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

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21  
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30

31 **Highlights**

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

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44 **Abstract**

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

62

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

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## 68 **1. Background**

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

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

106 Advances in scientific knowledge are driven by the accessibility of new technologies,  
107 i.e. that are relatively inexpensive and reliable, for use in monitoring and research.  
108 Biotelemetry and biologging representing one such advance, and animal-borne cameras  
109 another (Wilmers et al., 2015; Hays and Hawkes, 2018). Unmanned aerial vehicles (UAVs),  
110 often referred to as drones, have been used in ecological studies for some time (e.g. Jones et  
111 al. 2006), but the recent advent of inexpensive, reliable, easy-to-fly UAVs has led to a  
112 profusion of studies that utilize this technology (e.g. Koh and Wich, 2012; Chabot and Bird,  
113 2015; Johnston, 2019). UAVs provide the opportunity to collect high-resolution aerial  
114 imagery of animals over multiple scales in a way that is both unobtrusive and repeatable over  
115 time and space (Anderson et al., 2013; Christie et al., 2016; Colefax et al., 2018), in parallel  
116 to documenting behaviour and how it is correlated by the density and distribution of other  
117 animals and the environment (Marvin et al., 2016; Raoult et al., 2018; Torres et al., 2018;

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

123 The potential for UAV studies with sea turtles was recently reviewed by Rees et al.  
124 (2018). Here, we build on this work by examining how the potential of UAVs is being  
125 realised with respect to sea turtles, by highlighting some of the key findings that have  
126 recently emerged using this technology. We also identify some of the commonalities and  
127 differences with studies with other marine vertebrates, such as marine mammals and fish, to  
128 identify potential gaps in current uses.

129

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

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

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

156 Most UAV studies focus on the abundance and distribution of marine vertebrates,  
157 with limited studies on behaviour (**Figure 1d**). Studies on marine mammals primarily focus  
158 on abundance (including detection, distribution and density) and body condition assessment.  
159 For marine reptiles, the primary focus has been abundance. For fishes, interestingly,  
160 behavioural studies exceed abundance-distribution studies, with a primary focus on schooling  
161 behaviour, foraging behaviour and the speed of movement (Gallagher et al., 2018; Lea et al.,  
162 2018; Raoult et al., 2018; Rieucan et al., 2018; **Supplementary Table 1**).

163

## 164 **3. Abundance and distribution**

165 Six peer-reviewed studies using UAVs have investigated the abundance and distribution of  
166 five sea turtle species (Bevan et al., 2015; Brooke et al., 2015; Schofield et al., 2017a;  
167 Sykora-Bodie et al., 2017; Hays et al. 2018; Hensel et al., 2018). These studies were

168 primarily conducted in breeding areas (four out of six), counting turtles in the water. Here, a  
169 key issue is what proportion of turtles in an area are visible in the UAV footage, with an  
170 accurate estimate of this proportion being needed if counts from UAV footage are to be  
171 reliably converted to abundance estimates. So, some studies have attempted to estimate the  
172 “detection probability,” i.e. likelihood of a turtle being counted when the UAV is flown  
173 overhead (Schofield et al., 2017a; Sykora-Bodie et al. 2017; Hensel et al., 2018). This issue  
174 of detection probability is also important to address in other line transect sampling, e.g. when  
175 using boat or aircraft surveys (Buckland et al., 2001).

176 Studies with other marine taxa have started to compare the performance of UAV  
177 surveys compared to other survey techniques and have shown that the detection probability is  
178 sometimes better with UAVs and sometimes better with manned aircraft, depending on  
179 various factors. Such factors include the conditions (e.g. turbidity and glare), species, its  
180 morphology and behaviour (e.g. diving/surfacing behaviour; Buckland et al., 2001; Marques  
181 and Buckland, 2003; Thomas et al., 2010; Hodgson et al., 2013; Ferguson et al., 2018; **Figure**  
182 **2a**). This work highlights the need for consistency in methodologies if the goal is to generate  
183 time-series of abundance to assess population changes.

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

197 As well as estimating abundance, UAV surveys might also be used to provide density  
198 estimates of conspecifics or co-occurring species across a range of habitats (Kiszka et al.,  
199 2016; **Figure 2b**). Included in the published sea turtle studies, Sykora-Bodie et al. (2017)  
200 continuously surveyed a 3-km stretch of coastline, leading to density estimates of  $1299 \pm 458$   
201 to  $2086 \pm 803$  olive ridley turtles per square kilometre adjacent to the nesting site of Ostional  
202 in Costa Rica. In comparison, Schofield et al. (2017a) continuously surveyed an 8 km stretch  
203 of coastline to explore the relative abundance of male and female loggerhead sea turtles over  
204 the breeding period, demonstrating seasonal variation in male-female sex ratios and mating  
205 activity. At present, the abundance of sea turtles is primarily assessed from counts of tracks  
206 or nests on beaches, but translating from the number of nests to number of nesting females is  
207 not straightforward, as the mean number of clutches per female is often poorly known  
208 (Esteban et al. 2017). UAV surveys during the breeding period could open up opportunities to  
209 both finally provide quantitative information on the number of males at breeding sites  
210 (Rankin and Kokko, 2007; Hays and Hawkes, 2018), as well as reliable estimates of the  
211 number of nesting females, validating estimates based on nest counts (Schofield et al.,  
212 2017a). Furthermore, for very long nesting beaches (10s of km), it is often impractical to  
213 count turtle tracks using foot surveys and, here, aerial surveys have been successfully used  
214 (Witt et al., 2009). UAVs offer a less expensive alternative to aerial surveys at sites where the  
215 operation of UAVs (e.g. extent of flight paths) is appropriate for the amount of beach that  
216 needs to be surveyed.

