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Short Communication

Animal-borne video reveals atypical behaviour in provisioned green turtles: A global perspective of a widespread tourist activity

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A B S T R A C T

Feeding wildlife as a tourist activity is a growing industry around the world. However, providing alternative food sources can affect wildlife ecology and behaviour. In this study, we combined animal-borne cameras on five sub-adult green turtles (*Chelonia mydas)* from the Bahamas with a global review to directly assess impacts of provisioning on the behaviour of an endangered marine species for the first time. Descriptive evidence from video footage, with videos included in the manuscript, showed that the tagged turtles spent 86% of their time in shallow water (<1.5 m) at a provisioning site. All individuals observed, both tagged and untagged, actively approached people and boats, with up to 10 turtles recorded feeding on squid offered by tourists at one time. During these feeding events, multiple accounts of atypical aggressive behaviour such as biting and ramming conspecifics were recorded. Furthermore, a review of online sources revealed the widespread significance of turtle feeding as a tourist activity in at least 20 locations within the global range of green sea turtles, as well as five locations with regular provisioning of either loggerhead (*Caretta Caretta*) or hawksbill (*Eretmochelys imbracata*) turtles. At the majority of the locations, turtles were fed animal matter such as fish scraps and squid. Although sample size limited quantitative analyses, we found indications of relatively high growth rates of two tagged turtles and low seagrass intake rates of all five tagged turtles. Therefore, our results emphasize the need to further investigate the impacts of turtle provisioning on natural foraging behaviour, ecosystem functioning as well as turtle growth rates and health implications. Supplemental feeding may increase habituation and dependency of turtles on humans with risks for turtle conservation. The innovative use of animal-borne camera technology may provide novel insights to behavioural consequences of human-wildlife interactions that can aid in the management and conservation of rare or endangered species.

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1. Introduction

Globally, wildlife tourism is a rapidly growing industry centred around observation and interaction with wild animals. One such method employed to predictably experience wildlife, is the use of bait to attract and feed the animals, referred to hereafter as 'provisioning'. This tourist activity started in terrestrial ecosystems as reported for wild monkeys and bears (Knight, 2010; Kojola and Heikkinen, 2012), and is now widely reported in marine systems, such as provisioning of sharks, dolphins, stingrays, teleost fish and other species (Feitosa et al., 2012; Foroughirad and Mann, 2013; Maljković and Côté, 2011; Shackley, 1998). Provisioning can lead to positive impacts on wildlife conservation through increased awareness and connecting people with nature, which, in some cases has been demonstrated to have little to no negative effect to marine animal behaviour and functioning (Hammerschlag et al., 2017; Maljković and Côté, 2011). However, provisioning wildlife can also have both short and long-term negative effects, such as reduced health of the animals, dependency on the food provided by humans and inter or intraspecific aggressive behaviour (Dubois and Fraser, 2013; Murray et al., 2016; Orams, 2002). Eventually, this could impact the breeding success of entire populations (Higginbottom, 2004; Orams, 2002). For example, southern stingrays (*Hypanus americanus*) that were fed by tourists in the Caribbean, were more likely to contain ecto-dermal parasites and more likely to be injured by boats or predators than non-fed stingrays (Semeniuk and Rothley, 2008). Furthermore, provisioning bottlenose dolphins (*Tursiops aduncus/truncatus*) has resulted in both agonistic behaviour towards tourists and conspecifics as well as decreased female reproductive success compared to non-provisioned females (Orams et al., 1996; Senigaglia et al., 2019). Given the global increase in wildlife tourism, it is critical to develop research tools to closely monitor these interactions in order to mitigate potential impacts to wildlife.

