow at Tungsten; otherwise known in the District of Mackenzie from a single collection at Hole-in-the-Wall Lake (Porsild, 1961).

LINACEAE

Linum lewisii Pursh — 12795 [32]; 12038 [54]. Sole occurrences noted; collected from dry, open habitats.

EMPETRACEAE

Empetrum nigrum L. var. *hermaphroditum* (Lange) Sor. — 12489 [14]; 12944 [41]; 1781, 17932 [56]; 1812 [57]; 1519A, 1653 [59]; 1701, 17724 [60]. Fairly frequent in lodgepole and jack pine forests and in other habitats.

VIOLACEAE

Viola epipsila Ledeb. ssp. *repens* (Turcz.) Becker — 17935 [56]. In partial shade. In moss over boulders; rare.

Viola nephrophylla Greene — 12748 [30]. Found at a hotspring site; first collection from the Mackenzie Mountains; other collections from the District are from lowland situations.

Viola rugulosa Greene — 12241, 12245 [1]. Abundant near a hotspring; the only other Mackenzie District collection is that of Jeffrey (1961) from along the Liard River.

Viola tricolor L. — 12333 [3]. Occasional in an abandoned garden and around a cabin; an escape from cultivation. New to the Mackenzie District in Zone 6.

ELAEAGNACEAE

Elaeagnus commutata Bernh. — 12391 [7]. Fairly frequent along riverbanks.

Shepherdia canadensis (L.) Nutt. — 12394 [7]; 1761, 17899, 17915 [55]; 1628 [58]. Frequent on floodplains and terraces; often associated with white spruce and balsam poplar forests.

ONAGRACEAE

Circaea alpina L. — 16364 [58]. Hotspring site; otherwise known in the District of Mackenzie only from the Liard River valley (Jeffrey 1961 and several specimens gathered by Cody in 1961).

Epilobium angustifolium L. — 12392 [7]; 17927 [55]; 1787 [56]; 1552 (fls. pink), 1757, 16372 (fls. white), 16373 [58]. Fairly common on disturbed sites. Flowering June 27.

Epilobium ciliatum Raf. — 1506 [58]. By hotspring stream.

Epilobium glandulosum Lehm. var. *adenocaulon* (Haussk.) Fern. — 12746C [30]. Sole occurrence noted at a spring.

Epilobium latifolium L. — 12363 [5]; 1714, 17725 [60]. Fairly frequent on gravel bars along the river.

Epilobium palustre L. — 12728B, 12751 [30]; 17827 [60]. Frequent around hotspring pools and occasional in wet places elsewhere.

HALORAGACEAE

Hippuris vulgaris L. — 12875 [35]; 12906 [39]; 1630 [58]. Collected in shallow lakes and from hotspring streams.

Myriophyllum exalbescens Fern. — 12731 [30]; 12876 [35]. First collections from the Mackenzie Mountains; from shallow water of hotspring pools.

ARALIACEAE

Aralia nudicaulis L. — 12314 [2]; 12918C [39]; 12051 [54]. Fairly frequent in mixed white spruce and balsam poplar forests. New to the Mackenzie Mountains.

UMBELLIFERAE

Cicuta mackenzieana Raup — 12759 [30]. First collection from the Mackenzie Mountains; growing in a meadow near a hotspring; the nearest known sites for this species are from along the Liard River.

Heracleum lanatum Michx. — 12741 [30]; photo [58]. Wet meadows near hotspring pools.

Pastinaca sativa L. — 12249 [1]. Introduced plant, new to the flora of the District of Mackenzie in Zone 6.

Sium suave Walt. — 12647 [24]. Growing in shallow water of Yohin Lake.

CORNACEAE

Cornus canadensis L. — 12279 [2]; 1672 [59]; 1751, 17792 [60]. Common in several forest habitats.

Cornus stolonifera Michx. — 12290 [2]. Common on a floodplain and a terrace at this one site.

PYROLACEAE

Moneses uniflora (L.) Gray — 12426 [8]; 12435 [9]; 12526 [15]; 1525 [59]. Infrequent in spruce forests.

Pyrola asarifolia Michx. — 12397 [7]; 12824 [32]; 17919 [55]; 17987 [57]; 1528, 1601 [59]. Infrequent in white spruce and balsam poplar and white spruce forests.

Pyrola grandiflora Radius — 12347 [4]; 1805 [57]; 1586 [59]. White spruce forest and subalpine situations.

Pyrola minor L. — 1732, 17775 [60]. Alpine valley; rare in the Mackenzie Mountains.

Pyrola secunda L. var. *secunda* — 12300 [2]; 12415 [8]; 12825 [32]; 17909 [55]. Fairly frequent on floodplains and terraces with white spruce or mixed forests.

Pyrola secunda var. *obtusata* Turcz. — 12346 [4]; 12418 [8]; 12437 [9]. Fairly frequent in spruce forests.

Pyrola virens Schweigg. — 12407B [8]. Occasional in white spruce forests.

ERICACEAE

Andromeda polifolia L. — 12500 [14]. From a wet meadow near Virginia Falls.

Arctostaphylos rubra (Rehd. & Wils.) Fern. — 12422 [8]; 12571 [21]; 12711 [39]; 17924 [55]; 1810, 18011 [57]; 1591, 1661 [59]. Occasional from lowlands to alpine tundra.

Arctostaphylos uva-ursi (L.) Spreng. — 12388 [7]; 1765, 17905 [55]. Occasional in opening on south-facing slopes and in lodgepole and jack pine forests.

Cassiope tetragona (L.) D. Don ssp. *tetragona* — 12506 [14]; 12574 [21]; 1621A [59]; 1737A [60]. Frequent in alpine tundra and occasional at other sites such as Virginia Falls.

Cassiope tetragona (L.) D. Don ssp. *saximontana (Small) Porsild* — 12576 [21]; 12660 [26]; 1584 [59]. Collected from alpine tundra.

Kalmia polifolia Wang. — 12664 [26]; 17952 [56]. From wet meadows in alpine tundra. Omitted in error by Porsild and Cody (1968) from Zone 1, but previously reported from the area by Porsild (1945), Raup (1947) and Porsild (1961). The collection reported here is the third from the Mackenzie Mountains.

Ledum decumbens (Ait.) Lodd. — 12662 [26]. Occasional in alpine tundra.

Ledum groenlandicum Oed. — 12357 [4]; 12821 [32]; 1655, 1673 [59]; 1705 [60]. Common in black and white spruce forests.

Loiseleuria procumbens (L.) Desv. — 12671 [26]; 12684 [27]. Fairly frequent in alpine tundra.

Oxycoccus microcarpus Turcz. — 12883 [35]. Sole occurrence noted.

Oxycoccus quadripetalus Gil. — 12648 [24]. Peat bog habitat near Yohin Lake.

Phyllodoce glanduliflora (Hook.) Cov. — 1711, 17719 [60]. Terminal moraine in subalpine zone; rare in the western part of the Mackenzie Mountains.

Rhododendron lapponicum (L) Wahl. — 12369A [6]; 12592 [21]; 12614 [22]; 16402 [59]. Fairly frequent in alpine tundra; occasional at lower elevations.

Vaccinium uliginosum L. s.lat. — 12451 [10]; 12945 [41]; 1675, 1676 [59]; 1700 [60]. In bogs from lowlands to alpine tundra.

Vaccinium vitis-idaea L. var. *minus* Lodd. — 12368 [6]; 12892 [37]; 12903 [39]; 12939 [41]; 1654 [59] 1736 [60]. A common plant in spruce forests.

DIAPENSIACEAE

Diapensia obovata (Fr. Schm.) Nakai — 12676 [26]; 12685A [27]. These collections extend its known range well to the south from the Richardson Mountains, an extension of approximately 500 miles. New to the Mackenzie Mountains.

PRIMULACEAE

Androsace chamaejasme Host s. lat. — 12351 [4]; 12587 [21]; 12902 [39]; 12940 [41]. Rocky habitats from low mountain slopes to alpine tundra.

Androsace septentrionalis L. — 12027 [54]. Steep lower slopes of Nahanni Butte. Omitted in error by Porsild and Cody (1968) from Zone 1, but previously reported from that area on the basis of this collection (Cody, 1963).

Lysimachia thyrsiflora L. — 12655 [24]. Sole occurrence noted; from shallow water of Yohin Lake; the nearest collection is from along the Mackenzie River halfway between Fort Simpson and Fort Providence.

Primula egaliksensis Wormskj. — 12494 [14]; 17986 [57]. Occasional in wet meadows near Virginia Falls and at «Grizzly Bear» Lake.

Primula stricta Hornem. — 12452 [10]; 12494A [14]; 12741 [30]. Occasional in wet meadows and along riverbanks.

GENTIANACEAE

Gentiana acuta Michx. — 12733A [30]; 12843 [33]; 12927 [40]; 12050 [54]. Occasional in moist meadows and along streams. First collection from the Mackenzie Mountains, but known from the adjacent Liard and Mackenzie River lowlands.

Gentiana glauca Pall. — 12661 [26]; 12683 [27]; 1740, 17749 [60]. Meadows of the alpine tundra; infrequent.

Gentiana propinqua Richards. s. lat. — 12455 [10]; 12498 [14]; 12563 [20]; 12733B [30]; 12799 [32]; 12853 [33]; 17962 [56]; 1807, 17971B [57]; 1530, 1579, 1595 [59]; 17807 [60]. Occasional in a variety of habitats.

Gentiana prostrata Haenke — 1825, 17971A [57]. Turf at back of beach.

Gentiana raupii Porsild — 12060 [33]. Rare in sod in cabin clearing; this is an extension of range up the Liard River from Fort Simpson where it is fairly common on the banks of the Mackenzie River.

Lomatogonium rotatum (L.) Fries ssp. *tenuifolium* (Griseb.) Porsild — 17922 [55]. Apparently rare in the Mackenzie Mountains.

MENYANTHACEAE

Menyanthes trifoliata L. — 12745 [30]. Occasional in ponds and shallow lakes.

APOCYNACEAE

Apocynum androsaemifolium L. — 12042 [54]. In shade of *Populus tremuloides* on a steep slope of Nahanni Butte. Omitted in error by Porsild and Cody (1968) from Zone 1, but previously reported from that area on the basis of a specimen collected on Nahanni Butte, where the present collection was also gathered, by Jeffrey (1961).

POLEMONIACEAE

Polemonium acutiflorum Willd. — 17942 [56]; 1519 [58]; 1724, 17769 [60]. Moist subalpine meadows and beaches.

BORAGINACEAE

Mertensia paniculata (Ait.) G. Don — 12303 [2]; 12410 [8]; 18019 [57]; 1593, 1605 [59]; 1723 [60]. Occasional on floodplains and terraces.

LABIATAE

Mentha arvensis L. var. *villosa* (Benth.), S. R. Stewart — 12772 [30]; 12867 [34]; 12913 [39]; 17426 [50]; 1561 [58]. Abundant at hotsprings.

SCROPHULARIACEAE

Castilleja pallida (L.) Spreng. ssp. *caudata* Pennell — 12470 [13]. Infrequently noted; collected from an island in the South Nahanni River.

Castilleja raupii Pennell — 12358 [5]. Infrequently noted; collected from a gravel bar.

Mimulus guttatus DC. — 12754, 12769 [30]; 12868 [34]; 12881 [35]. New to the flora of the District of Mackenzie and the Mackenzie Mountains; in the distribution map for this species given in Hultén (1968), the nearest collection sites to those recorded here are in the southern Yukon.

Pedicularis capitata Adams — 1619 [59]; 17787 [60]. Moist alpine tundra and meadows.

Pedicularis labradorica Wirsing — 12432 [9]; 12458 [11]; 12658 [26]; 1785, 17940 [56]; 18013 [57]; 1727, 1750, 17772 [60]. An occasional plant in black spruce forests and alpine tundra.

Pedicularis lanata Cham. & Schlecht. — 12593 [21]; 12611, 12628 [22]; 12673 [26]; 12784 [31]; 1612A, 16381 [59]. Frequent in a variety of alpine habitats.

Pedicularis sudetica Willd. s. lat. — 12484 [14]; 1823, 18014, [57]; 1518, 1567 [58]; 1718, 1739, 17751 [60]. Usually wet alpine and subalpine meadows.

Rhinanthus borealis (Sterneck) Chab. — 17692 [58]. On bank by hotsprings at Tungsten; this is the only record from the Mackenzie Mountain region, but it is known along the Mackenzie River as far downstream as Norman Wells.

Veronica alpina L. var. *unalaschcensis* Cham. & Schlecht. — 17991 [57]; 1677, 16368 [59]; 1729, 17765 [60]. Moist tundra turf and rocky slopes.

Veronica americana (Raf.) Schwein. — 12763 [30]; 17418 [48]; 17426 [50]; 1515 [58]. Abundant surrounding hotspring pools; Porsild (1961) reported this species as new to the District of Mackenzie on the basis of a specimen collected by Arnold in a hotspring meadow at Hole-in-the-Wall Lake.

OROBANCHACEAE

Boschniakia rossica (Cham. & Schlecht.) Fedtsch. — 12444 [10]. A parasitic plant growing on the roots of *Alnus crispa*.

LENTIBULARIACEAE

Pinguicula vulgaris L. — 12442 [10]; 12734 [30]; 12800 [32]; 17921 [55]; Infrequent in moist habitats.

Utricularia minor L. — 12757 [30]. In hotspring pools. First collection from the Mackenzie Mountains; other District of Mackenzie collections are from about Great Slave and Great Bear Lakes.

Utricularia vulgaris L. — 12652 [24]; 12738, 12756 [30]. From hotspring ponds and a shallow lake. First collections from the Mackenzie Mountains, but known from the adjacent lowlands of the Mackenzie River.

PLANTAGINACEAE

Plantago canescens Adams — 12028 [56]. Steep lower slopes of Nahanni Butte. Not previously reported from the Mackenzie Mountains.
Plantago major L. — 12340 [3]; 1513, 1514, 1560 [58]. Noted in a forest opening and about the hotsprings at Tungsten.

RUBIACEAE

Galium boreale L. — 12292 [2]; 12495 [14]; 12801 [32]; 1644 [58]. Occasional on floodplains and terraces. Flowering June 26.
Galium trifidum L. — 12550 [18]; 12764 [30]. Infrequent in moist habitats such as muskegs and meadows.
Galium triflorum Michx. — 12263 [1]; 12730 [30]; 16365, 18028 [58]. Infrequent on floodplains and terraces and at a hotspring; these are the first records from the Mackenzie Mountain region but it is known from a number of sites along the Liard River (Cody 1961; Jeffrey 1961).

CAPRIFOLIACEAE

Linnaea borealis L. var. *americana (Forbes) Rehd.* — 12278 [2]; 1811 [57]; 1571 [58]. A fairly common species in forests.
Lonicera dioica L. var. *glaucescens* (Rydb.) Butters — 12291 [2]; 12056 [54]. On floodplains and terraces at the first site but on a steep slope among *Populus tremuloides* on Nahanni Butte. New to the Mackenzie Mountains.
Symphoricarpos occidentalis Hook. — 12043 [54]. Among *Populus tremuloides* on steep slope of Nahanni Butte; other District of Mackenzie collections have been from lowland sites. New to the Mackenzie Mountains.
Viburnum edule (Michx.) Raf. — 12301 [2]; 17910 [55]. Frequent in mixed forests on floodplains and terraces in the eastern portion of the region.

VALERIANACEAE

Valeriana septentrionalis Rydb. — 1533 [59]. In wet mossy area beside mountain stream.
Valeriana sitchensis Bong. — 1554 [58]; 1737, 17780 [60]. Hotsprings and alpine meadow slope.

CAMPANULACEAE

Campanula aurita Greene — 12344 [4]; 12488 [14]; 12532 [16]; 12813 [32]. Infrequent in forest opening and on grassy slopes.
Campanula lasiocarpa Cham. — 1587 [59]; 1715, 17762 [60]; in moist tundra turf and on steep mountain slopes.
Campanula rotundifolia L. — 12851, 12015 [33]. Sole occurrence noted was at Nahanni Butte.

LOBELIACEAE

Lobelia kalmii L. — 12740A, 12760, 12766 [30]; 12871 [34]; 12891 [36]; Common in hotspring areas. New to the Mackenzie Mountains; other District of Mackenzie collections are from about Great Slave Lake, at the foot of the Nahanni Range just north of Fort Simpson, and near a lake between the southern extremities of the Franklin Mountains.

COMPOSITAE

Achillea nigrescens (E.Mey.) Rydb. — 12297 [2]; 12424 [8]; 12566 [20]. Infrequent along rivers and in lowlands. Flowering June 26.
Achillea sibirica Ledeb. — 17435 [1]; 12858 [33]; 12899 [39]. Occasional near settlements at Nahanni Butte and a hotspring.
Agoseris aurantiaca (Hook.) Greene — 1508, 16356, 18027 [58]. Disturbed areas by the hotsprings; this locality and one other at "Canex Lake" a few miles to the north are the only known sites for the District of Mackenzie (Cody and Porsild 1968).
Antennaria densifolia Porsild — 12570 [21]; 12642 [23]; 12707 [29]; 12926 [40]; 1596A [59]. Occasional on alpine tundra and floodplains.
Antennaria isolepis Greene — 1782, 17947 [56]; 17777 [60]. In moss among stones in protected alpine situations.
Antennaria media Greene — 1734, 1741 [60]. Stream valley below glacier (Cody and Porsild 1968).
Antennaria moncephala DC. — 12601 [22]; 12699 [28]; 16375 [58]; 1596B [59]; 17753, 17758 [60]. Occasional on alpine tundra.
Antennaria nitida Greene — 12474 [13]. Sole occurrence noted on an island in the South Nahanni River. First collection in the Mackenzie Mountains.
Antennaria pulcherrima (Hook.) Greene — 12791 [32]. Sole occurrence noted on a mountain slope.
Antennaria rosea (Eaton) Greene — 12044 [54]. Steep open lower slopes of Nahanni Butte. New to the Mackenzie Mountains.
Arnica alpina (L.) Olin ssp. *angustifolia* (Vahl) Maguire — 12584 [21]; 12636 [23] 12674 [26]; 12696 [28]; 1803, 18001 [57]. Frequent on dry alpine sites.
Arnica alpina (L.) Olin ssp. *attenuata* (Greene) Maguire — 12386 [7]. Sole occurrence in an arti-

ficial clearing. First collection from the Mackenzie Mountains.

Arnica amplexicaulis Nutt. — 17416 [48]. Sole occurrence noted along a stream from a cool spring; this is only the second report of the species from the District of Mackenzie. The species was first reported by Porsild (1961) from Hole-in-the-Wall Lake.

Arnica chamissonis Less. ssp. *foliosa* (Nutt.) Maguire — 12735 [30]; 1510, 1564 [58]. Noted only at hotspring sites.

Arnica latifolia Bong. — 1743, 17788 [60]. Alpine meadow; this is the only locality known in the District of Mackenzie (Cody and Porsild 1968).

Arnica lessingii Greene — 1819, 18002 [57]; 1550, 1667, 16398 [59]; 1704 [60]. Rocky alpine slopes.

Arnica louiseana Farr ssp. *frigida* (Meyer) Maguire — 12353 [4]; 12808C [32]; 17721 [59]; 1615A [60]. Dry, rocky habitats; infrequent occurrence.

Artemisia arctica Less. — 17411 [47]; 1777, 17943 [56]; 1821, 17981 [57]; 1580, 1609, 1666 [59]; 1703, 17744 [60]. Alpine meadows and moist rocky slopes in the western parts of the Mackenzie Mountains.

Artemisia biennis Willd. — 12330 [3]. Occasional in a disturbed site near a cabin. Sole occurrence noted.

Artemisia frigida Willd. — 12457 [11]; 12934 [41]. 12026 [54]. Occasional on dry, open slopes with southern exposure. First collections from the Mackenzie Mountains; known nearby from the Liard and Mackenzie River valleys.

Artemisia tilesii Lebed. var. *tilesii* — 12538 [17]. Infrequent on sandy sites.

Artemisia tilesii var. *elatior* (T. & G.) Rydb. — 12269, 12277 [1]; 12924 [39]. Infrequent on a terrace near a hotspring.

Aster alpinus L. ssp. *vierhapperi* Onno — 12520 [14]; 12928 [40]; 12046 [54]. Infrequent on dry, open sites.

Aster ciliolatus Lindl. — 12857, 12008 [33]; 12898 [39]. Infrequent in thickets and mixed forests.

Aster ericoides L. — 12935 [41]; 12057 [54]. Dry, open slopes. First collections from the Mackenzie Mountains, but known from along the Mackenzie River valley.

Aster franklinianus Rydb. — 12755 [30]. From hotspring site. First collection from the Mackenzie Mountains; the nearest collections are from along the Liard River and at Fort Simpson.

Aster **nahanniensis** W. J. Cody *sp. nov.* Complexa *A. ericoide* ut videtur proxima sed capitulis majoribus in terminalibus ramulorum singularibus et marginibus phyllariorum papyraceis eroso-ciliatis prompte distinguenda.

Usque 35 cm alta subramosa. Caules puberulentes. Folia ad marginem prorsum scabra cetera glabra; radicalia usque 1.3 cm longa, breviter spathulata, obtusa; caulina usque 6.5 cm longa, linearia vel lineari-lanceolata, sessilia, subamplexicaulia, subacuta; ramulina 0.5 — 1.8 cm longa, oblonga vel ovato-oblonga, subacuta. Capitula 1.5 — 2 cm diam., caulem vel ramulos debiles terminantia. Phyllaria 3-4-seriata, exteriora spathulata, interiora lanceolata; margines papyraceae, eroso-ciliatae, purpurascentes. Corollae radiatae albae; ligula ca. 1.5 cm longa. Flosculi disci Flavi. Achenia 2 - 3 mm longa, pubescentia; pappus albus.

Typus: Canada: Mackenzie District: Mackenzie Mountains, South Nahanni River area; along stream near "Old Pots" spring; 61° 31' 30" N, 126° 29' W; 2500 ft [760 m]; Sept. 16, 1971. *George W. Scotter 17412:* holo.: DAO. See Figure 15.

Paratypus: South Nahanni River area: Hot mineral springs region south of the Flat River; 61°25'N, 126°36'W; 2500 ft. [760 m]; *George W. Scotter 12870;* DAO.

Aster sibiricus L. — 12382 [7]; 12414 [8]; 12464 [13]; 12482 [14]; 12844, 17438 [33]; 12923 [39]; 12942 [41]; 1798, 17977 [57]. Fairly frequently associated with riparian vegetation and in meadows.

Bidens cernua L. — 12873 [34]; 1562 [58]. Infrequent near hotspring pools; new to the Mackenzie Mountains; elsewhere in the District of Mackenzie this species is known from Great Slave Lake and along the Slave River.

Chrysanthemum integrifolium Richards. — 12586 [21]; 12637 [23]; 1589 [59]. Infrequent on rocky slopes of the alpine tundra zone.

Crepis elegans Hook. — 12408 [8]; 12537 [17]; 12562 [19]. Infrequent on gravelly sites. First collections from the Mackenzie Mountains, but known from banks along the Mackenzie River.

Erigeron angulosus Gaud. var. *kamtschaticus* (DC.) Hara — 12559 [19]; 1771 [55]. Noted in recently burned-over areas.

Erigeron elatus (Hook.) Greene — 12560 [19]. Infrequent in moist habitats.

Erigeron hyssopifolius Michx. — 12430 [8]; 12533 [16]; 12565 [20]; 12590 [21]; 12639 [23]; 12794 [32]. Fairly frequent in rocky habitats from riverbanks to alpine tundra.

Erigeron jucundus Greene — 1568 [58]; 17821 [59]. Talus slope and disturbed situations at Tungsten; otherwise known in the District of Mackenzie only from the vicinity of Glacier Lake in the Mackenzie Mountains (Raup, 1947, *pro parte).*

Erigeron lonchophyllus Hook. — 12544 [17] 12839, 12855 [33]. Infrequent in moist habitats. First collection from the Mackenzie Mountains; known from the Mackenzie valley as far north as Norman Wells.

Figure 15. *Aster nahanniensis*, a new species, was found along a stream below "Old Pots" Spring. Photo — Canada Department of Agriculture.

Erigeron philadelphicus L — 12262 [1]; 12302 [2]; 12331 [3]; 12840 [33]. Infrequent in moist habitats.

Erigeron yukonensis Rydb. — 12792 [32]. Sole occurrence was noted on a gravelly floodplain. First collection from the Mackenzie Mountains.

Hieracium gracile Hook. var. *yukonense* Porsild — 1509 [58]. Disturbed gravel; this is the only known locality in the District of Mackenzie (Cody and Porsild, 1968).

Hieracium scabriusculum Schwein. — 12035 [54]. Steep open slope of Nahanni Butte. New to the Mackenzie Mountains.

Hieracium triste Willd. — 1733, 17771 [60]. Rocky alpine situations in the western parts of the Mackenzie Mountains; this species was recorded as new to the District of Mackenzie on the basis of these specimens and a collection from near O'Grady Lake to the north (Cody and Porsild, 1968).

Matricaria matricarioides (Less.) Porter — 12854, 12021 [33]. An introduced plant at Nahanni Butte.

Petasites arcticus A.E. Porsild — 12678 [26]. Sole occurrence was noted at a bog in the alpine tundra zone. First collection from the Mackenzie Mountains.

Petasites frigidus (L.) Fries — 1702, 17713, 17723, 17793 [60]. In gravel of terminal moraine and in protected situations along alpine streams.

Petasites sagittatus (Pursh) Gray — 12849 [33]; 1547 [58]. Fairly common at the margins of meadows and bogs.

Senecio lugens Richards. — 12352 [4]; 12585 [21]; 12808B [32]; 1799, 17992 [57]; 1664, 16397 [59]; 17731 [60]. Infrequent from low elevations to alpine tundra. Flowering June 26.

Senecio pauciflorus Pursh — 1535, 17688 [58]. In disturbed situations and by the hotsprings at Tungsten (Cody and Porsild, 1968).

Senecio pauperculus Michx. — 12332, 12335B [3]; 12476 [13]; 12749 [30]. Fairly frequent in moist habitats at low elevations.

Senecio resedifolius Less. — 12617 [22]; 18004 [57]. Infrequent in rocky habitats in alpine tundra.

Senecio triangularis Hook. — 1563 [58]; 1730, 17761 [60]. Hotspring meadow at Tungsten and wet, springy, protected subalpine situations; found in the western parts of the Mackenzie Mountains.

Senecio yukonensis Porsild — 12657 [26]. Rare in alpine tundra.

Solidago canadensis L. var. *salebrosa* (Piper) M. E. Jones — 12341 [3]; 12475 [13]; 12761, 12774 [30]; 12845, 12010 [33]; 12897 [39]; 1557 [58]. Fairly frequent in moist habitats.

Solidago decumbens Greene var. *oreophila* (Rydb.) Fern. — 12846, 12859 [33]; 12930 [40]; 1768, 17906 [55]. Occasional throughout the area.

Solidago multiradiata Ait. s. lat. — 12371 [6]; 12419 [8]; 12446, 12453 [10]; 12641 [23]; 12808A [32]; 1797, 17965 [57]; 1588, 1600, 1663 [58]. Rocky sites from lowlands to alpine tundra.

Taraxacum alaskanum Rydb. 17766 [60]. Rare in moist tundra.

Taraxacum dumetorum Greene — 1570 [58]. In sod by hotspring meadow. New to the Mackenzie Mountains.

Taraxacum officinale Weber — 12337 [3]; 12013 [33]; 1540 [58]. An introduced weed. New to the Mackenzie Mountains.

Taraxacum scopulorum (Gray) Rydb. — 1719 [60]. In gravel of terminal moraine below glacier.

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CLASSIFICATION ÉCOLOGIQUE DES FORMES DE CROISSANCE DE *PICEA GLAUCA* (MOENCH.) VOSS ET DE *PICEA MARIANA* (MILL.) BSP. EN MILIEUX SUBARCTIQUES ET SUBALPINS

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Résumé

L'épinette blanche (*Picea glauca* (Moench.) Voss) et l'épinette noire (*Picea mariana* (Mill.) BSP.) adoptent plusieurs formes de croissance dans la toundra forestière. Le but de ce travail est de décrire les formes les plus fréquentes et d'en déterminer la signification écologique. L'ensemble des formes décrites est aligné le long d'un gradient climatique exprimé par le degré d'exposition aux vents froids et érosifs et l'enneigement variable des milieux au cours de la période la plus froide de l'hiver. La dessication et le verglas peuvent intervenir en tant que facteurs de genèse des formes décrites. Des milieux exposés aux milieux protégés, on note la dominance successive des formes empétroïde, fruticoïde, en bougeoir, en verticille, en drapeau et arborescente. Sachant que l'environnement est fluctuant, ces formes peuvent évoluer selon l'importance des variations écologiques.

Abstract

White spruce (*Picea glauca* (Moench.) Voss) and black spruce (*Picea mariana* (Mill.) BSP.) are characterized by many growth-forms in the forest-tundra. This paper describes the most frequent growth-forms and gives their origin and formation. These growth-forms may be individuals or agglomerated into krummholz. They express a climatic gradient determined by exposure to cold and erosive winds and by snow conditions during the coldest period of winter time. Dessication and icing may act also in the genesis of growth-forms. From exposed to protected sites, we observe the successive dominance of mat, infra-nival, supra-nival skirted, verticillate, flag and tree growth-forms. These growth-forms are not static since the environment is normally fluctuating and they can evolve according to the importance of ecological changes.

Introduction

Les chercheurs notent depuis longtemps la présence de diverses formes de croissance chez les espèces conifériennes arborescentes, localisées dans les régions de haute altitude (Daubenmire, 1954; Bliss, 1963; Wardle, 1965 et 1968; Billings et Mooney, 1968; Brooke *et al.*, 1970; Löve *et al.*, 1970;) et dans les régions de haute latitude (Marr, 1948; Hustich, 1950 et 1966; Rousseau, 1968; Savile, 1972; etc.). Bien que la majorité de ces formes se rencontre dans les régions subarctiques et subalpines (*sensu* Löve, 1970), on en retrouve à l'état sporadique dans les domaines de la forêt coniférienne boréale et de la forêt à feuillage décidu.

L'importance géographique de certaines formes prostrées a amené les taxonomistes (Fernald, 1950) à les décrire en tant que variétés ou formes des espèces considérées. Cependant, nous admettons aujourd'hui que ces formes constituent des accomodats et peuvent difficilement être incluses dans une classification phylogénétique.

Le but du présent travail est de proposer une classification des principales formes rencontrées chez *Picea glauca* (Moench.) Voss et *Picea mariana* (Mill.) BSP. dans la toundra forestière de l'est de l'Amérique du Nord, et plus particulièrement au Québec, et d'en suggérer une interprétation écologique. Bien que certaines formes de croissance aient déjà été sommairement décrites dans la littérature (Wardle, 1965 et 1968; Löve *et al.*, 1970), nous ne possédons pas encore une synthèse globale sur leurs principales variations morphologiques ainsi que sur leur véritable signification écologique. La principale région étudiée s'étend sur environ trois degrés de latitude, entre Poste-de-la-Baleine (55°17'N) et le Boniface (57°48'N), et sur trois degrés de longitude, depuis le littoral de la baie d'Hudson (77°W) jusqu'au cours supérieur de la rivière aux Feuilles (74°45'W). Des observations ont été effectuées aussi dans les étages subalpin et alpin du mont Jacques-Cartier, Parc de la Gaspésie, Québec.

Classification des formes de croissance

Les formes de croissance comprennent soit des individus isolés, soit des individus agglomérés en formation. Ces deux modes de distribution se retrouvent chez les deux espèces d'épinettes. Les diverses formes de croissance peuvent être groupées parmi les types suivants:

individu	*formation*
forme empétroïde	krummholz empétroïde
forme fruticoïde	krummholz fruticoïde
forme en bougeoir	krummholz-bougeoir
forme en verticille	krummholz-verticille
forme en drapeau	lisière en drapeau
forme arborescente symétrique	forêt (ou arboraie)

FORME EMPÉTROÏDE ET KRUMMHOLZ EMPÉTROÏDE
(«*MAT GROWTH FORM*» DES AUTEURS ANGLOPHONES)

Cette forme a été décrite sous la dénomination de forma *empetroïdes* Vict. & Rousseau (Fernald, 1950) pour *Picea mariana* et forma *parva* (Vict.) Fern. & Weath. (Fernald, 1950) pour *Picea glauca*. Les épinettes empétroïdes rappellent le port prostré d'*Empetrum*. Cette forme dépasse rarement 30 cm de hauteur et se retrouve intimement mêlée avec les individus des espèces composant la strate muscinale de nombreuses communautés végétales. Le tronc est prostré et suit la surface du sol. Le profil longitudinal des individus empétroïdes est relativement linéaire (fig. 1). Cette forme occupe ordinairement une surface de quelques centimètres carrés.

