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Fidelity and over-wintering of sea turtles

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While fidelity to breeding sites is well demonstrated in marine turtles, emerging knowledge of migratory routes and key foraging sites is of limited conservation value unless levels of fidelity can be established. We tracked green (*Chelonia mydas*, $n=10$) and loggerhead (*Caretta caretta*, $n=10$) turtles during their post-nesting migration from the island of Cyprus to their foraging grounds. After intervals of 2–5 years, five of these females were recaptured at the nesting beach and tracked for a second migration. All five used highly similar migratory routes to return to the same foraging and over-wintering areas. None of the females visited other foraging habitats over the study period (units lasted on average 305 days; maximum, 1356 days), moving only to deeper waters during the winter months where they demonstrated extremely long resting dives of up to 10.2 h (the longest breath-holding dive recorded for a marine vertebrate). High levels of fidelity and the relatively discrete nature of the home ranges demonstrate that protection of key migratory pathways, foraging and over-wintering sites can serve as an important tool for the future conservation of marine turtles.

Keywords: migration; fidelity; foraging; over-wintering; *Chelonia mydas*; *Caretta caretta*

1. INTRODUCTION

Marine turtles typically migrate hundreds or thousands of kilometres between specific breeding and foraging grounds (Plotkin 2003) and exhibit natal philopatry to colonial nesting beaches (Bowen *et al.* 1992). Forming large seasonally predictable breeding aggregations has predisposed this group to over exploitation since pre-history, causing the reduction of many populations (Frazier 2003). Modern conservation efforts initially focused on nesting females and their eggs, with the majority of protected areas for marine turtles being nesting beaches and their nearby coastal waters (e.g. Troëng *et al.* 2005). Considering that such a small proportion of the life cycle is spent at the breeding site (several months in every 2–4 years following an extended maturation period; Miller 1997), such areas offer limited protection to the population as a whole. Although electronic tracking studies of marine turtles have begun to highlight migratory corridors (e.g. Morreale *et al.* 1996) and important foraging sites (e.g. James *et al.* 2005), for most populations, knowledge of the biology of these species beyond the nesting beach remains deficient.

In recent years, there has been a rising awareness of the global threats posed to sea turtles through incidental mortality as a result of fisheries by-catch (Lewison *et al.* 2003; Carranza *et al.* 2006). Long-line fisheries are estimated to catch hundreds of thousands of turtles per year (Lewison *et al.* 2004*a*), suggested as the cause of the precipitous decline of the leatherback turtle (*Dermochelys coriacea*) in the Pacific Ocean (Spotila *et al.* 2000). For pelagic (oceanic) foragers, satellite tracking studies have recorded diffuse ranges (James *et al.* 2005; Hawkes *et al.* 2006), in some cases at the scale of ocean basins (Ferraroli *et al.* 2004; Eckert 2006). For those species feeding benthically (on bottom-dwelling organisms) in coastal waters (e.g. some green, *Chelonia mydas*; Bjorndal 1980; Godley *et al.* 2002 and loggerhead, *Caretta caretta*, turtles; Hatase *et al.* 2002; Hawkes *et al.* 2006), net-based fisheries pose a significant threat (Lewison *et al.* 2003). These benthic feeders have multiple, yet discrete, foraging sites within populations (Hatase *et al.* 2002; Hays *et al.* 2002). For example, green turtles flipper tagged at Ascension Island have been recorded along the entire coast of Brazil (Mortimer & Carr 1987) and those tagged at Tortuguero, Costa Rica across the Caribbean Sea (Troëng *et al.* 2005).