Green turtles (*Chelonia mydas*) are considered herbivorous during most of their juvenile to adult life stages but have been reported as omnivorous in some locations (Bjorndal, 1980; Mortimer, 1981; Nagaoka et al., 2012; Seminoff et al., 2002). Further, they have been demonstrated to prefer a food source that is high in protein, such as fish, when presented with the opportunity (Monzón-Argüello et al., 2018; Stewart et al., 2016). Therefore, green turtles are reliable candidates for tour operators to attract using fish as bait. Green turtles are internationally protected by law preventing global trade (CITES convention, 1973), after (sub) populations were historically decimated due to decades of exploitation (Jackson et al., 2001). National laws have incorporated further protection of sea turtles. For example, in The Bahamas, turtles have been fully protected since 2009, prohibiting the harvesting, possession, purchase and sale of all species and their eggs (Bjorndal and Bolten, 2010). However, in many nations, legislation does not extend to touching, handling or feeding turtles. This is of concern, as turtles can be exploited in novel ways due to global demand for wildlife tourism and provisioning activities may be having unknown impacts on turtle behaviour as well as their habitats throughout their range. Furthermore, insight into the global scale at which provisioning activities currently occurs and how those activities impact the behaviour of green turtles is urgently required to improve management and future conservation of this endangered species.

Here, we used camera tag technology as a novel method to investigate how turtle provisioning may affect the behaviour of sub-adult green turtles at an established tourism site from The Bahamas. In addition, we collated online sources in the assessment of a global review of turtle provisioning from similar tourism operations, and through our own study, propose important considerations for future research efforts.

2. Materials and methods

This study was conducted at Bottom Harbour, north Eleuthera, The Bahamas (25°.465294, −76°.634903) in November 2019. Bottom Harbour is a shallow water inlet of the western Atlantic Ocean with a mean depth of approximately 3.5 m and dominated by vast, continuous *Thalassia testudinum* seagrass meadows, interspersed with soft sediments and low-profile coral reef (Figures in Appendix A). The site was selected because of the high volume of green turtles historically encountered there, and subsequent tourist provisioning operations that have since been established. Provisioning of turtles at this site started in August 2017, and both guided tour and private boat visits have increased since then up to a current rate of about 10 boats day^{-1} in low season (April to November) and 30 to 40 boats day^{-1} in high season (November to April) (O'Shea. Pers. Obs.).

Activity of green turtles was recorded using animal-borne camera tags. Turtles were captured by hand in the morning at a location where feeding regularly takes place (1 m deep, Fig. A2). Metrics of size were recorded (curved carapace length *CCL* (cm), curved carapace width *CCW* (cm) and weight (kg)) before camera tags were attached. Tag packages consisted of an action camera in a housing (Drift Ghost X), depth and temperature datalogger (Sensus Ultra), a GPS tracker for retrieval (Spy Spot investigations, GL300-W) attached to a foam float (30 g of ethylene-vinyl acetate copolymer, 120 kg m^{-1}). The design of the camera package allowed its dry weight to be offset whilst submerged, so to minimize positive buoyancy that may influence turtle behaviour (dry weight: 407 g, wet weight: 420 g, 89 g upward buoyancy). The camera tags were attached via corrodible pop-up links to the carapace of the turtle with cool-setting epoxy (after Thomson and Heithaus, 2014). Turtles were subsequently released over one km from the position of capture at the opposite side of the bay, to a shallow (2 m) high-canopy seagrass meadow (Fig. A2). Cameras recorded turtle behaviour for a maximum of 5 h or until darkness. The camera tag was released from the turtle ~5–9 h after deployment and retrieved through real-time GPS tracking.

To investigate behaviour and habitat use, all videos were viewed in their entirety by one observer and the behaviour of the tagged turtles was classified every second into the main behaviour types: swimming, resting, natural grazing and provisioning. All turtles resumed typical behaviours (feeding, resting) within 30 min of deployment; therefore, the first 30 min were removed from video and depth data analyses. Additionally, untagged turtles recorded on camera were identified by morphological irregularities (such as irregular carapace scutes and scars) in combination with identification of unique facial scute patterns (Reisser et al., 2008). Turtles that could be identified this way were separately labelled (Appendix C). The number of feeding events during provisioning of both untagged and tagged turtles was counted. Aggressive encounters, which were defined by turtles specifically targeting other turtles (both tagged and non-tagged) by either biting, ramming, high-speed chasing and stealing bait were recorded, and treated as separate observations. Daily seagrass intake rates were extrapolated using camera observations and seagrass field measurements. Growth rates of recaptured individuals were calculated (see Appendix F for methods).