Le krummholz empétroïde constitue une formation arbustive rase. Il ressemble à la forme empétroïde quant à la hauteur et au profil longitudinal. Cependant, cette formation comprend plusieurs tigelles ou rameaux densément agglomérés. Il est difficile de distinguer le nombre d'individus qui la composent. Les plants se multiplient par voie végétative, de sorte que plusieurs tigelles peuvent appartenir à un seul individu comme c'est le cas chez les épinettes arborescentes en candélabre. La forme et la disposition des troncs sont semblables à celles des plants empétroïdes. Cette formation couvre une surface supérieure à un mètre carré (fig. 2) et est soit en colonie pure ou en mélange avec les individus des espèces de la strate muscinale.

FORME FRUTICOÏDE ET KRUMMHOLZ FRUTICOÏDE
(«*INFRA-NIVAL CUSHION*» DES AUTEURS ANGLOPHONES)

Cette forme correspond sans doute chez l'épinette noire à forma *semi-*

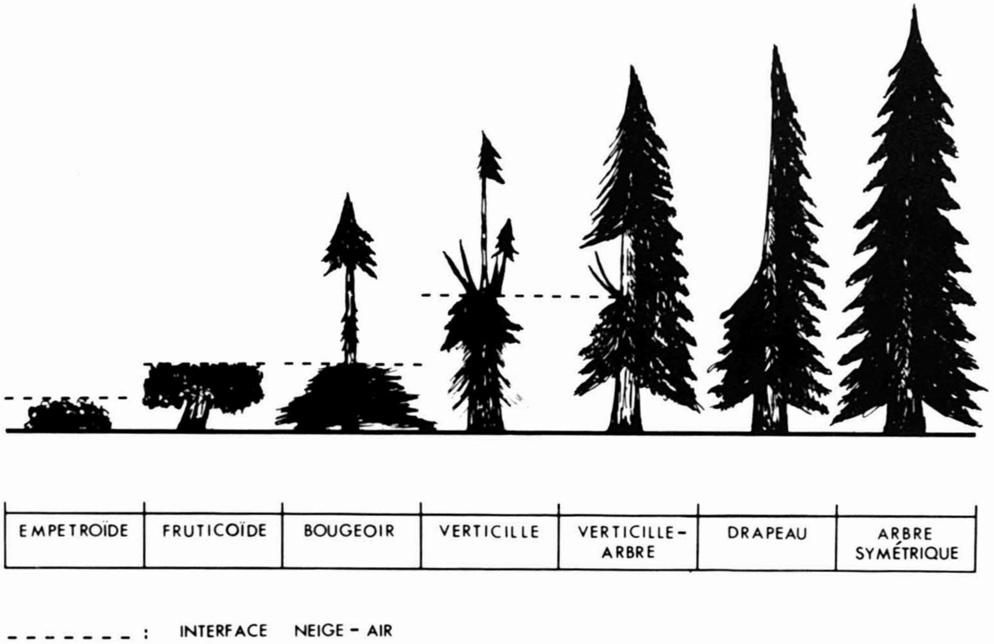

Figure 1. Formes de croissance de *Picea glauca* et de *Picea mariana* dans la toundra forestière.

prostrata (Peck) Blake (Fernald, 1950). Cette forme caractérise les épinettes arbustives non rases, mais à profil longitudinal souvent linéaire comme chez la forme empétroïde. On note la présence d'un tronc dressé de hauteur variable mais ne dépassant pas généralement deux mètres. Le tronc est soit vertical ou oblique et supporte de nombreuses branches parfois orientées dans une même direction. Plusieurs plants peuvent montrer une disposition flabelliforme des branches avec concavité plus ou moins prononcée près de l'axe du tronc. Dans certains cas, les branches sont présentes d'un seul côté de la tige. Les épinettes fruticoïdes épousent souvent la forme d'un triangle (fig. 1).

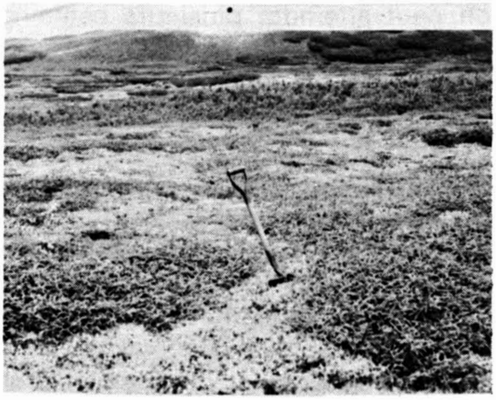

Figure 2. Krummholz empétroide à l'avant-plan ; Krummholz fruticoïde à l'arrière-plan : Golfe de Richmond.

Le krummholz fruticoïde est constitué de plusieurs tiges appartenant à un ou plusieurs individus et formant une masse compacte, rigide et à profil relativement régulier. Il possède les mêmes caractéristiques morphologiques générales que la forme fruticoïde. Le profil général de cette formation peut être triangulaire, rectangulaire ou ondulé (fig. 3). Le krummholz fruticoïde adopte parfois les formes du microrelief et prend l'aspect de haies soigneusement taillées au ciseau.

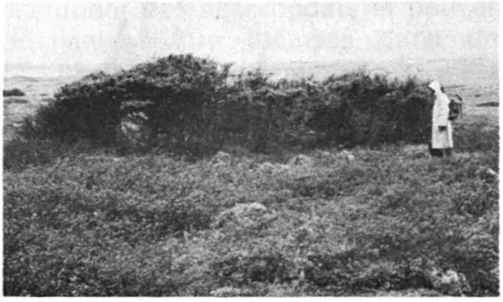

Figure 3. Krummholz fruticoïde triangulaire, Golfe de Richmond. Noter la différence de structures végétales associée à la présence du Krummholz.

FORME EN BOUGEOIR ET KRUMMHOLZ-BOUGEOIR («*SUPRA-NIVAL SKIRTED FLAG-TYPE*» DES AUTEURS ANGLOPHONES)

J. Rousseau (comm. verb.) a déjà utilisé le terme «yuccoïde» pour décrire cette forme. Cet auteur (Rousseau, 1968, p. 543) montre une photographie d'une telle forme chez le sapin (*Abies balsamea* (L.) Mill.). La forme en bougeoir se caractérise ordinairement par la présence d'une tige unique dont la partie basale est densément branchée et feuillue, la partie médiane complètement nue ou presque et la partie apicale légèrement branchée et feuillue. C'est le cas des formes en bougeoir arbustives. Cependant, la tige peut posséder un diamètre et une hauteur variables. Dans certains cas, la forme en bougeoir est arborescente; la partie dégarnie n'occupe plus la section médiane de la tige (fig. 1).

Le krummholz-bougeoir se réfère à un ensemble très irrégulier de formes en bougeoir, projetant des tiges dégarnies au centre et feuillues à l'apex, surplombant une masse touffue, dense et rigide. Les tiges peuvent atteindre deux à trois mètres de hauteur, alors que le massif proprement dit n'excède pas ordinairement deux mètres. La formation en krummholz-bougeoir peut renfermer des formes fruticoïdes et en verticille. Elle peut couvrir une surface de quelques dizaines de mètres carrés.

FORME EN VERTICILLE ET KRUMMHOLZ-VERTICILLE (AUCUN ÉQUIVALENT CHEZ LES AUTEURS ANGLOPHONES)

La forme en verticille se présente comme une suite de tiges et de tigelles, variables en nombre, et centrées radialement sur un tronc principal relativement bien développé. Chez certains individus, on a déjà dénombré une trentaine et même une quarantaine de branches, dont plusieurs sont transformées en tiges et tigelles, partant autour d'un même plan. Ces tiges et tigelles possèdent généralement un petit diamètre par rapport au tronc. Elles constituent une expansion irrégulière de l'axe principal. Le passage du tronc en tiges et en tigelles se fait abruptement. La forme de ces dernières peut varier grandement d'un individu à l'autre et plusieurs d'entre elles sont mortes. La hauteur des épinettes en verticille peut atteindre quatre à cinq mètres (fig. 1).

Le krummholz-verticille a l'aspect d'un peuplement forestier. Toutefois, il est ordinairement associé à d'autres formes de croissance voisines, comme la forme arborescente, dont les proportions varient selon les milieux écologiques. La surface occupée par une telle formation peut atteindre plusieurs centaines de mètres carrés (fig. 4).

FORME ET LISIÈRE EN DRAPEAU («*FLAG-TYPE*» DES AUTEURS ANGLOPHONES)

Cette forme est reconnue depuis longtemps et elle est très répandue dans de nombreuses régions du globe. Elle se caractérise par une dissymétrie marquée dans le port arborescent des épinettes. Une section importante de la tige est partiellement ou complètement dégarnie de branches sur un côté. À part cette irrégularité, la forme en drapeau ressemble à la forme arborescente

Figure 4. Formes en verticille, Golfe de Richmond. À gauche, verticille régressant vers un profil fruticoïde. Forte irrégularité dans la croissance du tronc et des tiges.

(fig. 1.). Il est très important de noter que des formes mixtes en bougeoir et en drapeau, de même qu'en verticille et en drapeau existent.

À la marge des forêts, il peut y avoir une lisière constituée d'épinettes en drapeau. Cette lisière n'est jamais large, quelques mètres, mais peut s'étendre sur plusieurs dizaines de mètres. Elle comprend souvent des formes mixtes.

FORME ARBORESCENTE SYMÉTRIQUE ET FORÊT («*TREE FORM*» DES AUTEURS ANGLOPHONES)

C'est la forme et la formation les mieux connues et les plus répandues chez les épinettes. La forme arborescente est soit monocaule ou en candélabre (fig. 1). La forme arborescente en candélabre a été décrite par Hustich (1950) et semble apparemment exclusive aux domaines des forêts conifériennes froides de latitude et d'altitude. La formation des clones par marcottage n'est pas encore expliquée d'une façon générale. La forme arborescente symétrique atteint une taille très variable; elle est généralement supérieure à cinq mètres de hauteur. Les forêts peuvent occuper évidemment une grande surface.

Origine des formes et des formations.

Les formes et les formations décrites apparaissent le long d'un gradient écologique relié principalement aux conditions climatiques. L'exposition aux vents froids et violents, ainsi que l'enneigement et parfois la dessication et le verglas, constituent les variables écologiques prépondérantes déterminant l'origine et l'importance géographique de chaque forme. La nature des sols intervient dans la distribution de certaines formations.

ÉPINETTES EMPÉTROÏDES

La forme empétroïde et le krummholz empétroïde sont associés à une très forte exposition aux vents hivernaux, causant un enneigement négligeable et un manque de protection contre les basses températures et l'érosion mécanique par les cristaux de neige et de glace. Ces cristaux peuvent atteindre une dureté égale à la calcite par temps très froid, comme −15° C et −20° C (Rikhter, 1963). Dans ces conditions la déflation nivale exerce un effet comparable à la déflation de grains de sable. Même si la croissance des épinettes empétroïdes peut être favorisée par des températures estivales relativement élevées, les conditions hivernales limitent l'expansion en hauteur des plants. Les bourgeons apicaux sont continuellement tués ou coupés. La hauteur des épinettes correspond à quelques centimètres près à la hauteur du couvert de neige pendant la période la plus froide et la plus venteuse de l'hiver (Payette et Lagarec, 1972).

ÉPINETTES FRUTICOÏDES

La forme fruticoïde correspond à la forme empétroïde quant aux conditions d'exposition éolienne à la surface du plant. La présence d'un tronc dressé de taille variable signifie que les épinettes fruticoïdes croissent dans des conditions moins restrictives au niveau de la surface du sol. La taille plus élevée est reliée sinon à un enneigement plus important, du moins à un hiver moins rigoureux. Cette situation peut être modulée par le microrelief (dépression, obstacle, etc.). La présence d'un obstacle à l'amont des plants, selon la direction des vents dominants et érosifs de l'hiver, ne saurait être vue comme une condition nécessaire à leur maintien, car plusieurs épinettes fruticoïdes se retrouvent dans des stations non abritées.

Le krummholz fruticoïde subit les mêmes conditions d'exposition éolienne que les formes précédentes, du moins à la surface de la formation. La forme et la hauteur des profils fruticoïdes coïncident avec la profondeur et la forme du couvert nival au cours de la période la plus froide et la plus venteuse de l'hiver (masse d'air arctique). L'épaisseur du tapis de neige est réglée par le processus nival de saturation topographique (Thom et Granberg, 1970; Payette *et al.*, 1973).

Chez le krummholz fruticoïde triangulaire, l'enneigement est minimal et l'exposition éolienne maximale dans la partie amont de la formation (c'est-à-dire dans le sens des vents érosifs); cette partie possède les mêmes caractéristiques écologiques que les épinettes empétroïdes. La partie aval de la formation est plus élevée et plus enneigée et n'est pas nécessairement associée à la protection par effet de masse des épinettes de l'amont. Cette partie aval se termine abruptement et, par appel au vide, favorise une accumulation sensible de neige. Plusieurs phanérogames et cryptogames bénéficient de cette protection et constituent des phytocénoses distinctes. Les formations fruticoïdes rectangulaires et ondulées ont deux origines possibles: a) d'exposition éolienne proprement dite; b) de saturation topographique par l'enneigement, au-delà de laquelle l'érosion est intense et modèle les formations à la topographie d'hiver des stations.

ÉPINETTES EN BOUGEOIR

La forme en bougeoir est très répandue dans la toundra forestière et reflète des conditions d'exposition moins sévères que les formes précédentes. La partie inférieure du plant est toujours enneigée, alors que la partie dégarnie de la tige est exposée aux vents érosifs. La partie apicale feuillue se situe dans une zone moins critique, où l'influence érosive des cristaux de neige et de glace est moins grande qu'à l'interface neige-air. Lorsque la plante au cours de sa croissance dépasse la couche de neige protectrice, elle se situe dans une zone très érosive. Elle risque deux situations: a) soit d'être étêtée ou tuée; b) soit résister et poursuivre sa croissance en hauteur. Dans la première situation, le plant peut évoluer soit vers une forme empétroïde ou fruticoïde, soit vers une forme en verticille (voir plus loin). Le verglas peut causer parfois une cassure de la tige et conduire aux conséquences de la première situation. Dans le second cas, il semble que la plante profite de conditions favorables (hiver doux, diminution de la vitesse des vents, changement d'orientation des vents, augmentation de l'enneigement, etc.) au cours d'une période suffisamment longue pour permettre au bourgeon apical d'atteindre une zone moins critique. Une fois cette étape accomplie, de nouvelles conditions érosives peuvent se faire sentir au niveau des rameaux et des branches latérales de la tige situés au contact neige-air. L'avènement de conditions favorables ne nécessite pas des fluctuations climatiques importantes. Seules les variations climatiques observées d'une année à l'autre dans la toundra forestière sont probablement suffisantes. La suite plus ou moins longue de bonnes années, comprenant autant la période hivernale que la période estivale, détermine le succès des plants à traverser la zone critique en conservant le bourgeon apical. Bien que la dessication des pseudophylles puisse jouer un certain rôle dans l'origine de la morphologie des types décrits (Wardle, 1965 et 1968), il semble que la relation position du bourgeon apical-fréquence et durée des variations climatiques soit plus importante.

Le krummholz-bougeoir représente une manifestation collective de la forme en bougeoir. On doit noter qu'il est le plus souvent mêlé à d'autres formes de croissance présentant une parenté génétique, comme la forme en verticille, à cause d'une protection par effet de masse. Soulignons qu'en dehors du krummholz empétroïde, une formation est rarement monomorphe. Compte tenu des conditions écologiques, les formes fruticoïdes, en bougeoir et en verticille occuperont une proportion variable de chaque krummholz.

ÉPINETTES EN VERTICILLE

La forme en verticille est vue comme une expression morphologique plus complexe que la forme précédente. Elle se rencontre dans des milieux souvent moins limitants que la forme en bougeoir. Ces deux formes apparaissent parfois dans des situations écologiques identiques. La zone de déflation nivale peut se situer à une plus grande hauteur, laquelle semble déterminée par les conditions de saturation topographique, soit à cause d'un relief protecteur et/ou de structures de végétation adjacentes assurant une protection contre l'érosion. L'origine de cette forme est aussi redevable à la fréquence d'apparition de séquences d'années favorables à la croissance.

Lorsque le bourgeon apical atteint la zone critique, il fait face aux deux situations décrites chez la forme en bougeoir. Si le bourgeon apical est tué, il se produit une perte de dominance apicale. Ceci a pour effet de permettre l'érection d'une ou de plusieurs branches latérales, pouvant éventuellement subir le même traitement. Dans le cas de conditions climatiques défavorables, la surface du plant présente un profil semblable à celui des formes empétroïde ou fruticoïde. Au contraire, si les conditions sont épisodiquement favorables, des tiges ou des tigelles se forment, par suite de pertes répétées de dominance apicale. Le résultat d'une telle taille naturelle est l'obtention d'une grande diversité de formes qui présentent un patron analogue. On note généralement une forte variation du diamètre des branches transformées en tige ou en tigelle. Si le nombre d'années favorables est long, on verra la formation d'une tige, le contraire donnant une tigelle. Ce processus de taille naturelle agit à l'interface neige-air ou au-delà si la zone érosive est déterminée par la topographie locale (relief et structure végétale). Notons tout de même qu'une tige bien formée et portant des branches feuillées peut être complètement endommagée par les basses températures sans que le bourgeon apical soit coupé. La mort de la tige favorise ainsi la transformation des branches en de nouvelles tiges à partir de la zone de contact neige-air. Il peut y avoir cependant des exceptions, lorsqu'un bourgeon latéral sur l'ensemble n'est pas tué. Les pertes successives de dominance apicale surviennent au cours d'une longue période de temps. Cette situation explique le fait que le tronc se développe normalement et la partie non enneigée fort irrégulièrement. La fréquence d'apparition et la durée des séquences favorables par rapport à celles des séquences défavorables déterminent le nombre de tiges et de tigelles de hauteur et de diamètre variables. Certaines épinettes en verticille ressemblent à la forme en bougeoir; d'autres se rapprochent morphologiquement de la forme arborescente. Il existe plusieurs intermédiaires entre ces deux dernières formes, soulignant une diminution sensible de l'érosion.

ÉPINETTES EN DRAPEAU ET ÉPINETTES SYMÉTRIQUES

La forme en drapeau représente le dernier maillon des formes érodées. Étant avant tout une forme arborescente, elle montre des signes mineurs d'érosion mécanique, face aux vents dominants de l'hiver et du printemps. Il est possible que la dessication ait un rôle à jouer, notamment au printemps (Wardle, 1965 et 1968), mais ceci ne peut être généralisé pour l'ensemble des épinettes en drapeau de la toundra forestière. Cette forme a déjà été associée à l'influence nocive des sels marins (Boyce, 1954). Ce facteur ne semble pas jouer dans les régions étudiées; la baie d'Hudson demeure gelée pendant plusieurs mois de l'année (Danielson, 1971) et plusieurs épinettes en drapeau se retrouvent loin de la mer et en altitude. Art *et al.* (1974) ont, cependant, souligné qu'un excès de sels marins peut conduire à une taille naturelle des arbres par mort successive de bourgeons axillaires. Cette forme de croissance est donc polygénétique.

La forme arborescente symétrique et la formation forestière proprement dites ne montrent aucun signe d'érosion. La présence d'arbres signifie ordinairement que ces milieux sont protégés contre les vents froids et érosifs.

Relations entre les différentes formes

Sachant que les formes décrites sont alignées le long d'un gradient climatique, elles manifestent un dynamisme relié aux fluctuations écologiques des stations où elles se retrouvent. C'est ainsi que des individus peuvent progresser ou régresser vers une autre forme selon l'amplitude des fluctuations du milieu. Une telle évolution des formes est schématisée à la fig. 5.

Sur une surface de quelques hectares, nous pouvons retrouver toutes ces formes. Il est même possible de noter la présence d'une épinette empétroïde ou fruticoïde à côté d'un verticille ou d'un arbre. Ceci suggère que les formes de croissance répondent à des conditions microclimatiques reliées à l'exposition (température et vent) variant considérablement dans le temps. Certains individus portent la marque historique de conditions écologiques difficiles bien qu'actuellement ces conditions soient moins restrictives ou vice versa. Des modifications plus ou moins profondes de ces conditions peuvent être uniquement fonction du dynamisme végétal (ou succession écologique) dans les stations adjacentes. Cet aspect peut devenir important car la succession végétale change les conditions géographiques soit par une diminution de la vitesse des vents froids, soit en modifiant l'enneigement dans le temps, ce qui détermine un nouveau seuil de saturation topographique. Par exemple, l'augmentation de la phytomasse d'une station située en amont (dans le sens des vents dominants) d'une station exposée a pour effet de diminuer localement l'influence éolienne et permettre l'installation de formes moins érodées. D'une façon plus générale, des changements dans la distribution des phytomasses modifient la nature de l'enneigement et le degré d'exposition des différents milieux.

Ces considérations nous permettent de penser que la forme en bougeoir est l'expression morphologique d'un milieu fluctuant. Elle est reliée à la probabilité d'apparition du bourgeon apical dans la zone de déflation nivale au cours d'une séquence d'années favorables, elle-même caractérisée par une fréquence et une durée variables d'apparition. Cette situation est commune dans la toundra forestière de latitude et souligne l'importance de l'opportunisme écologique de certaines espèces s'introduisant et se maintenant dans un site microclimatiquement variable. La forme en verticille représente sur ce plan une plus grande probabilité d'apparition conjointe des bourgeons apicaux dans la zone critique et de conditions peu ou pas limitantes au-dessus de la surface de la neige.

Les sections centrale et méridionale de la côte orientale de la baie d'Hudson possèdent un climat forestier. Pour une telle zone, il est moins écologiquement difficile d'obtenir une progression d'une forme à une autre qu'une régression. L'installation d'un individu en bougeoir est fonction d'un certain opportunisme écologique, tandis que l'installation d'un arbre nécessite une

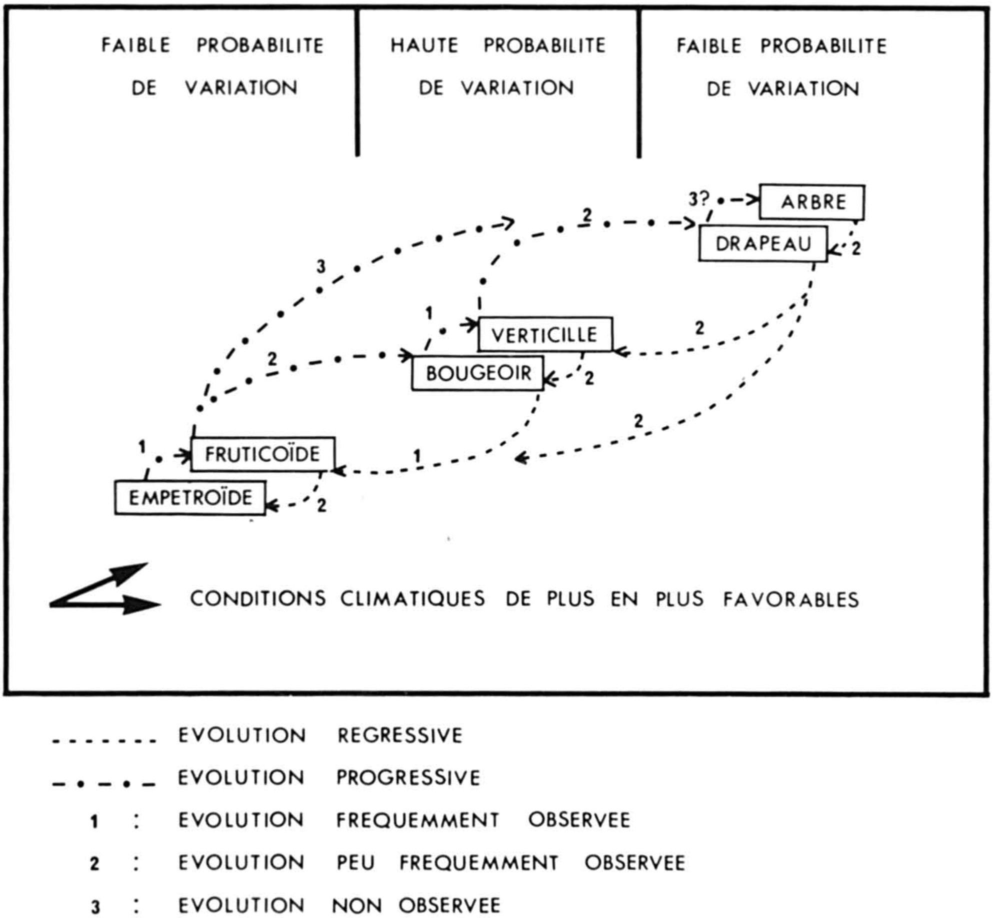

Figure 5. Évolution des formes de croissance en toundra forestière.

certaine régularité et stabilité climatiques pendant plusieurs années. La présence et l'abondance d'individus arborescents dans une région donnée supposent l'existence de conditions climatiques peu fluctuantes par rapport aux conditions climatiques où se retrouvent des plants en bougeoir. Ceci revient à dire qu'il y a plus de chances que la forme en bougeoir évolue vers une forme moins érodée que la forme arborescente vers une forme érodée.

Au-delà de la limite latitudinale ou altitudinale des forêts, la situation a toutes les chances d'être contraire. Dans ce cas, la présence d'une forme arborescente suppose une fluctuation écologique significative de faible fréquence d'apparition, laquelle est soulignée par la faible abondance d'arbres. La régression de cette forme vers une forme fruticoïde a déjà été observée sur le littoral québécois de la baie d'Hudson. Cela permet de penser que la présence d'un arbre devient aussi un cas d'opportunisme écologique.

Conclusion

L'étude des formes de croissance des épinettes met en évidence l'influence de l'hiver sur la végétation de la toundra forestière. Ces formes sont le reflet de conditions climatiques variables dans l'espace et le temps des régions subarctiques et subalpines. De plus, elle souligne l'opportunisme écologique des espèces soumises à des situations limitantes.

L'importance prise par ces formes dans les régions froides exprime, dans une grande mesure, l'impact d'un climat sévère sur la croissance des végétaux. S'il n'a pas été jugé utile de distinguer plus de formes que celles décrites dans ce travail, cela ne signifie en rien que l'on ne puisse pas mettre en évidence un continuum de formes de croissance relié à un continuum climatique au sein de la toundra forestière.

Il serait important de quantifier la signification écologique des formes de croissance au sein des toundras forestières afin de mieux définir cette zone (ou étage) de végétation. Quand il s'agit de problèmes de limites d'aires de régions biologiques et d'espèces, l'opportunisme écologique doit être retenu comme élément d'explication de tout phénomène biologique.

Remerciements

Cette partie d'un travail d'ensemble sur l'écologie de la limite des forêts a été stimulée par le regretté Jacques Rousseau, lors de sa présence au Centre d'Études nordiques de l'Université Laval. M. Pierre Morisset a bien voulu relire et critiquer le manuscrit. M. Francis Boudreau et Mlle Louise Filion ont aussi apporté des remarques pertinentes au cours de l'élaboration de ce travail. Je remercie vivement les organismes suivants qui ont permis la réalisation de cette recherche: Le Programme biologique international, le Service de Conservation du Ministère des terres et forêts du Québec, le Ministère de l'éducation (DGES) du Québec et le Conseil national de recherches (Canada).

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CONTRIBUTIONS TO THE FLORA OF MARINE ALGAE OF EASTERN CANADA, II. FAMILY CHAETOPHORACEAE[1]

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Résumé

L'auteur décrit et illustre les treize espèces (neuf genres) de Chaetophoracées (Chaetophorales) marines qu'on rencontre dans la flore algale de l'est du Canada. Des clefs d'identification sont présentées. Deux taxons qui apparaissaient dans la liste de South et Cardinal (1970) ne sont pas considérés ici ; ce sont *Endoderma (= Ectochaete) cladophorae* et *Ectochaete leptochaete.*

Abstract

Descriptions and original illustrations are provided for the thirteen species (nine genera) of marine Chaetophoraceae, Order Chaetophorales, presently included in the marine algal flora of eastern Canada. Keys to the species are included. Taxa previously included in the Checklist of Marine Algae of Eastern Canada (South and Cardinal, 1970) and omitted from this treatment are *Endoderma (= Ectochaete) cladophorae* and *Ectochaete leptochaete.*

Introduction

The following descriptions, illustrations and keys include the thirteen species of marine Chaetophoraceae, order Chaetophorales presently acceptable in the eastern Canadian benthic flora. The article represents part of a series in which aspects of the marine algal flora of eastern Canada will be considered (South and Cardinal, 1973). As a first step in using this work, reference should be made to the key to the genera of eastern Canadian marine algae given in South and Cardinal (1973).

The work in no way pretends to provide an exhaustive treatment of the eastern Canadian Chaetophoraceae; rather, an attempt is made to give a preliminary assessment of the group. The many gaps in knowledge of taxonomy, ecology, morphological variation and life history will become evident. It is hoped that as a result investigators will be stimulated to undertake the necessary research in the region.

Arrangement

Nomenclature used follows that of South and Cardinal (1970). The author's interpretation of species is based on study of eastern Canadian and northeast American material, together with an extensive survey of literature, standard exsiccatae and herbarium material from numerous sources. A comprehensive system of specimen citation was considered beyond the scope of a work of this type. Further, reference to type material is not included: in many instances type material cannot be traced, or when

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[1] Studies in Biology from Memorial University of Newfoundland, No. 358.

it is available proves to be inadequate for study. A system for placement of critically studied cultures in recognized culture collections should be strongly advocated for the marine Chaetophoraceae, so that material would be readily available to future workers.

Descriptions of genera are omitted. Generic concepts for many of the Chaetophoraceae are in a chaotic state; a review of the author's references, species descriptions and explanatory remarks will guide the reader to the appropriate sources. Descriptions of the species are based on study of eastern Canadian material, with reference to original and subsequent works. The author's location in Newfoundland has resulted in greater familiarity with that Province, and the collections in the Phycological Herbarium, Memorial University of Newfoundland (NFLD) were a frequent source of reference.

The marine Chaetophoraceae present considerable difficulty for the student. Their habit is frequently cryptic and the plants microscopic. Extensive taxonomic confusion in the group has led to a general neglect and there is a great need for monographic treatment. Culture and much more extensive field studies are greatly needed in eastern Canada. The life-history of most is poorly known, if at all, with the exception of selected species in the genera *Acrochaete, Bolbocoleon* and *Pseudopringsheimia.* The distribution of the taxa reported here is probably much broader than indicated. Distributions are based on published records and, when possible, examination of voucher specimens, especially for critical species.

Examination of live material is more or less essential for accurate determination of many of the species included here. Preservation destroys a number of important taxonomic criteria, especially delicate hairs, and reconstitution of herbarium material is unsatisfactory, unless sufficient experience with the group is first obtained.

Order **CHAETOPHORALES**

Family CHAETOPHORACEAE

ACROCHAETE N. Pringsheim, 1863

Type species: *Acrochaete repens* N. Pringsheim, 1863, p. 8, Pl. 2, Figs. 1-9.

Key to eastern Canadian species

1. Plants endophytic in *Fucus*, forming necrotic patches in the host surface tissues; cells with a single pyrenoid, rarely more .... (i) *A. parasitica*
1. Plants endophytic in *Chorda filum, Ralfsia, Laminaria, Leathesia* and other Phaeophyceae; not necessarily forming necrotic patches in the host tissues; cells with 1-5 pyrenoids, usually more than one .... (ii) *A. repens*

(i) *Acrochaete parasitica* Oltmanns 1894, p. 208, Pl. 7, Figs. 1-10;
Edelstein and McLachlan, 1968, p. 996; Edelstein *et al.*, 1970, p. 623; Cardinal, 1968, p. 13; South, 1968, p. 112; 1970, p. 16; South and Cardinal, 1970, p. 2086.

TYPE LOCALITY: Warnemünde, Greenland (in *Fucus vesiculosus* and *F. serratus)* and Egedesminde, Greenland (in *F. inflatus*).

DESCRIPTION (Fig. 1): This species can be found by macroscopic examination of the stipes and "wings" of *Fucus*, where dark necrotic patches are readily observed.

