RESEARCH ARTICLE

Individual variation in home-range across an ocean basin and links to habitat quality and management

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Abstract

1. Overgrazing may lead to management intervention (e.g. culling, animal relocation) to try and prevent habitat destruction. Overgrazing leading to seagrass meadow collapse has been recorded for green turtles (*Chelonia mydas*) at several sites around the world, although the generality of this phenomenon and the need for intervention to prevent widespread seagrass destruction is unknown.

2. Where turtles have degraded seagrass meadows, home-ranges are expected to be large and turtles will relocate as meadows are destroyed. We used high resolution Fastloc GPS tracking ($n = 32$ individuals, mean = 171 days per individual, SD = 99) to record the home-range of adult green turtles at foraging sites spanning 4523 km of longitude across the Western Indian Ocean. Contrary to predictions if overgrazing was occurring, we recorded small home-ranges and turtles rarely relocated their daytime foraging areas.

3. Based on all locations received, the mean 50% and 95% utilisation distributions (UD50 and UD95) were 2.4 km^2 (SD = 2.7) and 15.4 km^2 (SD = 17.7). Space use was often particularly small at night, when turtles rest, averaging 11% of the overall space use with the mean night-time UD50 and UD95 being 0.15 km^2 (SD = 0.1) and 1.1 km^2 (SD = 0.8), respectively. Variation in home-range across individuals was not influenced by the data volume (number of locations per day, duration of tracking) or animal size (carapace length) but increased significantly as the distance between the centre of day and night areas increased, that is individuals that had a larger daily commute had the larger home-ranges.

4. *Synthesis and applications.* Comparisons with home-range estimates from 16 previous studies, showed that those we recorded are among the smallest for adult green turtles globally. These results suggest that despite population size increases at several major nesting sites in the Western Indian Ocean, green turtles are generally not destroying the seagrass meadows on which they forage and so management intervention to prevent overgrazing is not needed. In this way, our work illustrates how movement data may inform management decisions for green turtles. Further targeted work on the seagrass ecosystem health could help confirm this suggestion.

1 | INTRODUCTION

Understanding patterns of space use lies at the heart of understanding the ecology of species and allows informed conservation management, such as the designation of protected areas (Sequeira et al., 2019). Decades of research across taxa have shown that, at local scales, habitat quality can drive individual variation in home-range (e.g. Fryxell et al., 2004; Goldingay, 2015; van Beest et al., 2011) with good quality habitats generally leading to smaller home-ranges, that is the area in which an animal generally lives and moves. Hence it might be expected that for animals with a wide distribution, individual home-range will vary in line with regional patterns in habitat quality. However, information on how the home-range varies for individuals foraging 1000s of km apart is much more scant, due to the logistic challenges of tracking individuals foraging across such broad areas. In some cases, space use patterns may have acute conservation implications because they may indicate where animals are over-depleting their foraging areas, which can lead to management intervention, such as culling or animal relocations, to try and prevent habitat destruction and population collapse (e.g. Fischer & Lindenmayer, 2000; Robson & van Aarde, 2018).

Green turtles (*Chelonia mydas*) are a predominantly marine herbivore that are a keystone species, often feeding on seagrass and shaping seagrass ecosystems through their grazing (Christianen et al., 2023; Fourqurean et al., 2019; Gangal et al., 2021). Recently a conservation concern has been highlighted in marine environments with green turtles overgrazing and hence destroying seagrass meadows, which they then abandon (Christianen et al., 2021). However, in other cases where green turtle numbers are presumably not above the carrying capacity of the environment, individuals may maintain discrete pastures where they serially crop new seagrass growth (Gulick et al., 2021). Hence where they feed on seagrass, which includes many regions around the world (Esteban et al., 2020), there appears to be a dichotomy between areas where green turtles overgraze areas and move on, versus areas with grazing plots that are maintained indefinitely. The relative occurrence of these two scenarios is poorly resolved but might be assessed by tracking individuals and assessing their patterns of space use. Furthermore, there are growing efforts to resolve space use by green turtles as they may provide an indication of the areal extent of seagrass meadows (Esteban et al., 2018), which is often poorly known, and hence help resolve the role of seagrass meadows in carbon sequestration (Kennedy et al., 2010). Finally, space use is of interest given the growing interest in how the risk of predation might impact movement patterns (Smulders et al., 2023). For example, green turtles are threatened by shark predation and so it is expected that they alternate foraging where seagrass habitat is optimal and then resting, particularly at night (Christiansen et al., 2017), in other areas that afford better protection.

Given this broad interest in space use by foraging green turtles, we set out to use state-of-the-art, high accuracy tracking (Fastloc GPS) to examine how home-range varied between individuals foraging in different areas 1000s of km apart across an ocean basin with the hypotheses that (i) home-range should be small where habitat quality is good, (ii) switches between the core areas used should often occur in long-term tracking if animals are destroying their habitat quickly and so need to move to find new seagrass meadows, (iii) clear diel patterns in space use should be evident given importance of sheltered night-time resting areas.

2 | MATERIALS AND METHODS

2.1 | Ethical and regulatory aspects

The experimental subjects were green sea turtles (*Chelonia mydas*). All work was approved by Swansea University and Deakin University Ethics Committees and the British Indian Ocean Territory (BIOT) Administration of the UK Foreign and Commonwealth Office.

