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# Large-scale movement patterns of male loggerhead sea turtles (*Caretta caretta*) in Shark Bay, Australia

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**Abstract.** Large marine vertebrates are particularly susceptible to anthropogenic threats because they tend to be long-lived, late to mature and wide-ranging. Loggerhead sea turtles (*Caretta caretta*) are characterised by such life history traits and are listed as 'Endangered' by The World Conservation Union. Although juvenile movements and at-sea behaviour of adult females are relatively well studied, little is known about the movements of males and their subsequent exposure to threats. Shark Bay, Western Australia, is home to the largest breeding population of loggerhead turtles in Australia. We assessed the large-scale movements of nine adult male loggerhead turtles, with the goal of aiding conservation and management policies. During 7 months outside the breeding season, all nine turtles stayed within the Shark Bay World Heritage Area, with most showing fidelity to small coastal foraging areas. Several turtles, however, showed relatively large movements between core foraging areas. None of the four turtles that continued transmitting through the breeding season exhibited obvious movements towards nesting beaches, suggesting that mating may occur on foraging grounds or that males are not mating every year. Quantifying male loggerhead movements assists conservation planning by identifying biologically relevant spatial scales at which research and management strategies should be designed.

**Additional keywords:** Argos, habitat use, Indian Ocean, kernel density estimation, satellite telemetry, spatial ecology.

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## Introduction

Large marine vertebrates tend to be wide-ranging, long-lived, and can take decades to reach maturity, making them particularly susceptible to anthropogenic threats (Godley *et al.* 2010; Maxwell *et al.* 2011; Scott *et al.* 2012). Accordingly, there is a critical need for an improved understanding of their distribution and movement patterns, including those of all age and sex classes, so as to assess threats to which individuals are exposed and to develop effective conservation and recovery strategies (Block *et al.* 2001; James *et al.* 2005; Schofield *et al.* 2007). Until recently, ascertaining these basic properties for large marine vertebrates has been complicated by the difficulty of tracking vagile taxa in the ocean. The advent of satellite telemetry, however, has revolutionised our ability to closely monitor these species and has yielded new insights into their ecology.

Distributed throughout tropical and temperate oceans worldwide, loggerhead sea turtles (*Caretta caretta*) are listed as 'Endangered' by The World Conservation Union (Eckert *et al.* 2008). To date, studies of loggerhead turtle movements have focussed on juveniles and females departing nesting beaches (Rees *et al.* 2010; Hawkes *et al.* 2011). Unlike females, males do not emerge onto nesting beaches, making attachment of tracking devices more difficult, studies less frequent and movement patterns of adult males less well known (Godley *et al.* 2008). Because differential use of habitat between sexes has been observed in a wide range of species, movement patterns and habitat use information for female loggerhead turtles cannot be applied to males (Breed *et al.* 2006; Van Dam *et al.* 2008; Schofield *et al.* 2010). Moreover, tracking male loggerhead turtles has the potential to identify sex differences in foraging habitats, reveal breeding areas and uncover anthropogenic threats to which only male loggerheads are exposed. Recently, in-water capture and tracking of males has begun to address the lack of information on male movements (e.g. Hays *et al.* 2010; Schofield *et al.* 2010; Arendt *et al.* 2012); however, these studies have been undertaken only in a few locations.

Much of what is known about sea turtle foraging ecology has been acquired from habitats that have been degraded by substantial anthropogenic impacts. Because anthropogenic activity can alter factors shaping movement patterns, such as population density, resource availability, abundance of predators and abiotic factors, turtles in human-affected areas could exhibit different movement patterns than they would under more natural conditions. Thus, undertaking studies in relatively pristine locations is a priority (e.g. Heithaus *et al.* 2005; Hamann *et al.* 2010).

The Shark Bay World Heritage Area (SBWHA), in Western Australia, provides a unique opportunity to examine the spatial ecology of loggerhead turtles in a relatively pristine seagrass ecosystem (Heithaus *et al.* 2005). Monitoring of loggerhead turtle nesting in Shark Bay began in 1994, when the Western Australia Department of Environment and Conservation started an annual tagging program on the Dirk Hartog Island nesting beach (Baldwin *et al.* 2003). In 1999, the Shark Bay Ecosystem Research Project began monitoring and tagging loggerheads on a foraging ground in the Eastern Gulf of Shark Bay. These initiatives have revealed that Shark Bay contains the largest nesting population of loggerhead sea turtles in Australia and that many females nesting on Dirk Hartog Island migrate to the foraging grounds in the Eastern Gulf (Heithaus *et al.* 2002; Baldwin *et al.* 2003). Yet, long-term and large-scale space use by loggerhead turtles in the bay, and especially the movements of males in this population, remain poorly understood. In Shark Bay, however, a pilot study in 2004 revealed that after 7 months, two females stayed within 10 km of their initial capture location, whereas the only tagged male moved ~140 km north, out of the SBWHA (Wirsing *et al.* 2004). Expanding on this preliminary effort, we used satellite telemetry and kernel density estimation to quantify large-scale movement and habitat use patterns of adult male loggerhead turtles, with the aim of informing conservation strategies and gaining insights into foraging and reproductive movements of male turtles.

