Sea Turtle Navigation and the Detection of Geomagnetic Field Features

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1. INTRODUCTION. The lives of sea turtles consist of a continuous series of migrations. As hatchlings, the turtles swim from their natal beaches into the open sea,[1,2] often taking refuge in circular current systems (gyres) that serve as moving, open-ocean nursery grounds[3]. The juveniles of many populations subsequently take up residence in coastal feeding areas that are located hundreds or thousands of kilometres from the beaches on which the turtles hatched;[4,5,6] some juveniles also migrate between summer and winter habitats.[7] As adults, turtles periodically leave their feeding grounds and migrate to breeding and nesting regions, after which many return to their own specific feeding sites.[7,8] The itinerant lifestyle characteristic of most sea turtle species is thus inextricably linked to an ability to orient and navigate accurately across large expanses of seemingly featureless ocean.

In some sea turtle populations, migratory performance reaches extremes. The total distances certain green turtles (*Chelonia mydas*) and loggerheads (*Caretta caretta*) traverse over the span of their lifetimes exceed tens of thousands of kilometres, several times the diameter of the turtle's home ocean basin.[9,10,11] Adult migrations between feeding and nesting habitats can require continuous swimming for periods of several weeks.[8,12] In addition, the paths of migrating turtles often lead almost straight across the open ocean and directly to the destination,[13,14,15] leaving little doubt that turtles can navigate to distant target sites with remarkable efficiency.

The migrations of hatchling turtles are equally impressive. Within seconds of emerging from their underground nests at night, hatchlings begin to crawl directly toward an ocean that cannot be seen from the emergence site.[16] Upon entering the sea, the young turtles immediately establish offshore headings and then maintain them long after visual contact with land is lost.[1,2,17] Thus, even moments after emerging from their nests, sea turtles are equipped with an array of mechanisms that permit well-oriented movements.

For logistical reasons, most studies on orientation mechanisms in sea turtles have focused on hatchlings rather than adults. Adults are powerful animals that often exceed one hundred kilograms in weight; they are also difficult to keep in captivity, and migrate only intermittently. In contrast, hatchlings are small,

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Fig. 1. Generalised diagram of the North Atlantic gyre, the current system that encircles the Sargasso Sea

seasonally abundant, easy to manipulate in laboratory and field studies, and strongly motivated to migrate offshore. In recent years, considerable progress has been made in characterising the orientation cues that guide hatchling turtles during their offshore migration.[16,18] In contrast, the navigational mechanisms that guide adult turtles have remained almost entirely unknown.

One of several orientation mechanisms present in hatchling sea turtles is a magnetic compass.[19,20,21,22,23] However, in addition to deriving directional information from the Earth's magnetic field, loggerhead hatchlings can apparently sense two different magnetic field features that vary across the surface of the Earth and may provide information on global position.[24,25] In this paper, we briefly summarise experimental evidence indicating that loggerhead turtles can detect magnetic inclination angle and magnetic field intensity. In addition, we discuss how hatchling and juvenile turtles may exploit this information to keep themselves within an oceanic area favourable for development. We conclude by speculating about how adult turtles might use geomagnetic features as components of a long-distance navigational system.

2. ORIENTED MOVEMENTS IN THE OPEN OCEAN. Hatchling loggerheads from the east coast of Florida enter the sea and swim from their natal beach to