The study was endorsed through research permits (0002SE12, 0007SE15, 0002SE17, 0006SE18) from the Commissioner for BIOT and research complied with all relevant local and national legislation.

2.2 | Satellite tracking

Satellite tags were attached to nesting green turtles on the island of Diego Garcia (7.428° S, 72.458° E) within the Chagos Archipelago during October 2012, July 2015, September–October 2017, and June–July 2018 using techniques described previously (Esteban et al., 2017). We used two models of Fastloc GPS Argos tags (SPLASH10-BF, Wildlife Computers, Seattle, Washington and model F4G 291A, Sirtrack, Havelock North, New Zealand). These units receive GPS ephemeris when a turtle surfaces, then part process those data onboard before relay via the Argos system. From the received GPS ephemeris, Fastloc GPS locations are derived (Dujon et al., 2014). FastLoc GPS satellite telemetry data were screened prior to analysis to exclude locations with temporal duplicates and unrealistic movement speed (>10 km h^{-1}). Only Fastloc GPS positions obtained with a minimum of 5 satellites and with a residual error value of <35 were used. These locations are generally within a few to tens of meters of the true location (Dujon et al., 2014). We analysed only Fastloc GPS locations, as

their high accuracy allows more reliable estimates of overall space use to be determined than Argos locations (Thomson et al., 2017), which are generally accurate to within a kilometre or more of the true location (Hoenner et al., 2012). Turtles were tracked to their foraging grounds after continuous migrations in the open ocean, often over many thousands of kilometres (Hays et al., 2020). We identified their arrival at post-nesting foraging grounds when individuals travelled to localised, relatively shallow areas where they remained for many weeks or months before tags stopped relaying data. This arrival was readily apparent with the high-accuracy Fastloc GPS locations.

2.3 | Home-range estimates

Home-ranges for individual turtles were calculated for 50% and 95% probability contours (hereafter UD50 and UD95), representing core and whole home-ranges respectively, using the biased random bridge (BRB) method (Benhamou, 2011) in R version 3.5.1 (R Development Core Team, Vienna, Austria) with package adehabitatHR v0.4.18 (Calenge, 2023). The BRB method assumes an advective-diffusive movement process between locations where movement direction is biased towards preferred areas, thereby incorporating the ability for preferential selection by individuals of more attractive areas within home-ranges. By accounting for the dynamic nature of successive locations, the BRB approach provides a reliable way of estimating home-range utilisation distributions given the often serially correlated nature of location data (Benhamou, 2011). The diffusion parameter D for foraging locations was estimated using a maximum-likelihood function (Calenge, 2023), with the maximum time threshold for inclusion of path segments between successive locations set to 12h, based on the rate at which locations were obtained. Utilisation distributions were calculated over a grid of 50m cell size that covered the spatial extent of GPS locations for each individual, with this value providing a good balance between data availability and the spatial extent of locations of the foraging grounds. To conservatively account for spatial uncertainty in location data, the minimum uncertainty parameter hmin was set to 100m based on Dujon et al. (2014). We examined if the home-range estimates were influenced by the size of individuals (curve carapace length or CCL, in cm), the longitude and latitude, whether the foraging areas were on a mainland coast or an oceanic island or bank, the distance of foraging sites from the nesting beach, the length of tracking, the mean number of locations per day, the number of switches between core areas and the distance between centroids of the day and night distributions.

When the home-ranges of multiple turtles overlapped, we estimated the likely number of forage patches for this result to occur, that is if multiple turtles use the same forage patch, then the likely number of forage patches was small. We did this estimation by running 1000 iterations where each of seven individuals randomly selected a foraging site from n available foraging sites and seeing how many times three or more individuals selected the same foraging site, with n varying from 20 to 70.

2.4 | Fixed transmitter home-range

We quantified the magnitude of error expected in estimates of home-range, which are introduced by varying accuracy of Fastloc GPS locations (see Appendix S1).

2.5 | Diel variation

To examine diel variation of space use the data were segmented into day and night-time locations. The geographic centroid and middle date of locations were used to calculate solar noon and nadir for foraging locations using the R package Suncalc v0.5.1 (Thieurmel, 2022). Locations occurring ±3h from local solar noon were assigned as daytime locations and locations occurring ±3h from local midnight were assigned as night-time locations. Approximately 50% of the locations fell outside the two 6-h periods around local noon and midnight. These locations were not used in analysis of diel variation in space-use to reduce the risk of introducing crepuscular 'commuting' locations into focal area estimation.

2.6 | Cluster analysis

To objectively identify movement between clusters of night-time locations that were visually distinct in the data, we constructed a distance matrix for each pair of night-time locations for each individual for the duration of tracking. The distance matrix was then subjected to hierarchical clustering using the 'single' linkage method in R version 3.5.1 (R Development Core Team, Vienna, Austria). This method was chosen due to its sensitivity to identifying elongated clusters, which can be particularly relevant for tracking the movement patterns of marine animals. The 'single' linkage method forms clusters based on the shortest distance between any two points in different clusters. To segment the resulting dendrogram and define distinct clusters of locations, a distance threshold of 250m was applied, beyond which tracking locations were considered to belong to separate clusters. This threshold was chosen based on visual analysis of the night-time locations which were often closely clustered. Essentially this threshold allowed us to objectively define clusters which were clearly evident by visual inspection and provides an objective method for others to reproduce our analysis. To ensure that distinct clusters were retained for further analysis, clusters with six or more Fastloc GPS locations were selected. Switches between clusters of locations were then quantified for the duration of tracking, that is where new clusters of locations emerged generally >1km from the original cluster.

