

Behavioural polymorphism in one of the world's largest populations of loggerhead sea turtles *Caretta caretta*

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ABSTRACT: To aid management and conservation of widely distributed marine vertebrate species, it is necessary to have a knowledge and understanding of their spatial ecology. We tracked 10 adult female loggerhead turtles *Caretta caretta* from Masirah Island, Sultanate of Oman, which hosts one of the world's largest breeding aggregations. Transmitters were specifically deployed early in the nesting season to enable tracking throughout the internesting and post-nesting habitats. Turtles displayed a dichotomy in behaviour during the internesting period, with 6 remaining close to Masirah Island and the others undertaking circuitous oceanic loops, hundreds of kilometres in length. This behaviour did not appear to be related to body size. Tracking-derived minimum clutch frequency was on average (\pm SD) 4.8 ± 1.2 nests ($n = 8$ ind.). Post-nesting migrations revealed a propensity towards long-term utilisation of oceanic habitats in the region between Socotra Island (Yemen) and the mainland of Yemen/Oman, with $76 \pm 15.4\%$ of time spent in oceanic habitat ($n = 8$ ind.). The spatial footprint of our tracked turtles was found to be far less than that of a similar number of turtles that were tagged later in the same season (from a separate unpublished study) and from long-distance returns of flipper tags. The spatial and temporal sub-structuring of the population highlights the need for more comprehensive tracking projects, with deployments across the breeding season in multiple years, in order to obtain reliable estimations of high-use foraging habitats of widely dispersed marine vertebrates. Variation in behaviour patterns suggests the need for diverse conservation measures.

KEY WORDS: *Caretta caretta* · Satellite tracking · Migration · Nesting · Sampling strategy · Oman

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INTRODUCTION

Many megavertebrate taxa utilise large expanses of the marine environment, with differential spatial use according to life stage (e.g. tuna: Dickhut et al. 2009; albatrosses: Croxall et al. 2005; penguins: Jouventin et al. 1994; seals: Field et al. 2005, 2007; whales: Zerbini et al. 2006). The range of marine turtles may encompass entire ocean basins as foraging and development habitats (Bolten et al. 1998, Hays et al. 2004). This places them in contact with a wide range of spatially

explicit threats such as incidental capture in marine fisheries in oceanic (Ferraroli et al. 2004, Lewison et al. 2004, Carranza et al. 2006) and coastal waters (James et al. 2005a, Peckham et al. 2008). This mandates the generation of a more effective understanding of their spatial ecology.

Flipper tagging has provided many important insights on migratory capabilities of marine turtles and point-to-point identification of long-distance movements and/or long-term residency to specific areas (Hendrickson 1958, Balazs 1976, Carr et al. 1978,

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Meylan 1995, Limpus & Limpus 2001). However, the adoption of satellite telemetry in recent decades has revealed a wealth of hitherto unobtainable insights (Godley et al. 2008). Researchers are now able to accurately and remotely track individual turtles over many hundreds of kilometres for many months and in some cases multiple years (Broderick et al. 2007). Although sample sizes are often constrained, findings are almost instant and spatial information often surpasses that resulting from flipper tagging of hundreds or thousands of turtles over a number of years (e.g. Godley et al. 2003a, Troeng et al. 2005, and compare Margaritoulis et al. 2003 with Zbinden et al. 2008). Movement data have facilitated the questioning of existing management methods (Zbinden et al. 2007, Witt et al. 2008, Schofield et al. 2009) and suggestion of new ones (Shaver & Rubio 2008, Shillinger et al. 2008).

Of the sea turtles, the loggerhead turtle *Caretta caretta* is the species for which the spatial ecology has been best elaborated. For example, neonate turtles from the NW Atlantic rookeries spend their first years in the open oceanic realm (Witherington 2002), moving within the North Atlantic Gyre (Bolten et al. 1998, Bolten 2003) before returning to the neritic coastal zone to complete their maturation (Bolten 2003, Schroeder et al. 2003). Once adult, the turtles undertake regular migrations between nesting grounds and foraging areas, which may or may not involve oceanic periods (Plotkin & Spotila 2002, Hawkes et al. 2007). Evidence is accumulating that this life-history pattern is not so rigidly adhered to, in that ontogenetic shifts between oceanic and neritic developmental habitats may be reversible (Kamezaki & Matsui 1997, Bolten 2003, McClellan & Read 2007, McClellan et al. 2010) and that variation exists in behaviour during both internesting and intranesting periods (Blumenthal et al. 2006, Hawkes et al. 2006, see also Seminoff et al. 2008 and Hatase et al. 2006 for green turtles *Chelonia mydas*).

The loggerhead population at Masirah Island, off the coast of the Sultanate of Oman, was first researched in the 1970s and was determined to be one of the largest nesting aggregations in the world, comprising several tens of thousands of individual turtles nesting annually (Ross & Barwani 1995). In the ensuing decades, flipper tagging has been undertaken to some extent and nesting beach surveys generated a more recent update on the population at 20 000 to 40 000 turtles nesting annually (Baldwin

et al. 2003). However, certain key facts relevant for conservation management—interesting habitat, reproductive output and details of post nesting migrations—are lacking.

In the present study we sought to gain insights into the spatial ecology of this population by equipping nesting turtles with satellite transmitters. We deliberately deployed near the beginning of the breeding season to facilitate insights into movements during their breeding season and post-nesting migration.

