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ARTICLE

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Synergistic use of UAV surveys, satellite tracking data, and mark-recapture to estimate abundance of elusive species

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Abstract

Estimating population abundance is central to many ecological studies and important in conservation planning. Yet the elusive nature of many species makes estimating their abundance challenging. Abundance estimates of sea turtles, marine birds, and seals are usually made when breeding adults are ashore, while life stages spent at sea, including as juveniles, are often poorly sampled. We used a combination of high-resolution satellite tracking (Fastloc-GPS), uncrewed aerial vehicle (UAV) surveys, and capture-mark-recapture approaches to assess the abundance of immature hawksbill (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*) in a tidal lagoon of the Chagos Archipelago (Indian Ocean). We captured, marked, and released 50 turtles (48 hawksbill and 2 green turtles) prior to UAV surveys and used satellite tracking data from 27 immature turtles (25 hawksbill and 2 green turtles) to refine the estimated numbers of marked turtles available for resighting and those likely to have emigrated from the study area. We estimated a total of 339 turtles in the lagoon with a density variation at different tidal heights between 265 turtles km^{-2} at high water and 499 turtles km^{-2} at low water. Of these, 91% were hawksbills and 9% were green turtles. These hawksbill densities are the highest reported among 17 foraging sites recorded around the world and likely reflect successful long-term protection of turtles in the Chagos Archipelago.

KEYWORDS

conservation, density, drone, endangered species, marine megafauna, marine protected area (MPA), mark-resight, satellite tracking, shifting baseline

INTRODUCTION

Population estimates are integral to conservation planning, for example, to allow high-use areas to be defined and population trends to be assessed (Lotze et al., 2011; Santini et al., 2018), and various census techniques have been widely used. Capture-mark-recapture (CMR) or capture-mark-resight are classic approaches, particularly in terrestrial systems (Lindberg, 2012). Sometimes census data involve direct counts of animals visible onshore, such as nesting seabirds or seals with pups (Clarke et al., 2011; Russell et al., 2019). In other cases, a population is sampled and numbers or biomass per unit effort are recorded, as in plankton, benthos, and fisheries surveys (Dutta et al., 2016; Keller et al., 2010). Yet despite the broad success of these approaches, in some cases, census data remain difficult to obtain, such as for elusive, rare, or widely distributed species or life history stages (e.g., beaked whales; Hildebrand et al., 2015). Obtaining census data in such cases is increasingly facilitated by modern technology and the development of new approaches. For example, camera traps are now widely used for elusive species such as cheetahs (*Acinonyx jubatus*; Brassine & Parker, 2015) and otters (e.g., Eurasian otter, *Lutra lutra*; Gil-Sánchez & Antorán-Pilar, 2020), and thermography for cryptic species (e.g., brown hare leverets, *Lepus europaeus*; Karp, 2020). Uncrewed aerial vehicle (UAV) surveys allow for ease of sampling expansive areas (Koh & Wich, 2012).

Here, we develop an approach that combines UAV surveys, CMR estimates, and high-resolution satellite tracking data to produce abundance estimates for a little-known life stage of a critically endangered species. We also highlight the value of this synergistic use of these three methods for population estimation surveys across varied taxa. Sea turtles are a group for which information on the abundance of certain life stages remains scant. Although the abundance of adult females is routinely measured using counts of nests or tracks on nesting beaches (Mazaris et al., 2017), the abundance of male turtles and the juvenile life stages are poorly known, and filling this knowledge gap is a key issue for sea turtle ecology and conservation (Rees et al., 2016; Wildermann et al., 2018). Although nesting numbers of some species and populations of sea turtles have shown encouraging upward trends (Mazaris et al., 2017), the hawksbill turtle (*Eretmochelys imbricata*) is listed globally as critically endangered (Mortimer & Donnelly, 2008). Therefore, understanding the population status of cryptic life history stages of this species is fundamental for identifying priority conservation regions and habitats, as well as for measuring population status at protected sites. Here, we examine the abundance and density of immature hawksbill turtles at a site that has been well-protected and free of negative anthropogenic impacts for many decades.

METHODS

Study site

Diego Garcia is the largest and only inhabited island in the Chagos Archipelago in the Indian Ocean. Research was undertaken at Turtle Cove (7.4309° S, 72.4349° E) situated in the south of Diego Garcia lagoon, which is a Ramsar site. Maximum depth at the cove entrance is 3.22 m (measured using a G5 logger, CTS, UK, from 5 February to 10 August 2021). Turtle Cove provides foraging habitat for immature hawksbill and green turtles (*Chelonia mydas*), and both species have been protected by conservation legislation since 1968 and 1970, respectively (Mortimer et al., 2020; Figure 1).

