Time-restricted orientation of green turtles

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ABSTRACT

Sea turtles have an exceptional ability to travel accurately between known habitats as well as from unknown areas back to familiar habitats. Previous studies indicate that their ability to migrate long distances depends upon geomagnetic cues, but that they may rely on other undetermined cues once they are close to their destination. It has been suggested that they may then use visual cues for orientation during daylight hours, but detailed analysis of their movements when approaching their destination, particularly in relation to time of day, are lacking. This study examined the orientation behaviour of 22 displaced green turtles (Chelonia mydas), tracked en route back to their foraging habitats in eastern Australia. Study turtles tended to alternate stationary and travelling states during their trip home. Orientation corrections predominantly occurred immediately after a stationary state and after sunrise. This is the first study to demonstrate time-restricted orientation by sea turtles and provided a new insight into their sophisticated way-finding abilities.

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1. Introduction

Migration is a critical component of the life history of many animals, ranging from plankton to large vertebrates (Dingle, 1996). Migratory animals travel between distant locations to meet needs such as food acquisition, reproduction, shelter, competition, and to respond to fluctuating environmental conditions (Dingle and Drake, 2007; Pulido, 2007; Ramenofsky and Wingfield, 2007). To complete migrations, the animals rely on their way-finding abilities, which enable them to stay on the right course (Åkesson and Hedenström, 2007; Lohmann et al., 2008a; Salewski and Bruderer, 2007).

The key components of way-finding ability are map sense (i.e. navigation) and compass sense (i.e. orientation). Map sense allows animals to determine their position on earth relative to a goal, and compass sense aids them to determine the direction of the direct path to a goal (Able, 2001; Bauer et al., 2011). The processes of navigation and orientation vary among animals (Milner-Gulland et al., 2011; Papi, 1992; Piersma et al., 2005) and assessing the underlying mechanism has been identified as a key question in the field of movement ecology (Hays et al., 2016; Nathan et al., 2008).

Natural scientists investigating animal navigation and orientation mechanisms have given much attention to sea turtles because they exhibit exceptional way-finding abilities (e.g. Carr, 1967; Darwin, 1873; Lohmann et al., 2008b). Generally, sea turtles use multiple habitats that are often separated by long distances (e.g. breeding and foraging habitats) and they are able to travel between those habitats with great accuracy (Limpus and Limpus, 2001; Schofield et al., 2010). Furthermore, displacement experiments have shown that sea turtles are also capable of travelling through unknown waters and consistently return to the area of capture following human-induced displacement (Avens et al., 2003; Luschi et al., 2003; Shimada et al., 2016).

Sea turtles appear to use the earth's magnetic field as the main source of information for navigation and orientation over long distances (Lohmann et al., 2013). For example, an experimental study using a coil system exposed juvenile green turtles (Chelonia mydas) to a magnetic field 337 km south or north of the test sites, and demonstrated that each turtle swam toward the general area of the magnetic field to which they were exposed (Lohmann et al., 2004). Yet, directional cues other than the geomagnetic field may also guide turtles to a specific end point given successful homing by magnetically-disrupted turtles after displacement (Benhamou et al., 2011; Papi et al., 2000). In particular, Benhamou et al. (2011) found that magnetic disruption had a very small effect on fine-scale orientation as the turtles approached their destinations. The orientation process during the last stage of migration appears critical because that is when breeding loggerhead turtles (Caretta caretta) and a breeding green turtle, tracked by satellite telemetry, were observed to make major course corrections in relation to their observed end point (Hays et al., 2014; Shimada, 2016b).

The fine-scale orientation process may involve chemical cues carried by wind or currents but these cues can only provide useful directional information in situations where a turtle swims against the current or wind thereby allowing detection of cues from the target destination

(Endres and Lohmann, 2013; Hays et al., 2003; Lohmann et al., 2013). Alternative hypotheses suggest that sea turtles may obtain other orientation cues during the day (Avens and Lohmann, 2003; Mott and Salmon, 2011; Shimada et al., 2016); however, details of fine-scale at-sea orientation behaviour, particularly in relation to time of day, are lacking for sea turtles.

Most displaced turtles tracked by Shimada et al. (2016) were relocated relatively short distances from their capture site, hence their travels back to their home habitat are in the category of short-distance migration. In this case, since the target the turtles were aiming for is known, the tracks of these displaced turtles provide an opportunity to examine possible hypotheses about the mechanisms controlling short-range orientation. Here, detailed analyses were conducted for the actual tracks taken by displaced turtles during the final stage of their homeward journey. Their movements in relation to time of day was also explored to seek any insights into potential orientation mechanisms.

2. Materials and methods

2.1. Data acquisition & pre-processing

This study used satellite-derived tracks collected from 22 green turtles at various foraging habitats in north-eastern Australia between 2008 and 2014 (Fig. S1, Table S1). All the turtles were captured by the rodeo method (Limpus, 1978) and identified as sexually mature females and males by gonad examination via laparoscopy or by a combination of curved carapace length and the tail length from carapace (Limpus et al., 2005). Each turtle was deployed with an Argos-linked Fastloc GPS (FGPS) tag (Sirtrack, Wildlife Computers, or SMRU Instrumentation) on the carapace with Sika AnchorFix®-3 + epoxy glue and fibreglass (Shimada et al., 2012). Study turtles were relocated from the capture site by boats and cars (range = 8.0 to 28.1 km, mean ± SD = 18.0 ± 4.6 km) and tracked back to the area of capture (Shimada et al., 2016). During relocation, the turtles were not able to see the benthic topography nor sense current-borne chemical cues, but geomagnetic, celestial and air-borne chemical cues were available. Study turtles did not approach terrestrial obstacles (e.g. islands) closer than 100 m during their homeward journey (first 3 h after release were exempted), and therefore it was assumed that the turtles' directional choices were not affected by physical boundaries.

