MAGNETIC ORIENTATION AND NAVIGATION BEHAVIOR OF LOGGERHEAD SEA TURTLE HATCHLINGS (*Caretta caretta*) DURING THEIR TRANSOCEANIC MIGRATION

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ABSTRACT

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Magnetic orientation and navigation behavior of hatchling loggerhead sea turtles (*Caretta caretta*) during their transoceanic migration
(Under the direction of Dr. Kenneth J. Lohmann)

Numerous animals embark on long-distance migrations, during which some of these animals can use the Earth's magnetic field as a cue in orientation and navigation. Here, I study how loggerhead sea turtle hatchlings (*Caretta caretta*) use geomagnetic cues to guide themselves during their migration around the north Atlantic gyre, a current system that encircles the Sargasso Sea. My results suggest that hatchling turtles can use regional magnetic fields from numerous locations along the northern segment of their migratory pathway as open ocean guideposts. Exceptions may exist, however, in cases where regional fields have changed significantly in the recent past because of secular variation. My results also suggest that the magnetic field in which sea turtle eggs incubate influences the hatchlings' subsequent ability to use regional fields for navigation. This finding has important implications for sea turtle conservation, as anthropogenic magnetic anomalies encountered by developing hatchlings at nesting beaches might disrupt their magnetic navigation abilities later in life.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Introduction

Long-distance migrations and magnetic orientation

Diverse animals undergo spectacular long-distance migrations, the function of which have been discussed extensively (Alerstam et al. 2003; Dingle 1996). Migration is primarily thought to help animals move among environments in order to enhance growth, survival and reproduction (Dingle & Drake 2007). For example, the arctic tern (*Sterna paradisaea*) migrates between nesting grounds along the Arctic rim of North America and Asia and feeding areas off the shores of Antarctica (Alerstam et al. 2003). Other examples include wildebeests (*Connochaetes taurinus*) that seasonally travel in single-file lines across the Serengeti Plains of East Africa, as well as emus (*Dromaius novaehollandiae*) that move across the arid Australian outback toward foraging grounds recently showered by rainfall (Dingle 1996).

Equally astonishing are the long-distance migrations of various marine vertebrates. Some of these animals can swim thousands of kilometers through the open ocean, such as adult salmon that migrate from regions in the middle of the Gulf of Alaska to estuaries along the southern coast of British Columbia and then up rivers to their natal stream to spawn (Quinn 2005). Some species of seal also travel great distances between feeding areas in the open sea and coastal reproductive grounds (Le Boeuf et al. 2000).

The ocean is a seemingly featureless environment. Thus, understanding how marine animals navigate during their migrations at sea has generated much interest. Since marine migrants mostly travel underwater, they are unlikely to have access to orientation cues available to many terrestrial animals, such as visual landmarks, airborne odors, or celestial information. However, the Earth's magnetic field is a pervasive environmental cue that is relatively stable and accessible at any ocean depth or during any weather condition (Cain et al. 2005; Johnsen & Lohmann 2005; Wiltschko & Wiltschko 2005).

Many animals are capable of sensing the Earth's magnetic field and using it as a cue for orientation and navigation (Wiltschko & Wiltschko 1995; Wiltschko & Wiltschko 2005). Animals can derive two types of information from the Earth's magnetic field. The first type of information is directional or compass information, which is characterized by using the magnetic field to maintain a constant heading in a particular direction (Able 2001). Various mammals (Kimchi et al. 2004), birds (Cochran et al. 2004; Viehmann 1979), reptiles (Lohmann 1993; Lohmann & Lohmann 1993), amphibians (Deutschlander et al. 1999), and fishes (Quinn 1980) have all been documented to possess a magnetic compass.

The second type of information that the Earth's magnetic field can provide is positional information. The geomagnetic field resembles a bar magnet (Figure 1.1). Magnetic field lines emerge from the southern hemisphere and then re-enter the northern hemisphere. Additionally, different components of the Earth's magnetic field, such as inclination angle and intensity, vary predictably across the surface of the planet so that each geographic location is associated with a unique magnetic field (Figure 1.2). Thus, if an animal can sense the field differences between separate locations, then it is possible to use this information to assess its geographic position. Past research suggests that a number of bird species are capable of using the geomagnetic field as a source of positional information (Beck & Wiltschko 1982; Mouritsen 2001; Wiltschko & Wiltschko 1995), as well as some species of newts (Phillips et al. 2002), sea turtles (Lohmann et al. 2001; Lohmann et al. 2004), and lobsters (Boles & Lohmann 2003). Although there is no evidence to support it, some mammals are hypothesized to also use magnetic cues for positional information (Davis et al. 2001).

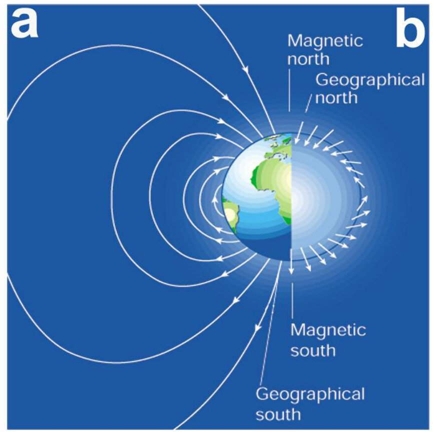

Figure 1.1. Diagram of the Earth's magnetic field. (a) Geomagnetic field lines emerging from the southern hemisphere and entering into the northern hemisphere. (b) Representation of the geomagnetic field's parameters that vary across the surface of the Earth. Arrows represent magnetic field vectors. The angle at which each arrow intersects the Earth indicates the field's inclination angle at the region of the planet, and the length of each arrow indicates the field's intensity at a given region of the planet, with shorter arrows signifying lower field intensity. The inclination angle is 90° at each magnetic pole and predictably decreases with latitude so that it is 0° at the magnetic equator. Field intensity decreases along a similar latitudinal gradient from the magnetic poles toward the magnetic equator. Taken from Alerstam (2003).

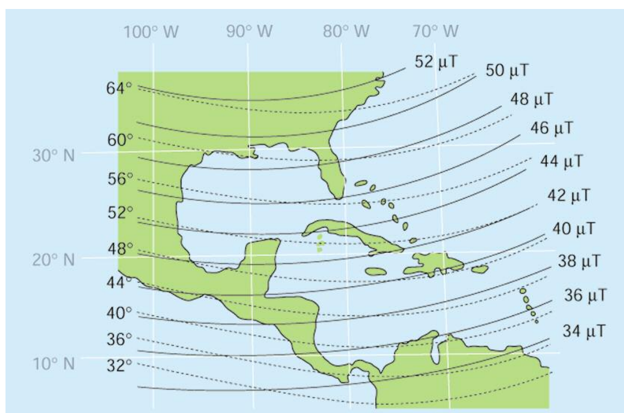

Figure 1.2. Map of the geomagnetic isolines across the Caribbean Sea. Solid lines are isodynamics, or lines of equal field intensity, and dotted lines are isoclinics, or lines of equal inclination angle. Since the isolines are not parallel, each geographic location is associated with a unique magnetic field (i.e. unique combination of intensity and inclination angle) Taken from Alerstam (2003).

One possible complication that animals using magnetic position-finding systems might encounter is that the Earth's magnetic field gradually and continuously changes over time, a geophysical phenomenon called secular variation (Skiles 1985). The degree to which secular variation occurs varies largely among the different regions of the planet, but in all cases it means that the pattern of geomagnetic isolines (i.e. lines of equal field intensity and equal inclination angle) on the surface of the Earth gradually changes so that the fields marking given locations do not stay the same (Lohmann et al. 1999; Lohmann & Lohmann 2006). In fact, normally specific fields "move" from one geographic location to another over time. In a hypothetical situation, for example, the Earth's magnetic field might change over 20 years so that the field that exists at New York City, New York in 2007 might subsequently exist in Philadelphia, Pennsylvania in 2027. Sometimes changes in the Earth's magnetic field can cause a specific field to no longer exist, or the same field can simultaneously exist in more than one geographic location. Although the topic has been briefly mentioned and discussed in the past (Alerstam 2003; Courtillot et al. 1997; Freake et al. 2006; Lohmann et al. 1999; Lohmann & Lohmann 2006), the effect of secular variation on magnetic position finding strategies has never been investigated.

Study system

Sea turtles undergo some of the most impressive long-distance migrations known to biologists, crossing vast oceanic regions (Bowen et al. 1995; Papi et al. 1995; Papi et al. 2000). As soon as the hatchlings emerge from their nest and enter the ocean, they establish a heading offshore and swim to the open ocean. Nearly all species of sea turtle then commence a post-hatchling oceanic life history stage, during which individuals inhabit the open ocean for a number of years before breeding later in life (Bolten 2003). Turtles in neritic waters are subject to high levels of predation; thus, there is strong selection for hatchlings and post-hatchlings to leave this zone and inhabit the open ocean, where predation rates are presumably less (Bolten 2003). The flatback sea turtle (*Natator depressus*) is the only sea turtle species that does not have a post-hatchling oceanic phase. Hatchling flatbacks are much larger than hatchlings of other sea turtle species, a feature thought to help young flatbacks resist intense predation (Walker & Parmenter 1990).

Eventually juvenile sea turtles inhabiting the open ocean grow larger and undergo an ontogenetic habitat shift, returning to neritic zones near the coast to take up residence. After turtles reach reproductive maturity, they migrate between their foraging grounds and breeding areas to mate and nest (Allard et al. 1994; Bowen et al. 2004; FitzSimmons et al. 1997; Meylan et al. 1990).

The loggerhead sea turtle is perhaps the best studied sea turtle species in terms of its migratory behavior. Once they reach the open sea, loggerhead hatchlings begin their transoceanic migration around the north Atlantic gyre, a circular current system that flows around the Sargasso

Sea (Carr 1987; Hays & Marsh 1997; Lohmann et al. 2001; Lohmann & Lohmann 2006). Young loggerheads remain in the gyre for approximately a decade (Bjorndal et al. 2000) and are frequently found foraging near the Azores, Maderia Islands, and Canary Islands (Bolten 2003; Bolten et al. 1998). Conditions inside the gyre are optimal for turtle growth and maturation (Bjorndal et al. 2000; Bolten 2003; Bolten et al. 1998), whereas conditions outside of the gyre can be fatal. For instance, the oceanic waters that exist to the gyre's north are lethally cold to sea turtles (Cain et al. 2005; Carr 1987; Hays & Marsh 1997; Lohmann et al. 2001). After their time in the gyre current system, loggerheads travel back to the southeastern United States and establish feeding grounds along the coast (Musick & Limpus 1997).

Similar to other animals (Dingle 1996; Papi 1992), sea turtles use many environmental cues in orientation and navigation. However, a growing body of research suggests that sea turtles rely on the Earth's magnetic field as a source of both directional and positional information while navigating in the open ocean (Lohmann et al. 1999; Lohmann & Lohmann 1996b; Lohmann & Lohmann 2006; Luschi et al. 2007). Hatchling loggerheads, for instance, have a magnetic compass sense that is thought to help direct them offshore after first entering the ocean (Irwin & Lohmann 2003; Lohmann 1991; Lohmann 1993).

Once in the open sea, turtles begin their transoceanic migration and can use the geomagnetic field as a source of positional information to help them do so (Lohmann et al. 2001). Experiments have shown that loggerheads can sense two components of the Earth's magnetic field that vary predictably across the surface of the globe, inclination angle (Lohmann & Lohmann 1994b) and intensity (Lohmann & Lohmann 1996a). These elements of the geomagnetic field can, in theory, provide young turtles with the necessary information to help them assess their geographic location (Lohmann et al. 1999; Lohmann & Lohmann 2003) in the North Atlantic Ocean.

Additionally, Lohmann et al. (2001) showed that hatchling loggerheads that have never before entered the ocean can distinguish among magnetic fields like those that exist at widely separated locations along their migratory pathway around the gyre (Figure 1.3). Hatchlings respond to these regional magnetic fields by swimming in directions that would, in each case, help them stay inside the gyre current system and progress along their migration. More specifically, as Lohmann et al. (2001) explain, hatchlings exposed to a field like one that is found near northern Florida swim southeastward, a response that likely helps turtles position themselves safely inside the east-veering Gulf Stream current and avoid being ejected from the gyre into the lethally cold waters that exist to the north. Next, hatchling turtles subjected to a field that exists at the northeastern boundary of the gyre orient southward. The current at this region of the gyre divides into two branches, one that flows northward into cold polar waters and another that flows southward into temperate waters. Thus, swimming southward likely decreases the turtles' likelihood of being swept north and helps them remain where conditions are optimal for their survival (Carr 1987; Hays & Marsh 1997; Lohmann et al. 2001). Finally, hatchlings exposed to a field at the southern border of the gyre orient toward the northeast. This orientation response likely helps keep turtles from drifting too far south of the gyre where they can be carried off course and away from the North American coast where juveniles usually take up residence (Musick & Limpus 1997). Thus, hatchlings appear capable of using a few regional magnetic fields located along their migratory pathway as navigational markers. Moreover, hatchlings are able to do so without having any prior migratory experience.

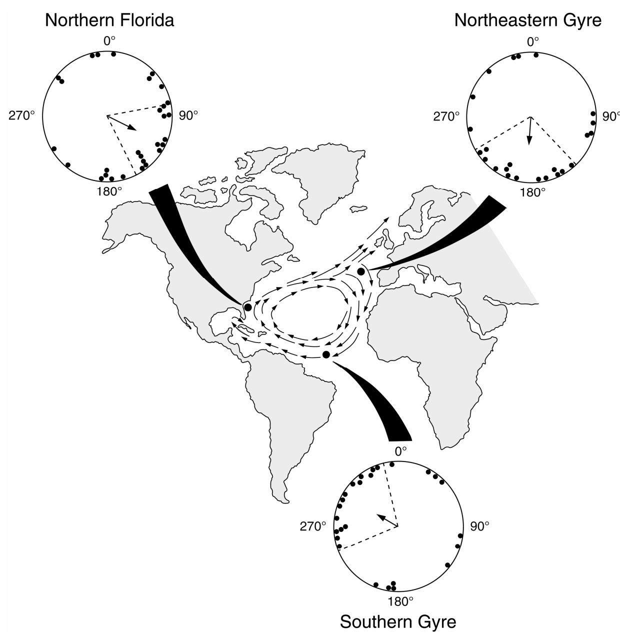

Figure 1.3. Diagram of hatchling responses to magnetic fields replicating those from three widely separated geographic locations (represented by back dots) along the north Atlantic gyre current system (indicated by the arrows on the map). Turtles exposed to a field like one that exists near the coast of northern Florida were significantly oriented to the southeast. Turtles exposed to a field like one found at the gyre's northeastern border responded by swimming southward. Finally, turtles subjected to a field like one that occurs at the gyre's southern border responded by swimming northwest. In each circular distribution, individual dots represent the

mean heading of a single turtle, the arrow indicates the mean heading of the group, and the dashed lines signify the 95% confidence intervals for the group. Taken from Lohmann et al. (2001).

Thesis objectives

In this thesis, I examine the magnetic navigation system that hatchling loggerhead sea turtles use to help them migrate around the gyre current system. Previous studies have suggested that hatchling loggerheads are capable of exploiting as navigational markers regional magnetic fields found along their migratory pathway. Yet, much remains unknown about this navigational strategy. Specifically, I investigate: (1) whether several fields found along the northern half of the turtles' migratory route elicit orientation responses that are consistent with the turtles' migration, or if turtles respond to only a limited few fields that mark crucial geographic boundaries of the gyre; (2) whether magnetic fields that exist outside the turtles' normal migratory pathway elicit orientation responses that would help turtles return to the gyre current system; (3) how secular variation might impact the turtles' magnetic position finding strategy in cases where regional fields have moved locations within the gyre significantly in the recent past; (4) the early ontogeny of the turtles' magnetic position-finding strategy by exploring how the magnetic environment in which hatchling turtles incubate might influence their ability to use regional fields as navigational markers; and (5) whether sea walls built upon sea turtle nesting beaches generate magnetic anomalies that incubating turtles might encounter while in the nest, which could therefore impede hatchling magnetic orientation behavior and have implications for sea turtle conservation. My results help explain the magnetic position-finding strategy that young loggerheads use to guide themselves during their transoceanic migrations. More broadly, my work will explore further how the Earth's magnetic field can be used as a source of positional information for long-distance migrants traveling complex migratory routes.