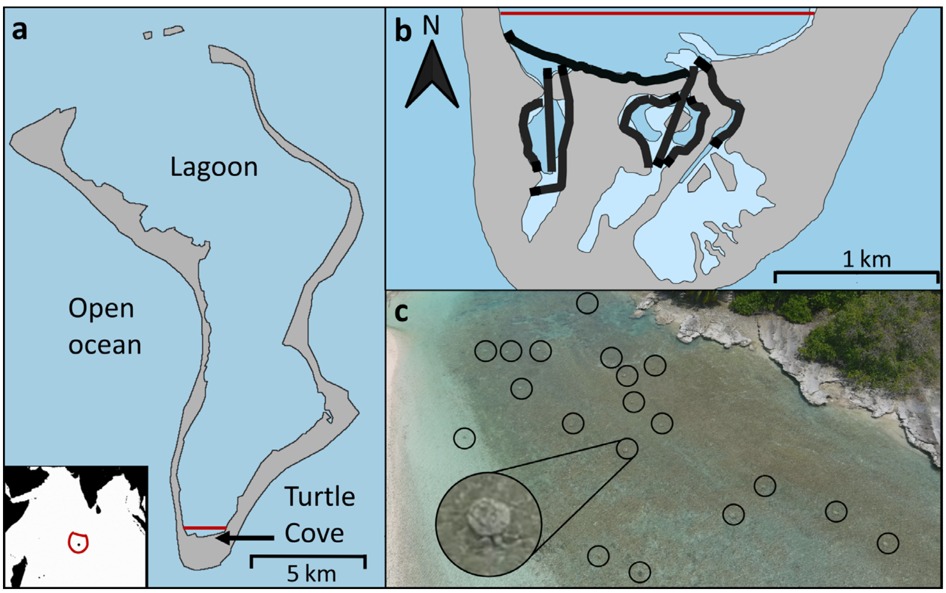

FIGURE 1 (a) Diego Garcia with an inset map of the Chagos Archipelago in relation to the wider Indian Ocean, including the British Indian Ocean Territory, marine protected area, and exclusive economic zone boundary (red polygon). (b) Uncrewed aerial vehicle (UAV) flight paths (black) over Turtle Cove showing areas exposed at low water (light blue) and the boundary of Turtle Cove (red line). (c) Image of turtles (black circles) from the UAV at 30-m altitude.

Physical captures and marking turtles

In February 2021, turtles were captured by hand, following methods detailed in Hays et al. (2021). Straight carapace length notch-tip (SCLn-t), straight carapace width (SCW), curved carapace length notch-tip (CCLn-t), and curved carapace width (CCW) (Bolten, 1999) were measured for all captured turtles. These measurements add to our morphometric dataset (compiled since 1996) along with CCL from nesting hawksbill ($n = 23$) and green turtle ($n = 49$) females since 2012. Captured turtles were marked with a broad line or cross of white paint on the carapace, following procedures outlined in Dunstan et al. (2020), and released back into Turtle Cove within 2 h of capture. Field observations showed the paint was clearly visible on the carapace for up to 2 weeks.

Satellite tagging

UAV surveys were conducted within five days of marking turtles, and counts of marked versus unmarked turtles were made. In theory, turtles might leave Turtle Cove within five days of release and so would not be available for resighting within the UAV surveys. To estimate what proportion of turtles would leave Turtle Cove within five days of release, we used high-resolution tracking data from 27 immature turtles (25 hawksbills and 2 greens) equipped with Fastloc-GPS Argos tags (SPLASH10-BF-297B-01, Wildlife Computers, Seattle, WA, USA) at the same site between 2018 and 2021 (see Hays et al., 2021 for satellite tag attachment details). Fastloc-GPS locations were filtered, by excluding residual values >30 and locations with <5 satellites, to improve accuracy. During days 1–5 after release, we calculated the percentage of time satellite-tracked turtles spent inside and outside of Turtle Cove.

UAV surveys

A quadcopter UAV (Autel Robotics EVO II, USA) recording 4K ultra-HD videos at 30 frames per second (fps) was flown by NE, a licensed UAV operator. As per safety guidelines, an observer was present for each flight to assist the pilot. Flights were manually flown at 5 m s^{-2}, though flight speed fluctuated due to factors including wind and obstructions. Transect lengths varied to accommodate for the shape and conditions of each cove. A pilot study was conducted in 2018 to establish the best conditions to undertake surveys at Turtle Cove, and initial analysis of data informed our 2021 survey design. Flight altitude of 30 m was chosen to not disturb turtles (Bevan et al., 2016; Schofield, Katselidis, et al., 2017), while maintaining video resolution to identify turtles. Eight transects were flown repeatedly over 3 days in the late morning (on day 3, the survey was also repeated in the afternoon). The order of transects was altered during each survey period to cover each area during different tidal states. For each flight, metadata including dates, start and end time, and start and end coordinates were recorded. An anemometer was used on the ground to measure wind speed (in meters per second) before each survey. Tide state and times were obtained for Diego Garcia (National Tidal and Sea Level Facility, 2021). In some cases, the UAV was flown in both directions along a transect to determine which footage had the least sun glare. Where these repeat surveys were undertaken, the transect with the best conditions (e.g., low glare) was chosen to count turtles.

Video processing

Image analysis was conducted by one observer (HJS). Data recorded included turtle counts and absence/presence of markings (white paint and/or satellite tags; Figure 2). For optimal analysis, UAV footage was processed on a 69 cm 4K ultra-HD monitor and a high-performance desktop with a high-quality graphics card. Adobe Premier Pro (Adobe, 2021) was used to aid in processing UAV videos and extracting high-quality images. Videos were moved frame by frame when a turtle was detected to capture the clearest image. Turtles were assigned a category of confidence in detection (certain, probable, or possible; Figure 2). Only turtles of the category "certain" were included in our abundance and density estimations. UAV flight data were extracted using Airdata (Airdata UAV, 2021), an application for UAV flight logs and management. The area of each transect was measured by multiplying the length of the transect by the width of the frame (30 m), following the standard approach of strip transect analysis (Marsh & Sinclair, 1989). Unavailable area in the footage was identified (e.g., over land and shadow), measured, and calculated using the ImageJ polygon tool (Schneider et al., 2012) and subtracted from the total area when estimating turtle densities.