217 Sea turtles exhibit temperature dependent sex determination, with the offspring sex  
218 ratios of all seven species already being highly female biased at most sites globally  
219 (Katselidis et al., 2012; Santidrian Tomillo et al., 2015; Hays et al., 2017). However, little is  
220 known about operational sex ratios (OSRs), i.e. adult sex ratios on the breeding grounds.  
221 Here UAV surveys have great potential. For example, Schofield et al. (2017a) used UAV  
222 surveys to assess adult sex ratios at a major loggerhead turtle breeding site, confirming  
223 conclusions based on previous boat-surveys and photo-id at the same study site (Hays et al.,  
224 2010). Importantly, Schofield et al. (2017a) showed that it is possible to readily distinguish  
225 adult males from females in UAV footage, opening up the way for studies around the world  
226 to assess operational sex ratios with this approach (**Figure 3a, c**). Assessing OSRs is a key  
227 question for sea turtle studies (Rees et al. 2016), particularly in the light of climate change  
228 which is predicted to cause increasingly female biased hatchling sex ratios.

229 UAV surveys also offer great potential to address other questions about the breeding  
230 biology of sea turtles. For example, the density of adult males and females on the breeding  
231 grounds is thought to be a key driver of the levels of multiple paternity within clutches, with  
232 increased male-female encounters leading to higher levels of multiple paternity (Lee et al.,  
233 2018). So, for example, low levels of multiple paternity have generally been reported for  
234 leatherback turtles, where females disperse widely during the breeding season, so even when  
235 nesting abundance is high, the density of individuals in a given area (or packing density) is  
236 likely to be low. In contrast, limited movements in the breeding season have been reported in  
237 the populations of other sea turtle species. For example, Sykora-Bodie et al. (2017) reported  
238 densities of  $1299 \pm 458$  to  $2086 \pm 803$  olive ridley turtles per square kilometre in the marine  
239 area adjacent to the nesting site of Ostional in Costa Rica, where around 125,000 sea turtles  
240 nest each season (Conant et al. 2014). However, similarly high packing densities can occur in  
241 relatively small populations, such as Zakynthos, Greece (around 300 individuals; Schofield et  
242 al., 2017a), which could be linked to high levels of multiple paternity comparable to sites  
243 with large numbers of turtles, such as Ostional (Zbinden et al., 2007; Lee et al., 2018). Turtle  
244 densities are readily derived from UAV surveys (for example, see **Figure 3b**) and so offer  
245 great potential to fully resolve links between density and multiple paternity.

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

#### 253 254 **4. Behaviour**

255 Four peer-reviewed studies using UAVs have investigated the behaviour of three sea turtle  
256 species; green, loggerhead and leatherback (Bevan et al., 2016; Schofield et al., 2017ab;  
257 Tapilatu et al., 2017). As well as distinguishing adult males from females (Bevan et al. 2016,  
258 Schofield et al., 2017ab; **Figure 2**), UAV footage can be analysed to quantify interactions  
259 between individuals. Thus, it is possible to examine, for example, if the departure of males  
260 from breeding sites is driven by changes in the receptiveness of females and the probability  
261 of successful mating attempts (Schofield et al., 2017a). Furthermore, UAVs can be applied to  
262 evaluate the learning and memory of marine vertebrates in relation to isolated sites containing  
263 important resources (Fagan et al., 2013), such as fish cleaning stations (Schofield et al.,  
264 2017b; **Figure 4**). Tapilatu et al. (2017) also used UAVs to record the offshore movement  
265 and swimming speeds of leatherback hatchlings, following emergence from nests on the  
266 beaches.



267           These fledgling UAV studies with sea turtles are mirrored by studies with other  
268 marine taxa which demonstrate how UAV surveys can complement the wealth of information  
269 provided by animal-borne data loggers and transmitters (e.g. recording location, depth, speed  
270 of travel) (Hays et al., 2016). UAV studies of sea turtles could be used to quantify the  
271 frequency of different behaviours of sea turtles in relation to habitat, conspecifics, density  
272 and/or detection of prey, as well as potential competitors or predators, which has previously  
273 been restricted to observations of focal animals directly or with various underwater camera  
274 technologies (e.g., hand-held, animal borne, baited remote underwater video systems, and  
275 underwater remote operated vehicles; Letessier et al., 2015; Smolowitz et al., 2015; Thomson  
276 et al., 2015; Schofield et al. 2017b;). Such information could help to generate activity, and  
277 hence, energy budgets, for this group of animals. (Goldbogen et al., 2017; Raoult et al., 2018;  
278 Rieucau et al., 2018; Torres et al., 2018) (**Figure 5**). Torres et al. (2018), for example,  
279 quantified the energy budget of grey seals (*Halichoerus grypus*) using UAVs (**Figure 5a, b**).  
280 Rieucau et al. (2018), on the other hand, showed how blacktip sharks (*Carcharhinus*  
281 *limbatus*) aligned differently in relation to one another depending on habitat type when  
282 forming shoals (**Figure 5c, d**), facilitating parallel comparisons with studies on the flocking  
283 behaviour of birds (Jullien and Clobert, 2000), synchronous swimming in wild dolphins  
284 (Fellner et al., 2006) or the relative positioning of sea turtles in breeding and foraging  
285 aggregations. UAVs could inform us of how sea turtles change their movement patterns in  
286 different habitat types or when searching for different prey items. For example, Raoult et al.  
287 (2018) showed that epaulette sharks (*Hemiscyllium ocellatum*) exhibit more sinuous, and  
288 hence slower swimming speeds, compared to reef sharks (*Carcharhinus perezii*) and a lemon  
289 shark (*Negaprion brevirostris*) occupying the same habitat (**Figure 5e, f**). Two other studies  
290 have explored the scavenging behaviour of sharks and crocodiles on carcasses (Lea et al.,  
291 2008; Gallagher et al., 2018). These approaches could be used to provide novel insights on  
292 the behaviour of sea turtles, particularly when in breeding or foraging aggregations.

