Vol. 703: 161–175, 2023
https://doi.org/10.3354/meps14225

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 12

Spatial distribution of inter-nesting green turtles from the largest Eastern Atlantic rookery and overlap with a marine protected area

Cheila Raposo[1,#,*], Julie Mestre[1,#], Rui Rebelo[2], Aissa Regalla[3], Alasdair Davies[4], Castro Barbosa[3], Ana Rita Patrício[1,5]

[1]MARE – Marine and Environmental Sciences Centre / ARNET – Aquatic Research Network, Ispa – Instituto Universitário, 1149-041, Lisboa, Portugal

[2]cE3c Centre for Ecology, Evolution and Environmental Changes & CHANGE – Global Change and Sustainability Institute, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

[3]Instituto da Biodiversidade e das Áreas Protegidas Dr. Alfredo Simão da Silva (IBAP), Av. Dom Settimio Arturro Ferrazzetta, CP 70, Bissau, Guinea-Bissau

[4]Zoological Society of London, Regent's Park, London NW1 4RY, UK

[5]Centre for Ecology & Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Penryn TR10 9EZ, UK

ABSTRACT: Understanding the spatial distribution of wildlife is fundamental to establish effective conservation measures. Tracking has been key to assess movement patterns and connectivity of sea turtles, yet some regions of great significance are largely understudied. We tracked 44 green turtles from the largest rookery in the Eastern Atlantic, on Poilão Island, Guinea-Bissau, during 2018 through 2020, to assess their inter-nesting movements, connectivity with nearby islands and fidelity to inter-nesting sites. Additionally, we investigated individual and environmental factors that may guide inter-nesting distribution and assessed the adequacy of a marine protected area to support this population during the breeding period. Green turtles had an overall home range of 124.45 km^2, mostly occupying a restricted area around Poilão Island, with 52 % of this home range falling within the no-take zone of the João Vieira-Poilão Marine National Park. Turtles exhibited strong fidelity to inter-nesting sites, likely as a strategy to save energy. Only 2 turtles performed significant excursions out of the park, and connectivity between Poilão and nearby islands within the park was limited. Larger turtles and turtles tagged later in the nesting season tended to have smaller core areas and home ranges; thus, experienced breeders may be moving less and potentially benefit from energy saving. This study highlights the importance of a marine protected area for the conservation of one of the largest green turtle breeding populations globally, and provides suggestions for further increasing its effectiveness.

KEY WORDS: Sea turtle · Inter-nesting behaviour · Breeding period · Home range · Tracking · Spatial distribution · Site fidelity · West Africa

1. INTRODUCTION

Understanding the spatial distribution of a species is key to defining areas of conflict with human activities (Tuda et al. 2014) and establishing effective conservation measures (Allen & Singh 2016, Fraser et al. 2018, Hays et al. 2019). For instance, the development of bio-logging technologies has enabled researchers to assess the spatial distribution and movement patterns of free-ranging marine spe-

*Corresponding author: cheila.raposo@gmail.com
#These authors have contributed equally to this work and share first authorship

cies (Ropert-Coudert & Wilson 2005), an essential step for the implementation of marine protected areas (MPAs; Trathan et al. 2014, Hindell et al. 2020).

Sea turtles, a group of charismatic species (Eckert & Hemphill 2005, Veríssimo et al. 2012) of great ecological value (Coleman & Williams 2002, León & Bjorndal 2002, Pawlik et al. 2018), are considered as conservation-dependent due to worldwide population declines (Mazaris et al. 2017) and ongoing threats (Rees et al. 2016), although recent years have seen the recovery of some major populations (Chaloupka et al. 2008). Historically, most conservation efforts have been focused on the nesting beaches during the breeding season (Mazaris et al. 2017) to prevent poaching of female turtles and their eggs. However, the life cycle of sea turtles mostly occurs at sea, where they are subjected to targeted illegal fishing (Riskas et al. 2018), bycatch (López-Mendilaharsu et al. 2020), boat strikes (Shimada et al. 2017), habitat destruction (Goldberg et al. 2015) and plastic pollution (Roman et al. 2021).

Nowadays, tracking studies are widely used and contribute to our understanding of how sea turtles behave while at sea (Hays & Hawkes 2018). Several tracking studies have focussed on post-breeding movements (Hays & Hawkes 2018) and on the inter-nesting habitat of female turtles (e.g. Eckert et al. 2006, Zbinden et al. 2007, Schofield et al. 2009, Godley et al. 2010, Chambault et al. 2016, Esteban et al. 2017, Hamilton et al. 2021, Shimada et al. 2021), increasing our knowledge of their ecology and population connectivity. We know that during the breeding period females nest several times and may spend several months near nesting sites, incurring energy-costly activities such as mating, oogenesis, travelling to and from the nesting beaches, crawling on land and egg-laying (Hamann et al. 2002, 2022, Chambault et al. 2016). The inter-nesting interval corresponds to the period between successive clutches being laid by a turtle during a single breeding season (Hays et al. 2002a, Price et al. 2019). In order to optimize their energy expenditure during the sequential inter-nesting intervals, green turtles *Chelonia mydas* have been shown to remain in the vicinity of nesting beaches (Waayers et al. 2011, Blanco et al. 2013, Esteban et al. 2015), resting on the seabed (Hays et al. 2000), or exhibiting assisted resting (i.e. remaining motionless at the seabed whilst aided by a structure, such as rocks; Reisser et al. 2013, Walcott et al. 2014, Fernandes et al. 2017). Sea turtles are mostly thought to fast during inter-nesting intervals (e.g. green turtles: Hamann et al. 2002, Chambault et al. 2016, Page-Karjian et al. 2020; hawksbill turtles *Eretmochelys imbricata*: Santos et al. 2010, Walcott et al. 2012, Goldberg et al. 2013; leatherback turtles *Dermochelys coriacea*: Plot et al. 2013, Asada et al. 2022). Nevertheless, at sites where food is available, inter-nesting turtles may opportunistically feed, as observed for example among leatherback (Asada et al. 2022) and green turtles (Hays et al. 2002b, Richardson et al. 2013).

Tracking studies of breeding green turtles show that they tend to have small home ranges (Blanco et al. 2013, Hart et al. 2013, 2017, Chambault et al. 2016, Snape et al. 2018, Shimada et al. 2021). Yet, larger home ranges were also found for green turtle populations in Sri Lanka (Richardson et al. 2013) and in the Mediterranean Sea (Levy et al. 2017). Overlap between home ranges and MPAs during the breeding period has been assessed for several green turtle populations worldwide (Hays et al. 2014, Revuelta et al. 2015, Hamilton et al. 2021), and tracking studies conducted during the breeding period have contributed to the designation and management of MPAs (Dawson et al. 2017).

The Bijagós Archipelago, in Guinea-Bissau, West Africa, hosts one of the largest nesting aggregations of green turtles worldwide (Catry et al. 2009, Patrício et al. 2019). Females nest on several islands of the archipelago, but the vast majority nest at Poilão Island (Catry et al. 2009). Two previous studies have shown that green turtles remain within the limits of the local MPA, the João Vieira-Poilão Marine National Park (hereafter 'JVPMNP'), during inter-nesting intervals (Godley et al. 2010, Patrício et al. 2022). However, no assessment has been made of the importance of the zones of the park — encompassing a central no-take zone and a buffer area subject to different protection measures — and no attempt has been made to explore individual and environmental aspects that may guide inter-nesting distribution.

Here, we analyse 3 years of tracking data from 59 female green turtles and evaluate their fine-scale movements during the breeding period. We assess their usage of the different zones of the JVPMNP, the fidelity to inter-nesting sites, and the connectivity between Poilão and the nearby JVPMNP islands. We explore how individual and extrinsic factors affect home ranges and core areas. This study will inform national management authorities on the suitability of the zonation of the JVPMNP for protecting this population, since this MPA was established in 2000 when no data on the inter-nesting distribution of turtles nesting at Poilão was available. It also provides novel information on the ecology of green turtles over the breeding period.

2. MATERIALS AND METHODS

2.1. Study site

Fieldwork was carried out at Poilão (10° 52′ N, 15° 43′ W; Fig. 1), an island surrounded by intertidal rocks and sandy areas, located in the southeast of the Bijagós Archipelago, Guinea-Bissau, West Africa (Fig. 1A). Together with 3 other main islands (João Vieira, Cavalos and Meio) and one islet (Cabras), Poilão is located within the JVPMNP (Fig. 1B). This MPA encompasses a central no-take zone (11 029 ha) where fishing activities are forbidden, and a peripheral zone (37 838 ha) where fishing is allowed to local residents and licensed recreational fishers using regulated equipment (Fig. 1B; see Patrício et al. 2022). With only 43 ha, Poilão hosts the largest green turtle nesting aggregation in the Bijagós Archipelago (Catry et al. 2002, 2009) and in the Eastern Atlantic (Patrício et al. 2019), with an annual average of 25 436 clutches (2013–2016; Patrício et al. 2019). Although nesting has been recorded year-round (Catry et al. 2009), a marked breeding season occurs from mid-June to mid-December, with a peak nesting activity between August and September (Catry et al. 2002). For the purpose of this study, the coastline of Poilão was divided in 4 sectors from west to east (FAR, AO, AE, CAB; see Fig. 1C). With the exception of AE, all beach sectors are characterized by the presence of a barrier of intertidal rocks.