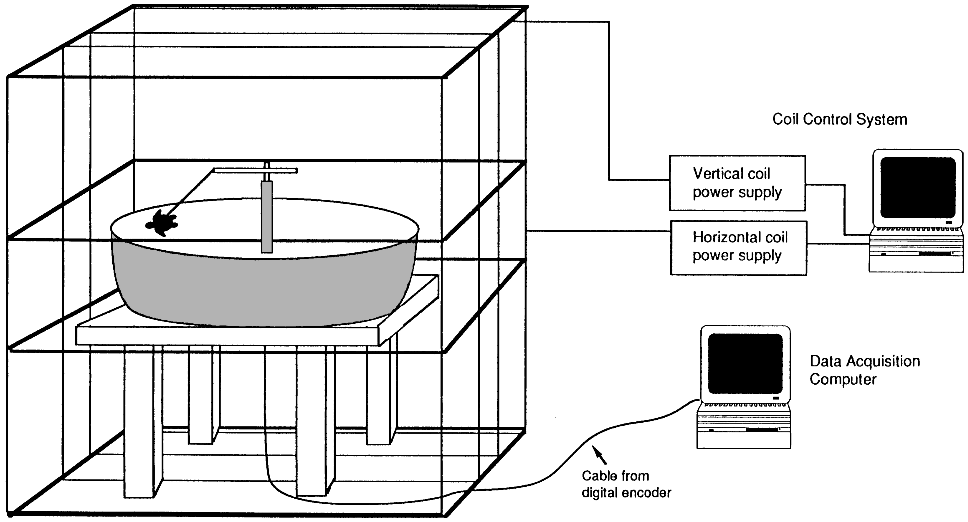

Fig. 2. Diagram of the orientation arena, magnetic coil system, and data acquisition system used in studies of hatchling responses to magnetic field features.[24] Each hatchling was tethered to a rotatable lever-arm mounted on a digital encoder (located inside the central post of the orientation arena). The lever arm tracked the direction toward which the turtle swam; signals from the encoder were relayed to the data acquisition computer, which recorded the orientation of the turtle every 10 seconds. The arena was enclosed by a magnetic coil system consisting of two different coils arranged orthogonally. One controlled the horizontal component of the field while the other controlled the vertical component.

the Gulf Stream current. During the offshore migration, hatchlings appear to use three distinct types of orientation cues sequentially.[16] On the beach, hatchlings crawl seaward by orienting toward the bright, low oceanic horizon. Once in the ocean, turtles initially swim offshore by orienting into waves. As the turtles move seaward (first by crawling and then by swimming), they apparently transfer their initial headings to their magnetic compasses, enabling them to maintain offshore courses after swimming beyond the wave refraction zone and into deep water where wave movement no longer reliably indicates the offshore direction.

The offshore migration to the Gulf Stream is just the first step in a much longer transoceanic journey. Young loggerheads evidently remain in the North Atlantic gyre (Fig. 1) for several years.[3] During this time they cross to the eastern side of the Atlantic Ocean before returning to the southeastern United States coast as subadults.[26,27] Analyses of mitochondrial DNA from nesting loggerheads has provided evidence that adult females eventually return to nest in the same geographic region where they themselves emerged as hatchlings.[4,5,28]

Hatchling and juvenile loggerheads in the open sea may benefit from oriented movements that serve to keep them within oceanic regions favourable for growth and development. For example, whereas the warm waters of the Gulf Stream provide a suitable environment for young turtles, straying beyond the latitudinal extremes of the North Atlantic gyre can be fatal. As the northern edge of the gyre approaches Portugal, the east-flowing current divides (Fig. 1). The northern

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branch continues past Great Britain and the water temperature decreases rapidly. Loggerheads swept north in this current soon die from the cold.[3,26] Similarly, turtles that venture south of the gyre risk being swept into the south Atlantic current system and carried far from their normal range. An ability to recognise the latitudinal extremes of the gyre, and to respond by orienting in an appropriate direction, might therefore have considerable adaptive value.

3. DETECTION OF MAGNETIC INCLINATION ANGLE. Several features of the Earth's magnetic field vary in a predictable way across the surface of the Earth. One such geomagnetic parameter, strongly correlated with latitude, is field line inclination.[29] At each position on the globe, magnetic field lines intersect the Earth's surface at a specific angle ranging from 0° (parallel to the Earth) at the geomagnetic equator to 90° at the magnetic poles. Thus, an animal able to distinguish between different inclination angles might be able to approximate its latitude.

