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RESEARCH ARTICLE

Orientation of hatchling loggerhead sea turtles to regional magnetic fields along a transoceanic migratory pathway

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SUMMARY

Young loggerhead sea turtles (*Caretta caretta*) from the east coast of Florida, USA, undertake a transoceanic migration around the North Atlantic Gyre, the circular current system that flows around the Sargasso Sea. Previous experiments indicated that loggerhead hatchlings, when exposed to magnetic fields replicating those that exist at five widely separated locations along the migratory pathway, responded by swimming in directions that would, in each case, help turtles remain in the gyre and advance along the migratory route. In this study, hatchlings were exposed to several additional magnetic fields that exist along or outside of the gyre's northern boundary. Hatchlings responded to fields that exist within the gyre currents by swimming in directions consistent with their migratory route at each location, whereas turtles exposed to a field that exists north of the gyre had an orientation that was statistically indistinguishable from random. These results are consistent with the hypothesis that loggerhead turtles entering the sea for the first time possess a navigational system in which a series of regional magnetic fields sequentially trigger orientation responses that help steer turtles along the migratory route. By contrast, hatchlings may fail to respond to fields that exist in locations beyond the turtles' normal geographic range.

Key words: magnetic orientation, navigation, magnetoreception, sea turtle, *Caretta caretta*, secular variation.

INTRODUCTION

Numerous marine vertebrates undergo long-distance migrations, including various fishes (Block et al., 2001; Bonfil et al., 2005), reptiles (James et al., 2005; Reich et al., 2007), seabirds (Gonzalez-Solis et al., 2007; Shaffer et al., 2006) and mammals (Lagerquist et al., 2008; Le Boeuf et al., 2000). In some cases, first-time migrants travel alone but nevertheless follow complex migratory routes that span hundreds or thousands of kilometres (Bolten et al., 1998; Kooyman et al., 1996; Quinn and Dittman, 1990). Little is known about the mechanisms that guide these long-distance migrations.

After emerging from underground nests, hatchling loggerhead sea turtles (*Caretta caretta*) from the east coast of Florida, USA, embark on one of the most spectacular marine migrations. Turtles enter the sea and swim to the North Atlantic Gyre, a circular current system that flows around the Sargasso Sea (Carr, 1987; Lohmann and Lohmann, 2003; Musick and Limpus, 1997). Turtles remain within the gyre for several years, during which time many cross to the eastern side of the Atlantic before eventually returning to the North American coast (Bolten, 2003; Musick and Limpus, 1997).

For young loggerheads, conditions within the North Atlantic Gyre are favourable for survival and growth (Bjorndal et al., 2000), whereas straying outside of the gyre is often fatal. For example, in the northeastern region of the gyre, the east-flowing current divides into a north-flowing branch and a south-flowing branch. Loggerheads swept to the north are likely to be carried into lethally cold waters (Cain et al., 2005; Carr, 1987; Hays and Marsh, 1997; Lohmann and Lohmann, 2003). Under these conditions, the ability to remain in the gyre by altering swimming direction at appropriate geographic locations might have considerable adaptive value.

The Earth's magnetic field provides a pervasive source of directional and positional information that is used by diverse animals for orientation and navigation (reviewed by Johnsen and Lohmann, 2005; Lohmann, 2010; Wiltschko and Wiltschko, 1995). The field varies predictably across the surface of the planet in such a way that most oceanic regions are marked by unique magnetic fields (Lohmann et al., 2008; Lohmann et al., 2007). Loggerhead hatchlings can detect the inclination angle of field lines (Lohmann and Lohmann, 1994b) and total field intensity (Lohmann and Lohmann, 1996a), two magnetic elements that might, in principle, provide sufficient positional information to guide movements around the gyre (Lohmann and Lohmann, 1996b; Wiltschko and Wiltschko, 2005). When subjected to magnetic fields such as those found at five widely separated locations along the migratory route, hatchling loggerheads responded by swimming in directions that would, in each case, help them remain within the gyre currents and advance along the migratory pathway (Lohmann et al., 2001; Putman et al., 2011). These results suggest that young loggerheads are equipped with a magnetic position-finding system in which regional magnetic fields elicit changes in swimming direction at particular geographic locations.