To analyse the global significance of provisioning of sea turtles by tourists, we compiled a database with locations where feeding activity has been reported multiple times in the last five years. This was done by searching on various social media and repository websites, such as Web of Science, Youtube, Instagram, Twitter and TripAdvisor for keywords "feeding" or "fed" and "turtle(s)" or "sea turtle(s)". Only locations where photographs or videos provided direct evidence of feeding activity were included.

3. Results and discussion

3.1. Behavioural observations from camera tags

In total, we analysed 1088 min (~18 h) of video footage from cameras retrieved from five individual turtles and we were able to identify and observe the behaviour of a further 12 individuals through filmed encounters. One turtle was tagged on a day when tourist boats were absent. Six videos show compilations of observed atypical turtle behaviour and encounters with conspecifics and humans (all videos accessible through digital version of the paper).

All tagged turtles showed habituation to regular provisioning activity by spending on average 406 ± 66 min (86% ± 6) of their time resting, swimming and feeding in the shallows (<1.5 m) in immediate proximity to the primary provisioning site (Appendix B), resting in groups of up to 12 individuals (Fig. 1A, Video 1). Turtles were shown to return to the provisioning site (17 ± 4 min) after release. Resting in very shallow habitats is uncommon for this species, as shallow, higher-energy zones are known to exacerbate buoyancy regulation in turtles (as seen in Video 1) (Hays et al., 2004; Seminoff et al., 2006). This suggests that the camera tags were not negatively influencing the buoyancy in these individuals. Lastly, observing these turtles resting in loose aggregations as observed here, particularly during diurnal periods, is further confounding from what we know for this species (Bjorndal, 1980; Fujisaki et al., 2016; Ogden et al., 1983).

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Adaptive behaviour of solitary animals gathering in anticipation of provisioning activity was also seen in bull sharks (*Carcharhinus leucas*) and multiple ray species (as summarized by Burgin and Hardiman, 2015). All turtles in this study were resting at the provisioning site at sunset, thus, corroborating behavioural responses of other known provisioned sub-populations, for example, whitetip reef sharks (*Triaenodon obesus*), southern stingrays and long-tailed macaques (*Macaca fascicularis*) (Corcoran et al., 2013; Fitzpatrick et al., 2011; Ilham et al., 2018). Therefore, these turtles may have optimized their diurnal spatial movements in order to benefit most from the provisioning activity.

One tagged turtle and at least nine untagged individual turtles recorded on camera were offered squid and all were observed to consume the squid during multiple provisioning events from multiple operators (Fig. 1C and D, Video 2,3,4). The tagged turtle consumed 35 portions of squid supplemented by at least five separate tourist boat tours within a period of 1 h. Although videos of the other four tagged turtles did not record provisioning activity, their behaviour suggested they are regularly fed squid, including their capture by hand, at the provisioning site for the present study. This was further evidenced by individuals being identified and observed feeding at the provisioning site on different days prior to and after their camera tag was released (Appendix E).

Provisioning resulted in an increase of behaviours considered atypical, both among turtles as well as between turtles and people feeding them. The provisioned turtle that was fitted with a camera tag was involved in 15 separate events of intra-specific aggressive behaviour, while five untagged turtles were recorded displaying aggressive behaviour towards conspecifics, all during provisioning (Fig. 1B, Video 2). A single southern stingray and various teleost species were observed during provisioning events competing for squid and resulting in direct competition with the turtles (Fig. 1B and C, Video 2,3). Aggression during foraging is not considered natural behaviour for green turtles from this region (Bjorndal, 1980); however, aggressive behaviour linked to provisioning was earlier reported in tourist-fed loggerhead turtles (*Caretta caretta*) in the Mediterranean Sea (Comis et al., 2015), and many other marine animals, such as various stingray and dolphin species (Orams et al., 1996; Semeniuk and Rothley, 2008), with potential impacts on social behaviour and structure of the fed animals (Orams, 2002).