2.7 | Published estimates of green turtle foraging ground home-range

A literature search was conducted (April 2023) using Web of Science (https://www.webofscience.com) using the search term: ALL=("green turtle*" OR "Chelonia mydas"), AND ALL=("space use" OR "home-range"). We then used Google Scholar to do both forward and backward citation searches of the results and worked through each article for reported home-ranges of adult female green turtles excluding results for males, immatures or turtles of unknown sex.

2.8 | Software

Analysis were run in R version 3.5.1 (R Development Core Team, Vienna, Austria) or in Minitab 8.2 Extended using the function "step" (https://www.minitab.com/en-us/).

3 | RESULTS

3.1 | Foraging site locations

A total of 5472 days of tracking data and 33,559 locations were obtained on the foraging grounds from 32 individuals, with the mean number of 171 tracking days per individual ($n=32$, SD=99, range=37–537 days) (Hays et al., 2024). These 32 individuals had been tracked from their nesting beaches on Diego Garcia to foraging sites in Kenya, Somalia, Mozambique, the Seychelles, the Maldives, Madagascar and the Chagos Archipelago, a longitudinal range spanning 4253 km and a latitudinal range spanning 2904 km (Figure 1). The mean number of daily locations was 6.1 ($n=32$, SD=3.1) and was not linked to duration of tracking, that is individuals that were tracked for longer did not provide fewer locations per day ($F_{1,30}=0.02$, $p=0.88$).

3.2 | Switches between core areas

Occasionally turtles relocated, particularly their night focal areas. These switches between core areas were readily evident both when locations were mapped and also in a plot of distance of each location from the first location versus time (Figure 2), that is there were no examples where a turtle relocated to a new foraging area, but that foraging area was relatively equidistant to the start point and so not evident in the distance from the first location. Such switches of core night-time clusters were relatively rare. For example, across 32 individuals the modal number of night-time clusters was one and the number of individuals using two, three or four clusters was nine, six and two individuals, respectively (mean 1.75 clusters, range 1–4, SD=0.88). All switches between core areas were to sites within a few kilometres of the original location and in some cases the animal returned to the original location sometime later (Figure 2b). In other words, while some individuals occupied the same night-time focal sites throughout tracking, others relocated between a number of distinct sites within a few kilometres of each other (Figure 2). In contrast, day locations generally
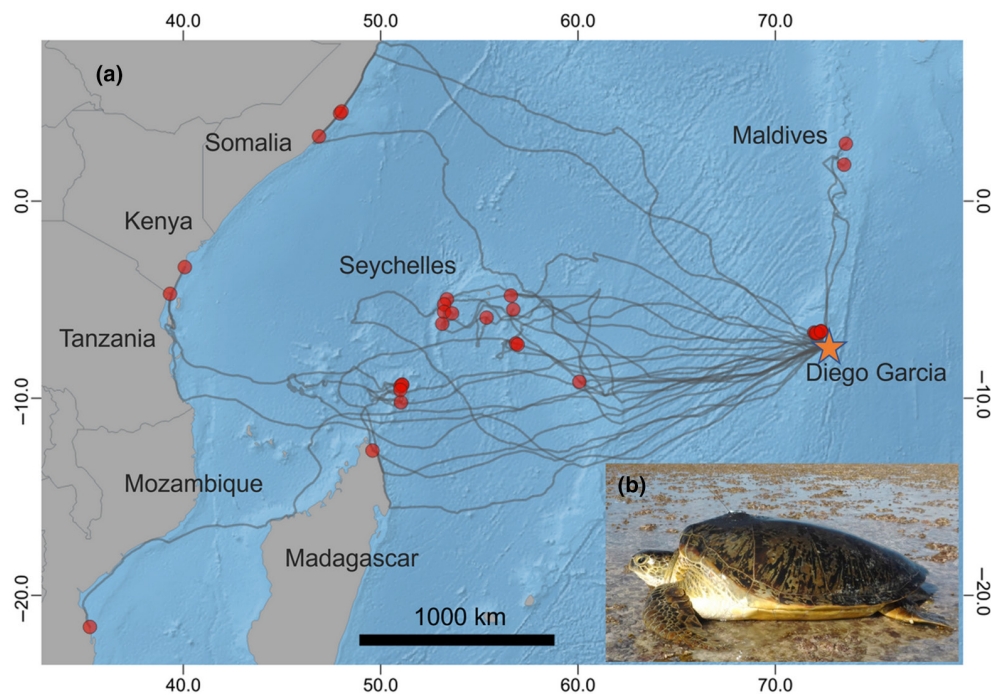
FIGURE 1 (a) The location of the foraging sites for 32 tracked green turtles indicated by closed red circles. Migration tracks from the nesting beach on Diego Garcia Atoll (orange star) are shown in grey. (b) A nesting green turtle equipped with a Fastloc GPS Argos tag on the nesting beach in the Chagos Archipelago.
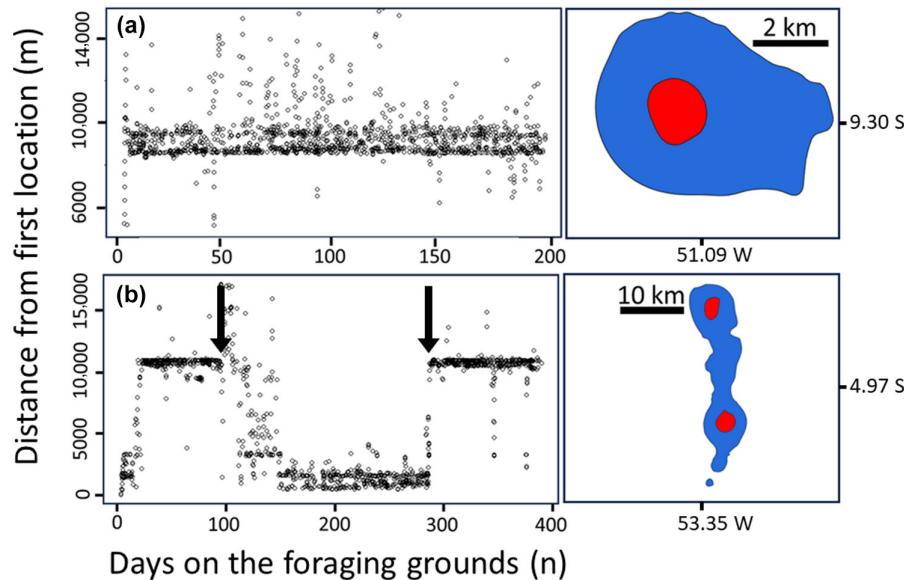
FIGURE 2 (a) An example of an individual that used one focal foraging area throughout tracking. This individual was foraging in the Farquhar Islands (Seychelles) with tracking data on the foraging grounds across 232 days. (b) An example of an individual that relocated a few kilometres. This individual was foraging on the Amirante Bank (Seychelles) and was tracked for 380 days. Indicated with arrows are the times when turtles switched to a new focal site and then returned to the original site a few months later, evident both when maps of locations were examined but also when the distance of locations from the start point was plotted versus time. Distance is the linear distance of locations from the first location. Red and blue colour indicate the 50% and 95% utilisation distribution, respectively.