293           UAVs provide researchers with the ability to assess the context of behavioural choices  
294 by animals (including intra- or inter-specific interactions, habitat associations and human  
295 influence) in relation to information on their abundance, distribution and density (Torres et  
296 al., 2018; Johnston, 2019). UAVs allow us to evaluate these behaviours at the group level, in  
297 a way that direct observations or remote tracking of focal individuals cannot (Hays et al.,  
298 2016) In addition, UAVs allow us to monitor both prey and predators simultaneously so, for  
299 example, we can now document the mechanism of prey engulfment by whales (Goldbogen et  
300 al., 2017). UAV studies are already exploring various components of “apparent competition”  
301 (Holt, 1977), showing how different species compete for and/or share the same space to  
302 access the same forage resources (Gallagher et al., 2018; Hodgson et al., 2013; Raoult et al.,  
303 2018), another factor that cannot be gleaned from remote telemetry. As UAV studies  
304 continue to accumulate, we will be able to objectively quantify how marine vertebrates  
305 contribute to community and ecosystem level dynamics, and how these dynamics influence  
306 their relative abundance and distribution to other species across space and time (Abrams,  
307 1984).

308

## 309 **5. Body condition**

310 To date, UAVs have not been used to evaluate the body condition of sea turtles, with this  
311 possibility potentially being hindered by the hard carapace covering the bodies of six of the  
312 seven species. Such studies remain limited to marine mammals (n = 7 studies; see  
313 **Supplementary Table 1**), quantifying the provisioning of offspring (Christiansen et al.,  
314 2016, 2018; Krause et al., 2017; **Figure 6a, b**). These studies build on a long-history of  
315 external morphological measurements being used to assess body condition in this group  
316 (Durban et al., 2015 2016; Dawson et al., 2017; Burnett et al., 2019), with UAVs providing a

317 new way to make these visual observations. For sea turtles, morphological traits have been  
318 applied to distinguish sex, age class, and species in UAV studies (Bevan et al., 2015;  
319 Schofield et al., 2017a) (see **Figure 3d**). Body condition in sea turtles is usually assessed by  
320 visual examination of the underside (plastron) of a turtle (Heithaus et al., 2007), which is  
321 relatively soft and changes shape with fat levels. By contrast, UAV footage captures the  
322 dorsal view of a turtle, which is rigid in hard-shelled species, and so less likely to change  
323 shape in relation to body condition, which may present limitations. However, it might be  
324 possible to measure changes in neck condition from aerial surveys flown at low altitudes;  
325 even as close as just 2 m above the sea surface as demonstrated by Rieucan et al. (2018) in  
326 their study on shark movement. The leatherback turtle poses an exception, as its pliant  
327 carapace changes shape, being expanded in fatter turtles encountered on the foraging grounds  
328 compared to thinner turtle encountered breeding (Davenport et al., 2011; Wallace et al., 2018;  
329 **Figure 6c, d**). Near-infrared hyperspectral imaging has been applied to detect and quantify  
330 fat levels in salmon (Fengle et al., 2012) and to detect marine mammals in aerial surveys  
331 (Podobna et al., 2010), with the potential to facilitate body condition assessments in  
332 leatherback turtles.