Plants filamentous, richly branched, endophytic in the tissues of *Fucus* species, deeply penetrating the host tissues, including the medullary region; plants impart dark brown colouration to the host surface, the host surface cells regenerating following infection. Cells 8 — 12μ broad, variable in length and thread-like in deeply penetrating filaments; cells containing a dense plate-like chloroplast and usually a single

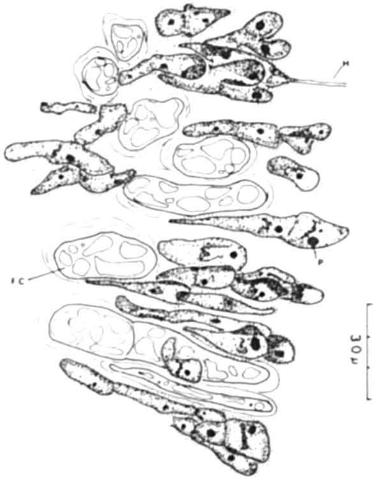

Figure 1. *Acrochaete parasitica* Oltm., endophytic in *Fucus distichus* L. subsp. *distichus*. Drawn from formalin preserved material. Sterile. FC = *Fucus* cell; H = hair; P = pyrenoid. Portugal Cove, Newfoundland, 17 May 1968. [In Herb. NFLD, Wet Stack No. 510].

pyrenoid. Upright branches formed at maturity, projecting slightly above the host surface and terminating in long hyaline hairs or clavate sporangia; mature plants erupting above host surface, the upright filaments aggregated laterally, branched, forming a superficially expanding growth form.

REPRODUCTION AND SEASONAL OCCURRENCE: Sporangia clavate, terminal on upright branches, 10-12μ broad and up to 25μ long; swarmers non-pairing, incompletely studied, reportedly germinating directly to repeat the filamentous phase. Filaments are probably perennial in eastern Canada, in Nova Scotia reproductive in November; specimens studied by the author in Newfoundland from November to May were sterile.

HABITAT: Endophytic or epi-endophytic in the tissues of *Fucus* species, in eastern Canada especially *Fucus distichus* subsp. *distichus* in high intertidal pools, frequently in exposed localities.

DISTRIBUTION: Widely distributed in the northern North Atlantic Ocean, extending further north than *A. repens*. N. E. Coast of North America: Nova Scotia to Newfoundland, Greenland. Eastern Canada: Probably very widely distributed and much commoner than indicated by present published records. Nova Scotia (Bay of Fundy); Newfoundland (Conception Bay; Bonne Bay; Avalon Peninsula).

(ii) *Acrochaete repens* N. Pringsheim 1863, p. 8, Pl. 2, Figs. 1-9;

Huber, 1892a, p. 306, Pl. 13, Figs. 1-7; 1892b, p. 328, Fig. 3a,b; Collins, *et al.*, 1905, No. 1279; Collins, 1906, p. 124; 1909, p. 282. Taylor, 1937, p. 51; 1957, p. 52; Edelstein and McLachlan, 1967, p. 211; South, 1968, p. 102; 1970, p. 17; Cardinal, 1968, p. 13; Hill, 1970, p. 9; South and Cardinal, 1970, p. 2086.

TYPE LOCALITY: Heligoland, in *Chorda filum* and *Leathesia difformis*.

DESCRIPTION (Fig. 2): Plants filamentous, irregularly branched, the prostrate filaments giving rise to upright branches of one-several cells; upright branches ter-

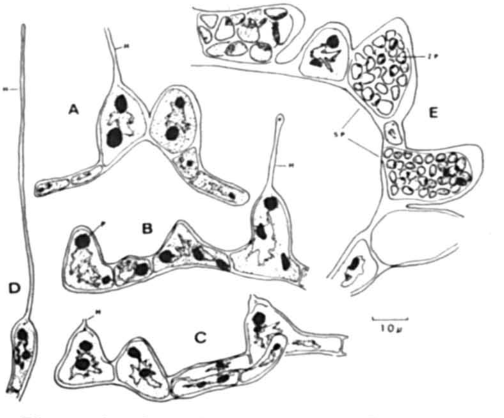

Figure 2. *Acrochaete repens* Pringsh., endophytic in *Chorda filum* (L.) Stackh. (drawn after South, 1968, Figs. 1-8 pp.) A. Part of a vegetative filament, with hair (H). B. Part of a vegetative filament, showing a young hair cell, chloroplast appearance and pyrenoids. C. Part of a vegetative filament showing branching. D. Mature hair, terminating an upright branch. E. Stages in formation of zoospores (ZP) and mature sporangia (SP). Drawn from living material. [B-D from Pomquet Harbour, Nova Scotia, October 1965; A and E from Rhosneigr, Anglesey, U. K., October 1964].

minating in sporangia or fine hairs less than 2.0μ in diam., the latter produced as an extension of the upper cell wall and not from a special hair-bearing cell; hairs also directly from prostrate cells, more rarely; filaments penetrating deeply in host tissues, or more superficial, and aggregated in cushionlike growths; cell shape extremely variable, from contorted threads in deeply penetrating filaments, to rounded cells in more superficial growth; chloroplast parietal, platelike, dark green with 1-3 or 4 pyrenoids; chloroplast occasionally parietal and netlike, when confusion of this species with *Bolbocoleon piliferum* may occur, especially in young *A. repens* which may lack upright branches and hairs. In culture a cushion-like mode of development predominates.

REPRODUCTION AND SEASONAL OCCURRENCE: Sporangia terminal, containing ca. 30 biflagellate swarmers formed by progressive subdivision of the mother-cell contents; swarmers 2.0μ in diameter before release, 2 × 2-3μ when motile, the flagella 3-4 × the length of the body; life history not known, although swarmers reportedly non-pairing, giving rise once more to the filamentous phase; reproduction reaches a peak in winter in Britain (November — April), but known in August in Massachusetts; reproductive period in eastern Canada undefined, but vegetative filaments probably throughout the year.

HABITAT: endophytic and epi-endophytic in the tissues of various Phaeophyceae. In eastern Canada known chiefly from *Chorda filum*, where it frequently occurs with *Bolbocoleon piliferum*; also not uncommon on *Ralfsia*, *Laminaria* (especially the terminal portions of laminae) and *Leathesia*. Elsewhere in its range recorded also from *Spermatochnus*, *Acrothrix* and *Stictyosiphon*.

DISTRIBUTION: Widely distributed in the northern North Atlantic Ocean. N. E. coast of North America: Southern Massachusetts to Newfoundland. Eastern Canada: Nova Scotia (Northumberland Strait); Newfoundland (Alexander Bay; Bonavista Bay).

BOLBOCOLEON N. Pringsheim, 1863.

Type species: *Bolbocoleon piliferum* N. Pringsheim 1863, p. 1-4, Pl. 1, Fig. 1

Bolbocoleon piliferum N. Pringsheim

N. Pringsheim, 1863, p. 1-4, Pl. 1, Fig. 1; Huber, 1892a, p. 308, Pl. 13, Figs. 8-12; 1892b, p. 329, Fig. 4 a-c; Hazen, 1902, p. 227; Collins, 1909, p. 283; Collins et al., 1905, No. 1225; Taylor 1937, p. 52; 1957, p. 52.

MacFarlane and Milligan, 1965, p. 4; Cardinal, 1967a, p. 460; 1967b, p. 30; 1968, p. 14; South, 1968, p. 103; 1969; 1970, p. 16; South and Cardinal, 1970, p. 2086; Lee, 1969, p. 140; Edelstein *et al.*, 1970, p. 623; McLachlan and Edelstein, 1971, p. 21.

TYPE LOCALITY: Heligoland.

DESCRIPTION (Fig. 3): Plants filamentous, prostrate; creeping superficially on a variety of marine Phaeophyceae and Rhodophyceae; branching irregular and cell division principally in the terminal region of the filaments; upright system reduced to bulb-shaped hair-bearing cells which give rise to hairs, the hair-bearing cells seldom separated from the prostrate system by a further division; hairs sometimes borne in dense clusters.

Hairs robust, brittle, up to 2.5μ in diameter and not sheathed except when injury to the original hair occurs and a new hair arises from the open base of the old; hairs only exceptionally arising directly from a cell of the prostrate system; old hairs frequently golden-brown in colour at the base.

Prostate cells up to 15.0μ broad and 50.0μ long, very variable in size and shape and frequently with a characteristic pouch-like dorsal protuberance;

chloroplast of the prostrate cells parietal and in the form of a network, with one to ten conspicuous pyrenoids; chloroplast of the hair-bearing cells generally plate-like, with one to two pyrenoids (Fig. 3).

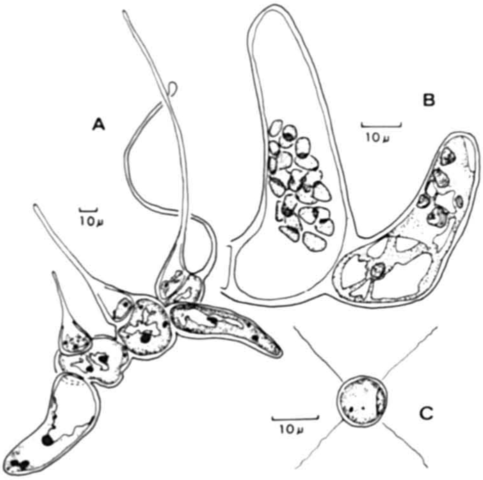

Figure 3. *Bolbocoleon piliferum* Pringsh. (drawn after South, 1968, Figs. 26-45 pp.). A. Vegetative filament with three hair cells and hairs. B. Mature zoosporangium with zoospores and mature vegetative cell showing dorsal protuberance, reticulate chloroplast and conspicuous pyrenoids. C. Zoospore after settlement and prior to casting off flagella. Based on British material.

REPRODUCTION AND SEASONAL OCCURRENCE: Sporangia formed from modified prostrate cells by an upward extension of the pouch-like outgrowth of the mother cell; up to thirty quadriflagellate swarmers produced by successive division of the mother cell contents; swarmers 8.3µ × 3.4-3.5µ, and 4.5µ in diam. when settled, containing a chloroplast, eyespot and at least one pyrenoid. Reproduction known in detail only from culture. Swarmers asexual and formed mitotically in sporangia (Moestrup, 1969). The chromosome number has been given as $n = 8$ (Moestrup, 1969) or $n = 11$ (Kermarrec, 1970). In culture, swarmers are non-pairing and germinate into self replicating, apparently asexual generations; two forms of the parent type occur, one "normal" with hair cells and hairs, the other "reduced" and highly reproductive, with few hair cells or hairs; quadriflagellate swarmers produced from the first generation of either type germinate once more into culture forms of either type. Moestrup (1969) attributes the more "normal" hair-bearing form to relatively poor availability of nutrients in culture; richer conditions cause a reduction in the abundance of hair cells and hairs. In eastern Canada probably occurs in a vegetative condition throughout the year; probably also reproductive at all times of year, but more so in winter.

HABITAT: Endo- or epiphytic on numerous species of loosely constructed Phaeophyceae or Rhodophyceae, but especially in the tissues of *Chorda filum*. Tolerant of a wide variety of conditions of exposure, depth and salinity.

DISTRIBUTION: Widely distributed in the North Atlantic Ocean. N. E. coast of North America: Long Island, Rhode Island, Maine to Newfoundland. Eastern Canada: Québec (Chaleur Bay; Magdalen Islands); Nova Scotia ((Bay of Fundy; Bras d'Or Lake); Newfoundland (south and east coasts).

ECTOCHAETE (Huber) Wille, 1909

Type species: *Ectochaete leptochaete* (Huber) Wille, 1909, p. 79.

Huber, 1892a, p. 326; Kylin, 1938, p. 71; Moevus, 1949, p. 309; Waern, 1952, p. 51; Pankow, 1971, p. 101.

On the basis of published information, three taxa could be included in this genus in eastern Canada: *E. cladophorae* (Hornby) Pankow, *E. leptochaete* (Huber) Wille and *E. wittrockii* (Wille) Kylin. Circumscription of the genus is vague, and there is considerable confusion at the species level on important taxonomic criteria, such as the presence or absence of hairs, the form of the chloroplasts, the number of pyrenoids, and the mode of growth. The similarity of *Ectochaete* to the non hair-bearing endophytic threads such as *Entocladia* or *Endoderma* sensu lato further compounds the confusion, a matter fully discussed in Waern (1952).

E. cladophorae has been reported only once from eastern Canada, from Nova Scotia (Edelstein and McLachlan, 1969; South and Cardinal, 1970; both as? *Endoderma*? *cladophorae* Hornby.) Waern (1952) emphasied the difficulty of identifying this species accurately; his discovery of hairs on Baltic material led Pankow (1971) to transfer it to *Ectochaete*. The single eastern Canadian record of *E. leptochaete* (South and Cardinal, 1970) is from Nova Scotia. Reexamination of the Nova Scotia specimens (Atlantic Regional Laboratory No. 2809) by Drs. Edelstein and McLachlan and the present author has led to the mutual conclusion that the specimens should be referred to *E. wittrockii*. *E. wittrockii*-like specimens are by far the most commonly encountered members of this genus in eastern Canada. Although Waern (1952) stated (p. 52)... "It is at present not possible to identify *E. wittrockii* from the pictures and descriptions available", and although there is presently a paucity of records from eastern Canada to clarify the situation, the genus will be included here, represented by a single species, *E. wittrockii*.

Ectochaete wittrockii (Wille) Kylin 1938, p. 72

Synonymy: *Entocladia wittrockii* Wille 1800, p. 1; *Endoderma wittrockii* (Wille) Lagerheim 1883, p. 75.

Hansgirg, 1888; Huber, 1892a, p. 326; Collins *et al.*, 1897, No. 265; 1908, No. 1469; Collins, 1909, p. 279 (all as *Endoderma wittrockii);* Taylor, 1937, p. 53; 1957, p. 54 (as *Entocladia wittrockii*); Kylin, 1938, p. 75; Waern, 1952, p. 51.

Cardinal, 1967a, p. 461; 1967b, p. 30; 1968, p. 27, p. 39 (as *Entocladia wittrockii*); Edelstein and McLachlan, 1967, p. 213 (as *Entocladia wittrockii*); 1968, p. 997; Mathieson *et al.*, 1969, p. 117; South, 1970, p. 17; South and Cardinal, 1970, p. 2086 (including their *Ectochaete leptochaete*).

DESCRIPTION (Figs. 4, 5): (the following description will require revision following detailed study of eastern Canadian *E. wittrockii*).

Plants filamentous, entirely prostrate, the filaments simple or more generally irregularly branched; cells cylindrical, 5-10μ diam. × 1-1.5 diam. long; terminal cells tapering, to 6.0μ diam., up to 26μ long; chloroplast parietal, containing a single pyrenoid, hairs present or absent, not on every cell and fine, 2.0μ diam., produced directly as an extension of the hair-bearing cell wall; a common epi-endophyte possibly referrable to *E. wittrockii* and frequently encountered in Newfoundland generally lacks hairs.

REPRODUCTION AND SEASONAL OCCURRENCE: Kylin (1938) described some unusual

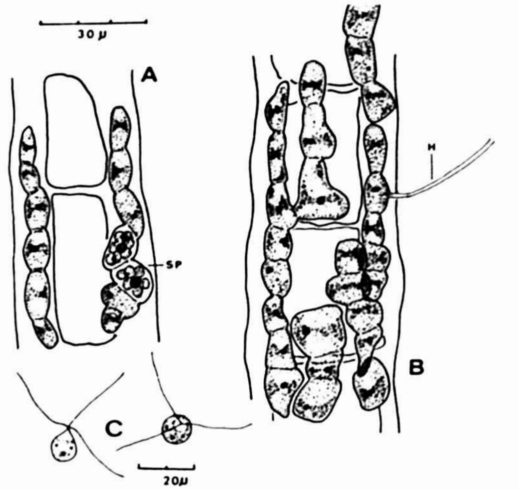

Figure 4. *Ectochaete wittrockii* (Wille) Kylin *sensu lato*. A. Fertile filament showing sporangia (SP) containing ca. 8 zoospores. Malet Hill, Rhode Island (drawn from reconstituted material, UC 97935. Coll. W. A. Setchell, 9 July 1889). Growing in *Elachista fucicola*. Compare with Figure 5A. B. Sterile filaments from same collection as A, showing branching pattern and a single hair (H). C. Triflagellate zoospores, redrawn from Kylin (1938, Fig. 4, B, C.).

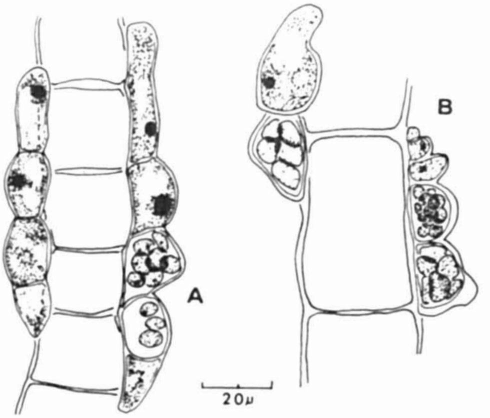

Figure 5. *?Ectochaete wittrockii* (Wille) Kylin *sensu lato*. A and B. Fertile specimens lacking hairs and on *Pilayella littoralis*. The larger cell size than shown in Figure 4 is a result of using living rather than reconstituted specimens. English Bay, Newfoundland. 5 May 1972 [In Herb. NFLD, No. 9084a], from living material.

features of reproduction in *E. wittrockii* from Scandinavia. Sporangia formed from any vegetative cell, ca. 16 zoospores per cell; zoospores 4.6-5.2 × 5,8-6.5μ, containing a single pyrenoid and chloroplast and two eyespots; zoospores tri-flagellate, the flagella 2-2.5 × the length of the zoospore; zoospores germinate to form a single sporangium measuring 15 × 20μ, this subdividing to form 16-32 zoospores, these similar to the original zoospores, with three flagella and two eyespots; Kylin (1938) did not follow the further development of these zoospores. Eastern Canadian (especially Newfoundland) material referred to *E. wittrockii* normally produces ca. 8 zoospores in the filamentous phase found in the field, these not as yet critically examined in the laboratory; Kylin's observations require substantiation in our material; the single celled zoosporangium described by him has not been discovered anywhere in the field to date. In Eastern Canada *E. wittrockii* sensu lato has been recorded in most months, although most commonly in summer and autumn; fertile plants occur predominantly in summer.

HABITAT: In the cell walls of various filamentous Phaeophyceae, in eastern Canada especially of *Elachista fucicola*, *Pilayella littoralis* and *Ectocarpus* spp., occasionally *Sphacelaria*. In other parts of its range known from *Desmotrichum* and *Cladophora*. The hairless variety described from Newfoundland (above) has a more superficial growth on the host. In exposed and sheltered localities in the lower intertidal and upper subtidal zones, not infrequently in areas subjected to reduced or fluctuating salinity.

DISTRIBUTION: Common in the eastern and western North Atlantic Ocean. N. E. coast of North America: Connecticut, Maine to Newfoundland. Eastern Canada: Québec (Malbaie; Magdalen Islands); Nova Scotia (Atlantic Coast); Newfoundland (widely distributed, including the south coast, Bonavista Bay, Bonne Bay, Fortune Bay).

ENTOCLADIA Reinke 1879

Type species: *Entocladia viridis* Reinke, 1879, p. 476, Pl. 6, Figs. 1-9.

Wille, 1890, p. 94, Fig. 57 (as *Entoderma*); Huber, 1892a, p. 313-326, Pls. 14, 15 (as *Endoderma*); Collins, 1909, p. 279 (as *Endoderma*).

The confusion between *Entocladia* and *Ectochaete* has already been referred to under *Ectochaete*. Of the two eastern Canadian species of *Entocladia* considered here, *E. perforans* and *E. viridis*, the status of the former is especially dubious in our area. Wilkinson and Burrows (1972 a, b) regard *E. perforans* as a common shell-boring species in Britain, likely to be confused with *Gomontia polyrhiza* (Lagerh.) Born. et Flah., along with several other minute, filamentous forms. Although their study is the first to describe *E. perforans* from shells, Anand (1937) had earlier reported it as a chalk-boring species in British chalk cliffs. Wilkinson and Burrows (1972a) did remark on the similar shell-boring species *E. tenuis* and *E. testarum* reported by Kylin (1935), but regarded their material as closer to *E. perforans.*

A shell- or chalk-boring habit has yet to be described for eastern Canadian *E. perforans. E. perforans sensu stricto* is a *Zostera* inhabiting species. Only by detailed comparative studies will it be possible to determine whether the *Zostera* inhabiting and chalk/shell-boring forms are a single or two different species.

Key to eastern Canadian species

1. In the leaves of dead or dying *Zostera* .... (i) *E. perforans*

1. In marine algae .... (ii) *E. viridis*

(i) *Entocladia perforans* (Huber) Levring, 1937, p. 26

Synonymy: *Endoderma perforans* Huber, 1892a, p.316.

Collins, 1909, p. 279; Collins *et al.*, 1910, No. 1625 (both as *Endoderma perforans*); Taylor, 1937, p. 53 (as *Endoderma perforans);* 1957, p. 54.

Cardinal, 1968, p. 39; Cardinal and Villalard, 1971, p. 894; Edelstein and McLachlan, 1967, p. 213; South and Cardinal, 1970, p. 2086.

TYPE LOCALITY: Golfe du Lion, France.

DESCRIPTION (Fig. 6): Plants filamentous, prostrate, endophytic, richly branched, often rather pale green in colour, lacking hairs; in dead and decaying *Zostera.* Filaments free, not aggregated into disciform structures; frequently ramifying the substrate between the lower and upper epidermal layers, or cells inside dead *Zostera* cells; cell shape very variable, cells 3-7μ diam. in superficial growths, or up to 14μ diam. in inner regions of the host; cells often swollen, or thread-like in penetrating filaments; cells with a single pyrenoid and nucleus, chloroplast parietal.

REPRODUCTION AND SEASONAL OCCURRENCE: sporangia enlarged vegetative cells, forming 8 quadri-flagellate zoospores; zoospores ovoid-spherical, with a conspicuous eyespot and a posterior chloroplast. According to Huber (1892a) germination of the zoospores results in reinstatement of the filamentous phase. Seasonal occurrence in eastern Canada not fully known, but reported in a reproductive condition in April in Nova Scotia. Known in a vegetative condition in July in the St. Lawrence Estuary and in Bonavista Bay, Newfoundland. Pankow (1971) reported sporangia throughout the year in the Baltic, but noted that reproductive plants were especially abundant in the spring.

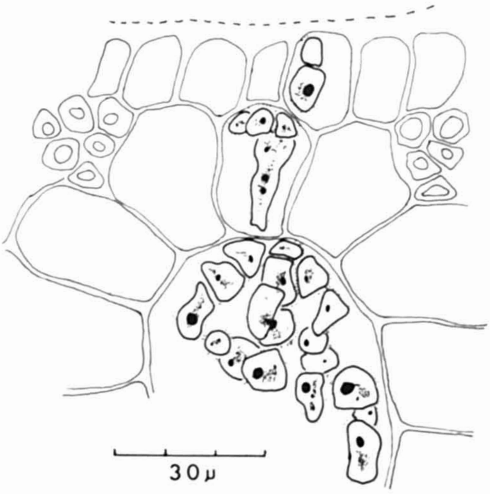

Figure 6. *Entocladia perforans* (Huber) Levr. in *Zostera marina* L., sterile. Terra Nova National Park Wharf, Newman Sound, Bonavista Bay, Newfoundland, 10 July 1972. [In Herb. NFLD, No. 9619]. Drawn from living material.

The shell-boring filaments attributed to this species by Wilkinson and Burrows (1972 a, b) were collected throughout most of the year in Britain, although no reproductive period was stated.

HABITAT: In dead or dying *Zostera* leaves, especially in sheltered areas with reduced or fluctuating salinity. Best observed on the bleached portions of the host leaves, where a number of other small epiphytic species will be found.

DISTRIBUTION: Known from Europe and the North Atlantic Ocean; N. E. Coast of North America: Massachusetts to Newfoundland. Eastern Canada: seemingly a scarce species, although careful searching would probably indicate a much wider distribution than indicated here. Québec (St. Lawrence Estuary); Nova Scotia (Pomquet Harbour, Antigonish County); Newfoundland (Alexander Bay, Bonavista Bay.)

(ii) *Entocladia viridis* Reinke, 1879 (loc. cit.)

Synonymy: *Endoderma viride* (Reinke) Lagerheim, 1883, p. 74.

Collins, 1909, p. 279; Collins *et al.*, 1910, No. 1626; 1915, No. 2006; 1917, No. 2236 (all as *Endoderma viride*); Taylor, 1937, p. 53; 1957, p. 54, Pl. 2, Figs. 1-2.

Cardinal 1967b, p. 461; 1968, p. 39; Cardinal and Villalard, 1971, p. 894; Edelstein and McLachlan, 1966, p. 1046; Edelstein *et al.*, 1970, p. 623; South, 1971, p. 1029; South and Cardinal, 1970, p. 2086.

TYPE LOCALITY: Naples.

DESCRIPTION (Fig. 7): Plants endophytic in various algae, lacking hairs; filamentous, profusely branched, the thalli only rarely forming a pseudoparenchyma centrally; cells variable in size, often irregular, the terminal cells blunt or tapering; cells 3-6μ × 5-10μ in diam., usually 1-6 diam. long; cells with a single pyrenoid, uninucleate, with a parietal chloroplast.
The delimitations of this poorly circumscribed species are at best vague.

REPRODUCTION AND SEASONAL OCCURRENCE: Asexual reproduction reportedly by quadriflagellate zoospores formed in enlarged (up to 20 × 40μ) intercalary cells; sexual reproduction reportedly by biflagellate gametes, incompletely described. Probably occurs in a vegetative state throughout the year in eastern Canada.

HABITAT: On the thallus of various algae, especially Rhodophyceae; hosts in in eastern Canada include *Halosaccion ramentaceum* (L.) J. Ag., *Phycodrys rubens* (L.) Batt., *Membranoptera alata* (Huds.) Stackh., and *Turnerella pennyi* (Harv.) Schmitz. Occurs over a wide range of depths, from the upper subtidal zone to more than 30 m subtidally, in moderately exposed to exposed localities.

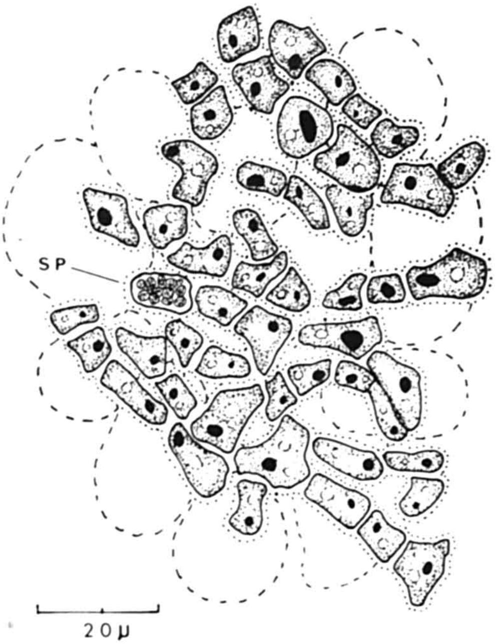

Figure 7. *Entocladia viridis* Reinke on *Membranoptera alata*, Bellevue, Trinity Bay, Newfounland, 13 November 1969 [In Herb. NFLD, No. 5345a]. Drawn from formalin preserved material. A sporangium (SP) and the variable shape and size of the pyrenoids are evident. The nuclear region is often conspicuous in cells of this species.

DISTRIBUTION: Widely distributed in the North Atlantic Ocean. N. E. coast of North America: Bermuda, Florida, North Carolina, Massachusetts, to Newfoundland. Eastern Canada: Québec (St. Lawrence Estuary; Chaleur Bay); Nova Scotia (Atlantic Coast and Bay of Fundy); Newfoundland (Avalon Peninsula).

EPICLADIA Reinke, 1889a

Reinke, 1889b, p. 31; Hazen, 1902, p. 225; Kylin 1938, p. 70

Type species: *Epicladia flustrae* Reinke (loc. cit.).

Epicladia flustrae Reinke

Synonymy: *Endoderma flustrae* Batters, 1902, p. 14.

Entocladia flustrae (Reinke) Batters (*in* Taylor 1937, p. 54).

Collins *et al.*, 1896, No. 160; Collins, 1909, p. 287, fig. 94; Taylor 1937, p. 54; 1957, p. 55 (all as *Entocladia flustrae*).

Wilce, 1959, p. 65; Edelstein and McLachlan, 1966; Cardinal, 1967a, p. 461; 1967b, p. 30 (as *Entocladia flustrae*); 1968, p. 38 (as *Entocladia flustrae);* p. 39; Cardinal and Villalard, 1971, p. 894; South, 1970, p. 17; 1968-71.

TYPE LOCALITY: west Baltic Sea.

DESCRIPTION (Fig. 8): Plants epizoic, or endozoic on or in the surface of Bryozoa; of irregularly and densely branched postrate filaments lacking upright branches; centrally, forming a pseudoparenchyma of irregularly polygonal cells 7-12 (20)μ in diam.; marginally, of free, radiating prostrate filaments, cylindrical, 5-10μ diam., becoming broaer terminally; chloroplast dense parietal, non-perforate, with a single pyrenoid; hairs lacking.

REPRODUCTION AND SEASONAL PERIODICITY: vegetative stage known throughout the year in Europe; probably perennial in eastern Canada, although collections to date known only from February — July. Reproduction not fully described: numerous zoospores (gametes?) formed in the vegetative cells, released from a round pore in the sporangium wall. Only sterile plants known from eastern Canada: Lund (1959) reported fertile plants in July from Greenland.

HABITAT: Readily observed on epiphytic Bryozoa, to which it imparts a dark green colouration in contrast to the normal whitish or yellowish appearance of the host. According to Levring (1937) the outer membrane of the Bryozoa is penetrated by *E. flustrae* filaments, in addition to their usual superficial habit.

Figure 8. *Epicladia flustrae* Reinke on a Sertularian. Harbour Mille, Fortune Bay, Newfoundland, 15 March 1971 [In Herb. NFLD, No. 5338]. Drawn from living material. Portion of a plant showing the smaller-celled pseudoparenchymatous central region and the larger-celled, branched, filamentous marginal region.

DISTRIBUTION: Common on the Atlantic coasts of Europe, including the Baltic Sea, and of North America. N. E. coast of North America: New York to Labrador, and east and west Greenland. Eastern Canada: Nova Scotia (Atlantic Coast); New Brunswick (Bay of Fundy); Québec (Chaleur Bay; St. Lawrence Estuary); Newfoundland (Fortune Bay, Conception Bay; Bonne Bay).

OCHLOCHAETE Thwaites *ex* Harvey, 1849, Pl. 226. Waern, 1952, p. 59.

Type species: *Ochlochaete hystrix* Thwaites *ex* Harvey, 1849, *(loc. cit.).*

Ochlochaete ferox Huber, 1892a, p. 292, Pl. 11, Figs. 1-3.

Synonymy: ? *Chaetobolos gibbus* Rosenvinge, 1893, p. 928: according to Waern, 1952, this species could well be synonymised with *O. ferox,* although the synonymy was not officially made by him.

Rosenvinge, 1893, p. 931; Collins *et al.*, 1908, No. 1521; Collins, 1908, p. 157; 1909, p. 285, Fig. 92; Taylor, 1937, p. 55; 1957, p. 56; Waern, 1952, p. 59, fig. 27.

Cardinal, 1967a, p. 461, fig. 1; 1968, p. 43; Edelstein and McLachlan, 1968, p. 997, figs 35-37; Edelstein *et al.*, 1970, p. 623; South, 1971, p. 1029; South and Cardinal, 1970, p. 2086.

TYPE LOCALITY: Croisic, France.

DESCRIPTION (Fig. 9): Plants regular, disc-like, or tending to irregular, the disc marginally filamentous, centrally pseudoparenchymatous, usually at most two-layered; cells rounded or angular centrally, up to 30 μ diam., marginally more elongate, 3.5-7.5 μ diam.; hairs numerous or sparse, open, aseptate and borne singly as continuations of vegetative cells, very conspicuous; chloroplast parietal, with irregular lobes projecting inwardly and with one, rarely two pyrenoids, or cell contents granular.

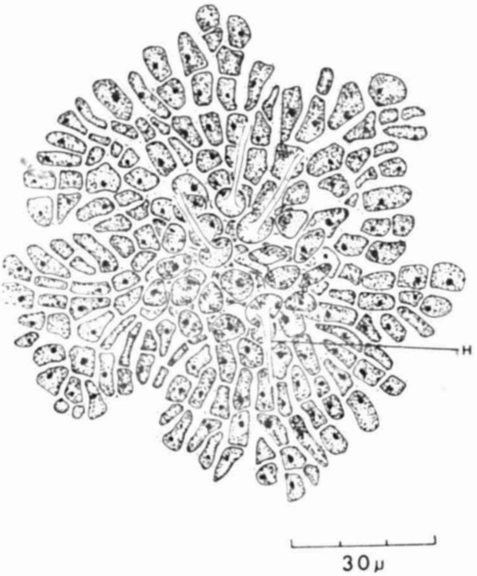

Figure 9. *Ochlochaete ferox* Huber. Drawn from reconstituted material of Collins *et al.*, 1908, No. 1521. [In Herb. NY]. On *Zostera*, "Salt Pond", Eastham, Massachusetts, 16 August 1908, F. S. Collins. Hairs (H) are poorly reconstituted in this material, but serve as an important distinction between this species and *Pringsheimiella scutata*, with which it frequently occurs on the same host.

