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Biphasal long-distance migration in green turtles

G. C. HAYS*, A. C. BRODERICK*, B. J. GODLEY*, P. LOVELL†, C. MARTIN*, B. J. McCONNELL† & S. RICHARDSON*
*School of Biological Sciences, University of Wales Swansea
†Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews

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Sea turtles have recently been shown to have the sensory ability to use magnetic information for guidance in the open ocean, although the importance of different potential navigational cues remains unknown. Between May and August 2001, we satellite-tracked green turtles, *Chelonia mydas*, during their >2000-km postnesting migration from Ascension Island to Brazil, following five individuals both during their transoceanic crossing and while on the Brazilian coast. None of the turtles travelled directly to its final destination but, instead, there were extended (up to 792 km) movements along the coast after the oceanic crossings. The extent of movement along the coast was unrelated to the oceanic crossing route. For example, individuals whose final destination was in the north of Brazil did not follow a more northerly oceanic crossing than those with a more southerly final destination. These observations show that green turtles returning from Ascension Island do not swim directly to their final destination, but instead conduct migration in two distinct phases: a fairly direct open ocean crossing, following which they turn north or south along the coast to reach their final destination. This long-distance migration may therefore be conducted without turtles needing to resort to sophisticated navigational skills. These previously unidentified long coastal movements may heighten the risk of turtles being captured by fishermen.

How animals complete long-distance migration remains enigmatic although, certainly for birds, some of the navigational cues that are used are known (Alerstam 2001a; Fransson et al. 2001). Sea turtles are thought to be among the most proficient navigators, often travelling thousands of kilometres between nesting and foraging sites (Carr 1968; Chelazzi 1992; Balazs 1994; Meylan 1995; Luschi et al. 1996; Papi & Luschi 1996; Pough et al. 2001). The navigational challenges facing marine turtles vary both between populations and during different life history stages. For example, to maximize their chances of staying within the North Atlantic gyre, juvenile loggerhead turtles, *Caretta caretta*, may use the inclination and intensity of the Earth's magnetic field as 'signposts' so that they swim south when in the northern parts of the gyre and vice versa (Lohmann & Lohmann 1996; Lohmann et al. 2001). However, the orientation cues used by adult turtles during their regular migrations between nesting and foraging areas are not known.

A classic example of adult migration concerns the green turtles, *Chelonia mydas*, that swim to and from their foraging grounds along the Brazilian coast to their nesting beaches on Ascension Island in the middle of the Atlantic (Carr 1968; Chelazzi 1992; Pough et al. 2001). Turtles tagged at Ascension Island have been recaptured over much of the Brazilian coast (between about 3°S to 23°S; Mortimer & Carr 1987) while satellite tracking has shown a tendency for individuals to swim fairly directly between Ascension and Brazil so that their oceanic crossing distance is reduced, with potentially celestial compasses being used (Luschi et al. 1998). Unfortunately in the past transmitters have almost always failed prematurely and so it has not been possible routinely to follow turtles to their final destination (Luschi et al. 1998). Here we describe how, by using more robust satellite transmitters and improved attachment methods, we followed the complete migration of turtles during their postnesting migration from Ascension Island to their final foraging grounds and hence identified the link between their oceanic crossing route and their final destination. We use these long-distance tracking results to consider whether complex navigational mechanisms need to be invoked to explain how migration in this species is accomplished.

Correspondence: G. Hays, School of Biological Sciences, University of Wales Swansea, Singleton Park, Swansea SA2 8PP, U.K. (email: g.hays@swan.ac.uk). P. Lovell and B. J. McConnell are at the Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews, Fife KY16 9TS, U.K.

METHODS

Between 24 May and 9 July 2001 we attached seven series 7000 Satellite Relay Data Loggers (SRDLs; manufactured by the Sea Mammal Research Unit of the U.K., McConnell

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et al. 1999) to green turtles at Ascension Island (7°57′S, 14°22′W). SRDLs were originally designed for deployment on to marine mammals and have a robust construction. We used a quick-setting epoxy resin (Foilfast, SFS components, Cheltenham, U.K.) to attach units to the carapace of females that had just completed nesting. To maximize the strength of attachment, the carapace was first cleaned with acetone and then lightly sandpapered. The epoxy was shaped to remove any possibility of direct impacts on the base of the aerial (which is a potential weak point), for example by turtles bumping up against underwater rocks. Attachment took about 20 min, during which time the turtles completed egg laying and covering up their nest site. Hence there was no need to restrain the turtles prior to their natural return to the sea. SRDLs were tiny, <1% by weight (700 g, physical dimensions $10 \times 7 \times 4$ cm) compared to the size of the turtles (typical weight 200 kg and carapace length 115 cm) and so their effect on the turtles' behaviour is probably minimal. All SRDLs eventually failed well before their expected battery life. This is almost certainly because they had fallen off the turtles and indeed we have evidence, from flipper-tagged turtles returning without equipment, that certainly within a few months equipment attached to the carapace will have been lost. Fieldwork was conducted with permission of the Ascension Island Administrator, His Honour Geoffrey Fairhurst.