While fidelity to nesting beaches has been well documented (Bowen *et al.* 2002), there are few studies that demonstrate fidelity to foraging grounds. Flipper tagging studies have recorded the same individuals at foraging sites after breeding intervals (Limpus *et al.* 1992), although the degree of fidelity to these sites and migratory routes cannot be determined using such methods. Juvenile loggerhead turtles have also been shown to exhibit site fidelity to feeding areas, returning to the same site following experimental displacement (Avens *et al.* 2003). Similarly, molecular analyses indicate that juvenile turtles return to foraging areas close to the natal beach (Bowen *et al.* 2004). No studies have systematically investigated whether marine turtles use the same migratory routes in different years and remain at the same foraging sites throughout the inter-breeding interval. Here, we set out to test whether sea turtles show fidelity to migratory routes

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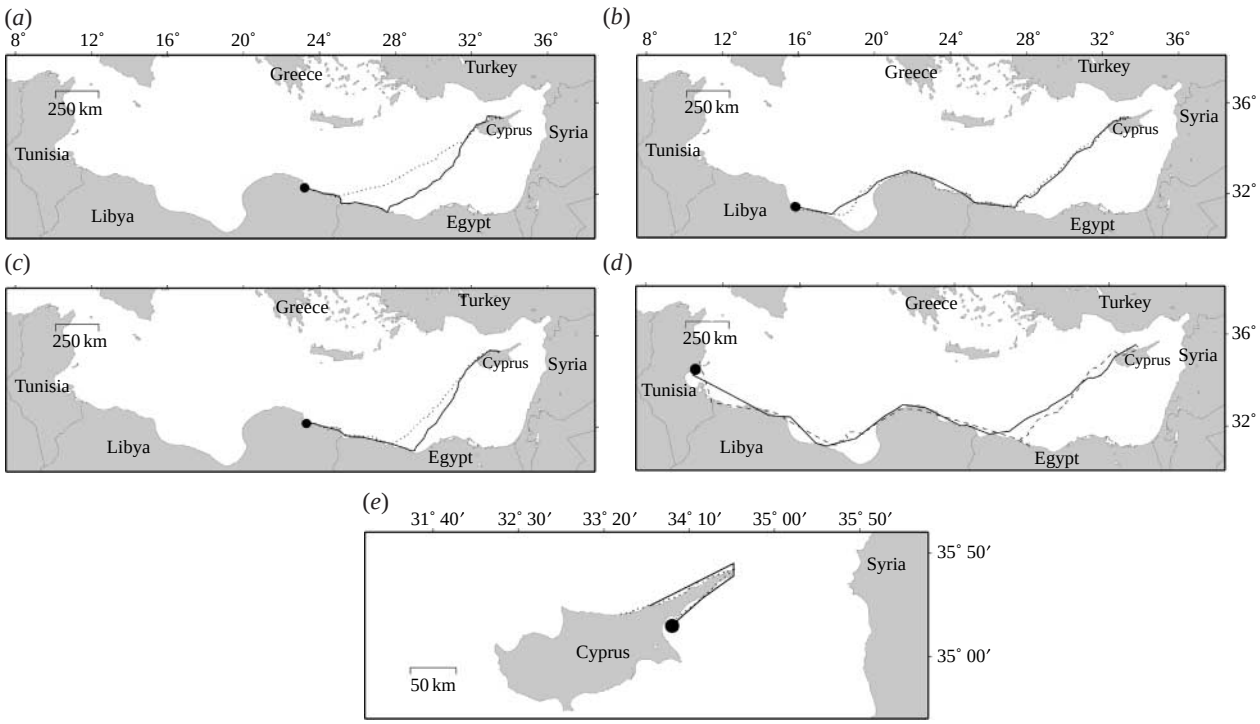

Figure 1. High fidelity to migratory routes. Routes taken by three green turtles (A, E, F) and two loggerhead turtles (K, R) to their foraging sites after two consecutive breeding seasons. Solid lines represent the first year of tracking and dotted lines the second. (*a*) Female A, 1999 and 2004. (*b*) Female E, 1998 and 2002. (*c*) Female F, 1998 and 2002. (*d*) Female K, 2002 and 2005. (*e*) Female R, 2001 and 2003. Routes are constructed from locations of class 3, 2, 1, A (see electronic supplementary material for routes and destinations of all individuals A–T).

and foraging sites through repeat satellite tracking of individual females in the Mediterranean, where there are an estimated 2000–3000 loggerheads and 300–400 green turtles nesting annually (Broderick *et al.* 2002), making these geographically isolated populations of conservation concern.

