Diel and seasonal patterns in activity and home range size of green turtles on their foraging grounds revealed by extended Fastloc-GPS tracking

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Abstract

An animal's home range is driven by a range of factors including top-down (predation risk) and bottom-up (habitat quality) processes, which often vary in both space and time. We assessed the role of these processes in driving spatiotemporal patterns in the home range of the green turtle (*Chelonia mydas*), an important marine megaherbivore. We satellite tracked adult green turtles using Fastloc-GPS telemetry in the Chagos Archipelago and tracked their fine-scale movement in different foraging areas in the Indian Ocean. Using this extensive data set (5,081 locations over 1,675 tracking days for 8 individuals) we showed that green

turtles exhibit both diel and seasonal patterns in activity and home range size. At night, turtles had smaller home ranges and lower activity levels, suggesting they were resting. In the daytime, home ranges were larger and activity levels higher, indicating that turtles were actively feeding. The transit distance between diurnal and nocturnal sites varied considerably between individuals. Further, some turtles changed resting and foraging sites seasonally. These structured movements indicate that turtles had a good understanding of their foraging grounds in regards to suitable areas for foraging and sheltered areas for resting. The clear diel patterns and the restricted size of nocturnal sites could be caused by spatiotemporal variations in predation risk, although other factors (e.g. depth, tides and currents) could also be important. The diurnal and seasonal pattern in home range sizes could similarly be driven by spatiotemporal variations in habitat (e.g. seagrass or algae) quality, although this could not be confirmed.

Keywords: activity patterns; bottom-up effects; home range; spatial ecology; top-down effects

Introduction

An animal's home range is the spatial expression of its movement pattern (Börger et al. 2008), which is the result of complex and dynamic interactions between top-down (Mech 1977; Kittle et al. 2008) and bottom-up processes (Heithaus and Dill 2002; Fryxell et al. 2004), which can affect both individual fitness (Lima and Dill 1990; Heithaus and Dill 2006; Heithaus et al. 2007) and population dynamics (Wang and Grimm 2007). Hence, understanding what factors influence the home range of animals is important for predicting the potential consequences of human induced top-down effects, such as fisheries induced

apex predator declines, and bottom-up effects, such as global warming, at both an individual and population level (Boyce and McDonald 1999).

In the absence of predators, animals generally distribute themselves in a way that maximize their net energy intake, and hence fitness, over time (Lima and Dill 1990; Langvatn and Hanley 1993; Storch 1993; Heithaus and Dill 2002). Depending on the ability of an animal to perceive its environment, a forager should direct its foraging effort to subsets of the environment (patches) that on average yield higher benefits than the environment at large, and move between these patches in a way that maximizes the total net energy intake (Charnov 1976; Brown 1988). Both terrestrial and marine mammalian grazers forage in spatiotemporally complex habitats characterized by patchy distributions of food (Wallis de Vries et al. 1999; Robbins and Bell 2000). The spatial distribution of quality food patches have been shown to strongly influence the movement patterns and home ranges of large terrestrial mammalian grazers, which in turn impose patterns on the landscape, which further enforce this behaviour (Fryxell 1991; Hobbs 1996; Fryxell et al. 2004).

Under the risk of predation, animals generally alter their movement patterns, and consequently home ranges, in ways that reduce risk at the cost of reduced energy intake from having to reside in sub-optimal areas (Lima and Dill 1990; Houston et al. 1993; Brown 1999; Heithaus and Dill 2002). From this comes the notion that herbivores exist in a ‘‘landscape of fear’’ (Laundré et al. 2001), with their home range being the result of a trade-off between energy maximizing and risk minimizing (Lima and Dill 1990; Houston et al. 1993; Brown and Kotler 2004), with selection favouring animals that optimally balance these two components in a way that maximize fitness over time (Sih 1980; Illius and Fitzgibbon 1994; Lima 2002). The trade-off between predation risk and energy acquisition is a dynamic

process, with both components often varying both spatially and temporally (Heithaus and Dill 2002). For example, using fine-scaled data from GPS radio collars, Creel et al. (2005) showed that elks (*Cervus elaphus*) reduced their use of preferred, but more risky, grassland foraging habitats when wolves (*Canis lupus*) were present in the area. Similarly, foraging bottlenose dolphins (*Tursiops aduncus*) matched the distribution of their prey when tiger sharks (*Galeocerdo cuvier*) were absent, but significantly deviated from these preferred habitats when shark density increased (Heithaus and Dill 2002). Similar trade-offs have also been documented for African savannah herbivores (Riginos and Grace 2008; Valeix et al. 2009; Hopcraft et al. 2014), as well as dugongs and green turtles (Heithaus et al. 2007; Wirsing et al. 2007).

Apart from habitat quality and predation risk, other variables can influence the movement patterns and home ranges of animals. These variables relates to individual characteristics (e.g. age, body mass and reproductive status), the state of the individual (e.g. hungry, satiated), as well as external environmental variables, both biotic (e.g. competition, conspecific behaviour and habitat type) and abiotic (e.g. topography, temperature and precipitation) (McLoughlin and Ferguson 2000; Forester et al. 2007; Börger et al. 2008; Van Beest et al. 2011).

Megaherbivores play an important role in structuring primary producer communities in terrestrial, freshwater and marine habitats. Grazers can have positive effects on plant productivity, distribution, community structure, tissue nutrient content, as well as nutrient recycling (McNaughton et al. 1997; Ritchie et al. 1998; Atwood et al. 2015). While considerable work has been done to understand the behaviour and home range of terrestrial megaherbivores (Bailey et al. 1996; Fryxell et al. 2004), relatively little attention has been focused on marine megaherbivores, despite these varied ecosystem roles. We therefore set

out to assess the extent and drivers of spatiotemporal patterns in the home range of green turtles. This study is timely as it is now feasible to track this species with high resolution, for protracted periods and in remote locations using Fastloc-GPS tags that remotely relay data via the Argos satellite system (Dujon et al. 2014).

