Ethology Ecology & Evolution 11: 1-23, 1999

Long-distance navigation in sea turtles

K.J. LOHMANN [1], J.T. HESTER [2] and C.M.F. LOHMANN [1]

[1] *Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599-3280, U.S.A.* (E-mail address: KLohmann@email.unc.edu)
[2] *Department of Biomedical Engineering, University of North Carolina, Chapel Hill, North Carolina 27599 U.S.A.*

Received 31 March 1998, accepted 21 May 1998

Adult sea turtles of several species migrate across vast expanses of ocean to arrive at specific nesting areas and feeding sites. Two hypotheses have been proposed to account for this remarkable navigation. The first is that chemical cues emanating from target areas guide turtles to their destinations. The second is that turtles can approximate their position relative to target regions using features of the earth's magnetic field. Because animals often rely on multiple cues while migrating, the two hypotheses are not mutually exclusive.

Satellite tracking experiments have revealed that migrating turtles often swim directly to distant goals, even when traveling perpendicularly to water currents. Because animals usually change course frequently while seeking the source of a chemical plume, the consistency of headings casts doubt on the hypothesis that turtles follow such plumes over great distances. Chemical cues may nevertheless play a role in enabling turtles to recognize a target area in the final stages of a long migration.

The magnetic navigation hypothesis is based on the finding that hatchling loggerhead turtles can detect two different features of the geomagnetic field (inclination angle and intensity) that vary across the earth's surface. Hatchlings from Florida, U.S.A., respond to magnetic features found along their migratory route by swimming in directions that may help keep them safely within the North Atlantic gyre, a circular warm-water current system favorable for growth and development. These results suggest that young turtles can derive positional information from features of the earth's field, and that such information may play an important role in guiding trans-oceanic migrations.

Adults might also exploit geomagnetic features in long-distance navigation. In principle, turtles nesting on coastlines might locate the appropriate region by returning to an area marked by the intersection of the shoreline and a magnetic isoline (e.g., a particular inclination angle or intensity). Turtles that migrate to remote islands may be able to exploit bicoordinate magnetic maps for position-finding, although secular variation and other factors may limit the conditions under which such a system can be used.

KEY WORDS: sea turtles, *Caretta caretta*, *Chelonia mydas*, orientation, navigation, chemical, olfactory, magnetic, magnetoreception, migration.

Introduction 2
Chemical cues and navigation 3
Magnetic navigation hypothesis 5
Future directions 18
Acknowledgments 19
References 19

INTRODUCTION

Most sea turtles migrate intermittently throughout their lives. As hatchlings, the turtles swim from their natal beaches into the open ocean (FRICK 1976, SALMON & WYNEKEN 1987), often taking refuge in circular current systems (gyres) that serve as moving, open-sea nursery grounds (CARR 1986, BOLTEN et al. 1998). As juveniles, many take up residence in coastal areas but migrate seasonally between summer and winter habitats (MUSICK & LIMPUS 1997). Finally, as adults, turtles periodically leave their feeding grounds and migrate to mating and nesting areas, after which many return to their individual feeding sites (LIMPUS et al. 1992, MUSICK & LIMPUS 1997). The itinerant lifestyle characteristic of sea turtles is thus inextricably linked to an ability to navigate accurately across large expanses of seemingly featureless ocean.

In some populations, migratory performance reaches extremes. The total distances certain green turtles (*Chelonia mydas*) and loggerheads (*Caretta caretta*) traverse over the span of their lifetimes exceed tens of thousands of kilometers, several times the diameter of the turtle's home ocean basin (CARR 1984, MORTIMER & PORTIER 1989, BOWEN et al. 1995). For example, green turtles that nest on Ascension Island in the South Atlantic regularly migrate between their nesting beach and Brazilian feeding grounds, a straight-line distance of more than 2,000 km (CARR 1975, 1984). Even more impressively, loggerheads that hatch on Japanese beaches apparently traverse the entire Pacific Ocean to Baja California before returning to Japan to nest (BOWEN et al. 1995).

Researchers have long hypothesized that adult turtles nest on or near the same beaches where they themselves emerged as hatchlings (MROSOVSKY 1983). Genetic analyses have now confirmed that the adults of at least some populations do indeed return to their natal region for nesting after first migrating to distant oceanic areas (MEYLAN et al. 1990; BOWEN et al. 1993, 1994, 1995).

Sea turtles can also pinpoint small, isolated feeding areas. Loggerheads and green turtles that nest along the Great Barrier Reef, for example, return afterwards to specific, widely dispersed feeding grounds that are sometimes located hundreds or thousands of kilometers from their nesting sites (LIMPUS et al. 1992). Although the feeding grounds of different individuals may lie in nearly any direction from the nesting region, adult turtles show great fidelity to both their feeding and nesting areas and migrate between them at appropriate times.

Satellite tracking experiments have revealed that turtles can navigate to such distant sites with remarkable efficiency. Paths of migrating turtles often lead nearly straight across the open sea to destinations hundreds of kilometers away (BALAZS et al. 1994, PAPI et al. 1995, PAPI & LUSCHI 1996). Such unwavering courses seem to imply that turtles possess an awareness of their position, the location of the distant goal, and the directional relationship between the two (PAPI & LUSCHI 1996, LOHMANN et al. 1997).

For logistical reasons, most studies on orientation and navigation in sea turtles have focused on hatchlings rather than adults. Adults are powerful animals that often exceed one hundred kilograms in weight; they are also difficult to keep in captivity, and migrate only intermittently. In contrast, hatchlings are small, seasonally abundant, easy to manipulate in laboratory and field studies, and strongly motivated to migrate offshore. In recent years, considerable progress has been made in characterizing the orientation cues that guide hatchlings during their offshore migration (reviewed by LOHMANN & LOHMANN 1996a, LOHMANN et al. 1997).

Relatively little is known, however, about how adult turtles navigate over long distances or how they relocate their natal region for mating and nesting. For now, hypotheses of adult navigation are based primarily on inferences from studies with hatchlings and juveniles, from analyses of migratory routes, and from theoretical considerations. In this paper we review and discuss two major hypotheses of long-distance navigation. The first is that chemical cues emanating from target areas guide turtles to their destinations. The second is that turtles can approximate their global position and navigate to nesting and feeding areas using features of the earth's magnetic field. Because long-distance migrants frequently use multiple cues in navigation (ABLE 1991), the two hypotheses are not mutually exclusive.

CHEMICAL CUES AND NAVIGATION

The discovery that chemical cues play a critical role in enabling salmon to recognize the tributaries in which they hatched (HASLER & WISBY 1951, HASLER et al. 1978, HASLER & SCHOLZ 1983, NORTHCOTE 1984) prompted speculation that similar cues may be important in sea turtle navigation. The chemical imprinting hypothesis for sea turtles proposes that hatchlings imprint on chemical cues unique to their natal beach and use this information as adults to return to that same beach for nesting and mating (CARR 1984, GRASSMAN 1993).

Relatively little evidence has been obtained to either support or refute this hypothesis. Behavioral experiments have revealed that sea turtles, like most aquatic animals (CARR 1988), can detect chemicals dissolved in water (MANTON et al. 1972a, 1972b; GRASSMAN & OWENS 1982). Whether such cues play a role in navigation or natal beach recognition, however, remains to be determined.

The spatial scale over which chemical cues are proposed to function is an important consideration in an oceanic environment where waves, currents, and eddies rapidly disrupt chemical gradients. Salmon, for example, appear to use chemical cues only at the end of their migrations when the fish have moved into coastal waters and drawn close to the natal river (HASLER et al. 1978). Different, as yet unidentified cues are thought to guide salmon during the open-ocean phase of their migration (QUINN 1984).

Some researchers, however, have hypothesized that sea turtles guide themselves over hundreds or thousands of kilometers of open sea by homing in on the source of a particular odor plume (KOCH et al. 1969, CARR 1972). Others have speculated that turtles, like salmon, may use chemical cues only to identify a final target area after other cues have already brought the animals into close proximity of the goal (LOHMANN & LOHMANN 1996b). We will consider the two possibilities separately.

Chemosensory cues in long-distance navigation

In an attempt to explain the remarkable migration of green turtles from the coast of Brazil to Ascension Island, KOCH et al. (1969) hypothesized that green turtles in Brazilian waters detect a chemical plume that originates at the island and then follow it across more than 2,000 km of ocean to its source. The putative chemical markers would need to persist in the sea without degrading for at least several weeks, and a sufficient gradient would need to exist so that turtles in distant locations could detect not only the chemical but the direction of increasing concentration (CARR 1972, 1984).

As the migratory paths of turtles have become better characterized, however, evidence against the use of such cues in long-distance navigation has begun to accumulate. Satellite tracking experiments have revealed that turtles often follow essentially straight paths to target sites hundreds of kilometers away (BALAZS et al. 1994, PAPI & LUSCHI 1996, LUSCHI et al. 1996), even when swimming directly across water currents (PAPI et al. 1995). Because animals orienting in a chemical plume are seldom able to move directly to the source without employing a search strategy that involves frequent course changes (BAKER 1985, DUSENBERY 1992), the consistency of the headings casts doubt on the hypothesis that turtles follow such plumes over great distances (PAPI et al. 1995, PAPI & LUSCHI 1996).

