


Detecting elusive aspects of wildlife ecology using drones: New insights on the mating dynamics and operational sex ratios of sea turtles

Gail Schofield¹  | Kostas A. Katselidis² | Martin K. S. Lilley³ | Richard D. Reina⁴ | Graeme C. Hays¹

¹Deakin University, School of Life and Environmental Sciences, Centre for Integrative Ecology, Warrnambool, Vic., Australia

²National Marine Park of Zakynthos, Zakynthos, Greece

³School of Biological and Chemical Sciences, Queen Mary University of London, London, UK

⁴School of Biological Sciences, Monash University, Clayton, Vic., Australia

Correspondence

Gail Schofield
Email: g.schof@gmail.com

Funding information

Deakin University

Handling Editor: David Gremillet

Abstract

1. Offspring and breeding (operational) sex ratios (OSR) are a key component of demographic studies. While offspring sex ratios are often relatively easy to measure, measuring OSRs is often far more problematic. Yet, highly skewed OSRs, and a lack of male–female encounters, may be an important extinction driver.
2. Using loggerhead sea turtles (*Caretta caretta*) as a case study, we showed the utility of drones, i.e. unmanned aerial vehicles (UAVs), to distinguish adult males and females in a marine breeding area, using a combination of morphological characteristics (tail length) and behavioural differences (active mating, courting and searching by males versus resting by females). Through repeated surveys, we documented seasonal changes in the OSR.
3. While the number, and ratio, of males and females on the breeding grounds changed massively, the ratio of receptive females (derived from the rate of influx of new individuals to the area) to breeding males remained close to 1:1 for much of the period before nesting commenced. Hence, we show how large imbalances in the number of adult males and females may translate into relatively balanced OSRs.
4. Our results suggest that the departure of males from the breeding grounds is linked to a decline in female receptivity, with female sea turtles being known to store sperm to ensure high clutch fertility throughout the nesting season.
5. In conclusion, while we detected up to three times more females than males at the breeding ground, at present, OSRs appear stable. However, because most males breed annually (vs. biannually by females), there might only be c. 100 males in the adult population (i.e. adult sex ratio of 1:7.5), which might become further skewed under expected climate change scenarios; thus, we need to identify the minimum number of males required to prevent extinction. Finally, we highlight the use of UAVs for assessing the mating dynamics of other marine, terrestrial or avian species, in which adults might exhibit visually detectable differences, such as sexual dimorphism, external body characteristics or grouping tendencies.

KEYWORDS

conservation policy, demography, drone, extinction, mating system, polyandry, potential reproductive rates

1 | INTRODUCTION

Studies of terrestrial, avian and marine wildlife stress the importance of understanding local population dynamics and sex ratios of endangered species for effective management to maintain health and viability, particularly for broadly dispersed populations (e.g. Di Fonzo, Collen, Chauvenet, & Mace, 2016; Gerber & White, 2014). Given widespread concerns over highly female-biased offspring sex ratios in reptiles, including sea turtles, caused by temperature-dependent sex-determination (TSD; Bull, 1980; Hays, Mazaris, & Schofield, 2014; Le Galliard, Fitze, Ferriere, & Clobert, 2005), key questions for implementing appropriate conservation actions and understanding the evolution of life-histories need to be directed towards understanding how adult male–female encounters occur to ensure the fertility of clutches (Hamann et al., 2010; Hays et al., 2016; Reina, Abernathy, Marshall, & Spotila, 2005). Thus, it is essential to quantify seasonal changes in the operational sex ratio (OSR; Emlen & Oring, 1977) and the time that individuals are no longer receptive to further mating opportunities (termed “time out” or potential reproductive rates, PRR; Clutton-Brock & Parker, 1992; Parker & Simmons, 1996).

The operational sex ratio is defined as the ratio of sexually active males to receptive females in a population, or, alternatively, the ratio of adult male to female individuals that are “ready to mate” at a given time (Clutton-Brock & Parker, 1992; Emlen & Oring, 1977). It is considered a main determinant of the intensity and type of competition for mates in populations (Kvarnemo & Ahnesjo, 1996; Weir, Grant, & Hutchings, 2011). In sea turtle populations, varying levels of competition for females have been detected, including male–male contests and scramble polygamy (Jessop, FitzSimmons, Limpus, & Whittier, 1999; Schofield, Katselidis, Pantis, Dimopoulos, & Hays, 2006). Most females copulate with several males (polyandry). However, variable rates of multiple paternity have been recorded for different sea turtle species (e.g. Crim et al., 2002; Fitzsimmons, 1998), suggesting that encounter rates drive the intensity of competition. In addition, males have been reported to precede females to the breeding grounds and become scarcer relative to females as the season progresses (Godley, Broderick, Frauenstein, Glen, & Hays, 2002; Hays, Fossette, Katselidis, Schofield, & Gravenor, 2010; Schofield, Scott, et al., 2013), leading to sex ratios shifting from highly male biased to highly female biased over the breeding period.

Measuring OSR in natural populations is difficult (Kokko & Monaghan, 2001). As a result, to date, the ratio of all reproductively active sea turtles in a population for a given season is used as a proxy of OSR (Hays et al., 2010, 2014). Yet, individual females are only thought to be receptive for c. 10 days (Comuzzie & Owens, 1990; Hamann, Limpus, & Owens, 2003; Kawazu et al., 2015; Wood & Wood, 1980); thus, the absolute number of females present in the study area might not actually reflect the number of receptive females at any one time. Furthermore, empirical proof of the actual number of male sea turtles frequenting breeding sites remains elusive globally. Sea turtles are a classic example of a group of species where population estimates are often based on imperfect detection (e.g. Bland et al., 2015; Frederiksen, Lebreton, Pradel, Choquet, & Gimenez, 2014), using the counts of female sea turtles ashore nesting or their tracks on beaches (Pfaller et al., 2013; Whiting, Chaloupka, & Limpus, 2013), failing to factor in the number

of males because they do not come ashore. The fact that males tend to breed more frequently (every 1–2 years) than females (every 2+ years; Hays et al., 2014; Limpus, 1993) also supports that this component of the population is already a highly limited resource (Hays et al., 2014). Therefore, to quantify the number of males and the population dynamics in sea turtle mating systems, techniques that facilitate the regular and rapid monitoring of the marine environment are required.

Commercially available lightweight drones, i.e. unmanned aerial vehicles (UAVs: quadcopters, balloons, and blimps) are being increasingly used to monitor the demographics, behaviour, and physiology of wildlife populations, particularly for elusive, dangerous and wide-ranging animals inhabiting difficult-to-access areas (Chambot & Bird, 2015; Jones, Pearlstine, & Percival, 2006). For instance, UAVs are revealing the distribution and numbers of animals under a variety of conditions, including marine areas (dugong *Dugong dugon*; Hodgson, Kelly, & Peel, 2013), precipitous coastal cliffs (gulls, Sardà-Palomera et al., 2012), forest canopies (orangutans *Pongo abelii*; Kohl & Wich, 2012), and in the dark using infra-red imagery (white-tailed deer *Odocoileus virginianus*; Kissell & Nimmo, 2011). Unmanned aerial vehicles are also being used to distinguish sex, age/size class, unique individuals, and changes in body condition (humpback whales *Megaptera novaeangliae*; Christiansen, Dujon, Sprogis, Arnould, & Bejder, 2016; killer whales *Orcinus orca*; Durban, Fearnbach, Barrett-Lennard, Perryman, & Leroi, 2015; bowhead whales *Balaena mysticetus*; Koski et al., 2015). Compared to conventional aerial or ground monitoring techniques, UAVs offer high operational flexibility, in addition to providing data of high spatial and temporal resolution at low operational costs and low manpower effort (Chambot & Bird, 2015). Thus, UAVs could be used to answer long-standing questions about the performance, energetics, habitat selection and social interactions of cryptic animals (Chambot & Bird, 2015; Hays et al., 2016; Wilmers et al., 2015). Such information could help improve the management and delimitation of nature reserves established to protect threatened wildlife (Linchant, Lisein, Semeki, Lejeune, & Vermuelen, 2015).