Materials and methods

Tag deployment and data processing

All fieldwork was approved by the Swansea University Ethics Committee, the British Indian Ocean Territory (BIOT) Scientific Advisory Group (SAG) of the U.K. Foreign and Commonwealth Office and the Commissioner for BIOT (research permit dated 2 October 2012). Research complied with all relevant local and national legislation. We attached Fastloc-GPS-Argos transmitters to eight adult female green turtles nesting at night on the island of Diego Garcia (7°25'S, 72°27'E) within the Chagos Archipelago during October 2012 (see Hays et al. (2014) for details). The size of the tagged turtles and tracking details are shown in Table 1. To each Turtle ID number a suffix was assigned corresponding to the country in which the eventual foraging grounds were located (Se=Seychelles, Ch=Chagos, Ma=Maldives, So=Somalia). We used two models of satellite tags (model F4G 291A, Sirtrack, Havelock North, New Zealand, and SPLASH10-BF, Wildlife Computers, Seattle, Washington), both of which relayed Fastloc-GPS data via the Argos satellite system (http://www.argos-system.org/). Satellite tags were programmed to acquire a maximum of one Fastloc-GPS location every 15 min, although the irregular surfacing pattern of the turtle and intermittent satellite overpasses for data relay resulted in fewer locations being obtained. From the Fastloc-GPS locations, the turtle's net swim speed was calculated. Before doing so however, the data was filtered to reduce measurement errors. First, locations with residual value above 35 were removed, in accordance with most Fastloc-GPS tracking studies (Dujon

et al. 2014). We then processed the data through a speed filter where we removed all positions which would require the turtle to swim at unrealistic speeds (>2.3 m sec^{-1}) (Dujon et al. 2014; Hays et al. 2014). We further restricted our location data to those points recorded by five or more satellites, which should result in an accuracy of 55 and 29m for 75% and 50% of locations, respectively (Dujon et al. 2014). This threshold further assured that more than 95% of the speed estimations had less than 10% errors (Dujon et al. 2014). Hazel (2009) estimated the mean linear error of Fastloc GPS locations to be 54 (±79.0), 42 (±52.9), 33 (±41.9) and 26m (±19.2) for five, six, seven and eight satellites, respectively. Finally, a small number (<0.05%) of locations were removed because they looked visibly erroneous (were far away from the remaining locations on the foraging grounds) when plotted spatially in R (R Core Team 2014).

Visual examinations of plotted tracks were used to identify when the turtles reached their foraging grounds. At this point, the turtles stopped traveling in a persistent direction and instead started to move back and forth within a relatively restricted area. All location data prior to this time were excluded from analyses, while the remaining data were analysed until the tags stopped working (Table 1).

Diel patterns in movement

To investigate diel movement patterns of the turtles, locations were first assigned as either daytime or nighttime based on the time of sunrise and sunset for the specific area and season, which was obtained using the package `insol` in R. The net movement of sea turtles as a function of time of day was investigated using Generalized Additive Models (GAMs) and generalized additive mixed models (GAMMs) in R. To bind the fitted values above zero, and to make residuals homogenous, net speed was first log transformed. Because time of day is a

149 circular variable, a cyclic cubic regression spline (type “cc” in the R-package `mgcv`) was
150 used, where the ends of the regression splines match up. To account for individual variation
151 in movement, turtle ID was added as a random effect in the model. To account for temporal
152 dependence between observations, a temporal auto-correlation structure within each turtle ID
153 was incorporated in the model, where the residuals at any given time were modelled as a
154 function of the residuals of the previous time point. Restricted maximum likelihood
155 estimation was used for estimating model parameters.
156
157 Model validation tests were run to identify potential violations of the assumptions of the
158 GAMM. Scatter plots of residuals versus fitted values were used to test the assumption of
159 equal variances (homogeneity) in the model. Normality of residuals was interpreted from
160 Quantile-Quantile plots and from residual histograms. Auto-correlation function and partial
161 auto-correlation function plots were used to visually detect patterns of temporal auto-
162 regressive and moving average parameters before and after adding the different correlation
163 structures. Because of the irregular surfacing pattern of the turtles, net speeds were estimated
164 over time periods of varying length. To investigate the sensitivity of the model output to this
165 variation, the time periods over which net speed was estimated was artificially restricted to an
166 upper threshold value ranging from 1 to 24 hours. The model output was then examined
167 visually (Supplementary Material Fig. S1).
168
169 **Seasonal patterns in movement**
170 To identify the number of unique diurnal and nocturnal sites for each turtle, we used a
171 Bayesian multivariate behavioural change point analysis (BCPA) on the time series of
172 latitude and longitude for each animal, using the `bcp` package in R (Barry and Hartigan
173 1993; Erdman and Emerson 2007). BCPA identifies partitions of sequences (time series) into

contiguous blocks with constant means within each block, while assuming independence between observations, normal distributed errors and constant variance throughout each sequence (see Erdman and Emerson (2007) for details). Because the distance of one degree longitude varies across latitudes, both latitude and longitude were converted to Northings and Eastings, expressed in meters. Since a turtle could potentially change its diurnal site seasonally without having to necessarily change its nocturnal site, and vice versa, we ran separate BCPAs for the daytime and nighttime positions. To fulfil the assumption of independence between locations (location data are naturally temporally auto-correlated), only a single location was used for each day and night, respectively. To make sure that the locations corresponded to actual daytime and nighttime hours, we only included positions recorded within three hours of midday and midnight, respectively. We used the default setting of the BCPA model (see Erdman and Emerson (2007), following the recommendations by Barry and Hartigan (1993). For the Markov Chain Monte Carlo methods, 10,000 iterations were run, with a burn in period of 1,000 iterations. From the resulting posterior probability, a lower threshold value of 0.95 (95% probability that a given time point is a change point) was used to identify change points. Because we were interested in persistent changes in diurnal and/or nocturnal sites, rather than short term deviations in diurnal and/or nocturnal sites, we ignored change points occurring within ten days of another change point. Locations that ended up in time periods between two identified blocks were allocated to the block located closest in space.

