
Commentary

Magnetic maps in animals: nature's GPS

Kenneth J. Lohmann*, Catherine M. F. Lohmann and Nathan F. Putman
Department of Biology, University of North Carolina, Chapel Hill, NC 27599 USA

*Author for correspondence (e-mail: klohmann@email.unc.edu)

Accepted 11 July 2007

Summary

Diverse animals detect the Earth's magnetic field and use it as a cue in orientation and navigation. Most research on magnetoreception has focused on the directional or 'compass' information that can be extracted from the Earth's field. Because the field varies predictably across the surface of the globe, however, it also provides a potential source of positional or 'map' information, which some animals use to steer themselves along migratory pathways or to navigate toward specific target areas. The use of magnetic positional information has been demonstrated in several diverse animals including sea turtles, spiny lobsters,

newts and birds, suggesting that such systems are phylogenetically widespread and can function over a wide range of spatial scales. These 'magnetic maps' have not yet been fully characterized. They may be organized in several fundamentally different ways, some of which bear little resemblance to human maps, and they may also be used in conjunction with unconventional navigational strategies.

Key words: magnetic, map, orientation, navigation, magnetoreception, secular variation, sea turtle.

Introduction

Animals exploit numerous sources of information while migrating, homing, or moving around their habitats. Among these, the Earth's magnetic field is a particularly pervasive environmental feature (Skiles, 1985). In contrast with most other cues, the field is present both night and day, is largely unaffected by weather and season, and exists virtually everywhere on the planet, from the deepest ocean trenches to the highest elevations that a bird can fly. Thus, it is perhaps not surprising that diverse organisms, ranging from bacteria to vertebrate animals (Wiltschko and Wiltschko, 1995), have evolved ways to exploit the geomagnetic field to guide their movements.

The Earth's field provides animals with two potential types of information. The simplest of these is directional or compass information, which enables an animal to maintain a consistent heading in a particular direction such as north or south. Magnetic compasses are phylogenetically widespread and exist in several invertebrate groups, as well as in all major groups of vertebrate animals (Wiltschko and Wiltschko, 1995; Wiltschko and Wiltschko, 2005; Johnsen and Lohmann, 2005).

Alone, a compass is often insufficient to guide an animal to a specific destination or to steer it reliably along a long and complex migratory route. For example, a sea turtle migrating through the ocean toward a distant target can be swept off course by currents, and a migratory bird's heading can be altered by wind. Navigation can therefore be enhanced by an ability to determine geographic position. For human navigators, this need

is now usually met by a global positioning system (GPS), which can provide geographic position and, when necessary, compute the direction to a specific goal. For some migratory animals, positional information inherent in the Earth's magnetic field provides a similar, although considerably less precise, way of assessing geographic location. Animals that can derive positional information from the Earth's field (as opposed to directional information) are often said to have a 'magnetic map'.

It is important to recognize that the term 'map', although ingrained in the animal navigation literature, is imprecise and perhaps unfortunate, inasmuch as it connotes specific spatial representations used by humans (Walcott, 1996). In reality, little is known about whether internal spatial representations exist in animals and, if they do, how closely they conform to human concepts of maps (Bennett, 1996). To further complicate matters, no universally accepted definition exists for the term 'map' among animal navigation researchers, and different authors have applied the term in different and sometimes contradictory ways (reviewed by Lohmann and Lohmann, 2006).

Increasingly, however, 'map' has come to be used in a broad and almost metaphorical sense (e.g. Walcott, 1996; Gould, 1998; Mouritsen, 2001; Boles and Lohmann, 2003). In this usage, which we adopt here, the term 'magnetic map' is a convenient shorthand that encompasses all uses of positional information in the Earth's field and makes no assumptions about the nature of the internal spatial representation (if any) that a particular animal has. Thus, the information in a magnetic map

may be inherited or learned, specific or very general, and used for diverse purposes depending on the needs of the animal. A magnetic map might, for example, tell an animal that it has arrived at a point in a migratory route where it should orient westward or that it is approximately north or south of the area where it lives. In sum, an animal has a magnetic map if it uses the Earth's magnetic field as a source of positional information, whereas it has a magnetic compass if it uses the field as a source of directional information. Some animals, of course, have both (Wiltschko and Wiltschko, 2003; Lohmann and Lohmann, 2006).