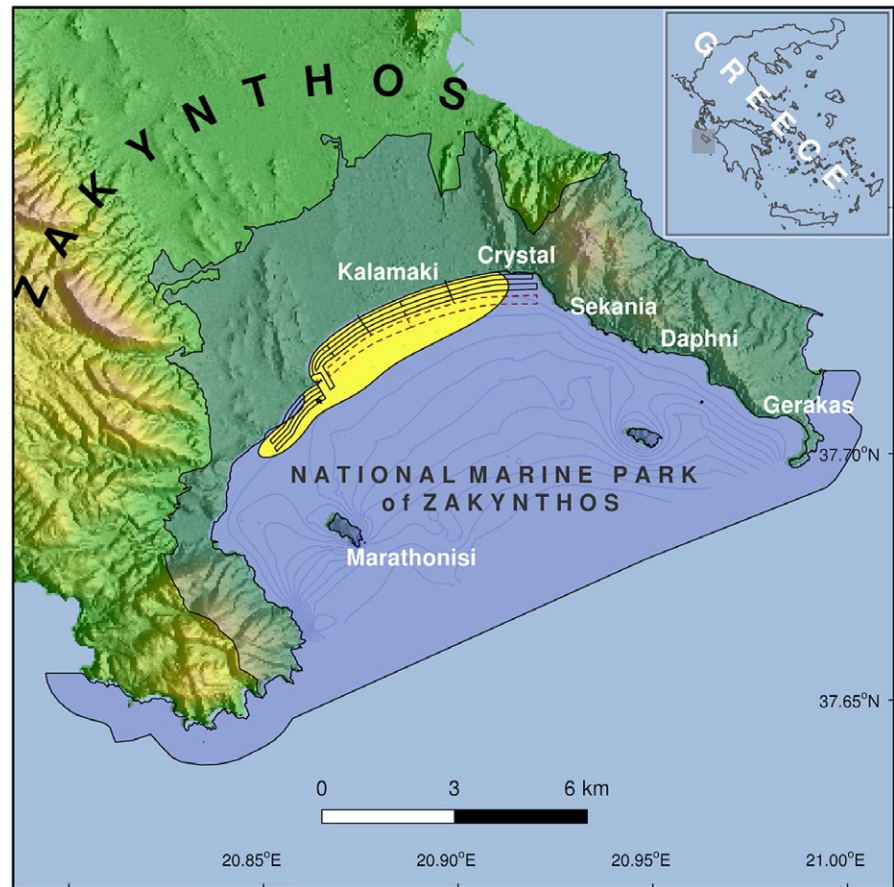
Preliminary studies have advocated the utility of UAVs to detect sea turtles (Brooke et al., 2015; Hodgson et al., 2013) and distinguish males (Bevan et al., 2016) in the marine environment, without causing the disturbance experienced using traditional plane surveys (Frick et al., 2000). Thus, here, we set out to explore whether rigorous UAV surveys could be used to provide the first reliable estimates of changes in the relative numbers of reproductively active male and female loggerhead sea turtles (*Caretta caretta*) during breeding from which to elucidate the actual OSR. Our results are expected to provide first estimates of male numbers in sea turtle breeding populations and help guide the development of effective conservation management practices, with potential wider application to other wildlife populations that exhibit visible morphological or behavioural differences between the sexes.

2 | MATERIALS AND METHODS

2.1 | Study area and species

Laganas Bay at the southeastern part of Zakynthos Island, Greece (Figure 1; Figure S1; 37°43'N, 20°52'E) is ideal for examining the

FIGURE 1 Laganas Bay on Zakynthos Island (Greece) showing the study area with the 50% kernel utilization distribution (see the Materials and Methods section for more details) of tracked turtles in May and June (yellow shaded area; $n = 63$ males and females; derived from Schofield, Scott, et al., 2013) and the transect lines. Regular transects = bold black lines, 50, 150, 250, 350 m offshore; additional transects = dashed red lines, 500 and 700 m offshore along which the unmanned aerial vehicles was flown during surveys; blue lines = isobaths; blue shaded area = outer limits of the marine area of the National Marine Park of Zakynthos; dark green = terrestrial area of the National Marine Park of Zakynthos. See Figure S1 for zoomed version of the transects. Note, in older publications, Crystal may be referred to as Kalamaki, while Kalamaki may be referred to as E. Laganas



breeding behaviour of sea turtles, because the turtle population forms a tight nearshore aggregation in shallow waters, with generally good underwater visibility (Hays et al., 2014; Schofield, Scott, et al., 2013). The bay is generally shallow, with a maximum depth of about 50 m and a marine area of 105.9 km², and a coastline of 27.8 km in length, forming the Marine Protection Area of the National Marine Park of Zakynthos. Within the bay are six discrete loggerhead sea turtle (*C. caretta*) nesting beaches with a total length of 6.16 km. Each year, a mean of 1,244 clutches are laid (based on 23 years of data extending from 1984 to 2007; Casale & Margaritoulis, 2010). Because females lay between three and five clutches (Schofield, Scott, et al., 2013; Zbinden, Aebischer, Margaritoulis, & Arlettaz, 2007), an estimated 249–415 female turtles are present each season (Katselidis, Schofield, Dimopoulos, Stamou, & Pantis, 2013; Schofield, Scott, Katselidis, Mazaris, & Hays, 2015), while around 100 males are predicted to be reproductively active based on the observed sex ratios from photo-identification surveys during the breeding period (Hays et al., 2010). Mating activity starts in early March and continues until late June, primarily along the central nearshore area of the bay (Figure 1; Schofield, Scott, et al., 2013). Most migratory males depart for foraging grounds in late May (Schofield, Scott, et al., 2013), while females start nesting from late May (Margaritoulis, 2005; Schofield, Scott, et al., 2013), and start migrating back to foraging grounds from early July until August to 1,000 km distant (Hays et al., 2014; Schofield, Scott, et al., 2013).

2.2 | Survey equipment

The DJI Phantom 3 Professional™ (Shenzhen, China; <http://www.dji.com>) is a relatively small, low-cost, and commercially available UAV that can travel up to 2 km from the launch point. The aircraft is controlled through the GO app from DJI™ that runs on a tablet computer. Each UAV battery allows approximately 15–20 min total flight time (using the DJI TB48 battery which provides the longest flight time). This UAV model includes a camera capable of recording up to 4K-quality video. In this study, all surveys were recorded in 3,840 × 2,160 pixel video quality at 30 frames/s. The camera is attached to a three-axis gimbal system that stabilizes the video in flight and allows the operator to remotely control multiple aspects of the camera angle. The aircraft has a GPS-stabilized flight control system and is stable in relatively windy conditions (e.g. up to 25 km/h wind speeds).