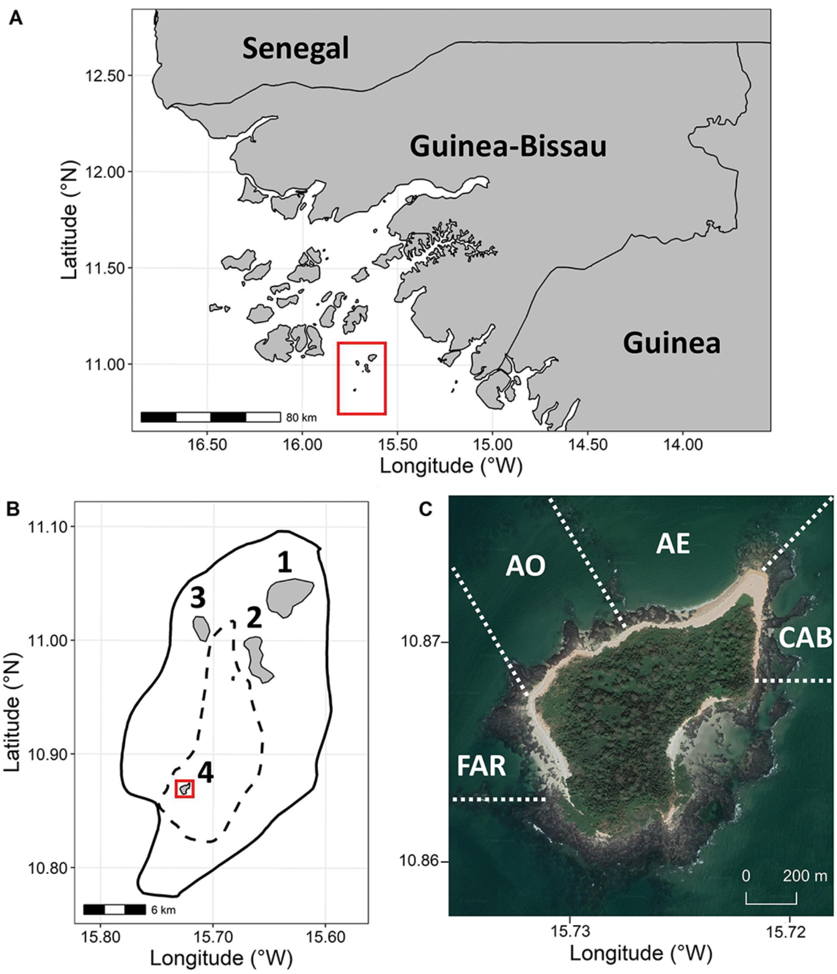

Fig. 1. (A) Location of the study area (red box) within the Bijagós Archipelago, Guinea-Bissau. (B) Close-up on the conservation areas. The peripheral solid black line and the central black dotted line depict the contours of the João Vieira-Poilão Marine National Park and the limit of the central no-take zone, respectively. The islands located within the Park are João Vieira (1), Meio (2), Cavalos (3) and Poilão (4, red box). Cabras is an islet located southwest of Meio, at the limit of the no-take zone. (C) For the purpose of this study, Poilão's coastline was divided in 4 sectors from west to east (FAR, AO, AE, CAB)

2.2. Tag deployment

Satellite and archival tags were deployed on 59 female green turtles during the 2018, 2019 and 2020 breeding seasons, between August 13 and November 8. In 2018, 20 turtles were equipped with SPOT-375B tags (99 × 55 × 21 mm, 152 g, ®Wildlife Computers), which rely on the Argos satellite system only and have an accuracy of hundreds of meters to >1 km (Thomson et al. 2017). In 2019 and 2020, FastGPS tags (F6G 376B, 115 × 64 × 43.5 mm, 220 g, ®Lotek), which provide both Argos and GPS locations (mean ± SD accuracy of fast-acquisition GPS ranging from 172.0 ± 317.5 m for a minimum of 4 satellites to 26.0 ± 19.2 m for a maximum of 8 satellites; Hazel 2009), were deployed on 9 and 15 females, respectively. In 2019, 15 additional turtles were equipped with Arribada Horizon GPS archival tags (Horizon version 3.95 × 64 × 32 mm, Arribada/Zoological Society of London), that provide GPS locations (mean ± SD horizontal accuracy: 12.05 ± 25.95 m) upon retrieval and download. SPOT-375B tags were not configured to provide haul-out data, and FastGPS and Arribada Horizon GPS tags were not fitted with a wet/dry sensor.

Tag deployment occurred after oviposition had begun, and tracking devices were deployed within 20 min. Details of tag deployment can be found in Protocol S1 in the Supplement at www.int-res.com/articles/suppl/m703p161_supp.pdf. Turtles fitted with the tracking devices were identified by their satellite tag (platform terminal transmitter, PTT) number (Table S1). Although clutch frequency can be estimated through satellite tracking (Esteban et al. 2017), we did not attempt to estimate this parameter because tags were not deployed at the beginning of the breeding season.

Uniquely numbered self-piercing tags were applied on both front flippers, and curved carapace length (hereafter 'CCL') was measured from the base of the nuchal scute to the tip of the furthest marginal scute to the nearest 1 mm using a flexible measuring tape, according to standard biometry measurement procedures (Bolten 1999). The beach sector where turtles were nesting was noted. Handling time was reduced to what was strictly necessary to minimize disturbance to turtles. All turtles maintained their nesting activity and returned safely to the sea.

2.3. Tracking data processing

The breeding period was defined as the time from tag deployment until a turtle exhibited a directed movement away from Poilão with no return. Locations corresponding to post-nesting movements were discarded from analyses. The individuals for which tags had a low frequency acquisition (ca. one location per day) or with a recording duration shorter than 4 d were excluded from the dataset. Four days was selected as the minimum recording duration because this is half the minimum inter-nesting interval reported for green turtles in Poilão (mean ± SD: 12.2 ± 1.6 d, range: 8–17 d; Catry et al. 2009), and we observed that turtles tended to reach the maximum distance from their nesting site within 4 d. The retained tracks were processed and analysed using R v3.6.1 software (R Core Team 2019).

The Argos tracking data were first filtered by removing the class Z locations, corresponding to the lowest location class provided by the Argos service (considered as error locations; Witt et al. 2010, Thomson et al. 2017). All GPS locations were obtained from at least 4 satellites. A speed filter of >5 km h^{-1} and an azimuth filter of $<20°$ were applied to all tracks using the sdafilter function from the argosfilter R package (Freitas 2012) to discard unrealistic fixes (Metcalfe et al. 2020). The McConnell speed filter (McConnell et al. 1992) was then executed with a 5 km h^{-1} threshold using the speedfilter function from the trip R package (Sumner et al. 2009, Sumner 2011), to further remove implausible locations (Patterson et al. 2010). A Kalman filter was then fitted with the crwMLE function from the crawl R package (Johnson et al. 2008, Johnson & London 2018), implementing error multiplication factors from the foiegras R package (Jonsen & Patterson 2019), to increase estimates of positioning accuracy (Patterson et al. 2010, Lopez et al. 2014). Locations were interpolated at 2 h time steps, corresponding to the mean time interval between 2 raw consecutive locations, through the crwPredict function from the crawl R package (Johnson et al. 2008, Johnson & London 2018). The original locations were not retained in the analyses (Calenge 2006).

2.4. Movement patterns, home ranges, core areas and overlap with a marine protected area

The geoDist function from the oce R package (Kelley et al. 2019) was used to calculate, for each turtle position, the distance to the previous location and the distance to the tag deployment site. The distance to the nearest point of the coastline of each island of the JVPMNP was calculated by assessing the distance between each turtle location and custom island shapefiles obtained from Google Earth, using the st_distance function (sf R package; Pebesma 2018). Bathymetry was obtained from the ETOPO1 (1-arc minute resolution) bedrock database (NOAA National Geophysical Data Center 2009) and associated to each turtle location.

For each individual, the proportion of locations falling within the protected areas of the JVPMNP was assessed and kernel utilization distributions (KUDs) were calculated, using the kernelUD function from the adehabitat R package (Calenge 2006), with a 1000 m smoothing parameter. This threshold was determined as the reference bandwidth computed by the function when including all individuals. KUDs of 50 and 95% were used to represent the core areas and home ranges, respectively (e.g. Hamilton et al. 2021).