did not occur in readily discernible clusters but were distributed more evenly across the foraging grounds. A notable exception were foraging areas on the south-eastern edge of the Great Chagos Bank where day foraging locations showed distinct clustering for two of the seven individuals at this site, although clusters were always close (within a few kilometres) of each other (see Figure 3c).

3.3 | Diel patterns of space-use

The mean UD50 and UD95 using all locations per individual, were 2.4 km² (n = 32 individuals, SD = 2.7) and 15.4 km² (n = 32 individuals, SD = 17.7), respectively. Individual home-ranges were entered into a step-wise multiple regression with the size of individuals (CCL in cm), the longitude and latitude at the centre of the foraging area, whether the foraging areas were on a mainland coast or an oceanic island or bank, the distance of foraging sites from the nesting beach, the length of tracking, the mean number of locations per day, the number of switches of core areas and the distance between centroids of the day and night distributions. The only factors significant enough to be included in the final equation were the distance between the day and night locations (Figure 3) and the number of switches between core areas. Often turtles occupied distinct areas in the day versus night, with a daily commute between these two areas. The distance between the centre of the area used during the day and the corresponding night-time area averaged 1.57 km (SD = 1.18, range = 0.08–4.03 km). As this commuting distance between the day and night locations increased, so did the overall space use (Figure 3a), with

this distance explaining 40% and 28% of the variation in UD50 and UD95 respectively (for the UD50, $F_{1,30} = 20.1$, $r^2 = 0.40$, $p < 0.001$ and for the UD95, $F_{1,30} = 11.9$, $r^2 = 0.28$, $p = 0.002$). Further, the number of distinct night-time clusters that were used explained 9.2% and 13.2% respectively of the residual variation in the UD50 and UD95.