In addition, turtles in many geographic areas appear to approach their nesting and feeding sites from directions that are seemingly independent of current direction. For example, green turtles that nest at Tortuguero, Costa Rica, apparently converge on their nesting sites from feeding grounds that are both upcurrent and downcurrent (CARR 1984). The same appears to be true for Kemp's ridleys (*Lepidochelys kempi*) that nest at Rancho Nuevo, Mexico (CARR 1963), loggerheads that nest in the United States (MEYLAN et al. 1983) and in South Africa (HUGHES 1995), and green turtles and loggerheads that nest along the Great Barrier Reef (LIMPUS et al. 1992). Oceanographic analyses have also suggested that currents at Ascension Island move eastward during the time when turtles migrate to the island from Brazil (BROWN 1990). If this is true, then an odor plume originating at the island would presumably move toward Africa and could not guide turtles approaching from the west.

Chemical cues and recognition of the natal beach region

Even if chemical cues are not involved in long-distance navigation, they might still enable turtles to recognize a specific nesting area after other navigational mechanisms have brought the turtles into the vicinity. Some limited evidence exists to support this hypothesis, but results are not yet conclusive.

In one study (GRASSMAN et al. 1984), Kemp's ridley turtle eggs from Rancho Nuevo, Mexico, were incubated in sand from Padre Island, Texas, U.S.A. After emerging from their eggs, hatchlings were permitted to crawl across the Padre Island beach and swim through the surf. They were then recaptured and held in captivity for 4 months, after which the turtles were tested in a water-filled arena consisting of four compartments. One contained a solution made from Padre Island sand and sea water, a second contained a similar solution made from sand and sea water from a different location (Galveston, Texas, U.S.A.), and two others contained untreated sea water. The time that turtles spent in each compartment after entering

was monitored, and results indicated that turtles spent significantly more time per entry in the Padre Island compartment than they spent in any of the others.

Although these results are suggestive, all turtles tested in this initial study had been "imprinted" to Padre Island sand and water; no attempt was made to test the responses of turtles that had been similarly "imprinted" to water from another location. Thus, the possibility remained that turtles preferred Padre Island water to the alternatives for reasons unrelated to early experience. A second experiment was therefore carried out to determine whether turtles "imprinted" to either Padre Island or Rancho Nuevo preferred water from their respective natal beaches (GRASSMAN & OWENS 1989). No such preferences could be discerned, but poor health of the turtles may have adversely affected their performance (GRASSMAN & OWENS 1989).

In an additional experiment, GRASSMAN & OWENS (1987) incubated green turtle eggs in sand that was scented with one of two chemicals (morpholine or 2-phenylethanol) that do not exist in the natural habitat. After the eggs hatched, each turtle was held for 3 months in water containing the same chemical to which the turtle had been exposed as an embryo. After 2 additional months without exposure to either chemical, the turtles were tested in a compartmentalized arena containing solutions of morpholine, 2-phenylethanol, and untreated sea water. Turtles that had previously been exposed to morpholine preferred morpholine to 2-phenylethanol, whereas the opposite was true for turtles that had been exposed to the 2-phenylethanol. Interestingly, however, additional groups of turtles that had been exposed to the chemicals only while in the nest (for about 2 months) or only after emerging from the nest (i.e., while living in the water of the holding tank for 3 months) failed to show these preferences.

These results provide additional evidence that turtles can detect chemical cues. Moreover, they demonstrate that, during at least certain developmental periods, turtles can retain the ability to recognize a chemical for at least 2 months. The significance of these findings, however, is not yet clear. Only turtles exposed to the chemicals for about 5 months duration (approximately 2 months in the nest, followed by 3 months in water) acquired the preference. Under natural conditions, hatchlings migrate beyond the waters of their natal beach within a few hours after emerging from their nests (FRICK 1976, IRELAND et al. 1978). Thus, if exposure to the chemical for 3 months after hatching is essential for the response to develop, then it is difficult to envision how such a process could occur during the offshore migration. Nevertheless, the initial results are intriguing, and additional studies are clearly needed.

MAGNETIC NAVIGATION HYPOTHESIS

Hatchling sea turtles possess a magnetic compass sense that enables them to establish and maintain courses relative to the earth's magnetic field (LOHMANN 1991; LIGHT et al. 1993; LOHMANN & LOHMANN 1993, 1994a; GOFF et al. 1998). For animals that migrate long distances, the earth's field provides not only a source of directional information, but a potential source of positional information as well (GOULD 1985, 1998; WILTSCHKO & WILTSCHKO 1995). The possibility therefore exists that turtles can approximate their position within the ocean, and their position relative to a goal, using geomagnetic field features (LOHMANN & LOHMANN 1994b, 1996b, 1998).

Positional information in the earth's magnetic field

Several features of the earth's field vary in a predictable way across the surface of the earth and might, in principle, be used in position-finding (SKILES 1985). For example, at each location on the globe, the geomagnetic field lines intersect the earth's surface at a specific angle of inclination (Fig. 1). Because inclination angles vary with latitude, an animal able to distinguish between different field inclinations might, in principle, determine its approximate latitude.

In addition to inclination angle, at least three other magnetic parameters could hypothetically be used in assessing position (Fig. 1). These include: (1) the intensity (strength) of the total field; (2) the intensity of the horizontal field; (3) the intensity of the vertical field. Additional magnetic features such as declination potentially exist for an animal that can detect geographic north as well as magnetic north (QUINN 1984, GOULD 1985). For sea turtles, however, limited visual abilities probably preclude the use of star patterns and other celestial cues that might conceivably be used to determine geographic north (EHRENFELD & KOCH 1967).

Field parameters at a given location are usually defined in terms of an inclination angle and a total field intensity. Specifying any two of the four parameters listed above, however, defines a local field.

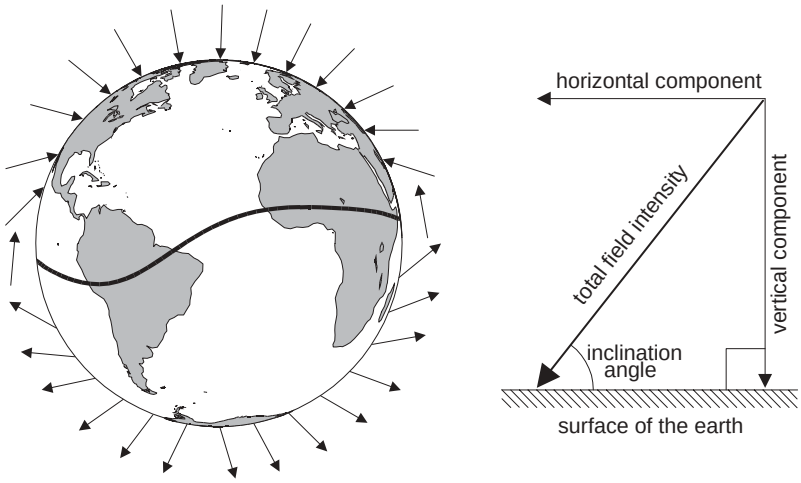

Fig. 1. — Left: Diagram of the earth's magnetic field illustrating how field lines (represented by arrows) intersect the earth's surface, and how inclination angle (the angle formed between the field lines and the earth) varies with latitude. At the magnetic equator (the curving line across the earth), field lines are parallel to the earth's surface and the inclination angle is 0°. An animal migrating north from the magnetic equator to the magnetic pole encounters progressively steeper inclination angles along its journey. At the magnetic pole, field lines are directed straight down into the earth and the inclination angle is 90°.
Right: Diagram illustrating four features of geomagnetic field vectors that might, in principle, provide sea turtles or other long-distance migrants with positional information. The field present at each location on earth can be described in terms of a total field intensity and an inclination angle. The total intensity of the field can be resolved into two vector components: the horizontal field intensity and the vertical field intensity. (Whether animals are able to resolve the total field into vector components, however, is not known).

Migratory route of Florida loggerheads

Hatchling loggerheads from the east coast of Florida, U.S.A., enter the sea and swim from their natal beach to the Gulf Stream current. This offshore migration, however, is just the first step in a much longer transoceanic journey. Young loggerheads evidently remain for at least several years in the North Atlantic gyre, the circular current system that encircles the Sargasso Sea (CARR 1986, HAYS & MARSH 1997). During this time many cross to the eastern side of the Atlantic Ocean (BOLTEN et al. 1994, 1998) before returning to the vicinity of the southeastern United States to take up residence in coastal feeding grounds (CARR 1987, SEARS et al. 1995, MUSICK & LIMPUS 1997).