To determine if loggerheads can distinguish between different magnetic inclination angles, hatchlings were tethered in a water-filled arena surrounded by a computerised coil system (Fig. 2) that was used to generate Earth-strength fields with different inclinations.[24] Hatchlings exposed to a field with an inclination angle found on the northern boundary of the North Atlantic gyre swam south-southwest (Fig. 3). In contrast, hatchlings exposed to an inclination

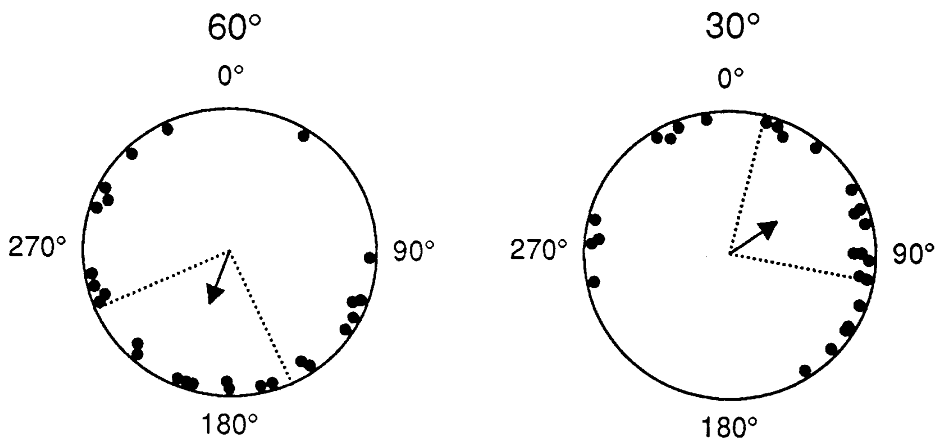

Fig. 3. Orientation of hatchling loggerheads tested in magnetic fields of the same intensity but different inclinations.[24] Turtles exposed to a 60° inclination angle (an angle found near the northern edge of the North Atlantic gyre) were significantly oriented toward the south-southwest, whereas those exposed to an inclination angle of 30° (found near the southern border of the gyre) swam in a northeasterly direction.

angle found near the southern boundary of the gyre swam in a northeasterly direction (Fig. 3). Turtles exposed to inclination angles they do not normally encounter (that is, from north or south of the North Atlantic gyre), or to a field inclination found well within the northern and southern extremes of the gyre, were not significantly oriented.

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These results demonstrate that loggerheads can distinguish between different magnetic inclination angles. In addition, inclination angles found near the northern and southern gyre boundaries elicited orientation that would direct turtles toward the gyre centre. The results are therefore consistent with the hypothesis that specific inclination angles in effect warn turtles that they have reached the latitudinal extremes of the gyre and must swim toward the gyre centre to avoid straying out of the warm-water current system.[24] For turtles that are safely within the gyre, drifting passively presumably poses no danger of displacement into undesirable areas. The absence of a directional preference among turtles exposed to an inclination angle found near the gyre's latitudinal centre is consistent with this interpretation.

4. DETECTION OF MAGNETIC FIELD INTENSITY. A second geomagnetic feature that varies across the surface of the Earth is field intensity. To determine if hatchling loggerheads can perceive differences in intensity that they encounter along their migratory route, hatchlings were exposed to one of two intensities that they normally encounter during their first months in the sea.[25] The inclination angle of the field was held constant in these trials. Turtles tested in a field of 52 000 nT (a field 10·6 percent stronger than the natal beach field, and one that hatchlings first encounter near South and North Carolina, USA) swam eastward (Fig. 4). Those exposed to a 43 000 nT field (a field 8·5 percent weaker than the natal beach field, and one first encountered on the eastern side of the Atlantic near Portugal) swam westward (Fig. 4).

These results demonstrate that hatchlings can distinguish between field intensities that occur in different locations along their migratory route. Moreover, because eastward orientation near South Carolina and westward orientation near the coast of Portugal would both function to keep young turtles within the gyre, the results imply that turtles can in effect derive positional information from geomagnetic field features.