The night-time home-ranges were typically relatively small (mean UD50 = 0.15 km², SD = 0.14; mean UD95 = 1.1 km², SD = 0.8). These night-time home-ranges were significantly smaller than the overall home-range, both for the UD50 (means 0.15 and 2.41 km² respectively, $t_{31} = 4.73$, $p < 0.001$) as well as for the UD95 (means 1.1 and 15.4 km² respectively, $t_{31} = 4.56$, $p < 0.001$), that is the night-time home-range was around 11% of the overall home-range. Night-time home-ranges were also significantly smaller than day-time home-ranges (UD50, means 0.15 and 1.66 km² respectively, $t_{31} = 3.54$, $p < 0.01$; UD95, means 1.1 and 12.12 km² respectively, $t_{31} = 3.81$, $p < 0.001$). For smaller home ranges, where individuals had a smaller daily commute between day and night-time focal areas, home ranges (day and night) tended to overlap. that is night-time UDs were located within day-time UDs. Where diel commuting distances were longer, for example those on the south-east Great Chagos Bank, day and night-time home ranges were distinct from one another. For a fixed transmitter, that is where any movement between locations was simply due to location inaccuracies, we calculated the UD95 as 0.249 km² and the UD50 as 0.056 km². In other words, the vast majority (>98%) of the calculated overall home-ranges for green turtles were likely due to animal movements rather than location errors. The calculated night-time home-ranges of some individuals were similar or even less than this calculated home-range for a fixed transmitter (Figure 4).
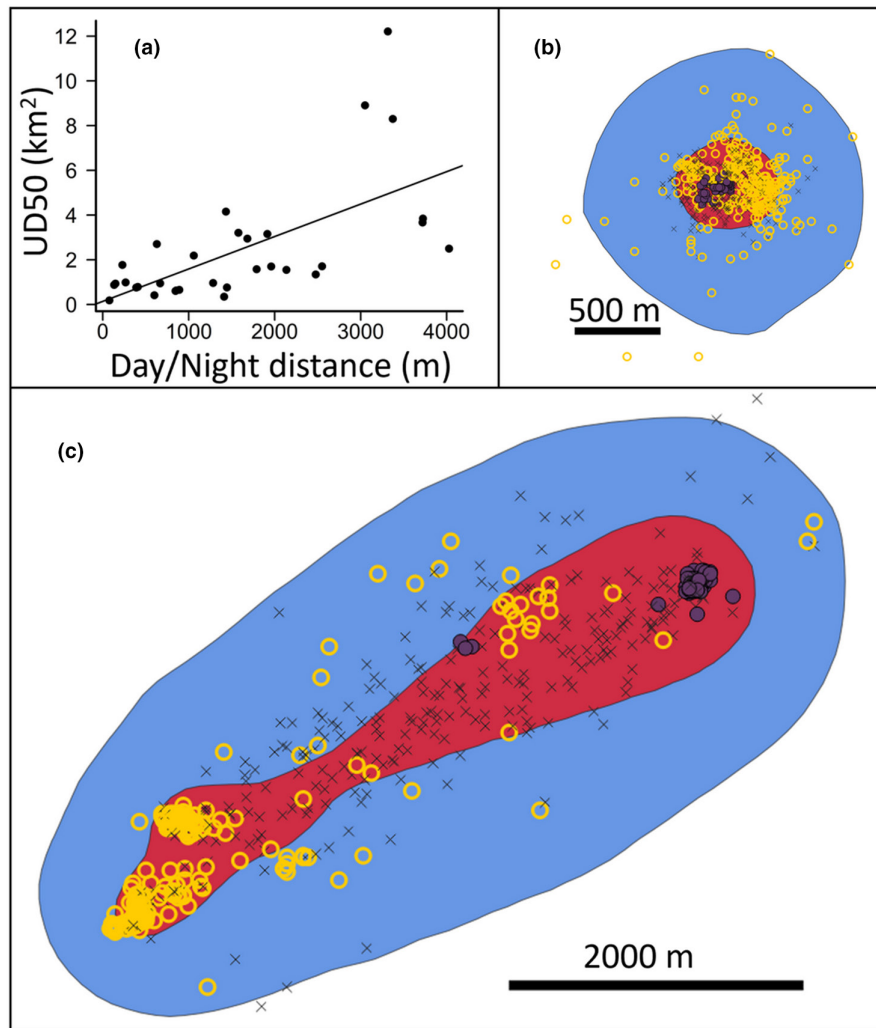
FIGURE 3 (a) The relationships between both the UD50 and the distance between the centroids of the day and night distributions. For the UD50, $F_{1,30} = 20.1$, $r^2 = 0.40$, $p < 0.001$ and for the UD95, $F_{1,30} = 11.9$, $r^2 = 0.28$, $p = 0.002$. The number of distinct night-time clusters that were used explained 9.2% and 13.2%, respectively of the residual variation in the UD50 and UD95. (b) An example of a relatively short distance between the day and night locations, for an individual foraging in the Maldives tracked for 103 days (226 day-time locations, 352 night-time locations and 603 transition locations). (c) An example of a relatively long distance between the day and night locations for an individual tracked for 537 days foraging on the Great Chagos Bank (565 day-time locations, 359 night-time locations and 1036 transition locations). Yellow open circles show daytime locations 3 h before and after local noon, and dark closed circles show night-time resting locations 3 h before and after local midnight. Crosses indicate locations from other times that were not included in analysis of diel variation in home range. Red and blue shaded areas show respectively the UD50 and UD95 for each individual for the duration of tracking. UD, utilisation distribution.