333

## 334 **6. Conclusions**

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

346

347

348

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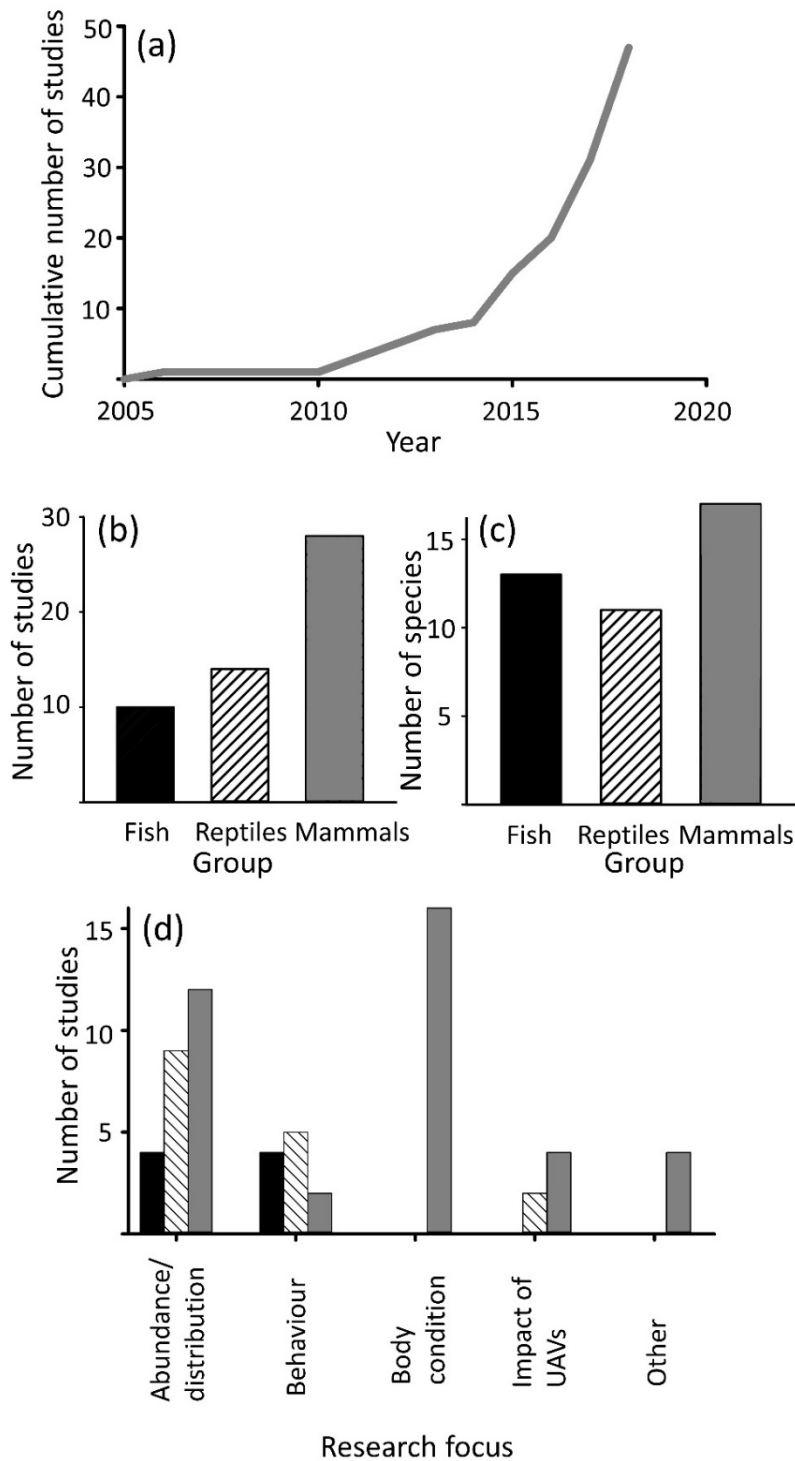
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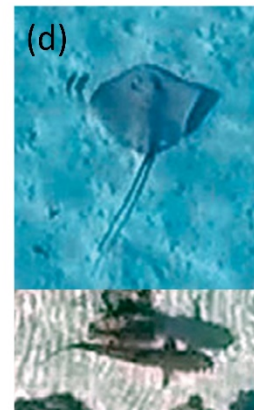
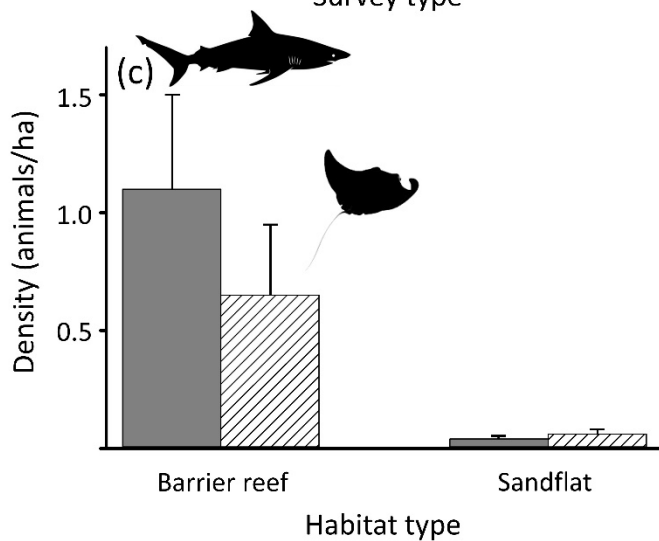
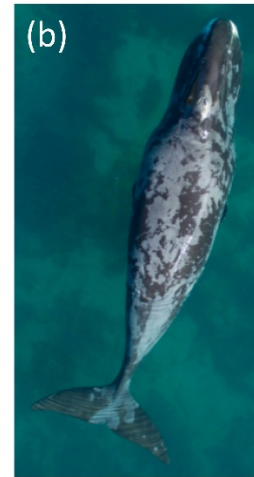
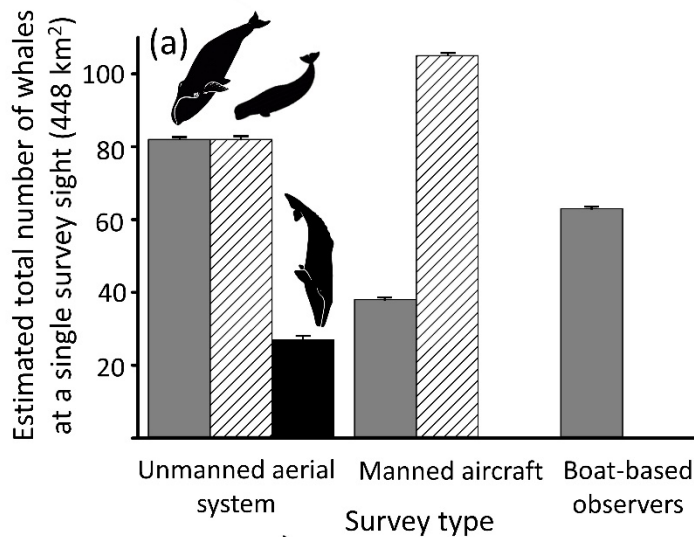
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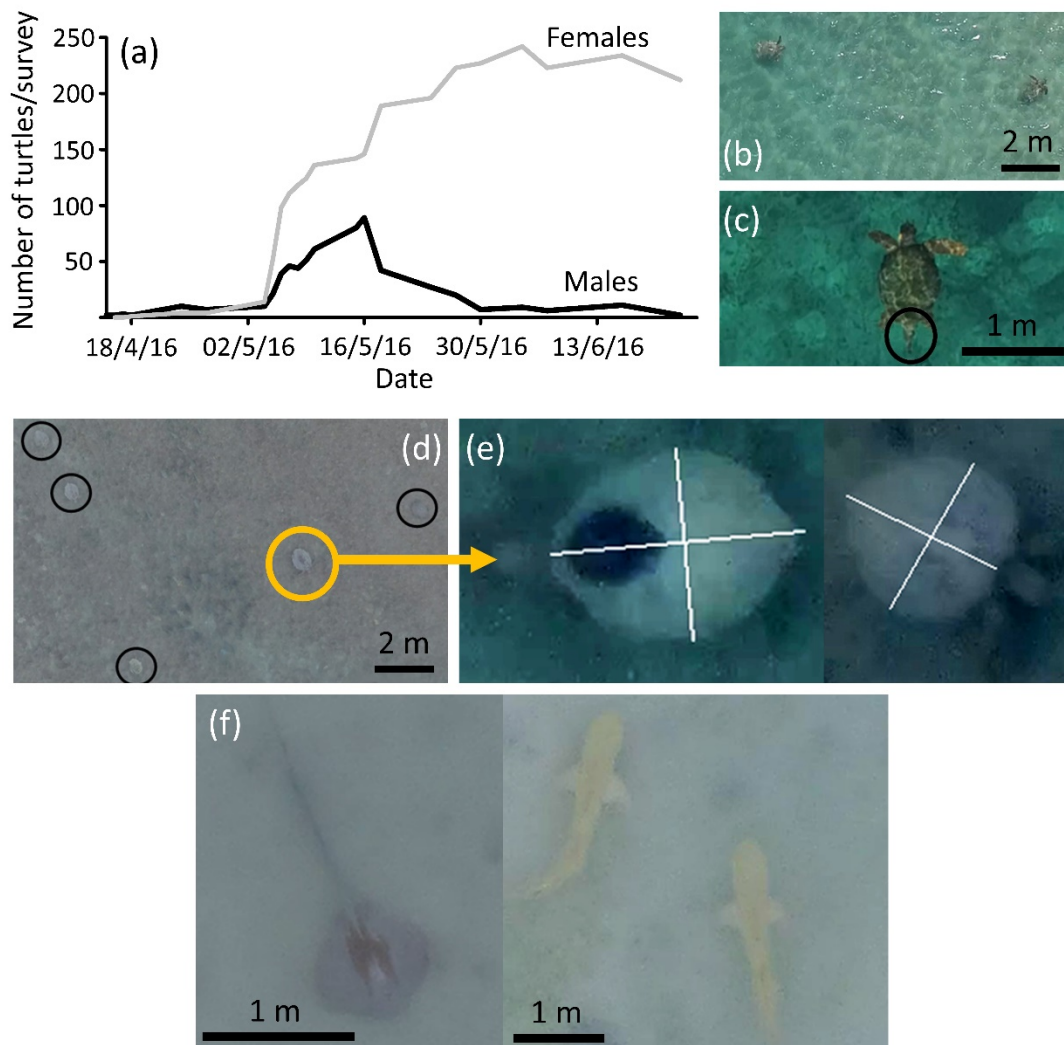