CHAPTER 2

Geomagnetic navigation in loggerhead sea turtles: responses to regional magnetic fields along a transoceanic migratory pathway

Abstract

Hatchling loggerhead sea turtles (*Caretta caretta*) embark on a long-distance migration around the north Atlantic gyre, a current system that encircles the Sargasso Sea. Previous experiments suggest that hatchling turtles can use regional magnetic fields that exist at widely separated locations along their migratory route as navigational markers. In this study, we exposed hatchlings to several other regional magnetic fields that exist along the northern half of the turtles' migratory route, and one located north of the gyre, where turtles are unlikely to survive. Hatchlings subjected to fields that occur along their migratory pathway responded by swimming in directions that would, in each case, help them remain inside the gyre current system and advance along their migratory pathway. Turtles exposed to a field that exists north of the gyre were not significantly oriented as a group. These results, combined with those of earlier studies, suggest that loggerhead turtles complete some or all of their first transoceanic migration using a form of magnetic waymark navigation, in which regional magnetic fields trigger directional responses that help steer the turtles along their migratory pathway. Although natural selection has apparently sculpted responses to multiple fields that exist along the migratory route, turtles may fail to respond to fields that exist in locations where they never go.

Introduction

Numerous marine animals undergo long distance migrations, including species of fish (Block et al. 2001; Quinn 2005), reptiles (Bolten et al. 1998; Bowen et al. 1995), and mammals (Darling & McSweeney 1985; Le Boeuf et al. 2000). In some cases, first time migrants successfully follow complex migratory routes that span hundreds or thousands of kilometers, despite traveling alone.

How these animals guide themselves during their first oceanic migration has long been of interest to behavioral biologists.

Young loggerhead sea turtles (*Caretta caretta*) embark on one of the most spectacular marine migrations. Hatchling turtles from the east coast of Florida, U.S.A. emerge from their nests and swim offshore to the north Atlantic gyre, a current system that encircles the Sargasso Sea (Carr 1987; Lohmann & Lohmann 2003; Musick & Limpus 1997). Turtles typically remain in the gyre for nearly a decade (Bjorndal et al. 2000). During this time, many young loggerheads swim to the eastern side of the Atlantic Ocean, as they have been documented foraging near the Azores, Maderia Islands, and Canary Islands (Bolten 2003; Bolten et al. 1998) before eventually returning to the southeastern United States to establish feeding grounds (Musick & Limpus 1997).

For migrating loggerheads, conditions along their migratory pathway, and within the north Atlantic gyre, are favorable for survival and growth (Bjorndal et al. 2000; Bolten 2003; Bolten et al. 1998), whereas straying outside of the gyre is often fatal. For example, in the northeastern region of the gyre, the current diverges into two branches, one of which flows northward toward the United Kingdom and Scandinavia, and the other of which flows southward past Portugal and the northwestern coast of Africa. Loggerheads swept into the north-flowing current likely die from the cold, polar waters that exist in this oceanic region (Cain et al. 2005; Carr 1987; Hays & Marsh 1997; Lohmann & Lohmann 2003; Lohmann & Lohmann 2006). Thus, having the ability to alter swimming direction at appropriate geographic areas in order to remain inside the gyre current system likely has considerable adaptive value.

The Earth’s magnetic field provides a pervasive source of directional and positional information used by diverse animals for orientation and navigation (Wiltschko & Wiltschko 1995; Wiltschko & Wiltschko 2005), including sea turtles (Lohmann et al. 2001; Lohmann & Lohmann 1994a; Lohmann et al. 2004; Luschi et al. 2007). Different features of the geomagnetic field vary predictably across the surface of the planet so that each geographic location is marked with a unique magnetic field. Previous research has shown that loggerhead hatchlings can detect two of these features, inclination angle (Lohmann & Lohmann 1994b) and total intensity (Lohmann & Lohmann 1996a), which, in theory, could provide them with the necessary positional information to migrate around the gyre (Lohmann & Lohmann 1996a; Lohmann & Lohmann 2006; Wiltschko & Wiltschko 2005). Additional studies have revealed that when subjected to magnetic fields like those found at three widely separated geographic regions of the gyre, hatchling loggerheads respond by swimming in directions that would, in each case, help them remain inside the gyre current system (Lohmann et al. 2001). These results suggest that young loggerheads are equipped with a magnetic position-finding system in which regional magnetic fields provide information that elicit changes in swimming direction at different geographic areas of the gyre. Here we investigate further this magnetic guidance system by exposing hatchling loggerheads to several additional magnetic fields like those that exist along the northern segment of the turtles' migratory route, as well as a field like one that exists to the north of the gyre current system, where turtles are unlikely to go or survive.

Methods

Animals

Hatchling loggerheads were collected from nests deposited along an 8 km stretch of coastline in Melbourne Beach, Florida, U.S.A. The date each nest was deposited was recorded, as well as the predicted date of emergence. 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 15-25 hatchlings. Turtles were immediately placed into a lightproof, Styrofoam container and transported to a nearby lab. Hatchlings were kept in complete darkness until testing and were used only once in an experiment before being released that same night.

Orientation tank

Turtles were tested in a circular orientation tank, with a diameter of 91.4cm (Figure 2.1). The inside of this tank was filled with water ranging in temperature from 26.0°C to 28.0°C and was completely black. In each trial, a hatchling was placed into a nylon-lycra harness that encircled its carapace, but did not impede its swimming (Salmon & Wyneken 1987). A 10.2 cm monofilament line connected the harness to a lever arm, which measured 25.4 cm from the center of the tank to the tip of the lever arm. The lever arm was attached to a digital encoder that was enclosed by a plastic vertical post mounted in the center of the tank. Thus, the lever arm could freely rotate 360° in the horizontal plane so that turtles could swim in any direction without touching either the edge of the tank or the plastic post mounted in the center. The digital encoder inside the plastic post was wired to a laptop computer in a nearby room. Before each trial began, we covered the tank with a black, 1.9 cm-thick plywood lid, as well as four sheets of 6 mm black plastic, to ensure that no light entered.

Magnetic coil

The orientation tank was surrounded by a computer-controlled magnetic coil system (Figure 2.1), which consisted of two orthogonally arranged Merritt-4 coils (Merritt et al. 1983) capable of generating uniform, Earth-strength magnetic fields. The first coil (2.41 m on a side) was aligned along the north-south axis and controlled the horizontal component of the magnetic field. The second coil (2.54m on a side) controlled the vertical component of the field. The current to the coils was controlled by computer software allowing us to generate any magnetic field that could be found in the Atlantic Ocean in the center of the coil where the turtles swam. This entire coil structure and orientation tank was located outdoors and more than 15m from where the computer was housed. Prior to locating the magnetic coils, we used a tri-axial fluxgate magnetometer (Applied Physics Systems, Model 520*)* to determine that the coil's location was free of magnetic distortions.

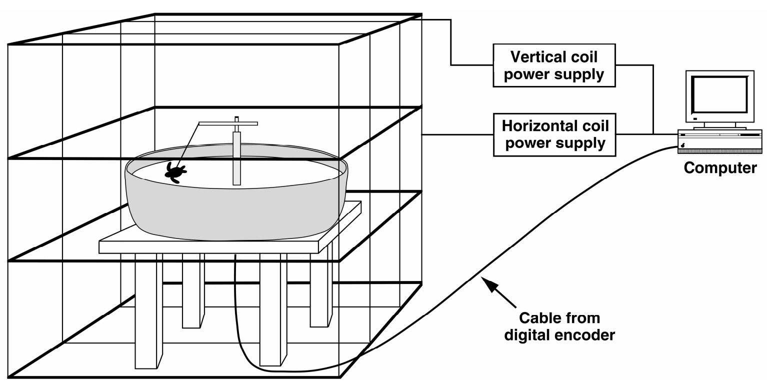

Figure 2.1. Schematic of experimental apparatus, including the orientation arena, magnetic coil structure, and data acquisition system. Turtles were tethered to a lever arm mounted to a digital encoder and capable of rotating 360° along the horizontal plane. Thus, the tracker arm monitored the direction in which the turtle swam via signals sent from the encoder to the computer system located in an adjacent room. The arena was enclosed by a magnetic coil structure capable of replicating magnetic fields found at different locations along the turtles' migratory route. Modified from (Lohmann & Lohmann 1994b).

The animals were tested with four different magnetic fields (Table 2.1). The first field, similar to one used in previous experiments (Lohmann et al. 2001), is identical to a field found at the northeastern boundary of the north Atlantic gyre. The second field is comparable to one that occurs approximately in the middle of the north Atlantic, and within the east-flowing currents that comprise the gyre's northern segment. The third field is like one found offshore from Portugal's southern coast. Finally, the fourth field replicates one located significantly north of the gyre current system, a location where turtles are unlikely to go or survive.

Table 2.1. Information on the different magnetic fields that turtles were exposed to during experiments. Each point is named based on its general location in the Atlantic Ocean. The exact latitudinal and longitudinal coordinates are provided as well as the magnetic parameters estimated from the IGRF model, 2005 version, for July 1st, 2006.

Location of Point	Latitude	Longitude	Field Inclination Angle (degrees)	Total Field Intensity (μT)
Melbourne Beach	28.1° N	80.7° W	58.1	46.8
Northeastern Boundary	44.5° N	20.0° W	60.1	46.2
Mid-Atlantic	40.0° N	45.0° W	59.4	46.7
Offshore Portugal	39.6° N	14.0° W	54.3	44.0
North of Gyre	52.0° N	40.0° W	69.0	51.1

The parameters for each field are based on estimates provided by the International Geomagnetic Reference Field (IGRF) model, version 2005, for July 1, 2006, which corresponds to the approximate months in which experiments were conducted. Using a tri-axial fluxgate magnetometer (Applied Physics Systems, Model 520), we confirmed that the coils produced the field parameters estimated from the IGRF software. Additionally, the measured deviations from perfect field uniformity in the center of the coil where the turtles swam were less than 0.55%.

Testing procedure

Experiments were conducted between late June and early August, 2006. All trials were carried out between the hours of 20:30 and 02:00, the time when loggerhead hatchlings usually emerge from their nests and enter the ocean (Witherington et al. 1990). Prior to each trial, the magnetic coils were turned off, and a light emitting diode (peak λ=550nm) located at the east side of the tank was illuminated. Each hatchling was placed in the harness and released into the water.

Healthy hatchling turtles are known to swim vigorously toward light after emerging from their nest (Lohmann & Lohmann 1994a; Lohmann & Lohmann 1994b; Lohmann & Lohmann 1996a; Salmon & Wyneken 1987); thus, the hatchling's swimming response after being placed in the tank verified whether the animal was behaviorally competent (Irwin & Lohmann 2003; Irwin & Lohmann 2005; Lohmann & Lohmann 1994a; Lohmann & Lohmann 1994b; Lohmann & Lohmann 1996a). If a turtle failed to maintain a direct course toward the LED in the first minutes of the experiment (less than 5% of turtles), then the trial was terminated and the hatchling was replaced with another individual.

Each turtle was permitted to swim toward the light in the local field for 10 minutes. After this time, the light was 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 minutes to acclimate to swimming in complete darkness in the new field. Once the acclimation period was complete, the hatchling's heading was recorded every 10 seconds for the next 5 minutes. Each hatchling was only tested once and was released later in the night after all the trials were completed.

The data presented here are from two separately run experiments. The first experiment was conducted from the end of June 2006 to the middle of July 2006. In this experiment, turtles were exposed to either the field resembling one found at the gyre's northeastern boundary or a field like one that exists at the mid-Atlantic region of the gyre's northern east-flowing segment (Table 2.1). The second experiment was conducted from mid-July 2006 to late July 2006. In it hatchlings were exposed to either a field replicating one that exists at the gyre's northeastern boundary (the same field used in the first experiment), a field similar to one found to the north of the gyre current system, or a field like one that exists offshore from the southern coast of Portugal.

Turtles from the same nest were distributed equally among the four treatments (i.e. fields). However, no more than 3 turtles from the same nest were tested in any single magnetic field. In each experiment, the order in which the different fields were presented to turtles was alternated every night.

Data analysis and statistics

After each trial was completed, the turtle's mean heading was calculated using all the data points recorded during the 5-minute trial period. We then used a Rayleigh test to determine whether hatchlings in each treatment group were significantly oriented in any particular direction (Batschelet 1981). The distributions from the four different treatment groups were compared using a multisample Mardia-Watson-Wheeler test (Batschelet 1981).

Results

In both experiments, hatchlings were subjected to a magnetic field that exists at the gyre's northeastern boundary, and, in each case, turtles were significantly oriented as a group, with mean headings directed southward. These two distributions are not significantly different (Watson U^2; U^2=0.089; 0.50>p>0.20). Thus, we combined the data from both experiments, and found that all turtles exposed to the field like one that exists at the gyre's northeastern boundary were significantly oriented as a group, with a mean angle to the south (Figure 2.2; mean angle=164.7°, n=54 p<0.01).

Hatchlings exposed to the magnetic field that exists in the middle of the North Atlantic within the east-flowing segment of the gyre were oriented significantly as a group, with a mean heading to the east (Figure 2.2; mean angle=70.8°, n=30, p=0.036). When turtles were exposed to the magnetic field offshore from southern Portugal, they were significantly oriented as a group, with a mean angle toward the southwest (Figure 2.2; mean angle=242.0°, n=27, p=0.028). The orientation responses of turtles exposed to a field like one that exists north of the gyre were statistically indistinguishable from random (Figure 2.2; mean angle=121.0°, n=27, p=0.506). Finally, significant differences exist among these four distributions (Mardia-Watson-Wheeler test; W=21.715; p<0.01).

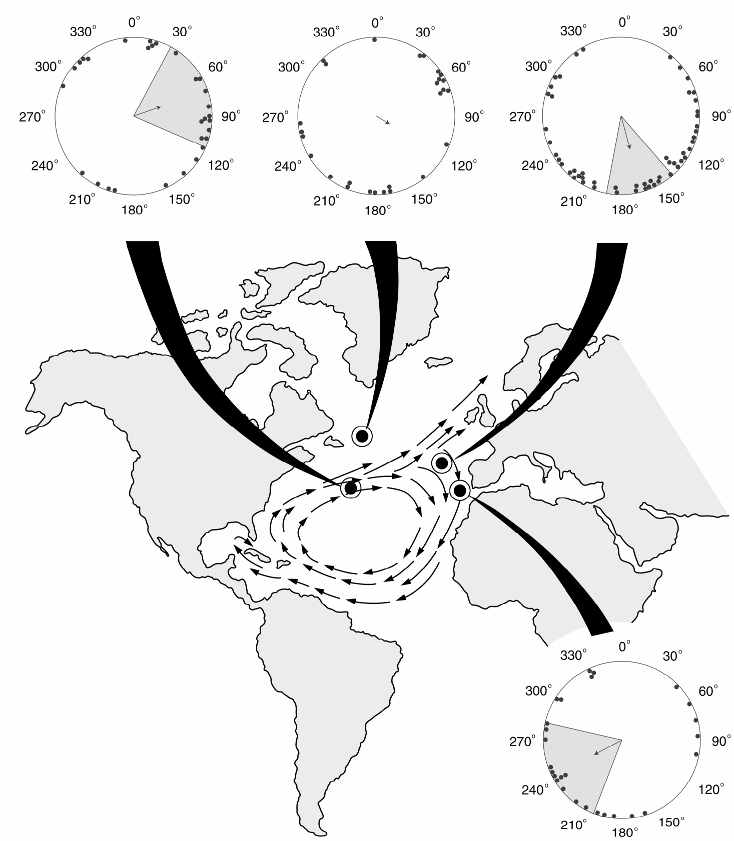

Figure 2.2. Diagram of hatchling orientation responses to magnetic fields that exist at different locations throughout the North Atlantic Ocean (indicated by the black target symbols). The arrows on the map show the direction in which the gyre current flows. In the circular orientation diagrams, each dot represents the mean heading of a single hatchling. The arrow indicates the mean direction of turtles in the group, and the length of the arrow is proportional to the magnitude of the mean vector *r* (with the radius of the circle corresponding to *r*=1). The shaded area inside the circle represents the values that fall with the 95% confidence intervals of the distribution. Data are plotted relative to magnetic north, with north indicated by 0°. Hatchlings subjected to a field that exists in the middle of the Atlantic Ocean, and within the northern east-flowing segment of the gyre, were significantly oriented as a group (Rayleigh Test, *z*=,3.298, *r*=0.332, *n*=30, *p*=0.036), with a mean heading of 70.8°. Hatchlings exposed to a field that exists north of the gyre were statistically indistinguishable from random (Rayleigh Test, *z*=0.69, *r*=0.16, *n*=27, *p*=0.506). Turtles subjected to a magnetic field that exists at the gyre's northeast boundary were significantly oriented as a group (Rayleigh Test, *z*=8.65, *r*=0.40, *n*=54, *p*<0.01), with a mean heading of 164.7°. Hatchlings exposed to a field located offshore from the southern coast of Portugal were significantly oriented as a group (Rayleigh Test, *z*=3.532, *r*=0.362, *n*=27, *p*=0.028) with a mean angle at 242.0°.

