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Paper:

Schofield, G., Esteban, N., Katselidis, K. & Hays, G. (2019). Drones for research on sea turtles and other marine vertebrates – A review. *Biological Conservation, 238*, 108214

http://dx.doi.org/10.1016/j.biocon.2019.108214

Biological Conservation Special Issue on drones

Drones for research on sea turtles and other marine vertebrates – a review

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Acknowledgements

GCH and NE were supported by the Bertarelli Foundation as part of the Bertarelli Programme in Marine Science. UAV operations in Diego Garcia, British Indian Ocean Territory were approved by permit (dated 12 October 2018) from the Commissioner's Representative of British Indian Ocean Territory. UAV operations in Greece were approved by permits from the Greek Ministry of Environment (ΓΓΓ & ΓΞ 151503/162/16-1-2017, ΥΠΕΝ/ΓΔΔ&ΔΠ 181806/941/18-04-2019). We also thank the editor and two anonymous reviewers for their constructive suggestions.

Highlights

- Use of unmanned aerial systems (UAVs), or drones, is rising to study marine vertebrates
- Many UAV studies focus on estimating abundance, distribution and density
- Coupled with traditional capture-mark-recapture approaches, UAVs can be used to estimate abundance of hard to study species
- Some UAV studies complement biologging techniques to assess the complexity of behaviours
- UAVs may have great utility in climate change studies, such as assessing breeding sex ratios in sea turtles

Abstract

We review how unmanned aerial vehicles (UAVs), often referred to as drones, are being deployed to study the abundance and behaviour of sea turtles, identifying some of the commonalities and differences with studies on other marine vertebrates, including marine mammals and fish. UAV studies of all three groups primarily focus on obtaining estimates of abundance, distribution and density, while some studies have provided novel insights on the body condition, movement and behaviour of individuals (including inter-specific interactions). We discuss the emerging possibilities of how UAVs can become part of the standard methodologies for sea turtle ecologists through combining information on abundance and behaviour. For instance, UAV surveys can reveal turtle densities and hence operational sex ratios of sea turtles, which could be linked to levels of multiple paternity. Furthermore, embedding UAV surveys within a mark-recapture framework will enable improved abundance estimates. The complexity of behaviours revealed by direct observations of sea turtles and animal-borne cameras can also be examined using UAV footage, complementing studies using electronic tags, such as time-depth recorders and satellite transmitters. Overall, UAVs provide a low-cost approach of quantifying the flexibility of marine animal behaviour, allowing us to integrate information on abundance to establish how individuals respond to the presence of other organisms and the immediate environment.

Keywords: aerial surveys, automation, drone, ecological monitoring, unmanned aircraft system, UAS

1. Background

A longstanding ecological challenge is the collection of sufficient data on the abundance, distribution and behaviour of free-ranging marine vertebrates to inform science and conservation (Nowacek et al., 2016; Hays et al., 2016, 2019). This is because free-ranging animals are often difficult to monitor regularly, due to their unpredictable movement patterns, occupation of hard-to-reach habitats and/or being easily disturbed by human presence (Sutherland et al., 2013; Nowacek et al., 2016). For example, marine mammals and sea turtles can sometimes be extremely difficult to monitor at sea, as they only surface to breathe for short periods, and are often not visible when submerged, even in coastal waters, while marine fishes rarely surface (Nowacek et al., 2016; Rees et al., 2016). As a result, only small numbers of individuals are targeted by studies (and not necessarily at the same time) that might not be representative of the population (Chabot and Bird, 2015; Sequeria et al., 2018). In particular, even today, most studies of sea turtles estimate abundance based on counts of nesting females, or counts of their tracks or nests, on beaches (Pfaller et al., 2013; Mazaris et al., 2017), failing to account for males, juveniles and non-breeding females (Rees et al., 2016; Schofield et al., 2017a, but see Chaloupka and Limpus, 2001). This lack of understanding of the population structure of sea turtles globally limits our ability to develop robust models to predict population trends, and implement conservation measures that are effective across all age classes (Rankin and Kokko, 2007; Rees et al., 2016).

While the behaviour of turtles at sea has been documented through direct observations (Booth and Peters, 1972; Schofield, 2006), only small numbers of individuals can generally be viewed underwater at once. As a result, over the last 40 years, various biologging and biotelemetry approaches (e.g. radio tracking, satellite telemetry, GPS tracking) have been implemented to infer behaviour, movement and distribution patterns of sea turtles and other marine wildlife (Hussey et al., 2015; Wilmers et al., 2015; Hays and Hawkes, 2018). Recent advances (e.g. miniaturization, lighter batteries, materials for waterproof casing) in animal-borne cameras have allowed researchers to match actual behaviour with that inferred from biologging or biotelemetry devices (Thomson et al., 2011; Smolowitz et al., 2015), along with providing brief glimpses of interactions with conspecifics, symbionts, prey and predators (Dell et al., 2014; Thomson and Heithaus, 2014; Thomson et al., 2015). However, all of these techniques require the invasive capture of animals to attach units, with inherent impacts on animal behaviour (McMahon et al., 2011; Hays et al., 2016). Furthermore, these techniques are expensive, making it difficult to track sufficient numbers of individuals at one time, or across time, to make sound population level inferences (Börger et al., 2006; Lindberg & Walker, 2007; Sequeria et al., 2018). Fundamentally, animal behaviour does not occur in isolation, with the behaviour of one individual being influenced by the surrounding environment and organisms (Dill, 1987). Therefore, it is essential to have knowledge of the density and distribution of animals when evaluating behaviour, and vice versa.

Advances in scientific knowledge are driven by the accessibility of new technologies, i.e. that are relatively inexpensive and reliable, for use in monitoring and research. Biotelemetry and biologging representing one such advance, and animal-borne cameras another (Wilmers et al., 2015; Hays and Hawkes, 2018). Unmanned aerial vehicles (UAVs), often referred to as drones, have been used in ecological studies for some time (e.g. Jones et al. 2006), but the recent advent of inexpensive, reliable, easy-to-fly UAVs has led to a profusion of studies that utilize this technology (e.g. Koh and Wich, 2012; Chabot and Bird, 2015; Johnston, 2019). UAVs provide the opportunity to collect high-resolution aerial imagery of animals over multiple scales in a way that is both unobtrusive and repeatable over time and space (Anderson et al., 2013; Christie et al., 2016; Colefax et al., 2018), in parallel to documenting behaviour and how it is correlated by the density and distribution of other animals and the environment (Marvin et al., 2016; Raoult et al., 2018; Torres et al., 2018;

Johnston, 2019). Comparatively, a single UAV has a similar cost to a single biologging unit or biotelemetry unit (excluding Argos charges), but can be used to monitor all individuals in a given area at once, rather than just a single individual. Thus, UAVs could be used to answer key questions on the ecology of marine vertebrates in ways that have not been previously possible (Hays et al., 2016, 2019; Nowacek et al., 2016; Rees et al., 2018).