Young loggerheads in the open sea may benefit from oriented movements that serve to keep them within oceanic regions favorable for growth and development. For example, whereas the warm waters of the Gulf Stream provide a suitable environment for young turtles, straying beyond the latitudinal extremes of the North Atlantic gyre can be fatal. As the northern edge of the gyre approaches Portugal, the east-flowing current divides. The northern branch continues past Great Britain and the water temperature decreases rapidly. Loggerheads swept north in this current soon die from the cold (CARR 1986, 1987; HAYS & MARSH 1997). Similarly, turtles that venture south of the gyre risk being swept into the south Atlantic current system and carried far from their normal range. An ability to recognize the latitudinal extremes of the gyre, and to respond by orienting in an appropriate direction, might therefore have considerable adaptive value.

Detection of magnetic inclination angle

The geomagnetic parameter most strongly correlated with latitude is field line inclination (SKILES 1985). To determine if loggerheads can distinguish between different inclination angles, hatchlings were tethered in a water-filled arena surrounded by a computerized coil system (Fig. 2) that was used to generate earth-strength fields with different inclinations (LOHMANN & LOHMANN 1994b). Hatchlings exposed to a field with an inclination angle found along the northern boundary of the North Atlantic gyre swam south-southwest (Fig. 3). In contrast, hatchlings exposed to an inclination angle found near the southern boundary of the gyre swam in a northeasterly direction (Fig. 3). Turtles exposed to inclination angles they do not normally encounter (i.e., from north or south of the North Atlantic gyre), or to a field inclination found well within the northern and southern extremes of the gyre, were not significantly oriented.

These results demonstrate that loggerheads can distinguish between different magnetic inclination angles. In addition, inclination angles found near the northern and southern gyre boundaries elicited orientation that would, in each case, direct turtles approximately toward the gyre center. The results are therefore consistent with the hypothesis that specific inclination angles in effect warn turtles that they have reached the latitudinal extremes of the gyre and must swim toward the gyre center to avoid straying out of the warm-water current system (LOHMANN & LOHMANN 1994b). For turtles that are safely within the gyre, drifting passively presumably poses no danger of displacement into undesirable areas. The absence of a directional preference among turtles exposed to an inclination angle found near the gyre's latitudinal center is consistent with this interpretation.

Detection of magnetic field intensity

A second geomagnetic feature that varies across the surface of the earth is field intensity. To determine if hatchling loggerheads can perceive differences in intensity that they experience along their migratory route, hatchlings were exposed

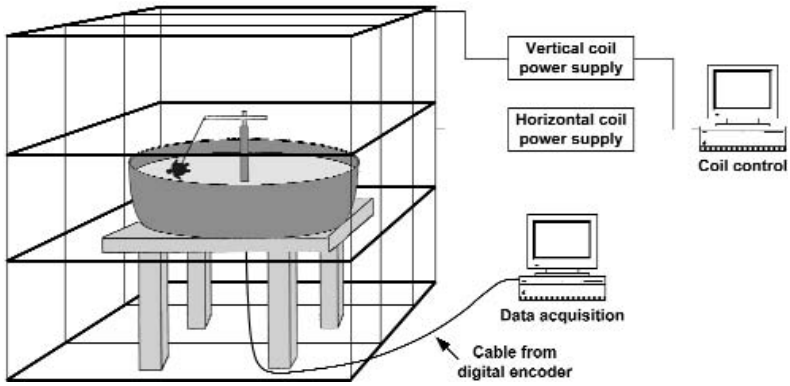

Fig. 2. — Diagram of the orientation arena, magnetic coil system, and data acquisition system used in studies of hatchling responses to magnetic field features (after LOHMANN & LOHMANN 1994b). Each hatchling was tethered to a rotatable lever-arm mounted on a digital encoder (located inside the central post of the orientation arena). The lever arm tracked the direction toward which the turtle swam; signals from the encoder were relayed to the data acquisition computer, which recorded the orientation of the turtle every 10 sec. The arena was enclosed by a magnetic coil system consisting of two different coils arranged orthogonally. One coil controlled the horizontal component of the field while the other controlled the vertical component.

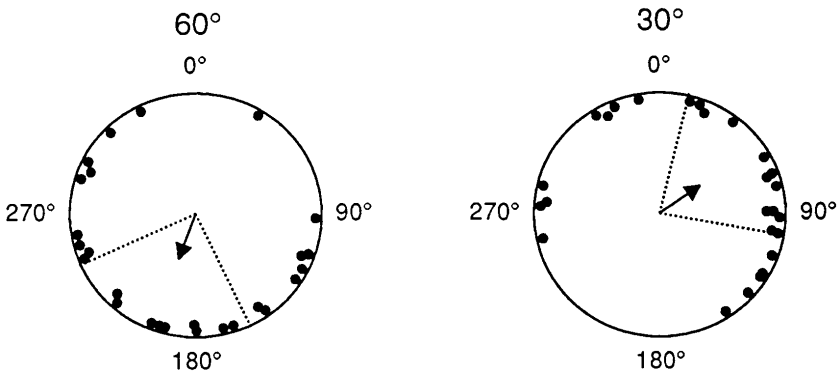

Fig. 3. — Orientation of hatchling loggerheads tested in magnetic fields of the same intensity but different inclinations (data from LOHMANN & LOHMANN 1994b). Turtles exposed to a 60° inclination angle (an angle found near the northern edge of the North Atlantic gyre) were significantly oriented toward the south-southwest, whereas those exposed to an inclination angle of 30° (found near the southern border of the gyre) swam in a northeasterly direction. Dashed lines represent the 95% confidence interval for the mean bearing.

to one of two intensities that they normally encounter during their first months in the sea (LOHMANN & LOHMANN 1996b). The inclination angle of the field was held constant in these trials. Turtles tested in a field of 52,000 nT (a field 10.6% stronger than the natal beach field, and one that hatchlings first encounter near South and North Carolina, USA) swam eastward (Fig. 4). Those exposed to a 43,000 nT field (a field 8.5% weaker than the natal beach field, and one first encountered on the eastern side of the Atlantic near Portugal) swam westward (Fig. 4).

These results demonstrate that hatchlings can distinguish between field intensities that occur in different locations along their migratory route. Moreover, because eastward orientation near South Carolina and westward orientation near

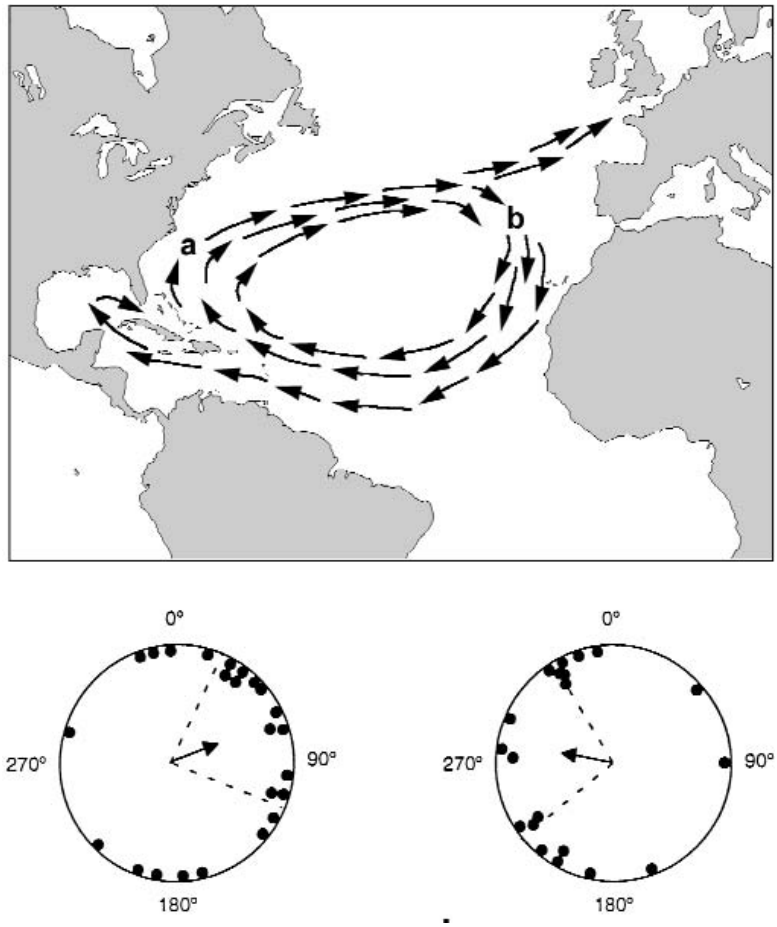

Fig. 4. — Top: Generalized diagram of the North Atlantic gyre (after GROSS 1977, CARR 1986) indicating the only location within the gyre where the field intensity is 52,000 nT (marked by "a") and the location where Florida loggerheads in the gyre presumably first encounter a field intensity of 43,000 nT (marked by "b").
Bottom: Orientation of hatchling loggerheads tested in a magnetic field of 52,000 nT (left) and 43,000 nT (right). Conventions as in Fig. 3. Diagrams are modified from LOHMANN & LOHMANN (1996b).

the coast of Portugal would both function to keep young turtles within the gyre, the results imply that turtles can derive positional information from geomagnetic field features.