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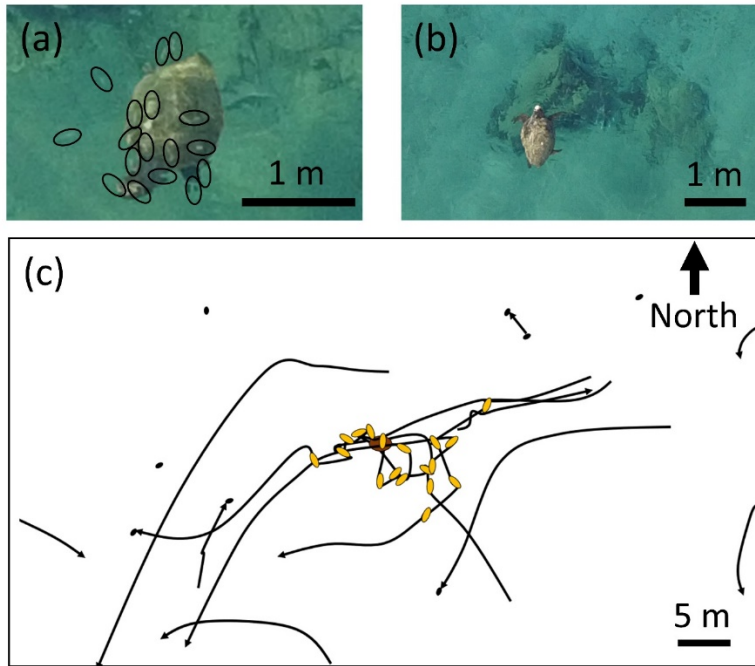
**Figure 1.** (a) Cumulative number of UAV studies on submerged marine mammals, marine reptiles and fishes to December 2018, showing an influx following 2010. Number of (b) studies and (c) species for each of the three groups. (d) Focus of studies on the three groups; black bars are fishes (bony and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