MATERIALS AND METHODS

Adult female turtles (turtles A to J; see Table 1) were located on the nesting beaches of Masirah Island (20.62°N 58.91°E, n = 8; 20.49°N 58.94°E, n = 2; Fig. 1). After completion of nesting and egg covering, turtles were equipped with Kiwisat 101 platform transmitter terminal (PTT) satellite tags (Sirtrack). All deployments were undertaken between 11 and 16 May 2006, which was early in the nesting season, shown in Ross & Barwani (1995) as starting in April.

The precise level of nesting occurring prior to tag deployment was not available for the current season. Previous data (Ross 1979) suggest that approximately 26% of the study individuals would have nested

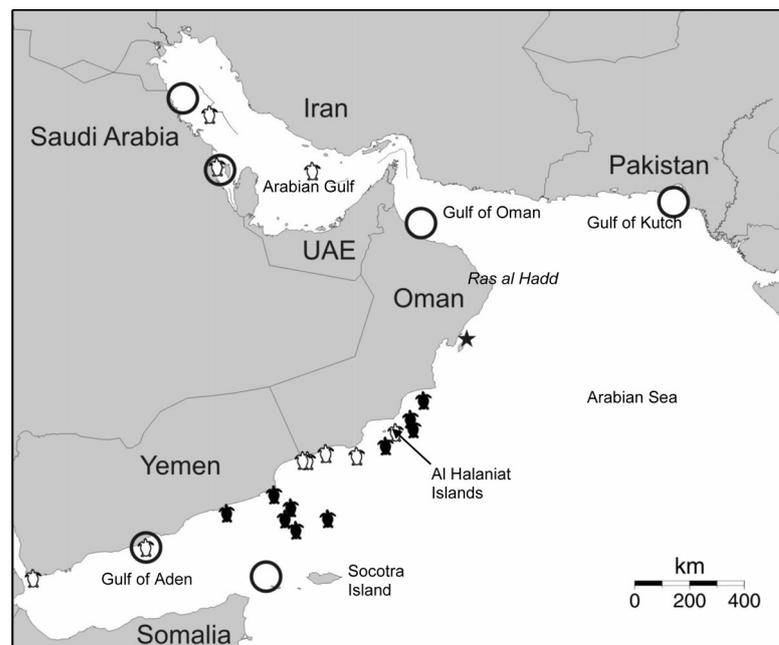


Fig. 1. Study region for *Caretta caretta*. ★ indicates tagged turtle origin (Masirah Island). 🐢 indicate the end locations of turtles tracked in the present study. 🐢 indicate final locations of a further 10 transmitters placed on loggerheads at Masirah, August 2006 (B. E. Witherington & E. Possardt pers. comm.). Circles indicate the locations of long-distance tag recoveries published prior to the present study; no indication of numbers given (Baldwin et al. 2003)

once prior to instrumentation; therefore the clutch-frequency estimations derived for our study animals should be considered minima. No animals bore tags from a previous nesting season. Curved carapace length (CCL, measured from the nuchal notch to the tip of the longest marginal scute; i.e. CCL_{n-t} from Bolten 1999) was recorded prior to transmitter deployment. Transmitters were programmed to be continuously on, with salt water switches used to inhibit signals during submergence, and were attached using 2-part epoxy resin (Foilfast, SFS Stadler; see Godley et al. 2002 for attachment methodology). Tags and epoxy were also coated with antifouling paint to minimise epibiont encrustation. The turtles were additionally flipper-tagged to facilitate re-identification following possible loss of the transmitter.

Telemetry data were generated utilising the Argos data collection system (CLS 2007) that were subsequently retrieved, managed and manipulated through the Satellite Tracking and Analysis Tool (STAT; details of this system are reported in Coyne & Godley 2005).

Locations that were used for assessing movements were taken from Argos Location Classes 3, 2, 1, A and B (shown to be the most accurate locations; Witt et al. 2010) and filtered to remove locations which required unlikely swimming speeds (5 km h^{-1} ; see Luschi et al. 1998), turning behaviour ($<25^\circ$ turn angle) or were inland (1 m above sea level). Locations were then interpolated to provide a single location per 24 h period. No interpolation was undertaken for days where no locations were received.

To facilitate comparison, data for nesting activity assessment were filtered as per Tucker (2010) and nesting was inferred from evaluating 6 of the 8 criteria used by that author; namely (1) distance criterion from a nearest coastline of 1 km, (2) temporal criterion of emergences coinciding within the expected internesting intervals for loggerheads, (3) behavioural criterion for the turtle movements directed onshore for nesting followed by an immediate offshore departure, (4) depth criterion for bathymetry locations associated with depths of -0.5 to 0.5 m indicating time ashore, (5) location quality criterion for an improvement in multiple Argos Location Classes 2 or 3 within a short time span, and (6) signal frequency criterion for evidence of an increased surface interval in the PTT data. Logistical limitations meant that the final 2 criteria of Tucker (2010), ground truthing and genetic verification, were not possible.

Using the above criteria we were unable to distinguish, with any certainty, non-nesting from nesting emergences. Consequently, internesting periods determined here equate to 'egg-laying to egg-laying'. These may be several days longer than the 'egg-laying to next emergence' period, defined by Limpus

(1985) and shown to have a temperature-dependent relationship (Hays et al. 2002a), for turtles that required attempts over several nights to successfully deposit a clutch.

Two distinct behaviours were identified with regards to movements and habitat use during the internesting period: sedentary or wide-ranging. We defined as wide-ranging those turtles whose maximum displacement was >50 km from their initial nesting site during the internesting period. Those not displaying this behaviour were termed sedentary.