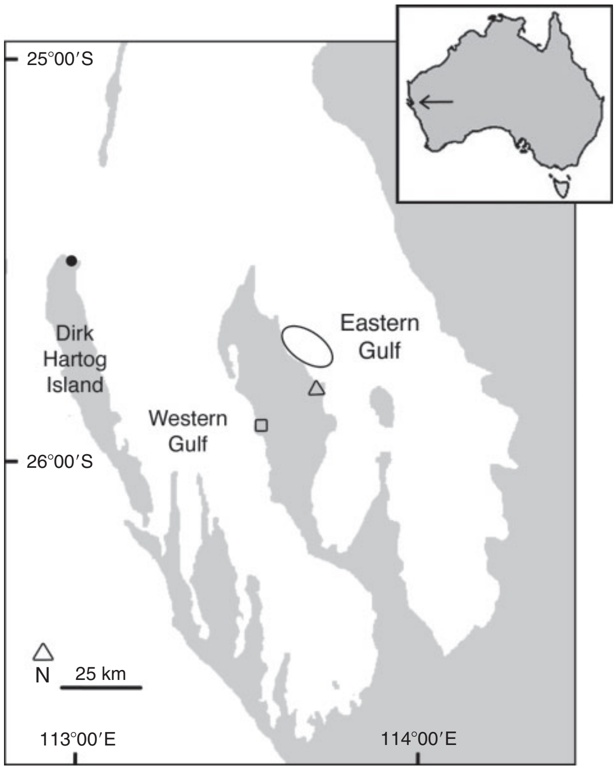


**Fig. 1.** Study site in the eastern gulf of Shark Bay, Western Australia. The square indicates the location of Denham. The triangle indicates the location of the Monkey Mia Dolphin Resort. The solid circle indicates the location of the nesting beach. The open circle indicates the area where the turtles were captured. Grey indicates land; white indicates ocean.

## Materials and methods

### *Study area*

Shark Bay, Western Australia (Fig. 1), is a World Heritage Area featuring expansive seagrass meadows (Walker *et al.* 1988) that have experienced minimal human impacts and support intact populations of large-bodied herbivores and predators (Preen *et al.* 1997; Heithaus *et al.* 2005; Vaudo and Heithaus 2009). Located at a latitudinal transition between tropical and temperate marine ecosystems, Shark Bay is at the southern end of Western Australia's loggerhead turtle breeding range (Baldwin *et al.* 2003). The northern beaches of Dirk Hartog Island, found along the bay's western margin, are home to the largest nesting population of loggerhead sea turtles in Australia (Baldwin *et al.* 2003). Both the Eastern and Western gulfs of Shark Bay are foraging grounds for large numbers of adult and subadult loggerhead turtles that may frequent nesting beaches of Dirk Hartog Island or those along the north-west coast of Western Australia (Heithaus *et al.* 2005; Thomson *et al.* 2012).

This research was conducted in the Eastern Gulf (~25°45′S, 113°44′E), offshore of the Monkey Mia Dolphin Resort (Fig. 1). This region encompasses extensive nearshore sandflats that support loggerhead turtles and other large benthic predators (Vaudo and Heithaus 2009; Thomson *et al.* 2012), numerous offshore seagrass banks (<4.0 m depth), and largely unvegetated deeper waters (6.5–15.0 m depth) (Heithaus *et al.* 2005).

### *Turtle capture and tagging*

In February and March 2009, nine male loggerhead turtles (based on tail lengths >25 cm) were captured by hand while searching haphazardly in shallow waters (<5.0 m depth) from a 5.5 m boat. Once captured, each turtle was brought alongside the boat, placed in a harness and weighed (±1 kg) using a hanging Salter scale (see Thomson *et al.* 2009). Turtles were brought onboard, measured (curved carapace length, CCL) and equipped with a titanium flipper tag. Each turtle was fitted with a Wildlife Computers SPOT5 ($n = 8$) or SPOT4 ($n = 1$) satellite transmitter (Wildlife Computers, Redmond, WA, USA; Fig. 2). Satellite tags were attached to the highest part of the carapace, using West Systems 105 epoxy with 205 hardener and borosilicate microballoons (see Eckert *et al.* 2008). Each tag was covered in dark blue Interlux Micron 66 antifouling paint (International Paint, Union, New Jersey, USA), which was allowed to dry before each turtle was released.