Secular variation and responses of hatchlings

In these experiments, hatchlings responded to magnetic field features that they had never before encountered. The responses to such features therefore appear to be fully functional when the turtles first emerge from their nests. Indeed, this may be essential because turtles swept out of the gyre usually die before they can regain entry (Carr 1986, Hays & Marsh 1997). Thus, young turtles probably cannot learn to recognize dangerous geographic areas because entering such regions is in itself fatal.

Although hatchlings evidently respond to specific magnetic features, the field that marks a given location changes gradually over time (Skiles 1985). In light of this secular variation, how can hatchlings respond appropriately to magnetic field features that may differ significantly from those that their ancestors encountered?

One possibility is that strong selective pressure acts to ensure a continuous match between the responses of hatchlings and the field features that exist at any point in time. For example, natural selection presumably removes from the population those young Florida loggerheads that stray out of the gyre, while favoring those with orientation responses that keep them safely inside. As the magnetic values marking the gyre boundaries change, turtles that fail to respond "correctly" to the new field conditions will be quickly eliminated and replaced by other turtles with slightly different responses that enhance the likelihood of survival under the new conditions. In this way, the responses of hatchlings may evolve rapidly to complement the continuously changing field.

Precedents exist for the rapid evolution of similar migratory adaptations. For example, monarch butterflies were introduced into Australia only about a century ago but now have a migration in which the timing and direction are altered by 6 months and 180° relative to the North American population from which they probably descended (James 1993, Brower 1996). Part of the central European population of a migratory bird, the blackcap *Sylvia atricapilla*, evolved a new migration route to the British Isles within only three decades (Berthold et al. 1992). In blackcaps, the direction of first migration appears to be encoded by at most a few genes (Helbig 1991, 1996), and the new route appears to be based on a novel, genetically programmed westnorthwesterly orientation preference that is spreading rapidly through the population (Berthold et al. 1992, Helbig 1996). These examples, and many others (Terrill 1991, Dingle 1996), highlight the evolutionary flexibility of migratory adaptations and the rapidity with which changes in orientation behavior can arise.

Navigation in adult turtles

The movements of hatchlings differ from those of adults in that the destination for young turtles is a large oceanic region rather than a relatively restricted nesting or feeding area. Thus, although hatchlings appear to derive at least some positional information from the earth's field, whether they can navigate with the

same precision as adults is not known. Hatchlings might conceivably emerge from their nests programmed only to swim toward specific directions in response to particular magnetic features found along the migratory route. For example, magnetic parameters along the far northern border of the gyre might elicit southward orientation, whereas features along the southern border of the gyre might elicit northward swimming. Thus, young turtles might remain within a favorable gyre or other oceanic region without possessing the navigational abilities needed to locate specific nesting and feeding areas.

Adult turtles, however, can return to nesting sites following forced displacements (Luschi et al. 1996, Papi et al. 1997). Moreover, adults often follow essentially straight courses both day and night while migrating to specific destinations hundreds of kilometers away (Balazs et al. 1994, Papi et al. 1995, Papi & Luschi 1996). Such precise targeting of specific destinations over immense distances is difficult to explain without hypothesizing an ability to determine geographic position relative to the goal (Gould 1985, Papi et al. 1995, Papi & Luschi 1996, Lohmann et al. 1997).

Although the nature of the sea turtle position-finding system remains unknown, one hypothesis is that adult turtles use geomagnetic field features such as inclination and intensity to assess position during long-distance migrations (Lohmann & Lohmann 1994b, 1996b; Lohmann et al. 1997). Geomagnetic field features could potentially be used by migrating adults in several different ways depending on the navigational task and the nature of the environment. Below we draw on several examples to outline how turtles might, in principle, use inclination and intensity to locate: (1) specific nesting regions along continental coastlines, and (2) isolated islands that serve as rookeries.

Magnetic cues as markers of continental nesting beaches

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

In principle, the ability to detect either inclination angle or intensity could allow turtles to identify a particular area of a continental beach. Inclination angle, in particular, is strongly correlated with latitude; thus, for shorelines running approximately north-south, each beach segment is marked by a unique angle (Lohmann & Lohmann 1994b).

Loggerhead turtles that nest in KwaZulu-Natal, South Africa, provide one example of a population that might plausibly use such a strategy. Most turtles tagged while nesting in this area have been recovered at widely dispersed locations along the African east coast (Hughes 1995), suggesting that many adults in this population undertake migrations that parallel the African coastline for hundreds of kilometers. Four turtles tracked by satellite did indeed swim along the coast as they traveled between their nesting beaches and feeding areas (Papi et al. 1997).

If turtles learn the inclination angle of their home beach as hatchlings, an adult attempting to return to the area might need only to swim along the African

coast until the appropriate angle is encountered (Fig. 5). Such turtles might also assess whether they are north or south of the goal by determining if the inclination angle is smaller or larger than that of the natal beach region. A similar process based on other magnetic features that vary latitudinally (e.g., total intensity, horizontal field intensity, or vertical field intensity) could also hypothetically be used.

Island-finding and bicoordinate magnetic maps

Turtles that nest on small, remote islands cannot follow a coastline until the appropriate destination is reached. However, the ability to perceive two field parameters, such as inclination and intensity, might provide turtles with the sensory abilities necessary to approximate position using a bicoordinate magnetic map (LOHMANN & LOHMANN 1996b). In most oceanic regions, isoclinics (lines of equal field inclination) and isodynamics (lines of equal field intensity) vary in different directions. Thus, each area within an ocean is usually marked by a different combination of magnetic features.

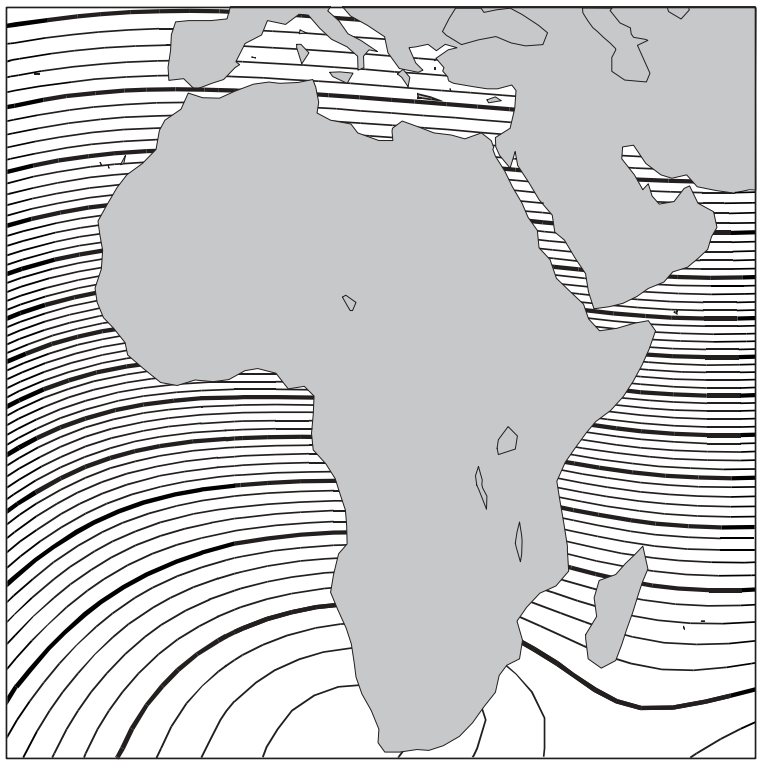

Fig. 5. — Isoclinics along the African coast. Each region of the eastern coastline is marked by a different inclination angle; a similar situation exists for the west coast. Adjacent isoclinics represent differences in inclination of 2°, while dark lines are spaced 10° apart. Isoclinics were derived from the IGRF 1995 model (CAMPBELL 1997) for the year 1995.

The migration of green turtles from the Brazilian coast to Ascension Island provides an example of how a bicoordinate magnetic map might permit navigation over a large oceanic region. Isoclinics and isodynamics form a nonorthogonal grid between South America and Africa, so that all locations between feeding grounds in Brazil and nesting beaches at Ascension Island are defined by unique combinations of inclination and intensity (LOHMANN & LOHMANN 1996b; Fig. 6). A migrating turtle using a bicoordinate map based on these two parameters might therefore be able to approximate its position anywhere along its route, provided it had learned the magnetic features of Ascension and the gradients of inclination and intensity in the South Atlantic.

A similar situation exists at Tromelin Island in the Indian Ocean (Fig. 7). Green turtles tagged while nesting at Tromelin have been recaptured in feeding grounds at various distant islands and along the coast of Madagascar (HUGHES 1995). Because green turtles show great fidelity to both feeding areas and nesting sites (CARR & CARR 1972, LIMPUS et al. 1992), turtles at Tromelin, like those at Ascension, apparently migrate across hundreds of kilometers of open sea to arrive at a tiny, remote island. The isoclinics and isodynamics in this region also form a grid that might, in principle, enable turtles to determine their position relative to the goal (Fig. 7).