Species identification

The length-to-width (L/W) ratios of turtles in the UAV footage were calculated by measuring the SCL and SCW from images where the whole carapace was clearly visible. Measurements were conducted using ImageJ (Schneider et al., 2012), and UAV footage was calibrated

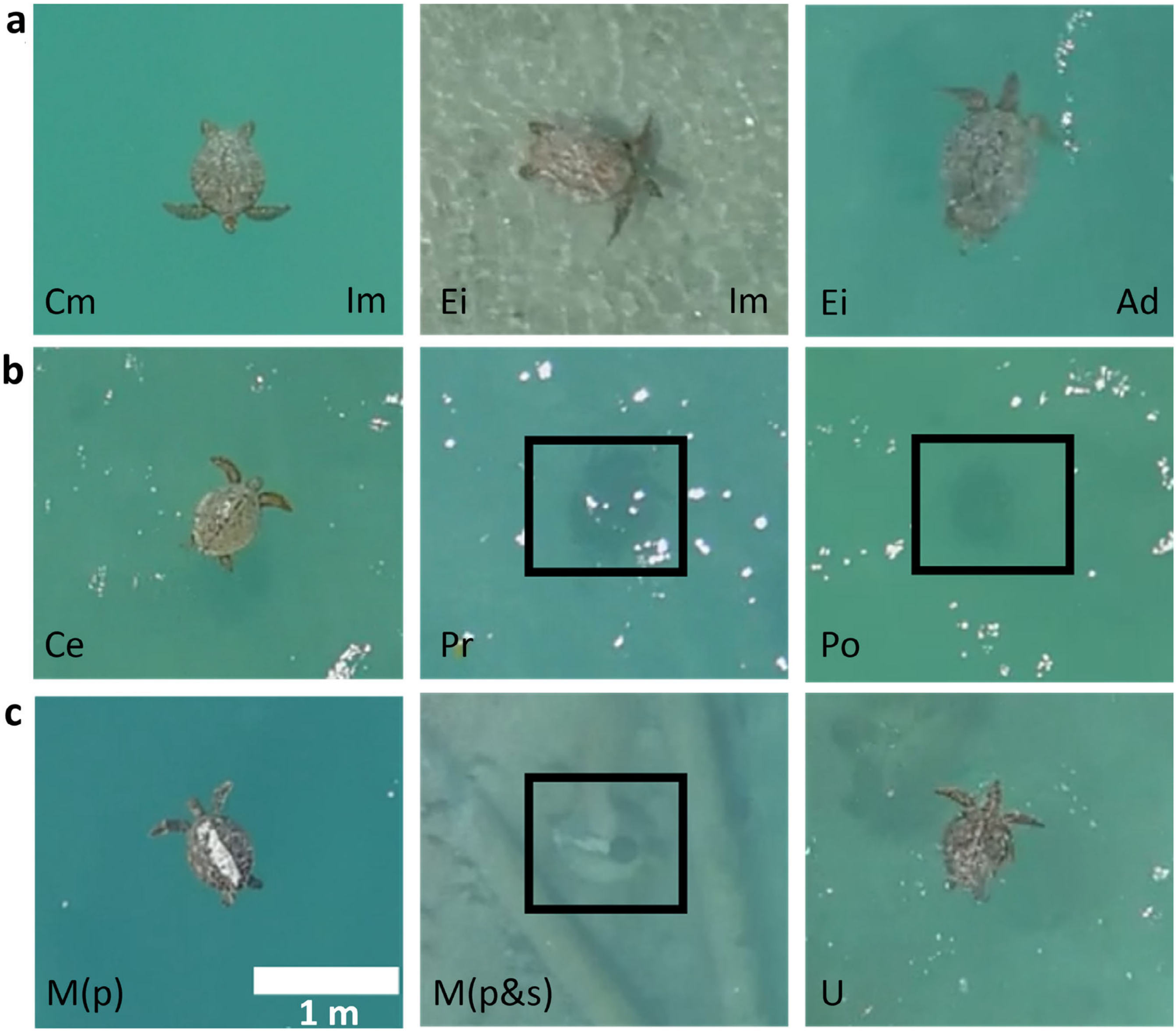

FIGURE 2 Examples of images from uncrewed aerial vehicle video surveys showing (a) an immature green turtle (Cm; Im), immature hawksbill turtle (Ei; Im), and an adult male hawksbill (Ei; Ad) turtle; (b) certain (Ce), probable (Pr), and possible (Po) turtles; and (c) marked turtles with white nontoxic paint (M; p), paint and satellite tag (M; p&s), and an unmarked turtle (U). Images have been cropped. Scale bar applies to all images.

using a transect of known length at 30-m altitude. In some cases, turtles could not be measured due to factors including turbidity, glare, depth, obstruction by overhangs or trees, partly obscured carapace, or obstruction of view of whole carapace due to dive angle.

To assess the L/W ratio of each species, calculate boundaries, and assign species to individuals, we used SCL and SCW measurements from immature hawksbill (<60 cm SCL) and green turtles (<65 cm SCL) captured in Turtle Cove between 1996 and 2021 and from green turtles captured in Seychelles (due to scarcity of green turtle captures in Turtle Cove) between 1981 and 2012. Green turtle carapaces were generally wider with a lower L/W ratio, whereas hawksbill turtle carapaces were more elongated and had a higher L/W ratio. Turtles observed in the UAV footage were identified using these respective L/W ratios. To confirm numbers of hawksbill and green turtles in the population, we applied the ratio of hawksbill to green turtles identified (using the L/W measurements from live-captured turtles) to the total number of observed turtles in the UAV footage.