Discussion

Hatchlings exposed to three magnetic fields replicating those found at separate geographic regions along the northern segment of the turtles' migratory pathway responded by, in each case, swimming in directions consistent with the migratory route. Additionally, a field like one found north of the gyre did not elicit an orientation response (Figure 2.2). Thus, our results show that hatchling loggerheads can distinguish among magnetic fields like those that exist at widely separated regions of the north Atlantic gyre.

Functional significance of orientation responses

Each magnetic field used in our experiment triggers an orientation response that is functionally significant to the turtles' migration at the particular field's given geographic location. For instance, turtles exposed to a field like one that exists at the northeastern boundary of the gyre oriented toward the south. This orientation response is consistent with previously published results, in which hatchlings were subjected to a similar magnetic field (Lohmann et al. 2001). The currents at this region of the gyre divide into two branches, one that flows northward into the polar-waters off of the United Kingdom and Scandinavia, and the other that flows into temperate waters off the coast of Portugal and the northwestern coast of continental Africa. Thus, by swimming south at this location within the gyre the turtles may avoid being swept northward into the lethally cold waters (Carr 1987; Hays & Marsh 1997; Lohmann et al. 2001; Lohmann & Lohmann 2003; Lohmann & Lohmann 2006). This response also likely helps the turtles progress into the temperate waters of the subsequent segment of the migratory pathway.

Next, hatchlings oriented eastward when exposed to a field resembling one that exists approximately in the middle of the North Atlantic Ocean, and within the east-flowing segment of the gyre. This orientation response would likely lead turtles in the same direction as the flow of the current, which probably helps turtles propel themselves through this oceanic area to the next part of their migratory pathway. Additionally, this area of the gyre is characterized by having a high degree of eddy activity and surface current variation (Richardson 1985). Environmental obstacles, such as these, could potentially delay hatchlings in the open ocean so that they are unable to reach important foraging grounds in the eastern North Atlantic (Bolten 2003; Bolten et al. 1998), or perhaps eject hatchlings into the lethally cold waters that exist north of the gyre (Carr 1987; Hays & Marsh 1997; Lohmann et al. 2001). Thus, by actively swimming through this region of the gyre, hatchlings might reduce the likelihood of being caught in eddy currents for prolonged periods or being altogether displaced from the current system.

When hatchlings were subjected to a field like one that exists offshore from southern Portugal, they swam approximately southwestward, a response consistent with the turtles' migration.

Swimming to southwest here might function to guide turtles away from the coastal waters of Europe and Africa, where predators are likely more abundant, and lead them toward the archipelagoes present in the eastern North Atlantic, such as the Azores, Maderia Islands, and Canary Islands. These island chains are located in oceanic areas in which young loggerheads from the southeastern United States are frequently documented foraging (Bjorndal et al. 2000; Bolten 2003; Bolten et al. 1998) before returning to North America (Musick & Limpus 1997).

The magnetic field located off the southern coast of Portugal is unusual in that this same field exists at multiple geographic locations in the Atlantic Ocean. The geomagnetic isolines of inclination angle and total intensity run approximately parallel to each other across much of the North Atlantic Ocean, intersecting at three widely separated geographic locations: offshore from southern Portugal, in the Sargasso Sea, and near the Bahamian Islands. Thus, the same magnetic field marks these three sites. Although young loggerheads migrating in the gyre are known to pass the oceanic region near Portugal (Bjorndal et al. 2000; Bolten 2003; Bolten et al. 1998), and thus presumably encounter this field there, whether the turtles travel through the other geographic areas where this field exists is unknown. If turtles do encounter this field elsewhere in the North Atlantic and respond to it in the same way, the southwesterly orientation might help function in helping steer young turtles back toward the North American coast.

Finally, hatchlings oriented randomly in response to a field like one that exists far to the north of the gyre. This result is consistent with the hypothesis that hatchling loggerheads are not programmed to respond to regional fields that exist outside of the gyre and in locations where turtles are unlikely to go. Because entering oceanic areas north of the gyre would likely kill hatchlings before they could ever return to their migratory pathway to complete their migration and eventually reproduce and pass on their genes, natural selection is unlikely to alter the hatchlings' magnetic guidance system so that they are capable of responding to fields that exist outside their normal range. Testing this hypothesis further will require additional experiments in which hatchlings are exposed to several other magnetic fields that exist outside the gyre currents.

However, this finding must be interpreted with caution, as the observed random orientation is a negative. There are other possible interpretations of these data. For instance, migratory experience might enhance the magnetic guidance system of young loggerheads, such that after many months or years migrating at sea, turtles would be able to extrapolate their geographic position from magnetic fields that they would not likely experience along their migratory pathway. Such ontogenetic changes in orientation and navigation behavior have been documented previously in migratory animals (Able & Able 1996; Able & Bingman 1987; Rodda & Phillips 1992; Wiltschko & Wiltschko 1985), including sea turtles, which appear to learn the magnetic topography of areas where they live as juveniles (Lohmann et al. 2004).

Magnetic field as navigational waymarks

Previous studies have found that hatchling loggerheads can distinguish among magnetic fields like those that exist at widely separated geographic boundary points of the gyre where turtles have a high risk of being swept outside of the gyre (Lohmann et al. 2001). Hatchling turtles respond to these fields by swimming in directions that would, in each case, help young turtles remain inside the gyre and progress around the migratory path (Cain et al. 2005; Lohmann et al. 2001; Lohmann & Lohmann 2003; Lohmann & Lohmann 2006; Wiltschko & Wiltschko 2005). Our data are consistent with this past experiment, but suggest that the hatchlings' ability to use regional magnetic fields as open ocean guideposts is more extensive than previously recognized. Hatchlings have evolved orientation responses to numerous regional fields that occur along their migratory pathway, as opposed to only a few fields that exist at locations where, for instance, the risk of displacement from the gyre is very great.

One possible interpretation of these results is that hatchlings use regional magnetic fields along their migratory pathway as a series of magnetic waymarks (Lohmann & Lohmann 2006). In effect, each magnetic waymark might trigger an orientation response that helps steer a turtle's movement through a given geographic region and toward the next segment of the migratory pathway. By orienting to multiple, sequential magnetic waymarks located around their migratory pathway, hatchlings might be able to navigate around the entire gyre over the course of many years.

A similar form of navigation has been documented in some invertebrates that learn to associate compass directions with visual landmarks in their environment (Collett et al. 1998; Menzel et al. 1998). Additionally, juvenile salmon are thought to learn a series of olfactory waymarks as they migrate down river systems toward the sea, and then retrace these odor waymarks as adults later in life when homing to their natal stream to spawn (Dittman & Quinn 1996). Our data suggests, however, that the turtles' ability to use magnetic waymarks differs from how these other animals use visual or olfactory waymarks in one important way. That is, hatchlings do not require migratory experience in order to respond to regional magnetic fields because, as our findings show, fields elicit responses before the turtles ever enter the ocean. Thus, turtles apparently do not have to learn to associate specific magnetic fields with particular geographic regions along the gyre current system prior to migration. This does not, however, preclude the possibility that learned responses might become more important with migratory experience and maturation.

Secular variation and orientation responses

The ability to navigate along a complex migratory pathway using regional magnetic fields as open ocean guideposts or magnetic waymarks is not incompatible with the fact that the Earth's magnetic field gradually changes over time (Lohmann et al. 2001). This phenomenon is referred to as secular variation (Skiles 1985). Thus, even though the Earth's field continually changes, strong selective pressure probably acts to maintain an approximate coupling between the turtles' orientation response and the magnetic fields that exist at various locations along the migratory pathway at any point in time (Lohmann et al. 2001). As Lohmann and Lohmann (2003) suggest, under the present conditions of the North Atlantic, turtles that stray out of the gyre are likely removed from the population, and selection probably favors those individuals with orientation responses that help keep young turtles inside the gyre current system. As the field that exists at a specific region of the migratory pathway changes, only those turtles that respond to the new field in a manner that allows them to continue their migration will survive and pass on their genes. Thus, it is in this way that orientation responses could evolve with the constantly changing geomagnetic field.

Past research has suggested that many migratory adaptations are evolutionarily flexible and can rapidly evolve (Brown & Brown 2000; Pulido 2007; Pulido et al. 2001), including elements of orientation behavior (Berthold et al. 1992; Helbig 1991; Helbig 1996). For instance, studies involving a population of blackcaps (*Sylvia atricapilla*) from central Europe have revealed that these birds have evolved a new migratory route to the United Kingdom within three decades (Berthold et al. 1992), and it is thought that the directional preference that blackcaps use to guide themselves at the onset of their first migration is controlled by only a few genes (Helbig 1996). Thus, the magnetic navigation strategy used by young loggerheads might have a similar degree of flexibility, which would allow hatchlings to adapt their magnetic orientation mechanisms in concert with secular variation.

Acknowledgements

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CHAPTER 3

Possible effects of secular variation on magnetic navigation behavior of loggerhead sea turtles

Abstract

Hatchling loggerhead sea turtles (*Caretta caretta*) embark on a long-distance migration around the north Atlantic gyre, a current system that encircles the Sargasso Sea. Before they even enter the ocean, hatchlings are programmed to respond to magnetic fields that exist at widely separated geographic regions of the gyre by swimming in directions that, in each case, help them advance along their migratory pathway and stay inside the gyre current system. However, as the geomagnetic field gradually changes over time (referred to as secular variation), magnetic fields that exist at specific areas can move from one location to another. Here we investigated how the movement of a regional magnetic field within the gyre might impact the turtles' magnetic navigation system. To do so, we exposed hatchling loggerheads to either a magnetic field that has remained in the same geographic vicinity during the past century, or to a field that has significantly moved locations within the gyre in the recent past. The field that has remains in the same region during the past century elicits a southward orientation response, which would likely have functional significance to the turtles' migration at nearly all of the locations at which this field existed during the past 100 years. The field that has recently moved locations within the gyre elicits a northeastward orientation response, which is unlikely to be functionally relevant to the turtles' migration at the location where the field presently exists. However, this orientation response is consistent with the turtles' migratory route at the region of the gyre where this field previously existed for most of the past century. Our findings suggest that turtles are capable of using regional fields as a source of positional information, but there might be an evolutionary time lag between hatchling orientation responses and the magnetic fields that exist at given locations within the gyre to which turtles respond.

Introduction

Numerous animals embark on long-distance migrations, including species of mammals (Darling & McSweeney 1985; Le Boeuf et al. 2000; Thompson et al. 1991), birds (Alerstam et al. 2003; Dingle 1996), fish (Block et al. 2001; Quinn 2005), reptiles (Madsen & Shine 1996; Papi et al. 2000), and invertebrates (Brower 1996; James 1993; Rose et al. 1985). Most of the migratory programs of these animals have evolved so that individuals can, in some cases, travel hundreds or thousands of kilometers and inhabit vastly different environments (Alerstam et al. 2003). The evolutionary flexibility of such migratory adaptations has interested biologists for many decades (Berthold & Helbig 1992; Pulido 2007).

One migratory adaptation that has been studied extensively is orientation and navigation, particularly the role that the Earth's magnetic field plays in helping guide animals during migration. Different elements of the geomagnetic field vary predictably across the globe's surface so that each geographic region is associated with a unique magnetic field. In theory, if an animal can detect the differences between fields that exist at separate geographic locations, it can then use this information to assess its geographic position. Diverse organisms, such as lobsters (Boles & Lohmann 2003), sea turtles (Lohmann et al. 2001; Lohmann et al. 2004), birds (Beck & Wiltschko 1982), and amphibians (Phillips et al. 2002), have been documented to use the geomagnetic field for positional information.

A potential complication for magnetic position-finding systems is that the Earth's magnetic field gradually changes over time (Lohmann & Lohmann 2006). This phenomenon is referred to as secular variation (Skiles 1985), in which the pattern of geomagnetic isolines (i.e. lines of equal inclination angle and lines of equal intensity) slowly change with time so that the magnetic field that exists at any particular location is not constant (Lohmann et al. 1999; Lohmann & Lohmann 2006), although the degree to which the magnetic field changes varies among the different regions of the planet. Possible effects of secular variation on magnetic position-finding strategies has been discussed briefly in the literature (Alerstam 2003; Courtillot et al. 1997; Freake et al. 2006; Lohmann et al. 1999; Lohmann & Lohmann 2006), but few experiments have attempted to investigate this topic.

Loggerhead sea turtles (*Caretta caretta*) are a long-distance migrant thought to use the Earth's magnetic field as a source of positional information during their movements at sea (Lohmann et al. 1999; Lohmann & Lohmann 1996b; Lohmann & Lohmann 2003). Immediately after hatching and entering the ocean, loggerhead sea turtle hatchlings from the east coast of Florida, U.S.A. begin a migration around the north Atlantic gyre, a current system that encircles the Sargasso Sea (Bjorndal et al. 2000; Carr 1987). Turtles spend approximately 10 years migrating around the gyre (Bjorndal et al. 2000) before returning to the southeastern United States to take up residence (Musick & Limpus 1997). Hatchlings can sense both the inclination angle (Lohmann & Lohmann 1994b) and total intensity (Lohmann & Lohmann 1996a) of the Earth's magnetic field, two components that vary predictably across the Earth and, in theory, could provide turtles with a source of positional information during their migrations (Lohmann et al. 1999; Lohmann & Lohmann 2003). Additionally, past studies indicate that hatchlings can use regional magnetic fields as navigational markers. In effect, these fields trigger orientation responses that, in each case, help turtles advance along their migratory pathway and stay inside the gyre current system (Lohmann et al. 2001).

The hatchlings exhibiting this behavior have not yet entered the ocean (Lohmann et al. 2001; Lohmann & Lohmann 1994b; Lohmann & Lohmann 1996a), suggesting that turtles emerge from their nest programmed to respond to specific field characteristics that exist along their migratory pathway by swimming in directions that would, in each case, help them advance along their migratory route and stay inside the gyre current system (Lohmann et al. 2001). However, in some cases, secular variation might cause fields to move from one location to another, within and around the gyre current system. In this study, we investigate how such changes in the magnetic field might affect the turtles' ability to use regional magnetic fields as navigational markers.