Furthermore, turtles were observed to actively approach and bite tourists with and without the provision of squid (Fig. 1E, Video 5). This behaviour is becoming increasingly frequent near the provisioning site and has seemingly been exacerbated by the sudden decrease in tourism and associated provisioning activity in 2020 due to COVID-19 restrictions (pers. comms. with local residents). Increases in agonistic behaviour towards people or biting incidents as a consequence of wildlife provisioning

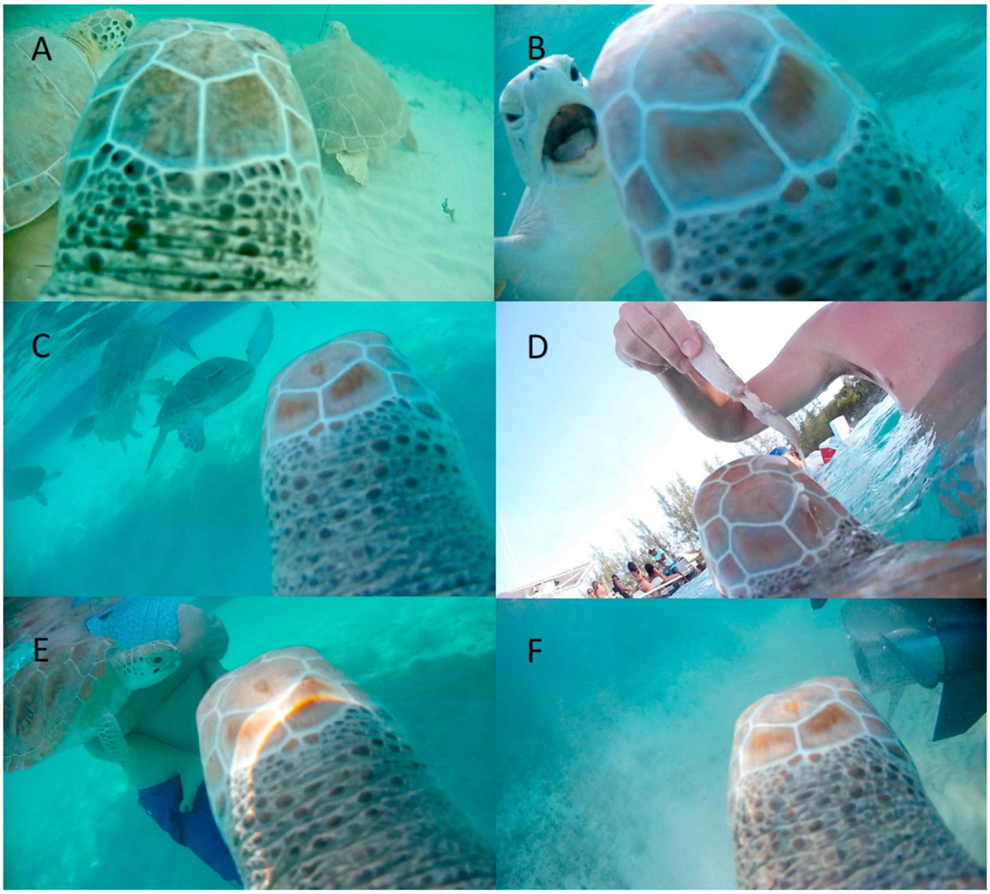

Figure 1. Video stills A-F correspond to videos 1-6 of atypical behaviour associated with the provisioning on green sea turtles (*Chelonia mydas*) behaviour. A) Turtles resting in groups near the provisioning site (Video 1). B) Turtles displaying aggressive behaviour during provisioning (Video 2). C) Provisioning of a group of turtles by multiple tourist boats (Video 3). D) Turtles being hand-fed by tourists (Video 4). E) Turtles approaching and biting tourists in the water (Video 5). F) Turtles approaching jetties, boats and engine propellers (Video 6).

has been reported for a large range of animals such as sharks, bears, dolphins and groupers (Hammerschlag et al., 2012; Kojola and Heikkinen, 2012; Orams et al., 1996; Perrine, 1989), potentially leading to counter-productive perceptions of wildlife by tourists, subsequently harming conservation efforts for endangered species (Hobday, 2012).