2.3 | Survey design

Previously, we showed that the 50% kernel utilization distribution (KUD) of 63 male and female loggerheads tracked in May and June with high-resolution GPS transmitters (Argos-linked Fastloc-GPS) and loggers (TrackTag) falls along an 8-km nearshore stretch of Laganas Bay during the breeding period (see Figure 1, derived from May and June data presented in the online supplement of Schofield, Scott, et al., 2013). The KUD was generated using the kernel density tool in the Geospatial modelling environment of ESRI ArcGIS (for full details see

Schofield, Scott, et al., 2013). The delineated survey area is characterised by shallow submerged sandbanks (NATURA 2,000 habitat 1,100, in Annex I of the 92/43 EEC Directive). Thus, we divided this section into six zones, using up a single battery in each zone. The line transects in each zone were 1–2 km in length parallel to shore and encompassing an area up to 400 m offshore (Figure 1). The line transects were run at 50 m, and 150 m, 250 m and 350 m (approximately representing 0.5–3.5-m seabed depth along the central line) from shore. The UAV was flown along predefined autonomous routes at a continuous speed of 12 m/s and height of 30 m above sea level, which provided a horizontal field of view of 50 m, preventing transect lines from overlapping. Faster and slower speeds of the UAV were initially tested, with 12 m/s being optimal to complete all transects. We assumed that the same individuals were not repeat sighted (double counted) across multiple transect lines or between zones, because (1) the transects were completed quickly (c. 2 min/1–2 km transect line), with turtles swimming at speeds of <0.2 km/hr (i.e. <4 m/min) in the breeding area (Schofield et al., 2010), (2) females general rest/bask during this period (Schofield et al., 2006), and (3) males search for females by moving parallel to shore, and were unlikely to traverse across transect lines (Schofield et al., 2006). We ran all transects in continuous flight mode and viewed the data during the processing stage only. We did not operate the UAV when there was a high chance of rain or when wind speeds exceeded 25 km/hr.

From 10 April to 23 June, 2016, we flew the UAV along all transects every 1–4 days. Surveys were completed between 16.00 and 19.00 (including the time required for setting up, flying the UAV and travelling to the next zone). This time of day was selected because it was when sea turtles were most easily detected during boat surveys that had been previously trialled at different times of the day (Schofield et al., 2009). Once every 14 days, we also ran additional transect lines at 500 m and 700 m to confirm that turtles were not distributed further out. In general, the majority of turtles were detected along the 50–150 m lines, with numbers declining to single turtles along the 250–350 m lines, and usually no individuals were sighted beyond these distances.

2.4 | Field-based validation trials

First, we ran trials on calm weather days when the underwater visibility was clear, to determine the optimal height to fly the UAV to maintain a sufficiently wide field of view, but also (1) detect adult turtles to a seabed depth of 5–7 m and (2) distinguish the tails of swimming males. Based on the random capture of adult male ($n = 45$ unique individuals) and female ($n = 43$ unique individuals) turtles within the breeding area from 2006 to 2012 (Schofield, Dimadi, et al., 2013; Schofield, Scott, et al., 2013), we obtained a mean curved carapace length of 83 cm for both sexes (range: 71–102 cm for males; 74–96 cm for females). These values support those obtained by Margaritoulis et al. (2003), who recorded a mean curved carapace length of 83 cm for nesting females on Zakynthos (range: 70–96.5 cm; $n = 395$ individuals). In the Mediterranean (Casale et al., 2005) and Greece (Rees et al., 2013), adult males had tails reported to extend >5 and >6 cm, respectively, often exceeding 25 cm, beyond the tip of the carapace, whereas females have tails that extend <5 cm beyond the tip of the carapace.

We used a wooden cut-out of a turtle that was 80-cm in size (i.e. reflecting the mean size of male and female turtles at the breeding area; Margaritoulis et al., 2003; Schofield, Scott, et al., 2013) and painted the same brown colour as turtles in our study population. We placed the model on the sea surface and on the seabed at 1, 2, 3, 4, 5, 6, and 7 m depth and flew the UAV over the turtle at heights ranging from 10 to 100 m. A minimum height of 10 m was selected, to ensure nearby animals were not disturbed (Bevan et al., 2016). A maximum height of 100 m was selected to ensure that we were operating well within the maximum allowed height of 120 m (400-feet) of general UAV operational guidelines.

To determine the optimum height to distinguish the tails of males, we used male turtles that were swimming within a few metres of shore (and were visually confirmed to have long tails by one observer (G.S.) wading in the water and viewing them directly), we again operated the UAV at different heights ranging from 10 to 100 m. Juvenile turtles are sometimes found in the breeding site (although not generally during the mating period; pers. comm. Kostas Papafitsoros); thus, we also made a wooden cut-out of a 40-cm turtle (i.e. juvenile), which we placed at a distance of 20-m from the adult cut-out, and again operated the UAV at different heights from 10 to 100 m to confirm that it is possible to distinguish between definite adult and juvenile size classes if necessary. We further validated this test by operating the UAV in an area containing a mixture of adults and juveniles.

In general, males swim with their tail extended, only curling it when they lose an encounter with another male or female, but immediately straightening it again on departure (Schofield et al., 2006). During the mating period, males actively swim (patrol) for receptive females, whereas females tend to primarily rest on the seabed and/or bask near the sea surface (Schofield et al., 2006). To confirm this observation in 2016, we ran four boat transects on fair weather days (<15 km/h wind speeds, and good underwater visibility conditions) between 9 May and 4 June in parallel (but lagging behind, due to slower boat speeds, but also to minimise interference) to the full or partial UAV line transects, during which we distinguished males from females based on tail length and behaviour. For the purpose of this study, we assumed that females had tails extending <5 cm from the tip of the carapace, with or without flipper tags, and were primarily resting on the seabed, being mated or courted or were avoiding males (Schofield et al., 2006). In comparison, we assumed that males had a tail extending >5 cm (none of which had flipper tags, even though males are tagged at other sites, Rees et al., 2013, 2017), and were exhibiting directional swimming, courtship, mating or fighting behaviour (Schofield et al., 2006). We assumed that immature turtles were not present during our surveys, as we have not encountered or accidentally attached tracking units ($n = 100$) to immature turtles during intensive in-water surveys since 2001, with incidental observations of a few immature turtles occurring later in the season and in deeper waters (Kostas Papafitsoros, personal communication).

On two occasions (9 May and 4 June 2016), we followed the same line transects at the same time of day as the UAV to quantify differences in the numbers turtles sighted between the two techniques. Boat surveys were conducted by two observers on a 4-m boat with an outboard engine and maximum boat speed of 5 knots. The maximum

field of view of turtles was *c.* 20 m on either side (for methodological details and validation see Schofield et al., 2006, 2009), making it comparable to the UAV, but primarily of individuals near the surface (excluding breathing individuals) or on the seabed when immediately adjacent to the boat. On the other two occasions, we focused detection effort in the areas of highest turtle aggregation (i.e. where the prevailing wind blows to shore; Schofield et al., 2009), and, using the boat, we followed the UAV along subsections of transect at the same time as the UAV flew past, to provide detailed comparisons of turtle sightings to validate sex and behaviour.