We assessed the abundance of hawksbill and green turtles live-captured between February and August 2021 to compare differences in the relative species abundance derived from live-capture versus UAV surveys.

Global immature hawksbill density review

A literature search was conducted in August 2020 and December 2021 for papers on Web of Science using the search term: ALL = ("Hawksbill turtle*" OR "*Eretmochelys imbricata*"), AND ALL = ("Immature*" OR "Juvenile*"), AND ALL = ("Abundance*" OR "Densit*" OR "Population estimate*" OR "Foraging site*" OR "Developmental site*"). We used Google Scholar to find all articles that had cited the first study to quantify hawksbills at a foraging site (Limpus, 1992) and worked our way through each article (~173 results) for immature hawksbill density results. We checked all available Marine Turtle Newsletters (MTNs) and International Sea Turtle Symposium (ISTS) proceedings for "Densit*" OR "Abundance*" OR "Population estimate*." Results using catch per unit effort were not included in our results. To compare hawksbill density results around the world, we calculated the mean and SD for sites that had included multiple density results for "zones" in close proximity and for studies over multiple years (e.g., Whiting et al., 2014). If a study had more than one estimate reported, then the mean was taken. If a site was reported in two separate studies, we chose the study that was the most recent and opted for an article (e.g., for Yucatan, Mexico; Cuevas et al., 2007). Data from theses and symposium proceedings were not included in our results.

Data analysis

Density was calculated using total population counts, divided by the available area within each transect, and calculated as number of turtles per square kilometer (turtles km^{-2}). Population density for each transect could then be used to calculate and extrapolate to the whole Turtle Cove area at different tidal heights of low, mid, and high water. The marking of white paint and satellite tag locations provided an opportunity for a mark-resight approach to calculate the population of immature sea turtles. We used the Chapman estimator (Chapman, 1951) to calculate the abundance of immature turtles:

$$\widehat{N}_c = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1$$

where $\widehat{N}_c$ is the population estimate, n_1 is the number of marked turtles available to be resighted, n_2 is the number of turtles observed from the UAV transects, and m_2 is the number of marked turtles resighted from the UAV transects.

The abundance estimates from the Chapman estimator were divided by the area of Turtle Cove to calculate the number of turtles per square kilometer (turtles km^{-2}), which are the density results used in our study. Differences in perception bias (i.e., the ability to observe turtles in different conditions of glare, shade, etc.) and availability bias (when animals present in the area were submerged and not visible due to turbidity, obstructions, overhangs, etc.) (Marsh & Sinclair, 1989) were accommodated within the CMR framework since any perception or availability bias would equally impact the ability to see both marked and unmarked turtles. Likewise, we did not use any of the classic distance sampling approaches, which assume that perception of objects decreases the further they are away from the ground track (Thomas et al., 2010).

To compare our results to global hawksbill density results, the average density was calculated from the available habitat area at low, mid, and high water, which gave a range of densities at different tidal heights.

RESULTS

Physical captures

Length and width measurements were collected from 227 hawksbill and 35 green turtles from Turtle Cove between 1996 and 2021, supplemented with measurements from 88 green turtles from the Seychelles. Most turtles captured in Turtle Cove were <60 cm SCL (Figure 3). Only 9% (15 out of 169) of all captured turtles in Turtle Cove between February and August 2021 exceeded this length and so were categorized as subadults or adults, of which two were males as indicated by the presence of a long tail. All hawksbill and green turtles captured in Turtle Cove since 1996 were <81 cm and <56.5 cm CCL, respectively, while our measured range of sizes for nesting turtles of each species is 74.0–87.1 cm and 97.5–124 cm CCL.

Satellite tagging and marking turtles

High-resolution Fastloc-GPS satellite tags were attached to 27 immature sea turtles (25 hawksbills and 2 greens) between 2018 and 2021. Immature turtles showed high fidelity to Turtle Cove, and during the 5 days after release, 85% of filtered Fastloc-GPS locations for the 27 turtles were within the Turtle Cove area (SD = 25.5%; range = 19%–100%; number of locations = 2888; Figure 4). Over two days in February 2021, 50 immature turtles (48 hawksbills and 2 greens) were captured, marked, and released. Given the results from the satellite tracking, we estimated that $0.85 \times 50 = 42.5$ of the 50 turtles were available for resighting during the UAV surveys.

