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ORIGINAL PAPER

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 (5081 locations over 1675 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 regard 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.

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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 fishery-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

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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 has 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-scale 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 Indo-Pacific 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 (*Dugong dugon*) and green turtles (*Chelonia mydas*) (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. Some of these variables are related to individual characteristics (e.g. age, body condition and reproductive status) as well as the state of the individual (e.g. hungry, satiated), whereas others are external, 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). Cederlund and Sand (1994) found that male moose (*Alces alces*) had larger home range sizes than females, due to sex-specific differences in body size. Differences in mating strategies are believed to be driving differences in home range sizes between male and female Indo-Pacific bottlenose dolphins, with males having larger home ranges to maximize mating opportunities with multiple females (Sprogis et al. 2016). In green turtles in Shark Bay, Australia, body condition has been found to influence habitat use, and consequently home ranges, with turtles in poor condition selecting more profitable, but risky, microhabitats, during periods of high predation risk, compared to turtles in good condition (Heithaus et al. 2007). Finally, dugongs in Queensland, Australia, forage closer to land during high tide compared to low tide, due to, at least partly, restricted access to intertidal food resources (Sheppard et al. 2009).

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, which in turn can influence the foraging behaviour and home range pattern of the grazers (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 UK 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

Table 1 Summary data of the eight satellite tracked adult female green turtles on their foraging grounds in the Indian Ocean

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[a]	4.71[a]	1.99[a]	2.89[a]
61813-So	106.0	Somalia	90	2013-03-07	2013-06-05	151	1.68	1.06	3.66

Turtle ID suffixes (Se, Ch, Ma, So) refer to the location of their foraging grounds

CCL curved carapace length, *Lat. dist.* latitudinal distance, *Long. dist.* longitudinal distance

[a] Turtle 61811-So made a 10-day excursion, 64 km in total, before returning back to its foraging ground. The excursion occurred after spending 152 days on the foraging ground

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 were filtered to reduce measurement errors. First, locations with residual values 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 s^{-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 29 m 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 26 m (±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 travelling 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 night-time 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 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 circular variable, a cyclic cubic regression spline (type "cc" in the R-package mgcv) was used, where the ends of the regression splines match up. To account for individual variation in movement, turtle ID was added as a random effect in the model. To account for temporal dependence between observations, a temporal auto-correlation structure within each turtle ID was incorporated in the model, where the residuals at any given time were modelled as a function of the residuals of the previous time point. Restricted maximum likelihood estimation was used for estimating model parameters.

Model validation tests were run to identify potential violations of the assumptions of the GAMM. Scatter plots of residuals versus fitted values were used to test the

assumption of equal variances (homogeneity) in the model. Normality of residuals was interpreted from quantile–quantile plots and from residual histograms. Auto-correlation function and partial auto-correlation function plots were used to visually detect patterns of temporal auto-regressive and moving average parameters before and after adding the different correlation structures. Because of the irregular surfacing pattern of the turtles, net speeds were estimated over time periods of varying length. To investigate the sensitivity of the model output to this variation, the time periods over which net speed was estimated were artificially restricted to an upper threshold value ranging from 1 to 24 h. The model output was then examined visually (Supplementary Material Fig. S1).

Seasonal patterns in movement

To identify the number of unique diurnal and nocturnal sites for each turtle, we used a Bayesian multivariate behavioural change point analysis (BCPA) on the time series of latitude and longitude for each animal, using the bcp package in R (Barry and Hartigan 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 metres. 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 night-time 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 night-time hours, we only included positions recorded within 3 h 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 1000 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 independently for each turtle. Diurnal and nocturnal activity centres were identified using 50% KUD (Worton 2002). As for the BCPA, temporal auto-correlation was accounted for by using only a single location for each day and each night, respectively.

To investigate how spatiotemporal patterns in the movement of turtles influence the home range size estimates, the 95% (overall home range) and 50% KUD (core area) were estimated for each individual at decreasing level of spatiotemporal complexity: High = KUD was estimated for each diurnal and nocturnal site separately and summed together for each individual to take into account both diel and seasonal patterns in home range; Medium = KUD was estimated for daytime and night-time positions separately and then summed together for each individual, to account for diel patterns in home range; Low = a single KUD was estimated for each individual, using one daytime and one night-time location for every 24-h period to account for temporal auto-correlation between locations; None = KUD was estimated directly from the filtered raw data.