3.4 | Co-occupancy of the same area by different turtles

Although turtles travelled from Diego Garcia to foraging sites spread across the Western Indian Ocean, some individuals travelled to the same foraging areas and their home-ranges overlapped. Of 32 tracked individuals, three of seven turtles tracked to the Great Chagos Bank overlapped in their home-range, as did also three turtles on the Amirantes Bank (Seychelles). We estimated the probability of three of seven turtles using the same forage patch depending on how many total available forage patches there were (Figure 5). These calculations show that there is only a relatively high ($p > 0.05$)
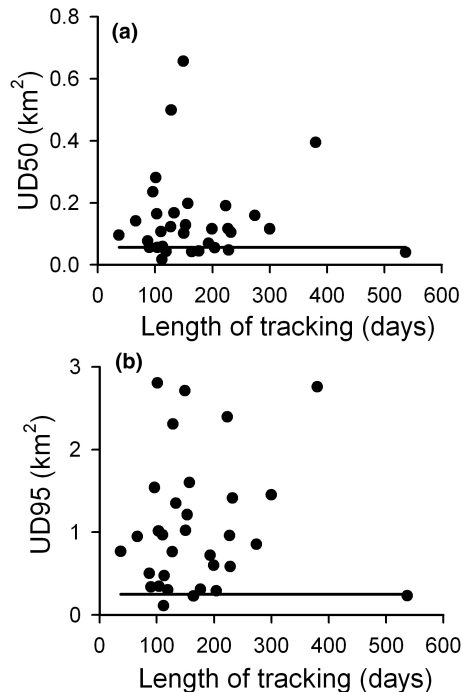
probability of three of seven turtles using the same area if the total number of forage patches was <50. If the number of forage patches is >50, then the probability of three of seven turtles using the same area is increasingly very small ($p < 0.05$).

## 3.5 | Literature values on home-range of adult green turtles

We located 14 published studies that reported foraging home-range estimates for adult female green turtles. Tagging locations were predominantly located in the Gulf of Mexico/Caribbean Sea and the

Western Pacific, with sites also located in the central Pacific and east Atlantic Oceans, Red Sea, Mediterranean Sea, Persian Gulf, Indian Ocean and South China Sea. Home-range estimates were derived from acoustic ($n=2$ studies and 14 individuals), Argos satellite ($n=10$ studies and 131 individuals) and FastGPS satellite tags ($n=2$ studies and 42 individuals). Across studies, home-range estimates tended to be highest for Argos tracking and lowest for Fastloc GPS tracking. Mean values of reported home-ranges (UD95) for acoustic, Argos and Fastloc GPS methods were: were 4.7 km^2 (SD $=1.4$, range $=3.15$–5.86 km^2), 349 km^2 (SD $=370.1$, range $=5.1$–1348.7 km^2) and 46 km^2 (SD $=51$, range $=5.7$–193.9 km^2) respectively. Comparatively, the mean home-range estimates of 15.4 km^2 (SD $=17.7$, range $=1.7$–79.2 km^2) found in this study were among the smallest reported for adult green turtles (Figure 6).

4 | DISCUSSION

We recorded the space use by green turtles across the Western Indian Ocean, which is a region where they feed primarily on seagrass (Stokes et al., 2019). Consequently, their space use while foraging is likely closely linked to the quality of seagrass meadows, with turtles using smaller areas where the quality of seagrass is higher. Our key findings were that green turtles used relatively small areas regardless of where their foraging sites were located across the Western Indian Ocean and that the commute distance between the day and night areas had the strongest influence on the overall home-range for each individual. These generally small foraging areas, point to broadly high-quality seagrass foraging environments throughout the region. Our conclusions are directly relevant to adult females but further work might target space use in adult males.

We found that turtles maintained fidelity to focal foraging and resting sites with only occasional switches between core areas of a few kilometres. It has been described how hard-shelled sea turtles (e.g. green turtles, hawksbills (*Eretmochelys imbricata*) and loggerheads (*Caretta caretta*)) often have fidelity to particular foraging sites across many years and perhaps even their entire adult lives (Shimada et al., 2020). However, where there is severe loss of habitat, for example associated with environmental pertubations, then individuals may relocate to new sites (Shimada et al., 2020). In this context, it has been reported that where green turtles occur at very high density as a result of population recovery, they may denude seagrass meadows and then move to new areas (Gangal et al., 2021). With this scenario, we might expect to see long

FIGURE 4 For (a) UD50 and (b) UD95, the night-time space use versus the length of tracking on the foraging grounds. Points represent space use in the night-time focal areas of individual turtles estimated over the full duration of tracking. The horizontal lines reflect the calculated space use values assuming a transmitter never moved. These plots suggest that several individuals moved very little at night, that is resting in almost exactly the same spot night after night across many months. UD, utilisation distribution.
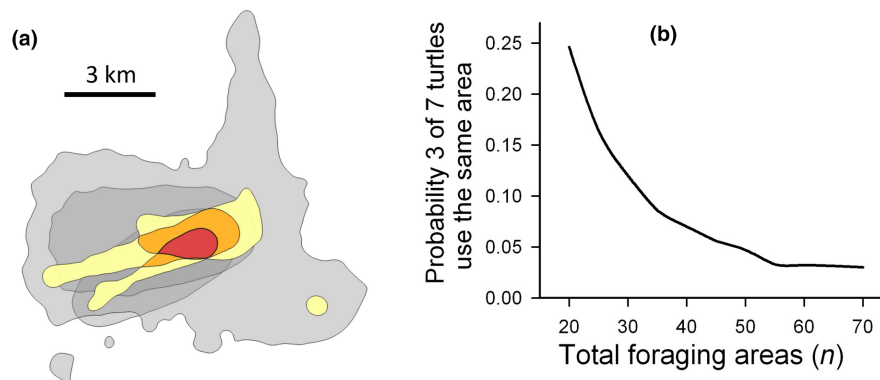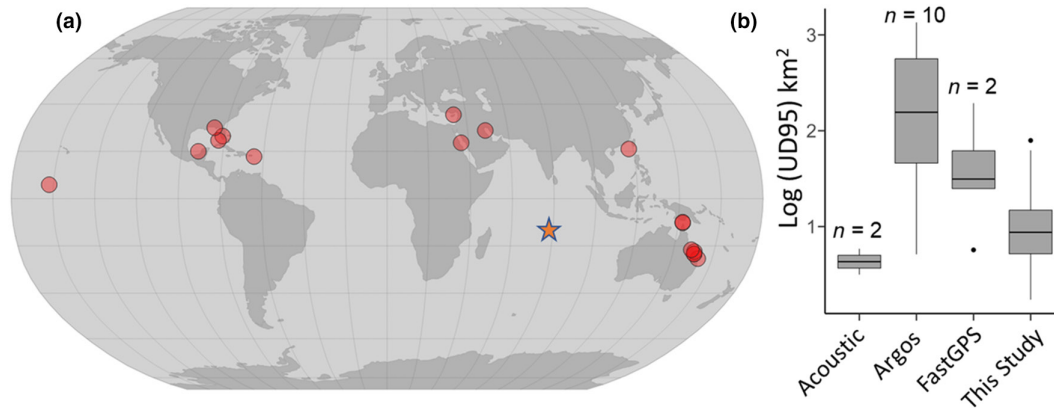