The overall home range and core area were also assessed, as well as their overlap with the limits of the park and of the central no-take zone.

2.5. In-water site fidelity

We aimed to determine whether female green turtles use the same in-water sites over a breeding season. To do this, we divided the tracks into inter-nesting intervals by identifying or estimating haul-out events. We then estimated the overlap of home ranges and core areas between inter-nesting intervals.

We selected all turtles with location data encompassing at least 2 complete theoretical inter-nesting intervals (i.e. recording duration >24 d; mean inter-nesting intervals = 12.2 d; Catry et al. 2009), and then randomly selected 2 of those intervals for each turtle. The areas (km^2) of the 50 and 95% KUDs were assessed for each interval as well as the overlap (%) between the 2 intervals of the same turtle. The overlap was defined as the proportion of the second interval included in the first.

For a visual observation of in-water site fidelity over time, we plotted successive home ranges and core areas of 3 turtles for which we had the longest recording durations (encompassing more than 2 inter-nesting intervals) and the highest confidence on the nights of haul-out events. For these individuals, the inter-nesting intervals were clearly identified either through direct observations at the nesting beaches and/or by locations ashore or very close to shore between dusk and dawn compatible with the timing of a nesting event. For one of these turtles, we calculated the overlaps of home ranges and core areas over time, first using the estimates of the first inter-nesting interval as a reference (% of any following inter-nesting interval within the first inter-nesting interval) and then the estimates of the previous inter-nesting interval (% of inter-nesting interval 'n' in inter-nesting interval 'n−1').

2.6. Connectivity between nesting sites

We inspected tracking data for movements close to other JVPMNP islands, indicative of possible nesting events. Additionally, we assessed flipper-tag data collected between 2018 and 2020 from turtles observed nesting at Poilão and Meio islands to further evaluate potential connectivity between adjacent islands within the JVPMNP.

2.7. Statistical analysis

A multiple linear model was first used to investigate the influence of the CCL, nesting beach sector, date of tag deployment (day-of-year), recording duration and year on the extent of the KUD areas. Because not all tag types were deployed each year (in 2018, only SPOT-375B tags were deployed), we cannot disentangle the effects of year and tag type in a general model. We thus performed 2 other models to independently test the effect of these 2 variables on the extent of the 50 and 95% KUDs. We investigated the year effect for turtles equipped with FastGPS tags in 2019 and 2020. We expected a higher competition for space around nesting sites in 2020 compared to 2019, since the number of emergences was much larger in that year (79 859 vs. 9606 in 2019). We investigated the effect of the tag type in 2019, when both FastGPS and Arribada Horizon GPS tags were deployed.

The models included all individuals for which CCL measurements were available. All model prerequisites (absence of heteroscedasticity, multicollinearity and correlation) were verified, and continuous explanatory variables were centered and scaled prior to analyses. Models were backward selected with the Akaike information criterion (Akaike 1998) using the stepAIC function (Venables & Ripley 2002). The diagnostic plots of the models were visually inspected. If the model residuals were not adequate to enable model validation, outliers were discarded, and the model was fitted again. All descriptive statistics are presented as mean ± SD.

3. RESULTS

Of the 59 turtles equipped with tracking devices, 15 were excluded from spatial analyses due to tag failure or insufficient data. The remaining 44 turtles were tracked for 27.5 ± 21.5 d (range 4–82 d; Table S1); they travelled a horizontal distance of 182.7 ± 178.7 km (range <1–643.9 km), and their horizontal speed was 0.24 ± 0.16 km h^{-1} (range 0–0.65 km h^{-1}). These individuals remained within a distance of 3.5 ± 5.0 km (range <1–27 km) from their tagging sites and within 1.5 ± 0.2 km (range 0.1–18.2 km) from the coastline of any JVPMNP island, using very shallow areas ranging between 2.3 and 6.0 m deep (4.0 ± 0.9 m). Their CCL was 99.5 ± 8.8 cm (range 78.0–121.5 cm, n = 42; 2 individuals were not measured).

3.1. Distribution of turtles and overlap with a marine protected area

The inter-nesting habitats of individual turtles ranged from 4.36 to 54.06 km^2 (10.37 ± 7.96 km^2, n = 44) and 18.83 to 495.56 km^2 (79.63 ± 86.92 km^2, n = 44) for 50 and 95% KUDs, respectively (Table S1). The overall core area of turtles spanned over 10.85 km^2

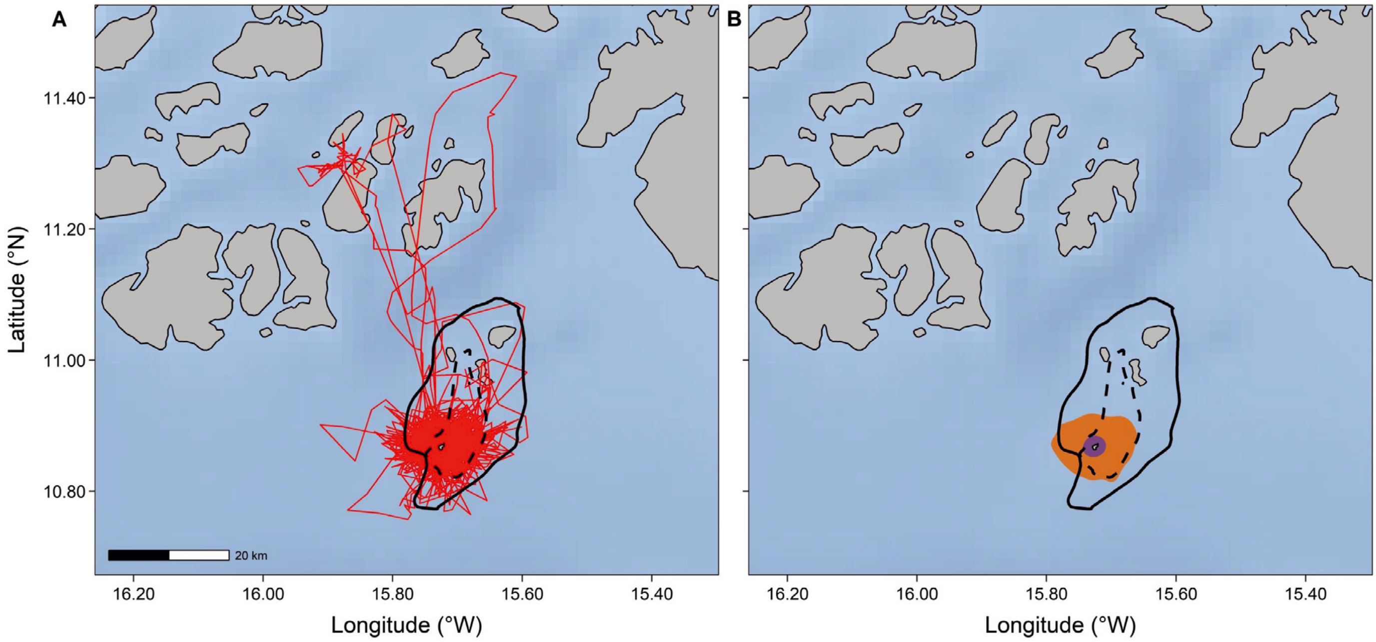

Fig. 2. Movements and estimated inter-nesting spatial distribution of 44 female green turtles tracked within the Bijagós Archipelago, Guinea Bissau, over the 2018, 2019 and 2020 breeding periods. The dotted and solid black lines represent the contours of the no-take zone and of the João Vieira-Poilão Marine National Park, respectively. (A) The red lines show the tracks of female turtles. (B) The purple and orange areas depict their overall core area (50% kernel utilization distribution) and home range (95% kernel utilization distribution), respectively

and was entirely included within the JVPMNP for the duration of the tracking periods (Fig. 2B). An expressive majority (95%) of this core area was encompassed within the central no-take zone (Fig. 2B). The overall home range of these turtles spread over 124.45 km^2 (Fig. 2B), with 88 and 52% of the 95% KUD included within the limits of the JVPMNP and of the no-take zone, respectively (Fig. 2B). Individual turtles spent a considerable amount of time within the protected area, with 96.2 ± 10% of locations within the JVPMNP and 86.5 ± 14.5% of locations within the no-take zone (Table S1, Fig. S1).

The smallest tracked turtle (PTT60897; CCL = 78 cm) swam off the limits of the JVPMNP and the farthest from Poilão, and was discarded from the general linear model explaining the 50% KUD. Another individual that travelled out of the JVPMNP was discarded from the model explaining the 95% KUD: PTT60891 (CCL = 92.5 cm).