Methods

Animals

Loggerhead sea turtle hatchlings were obtained from clutches deposited on nesting beaches at Melbourne Beach, Florida. The morning after they were laid, nests were marked and then monitored during the incubation period. Hatchlings were collected the evening before they would otherwise naturally emerge. We removed approximately 20 turtles from each nest by gently digging into the sand with our hands. The animals were placed in a lightproof Styrofoam container for transportation back to the lab. Hatchlings were kept in complete darkness and were used only once in an experiment before being released that same night.

Orientation tank

Orientation behavior was tested in a water-filled, circular arena, with a diameter of 91.4 cm (Figure 3.1). The tank's walls were black. The water temperature was 26.0°C to 28.0°C during the experimental trials. For each trial, a hatchling was placed in a nylon-lycra harness that did not interfere with swimming (Salmon & Wyneken 1987). The harness was attached to a 25.4 cm-long lever arm by 10.2 cm of monofilament line. The lever arm was connected to a digital encoder that was encased by a plastic, vertical post. This post was mounted in the center of the orientation tank. The lever arm was free to rotate 360° in the horizontal plane so that the turtle could swim in any direction. In addition, the animals were neither able to contact the edge of the orientation tank nor the center post. The digital encoder was wired to a computer in an adjacent room. To ensure that no outside light entered the orientation arena during a trial, the top of the tank was covered with a 1.9cm-thick, black plywood lid, as well as an additional four sheets of 6mm black plastic.

Magnetic coil

This orientation arena was placed in the center of a magnetic coil system capable of producing Earth-strength magnetic fields (Figure 3.1). The coil system consisted of two orthogonally arranged Merritt-4 coils (Merritt et al. 1983). The first coil (2.41m on a side) was aligned along the north-south axis of the ambient magnetic field and controlled the field's horizontal component. The second coil (2.54m on a side) controlled the field's vertical component. The electric current to the two coils was controlled by a computer, allowing us to generate magnetic fields from anywhere in the Atlantic Ocean in the center of the coils where the turtles swam. The entire experimental apparatus was located outside and at least 15m away from where the computer and power supplied were located. Additionally, we used a tri-axial magnetometer (Applied Physics System, model 520) to measure the magnetic field in the area where the coils were installed and ensure that there were no magnetic field distortions there.

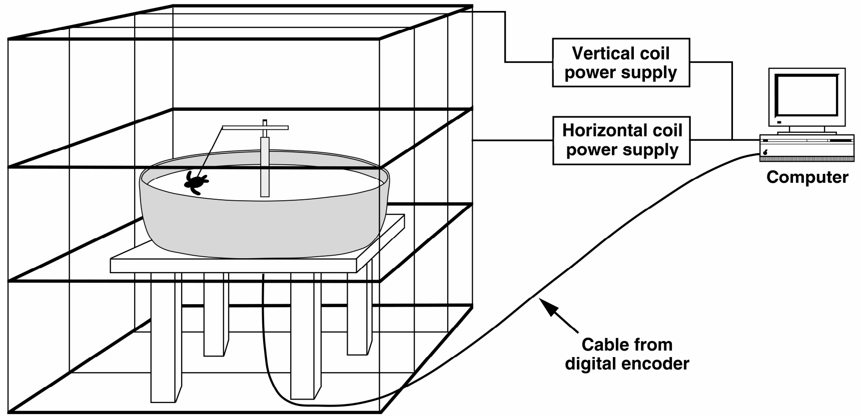

Figure 3.1. Diagram of the experimental apparatus, including the orientation arena, the magnetic coil system, and the computer that collected data and controlled the power supplies. Hatchlings were tethered to a lever arm that could rotate 360° along the horizontal plane. The lever arm was attached to a digital encoder which was encased by a vertical post in the center of the arena. The tracker arm recorded the turtle's heading and sent this information from the encoder to the computer located in a nearby room. The arena was placed inside two orthogonally arranged coil structures capable of replicating magnetic fields found at different locations along the turtle's migratory route. Modified from (Lohmann & Lohmann 1994b).

Magnetic fields and their movement as a result of secular variation

For this experiment, we programmed the power supplies so that they produced two different magnetic fields identical to ones found at separate locations along the loggerhead sea turtle's migratory pathway. The first field simulated the magnetic field conditions presently found at the gyre's northeastern boundary (LAT 44.5°N, LONG 20.0°W), and it has remained in this same geographic vicinity for much of the past century. To approximate the magnetic conditions at this geographic location, we generated a field that had an inclination of 60.1° and an intensity of 46.2μT. A field very similar to this one was used in a previous study and elicited a southward orientation response (Lohmann et al. 2001). The second field simulated the magnetic field conditions presently located offshore from Morocco, Africa (LAT 30.0°N, LONG 21.0°W), but this field moved to this geographic region of the gyre in the recent past. To approximate the magnetic conditions found at this geographic location, we generated a field that had an inclination angle of 41.2° and an intensity of 39.3μT. The parameters for each field were based on estimates provided by the International Geomagnetic Reference Field (IGRF) model, version 2005, projected for July 1st, 2006, which corresponded to the approximate time of data collection. The field uniformity in the middle of the coils where the turtles swam deviated from perfect field uniformity by less than 0.55%.

We used IGRF, version 2000, Applet software (Korhonen 2000) to determine the locations in which these two magnetic fields previously existed during the past century. The Applet software produces maps of specific geomagnetic isolines of inclination angle and intensity at any region of the globe. To pinpoint the location of each magnetic field during a given year, we first programmed the Applet to produce a map of the North Atlantic Ocean that showed only the 60.1° and 41.2° isoclinics (lines of equal inclination angle). Then, we programmed the Applet to produce a map of the North Atlantic that showed only the 46.2μT and 39.3μT isodynamics (lines of equal intensity). We subsequently transposed these two maps and recorded the latitudinal and longitudinal coordinates of the geographic locations at which the respective isoclinics and isodynamics intersected. The location of each field was determined at 5-year intervals between 1900 and the present. The data were illustrated on a separate map by plotting the locations of these fields over the past century.

Testing procedure

All experiments were conducted between mid to late July 2006, and trials were run between 20:30 and 02:00, which corresponds to the time when loggerhead hatchlings usually emerge from their nest and enter the ocean (Witherington et al. 1990). Prior to each trial, the magnetic coils were turned off, and a light emitting diode (peak λ=550nm) placed in the east of the orientation tank was turned on. A hatchling was placed into the harness and released in the water. The hatchling's swimming responses were monitored briefly after being placed in the tank, as healthy hatchlings are known to swim vigorously toward light after emergence from their nest (Lohmann & Lohmann 1994a; Lohmann & Lohmann 1994b; Lohmann & Lohmann 1996a; Salmon & Wyneken 1987; Wyneken et al. 1990). Thus, turtles capable of maintaining a constant course toward the light source were considered behaviorally competent and healthy (Irwin & Lohmann 2003; Irwin & Lohmann 2005; Lohmann 1991; Salmon & Wyneken 1987). Those turtles unable to maintain a direct course toward the LED in the first minutes of the experiment (less than 5% of turtles) were replaced with other individuals.

Turtles that swam to the LED were permitted to do so in the local field for 10 minutes. After this time, the light was switched off and the magnetic coils were simultaneously turned on, exposing the hatchlings to one of the two different magnetic fields discussed above. Turtles were given 3 minutes to adjust to swimming in darkness in the new field. After this initial acclimation, data acquisition began and each hatchling's heading was recorded every 10 seconds for the next 5 minutes. Turtles were tested once and were subsequently released later that night. No more than three turtles from the same nest were tested in any given magnetic field.

The field to which turtles were exposed was alternated throughout the night as trials were conducted. This experiment was conducted synchronously with another experiment (Chapter 1 of this thesis). Thus, the orientation responses in response to the field at the northeastern gyre boundary reported here were also shown in the first chapter of this thesis.

Data analysis and statistics

After each trial was completed, the data acquisition software calculated the turtle's mean heading using all the data collected during the 5-minute trial period in which the animal was exposed to one of the two fields. We then used a Rayleigh test to analyze whether all the turtles in each treatment group were significantly oriented (Batschelet 1981). Finally, we compared the two distributions using a Watson U^2 test (Batschelet 1981).

Results

The movement patterns of the two magnetic fields used in this experiment appear to be different from each other (Figure 3.2). The magnetic field that presently exists at the northeastern boundary of the gyre has remained in this geographic vicinity in the North Atlantic Ocean for much of the past century. In 1900, this field existed south of the Azores, and then from this location the field moved approximately southwestward toward the Sargasso Sea. In 1940, the field then began gradually moving northeastward to its present location.

The movement pattern of the field that presently exists off the shores of Morocco is markedly different. In 1900, this field existed exclusively in the oceanic region north of Surinam and French Guiana. Between 1900 and 1970, this field moved approximately west along the northern coastline of South America and toward Nicaragua. For a brief period between 1975 and 1980, this field simultaneously existed offshore from Nicaragua and Morocco. From 1985 to the present, however, the field has only existed offshore from Morocco and not anywhere in the Caribbean Sea.

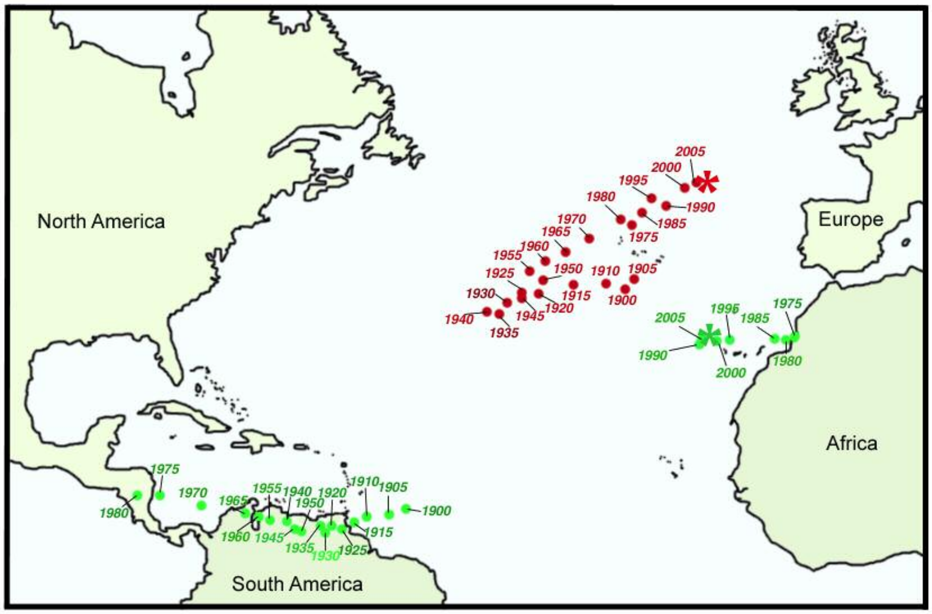

Figure 3.2. Map showing the location of the two magnetic fields used in this experiment during the past century as a result of secular variation. The asterisks indicate the geographic locations where the two separate fields existed on July 1, 2006, and subsequent dots indicate where the field existed at past times, which are noted next to each dot. The red asterisk and dots represent the field used in the experiment from the northeastern boundary of the gyre. The green asterisk and dots represent the field used in this experiment that currently exists off the west coast of North Africa.

Consistent with previous experiments (Lohmann et al. 2001), turtles subjected to a magnetic field like one found at the northeastern boundary of the north Atlantic gyre were significantly oriented as a group (Figure 3.3; Rayleigh test, n=27, r=0.40, p=0.012), with a mean heading of 150.8°. Turtles exposed to a magnetic field like one found off North Africa's west coast were also significantly oriented as a group (Figure 3.3; Rayleigh test, n=27, r=0.37, p=0.022), with a mean heading of 36.2°. Finally, the two distributions were significantly different (Watson U^2; U^2=0.31, p<0.005).

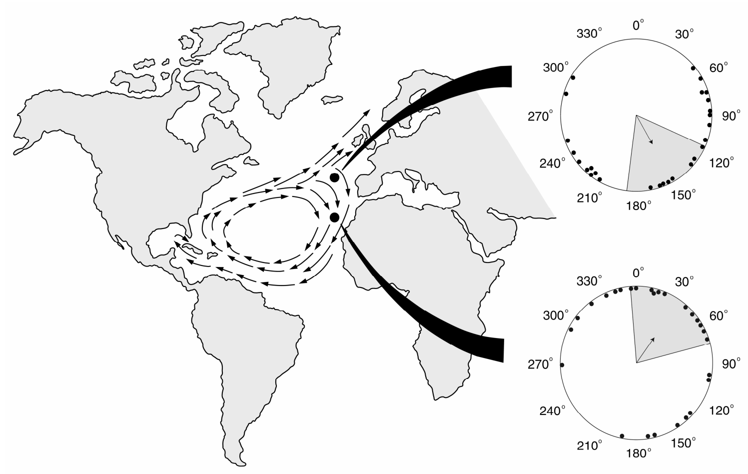

Figure 3.3. Hatchling orientation responses elicited by two magnetic fields that currently exist at separate locations along the north Atlantic gyre (indicated by the black dots). The arrows on the map indicate the direction in which the gyre current flows. In the two circular orientation diagrams, each dot represents the mean heading of a hatchling. The arrow indicates the mean heading of groups of turtles, and the length of the arrow is proportional to the magnitude of the mean vector r (with the radius of the circle corresponding to r=1). The shaded areas represent values within the 95% confidence intervals of the respective distributions. The data are plotted relative to magnetic north, with 0° indicating magnetic north and 180° indicating magnetic south. Turtles exposed to a magnetic field like one that exists at the northeast gyre boundary were significantly oriented as a group (Rayleigh Test, z=4.357, r=0.402, n=27, p=0.012), with a mean heading of 150.8°. Hatchlings subjected to a field like one that currently exists off the northwest coast of Africa were significantly oriented as a group (Rayleigh Test, z=3.734, r=0.372, n=27, p=0.022), with a mean heading of 36.2°. These two distributions were significantly different from each other (Watson U^2 test; U^2=0.31, p<0.005).

Discussion

When exposed to the field replicating one that presently exists near the north Atlantic gyre's northeastern boundary, hatchlings swam approximately southward. Turtles subjected to a field similar to one that currently exists offshore of Morocco swam toward the northeast. Thus, these results show that hatchling loggerheads can distinguish between two magnetic fields that exist at separate geographic areas of the north Atlantic gyre.

Functional significance of orientation responses

In previous experiments, the orientation responses elicited by several regional magnetic fields within the north Atlantic gyre appear to have functional significance to the turtles' migration. In effect, the fields trigger responses that would, in each case, help turtles advance along their migratory pathway and remain inside the gyre current system. In this experiment, hatchlings subjected to a magnetic field identical to one found at the northeastern boundary of the gyre oriented southward, a finding consistent with previous studies. At the northeastern segment of the gyre, the current splits into a north-flowing branch and a south-flowing branch. Thus, swimming south in this area probably helps turtles avoid being swept into the north-flowing currents that presumably carry young turtles into lethally cold waters that exist off the shores of the United Kingdom and Scandinavia (Cain et al. 2005; Lohmann et al. 2001; Lohmann & Lohmann 2006).

However, the orientation response we observed when we subjected turtles to a field like one that presently exists offshore from Morocco does not appear to serve an obvious function in terms of keeping turtles inside the gyre or helping them progress along their migratory pathway. The gyre currents offshore from the northeast coast of Africa flow to the southwest (Batteen et al. 2000; Oberhuber 1993), and thus turtles that swim to the northeast in this region would travel against the current. Based on these and previously published results (Lohmann et al. 2001), we would predict that turtles would swim in the same approximate direction of the currents in order to best progress along the migratory pathway.