Positional information in the Earth's field

To a first approximation, the Earth's magnetic field resembles the dipole field of a giant bar magnet (Fig. 1). Field lines leave the southern hemisphere and curve around the globe before re-entering the planet in the northern hemisphere.

Several geomagnetic elements vary in a predictable way across the surface of the Earth (Fig. 1). For example, at each location on the globe, the magnetic field lines intersect the Earth's field at a specific angle of inclination. At the magnetic equator, the field lines are parallel to the Earth's surface and the inclination angle is said to be 0° . The field lines become progressively steeper as one moves toward the magnetic poles; at the poles themselves, the field lines are perpendicular to the Earth's surface. Thus, inclination angle varies predictably with latitude, and an animal able to detect this field element may be able to determine if it is north or south of a particular area.

In addition to inclination angle, at least three other magnetic field elements vary across the Earth's surface in ways that make

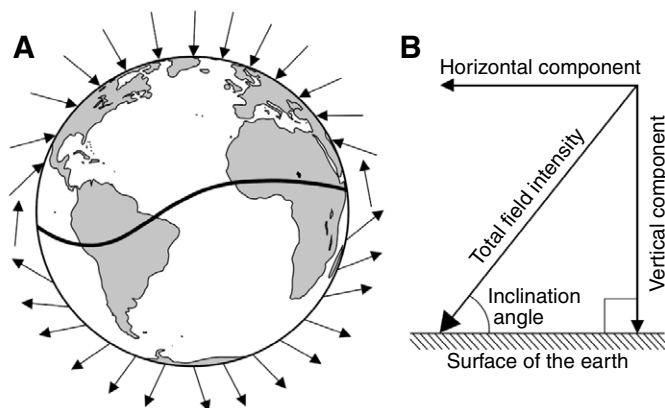


Fig. 1. (A) Diagrammatic representation of the Earth's magnetic field illustrating how field lines (represented by arrows) intersect the Earth's surface, and how inclination angle (the angle formed between the field lines and the Earth) varies with latitude. At the magnetic equator (the curving line across the Earth), field lines are parallel to the Earth's surface. The field lines become progressively steeper as one travels north toward the magnetic pole, where the field lines are directed straight down into the Earth and the inclination angle is 90° . (B) Diagram illustrating four elements of geomagnetic field vectors that might, in principle, provide animals 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.)

them suitable for a position-finding sense (Skiles, 1985; Lohmann and Lohmann, 1999). These include: (1) the intensity (strength) of the total field; (2) the intensity of the horizontal field; (3) the intensity of the vertical field. For animals that can perceive the direction of true geographic north (for example, by using the star patterns to determine the axis of Earth's rotation), additional magnetic parameters such as declination (the difference between true north and magnetic north) are also potential cues.

An important caveat is that fine-scale or local patterns of magnetic field contours are more complex than the general regional patterns because concentrations of magnetic minerals in the Earth's crust often generate local field anomalies (Skiles, 1985). Although these variations are typically less than 1% of the total field, their gradients (i.e. variation per distance) can be significantly greater than the gradients due to the main dipole field, and they can also be aligned in different directions. The larger gradients might be easier for a short-distance migrant or homing animal to detect, but the complexity of local magnetic contours indicates that any navigational strategies that exploit magnetic topography over these smaller spatial scales are likely to be site-specific, difficult to generalize, and learned rather than inherited.

The strength of local anomalies diminishes rapidly with distance from them. Thus, for animals such as sea turtles and migratory birds that travel relatively quickly and which swim or fly considerable distances above geological formations, local anomalies are probably of little consequence in most situations. Such animals can presumably pass rapidly across small anomalous regions, encountering only slight, transient irregularities before re-entering a magnetic environment dominated by the much larger main (dipole) field. Animals that crawl slowly on the surface of the Earth and move only over short distances, however, live in a world in which the crucial magnetic gradients can be influenced greatly by local anomalies. Thus, the spatial scale over which an animal moves, its speed of travel, and its proximity to the Earth's surface are all important factors in evaluating the magnetic environment in which an animal must navigate.

Magnetic maps and migratory pathways

Two animals that undertake long-distance migrations are known to use positional information in the Earth's magnetic field to help them navigate along their migratory pathways. In both cases, magnetic fields specific to particular geographic regions elicit directional changes at crucial points in the route.