### *Satellite telemetry, accuracy and filtering*

SPOT tags used the Argos system (www.argos-system.org, verified 30 October 2012) to derive positional information (CLS 2011). Position estimates were then managed using the Satellite Tracking and Analysis Tool (STAT; Coyne and Godley 2005). Each Argos position estimate contains a location classification (LC) representing an estimated accuracy, which enables

**Fig. 2.** Male loggerhead with SPOT satellite tag and antifouling paint.

filtration of points on the basis of accuracy requirements. LCs 3, 2, and 1 have Argos estimated errors of less than 250 m, 500 m and 1500 m, respectively. LCs 0, A and B have no associated error estimations provided by Argos. Empirical studies by Hays *et al.* (2001) and Royer and Lutcavage (2008) found location class A comparable in accuracy to location class 1 (errors from Hays *et al.* (2001): LC1 = 1.33 km ± 1.35 s.d., LCA = 0.99 km ± 1.36 s.d.; errors from Royer and Lutcavage (2008): LC1 = 2.01 km, LCA = 2.78 km). More recently, Witt *et al.* (2010) found errors such that LC3 < LC2 < LC1 < LCA < LCB < LC0; with error for LC1 = 0.8 km ± 0.7 s.d., and error for LCA = 1.4 km ± 2.5 s.d.

Acknowledging the trade-off between filtering out location classes with greater error and retaining enough position estimates to get a realistic estimate of a turtle's space use, we filtered positions by removing points classified as LC 0 or B. Including LC A positions nearly doubled (and in some cases tripled) the number of position estimations gathered during the 7-month tracking period. Because the methods we used to estimate activity space place a high probability of use where the density of points is greater, the cost of including points that could be less accurate was offset by the value of having more points to provide a more complete representation of the space used. Retention of LCs 3, 2, 1 and A is consistent with recent studies of marine turtles by Hawkes *et al.* (2011) and Zbinden *et al.* (2008). Further filtering removed obviously erroneous points (e.g. on land) and points requiring a swimming speed $>5\,\mathrm{km\,h^{-1}}$ (Luschi *et al.* 1998; Mangel *et al.* 2011). Filtered positions were plotted using ArcGIS 9.3 (ESRI, Redlands, California, USA).

### *Activity-space analysis*

We estimated loggerhead movement patterns with kernel density estimation in ArcGIS 9.3 (ESRI) by using Hawth's tools fixed kernel density estimator (www.spatialecology.com/htools, verified 30 October 2012) with a bivariate normal kernel (Worton 1989). This method generates probability density functions with percent volume contours (pvc) that delineate the space where there is a specified probability that an animal will be found over a particular time period (Kernohan *et al.* 2001). Thus, an 85 pvc activity space displays an area in which there is an 85% probability of finding the animal, given a particular time period.

Bandwidth selection is critical in kernel density estimation because, as a smoothing parameter, it controls the width of each point's probability density kernel. Various bandwidth selectors have been developed that use spatial data to minimise the mean integrated square error between the estimated density and the true unknown density. Two of the most robust bandwidth selectors are least-squares cross-validation (LSCV) and direct plug-in (Lichti and Swihart 2011). We used the 'ks' package in R (http://www.r-project.org) to produce 85 pvc activity spaces for each of the nine turtles using both the LSCV and direct plug-in methods. Although LSCV and direct plug-in performed similarly for most of the turtles (mean difference for seven of the turtles: $11\,\mathrm{km^2} \pm 6.5$ s.d.), the LSCV bandwidth for a turtle with two foraging sites that were far apart (see below) was not ecologically realistic. On the basis of this and previous studies suggesting that direct plug-in methods are more precise (Wand and Jones 1995; Duong 2007; Lichti and Swihart 2011), we chose to use the direct plug-in bandwidth selector.

Kernel density estimates were generated for each of the nine male loggerhead turtles using data transmitted between release (22 February – 27 March 2009) and 1 October 2009. We then calculated 50 pvc activity spaces to identify highly used, or core, spaces within each turtle's home range, 85 pvc activity spaces to encompass a larger amount of each turtle's movements, and 95 pvc activity spaces to incorporate area closer to the edges of each turtle's range. Although 95 pvc areas are frequently used in animal space use studies (Seaman *et al.* 1999), we included 85 pvc activity spaces because inner contours are more reliable (Seaman *et al.* 1999) and 85 pvc spaces are less susceptible to position errors of LC A points (i.e. many LC A points that are outliers as a result of error will be in a space of low probability and be excluded by a smaller pvc area).

### *Location class sensitivity*

To examine the sensitivity of activity spaces due to location-class filtering, kernel density estimates were generated and 50, 85 and 95 pvc activity spaces calculated using the datasets of LCs 3, 2 and 1 (filtered for obviously erroneous and speed $>5\,\mathrm{km\,h^{-1}}$) and compared with those that included LC A positions. Also, because sample size could influence pvc areas, 50, 85 and 95 pvc activity spaces were generated for each turtle by using randomly selected points from the datasets of LCs 3, 2, 1 and A (filtered for obviously erroneous and speed $>5\,\mathrm{km\,h^{-1}}$), with an identical number of points to the datasets with LCs 3, 2 and 1 for that individual. This random selection and activity space calculation was performed five times to determine a mean and standard error for each turtle.