2. MATERIAL AND METHODS

We deployed 26 satellite transmitters on 10 green and 10 loggerhead females nesting at two beaches (Alagadi 35°33′ N, 33°47′ E; Esentepe 35°36′ N, 33°69′ E) in Cyprus (1998–2005); included in this study are those previously published by Godley *et al.* (2002, 2003). Six females (three of each species) were tracked on two occasions after consecutive breeding years. Units were attached according to the protocol outlined by Godley *et al.* (2002), once females had finished laying their clutch and were camouflaging their nest. We used a variety of different models of transmitter over the course of this 8-year study (Telonics ($n=13$) Mesa, AZ, USA models ST6, ST14, ST18; Wildlife Computers SDR-SSC3 ($n=3$), Redmond, WA, USA; Sea Mammal Research Unit–Satellite Relay Data Loggers (SMRU–SRDLs; $n=3$), St Andrews, UK and Sirtrack Kiwisats ($n=7$), New Zealand). Some units provided location only (Telonics ST18; Sirtrack Kiwisats 101) while others also provided limited dive data (Telonics ST6 and ST14; Wildlife Computers SDR–SSC3) with SMRU–SRDLs recording individual dive profiles.

Units on green turtles lasted on average 291 days (s.d. 123; range 43–424 days, $n=13$; median 311 days) and for loggerhead turtles 322 days (s.d. 352, range 59–1356 (this unit is still transmitting at time of writing), $n=13$; median 176 days). Seventeen of our units lasted more than six months.

Data were downloaded and managed via the Argos system, which attributes a class of accuracy to a given location. Of the highest accuracy is class 3, with an approximate error of 150 m on both the axes (longitude and latitude), class 2, 300 m error; class 1, less than 1000 m error; class 0, more than 1000 m error; classes A and B are of unclassified accuracy (ARGOS 1996). Variation in these accuracy levels has been described when tested in the field (Hays *et al.* 2001; Vincent *et al.* 2002). We used the Satellite Tracking and Analysis Tool (STAT; Coyne & Godley 2005) to manage and manipulate data, and constructed routes using locations of class 3, 2, 1 and A. The distance between successive locations was calculated using a great circle route equation. To exclude implausible locations, minimum speed of travel was calculated between successive fixes and only locations corresponding to speeds of less than 5 km h^{-1} were included. In the foraging sites, only locations of class 3, 2 and 1 were used. Minimum convex polygons (MCP; the smallest polygon which contains all points that the animal has visited) were calculated from these locations to give an estimate of home range size. Ranges were estimated only where we had more than 10 locations of classes 3, 2 and 1 in each of the foraging and over-wintering grounds. Centroids (the central point of all locations) were calculated to compare site fidelity between years for the same individuals.

3. RESULTS

Our 20 study females migrated from Cyprus to foraging grounds in Egypt, Libya, Syria, Tunisia and Turkey (see electronic supplementary material, S1) between 22 June and 23 October. In addition to identifying foraging areas for these populations, these results also highlight the importance of the pelagic areas south to southwest of Cyprus and much of the coastal waters of North Africa as migration corridors for both species.