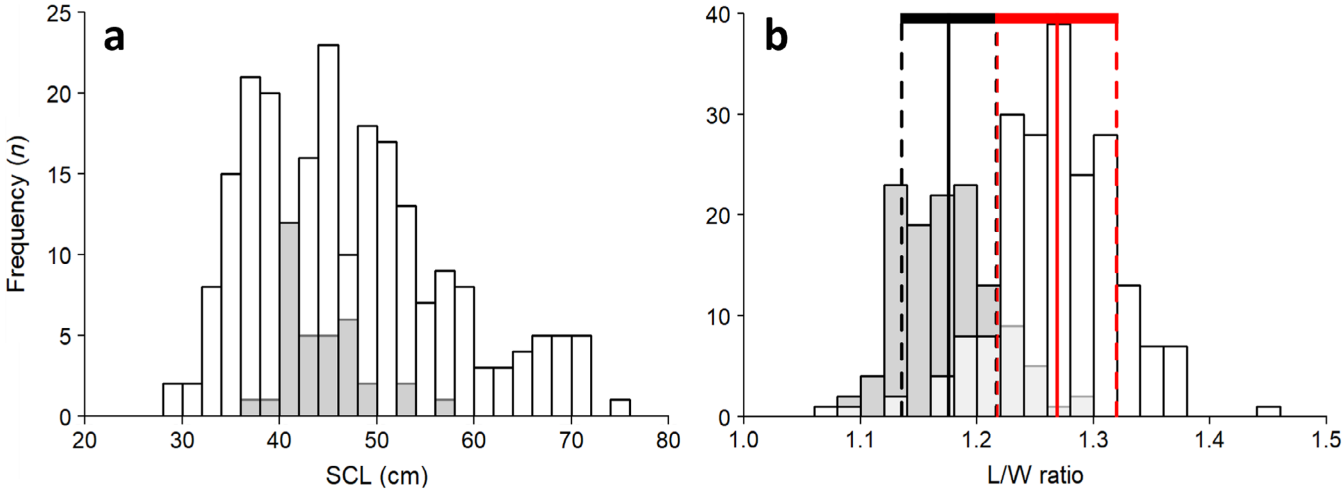

FIGURE 3 (a) Range and frequency of hawksbill (white bars; $n = 227$) and green (gray bars; $n = 35$) turtle straight carapace lengths (SCLs) for individuals captured in Turtle Cove (1996–2021). (b) Frequency of length/width (L/W) ratios calculated from straight carapace lengths and widths for immature hawksbill ($n = 201$; <60 cm SCL; white bars) and green turtles ($n = 123$; <65 cm SCL; gray bars) in Turtle Cove (1996–2021) and Seychelles (1981–2012). For each species, mean L/W ratios are indicated by solid vertical lines and standard deviation by dashed vertical lines (hawksbills = red and green turtles = black). The L/W ratios were used to inform species identification for turtles measured from uncrewed aerial vehicle imagery, with L/W ratio >1.22 for hawksbills and <1.22 for green turtles.

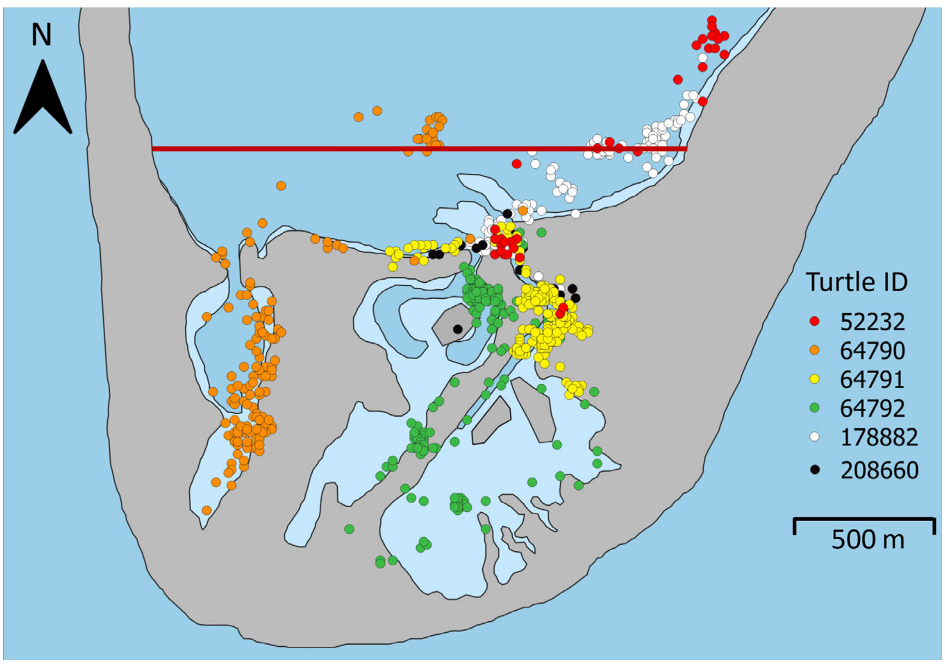

FIGURE 4 Filtered Fastloc-GPS locations after release (days 1–5) from six tracked immature turtles in 2018–2021, at Turtle Cove, Diego Garcia, Chagos Archipelago. Each coloured circle represents an individual Fastloc-GPS turtle location.

Species identification

The mean L/W ratios we calculated from captured turtles were 1.27 (SD = 0.05) for hawksbills and 1.18 (SD = 0.04) for green turtles. For turtles that we were able to measure from clear UAV images ($n = 67$), those with a L/W > 1.22 we assigned as hawksbills, and those <1.22 as green turtles (Figure 3), and on that basis we extrapolated the proportion of each species sighted in the UAV footage ($n = 257$). This L/W division assigned 203 as hawksbills. However, given the mean and SD in the measured L/W of hawksbills and assuming a normal distribution, 16% of hawksbills would be wrongly assigned as green turtles based on their L/W, that is, would have a L/W of <1.22. So, for example, if 100% of the 257 turtles were actually hawksbills, then, on average, the L/W division would be expected to wrongly identify 41 turtles as green turtles. So, it is likely that the true proportion of hawksbill turtles is closer to $(203 + 41)/257 = 95\%$. Of 169 turtles physically captured at Turtle Cove between February and August 2021, 87% were hawksbills and 13% were green turtles. We therefore assumed that the true percentage of hawksbill turtles was midway between these two estimates from the drone footage (95%) and from physical captures (87%), that is, 91% of turtles were hawksbills.