3.2. Global scale and prospective regulation of sea turtle provisioning activity

Across their global range, green turtles are regularly being fed from at least 20 locations in 15 countries in-situ to their natural habitat (Fig. 2, Appendix D, E), which may be having unreported deleterious effects on this species. At 13 of these locations (65%), the main food type offered to the turtles consisted of animal matter such as fish scraps, squid or conch. At seven other locations, plant matter such as fruit, lettuce or macroalgae was fed to the turtles. This global concept is not only restricted to green turtles, as we found evidence of loggerhead turtles being fed at four locations in two countries in the Mediterranean Sea, and hawksbill turtles at one location in the Pacific Ocean (Fig. 2). Habituation of turtles to humans and provisioning activity — such as groups of gathered turtles and tourists handling turtles above water - is clearly visible on the images provided by tour operators and their customers worldwide and in line with results from our camera study (Video 3, 5, Appendix E). Manipulating site fidelity and habituation to people may exacerbate poaching activity, which, despite local and regional laws, does still occur in various locations throughout these turtle's range, such as in Malaysia and in the Gulf of Venezuela (Barrios-Garrido et al., 2020; Joseph et al., 2019). The anticipated increased risk of poaching became reality for this research site in The Bahamas. Within a year after completing the fieldwork, a local tour operator illegally removed eight turtles from this provisioning site to presumably sell within a nearby island community (this was witnessed and relayed to the authors on the condition of anonymity).

Provisioned turtles may also be at greater risk of boat strike incidents, as postulated earlier by Stewart et al. (2016) and Monzón-Argüello et al. (2018). In our study, turtles were observed to actively approach jetties and boats - likely due to a conditioning of engine noise - and seemed unperturbed by propellers until they were in very close proximity (Fig. 1F, video 6).

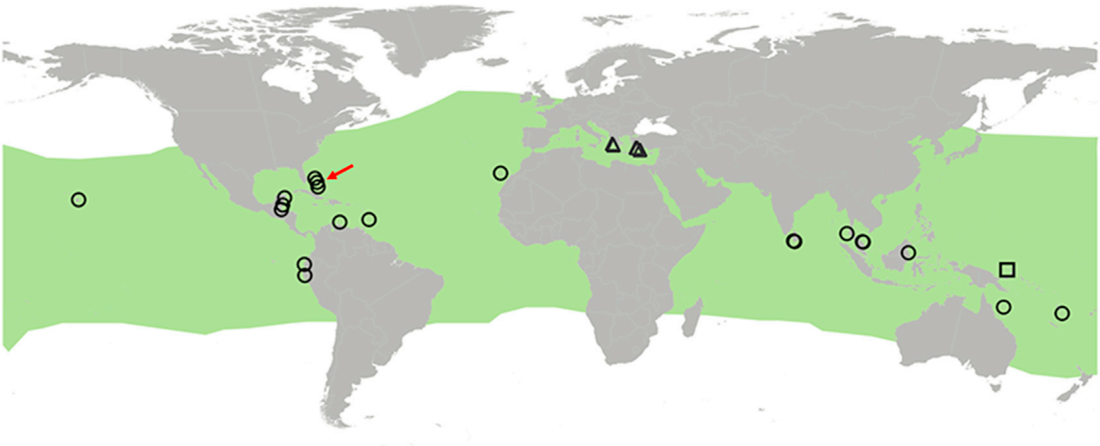

Fig. 2. Locations where regular provisioning of green sea turtles (*Chelonia mydas*, circles), loggerhead turtles (*Caretta caretta*, triangles) and hawksbill turtles (*Eretmochelys imbricata*, rectangles) as a tourist activity has been reported. Arrow points to the location of this study. In green: main habitat range of green sea turtles (adjusted from (Seminoff, 2004))

Consequences of similar behaviour were reported for tourist-fed southern stingrays, where 85% of the individuals had injuries such as propeller cuts, related to feeding activity in Grand Cayman (Semeniuk and Rothley, 2008). Another potential threat is that apex predators such as sharks are attracted to sites where tourists are provisioning their prey, increasing the risk of incidental attacks (Brena et al., 2015) and disrupting natural predator-prey behaviour with impacts on the wider ecosystem (Kiszka et al., 2015). Turtle provisioning most likely increases the dependency on humans for food, causing behavioural anomalies and under-nourishment when tourist activity fluctuates or is suddenly terminated, such as seen globally during the decreasing tourist numbers following the COVID-19 pandemic (Higginbottom, 2004; Nicola et al., 2020).