FIGURE 5 (a) An example of overlapping home-ranges of 3 turtles foraging on the Great Chagos Bank. Home-ranges are represented in grey with darker tones representing areas of overlap. Core home-ranges are in yellow (no overlap), orange (2 overlapping core home- ranges) and red (3 overlapping core home-ranges). (b) The probability that three of seven tracked turtles would use the same foraging area, given different numbers of suitable foraging areas.

FIGURE 6 (a) Locations of tag attachments for each of the different studies. The tag attachment location of the current study is indicated by an orange star. (b) Mean home-range estimates for studies using acoustic (e.g. Pillans et al., 2021; Whiting & Miller, 1998), Argos tracking (e.g. Attum et al., 2014; Broderick et al., 2007; Fujisaki et al., 2016; Hart et al., 2017; Lamont et al., 2023; Naro-Maciel et al., 2018; Ng et al., 2018; Rees et al., 2013; Sloan et al., 2022; Uribe-Martínez et al., 2021) and Fastloc GPS techniques (e.g. Gredzens et al., 2014; Shimada, Jones, Limpus, Groom, et al., 2016). Number of studies included for each technique is indicated in plot.

switches between core areas for many turtles. However, this was not the case, even when individuals were tracked for >1 year on their foraging grounds. This evidence might suggest that broadly across the Western Indian Ocean, green turtles are not exceeding the carrying capacity of seagrass meadows. This conclusion is supported by the generally small foraging areas used by green turtles in the Western Indian Ocean when compared to other regions where turtles have been GPS tracked, with these small areas suggestive of relatively high-quality food patches. While there have been population recoveries of green turtles in the Chagos Archipelago and elsewhere in the Western Indian Ocean (Mortimer et al., 2020; Pritchard et al., 2022), our finding of generally fixed, small home-ranges suggests that these recoveries are presumably still insufficient for turtles to be overexploiting seagrass generally in the region although over-exploitation of seagrass may be occurring elsewhere outside of the Western Indian Ocean such as the Lakshadsweep Archipelago (Gangal et al., 2021). In this context, the potential indirect benefit of continued tracking of green turtles is evident. If turtles' space-use is linked to seagrass quality, then if seagrass meadows become denuded through over-grazing it might be predicted that the space-use of individual turtles will increase as they need to search a wider area to find sufficient food. The pattern of movement that we occasionally observed where a turtle relocated to a site a few km from original and then subsequently relocated back to the original site a few weeks or months later, might represent an extension of the serial cropping of discrete seagrass meadows previously observed (Gulick et al., 2021). In these cases, turtles might have a good cognitive map of their local area and serially crop several available seagrass patches within that local area.

Night-time space use by turtles was only a small fraction of their overall space use. It has been described before how green turtles may have diel patterns of space use (e.g. Christiansen et al., 2017; Seminoff & Jones, 2006) and that green turtles tend to rest at night (e.g. Hart et al., 2016; Hays et al., 2000; MacDonald

et al., 2013). The most pragmatic explanation for the diel patterns of space use is that the habitat required for daytime foraging (i.e. seagrass meadows) is different to the optimum habitat for resting, which is likely to be areas with shelter or cover (e.g. caves, rocks, gullies, etc). Indeed direct observations at sites around the world have described resting by turtles on the seabed and also "assisted resting", where a turtle is wedged into coral reef or other structures (Houghton et al., 2003; Stimmelmayr et al., 2010). Interestingly when we built in considerations of location inaccuracy, the implication is that at night-time some individuals were returning to almost the exact same spot night after night and barely moving at all in their night-time locations, that is tiny areas were often used by green turtles at night. In such cases, highly desirable resting sites were clearly not ubiquitous, since turtles maintained fidelity to tiny night-time sites for long periods. The importance of a suitable night-time resting areas was evident in the fact that turtles might commute on average 1.6 km between their day and night areas. Given typical swim speed of foraging green turtles of around 1 km h^{-1} (e.g. Shimada, Jones, Limpus, & Hamann, 2016), the daily commute time between the centre of the day and night areas could take 1–2 h each way or 3–4 h per day. This represents a sizeable fraction of the daily time-budget. The implication is that the selection of the best night-time resting spots is important for green turtles, regardless of whether this increases their daily commute time and hence their time available for feeding. This finding adds to the growing evidence of the importance of safe resting areas and more generally for the important role of the risk of predation in shaping animal movements, not just with sea turtles (e.g. Christianen et al., 2023; Heithaus et al., 2007) but more broadly across marine taxa (Lubitz et al., 2022).