Loggerhead sea turtles *Caretta caretta* undergo one of the longest and most spectacular marine migrations. Hatchlings that emerge on beaches along the east coast of Florida, USA, migrate offshore to the North Atlantic gyre, the circular current system that encircles the Sargasso Sea. Young loggerheads remain for several years in the gyre system, during which time many cross to the eastern side of the Atlantic Ocean (Bolten et al., 1998; Bolten, 2003) before returning to the vicinity of the southeastern United States to take up residence in coastal feeding grounds (Sears et al., 1995; Musick and Limpus, 1997).

Experiments with loggerhead hatchlings revealed that they can detect at least two parameters of the Earth's magnetic field: magnetic inclination angle (Lohmann and Lohmann, 1994) and

magnetic field intensity (Lohmann and Lohmann, 1996). Furthermore, when hatchlings were subjected to fields replicating those found in three widely separated locations along the perimeter of the North Atlantic gyre (Lohmann et al., 2001), they responded in ways that appear to have functional significance in the migration. Turtles tested in a magnetic field replicating one that exists offshore near northern Florida swam east-southeast (Fig. 2) whereas those exposed to a field replicating one found near the northeastern edge of the gyre swam approximately south (Fig. 2). Turtles exposed to a field like one found near the southernmost part of the gyre swam west-northwest (Fig. 2). Thus, the results confirmed that loggerhead turtles can distinguish among magnetic fields that exist in widely separated oceanic regions and, moreover, the responses appear likely to keep the turtles within the confines of the gyre and help them advance along the migratory route.

A similar use of magnetic positional information occurs in the pied flycatcher *Ficedula hypoleuca*, a migratory bird that must change direction to avoid ecological barriers. The central European population of pied flycatchers begins its migration by flying southwest to Iberia, after which it changes to a southeasterly course. This two-step migratory pathway enables the birds to skirt the Alps, the Mediterranean Sea, and the central Sahara.

Captive flycatchers exposed to a sequence of magnetic fields approximately matching those they normally encounter while

migrating shifted orientation in the same direction and at the same time as conspecifics during the natural migration (Fig. 3). Such shifts in orientation did not occur in birds maintained in the ambient field at the migration start point, or in birds maintained in a field replicating that at the migratory endpoint. Thus, the results suggest a complex interaction between an endogenous time program and magnetic parameters, in which the birds must apparently experience sequentially the fields of specific locations at the appropriate times in order to orient appropriately at each point in the migration (Beck and Wiltschko, 1988).

In at least one species of bird, magnetic positional information is used in a different way. The thrush nightingale *Luscinia luscinia* migrates south across the Saharan desert, a vast region over which food is seldom available. Birds held in Sweden but exposed to a sequence of regional fields along the migratory route, the last from a location just north of the desert, gained significantly more weight than control birds held under identical conditions but in the local Swedish field (Fransson et al., 2001; Kullberg et al., 2003). Thus, the results imply that either a regional field just north of the Sahara, or a sequence of