Waern (1952) presents considerable evidence to suggest that *O. hystrix* and *O. ferox* might represent one and the same species. The epilithic habit of the latter in the Baltic throws some doubt on the validity of *O. lentiformis* Huber, known from southern Massachusetts (Taylor, 1957) a species frequently distinguished from *O. ferox* by its occurrence on stones and shells rather than as an epiphyte.

REPRODUCTION AND SEASONAL OCCURRENCE: Up to 20-30 quadriflagellate zoospores formed in central cells of the disc, the sporangia up to 30 μ diam.; zoospores reportedly germinate immediately to re-instate the vegetative disc phase; vegetative plants found throughout the year in some regions, but in North America apparently a summer species; in eastern Canada reported in September and January.

HABITAT: Epiphytic, especially on *Zostera*. Other hosts recorded include *Cladophora*, *Chaetomorpha*, *Polysiphonia*, *Gloiosiphonia*, *Vaucheria*, *Stictyosiphon*, *Pseudolithoderma* and, in the Baltic sea, various aquatic phanerogams. Reported by Waern (1952) as a common element of the epilithic flora in the Baltic, but to date not reported as a lithophyte under this name in eastern Canada.

DISTRIBUTION: Widely distributed in the North Atlantic Ocean. N. E. coast of North America: Southern Massachusetts to Newfoundland, Greenland. Eastern Canada: Uncommon, recorded from Québec (Chaleur Bay); Nova Scotia (Bay of Fundy; Northumberland Strait); Newfoundland (Fortune Bay).

PHAEOPHILA Hauck, 1876, p. 57, Fig. 1.

Type species: *Phaeophila dendroides* (Crouan frat.) Batt.

Phaeophila dendroides (Crouan frat.) Batters, 1902, p. 13

Synonymy: *Ochlochaete dendroides* Crouan and Crouan, 1867, p. 128, Pl. 8, fig. 59.
Phaeophila floridearum Hauck, 1876, p. 57, fig. 1.
Hauck, 1885, p. 464, fig. 200; Huber, 1892a, p. 290; Collins, 1918, p. 73, fig. 23; Taylor, 1928, p. 58, Pl. 3 figs. 4-6; 1937, p. 51 (all as *P. floridearum*); 1957, p. 51, Pl. 2, figs. 4-5; 1961, p. 48, Pl. 2, fig. 4. Edelstein and McLachlan, 1967, p. 214, figs. 5-6; Cardinal, 1968, p. 44; South and Cardinal, 1970, p. 2086.

TYPE LOCALITY: Brest.

DESCRIPTION (Fig. 10): Plants epi- or endophytic, entirely prostrate, filamentous, non-pseudoparenchymatous, irregularly or much branched; cells cylindrical or irregular, 9-40μ diam., 15-50μ long, containing a lobed, parietal chloroplast with one-several pyrenoids; cells frequently bearing one-three aseptate, inarticulate processes or hairs, the bases often spirally twisted; hairs neither separated from the supporting cell, nor swollen basally.

REPRODUCTION AND SEASONAL OCCURRENCE: Reproduction by numerous zoospores, borne in regularly or irregularly swollen intercalary or terminal zoosporangia; zoospores quadriflagellate, $5 \times 12.5\mu$. In eastern Canada plants found only in February, and sterile.

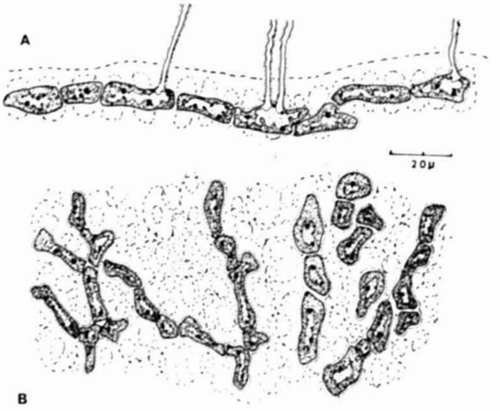

Figure 10. *Phaeophila dendroides* (Crouan frat.) Batt. Drawn from UC 98142, Coll. W. A. Setchell No. 824, Woods Hole, Massachusetts; in *Agardhiella tenera*. Sectional (A) and surface (B) views are shown. Cell size is considerably reduced here, owing to reconstitution of dried material — consult text for sizes of living cells.

HABITAT: creeping superficially between or on the cells of loosely constructed larger algae, Chlorophyceae, Phaeophyceae or Rhodophyceae being recorded as hosts elsewhere in the species' range; intertidal to the subtidal; reported from *Gracilaria* in eastern Canada.

DISTRIBUTION: widely distributed in the North Atlantic Ocean. N. E. coast of North America: Bermuda to Nova Scotia. Eastern Canada: seemingly very rare, with only a single record, from Pomquet Harbour, Antigonish, Nova Scotia.

PRINSHEIMIELLA Höhnel, 1920, p. 97

Type species: *Pringsheimiella scutata* (Reinke) Marchewianka 1924, p. 42.

Pringsheimiella scutata (Reinke) Marchew.

Synonymy: *Pringsheimia scutata* Reinke, 1889a, p. 33, Pl. 25.
Pringsheimiella scutata (Reinke) Schmidt et Petrak *in* Schmidt, 1935, p. 29.
Reinke, 1889b, p. 81; Huber, 1892a, p. 294; Collins *et al.*, 1908, No 1524; Collins, 1909, p. 288, fig. 95; Printz, 1926 p. 242, Pl. 6, figs. 58-61; Taylor, 1937, p. 56 (all as *Pringsheimia scutata*); 1957, p. 57; Waern, 1952, p. 62; Lund, 1959, p. 28.
Wilce, 1959, p. 65; Colinvaux, 1959, p. 11; MacFarlane and Milligan, 1965, p. 4; Edelstein and McLachlan, 1966, p. 1046; Edelstein *et al.*, 1970, p. 623; Cardinal, 1968, p. 45; Cardinal and Villalard, 1971, p. 894; Mathieson *et al.*, 1969, p. 117; South, 1970, p. 17; 1968-71, No. 82; South and Cardinal, 1970, p. 2086; Wille, 1901, p. 29, pl. 3, figs. 101-134.

TYPE LOCALITY: Baltic Sea (?Kiel).

DESCRIPTION (Fig. 11): Plants disc-like, filamentous, the filaments aggregated to form a single-layered cushion 0.1-0.2mm diam., with marginal growth; central cells longer than broad, up to 12μ diam.; marginal cells elongate, the filaments laterally branched, tending to dichotomous; chloroplast dense, parietal, containing a single pyrenoid. The presence of fine hairs on some plants was

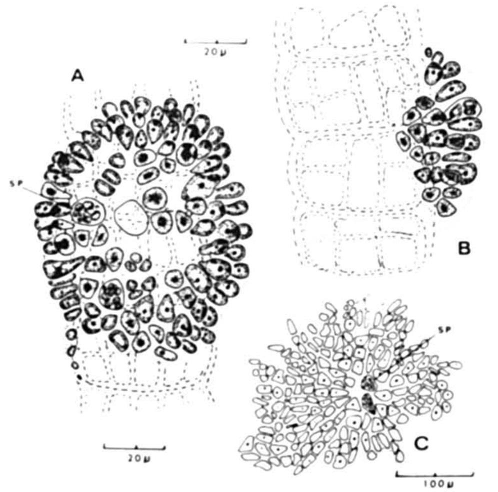

Figure 11. *Pringsheimella scutata* (Reinke) Marchew. A. Mature fertile specimen on *Sphacelaria*, showing a ripe sporangium (SP) adjacent to an emptied sporangium. Cells shown in surface and side views; drawn from slide-preserved material. Cobbler's Beach, Terra Nova National Park, Bonavista Bay, Newfoundland, 21 March 1969. [In Herb. NFLD, No. 3747a]. B. Less mature speciment than A, same host and collection. A partially formed sporangium is present. C. Reconstituted specimen, surface view, from Massachusetts. ALG. BOR. AM. No. 183, Coll. W. A. Setchell, 21 July 1890. [In Herb. NY].

reported by Reinke (1889b) although these were not shown in his figures. Huber (1892a) remarked that hairs might be formed only under certain conditions and Printz (1926) detected fine hairs on material from the Trondheimfjord in spring, although again they were not illustrated. Experience with this species in eastern Canada indicates that hairs are always lacking; the possibility, however, of confusing a sterile specimen with fine hairs with a young *Ochlochaete ferox* should not be overlooked. Huber (1892a) earlier suggested that the presence of a common membrane around the disc of *P. scutata* might be a distinguishing feature, but on asexual specimens only.

REPRODUCTION AND SEASONAL OCCURRENCE: Reinke (1889b) indicated the existence of both sexual and asexual generations, morphologically distinct. Kylin (1949) suggested that the two stages might represent distinct species. Asexual plants are more compact, with gelatinously thickened external walls, the central cells producing numerous quadriflagellate zoospores, measuring 8 × 15μ, the zoosporangia measuring 28-38μ tall. Sexual plants are more diffuse, with intercellular spaces and walls of equal thickness, the central gametangia producing 16-32 biflagellate (not quadriflagellate as in Taylor 1957) gametes measuring 3 × 4μ, the gametangia 13-18μ diam. Gametes copulate after liberation through an apical pore in the gametangial cell membrane; further development of the quadriflagellate zygote is not known.

In eastern Canada the species is known throughout the year; to date only the asexual phase has been reported. According to detailed observations on the species by Printz (1926) in the Trondheimfjord, vegetative growth commences in February and is rapid; in the autumn numerous gametangia are produced, and from then on numerous young individuals are in evidence. Observations on the species in Newfoundland suggest that a comparable seasonal cycle occurs, but only for asexual plants.

HABITAT: on various filamentous algae, or *Zostera;* subtidal, usually in rather protected, shallow locations.

DISTRIBUTION: Widely distributed in the northern Atlantic Ocean. N. E. coast of North America: Bermuda to Labrador and Greenland. Eastern Canada: Probably widely distributed throughout the area, except for the St. Lawrence estuary. Recorded from New Brunswick, Nova Scotia, Newfoundland and Labrador.

PSEUDENDOCLONIUM Wille, 1901, p. 29, Pl. 3, Figs. 101-134.

Type species: *Pseudendoclonium sub-*

marinum Wille, 1901 ; Wille, 1910, p. 282, Pl. 1, figs. 1-9.

Pseudendoclonium submarinum Wille

Synonymy: *Protoderma marinum* Reinke. 1889b. p. 81.

Pseudendoclonium marinum (Reinke) Aleem et Schulz, 1952, p. 72, fig. 5, a-c.

Collins, 1909, p. 284, fig. 87; Collins *et al.*, 1903, No. 1124 (both as *Protoderma marinum*); Waern, 1952, p. 49; Lund, 1959, p. 26; Pankow, 1971, p. 97; Taylor, 1937, p. 56; 1957, p. 58 (both as *Protoderma marinum);* MacFarlane and Milligan, 1965, p. 4 (as *Protoderma marinum);* Edelstein and McLachlan, 1966, p. 1046 (as *Protoderma marinum*); 1967, p. 214; Cardinal, 1967a, p. 462; 1968, p. 45 (as *Protoderma marinum*), p. 46 (including *Pseudendoclonium marinum)*; Cardinal and Villalard, 1971, p. 894; Mathieson *et al.*, 1969, p. 118 (as *Pseudendoclonium marinum*); South, 1970, p. 17; South and Cardinal, 1970, p. 2086; South and Steele, 1971, p. 32.

TYPE LOCALITY: Kiel Harbour.

DESCRIPTION (Fig. 12); Plants subparenchymatous, crustose, forming spreading monostromatic patches, occasionally more than one cell thick centrally; margins of short, radiating filaments, hairs entirely lacking; cells irregular in shape and centrally rather angular, 6-12μ diam.; marginally more elongate, the apices rounded; cells containing a dense parietal chloroplast and usually a single pyrenoid, or in older specimens cell contents granular, pyrenoid indistinct.

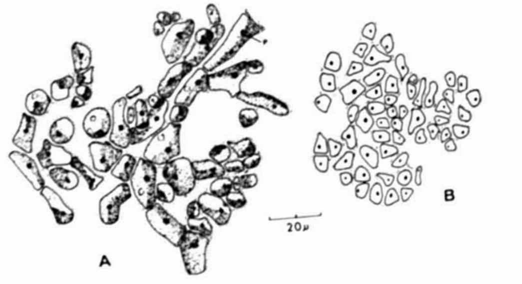

Figure 12. *Pseudendoclonium submarinum* Wille. A. Marginal region of plant with open branching, larger cells. B. Central portion of crust showing smaller cells and pseudoparenchymatous habit. Drawn from living material. [In Herb. NFLD].

REPRODUCTION AND SEASONAL OCCURRENCE: Reproduction by bi-flagellate zoospores, 4-8 in each cell, the sporangia developing from vegetative cells with little modification; aplanospores also reported; present throughout the year in eastern Canada, although reproductive periodicity not yet defined.

HABITAT: encrusting rocks, pebbles or dead shells; predominantly intertidal and especially abundant in rather protected estuarine habitats where it occurs together with encrusting Cyanophyceae and Phaeophyceae.

DISTRIBUTION: Abundant throughout the North Atlantic Ocean and an important encrusting species in the Baltic Sea. N. E. coast of North America: Florida to Newfoundland and Greenland. Eastern Canada: Québec (Chaleur Bay, St. Lawrence Estuary); New Brunswick (Bay of Fundy); Nova Scotia (Bay of Fundy and Atlantic Coast); Newfoundland (south coast and Bonavista Bay). Probably more widely distributed than indicated here, doubtless extending northwards to Labrador.

PSEUDOPRINGSHEIMA Wille, 1909, p. 89[1]

Type species: *Pseudopringsheimia confluens* (Rosenv.) Wille.

Key to eastern Canadian species

1. Thallus cushion-like, the cushions not confluent; somewhat gelatin-

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[1] In a study of the circumscription of the genus *Ulvella* (Crouan and Crouan, 1859), Papenfuss (1962) outlined the difficulties of determining the differences, if any, among *Ulvella*, *Pseudopringsheimia* and *Pseudulvella*. The problems cannot be resolved until the life history of *Ulvella lens*, the type of the oldest genus in the complex, has been worked out. The number of flagella on the zoospores is critical. For *Pseudopringsheimia confluens* Perrot (1969) conclusively showed that the plant normally occurring in nature is gametophytic and produces isogametes. A culture investigation of this species in eastern Canada, together with similar studies of other entities in the complex in Canada and Europe, will resolve the problems outlined by Papenfuss (1962).

ous, to 80μ thick, epi-endophytic on *Fucus* .... (ii) *P. fucicola*

1. Thallus cushion-like, the cushions confluent; not gelatinous, to 260μ thick; epi-endophytic on *Laminaria*, especially *L. longicruris* .... (i) *P. confluens*

(i) *Pseudopringsheimia confluens* (Rosenv.) Wille

Synonymy: *Ulvella confluens* Rosenvinge, 1893, p. 924, fig. 39.
Pseudopringsheimia penetrans Kylin, 1910, p. 6.
Rosenvinge, 1894, p. 212; Jønsson, 1904, p. 52; Collins, 1909 p. 286 (all as *Ulvella confluens*); Levring, 1937, p. 27; Lund, 1959, p. 29; Perrot, 1969, p. 279, Figs. 1-4.
Cardinal 1967b, p. 462; 1968, p. 46; Cardinal and Villalard, 1971, p. 894; Edelstein and McLachlan, 1967, p. 214; Edelstein et al., 1970, p. 623; South and Cardinal, 1970, p. 2086.

DESCRIPTION (Fig. 13a): Plants cushion-like, polystromatic, the cushion confluent and spreading extensively on the host; penetrating rhizoids present; cushions centrally to 260μ thick, the upright filaments branched and compacted laterally; hairs lacking; cell divisions transverse or oblique, the upper cells with denser contents than the lower; chloroplast cup-shaped or rounded, often confined to the upper part of the cell and containing a single pyrenoid.

REPRODUCTION AND SEASONAL OCCURRENCE: In eastern Canada reproductive plants recorded in March, sterile plants from March-June. Sporangia terminal, 10-12 × 27-44μ, containing 30-40 spores which escape from an apical orifice; sporangia may be formed in series. The life-history has not been studied for eastern Canadian plants.

Perrot (1969) has demonstrated an heteromorphic alternation of generations for this species in culture, using Roscoff material. Biflagellate isogametes are produced on the cushion phase occurring in nature on the stipes of *Laminaria*. The gametes measure 3-4 μ × 2.5-3.0μ. The zygotes developed in culture into a filamentous phase hitherto unknown from the field. Terminal cells of the filamentous phase became swollen, often detached and produced 6-12 spores which germinated to re-instate the gametophyte, cushion phase. Perrot (1969) showed that the vegetative alternation was coupled with a chromosomal sequence of $n = 6$, $2n = 12$, meiosis occurring in the gametangia found on the cushion phase. Perrot's (1969) descriptions and illustrations closely resemble the species as it occurs in eastern Canada. Comparable culture studies of eastern Canadian plants will reveal whether or not the same entity is involved in both regions.

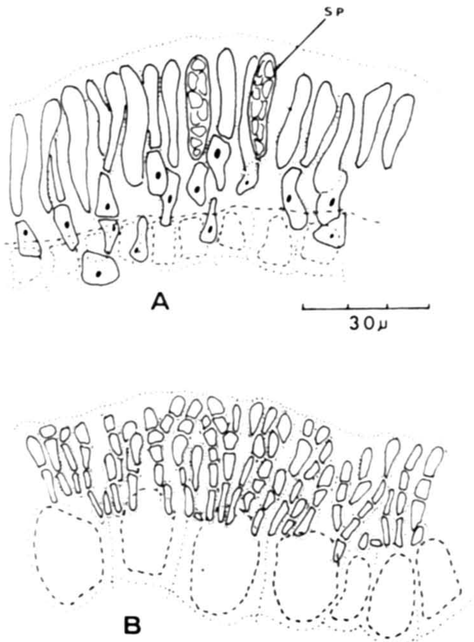

Figure 13. A. *Pseudopringsheimia confluens* (Rosenv.) Wille on *Laminaria*, showing sporangia (SP). Redrawn from reconstituted material. Holmes, Algae Rariores Exsiccatae No. 199. [in Herb. UC No 020392]. B. *Pseudopringsheimia fucicola* (Rosenv.) Wille on *Fucus*. Redrawn from reconstituted material, Levring, Kristineberg, Sweden. [In Herb. UC No. 737379]. Cell sizes for both *Pseudopringsheimia* species shown here are considerably reduced from nature, owing to reconstitution and shrinkage. Consult text for dimensions of plants in nature.

HABITAT: In the sublittoral zone, on the stipes of *Laminaria* species, in eastern Canada especially *L. longicruris*.

DISTRIBUTION: Widely distributed in the North Atlantic Ocean. N. E. coast of North America: Nova Scotia and Newfoundland, to Greenland. Eastern Canada: Nova Scotia (Bay of Fundy); Québec (Chaleur Bay; Gulf of St. Lawrence); Newfoundland (Fortune Bay). Probably much more widespread than present records indicate.

(ii) *Pseudopringsheimia fucicola* (Rosenv.) Wille, 1909, p. 89.

Synonymy: *Ulvella fucicola* Rosenvinge, 1893, p. 926, fig. 40.

Oltmanns, 1894, p. 211, Pl. 7, figs. 11-13; Collins, 1909, p. 286 (both as *Ulvella fucicola*); Kylin, 1949, p. 44, fig. 47; Waern, 1952, p. 62; Lund, 1959, p. 29; Pankow, 1971, p. 106, fig. 107.

Edelstein and McLachlan, 1966, p. 1046; Edelstein *et al.*, 1970, p. 623; Cardinal, 1968, p. 46; South and Cardinal, 1970, p. 2086.

DESCRIPTION (Fig. 13b): Plants cushion-like, hemispherical, polystromatic, the cushions not confluent, somewhat gelatinous; penetrating rhizoids present, hairs absent; cushions centrally to 75-80μ thick, composed of several radiating layers of oblong cells 5-7μ diam., 3-5 × the diameter long; cells containing a single parietal centrally located chloroplast and a single pyrenoid. Distinguishable from *P. confluens* by the host, the smaller cell size, the more gelatinous nature of the cell membranes and the more central position of the chloroplast.

REPRODUCTION AND SEASONAL OCCURRENCE: most cells transformed into sporangia twice the size of the vegetative cells, containing 6-10 zoospores; sporangia ellipsoidal or oblong. Mode of spore release and spore development unknown. In eastern Canada recorded from February to May; reproductive season undetermined.

HABITAT: on *Fucus* species, penetrating the surface layers of the host and especially invading the stipe region.

DISTRIBUTION: Europe, general in the North Atlantic Ocean. N. E. coast of North America: Nova Scotia and Greenland. Eastern Canada: Apparently a rare species; Nova Scotia (Bay of Fundy; Atlantic coast).

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Naturaliste can., 101 : 925-929 (1974).

ADDITIONS ET EXTENSIONS D'AIRES DANS LA FLORE DU QUÉBEC, LA NATURE DE L'*ERIOCAULON ROLLANDII* ROUSSEAU ET DESCRIPTION D'UN NOUVEL HYBRIDE DE *PRIMULA*

Ernest LEPAGE

Saint-Simon (Rimouski),
Québec

Résumé

Nous signalons l'addition de 4 plantes pour le Québec et des extensions d'aires pour 13 autres, dont la plus remarquable est l'*Eleocharis olivacea* Torr.. De plus, *Primula* x **Morissetii**, est décrit, tandis que l'*Eriocaulon septangulare* f. *Rollandii* représente un alignement nouveau.

Abstract

We report 4 plants as new to the Québec flora and some extensions of range for 13 more plants, of which *Eleocharis olivacea* Torr. is the most conspicuous. Furthermore *Primula* x **Morissetii** is described and *Eriocaulon septangulare* f. *Rollandii* is a new transfer.

Additions à la flore du Québec

CAREX LENTICULARIS Michx. var. EUCYCLA Fern., Rhodora **15**: 134 (1913). — Riv. Bonaventure (Bonaventure), rive humide près du pont, environ 5-6 milles en amont de l'embouchure, 20 juillet 1972, *Lepage et Cinq-Mars 16886.* — Saint-Hubert (Témiscouata), rive humide du lac Saint-François, 2 juillet 1973, *Lepage 16932.*

Cette variété à akènes largement ovales à orbiculaires, arrondis à la base et à l'apex, fut décrite sur des récoltes provenant de Terre-Neuve, le long de la branche est de la rivière Humber, et ne semble pas connue des autres provinces.

HIERACIUM X APATELIUM Naegeli & Peter nm. **pilosellifIorum** (Naegeli & Peter), stat. nov. — *H. pilosellifIorum* Naegeli et Peter, Hier. Mittel-Eur. Piloselloiden, p. 707 (1885). — *H. floribundum* Wimm. & Grab. X *H.Pilosella* L.

Cette plante ressemble beaucoup à *H.* x *flagellare* Willd. nm. *cernuiforme* (NP.) Lepage. Chez celui-ci le dessus des feuilles porte un mélange de poils courts, fins et flexueux provenant de *H. caespitosum* Dumort, et de poils longs et droits, héritage de *H. Pilosella* L.; chez H. x *apatelium*, les feuilles plus pâles, parfois un peu glauques, ne portent que des poils longs et droits. Nous le connaissons maintenant des endroits suivants: Rivière-du-Loup (Riv.-du-Loup), *Lepage 16790, 16791, 16792, 16794, 16800, 16801, 16802, 16803, 16805, 16806.* — Trois-Pistoles (Riv.-du-Loup), *Lepage 16627* (distribué sous le nom de *H.* x *flagellare* nm. *cernuiforme).* — Saint-Simon (Rimouski), *Lepage 16625* (distribué sub *H.* x *flagellare* nm. *cernuiforme).* — Saint-Fabien (Rimouski), près de l'îlet au Flacon, *Lepage 16858.* — Saint-Fabien, cap à l'Orignal, *Lepage 16636, 16818, 16819.*

HIERACIUM X FUSCOATRUM Naegeli & Peter. — H. *aurantiacum* L. X *H. caespitosum* Dumort.

Quand nous avons signalé cet hybride pour la première fois (Lepage, 1967), nous n'en connaissions aucune récolte du Québec, ni même du Canada, tout en notant que «cet hybride est sans doute plus fréquent que cette unique récolte semble l'indiquer». Nous l'avons maintenant des endroits suivants: Cacouna (Riv.-du-Loup), *Lepage 16697.* Saint-Simon (Rimouski), *Lepage 16930.* — Saint-Fabien (Rimouski), *Lepage 16837, 16841, 16846, 16852.* — On peut le reconnaître assez facilement par ses fleurs jaunes et maculées de rouge. L'involucre et le haut de la tige sont presque aussi poilus que chez *H. aurantiacum.*

HIERACIUM FLORIBUNDUM Wimm. & Grab.

Ce que nous identifions généralement sous ce nom comprend en réalité un agrégat de petites espèces, vraisemblablement d'origine hybride assez ancienne, qui se propagent maintenant de façon autonome. Dans la région de Rimouski particulièrement, cette plante possède des feuilles peu glauques et les premières du printemps, qu'on trouve à la base des tiges fertiles, sont souvent poilues supérieurement. La moitié supérieure de la tige est violacée; les fleurs jaune foncé sont souvent maculées de rouge et les stolons sont peu poilus. Cette plante correspond assez bien à *H. cochleatum* NP., qui serait l'hybride *H. auricula* L. X *H. caespitosum* Dumort. *H. caespitosum* est fréquent, mais *H. auricula* n'a pas encore été signalé au Québec. Il ne s'agirait donc pas d'un hybride récent.

En plus de nombreuses récoltes de Saint-Fabien, du Bic et de Rivière-du-Loup, nous l'avons aussi des endroits suivants: Lac Aylmer, canton Weedon (Wolfe), 20 juin 1967, *Brisson et Hamel 12296.* — Nouvelle-Écosse: Waterville, June 11, 1928, *H. Groh,* s.n. (dét. van Soest).

Extensions d'aires

LYCOPODIUM INUNDATUM L. — Saint-Simon (Rimouski), abondant autour d'un petit lac en voie de desséchement, 3 milles est du village, 17 sept. 1973, *Lepage 17024* — Autour d'un petit lac au bas du mont Nicolalbert (Gaspé), 17 juillet 1950, *Lepage 12411.* Ce sont apparemment les seules récoltes connues entre Québec et Gaspé sur la rive sud du Saint-Laurent. Carte de distrib.: Hultén (1958, map 198).

LEERSIA ORYZOIDES (L.) Sw. — Saint-Fabien (Rimouski), platière humide de la riv. du Sud-Ouest, 3 sept. 1973, *Lepage 17005.* C'est la seconde station connue dans la région de Rimouski-Riv.-du-Loup, l'autre étant le Lac-des-Aigles (Lepage, 1971).

PANICUM CAPILLARE L. — Bic (Rimouski), abondant dans la cour du chemin de fer, 4 sept. 1973, *Lepage 17017.* Scoggan (1950) l'avait déjà signalé de Matapédia.

ELEOCHARIS OLIVACEA Torr. — Saint-Simon (Rimouski), sur boues fines à la décharge d'un petit lac en voie de desséchement, 3 milles à l'est du village, 17 sept. 1973, *Lepage 17021.* Plante minuscule, bien différente des autres espèces du genre par ses tiges courbées et aplaties au sol. D'après la carte de distribution de Svenson (1939), il s'agit d'une extension d'aire considérable depuis le sud-ouest du Québec et cette nouvelle station marque sa limite nord en Amérique.

SALIX PADOPHYLLA Rydb. (Syn.: *S. pseudomonticola* Ball et var. *padophylla* (Rydb.) Ball; *Salix* x *ungavensis* Lepage, Naturaliste can. **89**: 117, 1962). — Après avoir comparé attentivement l'holotype du *S.* x *ungavensis* avec de bons échantillons de *S. padophylla*, nous constatons qu'il ne diffère de ce dernier que par ses capsules un peu pubescentes à la base, alors que généralement elles sont tout à fait glabres chez *S. padophylla*. Aux stations déjà connues (riv. Harricana et Nottaway, poste de Rupert et riv. Wiachouan), nous pouvons maintenant ajouter les suivantes pour le centre de l'Ungava : Rive humide de la riv. Swampy Bay, rapide en amont du lac Wakuach, 55° 27′ N., 67° 25′ W., 7 août 1961, *Dutilly et Lepage 39121* (rapporté sous le nom de *S. myrtillifolia* var. *brachypoda)*. — Riv. Swampy Bay, replat caillouteux de l'escarpement au bas du rapide en aval du lac Patu, 56° 40′ N., 68° 35′ W., 19 août 1961, *Dutilly* & *Lepage 39344* (holotype de *Salix* x *ungavensis*). — Riv. Caniapiscau, colline de dolomie, 57° 18′ N., 69° 13′ W., 24 août 1961, *Dutilly et Lepage 39443, 39456* (rapportés sub *S. myrtillifolia* var. *brachypoda)*. Vu sa distribution depuis l'Alaska jusqu'au centre de l'Ungava, on ne peut plus considérer cette espèce comme cordilérienne, car il s'agit bien d'une trans-américaine. Carte de distrib. : fig. 1.

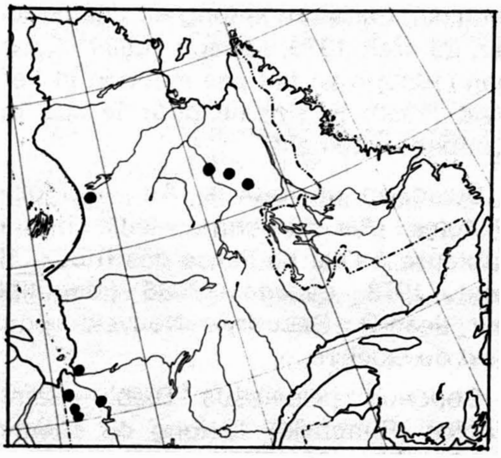

Figure 1. Distribution du *Salix padophylla* au Québec. (Goode's Base Map No. 111. Copyright 1939 par The University of Chicago. Utilisé avec la permission de l'University of Chicago Press).

POLYGONUM NEGLECTUM Bess. — Saint-Siméon (Rimouski), sur la voie ferrée, 27 août 1973, *Lepage 16980, 16985.* Regardé parfois comme variété (var. *angustissimum* Meisn.; var. *neglectum* (Bess.) Achers. & Grab.) ou même comme synonyme de *P. aviculare* L. Löve et Löve (1956) le considèrent comme une bonne espèce, avec ses feuilles aiguës, linéaires à étroitement lancéolées et ses akènes poncticulés.

DESCURAINIA RICHARDSONII (Sweet) O. E. Schulz. — Trois-Pistoles (Riv.-du-Loup), haut de la grève du Fleuve, 9 août 1973, *Lepage 16949.* Déjà connu de la péninsule de Gaspé (Scoggan, 1950), mais apparemment rare dans la région de Rimouski à Rivière-du-Loup.

ROSA VIRGINIANA Mill. — Saint-Fabien (Rimouski), le long du chemin de fer, 3 sept. 1973, *Lepage 17004.* — Saint-Simon (Rimouski), bord de la route, 29 août 1973, *Lepage 16995.* — Trois-Pistoles (Riv.-du-Loup), bord de la rivière débouchant dans l'anse des Rioux, 19 sept. 1973, *Lepage 17025.* Bien qu'assez fréquent en Gaspésie, ce sont nos premières récoltes dans la région de Rimouski à Rivière-du-Loup.

ASCLEPIAS SYRIACA L. — Saint-Fabien (Rimouski), 31 août 1973, *Lepage 16996.* — Saint-Simon (Rimouski), 29 août 1973, *Lepage 16990.* En consultant la carte de Doyon (1958), on voit que ces deux stations comblent une lacune assez importante dans l'aire de distribution de cette espèce, dans l'est de la Province.

COLLOMIA LINEARIS Nutt. — Saint-Fabien (Rimouski), le long du chemin de fer, 31 août 1973, *Lepage 16999.* C'est une autre plante très rare dans notre région.

ASTER SIMPLEX Wild. var. RAMOSISSIMUS (T. & G.) Cronq. — Saint-Simon (Rimouski), baissière le long du chemin de fer, 29 août 1973, *Lepage 16989*. Scoggan (1950) n'en fait pas mention et Fernald (1950) le signale pour le sud du Québec seulement.

SOLIDAGO NEMORALIS Ait. — Trois-Pistoles (Riv.-du-Loup), vieille prairie sableuse à l'est de l'anse des Rioux, 19 sept. 1973, *Lepage 17038* (identifiée par Jean-R. Beaudry). Nouveau pour l'est du Québec.