An Argos-linked FGPS tag uses two different satellite systems (i.e. GPS and Argos) to acquire location fixes. This study merged FGPS fixes (>3 GPS satellites and residual error value <30) with high quality Argos fixes (location class 3, 2, 1), and then applied screening as follows using the R package SDLfilter (Shimada, 2016a). Spatial and temporal duplicates were removed following Shimada et al. (2016) and only a single fix was retained per time and location. Biologically unrealistic movements (e.g. excessively fast speed) were identified and screened by the data driven filter (Shimada et al., 2012) using the threshold values estimated in Shimada et al. (2016). When the data driven filter is used, the estimated error (mean ± SD) for FGPS fixes is 0.05 ± 0.06 km (Shimada et al., 2012). Fixes above high tide line (i.e. on land) were also excluded following Shimada et al. (2016). The high tide line was estimated using bathymetry models (Beaman, 2010; Daniell, 2008) and tidal data obtained from the Australian Bureau of Meteorology and Queensland Department of Transport and Main Roads.

2.2. Behaviour analysis

Turtle tracks used in the analyses started at the point of release and ended when the turtles had returned to their 'home' habitat (Shimada et al., 2016). The data contained 714 FGPS fixes and 31 high quality Argos fixes from the 22 tracks. All analyses were executed with R software (R Core Team, 2015).

2.2.1. General patterns in tracks

First provided is a description of general spatial and temporal patterns seen in the tracks as a whole (i.e. distance, turn, direction, duration, timing), with a particular focus on sequences of consistent behaviour ("travelling" versus "stationary" states) and the transitions between them.

The residence time method (Barraquand and Benhamou, 2008) and a partitioning method (Lavielle, 2005) were used to divide each track into travelling or stationary periods (Fig. 1). The residence time method estimates the amount of time spent by an animal within a circle of a given radius centred at each observed location. The Lavielle's partitioning method, which identifies the point of change in residence time based on a penalised contrast, was then used to delineate successive locations of relatively high residency (i.e. a stationary period) from those of relatively low residency (i.e. a travelling period). The R package adehabitatLT (Calenge, 2006, 2015) was used to execute residence time calculation and track partitioning (see Table S2 for the parameters used).

Distances moved during each travelling or stationary period were quantified in two different ways: beeline distance and track distance. For each period, beeline distance is the straight-line distance from the first and last fixes, and track distance is the sum of distances between consecutive fixes. Beeline distance represents how far each turtle relocated, and track distance represents minimum actual distance moved during each travelling and stationary period. Duration was calculated as the time between the first and the last fixes within each movement period. Average travelling speed was estimated over each beeline distance and track distance.

The absolute turning angle was estimated at each fix within travelling periods. Turning angles were not estimated at each fix within a stationary period. Instead, the stationary period was treated as a single point. The absolute turning angle associated with a stationary period was estimated as the difference in travel direction immediately prior to, and immediately after the stationary period (Fig. 2A). That is, the absolute turning angle over the stationary period was the difference in direction between the two line segments:
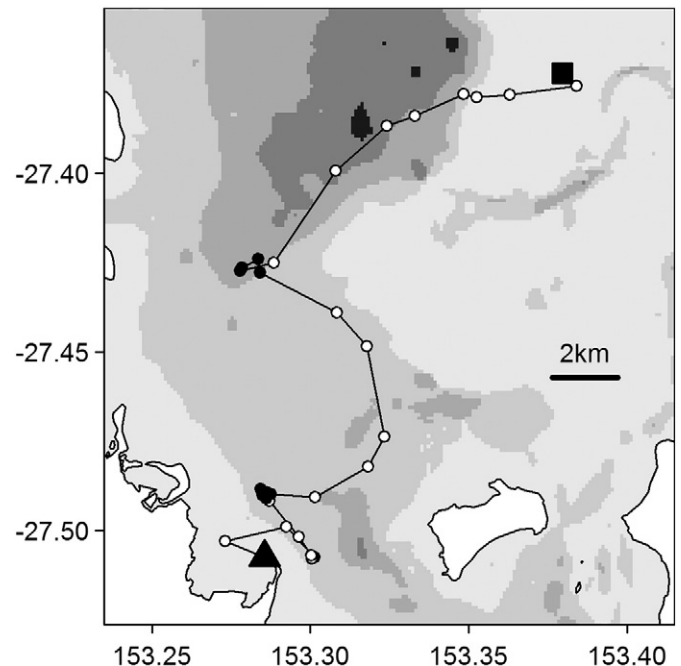
Fig. 1. *Chelonia mydas*. A homing track of a study turtle following displacement. Triangle = release point, empty circle = travelling state, filled circle = stationary state, square = end point. Successive locations are connected by black lines. Grey gradients show water depth ranges at mean sea level (0–5 m, 5–10 m, 10–15 m, 15-20 m, >20 m): the darker the colour the deeper the water.