Population estimation

UAV surveys in March 2021 totaled 23.2 km in length with a field of view width of 30 m, and sea turtles were recorded on 257 occasions. Using the ratio of marked to unmarked turtles in the UAV footage, we estimated an abundance of 339 turtles (95% CI: 287–392) in Turtle Cove and population densities of between 265 turtles km^{-2} at high water and 499 turtles km^{-2} at low water. These are conservative estimates, as we only included images categorized as "certain" turtles and did not consider those categorized as "potential" or "probable" turtles. The ratio of "potential or probable" to "certain" turtles in the footage was 5.97 (86% certain and 14% potential or probable). Given the proportion of hawksbill to green turtles derived from the L/W measurements, we therefore estimated densities at high and low water of between 241 and 454 turtles km^{-2} for hawksbills and 24–45 turtles km^{-2} for green turtles.

Review of immature hawksbill population densities

Our literature search located nine studies reporting immature hawksbill densities. Developmental habitat sites with density data included those in the Western Atlantic (mainly the Gulf of Mexico and Caribbean Sea), southern Indian Ocean (Mauritius and Cocos Keeling Islands), and one site in the Western Pacific (Heron Reef). Density estimates for hawksbill turtles at Turtle Cove were higher than all other densities recorded among comparable developmental habitats across the world (Figure 5; Appendix S1: Table S1), which ranged from <0.01 to 201 turtles km^{-2}. The average density calculated from available habitat at low, mid, and high water tidal heights at Turtle Cove (343 hawksbill turtles km^{-2}) is greater than all other sites reported around the world.

DISCUSSION

By combining UAV surveys, satellite tracking data, and a mark-resight approach, we demonstrated how population abundance can be estimated and revealed an exceptionally high density of foraging turtles. This synergistic use of approaches may have wide utility across a broad range of taxa. Although UAVs are becoming a routine method for wildlife census surveys, species identification is not always straightforward. For example, Hensel et al. (2018) observed hawksbill and green turtles in the Bahamas and were not able to distinguish between these two sympatric species. Similarly, Kelaher et al. (2020) found difficulty in identifying between offshore bottlenose dolphins (*Tursiops truncatus*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*).

To address issues with species identification, we developed an objective way of distinguishing species using morphological data based on their relative width versus length. This general approach of objective species identification might have wide applicability, especially where different species can be captured and detailed morphometric measurements are taken. The similarity in the proportions of each species recorded using both physical captures and UAV, validates our species assignment and supports the use of L/W ratios in future studies that need to distinguish between sea turtle species. Further automated procedures for assessing morphology in UAV footage may have applicability, such as the use of a convolutional neural network to detect whale species in UAV footage through morphological measurements (Gray et al., 2019) and machine learning algorithms to differentiate between shark species (Butcher et al., 2021). Our measurements of captured turtles revealed morphometric differences between two sympatric species and demonstrated that the foraging site is used primarily by small immature turtles. Notably, all green turtles and most of the hawksbill turtles captured had smaller carapace length than adults measured at this study site while nesting.

Green turtles display an ontogenetic shift in diet toward herbivory at sizes greater than 30 cm CCL in benthic habitats (Burgett et al., 2018) and have a predominantly seagrass-based diet in the Western Indian Ocean (Stokes et al., 2019). For example, juvenile green turtles forage on animal matter in coastal habitats of southern Peru and then transition from a high- to low-calorie diet when they migrate north to feed on abundant vegetation (Quiñones et al., 2022). Given the lack of seagrass in Turtle Cove, green turtles might not be expected to remain in this developmental habitat for extended periods. Very few adult hawksbills have been captured in Turtle Cove, which could be linked to the niche segregation between juvenile and adult hawksbill turtles as