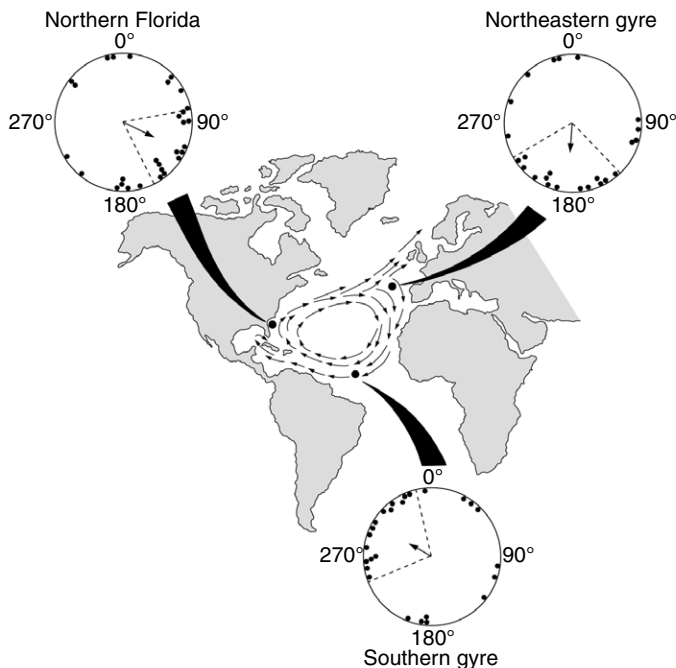


Fig. 2. Orientation of hatchling loggerhead turtles in magnetic fields characteristic of three widely separated locations (marked by black dots on the map) along the migratory route. Generalized main currents of the North Atlantic gyre are represented on the map by arrows. In the orientation diagrams, each dot represents the mean angle of a single hatchling. The arrow in the center of each circle represents the mean angle of the group. Broken lines represent the 95% confidence interval for the mean angle. See text for details. (Modified from Lohmann et al., 2001.)

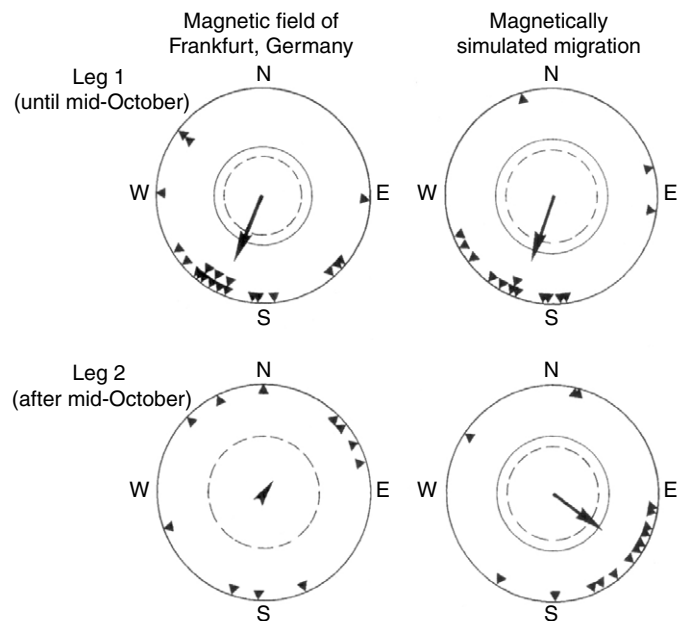


Fig. 3. Orientation of young pied flycatchers held in captivity during the time of their first migration. Results are shown from birds maintained in the magnetic field of Frankfurt, Germany (left), and birds subjected to a sequence of magnetic fields approximately matching those that they encounter along the migratory pathway (right). During the time corresponding to the first leg of the migration (Leg 1), both groups of birds were significantly oriented toward the south-southwest, corresponding with the direction that they initially travel. Only the birds exposed to the magnetically simulated migration, however, adopted appropriate southeasterly orientation during the time corresponding to the second leg of the migration (Leg 2). The arrow in the center of each circle represents the mean angle of the group. Arrows that extend across the first inner circle (dotted line) denote distributions that are significantly oriented at $P < 0.05$, whereas those that extend across the second inner circle (solid line) denote $P < 0.01$. (Modified from Beck and Wiltschko, 1988; Wiltschko and Wiltschko, 2005.)

fields normally encountered during the migration, triggers changes in behavior and physiology that result in the birds accumulating fat needed for their trans-desert flight.

Magnetic maps and target areas

In addition to exploiting magnetic positional information to follow migratory pathways, animals can also use magnetic map information to travel to specific target areas. In this case, they apparently learn the magnetic topography of the areas in which they settle and develop a magnetic map that can be used to facilitate navigation toward specific goals (Lohmann et al., 2004; Lohmann and Lohmann, 2006).

After a period of years in the open ocean, for example, juvenile sea turtles of several species leave the pelagic environment and take up residence in feeding grounds in shallow, coastal regions (Musick and Limpus, 1997). Such turtles often show fidelity to specific foraging areas, returning to them reliably after long, seasonal migrations or experimental displacements (Ireland, 1980; Avens et al., 2003; Avens and Lohmann, 2004). How the turtles return to these foraging areas was investigated using juvenile green turtles *Chelonia mydas* captured in their feeding grounds near the central east coast of Florida. The turtles were placed in an orientation arena near the capture site and exposed to one of two magnetic fields: a field that exists at a location 337 km to the north or one that occurs an equivalent distance to the south. Turtles exposed to the northern field swam southward, whereas those exposed to the southern field swam northward (Fig. 4). Thus, the turtles behaved as if they had been physically displaced to the locations where the magnetic fields exist in nature and were attempting to home from each site.