It is not known, however, whether hatchlings respond only to a few fields that exist at crucial geographic boundaries, or also to fields that exist anywhere along the migratory route or even outside of the gyre. Here we investigate this issue by exposing hatchling loggerheads to additional magnetic fields that exist at three different locations along the northern portion of the migratory route, as well as to a field that exists north of the migratory pathway where turtles probably cannot go because the water temperature is too cold.

MATERIALS AND METHODS

Animals

Hatchling loggerheads, *Caretta caretta* (Linnaeus 1758), were collected from nests deposited along an 8 km stretch of coastline in Melbourne Beach, Florida, USA. We recorded the date each nest was deposited and then monitored the time to emergence for nests in the same area, allowing us to accurately predict when hatchlings from a given nest would emerge. In the late afternoon, a few hours before the turtles would otherwise have emerged naturally, we gently dug into the sand with our hands and removed 15–20 hatchlings. Turtles were immediately placed into a lightproof, Styrofoam^{TM} container and transported to a nearby laboratory. Hatchlings were maintained in complete darkness until testing.

Orientation arena and tracking system

Turtles were tested in a circular orientation arena (91.4 cm diameter) that was filled with water to a depth of approximately 40 cm (Fig. 1). Water temperature during trials ranged from 26.0 to 28.0°C.

In each trial, a hatchling was placed into a nylon–lycra harness that encircled its carapace but did not impede swimming (Salmon and Wyneken, 1987). A monofilament line 10.2 cm in length connected the harness to a tracker arm, which measured 25.4 cm from its tip to the centre of the arena. The tracker arm could rotate 360 deg in the horizontal plane so that turtles could swim in any direction without touching either the edge of the arena or the central post. The arm was attached to a digital encoder encased inside a plastic post mounted in the centre of the tank. The digital encoder was wired to a computer in a nearby room so that the orientation of each turtle could be monitored. To ensure that no light entered the orientation arena during a trial, we covered the tank before each trial with a plywood lid (1.9 cm thick) and then four layers of black plastic sheeting.

Magnetic coil system

The orientation arena was surrounded by a computer-controlled magnetic coil system capable of generating uniform, Earth-strength magnetic fields (Fig. 1). The system consisted of two coils arranged orthogonally, each designed in accordance with the four-square design of Merritt and colleagues (Merritt et al., 1983). The first coil measured 2.41 m on a side and was aligned along the north–south axis so that it could be used to control the horizontal component of the magnetic field. The second coil, constructed around the first, measured 2.57 m on a side and controlled the vertical component of the field. The current to the two coils was controlled by computer software, which enabled us to replicate the magnetic field existing at any location in the Atlantic Ocean. To avoid field distortions from buildings or electrical wiring, the coil was located outdoors more than 15 m from the building in which the data-acquisition computer was housed.

During experiments, turtles were restricted to an area in the centre of the coil defined by a horizontal circle of radius 30 cm and a vertical area of about 5 cm. In this region, calculated (Kirschvink, 1992) and measured deviations from perfect field uniformity were less than 0.3%.

Magnetic field parameters

Turtles were tested in four different magnetic fields that approximate those at different locations in the Atlantic: (1) the mid-Atlantic along the northern gyre currents (40.0°N, 45.0°W); (2) near the northeastern boundary of the gyre (44.5°N, 20.0°W); (3) off the southern coast of Portugal (39.6°N, 14.0°W), an area that is unique because the magnetic field that exists there also exists elsewhere in the Atlantic (Lohmann and Lohmann, 1996b); and (4) north of the gyre currents (52.0°N, 40.0°W), an area with temperatures too cold for loggerheads (Witt et al., 2010).

The parameters for each field were based on estimates provided by the International Geomagnetic Reference Field (IGRF) model, version 2005, for July 2006, the month when most of the data were collected. The fields produced by the coil system replicated the IGRF estimates to within 0.1 deg of inclination and 0.1 μT of intensity, based on five independent measurements in each field with a tri-axial fluxgate magnetometer (Applied Physics Systems, Model 520). Field parameters were as follows: (1) mid-Atlantic location: inclination 59.5 deg, intensity 46.7 μT; (2) northeastern gyre: inclination 60.2 deg, intensity 46.2 μT; (3) south Portugal location: inclination 54.4°, intensity 44.0 μT; (4) north of gyre: inclination 69.0 deg, intensity 51.1 μT.