All explanatory variables were kept during the stepwise model selection for the 50% KUD general model and explained approximately 37% of its variance (n = 41, adjusted r^2 = 0.37, $F_{8,32}$ = 3.9, $p < 0.01$). Inter-nesting core areas increased significantly with the recording duration and were significantly smaller in 2019 compared to 2018 (Tables 1 & S2). Turtle size had a marginally significant negative effect on core areas (Table 1). Lastly, core areas tended to decrease when tag deployment occurred later in the breeding season, but this effect was not significant (Table S2).

Table 1. ANOVA table from the general multiple linear model predicting the extent of the 50 and 95% kernel utilization distribution (KUDs). **Bold** indicates significant values ($p < 0.05$)

Response variable	Explanatory variable	df	SS	MS	F	p
50% KUD	CCL	1	38.75	38.75	3.23	0.08
	Nesting beach sector	3	64.51	21.50	1.79	0.17
	Date of tag deployment	1	16.45	16.45	1.37	0.25
	Recording duration	1	95.04	95.04	7.93	**<0.01**
	Year	2	160.21	80.11	6.69	**<0.01**
	Residuals	32	383.46	11.98	–	–
95% KUD	Nesting beach sector	3	6313.00	2104.50	1.58	0.21
	Date of tag deployment	1	80.00	80.30	0.06	0.81
	Recording duration	1	17949.00	17949.10	13.50	**<0.001**
	Year	2	8375.00	4187.50	3.15	0.06
	Residuals	34	45208.00	1329.60	–	–

For the 95% KUD general model, CCL was dropped during the stepwise model selection. The remaining explanatory variables explained 30% of the variance (n = 42, adjusted $r^2 = 0.30$, $F_{7,34} = 3.5$, $p < 0.01$). As with core areas, home ranges were significantly larger for longer recording durations (Tables 1 & S2). Turtles tended to display smaller home ranges in 2019 and larger ones in 2020 compared to 2018, and this effect was marginally significant (Table 1). Home ranges also tended to be smaller for late tag deployments and among turtles tagged at beach sectors surrounded by a rocky reef (all but AE; Table S2), but these effects were not significant.

In the model testing the effect of year (2019 vs. 2020), none of the explanatory variables had a significant effect on both 50% (n = 19, p = 0.15) and 95% KUDs (n = 19, all explanatory variables were dropped during the stepwise model selection).

There was no effect of tag type on 50% KUD in 2019; in fact, this variable was dropped during stepwise model selection (only CCL, date of tag deployment and recording duration were kept, explaining 34% of the variance: n = 19, adjusted $r^2 = 0.34$, $F_{3,15} = 4.2$, $p < 0.05$; Table S3). All explanatory variables were kept in the model to test tag type effect on 95% KUD in 2019, accounting for 59% of the variance (n = 19, adjusted $r^2 = 0.59$, $F_{7,11} = 4.8$, $p < 0.05$). However, tag type did not significantly affect home ranges, although there was a trend for turtles tracked with FastGPS tags to display larger homes ranges compared to turtles fitted with Arribada Horizon GPS tags (Table S4).

3.2. Inter-nesting site fidelity

At least 2 complete theoretical inter-nesting intervals (i.e. 12 d duration each) were recorded for 45.45% of the tracked turtles (range: 2–6 inter-nesting intervals per individual). These turtles showed strong fidelity to inter-nesting sites over 2 randomly selected inter-nesting intervals (Table S5). Nevertheless, inter-individual variability was noticed with 77.44 ± 15.34% and 75.01 ± 18.58% of overlap between first and later inter-nesting intervals for 50 and 95% KUDs, respectively (Table S5).

We visually depicted overlapping home ranges and core areas for 3 turtles (PTT182458, PTT182451 and PTT60887; Fig. 3) and present the detailed example of one of these turtles (PTT60887, with the longest recording duration; Table 2), for which the true inter-nesting intervals (i.e. with varying durations) were assessed relying on direct observations from the beach patrols and on the fine-scale analysis of tracking data. The 50 and 95% KUDs of the 3 to 5 inter-nesting intervals recorded for the 3 individuals had a similar extent and a high overlap (Table 2, Fig. 3).

3.3. Connectivity between nesting sites

Despite some tracked turtles performing incursions close to the islands of Meio and João Vieira (Fig. 2A), there was no clear evidence that they laid eggs in these or other nearby islands. The flipper-tag observations from 2018 to 2020, on the other hand, revealed movements between the main nesting site of Poilão and the nesting areas of Meio and João Vieira. In 2018, 20 female turtles were flipper-tagged at Meio and re-sighted at Poilão (42.55% of 47 tagged turtles), while 1 female flipper-tagged at Poilão was re-sighted at Meio (0.35% of 288 tagged females in Poilão that year; Table 3). In 2020, 11 females that were flipper-tagged at Meio (13.10% of 84 tagged) were seen nesting at Poilão, and 1 turtle flipper-tagged at Meio was seen nesting at João Vieira (1.19%; Table 3).

4. DISCUSSION

Understanding the spatial distribution of sea turtles during the breeding period is essential to the implementation of conservation measures or assessment of whether measures in place, such as MPAs, effectively support populations. We assessed the movement patterns of the largest breeding aggregation of green turtles in the Eastern Atlantic during inter-nesting intervals and the distribution of turtles according to the zonation of the JVPMNP. We found that females nesting on Poilão exhibited restricted movements around the island. They displayed strong fidelity towards their at-sea inter-nesting sites and limited connectivity to nearby islands within this MPA. The protection of this population during the breeding period can further be enhanced by increasing the no-take zone of the MPA.

4.1. Individual variation in home ranges and core areas

Female turtles tracked in this study mostly resided in overlapping and restricted inter-nesting habitats with similar extents and remained within shallow

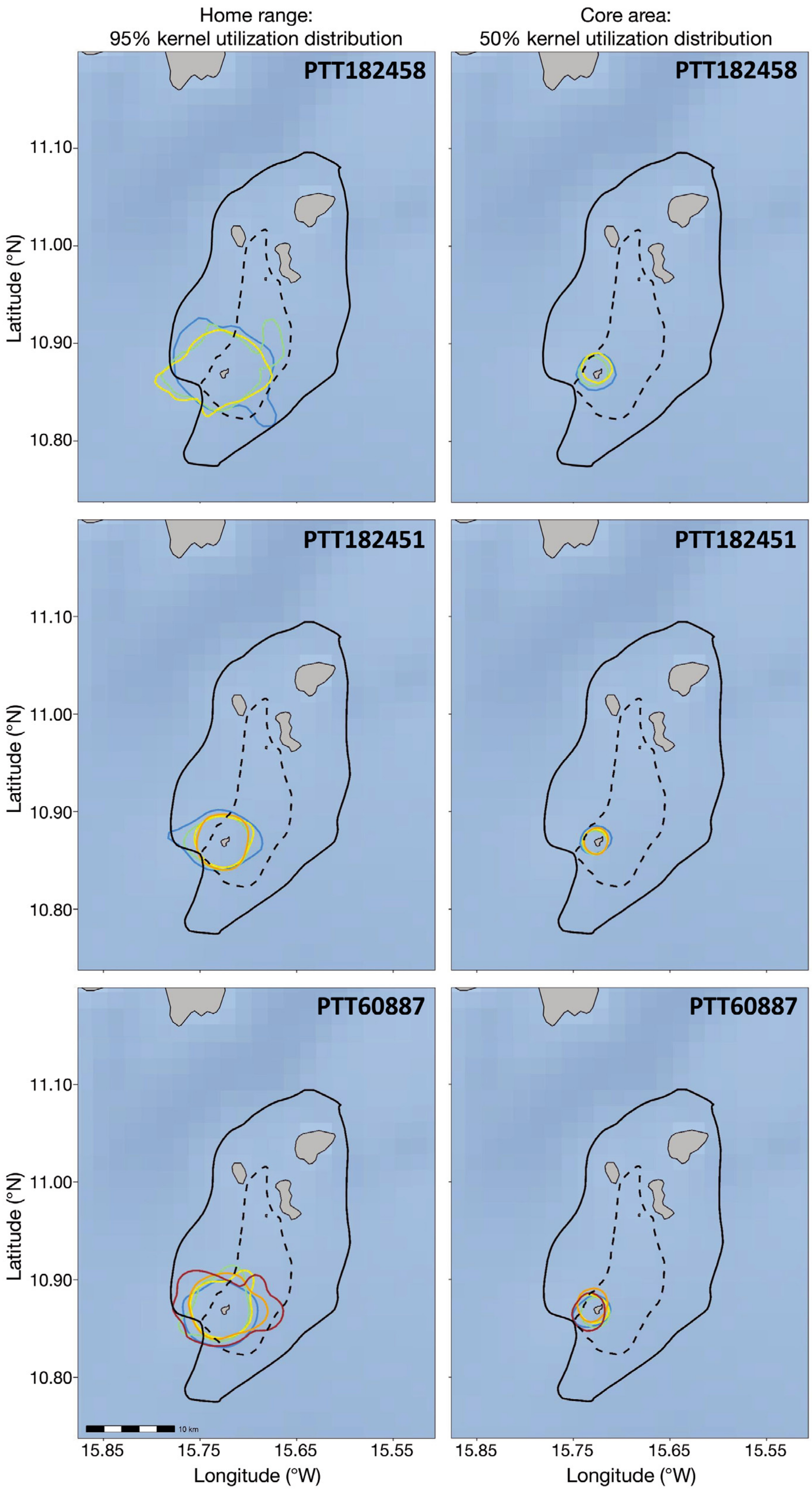

Fig. 3. Home ranges and core areas estimated over successive inter-nesting intervals for 3 female green turtles tracked within the Bijagós Archipelago, Guinea-Bissau. The dotted and solid black lines represent the contours of the no-take zone and the João Vieira-Poilão Marine National Park, respectively. Blue line: first recorded inter-nesting interval; green: second; yellow: third; orange: fourth; brown: fifth. The number of inter-nesting intervals differs among individuals