**Table 1. Summary of physical and tracking information for nine male loggerhead turtles fitted with SPOT satellite transmitters from Wildlife Computers (Redmond, WA, USA)**

Turtles were tracked between 22 February and 1 October 2009. Data points retained are of location classes 3, 2, 1 and A. Displacement is based on distance between release location and final transmission location. Percent volume contours (pvc) were calculated from kernel density estimations generated for each turtle. CCL, curved carapace length

| Turtle | Length (CCL in cm) | Weight (kg) | No. of days tracked | No. of data points | Displacement (km) | Activity spaces | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | 50 pvc (km$^2$) | 85 pvc (km$^2$) | 95 pvc (km$^2$) |
| 1 | 98 | 120 | 215 | 203 | 2.5 | 25.5 | 182.8 | 309.1 |
| 2 | 100 | 108 | 220 | 298 | 2.2 | 7.8 | 52.3 | 107.4 |
| 3 | 102 | 120 | 219 | 232 | 26.7 | 5.5 | 27.9 | 60.3 |
| 4 | 101 | – | 219 | 249 | 2.7 | 5.2 | 36.5 | 81.5 |
| 5 | 98 | 115 | 219 | 311 | 100.4 | 171.5 | 586.8 | 1771.9 |
| 6 | 96 | 106 | 202 | 208 | 3.3 | 10.3 | 62.0 | 131.9 |
| 7 | 99 | 120 | 105 | 83 | 49.8 | 7.3 | 52.8 | 90.3 |
| 8 | 103 | 135 | 217 | 336 | 25.5 | 35.1 | 139.3 | 297.9 |
| 9 | 90 | – | 146 | 128 | 33.9 | 123.0 | 533.5 | 1099.6 |

### *Seasonality of spatial activity*

To test if loggerhead space use varies as a function of season, we calculated 85 pvc activity spaces for 3-month periods during the breeding season (1 November 2009 – 1 February 2010) and outside the breeding season (1 May – 1 August 2009) (Baldwin *et al.* 2003) for the four turtles that continued transmitting through 1 February 2010. The effect of season on activity space size was tested with a paired *t*-test on normalised data.

## Results

### *Activity spaces*

The nine male loggerhead turtles on which we deployed satellite transmitters ranged in size from 90 to 103 cm CCL (mean 98.6 ± 3.7 s.d.) and from 106 to 135 kg (mean 117.7 ± 8.9 s.d.) (Table 1). The mean number of days tracked was 172 (±41 s.d.) and the mean number of data points (LCs 3, 2, 1, A) for each turtle was 227 (±79 s.d.) (Table 1). Displacements between release locations and final position points ranged from 2.2 to 100.4 km, with a mean of 27.4 km (±32.3 s.d.) (Table 1). Core activity spaces varied considerably among individuals. The 50% probability of occurrence ranged from 5.2 km$^2$ to 171.5 km$^2$ (mean 43.5 km$^2$ ± 57.5 s.d.), 85% probability of occurrence ranged from 27.9 km$^2$ to 586.8 km$^2$ (mean 186.0 km$^2$ ± 206.0 s.d.) and 95% probability of occurrence ranged from 60.3 km$^2$ to 1771.9 km$^2$ (mean 438.9 km$^2$ ± 562.4 s.d.) (Table 1, Fig. 3).

Individual turtles exhibited one of two major types of movement. Four turtles (2, 3, 4, 7) used a single continuous area <53 km$^2$ (based on 85 pvc activity spaces) exclusively for the duration of the tracking period (22 February – 1 October 2009). The other five individuals (1, 5, 6, 8, 9) used one area for a period of time, but then transited to another area where they took up residence and remained for anywhere from a week to several months (Fig. 3). For example, Turtle 5 inhabited an area in the Eastern Gulf for several months, and then, over the course of 3 days in June, moved roughly 85 km, to the coastal waters off of Bernier and Dorre Islands, where it stayed until the end of September (Fig. 3). Four (1, 6, 8, 9) of the five turtles that used more than one core area returned to the area they used immediately following capture and tagging (Fig. 4). Turtle 8 transited between its two core areas, spaced ~10 km apart, three times, whereas Turtle 9 moved between its two core areas, which were ~15 km apart, 11 times over 7 months of tracking.

### *Location class analysis*

When we used LCs 3, 2 and 1, the 85 pvc activity spaces (mean 84.4 km$^2$ ± 140.7 s.d.) generated were 20.7–87.5% smaller than the 85 pvc activity spaces generated using points with LCs 3, 2, 1 and A (mean 186.0 km$^2$ ± 206.0 s.d.) (Table 2, Fig. 5*a*). Similarly, 85 pvc activity spaces using LCs 3, 2 and 1 (mean 84.4 km$^2$ ± 140.7 s.d.) were 51.4–79.7% smaller than 85 pvc activity spaces generated by randomly selecting an equal number of points from the dataset with LCs 3, 2, 1 and A (mean 233.0 km$^2$ ± 303.4 s.d.) (Table 2, Fig. 5*b*).