The potential for UAV studies with sea turtles was recently reviewed by Rees et al. (2018). Here, we build on this work by examining how the potential of UAVs is being realised with respect to sea turtles, by highlighting some of the key findings that have recently emerged using this technology. We also identify some of the commonalities and differences with studies with other marine vertebrates, such as marine mammals and fish, to identify potential gaps in current uses.

2. The growth of UAV studies on sea turtles and other marine vertebrates

We assembled data on ecological studies using UAVs of marine mammals, marine reptiles and fishes. We searched the Thomson Reuters ISI Web of Science^{TM} database and Google Scholar for papers that included any combinations of terms in the topic field: 'drone' + 'UAV' + 'UAS' + 'marine' + 'vertebrate' + 'ecology' + 'behaviour' + 'behavior' + 'population' + 'abundance' + 'distribution' + 'density' + 'movement'. The topic field included the title, abstract, keywords and Keywords Plus (i.e. words that frequently appear in the titles of the articles cited within a publication). To locate additional articles that might not have been identified by the initial search, we also checked the reference lists of relevant papers based on the pre-defined terminology. We only included papers published before December 2018. For illustrative purposes, we also made use of some of our unpublished UAV footage. Papers that focused on detecting nests or animals on land were excluded. In total, we located 48 publications that met our criteria, of which 10 were on sea turtles (**Supplementary Table 1**).

While studies began experimenting with UAV surveys of marine vertebrates in the mid-2000s (Jones et al., 2006), a surge in studies is evident since 2013, when UAVs became commercially accessible (i.e. inexpensive) (**Figure 1a**). Most UAV studies (>50%) have focused on marine mammals, followed by marine reptiles and fishes (including sharks) (**Figure 1b**). The highest diversity of species targeted were marine mammals, followed by marine reptiles and fishes (**Figure 1c**). The eleven species of marine reptiles targeted so far included all seven species of sea turtles and four crocodilians; namely, loggerhead turtle (*Caretta caretta*), green turtle (*Chelonia mydas*), Kemps ridley turtle (*Lepidochelys kempii*), Olive ridley (*Lepidochelys olivacea*), hawksbill turtle (*Eretmochelys imbricata*), flatback turtle (*Natator depressus*), leatherback turtle (*Dermochelys coriacea*), gharial (*Gavialis gangeticus*), mugger crocodile (*Crocodylus palustris*), saltwater crocodile (*Crocodylus porosus*), and American alligator (*Alligator mississippiensis*).

Most UAV studies focus on the abundance and distribution of marine vertebrates, with limited studies on behaviour (**Figure 1d**). Studies on marine mammals primarily focus on abundance (including detection, distribution and density) and body condition assessment. For marine reptiles, the primary focus has been abundance. For fishes, interestingly, behavioural studies exceed abundance-distribution studies, with a primary focus on schooling behaviour, foraging behaviour and the speed of movement (Gallagher et al., 2018: Lea et al., 2018; Raoult et al., 2018; Rieucau et al., 2018; **Supplementary Table 1**).

3. Abundance and distribution

Six peer-reviewed studies using UAVs have investigated the abundance and distribution of five sea turtle species (Bevan et al., 2015; Brooke et al., 2015; Schofield et al., 2017a; Sykora-Bodie et al., 2017; Hays et al. 2018; Hensel et al., 2018). These studies were primarily conducted in breeding areas (four out of six), counting turtles in the water. Here, a key issue is what proportion of turtles in an area are visible in the UAV footage, with an accurate estimate of this proportion being needed if counts from UAV footage are to be reliably converted to abundance estimates. So, some studies have attempted to estimate the “detection probability,” i.e. likelihood of a turtle being counted when the UAV is flown overhead (Schofield et al., 2017a; Sykora-Bodie et al. 2017; Hensel et al., 2018). This issue of detection probability is also important to address in other line transect sampling, e.g. when using boat or aircraft surveys (Buckland et al., 2001).

Studies with other marine taxa have started to compare the performance of UAV surveys compared to other survey techniques and have shown that the detection probability is sometimes better with UAVs and sometimes better with manned aircraft, depending on various factors. Such factors include the conditions (e.g. turbidity and glare), species, its morphology and behaviour (e.g. diving/surfacing behaviour; Buckland et al., 2001; Marques and Buckland, 2003; Thomas et al., 2010; Hodgson et al., 2013; Ferguson et al., 2018; **Figure 2a**). This work highlights the need for consistency in methodologies if the goal is to generate time-series of abundance to assess population changes.

Another approach to assess what proportion of individuals are counted in UAV surveys is to embed traditional capture-mark-recapture approaches within UAV studies (e.g. Ferguson et al., 2018). For example, if a sample of individuals is captured, marked and then released so they can redistribute within the population, then within the subsequent UAV surveys the numbers of marked versus unmarked individuals can be used to estimate the total population size. For example, in a simple example, if 50 individuals were marked, but then only 1 in 10 (0.1) individuals in a subsequent UAV survey were seen to be marked, the population estimate would be 50 / 0.1 = 500 individuals. These sorts of studies will need to consider all of the well-known caveats of capture-mark-recapture studies (Seber, 1986; Buckland et al., 2001) but offer great promise for assessing abundance in a diverse range of habitats for sea turtles, including breeding areas (e.g. assessing number of breeding females) and foraging grounds (e.g. number of immature turtles of two different species resident in an area, see **Figure 3b, d**).

As well as estimating abundance, UAV surveys might also be used to provide density estimates of conspecifics or co-occurring species across a range of habitats (Kiszka et al., 2016; **Figure 2b**). Included in the published sea turtle studies, Sykora-Bodie et al. (2017) continuously surveyed a 3-km stretch of coastline, leading to density estimates of 1299 ± 458 to 2086 ± 803 olive ridley turtles per square kilometre adjacent to the nesting site of Ostional in Costa Rica. In comparison, Schofield et al. (2017a) continuously surveyed an 8 km stretch of coastline to explore the relative abundance of male and female loggerhead sea turtles over the breeding period, demonstrating seasonal variation in male-female sex ratios and mating activity. At present, the abundance of sea turtles is primarily assessed from counts of tracks or nests on beaches, but translating from the number of nests to number of nesting females is not straightforward, as the mean number of clutches per female is often poorly known (Esteban et al. 2017). UAV surveys during the breeding period could open up opportunities to both finally provide quantitative information on the number of males at breeding sites (Rankin and Kokko, 2007; Hays and Hawkes, 2018), as well as reliable estimates of the number of nesting females, validating estimates based on nest counts (Schofield et al., 2017a). Furthermore, for very long nesting beaches (10s of km), it is often impractical to count turtle tracks using foot surveys and, here, aerial surveys have been successfully used (Witt et al., 2009). UAVs offer a less expensive alternative to aerial surveys at sites where the operation of UAVs (e.g. extent of flight paths) is appropriate for the amount of beach that needs to be surveyed.