5. NAVIGATION OF ADULT TURTLES. Although hatchlings appear to derive at least some positional information from the Earth's field, whether they can actually determine their position relative to a goal and navigate as adults do is not known. Hatchlings might conceivably emerge from their nests programmed only to swim toward specific directions in response to particular magnetic features found along the migratory route. For example, magnetic parameters along the far northern border of the gyre might elicit southward orientation, whereas features along the southern border of the gyre might elicit northward swimming. Thus, young turtles might remain within a favourable gyre or other oceanic region without possessing the same navigational abilities that enable adults to locate specific nesting areas.

Adult turtles of several species are now known to navigate to specific nesting regions from hundreds or thousands of kilometres away. Green turtles that nest on Ascension Island in the South Atlantic, for example, regularly migrate between their nesting beach and Brazilian feeding grounds, a straightline distance of more than 2000 kilometres.[9,12] Most Kemp's ridley turtles (*Lepidochelys kempi*) throughout the Atlantic, Caribbean, and Gulf of Mexico converge on a single, isolated beach in Mexico at nesting time.[9,30] And loggerheads that nest in Japan

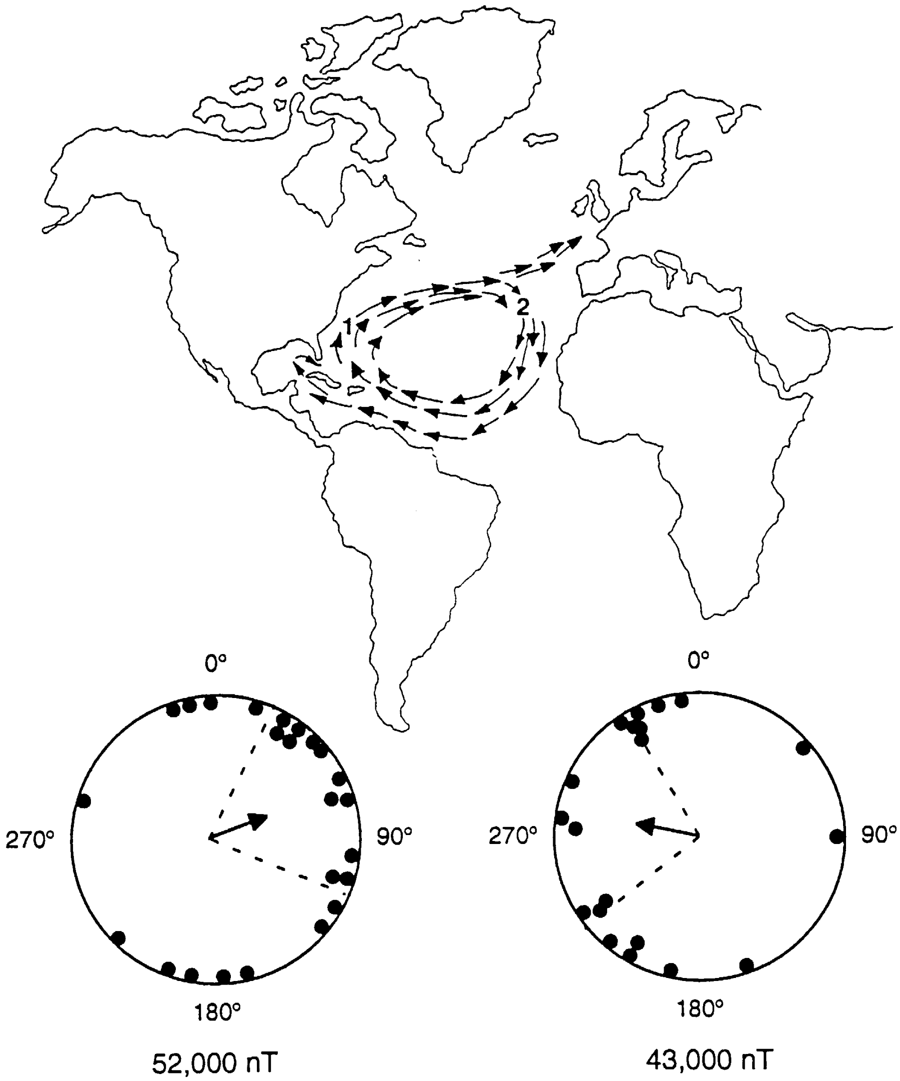

Fig. 4. Top: Diagram of the North Atlantic gyre indicating the only location within the gyre where the field intensity is 52 000 nT (marked by the number 1) and the location where Florida loggerheads in the gyre presumably first encounter a field intensity of 43 000 nT (marked by the number 2). Bottom: Orientation of hatchling loggerheads tested in a magnetic field of 52 000 nT (left) and 43 000 nT (right). Diagrams are from Reference 25.

apparently traverse the entire Pacific Ocean to Baja California before returning to their natal region to lay their eggs.[11]

Sea turtles can also pinpoint small, isolated areas that are not nesting beaches. Loggerheads and green turtles that nest along the Great Barrier Reef, for example, return afterwards to specific, widely dispersed feeding grounds that are sometimes located hundreds or thousands of kilometres from their nesting sites.[8]

Although the feeding grounds of different individuals are often separated by hundreds of kilometres and may lie in nearly any direction from the nesting area, adult turtles show great fidelity to both their feeding and nesting sites, and migrate between them at appropriate times.

Researchers have long hypothesised that the nesting sites selected by adult turtles are located on or near the same beaches where the turtles themselves emerged as hatchlings.[31] Genetic analyses have now confirmed that the adults of at least some populations do indeed reliably return to nest in their natal region after first migrating to distant oceanic areas.[4,5,28,32]