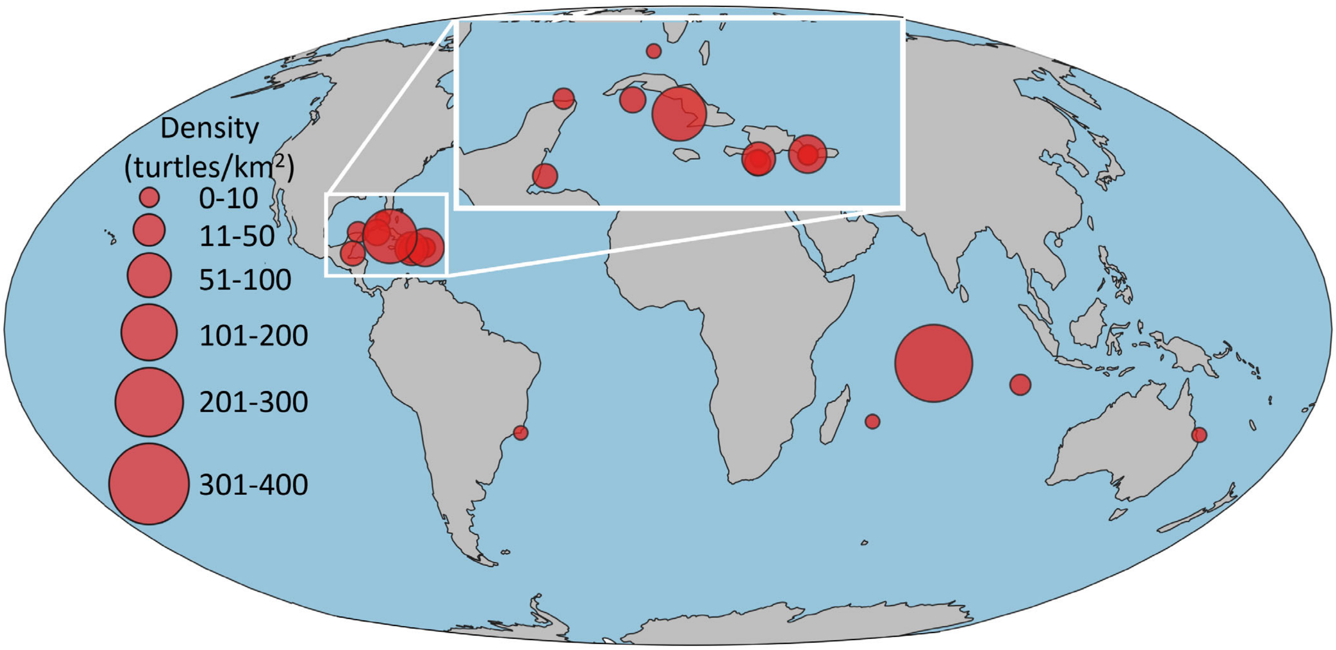

FIGURE 5 Juvenile hawksbill population densities (indicated by circle size) at development sites around the world. Where multiple densities were recorded for one site, the mean density was calculated. Source data may be found in Appendix S1: Table S1 (numbers correspond to ID numbers listed in Table S1): (1) Key West, Florida; 1.8 turtles km^{-2} (Herren et al., 2018); (2) Rio Lagartos, Mexico; 34 turtles km^{-2} (Cuevas et al., 2007); (3) Doce Leguas, Cuba; 201 turtles km^{-2} (ROC, 2000); (4) Isle of Youth, Cuba; 59 turtles km^{-2} (ROC, 2000); (5) Playa Norte, Dominican Republic; 5.6 turtles km^{-2} (Leon & Diez, 1999); (6) Bahia de las Aguilas, Dominican Republic; 6.6 turtles km^{-2} (Leon & Diez, 1999); (7) Cabo Rojo, Dominican Republic; 8.2 turtles km^{-2} (Leon & Diez, 1999); (8) Los Frailes, Dominican Republic; 58.3 turtles km^{-2} (Leon & Diez, 1999); (9) Colita, Dominican Republic; 96.8 turtles km^{-2} (Leon & Diez, 1999); (10) Mona Reef, Puerto Rico; 24.1 turtles km^{-2} (Diez & van Dam, 2002); (11) Mona cliff wall, Puerto Rico; 28.6 turtles km^{-2} (Diez & van Dam, 2002); (12) Monita cliff wall, Puerto Rico; 120 turtles km^{-2} (Diez & van Dam, 2002); (13) Glover's Reef, Belize; 53 turtles km^{-2} (Strindberg et al., 2016); (14) Arraial do Cabo, Brazil; 1×10^{-10} turtles km^{-2} (Mello-Fonseca et al., 2021); (15) Mauritius; 0.49 turtles km^{-2} (Reyne et al., 2017); (16) Diego Garcia, Chagos Archipelago; 343 turtles km^{-2} (present study); (17) Cocos Keeling; 32.5 turtles km^{-2} (Whiting et al., 2014); (18) Heron Reef, Australia; 3.3 turtles km^{-2} (Limpus, 1992).

seen at other sites, such as Príncipe Island, West Africa (Ferreira et al., 2018).

The ability to detect animals from UAV footage can be heavily influenced by the type of background over which the UAV is flown. Often, animals are a similar color to their habitat and blend in with their surroundings. For example, Chabot and Bird (2012) found that Snow Geese (*Chen caerulescens*) were easier to count as they stood out against their background compared to Canada Geese (*Branta canadensis*), which blended in. Most UAV surveys in the marine environment cover deeper, open water, and run into issues with sighting animals at depth (Bevan et al., 2016; Schofield, Papafitsoros, et al., 2017), although recent studies have found adjusting and accentuating the green colors in images during post-processing helps to detect submerged fauna (Colefax et al., 2021). Compared with other marine fauna such as dolphins, sharks, and rays, turtles have a lower probability of detection and are more difficult to classify (Colefax et al., 2019). Conducting a UAV survey over a shallow, sheltered lagoon minimized these challenges to some degree, as turtles were often visible resting on the seabed and wave action was minimal. However, in other turtle foraging habitats, such as coral reefs, it is often more difficult (especially in rough sea or turbid conditions) to distinguish between turtles and rocky or reef structures. Likewise, in the terrestrial world, the meerkat (*Suricata suricatta*) can be easily confused with bushes or rocks (Rey et al., 2017). Therefore, we classed turtle sightings as "certain," "probable," and "possible" and only included "certain" sightings in our calculations, leading to conservative estimates of turtle densities. Although machine learning algorithms are available, it is favorable to have a uniform background as increased habitat complexity has led to a decrease in detection rates, for example, detecting seals due to the presence of boulders of similar shape and size (Dujon et al., 2021). In cases of complex benthic or coastal habitats, perception and availability bias should be considered during analysis of aerial images (Fuentes et al., 2015).

Although our estimated ratios of species occurrence based on captures and UAV observations were very similar, in other cases UAV data may be biased to one species or another based on vigilance and escape reactions, or depth distribution, for example, missing animals or species at increased depths, such as rays buried or animals under structures (McIvor et al., 2022). So, we recommend validation of UAV species identifications in multispecies assemblages, as we have done using in-water captures at the same site. Similarly, it is well known that there may be sampling biases with studies across multiple taxa. For example, slowly towed plankton nets will tend to underestimate the abundance of faster moving plankton, such as fish larvae (Thayer et al., 1983), and traps often selectively catch certain species (Harvey et al., 2012). Our approach and findings show how UAV surveys, when combined with capture data, may inform future studies of foraging turtles where major knowledge gaps exist across species (Hamann et al., 2010).