The 50 and 95 pvc activity spaces followed the same trend as the 85 pvc activity spaces. Using LCs 3, 2 and 1, 50 pvc activity spaces (mean 29.5 ± 56.0 s.d.) were on average smaller than 50 pvc activity spaces generated with LCs 3, 2, 1 and A (mean 43.5 ± 57.5 s.d.) and on average smaller than 50 pvc activity spaces generated by randomly selecting an equal number of points from the dataset with LCs 3, 2, 1 and A (mean 70.9 ± 109.5 s.d.) (Table 3). Using LCs 3, 2 and 1, 95 pvc activity spaces (mean 130.1 ± 211.1 s.d.) were smaller than 95 pvc activity spaces generated using LCs 3, 2, 1 and A (mean 438.9 ± 562.4 s.d.) and smaller than activity spaces generated by randomly selecting an equal number of points from the dataset with LCs 3, 2, 1 and A (mean 421.9 ± 584.6 s.d.) (Table 4).

### *Seasonality of spatial activity*

Based on four turtles for which we had sufficient time series of spatially explicit data, there was no significant difference in loggerhead activity space as a function of breeding season ($n = 4$, $t = 2.14$, $P = 0.12$). Three turtles (1, 5, 9) exhibited smaller activity spaces during breeding season (Fig. 5*c*) and one turtle (2) manifested a larger activity space during breeding season (Fig. 5*c*). No turtles moved to waters close to nesting beaches in the Western Gulf of Shark Bay during the breeding season.

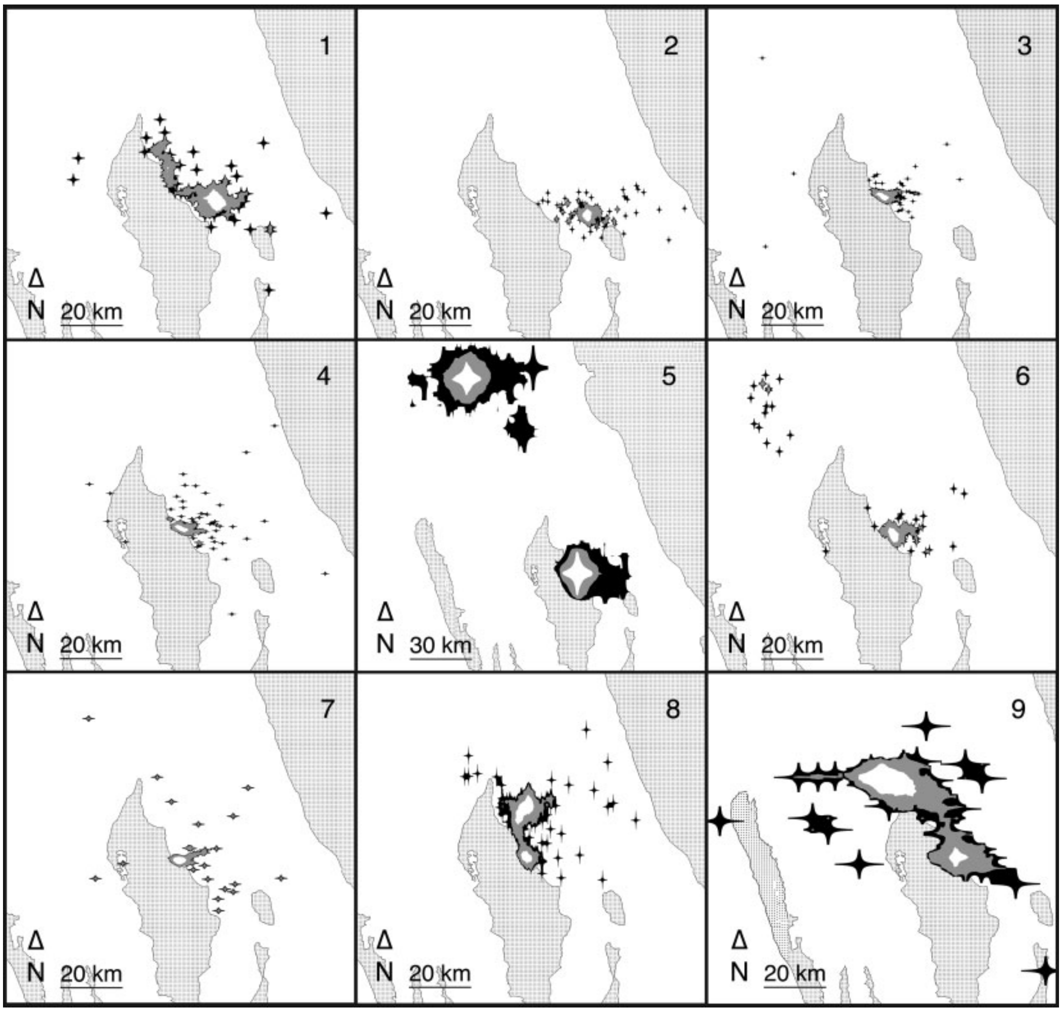


**Fig. 3.** Probability density functions generated from kernel density estimation for three percent volume contours (pvc) for nine turtles; 50 pvc areas (white), 85 pvc areas (grey) and 95 pvc areas (black). Note the variation in spatial scale for wide-ranging Turtle 5.