In addition, recent satellite tracking experiments have demonstrated that adult turtles can return to nesting sites following forced displacements[33] and that turtles often follow essentially straight courses both day and night while migrating directly to specific destinations from hundreds of kilometres away,[13,14,15] Such precise targeting of specific destinations over immense distances is difficult to explain without hypothesising an ability to determine geographic position relative to the goal.[14,15,16,34]

Although the nature of the sea turtle position-finding system remains unknown, one hypothesis is that adult turtles use geomagnetic field features such as inclination and intensity to assess position during long-distance migration.[16,24,25] Geomagnetic field features could potentially be used by migrating turtles in several different ways depending on the navigational task and the environment (for example, coastal or open ocean). Below we draw on two examples to outline how turtles might, in principle, use inclination and intensity to locate: (1) specific nesting areas along continental coastlines, and (2) isolated islands that serve as rookeries.

5.1. *Magnetic cues as markers of continental nesting beaches*. Many major sea turtle rookeries are located on continental coastlines that are aligned approximately north-south (e.g., Mexico, Costa Rica, and the southeastern United States). For turtles that feed in shallow coastal areas along the same continent on which they nest, the problem of navigating from a feeding area to a specific nesting region may be reduced to one of swimming north or south along a coastline until the nesting location is reached and recognised. Thus, turtles might need only to detect a single feature that varies latitudinally in order to discriminate between different coastal regions.

In principle, the ability to detect either inclination angle or intensity could allow turtles to identify a particular area of a continental beach. Inclination angle, in particular, is strongly correlated with latitude; thus, for shorelines running approximately north-south, each beach segment is marked by a unique angle.[24]

Loggerhead turtles that nest in Tongaland, Natal, South Africa, provide one example of a population that might plausibly use such a strategy. Most turtles tagged while nesting in this area have been recovered at widely distributed locations along the African east coast[35] (Fig. 5). Thus, many adults in this population presumably undertake migrations that parallel the African coastline for hundreds of kilometres.