Table 2. Haul-out events (crawling/egg-laying) of a female green turtle (PTT60887). Most inter-nesting (IN) intervals were clearly identified through direct observations at the nesting beaches. Unobserved nesting attempts were estimated from tracking data if locations occurred ashore or very close to shore between dusk and dawn around the expected nesting date (i.e. corresponding to the date of the previous haul-out event plus the theoretical duration of the IN interval for this population, range: 8–17 d; Catry et al. 2009). Missing data are denoted by '–'

End date of IN intervals	Assessment of haul-out events	IN interval identifier	IN interval duration (d)	50% KUD (km^2)	95% KUD (km^2)	Overlap with 1st recorded IN interval (%)		Overlap with previous IN interval (%)	
						50% KUD	95% KUD	50% KUD	95% KUD
14/09/2018	Sat tag deployment date, laid eggs	–	–	–	–	–	–	–	–
29/09/2018	Estimated from tracking	1	14	11.54	48.69	–	–	–	–
06/10/2018	Encountered by the beach patrol, laid eggs	2	7	8.68	45.73	93.38	82.99	93.38	82.99
13/10/2018	Estimated from tracking	3	7	8.84	40.70	92.15	86.75	80.52	89.47
27/10/2018	Encountered by the beach patrol but not known if it laid eggs as it was found stranded on the rocks	4	14	10.16	48.99	74.09	79.93	77.04	77.76
06/11/2018	Encountered by the beach patrol, laid eggs	5	10	12.39	77.10	81.06	62.37	63.98	60.11

Table 3. Evidence for connectivity between nesting beaches on the João Vieira-Poilão Marine National Park islands from female green turtles flipper-tagged during the 2018, 2019 and 2020 monitoring programs within the Bijagós Archipelago, Guinea-Bissau

Year	Location of observation	Location of re-observation	Number of re-observations	Total number of flipper-tagged females
2018	Meio	Poilão	20	47
2018	Poilão	Meio	1	288
2020	Meio	Poilão	11	84
2020	Meio	João Vieira	1	84

near-shore waters. Similar to our study, restricted inter-nesting areas have been previously reported among green (e.g. Hart et al. 2013, 2017, Chambault et al. 2016, Shimada et al. 2021), loggerhead *Caretta caretta* (e.g. Schofield et al. 2010) and hawksbill (e.g. Walcott et al. 2012, Revuelta et al. 2015, Hart et al. 2019, Hamilton et al. 2021) turtles, although the use of larger areas has also been reported for green (e.g. Richardson et al. 2013, Levy et al. 2017), loggerhead (e.g. Tucker et al. 1995, Levy et al. 2017, Snape et al. 2018) and flatback *Natator depressus* (e.g. Whittock et al. 2014, 2016, Hamann et al. 2017) turtles.

Inter-individual variability exists, with larger turtles tending to display smaller core areas. It has previously been shown that smaller turtles tend to nest over larger ranges (Shimada et al. 2021), suggesting that inter-nesting ranges decrease with experience. Two turtles travelled longer distances north of the JVPMNP during the breeding period. These could potentially be newly recruited females, lacking knowledge of inter-nesting habitat availability and thus performing exploratory forays to evaluate alternative areas, or returning to known areas between clutches. These 2 animals were below the average size of nesting females from Poilão (100 cm CCL), supporting this hypothesis, as smaller individuals are presumably younger (Lockley et al. 2020, Şirin & Başkale 2021). Notably, the smallest individual travelled twice to its foraging ground (approximately 50 km away from Poilão; Patrício et al. 2022) between consecutive nesting events.

Both core areas and home ranges of turtles were smaller when tag deployment occurred later in the breeding season. Hawksbill turtles have been shown to decrease their movements along the breeding season to save energy over consecutive inter-nesting intervals (Walcott et al. 2012). Green turtles may behave similarly at the JVPMNP.

4.2. Extrinsic factors affecting home ranges and core areas

The fact that longer recording durations led to larger home ranges and core areas was likely an effect of the number of recorded inter-nesting intervals and related proportion of locations recorded at the distal points of the trips. For instance, when testing for the tag type effect in 2019, turtles fitted with Arribada Horizon GPS tended to have smaller home ranges than those equipped with FastGPS. While Arribada GPS only recorded one inter-nesting interval per individual, FastGPS tags regularly recorded more than one inter-nesting interval, increasing the probability of larger KUDs.

A year effect was detected on the extent of the inter-nesting core areas and home ranges, with females having smaller core areas in 2019 than in 2018, and slightly larger home ranges in 2020 compared to 2018. Inter-annual variability in abundance was observed for nesting turtles at Poilão, with a lower number of nests estimated for 2019 compared to 2018 and 2020 (10 116, 14 406 and 59 676, respectively; Instituto da Biodiversidade e das Áreas Protegidas, unpubl. data). In years with high densities of nesting females, the expansion of inter-nesting core areas may decrease competition for preferred resting sites (Wood et al. 2017). Yet, the fact that we did not detect a year effect when comparing only 2019 (14 406 nests) with 2020 (59 676 nests) suggests that competition for resting sites is not noticeable in the waters surrounding Poilão Island, or perhaps the difference in abundance was not sufficient to lead turtles to explore larger areas to find suitable resting sites. Alternatively, the observed year effect may potentially be influenced by the use of the Argos system in 2018, which is less accurate and can lead to larger home ranges (Thomson et al. 2017). Further deployments using the same tag type across more years may elucidate this matter. Although the accuracy and number of locations as well as the recording duration are known to influence home range estimates (Börger et al. 2006, Dujon et al. 2014, Thomson et al. 2017), we are confident that the location system (Argos and/or GPS) had a negligible effect on the extent of the inter-nesting areas assessed from different tag types and on the assessments of overlap with the local MPA. Indeed, the proportion of GPS and Argos locations falling within the JVPMNP did not differ significantly (ANOVA, $F_{2,41}$ = 2.52, p = 0.09; Table S6).

4.3. Inter-nesting site fidelity

Tracked turtles for which at least 2 inter-nesting intervals were recorded exhibited strong fidelity to inter-nesting sites. This is consistent with studies conducted on green turtles in the Red Sea (Shimada et al. 2021) and at hawksbills nesting sites in Martinique (Nivière et al. 2018) and in Barbados (Walcott et al. 2012). Turtles probably return to the same inter-nesting areas where suitable conditions are found (Hart et al. 2010, Walcott et al. 2012), avoiding expending energy exploring unknown areas. Green turtles nesting at Poilão have also been shown to display high intra-season nest-site fidelity with 65.5% of clutches being laid within 150 m of the previous one from the same turtle (n = 110; Patrício et al. 2018). If most females return to nest in the same area of the beach, it might be a good strategy to stay within the same coastal inter-nesting area. Furthermore, by remaining near the nesting beaches, females can presumably save energy for oogenesis, trips to and from the nesting beach and egg-laying (Walcott et al. 2012, Chambault et al. 2016, Hart et al. 2019). Nonetheless, other satellite tracking (e.g. Esteban et al. 2015, 2017) and flipper-tagging studies (e.g. Moncada et al. 2006) have shown that green turtles can shift their nesting sites over the course of the breeding period.

Inter-nesting area and nesting site selection among green turtles from Poilão Island can also be linked to benthic topography. We found that turtles nesting in beach sectors surrounded by a barrier of intertidal rocks tended to display smaller home ranges. Potentially, turtles crossing rocky areas to reach nesting sites may have prior knowledge of these formations, that they may use as resting sites, a behaviour known to occur among green and hawksbill turtles (Reisser et al. 2013, Walcott et al. 2014, Fernandes et al. 2017). In Brazil, a green turtle was found resting under the same rock twice (Reisser et al. 2013), suggesting that turtles can find known features, avoiding the energy costs of looking for new resting sites during each inter-nesting interval. Previous studies estimate that green turtles prefer resting depths of 10 to 20 m, where they reach neutral buoyancy (Hays et al. 2000, Hatase et al. 2006, Cheng 2009). Here, turtles used shallower depths (2.3 to 6.0 m) so assisted resting is probably the best option to save energy. Reconstructing the time-energy budget of inter-nesting females would, however, require the use of time-depth recorders (Hazel et al. 2009, Ballorain et al. 2013) and accelerometers (Hounslow et al. 2022).