Sea turtles exhibit temperature dependent sex determination, with the offspring sex ratios of all seven species already being highly female biased at most sites globally (Katselidis et al., 2012; Santidrian Tomillo et al., 2015; Hays et al., 2017). However, little is known about operational sex ratios (OSRs), i.e. adult sex ratios on the breeding grounds. Here UAV surveys have great potential. For example, Schofield et al. (2017a) used UAV surveys to assess adult sex ratios at a major loggerhead turtle breeding site, confirming conclusions based on previous boat-surveys and photo-id at the same study site (Hays et al., 2010). Importantly, Schofield et al. (2017a) showed that it is possibly to readily distinguish adult males from females in UAV footage, opening up the way for studies around the world to assess operational sex ratios with this approach (**Figure 3a, c**). Assessing OSRs is a key question for sea turtle studies (Rees et al. 2016), particularly in the light of climate change which is predicted to cause increasingly female biased hatchling sex ratios.

UAV surveys also offer great potential to address other questions about the breeding biology of sea turtles. For example, the density of adult males and females on the breeding grounds is thought to be a key driver of the levels of multiple paternity within clutches, with increased male-female encounters leading to higher levels of multiple paternity (Lee et al., 2018). So, for example, low levels of multiple paternity have generally been reported for leatherback turtles, where females disperse widely during the breeding season, so even when nesting abundance is high, the density of individuals in a given area (or packing density) is likely to be low. In contrast, limited movements in the breeding season have been reported in the populations of other sea turtle species. For example, Sykora-Bodie et al. (2017) reported densities of 1299 ± 458 to 2086 ± 803 olive ridley turtles per square kilometre in the marine area adjacent to the nesting site of Ostional in Costa Rica, where around 125,000 sea turtles nest each season (Conant et al. 2014). However, similarly high packing densities can occur in relatively small populations, such as Zakynthos, Greece (around 300 individuals; Schofield et al., 2017a), which could be linked to high levels of multiple paternity comparable to sites with large numbers of turtles, such as Ostional (Zbinden et al., 2007; Lee et al., 2018). Turtle densities are readily derived from UAV surveys (for example, see **Figure 3b)** and so offer great potential to fully resolve links between density and multiple paternity.

Density information could also be used to investigate the importance of sea turtles as ecosystem engineers (Coleman and Williams, 2002; Heithaus et al., 2012; Hays et al., 2018). For example, high densities green turtles can have a dramatic impact on the seagrass meadows within which they forage (Christianen et al., 2013; Atwood et al., 2015). Furthermore, there is potential for opportunistic sightings of non-target taxa during UAV surveys. For example, abundance of sharks and rays co-habiting a series of lagoon inlets that are foraging grounds of immature hawksbill and green turtles (**Figure 3e**).

4. Behaviour

Four peer-reviewed studies using UAVs have investigated the behaviour of three sea turtle species; green, loggerhead and leatherback (Bevan et al., 2016; Schofield et al., 2017ab; Tapilatu et al., 2017). As well as distinguishing adult males from females (Bevan et al. 2016, Schofield et al., 2017ab; **Figure 2**), UAV footage can be analysed to quantify interactions between individuals. Thus, it is possible to examine, for example, if the departure of males from breeding sites is driven by changes in the receptiveness of females and the probability of successful mating attempts (Schofield et al., 2017a). Furthermore, UAVs can be applied to evaluate the learning and memory of marine vertebrates in relation to isolated sites containing important resources (Fagan et al., 2013), such as fish cleaning stations (Schofield et al., 2017b; **Figure 4**). Tapilatu et al. (2017) also used UAVs to record the offshore movement and swimming speeds of leatherback hatchlings, following emergence from nests on the beaches.

These fledgling UAV studies with sea turtles are mirrored by studies with other marine taxa which demonstrate how UAV surveys can complement the wealth of information provided by animal-borne data loggers and transmitters (e.g. recording location, depth, speed of travel) (Hays et al., 2016). UAV studies of sea turtles could be used to quantify the frequency of different behaviours of sea turtles in relation to habitat, conspecifics, density and/or detection of prey, as well as potential competitors or predators, which has previously been restricted to observations of focal animals directly or with various underwater camera technologies (e.g., hand-held, animal borne, baited remote underwater video systems, and underwater remote operated vehicles; Letessier et al., 2015; Smolowitz et al., 2015; Thomson et al., 2015; Schofield et al. 2017b;). Such information could help to generate activity, and hence, energy budgets, for this group of animals. (Goldbogen et al., 2017; Raoult et al., 2018; Rieucau et al., 2018; Torres et al., 2018) (**Figure 5**). Torres et al. (2018), for example, quantified the energy budget of grey seals (*Halichoerus grypus*) using UAVs (**Figure 5a, b)**. Rieucau et al. (2018), on the other hand, showed how blacktip sharks (*Carcharhinus limbatus*) aligned differently in relation to one another depending on habitat type when forming shoals (**Figure 5c, d)**, facilitating parallel comparisons with studies on the flocking behaviour of birds (Jullien and Clobert, 2000), synchronous swimming in wild dolphins (Fellner et al., 2006) or the relative positioning of sea turtles in breeding and foraging aggregations. UAVs could inform us of how sea turtles change their movement patterns in different habitat types or when searching for different prey items. For example, Raoult et al. (2018) showed that epaulette sharks (*Hemiscyllium ocellatum*) exhibit more sinuous, and hence slower swimming speeds, compared to reef sharks (*Carcharhinus perezii*) and a lemon shark (*Negaprion brevirostris*) occupying the same habitat (**Figure 5e, f**). Two other studies have explored the scavenging behaviour of sharks and crocodiles on carcasses (Lea et al., 2008; Gallagher et al., 2018). These approaches could be used to provide novel insights on the behaviour of sea turtles, particularly when in breeding or foraging aggregations.