Location accuracy will influence calculated space use (Thomson et al., 2017). Put simply, it is expected that where individual locations are highly inaccurate, then large home-ranges will tend to be calculated since more of the apparent movement is simply location inaccuracies. This issue will exist across tracking technologies, but

with high-accuracy Fastloc GPS tracking we expect any artefacts of location accuracy to be considerably less than with low accuracy tracking, for example Argos. This prediction was supported by our comparison of adult green turtle home-ranges reported across studies, with Argos tracking studies tending to provide much higher home-range estimates, than those studies using Fastloc GPS or acoustic tracking. This finding has important implications for trying to resolve differences in home-range across studies. Furthermore, in some cases acoustic tracking may underestimate home-range if studies are short-term (e.g. Whiting & Miller, 1998) or animals are only detected when close to receivers so that their longer distance movements are not recorded. Hence GPS tracking likely provide the most reliable, long-term indication of space-use by sea turtles. It is noteworthy that our calculated home-ranges are less than those calculated at almost all the sites where Fastloc GPS has been used previously with adult green turtles (Gredzens et al., 2014; Shimada, Jones, Limpus, Groom, et al., 2016), which again points to high-quality habitat in the Western Indian Ocean. Where the budget is restrictive and newer technologies such as GPS are not affordable or where different satellite systems and tag models are used over time, then approaches such as state space modelling might help to accommodate the different location accuracies of different technologies.

In our study, satellite tags typically provided several locations per day for extended periods. In other studies it has been shown that the data volume (e.g. number of locations or length or tracking) can influence home-range estimates (Börger et al., 2006). However, this was not the case in our study, presumably because any impacts of data volume were overshadowed by other factors such as the daily commuting distance between night and day locations. Nevertheless, data volume should be considered as a covariate when assessing potential drivers of home-range size in other studies (Börger et al., 2006).

It is noteworthy that several turtles could overlap in their space use in some regions. It is well-known that many green turtles may forage in a single area of seagrass (e.g. Gangal et al., 2021). The implications of our findings are that in those areas of space-use overlap, there is likely to be relatively less seagrass. For example, while the Great Chagos Bank covers 12,642 km^2, we estimate that there are likely 50 or fewer seagrass meadows in that area given that three of seven green turtles tracked to that region had overlapping home-ranges, that is there might not be a huge number of suitable forage patches (i.e. seagrass meadows) on the Great Chagos Bank. This conclusion may explain both why only seven of 32 tracked turtles travelled to the Great Chagos Bank, even though it is relatively close to the nesting areas (<100 km distant), as well as why many individuals travelled to foraging sites several 1000 km from the nesting beaches. In this way, green turtle movements and space use might be used to refine estimates of the location of seagrass meadows across ocean basins, which remain poorly resolved (McKenzie et al., 2020). Looking forward, repeating studies tracking green turtles over long periods, might reveal changes in space use patterns linked to loss of seagrass habitat. We note also that we only tracked a tiny proportion of the nesting turtles. For example, we tracked 32 individuals but there are thought to be >20,000 green turtle nests annually on the Chagos Archipelago (Mortimer et al., 2020). Hence our tracking data-set will not capture the total number of green turtles that use the same forage areas.

Our key conclusions from long-term, high-resolution tracking of green turtles are that (i) small home-ranges likely point to generally high quality seagrass forage habitat across the Western Indian Ocean; (ii) generally small night-time space use suggests that turtles may often rest in exactly the same spot night after-night, likely to reduce predation threat; (iii) high overlap in space use by green turtles in some areas (e.g. the Great Chagos Bank) likely points to relatively few seagrass meadows in those areas. Our findings suggest that generally across the Western Indian Ocean, green turtles are likely not destroying the seagrass meadows on which they forage and hence management intervention to prevent overgrazing is not yet needed. Our work illustrates how high-accuracy tracking from Fastloc-GPS and the resulting clear picture on home-range movements, can help inform about the likely habitat of sea turtles and whether management intervention is needed to prevent overgrazing. Further targeted work on the seagrass beds identified as green turtle forage sites, could help confirm the inferences of habitat quality made from tracking data.

AUTHOR CONTRIBUTIONS

Study design: Graeme C. Hays, Nicole Esteban. *Field work*: Graeme C. Hays, Nicole Esteban. *Statistical analyses*: Alex Rattray, Takahiro Shimada, Graeme C. Hays. *Writing and revision*: Graeme C. Hays, Nicole Esteban, Alex Rattray, Takahiro Shimada. *Statement on inclusion*: Our study brings together authors from a number of different countries, including scientists based in the country where the study was carried out (UK). All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset. Whenever relevant, literature published by scientists from the region was cited.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

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SUPPORTING INFORMATION

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

Appendix S1. Supplementary Materials and Methods. Fixed transmitter home-range.

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