Magnetic maps are known to exist in at least one other marine animal. The Caribbean spiny lobster *Panulirus argus* is a migratory crustacean found in the waters of the Caribbean and the southeastern United States. *P. argus* is nocturnal and spends the daylight hours within crevices and holes (Herrnkind, 1980). At night the lobsters emerge to forage over a considerable area before returning in darkness to the same den or to one of several

others nearby (Herrnkind and McLean, 1971; Herrnkind, 1980). Early tag and recapture studies (Creaser and Travis, 1950) provided evidence that lobsters are capable of homing after being displaced several kilometers from a capture site. More recent experiments have confirmed that lobsters do indeed orient reliably toward capture areas when displaced to unfamiliar sites, even when deprived of all known orientation cues *en route* (Boles and Lohmann, 2003).

To test the hypothesis that lobsters, like turtles, exploit positional information in the Earth's magnetic field, lobsters were exposed to fields replicating those that exist at specific locations in their environment (Boles and Lohmann, 2003). Lobsters tested in a field that exists north of the capture site oriented southward, whereas those tested in a field like one that exists an equivalent distance to the south oriented northward (Fig. 5). These results closely parallel those obtained with juvenile sea turtles (Fig. 4) and provide strong evidence that spiny lobsters possess a magnetic map that facilitates navigation toward specific geographic areas.

Whereas sea turtles migrate across entire ocean basins and spiny lobsters sometimes traverse distances of up to 200 km (Herrnkind, 1980), a surprising finding is that a magnetic map may also be used by a kind of salamander that never travels farther than a few kilometers. Red-spotted newts *Notophthalmus viridescens* exposed to a magnetic field with an intensity matching that of the home area but an inclination angle found to the north oriented southward, whereas those exposed to an inclination angle found south of their area walked northward (Fischer et al., 2001; Phillips et al., 2002). Thus newts, like sea turtles (Lohmann and Lohmann, 1994), can distinguish among different magnetic inclination angles. Whether they also detect field intensity, as turtles do (Lohmann and Lohmann, 1996), has not yet been determined.

One caveat is that the newt studies involved combinations of inclination and intensity that do not precisely match those that exist in nature. Thus, an important future step will be to determine how newts respond to fields that actually exist in their environment, as has been done with turtles (Lohmann et al.,

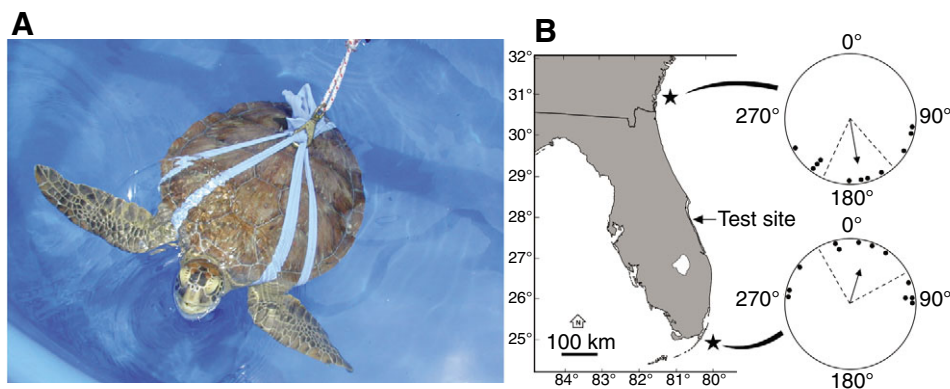


Fig. 4. (A) A juvenile green turtle swimming in a magnetic navigation experiment. Turtles were placed into soft cloth harnesses and tethered to an electronic tracking device that monitored their orientation as they swam in a water-filled arena surrounded by a magnetic coil system (Lohmann et al., 2004). (B) Evidence for a magnetic map in green turtles. Juvenile turtles were captured in feeding grounds near the test site in Melbourne Beach, Florida, USA. Each turtle was exposed to a magnetic field that exists at one of two distant locations along the coastline (represented by stars). Turtles exposed to the field from the northern site swam approximately southward, whereas those exposed to the field from the southern site swam approximately north. Conventions are as in Fig. 2. (Modified from Lohmann et al., 2004.) See text for details.