RESULTS

Internesting movements

Overall transmitter performance compared well with other studies of conspecifics. Mean \pm SD duration of tracking, from release to last transmission, was 266 ± 153 d (range: 84 to 665 d). Transmitter duration was sufficient to encompass part of each animal's nesting period and at least provide indications as to patterns of post-nesting dispersal and foraging habitats of all individuals. Transmitters on 2 turtles (turtles B and C) temporarily ceased to function during their internesting periods but resumed functionality (after 47 and 70 d respectively) when the turtles were distant from Masirah Island and did not return. These turtles are excluded from analysis of clutch-frequency values. A further transmitter (turtle I) temporarily ceased to function after 398 d and resumed transmissions after 112 d for an additional 154 d.

Six of the 10 turtles (turtles A to E and J) were classed as sedentary for their entire internesting periods. They remained in shallow water, averaging <10 m deep, with maximum displacement from point of deployment ranging from 9.1 to 42.3 km (Table 1, Fig. 2).

The remaining 4 turtles (turtles F, G, H and I) were classed as wide-ranging, undertaking circuitous movements away from the island to the northeast, following local sea currents, roughly parallel to the coastline of the Omani mainland to maximal displacement of 61 to 317 km (Table 1, Fig. 2). All but 1 of these wide-ranging turtles spent all of their time in waters averaging 29 to 51 m deep (Table 1) in which it might be possible to feed benthically (Hawkes et al. 2006, Hatase et al. 2007). However, the most wide-ranging of the turtles ranged into waters >3 km deep, averaging >1200 m in depth. Turtles F and G switched to sedentary behaviour for a single internesting period after the 5th and 3rd clutches, respectively. All turtles remained in the territorial waters of Oman during the internesting period.

Table 1. *Caretta caretta*. Details of each female's size, behaviour and habitat utilisation during interesting and post-breeding periods. CCL: curved carapace length. CF: clutch frequency. Water depth: average depth of water inhabited during interesting period, it includes positive values, as the daily-interpolated locations were obtained from turtles in near-shore habitat around a peninsula. Av. displ.: average displacement from initial tagging location. Values are means \pm SD, ranges in parentheses. Data-days: number of days with data from total number of days during the period (percentage in parentheses). Oceanic days: number of data-days spent in water depths >200 m from data-days (percentage in parentheses). Post-nesting data include migration and foraging periods. Max. displ.: maximum displacement from initial nesting location. Values for countries are the number of data-days the turtle spent within the country's territory (percentage in parentheses). Turtle I remigrated to Masirah to nest after a single year, hence the data is divided into first (P1) and second (P2) post-nesting periods

Turtle	CCL (cm)	CF (nests)	Water depth (m)	Interesting		Post-nesting											
				Av. displ. (km)	Data-days	Oceanic days	Max. displ. (km)	Data-days	Iran	Pakistan	Oman	Yemen	Somalia	International			
A^a	105.5	5	2 \pm 4 (8–26)	8.4 \pm 3.4 (1.7–21.7)	53/62 (85)	9/20 (45)	496	20/22 (91)			20 (100)						
B^b	98.0	\geq 5	1 \pm 3 (+15 to 9)	8.5 \pm 3.8 (1.1–15.4)	67/76 (88)	64/89 (72)	959	89/89 (100)			10 (11.2)	79 (88.8)					
C^c	108.5	\geq 3	1 \pm 2 (+6 to 6)	4.4 \pm 2.0 (0.5–9.1)	21/44 (48)	168/185 (91)	1427	185/200 (93)			26 (14)	149 (81)	10 (5)				
D	97.0	6	2 \pm 6 (18–21)	9.1 \pm 4.6 (0.2–18.9)	33/78 (42)	109/169 (64)	431	169/172 (98)	1 (0)	3 (2)	165 (98)						
E	102.0	4	2 \pm 3 (1–9)	7.4 \pm 4.0 (0.6–14.6)	17/47 (36)	101/121 (83)	1033	121/171 (71)			72 (60)	49 (40)					
F^a	101.0	6	41 \pm 139 (0–1238)	29.5 \pm 29.9 (1.4–139.9)	81/85 (95)	23/90 (26)	340	90/99 (91)			90 (100)						
G	94.5	4	51 \pm 147 (2–945)	20.9 \pm 28.7 (1.1–122.5)	47/58 (81)	77/152 (51)	533	152/223 (68)			152 (100)						
H	108.0	3	1217 \pm 1303 (8–3184)	121.3 \pm 96.4 (0.8–317.0)	32/32 (100)	184/197 (93)	1097	197/197 (100)		5 (3)	91 (46)	94 (48)				7 (4)	
I^d	99.0	4	29 \pm 40 (15–243)	21.9 \pm 15.8 (2.5–61.7)	58/58 (100)	P1: 148/232 (64) P2: 137/154 (89)	P1: 1182 P2: 1324	P1: 232/272 (85) P2: 154/154 (100)			P1: 116 (50) P2: 137 (89)	P1: 116 (50) P2: 137 (89)					
J	96.0	6	10 \pm 59 (10–384)	12.0 \pm 7.7 (0.4–42.3)	42/85 (49)	116/130 (89)	1000	130/138 (94)			41 (32)	89 (68)					

^aTransmitter ceased functioning before final foraging location was identified. ^bTransmitter temporarily ceased functioning on 27 July 2006, thus possibly missing a 6th nest, restarted when turtle was far from the island on 12 September. ^cTransmitter temporarily ceased functioning on 27 June 2006, thus missing possible subsequent nests until the transmitter resumed functioning far away from the island on 5 September 2006. ^dTurtle moved away from the island and returned again, finally departing on 12 August; however, timing and locations do not indicate the turtle re-nested after 12 July