When we consider how secular variation has impacted the movement of these two magnetic fields during the past century, a possible interpretation of the results emerges (Figure 3.3). The field that currently exists at the gyre's northeastern boundary has remained in the same geographic vicinity within the North Atlantic for much of the past 100 years. Swimming southward at any of the locations where this field has previously existed would likely be sufficient to, at the minimum, help young turtles stay inside the gyre where conditions are favorable for survival (Bjorndal et al. 2000; Bolten 2003; Bolten et al. 1998). However, the most important point is that southward orientation at all the locations where the field existed would most likely have *not* guided young loggerheads in a direction that would either delay or prolong their migration, or lead them outside the gyre current system where they would probably die.

In contrast, the field that currently exists offshore from Morocco has been present at this location during the past 25 years, and previously existed exclusively along the South American coast. Young loggerheads migrating near the northeastern coast of South America where this magnetic field previously existed would presumably be traveling north-northwestward in order to reach the southeastern coast of North America where they establish residence (Musick & Limpus 1997). By swimming approximately northeast, hatchlings might help steer themselves toward the North

American coast line and avoid being caught in the waters near the South American shore that have significant eddy activity (Arnault 1987). Thus, it is possible that this orientation response has a functional significance to the turtles' migratory pathway near the north and northeastern coastline of South America and in the Caribbean Sea, where the field previously existed. Since the field existed in this region of the gyre for much of the past century, the orientation response we observed might have evolved when the field was actually located near the Caribbean, and *not* offshore from Morocco.

It is important to note that we cannot rule out several other interpretations of these data, such as the possibility that the northeastern orientation response has a functional significance to the turtles' migration that we cannot determine based on the current knowledge of loggerhead migratory ecology. For example, turtles might swim in the opposite direction of the current so that they can prolong their stay in the oceanic area off the northwestern coast of Africa. These waters are highly productive due to heavy upwelling (Johnson & Stevens 2000), and thus might provide turtles with rich foraging grounds.

One limitation to our analysis of how secular variation has caused these two fields to move geographic locations is that we can only examine each of the fields' movements during the past century. Our analysis was unlikely to capture how these fields move geographic locations over a more realistic evolutionary time-period. Without such analysis, it is difficult to resolve or conclude exactly where the fields were located when the orientation responses were likely to have evolved. Future analysis should focus on lengthening the time-scale at which the movements of specific magnetic fields are tracked.

Secular variation and magnetic position-finding

The preliminary results presented here do not suggest that the loggerheads' magnetic position-finding system is incompatible with secular variation. Although the Earth's field gradually changes over time, natural selection probably acts to maintain an approximate coupling between the hatchlings' orientation responses and the magnetic fields that exist at various geographic regions of the turtles' migratory route (Lohmann et al. 2001). In this way under the present conditions of the North Atlantic Ocean, turtles that stray outside of the gyre current system likely die from exposure to cold waters or are swept off course (Cain et al. 2005; Lohmann et al. 2001; Lohmann & Lohmann 2003; Lohmann & Lohmann 2006) and are thus removed from the population. Selection probably favors those hatchlings equipped with orientation mechanisms that help them remain inside the gyre and advance along their migratory course. Moreover, as the field changes with time, turtles that respond to magnetic fields along their migratory route by swimming in directions that increase their likelihood of survival will be selected for (Lohmann & Lohmann 2003). Thus, it is possible that natural selection modifies the hatchlings' magnetic position-finding strategy as the geomagnetic field gradually changes over time, which would enable turtles to use regional magnetic fields along their migratory route as navigational markers.

Exceptions may exist, however, in geographic areas where the field has changed significantly in the recent past, such as the field that currently exists offshore from Morocco. Loggerheads are long-lived and reach reproductive maturity around 12-37 years of age (Witherington 2003). Since this particular field has only existed offshore from the African continent for the past 25 years, only relatively young turtles that recently reached maturity would have experienced this field in this present location while migrating. Thus, the majority of the loggerhead population that is currently reproductively mature would have only encountered this field near the Caribbean Sea, in a location along their migratory pathway where a northeastern orientation response would have been adaptive. Thus, it is possible that not enough time has transpired for natural selection to modify the orientation response so that it is suitable for guiding young turtles southward, which is in the direction of the Canary Current that flows along the northwestern coast of Africa. In effect, the response that we have observed could be a maladaptation resulting from an evolutionary time lag. Other examples of such maladaptations, albeit not regarding orientation behavior, have been documented in other organisms, such as birds (Hosoi & Rothstein 2000), insects (Spitzer 2006), and funguses (Kaltz et al. 1999).

It would not be surprising if selection eventually modifies this orientation response over time so that it is functionally significant to the turtles' migration at the location where the field currently exists. Many migratory adaptations are thought to be evolutionarily flexible, and some of which have been shown to rapidly evolve (Brown & Brown 2000; Pulido 2007; Pulido et al. 2001), including orientation programs (Berthold et al. 1992). For example, a population of blackcaps that inhabits central Europe has evolved a new migratory route to the United Kingdom within three decades (Berthold et al. 1992), and it is thought that the birds' directional preference is controlled by only a few genes (Helbig 1996). Thus, whether the magnetic position-finding system of loggerheads can also rapidly evolve is unknown, but simply a similar degree of flexibility would presumably enable the turtles' navigation system to adjust to the continually changing geomagnetic field.

Since loggerhead sea turtles, as well as many other animals, have maintained their ability to use the Earth's magnetic field as a source of positional information, the problems that secular variation might pose for magnetic maps and other magnetic position-finding mechanisms are certainly not insurmountable (Lohmann & Lohmann 2006). Additional empirical, as well as theoretical, studies investigating this fascinating issue would be useful in understanding the evolutionary implications of secular variation and magnetic navigation.

Acknowledgements

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CHAPTER 4

Effect of the geomagnetic environment in which sea turtle clutches incubate on the hatchlings' subsequent magnetic orientation behavior

Abstract

Loggerhead sea turtle hatchlings (*Caretta caretta*) are capable of using regional magnetic fields as open ocean navigational markers during their transoceanic migrations, yet the early ontogeny of this magnetic orientation behavior is unknown. We studied whether the magnetic environment in which loggerhead sea turtle hatchlings develop affects their subsequent magnetic orientation behavior. Clutches of eggs deposited by nesting females on the beach were permitted to develop in one of two ambient magnetic fields. Half of the clutches were subjected to an altered magnetic field generated by an array of magnets buried around the eggs. The other half of the clutches were treated identically, but surrounded by an array of non-magnetic aluminum bars so that the eggs developed in the natural magnetic field. Hatchling turtles from both groups were subjected to several behavioral assays designed to assess both their orientation behavior and general health. The results indicated that developing in an altered magnetic field affected the way in which hatchlings responded to a regional magnetic field that exists along their migratory route, which is used as an open-sea navigational marker. However, turtles that developed in the altered field did not differ from controls in other assays of orientation behavior and health unrelated to magnetic field perception. To our knowledge, these findings are the first to show that the magnetic environment in which a vertebrate animal develops can influence its subsequent magnetic orientation behavior and could further impact how individuals navigate throughout their lives.

Introduction

Numerous animals are capable of using the Earth's magnetic field as a cue for orientation and navigation (Wiltschko & Wiltschko 2006; Wiltschko & Wiltschko 2005). The geomagnetic field potentially provides animals with a source of directional and positional information (Cain et al. 2005;

Johnsen & Lohmann 2005; Wiltschko & Wiltschko 2005). Directional, or compass, information is used to help organisms maintain a constant heading (Bingman 1981; Kimchi & Terkel 2001; Lohmann 1993; Quinn 1980; Viehmann 1979), whereas positional information is used to help some animals assess their geographic location (Beck & Wiltschko 1982; Boles & Lohmann 2003; Lohmann et al. 2004; Phillips et al. 2002).

Although magnetic orientation is well documented in diverse animals (Wiltschko & Wiltschko 1995), relatively little is known about the early ontogeny of magnetic orientation behavior. For some animals, environmental cues present during critical periods of development can influence subsequent orientation and navigation, such as young salmon fry that imprint on site-specific odors from their natal stream and later use these odors to help recognize the stream as adults when returning to spawn (Dittman & Quinn 1996; Quinn 2005). However, few experiments have investigated whether magnetic fields encountered during early development have effects on subsequent magnetic orientation behavior.

Loggerhead sea turtles (*Caretta caretta*) offer a promising system for investigating this issue because much is known about loggerhead magnetic orientation and navigation behavior (Lohmann et al. 1999; Lohmann & Lohmann 2003). For example, immediately after emerging from their nest, hatchling loggerheads have a magnetic compass that is thought to help guide them offshore and toward the Gulf Stream current (Goff et al. 1998; Irwin & Lohmann 2003; Light et al. 1993; Lohmann 1993; Lohmann & Lohmann 1994a). Once they enter this current, young loggerheads begin their transoceanic migration around the north Atlantic gyre, a circular current system that flows around the Sargasso Sea (Bjorndal et al. 2000). Previous experiments have suggested that hatchlings can use magnetic fields from widely separated geographic regions of the gyre as navigation markers (Lohmann et al. 2001). In effect, these regional fields elicit orientation responses that, in each case, would help hatchlings remain inside the gyre current system and advance along their migratory pathway (Cain et al. 2005; Lohmann et al. 2001; Lohmann & Lohmann 2003). Finally, it is hypothesized, but not yet demonstrated, that hatchling sea turtles imprint on the magnetic field of their natal beach and use this information when returning to this beach later in life to nest (Lohmann et al. 1999). Thus, it remains unknown whether the magnetic environment that turtles encounter during incubation influences any of these magnetic orientation behaviors.

To study whether the magnetic field that an animal experiences during incubation influences magnetic orientation abilities later in life, we altered the magnetic field in which clutches of loggerhead sea turtle eggs incubated and then tested whether hatchlings from these nests were still able to use magnetic navigational markers to orient in a direction consistent with their migratory pathway. In addition, we subjected hatchlings to additional orientation tests and assays of general health to help determine whether the effects of the altered magnetic field were likely specific to the hatchlings' magneto-sensory abilities.

Methods

Locating turtle nests

The study was conducted in Melbourne Beach, Florida, USA. Every morning between 06:00 and 09:00, we patrolled a 5km stretch of beach to locate freshly deposited sea turtle nests. At each nest, the female's tracks were examined to determine the exact location of the clutch. The location of the nest was then marked by placing stakes into the nearby dune and measuring the distance to the clutch.

Manipulation of the magnetic field around the eggs

A square trench was dug around each nest's egg chamber using gardening trowels. The trench was dug far enough away from the egg chamber so that the eggs were neither exposed nor harmed during this process. A square frame (55.9cm by 55.9cm) made from plastic PVC pipe was placed in the trench so that it was 23cm below the top of the egg chamber, which corresponds to the approximate depth at the center of the egg chamber (Carthy, in press) (Figure 4.1). We then filled the trench with the same moist sand that was previously removed.

The frames placed around each nest were structurally identical. Half of the frames had magnets attached to them, while the other half of the frames held non-magnetic aluminum bars of equal size. Thus, nests surrounded by frames with magnets developed in an altered magnetic field, and nests surrounded by frames with aluminum bars developed in the local ambient field of the natal beach. All magnets and aluminum bars were wrapped in waterproof plastic bags so that neither could corrode and possibly alter the chemical composition of the sand surrounding the nest.

Bar magnets (0.64 cm x 1.27 cm x 10.16 cm; Neodymium rare Earth magnet; N40) were obtained from National Imports (Falls Church, Virginia, USA) and were attached to opposite sides of the PVC frame (55.9cm apart from each other) so that the north pole of the first magnet and the south pole of the second magnet faced inward toward each other. The sides of the PVC frame holding the magnets were positioned so that the magnets were on the north and south sides of each nest. The PVC frames holding aluminum bars were placed in the sand identically.

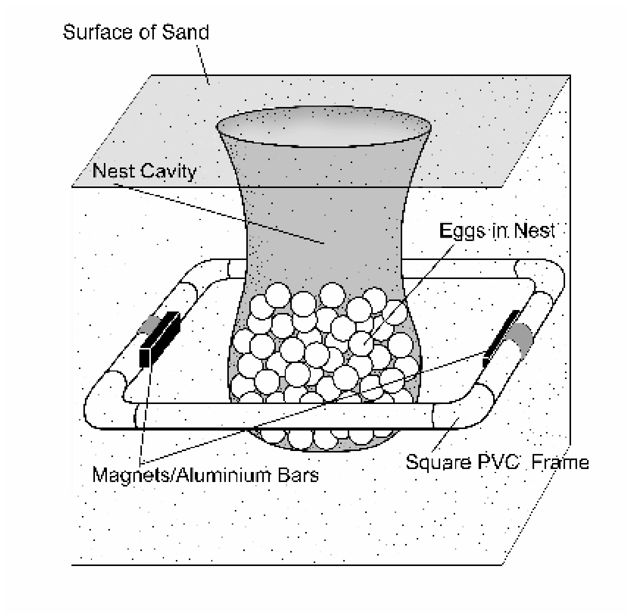

Figure 4.1. Diagram of PVC square buried around the nests with either magnets or aluminum bars attached. The square frames were placed around the middle point of the egg chamber of the nest and positioned so that the magnets/aluminum bars were always on the north and south sides of each nest.

Measurements of the magnetic field distortion

Using a gaussmeter (Indianapolis, Indiana, USA), we measured the field around the PVC frame containing magnets to ensure that the entire clutch would encounter an altered field and that field alteration between frames with magnets was the same. No area of the nests incubating in the altered field experienced a field intensity greater than 310μT or less than 36μT, and the intensity in the center of the PVC frame was 80μT. In comparison, all the eggs incubating in nests surrounded by frames with aluminum bars experienced a field intensity of approximately 47μT, which corresponds to the local magnetic field at Melbourne Beach, Florida, USA.

Collection of hatchlings

Nests were monitored daily. When emergence was imminent (often indicated by a small depression in the sand), we gently dug into the sand by hand and removed approximately 30 hatchlings. Turtles were placed into a Styrofoam cooler and transported to the laboratory for experiments and measurements. Each animal was used only once for a single experiment and released later that night.

Gyre responses

Orientation Arena. Magnetic orientation behavior was tested in a circular tank that was 91.4 cm in diameter (Figure 4.2). The inside of the tank was black. The water temperature was 28.0°C to 30.0°. Hatchlings were placed in a nylon-lycra harness that encircled each turtle without impeding its swimming (Salmon & Wyneken 1987). The harness was connected to a graphite lever arm by 10.2 cm of monofilament line. The lever arm measured 25.4 cm from the center of the tank to the tip of the lever arm. At the center of the tank, the lever arm was attached to a digital encoder encased by a PVC post. Thus, the lever arm could freely rotate 360° in the horizontal plane, and the hatchlings were able to swim in any direction. Yet, hatchlings were neither able to touch the PVC post in the center of the arena nor the outer edge of the arena. The digital encoder recorded the direction the turtle swam and was connected to a computer in an adjacent room. To ensure that no light entered the orientation arena during the experiments, the tank was covered by a 1.9 cm-thick, black plywood lid and four layers of 6 mm black plastic.

Magnetic Coil. The orientation arena was surrounded by two orthogonally arranged magnetic coils (Merritt et al. 1983), capable of producing uniform and Earth-strength fields in their center where the turtles swam (Figure 4.2). The first coil (2.28 m on a side) was aligned along the north-south axis of the ambient magnetic field and controlled the field's horizontal component. The second coil (2.51 m on a side) controlled the vertical component of the magnetic field. Each coil was powered by a computer-controlled power supply. Thus, by controlling the amount of current in the coil, we could produce magnetic fields in the center of the coil like any of those found across the Atlantic Ocean. The entire experimental apparatus was located outdoors and in an area free from magnetic distortions.

In this experiment, we replicated a field similar to one used in previous experiments (Lohmann et al. 2001) that is found at the northeast boundary of the north Atlantic gyre (LAT 44.5°, LONG 20°). The field parameters were based on estimates provided by the International Geomagnetic Reference Field (IGRF) model, version 2000, for July 1, 2005, which corresponds to the time of year when we collected data. The field used to approximate the magnetic conditions at the northeastern boundary of the gyre had an inclination angle of 60.1° and a total intensity of 46.2μT. Using a tri-axial fluxgate magnetometer (Applied Physics Systems 520), we confirmed that the coil system produced this field and the deviation from perfect field uniformity in the center of the coil where the turtles swam was less than 0.5%.