We obtained the locations of transmitters via the Argos system (http://www.argosinc.com/) and reconstructed routes by interpolating between Argos locations, ignoring a small number (26 out of 555 during migration) that were clearly erroneous as they were well off the route reconstructed by interpolating between other locations. Occasional erroneous locations are an inherent feature of the Argos system, with class B and class 0 locations, in particular, sometimes being tens of kilometres from the true position (Hays et al. 2001). Once directed movement along the coast had stopped, we calculated the mean position of locations to define the final destination for each turtle, again ignoring a few highly erroneous (three out of 186) locations. We determined the distance travelled during migration by splitting each route into four to six straight-line segments, each of which were several hundreds of kilometres long, and then determining the length of each segment. This approach removes the impact of location inaccuracies on the calculated speeds of travel (Hays et al. 2001). Segments along the shore never crossed inland. Times are listed as Greenwich Mean Time.

RESULTS

We followed five individuals, both during their oceanic crossing and after they had reached Brazil. In four of these cases the turtles were followed until they stopped moving along the coast and then stayed in the same locality for several weeks. We conclude, therefore, that they had completed their migration and reached their destination. The routes to Brazil varied slightly between these individuals (Fig. 1). For example, turtle D travelled along the most northerly route, before arriving at the mainland

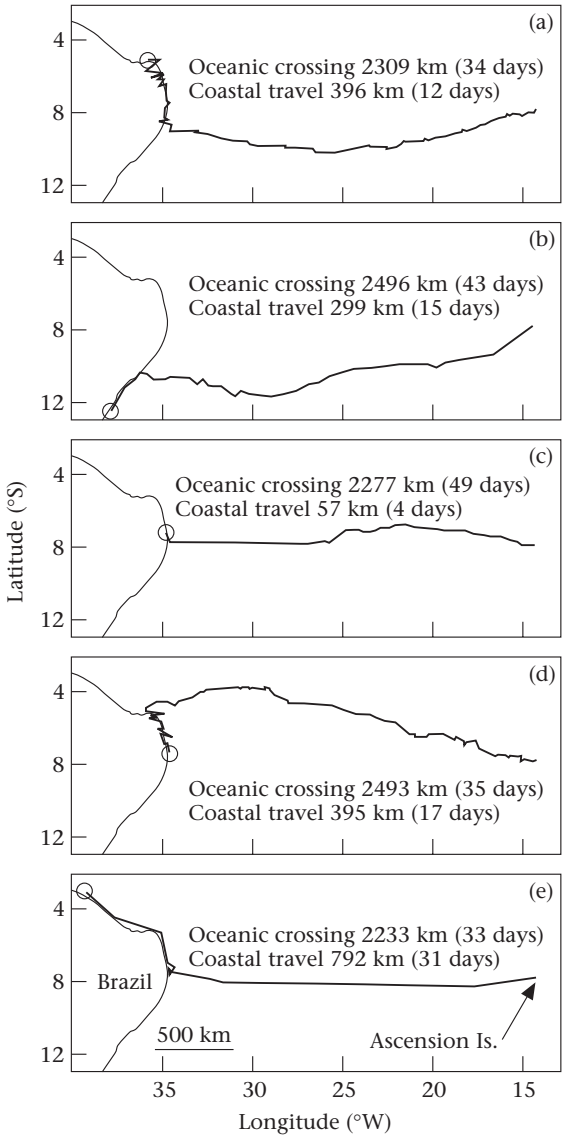

Figure 1. The routes followed by five turtles between Ascension Island and Brazil. Parts a–e represent turtles A–E, respectively. The recorded periods of residence in the vicinity of the final location were 33 days, 1 day, 43 days, 58 days and 21 days, respectively, and the mean position during these periods of residence are denoted by the open circle at the end of each track.

coast of Brazil at a latitude of about 5.1°S. In contrast, turtle B travelled in the most southerly direction and reached Brazil at a latitude of 10.4°S. Upon reaching Brazil, all five turtles conducted along-shore movements. The arrival point at the coast of Brazil appeared to have little bearing on the final destination. For example, while the turtle that followed the most southerly oceanic crossing route (turtle B) turned south after reaching the mainland, turtle D, which also turned south along the coast, had the most northerly arrival point at Brazil, while turtle E, which travelled 792 km northwards along the coast, had a relatively mid-latitude arrival point at Brazil. Furthermore, two of the turtles (C and D) had final destinations that were close to each other (7.2°S and 7.4°S, respectively), but took different routes to reach