Testing procedure

All experiments were conducted between late June and early August 2006. Trials were carried out between 20:30 and 02:00 h, the time when most loggerhead hatchlings emerge from their nests and enter the sea (Witherington et al., 1990).

Prior to each trial, the magnetic coils were turned off and a light-emitting diode (LED) with a peak wavelength of 550 nm was illuminated on the tank's east side. A hatchling was placed in the harness and released into the water. Healthy hatchlings swim vigorously towards light after emerging from their nest; thus, the hatchling's swimming response verified that the animal was behaviourally competent (Lohmann and Lohmann, 1994a; Salmon and Wyneken, 1987). Those few turtles that failed to swim toward

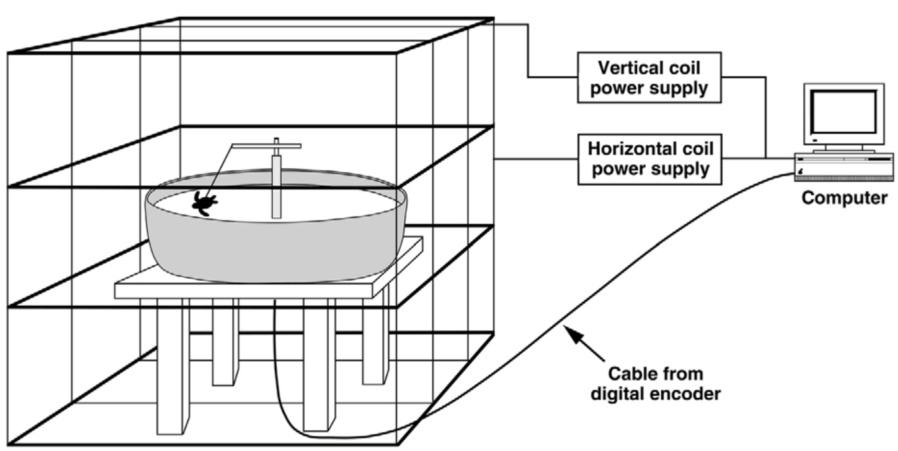

Fig. 1. Schematic of the experimental apparatus, including the orientation arena, magnetic coil structure and data-acquisition system. Turtles were tethered to a rotatable tracker arm attached to a digital encoder, which relayed the direction of swimming to a computer in a nearby building. The arena was enclosed by a magnetic coil capable of replicating magnetic fields found at different locations along the turtles' migratory route. Modified from Lohmann and Lohmann (Lohmann and Lohmann, 2003).

the LED (less than 5%) were replaced with other individuals prior to the start of the trial.

Each turtle was permitted to swim toward the light in the local field for 10 min. The light was then turned off and the magnetic coils were simultaneously turned on so that each hatchling was exposed to one of the four different magnetic fields. Turtles were then given 3 min to acclimate in the new field, after which the computer recorded each hatchling's heading once every 10 s for the next 5 min.

Each hatchling was tested a single time in one of the four fields. Hatchlings drawn from at least nine different nests were tested in each field, and no more than three turtles from the same nest were tested in any given field. Hatchlings were released on the beach after each night's testing was completed.

Data analysis and statistics

A mean heading for each turtle was calculated using all data points recorded during its 5 min trial period. Rayleigh tests were used to determine whether groups of hatchlings tested in each field were significantly oriented (Batschelet, 1981). The distributions in the four fields were compared using the Mardia–Watson–Wheeler test (Batschelet, 1981; Zar, 1999).

RESULTS

Hatchlings exposed to a magnetic field that exists within the gyre currents near the middle of the Atlantic (Fig. 2) were significantly oriented toward the east (mean angle=70.8 deg, Rayleigh test, r=0.33, N=30, P=0.036). Turtles exposed to a field like one that exists near the gyre's northeastern boundary were also significantly oriented, but in a southerly direction (mean angle=164.7 deg, r=0.40, N=56, P<0.001). Turtles exposed to a field that exists offshore near southern Portugal were significantly oriented approximately toward the southwest (mean angle=242.0 deg, r=0.36, N=27, P=0.028). In contrast, the orientation of turtles exposed to a field that exists north of the gyre was statistically indistinguishable from random (mean angle=121.0 deg, r=0.16, N=27, P=0.51). The Mardia–Watson–Wheeler test indicated that significant differences existed among the four distributions (W=21.72, P<0.01). Thus, the results indicate that loggerhead turtles can distinguish among magnetic fields that exist in these different locations.