2.5 | Post survey data processing

Post survey, following Hodgson et al. (2013), the lead author (G.S.), independently reviewed all video footage captured in real time during transects on a computer and recorded all turtle sightings, sex and activity. A second observer (KAK) also independently reviewed the video footage. The two observers exhibited no difference in detecting turtles, and when there was a difference in detecting the sex (<2% error rate), the still images from the video footage were used to resolve this issue. To obtain the stills, the video footage was extracted at one frame (photo) per second, using FFmpeg (<http://www.ffmpeg.org>), in Portable Network Graphics (.png) format, retaining the same resolution as the video footage (3,840 × 2,160 pixels). These stills were used to better assess the two records.

In addition, the environmental conditions for each video were scored using the methods described by Hodgson et al. (2013), including underwater sea visibility, glare and glitter, and sea state. Sighting data included recording the number of observed turtles, sex (confirmed male with tail visible, possible male in an interaction with another turtle, possible female for all other turtles), position of the turtle in water column (on seabed, in water column [i.e. the animal cast a shadow on the seabed], breaking the surface) and activity (resting, basking, breathing, swimming, interacting, mating). Glare and glitter were a minimal issue at the study site; at the time of day that the UAV was flown, at most 15% of the frame (i.e. field of view) was subject to glare, and even in these instances the top or bottom part of the frame could always be viewed along the path, allowing 100% detection. Even when turbidity was recorded, the seabed was still visible from the UAV (i.e. to 4 m), and only occurred in one of the six zones in surveys with NW and SW winds.

Because the survey area was characterised by submerged sandbanks, detection of sea turtles was relatively easy against the sandy bottom. Furthermore, because the UAV allowed 100% field of view across the 50-m surface and to 4-m seabed depth (maximum depth surveyed on most days), with no glare issues. Distance-Sampling analysis (Buckland, Anderson, Burnham, & Laake, 1993) was not required to estimate the abundance of sea turtles within the survey area.

2.6 | Data analyses

We recorded the total number of turtle sightings on each survey day, along with the numbers of males and females. To estimate our

detection rate (percentage) of females in the population, we compared the maximum number of females sighted across all surveys against the estimated mean number of females (249–415 females), which was extrapolated from the mean number of nests for the 23-year period (Casale & Margaritoulis, 2010) and assuming either three to five clutches per female (Schofield, Scott, et al., 2013; Zbinden et al., 2007). We also assessed the representativeness of this result, based on official press releases in Greek newspapers by the monitoring organisation (ARCHELON) at the end of the 2016 season, stating about 1,500 clutches (IMERA, Zakynthos 3 October 2016, p. 10).

To estimate the OSR, we first confirmed that the change in the relative numbers of males and females from April to June matched that detected in the field, by comparing our results against those obtained from 467 turtles sighted during 27 boat-based surveys from mid-April to mid-May in 2003 (Hays et al., 2010). To quantify the OSR (termed “functional OSR” [fOSR] here to distinguish it from the “seasonal” OSR), we assumed that the influx in females observed between surveys represented receptive females. We also assumed that females are only in oestrus for *c.* 10 days (Comuzzie & Owens, 1990; Hamann et al., 2003; Kawazu et al., 2015; Wood & Wood, 1980). Thus, we compared male numbers against the average rate of change (Δ) of female numbers per 10-day periods from the start to end of surveys, whereby:

$$\begin{aligned} \text{Rate of change}(\Delta/\text{day}) &= \frac{\Delta(y)}{\Delta(x)} \\ &= \frac{(\text{No. turtles on day 10}) - (\text{No. turtles on day 1})}{10(\text{days}) - 1(\text{day})} \end{aligned} \quad (1)$$

3 | RESULTS

3.1 | Field-based validation trials

It was possible to detect turtles on the sea surface at a height of 100-m above sea level, but very good weather and sea state conditions were required. To detect turtles reliably to the seabed at 5–7 m, we found that 60 m was maximum detection height in our study area. To distinguish reliably the tails of swimming males, we found that 30 m was the maximum detection height (Figure 2). When operating the UAV up to a height of 60-m above the sea surface, it was possible to reliably distinguish the 80-cm and 40-cm turtle models (adult and juvenile respectively) from one another (Figure 2), even when the 80-cm model was at a depth of 5-m and the 40-cm model was on the sea surface, using the equation:

$$\begin{aligned} \text{real size of object (mm)} \\ &= \frac{\text{distant to object (mm)} \times \text{object size (pixels)} \times \text{sensor size (mm)}}{\text{focal length (mm)} \times \text{image size (pixels)}} \end{aligned} \quad (2)$$

The 80-cm and 40-cm models had “object sizes” of 29.3 pixels and 14.7 pixels when using the still images from the UAV video footage obtained at 60-m height above the sea surface, respectively. See Figure S1 for an examples of UAV footage at 30-m height above sea level, which was the selected height at which all surveys in the subsequent sections were conducted.

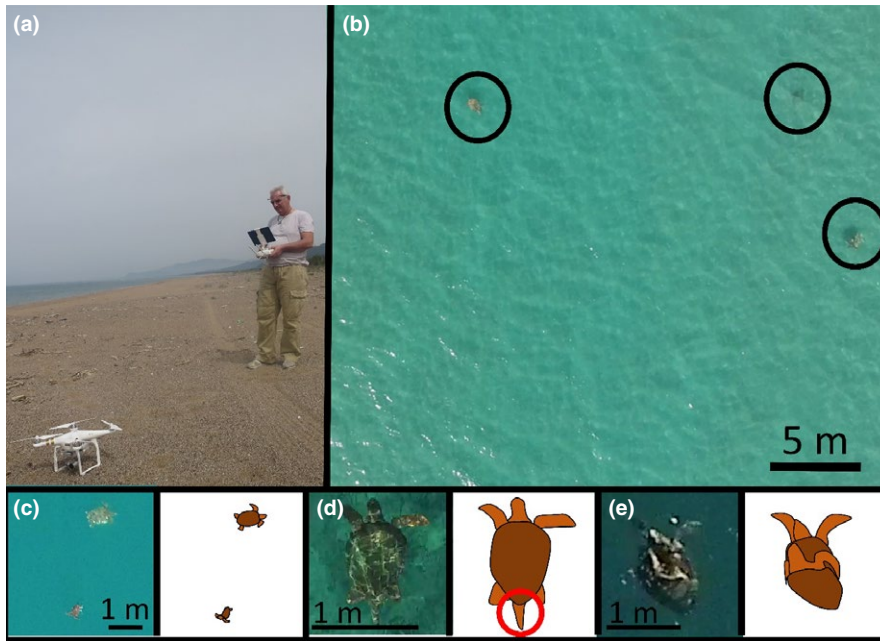


FIGURE 2 (a) Operation of the DJI Phantom 3 Professional™. (b) Observations of loggerhead sea turtles (*Caretta caretta*) (inside black open circles) from the unmanned aerial vehicles from a height of 30 m. (c) Distinguishing adult (top of image) from immature (bottom of image) sea turtles. (d) Distinguishing an adult male loggerhead sea turtle based on a tail (inside red open circle) that extends beyond the carapace. (e) Mating pair of loggerhead sea turtles. Images b, c, d, and e were zoomed in during the post-processing of high resolution images

The parallel boat transects confirmed that, during the survey period, all turtles observed resting on the seabed or basking near the sea surface were females, while all observed males were actively swimming or interacting with females. We also confirmed that >95% of interactions were between males and females during this period (Figure 2e). Male:male interactions and female:female interactions represented the remaining 5% in early-mid May and early June, respectively.