Home ranges

Green turtle home range sizes were estimated using Kernel Utility Distribution (KUD) (Worton 2002) using the `adehabitatHR` package in R, with the reference bandwidth as smoothing parameter. The area of each identified diurnal and nocturnal site was estimated

199 independently for each turtle. Diurnal and nocturnal activity centres were identified using
200 50% KUD (Worton 2002). As for the BCPA, temporal auto-correlation was accounted for by
201 using only a single location for each day and each night, respectively.
202
203 To investigate how spatiotemporal patterns in the movement of turtles influence the home
204 range size estimates, the 95% (overall home range) and 50% KUD (core area) were estimated
205 for each individual at decreasing level of spatiotemporal complexity: High = KUD was
206 estimated for each diurnal and nocturnal site separately, and summed together for each
207 individual to take into account both diel and seasonal patterns in home range; Medium =
208 KUD was estimated for daytime and nighttime positions separately and then summed
209 together for each individual, to account for diel patterns in home range; Low = a single KUD
210 was estimated for each individual, using one daytime and one nighttime location for every
211 24-hour period to account for temporal auto-correlation between locations; None = KUD was
212 estimated directly from the filtered raw data.
213
214 **Home range influence on activity budget**
215 The size and shape of a turtle's home range is likely to influence the proportion of time that it
216 spends foraging, resting and in transit, which constitute its activity budget. In particular, the
217 distance between the diurnal and nocturnal sites is likely to influence the proportion of time
218 that the turtle spend in transit between sites. The longer a turtle spends in transit, the less time
219 it will have available for foraging and/or resting, which over time could have consequences
220 on the animals bioenergetic budget, and ultimately fitness (New et al. 2014; Christiansen and
221 Lusseau 2015). To better understand the potential fitness consequences of variations in the
222 turtle's home ranges, we developed an individual based model for each of our eight turtles
223 where we simulated the daily movement for each turtle over a year. For each day in the

simulation, a diurnal and nocturnal site was allocated based on the number of unique sites for that individual identified by the BCPA. For animals with multiple diurnal and/or nocturnal sites, the number of simulated days spent in each site was set to be proportional to the relative amount of time spent in each site during the actual study period. After having allocated a diurnal and nocturnal site to each day, one daytime and one nighttime location were drawn at random from the corresponding KUDs for those sites for each day. The transit time between the two sites was then estimated based on the distance between the two locations and the swim speed of the turtle during transit. We set the swim speed during transit to be 0.6 m sec^{-1}, based on Watanabe et al. (2011). We further assumed that the speed of travel did not differ between individuals, as cost of transport for similar sized turtles should be similar. At the end of the simulation the mean proportion of time spent in transit over the year and the 95% highest posterior density intervals were estimated using bootstrapping resampling methods (1,000 iterations).

Results

Foraging ground locations and sample size

After being tagged, the turtles remained for varying lengths in the Chagos Archipelago breeding ground before starting their migrations back to their different foraging grounds across the Indian Ocean. Two turtles travelled west to the coast of Somalia, four to the Amirantes Islands, Seychelles, one travelled north to the Maldives, while the last turtle migrated to the Great Chagos Bank (Fig. 1). A detailed description of the migration of the eight tagged turtles can be found in Hays et al. (2014).

After the turtles had reached their foraging grounds, the tags kept transmitting for two to 18 months, resulting in a total of 1,675 tracking days (Table 1). After data filtering, 5,081

Fastloc-GPS locations remained, ranging between 103 and 1,637 per individual (Table 1). The average number of locations obtained per day per individual ranged between one and five. On their foraging ground, all eight turtles stayed within relatively small areas (Fig. 1, Table 1). The only exception was turtle 61811-So, which after spending 152 days on its foraging ground off the coast of Somalia, made a short excursion (circa 64 km) southwest along the coast before returning back to its foraging ground after 10 days. The accumulated distance travelled during this excursion was about 64 km. To simplify our analyses, this part of the track (35 locations) was excluded from the data set. For all individuals, the locations within the foraging ground were distributed heterogeneously in space, with clusters of positions occurring in specific areas within each foraging ground (Fig. 1).

Diel patterns in movement

Time of day had a significant effect on the net swim speed of turtles ($F_{7.8,2374.2}$=118.8, $p<0.001$, based on swim speeds estimated over time periods of < 3 hours). Individual variation accounted for 6.7% of the total variation in the data. Adding a temporal auto-correlation structure, an auto-regression structure of lag one, improved the model significantly (Log-likelihood ratio test: L=176.9, df=1, $p<0.0001$) and also removed any pattern of auto-correlation from the residuals. The full model explained 28.9% (adjusted R^2) of the variance in net speed.

There was a curvilinear relationship between net speed and hour of day for green turtles (Fig. 2). The activity level (i.e. net swim speed) during night was lower (~0.2 m s^{-1}) than during daytime hours (~0.4 m s^{-1}). Just before sunrise the activity of the turtles started to increase rapidly, with the turtles reaching a peak in activity between 6 and 8am. This peak was followed by a lower level of activity (~0.4 m s^{-1}) throughout most of the daylight hours,

although significantly higher than during night. Shortly before sunset there was a second peak in activity, between 4 and 6pm, before the activity level dropped again for the night (Fig. 2). While the second peak in activity was slightly lower than the first, this could be an artefact of fixing the time of sunrise to 6am in the analyses, while sunset was allowed to vary seasonally over the year. This was done to facilitate comparison between turtles located at different time zones and latitudes. Although the magnitude of both activity peaks varied depending on the upper threshold chosen for including net speed estimates, the general pattern was consistent across thresholds (Supplementary Material Fig. S1).