Although the Ascension and Tromelin Island examples are useful to illustrate the concept of a bicoordinate map, some elements of these maps cannot be gener-

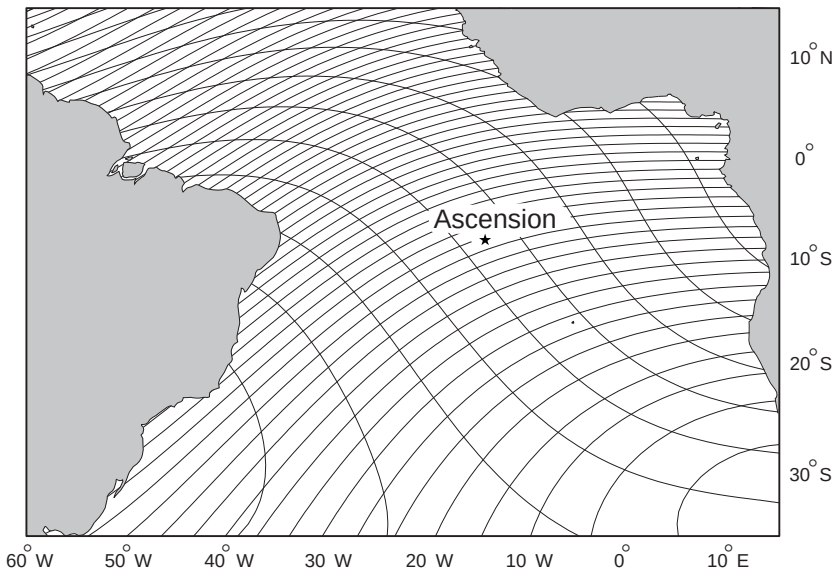

Fig. 6. — Isoclinics and isodynamics in the oceanic region surrounding Ascension Island. Isoclinics in this region are aligned approximately northeast-southwest. Adjacent isoclinics represent differences in inclination of 2°. Isodynamics are aligned approximately northwest-southeast and are shown in increments of 1,000 nT. The two geomagnetic features form a non-orthogonal grid that might, in principle, provide Ascension Island turtles with a bicoordinate position-finding system as they migrate between Ascension and the Brazilian coast. Isoclinics and isodynamics were derived for the year 1995 from the IGRF 1995 model (CAMPBELL 1997).

alized to all locations. In particular, the angle of intersection between isoclinics and isodynamics varies greatly between widely separated geographic areas. Thus, although the two sets of isolines are nearly perpendicular in parts of the south Atlantic (Fig. 6) and Indian Ocean (Fig. 7), this pattern is not universal; the intersection angle is smaller in other oceanic regions such as the North Atlantic and approaches 0° (parallel isolines) in a few locations (LOHMANN & LOHMANN 1996b). Bicoordinate maps based on inclination and intensity may therefore be of variable utility in different parts of the world, and indeed, might be exploited only by populations that inhabit geographic regions with the most favorable grids.

Magnetic features could hypothetically be exploited in several other ways (reviewed by WILTSCHKO & WILTSCHKO 1995, GOULD 1998). For example, field parameters might provide only one coordinate of a bicoordinate map that involves a second, as yet unidentified, cue (PHILLIPS 1996). An interesting navigational model involving total field intensity and the direction of the intensity gradient has also recently been proposed (WALKER 1998).

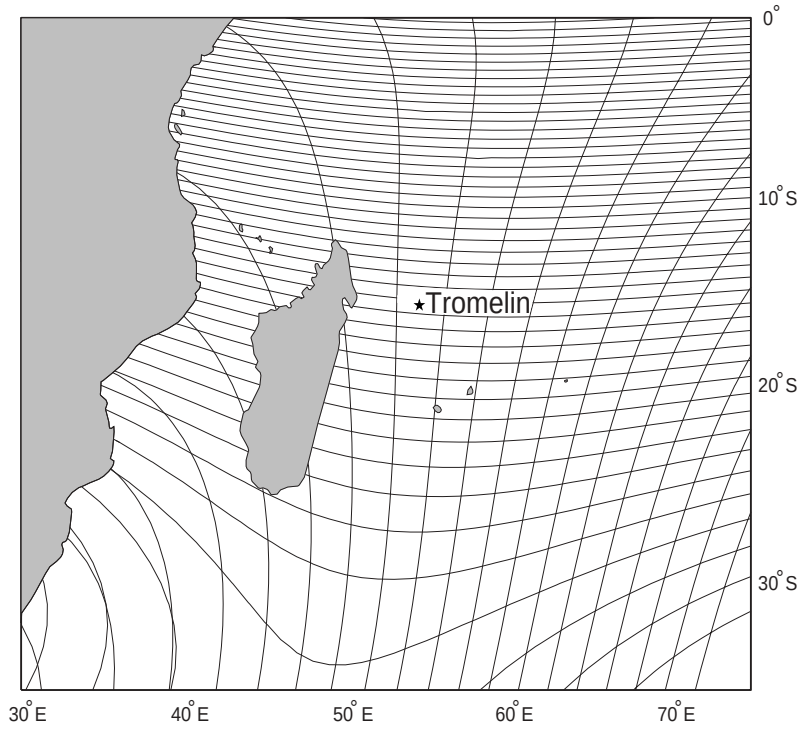

Fig. 7. — Isoclinics and isodynamics in the Indian Ocean surrounding Tromelin Island. Isoclinics run approximately east-west in this region and are shown in 1° contours. Isodynamics run approximately north-south and are represented in 1,000 nT increments. As is the case at Ascension, the two sets of isolines form a nonorthogonal grid that might, in principle, be used in position-finding. Isoclinics and isodynamics were derived for the year 1995 from the IGRF 1995 model (CAMPBELL 1997).

Magnetic imprinting hypothesis

The nesting sites of sea turtles possess certain, specific attributes. For example, the beach must consist of sand rather than rock or mud, and the sand must possess qualities favorable for nest construction and egg incubation (MORTIMER 1990, HENDRICKSON 1995). The area must be free of steep inclines, mangrove frontage, and other insurmountable obstacles that block access from the sea (HENDRICKSON 1958, MORTIMER 1995). Appropriate temperatures for incubation and sex determination are also required (ACKERMAN 1997), as are low densities of egg predators (MORTIMER 1995) and close proximity to ocean currents that can help transport hatchlings to suitable developmental habitats (MUSICK & LIMPUS 1997).

Given this suite of environmental factors, it is clear that nesting areas are created and destroyed rapidly over evolutionary time. Changes in sea level and climate, as well as storms and erosion, quickly render favorable areas unusable and produce suitable sites where none existed previously (HENDRICKSON 1958, BOWEN et al. 1989).

Because nesting areas are ephemeral, positional information specific to particular sites is probably learned by turtles rather than inherited (BOWEN et al. 1989, BOWEN & AVISE 1995). If the critical information involves magnetic features, then inheritance is also effectively precluded by the gradual change in field parameters; the field that exists at a nesting locality at any point in time usually differs from the field that existed there during earlier generations. These considerations imply that if turtles do indeed rely on magnetic features to recognize the natal region, then each turtle must learn the appropriate magnetic features during its lifetime (LOHMANN & LOHMANN 1994b, 1996b, 1998).

One possibility is that turtles imprint on the magnetic features of their natal beach as hatchlings (LOHMANN & LOHMANN 1994b, 1996a). Such a process would enable each turtle to begin its journey with knowledge of the field features that marked its natal region at the time it entered the sea. During its pelagic years a turtle might then learn how the various field parameters vary over a large oceanic region, so that eventually, as an adult, the animal is able to assess its position relative to its natal area.

Such magnetic imprinting, if it occurs, may represent the first of several occasions when a turtle learns the magnetic features that mark a specific location. For example, turtles might subsequently learn the features of feeding areas so that they can return to such sites after reproductive migrations. The flexibility inherent in such a system might also enable turtles to update their knowledge of the features in important areas each time they visit so as to minimize navigational errors that might otherwise accrue from secular variation (LOHMANN & LOHMANN 1998).

Secular variation and natal beach homing

If turtles do indeed imprint on the magnetic features of the natal region, then the change in the geomagnetic field that occurs during a turtle's absence from the area might cause navigational errors during return migrations (LOHMANN & LOHMANN 1998). Whether secular change poses a significant obstacle to magnetic navigation presumably depends on numerous factors, some of which vary greatly between species, populations, and geographic regions. Among critical variables are: (1) the magnetic feature(s) used; (2) the way in which such features are exploited; (3) the nature of the nesting area (e.g., continental coastline or island); (4) the

length of time a turtle is gone from a region; (5) the rate of field change in the critical area; (6) the navigational error represented by the change; (7) whether a turtle can update its knowledge of magnetic features when it returns to a site or region; (8) whether a turtle can estimate secular change or compensate for it; and (9) the distance from which a turtle can locate the target area using nonmagnetic cues.

At present, insufficient data exist to permit a reliable assessment for any situation. Analyses suggest, however, that the effects of secular change should be expected to differ greatly depending on precisely how magnetic features are used and on whether the target areas are along continental coastlines or on islands.

Continental nesting areas and secular change

For loggerheads and other species that nest predominantly on coastlines, potential effects of secular change may be mitigated by the tendency of turtles to return to natal regions rather than to highly specific natal sites. Both the pattern of population genetics and the nesting locations of individual loggerheads suggest that although females return to nest within the general geographic region of their natal beach, they may select nest sites anywhere within a considerable area (RICHARDSON 1982, BJORNDAL et al. 1983, BOWEN & AVISE 1995, MILLER 1997).