If Tongaland turtles learn the inclination angle of their home beach as

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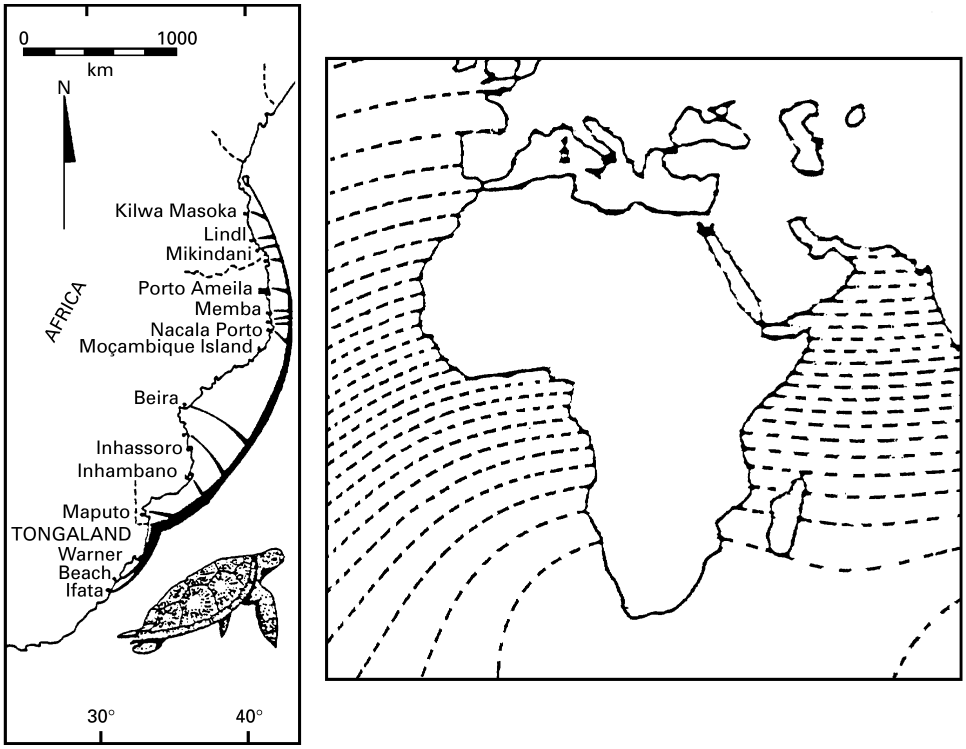

Fig. 5. Left: Locations where loggerhead females have been recaptured after nesting in Tongaland, Natal, South Africa (modified from Reference 35). Arrows indicate sites of recovery along the African coast; a few sites along the west coast of Madagascar are not shown. Right: Isoclinics (represented by dashed lines) along the African coast (modified from Reference 29). Each region of the east African coastline is marked by a different inclination angle. Adjacent isoclinics represent differences in inclination of 5°.

hatchlings, an adult attempting to relocate the area might need only to swim along the African coast until the appropriate angle is encountered (Fig. 5). Such a turtle might also assess whether it is north or south of the goal by determining if the inclination angle is smaller or larger than that of the natal beach region. An identical process based on one of several magnetic features other than inclination (total intensity, horizontal field intensity, or vertical field intensity) could also be used.

5.2. *Island-finding and bicoordinate magnetic maps*. Turtles that nest on small islands in remote oceanic areas cannot follow a coastline until the appropriate destination is reached. The ability to perceive both field inclination and intensity, however, may provide turtles with the sensory abilities necessary to approximate position using a bicoordinate magnetic map.[25] In most oceanic regions, isoclinics (lines of equal field inclination) and isodynamics (lines of equal field intensity) vary in different directions. Thus, each area within an ocean is usually marked by a different combination of magnetic features.

The migration of Ascension Island green turtles provides one intriguing example of how such a bicoordinate magnetic map might permit navigation over a large oceanic region. Isoclinics and isodynamics form a non-orthogonal grid between South America and Africa, so that all locations between feeding grounds in Brazil and nesting beaches at Ascension Island are defined by unique combinations of inclination and intensity[25] (Fig. 6). A migrating turtle using a