Seasonal patterns in movement

The BCPA identified 10 and 11 unique diurnal (Table 2) and nocturnal sites (Table 3) for our eight turtles, respectively. While most turtles were shuttling daily between a single diurnal and a single nocturnal site throughout the study period, three animals changed their diurnal and/or nocturnal site seasonally (Supplementary Material Figs. S2 and S3). Turtle 21923-Se foraged and rested in adjacent areas (F1 and R1) for the first 50 days, before abruptly changing both its diurnal and nocturnal site to a new area (F2 and R2) located approximately four km north, where it remained for the last 47 days of the track (Fig. 3, Supplementary Material Figs. S2 and S3). Turtle 117569-Se revisited the same diurnal and nocturnal sites over the course of the tag deployment. It spent the first 11 days in a restricted area located in the northern part of its home range (F4 and R4), before relocating to another area approximately 11 km south, where it spend 129 days (F5 and R5) (Fig. 3, Supplementary Material Figs. S2 and S3). The turtle then returned to its initial site (F4 and R4), where it stayed for 135 days, before again relocating to the second site (F5 and R5), where it spend the remaining 100 days of the track. Turtle 61811-So stayed in the same diurnal site over the duration of the study, but changed its nocturnal site (R9) after 187 days to a new site (R10)

299 located about 2 km west, where it stayed at night for the remaining 16 days of the track (Fig.
300 3, Supplementary Material Figs. S2 and S3).
301
302 **Home ranges**
303 Both during day and night, the turtles restricted their movement to relatively small areas,
304 identified from 50% KUD (Fig. 3). Although diurnal sites were generally larger in size
305 (95%KUD: mean=20.0 km^2, SD=14.4; 50%KUD: mean=3.6 km^2, SD=3.1) compared to
306 nocturnal sites (95%KUD: mean=10.2 km^2, SD=16.5; 50%KUD: mean=1.6 km^2, SD=2.1),
307 there were two exceptions (see ID 21923-Se and 61813-So, Fig. 3, Tables 2 and 3). The
308 degree of overlap between diurnal and nocturnal sites differed markedly between individuals,
309 as did the distance between sites (Fig. 3). While most diurnal and nocturnal sites had a single
310 centre of activity, some sites had two centres which the turtle regularly moved between (F7a
311 and F7b for Turtle ID:4394-Se, F9a and F9b for Turtle ID:61811-So, F10a and F10b and
312 R11a and R11b for Turtle ID:61813-So, Fig. 3). There were large differences in the size of
313 both diurnal and nocturnal sites, both within and between individuals (Tables 2 and 3).
314
315 Accounting for diel and seasonal patterns in movement had large effects on the estimated
316 home range sizes of the turtles (Supplementary Material Table S1). Accounting for temporal-
317 auto-correlation between locations (Low complexity) resulted in larger estimated home range
318 sizes compared to the raw location data (No complexity) (Supplementary Material Table S1).
319 Adding diel patterns into the home range estimation (Medium complexity) had a large effect
320 on the resulting size, however the direction and magnitude of this effect varied between
321 individuals (Supplementary Material Table S1). Finally, for individuals that had multiple
322 diurnal and/or nocturnal sites, incorporating both seasonal and diel patterns in movement

(High complexity) lead to a significant reduction in home range size, sometimes even below that of the raw data (No complexity) (Supplementary Material Table S1).

Home range influence on activity budget

Our simulations showed that the eight turtles varied significantly in the proportion of time they spent in transit on their foraging grounds (Fig. 4). While the size of the home ranges affected the daily variation in transit within individuals (the size of the error bars in Fig. 4), individual differences in the distance between diurnal and nocturnal sites was the main cause for the large variation in transit time between individuals (Fig. 4).

Discussion

The aim of this study was to investigate spatiotemporal patterns in the home range of green turtles to better understand the relative importance of top-down and bottom-up processes affecting this marine megaherbivore. Fastloc-GPS tags allowed us to track the fine-scale movement of green turtles for up to two years on their foraging grounds with the high quantity and quality of the locations giving us an unprecedented insight into the fine-scale movement patterns of green turtles compared to studies using conventional Argos tracking (Hays et al. 1999; Godley et al. 2002). Hence, in concurrence with Börger et al. (2008) we stress the importance of incorporating spatiotemporal patterns in animal movement when estimating home range sizes.

The low level of activity during night, coupled with restricted nocturnal home range sizes, suggest that turtles were resting at night. During daytime the activity levels was higher and the home range sizes larger, inferring that turtles were foraging within their diurnal sites at daytime. This diel movement between distinct foraging and resting sites, also observed in

several other studies (e.g. Makowski et al. 2006; Seminoff and Jones 2006; MacDonald et al. 2013; Gredzens et al. 2014), could be the result of top-down effects from predation risk resulting in turtles seeking sheltered habitats during night to avoid predation from large sharks. Turtles rely on vision to detect sharks and might therefore avoid foraging at night to reduce predation risk (Heithaus et al. 2002; Makowski et al. 2006). Turtles generally rest close to reef structures, where they can find shelter under reef ledges, in small caves and crevices in the sides of the reefs (Makowski et al. 2006; Hazel et al. 2009). Preference for safer habitats during resting has also been observed in other species, including desert baboons (*Papio cynocephalus ursinus*) (Cowlishaw 1997), dugongs (Sheppard et al. 2009), spinner dolphins (*Stenella longirostris*) (Tyne et al. 2015) and bottlenose dolphins (Heithaus and Dill 2002). Although the bottom substrate was unknown, nocturnal sites were generally smaller in size and often located closer to land presumably in habitats with more structure (e.g. caves) for shelter, although high-resolution habitat maps for these areas were not available. That the turtles showed such high fidelity to these specific sites suggests they must offer some level of protection for the turtles that makes it worthwhile returning to them. Predation risk could therefore help explain why the turtles sought out specific resting sites at night that were sometimes even spatially segregated from their daytime foraging sites.