Wildlife interactions that reduce harm or impact to the target species can be encouraged by local education, regulation and management. Education about the potential impacts of wildlife provisioning has shown to be important in the development of sustainable tourist-wildlife activities (Murray et al., 2016). Tour operators can be informed by local nature management agencies about the potential consequences of feeding, such as shifts in aggression towards people. Local governments or conservation agencies may consider enforcing bans on the feeding of sea turtles, as has been done for bears, dolphins and monkeys (Orams, 2002). With global increases in wildlife provisioning, attention is required to monitor and mitigate impacts associated with wildlife tourism and to develop sustainable tourist-wildlife activities.

3.3. Priority questions to motivate future research

Our results emphasize the need to study impacts of provisioning on seagrass intake rates, turtle health and ecosystem dynamics. Future studies should address increases in sample size and a direct comparison to non-provisioned turtles to investigate whether provisioning is causing the behavioural observations observed here (biased site fidelity, altered diet, aggressive behaviour), and validated though the wider assessments presented here. Additionally, a potential shift in diet may impact natural grazing behaviour and seagrass dynamics. The videos show that turtles would still eat seagrass outside of provisioning activity (Video 6). We calculated that the tagged turtles had a low average projected daily seagrass intake (6.4 g DW/day/turtle, appendix B2) when tourists were present, but that the turtle tagged on the day when tourists were absent, had a higher daily seagrass intake (34.3 g DW/day), which falls within the reported range of 30–220 g DW needed per sub-adult turtle per day (Bjorndal, 1982; Thayer et al., 1982; Williams, 1988). Therefore, turtles may either increase their seagrass uptake rate in absence of provisioning or have adjusted their seagrass intake as a direct result of provisioning, with potentially unknown impacts on wider ecosystem functioning.

Lastly, two of our studied turtles had been previously tagged and measured revealing rudimentary growth rates. One turtle, which was initially tagged in 2017, just after provisioning charters started, revealed values exceeding previous reported Bahamian turtle growth rates (Bjorndal and Bolten, 1988), with an increase in Body Condition Index (BCI) from 1.17 (2017) to 1.27 (2019), 5.49 cm CCL and 6.8 kg year^{-1}. Increases in weight, length and BCI as well as the well-fed appearance of other provisioned turtles in Video 3 and 4 suggest that provisioning may compensate for the recorded low seagrass intake rates in terms of growth. The global study revealed that mostly animal matter is fed to the turtles, which is a food source outside their usual trophic level and can increase growth rates and impact green turtle health (Bjorndal, 1985; Stewart et al., 2016). Therefore, it is worthwhile to study the impacts of potential atypical growth rates of provisioned turtles on turtle health and reproductive success.

4. Conclusion

Here, we demonstrated for the first time, behavioural impacts associated with tourist driven provisioning of wild marine turtles using a novel animal-borne tag package and applications of such technology. Further, addressing these types of manipulated wildlife interactions at a global scale, highlights the potential broader implications for animal welfare, conservation and wider ecosystem function. Animal-borne camera tags were found to be highly practical and efficient for data collection and this study serves as a pioneering proof of concept to observe interactions between wildlife and humans. Together with additional long-term and comparative studies with increased sample sizes these camera data will underpin more effective methods in assessing the impact that feeding has on wild animal behaviour, growth and reproductive success. Increased education, monitoring and regulation with regards to the feeding of sea turtles and other wildlife may ensure sustainable tourist-wildlife relationships in the future.

CRediT authorship contribution statement

Fee OH. Smulders: Conceptualization, Methodology, Investigation, Formal analysis, Data Curation, Visualization, Writing - original draft, Writing - review & editing, Funding acquisition **Owen OR. O'Shea:** Conceptualization, Investigation, Resources, Writing - review & editing **Marjolijn JA. Christianen:** Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A - F. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01417.

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