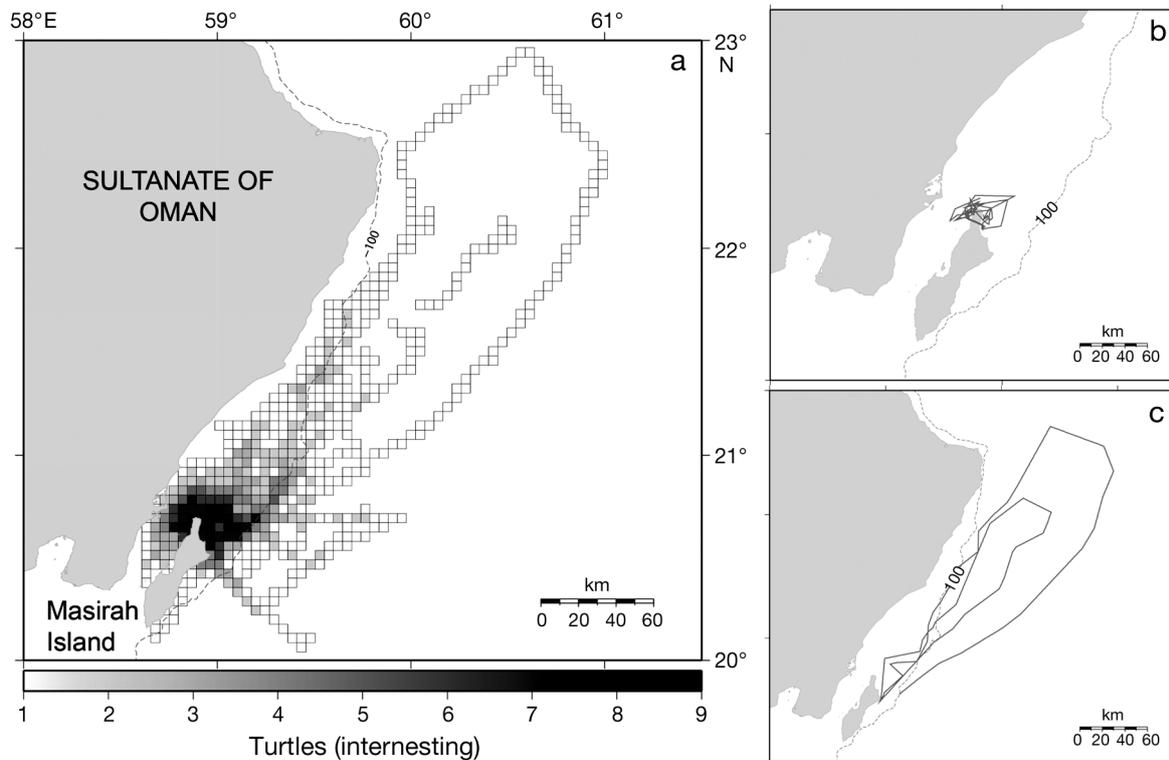


Fig. 2. *Caretta caretta*. Internesting period habitat ranges for 10 loggerhead turtles equipped with satellite transmitters early in the 2006 nesting season on Masirah Island. (a) Raster showing number of turtles that had passed through each location during the internesting period. (b) Example track for 'sedentary' internesting behaviour (turtle A). (c) The most wide-ranging track (turtle H). Each map shows the 100 m isobath. Raster shows 5 km grid cells and locations were determined using the filtering regime given in 'Materials and methods', except that a 1 h interpolation interval was used

Estimating internesting interval and clutch frequency

Time-depth recorder studies have shown that sea turtles become more active in the few days before a subsequent nesting event (e.g. Houghton et al. 2002). Increased surface time during this period raises the likelihood of the orbiting Argos satellites receiving uplinks from the transmitters. Coupling this with possible multi-night nesting activity made precise identification of individual nesting events difficult. However, close examination of the data enabled us to determine individual periods of nesting activity with some confidence (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m418p201_supp.pdf) and calculate a mean (\pm SD) time between nesting (internesting interval) of 16.4 ± 1.7 d (range: 13 to 20 d, $n = 36$ from all 10 ind.), which is in accordance with conspecifics elsewhere (Miller 1997).

Mean (\pm SD) minimum clutch frequency for the 8 animals for which we have complete tracking records was 4.8 ± 1.2 nests (range: 3 to 6 nests; Table 1). Mean (\pm SD) CCL for the sampled turtles was 101.0 ± 5.0 cm (range: 94.5 to 108.5 cm, $n = 10$; Table 1). There was no

difference in carapace size between wide-ranging and sedentary individuals (Mann-Whitney $U = 11$, $p = 0.91$; Table 1) and no significant difference was found between the internesting behavioural groups in relation to minimum clutch frequency (Mann-Whitney $U = 4$, $p = 0.35$). No significant correlation was found between carapace length and clutch frequency (Spearman's $r_s = -0.40$, $n = 8$, $p = 0.33$).

Post-nesting migrations

Post-nesting migrations of the 8 turtles which were tracked to a foraging area for 89 to 197 d spanned the whole Indian Ocean coast of Oman, the easterly waters of Yemen and the oceanic area north of Socotra Island (Yemen). There was, however, variation in the patterns of movement shown (Video S1 in Supplement 2 at www.int-res.com/articles/suppl/m418p201_supp/).