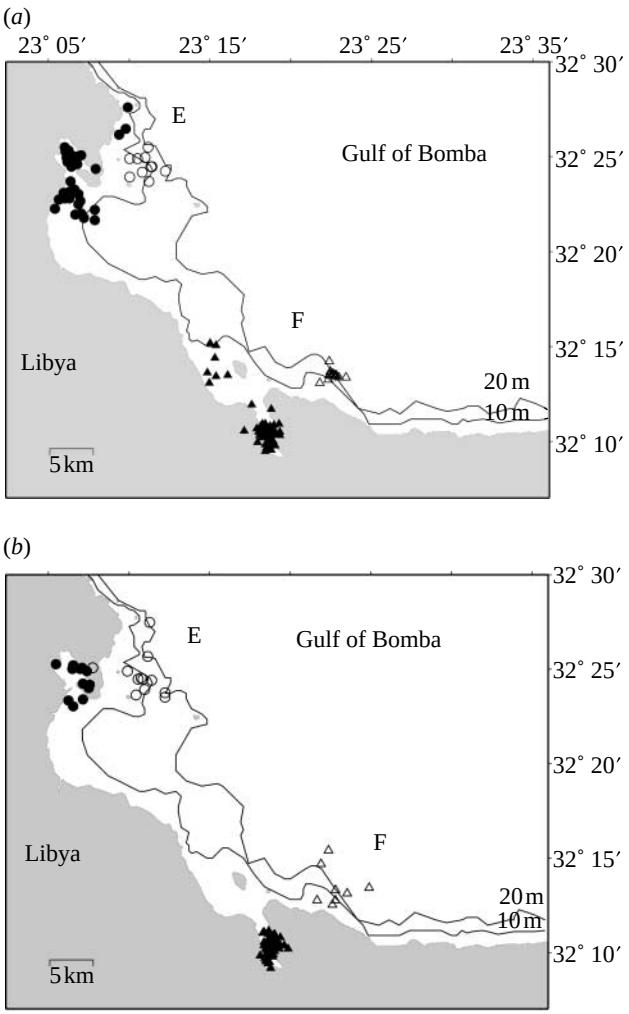

Figure 2. Foraging and wintering site fidelity within and between seasons by green turtles. Locations of class 3, 2 and 1, for (*a*) green turtles E (circles) and F (triangles) in their foraging (March–October; closed symbols) and over-wintering sites (November–February; open symbols) following their post-nesting migration in 1998 and (*b*) the same females following migration in 2002. Satellite transmitters lasted 7–15 months. During the 2002 tracking, individual dives were recorded for turtle E (figure 3*a–c*).

Six of our 20 study individuals returned to nest after intervals of 2–5 years and were tracked for a second migration. Five females, following extremely similar routes, returned to the same foraging locations (green turtles A, E, F, figure 1*a–c*; loggerhead turtles K and R, figure 1*d*,*e*). One unit failed before the female reached its final destination on the second migration although it appeared to be following the same route as its previous migration until the point of failure (loggerhead M, see electronic supplementary material, S2). Mean minimum distance between tracks at each location received during oceanic migration was 11.8 (s.d. 9.9), 55.3 ($\pm$46.5) and 18.6 km ($\pm$23.1) for green turtles (A, E and F, respectively), and 25.1 ($\pm$15.4) and 7.0 km ($\pm$8.3) for loggerhead turtles (K and R, respectively; figure 1).

All females tracked for more than six months (green turtles, $n=7$; loggerhead turtles, $n=7$) remained in the same foraging grounds, moving to deeper water in early November where they remained until returning to the foraging grounds in March/April (e.g. figure 2). Females of both species used a smaller area during this winter phase than during the summer months; green turtles: summer, 77 km^2 (s.d. 72; mean number of locations 43$\pm$29; range 12–90); winter, 37 km^2 ($\pm$37; mean locations 15$\pm$7; range 10–28), $n=6$; loggerhead turtle: summer, 331 km^2 ($\pm$494; mean locations 22$\pm$8; range 12–27); winter, 55 km^2 ($\pm$76; mean locations 17$\pm$6; range 10–22), $n=3$; indicative of reduced movement during these colder months. Dive data confirmed that both species conducted much longer deeper dives in winter (figure 3*a*,*b*). Data from green turtle E (figure 1*b*) illustrate short shallow dives in summer, indicative of active foraging (figure 3*c*; mean$\pm$s.d. duration of 724 dives September–October 2002; 0.36$\pm$0.34 h; range 0.01–1.23 h) while longer flat-bottomed dives recorded in winter are indicative of resting (figure 3*e*; January–February 2003, 1.67$\pm$1.09 h; range 0.13–5.12 h; $n=81$). Loggerhead turtles were also undertaking longer dives in the winter months (figure 3*b*). Indeed, deep bottom resting dives of more than 10 h duration were recorded in the coldest months (figure 3*d*; September–October 2002; 0.41$\pm$0.17; range 0.01–0.92 h; $n=638$; figure 3*f*; January–February 2003; 5.12$\pm$2.13; range 0.04–10.24 h, $n=135$), the longest breath-holding dives ever recorded in a marine vertebrate.