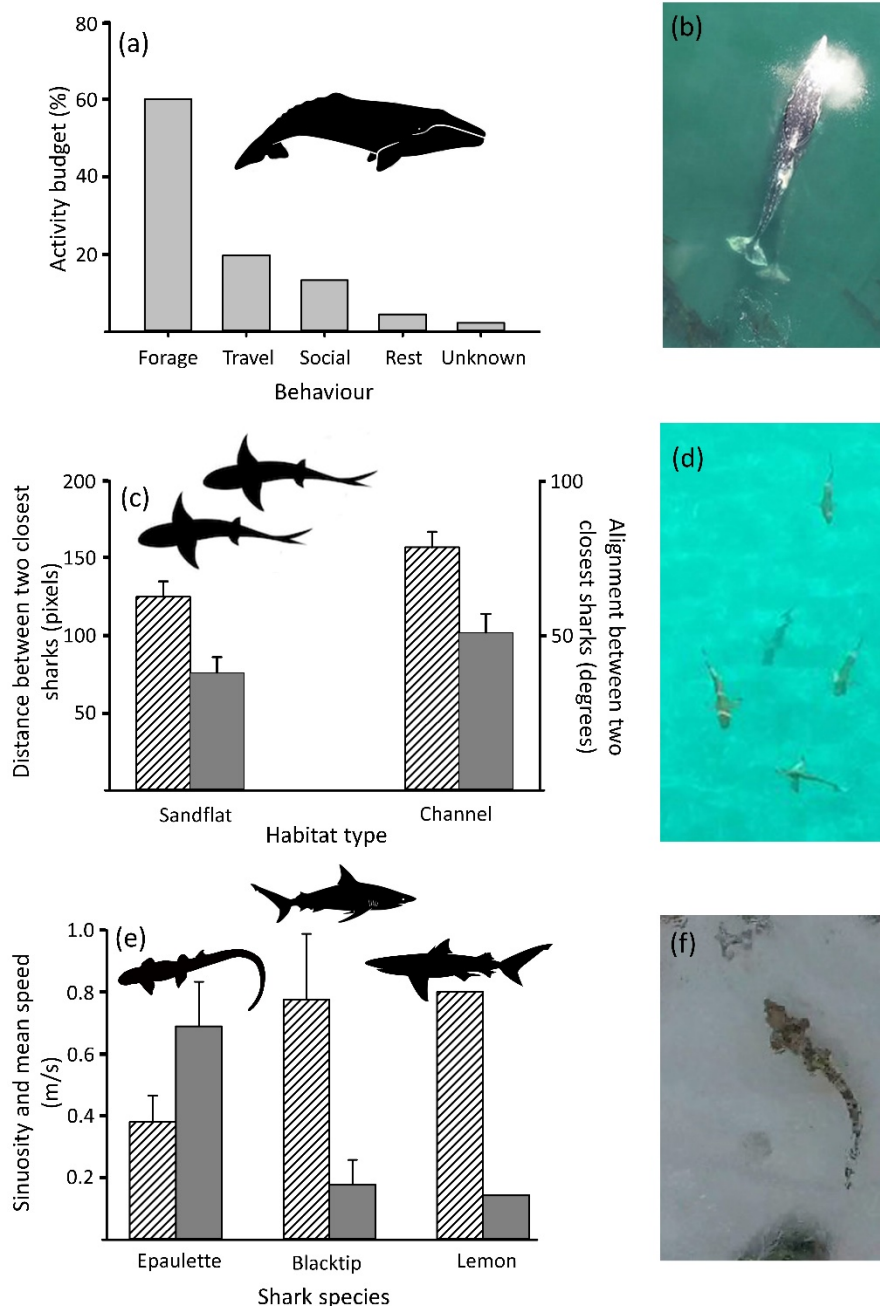
629  
 630 **Figure 2.** Examples of how UAVs have been used to study abundance and distribution in  
 631 other taxa: (a) abundance estimates of conspecific species in a single survey sector covering  
 632 448 km<sup>2</sup>: bowhead whale *Balaena mysticetus* (grey bars), beluga *Delphinapterus leucas*  
 633 (hatched bars) and grey whale *Eschrichtius robustus* (black bars) sightings and abundance  
 634 estimates (and coefficient of variance) vary with technology used: UAVs compared to  
 635 manned aircraft and boat-based observations (replotted and adapted from Ferguson et al.  
 636 2018); (b) aerial view of a bowhead from UAV flown at 12.9 m above the sea surface (reused  
 637 from Fortune et al. 2017); (c) Mean ( $\pm$ SD) density of blacktip reef sharks *Carcharhinus*  
 638 *melanopterus* (light grey bars) and pink whiprays *Himantura fai* (hatched bars) in two  
 639 habitats highlighting spatial heterogeneity in distribution (replotted and adapted from Kiszka  
 640 et al. 2016); (d) aerial view of a blacktip reef shark (upper panel) and a pink whipray taken  
 641 from an altitude of 12 m (reused from Kiszka et al. 2016).  
 642