We confirmed that the UAV was about seven times more effective than the boat surveys when turtle numbers were low (78 vs. 11 turtles sighted per survey respectively) and four times more effective when turtle numbers were high (251 vs. 64 turtles sighted per survey respectively). We confirmed that the UAV flew on the same path across different days based on repeat sightings of permanent features along transect lines in each zone, including buoys and concrete blocks.

3.2 | Breeding phenology

We recorded a total of 3,306 sightings of turtles over 33 daily UAV surveys at 30 m altitude from 10 April to 23 June in 2016, totalling 174 UAV flights covering more than 1,000 km distance.

The maximum number of males and females detected on a single survey day was 89 (16 May 2016) and 242 (4 June 2016) respectively (Figure 3). We also recorded over 326 mating and courtship events over the surveys, with a maximum of 89 mating/courtship interactions being recorded in a single survey (16 May) (Figure 3). The 242 females represented 58%–97% of estimated females extrapolated from mean annual nest numbers when assuming three or five clutches respectively.

From 4 to 16 May 2016, we observed a similar rate of increase in the numbers of males and females (Figure 3). At this point, the influx in female numbers slowed, with male numbers sharply declining. Mating and courtship activity followed a similar pattern to that of male numbers; however, the numbers of interacting turtles dropped faster

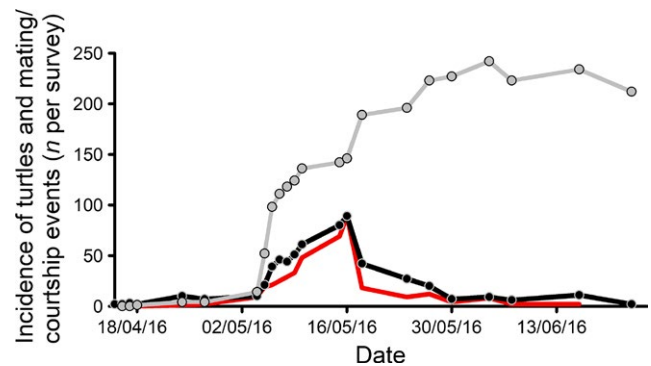


FIGURE 3 Incidence of male (black line) and female (grey line) loggerhead turtles and mating/courtship events (red line) in the study area (number per survey when the drone was flown at 30 m altitude)

than male numbers after 16 May, with more males being observed swimming than mating/interacting (Figure 3). Only 11 males remained in the study area through June.

3.3 | Operational sex ratios

The overall male:female OSR for the breeding season was 1:2.7 (based on the maximum number of males and females recorded across all surveys i.e. 89 males vs. 242 females). However, at different points in the season (from April to June), the sex ratio changed from highly male biased to highly female biased. Our UAV-derived time series (2016 surveys) of this sex ratio change was strongly correlated with the boat-based time series (2003 surveys) (Pearson's product-moment correlation $t = 8.27$, $p < .01$), with both series exhibiting strong negative trends over time (Mann-Kendall test: $\tau = -0.94$, $p < .01$; 2016: $\tau = -0.75$, $p < .01$; Mann, 1945; Kendall, 1948) (Figure 4a). When assessing the rate of change in the (Δ) influx of females, we found a strong positive correlation between the number of males

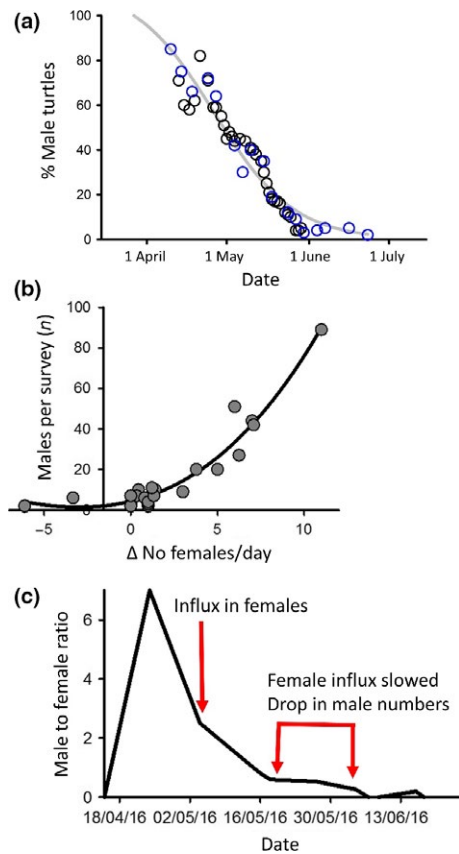


FIGURE 4 (a) Comparing the change in the sex ratio of adult turtles during the breeding season obtained from unmanned aerial vehicles observations at 30 m altitude (blue circles) and that obtained from in-water photo identification surveys (black circles). Adapted from Hays et al. (2010). (b) Maximum number of males present was correlated with the maximum influx in females entering the study area (i.e. reflecting females that are thought to be “receptive” to mating) ($F_{2,22} = 126.4$, adjusted $r^2 = .97$, $p < .001$). (c) Ratio of males to “receptive” females in the study area across time, assuming that females remain receptive for *c.* 10 days (based on Comuzzie & Owens, 1990; Hamann et al., 2003; Kawazu et al., 2015; Wood & Wood, 1980). Initially, the bias was highly male skewed, but became close to 1:1 when there was an influx in female numbers; subsequently, male numbers dropped, while the influx in females slowed, resulting in the ratio of males to receptive females remaining similar over this period. In fact, the actual sex ratio would be 1:4. It is likely that male departure is triggered by increased effort to detect receptive females among mated females

and “receptive” females (Figure 4b; $F_{2,22} = 126.4$, adjusted $r^2 = .97$, $p < .001$). While, initially, the fOSR was strongly male-biased, it became 1:1 immediately after the major influx in females, with this ratio being retained over the following month (Figure 4c), due to female influx slowing while male numbers declined (Figure 3).

4 | DISCUSSION

Here, we confirmed that the relative number of males and females changes through the breeding season, but that the fOSR is maintained

close to 1:1, due to the departure of males. In parallel, we provided the first estimates of male numbers in a sea turtle population globally, confirming that highly female-biased offspring sex ratios perpetuate into adulthood, with possible repercussions on future population viability in the light of global climate change (Hamann et al., 2010; Hays et al., 2016). Finally, we showed that UAVs represent a highly useful tool for managers to assimilate field-based information on population dynamics and sex structure of wildlife that exhibit clear morphological or behavioural differences during breeding. Such information could help resolve major knowledge gaps about male–female interactions in elusive wildlife during breeding.