## Discussion

Activity space sizes, based on 85 pvc, of nine male loggerhead sea turtles in Shark Bay, Australia, varied considerably and displayed two primary space-use tactics. Both of these tactics, however, tended to result in relatively little displacement of turtles. After 7 months of tracking, eight of the nine turtles were within 50 km of their original capture location, and four of those were within 4 km of their original capture location. We did not observe any large migratory movements out of Shark Bay and up the coast of Western Australia by the nine turtles in this 7-month tracking study. Early tracking research in the same study area showed that although turtles may remain in single, relatively small activity spaces, others may relocate, at least temporarily, to other core areas (Wirsing *et al.* 2004). More recently, tag–recapture data have shown that a considerable number of male loggerhead turtles show multi-year fidelity to a relatively small area along the western coast of the Eastern Gulf, where the current study took place (e.g. Heithaus *et al.* 2005; Thomson *et al.* 2012). Consequently, the patterns we report here are consistent with previous work in Shark Bay, but divergent from international studies documenting extremely vast loggerhead turtle movement elsewhere.

Movements and activity spaces of loggerhead turtles on foraging grounds vary considerably among locations. For example, female loggerheads in the north-western Atlantic occupy foraging areas anywhere from hundreds to thousands of square kilometres (Hawkes *et al.* 2011), females off the coast of Brazil occupy foraging areas between 500 and 1500 $km^2$ (Marcovaldi *et al.* 2010), and Mediterranean females use foraging areas between 3.5 and 1198 $km^2$ (Zbinden *et al.* 2008). Recent studies on adult male loggerheads in the Mediterranean suggest that they follow similar migratory patterns as adult females, but differ in the sites in which they forage (Schofield *et al.* 2009), with foraging areas ranging from 10 $km^2$ in neritic habitats to 1000 $km^2$ in oceanic habitats (Schofield *et al.* 2010). Studies tracking adult male loggerheads in the western Atlantic found foraging area sizes anywhere from 31 to 3234 $km^2$, with larger areas being associated with greater latitudes

(Arendt *et al.* 2012). This variation suggests that local factors play an important role in determining behaviour and hindered our capacity to predict the movements of male loggerheads in Shark Bay by using the results of studies in other areas. We found males to use foraging area sizes comparable to the smaller neritic foraging areas used by Mediterranean males, which is consistent with the idea that movements should be relatively restricted in resource-rich habitats such as Shark Bay.

Although all turtles in this study exhibited relatively small foraging areas, movement patterns on the foraging grounds differed, with individuals either (1) staying in one foraging area, or (2) moving between two different core foraging areas. Among the latter group, we observed differences in both the distance between core areas and the frequency with which turtles moved between them; the greater the distance between the two areas, the less often turtles switched foraging sites. For example, Turtle 5 travelled 85 km to a second site just once in 7 months, whereas Turtle 9 moved 11 times between two foraging areas that were only 15 km apart. Recaptures of tagged individuals suggest that short-distance movements along the shallow sandy habitats of the Eastern Gulf are probably common (Heithaus *et al.* 2005; Thomson *et al.* 2012). The factors driving individual variation in movement tactics remain unclear at this time, but may be caused by differential responses to variation in predation risk and resource abundance or prey types, or differences in social behaviour or mating tactics. Altered movement patterns in relation to mating are also possible, given that activity spaces tended to be smaller during the breeding season than outside of the breeding season.

Unlike male loggerhead turtles in the Mediterranean (Schofield *et al.* 2009) and along the eastern coast of Australia (Schroeder *et al.* 2003), those in Shark Bay did not show movements to waters offshore of nesting beaches. This finding suggests that males in Shark Bay may not be mating each year or may be mating within the foraging habitats and do not need to move seasonally to breed, possibly because of the proximity of nesting beaches. Indeed, mating has been observed on foraging grounds on multiple occasions. However, this result should be interpreted with caution because of relatively low sample sizes and long-distance movements found in one male turtle tracked before the current study (Wirsing *et al.* 2004).

Technological advances in satellite telemetry have allowed for increases in tracking durations; however, identifying causes of transmission cessation to improve future study designs remains difficult. Hays *et al.* (2007) identified battery exhaustion, salt-water switch failure, antenna breakage and animal mortality as causes for satellite transmitter cessation. Although specific causes of signal loss in this study are unknown, recapture of Turtle 3 in December 2011 revealed that its tag had been worn down, such that only the base of the housing remained. Animal-borne cameras deployed on loggerhead turtles in Shark