Individual animals displayed combinations of behavioural modes described by Godley et al. (2008). Eight turtles (turtles B to E and G to J) combined migration to neritic foraging areas (type A1 behaviour) with extended periods in oceanic waters (type B behaviour). One turtle

initially remained near Masirah before migrating southwards, but the transmissions ceased before final foraging habitat was determined (turtle F). Transmission for the final turtle (turtle A) ceased early into its southward migration; hence all turtle tracks ended south of Masirah, with 6 turtles entering territorial waters of Yemen, undertaking large-scale oceanic loops north of Socotra Island (Video S1). However, turtles D and H initially migrated north, circling the oceanic waters off Ras Al Hadd (Oman) (Table 1, Fig. 3). Further descriptions and figures of individual turtle routes can be found in Fig. S2 in Supplement 1 at www.int-res.com/articles/suppl/m418p201_supp.pdf.

High-use areas defined by residence time and number of turtles occupying the location clearly show 2 hotspots. The first was focused along the wide continental shelf of Oman, between 17.5 and 21.5°N, and the second was an extensive oceanic area north of Socotra Island (Fig. 4) spanning the waters of Oman and Yemen, with the latter area showing a denser utilisation.

Omitting turtles A and F, for which final destinations were not determined, we found that there was no sig-

nificant relationship (Mann-Whitney $U = 21$, $p = 0.77$) between interesting behaviour and maximum displacement from nesting area, and a positive but non-significant (Spearman's $r_s = 0.70$, $n = 8$, $p = 0.056$) relationship between turtle size and proportion of time spent in waters >200 m deep, with a suggestion that the largest turtles are resident in oceanic waters for a greater proportion of time.

The longest tracking duration (turtle I) exceeded 22 mo and in this period the turtle demonstrated several important life-history traits including remigration with a 1 yr remigration interval. The turtle initially migrated to the region north of Socotra Island, displaying both type A1 and B behaviours (P1 in Table 1) until it migrated towards Masirah Island, reaching there in mid-May the following year. She remained close to the island for almost a month, when she appears to have nested twice, before transmissions ceased. After 112 d without signals, transmitter activity resumed, showing the turtle to have returned to the north of Socotra Island, undertaking large-scale looping movements in the area once more, almost exclusively in oceanic waters (P2 in Table 1).

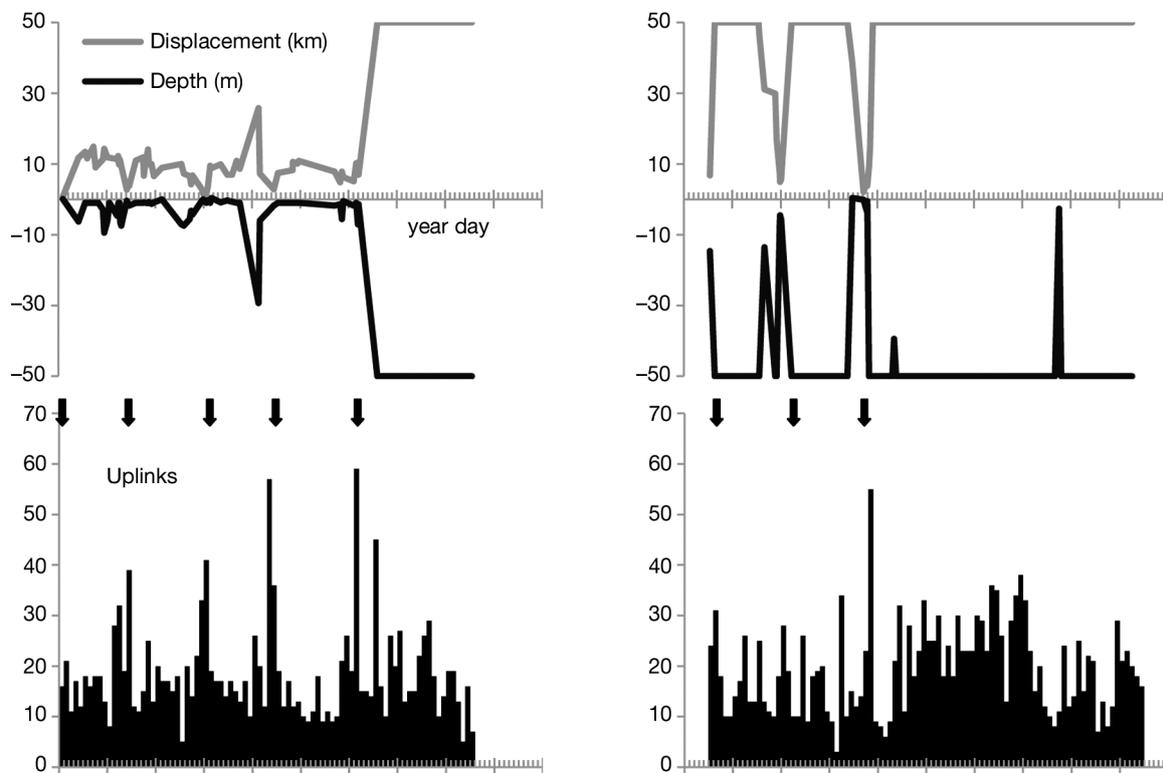


Fig. 3. *Caretta caretta*. Examples of data acquired during the interesting period for sedentary turtle A (left) and wide-ranging turtle H (right). Fidelity to nesting location is shown by water depth and displacement at near-zero. Data are synchronised at approx. 2-wk intervals. The increased activity and on-land time during nesting is generally represented in peaks in daily number of uplinks received by the Argos satellite system shown in the lower graphs. Arrows indicate inferred nesting activity. Depth and displacement are shown with values of -50 or 50 where these values were exceeded. Each tick on x-axes represents 1 day. Similar charts for all turtles are presented in Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m418p201_supp.pdf