SONCHUS ULIGINOSUS Bieb. — Saint-Fabien (Rimouski), le long du chemin de fer, 31 août 1973, *Lepage 16997*.— Lac-des-Aigles (Rimouski), 11 août 1972, *Lepage 16557*. — Lac du Pain de Sucre, entre Squattec et Lejeune (Témiscouata), 22 juil. 1970, *Lepage 16479*. — Lac Témiscouata (Témiscouata), 4 milles ouest de Squattec, 12 août 1969, *Lepage 16350*. Espèce souvent immergée dans le *S. arvensis* L. var *glabrescens* Guenth., Grab. & Wimm., quoique facilement séparable, surtout sur le terrain, par ses capitules plus corsés au sommet (turbinés ; caractère qui disparaît après pressage), ses tégules d'un vert plus pâle et à marge blanchâtre.

Une primevère hybride

PRIMULA x **Morissetii,** hybr. nov.

P. egaliksensis Wormskj. X *P. stricta* Hornem.

Lobulae calycis incisae more P. egaliksensis, *sed corolla pallidoviolacea, lobulae ejus incisae more* P. stricta. *Cum praesumptis genitoribus crescens.*

Baie d'Hudson, T.N.O.: îles Dormeuses (Sleepers Isl.) vers 57°30'N., 79° 45'W., partie nord-ouest de la pointe sud de l'île Kidney, endroits très humides sur sol mince le long du rivage, 25 août 1970, *Pierre Morisset 70-235-1* (holotype, Herbier Louis-Marie, Université Laval). De prime abord, on le prendrait pour le *P. egaliksensis* f. *violacea* Fern., mais la corolle et ses lobes appartiennent plutôt au *P. stricta*, bien que les lobes du calice soient incisés à la manière de *P. egaliksensis.*

Alignement nouveau

ERIOCAULON SEPTANGULARE With. f. **Rollandii** (Rousseau) stat. nov. — *E. Rollandii* Rousseau, Bull. Jard. Bot. (Bruxelles) 27: 372 (1957).

Il s'agit d'une forme écologique semblable au *Subularia aquatica* L. f. *terrestris* Warion. Les différences entre *E. septangulare* et *E. Rollandii* ne sont que quantitatives. Nous avons trouvé cette forme dans la région de Rimouski et du Témiscouata en compagnie de l'espèce typique. Les plantes aquatiques sont très sensibles à un changement d'habitat: les plantes des rives exondées sont parfois bien différentes des plantes de même espèce qui baignent dans l'eau, par exemple, le *Nuphar variegatum*, le *Potamogeton gramineus*, le *Sagittaria latifolia* et bien d'autres. Rousseau (1. c.) fait la remarque suivante: «Malgré des recherches intenses, il a été impossible de trouver dans tout le territoire de Mistassini des *Eriocaulon* baignant dans l'eau, comme c'est normalement le cas pour *E. septangulare.* » Nous avons fait la même constatation dans la région du lac Duncan. Nous n'avons pas de réponse exacte pour l'explication de ce phénomène, qui, d'ailleurs, ne se limite pas à l'*Eriocaulon.* Dans le Nord, on rencontre généralement le *Potentilla palustris* dans les lieux très humides, mais non inondés, alors que plus au sud il baigne dans plusieurs pouces d'eau ; il y a probablement une équivalence d'habitats, dont il faut tenir compte.

Les plantes mentionnées dans cet article sont conservées dans l'herbier de l'auteur.

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SOLIDAGO SHINNERSII (Beaudry) *STAT. ET COMB. NOV.*, UNE NOUVELLE ESPÈCE DU COMPLEXE DU *S. GIGANTEA*

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Résumé

Trois entités du complexe du *Solidago gigantea* constituent une série polyploïde régulière: *S. gigantea* Ait. ($2n = 18$), *S. serotina* Ait. ($2n = 36$), et *S.* **Shinnersii** (Beaudry) *stat. & comb. nov.* ($2n = 54$).

Abstract

Three entities of the *Solidago gigantea* complex constitute a regular polyploid series: *S. gigantea* Ait. ($2n = 18$), *S. serotina* Ait. ($2n = 36$), and *S.* **Shinnersii** (Beaudry) *stat. & comb. nov.* ($2n = 54$).

Les taxonomistes des plantes supérieures considèrent généralement que les complexes d'espèces sont constitués par des entités qui, par plusieurs des caractères morphologiques qui déterminent leur apparence générale, ont tellement en commun, qu'elles semblent avoir partagé un même ancêtre. Les trois entités nommées *Solidago gigantea* Ait. var. *gigantea*, *S. serotina* Ait., et *S. gigantea* var. *Shinnersii* Beaudry constituent un tel complexe, désigné ici complexe du *Solidago gigantea*. En effet, les caractères des inflorescences et des tiges de ces trois entités sont les mêmes, et toutes trois produisent aussi de longs et robustes rhizomes. De plus, leurs feuilles varient peu en longueur de haut en bas de la tige, sont lancéolées, nettement dentées par le même type de dents, trinervées, mais de largeur et de longueur moyennes différentes, *S. gigantea* var. *gigantea* ayant les plus petites et *S. gigantea* var. *Shinnersii* les plus grosses.

Mes concepts de ces trois entités ont déjà été exposés dans deux publications (Beaudry, 1963 et 1970). Dans la première, j'ai aussi rapporté des changements de phénotype observés dans mes cultures de ces plantes, certains individus d'une entité de ce groupe pouvant passer d'une année à l'autre au phénotype d'une autre entité du même groupe. Les observations suivantes faites subséquemment, ont cependant montré que ces supposés changements de phénotype ne se réalisaient pas, et que j'avais été induit en erreur par des mélanges de tiges appartenant à des plantes différentes. Ces mélanges ont été produits de la façon suivante.

J'ai éventuellement constaté que ces supposés changements de phénotype n'étaient observés que lorsque des individus du *S. gigantea* var. *gigantea*, du *S. serotina* et du *S. gigantea* var. *Shinnersii* étaient établis au voisinage les uns des autres. Dans mes parcelles, les plantes étaient toutes séparées par trois pieds de distance sur le rang et par quatre pieds entre les rangs. Pour éviter le mélange des systèmes radiculaires, des sarclages profonds étaient ré-

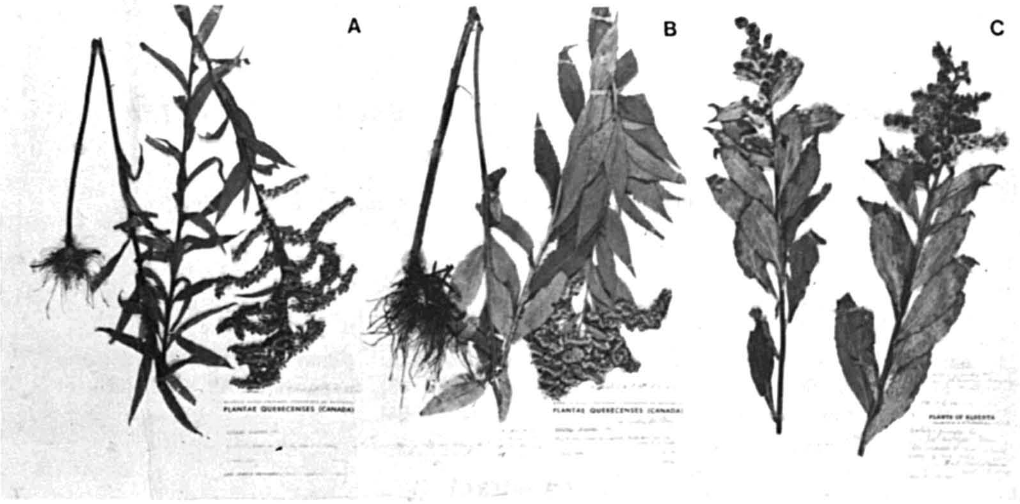

Figure 1. a. *Solidago gigantea* Ait. ($2n = 18$), b. *S. serotina* Ait. ($2n = 36$), c. *S. Shinnersii* (Beaudry) Beaudry ($2n = 54$).

gulièrement pratiqués au moyen d'un sarcleur du type «rototiller» entre les rangs et à la houe à la main entre les plantes sur les rangs. J'ai pu cependant constater que ces traitements, très efficaces pour la majorité des nombreuses espèces cultivées dans mes parcelles, ne limitaient qu'en partie la croissance des rhizomes des trois entités en cause. Ces dernières produisaient des rhizomes profonds, c'est-à-dire au-dessous de la zone sarclée, et si longs qu'ils atteignaient les emplacements de plantes voisines sur le même rang ou même sur un rang voisin, pour mêler ensuite leurs tiges aériennes à celles de ces voisins.

Lorsque les méprises faites au moment des déterminations d'identité à cause de ces mélanges sont éliminées, on constate que tous les individus du *S. gigantea* var. *gigantea* ont un nombre $2n$ de 18, ceux du *S. serotina* de 36 (Beaudry, 1970) et ceux du *S. gigantea* var. *Shinnersii* de 54 (Beaudry, 1963). Ces trois entités constituent donc une série polyploïde régulière, la première étant diploïde (2 ×), la deuxième tétraploïde (4 ×) et la troisième hexaploïde (6 ×), et les dimensions moyennes de leurs familles sont en corrélation positive avec leur nombre chromosomique respectif (fig. 1).

Lorsque le *S. gigantea* var. *Shinnersii* est ainsi débarrassé de ces individus à feuilles étroites qui empêchaient de le séparer facilement du *S. serotina*, on peut lui attribuer le statut d'espèce: *Solidago* **shinnersii** (Beaudry) *stat. et comb. nov.* (Basionyme: *S. gigantea* Ait. var. *Shinnersii* Beaudry, Canad. J. Genet. Cytol. 5: 168. 1963).

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COMMUNICATIONS BRÈVES

UN *RHYACOPHILA* NÉARCTIQUE MÉCONNU (TRIOCHOPTERA, RHYACOPHILIDAE)

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Les ♀♀ de *Rhyacophila* ont la réputation d'être difficiles à déterminer. En fait il n'en est rien, car le VIIIe segment montre des variations importantes, allant des formes les plus simples aux plus compliquées. D'autre part, elles sont pourvues d'un appareil vaginal interne également de forme et de structure complexes. Poursuivant mes études sur les *Rhyacophila* néarctiques, j'ai été surpris de constater que chez l'une des deux espèces dont l'aire de répartition est disjonctive, *acropedes* Banks, si les ♂♂ orientaux sont semblables aux ♂♂ occidentaux, il n'en n'est pas de même des ♀♀. Les différences entre les ♀♀ orientales et occidentales étant de même importance que celles que l'on observe entre les ♀♀ des trois autres espèce du groupe, je les considère comme de bons caractères spécifiques. Je figure ici les génitalia de ces quatre espèces, *vao* Milne, *inculta* Ross et Spencer, *ignorata* n. sp. et *acropedes,* pour montrer l'amplitude de leurs caractères distinctifs. Elles peuvent être classées en une série approximativement linéaire, le VIIIe segment montrant des caractères graduellement accusés, dans laquelle la nouvelle espèce occupe la troisième place.

Rhyacophila ignorata n. sp.

Taille et coloration du corps et des ailes semblables à celles d'*acropedes*.

Génitalia ♂ semblables à ceux d'*acropedes.* Les faibles différences que l'on peut noter entre les deux espèces ne sont pas plus importantes que celles que l'on peut observer entre divers spécimens d'*acropedes.*

Génitalia ♀ (fig. 3): vu de profil, le VIIIe segment apparaît assez fortement tronconique, avec son angle apical inférieur pincé latéralement et formant une carène à extrémité anguleuse, dépassant à peine le bord apical du segment. Vu de dessous, le VIIIe segment montre ses quatre angles bien saillants et ses faces latérales très légèrement bombées. Les caractères de l'appareil vaginal sont plus élusifs. Les pièces latérales sont plus étroites et moins longues que celles d'*acropedes* et l'anneau est plus épais et moins concave.

Holotype ♀ , allotype ♂ et 2 paratypes ♂♂ (CNC 13.309): Tuckerman Rav., Mt Washington, N.-H., U.S.A., 4-VIII-1958 (O.S. Flint). Paratypes: 3 ♂♂ I ♀ , Blue Jay Cove, Manitoulin Isl., Ontario, Canada, 30-VI et 8-VII-1957 (F.P. Ide), ROM.

Rh. ignorata n'est actuellement connu que de quelques localités isolées du New-Hampshire, de l'Ontario et du Québec. Il constitue le premier cas connu chez les Trichoptères d'une espèce se distinguant d'une autre par les caractères de la ♀ seulement.

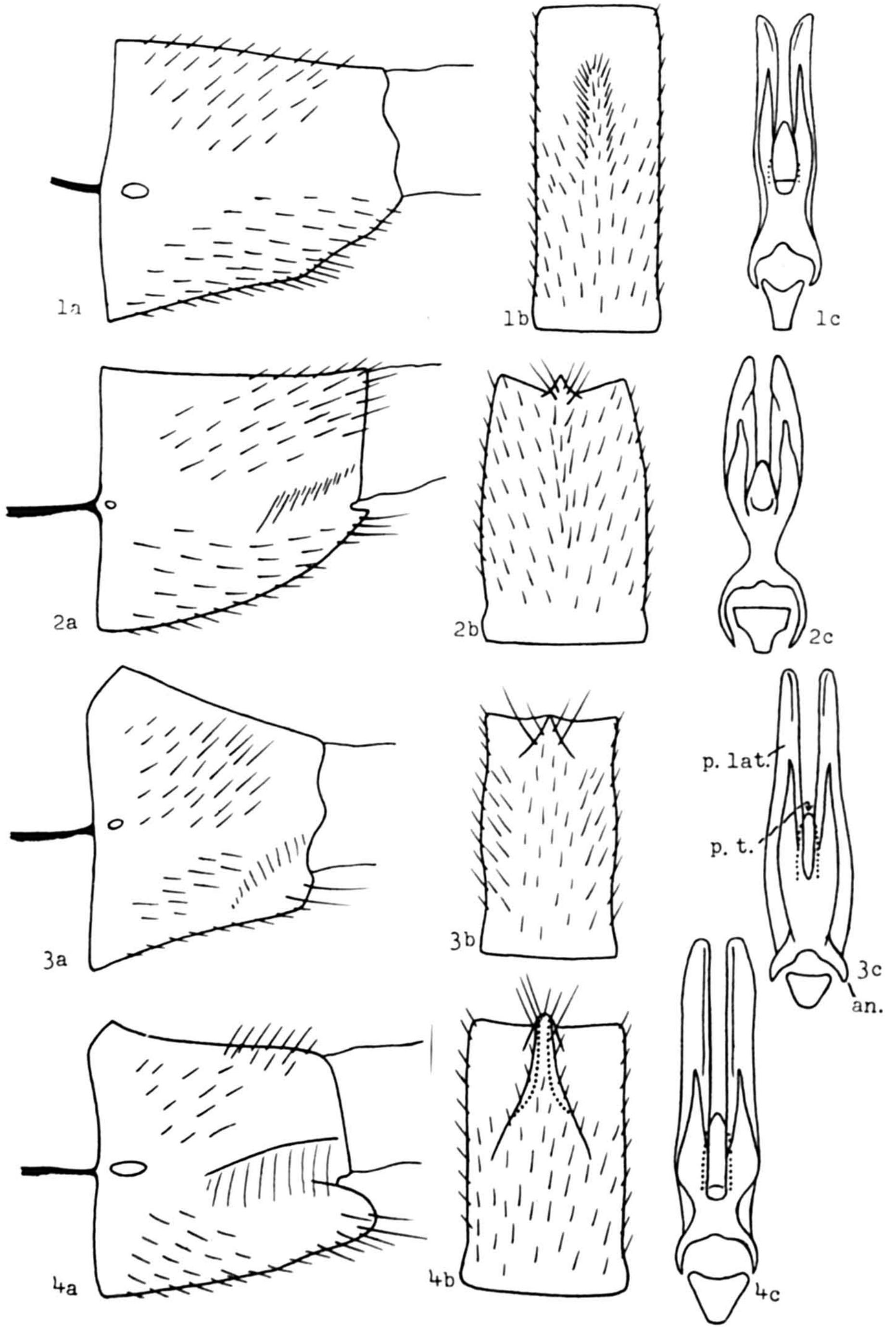

Figure 1, *vao.* Figure 2, *inculta.* Figure 3, *ignorata.* Figure 4, *acropedes.* a, VIIIe segment vu de profil. b, le même vu de dessous. c, appareil viginal vu de face (p. lat. : pièces latérales ; p. t. : pièce terminale ; an. : anneau).

NOUVELLES DONNÉES ET REMARQUES SUR LA RÉPARTITION NORDIQUE DE QUELQUES FORMICIDES (HYMÉNOPTÈRES) NÉARCTIQUES

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Les données sur la répartition des fourmis dans le nord de l'Amérique du Nord, c'est-à-dire au-delà du 52e degré de latitude nord, sont encore rares et fragmentaires. Certaines s'avèrent inutilisables parce qu'il est pratiquement impossible de déterminer s'il s'agit d'une présence accidentelle ou non (par exemple, cas de sexués emportés par le vent), tandis que d'autres ne peuvent être employées sans avoir pu retracer les spécimens discutés afin de vérifier la signification réelle des taxa utilisés. La mention de *Leptothorax acervorum canadensis* Provancher (maintenant appelée *L. muscorum* (Nylander)) à Umiat, Alaska, par Weber (1948) illustre le premier cas; l'usage du nom de *Formica fusca* Linné par Weber (1953), pour interpréter le nom de *Formica rubra* utilisé par Parry en 1826, caractérise bien le deuxième cas. (Pour ma part, je soutiendrais ici qu'il s'agissait plutôt de *Formica neorufibarbis* Emery). Aussi une liste exhaustive des données de la littérature, qui ne serait que répétive, procédé très contestable en particulier en écologie et en systématique, serait sans valeur. Toutefois quelques données peuvent être actuellement utilisées et interprétées pour préciser la répartition géographique de quelques espèces dans le nord de la région néarctique.

Brown, en 1949, a rapporté la présence de colonies de fourmis à la station Reindeer, dans le delta du fleuve Mackenzie, Territoire du Yukon, Canada. Cet endroit se situe à l'intérieur du cercle polaire arctique par 68° 42′ Lat.N. et 134° 07′ Long.O. Trois espèces sont identifiées: *Camponotus herculeanus* (Linné), *Formica fusca et Leptothorax acervorum canadensis.* Les spécimens nommés *F. fusca* représentent ce que j'ai appelé la forme toundra de *Formica neorufibarbis* (Francœur, 1973). À l'occasion d'une analyse des variations de *L. muscorum,* Brown (1955) apporte quelques données géographiques nouvelles sur cette espèce, ainsi que sur *F. neorufibarbis.* La baie de Kidluit à l'île Richards (69° 32′ Lat.N., 133° 47′ Long.O.) semble être le point le plus septentrional où une fourmi ait été capturée, en occurence *L. muscorum.* Mais un établissement permanent de cette espèce dans ce lieu reste à prouver selon les commentaires de l'auteur (Brown, 1955).

Gregg (1972) signale pour la région de Churchill (58° 45′ L.N.), au Manitoba, quatre espèces: *Myrmica brevinodis* Emery, *Leptothorax canadensis* Provancher (= *L. muscorum* (Nylander)), *Camponotus herculeanus* et *Formica neorufibarbis algida* Wheeler (= *F. neorufibarbis,* Francoeur, 1973). Après avoir examiné les spécimens récoltés par Gregg, il appert a) que les spécimens nommés *M. brevinodis* appartiennent en fait à *M. kuschei* Wheeler; b) que les individus rassemblés sous *F. algida* ne correspondent pas à la forme toundra de *F. neorufibarbis*, ce qui surprend. En outre, Francoeur et Béique (1966) ont démontré qu'il fallait abandonner l'usage du nom de *M. brevinodis* au profit de celui de *M. incompleta* Provancher.

Récemment, dans une révision taxonomique du groupe *Formica fusca* (Francœur, 1973), j'ai pu vérifier l'identité de plusieurs spécimens provenant de nouvelles récoltes ou rapportés antérieurement dans la littérature et ainsi préciser la répartition, au delà du 52e parallèle nord, de quatre espèces: *F. neoclara* Emery, *F. podzolica* Francœur, *F. fusca* et *F. neorufibarbis.*

Au Québec, la répartition nordique des fourmis reste globalement à déterminer. Gregg (1969) rapporte que *F. fusca* peut atteindre Pointe Comfort, sur la Baie James, au Nouveau-Québec. J'ai identifié les spécimens actuellement connus de ce lieu à *F. podzolica* et signalé l'existence de *F. neorufibarbis* au Poste-de-la-Baleine, sur la baie d'Hudson, au Nouveau-Québec (Francœur, 1973). À ce dernier endroit viennent maintenant s'ajouter les noms de quatre autres fourmis: *Myrmica kuschei, Leptothorax muscorum, Camponotus herculeanus et Formica subnuda* Emery. Les trois premières sont des espèces caractéristiques de la forêt boréale coniférienne de l'Amérique du Nord. Leurs colonies furent trouvées soit dans du bois mort (branches, troncs) ou dans le sol recouvert de matière organique (mousses, lichens). Seulement cinq femelles, sans ailes, représentent *F. subnuda* dans les échantillons que j'ai examinés; il faudra attendre la découverte d'une colonie pour confirmer la présence continue de cette espèce dans cette région de la baie d'Hudson.

Les fourmis du Poste-de-la-Baleine ont été récoltées par des étudiants au cours d'un stage de travail et par le Dr J.-M. Perron, de l'Université Laval. Je remercie ce dernier pour m'avoir fourni ces spécimens. Quelques séries représentatives sont conservées dans la collection du Département de biologie de l'Université Laval. Les autres séries sont déposées dans la collection de l'auteur et portent les numéros suivants 02812, 02844 à 02857 inclusivement.

Je remercie le Dr. R.E. Gregg pour m'avoir donné des spécimens récoltés à Churchill, Manitoba. Cette étude a été effectuée dans le cadre d'un projet supporté par une subvention (A-6501) du Conseil national de recherches du Canada.

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THE DISTRIBUTION OF *PELLAEA* IN QUÉBEC AND EASTERN ONTARIO

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In their recent study of the Cliff-brake ferns (genus *Pellaea)*, Rigby and Britton (1970) describe both Canadian species, *P. atropurpurea* (L.) Link and *P. glabella* Mett., as «...comparatively rare..., or at most only locally abundant...». They cite a total of 8 stations of *Pellaea* in southern Québec and eastern Ontario. Lafontaine and Brunton (1972) describe 4 additional stations of *P. atropurpurea* from southern Québec. This note describes 2 new stations for each species in Ontario and Québec.

Pellaea atropurpurea (L.) Link

ONTARIO — Renfrew County: 1/4 mile south of Mountain Chute Dam, Madawaska River; 10.2 miles southwest of Calabogie; lat. 45° 12′ N, long. 76° 53′ W. March 24, 1973. *Brunton and Lafontaine 553* (DAO).

A small colony (10 clumps) of stunted plants was found growing out from under marble rocks on the exposed, steep, debris-covered slope of a 200-foot southwest-facing cliff. It is the first record for this species in Renfrew County.[1]

QUEBEC — Gatineau County: 3 miles south of Poltimore; lat. 45° 45.5′ N, long. 75° 43.2′ W; April 23, 1973. *Brunton and Lafontaine 662* (DAO).

An enormous colony (many hundreds of clumps) was found covering most of the 1/4 mile-long cliff-face, on a steep, debris-covered slope of marble, under partial shade. *Woodsia oregana* D.C. Eat. and *Cryptogramma stelleri* Gmel.) Prantl. were notable associates. This is the largest station of *P. atropurpurea* yet discovered in Québec.

Pellaea glabella Mett.

ONTARIO — Nipissing District: the Natch cliffs, Petawawa River, Algonquin Provincial Park; lat. 46° 03′ N, long. 77° 52′ W. August 17, 1971. *Reznicek and Pratt.* Algonquin Park Herbarium *1776* (and DAO).

The fern is fairly common on the 350-foot, southwest-facing cliff, in exposed cracks in the cliff-face. A total of approximately 75 clumps were noted. In addition, a few (8 to 10) were noted on the northeast-facing cliff opposite the main colony (P.D. Pratt, pers. comm., 1973). Though primarily gneissic rock, some calcareous content was noted. The *Pellaea* grows in association with such species as *Dryopteris fragrans*

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[1] While this paper was in press, two stations of *Pellaea atropurpurea* were found on White Lake Mountain, Renfrew County, Ontario. These stations are approximately 25 miles northeast of the station at Mountain Chute Dam described above. The data for these stations are: (1) 2.4 miles east-north-east of White Lake, Ontario, lat. 45°22′N, long. 76°27′W, July 14, 1974. *Lafontaine* (DAO). (2) 1.9 miles east-north-east of White Lake, Ontario, lat. 45°22′N, long. 76°28′W, November 2, 1974. *Lafontaine and White* (CAN).

(L.) Schott. It constitutes the only known station for Algonquin Park, and appears as a checklist entry in Moore (1972).

QUEBEC — Gatineau County: 2 miles southwest of Poltimore; lat. 45° 47′N, long. 75° 43′ W. *Cody 21225*, July 5, 1973 (DAO), *Brunton and Lafontaine 626*, July 14, 1973 (DAO).

Fifty large (and numerous small) clumps were found growing in cracks in the exposed marble face of the 60-foot, southeast-facing cliff. The initial collection in July 1973 was made by W.J. Cody, Canada Department of Agriculture, as *P. atropurpurea*.
After consultation with Cody, the original collection was revised to *P. glabella*. This constitutes the third record for the province of Québec and the first record for the Ottawa-Hull district. Elsewhere in Québec it is known only from Petit lac Brompton, Richmond County (Britton, Legault and Rigby, 1967) and lac Montjoie, Sherbrooke County (*fide* D.M. Britton, 1974).

Discussion

P. atropurpurea and *P. glabella* have a similar status in Québec and eastern Ontario (being represented by 9 and 8 stations respectively). Both are rare here, being occasionally locally common on calcareous, south-facing cliffs and/or slopes. *P. glabella* is found only on the driest, most exposed rock-faces, projecting out from cracks in the rock in its characteristic « pin-cushion » — like clusters. *P. atropurpurea*, however, shows a marked preference for shaded rock slopes (exclusively on marble), growing in earth-filled fissures, on debris-covered ledges, and occasionally on talus slopes.

It is interesting to note that although the new Québec stations of *P. atropurpurea* and *P. glabella* (reported in this note) grow commonly on cliffs less than 3 miles apart, neither station has representation from both species. The only difference noted between the two sites is that the *P. glabella* cliff is southeast-facing while the *P. atropurpurea* cliff is southwest-facing.

Acknowledgements

The Algonquin Park station was discovered while Reznicek and Pratt were employed in ecological inventory work for the Ontario Ministry of Natural Resources.

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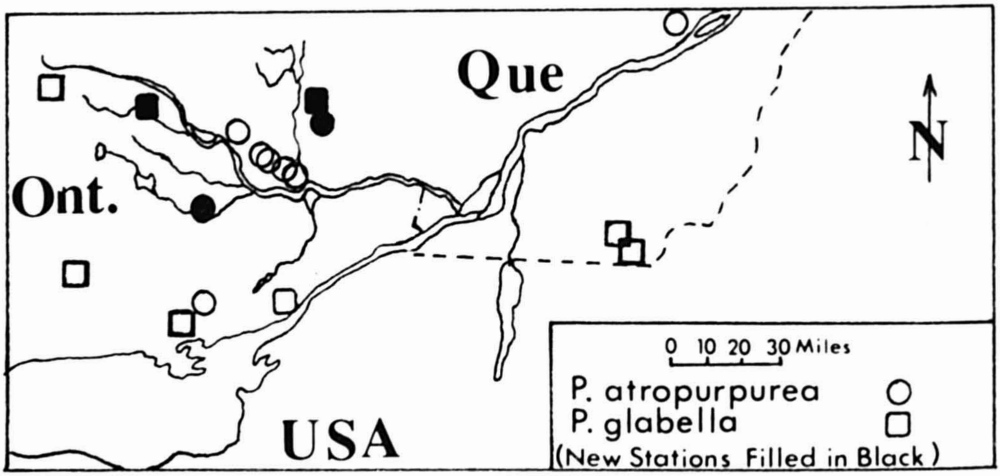
BRITTON, D.M., A. LEGAULT and S.J. RIGBY, 1967. *Pellaea atropurpurea* (L.) Link and *Pellaea glabella*. Mett. in Quebec. *Naturaliste can.*, 94:761-763.



Distribution of *Pellaea* in Québec and Eastern Ontario

LAFONTAINE, J.D. and D.F. BRUNTON, 1972. The Purple Cliff-brake, *Pellaea atropurpurea* (L). Link, in Western Quebec. *Can. Fld-Nat.*, 86: 85-86.

MOORE, M.I., 1972. Vascular plants of the Middle Ottawa Valley and Northeastern Algonquin Park. Petawawa Forest Experiment Station Information Report PS-X-34, Environment Canada, Chalk River.

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REVUE DES LIVRES

LASKIN, A.J. and H.A. LECHEVALIER, 1973. **Handbook of microbiology,** Vol. 1 : Organismic microbiology. CRC Press, Cleveland, Ohio. 940 p. 30 × 18.5 cm. Relié, $36.00.

Depuis fort longtemps, la société Chemical Rubber publie des manuels pratiques de laboratoire dans divers domaines scientifiques, dont le plus connu reste le *Handbook of chemistry and physics* rendu maintenant à sa 53e édition. À la liste déjà longue des ouvrages du même genre vient s'ajouter le premier tome d'une série de quatre gros volumes sur le champ très vaste de la microbiologie, intitulé *Organismic microbiology* ou, en français, la Microbiologie organismique, si ce néologisme est acceptable. Les éditeurs de ces manuels ont confié la rédaction de ce volume à MM. A.J. Laskin, de l'Esso research and engineering company et Hubert A. Lechevalier de l'Institut de microbiologie de l'Université Rutgers au New Jersey. Les trois autres tomes sur d'autres aspects de la microbiologie paraîtront sans doute dans un avenir pas trop éloigné.

Cet *in-16* de 940 pages contient une masse considérable de données les plus au point sur les organismes eux-mêmes, soit les bactéries, les champignons, les algues, les protozoaires et les virus, et sur la méthodologie microbiologique. Un comité consultatif, composé de 22 microbiologistes reconnus, a confié à 53 auteurs la tâche de rassembler les matériaux indispensables et de rédiger un ou plusieurs chapitres de chacune des parties. H.A. Lechevalier, pour sa part, en a écrit neuf en plus d'avoir colligé une grande partie de la matière de ce volume.

La masse énorme des connaissances accumulées dans les sphères si diverses de la microbiologie, répartie dans un nombre très élevé de publications qui peuvent remplir plusieurs bibliothèques spécialisées, doit être périodiquement condensée en des ouvrages de référence à l'usage des chercheurs et des techniciens de laboratoire. Dans ce premier tome, on trouve un résumé succint, mais à jour, des données les plus récentes sur la morphologie, le cycle vital, les caractères culturaux, l'habitat, la nutrition et autres traits jugés indispensables, selon les groupes de microorganismes, pour la détermination des genres sinon des espèces et pour les situer dans l'écosystème. À des notions aussi ramassées, s'ajoutent des tableaux d'une consultation commode, des dessins linéaires, des microphotographies et des listes bibliographiques plus ou moins longues selon l'importance des groupes traités. Sans doute, on peut juger insuffisant le traitement des classes d'organismes aussi nombreux et complexes que les champignons et les algues, mais on doit comprendre que ces indications peuvent au moins aiguiller l'utilisateur vers des ouvrages plus spécialisés. En revanche, les nombreux chapitres sur les bactéries, les levures, et les virus nous semblent aussi élaborés que possible dans un ouvrage de ce genre, et comprennent des tableaux sur les mensurations et autres traits qui peuvent conduire à l'identification précise. La partie réservée à la méthodologie paraît aussi adéquate autant par le choix des techniques que par la concision des méthodes d'étude, de purification des cultures et de conservations des microorganismes vivants. Enfin, comme dans les autres manuels de cette série, les éditeurs ont consacré quelques 70 pages aux renseignements généraux utiles tels qu'un glossaire, les normes bactériologiques des eaux potables aux États-Unis et ailleurs, les règles de nomenclature et quelques tableaux de conversion.

Réunir sous une seule couverture toute cette matière, généralement éparse dans les nombreux ouvrages de diverses spécialités, constitue une gageure que les éditeurs et les rédacteurs ont su relever et le résultat de cet effort remarquable sera fort apprécié dans la plupart des laboratoires voués à l'une ou l'autre des facettes de la microbiologie. Certes, les spécialistes pourront offrir des critiques constructives, car un ouvrage de ce genre reste perfectible quant à sa présentation et doit se rénover périodiquement quant à son contenu.