Other possible explanations for why turtles selected specific resting sites at night also need mentioning. Resting turtles might prefer certain depths where they can stay neutrally buoyant with greater oxygen stores (more inflated lungs) and remain submerged for longer periods of time before having to breath (Hays et al. 2000; Minamikawa et al. 2000). Unfortunately, detailed bathymetry maps of our study areas were not available to test this hypothesis. Tides and ocean currents can also influence turtle movement and habitat use, with turtles in some foraging grounds showing strong circatidal movement patterns (Brooks et al. 2009) or

restricted home ranges during low tide (Limpus and Limpus 2000). While the turtles in this study showed a clear diel, rather than circatidal pattern in activity and home range size, ocean currents still might influence habitat choice at night, with turtles selecting nocturnal sites that are protected from currents. The large variation in movement and home range patterns of green turtles recorded around the world (Bjorndal 1980; Seminoff et al. 2002; Makowski et al. 2006; Taquet et al. 2006; Hazel et al. 2009; Senko et al. 2010; MacDonald et al. 2013) indicate that green turtles have a high degree of plasticity in their behaviour and that their movement and home range patterns are influenced strongly by local environmental features.

We found large differences in diurnal home range sizes of turtles in this study. Further, three of our eight tracked turtles changed their home range pattern seasonally. Seasonal movement between foraging patches is a common behaviour observed in terrestrial grazers (Fryxell et al. 2004; Fryxell et al. 2008; Hopcraft et al. 2014), with animals moving between dense prey patches in a manner which maximizes energy intake over time (Charnov 1976; Brown 1988). Rather than being distributed homogenously over the sea floor, seagrass is generally found in well-defined patches (Robbins and Bell 2000), similar to terrestrial grass systems (Wallis de Vries et al. 1999). While green turtles are known to regraze seagrass patches within a foraging site (Bjorndal 1980; Zieman et al. 1984), this is the first study to measure seasonal patterns in grazing behaviour in sea turtles. Repeated grazing of seagrass patches may increase seagrass food quality by enhancing the production of new leaves that are higher in nutrient content and therefore more easily digested by the turtles (Bjorndal 1980; Zieman et al. 1984; Aragones et al. 2006). The timing of regrazing will depend on the recovery time of the seagrasses (which can vary substantially from a couple of weeks up to a year depending on the location of the seagrass bed), the timing and the intensity of the grazing (including turtle density), the seagrass species composition, depth and the location of grazing within the

beds (Zieman et al. 1984; Rasheed 1999; Aragones and Marsh 2000; Rasheed et al. 2014). While this study has provided insights into the movement pattern of foraging sea turtles, the lack of information about resource (i.e. seagrass and algae) quantity and quality prevented us from testing any further hypotheses in relation to optimal foraging behaviour in this species. Nevertheless, the measured individual variation in diurnal home range sizes and the structured seasonal movement of turtles between foraging sites suggest that bottom-up processes relating to resource (i.e. seagrass and/or algae) quantity and quality could be shaping these behavioural patterns.

The structured and predictable nature of the movement and home range patterns in this study suggest that the turtles had a good spatial understanding of their foraging grounds, which allowed them to make informed decisions on where and when to move to find suitable foraging and resting areas. This stands in stark contrast to the random walk foraging movement of pelagic marine predators where the knowledge of the prey field is generally poor (Sims et al. 2008; Humphries et al. 2010). However, while the tracked turtles showed some similarities in movement and home range patterns, there were also some considerable differences between individuals. The transit distance between foraging and resting sites varied considerable between individuals, which resulted in differences in activity budgets between turtles, with animals transiting further having less time available for foraging compared to turtles foraging closer to their resting sites. With all of the turtles being mature females of similar size (within 10% carapace length), it is unlikely that this difference is due to size-specific variations in food requirements and physiology, as observed by Ballorain et al. (2010). Instead, it is possible that the observed individual variation in home range sizes and transit distance reflect variation in habitat quality (food quantity and quality) between the different foraging grounds (Festa-Bianchet 1988). Turtles might be willing to travel further

from their resting sites in order to reach more profitable seagrass beds, even if this means that they will have less time available per day to forage there, as long as it maximizes net energy intake over time (Charnov 1976; Brown 1988). Hence, the estimated activity budgets in this study might not necessarily reflect the turtles' energetic budgets. In addition, other factors such as body condition and competition might also influence the movement and home range sizes of green turtles (Fretwell and Lucas 1970; Heithaus et al. 2007). A direct assessment of the seagrass quality and quantity of the foraging sites, in combination with direct observations of sea turtle behaviour and condition will help answer these questions. Seagrass ecosystems have been poorly studied in the western Indian Ocean and need to be given higher priority in regional habitat studies.

In summary we highlight the value of new generation Fastloc-GPS Argos tags for resolving the details of sea turtle movements at small scales. The complexity of movements over different spatial scales points to animals that have a good knowledge of their environment, commuting between suitable foraging and resting sites and changing these sites over time in a way that likely allows patch recovery and maximise energy intake. These complexities of shifts in foraging habitat patch use over time and the associated commuting to night-time refuges, likely occur broadly across marine and terrestrial systems although resolving these complexities and generalities remains key question (Hays et al. 2016).

Acknowledgments: We thank British Forces BIOT, MRAG Ltd, NAVFACFE PWD DG Environmental Department, and the many volunteers on Diego Garcia for logistical support. We thank L. Avens and two anonymous reviewers for their constructive comments which helped to improve this manuscript. FC and GCH developed the study, as part of a larger project initially conceived by GCH, NE and JAM. FC led the data processing, analyses and

interpretation of the data, with contribution from GCH and AMD. FC led the writing with input from GCH. All other authors commented on the manuscript.