643  
 644 **Figure 3.** UAV surveys can be used to estimate population size and operational sex ratio  
 645 (OSR), and opportunistically record other taxa to assess abundance, biomass and species  
 646 diversity. (a) Counts of the relative numbers of adult male and female loggerhead sea turtles  
 647 *Caretta caretta* in a population allow the operational sex ratio (OSR) to be assessed, i.e. the  
 648 adult sex ratio on the breeding grounds (replotted from Schofield et al. 2017a). (b) Breeding  
 649 individuals are counted through UAV surveys conducted at an altitude of 60 m and (c) adult  
 650 male sea turtles can be distinguished from adult females as the tails of males noticeably  
 651 protrude from the carapace. (d) Mark and recapture estimation of foraging immature turtle  
 652 population size in Diego Garcia lagoon, BIOT by repeated UAV transect surveys (each black  
 653 circle represents a sea turtle). Population size can be estimated by recording numbers of  
 654 marked (large yellow circle; turtle with satellite tag) and unmarked turtles (small circles). (e)  
 655 Transect surveys can inform species diversity and size of individuals, in this case  
 656 distinguishing a hawksbill *Eretmochelys imbricata* (left; 53 x 30 cm with satellite transmitter  
 657 visible as a black oval) and green *Chelonia mydas* (right; 41 x 41 cm) from the shape of the  
 658 carapace, based on Image analysis (e.g. ImageJ). (f) Opportunistic sightings of non-target  
 659 taxa. Here, sharks and ray sightings made during sea turtle surveys are shown. Photos in (b)  
 660 and (c) adapted from Schofield et al. 2017a; (d-f) unpublished images courtesy of Esteban,  
 661 Mortimer and Hays.  
 662