It is extremely difficult to record the OSR of sea turtles accurately in the marine environment, due to the limitations of sea state and underwater visibility, along with restricted fields of view on boats and aircraft, requiring estimates to be extrapolated using distance-sampling (Buckland et al., 1993). Consequently, to date, offspring sex ratios have been used to infer adult OSRs for sea turtles globally (Hays et al., 2014), leading to the suggestion that highly female biased offspring sex-ratios are adaptive, like that documented for lizards (Warner & Shine, 2008). Our UAV surveys provided the first opportunity to obtain actual count data of relative male and female numbers over the 3-month breeding period to test adult OSR predictions in the field. For sea turtles, it is not sufficient to obtain counts of all males and females on the breeding ground, because female turtles are only thought to be receptive for a short period of time, with most males departing over a period of several weeks when some females are still arriving. Through obtaining the exact OSR at different points through the breeding season, we were able to build the receptive period of females into the analysis to derive the fOSR. So, even though the seasonal sex ratio shifted from being highly male-biased to highly female-biased, only a small number of females are likely receptive at a given time, with similar numbers of males remaining to mate them, resulting in an fOSR close to 1:1 for most of the period. About 11 males were recorded to remain actively interacting with females until the end of June in our UAV surveys, and were probably residents of the island (Schofield, Scott, et al., 2013). These males had the potential to mate with all late-arriving females (up to the end of June based on Fastloc-GPS tracking data, Schofield, Scott, et al., 2013), assuming they were not already mated en-route (Meylan, Meylan, & Yeomans, 1992), thus enhancing their reproductive fitness.

Our UAV surveys showed that males began departing the breeding area as soon as the influx in females slowed, suggesting that females have a limited period of receptivity in our study population, supporting that reported for other populations (Comuzzie & Owens, 1990; Hamann et al., 2003; Kawazu et al., 2015; Wood & Wood, 1980). Thus, male departure might be triggered by a decline in receptive females (i.e. an increase in failed encounters) combined with increased effort to detect them among already-mated females and compete for them with other males when energetic reserves are dropping (Godley et al., 2002; Plotkin, Owens, Byles, & Patterson, 1996). Variable rates of multiple paternity for different sea turtle species (e.g. Crim et al., 2002; Fitzsimmons, 1998) also indicate that males often have limited success in attempting to mate with already-mated females. Our UAV

surveys showed that the influx in females peaked at the same time as mating activity, supporting previous hypotheses (Godley et al., 2002). However, peak mating occurred later than that detected in previous boat-based surveys (Hays et al., 2010). It is likely that peak mating shifts across years depending on a range of biotic and abiotic conditions, including temperature, weather, the timing of departure from distant foraging grounds and the conditions individuals experience after arriving at the breeding grounds (Baker, 1938; Both, Bijlsma, & Ouwehand, 2016; Visser et al., 2015). For instance, using Fastloc GPS data, males started departing from 1 May 2009, from 10 May in 2007, 2010 and 2012 and none departed before 20 May in 2008 and 2011 (Schofield, Scott, et al., 2013), indicating interannual variation in the spread and peak of mating activity.

Our UAV surveys provided the first minimum estimate of male numbers in the breeding population. Knowledge about the numbers and area use of males remains limited in for all populations of all sea turtle species globally (Arendt et al., 2012; James, Eckert, & Myers, 2005), despite the fact that offspring sex ratios are highly female skewed, indicating that males are a limited resource (Hays et al., 2014). It is possible that up to 91 or 151 males were present when extrapolating female estimates from nest counts; however, because most males breed annually (76% based on satellite tracking and photo-identification datasets; Schofield, Dimadi, et al., 2013; Schofield, Scott, et al., 2013), less than 200 males (just 112 to 187 males, respectively) might frequent this site. Thus, this study reasserts the importance of learning more about the male component of wildlife populations to improve conservation efforts (Gerber & White, 2014), advocating UAVs as an easy way to detect and count male sea turtles in the marine environment during the breeding period.

In conclusion, we showed that, in the context of sea turtles, OSR is not simply the number of adult male and females on the breeding grounds that is important, and it should incorporate the period of receptivity of females, along with the inflow and outflow of individuals over the breeding period. Furthermore, in single daily surveys we detected up to 65% of the females in the population, as well as obtaining preliminary estimates of male numbers. These findings confirm the utility of UAVs for monitoring sea turtle populations, with more turtles being detected through UAVs compared to boat-based surveys, particularly when small numbers of turtles (<100) were present in the survey area. While the potential of UAVs to contribute towards addressing long-standing research questions for cryptic species is still being explored, our study showed that this technology is particularly useful when individuals are dispersed or numbers are low, and might otherwise be missed by other surveying techniques. Ultimately, UAVs could change how we monitor and manage wildlife populations, particularly when it is possible to distinguish the sexes based on morphological or behavioural traits, as tools in their own right and in combination with other techniques.

ACKNOWLEDGMENTS

UAV flights conformed to Greek legislation during the period of our surveys (Zakynthos Airport protocol numbers: KAZAS/AR/1184 and KAZAS/AR/1190). Approval was given by the Animal Ethics

Committee of Deakin University (B062017). The research was part funded by Deakin University. The map was created following suggestions from <http://scalar.usc.edu/works/graphics-for-conservation/index>. None of the authors have any conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

G.S. and G.C.H. conceived the study. R.D.R. provided technical guidance. G.S. and K.A.K. conducted the fieldwork, with assistance by M.K.S.L. G.S. led the writing with contributions by all authors.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.j3572> (Schofield, Katselidis, Lilley, Reina, & Hays, 2017).

REFERENCES

- Arendt, M. D., Segards, A. L., Byrd, J. I., Boynton, J., Schwenter, J. A., Whitaker, J. D., & Parker, L. (2012). Migration, distribution, and diving behavior of adult male loggerhead sea turtles (*Caretta caretta*) following dispersal from a major breeding aggregation in the Western North Atlantic. *Marine Biology*, *159*, 113–125.
- Baker, J. R. (1938). The evolution of breeding seasons. In G. R. DeBeer (Ed.), *Evolution: Essays on aspects of evolutionary biology* (pp. 161–177). Oxford, UK: Clarendon.
- Bevan, E., Wibbels, T., Navarro, E., Rosas, M., Najera, B. M. Z., Sarti, L., ... Burchfield, P. (2016). Using Unmanned Aerial Vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (*Chelonia mydas*). *Herpetological Review*, *47*, 27–32.
- Bland, L. M., Orme, D. L., Bielby, J., Collen, B., Nicholson, E., & McCarthy, M. A. (2015). Cost-effective assessment of extinction risk with limited information. *Journal of Applied Ecology*, *52*, 861–870.
- Both, C., Bijlsma, R. G., & Ouwehand, J. (2016). Repeatability in spring arrival dates in Pied Flycatchers varies. *Ardea*, *104*, 3–21.
- Brooke, S., Graham, D., Jacobs, T., Littnan, C., Manuel, M., & O'Conner, R. (2015). Testing marine conservation applications of unmanned aerial systems (UAS) in a remote marine protected area. *Journal of Unmanned Vehicle Systems*, *3*, 237–251.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., & Laake, J. L. (1993). *Distance sampling: Estimating abundance of biological populations*. London, UK: Chapman and Hall.
- Bull, J. J. (1980). Sex determination in reptiles. *Quarterly Review of Biology*, *55*, 3–21.
- Casale, P., & Margaritoulis, D. (Eds.) (2010). *Sea turtles in the mediterranean: Distribution, threats and conservation priorities. IUCN/SSC Marine Turtle Specialist Group*. Gland, Switzerland: IUCN.
- Casale, P., Freggi, D., Basso, R., & Argano, R. (2005). Size at male maturity, sexing methods and adult sex ratio in loggerhead turtles (*Caretta caretta*) from Italian waters investigated through tail measurements. *Herpetological Journal*, *15*, 145–148.
- Chambot, D., & Bird, D. M. (2015). Wildlife research and management methods in the 21st century: Where do unmanned aircraft fit in? *Journal of Unmanned Vehicle Systems*, *3*, 137–155.
- Christiansen, F., Dujon, A. M., Sprogis, K. R., Arnould, J. P. Y., & Bejder, L. (2016). Non-invasive Unmanned Aerial Vehicle provides estimates of the energetic cost of reproduction in humpback whales. *Ecosphere*, *7*, e01468.
- Clutton-Brock, T. H., & Parker, G. A. (1992). Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology*, *67*, 437–546.