UAVs provide researchers with the ability to assess the context of behavioural choices by animals (including intra- or inter-specific interactions, habitat associations and human influence) in relation to information on their abundance, distribution and density (Torres et al., 2018; Johnston, 2019). UAVs allow us to evaluate these behaviours at the group level, in a way that direct observations or remote tracking of focal individuals cannot (Hays et al., 2016) In addition, UAVs allow us to monitor both prey and predators simultaneously so, for example, we can now document the mechanism of prey engulfment by whales (Goldbogen et al., 2017). UAV studies are already exploring various components of “apparent competition” (Holt, 1977), showing how different species compete for and/or share the same space to access the same forage resources (Gallagher et al., 2018; Hodgson et al., 2013; Raoult et al., 2018), another factor that cannot be gleaned from remote telemetry. As UAV studies continue to accumulate, we will be able to objectively quantify how marine vertebrates contribute to community and ecosystem level dynamics, and how these dynamics influence their relative abundance and distribution to other species across space and time (Abrams, 1984).

5. Body condition

To date, UAVs have not been used to evaluate the body condition of sea turtles, with this possibility potentially being hindered by the hard carapace covering the bodies of six of the seven species. Such studies remain limited to marine mammals (n = 7 studies; **see Supplementary Table 1**), quantifying the provisioning of offspring (Christiansen et al., 2016, 2018; Krause et al., 2017; **Figure 6a, b**). These studies build on a long-history of external morphological measurements being used to assess body condition in this group (Durban et al., 2015 2016; Dawson et al., 2017; Burnett et al., 2019), with UAVs providing a new way to make these visual observations. For sea turtles, morphological traits have been applied to distinguish sex, age class, and species in UAV studies (Bevan et al., 2015; Schofield et al., 2017a) (see **Figure 3d**). Body condition in sea turtles is usually assessed by visual examination of the underside (plastron) of a turtle (Heithaus et al., 2007), which is relatively soft and changes shape with fat levels. By contrast, UAV footage captures the dorsal view of a turtle, which is rigid in hard-shelled species, and so less likely to change shape in relation to body condition, which may present limitations. However, it might be possible to measure changes in neck condition from aerial surveys flown at low altitudes; even as close as just 2 m above the sea surface as demonstrated by Rieucau et al. (2018) in their study on shark movement. The leatherback turtle poses an exception, as its pliant carapace changes shape, being expanded in fatter turtles encountered on the foraging grounds compared to thinner turtle encountered breeding (Davenport et al., 2011; Wallace et al., 2018; **Figure 6c, d**). Near-infrared hyperspectral imaging has been applied to detect and quantify fat levels in salmon (Fengle et al., 2012) and to detect marine mammals in aerial surveys (Podobna et al., 2010), with the potential to facilitate body condition assessments in leatherback turtles.

6. Conclusions

Answering ecological questions associated with abundance and distribution requires information on the relative positioning of animals to other organisms, their behaviour and environmental conditions. Until now, for marine wildlife, the limitation has been acquiring sufficient information on large numbers of individuals occupying the same space at the same time and at different times. UAVs represent an approach for the research and monitoring of marine animals that “fill” the gaps other approaches cannot (e.g. biologging, biotelemetry and local human observations). In particular, UAVs are demonstrating the potential to provide new insights on animal behaviour linked to abundance, distribution and density under a variety of settings. In particular, UAVs provide us with the opportunity, at very low cost, to quantify the flexibility of animal behaviour and their ability to adjust to changing conditions, including environmental challenges, such as climate change.

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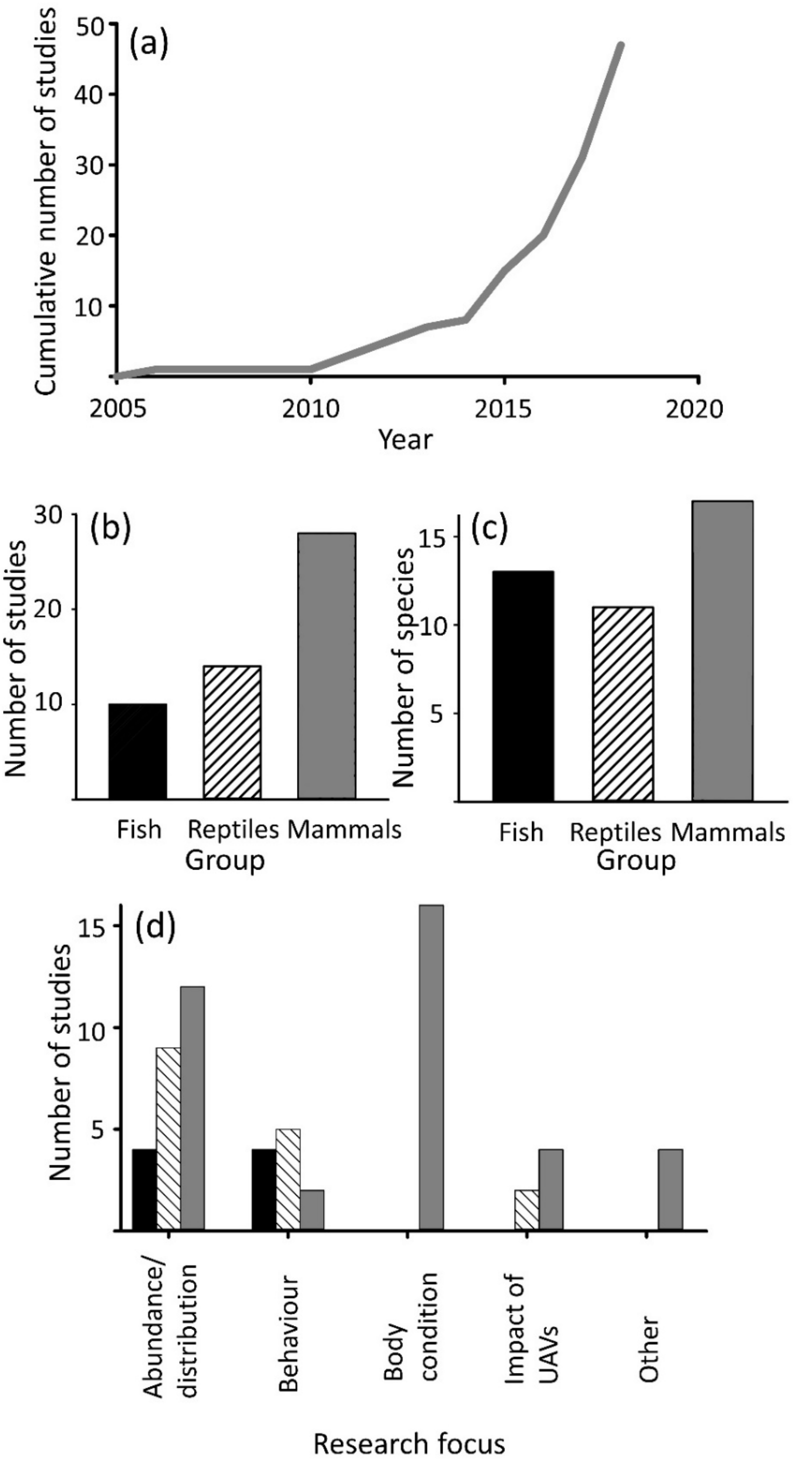

Figure 1. (a) Cumulative number of UAV studies on submerged marine mammals, marine reptiles and fishes to December 2018, showing an influx following 2010. Number of (b) studies and (c) species for each of the three groups. (d) Focus of studies on the three groups; black bars are fishes (bony and cartilaginous), hatched bars are marine reptiles and grey bars are marine mammals. See **Supplementary Table 1** for details on publications.