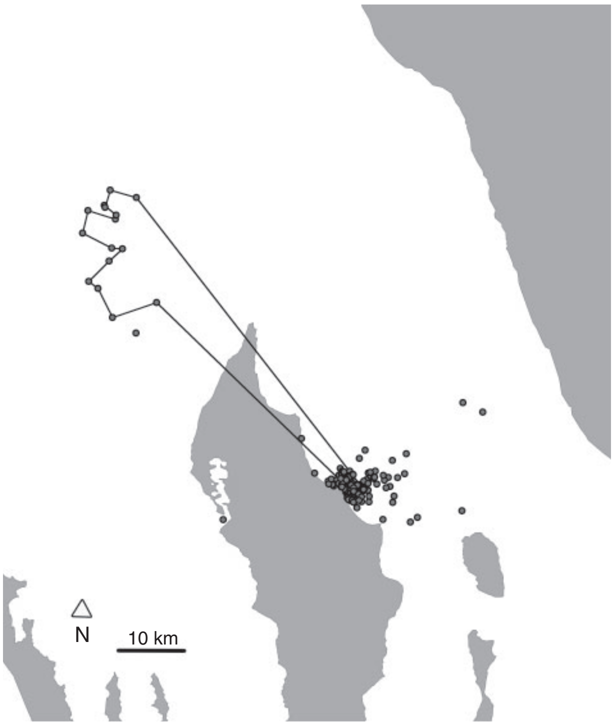


**Fig. 4.** Location estimates for Turtle 6. Lines chronologically connect points during 21 July – 4 September 2009, to highlight when the turtle travelled from one foraging area to a second foraging area, and back again.

**Table 2. Summary of 85 pvc activity spaces for each turtle, calculated using all points with LCs 3, 2 and 1, all points with LCs 3, 2, 1 and A and randomly selected points from the dataset with LCs 3, 2, 1 and A, to match the sample size of the dataset of LCs 3, 2 and 1, and repeated five times to generate a mean and standard error**

| Turtle | All LC321 | | All LC321A | | Randomly selected LC321A | |
|---|---|---|---|---|---|---|
| | No. of data points | 85 pvc activity space ($km^2$) | No. of data points | 85 pvc activity space ($km^2$) | No. of data points | 85 pvc activity space (mean ± s.e., $km^2$) |
| 1 | 60 | 49.5 | 203 | 182.8 | 60 | 205 ± 20.2 |
| 2 | 127 | 12.6 | 298 | 52.3 | 127 | 58.2 ± 4.7 |
| 3 | 96 | 6.6 | 232 | 27.9 | 96 | 26.5 ± 1.9 |
| 4 | 110 | 6.7 | 249 | 36.5 | 110 | 33.0 ± 1.9 |
| 5 | 107 | 465.5 | 311 | 586.8 | 107 | 957.4 ± 48.3 |
| 6 | 57 | 20.3 | 208 | 62.0 | 57 | 69.9 ± 10.9 |
| 7 | 21 | 6.6 | 83 | 52.8 | 21 | 23.3 ± 4.2 |
| 8 | 180 | 50.7 | 336 | 139.3 | 180 | 154.7 ± 5.1 |
| 9 | 27 | 141.4 | 128 | 533.5 | 27 | 569.1 ± 161.6 |

Bay have filmed individuals repeatedly scraping their carapace on the underside of rock and coral ledges (J. Thomson, pers. comm.), a behaviour also mentioned by Hays *et al.* (2007). Thus, satellite tags may cease working as a result of physical damage (including antenna breakage) and using a rigid bar or shield to protect tags in future deployments could facilitate longer transmission durations and allow for more behavioural information to be gathered.

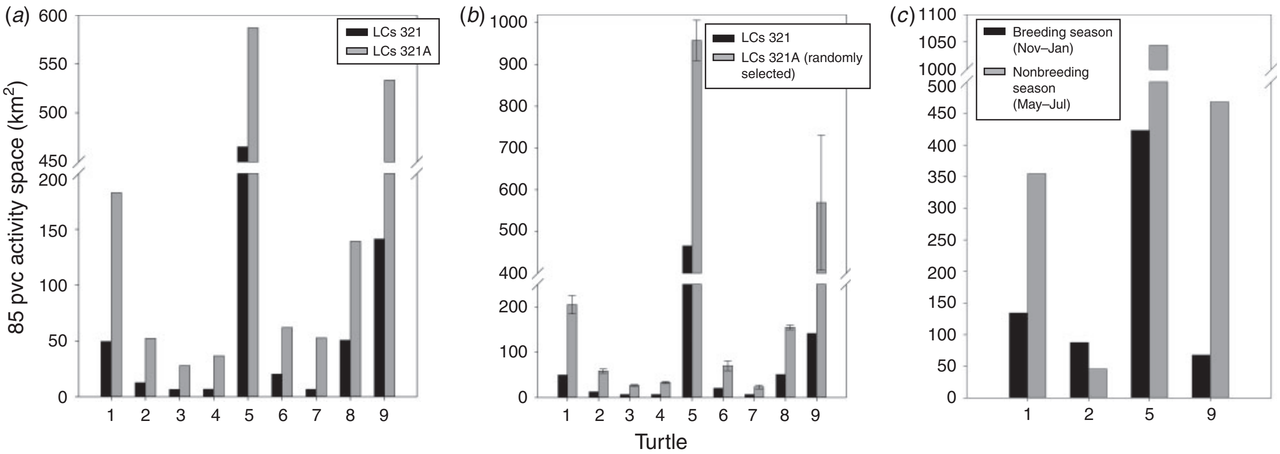


**Fig. 5.** 85 pvc activity spaces for each of the nine turtles generated using (*a*) LCs 321 and LCs 321A, (*b*) LCs 321 and randomly selected points from LCs 321A to match the number of points with LCs 321 (random selection was repeated five times to determine a mean and standard error), and (*c*) LCs 321A during and outside of the breeding season.