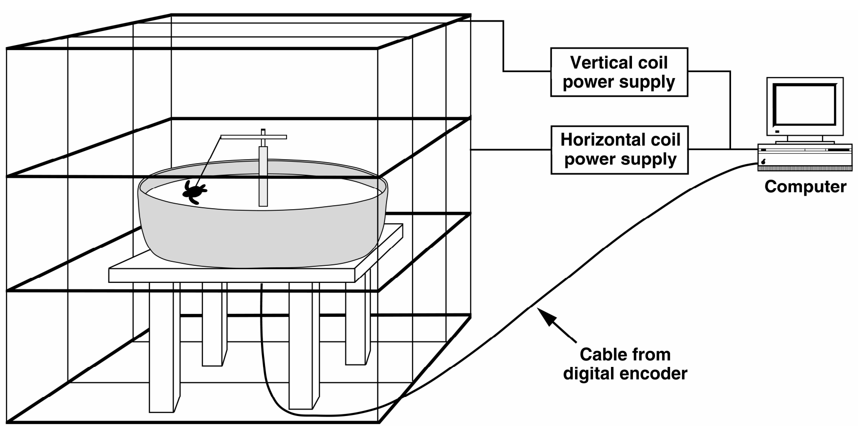

Figure 4.2. Diagram of the experimental apparatus and data acquisition system used to monitor the turtle's orientation. The turtle was harnessed in a nylon-lycra swimsuit and placed in a water-filled arena that was surrounded by two orthogonally arranged coil structures. Computer controlled power supplies located in an adjacent room altered the magnetic field in the center of the coil so that it replicated a geomagnetic field found at the northeastern boundary of the north Atlantic gyre and controlled the turtle's orientation while swimming. Modified from (Lohmann & Lohmann 1994b).

Testing procedure. Prior to each trial, the magnetic coils were turned off, and a light emitting diode (peak λ=520nm) located in the east side of the tank was illuminated. Each hatchling was placed in the harness and permitted to swim freely. Healthy hatchlings are known to swim toward light after they emerge from their nests (Lohmann 1991; Lohmann & Lohmann 1994a; Salmon & Lohmann 1989; Salmon & Wyneken 1987), so a hatchling's ability to swim toward the light was used to verify that the animal was behaviorally competent (Irwin & Lohmann 1999; Irwin & Lohmann 2003). If a turtle was unable to sustain a direct course toward the light source in the first minute of the experiment, the trial was aborted, and the hatchling was replaced.

Hatchlings from both incubation treatments were permitted to swim toward the light for 10 minutes. The LED was then turned off, and the coils were simultaneously turned on so that the turtles were exposed to the magnetic field described above. Turtles were given 3 minutes to adjust to the new field and to swimming in the dark. After the acclimation period, each hatchling's heading was recorded by the data acquisition software every 10 seconds for a total of 5 minutes. All trials were conducted between 20:30 and 02:00. No more than 3-4 turtles from the same nest were tested in this magnetic field. Additionally, we used turtles from 6 different control (incubation in local field) nests and 8 different experimental (incubation in altered field) nests.

Upon completion of each trial, the turtle's mean heading was calculated using all the data points recorded during the 5-minute trial period. We then used a Rayleigh test to determine whether hatchlings from each incubation treatment were significantly oriented in any particular direction (Batschelet 1981). These two distributions were compared using a Watson U^2 test (Batschelet 1981).

Additional tests of orientation and health

Hatchling turtles from both incubation treatments were subjected to additional assays of orientation behavior and health to determine whether the effects of the altered magnetic field during development were likely specific to hatchlings' magnetic field sensing abilities. Thus, we tested two orientation behaviors not known to rely on magnetoreception: (1) the turtles' ability to sense the orbital motions of waves and use them as an orientation cue, and (2) the turtles' ability to orient toward the sea after emerging from their nest. In addition, we recorded hatchling morphometrics from both incubation treatments to assess any possible obvious differences in growth or any morphological abnormalities.

Orientation into waves. After entering the ocean, hatchling sea turtles begin migrating offshore by swimming into waves (Lohmann & Lohmann 1992; Lohmann & Lohmann 2003; Lohmann et al. 1995). Studies have shown that hatchlings are able to detect wave direction by sensing the waves' orbital motions. Turtles can use their rear flippers as rudders in order to correct their orientation so that they are always swimming into a propagating wave (Lohmann et al. 1995). For example, when waves approach a turtle's right side, it will extend its right rear flipper to turn into the oncoming wave. Likewise, when waves approach a turtle's left side, it will extend its left rear flipper. Thus, it is possible to unambiguously determine the direction a turtle intends to turn by monitoring its rear flippers (Lohmann et al. 1995).

Using a mechanical wave simulator (Figure 4.3), we tested whether turtles from both incubation treatments were able to sense the orbital motions of waves and use them as an orientation cue. The wave simulator and experimental protocol we followed is described in detail in Lohmann et al. (1995).

The wave simulator was located in a completely dark room. Turtles were placed in a nylon-lycra harness attached to a wooden dowel that extended from the bottom of a vertical post on the simulator. An infrared camera was also mounted on this post above the hatchling and was wired to a monitor in an adjacent room. Thus, a hatchling on the simulator could be continuously observed during the experiments.

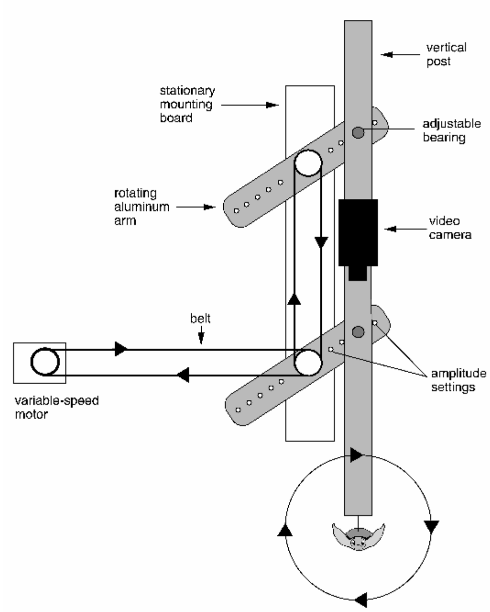

Figure 4.3. Mechanical wave simulator used to produce orbital movements of waves similar to those that hatchlings experience while swimming offshore of eastern Florida. An adjacent motor turns a belt, which in turn drives a second belt attached to two identical rotating aluminum arms. A vertical post is attached to the arms, on the bottom of which a hatchling is harnessed. A video camera mounted on the top of the post monitors the hatchling's movements. The machine subjects the animal to the orbital movements of waves approaching its right or left side. Modified from (Lohmann et al. 1995).

Before each trial, hatchlings were permitted to swim in a bucket of freshwater in complete darkness for 10 minutes to ensure that they were in the same behavioral state that they would otherwise normally be in if they were swimming into waves in the ocean (Lohmann et al. 1995). Next, hatchlings were placed into the harness on the simulator, and then the wave simulator was turned on. Each hatchling was subjected to a movement sequence that simulated waves approaching either the turtle's left side or its right side. The direction of waves was altered after every turtle so that, for example, one turtle experienced waves approaching the left side of its body and the next turtle experienced waves approaching the right side of its body. The circular movements that each hatchling experienced resembled the wave conditions off the east coast of Florida that turtles would naturally encounter, with the radius of circular movement being 0.16 m at a period of 5.0 sec (Lohmann et al. 1995).

After the wave simulator was turned on, hatchlings were given 1 minute to adjust to the movements in complete darkness. After this time, an observer recorded the amount of time that each hatchling extended its right rear flipper and its left rear flipper 90° perpendicular to the mid-sagittal plane of the hatchling's body. This information was recorded for 3 minutes. No more than 3-5 hatchlings from the same nest were subjected to each simulated wave condition. We used turtles from 7 different control nests and 7 different experimental nests.

We analyzed these data by comparing the times spent turning either left or right. First, we used a Wilcoxon signed-rank test for paired comparisons to determine whether hatchlings subjected to each wave condition preferred turning either right or left. Then, we used a Mann-Whitney U test to compare whether the time spent turning either right or left was different between hatchlings from each incubation treatment.

Orientation toward the sea. Hatchling sea turtles quickly crawl down to the ocean immediately after emerging from their nest. To find their way to the sea, hatchlings rely on visual cues (Mrosovsky & Kingsmill 1985; Salmon et al. 1992). We tested whether hatchlings from both incubation treatments were able to orient toward the sea on the night that they would have otherwise naturally emerged from their nest. To do so, hatchlings were placed in the center of a 15m-diameter circle inscribed on the beach. The direction that turtles faced when they were set down was alternated between north, west, east, and south. Once the turtle had been placed in the circle, the experimenter stepped away from the turtle as much as possible without losing sight of the animal and watched the turtle crawl freely in any direction. Thus, the location of the experimenter varied. Using a digital compass (Autohelm personal compass, Nautech Limited, England), the observer recorded the bearing at which the turtle crossed the circumference of the circle. The time each turtle spent crawling from the circle's center to its circumference was also recorded using a standard stopwatch. The most direct route from the circle's center to the sea was between 40° and 80°.

The experiments were conducted between 21:00 and 00:30, and turtles were stored in a lightproof Styrofoam cooler up until the time that they were individually retrieved for the experiment. We tested the sea finding ability of no more than 4-5 turtles from the same nest, and we used turtles from 4 different control nests and 4 different experimental nests. We used a Rayleigh test to determine if hatchlings from each incubation group were significantly oriented in any particular direction, and then compared these two distributions using a Watson U^2 test (Batschelet 1981).

Morphometrics. We recorded measurements including straight carapace length, straight carapace width, right flipper length, head width, and weight, using 15 randomly chosen hatchlings per nest (taken from 7 nests from each incubation treatment). For each morphological character, we calculated a nest average using all the data recorded from the 15 hatchlings of the particular nest. We then computed an overall mean for each morphometric character by averaging the 7 nest averages within a given incubation treatment. Weight was measured with a spring scale (Pesola®), and the remaining morphometrics were measured with digital calipers. Morphometrics were defined by (Wyneken 2001) and were as follows: (1) straight carapace length is the straight-line distance from anterior most point on the midpoint of the nuchal scute to the anterior most tip of the last marginal scute; (2) straight carapace width is the widest distance between the left and right marginal scutes; (3) right flipper length is the distance on the right front flipper from the distal tip of the humerus to the distal tip of the flipper; and (4) head width is the widest part of the head. We used a two-tailed t test to compare the overall means for each morphometric character between incubation treatments.

Results

When exposed to a magnetic field like one found at the northeastern boundary of the north Atlantic gyre, hatchlings that incubated in the local magnetic field of the natal beach were significantly oriented as a group (Figure 4.4; Rayleigh Test; r=0.39, n=23, p=0.03), with a mean angle of 166°. In contrast, the orientation responses of hatchlings that incubated in an altered magnetic field when exposed to the same field were statistically indistinguishable from random (Figure 4.4; Rayleigh Test; r=0.13, n=29, p=0.61). These two distributions are statistically different (Watson U^2 test; U^2=0.189, p<0.05).

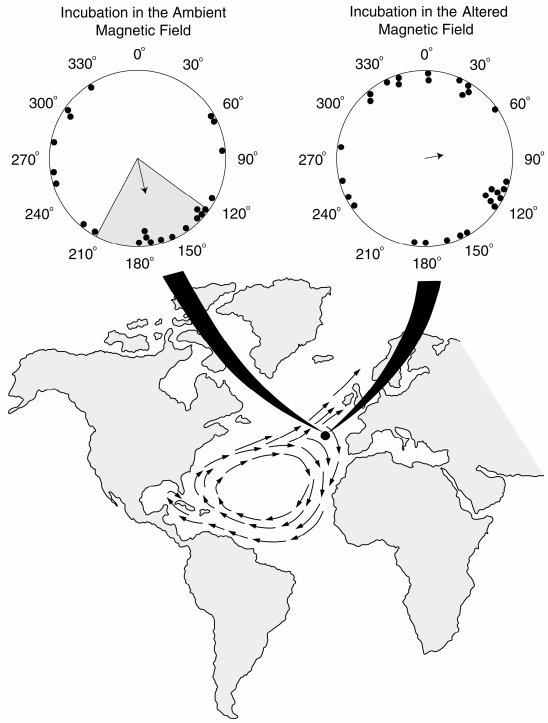

Figure 4.4. Orientation of hatchlings that incubated in either the natural magnetic field or a slightly distorted magnetic field when exposed to a magnetic field along the northeastern boundary of the north Atlantic gyre (indicated by the black dot). In the circular orientation diagrams, each dot represents the mean heading of a hatchling. The arrow indicates the mean direction of turtles in the group. The length of the arrow is proportional to the magnitude of the mean vector *r*, while the radius of the circle corresponds to r=1. The shaded area inside the circle represents the values that fall within the 95% confidence intervals of the distribution. Data are plotted relative to magnetic north, with 0° indicating magnetic north and 180° indicating magnetic south. Turtles that incubated in the natural magnetic field of the beach were significantly oriented as a group (Rayleigh Test, z=3.44, r=0.39, n=23; p=0.03) and had a mean heading of 166°. Turtles that incubated in a slightly distorted magnetic field were not significantly oriented as a group (Rayleigh Test, z=0.50, r=0.13, n=29, p=0.61) with a mean. The two distributions are significantly different (Waston's U^2 test, U^2=0.189, p<0.05).

Hatchling turtles from both incubation treatments showed similar turning behavior on the wave simulator (Table 4.1). Additionally, this turning behavior was consistent with findings from previous studies (Lohmann et al. 1995). First, when simulated waves approached the turtles' left sides, hatchlings from both incubation treatments spent significantly more time turning left than turning right (distorted field; W=329.0, n=25, p<0.01; ambient field, W=323.0, n=25, p<0.01). There was also no statistically significant difference between the amount of time that turtles from both incubation treatments spent turning left (U=623.5, p=0.79) or turning right (U=659.0, p=0.68) with simulated waves approaching from the left.

Likewise, when simulated waves approached the turtles' right sides, hatchlings from both incubation treatments spent significantly more time turning to the right instead of the left (distorted field; W=323.0, n=25, p<0.01; ambient field; W=325.0, n=25, p<0.01). Again, there was no significant difference found between the amount of time that hatchlings from both groups spent turning right (U=586.5, p=0.33) or turning left (U=716.5, p=0.13) with waves approaching from the right.

Table 4.1. Results from the wave simulator experiment in which hatchlings from both incubation treatments were subjected to simulated waves approaching from either the animal's left or right side. When waves were simulated to approach the turtles' left sides, there was neither a significant difference between the amounts of time that turtles from both incubation treatments spent turning right (Mann-Whitney U Test; n=25, p=0.68, U=659.0), nor the time they spent turning left (Mann-Whitney U Test; n=25, p=0.79, U=623.5). When waves were simulated to approach the turtles' right sides, there was no significant difference between the amounts of time that turtles from both incubation treatments spent turning left (n=25, p=0.13, U=716.5) or right (n=25, p=0.33, U=586.5). Since data were collected in each trial for a total of 3 minutes, the maximum number of seconds that a turtle could spend turning in a given direction is 180.

	Waves approach hatchling's left side		Waves approach hatchling's right side	
	Seconds spent turning left (mean ± SD)	Seconds spent turning right (mean ± SD)	Seconds spent turning left (mean ± SD)	Seconds spent turning right (mean ± SD)
Hatchlings that Incubated in the Local Magnetic Field	156.1 ± 11.0	2.9 ± 27.4	8.0 ± 17.6	153.3 ± 7.0
Hatchlings that Incubated in the Altered Magnetic Field	154.8 ± 5.2	4.8 ± 15.9	3.4 ± 12.7	158.9 ± 20.3
p-value	N.S.	N.S.	N.S.	N.S.