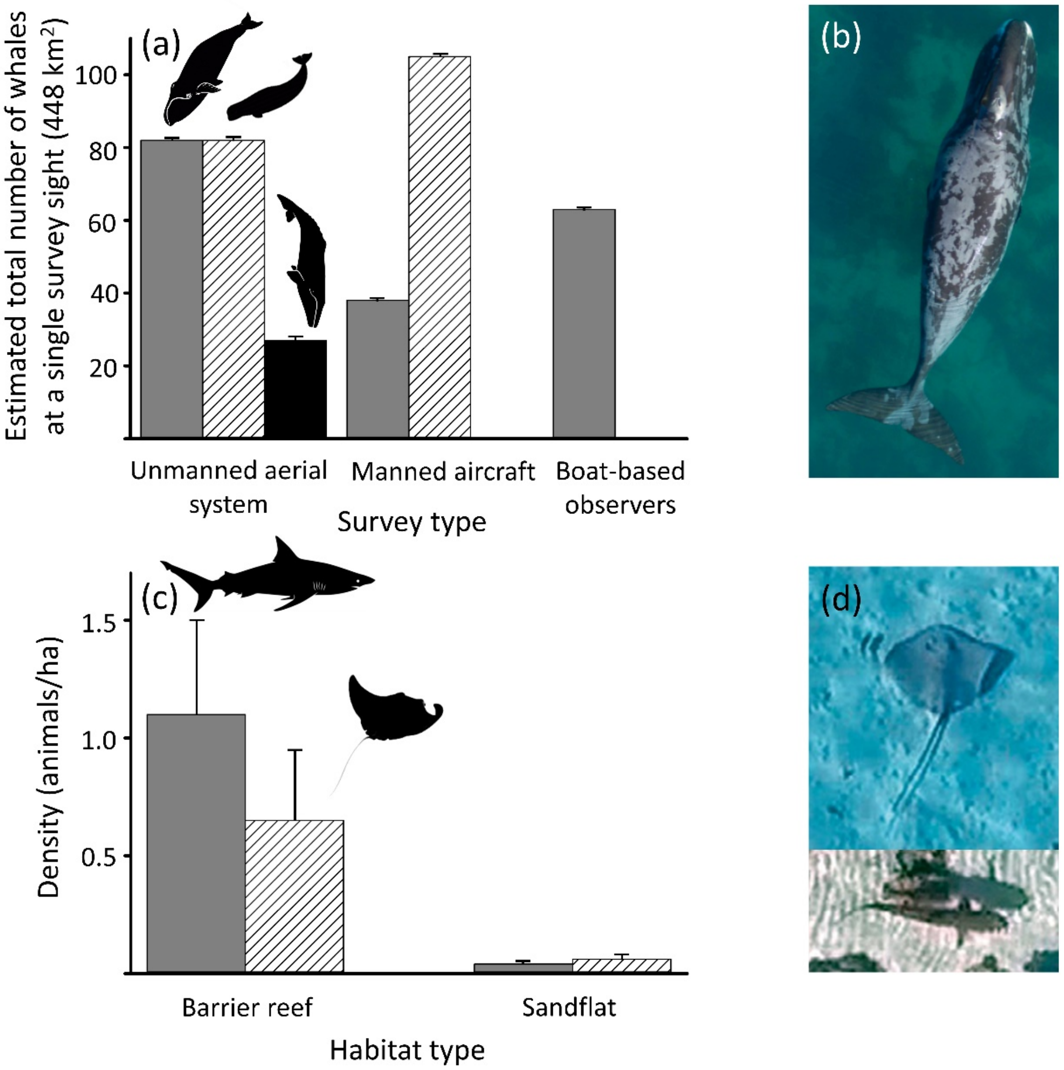

Figure 2. Examples of how UAVs have been used to study abundance and distribution in other taxa: (a) abundance estimates of conspecific species in a single survey sector covering 448 km^2: bowhead whale *Balaena mysticetus* (grey bars), beluga *Delphinapterus leucas* (hatched bars) and grey whale *Eschrichtius robustus* (black bars) sightings and abundance estimates (and coefficient of variance) vary with technology used: UAVs compared to manned aircraft and boat-based observations (replotted and adapted from Ferguson et al. 2018); (b) aerial view of a bowhead from UAV flown at 12.9 m above the sea surface (reused from Fortune et al. 2017); (c) Mean (±SD) density of blacktip reef sharks *Carcharhinus melanopterus* (light grey bars) and pink whiprays *Himantura fai* (hatched bars) in two habitats highlighting spatial heterogeneity in distribution (replotted and adapted from Kiszka et al. 2016); (d) aerial view of a blacktip reef shark (upper panel) and a pink whipray taken from an altitude of 12 m (reused from Kiszka et al. 2016).