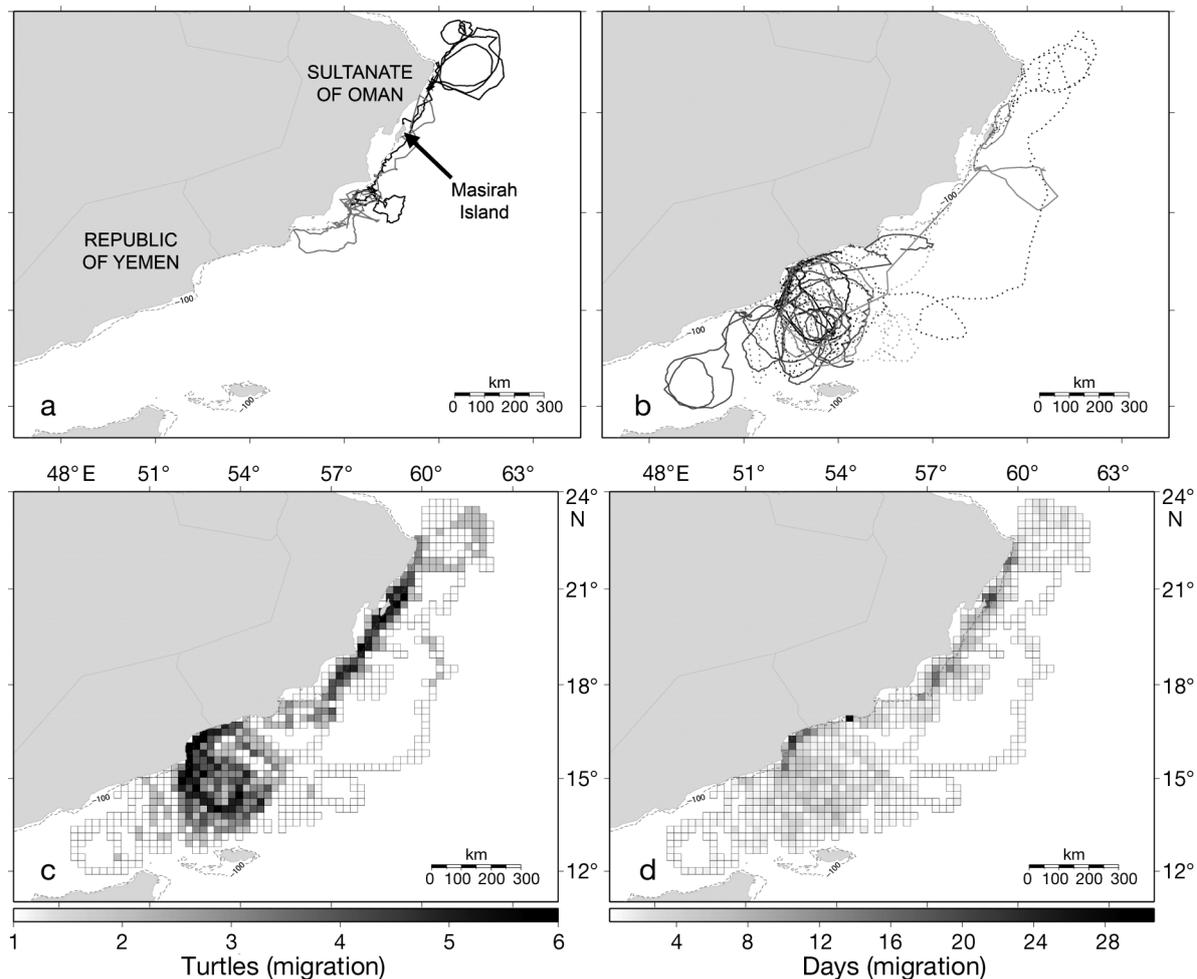


Fig. 4. *Caretta caretta*. Post-nesting spatial utilisation of the 10 turtles tracked. (a) Movements of 2 turtles (D and G) which, despite lengthy tracking (>250 d), did not migrate into Yemeni waters. (b) The other 6 turtles (B, C, E, H, I and J) for which extensive post-nesting movements were obtained. (c) Total number of turtles having passed through a location. (d) Sum of number of days turtles were in each location. See Fig. 1 for additional geographic locations. Rasters show 25 km grid cells and locations were determined using the filtering regime given in 'Materials and methods', except that a 6 h interpolation interval was used. See Fig. S2 in Supplement 1 at www.int-res.com/articles/suppl/m418p201_supp.pdf for post-nesting tracks of individual turtles

DISCUSSION

Depending on species, marine turtles display highly variable levels of ontogenetic shift in habitat selection. Juveniles of most species live in oceanic conditions (Bjorndal 1997) and the leatherback turtle *Dermodochelys coriacea* shows least shift, with adults remaining in oceanic waters to feed mainly on gelatinous plankton (Hays et al. 2004). Some hard-shelled species (e.g. hawksbill turtles *Eretmodochelys imbricata* and green turtles *Chelonia mydas*) generally change to become inhabitants of shallow, coastal environments and feed on benthos as adults (Bjorndal 1997). The olive ridley turtle *Lepidochelys olivacea* is a generalist exhibiting a somewhat intermediary behaviour — with adults capable of foraging benthically in relatively deep neritic

water (McMahon et al. 2007) — but is shown to also inhabit shallow coastal and the open oceanic environment (Polovina et al. 2004, Whiting et al. 2007).