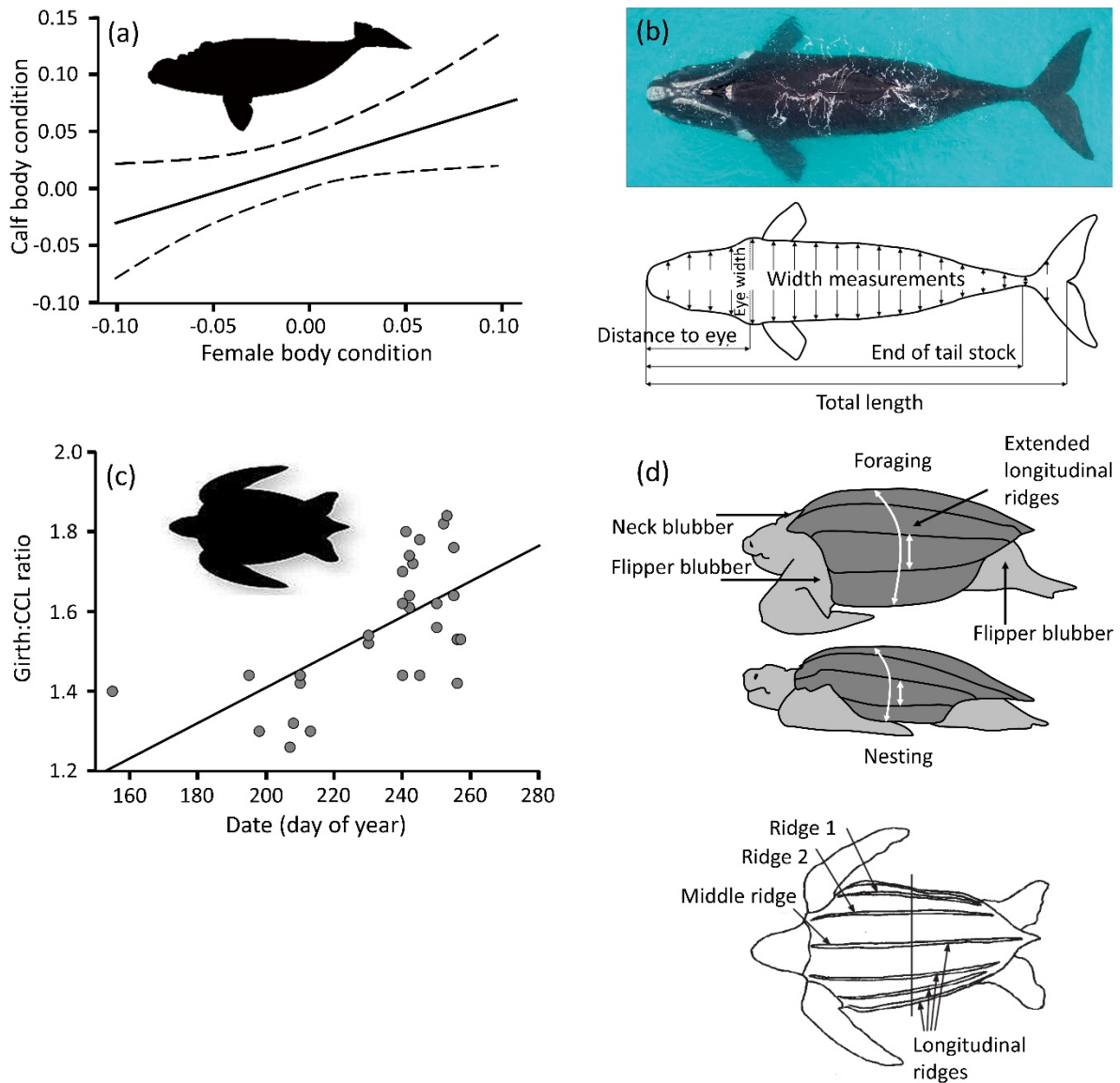


663  
 664 **Figure 4** (a) UAVs can be used to document interspecific interactions; in this case, an adult  
 665 female loggerhead sea turtle *Caretta caretta* frequenting a fish-cleaning station (open black  
 666 ovals are the cleaner fish). (b) Sea turtle positioned directly over the fish-cleaning station. (c)  
 667 By hovering the UAV over a pre-designated site for prolonged periods (i.e. 40 min or more),  
 668 the movement of animals in relation to important resources (such as sea turtles and cleaning  
 669 stations) can be monitored in relation to other animals and the surrounding environment.  
 670 Panel (c) adapted from Schofield et al. (2017b): Movement of nine turtles over a 40 min  
 671 period during a NE wind; arrows show the direction of movement of turtles; yellow ovals are  
 672 where turtles were cleaned; black ovals are resting turtles.  
 673



674  
 675 **Figure 5** Examples of how UAVs have been used to study behaviour in other taxa: (a)  
 676 measuring the activity budgets of grey whales, *Eschrichtius robustus* (replotted and adapted  
 677 from Torres et al. 2018); (b) UAV image of a nursing grey whale taken at 25–40 m altitude  
 678 (reused from Torres et al. 2018); (c) variation in the mean ( $\pm$ SD) distance (hatched bars) and  
 679 alignment (grey bars) of neighbouring reef sharks *Carcharhinus melanopterus* in different  
 680 habitats (replotted and adapted from Rieucau et al. 2018); (d) UAV image of shoaling reef  
 681 sharks taken at an altitude of 12 m (reused from Rieucau et al. 2018 with permission from  
 682 publisher); (e) differences in the mean ( $\pm$ SD) speed (hatched bars) and sinuosity (grey bars)  
 683 of three shark species occupying the same habitat; epaulette sharks (*Hemiscyllium ocellatum*)  
 684 display sinusoidal movement patterns, while blacktip reef sharks (*Carcharhinus*  
 685 *melanopterus*) and a lemon shark (*Negaprion acutidens*) exhibited more linear trajectories  
 686 (replotted and adapted from Raoult et al. 2018); (f) zoomed in UAV image of an epaulette  
 687 shark taken at an altitude of 15 m (reused from Raoult et al. 2018). Examples of target  
 688 individuals are shown in white boxes.





690  
 691 **Figure 6** A body condition index can be calculated from the width and length measurements,  
 692 i.e. distinguishing fatter versus thinner individuals. (a) Example of how UAVs have been  
 693 used to assess female vs calf body condition in southern right whales, *Eubalaena australis*  
 694 (replotted from Christiansen et al. 2018); (b) UAV image of southern right whale and width  
 695 and length measurements made to quantify body condition (reused from Christiansen et al.  
 696 2018); (c) Examples of how body condition is measured in leatherback sea turtles  
 697 *Dermochelys coriacea* (replotted from Davenport et al. 2011), which could be examined  
 698 using UAV imagery; (d) differences in the body fat deposition and girth of carapace between  
 699 foraging and nesting leatherbacks (upper panel; adapted from Davenport et al. 2011) and  
 700 body measurement parameters (lower panel) (reused from Davenport et al. 2011 with  
 701 permission from publisher).  
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704

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

<b>Abundance and Distribution</b>			
<b>Class</b>	<b>Group</b>	<b>Species</b>	<b>Study focus</b>
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	Crocodylian	American alligator	Detection
Reptile	Crocodylian	American alligator	Detection
Reptile	Crocodylian	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
<b>Behaviour</b>			
<b>Class</b>	<b>Group</b>	<b>Species</b>	<b>Study focus</b>



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 station
Reptile	Sea turtle	Leatherback	Fitness - swimming speeds
Reptile	Crocodylian	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, activity budget
Marine Mammals	Cetacean	Gray whales	Behaviour states and events, activity budget

<b>Physiology/Morphometrics</b>			
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
<b>Disturbance from UAVs</b>			
Reptile	Sea turtle	Green turtle, flatback, hawksbill	
Reptile	Crocodylian	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	

<b>Other</b>			
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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