Funding: This project was funded by a Darwin Initiative Challenge Fund grant (EIDCF008), the Department of the Environment Food and Rural Affairs (DEFRA), the Foreign and Commonwealth Office (FCO), College of Science of Swansea University, and the BIOT Scientific Advisory Group (SAG) of the FCO.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: All applicable international, national and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

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Tables

Table 1 Summary data of the eight satellite tracked adult female green turtles on their foraging grounds in the Indian Ocean. CCL=curved carapace length, Lat. dist.= latitudinal distance, Long. dist.= longitudinal distance. Turtle ID suffixes (Se, Ch, Ma, So) refer to the location of their foraging grounds.

Turtle ID	CCL (cm)	Location	Track duration (days)	Start date	End date	Nb. locations	Locations day^{-1}	Lat. dist. (km)	Long. dist. (km)
21923-Se	110.0	Seychelles	96	2013-02-28	2013-06-04	146	1.52	5.50	4.67
117568-Ch	104.0	Chagos	538	2012-11-08	2014-04-30	1637	3.04	5.65	5.65
117569-Se	101.5	Seychelles	381	2013-01-03	2014-01-19	1178	3.09	20.80	5.57
117570-Ma	103.0	Maldives	128	2013-03-13	2013-07-19	103	0.80	5.77	4.29
4394-Se	104.0	Seychelles	66	2012-11-27	2013-02-01	154	2.33	6.58	6.08
21914-Se	105.0	Seychelles	153	2012-12-23	2013-05-25	662	4.33	11.72	7.60
61811-So	111.5	Somalia	223	2012-12-21	2013-08-01	1050*	4.71*	1.99*	2.89*
61813-So	106.0	Somalia	90	2013-03-07	2013-06-05	151	1.68	1.06	3.66

*Turtle 61811-So made a 10 day excursion, 64 km in total, before returning back to its foraging ground. The excursion occurred after spending 150 days on the foraging ground

646 **Table 2** Summary table of the 10 identified diurnal sites of the eight tracked green turtles on
647 their foraging grounds in the Indian Ocean. KUD=Kernel Utility Distribution

Diurnal site ID	Turtle ID	N	Duration (days)	95% KUD Area	50% KUD Area
D1	21923-Se	15	51	1.18	0.27
D2	21923-Se	5	36	7.72	1.55
D3	117568-Ch	268	537	8.51	0.93
D4	117569-Se	71	145	26.16	2.60
D5	117569-Se	127	228	10.08	0.97
D6	117570-Ma	25	127	20.94	4.91
D7	4394-Se	28	61	44.14	10.56
D8	21914-Se	109	154	25.06	2.91
D9	61811-So	127	222	3.78	0.89
D10	61813-So	21	55	12.04	2.97

648

649 **Table 3** Summary table of the 11 identified nocturnal sites of the eight tracked green turtles

650 on their foraging grounds in the Indian Ocean. KUD=Kernel Utility Distribution

Nocturnal site ID	Turtle ID	N	Duration (days)	95% KUD Area	50% KUD Area
N1	21923-Se	17	50	6.13	1.18
N2	21923-Se	6	47	0.27	0.08
N3	117568-Ch	183	532	0.09	0.00
N4	117569-Se	74	186	22.75	3.53
N5	117569-Se	75	178	27.00	2.64
N6	117570-Ma	13	119	3.42	0.74
N7	4394-Se	19	66	4.42	0.94
N8	21914-Se	84	152	2.54	0.38
N9	61811-So	84	187	0.73	0.11
N10	61811-So	13	16	0.44	0.11
N11	61813-So	21	89	13.43	3.20

651

Figure legends

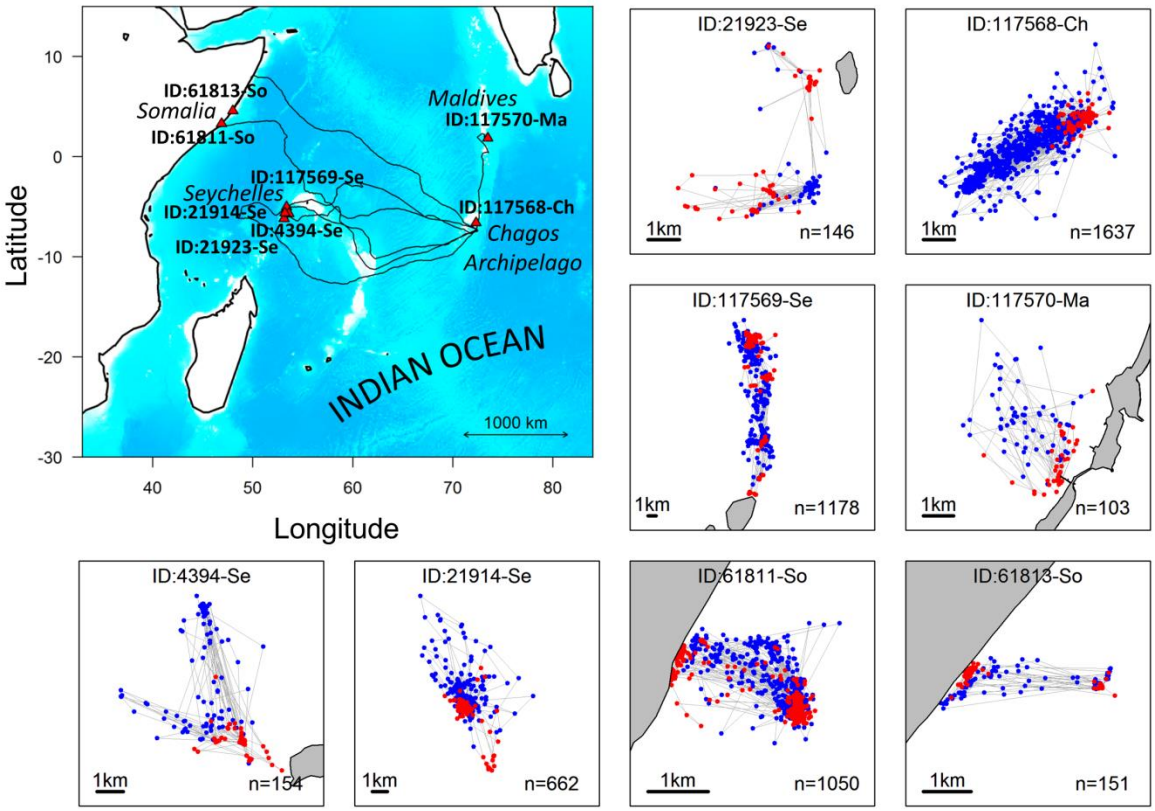
Fig. 1 The top-left subfigure shows the migratory movements of the eight tracked adult female green turtles (solid black lines) from their nesting beach on Diego Garcia, Chagos Archipelago, to their respective foraging grounds (red triangles) in the Indian Ocean. The smaller subfigures show the foraging grounds of each turtle (see ID number at the top of each subfigure), with blue and red dots indicating daytime and nighttime locations, respectively (the sample size is shown in the lower-left corner of each subfigure). The light grey lines show the movement tracks of turtles within their foraging grounds. Grey areas indicate land