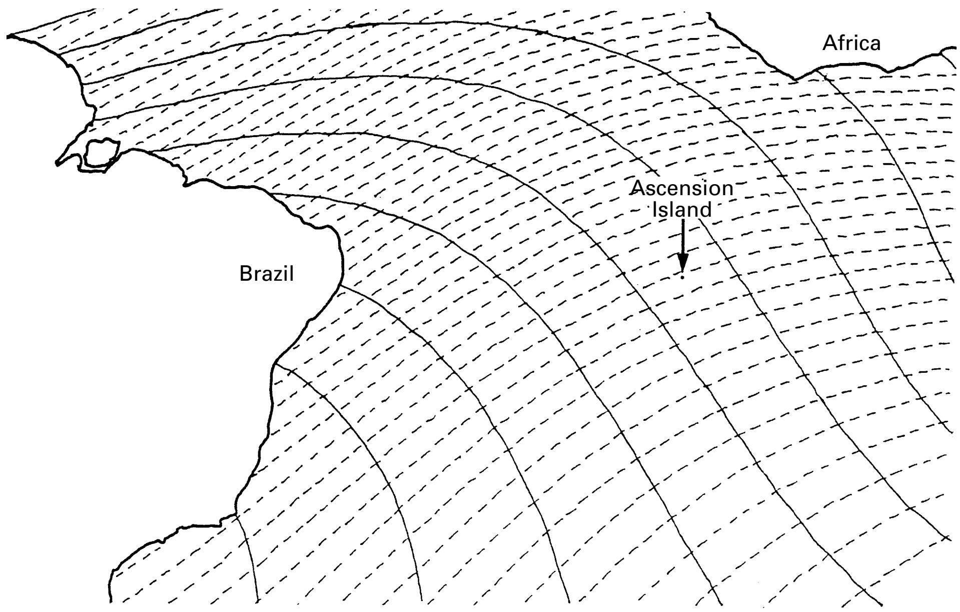

Fig. 6. Isoclinics (dashed lines) and isodynamics (solid lines) in the oceanic region surrounding Ascension Island.[25] Adjacent isoclinics differ by 2° and adjacent isodynamics by 1000 nT. The two geomagnetic features form a non-orthogonal grid that might, in principle, provide Ascension Island turtles with a bicoordinate position-finding system as they migrate between Ascension and the Brazilian coast.

bicoordinate map based on these two parameters might therefore be able to approximate its position anywhere along its route, provided it had learned the magnetic features of Ascension and the gradients of inclination and intensity in the South Atlantic.

6. SECULAR VARIATION AND MAGNETIC NAVIGATION. The responses of hatchling Florida loggerheads to inclination[24] and intensity[25] are consistent with the hypothesis that specific magnetic features elicit orientation that functions to keep young turtles safely within the North Atlantic gyre. Because turtles in these experiments responded to field conditions that they had never before encountered, such responses appear to be fully functional when the hatchlings first emerge from their nests. Indeed, for such responses to play a meaningful role in keeping young turtles within the gyre, the responses probably *must* function the first time the appropriate field values are encountered because

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turtles swept out of the gyre usually die before they can regain entry.[3] Thus, young turtles probably cannot learn to recognise dangerous geographic areas through experience because entering such regions is in itself fatal.

Although hatchlings can clearly detect and respond to magnetic field features, the Earth's magnetic field and the values of the various field parameters change gradually over time.[29] In light of this secular variation, how can hatchling turtles respond appropriately to magnetic field features that may differ significantly from those that their ancestors encountered?

The answer may be that strong selective pressure acts to ensure a continuous 'match' between the responses of hatchlings and the magnetic field features that exist at any point in time. In the case of Florida loggerheads, natural selection removes from the population those turtles that stray out of the gyre and may favour those that swim toward the gyre centre in response to magnetic field features marking the gyre's latitudinal extremes. As the Earth's field changes over time, the magnetic values marking the critical boundaries will change, and those turtles that fail to respond in a way that keeps them within the gyre under the new field conditions will be eliminated. Simultaneously, other turtles possessing slightly different responses that lead to increased survivorship under the new conditions will be favoured. In this way, the responses of hatchlings may evolve rapidly to complement the continuously changing field.