Home range influence on activity budget

The size and shape of a turtle's home range are likely to influence the proportion of time that it spends foraging, resting and in transit, which constitute its activity budget. In particular, the distance between the diurnal and nocturnal sites is likely to influence the proportion of time that the turtle spend in transit between sites. The longer a turtle spends in transit, the less time it will have available for foraging and/or resting, which over time could have consequences for the animals bioenergetic budget, and ultimately fitness (New et al. 2014; Christiansen and Lusseau 2015). To better understand the potential fitness consequences of variations in the turtle's home ranges, we developed an individual-based model for each of our eight turtles 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 night-time locations were drawn at random from the corresponding KUDs for those sites for each day. The transit

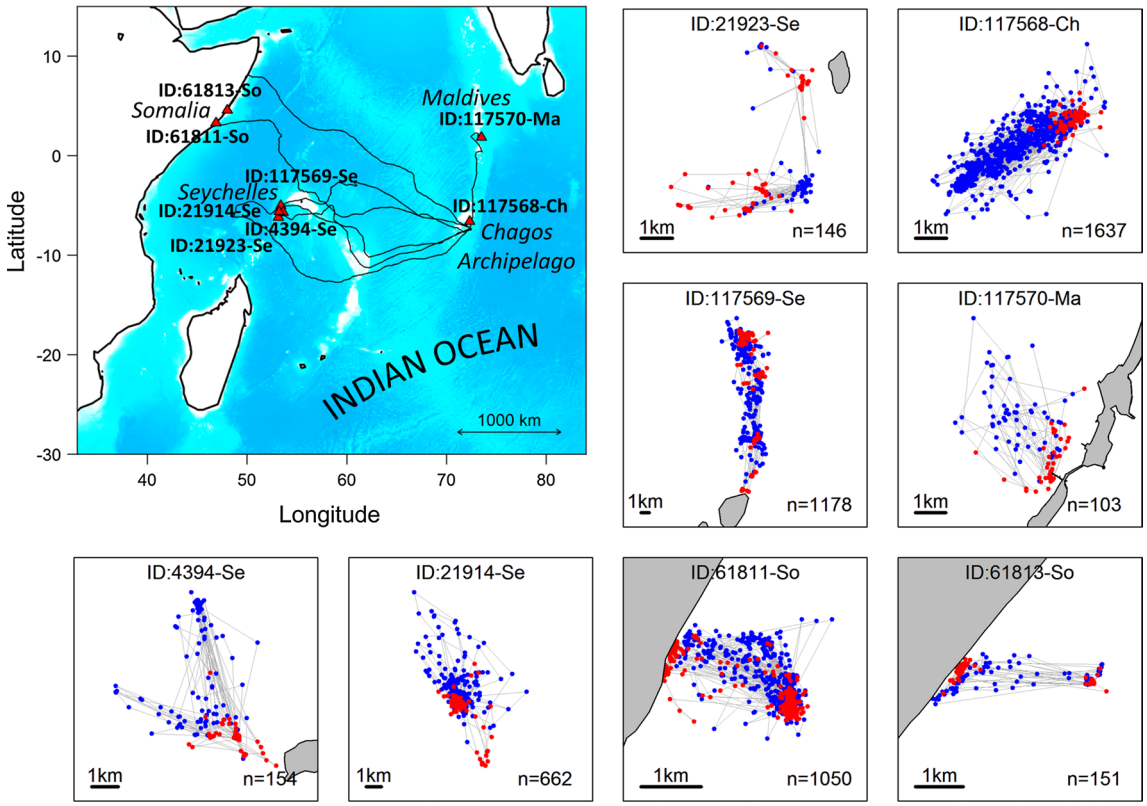

Fig. 1 *Top-left subfigure* shows the migratory movements of the eight tracked adult female green turtles (*solid black lines*) from their nesting beach on Diego Garcia, Chagos Archipelago, to their respective foraging grounds (*red triangles*) in the Indian Ocean. The *smaller subfigures* show the foraging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

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 s^{-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 (1000 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 1675 tracking days (Table 1). After data filtering, 5081 Fastloc-GPS locations remained, ranging between 103 and 1637 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) south-west 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 grounds were distributed heterogeneously in space, with clusters of positions occurring in specific areas within each foraging ground (Fig. 1).