Green turtles tracked following breeding in both 1998 and 2002 (figure 1*b*, female E; figure 1*c*, female F) demonstrated very high site fidelity, using the same inshore foraging and deeper wintering sites within and between breeding intervals (figure 2). Centroids (central point of all locations) of the foraging areas used by female E in the two study years were 2.4 km apart, with over-wintering sites only 1.2 km apart (figure 2*a*). For female F, centroids were 1.3 (foraging) and 0.4 km (wintering) apart (figure 2*b*). In the first year of tracking, the transmitter on green turtle A (figure 1*a*) lasted only a few weeks once in the foraging ground, although it returned to the same site we could not quantify fidelity. Similarly, for loggerhead turtles (figure 1*d*,*e*) tracked twice, locations on the foraging grounds in one season were not of the accuracy to allow spatial analysis.

4. DISCUSSION

In this study, we have demonstrated that both green and loggerhead turtles exhibit high levels of fidelity to migratory routes, foraging areas and wintering sites both between and within years and after successive breeding migrations. Our study females tracked for two consecutive migrations used highly similar routes to return to the same foraging locations. Many of our study females passed suitable foraging habitat on their migration, indeed some passed through areas used by other conspecific study animals. Previous satellite tracking studies have also shown that females appear to pass suitable foraging habitats although possibly foraging *en route* (Hays *et al.* 2002; Troëng *et al.* 2005). Why then return to a specific site? There are many factors that may influence this behaviour—food resource limitation, territorial defence or perhaps the proximity of good over-wintering sites define site selection.

Direct observations have shown that green turtles serially crop seagrass gardens, to encourage new energetically rich growth (Bjorndal 1997). Returning to an area that has been cropped may therefore be of nutritional