Although there are exceptions (McClellan & Read 2007, McClellan et al. 2010), juvenile loggerhead turtles undergo an ontogenetic shift in habitat use as they mature and grow, moving from oceanic to neritic waters. This is thought to be explained by higher growth rates prevalent in neritic conditions (Bolten 2003) due to increased availability of food (Snover 2008). Thus, post-nesting migrations normally terminate at neritic foraging habitats (Papi et al. 1997, Godley et al. 2003b, Schroeder et al. 2003, Hawkes et al. 2007, Zbinden et al. 2008). Recently, a dichotomy in behaviour for adult female loggerheads has been identified during post-breeding migrations and resi-

dencies from Cape Verde, West Africa (Hawkes et al. 2006) and Japan (Hatase et al. 2002, 2007). In both cases smaller turtles used oceanic habitats with the more usual neritic habitats only used by larger individuals.

In contrast, most of the turtles in the present study extensively used pelagic habitats in addition to coastal neritic ones during the post-nesting phase, with the largest individuals mostly utilising the oceanic realm. We suggest that a polymodal foraging strategy for individuals is widespread in this population; this was recently suggested at population level for loggerheads breeding in southeastern USA (Reich et al. 2010). Additionally it should be noted that sizes of all turtles in the present study were equivalent to the larger neritic dwelling individuals from Cape Verde (Hawkes et al. 2006). We suggest that oceanic foraging may be equally if not more beneficial in energetic terms as neritic foraging in the Arabian Sea region. The lack of strong size differentiation between neritic and oceanic-dwelling individuals has also been shown in green turtles (Hatase et al. 2006, Seminoff et al. 2008).

The spatial footprint of the turtles tagged in the present study ranged from northeast Oman to the entrance to the Gulf of Aden, with maximum migratory distances from the nesting region ranging from approximately 400 to 1400 km. Turtles tagged and tracked at Masirah Island later in the same season as part of a separate study also utilised the core foraging area, above Socotra Island, but half the individuals either progressed further southwest into the Gulf of Aden or north and west into the Arabian Gulf (Fig. 1, B. E. Witherington & E. Possardt pers. comm.). Limpus (1985) found that loggerheads from different foraging areas in Australia begin migrations to a single nesting area at different times. Therefore there may be intraseasonal temporal sub-structuring of the population, leading the cohorts to experience diverse threats, separated both spatially and temporally.

Furthermore, long-distance recoveries of loggerhead turtles tagged on Masirah Island have been reported by Baldwin et al. (2003) (see Fig. 1). They indicate that turtles travelled south and west to the Gulf of Aden, north and northwest to the Gulf of Oman and the Arabian Gulf and additionally to the northeast to Pakistan or the Gulf of Kutch. Our present study and the other telemetry results broadly concur with this distribution. However, both satellite-tracking studies lack turtles that migrated across the Arabian Sea to the Indian subcontinent. The significance of this omission needs to be determined. It may be that dispersal to this region is rare or it is only demonstrated by mid-season turtles or those from a different year-cohort not yet tracked.

Some seminal sea-turtle satellite-tracking studies (e.g. Hays et al. 1991) noted the utility of satellite tracking for deriving clutch-frequency estimations. However, as the technique became more widespread, a shift in emphasis on examining post-nesting migrations occurred (e.g. Luschi et al. 1998, Godley et al. 2002, Hays et al. 2002b). Many studies then focused on end-of-season deployment to avoid dangers to the transmitter in the internesting environment (e.g. cleaning behaviour in Schofield et al. 2006). Their findings may present a biased representation of the true spread of post-nesting movements for the population as a whole, as suggested here. This bias may be exacerbated with results obtained from a single nesting season, strongly suggesting that to obtain a full representation of a population, both intra-seasonal temporal spread and multi-annual telemetry need to be undertaken, as demonstrated by Whiting et al. (2007) and indicated by Shillinger et al. (2010). This flags the necessity for existing studies of marine turtles and other megafauna to be revisited to determine if suitable spread of sampling has been achieved to substantiate the inferences made.

The results of the present study also identify plasticity in behaviour during the breeding season. No link between body size and behaviour was established and some individuals carried out coastal sedentary and wider-ranging movements involving oceanic looping. This is the third population of loggerheads, in addition to those of Japan (Sakamoto et al. 1990) and the Cayman Islands (Blumenthal et al. 2006), in which individuals demonstrate oceanic habitat utilisation during internesting periods, contrasting with other populations (e.g. Greece: Zbinden et al. 2007; Cyprus: Fuller et al. 2008; USA: Stoneburner 1982, Plotkin & Spotila 2002; Australia: Tucker et al. 1996) and further highlights the highly plastic behaviour of this species. We would note, however, that in a recent study of 12 loggerhead turtles in the USA (Hawkes et al. 2007), one female spent at least some time in oceanic habitats before returning to neritic habitats. Thus, as our knowledge base expands it is likely that we will discover that multiple behavioural strategies are employed in other populations previously thought to conform to the typical model.

Female loggerhead turtles typically have 2.5 to 3 yr remigration intervals between breeding years (Schroeder et al. 2003); however, evidence is accumulating for the common occurrence of single-year remigrations from flipper-tag returns (Broderick et al. 2001, Schroeder et al. 2003) and using satellite tracking (Cape Verde: B. J. Godley et al. unpubl.; Cayman Islands: Blumenthal et al. 2006). We confirm, as previously reported (Ross 1979), that single-year remigrations occur within the Masirah population at an un-

quantified level, which has implications for population modelling requiring accurate fertility and migration rates to produce meaningful population estimates (Hays 2000, Heppell et al. 2003).