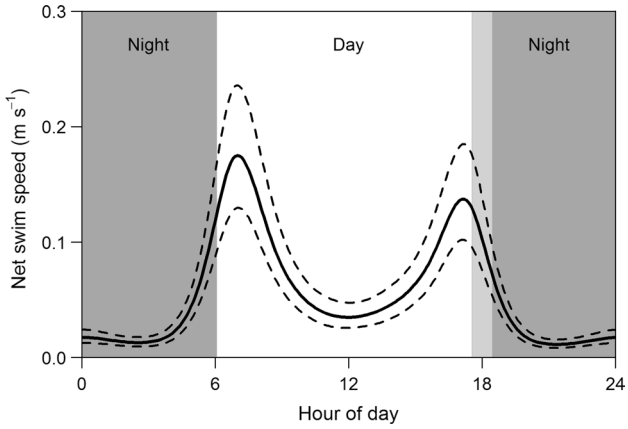

Fig. 2 Back-transformed swim speed as a function of hour of day for the eight tracked green turtles in their Indian Ocean foraging grounds. The *solid black line* represents the fitted values of the best fitting GAMM. The *white* and *dark grey background colours* indicate day-time and night-time hours, respectively. The time of sunrise was fixed to 6 am 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 3 h and less. $n = 2383$ speed estimates

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 h). 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 8 am. 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 6 pm, 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 6 am 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 spent its daytime and night-time hours in adjacent areas (D1 and N1) for the first 50 days, before abruptly changing both its diurnal and nocturnal sites to a new area (D2 and N2) 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 (D4 and N4), before relocating to another area approximately 11 km south, where it spent 129 days (D5 and N5)

Table 2 Summary table of the 10 identified diurnal sites of the eight tracked green turtles on their foraging grounds in the Indian Ocean

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

KUD Kernel Utility Distribution

Table 3 Summary table of the 11 identified nocturnal sites of the eight tracked green turtles on their foraging grounds in the Indian Ocean

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

KUD Kernel Utility Distribution

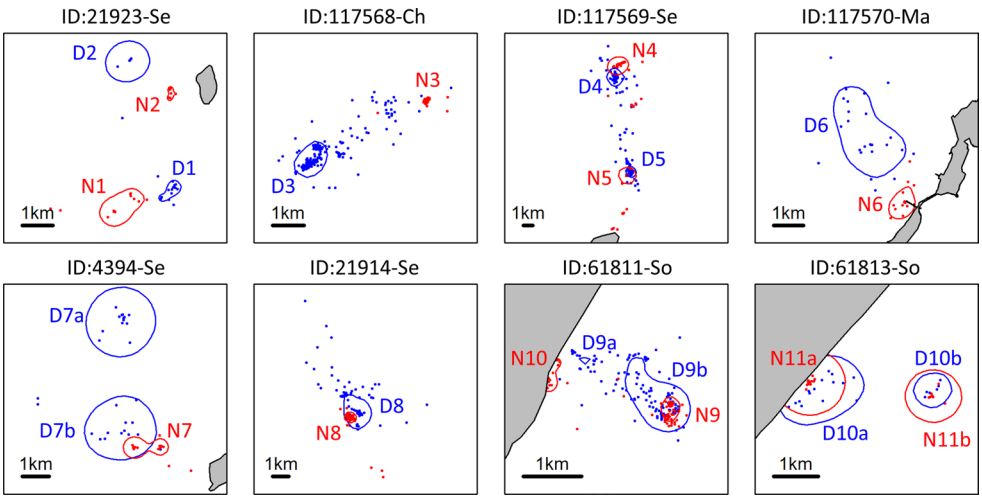

Fig. 3 Diurnal (D; *blue contour lines*) and nocturnal (N; *red contour lines*) sites of the eight tagged female green turtles on their foraging grounds in the Indian Ocean, estimated using 50% Kernel Utility Distributions. *The numbers next to the letters* indicate the ID number of the specific site, 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 night-time location data that were used to estimate the home ranges are shown as *blue* and *red dots*, respectively. Only one daytime and one night-time location for every 24-h period was used to account for temporal auto-correlation between locations. No locations during transit were used. *Grey areas* indicate land

(Fig. 3, Supplementary Material Figs. S2 and S3). The turtle then returned to its initial site (D4 and N4), where it stayed for 135 days, before again relocating to the second site (D5 and N5), where it spent 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 (N9) after 187 days to a new site (N10) located about 2 km west, where it stayed at night for the remaining 16 days of the track (Fig. 3, Supplementary Material Figs. S2 and S3).