Population estimates from CMR studies are often based on assumptions of immigration and emigration. Closed population models assume births, deaths, immigration, and emigration are not occurring (Dail & Madsen, 2011), whereas these assumptions are relaxed in different ways for open population models (Kendall & Bjorkland, 2001). Often, these assumptions are ignored or not met (Pollock, 1991). It is important to know what proportion of marked individuals remain in the study area and are therefore available to be recounted in the recapture/resights. Although UAVs have been used in combination with a mark-resight approach to estimate nesting turtle abundance (Dunstan et al., 2020), the added value of satellite tracking individuals to assess emigration rates has not been considered. Both UAV and tracking studies are now increasingly used across various wildlife species, including sea turtles (Hays & Hawkes, 2018; Schofield et al., 2019) and, we have shown the added benefit of performing both of these types of studies at the same site, with the tracking data enhancing the value of UAV surveys. Our finding that in the five days after release most turtles remained within the locality of the capture site accords with detailed movement analysis showing generally very small home ranges for immature turtles in the Chagos Archipelago (Hays et al., 2021). Given this benefit of knowing the proportion of marked individuals available for recapture or resighting, we advocate this use of animal tracking within mark-resighting UAV surveys across taxa and not only for sea turtle studies.

Our findings show immature hawksbill turtle densities at Turtle Cove to be higher than those reported at hawksbill developmental sites elsewhere in the world. Despite the circum-tropical distribution of hawksbill turtles (Mortimer & Donnelly, 2008), relatively few estimates of turtle density on their foraging grounds have been calculated, likely reflecting the inherent difficulties of obtaining these density estimates, but this is likely to change given the increased use of UAV surveys. For immature turtles, reported density estimates vary widely from <0.01 turtles km^{-2} in Brazil (Mello-Fonseca et al., 2021) to 201 turtles km^{-2} in Cuba (ROC, 2000). This wide variation in density might reflect several factors, such as the proximity of large nesting populations that provide a source of juveniles, the varying suitability of different habitats, or the extent of long-term protection. The importance of long-term protection is implicated in the results from Doce Leguas, Cuba, with a mean hawksbill density of 201 turtles km^{-2}, where all marine turtles have been protected since 1995 and traditional harvesting by local communities is controlled and regulated (ROC, 2000). Our findings provide further evidence that long-term protection helps drive high densities of foraging turtles, given that Turtle Cove has been well-protected for several decades (Sheppard et al., 2012). The human population on Diego Garcia is relatively small (usually less than 2000 people), and the prohibition of people entering the water at Turtle Cove is supported by regular enforcement patrols and severe fines for any unauthorized activity in the water. Our data provide evidence that restricted military sites often support high biodiversity due to the exclusion of the general population and a reduction in certain anthropogenic impacts (Zentelis & Lindenmayer, 2015). Human activity in restricted military areas is typically strictly controlled with little or no disturbance over long periods. Another example is that of Donna Nook in the Humber estuary, a military site used as a weapon and bombing range, where gray seal pups have increased in number from around 30 to almost 2000 between 1984 and 2016 (Russell et al., 2019).

Broader ecological consequences of the high densities of foraging hawksbills that we report might be expected. Experimental studies in Indonesian seagrass meadows have shown that increased rates of grazing by green turtles may increase primary productivity and biomass as well as potentially increase tolerance to high nutrient loads (Christianen et al., 2011). On the other hand, high densities of foraging green turtles have been linked to overgrazing of seagrass meadows at sites in Bermuda, North Atlantic (Fourqurean et al., 2010), the Great Barrier Reef, Australia (Scott et al., 2020), and the Lakshadweep archipelago, Indian Ocean (Gangal et al., 2021). Turtle body condition is likely to deteriorate in habitats that they have overgrazed, but the links between hawksbill turtle foraging density, grazing impacts, and body condition are yet to be identified.

Marine protected areas (MPAs) can help protect biodiversity (Sala & Giakoumi, 2018), and Diego Garcia lies at the heart of one of the world's largest MPAs, with the benefits of minimal anthropogenic impacts extending to fish stocks, coral reef health, and seabird abundance (Hays et al., 2020). We have previously shown that the numbers of nesting hawksbill and green turtles are increasing (Mortimer et al., 2020). Our findings presented here that Turtle Cove on Diego Garcia has the highest density of foraging hawksbill turtles ever reported provide further evidence of the value of long-term protection of developmental habitats.

AUTHOR CONTRIBUTIONS

Nicole Esteban and Graeme C. Hays conceived the study. Nicole Esteban, Holly J. Stokes, Jeanne A. Mortimer, and Jacques-Olivier Laloë completed the fieldwork. Holly J. Stokes led the data analysis. Holly J. Stokes, Graeme C. Hays, and Nicole Esteban led the writing with contributions from all authors.

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CONFLICT OF INTEREST STATEMENT

All authors certify that there are no conflicts of interest or competing interests to declare.

DATA AVAILABILITY STATEMENT

The uncrewed aerial vehicle survey data and turtle measurements are available from Dryad: https://doi.org/10.5061/dryad.ttdz08m1p (Stokes et al., 2022). The satellite tracking data are available from the Movebank Data Repository: https://doi.org/10.5441/001/1.r72ph75f (Hays et al., 2021) and from Dryad: https://doi.org/10.5061/dryad.ttdz08m1p (Stokes et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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