In the sea finding experiments, hatchlings from both incubation treatments were significantly oriented as a group (Figure 4.5). Hatchlings that incubated in the local field (Rayleigh Test; r=0.97, n=31, p<0.001) had a mean heading of 56°, and hatchlings that incubated in the altered magnetic field (Rayleigh Test; r=0.97, n=25, p<0.001) had a mean heading of 55°. The mean headings from both groups were directed toward the ocean and were statistically indistinguishable from one another (Watson U^2 Test; U^2=0.056, p>0.50).

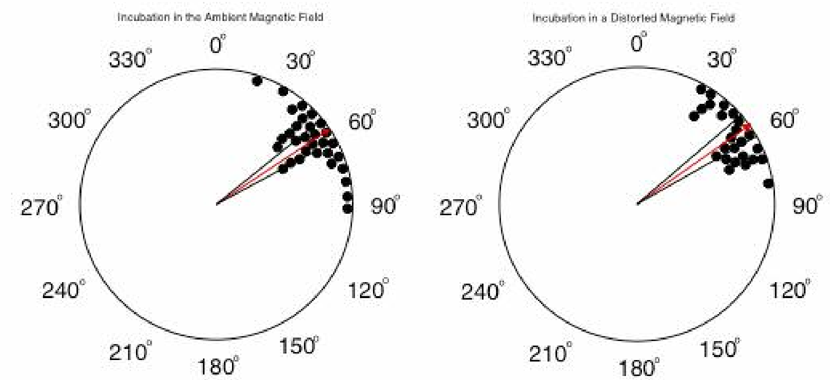

Figure 4.5. Orientation of hatchlings from both incubation treatments when placed on the beach to test their sea finding ability. Each dot within the circular diagram represents the point at which the hatchling crossed the perimeter of the experimental circle after being placed on the beach. The red arrow indicates the mean direction of turtles in the group. The length of the arrow is proportional to the magnitude of the mean vector *r*, while the radius of the circle corresponds to r=1. The lines inside the circular diagram represent the 95% confidence intervals of the distribution. Data are plotted relative to magnetic north, with 0° indicating magnetic north and 180° indicating magnetic south. Turtles that incubated in the ambient magnetic field were significantly oriented as a group (Rayleigh test, n=31, z= 28.9, r=0.97, p<<0.01) with a mean heading of 56°. Turtles that incubated in the slightly distorted magnetic field significantly oriented as a group (Rayleigh test, n=25, z=23.6, r=0.97, p<<0.01) and had a mean heading of 54°. The two distributions were not significantly different (Watson's U^2 test, U^2=0.056, p>0.50).

Finally, no significant morphological differences were detected between hatchlings that incubated in the altered magnetic field and those that incubated in the local field (Table 4.2; t-tests; weight, t=1.24, n=7, p=0.24; straight carapace length t=1.78, n=7, p=0.10; straight carapace width, t=1.14, n=7, p=0.28; right flipper length, t=1.16, n=7, p=0.27; head width t=2.28, n=7, p=0.21).

Table 4.2. Nest averages from both incubation treatments of hatchling morphometrics.. t-tests (two tailed) were used to compare means between incubation treatments. No significant differences were detected (SCL, n=7, t=1.78, p>0.05; SCW, n=7, t=1.14, p>0.05; head width, n=7, t=1.13, p>0.05; right flipper length, n=7, t=1.16, p>0.05; weight, n=7, t=1.24, p>0.05).

	Straight Carapace Length (cm)	Straight Carapace Width (cm)	Head Width (cm)	Right Flipper Length (cm)	Weight (g)
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Hatchling Incubating in Local Field	43.6 ± 0.9	32.8 ± 1.0	15.1 ± 0.2	34.2 ± 0.7	18.6 ± 1.3
Hatchling Incubating in Altered Field	44.5 ± 0.9	33.5 ± 1.2	15.2 ± 0.4	35.5 ± 1.8	19.4 ± 1.1
p-value	N.S.	N.S.	N.S.	N.S.	N.S.

Discussion

When hatchlings that incubated in the natural magnetic field of their natal beach were exposed to a magnetic field like one that exists at the northeastern boundary of the north Atlantic gyre, they responded by swimming southward. In contrast, hatchlings exposed to this same field that incubated in an altered magnetic environment oriented randomly (Figure 4.4). Thus, our results demonstrate that the magnetic environment in which loggerhead sea turtle eggs incubate affects the hatchlings' magnetic orientation behavior soon after emerging from the nest.

In addition, hatchling turtles from both incubation treatments appeared healthy and did not show any obvious morphological abnormalities or defects (Table 4.2). Irrespective of the magnetic environment in which they incubated, the hatchling turtles were capable of sensing the orbital movements of waves and using them as an orientation cue (Table 4.1), as well as finding the sea on the same night they would have naturally emerged from their nest (Figure 4.5). These findings suggest that the altered magnetic field did not cause any obvious health or behavioral abnormalities and that the effects of the altered field were likely specific to the turtles' ability to sense or respond appropriately to magnetic fields.

Functional significance of the nest's magnetic environment

The findings from control hatchlings are consistent with a previous study that showed that loggerhead hatchlings can distinguish among magnetic fields like those that exist at widely separated geographic regions of the north Atlantic gyre (Lohmann et al. 2001). In this experiment, hatchlings respond to the different regional magnetic fields by swimming in directions that would, in each case, likely help turtles stay inside the gyre current system and advance along their migratory pathway (Cain et al. 2005; Lohmann et al. 2001; Lohmann & Lohmann 2003; Lohmann & Lohmann 2006). Because hatchlings that incubated in an altered magnetic environment did not respond to a regional magnetic field in this same manner, it is likely that the magnetic field that developing turtles encounter in the nest somehow influences their ability to use the Earth's magnetic field as a cue for orientation. To our knowledge, this is the first demonstration of such an effect on magnetic orientation behavior, and our results therefore imply that the magnetic field in which loggerhead eggs incubate might affect the hatchlings' ability to use regional magnetic fields along their migratory pathway as navigational markers while migrating around the gyre.

How the magnetic environment turtles experience during development might impact the hatchlings' magnetic position-finding systems cannot be determined at this time, but there are three possible interpretations for how it might do so. First, turtles incubating in the altered field might be unable to obtain directional information from the Earth's magnetic field, but still be able to obtain positional information from it. In this case, in theory, young turtles migrating around the gyre that encounter a regional field would be able to determine the given direction they must swim in order to advance to the next segment of the migration, but then would not be able to maintain a constant heading in this direction. This situation would suggest that the magnetic environment encountered during incubation is critical for the proper development of the turtles' magnetic compass sense.

It is worth noting that experiments involving pied flycatchers (*Ficedula hypoleuca*) have suggested that the magnetic field these birds experience during incubation and as nestlings affects their magnetic compass for their first migration (Alerstam & Hogstedt 1983). However, these results should be interpreted with caution since attention has recently been drawn to potential flaws in this study's experimental apparatus, which could have significantly altered the results (Muheim et al. 2006). Thus, whether the magnetic field young passerine migrants experience during development influences their innate magnetic compass sense has not been settled.

Second, turtles incubating in an altered field might be unable to obtain positional information from the geomagnetic field, but still be able to obtain directional information from it. In this case, young turtles would not be able to determine the direction in which they should swim to progress along their migration, but they would still be able to maintain a constant heading in any given direction if they did in fact somehow choose one. This situation would therefore imply that the magnetic environment hatchlings encounter during incubation might be important for the development of the hatchlings' position-finding system.

To our knowledge, there are no studies investigating how the magnetic field experienced during early development impacts magnetic position-finding abilities later in life. For loggerhead sea turtles, one interesting possibility is that the orientation responses to regional fields located along the migratory pathway are set relative to the field that occurs at the turtles' natal beach. In this case, migrating loggerheads might respond to a particular regional field because it has a set difference of inclination angle and/or intensity relative to the field that the turtles encounter during development at the natal beach. If turtles use this strategy, then in this experiment, hatchlings incubating in the altered magnetic environment would have set their magnetic position-finding system relative to erroneous fields that either exist at random, distant geographic locations on the planet or that do not exist at all, both of which would cause navigational errors observed in the form of random orientation.

Finally, turtles incubating in the altered magnetic field might not be able to obtain either positional or directional information from the geomagnetic field upon emerging from their nest. In this situation, magnetic orientation and navigation would be impossible, as turtles that experienced a regional magnetic field in the open ocean could neither determine the proper heading they should travel in order to advance along their migratory route nor maintain a course in this or any other direction. Thus, this would suggest that the magnetic environment during incubation influences both the magnetic compass and position-finding system.

Our findings do not permit us to conclude that the observed effects on the hatchlings' magnetic guidance system are long lasting and thus would persist during the hatchlings' migration around the gyre. It is possible that experience in the ocean could help turtles adjust to the magnetic conditions of the North Atlantic, which could thereby enable them to exploit regional fields along their migratory path. However, this possibility is not necessarily likely, as we exposed the turtles used in our experiments to magnetic fields different from those of their nest for many hours prior to testing. Recent studies suggest that migratory birds can quickly acclimate their magnetic compass sense to fields that differ greatly from the ones to which they had previously been exposed (Wiltschko et al. 2006). If the effects of the altered field on the hatchlings were temporary, and assuming that the turtles' magnetic compass is similar to that of a migratory bird's, then the turtles would have had ample time to acclimate their magnetic guidance system to the field they encountered prior to testing and turtles from both incubation treatments would have oriented in the same manner. This issue, as well as how magnetic fields encountered during incubation affect magnetic orientation and navigation strategies, require further experimental testing in which eggs are permitted to incubate in controlled, Earth-strength magnetic fields.

Magnetic imprinting hypothesis

The magnetic environment that hatchlings encounter during their development in the nest might also affect the turtles' ability as adults to navigate back to their natal beach to nest. Although studies have established that adult female loggerhead turtles return to the vicinity of their natal beach to nest (Allard et al. 1994; Bowen et al. 1993; Bowen et al. 1992; Encalada et al. 1998), it is not known how females guide themselves to this particular location after being away for several years. Since beaches are ephemeral over evolutionary time, the information sea turtles use to return to their natal beach is probably learned and based on environmental cues present at the beach, rather than genetically programmed (Bowen et al. 1989). The magnetic imprinting hypothesis proposes that hatchlings imprint on the features of the magnetic field at their natal beach and use this information later in life when returning to nest (Lohmann et al. 1999; Lohmann & Lohmann 1994b; Lohmann & Lohmann 1996b).

Our results are consistent with the magnetic imprinting hypothesis, suggesting for the first time that the magnetic environment sea turtles experience during incubation might influence their subsequent orientation and navigation. If the magnetic field hatchlings encounter at their natal beach is an important source of information on which they base their migratory strategies, then they could also plausibly use this information to help guide them later in life when swimming to their natal beach to nest. Turtles in our experiment that incubated in the altered field were exposed to erroneous fields that either do not naturally occur on the planet or are found at distant locations, so imprinting on such fields would mean that adult loggerheads might have difficulty relocating this beach in the future.

Although further experiments regarding magnetic imprinting are likely to be logistically difficult, they are nevertheless necessary. Namely, studies must assess whether there is a critical period in which young or developing hatchlings imprint on the magnetic field parameters of their natal beach, much like young salmon do when they imprint on the odors of their natal stream (Quinn & Dittman 1990).

Conservation implications

Our findings also have implications for sea turtle conservation. For example, metal wire cages are commonly placed on top of incubating sea turtle nests in order to prevent naturally occurring predation of the eggs (Ratnaswamy et al. 1997; Yerli et al. 1997). However, these cages alter the magnetic field in which the eggs incubate (Irwin et al. 2004). It is possible that hatchlings that develop under a metal cage show a similar inability to use regional magnetic fields along their migratory pathway as navigational markers. If so, then these hatchlings might make navigational errors during their migrations offshore or in the open ocean, which could have damaging effects on endangered sea turtles at the population level. This practice is worth reconsidering, and perhaps conservationists will design new cages constructed from non-metal materials that will not alter the magnetic environment in which the clutches develop.

In addition, other anthropogenic magnetic anomalies that occur along sea turtle nesting beaches might impact the magnetic navigation system of sea turtles. For example, many sea turtles preferentially nest in front of large sea walls and beachfront condominiums (Mrosovsky et al. 1995; Salmon 1993) constructed from iron rebar and other magnetic materials that might distort the local field. If these anthropogenic magnetic anomalies negatively influence the magnetic navigation system of sea turtles, conservation practices to avoid these consequences should be considered.

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CHAPTER 5

Magnetic anomalies caused by metal sea walls: a possible effect on hatchling sea turtle magnetic orientation behavior?

Abstract

The Earth's magnetic field is an important environmental cue for sea turtle orientation and navigation, and recent studies indicate that sea turtle eggs that incubate in an altered magnetic field might impede the hatchlings' magnetic orientation behavior later in life. Man-made structures, such as sea walls, built on sea turtle nesting beaches might distort the magnetic field in which nearby nests incubate and possibly influence the hatchlings' magnetoreception abilities. To investigate whether sea walls do in fact distort the local magnetic field along sea turtle nesting beach habitat, we measured the magnetic field in front of two metal sea walls, one fiberglass sea wall, and sections of the beach without any nearby sea walls. The magnetic field in front of the two metal sea walls was different from the local ambient field, whereas the field in front of the fiberglass sea wall did not deviate from the local field. Sea turtle eggs that incubate in front of the two metal sea walls will therefore experience an altered magnetic field, which would impair the hatchlings' subsequent magnetic orientation and navigation behavior. If so, then turtles might have difficulty navigating through the open ocean during their migratory movements at numerous stages of their lives. The impact of anthropogenic magnetic anomalies on the navigational abilities of sea turtles might be an important consideration for conservation.

Introduction

Numerous studies indicate that sea turtles use the Earth's magnetic field to orient and navigate during their migrations in the open sea (Lohmann et al. 1999; Lohmann & Lohmann 1996b; Lohmann & Lohmann 2003; Luschi et al. 2007). For example, hatchling loggerhead sea turtles (*Caretta caretta*) have a magnetic compass (Lohmann 1991; Lohmann & Lohmann 1994a), which is thought to help turtles travel offshore after first entering the ocean (Lohmann & Lohmann 1996b;

Lohmann & Lohmann 2003). Also, hatchling loggerheads can sense magnetic field inclination angle (Lohmann & Lohmann 1994b) and intensity (Lohmann & Lohmann 1996a), which are two components of the geomagnetic field that vary predictably across the planet's surface and, in theory, can provide turtles with positional information (Lohmann et al. 1999; Lohmann & Lohmann 1996a; Lohmann & Lohmann 2003). Moreover, previous studies have suggested that hatchlings use regional magnetic fields found along their transoceanic migratory pathway as navigational markers (Lohmann et al. 2001; Wiltschko & Wiltschko 2005). Finally, it is hypothesized, although not yet demonstrated, that hatchling turtles imprint on the magnetic field at their natal beach and use this information later in life to return to this area to nest (Lohmann et al. 1999).

With increased interest in conservation physiology (Wikelski & Cooke 2006), recent studies have begun to investigate how anthropogenic magnetic anomalies might impact sea turtle magnetoreception (Irwin et al. 2004). For example, sometimes metal wire cages are placed over sea turtle nests to protect the eggs from predators (Ratnaswamy et al. 1997; Yerli et al. 1997). Yet, these cages can alter the magnetic field in which the eggs develop (Irwin et al. 2004), and past experiments suggest that the magnetic environment sea turtles experience during development might influence the hatchling magnetic orientation behavior (Chapter 4 of this thesis). If the effects of the magnetic environment are long lasting and do, in fact, influence sea turtle orientation and navigation in the open ocean, then metal wire protective cages and other human-imposed magnetic anomalies along sea turtle nesting beaches might impede the turtles' ability to guide themselves through the open sea. As a consequence, turtles may be delayed in or unable to complete their critical migrations.