4.4. Connectivity between islands

Our tracking data did not clearly indicate connectivity between Poilão and the other islands of the JVPMNP during the breeding period. High nest-site fidelity towards Poilão beaches (Patrício et al. 2018) further supports overall restricted linkages between the nesting islands, despite their close proximity.

However, connectivity between JVPMNP islands is supported by re-sightings of individuals flipper-tagged at Meio Island and later found nesting at Poilão. Connectivity between nesting sites has been reported in other nesting green and hawksbill turtle populations (Hart et al. 2013, Esteban et al. 2015, Iverson et al. 2016, Hamilton et al. 2021), a strategy that can yield evolutionary advantages and enhance overall reproductive success (Schofield et al. 2010, Hart et al. 2019, Hamilton et al. 2021), particularly if nesting beaches are subjected to variable levels of threats (e.g. sea-level rise, predation or poaching). We suggest reinforcing the beach monitoring on other islands besides Poilão to estimate the reproductive success and suitability of the MPA to enhance population resilience on each of the JVPMNP islands. Since a population may be overestimated if counts of turtles are performed independently on different islands (Esteban et al. 2017), detailed information on connectivity between islands is essential for conservation management of turtles within the JVPMNP.

4.5. Adequacy of MPA limits

We show that female green turtles spent most of the peak breeding season within the limits of the JVPMNP. These findings reinforce the value of MPAs around important sea turtle rookeries. Similar findings have been described for the Solomon Islands (Hamilton et al. 2021), Dominican Republic (Revuelta et al. 2015) and the Chagos Archipelago (Hays et al. 2014).

However, we further reveal that only 52% of the overall home range of tracked turtles fell within the central no-take zone of this MPA. We assume that the population spends half of its inter-nesting time within the peripheral zone of the JVPMNP, where turtles coexist with anthropogenic activities including recreational and artisanal fishing. Extending the no-take zone to encompass the area westwards of Poilão would reduce overlap between fishing activities and the habitat of turtles during the critical breeding period, enhancing the protection of turtles. This extension could be temporally restricted (Witt et al. 2008, Coelho Dias da Silva et al. 2010, Schofield et al. 2013, Santos et al. 2021) to the peak nesting season (August to September) if the fishing grounds immediately west of Poilão are very important for local fishers, to reduce conflict.

Additionally, despite restrictions in place, illegal fishing still occurs inside this MPA (C. Barbosa pers. comm.), perpetrated by national (38%) and foreign (62%) fishers (Catry et al. 2018), leading to turtle by-catch. We thus recommend increasing the frequency of at-sea patrolling within the waters of the park and enforcing existing regulations, particularly during the green turtle peak breeding season. Protection measures directed at female turtles will also benefit the reproductive males as a recent study shows that most males concentrate near Poilão Island during the peak breeding season (Beal et al. 2022). The risk of interaction between turtles and fishing activities outside of the peak breeding season is probably low, as both females (n = 35) and males (n = 12) migrate to foraging areas outside the PNMJVP (Beal et al. 2022, Patrício et al. 2022), suggesting that these coastal waters are not used for foraging.

Acknowledgements. We are sincerely grateful to Instituto da Biodiversidade e das Áreas Protegidas Dr. Alfredo Simão da Silva (IBAP), for permitting fieldwork and providing logistical support. We thank all fieldworkers, namely IBAP technicians and rangers, and community members from the Bijagós, who contributed to tag deployments in 2018, 2019 and 2020 as well as all people involved in the monitoring surveys of turtles. We thank Prof. Paulo Catry (MARE – Ispa), for his key role in the development of sea turtle research projects in Guinea-Bissau. This study was funded by the MAVA Foundation through the project 'Consolidation of sea turtle conservation at the Bijagós Archipelago, Guinea-Bissau'; the Regional Partnership for Coastal and Marine Conservation (PRCM), through the project 'Survie des Tortues Marines'; the 'La Caixa' Foundation (ID 100010434) through a fellowship awarded to A.R.P. (LCF/BQ/PR20/11770003); and the Fundação para a Ciência e a Tecnologia, Portugal, through a grant (UIDB/04292/2020 and UIDP/04292/2020) awarded to MARE, the project LA/P/0069/2020 granted to the Associate Laboratory ARNET, and a PhD grant (2020.08549.BD) awarded to C.R.

LITERATURE CITED

Akaike H (1998) Information theory and an extension of the maximum likelihood principle. In: Springer S, Parzen E, Tanabe K, Kitagawa G (eds) Selected papers of Hirotugu Akaike. Springer Series in Statistics. Springer, New York, NY

Allen AM, Singh NJ (2016) Linking movement ecology with wildlife management and conservation. Front Ecol Evol 3:155

Asada A, Eckert SA, Gelwick FP, Hagey WH, Davis RW (2022) Diving behavior and energetic strategy of leatherback sea turtles during internesting intervals on St. Croix, U.S. Virgin Islands. J Exp Mar Biol Ecol 550:151722

Ballorain K, Bourjea J, Ciccione S, Kato A and others (2013) Seasonal diving behaviour and feeding rhythms of green turtles at Mayotte Island. Mar Ecol Prog Ser 483: 289–302

Beal M, Catry P, Regalla A, Barbosa C and others (2022) Satellite tracking reveals sex-specific migration distance in green turtles (*Chelonia mydas*). Biol Lett 18:20220325

Blanco GS, Morreale SJ, Seminoff JA, Paladino FV, Piedra R, Spotila JR (2013) Movements and diving behavior of internesting green turtles along Pacific Costa Rica. Integr Zool 8:293–306

Bolten AB (1999) Techniques for measuring sea turtles. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group Publication, Washington, DC, p 110–114

Börger L, Franconi N, De Michelle G, Gantz A and others (2006) Effects of sampling regime on the mean and variance of home range size estimates. J Anim Ecol 75: 1393–1405

Calenge C (2006) The package 'adehabitat' for the R software: A tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Catry P, Barbosa C, Indjai B, Almeida A, Godley BJ, Vié JC (2002) First census of the green turtle at Poilão, Bijagós Archipelago, Guinea-Bissau: the most important nesting colony on the Atlantic coast of Africa. Oryx 36:400–403

Catry P, Barbosa C, Paris B, Indjai B and others (2009) Status, ecology, and conservation of sea turtles in Guinea-Bissau. Chelonian Conserv Biol 8:150–160

Catry P, Pires AJ, Barbosa C, Cordeiro JS, Tchantchalam Q, Regalla A (2018) Ameaças e Conservação. In: Catry P, Regalla A (eds) Parque Nacional Marinho João Vieira e Poilão: Biodiversidade e Conservação. IBAP - Instituto da Biodiversidade e das Áreas Protegidas, Bissau, p 359–395

Chaloupka M, Bjorndal KA, Balazs GH, Bolten AB and others (2008) Encouraging outlook for recovery of a once severely exploited marine megaherbivore. Glob Ecol Biogeogr 17:297–304

Chambault P, de Thoisy B, Kelle L, Berzins R and others (2016) Inter-nesting behavioural adjustments of green turtles to an estuarine habitat in French Guiana. Mar Ecol Prog Ser 555:235–248

Cheng IJ (2009) Changes in diving behaviour during the internesting period by green turtles. J Exp Mar Biol Ecol 381:18–24

Coelho Dias da Silva, AC, Comin de Castilhos J, Pinheiro dos Santos EA, Brondízio LS, Bugoni L (2010) Efforts to reduce sea turtle bycatch in the shrimp fishery in Northeastern Brazil through a co-management process. Ocean Coast Manage 53:570–576

Coleman FC, Williams SL (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends Ecol Evol 17:40–44

Dawson TM, Formia A, Agamboué PD, Asseko GM and others (2017) Informing marine protected area designation and management for nesting olive ridley sea turtles using satellite tracking. Front Mar Sci 4:1–12

Dujon AM, Lindstrom RT, Hays GC (2014) The accuracy of Fastloc-GPS locations and implications for animal tracking. Methods Ecol Evol 5:1162–1169

Eckert KL, Hemphill AH (2005) Sea turtles as flagships for the protection of the wider Caribbean region. Marit Stud 3(2):119–143

Eckert SA, Bagley D, Kubis S, Ehrhart L, Johnson C, Stewart K, DeFreese D (2006) Internesting and postnesting movements and foraging habitats of leatherback sea turtles (*Dermochelys coriacea*) nesting in Florida. Chelonian Conserv Biol 5:239–248