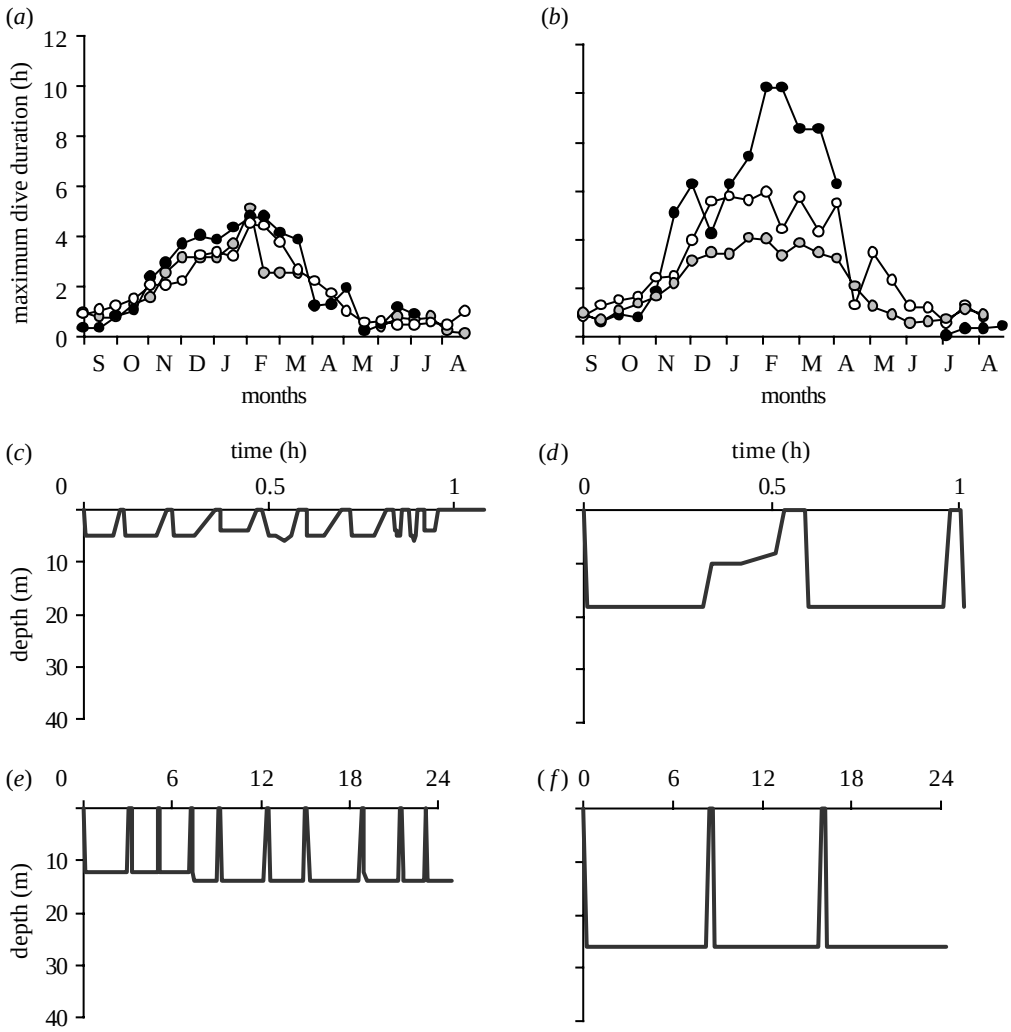

Figure 3. Diving behaviour of green and loggerhead turtles. Maximum dive durations for (*a*) green and (*b*) loggerhead turtles in each half month period between 1 September 2002 and 31 August 2003. Filled black circles are data for green turtle E and loggerhead turtle K fitted with SMRU-SRDL dive computers. Open and grey circles are females fitted with Telonics ST6 transmitters (green turtles, G and H and loggerhead turtles, N and Q). (*c*) Illustrative bouts of diving for green turtle E and (*d*) loggerhead turtle K in the summer foraging grounds (September 2002) and (*e*) green turtle E and (*f*) loggerhead turtle K in the over-winter grounds (January 2003). (Note: (1) Transmissions from SMRU-SRDLs in parts (*a*) and (*b*) were interrupted for a period in midwinter possibly due to biofouling resulting from reduced activity. (2) Differing scaling of *x*-axis in parts (*c*)–(*f*). (3) See electronic supplementary material for routes and destinatious of individuals A–T).

benefit. In addition, this sessile food source is highly predictable; likely to be there when a female returns after an interval of three to six months. The loggerhead turtle, with its omnivorous diet, including vagile organisms such as molluscs and crustaceans (Bjorndal 1997; Godley *et al.* 1997), might have been expected to have lower site fidelity, potentially having depleted resources during previous feeding bouts. Indeed, the larger home ranges recorded in this species may reflect this differing trophic status.

Although we have demonstrated fidelity to foraging and over-wintering sites within and between seasons, should a site become wholly unsuitable, e.g. excessively depleted of food, turtles must move to a new area, thus there may be movement across wider time-scales, dependent on the stability of these sites. This may be an explanation for the findings by Cheng (2000), in the only previous study where a marine turtle (*C. mydas*) was tracked after two consecutive breeding seasons and was not tracked to the same end location. An alternative explanation for this finding, however, may have been an artefact of the short duration of units (59 and 45 days after departure from nesting grounds).