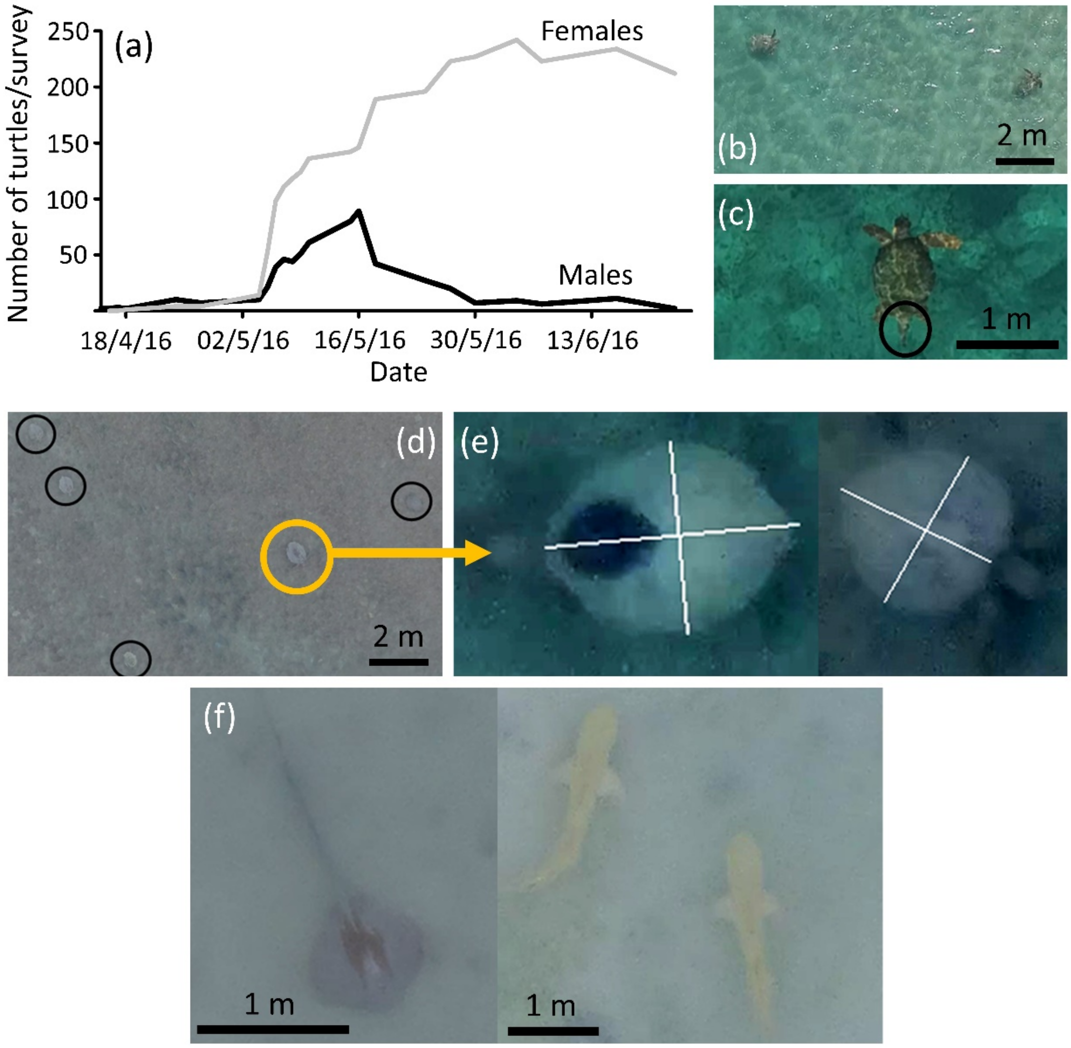

Figure 3. UAV surveys can be used to estimate population size and operational sex ratio (OSR), and opportunistically record other taxa to assess abundance, biomass and species diversity. (a) Counts of the relative numbers of adult male and female loggerhead sea turtles *Caretta caretta* in a population allow the operational sex ratio (OSR) to be assessed, i.e. the adult sex ratio on the breeding grounds (replotted from Schofield et al. 2017a). (b) Breeding individuals are counted through UAV surveys conducted at an altitude of 60 m and (c) adult male sea turtles can be distinguished from adult females as the tails of males noticeably protrude from the carapace. (d) Mark and recapture estimation of foraging immature turtle population size in Diego Garcia lagoon, BIOT by repeated UAV transect surveys (each black circle represents a sea turtle). Population size can be estimated by recording numbers of marked (large yellow circle; turtle with satellite tag) and unmarked turtles (small circles). (e) Transect surveys can inform species diversity and size of individuals, in this case distinguishing a hawksbill *Eretmochelys imbricata* (left; 53 x 30 cm with satellite transmitter visible as a black oval) and green *Chelonia mydas* (right; 41 x 41 cm) from the shape of the carapace, based on Image analysis (e.g. ImageJ). (f) Opportunistic sightings of non-target taxa. Here, sharks and ray sightings made during sea turtle surveys are shown. Photos in (b) and (c) adapted from Schofield et al. 2017a; (d-f) unpublished images courtesy of Esteban, Mortimer and Hays.

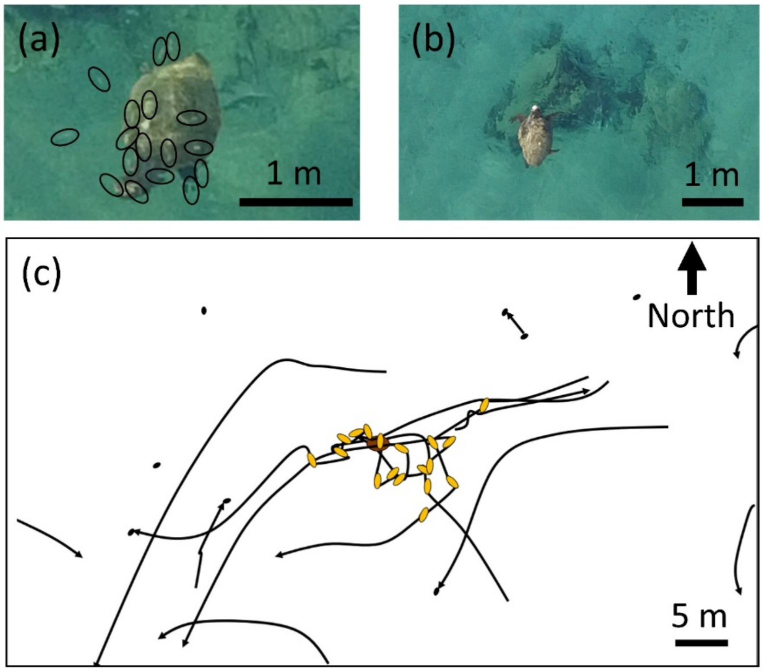

Figure 4 (a) UAVs can be used to document interspecific interactions; in this case, an adult female loggerhead sea turtle *Caretta caretta* frequenting a fish-cleaning station (open black ovals are the cleaner fish). (b) Sea turtle positioned directly over the fish-cleaning station. (c) By hovering the UAV over a pre-designated site for prolonged periods (i.e. 40 min or more), the movement of animals in relation to important resources (such as sea turtles and cleaning stations) can be monitored in relation to other animals and the surrounding environment. Panel (c) adapted from Schofield et al. (2017b): Movement of nine turtles over a 40 min period during a NE wind; arrows show the direction of movement of turtles; yellow ovals are where turtles were cleaned; black ovals are resting turtles.