Esteban N, van Dam RP, Harrison E, Herrera A, Berkel J (2015) Green and hawksbill turtles in the Lesser Antilles demonstrate behavioural plasticity in internesting behaviour and post-nesting migration. Mar Biol 162:1153–1163

Esteban N, Mortimer JA, Hays GC (2017) How numbers of nesting sea turtles can be overestimated by nearly a factor of two. Proc Biol Sci 284:20162581

Fernandes A, Bondioli ACV, Solé M, Schiavetti A (2017) Seasonal variation in the behavior of sea turtles at a Brazilian foraging area. Chelonian Conserv Biol 16:93–102

Fraser KC, Davies KTA, Davy CM, Ford AT, Flockhart DTT, Martins EG (2018) Tracking the conservation promise of movement ecology. Front Ecol Evol 6:150

Freitas C (2012) Argosfilter: Argos locations filter. R package version 0.63. https://CRAN.R-project.org/web/packages/argosfilter/argosfilter.pdf

Godley BJ, Barbosa C, Bruford M, Broderick AC and others (2010) Unravelling migratory connectivity in marine turtles using multiple methods. J Appl Ecol 47:769–778

Goldberg DW, Leitao SAT, Godfrey MH, Lopez GG and others (2013) Ghrelin and leptin modulate the feeding behaviour of the hawksbill turtle *Eretmochelys imbricata* during nesting season. Conserv Physiol 1:cot016

Goldberg DW, Almeida DT, Tognin F, Lopez GG, Pizetta GT, Junior NOL, Sforza R (2015) Hopper dredging impacts on sea turtles on the northern coast of Rio de Janeiro state, Brazil. Mar Turtle Newsl 147:16–20

Hamann M, Limpus CJ, Whittier JM (2002) Patterns of lipid storage and mobilisation in the female green sea turtle (*Chelonia mydas*). J Comp Physiol B 172:485–493

Hamann M, Wildermann N, Williams G, Daff K, Protection H (2017) Final report on inter-nesting habitat use by flatback turtles from the Curtis Island rookery — 2013 to 2015. Produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring. https://www.gpcl.com.au/wp-content/uploads/2022/08/ERMP_InterNesting_habitat_use_by_flatback_turtles_off_the_Curtis_Island_Coast_2013-2015_CA13002463-DOCSCQPA1380400.pdf

Hamann M, Shimada T, Duce S, Foster A, To ATY, Limpus C (2022) Patterns of nesting behaviour and nesting success for green turtles at Raine Island, Australia. Endang Species Res 47:217–229

Hamilton RJ, Desbiens A, Pita J, Brown CJ and others (2021) Satellite tracking improves conservation outcomes for nesting hawksbill turtles in Solomon Islands. Biol Conserv 261:109240

Hart KM, Zawada DG, Fujisaki I, Lidz BH (2010) Inter-nesting habitat-use patterns of loggerhead sea turtles: enhancing satellite tracking with benthic mapping. Aquat Biol 11:77–90

Hart KM, Zawada DG, Fujisaki I, Lidz BH (2013) Habitat use of breeding green turtles *Chelonia mydas* tagged in Dry Tortugas National Park: making use of local and regional MPAs. Biol Conserv 161:142–154

Hart KM, Iverson AR, Benscoter AM, Fujisaki I and others (2017) Resident areas and migrations of female green turtles nesting at Buck Island Reef National Monument, St. Croix, US Virgin Islands. Endang Species Res 32:89–101

Hart KM, Iverson AR, Benscoter AM, Fujisaki I and others (2019) Satellite tracking of hawksbill turtles nesting at Buck Island Reef National Monument, US Virgin Islands: Inter-nesting and foraging period movements and migrations. Biol Conserv 229:1–13

Hatase H, Sato K, Yamaguchi M, Takahashi K, Tsukamoto K (2006) Individual variation in feeding habitat use by adult female green sea turtles (*Chelonia mydas*): Are they obligately neritic herbivores? Oecologia 149:52–64

Hays GC, Hawkes LA (2018) Satellite tracking sea turtles: Opportunities and challenges to address key questions. Front Mar Sci 5:432

Hays GC, Adams CR, Broderick AC, Godley BJ, Lucas DJ, Metcalfe JD, Prior AA (2000) The diving behaviour of green turtles at Ascension Island. Anim Behav 59: 577–586

Hays GC, Broderick AC, Glen F, Godley BJ, Houghton JDR, Metcalfe JD (2002a) Water temperature and internesting intervals for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. J Therm Biol 27:429–432

Hays GC, Glen F, Broderick AC, Godley BJ, Metcalfe JD (2002b) Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations. Mar Biol 141:985–990

Hays GC, Mortimer JA, Ierodiaconou D, Esteban N (2014) Use of long-distance migration patterns of an endangered species to inform conservation planning for the world's largest marine protected area. Conserv Biol 28: 1636–1644

Hays GC, Bailey H, Bograd SJ, Bowen WD and others (2019) Translating marine animal tracking data into conservation policy and management. Trends Ecol Evol 34: 459–473

Hazel J (2009) Evaluation of fast-acquisition GPS in stationary tests and fine-scale tracking of green turtles. J Exp Mar Biol Ecol 374:58–68

Hazel J, Lawler IR, Hamann M (2009) Diving at the shallow end: green turtle behaviour in near-shore foraging habitat. J Exp Mar Biol Ecol 371:84–92

Hindell MA, Reisinger RR, Ropert-Coudert Y, Hückstädt LA and others (2020) Tracking of marine predators to protect Southern Ocean ecosystems. Nature 580:87–92

Hounslow JL, Fossette S, Byrnes EE, Whiting SD and others (2022) Multivariate analysis of biologging data reveals the environmental determinants of diving behaviour in a marine reptile. R Soc Open Sci 9:211860

Iverson A, Hart K, Fujisaki I, Cherkiss M, Pollock C, Lundgren I, Hillis-Starr Z-M (2016) Hawksbill satellite-tracking case study: Implications for remigration interval and population estimates. Mar Turt Newsl 148.

Johnson D, London J (2018) Crawl: an R package for fitting continuous-time correlated random walk models to animal movement data. Zenodo.

Johnson DS, London JM, Lea MA, Durban JW (2008) Continuous-time correlated random walk model for animal telemetry data. Ecology 89:1208–1215

Jonsen I, Patterson T (2019) FoieGras: Fit continuous-time state-space and latent variable models for quality control of Argos satellite (and other) telemetry data and for estimating movement behaviour. R package. https://CRAN.R-project.org/package=foieGras

Kelley D, Richards C, Layton C (2019) Oce: Analysis of Oceanographic Data. R package version 1.1-1. Retrieved from https://CRAN.R-project.org/package=oce

León YM, Bjorndal KA (2002) Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. Mar Ecol Prog Ser 245:249–258

Levy Y, Keren T, Leader N, Weil G, Tchernov D, Rilov G (2017) Spatiotemporal hotspots of habitat use by loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles in the Levant basin as tools for conservation. Mar Ecol Prog Ser 575:165–179

Lockley EC, Fouda L, Correia SM, Taxonera A and others (2020) Long-term survey of sea turtles (*Caretta caretta*) reveals correlations between parasite infection, feeding ecology, reproductive success and population dynamics. Sci Rep 10:18569

Lopez R, Malarde JP, Royer F, Gaspar P (2014) Improving Argos doppler location using multiple-model Kalman filtering. IEEE Trans Geosci Remote Sens 52:4744–4755

López-Mendilaharsu M, Giffoni B, Monteiro D, Prosdocimi L and others (2020) Multiple-threats analysis for loggerhead sea turtles in the southwest Atlantic Ocean. Endang Species Res 41:183–196

Mazaris AD, Schofield G, Gkazinou C, Almpanidou V, Hays GC (2017) Global sea turtle conservation successes. Sci Adv 3:e1600730

McConnell BJ, Chambers C, Fedak MA (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarct Sci 4:393–398

Metcalfe K, Bréheret N, Bal G, Chauvet E and others (2020) Tracking foraging green turtles in the Republic of the Congo: insights into spatial ecology from a data poor region. Oryx 54:299–306

Moncada F, Abreu-Grobois FA, Muhlia-Melo A, Bell C and others (2006) Movement patterns of green turtles (*Chelonia mydas*) in Cuba and adjacent Caribbean waters inferred from flipper tag recaptures. J Herpetol 40:22–34

Nivière M, Chambault P, Pérez T, Etienne D and others (2018) Identification of marine key areas across the Caribbean to ensure the conservation of the critically endangered hawksbill turtle. Biol Conserv 223:170–180