DISCUSSION

Hatchling loggerhead turtles oriented east-northeast when exposed to a magnetic field replicating one that exists in the Gulf Stream

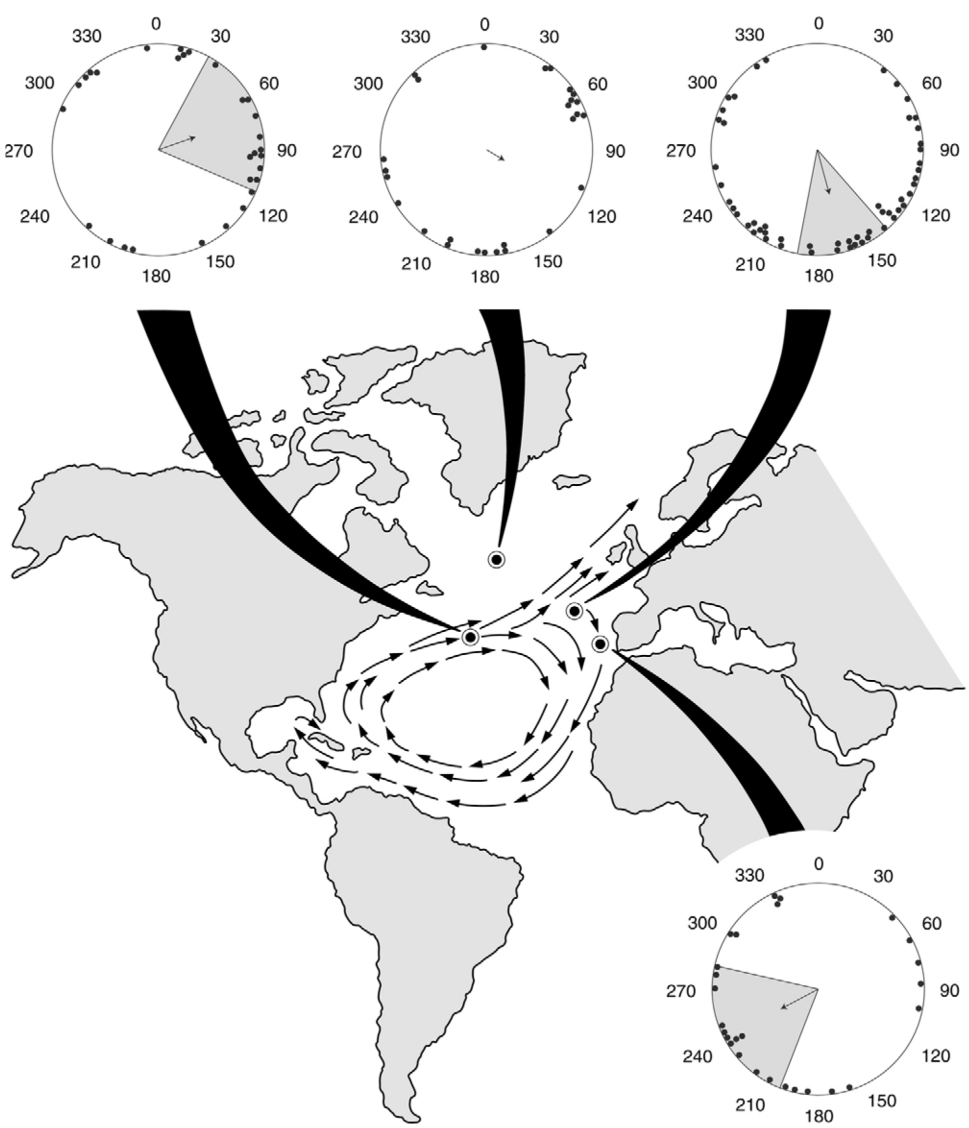

Fig. 2. Diagram of hatchling orientation responses to magnetic fields that exist at different locations (indicated by circled dots) in the North Atlantic Ocean. The arrows on the map represent the main gyre currents. In the orientation diagrams, each dot represents the mean heading of a single hatchling. The arrow indicates the mean direction of turtles in the group, with the length of the arrow proportional to the magnitude of the mean vector r (the radius of the circle corresponds to r=1). The shaded sector inside the circle indicates the 95% confidence interval for distributions that were significantly oriented. Data are plotted relative to magnetic north. Hatchlings subjected to a field that exists near the middle of the Atlantic and within the east-flowing gyre currents were significantly oriented (r=0.33, N=30, P=0.036, Rayleigh test), with a mean heading of 70.8 deg. Hatchlings exposed to a field that exists north of the gyre had orientation that was statistically indistinguishable from random (r=0.16, N=27, P=0.51). Hatchlings exposed to a field that exists at the gyre's northeast boundary were significantly oriented (r=0.40, N=54, P<0.001), with a mean heading of 164.7 deg. Hatchlings exposed to a field located offshore from the southern coast of Portugal were significantly oriented as a group (r=0.36, N=27, P=0.028), with a mean heading of 242.0 deg.

approximately halfway across the Atlantic. In contrast, turtles exposed to a field like one found near the coast of northern Portugal swam approximately south, and turtles exposed to a field that exists off the coast of southern Portugal swam approximately southwest. These three fields exist at locations within the gyre currents and along the normal migratory route of Florida loggerheads (Carr, 1987); thus, they are likely to be encountered by migrating turtles. One additional group of turtles was exposed to a magnetic field that exists in an area to the north of the gyre that is well outside the normal migratory route (Witt et al., 2010). Hatchlings tested in this field had orientation that was statistically indistinguishable from random.

Orientation responses to fields in the gyre