Home ranges

Both during day and night, the turtles restricted their movement to relatively small areas, identified from 50% KUD (Fig. 3). Although diurnal sites were generally larger in size (95% KUD: mean = 20.0 km^2, SD = 14.4; 50% KUD: mean = 3.6 km^2, SD = 3.1) compared to nocturnal sites (95% KUD: mean = 10.2 km^2, SD = 16.5; 50% KUD: mean = 1.6 km^2, SD = 2.1), there were two exceptions (see ID 21923-Se and 61813-So, Fig. 3; Tables 2, 3). The degree of overlap between diurnal and nocturnal sites differed markedly between individuals, as did the distance between sites (Fig. 3). While most diurnal and nocturnal sites had a single centre of activity, some sites had two centres which the turtle regularly moved between (D7a and D7b for Turtle ID:4394-Se, D9a and D9b for Turtle ID:61811-So, D10a and D10b and N11a and N11b for Turtle ID:61813-So, Fig. 3). There were large differences in

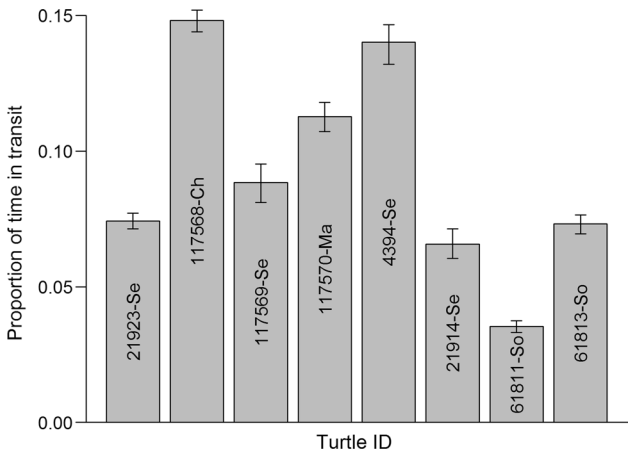

Fig. 4 Simulated proportion of time spent in transit for the eight green turtles on their foraging grounds in the Indian Ocean. *Error bars* represent 95% highest posterior density intervals. The means and density intervals are based on 1000 model simulations, where the daily movement for each turtle was simulated over a year. For each day in the simulation, a diurnal and nocturnal site was allocated based on the 50% Kernel Utility Distributions for the specific turtle (Fig. 3)

the size of both diurnal and nocturnal sites, both within and between individuals (Tables 2, 3).

Accounting for diel and seasonal patterns in movement had large effects on the estimated home range sizes of the turtles (Supplementary Material Table S1). Accounting for temporal auto-correlation between locations (low complexity) resulted in larger estimated home range sizes compared to the raw location data (no complexity) (Supplementary Material Table S1). Adding diel patterns into the home range estimation (medium complexity) had a large effect on the resulting size; however, the direction and magnitude of this effect varied between individuals (Supplementary Material Table S1). Finally, for individuals that had multiple diurnal and/or nocturnal sites, incorporating both seasonal and diel patterns in movement (high complexity) lead to a significant reduction in home range sizes, 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 were 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, suggests that turtles were resting at night. During daytime, the activity levels were higher and the home range sizes larger, inferring that turtles were foraging within their diurnal sites during 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 to return 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 breathe (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 some 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, 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). Green turtles are known to regraze seagrass patches within a foraging site (Bjorndal 1980; Zieman et al. 1984). 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 seagrass (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 maximize 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 a key question (Hays et al. 2016).

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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.

References

Aragones L, Marsh H (2000) Impact of dugong grazing and turtle cropping on tropical seagrass communities. Pac Conserv Biol 5:277–288

Aragones LV, Lawler IR, Foley WJ, Marsh H (2006) Dugong grazing and turtle cropping: grazing optimization in tropical seagrass systems? Oecologia 149:635–647

Atwood TB, Connolly RM, Ritchie EG et al (2015) Predators help protect carbon stocks in blue carbon ecosystems. Nat Clim Change 5:1038–1045

Bailey D, Gross J, Laca E et al (1996) Mechanisms that result in large herbivore grazing distribution patterns. J Range Manage 49:386–400

Ballorain K, Ciccione S, Bourjea J et al (2010) Habitat use of a multispecific seagrass meadow by green turtles *Chelonia mydas* at Mayotte Island. Mar Biol 157:2581–2590

Barry D, Hartigan JA (1993) A Bayesian analysis for change point problems. J Am Stat Assoc 88:309–319

Bjorndal KA (1980) Nutrition and grazing behavior of the green turtle *Chelonia mydas*. Mar Biol 56:147–154

Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecol Lett 11:637–650

Boyce MS, McDonald LL (1999) Relating populations to habitats using resource selection functions. Trends Ecol Evol 14:268–272

Brooks LB, Harvey JT, Nichols WJ (2009) Tidal movements of East Pacific green turtle *Chelonia mydas* at a foraging area in Baja California Sur, Mexico. Mar Ecol Prog Ser 386:263–274

Brown JS (1988) Patch use as an indication of habitat preference, predation risk, and competition. Behav Ecol Sociobiol 22:37–47

Brown JS (1999) Vigilance, patch use and habitat selection: foraging under predation risk. Evol Ecol Res 1:49–71

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–1014

Cederlund G, Sand H (1994) Home-range size in relation to age and sex in moose. J Mammal 75:1005–1012

Charnov EL (1976) Optimal foraging, the marginal value theorem. Theor Popul Biol 9:129–136

Christiansen F, Lusseau D (2015) Linking behavior to vital rates to measure the effects of non-lethal disturbance on wildlife. Conserv Lett 8:424–431

Cowlishaw G (1997) Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Anim Behav 53:667–686

Creel S, Winnie J, Maxwell B et al (2005) Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397

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

Erdman C, Emerson JW (2007) bcp: an R package for performing a Bayesian analysis of change point problems. J Stat Softw 23:1–13

Festa-Bianchet M (1988) Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580–586

Forester JD, Ives AR, Turner MG et al (2007) State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecol Monogr 77:285–299

Fretwell SD, Lucas HL (1970) On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biol 19:16–36

Fryxell JM (1991) Forage quality and aggregation by large herbivores. Am Nat 138:478–498

Fryxell JM, Wilmshurst JF, Sinclair ARE (2004) Predictive models of movement by serengeti grazers. Ecology 85:2429–2435

Fryxell JM, Hazell M, Börger L et al (2008) Multiple movement modes by large herbivores at multiple spatiotemporal scales. PNAS 105:19114–19119

Godley BJ, Richardson S, Broderick AC et al (2002) Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. Ecography 25:352–362

Gredzens C, Marsh H, Fuentes MMPB et al (2014) Satellite tracking of sympatric marine megafauna can inform the biological basis for species co-management. PLoS ONE 9:e98944

Hays GC, Luschi P, Papi F et al (1999) Changes in behaviour during the internesting period and postnesting migration for Ascension Island green turtles. Mar Ecol Prog Ser 189:263–273

Hays GC, Adams CR, Broderick AC et al (2000) The diving behaviour of green turtles at Ascension Island. Anim Behav 59:577–586

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, Ferreira LC, Sequeira AMM et al (2016) Key questions in marine megafauna movement ecology. Trends Ecol Evol 31:463–475

Hazel J (2009) Evaluation of fast-acquisition GPS in stationary tests and fine-scale tracking of green turtles. J Exp Mar Bio 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 Bio Ecol 371:84–92

Heithaus MR, Dill LM (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480–491