If hatchlings learn the magnetic environment of their home region in terms of a specific isoline intersecting the coast (Fig. 5), then the shoreline can function as one coordinate, so that drift in the critical feature results only in the perceived target area moving slightly along the coast in one direction or the other. Under such conditions, the limited field change that typically occurs between the time a turtle leaves an area and when it returns is unlikely to result in a navigational error that displaces the animal beyond its natal region. Indeed, the effect of such drift may be inconsequential if magnetic features near the home beach serve mainly as a landmark to turtles indicating the general area in which to begin searching for either: (i) any suitable nesting site, or (ii) distinctive local cues that permit fine-scale localization of particular nesting locations.

Bicoordinate maps and secular change

Secular variation may impose more significant constraints on the conditions under which bicoordinate magnetic maps can be used (LOHMANN & LOHMANN 1998). In cases of island-finding (e.g., Figs 6-7), a turtle cannot exploit a coastline to reduce the navigational task to one of detecting a single magnetic feature. Thus, the problem of drift is magnified by the change in two features rather than one, and the grid is gradually distorted over time so that the magnetic coordinates that initially marked the island move progressively farther away.

As a first step toward investigating possible effects of secular variation on island-finding, we examined how recent changes in the earth's field at Ascension Island and Tromelin Island might affect attempts to locate each island using a magnetic map. For our analysis we assumed that turtles use a bicoordinate map based on inclination and intensity (e.g., Figs 6 and 7). We further assumed that: (1) search patterns that might assist in locating the island are not used; (2) turtles are unable to compensate for secular change in any way; (3) navigation is based exclusively on the magnetic map (no supplemental, nonmagnetic cues are used).

Although each of these assumptions may be incorrect, the results of this "worst-case" analysis (Fig. 8) illustrate several points. First, considerable differences exist between different geographic regions. The field at Ascension, for example, is presently changing more rapidly than the field at Tromelin. Second, the navigational error that results from secular change over a few years is not large, at least not in the context of transoceanic migrations that may span thousands of kilometers. Thus, a 2 or 3-year absence from a nesting area, as is probably typical for adult female green turtles (CARR 1975, BJORNDAL et al. 1983, MILLER 1997), would result in a navigational error of about 20-30 nautical miles (NM) at Ascension; an identical absence from Tromelin would result in an error of only about 5-10 NM. If adult males return every year to the region for mating, as the males of some populations apparently do (MILLER 1997), then such turtles may encounter even less drift between visits (about 10 NM at Ascension and 3 NM at Tromelin). We conclude that the field change presently occurring between successive migra-

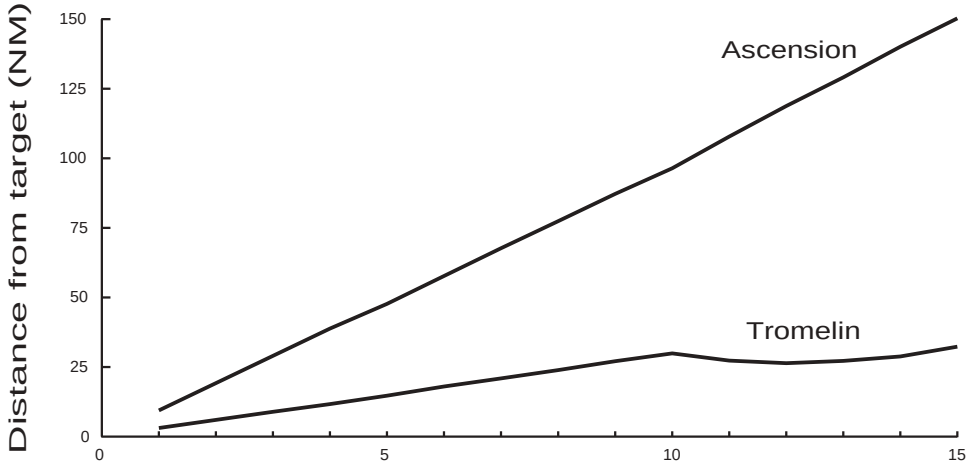

Fig. 8. — Estimates of worst-case navigational error due to secular change at Ascension Island and Tromelin Island. Potential error is graphed as a function of time away from each island; distances are in nautical miles (1 NM = 1.852 km). The analysis assumes that turtles: (1) rely exclusively on a bicoordinate map based on inclination angle and total intensity; (2) are unable to compensate for secular change; (3) do not use search strategies or any nonmagnetic cues to locate the island at the end of the migration; and (4) return to the exact magnetic coordinates that marked the island the last time the turtle was there. To calculate error, we first mapped the magnetic grid that existed around each island in 1995 (Figs 6-7) using the IGRF 1995 model (CAMPBELL 1997). We then used the model to determine the inclination and intensity that marked each island during each previous year back to 1980. The magnetic coordinates (inclination and intensity) for each year were plotted on the 1995 magnetic grid map, and we then measured the distance between each set of coordinates and the position of the island. The error thus represents how far from the island the magnetic coordinates that marked the location at various times between 1980 and 1995 had drifted by 1995. For example, a female turtle that nested at Ascension in 1992 and next returned to the island in 1995 would miss the island by about 25-30 NM if she returned to the magnetic coordinates that marked the island in 1992; a similar 3-year absence from Tromelin Island, however, would result in an error of only about 10 NM.

tions of adult turtles does not appear to preclude using magnetic grid maps in navigation, especially if supplemental cues or search patterns aid turtles in localizing the island at the end of the migration.

Whereas the field change that occurs over 1-3 years may cause little difficulty for adults once they begin making regular reproductive migrations, greater drift may occur during the period of a turtle's life that precedes its first return to the natal region. Little is known about the length of this interval, but it can be considerably less than the time to sexual maturity (SEARS et al. 1995). In addition, great variation probably exists between different populations and species (MUSICK & LIMPUS 1997), so that no generalized assessment can be made of the field change that occurs before a first return migration. For now, we can only conclude that if turtles rely exclusively on bicoordinate maps, and if they cannot compensate for field change, then navigational errors will generally increase with increasing periods away from the natal region (Fig. 8).

Under natural conditions, however, a magnetic map may function as only one part of a repertoire of navigational mechanisms (SALMON & WYNEKEN 1994). Thus, diverse cues or behavioral strategies might normally assist turtles in locating an island at the end of a migration (CARR 1984, LOHMANN et al. 1997). Among potentially useful cues are wave diffraction patterns around an island (LEWIS 1978), pheromones from nesting or mating conspecifics (EHRENFELD & EHRENFELD 1973), chemical cues unique to a natal beach area (GRASSMAN et al. 1984), chemical cues such as dimethyl sulfide that may signal nearby shallow water areas (TURNER & LISS 1985, NEVITT et al. 1995), long-range visual landmarks such as mountains (CARR 1984), and the sounds of waves breaking (MROSOVSKY 1972, LUSCHI et al. 1996). Mechanisms involving interactions with other turtles are also possible (OWENS et al. 1982), inasmuch as turtles that have navigated into the appropriate region for the first time might encounter other members of the population that are migrating to the same goal; thus, following an experienced conspecific at the end of a migration could lead an inexperienced turtle to an appropriate nesting site (HENDRICKSON 1958). Search patterns initiated at the end of a migration might also help a turtle to locate an island, just as searching behavior enables desert ants to overcome accumulated errors and locate a tiny nest entrance at the end of long foraging trips (WEHNER & SRINIVASAN 1981).

We tentatively conclude that, at least under favorable conditions, a turtle absent for even a decade or more could plausibly use magnetic features to navigate into the general vicinity of an island, close enough for local cues to permit final localization of the target. Once the island has been located, such a turtle would presumably need to update its knowledge of the magnetic features and regional grid in preparation for its next migration.

FUTURE DIRECTIONS

Conducting experiments to test hypotheses of open-sea navigation in adult turtles will be challenging. The large size of adults precludes the relatively simple laboratory manipulations that have proven successful with hatchlings. Field experiments are possible, yet the design must take into account the fact that long-distance migrants often exploit multiple cues in orientation and navigation (ABLE 1991, GOULD 1998). Thus, eliminating even a preferred source of information from

the natural habitat may fail to disrupt migratory headings if alternative cues are available (ABLE 1993). These potential pitfalls, along with the relative infrequency of adult migrations and the large distances involved, pose significant logistical and experimental obstacles.

Such difficulties notwithstanding, satellite tracking procedures now provide a possible avenue for experimentation with adults in the natural habitat (LUSCHI et al. 1996, MORREALE et al. 1996, PAPI et al. 1997). The continuing refinement of such tracking may eventually permit rudimentary tests of navigational hypotheses in turtles and other migratory animals (NOWAK & BERTHOLD 1991).

For now, experiments with hatchlings and juveniles have provided a first glimpse into the sensory cues that adult turtles may have at their disposal. How adults navigate across vast expanses of seemingly featureless ocean, however, remains an enduring mystery.