Fig. 2 Back transformed swim speed as a function of hour of day for the eight tracked green turtles in their Indian Ocean foraging grounds. The solid black line represents the fitted values of the best fitting GAMM. The white and dark grey background colours indicate daytime and nighttime hours, respectively. The time of sunrise was fixed to 6am for all turtles and the strip of light grey background colour represents dusk, which varied seasonally over the year. The dashed lines represent 95% confidence interval. Swim speeds were estimated over time periods of three hours and less. n=2,383 speed estimates

Fig. 3 Diurnal (D; blue contour lines) and nocturnal (N; red contour lines) sites of the eight tagged female green turtles on their foraging grounds in the Indian Ocean, estimated using 50% Kernel Utility Distributions. The numbers next to the letters indicate the ID number of the specific site, whereas *a* and *b* represent sites that had two centres of activity, but were not temporally segregated (the turtle moved back and forth between these two sites on a day to day basis). The ID number of each turtle can be seen on top of each sub-figure. The daytime and nighttime location data that was used to estimate the home ranges are shown as blue and red dots, respectively. Only one daytime and one nighttime location for every 24-hour period

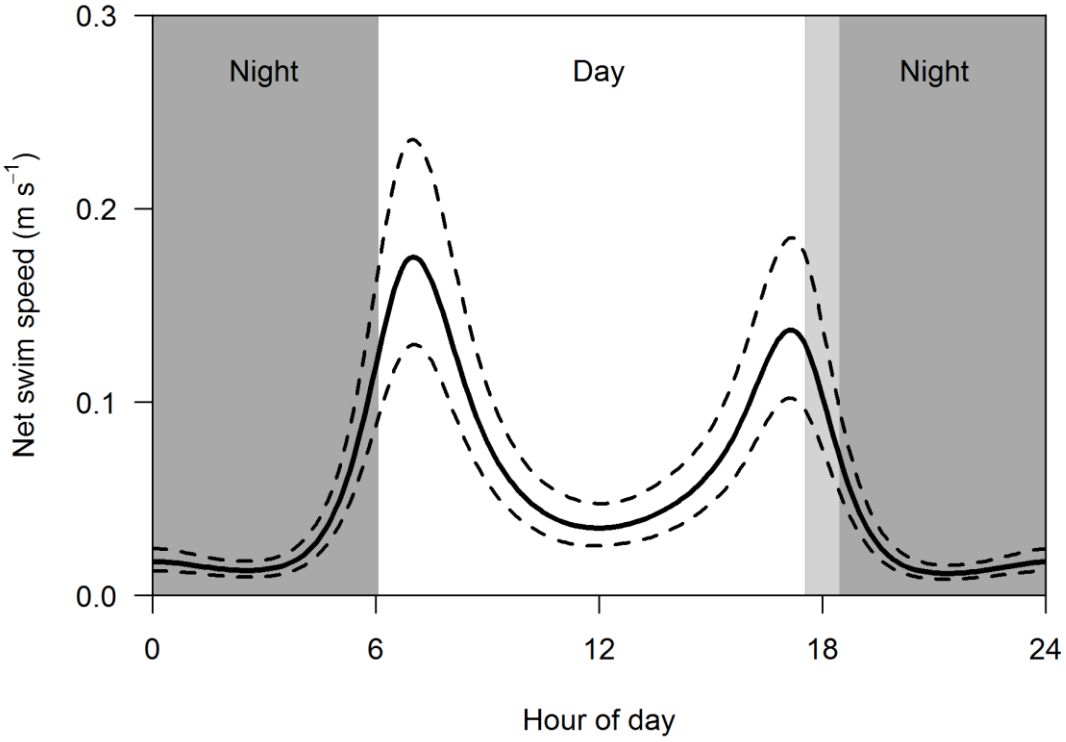
677 was used to account for temporal auto-correlation between locations. No locations during
678 transit were used. Grey areas indicate land
679
680 **Fig. 4** Simulated proportion of time spent in transit for the eight green turtles on their
681 foraging grounds in the Indian Ocean. Error bars represent 95% highest posterior density
682 intervals. The means and density intervals are based on 1,000 model simulations, where the
683 daily movement for each turtle was simulated over a year. For each day in the simulation, a
684 diurnal and nocturnal site was allocated based on the 50% Kernel Utility Distributions for the
685 specific turtle (Fig. 3)