their destination. If turtle D, which had a coastal migration of 395 km, had followed the oceanic crossing route of turtle E, then landfall would have been made within 50 km of the final destination. The coastal migration was certainly not a trivial component of the overall migration, with the distance travelled along the coast averaging 16.5% (range 2.5–35.5%) of the distance travelled across the open ocean. Turtle D, which had the most northerly landfall in Brazil, travelled via the island of Fernando de Noronha, about 350 km northeast off the coast of northern Brazil. On 4 August, turtle D was about 161 km east of Fernando de Noronha, was located at Fernando de Noronha three times between 0818 hours on 8 August and 0840 hours on 10 August, and by 2036 hours on 10 August was located 32 km west of this island as she continued her journey to mainland Brazil, that is the pattern of locations shows that the turtle stayed at the island for a maximum of only a few days. For all the turtles the speed of travel decreased markedly between the oceanic crossing (mean 61 km/day) and the period of coastal travel (mean 25 km/day).

DISCUSSION

Although there is some evidence that green turtles maintain fidelity to particular feeding areas between years (Limpus et al. 1992), the evidence is not conclusive (Cheng 2000). Therefore it is possible that the turtles returning to Brazil do not maintain fidelity to the particular foraging site they occupied prior to their migration to Ascension Island and so they might only have an approximate goal (e.g. the Brazilian coast) after which they move along the coast until they encounter a suitable area. However, such a scenario does not fit in well with the fact that the turtles did not take up residence in the first available location with suitable forage. This is clearly illustrated by turtle D which reached the island of Fernando de Noronha which has extensive macroalgal beds that support a year-round resident feeding population of green turtles (Marcovaldi et al. 1998). However, turtle D did not stay at this island but instead continued her journey to mainland Brazil. Also some of the tracked turtles moved long distances along the coast and so through areas that would have been 'suitable'. For example, turtle E travelled through the destination of turtle A, while turtle A travelled through the destination of turtle C. Furthermore, during their period of coastal travel, turtles did not follow circuitous 'searching' paths, but instead moved directly along the coast. In short, it is highly unlikely that the observed movements along the coast of several hundred kilometres simply reflect the turtles searching for a suitable foraging site.

Owing to the inaccuracies of the locations provided by the Argos system, speeds calculated over small time and distance scales can often be inaccurate (Hays et al. 2001). Therefore, if an animal is moving in approximately a straight line, then the most accurate way of determining the mean speed is to maximize the distance (and time interval) between the locations used in this calculation and this is what we have done here to show that while moving along the coast the speed of travel certainly decreased compared to the oceanic crossing. This relatively slow travel along the coast may reflect a combination of factors: during the oceanic crossing the turtles are aided by the westward flowing South Atlantic Equatorial Current and along the coast of Brazil they may stop to rest and feed.

For animals migrating to a small target such as an isolated island, precise orientation is required if the goal is to be attained without extended searching. However, the navigational task facing turtles migrating to an extended mainland coast is less demanding, as movements along the shore can be used to compensate for the exact landfall. Our results show that, freed of the necessity for direct navigation to their final destination, green turtles make use of this potential for coastal movements after their ocean crossing. In this way they can complete long-distance postnesting migrations in a relatively straightforward manner, crossing the open ocean in a fairly straight line, which would require only a compass sense (Luschi et al. 1998), and then hugging the coastline to their goal. The most well-known examples of indirect migration routes are shown by birds avoiding unfavourable areas, for example large expanses of water (Alerstam 2001b). In the case of green turtles migrating to their feeding grounds from Ascension Island, however, indirect routes are followed not to avoid unfavourable areas but simply as a pragmatic solution to completing a long journey successfully.

Our results help to complete a general conceptual framework for explaining how turtles migrate to and from nesting beaches. We can view these prenesting and postnesting migrations along a continuum of navigational difficulty. In the simplest case of nesting and foraging both taking place on the same mainland coast, then migration can readily be accomplished by simple along-shore travel (Papi et al. 1997). More involved are postnesting migrations where nesting occurs on an oceanic island and foraging on a mainland shore. In these cases, regardless of whether the island is close to the mainland (Cheng 2000) or distant (this study), migration seems to be completed though a combination of fairly direct oceanic crossings, necessitating only a crude compass sense, followed by coastal travel. The most exacting navigational task facing turtles involves finding a remote oceanic island, and although it is still not known how this task is accomplished, island finding may involve direct sensory contact (possibly olfactory) with the island (Luschi et al. 2001).

To summarize, our long-term tracking results show that green turtles do not complete migration along the shortest route but rather travel in a way that provides a simple pragmatic solution for eventually getting them to their destination. Although there is increasing localized protection of turtles in coastal foraging sites (Marcovaldi et al. 1998), both incidental and directed captures continue in many areas of the world. The identification of migration routes offers the potential of identifying potential threats to turtles (Lutcavage et al. 1997). In this regard extended along-shore movements increase the chances of turtles entering unprotected coastal areas and so are likely to raise their probability of capture.

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