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WAY, D.S., 1973. **Terrain analysis.** A guide to site selection using aerial photographic interpretation. John Wiley & Sons, New York. viii + 392 p., 253 fig., 99 tab. 28.5 × 22 cm. Relié, $29.50.

Dans cette première décade de prise de conscience de l'environnement, l'ouvrage du professeur Way se révèle une pièce à conviction fondamentale pour triompher des résistants de la vieille garde en leur faisant comprendre la nécessité des analyses de terrain sérieuses comme base valable à la recherche de solutions aux problèmes de plus en plus nombreux qui assaillent les dirigeants à tous les niveaux de gouvernement. L'exploitation stupide des richesses naturelles et une certaine inconscience collective à détruire le milieu où à le polluer, que ce soit par des déchets chimiques déversés par milliers de tonnes dans les cours d'eau ou simplement par un geste irréfléchi de l'automobiliste qui déverse sur la place publique le contenu du cendrier de sa puissante américaine, ont engendré une situation qu'il faut maintenant corriger par une utilisation rationnelle des ressources et un aménagement harmonieux du territoire.

Malgré des progrès accomplis dans quelques ministères, il reste encore beaucoup à faire pour tirer pleinement profit des études de terrain basées sur la géomorphologie et la photo-interprétation. Pourtant le cadre de référence minérotrophique se révèle fondamental pour assoir toute étude écologique sérieuse, comme l'a démontré entre autre l'étude du Saguenay-Lac-Saint-Jean, et celle-ci constitue la seule base valable pour un aménagement intégré et harmonieux des ressources. De plus en plus de gens en sont convaincus bien que certains « papes » de l'écologie et de l'aménagement continuent à dogmatiser et à proner des méthodes vétustes. Par ailleurs la formation donnée aux jeunes dans la plupart des universités demeure souvent insatisfaisante, de sorte que la communauté manque de spécialistes compétents.

L'ouvrage se divise en deux parties; l'une assez théorique et générale, (chapitres 1 à 5), l'autre essentiellement pratique (chapitres 6 à 11). Dans le premier chapitre l'auteur définit sa conception de l'analyse du terrain basée sur l'interprétation des formes et des dépôts à l'aide des photographies aériennes verticales et définit les éléments par lesquels les formes et les dépôts meubles peuvent être identifiés. Les chapitres 2 et 3 contiennent des données de base générales sur les processus géologiques et les sols. Dans le chapitre 4, l'auteur indique les sources de documentation et les types de photographies existant, puis au chapitre 5, il fait une brève revue des applications ou des résultats obtenus de l'analyse du terrain, notamment dans l'optique de la construction de routes, d'égoûts, d'aqueducs, de fosses septiques, de barrages ou lacs artificiels, la recherche de sources d'approvisionnement en matériaux de construction (sable, gravier, pierre), etc. Dans les chapitres 6 à 11, il fait l'analyse des diverses formes de terrain et des dépôts rencontrés dans les roches sédimentaires, ignées et métamorphiques, et dans les milieux glaciaire (63 p.), éolien (22 p.) et fluviatile (71 p.) Ce dernier chapitre déborde largement le cadre fluviatile, puisque l'auteur y traite aussi des deltas, des dépôts organiques, des plages et des estrans (*tidal flats*). L'ouvrage est complété par un glossaire de 214 termes ou expressions, d'appendices sur les services de conservation et de cartographie du sol aux États-Unis et d'un index général de 6 pages.

Pour chaque type de roche et de dépôt, l'auteur fournit des renseignements pertinents en rapport avec la qualité du site, les avantages et désavantages, les impératifs de son aménagement, les qualités et les défauts pour la construction des égouts, des dépotoirs, l'excavation, l'approvisionnement en eau potable, en matériaux de construction, les dangers de glissements de terrain, la construction de routes, l'aménagement de belvédères, etc. Il fournit aussi une clé d'interprétation sous forme de tableau commenté dans le texte. Un extrait de la carte topographique accompagne chaque cliché stéroscopique.

L'ouvrage est abondamment illustré : figures au trait fin, blocs diagrammes, cartes et photographies aériennes verticales en couples permettant la vision stéréoscopique. L'échantillonnage des photographies aériennes se révèle relativement bon quoique quelques exemples soient plutôt mal choisis. Les 63 clichés stéréoscopiques sont à des échelles variées : 21, au total, allant de la grande échelle (1/2 000) à la moyenne (1/69 000) ; toutefois plus de la moitié (57%) sont à l'échelle de 1/20 000. Leur origine est essentiellement américaine : 93% provenant de 30 états.

Ce serait induire le lecteur en erreur que de lui laisser croire en l'absence de lacunes ou de failles. On en trouve suffisamment pour altérer la qualité générale de l'ouvrage. Néanmoins, nous croyons que le lecteur pourra oublier assez facilement les nombreuses fautes typographiques (p. 84, 94, 199, 202, 228, 295, 316), les clichés trop ou pas assez contrastés ou même flous (p. 115, 165, 167, 272-273), les figures trop grandes ou ratées (p. 77, 243, 249), les commentaires trop laconiques accompagnant les photographies aériennes, l'absence de croquis géomorphologiques tirés de l'interprétation des photographies, l'imprécision des figures de généralisation (p. 19, 80, 140, 204, 292), les affirmations générales manquant de nuances (p. 263), et le vocabulaire parfois abusif voire même incorrect. Ainsi, parler de «*wind-drift dunes*» pour les dunes paraboliques, nous paraît un pléonasme, puisque toutes les dunes sont dues au vent; placer côte-à-côte des barchanes et des paraboliques (fig. 10.7, p. 269) nous semble une erreur grossière car les deux ne se forment pas aux mêmes endroits et de la même manière. L'auteur cite en exemple la coulée boueuse de Nicolet survenue en 1965 (sic); il faut lire 1955. Il est dit dans la légende de la figure 6.40 (p. 125) représentant un synclinal que «*The oldest beds are in the center of the fold*»; c'est le contraire qui est vrai, si l'auteur entend par là les couches qui affleurent.

Ce livre pourra décevoir le spécialiste parce qu'il ne va pas assez loin. Justement, il ne lui est pas destiné, mais s'adresse avant tout au débutant qui désire acquérir les notions fondamentales pour l'analyse du terrain. Dans cet optique, c'est un ouvrage bien fait, généralement bien informé, contenant des données de base valables et possédant des qualités pédagogiques. Il rendra d'utiles services non seulement aux étudiants en génie civil, géographie et géologie, mais aussi à plusieurs autres disciplines comme la foresterie, la pédologie, l'urbanisme et l'hydrologie. Nous le recommandons volontiers aux étudiants des premier et second cycles universitaires et même aux cégépiens. Son prix relativement élevé pourrait en limiter la diffusion.

Des ouvrages comme celui-ci permettent de constater le chemin parcouru par les géomorphologues depuis qu'ils ont abandonné la chasse aux insaisissables surfaces d'érosion, aux buttes témoins et à la néotectonique au profit d'analyses pratiques du terrain. Malheureusement ceux qui ont rendu rentable la géomorphologie demeurent peu nombreux et font souvent l'objet de critiques sévères de la part d'académiciens attardés. Par ailleurs un certain nombre d'amateurs ont ouvert des bureaux pour effectuer ce genre d'études avant même d'avoir acquis les connaissances suffisantes et la formation appropriée. On peut craindre non seulement l'insatisfaction de ceux qui leur accordent des contrats, mais aussi un certain discrédit dont les autres auront à souffrir. À ces amateurs, nous conseillons fortement de se faire la dent en étudiant à fond l'ouvrage de Way. Un bon vernis peut cacher bien des défauts.

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SCHUMANN, W., 1973. **Pierres et minéraux.** Delachaux et Niestlé, Neuchâtel/Suisse. 227 p., 306 photos en couleurs. 12.5 × 19 cm. Relié-carton, $10.00.

Au cours des deux dernières années plusieurs ouvrages de minéralogie abondamment illustrés de planches en couleurs ont été publiés. Le livre de Walter Schumann s'ajoute à cette liste et se classe parmi les mieux réussis.

Le but de ce livre est de mettre à la portée de tous le monde des pierres. L'auteur vise à atteindre son objectif en utilisant plus de 300 photos en couleurs bien réussies exposant la beauté des pierres. Chaque illustration est accompagnée d'une description en page opposée, ce qui permet une étroite liaison entre texte et illustration. L'arrière-plan des planches est de différentes couleurs et a été judicieusement choisi pour mieux exprimer les couleurs réelles des minéraux et des roches.

L'ouvrage réunit 4 sections principales qui traitent: a) des minéraux, gemmes et pierres précieuses, b) des roches, c) des minerais, d) des fossiles. On y retrouve, en plus des conseils pour collectionneurs, des tableaux de détermination des minéraux et des roches et un index détaillé. Les minéraux, gemmes, minerais, roches et fossiles décrits dans ce livre correspondent à ceux que le promeneur peut trouver sur le terrain ou acheter.

L'auteur ne s'est pas limité à présenter un recueil de magnifiques photos accompagnées de brèves descriptions précises; il expose au début de chaque section un résumé de notions et de principes permettant une information plus complète. Ce livre n'est pas un traité de minéralogie, cependant les nombreuses photos en couleurs et les textes fournissent une information rapide à des collectionneurs tout en leur permettant de reconnaître les différentes pierres et de les classer.

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IVERSEN, J., 1973. **The development of Denmark's nature since the last glacial.** Geological Survey of Denmark, Series 5, No 7-C, Geology of Denmark 3, 1 volume, 126 p., 77 fig., 5 photographies et 2 gravures en couleur. C.A. Reitzel, Copenhague. Relié, 60 couronnes danoises.

Le professeur Johannes Iversen mourait, le 17 octobre 1971. Pendant près de quarante ans, il fut la figure de proue de l'analyse pollinique en Europe du nord-ouest. Knut Faegri, de Bergen, Norvège, avec qui le professeur Iversen écrivit son fameux *Textbook of modern pollen analysis* qui devait demeurer la référence essentielle de l'analyse pollinique mondiale, s'est chargé de la notice nécrologique de ce grand homme (Pollen et spores, 13 (3)). Faegri commente en ces termes une des dernières œuvres du professeur Iversen: "*It is a master's synthesis of investigations in an* *area where the level and sophistication of pollen-analytic knowledge is higher than in any other country, not least because of the work performed or inspired by himself. Being written in Danish and published in this context, it is unfortunately not available to many readers outside the country, which can only be deplored."* Le Dr. Svend Th. Andersen, qui succéda au professeur Iversen à la direction du Département de paléobotanique de la Commission géologique du Danemark, a réalisé l'édition anglaise de cette œuvre admirable. Il la rendait ainsi accessible à l'ensemble de la communauté scientifique.

Il s'agit d'une vaste fresque, écrite dans une langue claire et vivante, décrivant les différentes facettes de l'évolution de l'environnement du Danemark depuis la dernière glaciation. L'auteur est un des rares palynologues à posséder une vision vraiment écologique de l'histoire des derniers 20 000 ans. Bien sûr, il relate les divers changements dans la végétation, en passant par les périodes bien connues du tardi-glaciaire, puis du Pin et de Bouleau, du Pin et du Noisetier, du Tilleul, du Hêtre; elles forment autant de chapitres. Mais pour chacune, l'auteur décrit la vie animale, les conditions climatiques, les sols, en un tableau d'un réalisme étonnant. Sur ce canevas, l'auteur reporte les activités humaines pré-historiques et proto-historiques, sans négliger l'action qu'elles ont exercée sur les changements de l'environnement. Mais pourquoi tenter de rendre si maladroitement le contenu de ce chef-d'œuvre! Ne suffirait-il pas de dire qu'on croirait, à la lecture, assister au déroulement des événements décisifs de l'Holocène du Danemark!

Pour les québécois, l'intérêt de ce livre réside dans la grande similitude des événements qui ont marqué les territoires du Québec et du Danemark depuis la dernière glaciation. Malgré des différences évidentes, le déroulement du retrait des glaces et de l'immigration des éléments floristiques s'est effectué selon des modalités analogues. Tous les quaternaristes trouveront plaisir à lire ce volume principalement les écologues, les botanistes et les archéologues. Reste à souhaiter qu'un jour, une œuvre semblable vienne dépeindre les derniers 13 000 ans de l'histoire naturelle du Québec.

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GAGNON, H., 1974. **La photo aérienne: son interprétation dans les études de l'environnement et de l'aménagement du territoire.** Éditions HRW, Montréal. 278 p., 50 fig., 187 photos, 8 pl. couleurs. 21,5 × 28cm. Broché, $16,50.

Le premier ouvrage traitant de la photo-interprétation à être publié au Québec vient d'être lancé par les éditions HRW de Montréal. Il convient de signaler l'événement si l'on considère la position défavorisée de la minorité francophone nord-américaine qui doit se nourrir soit d'ouvrages européens rédigés en français, soit d'ouvrages anglophones principalement américains. Les étudiants québécois disposent maintenant d'un manuel de base de bonne qualité pour une initiation valable à la photo-interprétation.

L'auteur, géographe de profession, a conçu son ouvrage dans une optique assez large quoique axée sur l'aménagement du territoire. Dans les deux premiers chapitres, il rappelle des notions élémentaires. Il définit d'abord la nature même de la photo-interprétation en précisant qu'elle comporte cinq opérations fondamentales distinctes, mais intimement reliées les unes aux autres, à savoir la détection, l'identification, l'analyse, la déduction et la classification. Les troisième et quatrième opérations sont probablement les plus importantes et confèrent à cette technique devenue populaire son originalité. Il ne saurait y avoir de véritable photo-interprétation sans analyse et déduction. Identifier une forme ou un objet quelconque à partir d'une photo constitue nullement un acte de photo-interprétation. C'est la signification de cette forme ou de cet objet qui constitue l'essence même de la photo-interprétation et qui rend d'incomparables services aux utilisateurs. Mais avant de procéder aux diverses opérations nécessaires à l'interprétation, il importe de connaître quelques notions de base sur la nature et les propriétés des photographies aériennes notamment la géométrie de la photographie aérienne, l'observation stéréoscopique, l'émulsion photographique, les éléments variables des photographies (teinte, texture, etc.) et les facteurs de modification des variables photographiques. L'auteur rappelle fort pertinemment (p. 4) qu'il n'existe à peu près pas de photo-interprètes universels, car à la base même de cette technique, il faut que l'utilisateur possède des connaissances dans la discipline impliquée. Il y aura donc des géographes, des géomorphologues, des forestiers, des pédologues interprètes, etc. Seule une longue expérience et des connaissances dans plusieurs disciplines peuvent conduire au métier de photo-interprète proprement dit.

Gagnon attache une grande importance à l'analyse des formes du relief (p. 23-77); il considère qu'à la base de tout travail d'inventaire des ressources, d'écologie et d'aménagement rationnel de l'espace, se situent l'analyse du relief et l'étude de ses processus de formation. Tout travail sérieux d'aménagement du territoire doit, au départ, classifier les ensembles géomorphologiques afin d'établir scientifiquement les zones d'utilisation potentielle. Comme membre d'une équipe multidisciplinaire d'inventaire écologique qui accorde à la géomorphologie une place de choix, nous appuyons entièrement cette affirmation. Il faut se garder, toutefois, de tomber dans le piège en concevant la géomorphologie comme un objectif en soi, alors qu'elle constitue un moyen ou un des maillons de la chaîne des opérations à accomplir.

L'auteur aborde ensuite l'étude de l'occupation de sol (chapitre 4), l'affectation des sols (chapitre 5) et la délimitation des régions homogènes (chapitre 6). Il présente aussi des considérations sur l'incidence historique et socio-économique de la photo-aérienne (chapitre 7) avant de démontrer que la photo-interprétation peut aider à la prévention de catastrophes naturelles ou empêcher une mauvaise utilisation des ressources et du milieu (chapitre 8); l'exemple éloquent des glissements de terrain sert à la démonstration. Dans le dernier chapitre, il aborde la question des nouvelles techniques de télédétection: photo-infrarouge, photo-radar, photographies de haute altitude transmises par satellites, senseurs à balayage multibandes, etc. Si ces divers progrès techniques permettent les plus beaux espoirs, il faut reconnaître qu'actuellement les résultats pratiques obtenus demeurent modestes. Dans la plupart des cas, on en est encore à la phase expérimentale.

En conclusion, l'auteur discute brièvement des implications économiques et pratiques de la photo-interprétation en soulignant quelques domaines spécifiques où la photo-interprétation a rendu d'utiles services et fait faire de substantielles économies de temps et d'argent. Le lecteur averti trouvera probablement peu convaincante cette démonstration plutôt mal documentée. Une bibliographie choisie (6 p.) et un glossaire laconique (2 p.) complètent l'ouvrage.

Dans l'ensemble, ce manuel de base de premier et second cycle universitaire est de bonne qualité et est relativement bien rédigé. L'illustration y est abondante, relativement bien choisie et assez variée, quoique de qualité fort inégale. Malheureusement une trentaine de clichés de qualité pauvre à médiocre altèrent sa valeur générale. Dans une prochaine édition, il conviendrait de remplacer ou d'enlever les figures ratées comme celles de la page 135. Il paraîtra étonnant, mais significatif à plusieurs, que 70% des photographies aériennes verticales offertes en exemple sont des photographies simples ne permettant pas la vision stéréoscopique. Diverses raisons peuvent expliquer ce choix. La question du coût de reproduction ne semble pas à elle seule justifier cette option puisque plusieurs clichés de grandes dimensions présentent un intérêt limité ou sont parfois des répétitions, notamment les photographies illustrant les glissements de terrain de Saint-Jean-Vianney et de Saint-Jérôme-de-Métabetchouane (p. 206 et 224). Le choix des photographies met le Québec en vedette, puisque 78% d'entre elles illustrent des portions de la Terre-Québec contre 10% par l'Ontario et 5% respectivement pour les Maritimes et l'Arctique canadien. Les légendes accompagnant les photographies sont souvent trop laconiques et obligent le lecteur à retourner au texte pour découvrir la justification de plusieurs d'entre elles. Par ailleurs, l'échelle des photographies n'est pas indiquée, ce qui se révèle gênant pour l'utilisateur. L'auteur aurait eu avantage aussi à indiquer sur les photographies, par un symbole quelconque, les phénomènes qu'il voulait mettre en évidence.

Somme toute, voici un ouvrage typiquement québécois qui ne manquera pas de capter l'attention de ceux qui s'intéressent à l'espace terrestre. Son prix modique le met à la portée de la plupart des étudiants. Nous n'hésitons pas à le recommander à ceux qui œuvrent dans le domaine des sciences de la terre, en particulier à ceux qui s'intéressent à l'environnement et à l'aménagement rationnel des ressources.

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AHMADJIAN, V. and M.E. HALE, (Editors), 1973. **The Lichens.** Academic Press, New York and London. xiv + 697 p. 16 × 23,5 cm. Clothbound, $35,00 U.S.

This book, a companion volume of Ainsworth and Susman: *The Fungi*, is the most comprehensive treatise on lichens to date and will be indispensable to anyone with a serious interest in these organisms or symbiotic systems in general. The editors are to be congratulated on finding authors for the nineteen chapters and three appendices, which mostly reach a commendable standard of excellence. Topics that might have been expected to be represented but are not, are those concerning the chemo-taxonomy of lichens, their phytosociology and phyto-geography. A key to the genera of lichens would also have been useful. The volume is not, however, integrative as the dust cover suggests; cross-references to other chapters often appear to have been added by the editors. The difficulties of producing a truly integrated text in the first edition of a multi-authored book such as this are almost insurmountable but this should be the primary aim of future editions which the editors hope will be forthcoming.

The chapters are divided into five parts, the first of which Structure and Development would have been more accurately titled Structure and Reproduction. It opens strongly with an article by Jahns on anatomy and morphology and is logically followed by Letrouit-Galinou's account of sexual reproduction in lichens. This contribution relies almost exclusively on the findings of French workers on ascus and ascocarp structure, and it remains for Poelt in the following article on the systematic evaluation of morphological characters to place these results in the context of Scandinavian, British and North American work in the field. The principles expounded in this excellent chapter are applied in the appendix (A) on classification, also written by Poelt. The section is completed with a contribution on fine structure by Peveling in which the micro-structure unique to lichens is emphasised.

Part II, Physiology of the Intact Thallus, commences with the chapter by Tuominen and Jaakkola on the absorption and accumulation of mineral elements and radioactive nuclides and is in many respects the most thought provoking chapter of the entire book. Other chapters in the section include one on photosynthesis and carbohydrate movement, another on nitrogen metabolism and a fourth by Syers and Iskandar on the pedogenic significance of lichens. This latter would have been more appropriately placed in Part III, Environmental Response and Effects. On the other hand Part II would have been strengthened further by the inclusion of the chapter on water relations by Blum. The third section begins on an unfortunate note with a statement at the beginning of the chapter on the response of lichens to extreme environments. To quote, "The question of what constitutes an extreme environment is difficult to answer. It could mean that habitat conditions are extreme for all organisms or... that conditions are extreme only for lichens." Or it could mean an extreme environment for only one species of lichen. The title has anthropomorphic overtones and should be ignored as the author wisely concludes. "This chapter will review the physiological and morphological responses of lichens to the most important environmental factors and consider the relationship of these factors to lichen distribution." It is a pity that it takes Kappen 69 pages to do this but he has served us well with an exhaustive eleven page list of references. After the chapter by Blum there follows another strong chapter by Brodo on substrate ecology in which the multi-variate nature of the problem and the effect of limiting factors are clearly recognized. This part of the book is concluded with chapters on air pollution and growth by Gilbert and Hale respectively.

Part IV concerns the secondary metabolic products of lichens and it will be of no surprise to learn that lichen acids receive the most attention. Chapters by Huneck and Mosbach deal with the nature and biosynthesis of lichen substances and in a third chapter on the antibiotic properties of lichen acids it is concluded that the use of lichens in folklore medicine has to a remarkable extent been quite logical. Appendix (B) by Johan Santesson on the identification and isolation of lichen substances completes the contributions on this topic. The fifth and final Part on Symbiont Interactions contains two papers. The first on the resynthesis of lichens is complimented by Appendix (C) dealing with methods of culturing the isolated symbionts and of recombining them, both authored by Ahmadjian. The final article by Scott on the evolutionary aspects of symbiosis is stimulating but suffers more than any other contribution from the lack of integration with the rest of the text; there is not a single reference to the preceding chapters.

The question might well be asked as to whether this volume tells us anything that is fundamentally new about the lichen symbiosis. The answer must be that it does not, at least not explicitly, but then perhaps it was not supposed to. An important and novel aspect of the study of the lichen symbiosis is, however, hinted at in a number of articles. Tuominen and Jaakkola are the most specific. "In principle, the uptake of metal cations is divided into the passive, physicochemical phase and an active phase that depends on metabolic sources of energy." The passive process is characterised by the reversible binding of cations and has therefore been amenable to analysis in terms of equilibrium thermodynamics. The elucidation of active uptake, if it occurs, is altogether more problematical and the authors suggest that it should be studied from the point of view of steady-state (irreversible) thermodynamics, since it is not a reversible process. Physiological immobilisation of cations, implying active translocation within the lichen has been demonstrated by comparing the responses of dead and living tissues. Blum also suspects that active processes influence water relations while Kershaw and Millbank believe that evidence from nitrogen metabolism suggests "controlled" (active?) parasitism of the alga by the fungus. Although Richardson in his lucid article on photosynthesis and carbohydrate movement emphasizes that it is still not certain whether the role of the fungus is active or passive in carbohydrate transfer, a new method is suggested which is dependent on the higher membrane potential of the mycobiont which is again indicative of an active process.

If active processes really are at the foundation of the lichen symbiosis then it cannot be assumed that we will learn more about the nature of the symbiosis by studying the component physiological systems in isolation and then regarding the lichen as a vector sum of the components. This approach has its logical basis in the belief that all chemical and biological phenomena are explainable in purely physical and mechanistic terms, a view to which few physicists would now subscribe. It is only valid where passive, reversible processes predominate. The understanding of irreversible systems, which include the directional phenomena of cell and tissue differentiation, growth, ecological succession and evolution, is perhaps the most important problem of biology to-day. With the increasing ability to culture lichens for extended periods of time these holobionts, characterised by relatively few differentiated tissues, may offer an unique opportunity for the study of steady-state processes.

Publication of *The Lichens* marks a new era in lichenology. Hitherto it has, in the main, been possible for lichen taxonomists, physiologists, morphologists and ecologists to follow progress in all fields. With the rapidly increasing knowledge of lichens it will be more difficult to do this in the future. It remains to be seen whether lichenologists will follow the well trodden path of reductionism, accumulating a vast knowledge of details while some of the most basic processes of life remain obscure, or whether they will take a more holistic approach in their attempts to understand the fundamental processes which have led to and maintain the unique symbiotic state characteristic of the lichens. Acceptance of this challenge could lead to results with implications beyond the lichen association and possibly beyond biology as well.

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WHITTAKER, R.H., (éditeur), 1973. **Ordination and classification of communities.** *Handbook of vegetation science*, part 5. Dr. W. Junk, The Hague. x + 738 p., 40 tab., 91 fig. 16 × 25cm. Relié-toile, 16,00 Guilders.

KNAPP, R., (éditeur), 1974. **Vegetation dynamics.** *Handbook of vegetation science*, part. 8. Dr. W. Junk, The Hague. xii + 368 p., 7 tab., 15 fig., 15 photos. 16 × 25cm. Relié-toile, 85,00 Guilders.

Le *Handbook of vegetation science* est édité par le Professeur Reinhold Tüxen. Il comprend 18 volumes consacrés à la publication des mises au point sur le savoir et les méthodes de recherche en phytosociologie. Les articles, provenant des auteurs du monde entier, et de tendances diverses, sont regroupés, sous l'autorité d'un éditeur, en fonction de leurs affinités dans des volumes autonomes.

Dans cet esprit, le volume 5 traite de l'*Ordination et de la classification des communautés*. L'ordination et la classification constituent une étape importante de l'étude de la végétation permettant d'effectuer le passage des données du terrain à la généralisation. Cette dernière étant, à son tour, indispensable aux applications pratiques. Il s'agit probablement du premier volume réunissant et évaluant les développements récents dans le domaine de l'ordination, incluant les techniques russes, et faisant en même temps, le point sur les techniques de classification de la méthode de Braun-Blanquet.

Quant au volume 8 de la série, il est consacré à la *Dynamique de la végétation*. La connaissance des tendances évolutives de la végétation est nécessaire lorsqu'on veut assoir les travaux d'aménagement et de protection sur une base rationnelle. Les successions secondaires sont dans ce sens spécialement importantes. Le volume débute par une discussion des différents types d'évolution, passe en revue les méthodes utilisées, pour leur étude, en examine les causes et la classification pour traiter, finalement, les questions de la productivité des divers stades. Le livre se termine par 63 pages de références bibliographiques et un index des matières.

Les deux volumes méritent leur place dans toute bibliothèque sérieuse comprenant une section d'écologie végétale.

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GUINOCHET, M., 1973. **Phytosociologie.** *Collection d'écologie*, 1. Masson, Paris. vi + 227 p., 36 fig., 9 tab., et 1 carte en couleurs hors-texte. 16,5 × 24cm. Broché, prix non indiqué.

LONG, G., 1974. **Diagnostic phyto-écologique et aménagement du territoire.** I. Principes généraux et méthodes. *Collection d'écologie*, 4. Masson, Paris. 252 p., 39 fig., 16 × 24 cm. Broché, prix non indiqué.

La *Collection d'écologie* éditée par la maison Masson de Paris, vient de s'enrichir de deux ouvrages importants consacrés à l'étude de la végétation.

Le premier, intitulé *Phytosociologie*, est l'œuvre du Professeur Guinochet, spécialiste renommé de la science de la végétation. Il s'agit d'un traité portant sur les méthodes phytosociologiques classiques et numériques, sur la dynamique et la systématique des associations végétales, sur les relations de ces dernières avec les facteurs édaphiques, climatiques et biotiques et sur le déterminisme, l'évolution et la genèse des associations végétales.

Le second ouvrage est consacré aux applications de la phyto-écologie en aménagement du territoire. Il comprend deux parties. Dans une première, l'auteur examine les bases théoriques de l'approche phyto-écologique générale alors que la deuxième traite de la cartographie des écosystèmes et du milieu naturel.

Ces deux livres sauront intéresser autant les étudiants que les enseignants préoccupés par les problèmes de l'étude et de l'aménagement de la végétation.

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SMITH, G.J.C., H.J. STECK and G. SURETTE, 1974. **Our ecological crisis.** Its biological, economic & political dimensions. Collier-Macmillan Canada, Don Mills, Ont. ix + 198 p. ill. 15.0 × 23.5 cm. Broché, $3.25.

Depuis le livre de Rachel L. Carson *Silent Spring* qui fut le point de départ des mouvements écologiques aux États-Unis, jusqu'au rapport du Club de Rome qui internationalisait la crise écologique menaçant l'humanité, le public, surtout anglo-saxon, se trouve devant une littérature traitant de la dégradation toujours plus abondante de son environnement.

Ce livre, selon le vœu des auteurs, est destiné au grand public des non spécialistes qui cherchent des éléments pour comprendre le développement de la crise écologique. Cette crise, du point de vue des auteurs, ne doit pas être réduite à des problèmes de pollution, mais elle résulte directement de «l'écologie sociale» de l'homme et est dépendante de la structure de la société aussi bien que de la culture, technologie, etc.

Les auteurs globalisent la crise. Cette tentative est intéressante et souvent originale, car l'écologie est aussi l'étude des relations entre l'homme et la nature et par là entre l'homme et l'homme. Nous ne pouvons plus définir de milieu dans la biosphère où l'homme n'intervient pas directement ou indirectement. Il faut que l'homme retrouve sa place dans un système écologique cyclique et non plus linéaire qui fournisse une accumulation de déchets et de pollutions, ainsi que des consommations d'énergie non renouvelables toujours plus vastes pour maintenir le système. On doit trouver un modèle alternatif à celui de la croissance continue. Ces thèses de départ sont exposées dans l'introduction.

La démonstration et le développement ont été divisés en trois centres d'intérêts (écologie, économie et politique) dont chacun des auteurs a rédigé une partie.

La première partie rédigée par G.S.C. Smith est une introduction à l'écologie. Dans une cinquantaine de pages, l'auteur réussit à donner au lecteur non spécialiste une vue assez complète, lui permettant de comprendre: la structure et le fonctionnement des écosystèmes, les cycles écologiques et la pollution, les lois gouvernant la croissance des populations, l'effet des différents polluants (pesticides, métaux toxiques et radiations) ainsi que les interactions de ces polluants. Le dernier paragraphe traitant des océans montre que les ressources de ce milieu sont loin d'être illimitées comme le laissait entendre une certaine presse.

Dans la deuxième partie, G. Surette analyse la nature du système économique et culturel qui contribue à la dégradation de l'environnement, si bien que ce chapitre n'étudie pas les coûts-bénéfices de l'antipollution mais examine plutôt la structure du système économique. L'économie prend comme vérité première que la nature de l'homme est à l'accroissement de ses biens matériels, si bien que cet accroissement est théoriquement indéfini alors que les ressources sont finies, d'où crise. G. Surette nous montre que cette vérité première a ses racines dans les doctrines religieuses, le système d'éducation et la culture. L'économie des marchés qui en découle favorise une concentration des pouvoirs de décision, de la production et de la technologie dans quelques firmes concurrentielles qui par leur nature même ne peuvent lutter contre la pollution. Malgré sa complexité, cette étude reste compréhensible grâce à un enchaînement clair et logique de l'argumentation. Mais comment sortir de ce cercle? Peut-être grâce à l'acceptation de la non croissance et la distinction entre désirs et besoins; encore faudrait-il un changement dans les processus de la production et de la décision comme le suggère l'auteur.

Dans la troisième partie, M.J. Steck examine la réponse des différentes administrations américaines qui se sont succédées au pouvoir depuis F. Roosevelt jusqu'à R. Nixon. Cette étude est très largement documentée, et le lecteur intéressé y trouvera de nombreuses références. L'auteur répond dans ce chapitre à un certain nombre de questions. Le système politique est-il capable de lutter contre la dégradation de l'environnement? Quels ont été les éléments moteurs dans l'établissement des lois anti-pollution (partis politiques, groupes de pression ou individus)? Ces lois sontelles suffisamment contraignantes...?