686 **Figures**



687

688 **Figure 1**



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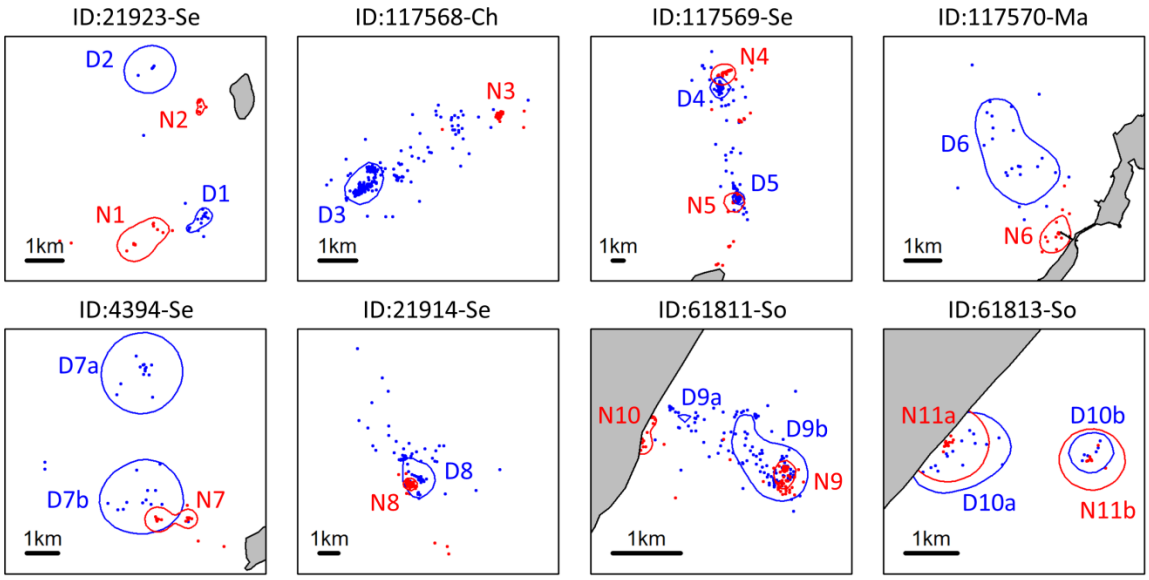
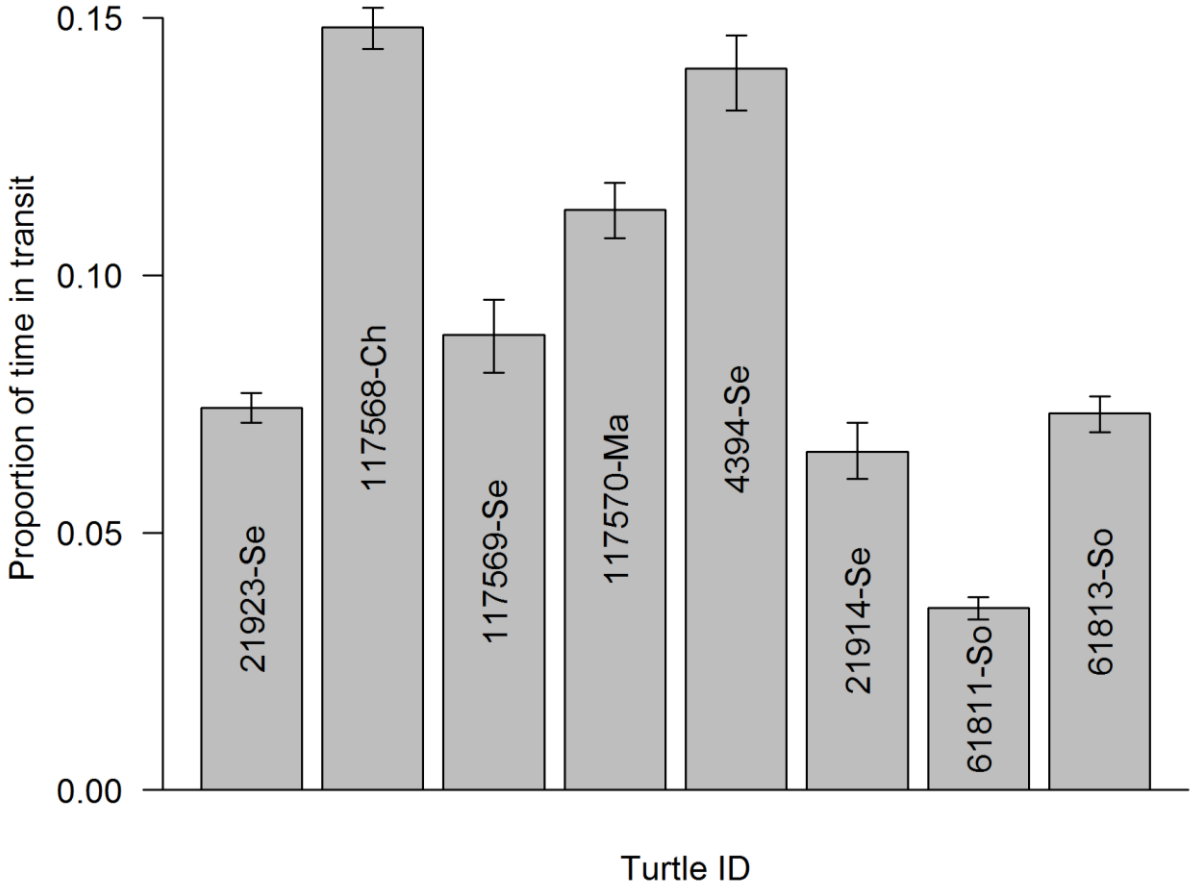
690 **Figure 2**



691

692 **Figure 3**



693

694 **Figure 4**