ACKNOWLEDGMENTS

We thank Mike Salmon, Jeanette Wyneken, Bill Irwin, and Larisa Avens for assistance with our research and for their many helpful insights. We are also grateful to Wolfgang Wiltschko, Floriano Papi, and Kimberly Delemos for their comments on earlier drafts of the manuscript. Our research has been supported by grants from the National Science Foundation (IBN 9120338 and IBN 9419993).

REFERENCES

ABLE K.P. 1991. Common themes and variations in animal orientation systems. *American Zoologist* 31: 157-167.

ABLE K.P. 1993. Orientation cues used by migratory birds: a review of cue-conflict experiments. *Trends in Ecology & Evolution* 8 (10): 367-371.

ACKERMAN R.A. 1997. The nest environment and the embryonic development of sea turtles, pp. 83-106. In: Lutz P.L. & Musick J.A., Edits. The biology of sea turtles. *Boca Raton: CRC Press*.

BAKER T.C. 1985. Chemical control of behavior, pp. 621-672. In: Kerkut G.A. & Gilbert L.I., Edits. Comprehensive insect physiology, biochemistry, and pharmacology. *Oxford: Pergamon*.

BALAZS G.H., CRAIG P., WINTON B.R. & MIYA R.K. 1994. Satellite telemetry of green turtles nesting at French Frigate Shoals, Hawaii, and Rose Atoll, American Samoa, pp. 184-187. In: Bjorndal K.A. et al., Edits. *Proceedings of the 14th Annual Symposium on Sea Turtle Biology and Conservation, NOAA Technical Memorandum, NMFS-SEFSC-351*.

BERTHOLD P., HELBIG A.J., MOHR G. & QUERNER U. 1992. Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360: 668-670.

BJORNDAL K.A., MEYLAN A.B. & TURNER B.J. 1983. Sea turtle nesting at Melbourne Beach, Florida, I. Size, growth, and reproductive biology. *Biological Conservation* 26: 65-77.

BOLTEN A.B., BJORNDAL K.A., MARTINS H.R., DELLINGER T., BISCOITO M.J., ENCALADA S.E. & BOWEN B.W. 1998. Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. *Ecological Applications* 8 (1): 1-7.

BOLTEN A.B., MARTINS H.R., BJORNDAL K.A. & GORDON J. 1994. Size distribution of pelagic-stage loggerhead sea turtles (*Caretta caretta*) in the waters around the Azores and Madeira. *Arquipélago* 11A: 49-54.

Bowen B.W., Abreu-Grobois F.A., Balazs G.H., Kamezaki N., Limpus C.J. & Ferl R.J. 1995. Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proceedings of the National Academy of Sciences of the USA* 92: 3731-3734.

Bowen B.W. & Avise J.C. 1995. Conservation genetics of marine turtles, pp. 190-237. In: Avise J.C. & Hamrick J.L., Edits. Conservation genetics: case histories from nature. *New York: Chapman and Hall*.

Bowen B.W., Avise J.C., Richardson J.I., Meylan A.B., Margaritoulis D. & Hopkins-Murphy S.R. 1993. Population structure of loggerhead turtles (*Caretta caretta*) in the northwestern Atlantic Ocean and Mediterranean Sea. *Conservation Biology* 7: 834-844.

Bowen B.W., Kamezaki N., Limpus C.J., Hughes G.R., Meylan A.B. & Avise J.C. 1994. Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. *Evolution* 48: 1820-1828.

Bowen B.W., Meylan A.B. & Avise J.C. 1989. An odyssey of the green turtle: Ascension Island revisited. *Proceedings of the National Academy of Sciences of the USA* 86: 573-576.

Brower L.P. 1996. Monarch butterfly orientation: missing pieces of a magnificent puzzle. *Journal of Experimental Biology* 199: 93-103.

Brown C.W. 1990. The significance of the South Atlantic equatorial countercurrent to the ecology of the green turtle breeding population of Ascension Island. *Journal of Herpetology* 24 (1): 81-84.

Campbell W.H. 1997. Introduction to geomagnetic fields. *Cambridge: Cambridge University Press*.

Carr A. 1963. Orientation problems in the high seas travel and terrestrial movements of marine turtles, pp. 179-193. In: Slater L.E., Edit. Bio-Telemetry. *New York: MacMillan Company*.

Carr A. 1975. The Ascension Island green turtle colony. *Copeia* (3): 547-555.

Carr A. 1984. The sea turtle: so excellent a fishe. *Austin, Texas: University of Texas Press*.

Carr A. 1986. Rips, FADS, and little loggerheads. *Bioscience* 36: 92-100.

Carr A. 1987. New perspectives on the pelagic stage of sea turtle development. *Conservation Biology* 1: 103-121.

Carr A. & Carr M.H. 1972. Site fixity in the Caribbean green turtle. *Ecology* 53 (3): 425-429.

Carr A.F. 1972. The case for long-range chemoreceptive piloting in *Chelonia*, pp. 469-483. In: Galler S.R. et al., Edits. Animal orientation and navigation (NASA SP-262). *Washington, D.C.: Scientific and Technical Information Office, National Aeronautics and Space Administration*.

Carr W.E.S. 1988. The molecular nature of chemical stimuli in the aquatic environment, pp. 3-27. In: Atema J. et al., Edits. Sensory biology of aquatic animals. *New York: Springer-Verlag*.

Dingle H. 1996. Migration. *New York: Oxford University Press*.

Dusenbery D.B. 1992. Sensory ecology. *New York: W.H. Freeman and Company*.

Ehrenfeld J.G. & Ehrenfeld D.W. 1973. Externally secreting glands of freshwater and sea turtles. *Copeia* (2): 305-314.

Ehrenfeld D.W. & Koch A.L. 1967. Visual accommodation in the green turtle. *Science* 155: 827-828.

Frick J. 1976. Orientation and behaviour of hatchling green sea turtles (*Chelonia mydas*) in the sea. *Animal Behaviour* 24: 849-857.

Goff M., Salmon M. & Lohmann K.J. 1998. Hatchling sea turtles use surface waves to establish a magnetic compass direction. *Animal Behaviour* 55: 69-77.

Gould J.L. 1985. Are animal maps magnetic?, pp. 257-268. In: Kirschvink J.L. et al., Edits. Magnetite biomineralization and magnetoreception in organisms. *New York: Plenum Press*.

Gould J.L. 1998. Sensory bases of navigation. *Current Biology* 8: R731-R738.

Grassman M. 1993. Chemosensory orientation behavior in juvenile sea turtles. *Brain, Behavior, and Evolution* 41: 224-228.

Grassman M. & Owens D. 1987. Chemosensory imprinting in juvenile green sea turtles, *Chelonia mydas*. *Animal Behaviour* 35: 929-931.

GRASSMAN M.A. & OWENS D.W. 1982. Development and extinction of food preferences in the loggerhead sea turtle, *Caretta caretta*. *Copeia* (4): 965-969.

GRASSMAN M.A. & OWENS D.W. 1989. A further evaluation of imprinting in Kemp's ridley sea turtle, p. 90. In: Caillouet C.W. Jr & Landry A.M. Jr, Edits. Proceedings of the first international symposium on Kemp's ridley sea turtle biology, conservation and management. *Texas A&M University Sea Grant College Program, TAMU-SG-89-105*.

GRASSMAN M.A., OWENS D.W., MCVEY J.P. & MARQUEZ R.M. 1984. Olfactory-based orientation in artificially imprinted sea turtles. *Science* 224: 83-84.

GROSS M.G. 1977. Oceanography. *Englewood Cliffs, New Jersey: Prentice-Hall, Inc.*

HAYS G.C. & MARSH R. 1997. Estimating the age of juvenile loggerhead sea turtles in the North Atlantic. *Canadian Journal of Zoology* 75: 40-46.

HASLER A.D. & SCHOLZ A.T. 1983. Olfactory imprinting and homing in salmon. *Berlin: Springer.*

HASLER A.D., SCHOLZ A.T. & HORRALL R.M. 1978. Olfactory imprinting and homing in salmon. *American Scientist* 66: 347-355.

HASLER A.D. & WISBY W.J. 1951. Discrimination of stream odors by fishes and relation to parent stream behavior. *The American Naturalist* 85: 223-238.

HELBIG A.J. 1991. Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). *Behavioral Ecology and Sociobiology* 28: 9-12.

HELBIG A.J. 1996. Genetic basis, mode of inheritance and evolutionary changes of migratory directions in palearctic warblers (Aves: Sylviidae). *Journal of Experimental Biology* 199: 49-55.

HENDRICKSON J.R. 1958. The green sea turtle, *Chelonia mydas* (Linn.) in Malaya and Sarawak. *Proceedings of the Zoological Society of London* 130: 455-535.

HENDRICKSON J.R. 1995. Nesting behavior of sea turtles with emphasis on physical and behavioral determinants of nesting success or failure, pp. 53-57. In: Bjorndal K.A., Edit. Biology and conservation of sea turtles (second edition). *Washington, D.C.: Smithsonian Institution Press*.