Another consequence of secular variation is that if adult turtles do indeed navigate to their natal beaches by relying in part on magnetic features, then turtles probably cannot inherit from their ancestors the magnetic positional information necessary to locate a particular nesting region; the field at such a locality will usually differ significantly from the field that existed there during earlier generations. In addition, the ephemeral nature of nesting sites over evolutionary time probably also necessitates that positional information specific to particular sites is learned rather than inherited.[11,36] Thus, turtles may learn the magnetic features of their natal beach for the first time as hatchlings;[18,24] they may also learn additional locations such as feeding sites later in life. Moreover, turtles may be able to update their knowledge of the magnetic features in important areas each time they visit so as to minimise navigational errors that might otherwise accrue from the secular variation.

For loggerhead turtles, and perhaps other species as well, the potential effects of secular variation on the navigation of adults may be mitigated by the tendency of turtles to home to natal regions rather than to highly specific natal sites. Both the pattern of population genetics and the nesting behaviour of tagged individuals suggest that although females return to nest within the general geographic region of their natal beach, they may select nest sites anywhere within a considerable area.[11,37]

Given the relatively large size of the apparent goal, the magnetic navigation hypothesis can easily account for the regional homing of turtles that nest on continental beaches, particularly if hatchlings learn the magnetic environment of their home region in terms of a specific isoline intersecting the coast (Fig. 5). The shoreline can then function as one coordinate, so that the drift of the critical magnetic feature results only in the perceived target area moving slightly along the coast in one direction or the other. Under such conditions, the limited field drift that occurs between the time a turtle leaves the area and when it tries to return will rarely result in a navigational error that displaces a turtle beyond its home region. Indeed, the effect of such drift may be altogether negligible if magnetic features near the home beach serve mainly as a landmark indicating the general area in which the search for a suitable nesting site should be carried out.

Secular variation may pose a greater problem for the bicoordinate grid hypothesis illustrated by the Ascension Island example (Fig. 6). In such cases of island-finding, a turtle cannot exploit a coastline to reduce the navigational task to one of detecting a single magnetic feature. Thus, the problem of drift is magnified by the change in two features rather than one, and the grid is gradually distorted over time so that the magnetic coordinates that initially marked the island drift progressively farther away. Clearly, a turtle absent from the area for too long and unable to compensate for the drift would be unsuccessful in locating the island if it returned to the magnetic coordinates that marked the island many years earlier. On the other hand, the problem might be overcome if a turtle is somehow able to correct for the drift or is not gone from the area for an overly long time, the critical period being determined by factors such as the rapidity of the field change, the navigational error represented by the drift, and the distance from which a turtle can locate the island using non-magnetic cues. Under favourable conditions, a turtle absent for a period of years might still be able to use magnetic features to navigate into the general vicinity of the island, close enough for local chemical cues,[38] visual cues, or the sounds of waves breaking[39] to be used in making landfall. Once the island has been located, such a turtle would presumably need to update its knowledge of the magnetic features and regional grid in preparation for its next migration.

7. SUMMARY. Laboratory experiments have demonstrated that hatchling loggerhead sea turtles have a magnetic compass sense and can also detect two different features of the Earth's magnetic field (inclination angle and intensity) that vary across the surface of the earth. Hatchlings responded to magnetic features found along their migratory route by swimming in directions that would presumably favour their retention within the North Atlantic gyre, a circular warm-water current system favourable for growth and development. These results suggest that young turtles can in effect derive positional information from features of the Earth's field, and that such information plays an important role in guiding the trans-oceanic migration of young turtles.

How adult turtles navigate to their natal regions to nest is not known. In principle, turtles nesting on coastlines might locate the appropriate region by returning to an area marked by the intersection of the shoreline and a magnetic isoline (for example, a particular inclination angle or intensity). Turtles that migrate to remote islands might be able to exploit bicoordinate magnetic maps in position-finding, but secular variation may limit the conditions under which such a bicoordinate system can be used. For now, experiments with hatchlings have provided a first glimpse into the sensory cues that adult turtles may have at their disposal, but the open-ocean navigational abilities of sea turtles and other marine animals remain an enduring mystery.

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1. Animal navigation. 2. Turtles. 3. Earth magnetism.