**Table 3. Summary of 50 pvc activity spaces for each turtle, calculated using all points with LCs 3, 2 and 1, all points with LCs 3, 2, 1 and A and randomly selected points from the dataset with LCs 3, 2, 1 and A, to match the sample size of the dataset of LCs 3, 2, and 1, and repeated five times to generate a mean and standard error**

| Turtle | All LC321 | | All LC321A | | Randomly selected LC321A | |
|---|---|---|---|---|---|---|
| | No. of data points | 50 pvc activity space (km$^2$) | No. of data points | 50 pvc activity space (km$^2$) | No. of data points | 50 pvc activity space (mean ± s.e., km$^2$) |
| 1 | 60 | 9.4 | 203 | 25.5 | 60 | 38.8 ± 5.0 |
| 2 | 127 | 4.0 | 298 | 7.8 | 127 | 10.2 ± 0.7 |
| 3 | 96 | 2.2 | 232 | 5.5 | 96 | 6.2 ± 0.4 |
| 4 | 110 | 2.1 | 249 | 5.2 | 110 | 5.9 ± 0.3 |
| 5 | 107 | 185.1 | 311 | 171.5 | 107 | 348.3 ± 10.3 |
| 6 | 57 | 6.1 | 208 | 10.3 | 57 | 13.9 ± 1.9 |
| 7 | 21 | 1.9 | 83 | 7.3 | 21 | 5.8 ± 0.9 |
| 8 | 180 | 17.6 | 336 | 35.1 | 180 | 41.2 ± 1.3 |

**Table 4. Summary of 95 pvc activity spaces for each turtle, calculated using all points with LCs 3, 2 and 1, all points with LCs 3, 2, 1 and A and randomly selected points from the dataset with LCs 3, 2, 1 and A, to match the sample size of the dataset of LCs 3, 2 and 1, and repeated five times to generate a mean and standard error**

| Turtle | All LC321 | | All LC321A | | Randomly selected LC321A | |
|---|---|---|---|---|---|---|
| | No. of data points | 95 pvc activity space (km$^2$) | No. of data points | 95 pvc activity space (km$^2$) | No. of data points | 95 pvc activity space (mean ± s.e., km$^2$) |
| 1 | 60 | 85.2 | 203 | 309.1 | 60 | 324.5 ± 40.2 |
| 2 | 127 | 20.7 | 298 | 107.4 | 127 | 101.5 ± 7.2 |
| 3 | 96 | 10.4 | 232 | 60.3 | 96 | 49.9 ± 3.3 |
| 4 | 110 | 11.9 | 249 | 81.5 | 110 | 64.7 ± 3.9 |
| 5 | 107 | 701.0 | 311 | 1771.9 | 107 | 1913.1 ± 166.2 |
| 6 | 57 | 36.8 | 208 | 131.9 | 57 | 116.8 ± 16.4 |
| 7 | 21 | 10.7 | 83 | 90.3 | 21 | 35.3 ± 6.1 |
| 8 | 180 | 78.5 | 336 | 297.9 | 180 | 303.3 ± 8.8 |
| 9 | 27 | 215.4 | 128 | 1099.6 | 27 | 888.4 ± 247.6 |

Identifying male loggerhead turtle movement patterns contributes to the global research priority for marine turtles of identifying loggerhead biogeography in foraging habitats (Hamann *et al.* 2010). Variation in loggerhead-turtle movement strategies around the world highlights the need for studies at multiple scales and locales. The nine turtles in this 7-month tracking study stayed within the Shark Bay World Heritage Area, suggesting that some turtles in the bay are likely part of a resident population and are therefore exposed to a different suite of threats than turtles that leave the bay. The high frequency of recaptures in ongoing research by the Shark Bay Ecosystem Research Project further supports this evidence of residence (Heithaus *et al.* 2005; Thomson *et al.* 2012). Findings from this study also suggest there are localised foraging hotspots within Shark Bay. Future research to uncover fine-scale movements of loggerheads within foraging hotspots may be aided by the deployment of Fastloc GPS tags, which despite involving a greater cost than conventional Argos satellite tags, provide location estimates that are roughly an order of magnitude more accurate (Rutz and Hays 2009; Witt *et al.* 2010).

Because Shark Bay has been designated a World Heritage Area and Marine Park, existing conservation frameworks can be implemented to protect this resident population at the biologically relevant scale at which turtles are moving in Shark Bay, including regulations such as zoning for slower boat speeds to reduce the risk of vessel strikes and fishing guidelines to reduce by-catch. Shark Bay has been deemed a hotspot in the Marine Turtle Recovery Plan for Western Australia (Department of Environment and Conservation 2009), making it an important site for which to continue research into the degree of behavioural plasticity around loggerhead turtle spatial ecology.

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