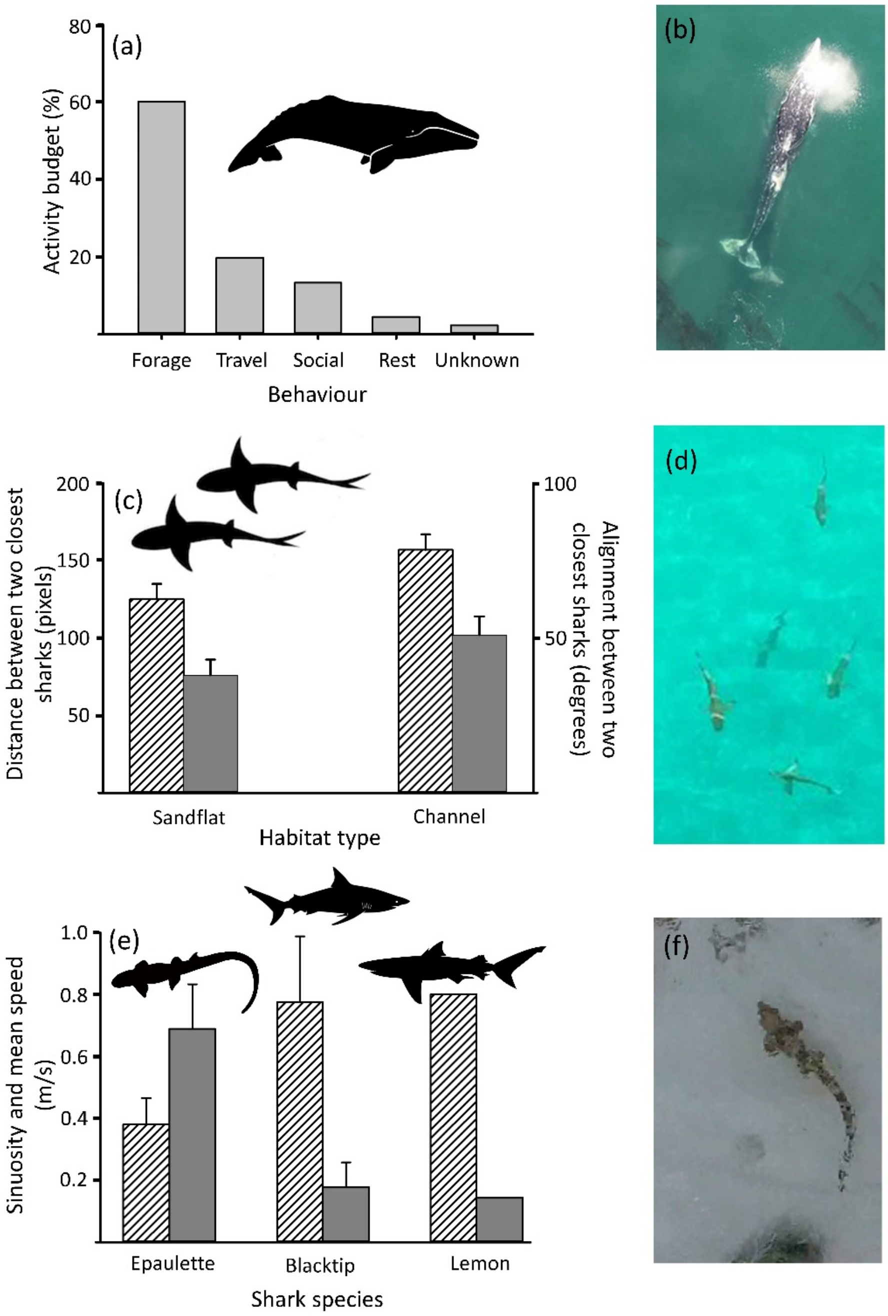

Figure 5 Examples of how UAVs have been used to study behaviour in other taxa: (a) measuring the activity budgets of grey whales, *Eschrichtius robustus* (replotted and adapted from Torres et al. 2018); (b) UAV image of a nursing grey whale taken at 25–40 m altitude (reused from Torres et al. 2018); (c) variation in the mean (±SD) distance (hatched bars) and alignment (grey bars) of neighbouring reef sharks *Carcharhinus melanopterus* in different habitats (replotted and adapted from Rieucau et al. 2018); (d) UAV image of shoaling reef sharks taken at an altitude of 12 m (reused from Rieucau et al. 2018 with permission from publisher); (e) differences in the mean (±SD) speed (hatched bars) and sinuosity (grey bars) of three shark species occupying the same habitat; epaulette sharks (*Hemiscyllium ocellatum*) display sinusoidal movement patterns, while blacktip reef sharks (*Carcharhinus melanopterus*) and a lemon shark (*Negaprion acutidens*) exhibited more linear trajectories (replotted and adapted from Raoult et al. 2018); (f) zoomed in UAV image of an epaulette shark taken at an altitude of 15 m (reused from Raoult et al. 2018). Examples of target individuals are shown in white boxes.