NOAA National Geophysical Data Center (2009) ETOPO1 1 Arc-Minute Global Relief Model. NOAA National Centers for Environmental Information. https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.ngdc.mgg.dem:316 (accessed 15 May 2021)

Page-Karjian A, Chabot R, Stacy NI, Morgan AS and others (2020) Comprehensive health assessment of green turtles *Chelonia mydas* nesting in southeastern Florida, USA. Endang Species Res 42:21–35

Patrício AR, Varela MR, Barbosa C, Broderick AC and others (2018) Nest site selection repeatability of green turtles, *Chelonia mydas*, and consequences for offspring. Anim Behav 139:91–102

Patrício AR, Varela MR, Barbosa C, Broderick AC and others (2019) Climate change resilience of a globally important sea turtle nesting population. Glob Change Biol 25: 522–535

Patrício AR, Beal M, Barbosa C, Diouck D and others (2022) Green turtles highlight connectivity across a regional marine protected area network in West Africa. Front Mar Sci 9:812144

Patterson TA, McConnell BJ, Fedak MA, Bravington MV, Hindell MA (2010) Using GPS data to evaluate the accuracy of state–space methods for correction of Argos satellite telemetry error. Ecology 91:273–285

Pawlik JR, Loh TL, McMurray SE (2018) A review of bottom-up vs. top-down control of sponges on Caribbean fore-reefs: what's old, what's new, and future directions. PeerJ 6:e4343

Pebesma E (2018) Simple features for R: Standardized support for spatial vector data. R J 10:439–446

Plot V, Jenkins T, Robin JP, Fossette S, Georges JY (2013) Leatherback turtles are capital breeders: morphometric and physiological evidence from longitudinal monitoring. Physiol Biochem Zool 86:385–397

Price ER, Sotherland PR, Wallace BP, Spotila JR, Dzialowski EM (2019) Physiological determinants of the internesting interval in sea turtles: a novel 'water-limitation' hypothesis. Biol Lett 15:20190248

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rees AF, Alfaro-Shigueto J, Barata PCR, Bjorndal KA and others (2016) Are we working towards global research priorities for management and conservation of sea turtles? Endang Species Res 31:337–382

Reisser J, Proietti M, Sazima I, Kinas P, Horta P, Secchi E (2013) Feeding ecology of the green turtle (*Chelonia mydas*) at rocky reefs in western South Atlantic. Mar Biol 160:3169–3179

Revuelta O, Hawkes L, León YM, Godley BJ, Raga JA, Tomás J (2015) Evaluating the importance of Marine Protected Areas for the conservation of hawksbill turtles *Eretmochelys imbricata* nesting in the Dominican Republic. Endang Species Res 27:169–180

Richardson PB, Broderick AC, Coyne MS, Ekanayake L and others (2013) Satellite telemetry reveals behavioural plasticity in a green turtle population nesting in Sri Lanka. Mar Biol 160:1415–1426

Riskas KA, Tobin RC, Fuentes MMPB, Hamann M (2018) Evaluating the threat of IUU fishing to sea turtles in the Indian Ocean and Southeast Asia using expert elicitation. Biol Conserv 217:232–239

Roman L, Schuyler Q, Wilcox C, Hardesty BD (2021) Plastic pollution is killing marine megafauna, but how do we prioritize policies to reduce mortality? Conserv Lett 14: e12781

Ropert-Coudert Y, Wilson RP (2005) Trends and perspectives in animal-attached remote sensing. Front Ecol Environ 3:437–444

Santos AJB, Freire EMX, Bellini C, Corso G (2010) Body mass and the energy budget of gravid hawksbill turtles (*Eretmochelys imbricata*) during the nesting season. J Herpetol 44:352–359

Santos AJB, Bellini C, Santos EAP, Sales G and others (2021) Effectiveness and design of marine protected areas for migratory species of conservation concern: a case study of post-nesting hawksbill turtles in Brazil. Biol Conserv 261:109229

Schofield G, Lilley MKS, Bishop CM, Brown P and others (2009) Conservation hotspots: implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery. Endang Species Res 10:191–202

Schofield G, Hobson VJ, Lilley MKS, Katselidis KA, Bishop CM, Brown P, Hays GC (2010) Inter-annual variability in the home range of breeding turtles: implications for current and future conservation management. Biol Conserv 143:722–730

Schofield G, Scott R, Dimadi A, Fossette S and others (2013) Evidence-based marine protected area planning for a highly mobile endangered marine vertebrate. Biol Conserv 161:101–109

Shimada T, Limpus C, Jones R, Hamann M (2017) Aligning habitat use with management zoning to reduce vessel strike of sea turtles. Ocean Coast Manage 142:163–172

Shimada T, Duarte CM, Al-Suwailem AM, Tanabe LK, Meekan MG (2021) Satellite tracking reveals nesting patterns, site fidelity, and potential impacts of warming on major green turtle rookeries in the Red Sea. Front Mar Sci 8:633814

Şirin A, Başkale E (2021) Age structure of stranded loggerhead turtles (*Caretta caretta*) in Turkey. Zool Middle East 67:302–308

Snape RTE, Bradshaw PJ, Broderick AC, Fuller WJ, Stokes KL, Godley BJ (2018) Off-the-shelf GPS technology to inform marine protected areas for marine turtles. Biol Conserv 227:301–309

Sumner M (2011) The tag location problem. PhD thesis, University of Tasmania. https://eprints.utas.edu.au/12273/3/sumner.pdf

Sumner MD, Wotherspoon SJ, Hindell MA (2009) Bayesian estimation of animal movement from archival and satellite tags. PLOS ONE 4:e7324

Thomson JA, Börger L, Christianen MJA, Esteban N, Laloë JO, Hays GC (2017) Implications of location accuracy and data volume for home range estimation and fine-scale movement analysis: comparing Argos and Fastloc-GPS tracking data. Mar Biol 164:204

Trathan PN, Collins MA, Grant SM, Belchier M, Barnes DKA, Brown J, Staniland IJ (2014) The South Georgia and the South Sandwich Islands MPA: protecting a biodiverse oceanic island chain situated in the flow of the Antartic cirCumpolar Current. In: Johnson ML, Sandell J (eds) Marine managed areas and fisheries. Advances in Marine Biology, 69. Academic Press, Amsterdam, p 15–78

Tucker AD, Fitzsimmons MN, Limpus CJ (1995) Conservation implications of internesting habitat use by loggerhead turtles *Caretta caretta* in Woongarra Marine Park, Queensland, Australia. Pac Conserv Biol 2:157–166

Tuda AO, Stevens TF, Rodwell LD (2014) Resolving coastal conflicts using marine spatial planning. J Environ Manage 133:59–68

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th ed. Springer, New York, NY

Veríssimo D, Jones DA, Chaverri R, Meyer SR (2012) Jaguar *Panthera onca* predation of marine turtles: Conflict between flagship species in Tortuguero, Costa Rica. Oryx 46:340–347

Waayers DA, Smith LM, Malseed BE (2011) Inter-nesting distribution of green turtles (*Chelonia mydas*) and flatback turtles (*Natator depressus*) at the Lacepede Islands, Western Australia. J R Soc West Aust 94:359–364

Walcott J, Eckert S, Horrocks JA (2012) Tracking hawksbill sea turtles (*Eretmochelys imbricata*) during inter-nesting intervals around Barbados. Mar Biol 159:927–938

Walcott J, Eckert S, Oxenford HA, Horrocks JA (2014) Use of a towed camera system to investigate benthic habitat use by inter-nesting female hawksbill sea turtles. Endang Species Res 24:159–170

Whittock PA, Pendoley KL, Hamann M (2014) Inter-nesting distribution of flatback turtles *Natator depressus* and industrial development in Western Australia. Endang Species Res 26:25–38

Whittock PA, Pendoley KL, Hamann M (2016) Using habitat suitability models in an industrial setting: the case for internesting flatback turtles. Ecosphere 7:e01551

Witt MJ, Broderick AC, Coyne MS, Formia A and others (2008) Satellite tracking highlights difficulties in the design of effective protected areas for Critically Endangered leatherback turtles *Dermochelys coriacea* during the inter-nesting period. Oryx 42: 296–300
Witt MJ, Åkesson S, Broderick AC, Coyne MS and others (2010) Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. Anim Behav 80: 571–581
Wood LD, Brunnick B, Milton SL (2017) Home range and movement patterns of subadult hawksbill sea turtles in Southeast Florida. J Herpetol 51:58–67
Zbinden JA, Aebischer A, Margaritoulis D, Arlettaz R (2007) Insights into the management of sea turtle internesting area through satellite telemetry. Biol Conserv 137:157–162

Editorial responsibility: Graeme Hays, Burwood, Victoria, Australia
Reviewed by: M. Hamann, J.-O.Laloe and 2 anonymous referees

Submitted: August 2, 2022
Accepted: December 12, 2022
Proofs received from author(s): January 9, 2023