HUGHES G.R. 1995. Conservation of sea turtles in the southern Africa region, pp. 397-404. In: Bjorndal K.A., Edit. Biology and conservation of sea turtles (second edition). *Washington, D.C.: Smithsonian Institution Press*.

IRELAND L.C., FRICK J.A. & WINGATE D.B. 1978. Nighttime orientation of hatchling green turtles (*Chelonia mydas*) in open ocean, pp. 420-429. In: Schmidt-Koenig K. & Keeton W.T., Edits. Animal migration, navigation, and homing. *New York: Springer-Verlag.*

JAMES D.G. 1993. Migration biology of the monarch butterfly in Australia, pp. 189-200. In: Malcom S.B. & Zalucki M.P., Edits. Biology and conservation of the monarch butterfly. *Los Angeles: Natural History Museum of Los Angeles County.*

KOCH A.L., CARR A. & EHRENFELD D.W. 1969. The problem of open-sea navigation: the migration of the green turtle to Ascension Island. *Journal of Theoretical Biology* 22: 163-179.

LEWIS D. 1978. The voyaging stars: secrets of the Pacific island navigators. *Sydney, Australia: Collins*.

LIGHT P., SALMON M. & LOHMANN K.J. 1993. Geomagnetic orientation of loggerhead sea turtles: evidence for an inclination compass. *Journal of Experimental Biology* 182: 1-10.

LIMPUS C.J., MILLER J.D., PARMENTER C.J., REIMER D., MCLACHLAND N. & WEBB R. 1992. Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildlife Research* 19: 347-358.

LOHMANN K.J. 1991. Magnetic orientation by hatchling loggerhead sea turtles (*Caretta caretta*). *Journal of Experimental Biology* 155: 37-49.

LOHMANN K.J. & LOHMANN C.M.F. 1993. A light-independent magnetic compass in the leatherback sea turtle. *Biological Bulletin* 185: 149-151.

LOHMANN K.J. & LOHMANN C.M.F. 1994a. Acquisition of magnetic directional preference in hatchling loggerhead sea turtles. *Journal of Experimental Biology* 190: 1-8.

LOHMANN K.J. & LOHMANN C.M.F. 1994b. Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *Journal of Experimental Biology* 194: 23-32.

Lohmann K.J. & Lohmann C.M.F. 1996a. Orientation and open-sea navigation in sea turtles. *Journal of Experimental Biology* 199: 73-81.

Lohmann K.J. & Lohmann C.M.F. 1996b. Detection of magnetic field intensity by sea turtles. *Nature* 380: 59-61.

Lohmann K.J. & Lohmann C.M.F. 1998. Migratory guidance mechanisms in marine turtles. *Journal of Avian Biology* 29: 585-596.

Lohmann K.J., Witherington B.E., Lohmann C.M.F. & Salmon M. 1997. Orientation, navigation, and natal beach homing in sea turtles, pp. 107-135. In: Lutz P.L. & Musick J.A., Edits. The biology of sea turtles. *Boca Raton: CRC Press*.

Luschi P., Papi F., Liew H.C., Chan E.H. & Bonadonna F. 1996. Long-distance migration and homing after displacement in the green turtle (*Chelonia mydas*): a satellite tracking study. *Journal of Comparative Physiology (A)* 178: 447-452.

Manton M., Karr A. & Ehrenfeld D.W. 1972a. Chemoreception in the migratory sea turtle, *Chelonia mydas*. *Biological Bulletin* 143: 184-195.

Manton M.L., Karr A. & Ehrenfeld W. 1972b. An operant method for the study of chemoreception in the green turtle, *Chelonia mydas*. *Brain, Behavior, and Evolution* 5: 188-201.

Meylan A.B., Bjorndal K.A. & Turner B.J. 1983. Sea turtles nesting at Melbourne Beach, Florida, II. Post-nesting movements of *Caretta caretta*. *Biological Conservation* 26: 79-90.

Meylan A.B., Bowen B.W. & Avise J.C. 1990. A genetic test of the natal homing versus social facilitation models for green turtle migration. *Science* 248: 724-727.

Miller J.D. 1997. Reproduction in sea turtles, pp. 51-81. In: Lutz P.L. & Musick J.A., Edits. The biology of sea turtles. *Boca Raton: CRC Press*.

Morreale S.J., Standora E.A., Spotila J.R. & Paladino F.V. 1996. Migration corridor for sea turtles. *Nature* 384: 319-320.

Mortimer J.A. 1990. The influence of beach sand characteristics on the nesting behavior and clutch survival of green turtles (*Chelonia mydas*). *Copeia* (3): 802-817.

Mortimer J.A. 1995. Factors influencing beach selection by nesting sea turtles, pp. 45-51. In: Bjorndal K.A., Edit. Biology and conservation of sea turtles (second edition). *Washington, D.C.: Smithsonian Institution Press*.

Mortimer J.A. & Portier K.M. 1989. Reproductive homing and internesting behavior of the green turtle (*Chelonia mydas*) at Ascension Island, South Atlantic Ocean. *Copeia* (4): 962-967.

Mrosovsky N. 1972. Spectrographs of the sounds of leatherback turtles. *Herpetologica* 28: 256-258.

Mrosovsky N. 1983. Conserving sea turtles. *London: British Herpetological Society.*

Musick J.A. & Limpus C.J. 1997. Habitat utilization and migration in juvenile sea turtles, pp. 137-163. In: Lutz P.L. & Musick J.A., Edits. The biology of sea turtles. *Boca Raton: CRC Press*.

Nevitt G.A., Veit R.R. & Kareiva P. 1995. Dimethyl sulfide as a foraging cue for Antarctic Procellariiform seabirds. *Nature* 376: 680-682.

Northcote T.G. 1984. Mechanisms of fish migration in rivers, pp. 317-355. In: McCleave J.D. et al., Edits. Mechanisms of migration in fishes. *New York: Plenum*.

Nowak E. & Berthold P. 1991. Satellite tracking: a new method in orientation research, pp. 307-321. In: Berthold P., Edit. Orientation in birds. *Basel: Birkhäuser Verlag.*

Owens D.W., Grassman M.A. & Hendrickson J.R. 1982. The imprinting hypothesis and sea turtle reproduction. *Herpetologica* 38 (1): 124-135.

Papi F., Liew H.C., Luschi P. & Chan E.H. 1995. Long-range migratory travel of a green turtle tracked by satellite: evidence for navigational ability in the open sea. *Marine Biology* 122: 171-175.

Papi F. & Luschi P. 1996. Pinpointing 'Isla Meta': the case of sea turtles and albatrosses. *Journal of Experimental Biology* 199: 65-71.

Papi F., Luschi P., Crosio E. & Hughes G.R. 1997. Satellite tracking experiments on the navigational ability and migratory behaviour of the loggerhead turtle *Caretta caretta*. *Marine Biology* 129: 215-220.

Phillips J.B. 1996. Magnetic navigation. *Journal of Theoretical Biology* 180: 309-319.

QUINN T.P. 1984. An experimental approach to fish compass and map orientation, pp. 113-123. In: McCleave J.D. et al., Edits. Mechanisms of migration in fishes. *New York: Plenum*.

RICHARDSON J.I. 1982. A population model for adult female loggerhead sea turtles (*Caretta caretta*) nesting in Georgia. *Ph.D. Dissertation, University of Georgia, Athens, Georgia, U.S.A.*

SALMON M. & WYNEKEN J. 1987. Orientation and swimming behavior of hatchling loggerhead turtles (*Caretta caretta* L.) during their offshore migration. *Journal of Experimental Marine Biology and Ecology* 109: 137-153.

SALMON M. & WYNEKEN J. 1994. Orientation by hatchling sea turtles: mechanisms and implications. *Herpetological Natural History* 2 (1): 13-24.

SEARS C.J., BOWEN B.W., CHAPMAN R.W., GALLOWAY S.B., HOPKINS-MURPHY S.R. & WOODLEY C.M. 1995. Demographic composition of the feeding population of juvenile loggerhead sea turtles (*Caretta caretta*) off Charleston, South Carolina: evidence from mitochondrial DNA markers. *Marine Biology* 123: 869-874.

SKILES D.D. 1985. The geomagnetic field: its nature, history, and biological relevance, pp. 43-102. In: Kirschvink J.L. et al., Edits. Magnetite biomineralization and magnetoreception in organisms. *New York: Plenum Press*.

TERRILL S.B. 1991. Evolutionary aspects of orientation and migration in birds, pp. 180-201. In: Berthold P., Edit. Orientation in birds. *Basel: Birkhäuser Verlag*.

TURNER S.M. & LISS P.S. 1985. Measurements of various sulfur gases in a coastal marine environment. *Journal of Atmospheric Chemistry* 2: 223-232.

WALKER M.M. 1998. On a wing and a vector: a model for magnetic navigation by homing pigeons. *Journal of Theoretical Biology* 192: 341-349.

WEHNER R. & SRINIVASAN M.V. 1981. Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *Journal of Comparative Physiology* 142: 315-338.

WILTSCHKO R. & WILTSCHKO W. 1995. Magnetic orientation in animals. *Berlin: Springer*.