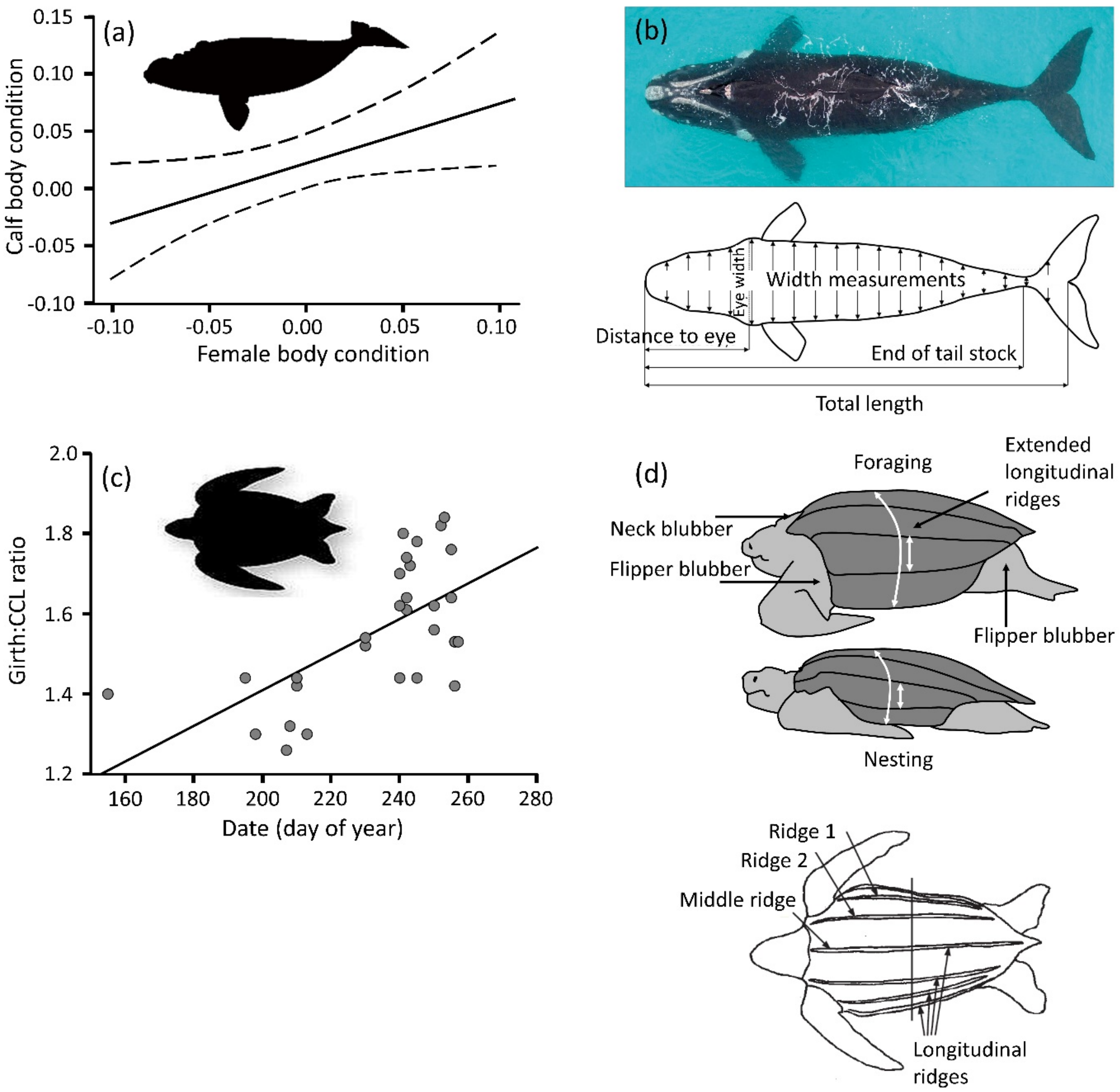

Figure 6 A body condition index can be calculated from the width and length measurements, i.e. distinguishing fatter versus thinner individuals. (a) Example of how UAVs have been used to assess female vs calf body condition in southern right whales, *Eubalaena australis* (replotted from Christiansen et al. 2018); (b) UAV image of southern right whale and width and length measurements made to quantify body condition (reused from Christiansen et al. 2018); (c) Examples of how body condition is measured in leatherback sea turtles *Dermochelys coriacea* (replotted from Davenport et al. 2011), which could be examined using UAV imagery; (d) differences in the body fat deposition and girth of carapace between foraging and nesting leatherbacks (upper panel; adapted from Davenport et al. 2011) and body measurement parameters (lower panel) (reused from Davenport et al. 2011 with permission from publisher).

Supplementary Table 1. UAV studies of marine vertebrates to December 2018.

Abundance and Distribution			
Class	**Group**	**Species**	**Study focus**
Reptile	Sea turtle	Green Turtle	Detection
Reptile	Sea turtle	Kemps Ridley	Detection
Reptile	Sea turtle	Loggerhead sea turtle	Abundance: sex ratios
Reptile	Sea turtle	Olive Ridley	Density
Reptile	Sea turtle	Green turtle	Detection
Reptile	Sea turtle	Green turtle, Hawksbill turtle	Detection
Reptile	Crocodilian	American alligator	Detection
Reptile	Crocodilian	American alligator	Detection
Reptile	Crocodilian	Gharial, Mugger Crocodile	Abundance
Fishes	Bony	Chum Salmon	Detection
Fishes	Bony	Fishes	Detection
Fishes	Cartilaginous	Blacktip reef shark, Pink Whipray	Density

Fishes	Cartilaginous	Lemon shark, Nurse shark, Bonnethead shark, Southern stingray, Spotted eagle ray	Detection
Marine Mammals	Sirenian	Manatee	Detection
Marine Mammals	Sirenian	Dugong	Detection
Marine Mammals	Pinniped	Leopard Seal	Abundance
Marine Mammals	Pinniped	Ribbon seals, spotted seals	Detection
Marine Mammals	Pinniped	Stellar Sea Lions	Abundance
Marine Mammals	Cetacean	River Dolphin	Detection
Marine Mammals	Pinniped	Grey Seal	Abundance
Marine Mammals	Pinniped	Grey Seal	Abundance
Marine Mammals	Cetacean	Bowhead whale	Distribution, density abundance
Marine Mammals	Cetacean	Humpback whales, Killer whales	Detection
Marine Mammals	Sirenian	Dugong	Detection estimates
Reptile	Sirenian	Dugong	Detection
Behaviour			
Class	**Group**	**Species**	**Study focus**

Reptile	Sea turtle	Green Turtle	Courtship, mating
Reptile	Sea turtle	Loggerhead sea turtle	Mating, interacting, swimming, resting
Reptile	Sea turtle	Loggerhead sea turtle	Movement to/from cleaning stat
Reptile	Sea turtle	Leatherback	Fitness - swimming speeds
Reptile	Crocodilian	Saltwater Crocodile	Foraging activity
Fishes	Cartilaginous	Tiger Shark	Foraging activity
Fishes	Cartilaginous	Reef Shark	Shoaling behaviour
Fishes	Cartilaginous	Tiger shark, Bull shark, Tawny nurse shark	Foraging activity
Fishes	Cartilaginous	Blacktip Reef Sharks, Lemon Sharks, Epaulette sharks	Movement, Speed, Direction
Marine Mammals	Cetacean	Baleen Whales	Foraging activity
Marine Mammals	Cetacean	Bowhead whales	Cleaning behaviour
Marine Mammals	Cetacean	Gray whales	Behaviour states and events, act budget
Marine Mammals	Cetacean	Gray whales	Behaviour states and events, act budget

Physiology/Morphometrics			
Marine mammals	Cetacean	Killer whale	Photogrammetry
Marine mammals	Cetacean	Blue whale	Photogrammetry
Marine mammals	Cetacean	Humpback whales	Energetic costs of reproduction
Marine mammals	Cetacean	Southern Right Whales	Photogrammetry
Marine mammals	Pinniped	Leopard seals	Photogrammetry
Marine mammals	Cetacean	Southern Right Whales	Maternal body size, calf growth
Marine mammals	Cetacean	Baleen Whales	Photogrammetry
Disturbance from UAVs			
Reptile	Sea turtle	Green turtle, flatback, hawksbill	
Reptile	Crocodilian	Saltwater crocodile	
Marine Mammals	Pinniped	Stellar sea lions, sea otters	
Marine Mammals	Pinniped	Grey Seal, Harbour seal	
Marine Mammals	Pinniped	Grey seal	
Marine Mammals	Cetacean	Blue whale	

Other			
Marine Mammals	Cetacean	Blue whale	Health monitoring
Marine Mammals	Cetacean	bowhead whales	Photo id
Marine Mammals	Cetacean	Humpback whale	Health monitoring
Marine Mammals	Cetacean	Humpback whale	Health monitoring

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