Ce livre relativement court donne au lecteur des éléments assez sûrs pour comprendre la crise écologique dans tous ses aspects. La bibliographie citée à la fin de chaque chapitre est intéressante et permet au lecteur motivé d'approfondir ses connaissances. Les auteurs ont réussi tout au long de ce livre à éviter deux écueils, la «tragédie journalistique» et l'exposé scientifique trop austère. On peut regretter que les deux dernières parties n'aient pas fait l'objet d'une rédaction commune qui aurait permis l'approfondissement de certains points et donné plus de poids à quelques démonstrations, car comme le montrent les auteurs dans de nombreux exemples, les frontières entre l'économique et le politique sont parfois bien tenues dans la société américaine. Les problèmes soulevés tout au long de ce volume dépassent très largement les frontières américaines, leurs solutions ne pouvant être trouvées à l'intérieur d'un seul pays, du fait que cette crise écologique est une menace pour la biosphère entière. À une période où la crise de l'énergie annonce le reflux de nombreux groupes de défense de l'environnement, ce livre tombe au fait, et peut-être comme le souhaitent les auteurs, permettra-t-il à chaque lecteur de prendre conscience et de comprendre sa vie dans des perspectives écologiques.

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MASTERS, M., 1974. **Introduction to environmental science and technology.** John Wiley & Sons, New York. xii+404 p., ill. 15,5×23,5 cm. Relié, prix non indiqué.

Ce livre se situe dans la meilleure tradition du *textbook* américain, en ce sens qu'il ne se borne pas à faire le point sur l'état des connaissances dans un domaine, mais tente plutôt de réaliser une synthèse originale. Le manuel s'adresse à ce public étudiant et professionnel, de plus en plus nombreux, qui cherche des solutions technologiques aux problèmes de l'environnement, solution que l'on tend à inscrire dans le cadre des grands équilibres écologiques.

L'auteur cherche à établir le pont entre les trois grands pôles du domaine de l'environnement: l'écologie, la technologie et l'idéologie. À ce propos, Masters semble faire partie de ces intellectuels américains qui ne refusent aucune question, mais pour qui les solutions consistent en une amélioration du système plutôt qu'en son changement radical.

L'ouvrage est divisé en quatre parties: écologie et population, pollution de l'eau, pollution de l'air, énergie et matières premières. La première section est assez décevante pour l'écologiste, puisqu'elle se limite aux concepts les plus classiques de l'écologie et de la dynamique des populations; le lecteur peu familier avec ces concepts lira cependant avec profit les trois chapitres de cette introduction. Notons que cet exposé présente tout de même une certaine originalité en ce qu'il débouche sur la démographie et l'écologie humaine, ouvrant ainsi de nombreuses perspectives qui seront exploitées dans les chapitres subséquents.

Les deux sections suivantes, sur la pollution de l'eau et de l'air, suivent un plan similaire: identification des sources de pollution, action des polluants sur le milieu, technologie du contrôle de la pollution. De très nombreux exemples, tirés de la situation américaine, illustrent aussi bien les cas de pollution que les solutions envisagées.

La dernière section traite du problème crucial de l'énergie et des matières premières. Après une revue de la situation énergétique et des perspectives à moyen terme, l'auteur examine la production d'énergie électrique par les centrales classiques et nucléaires, pour déboucher sur les sources nouvelles et futures d'énergie. Le chapitre sur les matières premières se situe dans la perspective du Club de Rome et les solutions proposées s'inscrivent dans le cadre d'un ralentissement, considéré comme inévitable, de la croissance. Les implications économiques et politiques des différentes solutions, tant aux États-Unis qu'au plan international, sont dégagées sans toutefois que ressortent clairement les perspectives favorisées par l'auteur.

La présentation matérielle de l'ouvrage est excellente et l'illustration, très abondante, par suite notamment de l'option de l'auteur en faveur de ce mode d'exposition, de préférence à la formulation mathématique. Chacun des chapitres comporte une bibliographie ainsi qu'une série de questions; un index général facilite la consultation du volume.

Instrument didactique de qualité, ce manuel constitue en outre une bonne source de référence pour le professionnel intéressé aux principes écologiques du contrôle de la pollution; on ne saurait cependant se dispenser de la consultation parallèle d'un ouvrage d'écologie moderne.

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VAN DEN BOSCH, R. and P.S. MESSANGER, 1973. **Biological control.** Intext Educational Publishers, New York. xii + 180 p., ill. 15 × 22,5cm. Relié, $10,50; cartonné, $4,95.

Ce travail définit clairement les divers aspects de la lutte biologique. C'est un ouvrage de référence essentiel, non seulement pour les étudiants en entomologie, mais aussi pour tous ceux qui voudraient se familiariser avec les principes de base de ce domaine.

Les auteurs définissent d'abord le phénomène de la lutte biologique, puis discutent successivement des aspects suivants: (1) les concepts écologiques qui jouent un rôle de première importance dans la compréhension de la théorie de lutte biologique; (2) l'histoire et le développement de la lutte biologique, particulièrement en Amérique du Nord; (3) les agents qu'on utilise dans les programmes de lutte biologique, tel que les parasites et les prédateurs; (4) le protocole de l'introduction des agents exotiques pour la lutte biologique: notamment la recherche d'agents de contrôle possibles dans un climat et un écosystème correspondants, les règlements de la quarantine, la technique de libération de l'agent et l'évaluation de son efficacité après l'introduction; (5) les facteurs qui peuvent limiter le succès des agents exotiques, y compris une liste des programmes où la lutte biologique a échoué ainsi qu'une discussion des causes d'échec; (6) les programmes qui ont succédé (complètement ou partiellement); un certain nombre de programmes sont discutés en profondeur pour expliquer les différentes techniques et les types de problèmes qu'on peut rencontrer dans la lutte biologique; (7) la lutte contre les insectes nuisibles à l'aide de parasites et de prédateurs indigènes et l'interférence possible causée par des pesticides dans ce système; le concept de la lutte intégrée est présenté et plusieurs exemples sont discutés; (8) le potentiel de la lutte biologique contre les insectes nuisibles et les mauvaises herbes dans le futur.

Aussi, il y a les questions de revision, la bibliographie et les références additionnelles inclus à la fin de chaque chapitre, ainsi que le glossaire des termes techniques qui aideront le lecteur dans la compréhension de ce sujet.

Cet ouvrage répond à un besoin urgent que ces auteurs viennent de combler avec succès. Tout en étant complet, ce travail est exempt de détails trop techniques souvent rencontrés dans des ouvrages de ce genre.

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HOLZ, R.K., (éd.), 1973. **The surveillant science.** Remote sensing of the environment. Houghton Mifflin Company, Boston. XII + 390 p., 373 fig., 90 tab. 21 × 28 cm. Cartonné, $7,95.

Par ce recueil de 44 articles, provenant pour la plupart, de chercheurs dont la réputation n'est plus à faire dans le domaine de la télédétection, R.K. Holz nous propose un ouvrage dont nous analyserons davantage la conception et l'à-propos du choix des articles que le contenu.

La constatation première que fait le lecteur en lisant cet ouvrage, est la date de parution originale des articles proposés. Bien que publié en 1973, *The surveillant science* contient plus de 75% de textes parus entre 1960 et 1970, contre 25% postérieurs (10 exactement). Or, c'est bien au cours des cinq dernières années, et plus particulièrement depuis l'avènement des satellites ERTS-1 et, à un degré moindre, Skylab, que nous avons assisté à une véritable explosion de techniques nouvelles dans ce domaine. Aussi ne nous étonnerons-nous pas de trouver si peu d'articles mentionnant par exemple, le traitement automatique des images, technique actuellement bien acquise. Toutefois, certains articles laissent entrevoir les énormes possibilités que permettaient d'envisager les diverses utilisations d'un satellite comme ERTS-1, possibilités d'alors, qui sont, pour la plupart, devenues réalités d'aujourd'hui. Seule, la présence de l'article de R.B. Barnes (*Diagnostic thermography*), dont le thème illustre la couverture, nous a vraiment surpris dans un tel recueil: les applications médicales de l'infrarouge thermique n'ont qu'un rapport très éloigné avec les problèmes de télédétection de l'environnement. Mais le reproche essentiel que nous adressons à l'éditeur est de n'avoir pas reproduit une bonne partie des illustrations (graphiques et/ou photographies) auxquels renvoient les textes. Était-il trop coûteux ou trop malaisé de le faire? Toujours est-il que le lecteur acquiert un sentiment croissant de frustration, car certaines illustrations absentes sembleraient indispensables à une meilleure compréhension du texte. Dans ces cas, somme toute assez fréquents, n'y aurait-il pas eu lieu de demander à l'auteur de remanier son texte en conséquence, ou bien de choisir d'autres textes ne présentant pas cet inconvénient?

Malgré ces quelques restrictions, force nous est de reconnaître que R.K. Holz, dans la conception de cet ouvrage, suit une logique très simple, mais irréfutable. Il en est comme preuve, le bel enchaînement proposé pour les dix chapitres du volume: (1) présentation du spectre électromagnétique, (2) la télédétection ou les moyens d'obtenir de l'information sur un phénomène éloigné, (3) la télédétection dans l'ultra-violet, (4) la télédétection dans la partie visible du spectre électromagnétique, (5) la télédétection dans le proche infra-rouge, (6) la télédétection dans l'infra-rouge thermique, (7) la télédétection par micro-ondes passives, (8) la télédétection par radar (micro-ondes actives), (9) la télédétection multispectrale, (10) les implications sociales de la télédétection.

Dans l'ensemble, une abondante bibliographie accompagne chaque article, suivie, à la fin de chacun des dix chapitres, d'une liste de lectures suggérées, articles ou volumes de références, ceux-ci venant en complément du thème traité dans le chapitre.

Paru cinq ans plus tôt, ce volume aurait reçu, sans aucun doute, un accueil enthousiaste. Cependant, s'il vient irrémédiablement trop tard pour le chercheur en quête des dernières techniques, il devrait encore trouver place dans la bibliothèque de tout étudiant et tout enseignant concernés par les problèmes de l'environnement. En effet, ce ne sont malheureusement pas les cours sur la télédétection dispensés dans les universités québécoises francophones qui leur permettront d'acquérir les indispensables connaissances de base. Cet ouvrage vient donc à point nommé, j'en suis sûr, pour combler une partie de cette lacune, d'autant plus que son prix modique nargue les ravages de l'inflation...

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ANDREWS, N.A., (éditeur), 1973. **Soil ecology.** *Series in studies of the environment.* Prentice-Hall of Canada, Scarborough, Ontario. v + 198 p. 17,5 × 23 cm. Broché, prix non indiqué.

L'éditeur Andrews a su présenter un livre d'écologie du sol qui saura être formateur aux gens s'intéressant à cette jeune science. Après avoir traité successivement des questions énergétiques, des aspects biotiques et abiotiques et des cycles nutritifs au chapitre premier, l'auteur donne, au second chapitre, une présentation intéressante de l'origine et de la nature du sol. Plus de vingt pages sont ensuite consacrées à la formation et la classification des sols. Les deux chapitres suivants traitent de la vie dans le sol. En premier, les représentants de la macrofaune (vers de terre, nématodes, escargots, arthropodes, etc.) sont étudiés dans leur milieu. Ensuite, les principaux groupes de microorganismes (protozoaires, champignons, bactéries, etc.) sont passés en revue. La cinquième partie traite de techniques d'étude au champ et au laboratoire. Le livre se termine par deux courts chapitres: les sujets de recherche et les cas d'étude.

Quelques oublis ou erreurs ont été notés: la structure du sol, le cycle de l'azote et la formation de l'humus en sont des exemples. Ce livre, sans références mais avec des lectures recommandées, s'adresse particulièrement au débutant. De fait, la moitié de l'ouvrage procure les notions élémentaires de base tandis que l'autre moitié présente des techniques ou des idées d'étude au terrain et en laboratoire. Le sixième chapitre aurait pu être intégré à celui traitant des études au laboratoire et au champ. Le dernier chapitre est plutôt interrogatif et apporte peu au lecteur.

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SMILEY, T.L. and J.H. ZUMBERGE, éditeurs, 1974. **Polar deserts and modern man.** The University of Arizona Press, Tucsson. 173 p., ill. 32 × 22,5 cm. Relié, $11,50.

Sixième ouvrage d'une série consacrée à l'étude des déserts du globe, les mélanges édités par Smiley et Zumberge sont le compte rendu d'un congrès tenu trois ans auparavant. Cet intérêt pour les déserts polaires prolonge comme un appendice un intérêt principal pour les déserts chauds.

L'ouvrage auquel ont participé 19 auteurs est composé de 14 chapitres dont la moitié traite de

Natural environment; en nombre de pages, cette partie physique comprend les deux tiers du livre. L'on y retrouve surtout des présentations thématiques sur la climatologie (R.G. Barry), la géomorphologie et la microbiologie. L'on y présente une notion de *corelessness* pour l'hiver de même qu'une liste des 15 adaptations des plantes vasculaires aux conditions polaires. En outre, Davies livre une étude des lacs du Grand Nord et Tedrow réexamine ses types de sol nordiques. Quelques cartes, par exemple en 2.4, suggèrent ici et là des limites singulières de la région polaire et la figure 1.11 fournit un schéma généralisé des couches supérieures d'une calotte glaciaire en fonction des phénomènes d'accumulation et d'ablation. L'autre tiers du livre, plus pauvre, est pourtant divisé en deux grandes parties dont la seconde est d'ailleurs mal titrée. Elles abordent différents thèmes économique et humain. La moitié des articles n'ont chacun que trois pages et une moitié de toutes les pages est consacrée à une revue du genre information sur les transports dans l'Arctique (article comportant un utile tableau). Le texte de Tussing sur les *Costs imposed by environmental stress* offre beaucoup d'intérêt. Un index de mille mentions termine ce recueil de grand format, illustré d'une figure (noir et blanc) par page et possédant un faciès de scientificité.

Que penser de ce livre sur les régions polaires? Le titre fait choc puisqu'il brise l'opposition naturelle entre le mot homme et le mot désert (ce dernier suggérant l'idée d'une très faible population). Nous ne pouvons nous empêcher d'écrire que le sujet annoncé n'est guère traité. Les *editors* en préface n'ont-ils pas écrit: «*This book examines the polar deserts with respect to their physical and biological characteristics in relation to intensified development*». Ce n'est pas en parlant surtout de la nature au début d'un livre et un peu de l'homme à la fin que les relations entre ces deux thèmes sont traités. Cet ouvrage met encore une fois en cause le rôle des *editors* car ils se font davantage des «recueilleurs» de travaux que des intégrateurs des textes sollicités. Faute de ce travail de finalisation, de tels livres ne dépassent pas le compendium d'articles d'experts. Leurs travaux se rattachent à l'une ou l'autre de trois catégories: a) des mises au point de ce que les auteurs connaissent bien, tels les écrits de Tedrow (sols) et de Pewé (géomorphologie); b) des réflexions plutôt nouvelles et de grande qualité, celles de Gionivetto et de Barry en climatologie; c) de courts textes insuffisamment préparés mais signés par des spécialistes connus. Qui a suivi la littérature scientifique du Nord trouve peu de choses neuves dans la première et la dernière catégories. Bref, un ensemble de textes d'intérêt inégal. De plus étant donné les glaces qui occupent l'Extrême Nord pendant la presque totalité de l'année, l'on reste peu exalté par la phrase suivante: «*It can be safely said that man is more in danger of drowning than dying of thirst in the arctic desert*».

L'ouvrage ne s'est pas préoccupé de définir la région à l'étude. Ici et là, l'on fait allusion à quelques critères de référence: température du mois le plus chaud, quantité faible de précipitations, indice d'évaporation. A aucun endroit, n'apparaît une pensée d'ensemble sur les limites globales de la région. A la limite, l'on peut dire que la notion même de désert polaire ne s'est guère développée par ce livre. De plus, au plan régional, on a procédé avec une grande élasticité; des auteurs portent référence à l'Alaska, d'autres au Canada, un autre à l'Antarctique, un autre à l'URSS. Une certaine systématisation dans les comparaisons aurait apporté au lecteur beaucoup plus de profits. Enfin, un livre tourné vers le développement peut-il éviter d'aborder les problèmes politiques et le code mental des «promoteurs»? Peut-il dire si peu sur les cultures indigènes?

Bref, si cet ouvrage groupe de bonnes informations au sujet des régions situées dans les hautes latitudes, il s'agit bien plutôt d'un autre livre sur le Polaire que d'un livre autre, ce dernier pourtant suggéré par le titre.

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LOGMAN, K.A. and J. JENIK, 1974. **Tropical forest and its environment.** Longman, London. 196 p. ill. 14 × 21,5 cm. Broché, L 1, 95.

L'objectif des auteurs est de présenter une vue dynamique de la forêt tropicale et d'analyser cet écosystème sur le plan écophysiologique.

Les peuplements forestiers concernés s'étendent dans la zone tropicale humide et dans celle soumise au climat de mousson. L'examen de l'environnement porte principalement sur les régimes photique, thermique et hydrique ainsi que sur le statut édaphique. Dans la description de la phytocénose forestière, les aspects abordés ont trait à la stratification, aux formes biologiques, aux types d'enracinement — l'un des auteurs a particulièrement étudié la morphologie racinaire —, et à la régénération en forêt primitive.

Les pages consacrées à la physiologie de la croissance constituent une lecture très enrichissante. Le débourrement, la vitesse d'élongation de la pousse, la dormance des bourgeons, la croissance foliaire, la défeuillaison, l'activité cambiale, la croissance racinaire, la floraison et la fructification sont étudiées chez des arbres à large distribution géographique. Un mécanisme encore mal connu chez nombre d'essences tropicales est le fonctionnement (vitesse, périodicité, dormance) de l'assise génératrice. Dans ce processus, on sait que des facteurs internes (auxines) et externes (climat) interfèrent. L'action de ces derniers est fort complexe: on a notamment montré (Bois et Forêts des Tropiques, 1970) l'existence possible de corrélations entre le photopériodisme, la durée d'ensoleillement et la quantité d'énergie reçue, la température, le déficit de saturation et les rythmes d'accroissement.

Un dernier chapitre traite de l'avenir de la forêt tropicale. Ce gigantesque réservoir de bois est soumis à un vaste gaspillage: en bien des régions, la destruction du capital ligneux et la dégradation des sols progressent à vive allure.

Cet ouvrage bien illustré et accompagné d'une bibliographie multilingue substantielle trouvera certainement une large audience parmi tous ceux qui — étudiants, praticiens et chercheurs —, s'intéressent à la sylve tropicale. Il est heureux que les éditeurs de *Tropical Ecology Series* aient choisi un tel sujet pour inaugurer leur collection.

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DURRENBERGER, R.W., 1973. **Dictionary of the environmental sciences.** National Press Books, California, U.S.A. 282 p., ill. 15 × 21 cm. Relié, $6,50.

L'intérêt accru pour l'environnement, au sens large, a certes, contribué au développement de plusieurs nouveaux cours dans les collèges et les universités. Plusieurs chercheurs, individuellement ou en équipes multidisciplinaires, travaillent à comprendre et à résoudre les problèmes liés aux différents aspects de la pollution et de l'aménagement des ressources. C'est ainsi que la terminologie et les concepts couvrant un large spectre de disciplines académiques sont maintenant fréquemment employés par ceux concernés par l'environnement.

Une des difficultés que rencontrent ces individus, se manifeste dans la communication de leurs idées aux autres: car nous savons que certains mots prennent des sens différents dans d'autres disciplines. Pour remédier à cela, Robert W. Durrenberger expose dans la préface de son livre *Dictionary of the environmental sciences* que celui-ci a été préparé pour aider amateurs et professionnels à établir un pont entre eux et leur permettre d'exprimer leurs idées et cela dans toute l'étendue des sciences de l'environnement avec clarté et compréhension.

Ce petit dictionnaire (282 pages) traite un grand nombre de termes sans toutefois être exhaustif: de nouveaux mots naissent continuellement dans notre vocabulaire et souvent les vieux mots prennent de nouvelles significations pour servir des besoins nouveaux. Tout de même, ce dictionnaire tente de couvrir un très grand nombre de disciplines académiques. Parmi celles-ci figurent la géologie, l'ingénérie, l'économique, la géographie, l'anthropologie, l'architecture, la botanique, la zoologie, l'agriculture, la climatologie, la physique, l'astronomie et de nombreuses autres.

Nous remarquons cependant que l'auteur traite d'une façon inégale ces domaines scientifiques. Ainsi, la climatologie, la géodésie, la physique et la géomorphologie reçoivent des traitements de faveur. Presque les deux tiers du dictionnaire définissent des termes qui leur sont propres. Quoique le nombre de pages soit restreint, l'auteur s'est permis d'inclure une grande quantité de mots d'intérêt très secondaire. Ainsi, les symboles chimiques, les dieux grecs, les multiples formes de représentation géodésique de la terre, les abréviations de termes de physique, les tribus africaines sont sur-représentés. L'auteur a aussi, a maintes reprises, défini un mot avec tous les adjectifs, noms et verbes s'y dérivant: exemple, *adiabatic* a 9 dérivés, *advection* en a 5, *fog* et *foehn* 4 chacun. Les quelques noms de plantes et d'animaux qui apparaissent sont, soit des espèces préhistoriques ou soit restreintes à des aires de distributions très petites. En plus, ces espèces sont nommées uniquement en anglais et jamais accompagnées de leur nom scientifique. Il est alors très difficile de connaître l'espèce exacte dont l'auteur parle. Dans la majorité des cas les mots sont définis dans un sens très restrictif. Il nous est alors impossible de savoir quelle signification prend un mot employé dans plusieurs disciplines scientifiques. Aussi, ne voit-on pas la différence que l'auteur fait entre les termes *hydrophyte* et *hygrophyte*, pas plus qu'entre *fen, march, muskeg, bog* et *peat bog*. Finalement, aucun mot est suivi de son origine latine ou grecque pas plus qu'il est indiqué s'il s'agit d'un adjectif, d'un nom ou d'un verbe. Malgré cela, ce dictionnaire contient un nombre impressionnant de photos, schémas qui permettent une visualisation de nombreuses définitions. Toutes ces figures sont d'excellentes qualités, très précises et comportent un grand nombre de détails. A la fin se trouvent deux appendices. Le premier porte sur un tableau des périodes géologiques de la terre avec les principaux phénomènes physiques et biologiques reliés à ces temps géologiques. L'autre concerne l'ensemble des mesures de longueur, d'aire, de volume, de poids, de pression et d'énergie avec leurs équivalences dans les systèmes métriques et anglais ainsi que les moyens de conversion d'un système à l'autre.

Ce dictionnaire reste un guide utile. Il permet de répondre à un certain nombre de questions, mais nous laisse trop souvent sur notre appétit. L'une des grandes difficultés de ce dictionnaire, est de traiter des termes soit d'une façon très générale soit d'une façon trop précise. Il en résulte alors un manque d'uniformité qui gêne l'utilisateur. Ce dictionnaire peut à la fois servir pour les amateurs et pour les professionnels des sciences de l'environnement. Il peut aussi trouver place aux niveaux collégial et universitaire. A la pratique, nous constatons qu'il aide beaucoup à la compréhension d'un texte de langue anglaise sur l'environnement. Le lecteur aura toutefois avantage de consulter d'autres dictionnaires plus spécialisés, s'il veut obtenir plus de précision sur les mots cherchés et réponse à toutes ses questions.

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HUNT, C.B., 1974. **Natural regions of the United States and Canada.** Freeman, San Francisco. xii + 725 p., 558 fig., 22 tab. 18,5 × 26 cm. Relié, $14,95.

Les études axées sur la physiographie (relief) ont connu leur période de popularité au cours de la première moitié du XXè siècle. Depuis une quinzaine d'années, elles ont progressivement été délaissées dans plusieurs pays d'Europe notamment en France et en Allemagne, mais survivent entre autres en Angleterre et en Roumanie. Au délà des modes passagères, on peut regretter cet abandon généralisé des études physiographiques, car malgré leur insuffisance géomorphologique, elles permettaient de fournir rapidement, à partir de l'analyse des cartes et de diverses publications, une image valable des éléments de géographie physique. On constate précisément une lacune sérieuse dans ce domaine pour les régions n'ayant jamais fait l'objet de telles synthèses. Les recherches géomorphologiques modernes qui ont remplacé les études physiographiques d'hier ont souvent un caractère spécialisé et sophistiqué. Si elles satisfassent mieux le spécialiste, elles se révèlent parfois peu accessibles au généraliste et demeurent trop largement inutilisées. Toutefois, tout plaidoyer en faveur d'une reprise des études sur la physiographie à la mode ancienne manquera de convaincre même les plus favorables. Pourtant, des ouvrages comme celui de Hunt rendent incontestablement d'utiles services, en particulier dans l'enseignement.

Natural regions of the United States and Canada est une réédition, avec quelques additions, modifications et changement de titre, d'un ouvrage paru en 1967 sous le titre de *Physiography of the United States.* Il est divisé en deux grandes parties totalisant 20 chapitres, et comprend en outre 4 appendices et 2 index. La première partie est consacrée aux processus et aux formes en général. L'auteur y aborde successivement les sujets suivants: les régions naturelles; l'ossature structurale du continent nord-américain; les formes du relief, en particulier les collines et les vallées; le climat et la température; l'eau; les formations meubles; l'érosion et la sédimentation; la biogéographie; les ressources naturelles.

Dans la seconde partie l'auteur présente les principales caractéristiques physiques et biophysiques des grandes régions des Etats-Unis et du Canada qu'il a regroupé en 11 unités géographiques, soit les plaines côtières du golfe du Mexique et de la côte est des Etats-Unis; les Appalaches; le Bouclier canadien; les plaines et plateaux du centre; les Montagnes Rocheuses; les bassins intérieurs et les chaines de l'ouest; la chaine côtière du Pacifique; l'Alaska et le Yukon; les complexes insulaires volcanique et corallien d'Hawaii et de Puerto Rico.

L'ouvrage est abondamment illustré; croquis au trait, graphiques, cartes de localisation, cartes thématiques, extraits de cartes topographiques blocs diagrammes et une soixantaine de photographies complètent admirablement bien le texte qui apparaît dans l'ensemble clair et relativement bien informé. Dans ce genre d'ouvrage, les nombreuses généralisations ou simplifications ne devraient pas surprendre le lecteur. Aussi devient-il gênant de critiquer le contenu. A titre d'exemple mentionnons que l'auteur considère les monts Otish ou de Marie-Victorin comme faisant partie des hautes-terres laurentiennes (sic) au Québec méridional. Quand donc comprendra-t-on que l'adjectif de Laurentides est *laurentidien* et non *laurentien?* aussi, les monts Otish font partie du Québec central subarctique et non du Québec méridional qui arrête vers le 50è degré de lat. N. et coïncide avec l'isotherme de 0°C de température moyenne annuelle de l'air.

La bonne qualité de l'édition fait honneur à la maison Freeman qui a su, une fois encore, mettre sur le marché un excellent produit à un prix relativement bas. Le titre de l'ouvrage ne couvre pas exactement la réalité, car en fait en dehors d'un chapitre sur le Bouclier canadien (20 p.), d'ailleurs pas exclusivement réservé au territoire canadien, et quelques autres passages ici et là, il est question exclusivement des Etats-Unis. D'aucuns seront déçus de constater qu'une fois de plus le Canada n'est que la projection septentrionale des U.S.A. Quoiqu'il en soit, cette réédition revue et augmentée sera fort appréciée des étudiants du premier cycle universitaire et du CEGEP comme du public en général. C'est un ouvrage de géographie physique régionale, classique, à avoir chez-soi.

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ALIMAN, M. and D.F. LAWRENCE, 1973. **Geological laboratory techniques.** Arco Publ., New York. 335 p., 180 fig., 9 pl. couleurs h. t., 43 tab. 18 × 25,5 cm. Relié, $25,00.

La géologie, comme quelques autres branches du savoir, a pour originalité d'être à la fois une science de terrain et de laboratoire. Malheureusement on la considère surtout sous le premier volet ce qui a pour conséquence de plonger injustement dans l'ombre les ouvriers du second qui accomplissent pourtant un travail aussi important que les géologues de terrain, car les roches doivent être étudiées sous tous les aspects allant du microscopique (échelle du minéral) ou mégascopique (échelle du batholite).

Les ouvrages consacrés aux techniques de laboratoire en géologie n'encombrent certes pas les bibliothèques spécialisées. Le nouveau venu en géologie apprend rapidement qu'il faut s'en remettre à l'expérience des ainés qui, à l'instar des grands chefs, semblent garder jalousement leurs «recettes». Pourtant, qui dépouille la littérature spécialisée se rend compte qu'il existe une abondante documentation sur les diverses méthodes et techniques utilisées dans les laboratoires de géologie. Le problème réside dans le fait que ces recettes demeurent dispersées. A de rares exceptions près, elles n'ont jamais été consignées dans des manuels pratiques, faciles d'accès. Cette lacune vient en partie d'être comblée par la parution de l'ouvrage d'Allman et de Lawrence, deux techniciens en géologie d'expérience du *Queen Mary College* de Londres.

L'ouvrage comprend 9 chapitres traitant de la coupe et du broyage des roches; de la préparation des coupes ou plaques minces; des techniques de teinture; des éléments d'optique du microscope; du broyage et du tamisage; des méthodes de séparation, de Rayons-X et de spectographie; des techniques de moulage, gravure, peinture et empreintes. Il comprend aussi 12 appendices contenant divers tableaux et tables de conversion, une liste des principaux manufacturiers et fournisseurs (principalement américains, britanniques et allemands) d'équipement de laboratoire et un index général. De courtes listes de références placées à la fin de chaque chapitre offrent un complément d'information à celui qui le désire. L'ouvrage est abondamment illustré: 165 croquis au trait, 15 photographies en noir et blanc et 48 photographies en couleurs dont 42 représentant des microphotographies de coupes minces. Relativement bien fait dans l'ensemble, on s'y retrouve facilement grâce à une table des matières détaillée. Bien que publié par une maison d'édition américaine, cet ouvrage, le premier du genre spécialement conçu pour la géologie, est de conception britannique.

Les professionnels qui souffrent du complexe du manque de techniques pourront désormais apaiser leur conscience. L'ouvrage d'Allman et Lawrence leur fournit de nombreuses «recettes»; ils n'ont plus qu'à les essayer. Evidemment il ne suffit pas de lire ou de posséder cet ouvrage pour devenir automatiquement un bon technicien en géologie. Il serait peut-être temps qu'à l'instar de d'autres pays dont l'Angleterre, on fonde, au Québec, une école de techniciens en géologie comme il en existe depuis longtemps dans plusieurs autres domaines: agriculture, foresterie, biologie, chimie, génie civil, etc. Malgré les immenses richesses de son sous-sol, le Québec accuse un net retard dans le domaine des sciences de la terre. Jusqu'à maintenant les spécialistes des roches semblent avoir mis un peu trop souvent leurs talents au service des intérêts capitalistes étrangers. Le temps semble venu de donner à la géologie la place qui lui revient puisqu'elle contient des éléments fondamentaux de culture qu'il serait regrettable d'ignorer.

Il va sans dire que *Geological laboratory techniques* trouvera sa place dans toutes les bibliothèques des sciences de la Terre et sera un outil apprécié de ceux qui œuvrent à l'ombre dans les laboratoires de géologie. Toutefois, son prix relativement élevé en limitera sans doute la diffusion parmi les étudiants et les professionnels.

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WASHBURN, A.L., 1972. **Periglacial processes and environments.** Edward Arnold, London et St. Martin's Press, New York. vi + 320 p., 145 fig., 10 tab. 19 × 25,5 cm. Relié, $23,95.

Le milieu périglaciaire prévaut actuellement sur environ 20% de la surface terrestre, soit dans les régions des hautes latitudes et des hautes altitudes. Au cours du Pleistocène, de vastes régions connaissant aujourd'hui un climat tempéré ont été soumises aux influences du froid; ce fut le cas notamment d'une grande partie de l'Europe et des Etats-Unis. Pourtant, les études sur le périglaciaire sont relativement jeunes. Si l'on met de côté les travaux des pionniers, le périglaciaire s'est affirmé comme une branche distincte des sciences de la terre au cours des deux dernières décennies grâce surtout aux efforts des européens, en particulier des polonais qui publient l'unique périodique entièrement consacré au sujet. En Amérique, les études sur le périglaciaire accusent un net retard notamment les études régionales et les inventaires des processus et des formes. La parution récente du premier ouvrage en anglais entièrement consacré au périglaciaire donnera sans doute un élan décisif. Il aura fallu attendre plusieurs années avant qu'un chercheur américain parvienne à réunir dans quelques centaines de pages les notions fondamentales relatives à l'action du froid hors du milieu glaciaire proprement dit.

L'ouvrage comprend 12 chapitres de longueur et de valeur très inégales, un index et une bibliographie de 50 pages en plusieurs langues, sans doute la plus multilingue des ouvrages anglo-saxons de cette catégorie. Autre caractéristique à l'honneur de l'auteur, les ouvrages consignés dans la bibliographie sont cités dans le texte.