Heithaus MR, Dill LM (2006) Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? Oikos 114:257–264
Heithaus MR, Frid A, Dill LM (2002) Shark-inflicted injury frequencies, escape ability, and habitat use of green and loggerhead turtles. Mar Biol 140:229–236
Heithaus MR, Frid A, Wirsing AJ et al (2007) State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. J Anim Ecol 76:837–844
Hobbs NT (1996) Modification of ecosystems by ungulates. J Wildl Manage 60:695–713
Hopcraft JGC, Morales JM, Beyer HL et al (2014) Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. Ecol Monogr 84:355–372
Houston AI, McNamara JM, Hutchinson JMC (1993) General results concerning the trade-off between gaining energy and avoiding predation. Philos Trans R Soc B 341:375–397
Humphries NE, Queiroz N, Dyer JR et al (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature 465:1066–1069
Illius AW, Fitzgibbon C (1994) Costs of vigilance in foraging ungulates. Anim Behav 47:481–484
Kittle AM, Fryxell JM, Desy GE, Hamr J (2008) The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. Oecologia 157:163–175
Langvatn R, Hanley TA (1993) Feeding-patch choice by red deer in relation to foraging efficiency. Oecologia 95:164–170
Laundré JW, Hernandez L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Can J Zool 79:1401–1409
Lima SL (2002) Putting predators back into predator-prey behavioral interactions. Trends Ecol Evol 17:70–75
Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640
Limpus CJ, Limpus DJ (2000) Mangroves in the diet of *Chelonia mydas* in Queensland, Australia. Mar Turt Newsl 89:13–15
MacDonald BD, Madrak SV, Lewison RL et al (2013) Fine scale diel movement of the east Pacific green turtle, *Chelonia mydas*, in a highly urbanized foraging environment. J Exp Mar Bio Ecol 443:56–64
Makowski C, Seminoff JA, Salmon M (2006) Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. Mar Biol 148:1167–1179
McLoughlin PD, Ferguson SH (2000) A hierarchical pattern of limiting factors helps explain variation in home range size. Écoscience 7:123–130
McNaughton SJ, Banyikwa FF, McNaughton MM (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278:1798–1800
Mech LD (1977) Productivity, mortality, and population trends of wolves in northeastern Minnesota. J Mammal 58:559–574
Minamikawa S, Naito Y, Sato K et al (2000) Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. J Exp Biol 203:2967–2975
New LF, Clark JS, Costa DP et al (2014) Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. Mar Ecol Prog Ser 496:99–108
R Core Team (2014) R: a language and environment for statistical computing. http://www.rproject.org/
Rasheed MA (1999) Recovery of experimentally created gaps within a tropical *Zostera capricorni* (Aschers.) seagrass meadow, Queensland Australia. J Exp Mar Bio Ecol 235:183–200
Rasheed MA, McKenna SA, Carter AB, Coles RG (2014) Contrasting recovery of shallow and deep water seagrass communities following climate associated losses in tropical north Queensland, Australia. Mar Pollut Bull 83:491–499
Riginos C, Grace JB (2008) Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. Ecology 89:2228–2238
Ritchie ME, Tilman D, Knops JMH (1998) Herbivore effects on plant and nitrogen dynamics in Oak savanna. Ecology 79:165–177
Robbins BD, Bell SS (2000) Dynamics of a subtidal seagrass landscape: seasonal and annual change in relation to water depth. Ecology 81:1193–1205
Seminoff JA, Jones TT (2006) Diel movements and activity ranges of Green turtle (*Chelonia mydas*) at a temperate foraging area in the Gulf of California, Mexico. Herpetol Conserv Biol 1:81–86
Seminoff JA, Resendiz A, Nichols WJ (2002) Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. Mar Ecol Prog Ser 242:253–265
Senko J, Koch V, Megill WM et al (2010) Fine scale daily movements and habitat use of East Pacific green turtles at a shallow coastal lagoon in Baja California Sur, Mexico. J Exp Mar Bio Ecol 391:92–100
Sheppard JK, Jones RE, Marsh H, Lawler IR (2009) Effects of tidal and diel cycles on dugong habitat use. J Wildl Manage 73:45–59
Sih A (1980) Optimal behavior: can foragers balance two conflicting demands? Science 210:1041–1043
Sims DW, Southall EJ, Humphries NE et al (2008) Scaling laws of marine predator search behaviour. Nature 451:1098–1102
Sprogis KR, Raudino HC, Rankin R et al (2016) Home range size of adult Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a coastal and estuarine system is habitat and sex-specific. Mar Mammal Sci 32:287–308
Storch I (1993) Habitat selection by capercaillie in summer and autumn: is bilberry important? Oecologia 95:257–265
Taquet C, Taquet M, Dempster T et al (2006) Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. Mar Ecol Prog Ser 306:295–302
Tyne JA, Johnston DW, Rankin R et al (2015) The importance of spinner dolphin (*Stenella longirostris*) resting habitat: implications for management. J Appl Ecol 52:621–630
Valeix M, Loveridge AJ, Chamaille-Jammes S et al (2009) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology 90:23–30
Van Beest FM, Rivrud IM, Loe LE et al (2011) What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? J Anim Ecol 80:771–785
Wallis de Vries MF, Laca EA, Demment MW (1999) The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia 121:355–363
Wang M, Grimm V (2007) Home range dynamics and population regulation: an individual-based model of the common shrew *Sorex ayaneus*. Ecol Modell 205:397–409
Watanabe YY, Sato K, Watanuki Y et al (2011) Scaling of swim speed in breath-hold divers. J Anim Ecol 80:57–68
Wirsing AJ, Heithaus MR, Dill LM (2007) Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. Anim Behav 74:93–101
Worton BJ (2002) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 83:3257–3265
Zieman JC, Iverson RL, Ogden JC (1984) Herbivory effects on *Thalassia testudinum* leaf growth and nitrogen content. Mar Ecol Prog Ser 15:151–158