The orientation responses of turtles to each of the three magnetic fields that exist along the migratory route appear likely to have functional significance in the migration of young loggerheads. For turtles moving along the northern gyre boundary in the mid-Atlantic, an east-northeasterly orientation would presumably help turtles pass through an unpredictable oceanic area characterized by considerable surface current variation, Gulf Stream meanders and a high degree of eddy formation (Richardson, 1975; Richardson, 1985). Current meanders and eddies have the potential to displace turtles from the migratory route and delay hatchlings from reaching foraging grounds in the eastern North Atlantic (Bolten, 2003; Bolten et al., 1998). By actively moving eastward through this region instead of drifting passively, hatchlings might reduce the likelihood of being displaced from the migratory route.

Turtles exposed to a field like one that exists off the coast of northern Portugal oriented southwards, a response consistent with results of a previous experiment in which hatchling turtles were exposed to a similar field (Lohmann et al., 2001). Swimming south in this geographic area presumably helps turtles remain within the warm-water gyre and avoid the lethally cold waters to the north (Cain et al., 2005; Locarnini et al., 2006; Lohmann et al., 2001).

Turtles subjected to a field like one that exists offshore near southern Portugal swam in a southwesterly direction, a response consistent with both the direction of the gyre currents in this area and the turtles' migratory route. As noted, the south Portugal field is unusual in that, whereas fields that exist in the north Atlantic are typically unique to a single geographic region, the field near south Portugal matches or closely resembles fields that exist within a narrow transoceanic corridor extending from south Portugal through the Sargasso Sea and towards the West Indies (Lohmann and Lohmann, 1996b). Thus, turtles might conceivably encounter this particular field in more than one location, although whether they actually travel through the Sargasso Sea and other geographic areas where the same field exists is not known.

Response to a field outside the gyre

Hatchlings exposed to a field that exists well north of the migratory route had orientation that was statistically indistinguishable from random. This result is consistent with the hypothesis that hatchling loggerheads are not programmed to respond to regional fields that exist outside of the normal migratory pathway.

In a previous experiment, turtles also oriented randomly when exposed to magnetic fields with inclination angles that exist north or south of the migratory route (Lohmann and Lohmann, 1994b). An important caveat, however, is that the fields used in the earlier study did not fully replicate fields that exist in nature; instead, the intensity was held constant, so that different inclination angles were each paired with a field intensity that existed near the natal beach in Florida. The present study is the first to test the responses of hatchlings to a field that fully replicates one that exists outside the gyre.