Le lecteur apprendra dans l'introduction que le terme *périglaciaire* introduit par Lozinski (1909) pour désigner le climat froid et les phénomènes se développant autour des calottes glaciaires a perdu son sens originel pour s'étendre à tout le domaine froid en dehors du glaciaire proprement dit. L'action du froid constitue donc l'objet principal du périglaciaire. Cette action souvent complexe et maintes fois imparfaitement connue se manifeste sous divers aspects: formation de lentilles de glace dans le sol, action des congères de neige et des glaces flottantes, triage du matériel, soulèvement de cailloux, solifluxion, etc. La variété des climats dits périglaciaires se traduit par des formes différentes et des processus d'intensité variable. Divers facteurs influencent ou guident l'action du froid en dehors du climat, notamment la topographie, les caractéristiques du sol ou de la roche en place, et le temps, i.e. la période au cours de laquelle le froid peut exercer son action. L'auteur souligne brièvement ces divers paramètres ou facteurs dans le deuxième chapitre avant d'aborder la question du gel saisonnier ou permanent du sol que l'on connaît partout au Québec pour le premier et par endroits au nord du 50° lat. N. pour le second. Il s'étend assez longuement sur le pergélisol, notamment sur son étendue, son épaisseur, ses caractéristiques, son origine et sur les formes de terrain qui s'y développent.

Les chapitres consacrés à l'action du froid et le mouvement en masse (*mass-wasting*) constituent le corps de l'ouvrage (154 p.) soit près de 60% si l'on exclut les références. Dans la partie consacrée à l'action du froid, l'auteur aborde successivement les processus de l'engel, la fissuration, le soulèvement et le chevauchement, le déplacement en masse, le craquellement, le triage, les sols réticulés, les involutions, les champs de blocs, les tourbières réticulées, les palses et les pingos, tous des phénomènes liés à des degrés divers à l'action du froid. Dans celui consacré au mouvement en masse, il traite successivement des avalanches, des coulées de slush, des glissements, de la reptation, de la gélifluxion et des dépôts qui lui sont associés, des glaciers rocheux, des talus d'éboulis, des ramparts de protalus et des grèzes litées. Dans l'ensemble ces divers sujets sont traités d'une façon fort honnête et toujours prudente. Aucune compromission de la part de l'auteur qui loin de saturer le lecteur lui donne le goût d'en savoir davantage et de puiser lui-même dans les nombreux travaux cités.

Les cinq chapitres qui suivent sont beaucoup moins bien étoffés. L'auteur a réussi à traiter de la nivation et des formes qu'elle engendre en moins de 3 pages de texte. De même, il consacre 3,5 pages de texte à l'action des cours d'eau en milieu froid, 4 pages à l'action lacustre et marine, 2,5 pages à l'action éolienne et environ 4 pages au thermokarst. D'aucuns trouveront un peu maigre le dossier de ces divers sujets. Il faut reconnaître à la décharge de l'auteur que jusqu'à maintenant les chercheurs ont attaché relativement peu d'importance à ces sujets qui révèlent plutôt des sciences naturelles ou de l'observation que des sciences expérimentales, appliquées ou de l'ingénieur.

L'ouvrage est abondamment illustré: 71 photographies et 74 figures au trait. Sa qualité et son originalité varient beaucoup. Si l'on considère la nouveauté du matériel offert dans les illustrations, on constate que 50% des photographies ont déjà été publiées ailleurs et que 90% des figures au trait ont été empruntées de publications diverses. Dans l'ensemble la qualité des photographies est bonne voire même excellente dans plusieurs cas. Néanmoins les éditeurs devraient s'abstenir de publier des photographies manquant de mise au point (cf. p. 33, 98, 121), ou des photographies reproduites directement de publications antérieures comme celle de la page 122 illustrant des polygones avec triage, ou encore des photographies hors du sujet comme celle de la page 224 montrant une souche avec un gros caillou logé entre les racines. Le lecteur aurait préféré plus d'exemples du glaciel en milieu littoral-marin, fluviatile et lacustre. La petite crête de blocs glacielle de la page 221 semble bien modeste à côté des crêtes glacielles de 10 à 15 m de hauteur que l'on rencontre le long des grandes rivières du Québec subarctique (e.g. La Grande, l'Eastmain, le Rupert, le Caniapiscau). D'ailleurs les phénomènes glaciels, probablement encore mal connus de l'auteur, ont été mal évalués. Contrairement aux indications du tableau p. 241, ce n'est pas dans les régions polaires que les phénomènes glaciels sont les plus actifs, les plus variés et les plus spectaculaires, mais plutôt dans les régions subpolaires et dans certains cas dans les régions froides des moyennes latitudes.

Par le petit nombre de cartes montrant la répartition des phénomènes périglaciaires en Amérique du Nord, on constate facilement que l'U.R.S.S. et l'Europe devancent de plusieurs années les chercheurs nord-américains dans le domaine du périglaciaire. A dire vrai, les aspects techniques reliés à l'ingéniérie ont reçu plus d'attention au Canada et aux Etats-Unis que l'inventaire et la cartographie des formes et des phénomènes actifs et reliques.

S'il faut se réjouir de constater que l'auteur considère le glaciel comme un phénomène périglaciaire, plusieurs regretteront qu'il n'ait pas saisi l'occasion pour banir l'usage du terme *permafrost* qui, selon Kirt Bryan, constitue un non-sens et devrait être remplacé par *pergélisol,* car il s'agit bien d'un sol gelé en permanence et non d'un gel permanent en soi. Il arrive parfois que l'habitude fasse place au bon sens, même en science. Le lecteur assoiffé de certitudes sera sans doute déçu d'apprendre qu'il reste encore beaucoup à découvrir et à préciser dans le domaine du périglaciaire. L'auteur le rappelle à maintes reprises et admet volontiers l'insuffisance de nos connaissances. Ce trait reflète la profonde honnêteté du chercheur consciencieux. Mais l'extrême prudence, les multiples réserves et les nuances apportées par l'auteur finissent par agacer le lecteur et trahissent un certain conservatisme ou un manque d'audace de bon aloi. Somme toute, c'est un ouvrage très correct, comme un professionnel bien habillé, cravate et complet classique, cheveux courts et visage rasé; rien de provoquant, quoi! Si! le format de l'ouvrage qui s'ouvre dans le sens de la longueur.

En dépit de quelques lacunes, cet ouvrage mérite d'être largement diffusé. Il consacre le périglaciaire en Amérique du Nord. Les étudiants font un bon placement en se le procurant. Ils pourront désormais se payer le luxe de sécher les cours. Souhaitons qu'il donne un essor aux études sur le périglaciaire du Québec.

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STEIN, J.R., (éditeur), 1973. **Handbook of phycological methods.** Culture methods & growth measurements. Cambridge University Press, London. xii + 448 p. ill. 23 × 15,5 cm. Relié, $19,50 U.S.

Ce volume est le premier à paraître d'une série de quatre qui, nous l'espérons, ne tardera pas trop à être complétée. Ce volume initial traite des méthodes de culture et des diverses techniques à utiliser pour évaluer leur croissance. Il se divise en cinq parties à l'intérieur desquelles plusieurs spécialistes sont mis à contribution. Ces cinq sections couvrent plus spécifiquement les aspects suivants: l'isolation et la purification des cultures, l'équipement et les méthodes, les techniques plus spécifiques (cultures continues, cultures massives, etc.), les méthodes de mesure de croissance de ces cultures, le dosage de vitamines dans le milieu et dans les organismes. Les 28 contributions qui constituent ce manuel pratique couvrent de façon très satisfaisante aussi bien les algues d'eau douce que les algues marines, les organismes unicellulaires, coénocytiques ou macroscopiques.

Il n'existait pas jusqu'à ce jour de référence bibliographique ou l'on pouvait espérer trouver avec quelqu'assurance la méthode de culture la plus adéquate pour l'organisme alors sous étude. Avec cette parution, le problème se trouve en partie résolu. En effet, en plus des nombreuses méthodes décrites, et de la multitude de milieux proposés, une bibliographie exhaustive accompagne chaque article, ce qui augmente considérablement les chances de trouver la voie à suivre.

Cette initiative de Janet Stein et de ses collaborateurs débouche donc sur un succès indiscutable pour lequel on doit les féliciter vivement.

On ne peut que recommander fortement l'acquisition de ce volume par tout laboratoire utilisant ce type de matériel.

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BYRDE, R.J.W. and C.V. CUTTING, 1973. **Fungal pathogenicity and the plant's response.** Academic Press, London & New York. v + 499 p., nombreux tab. et ill. 15 × 23,5 cm. Relié-toile, $23,50.

Ce troisième symposium Long Ashton, tenu à l'Université de Bristol, traita du mode d'action des champignons pathogènes, de la réaction de l'hôte et de l'interaction hôte-pathogène. Les comptes rendus groupés en cinq sections de deux à quatre articles sont publiés dans un volume dont la présentation est impeccable. Les textes sont accompagnés de photographies et diagrammes; ils sont suivis d'une liste de références citées et d'une discussion très vivante.

Précédant les articles scientifiques, un texte inaugural, présenté par le professeur R.K.S. Wood, président de la Société internationale de pathologie végétale, discute de la spécificité des microorganismes pathogènes et de la réponse de l'hôte. Les sections I et II groupent les textes traitant du rôle des enzymes et de l'éthylène dans le processus pathogénique. Les deux dernières sections formant la partie B du volume intitulé *La réponse de la plante*, traitent de la résistance aux maladies et des changements métaboliques apparaissant chez l'hôte. La section III forme cependant le corps du volume occupant 210 des 474 pages de texte. Quatre textes bien documentés sont groupés sous le titre *Parasitisme obligatoire*. La contribution la plus remarquable est sans doute celle de Bracker et de Littlefield dont le texte de 159 pages comprend 83 figures et 269 références. Ce chapitre constitue en quelque sorte un traité sur l'interface physique entre l'hôte et le pathogène. Les auteurs y discutent du concept d'interface (ou zone interfaciale), expliquent la terminologie se référant aux structures et aux interactions hôte-pathogène ou hôte-symbiote et discutent de nombreux exemples d'interfaces. Ce chapitre inclu également la première classification des types d'interfaces, accompagnée chacune d'un diagramme. Le texte est complété par une série de photographies très éloquentes au microscope électronique et photonique illustrant les structures interfaciales.

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MOORE, T.C., 1973. **Research experiences in plant physiology.** A laboratory manual. Springer-Verlag, New York. vi + 462 p., 23 fig., 8 tab. 21 × 27,5 cm. Broché, $9,50.

Ce manuel de laboratoire de physiologie végétale est destiné aux étudiants de 1^er^ et de 2^e^ cycles. L'objectif pédagogique poursuivi par l'auteur, le professeur T.C. Moore de l'Université d'Orégon, est de développer chez l'étudiant l'esprit scientifique, et plus précisément, de lui apprendre, par le biais d'investigations bien planifiées, comment fonctionne une plante. L'étudiant travaille habituellement en équipe de trois à huit membres. L'auteur lui soumet des problèmes actuels de recherche dans les principaux domaines de la physiologie végétale.

Le volume est constitué de 25 exercices formant chacun une unité complète comprenant cinq sections: état de la question ou du problème, matériel et méthodes (celles-ci proviennent le plus souvent d'articles scientifiques) références (en général, une vingtaine par exercice), recommandations et cédule de travail, rapports (tableaux, graphiques et interprétation des données).

Voici quelques titres ou sujets des exercices: perméabilité cellulaire, potentiel hydrique, activité enzymatique, électrophorèse, chromatographie et spectre d'absorption des pigments, mesure de l'intensité photosynthétique, facteurs influençant la photosynthèse, photorespiration, régulation de la croissance et du développement (13 exercices, soit environ 225 pages couvrent ce secteur important de la physiologie végétale), nutrition minérale, absorption et translocation de phosphate ^{32}P, fixation symbiotique de l'azote.

Ce manuel, en plus d'être pour les étudiants de biologie végétale un excellent outil de formation scientifique, sera d'une très grande utilité pour les professeurs et les assistants des travaux pratiques en physiologie végétale.

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NEEDHAM, A.E., 1974. **The significance of zoochromes.** Springer-Verlag, New York, Heidelberg et Berlin. 429 p. 24,5 × 17 cm. Relié, $26,00.

Ce troisième volume de la collection *Zoophysiology and Ecology* réunit les données relatives à la biologie des pigments dans le règne vivant et plus particulièrement dans le monde animal comme l'indique son titre. L'auteur se propose de mettre au point les connaissances propres à ce domaine acquises par les physiologistes, les biochimistes et les écologistes. Cette analyse approfondie est aussi complète que possible actuellement. Une bibliographie exhaustive, plus de 1200 références citées et rapportées, témoigne du sérieux de l'ouvrage et de l'effort de synthèse de son auteur.

Dans la première partie de l'ouvrage, l'auteur donne un bref aperçu des propriétés physiques des molécules organiques chromatiques. La seconde partie est consacrée à la nature chimique, à l'origine et à la distribution des pigments dans les tissus et organes des animaux. Ce chapitre représente une somme impressionnante de documents destinés aux spécialistes de chaque groupe zoologique qui y trouveront matière à enseignement et aussi à discussion. Les parties 3 et 4 traitent du rôle physiologique des pigments: adaptation chromatique en fonction du milieu (protection, camouflage, défense,...), rapports entre pigments et mécanismes sensoriels (photoperception, chimioperception, thermoperception), place fondamentale des pigments dans les métabolismes et en particulier dans celui de la respiration. La cinquième partie met en évidence l'importance des pigments dans la reproduction, un tableau énumère la distribution des différents pigments dans les œufs du règne animal (des Hydraires aux Vertébrés) avec références bibliographiques. Ce paragraphe aborde peut être trop succinctement la place des pigments dans l'ontogenèse et le développement post-embryonnaire, la mention faite à la mue et à la métamorphose aurait mérité plus d'attention. La biosynthèse des grandes familles de pigments ainsi que le contrôle génétique et physiologique de la chromatogenèse sont rapportés dans la sixième partie. L'intérêt de ces derniers chapitres est évident pour plusieurs disciplines. Enfin, l'ouvrage se termine par un essai réussi sur le rôle des pigments dans l'évolution animale soulignant leur valeur adaptative.

On peut regretter que les illustrations ne soient pas plus abondantes, que leur qualité ne soit pas parfaite et que ce livre, qui traite des pigments et de la pigmentation, ne renferme pas de planches en couleur. Ces défauts, qui doivent être attribués à la conception de l'édition, enlèvent un peu de modernisme à l'ouvrage. Ces imperfections n'ont pas empêché l'auteur d'atteindre son but ambitieux. En effet, l'ouvrage constitue une remarquable synthèse de nos connaissances actuelles sur les pigments des animaux. Il s'adresse à un public déjà averti, c'est un outil de travail utile non seulement aux chercheurs expérimentés ou débutants qui y trouveront une documentation complète sur le sujet qui les intéresse mais à l'enseignant biologiste de toutes catégories toujours à la recherche de données récentes.

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WIESER, W., 1973. **Effects of temperature on ectothermic organisms.** Springer-Verlag, New York. 298 p., ill. et nombreux tableaux. 17 × 24 cm. Relié, $25,00.

Cet ouvrage est l'un des fruits d'un symposium, *Effets de la température sur les organismes ectothermiques*, tenu à Obergurgl (Autriche) en septembre 1972. On y trouve donc les contributions de quelque 26 spécialistes qui explorent les différentes facettes du problème. On retrouve dans le regroupement des travaux sous trois rubriques (mécanismes, écologie et résistance au froid) une des préoccupations majeures de l'éditeur, Wolfgang Wieser, pour qui les questions relatives aux causes de l'adaptation thermique ne sont pas les seules à susciter des réponses importantes pour le biologiste; sont également significatives les questions ayant trait à la compréhension de l'adaptation thermique d'un organisme donné.

Il ne faudrait pas sous-estimer la portée des résultats de travaux sur l'ajustement thermique des ectothermes. Ceux-ci en effet font appel à un éventail fort riche de mécanismes adaptifs pour répondre aux sollicitations d'un milieu thermiquement instable. On trouvera d'ailleurs dans ce livre des contributions illustrant fort bien certains de ces mécanismes d'adaptation aux variations de température: changements dans les éléments du système nerveux, les complexes enzymatiques, la physiologie des membranes, la physiologie des mitochondries, etc.

Les réactions observées *in vitro* ne peuvent toutes mener à des conclusions valables sur leur rôle *in vivo*, ne serait-ce bien souvent parce que différents chercheurs, expérimentant avec des espèces différentes, selon des approches différentes, aboutissent à des conclusions divergentes quant aux relations thermiques des ectothermes avec leur milieu. Ainsi, certains voient une proportionnalité nette entre le métabolisme et la température, alors que d'autres voient jouer des mécanismes homéostasiques, d'autres encore décelant des relations plus complexes de type «multistable». Cette apparente confusion incite l'éditeur à considérer que toutes ces interprétations sont peut-être valables, vu notre ignorance de l'écologie détaillée de même un petit nombre d'espèces. L'impossibilité actuelle de construire un modèle satisfaisant, faute de données suffisantes, justifie les efforts des écologistes et éthologistes qui s'attachent à l'étude des effets des changements de température sur les organismes et leur comportement. On trouve d'ailleurs dans ce volume certains résultats qui ont trait soit à des phénomènes étudiés de façon générale ou comparée (facteurs mésologiques, effet du jeûne) soit à la réponse de différentes espèces d'ectothermes aux variations de température: Polychètes, Mollusque, Ecrevisse, Arachnides, Turbellariés triclades, Levure, Rotifères, Fourmis et Insectes à diapause, font l'objet de ces études. Le livre se termine sur quatre exposés qui traitent de la résistance au froid, chez les Reptiles, les Invertébrés marins et les Poissons, les Araignées et un Gastéropode pulmoné.

Les articles, forcément d'inégale valeur, sont en général d'une très bonne tenue et devraient permettre au biologiste peu familier avec les problèmes de l'adaptation thermique de rentrer de plein-pied dans le sujet. En biologie expérimentale, l'un des paramètres les plus omniprésents est très certainement la température. A la lecture de cet ouvrage on reste surpris devant la multiplicité des problèmes soulevés par les changements de température et quelque peu perplexe quant à la signification de bien des résultats de biologistes et autres qui ont traité ce paramètre comme probablement mineur. L'une des vertus de cet ouvrage est certainement de faire saisir au lecteur l'importance primordiale du facteur température sur les phénomènes biologiques et ouvre des perspectives intéressantes sur la régulation du métabolisme.

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PRECHT, H., J. CHRISTOPHERSEN, H. HENSEL and W. LARCHER, 1973. **Temperature and life**, 2ième édition. Springer-Verlag, New York, Heidelberg, Berlin. xix + 779 p., nombreux tab. et fig. 17 × 25cm. Relié-toile, $54,70.

Cette deuxième édition, anglaise, de *Temperatur und Leben* est beaucoup plus qu'une simple révision de la première, parue en 1955. En effet le texte a été si fortement remanié et enrichi de diverses additions que le présent ouvrage peut être considéré comme entièrement nouveau. Seize spécialistes, appartenant à la biochimie, la botanique, la microbiologie, la physiologie ou la zoologie, ont contribué à la rédaction de cette deuxième édition. Il n'est donc pas surprenant d'y voir discutés tous les phénomènes biologique, car en est-il sur lesquels la température est sans influence? Malgré la diversité des sujets traités, les auteurs ont su faire ressortir le thème de cet ouvrage: l'adaptation des organismes aux changements de température.

L'ouvrage est divisé en deux parties. La première traite des poïkilothermes et englobe les microorganismes, les plantes et les animaux dont la température corporelle varie en fonction de celle de l'environnement. La deuxième partie est consacrée aux homéothermes. Dans l'une et l'autre parties, les auteurs ont largement dépassé le cadre strict de l'adaptation. Ils y discutent, par exemple, la régulation génétique des réactions aux variations de température et l'influence de ces dernières sur la photosynthèse, la croissance et la distribution géographique des organismes. De la thermodynamique aux thermorécepteurs chez l'homme, rien n'a échappé aux auteurs de cet ouvrage d'une valeur exceptionnelle.

A l'index alphabétique s'ajoute une table des matières, bien faite et fort pratique, de plus de douze pages, qui témoigne des nombreux aspects de cette étude. La bibliographie constitue une source inépuisable d'information.

Cet ouvrage devrait être consulté par tout biologiste qui s'intéresse à l'étude de la température. Chercheurs, enseignants et étudiants des cycles supérieurs y trouveront plaisir et satisfaction.

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YARON, B., E. DANFORS, and Y. VAADIA, 1973. **Arid zone irrigation.** *Ecological studies*, volume 5. Springer — Verlag, New York. viii + 434 p., 60 tab., 181 fig. 16 × 24 cm. Relié, $36,20.

Ce livre a été écrit par plusieurs spécialistes dans le but de servir de texte de référence pour les agronomes, les spécialistes du sol, les ingénieurs en irrigation et les physiologistes. Ses huit chapitres comprennent trente deux textes qui peuvent être regroupés en cinq sujets. (1) L'environnement et les ressources en eau des régions arides, (2) les caractéristiques hydrologiques des sols et la physique du mouvement de l'eau dans le système sol-plante — atmosphère, en relation avec l'irrigation, (3) la chimie et la salinité des sols irrigués, (4) la technologie de l'irrigation et (5) l'analyse, à l'aide d'exemples appropriées, des besoins en eau des plantes des régions arides.

Ce texte ne remplace pas le livre intitulé *Irrigation of agricultural lands* publié en 1967 par la Société agronomique américaine. On peut le considérer comme une mise à jour des derniers développements en matière d'irrigation des régions arides. La théorie énoncée dans ce texte est à la portée des professionnels praticiens en irrigation. Nos praticiens pourront bénéficier d'une partie de la matière traitée, même si les problèmes d'irrigations des régions arides sont très différents des notres. Ce livre a sa place dans une bibliothèque scientifique.

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NATIONAL WATER COMMISSION, 1973. **Water policies for the future.** Water Information Center, Port Washington, N.Y. xxvii + 579 p., 51 tab., 8 fig., 74 photo. 18 × 24 cm. Relié, $17,50.

Ce document est une compilation complète des faits et des politiques d'aménagement concernant la ressource — eau aux Etats-Unis. On traite en profondeur des problèmes d'aménagement de l'eau. Il a été préparé par la Commission nationale de l'eau pour le président et le Congrès des Etats-Unis.

Le texte est divisé en 17 chapitres et traite globalement: (1) de la pollution, des problèmes urbains, des besoins en eau, des moyens d'augmenter le rendement en eau et de l'utilisation plus efficace de l'eau; (2) des relations entre l'eau, l'environnement et l'économie du pays; (3) des problèmes de juridiction de l'eau, des programmes d'aménagement et des agences en charges de la gestion de l'eau et (4) des coûts, de la collection des données et des besoins en recherche pour améliorer la gestion de l'eau.

La Commission nationale de l'eau réclame l'adoption de 232 recommandations afin de rendre l'aménagement de l'eau plus efficace et plus équitable tout en favorisant la conservation de l'environnement. Quoique ce document discute des problèmes confrontant nos voisins du Sud, il n'en demeure pas moins une importante source de références sur le sujet. Cette publication devrait être disponible aux hydrologues; principalement à ceux qui guident l'établissement des politiques d'aménagement de l'eau.

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MACHATTIE, L.B. and F. SCHNELIE, 1974. **An introduction to agrotopoclimatology.** World Meteorological Organization, Genève, Technical note no 133, 131 p. 16,5 × 22,5 cm. Relié-toile, prix non indiqué.

Si l'on veut assurer une bonne planification agricole, il est essentiel de connaître non seulement les grandes zones climatiques régionales mais il faut aussi connaître la grande influence qu'exerce la topographie sur le climat local. Il est nécessaire de comprendre les mécanismes par lesquels la topographie agit sur les éléments climatiques considérés individuellement ou collectivement. Ceci devient d'autant plus important que la superficie des sols arabes est limitée et que les besoins alimentaires sont croissants.

Ce domaine de la climatologie s'est donc rapidement développé dans les pays européens et asiatiques à forte densité de population, où l'on a dû récupérer pour la production agricole des territoires ayant une topographie très accidentée et un potentiel agricole variable selon les conditions du milieu. Cette publication nous fait part de l'expérience acquise dans ce type de travail au cours des années.

Dans un premier temps, on présente les connaissances générales acquises en ce qui a trait à l'influence de la topographie sur les éléments météorologiques tels que les précipitations, la radiation, la température, les vents, l'humidité de l'air et l'évapotranspiration. On présente par la suite une discussion sur, l'élaboration d'une étude agrotopoclimatologique considérant les besoins en personnel et en équipement de même que sur l'analyse et la présentation des résultats. Le tout est couronné par des exemples de travaux. Dans un deuxième temps, les auteurs présentent une extensive bibliographie (environ 1000 références) concernant des études agrotopoclimatologiques, l'instrumentation et la météorologie générale.

C'est une référence qui, sans être très poussée sur l'aspect technique, est une bonne source d'information pour toute personne intéressée par les relations climat-productions végétales.

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STEINHAUSER, F. et R. SCHNEIDER, 1974. **Conference to review the science of meteorology** et **Conference on economic and social benefits of meteorology.** Lectures presented at the IMO/WMO centenary conferences, Vienna and Geneva, September 1973. (Conférences présentées aux célébrations du centenaire de l'OMI/OMM, Vienne et Genève, septembre 1973). Organisation météorologique mondiale, Genève, Note technique no 130, 139 p. 27 × 29 cm. Relié-carton, prix non indiqué.

Il s'agit d'une collection de textes de deux séries de conférences données à l'occasion du centenaire de l'Organisation météorologique mondiale. La première conférence tenue à Vienne se proposait de faire une revue de la météorologie comme science. Le professeur F. Steinhauser de l'Institut central autrichien pour la météorologie en fut le directeur. La deuxième conférence, tenue à Genève, sous la direction de M. R. Schneider, directeur de l'Institut météorologique suisse, décrivait les bénéfices économiques et sociaux rattachés à l'application des connaissances météorologiques.

La première série résume les progrès scientifiques qui ont marqué la météorologie moderne. Cette série devrait être avidement lue par le météorologue. Elle le renseigne efficacement non seulement de l'état actuel de cette science mais aussi de la planification de la recherche dans le futur. Cette série est aussi utile aux scientifiques et technologues œuvrant dans des domaines connexes rattachés de près ou de loin aux problèmes de l'environnement humain.

L'historique de l'Organisation météorologique mondiale y est donné par le Dr. A. Nyberg de l'Institut météorologique de Suède. Il y montre comment les développements scientifiques dans les domaines de la connaissance, des instruments et des communications ont permis la création de l'Organisation météorologique internationale il y a cent ans. Celle-ci devint en 1950 l'Organisation météorologique mondiale ou simplement l'OMM. L'OMM fait partie intégrante des Nations Unies et possède un caractère purement technique dont le pouvoir de décision ne porte que sur l'aspect scientifique. L'aspect actuel important de l'OMM pour le lecteur est sûrement l'avènement du *Global Atmospheric Research Programme* ou GARP, qui régit une série d'expériences à l'échelle globale spatialement et à l'échelle internationale politiquement. GARP est une occasion unique et inédite d'obtenir une meilleure connaissance des processus physiques de l'atmosphère en combinant les efforts coordonnés des divers services météorologiques nationaux, des universités et des laboratoires de recherche du monde entier. L'importance de cette action coordonnée réside dans les progrès scientifiques anticipés en météorologie qui ajoutés aux recherches intensives dans des champs d'action autres produiront une amélioration sensible dans les services offerts au bénéfice du développement économique des pays du monde en tenant compte de l'environnement humain. Plusieurs conférenciers ont narré l'historique de la météorologie selon l'expérience nationale. M. J.S. Sawyer du Bureau météorologique du Royaume-Uni nous entretient de la prévision du temps, son passé, présent et futur. Il nous donne un aperçu très valable de l'état de la prévision numérique actuelle, de son actif, de ses limites anticipées.

Les développements et les tendances dans la recherche en climatologie ont été rapportés par le professeur H.E. Landsberg de l'Université du Maryland. On y voit que la climatologie a évolué de façon similaire à la météorologie. Aux modèles statistiques utilisés initialement se sont substitués les modèles mathématiques développés récemment et qui apparaissent très prometteurs à l'élucidation des causes des fluctuations climatiques. On y trouve enfin plusieurs aspects pratiques sur l'utilisation de la connaissance du climat. Ces aspects concernent surtout les actions en agriculture, en construction, en aménagement, en utilisation des terres, en loisirs et en sports. Une revue des buts de GARP est présentée par un Canadien, le Dr. R.W. Stewart du ministère de l'Environnement. Le Dr. Stewart spécifie que le GARP appartient au domaine de la recherche appliquée et a pour but d'une part de produire de meilleures prédictions pour des périodes plus longues et d'autre part de comprendre mieux ce qui à la fin produit le climat. On a répété plusieurs fois dans l'historique de la météorologie l'effet qu'ont eu les instruments sur l'évolution de cette science. Le professeur Morel de l'Université de Paris donne un compte rendu très à date des développements techniques réalisés dans l'observation de l'atmosphère. C'est une revue excellente de la technique moderne de mesure surtout basée sur les observations faites par satellites, de leur utilisation et des nouveaux modes d'assimilation de ces données.

La dernière conférence de la première série porte sur la modification du temps. Le professeur M. Neiburger de l'Université de Californie traite du sujet sous deux angles: les modifications intentionnelles (production de pluie, dissipation du brouillard, affaiblissement de la convection dans les nuages, suppression de la grêle, diminution des vents dans les ouragans) et les modifications non-intentionnelles (changement de l'état du sol par l'agriculture, par la pâture des animaux, par la création des villes et des cités et par la venue de la révolution industrielle).

La deuxième série de conférences est de portée économique et sociale. En effet, à partir des données et des connaissances actuelles de la météorologie on y décrit les bénéfices et les services pourvus à l'humanité en général dans les domaines économiques et sociaux, et compte tenu de l'état de développement de certains groupes humains, on y propose des modes d'action plus appropriés et plus propices. Cette deuxième série intéressera sûrement non seulement le météorologue mais aussi et peut-être surtout l'hydrologue, l'agronome, le sociologue et l'économiste. L'impact de la Veille météorologique mondiale (V.M.M.) de l'OMM sur le développement économique et social a été présenté par M. V.A. Bugaey du Service d'hydrométéorologie de l'URSS. Cette Veille a été créée en vue de coordonner les services techniques nationaux et pouvoir de l'assistance météorologique aux membres de l'OMM par l'entremise des organismes internationaux en place. Ce service est basé sur l'utilisation de l'ordinateur moderne afin de transférer l'information demandée de façon rapide et efficace. Il est à noter que la VMM permet d'acquérir les données sur lesquelles reposent les ambitions du GARP. On est actuellement à établir un programme international de la VMM pour dériver des avantages économiques des prévisions tant hydrologiques que météorologiques.

Le point de vue des pays en voie de développement fut présenté par M. S. Tewungwa du Département de météorologie de la Communauté de l'Afrique de l'Est. Il reconnaît l'assistance technique reçue de l'OMM et remarque que toutefois l'effort mis sur la formation est peut-être l'aspect le plus rentable. En effet graduellement ces pays deviennent auto-suffisants et peuvent prendre le contrôle de leur développement. La conférence la plus intéressante est peut-être celle du professeur E. Bernard de Belgique. Il propose une thèse, très convaincante du mode d'assistance météorologique selon le degré de développement économique et social d'un pays. Il est intéressant de se situer (soi-même) selon les critères du professeur Bernard.

Un autre Canadien, M.R.H. Clark de l'Energie, mines et ressources décrivit les problèmes d'interface de la météorologie et de l'hydrologie dans le service de gestion de l'eau. Il énonça les rapports et les interrelations existant entre la météorologie et l'hydrologie dans la gestion rationnelle et l'Opération des barrages, lacs, réseaux hydrologiques et dans la prévision de l'écoulement des cours d'eau. La dernière conférence fut présentée par M. J.P. Meade du Bureau météorologique du Royaume-Uni. La météorologie doit beaucoup aux marins d'antan. Elle semble s'être divorcée comme science du domaine marin. Avec la venue de cette nouvelle science, l'océanographie, M. Meade voudrait voir ces deux sciences plus intimement liées en les rattachant et les chapeautant par une science plus globale qui les contiendraient.

En résumé, la lecture des textes de conférences donne une très bonne idée de l'état de la météorologie actuellement et des grandes lignes de conduite pour le futur. Le mélange de l'aspect scientifique et des conséquences sociales et économiques est heureux car il permet de faire le point entre les deux sphères et de sortir, en d'autres mots, de sa tour d'ivoire. Finalement, ces textes illustrent bien l'action bénéfique que fournit l'OMM à l'humanité. On ne peut qu'envier et applaudir les résultats tangibles que cette organisation internationale a pu apporter en dépit des aléas politiques de ce dernier siècle.

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