High levels of fidelity to nesting beaches, as displayed by turtle I, are well documented and established (see Schroeder et al. 2003); however, overwintering-site fidelity is less well published. Broderick et al. (2007) showed that both loggerhead and green turtles from northern Cyprus returned to the same overwintering areas after successive breeding years. Limpus & Limpus (2003) had previously suggested that, for loggerhead turtles, the adults forage in the same areas as they grew to maturity. The propensity for foraging-site fidelity, albeit in this case a large and mainly oceanic area, is corroborated through the movements of turtle I in the present study. If this oceanic region is also the developmental habitat for the nesting population of Masirah then we can expect the at-sea population in the area to number tens of thousands. In identifying and describing the key foraging habitat for this globally significant population, we have contributed to one of the global research priorities for marine turtles (Hamann et al. 2010).

Accurate estimation of clutch frequency with appropriate error statistics is very important for estimating population size (Schroeder et al. 2003). Satellite tracking has recently been shown to provide accurate clutch-frequency counts for loggerheads in Florida (Tucker 2010), with a higher-than-previously estimated clutch frequency generated. Interpretation of tracking data was simpler for that study site, along a barrier island, in comparison with locations based around the head of a peninsula on an offshore island such as Masirah. However, technological advances in satellite tracking and data relay through the Argos system could still further improve assessments of clutch frequency. Advances include the use of haul-out times, demonstrated for leatherback turtles (Georges et al. 2007) and olive ridley turtles (Hamel et al. 2008), and GPS positioning, which is more accurate than the standard Argos system (Witt et al. 2010). It has been shown that a loggerhead population of small individuals becomes resource-limited after 4 clutches in a single season (Broderick et al. 2003), whereas larger turtles may deposit more (Tucker 2010; the present study). Despite this, the current clutch-frequency estimate (mean minimum: 4.8 nests) is higher than that used in previous population-estimate calculations and hence would significantly reduce estimates that incorporate this datum (e.g. Baldwin et al. 2003). It is clear that although the loggerhead population at Masirah Island is undoubtedly one of the world's largest, more up-to-date and extensive data are required to produce a current

population estimate and systematic annual surveying is necessary to identify any possible trend in population size.

The present study indicates that individual, early-nesting turtles remain in the Masirah region for nesting for a conservative average of 63 d (range: 32 to 85 d), with some turtles remaining for a period after their nesting season. This does not include the pre-nesting period during which the turtles congregate near the nesting beach (Miller 1997). If we assume this length of residency also applies to later-nesting turtles (nesting occurs April through September; Ross & Barwani 1995), we can infer that the Omani seas around Masirah and further north will be densely populated by reproductively active females and males for 6 full months of every year. This intensive habitat use should be a stimulus for at-sea studies and conservation measures to be adopted by the authorities. Additionally, Masirah hosts nesting populations of 3 other sea-turtle species whose nesting seasons fall outside that of the loggerhead's (olive ridley turtles and hawksbill turtles: Ross & Barwani 1995, Rees & Baker 2006; green turtles: Ross & Barwani 1995) from which we can infer that the seas around Masirah are of year-round importance for adult marine turtles.

In Oman, loggerhead turtles are reportedly not targeted for capture by fishermen to the same extent as green turtles (Baldwin & Al-Kiyumi 1999) and therefore directed take may not significantly impact on the population. However, with high-use locations covering large-scale oceanic habitats both for the inter- and intra-nesting period, the population is susceptible to the negative impacts of incidental capture in fisheries targeting other species. Trawling activities in Oman have been shown to negatively affect turtle populations, with an estimated mortality rate of 50% for incidentally caught specimens (Hare 1991). Lewison & Crowder (2007) suggest that fisheries possibly have a large, albeit largely unquantified impact on loggerhead turtle populations.

A loosely coastal migratory corridor heading southwest from Masirah has been determined together with extensive foraging habitats, both neritic and oceanic, between Socotra Island and the mainland. The predictability of large numbers of loggerhead turtles in the region supports further investigations on the impacts of fishing on the population and highlights the need for joint conservation initiatives between the Sultanate of Oman and the Republic of Yemen. Such actions could protect upwards of 50% of the adult population based on the current findings.

We now have an idea as to the spatial extent of adult females from this rookery, but do not yet have any indication as to the key areas for males. It appears that in multiple species, including loggerhead turtles, males

generally display migration patterns broadly similar to those observed in adult female conspecifics (Plotkin et al. 1996, Sakamoto et al. 1997, Hays et al. 2001, James et al. 2005a,b,c, Shaver et al. 2005). However, for hawksbill turtles, male patterns have been shown to be different to those of adult females from the same population (Van Dam et al. 2008).

Our findings covering plasticity of behaviour during the breeding season and temporal differences in dispersal from the nesting area for this globally significant population of loggerhead turtles have implications on conservation policy and management at a national and international level. We have suggested areas that should be the focus for further study, possibly to allow establishment of protected areas or other mitigation strategies (Grantham et al. 2008, Howell et al. 2008). In turn these measures need to be assessed in the context of other regional biodiversity, which includes populations of other marine turtle species. Furthermore, the spatial and temporal substructuring of the population highlights the need for more comprehensive tracking projects, with deployments across the breeding season in multiple years, in order to obtain reliable estimations for high-use foraging habitats of widely dispersed marine vertebrates.

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