- Comuzzie, D. K. C., & Owens, D. W. (1990). A quantitative analysis of courtship behaviour in green sea turtles (*Chelonia mydas*). *Herpetologica*, *46*, 195–202.
- Crim, J. L., Spotila, L. D., Spotila, J. R., O'Connor, M., Reina, R. D., Williams, C. J., & Paladino, F. V. (2002). The leatherback turtle, *Dermodochelys coriacea*, exhibits both polyandry and polygyny. *Molecular Ecology*, *11*, 2097–2106.
- Di Fonzo, M. M. I., Collen, B., Chauvenet, A. L. M., & Mace, G. M. (2016). Patterns of mammalian population decline inform conservation action. *Journal of Applied Ecology*, *53*, 1046–1054.
- Durban, J. W., Fearnbach, H., Barrett-Lennard, L. G., Perryman, W. L., & Leroi, D. J. (2015). Photogrammetry of killer whales using a small hexacopter launched at sea. *Journal of Unmanned Vehicle Systems*, *3*, 131–135.
- Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*, 215–223.
- Fitzsimmons, N. N. (1998). Single paternity of clutches and sperm storage in the promiscuous green turtle (*Chelonia mydas*). *Molecular Ecology*, *7*, 575–584.
- Frederiksen, M., Lebreton, J.-D., Pradel, R., Choquet, R., & Gimenez, O. (2014). Identifying links between vital rates and environment: A toolbox for the applied ecologist. *Journal of Applied Ecology*, *51*, 71–81.
- Frick, M. G., Slay, C. K., Quinn, C. A., Windham-Reid, A., Duley, P. A., Ryder, C. M., & Morse, L. J. (2000). Aerial observations of courtship behavior in loggerhead sea turtles (*Caretta caretta*) from southeastern Georgia and northeastern Florida. *Journal of Herpetology*, *34*, 153–158.
- Gerber, L. R., & White, E. R. (2014). Two-sex matrix models in assessing population viability: When do male dynamics matter? *Journal of Applied Ecology*, *51*, 270–278.
- Godley, B. J., Broderick, A. C., Frauenstein, F., Glen, F., & Hays, G. C. (2002). Reproductive seasonality and sexual dimorphism in green turtles. *Marine Ecology-Progress Series*, *226*, 125–133.
- Hamann, M., Godfrey, M. H., Seminoff, J. A., Arthur, K., Barata, P. C. R., Bjørndal, K. A., ... Godley, B. J. (2010). Global research priorities for sea turtles: Informing management and conservation in the 21st century. *Endangered Species Research*, *11*, 245–269.
- Hamann, M., Limpus, C. J., & Owens, D. W. (2003). Reproductive cycles of males and females. In P. L. Lutz, J. A. Musick, & J. Wyneken (Eds.), *The biology of sea turtles* (Vol. II, pp. 135–161). Boca Raton, FL: CRC Press.
- Hays, G. C., Ferreira, L. C., Sequeira, A. M. M., Meekan, M. G., Duarte, C. M., & Bailey, H., ... Thums, M. (2016). Key questions in marine megafauna movement ecology. *Trends in Ecology and Evolution*, *31*, 463–475.
- Hays, G. C., Fossette, S., Katselidis, K. A., Schofield, G., & Gravenor, M. B. (2010). Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change. *Conservation Biology*, *24*, 1636–1643.
- Hays, G. C., Mazaris, A. D., & Schofield, G. (2014). Different male versus female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Frontiers in Marine Science*, *1*, 43–52.
- Hodgson, A., Kelly, N., & Peel, D. (2013). Unmanned aerial vehicles (UAVs) for surveying marine fauna: A dugong case study. *PLoS ONE*, *8*, e79556.
- James, M. C., Eckert, S. A., & Myers, R. A. (2005). Migratory and reproductive movements of male leatherback turtles (*Dermodochelys coriacea*). *Marine Biology*, *147*, 845–853.
- Jessop, T. S., FitzSimmons, N., Limpus, C. J., & Whittier, T. S. (1999). Interactions between behaviour and plasma steroids within the scramble mating system of the promiscuous green turtle *Chelonia mydas*. *Hormones and Behaviour*, *36*, 86–97.
- Jones, G. P., Pearlstine, L. G., & Percival, H. F. (2006). An assessment of small unmanned aerial vehicles for wildlife research. *Wildlife Society Bulletin*, *34*, 750–758.
- Katselidis, K. A., Schofield, G., Dimopoulos, P., Stamou, G. N., & Pantis, J. D. (2013). Evidence based management to regulate the impact of tourism at a key sea turtle rookery. *Oryx*, *47*, 584–594.
- Kawazu, I., Kino, M., Yanagisawa, M., Maeda, K., Nakada, K., Yamaguchi, Y., & Sawamukai, Y. (2015). Signals of vitellogenesis and estrus in female hawksbill turtles. *Zoological Science*, *32*, 114–119.
- Kendall, M. G. (1948). *Rank correlation methods* (4th ed.). London, UK: Griffin.
- Kissell Jr., R. E., & Nimmo, S. K. (2011). A technique to estimate white-tailed deer *Odocoileus virginianus* density using vertical-looking infrared imagery. *Wildlife Biology*, *17*, 85–92.
- Kohl, L. P., & Wich, S. A. (2012). Dawn of UAV ecology: Low-cost autonomous aerial vehicles for conservation. *Tropical Conservation Science*, *5*, 121–132.
- Kokko, H., & Monaghan, P. (2001). Predicting the direction of sexual selection. *Ecology Letters*, *4*, 159–165.
- Koski, W. R., Gamage, G., Davis, A. R., Mathews, T., LeBlanc, B., & Ferguson, S. H. (2015). Evaluation of UAS for photographic re-identification of bowhead whales, *Balaena mysticetus*. *Journal of Unmanned Vehicle Systems*, *3*, 22–29.
- Kvarnemo, C., & Ahnesjö, I. (1996). The dynamics of operational sex ratio and competition for mates. *Trends in Ecology and Evolution*, *11*, 404–408.
- Le Galliard, J.-F., Fitze, P. S., Ferriere, R., & Clobert, J. (2005). Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences USA*, *102*, 18231–18236.
- Limpus, C. J. (1993). The green turtle, *Chelonia mydas*, in Queensland-breeding males in the southern great barrier reef. *Wildlife Research*, *20*, 513–525.
- Linchant, J., Lisein, J., Semeki, J., Lejeune, P., & Vermuelen, C. (2015). Are unmanned aircraft systems (UASs) the future of wildlife monitoring? A review of accomplishments and challenges. *Mammal Review*, *45*, 239–252.
- Mann, H. B. (1945). Nonparametric tests against trend. *Econometrica: Journal of the Econometric Society*, *13*, 245–259. <https://doi.org/10.2307/1907187>
- Margaritoulis, D. (2005). Nesting activity and reproductive output of loggerhead sea turtles, *Caretta caretta*, over 19 seasons (1984–2002) at Laganas Bay, Zakynthos, Greece: The largest rookery in the Mediterranean. *Chelonian Conservation and Biology*, *4*, 916–929.
- Margaritoulis, D., Argano, R., Baran, I., Bentivegna, F., Bradai, M. N., Caminas, J. A., ... Lazar, B. (2003). Loggerhead turtles in the Mediterranean sea. In A. B. Bolten, & B. E. Witherington (Eds.), *Loggerhead sea turtles* (pp. 175–198). Washington, DC: Smithsonian Books.
- Meylan, P. A., Meylan, A. B., & Yeomans, R. (1992). Interception of Tortuguero-bound green turtles at Bocas del Toro Province, Panama. In M. Salmon, & J. Wyneken (Eds.), *Proceedings of the eleventh, annual workshop on sea turtle biology and conservation*. NOAA Technical Memorandum NMFS-SEFSC-302 (p. 74).
- Parker, G. A., & Simmons, L. W. (1996). Parental investment and the control of sexual selection: Predicting the direction of sexual competition. *Proceedings of the Royal Society of London, Series B*, *263*, 315–321.
- Pfeller, J. B., Bjørndal, K. A., Chaloupka, M., Williams, K. L., Frick, M. G., & Bolten, A. B. (2013). Accounting for imperfect detection is critical for inferring marine turtle nesting population trends. *PlosOne*, *8*, e62326.
- Plotkin, P. T., Owens, D. W., Byles, R. A., & Patterson, R. (1996). Departure of male olive ridley turtles (*Lepidochelys olivacea*) from a nearshore breeding ground. *Herpetologica*, *52*, 1–7.
- Rees, A. F., Carreras, C., Broderick, A. C., Margaritoulis, D., Stingell, T. B., & Godley, B. J. (2017). Linking loggerhead locations: Using multiple methods to determine the origin of sea turtles in feeding grounds. *Marine Biology*, *164*, 30.
- Rees, A. F., Margaritoulis, D., Newman, R., Riggall, T. E., Tsaros, P., Zbinden, J. A., & Godley, B. J. (2013). Ecology of loggerhead marine turtles *Caretta caretta* in a neritic foraging habitat: Movements, sex ratios and growth rates. *Marine Biology*, *160*, 519–529.
- Reina, R. D., Abernathy, K. J., Marshall, G. J., & Spotila, J. R. (2005). Respiratory frequency, dive behaviour and social interactions of

- leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *Journal of Experimental Marine Biology and Ecology*, 316, 1–16.
- Sardà-Palamera, F., Bota, G., Vinolo, C., Pallares, O., Sazatornil, V., & Brotons, L., ... Sarda, F. (2012). Fine-scale bird monitoring from light unmanned aircraft systems. *Ibis*, 154, 177–183.
- Schofield, G., Bishop, C. M., Katselidis, K. A., Dimopoulos, P., Pantis, J. D., & Hays, G. C. (2009). Microhabitat selection by sea turtles in a dynamic thermal environment. *Journal of Animal Ecology*, 78, 14–22.
- Schofield, G., Dimadi, A., Fossette, S., Katselidis, K. A., Koutsoubas, D., Lilley, M. K. S., ... Hays, G. C. (2013). Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. *Diversity and Distributions*, 19, 834–844.
- Schofield, G., Hobson, V. J., Fossette, S., Lilley, M. K. S., Katselidis, K. A., & Hays, G. C. (2010). Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range on sea turtles. *Diversity and Distributions*, 16, 840–853.
- Schofield, G., Katselidis, K. A., Lilley, M. K. S., Reina, R. D., & Hays, G. C. (2017). Data from: Detecting elusive aspects of wildlife ecology using drones: new insights on the mating dynamics and operational sex ratios of sea turtles. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.j3572>
- Schofield, G., Katselidis, K. A., Pantis, J. D., Dimopoulos, P., & Hays, G. C. (2006). Behaviour analysis of the loggerhead sea turtle (*Caretta caretta*) from direct in-water observation. *Endangered Species Research*, 2, 51–61.
- Schofield, G., Scott, R., Dimadi, A., Fossette, S., Katselidis, K. A., & Koutsoubas, D., ... Hays, G. C. (2013). Evidence based marine protected area planning for a highly mobile endangered marine vertebrate. *Biological Conservation*, 161, 101–109.
- Schofield, G., Scott, R., Katselidis, K. A., Mazaris, A., & Hays, G. C. (2015). Quantifying wildlife watching ecotourism intensity on an endangered marine vertebrate. *Animal Conservation*, 18, 517–528.
- Visser, M. E., Gienapp, P., Husby, A., Morrissey, M., de la Hera, I., Pulido, F., & Both, C. (2015). Effects of spring temperatures on the strength of selection on timing of reproduction in a long-distance migratory bird. *PLoS Biology*, 13, e1002120.
- Warner, D. A., & Shine, R. (2008). The adaptive significance of temperature-dependent sex determination in a reptile. *Nature*, 451, 566–568.
- Weir, L. K., Grant, J. W. A., & Hutchings, J. A. (2011). The influence of operational sex ratio on the intensity of competition for mates. *American Naturalist*, 177, 167–176.
- Whiting, A. U., Chaloupka, M., & Limpus, C. J. (2013). Comparing sampling effort and errors in abundance estimates between short and protracted nesting seasons for sea turtles. *Journal of Experimental Marine Biology and Ecology*, 449, 165–170.
- Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, 96, 1741–1753.
- Wood, J. R., & Wood, F. E. (1980). Reproductive biology of captive green sea turtles (*Chelonia mydas*). *American Zoologist*, 20, 499–505.
- Zbinden, J. A., Aebischer, A. A., Margaritoulis, D., & Arlettaz, R. (2007). Insights into the management of sea turtle internesting area through satellite telemetry. *Biological Conservation*, 137, 157–162.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Schofield G, Katselidis KA, Lilley MKS, Reina RD, Hays GC. Detecting elusive aspects of wildlife ecology using drones: New insights on the mating dynamics and operational sex ratios of sea turtles. *Funct Ecol*. 2017;00:1–10. <https://doi.org/10.1111/1365-2435.12930>