It is therefore important to identify additional anthropogenic magnetic anomalies that sea turtles or sea turtle eggs might encounter at a nesting beach. Sea walls are one such potential structure that could disrupt the local magnetic field along a nesting beach. These structures are designed to reduce beach erosion and are often constructed out of metal materials, such as iron and steel, which are magnetic. Here we investigate whether three different sea walls built on sea turtle nesting beaches distort the magnetic field experienced by clutches of eggs laid in front of the walls.

Methods

To assess the effects of sea walls on the local magnetic field along sea turtle nesting beaches, we measured the field distortions produced by three separate sea walls built on beaches where loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and leatherback (*Dermochelys coriacea*) sea turtles commonly nest. The three walls were located in Indian River County, Florida, U.S.A. Although they varied in height and length, two of the sea walls were constructed from mainly metal materials (Wabasso wall and Estefan wall), and the third wall was built from fiberglass (Sanderling wall).

We used a tri-axial fluxgate magnetometer (Applied Physics Systems, model 520) to measure the magnetic field. Measurements were made along transects extending from the front of the sea wall toward the ocean (ending at the approximate high tide mark) (Figure 5.1). Transects were 13 m long, and measurements were made at one meter intervals along a plastic measuring tape, starting one meter back from the base of the wall. Thus, for each transect, the magnetic field was recorded 13 times.

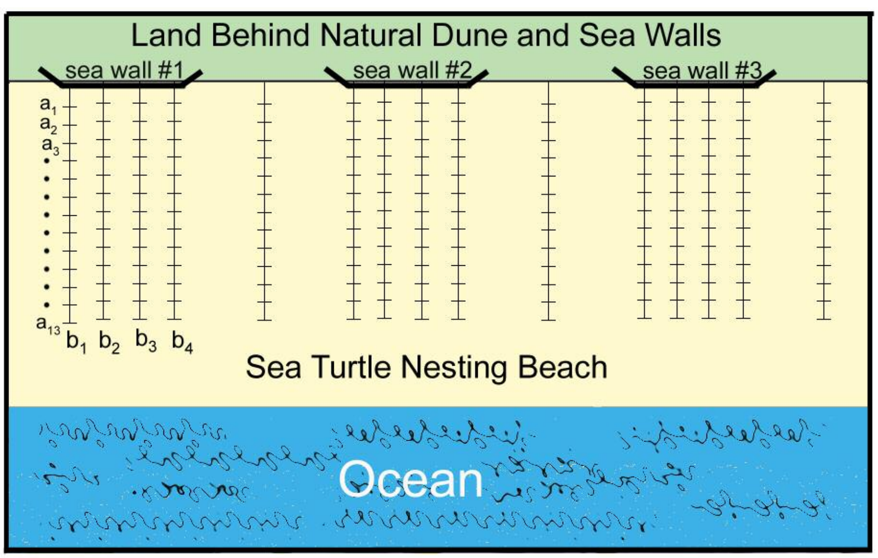

Figure 5.1. Schematic of how transects were laid out along the beach. b_1 to b_4 represent the individual transects taken at each wall. a_1 to a_{13} represent the locations that measurements were recorded along each transect. Transects not immediately in front of a sea wall represent control transects, one of which is not shown in this diagram.

When measuring the field at each location along a given transect, the probe of the tri-axial magnetometer, which simultaneously measures the three orthogonal axes, was placed on a stand 30 cm above the sand and leveled. The probe was then rotated in the horizontal plane so that the Y component of the field was 0. As a result, we were able to record the field's horizontal and vertical components and subsequently compute total magnetic field intensity and inclination angle for each location a measurement was taken.

For our control, the ambient magnetic field was measured in the exact same way, but control transects were laid out on areas of the beach without a sea wall. Each transect began at the base of the natural beach dune instead of the base of a sea wall. The natural dunes are very steep and prevent turtles from nesting behind them, much like a sea wall. We recorded measurements from four different control transects. One control transect was laid out to the north of the three sea walls, and another was laid out to the south of the three sea walls. The final two control transects were laid out along regions of the beach between the sea walls (Figure 5.1). Control transects were at least 40 meters away from any sea wall. The average values we recorded for the ambient field were compared to the value predicted by the International Geomagnetic Reference Field (IGRF), 2000 model, for July 1, 2005, a date that corresponded to the time this study was conducted.

Results

The two components of the geomagnetic field, inclination angle and total intensity, in front of the two metal sea walls were different from those of the local ambient magnetic field (Figures 5.2 and 5.3). The field differences were greatest at the base of each wall and decreased with distance from the wall. The inclination angle and intensity were nevertheless different from the local field 13 meters from the base of the wall, a distance that corresponds to the approximate high tide mark. In contrast, the inclination angle and total intensity in front of the fiberglass sea wall were the same as the local ambient magnetic field. The field values we recorded for the ambient field were similar to those estimated by the IGRF software (58.1° and 46.9μT).

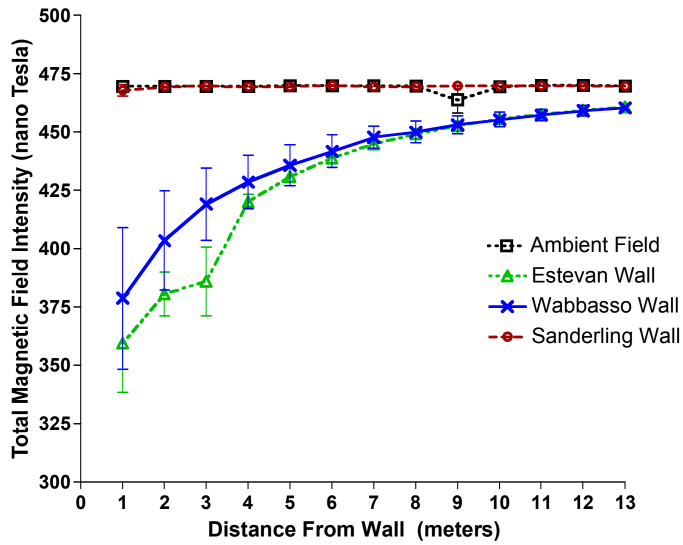

Figure 5.2. Graph of the mean distortion of the total magnetic field intensity in front of each of the three sea walls, as well as the ambient field. The x axis shows distance (in meters) the readings were taken from the base of the wall, and the y axis shows the total magnetic field intensity (in nT). The legend indicates the symbols that represent the three walls and the ambient field. The Wabasso wall and the Estefan wall were built from metal materials, and the Sanderling wall was constructed from mainly fiberglass. The error bars represent 1 standard deviation above and below the mean distortion for a given distance from the wall's base.

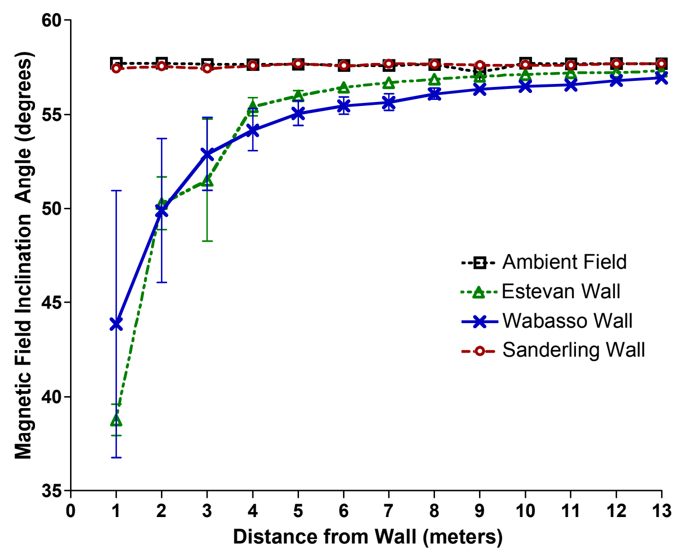

Figure 5.3. Graph of the mean distortion of the magnetic field inclination angle in front of each of the three sea walls, as well as the ambient field. The x axis shows distance (in meters) the readings were taken from the base of the wall, and the y axis shows the total magnetic field intensity (in degrees). The legend indicates the symbols that represent the three walls and the ambient field. The Wabasso wall and the Estefan wall were built from metal materials, and the Sanderling wall was constructed from mainly fiberglass. The error bars represent 1 standard deviation above and below the mean distortion for a given distance from the wall's base.

Discussion

Our results suggest that the two metal sea walls (Wabasso wall and Estefan wall) distort the inclination angle and total intensity of the nearby magnetic field. In each case, the field distortion is greatest at the wall's base and decreases with distance from the wall. Since these field distortions extend to the high tide mark, most of the suitable nesting habitat in front of the two metal sea walls has a magnetic field that is different from the undisturbed local field. In contrast, the field in front of the fiberglass sea wall (Sanderling wall) was not distorted.

Although we cannot conclude that the metal sea walls necessarily caused the field distortions we recorded, it is highly likely that this is the case because both walls were constructed primarily of iron and were magnetic in nature (Fuxjager and Katz, personal observation). It is possible that other nearby structures, such as the houses built behind the sea walls, were responsible for distorting the field. This is unlikely since houses of a similar size and distance from the beach were built behind the non-magnetic (Fuxjager and Katz, personal observation), fiberglass sea wall. Moreover, most houses along this region of the Florida coast appeared to be constructed mainly from non-magnetic materials, such as cinder blocks and wood, as opposed to iron and steel.

Behavioral effects of field distortions

The behavioral effects of incubating in front of a sea wall that distorts the local magnetic field are unknown. Previous studies imply that hatchlings normally use regional magnetic fields located along their migratory route as open ocean navigational markers. These fields elicit swimming responses that would, in each case, likely help turtles advance along their migratory pathway around the north Atlantic gyre, the circular current system that flows around the Sargasso Sea (Lohmann et al. 2001). However, recent evidence suggests that the magnetic field in which sea turtle eggs develop affects the hatchlings' subsequent ability to use regional magnetic fields in this manner. In this experiment, the magnetic field in which particular clutches of eggs incubated was experimentally altered using strong magnets, whereas other nests were permitted to incubate in the local field. Upon hatchling emergence, the magnetic orientation behavior of the turtles from both incubation treatments was tested, and hatchlings that incubated in the altered field, unlike those turtles that incubated in the local field, were randomly oriented when exposed to a regional magnetic field (Chapter 4 of this thesis).

When examined in the context of this study, the aforementioned results suggest that hatchlings that incubate in front of a sea wall that distorts the local field might be unable to use regional magnetic fields along their migratory route as navigational markers. If so, and if the observed effect on turtle orientation is long lasting or permanent, then the navigational abilities of young loggerheads migrating in the gyre after incubating in front of a metal sea wall might be impaired in a number of ways. For instance, young turtles unable to redirect their headings at crucial geographic boundaries of the gyre might be more vulnerable to displacement from the gyre current system and therefore subject to a higher risk of being swept into the lethally cold waters that exist to the gyre's north (Cain et al. 2005; Hays & Marsh 1997; Lohmann & Lohmann 2003).

Developing in a distorted magnetic field might impact other aspects of sea turtle magnetic orientation. For instance, hatchling turtles have a magnetic compass, which is thought to help guide them offshore after emerging from their nest (Irwin & Lohmann 2003; Lohmann & Lohmann 1994a; Lohmann & Lohmann 2003). If incubating in a distorted magnetic field causes the turtles' compass to function differently from normal, then turtles might be unable to establish headings that would lead them to the Gulf Stream Current while swimming offshore. Such a navigational error could be fatal for young turtles, as they might deplete their limited energy stores before reaching their offshore destination (Irwin et al. 2004).

Finally, turtles developing in an altered field in front of a sea wall might have trouble homing to their natal beach later in life when they are ready to nest. Numerous studies show that sea turtles return to the vicinity of their natal beach to lay their eggs once they reach reproductive maturity (Allard et al. 1994; Bowen et al. 2004; Bowen et al. 1994; Encalada et al. 1998). Although it has not yet been demonstrated, turtles are hypothesized to imprint on the magnetic field of their natal beach and use this information later in life to navigate back to the same geographic area (Lohmann et al. 1999). Salmon have a similar ability, as young fry imprint on the odors of their natal stream, and then adult salmon use this information to return to this same region later in life to spawn (Dittman & Quinn 1996; Quinn 2005). Thus, developing in a distorted field could make young hatchlings imprint on fields that do not exist in nature or exist at distant geographic locations. If so, then adult turtles might have difficulty relocating their natal beach when they are trying to return to nest.

Thus, the magnetic field distortions produced by some sea walls could potentially impede sea turtle magnetic orientation behavior in a number of different ways. Yet, at this time, it is difficult to assess the effects of magnetic field alterations of magnetic orientation and navigation. Nevertheless, we must consider the possibility that anthropogenic magnetic anomalies might adversely impact sea turtle navigation systems and we must evaluate other sources of human-induced magnetic disturbances, such as beachfront hotels and condominiums, since these are areas where loggerhead sea turtles preferentially nest (Salmon 1993). Solutions, such as constructing sea walls from non-magnetic materials like fiberglass, need to be considered when developing conservation policy.

Acknowledgments

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CHAPTER 6

Concluding Remarks

My data suggest that the magnetic navigation system that hatchling loggerhead sea turtles use to migrate around the north Atlantic gyre is more complex than previously thought. That is, several regional magnetic fields found along the northern half of the turtles' migratory pathway, as opposed to only a few fields from geographic boundary points, elicit orientation responses that probably help keep turtles safely inside the gyre current system and progress along their migratory route. It is possible that turtles use regional fields as open ocean magnetic waymarks that guide young loggerheads through a given geographic region and toward the next segment of their migratory path.

Yet, certain fields may fail to provide such positional information to turtles in cases where regional fields have changed geographic locations within the gyre in the recent past. In this situation, young turtles might experience a field and respond to it by swimming in a direction that is not conducive to progressing along their migratory pathway. One possibility is that there is an evolutionary time lag between hatchling orientation responses and the magnetic fields that exist at given locations within the gyre to which turtles respond.

Additionally, my results imply that the magnetic field in which sea turtle eggs incubate influences the hatchlings' subsequent ability to use regional magnetic fields as open ocean navigational markers. There are a number of possible explanations for how the magnetic environment experienced during development might influence the turtles' magnetic navigation system, but further experiments are needed in order to investigate these possibilities more thoroughly. These particular results are also consistent with the magnetic imprinting hypothesis and thus might provide insight into how adult turtles navigate back to their natal beach to nest.

Finally, from a conservation perspective, this thesis provides evidence that developing in anthropogenic magnetic anomalies might disrupt the ability of sea turtles to sense and respond to the

Earth’s magnetic field. Metal sea walls, for instance, distort the local magnetic field of the adjacent sea turtle nesting beaches on which these structures were built. Thus, hatchling sea turtles that develop in nests that are located in front of these walls might be unable to properly use the Earth’s magnetic field as an orientation cue while migrating through the open sea. Consequently, turtles could delay or be unable to complete their migrations.

These results provide insight into how long-distance migrants can use geomagnetic cues as a source of positional information when traveling between distant locations. For instance, exploiting regional magnetic fields as a source of positional information in order to navigate a complex pathway might be a guidance strategy employed by a number of different animals. My studies also provided other valuable information about the function and evolution of magnetic position-finding systems, as well as how human disturbances might influence them. This thesis provides a basis for future experiments exploring these topics, as well as answers a number of different questions that are raised regarding magnetic orientation and navigation, which could apply to phylogenetically diverse migratory vertebrates such as seals (Le Boeuf et al. 2000; McConnell et al. 1999), whales (Darling & McSweeney 1985), some species of birds (Alerstam et al. 2003; Mouritsen 2001), salmon (Quinn 1990; Quinn 2005), bats (Holland 2007) and butterflies (James 1993).

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