We recorded very long over-wintering dives suggestive of seasonally reduced activity (Ultsch 2006) in both species, with females moving to deeper water in the colder months. We anticipated that this would be the case for green turtles as a result of limited primary production at low temperatures and based upon preliminary data from this site (Godley *et al.* 2002). However, adult female loggerheads, located along the relatively warm North African coast of the Mediterranean and with a broader range of prey, might have been expected to continue active foraging during winter months. From direct observations of loggerhead turtles in North America, it was suggested that this species hibernates in the colder months (Carr *et al.* 1980). Prior to our study, the only previous records of individual over-wintering dives in this species were those recorded by Hochscheid *et al.* (2005) in one juvenile in the northern Mediterranean conducting dives of up to 6.2 h, and more recently adult loggerheads off the northeastern USA coast have been recorded diving for

up to 7.4 h (Hawkes *et al.* 2007). This species is very plastic in its ecology (Hatase *et al.* 2002; Hawkes *et al.* 2006), and it is possible that some loggerhead turtles oscillate between periods of resting and occasional foraging, or that individual differences in wintering strategy exist. Individuals of both species will be vulnerable to demersal fishing activities during the over-wintering phase, not only as a result of the increase in time spent on the seabed but also having slowed down their metabolism to enable this behaviour, they are likely to be sluggish in their response to threats.

Many populations of marine turtles are of profound conservation concern as a result of past over harvest and modern fisheries by-catch (Spotila *et al.* 2000; Frazier 2003; Lewison *et al.* 2003, 2004*a*). The problem of conserving populations of coastal living adults is perhaps more soluble than those which forage on the high seas. The case of the herbivorous green turtle, with its smaller inshore home range, is clearly more tractable and we have highlighted two small regions off the Libyan coast that should be considered a priority for this species. Considering that there are estimated to be as few as 300–400 female green turtles breeding annually in the Mediterranean (Broderick *et al.* 2002), such potential hotspots require detailed investigation. Also of concern is the fact that six of the ten loggerhead turtles tracked are located in areas (Gulf of Gabes and the Nile Delta) with significant fisheries activity (Lewison *et al.* 2004*b*) and mitigation efforts are needed to reduce this threat. While capture of juveniles in both neritic and pelagic areas must also be addressed (Carreras *et al.* 2004), excellent first steps will be the protection of reproductively valuable adults. The relatively localized inshore foraging grounds and the high degree of fidelity over extended time-scales demonstrated here offers potential for adults of these species to be more effectively protected through adaptive management strategies. In addition, fidelity to migratory corridors strengthens the argument for the monitoring and/or control of fisheries activity in important areas during migratory periods. In particular, we have highlighted the importance of the southwest corridor from Cyprus to the North African coast, a migratory route used by 11 of our 20 study females. These findings lend support to proposals to protect key migratory routes and foraging habitats and highlight the need to identify over-wintering habitats, where individuals are spending the majority of their time resting on the seabed and are highly susceptible to demersal fishing gear.

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NOTICE OF CORRECTION

The scale bar in figure 2*b* is now correct.

1 May 2007

PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2007) **274**, 3183–3184

Errata

Proc. R. Soc. B **274**, 183–197 (31 October 2006) (doi:10.1098/rspb.2006.3705)

Soft tissue and cellular preservation in vertebrate skeletal elements from the Cretaceous to the present

Mary Higby Schweitzer, Jennifer L. Wittmeyer and John R. Horner

The funding acknowledgement in the acknowledgement section was incorrect, and should read as follows:

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Proc. R. Soc. B **274**, 1533–1538 (22 June 2007) (doi:10.1098/rspb.2007.0211)

Fidelity and over-wintering of sea turtles

Annette C. Broderick, Michael S. Coyne, Wayne J. Fuller, Fiona Glen and Brendan J. Godley

The scale bar in figure 2*b* was incorrect, and should read as follows:

5 km.

Proc. R. Soc. B **274**, 2099–2107 (3 July 2007) (doi:10.1098/rspb.2007.0429)

A new probable stem lineage crustacean with three-dimensionally preserved soft parts from the Herefordshire (Silurian) Lagerstätte, UK

Derek J. Siveter, Mark D. Sutton, Derek E. G. Briggs and David J. Siveter

Figures 1 and 2 were incorrectly sized and the magnifications in the legend of figure 3 were incorrectly stated.

The online version of the article has now been corrected.