The finding that a field from outside the gyre failed to elicit an oriented swimming response from turtles must be interpreted with caution for several reasons. At present, only one field from a single location more than 2000 km north of the main gyre currents has been tested; thus, other fields that exist closer to the migratory route, but still outside it, might elicit oriented swimming. In addition, the turtles tested were hatchlings that had never been in the ocean. Migratory experience might enhance the magnetic guidance system of loggerheads, and after weeks or months migrating at sea, turtles might be able to extrapolate position more effectively from magnetic fields that exist beyond their normal geographic range. Ontogenetic changes in orientation and navigation behaviour are known to occur in some animals (Able and Able, 1996; Wiltschko and Wiltschko, 1985), including sea turtles, which as juveniles appear to learn the magnetic topography of areas where they live (Lohmann et al., 2004; Lohmann et al., 2008). Yet another possibility is that young turtles have an 'intensity window' similar to that of birds and thus need time to acclimate to fields that differ greatly from those they have encountered previously (Wiltschko and Wiltschko, 1995). If so, then turtles under natural conditions might respond differently to fields from outside the migratory route than did turtles in our experiment.

Regional magnetic fields as navigational waypoints

Our findings corroborate and extend previous results indicating that hatchling loggerheads can distinguish among magnetic fields that exist at different geographic locations along their migratory route (Lohmann et al., 2001; Putman et al., 2011). Our new data indicate, however, that the hatchlings' ability to exploit regional fields as open-ocean guideposts is more extensive than previously recognized. For example, not all fields along the northern boundary of the gyre elicited identical southerly orientation, which might function to keep turtles within an appropriate range of latitudes. Instead, a field that exists in the Gulf Stream about halfway across the Atlantic elicited east-northeasterly orientation, consistent with the migratory route (Fig. 2).

One possible interpretation of these results is that hatchlings use regional magnetic fields along their migratory pathway as a series of magnetic waypoints (Lohmann and Lohmann, 2006; Lohmann et al., 2007). In effect, the migration might be accomplished as a series of sequential steps, in which distinct regional magnetic fields each in turn trigger orientation responses that lead turtles in the appropriate direction for the next segment of the migration. Viewed in this way, couplings of directional swimming to regional fields may provide the building blocks or 'subroutines' (Wehner, 1998) from which natural selection can sculpt a sequence of responses capable of guiding first-time migrants along complex migratory routes. The existence of such responses does not rule out the possible involvement of additional cues and mechanisms in guiding the first migration, nor does it preclude the development of additional navigational strategies or mechanisms as the turtles mature.

Natural field change and orientation responses

Although regional magnetic fields evidently elicit directional swimming in young loggerheads, the field that marks a given geographic area changes gradually over time (Skiles, 1985). In light of this field change (known as secular variation), how can hatchlings evolve useful navigational responses to regional fields? A likely explanation is that strong selective pressure acts to maintain an appropriate coupling between the turtles' directional swimming responses and the magnetic fields that exist at crucial geographic locations along the migratory pathway at any point in time (Lohmann et al., 1999; Lohmann et al., 2001; Lohmann and Lohmann, 1998; Lohmann and Lohmann, 2003; Putman et al., 2011). Under the present conditions of the North Atlantic, for example, turtles that stray out of the gyre are likely removed from the population, whereas selection favours those individuals with orientation responses that help keep them inside the gyre currents. As the field that exists in a specific region of the migratory pathway changes, only those turtles that respond to the new field in a way that allows them to migrate successfully will survive to pass on their genes.

These considerations aside, responses to regional magnetic fields might be rendered useless during limited periods of exceedingly rapid field change (Camps et al., 1995; Coe and Prevot, 1989) that sometimes accompany polarity reversals of the Earth's field. Such transient periods of rapid change, however, do not preclude the evolution of magnetic responses during the intervening and usually longer intervals (Skiles, 1985) when the Earth's field changes slowly and is relatively stable. Indeed, responses similar to those we describe in sea turtles might also function in the navigation of diverse migratory animals (Block et al., 2001; Gonzalez-Solis et al., 2007; Henshaw et al., 2010; Le Boeuf et al., 2000; Quinn and Dittman, 1990).

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