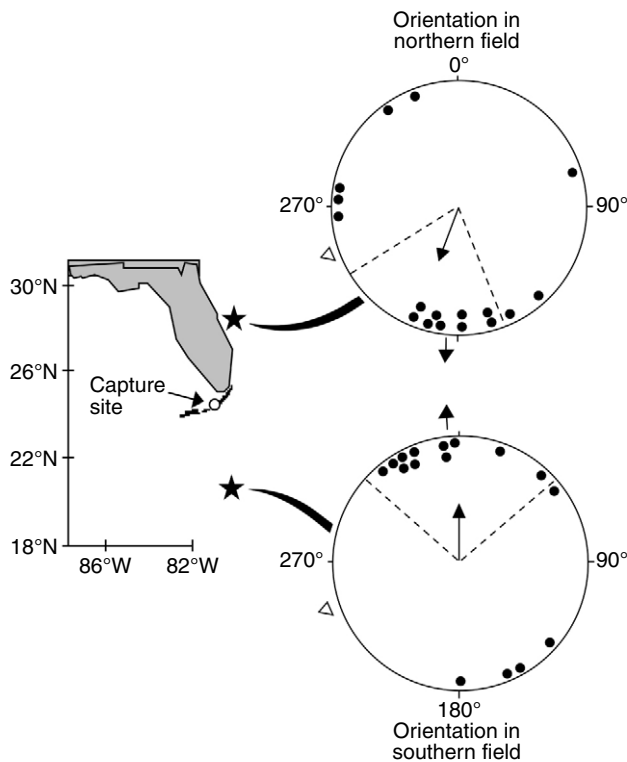


Fig. 5. A magnetic map in spiny lobsters. Lobsters from the middle Florida Keys were subjected to magnetic fields that exist in locations north or south of the location where they were captured. As with juvenile green turtles, lobsters subjected to the field from the northern site oriented approximately southward, whereas those exposed to the field from the southern site crawled approximately north. The open triangle outside each orientation diagram indicates the actual direction to the capture site from the test site. In each case, lobsters responded as if they had been displaced to the locations marked by the stars rather than orienting in the direction that was actually toward the capture site. Conventions are as in Fig. 2. (Modified from Boles and Lohmann, 2003.)

2001; Lohmann et al., 2004) and lobsters (Boles et al., 2003). Nevertheless, the initial results are consistent with the hypothesis that newts derive positional information from the Earth's field, and the existence of magnetic maps in three animals as evolutionarily distant as turtles, lobsters and newts suggest that such maps may be phylogenetically widespread.

Although young migratory birds of some species can derive positional information from the Earth's field during their first migration (e.g. Fig. 3), whether experienced birds use magnetic maps when traveling toward specific targets (in the same way, for example, as juvenile sea turtles; Fig. 4) is not known. Several lines of evidence consistent with magnetic maps in adult birds have been reported, including electrophysiological experiments suggesting high sensitivity to magnetic field intensity (Semm and Beason, 1990), effects of strong pulsed magnetic fields that are thought to affect a navigational map (Munro et al., 1997; Wiltschko and Wiltschko, 2005), and a report that the orientation behavior of a migratory bird was affected by changing the vertical component of the field, a treatment that also alters inclination angle and total intensity (Fischer et al.,

2003; Freake et al., 2006). Further investigation of magnetic maps in adult birds appears likely to be productive.

The possibility that homing pigeons exploit magnetic positional information as a component of their navigational maps has also been discussed for several decades. Evidence consistent with the hypothesis includes data showing increased dispersion when pigeons are released at magnetic anomalies (Walcott, 1978; Gould, 1982), increased dispersion correlated with temporal changes in the field (Keeton et al., 1974), the identification of possible magnetic intensity receptors (Fleissner et al., 2003), and recent analyses suggesting that the flight paths of pigeons are sometimes affected by subtle magnetic contours (Dennis et al., 2007). Opinions among pigeon experts, however, have remained divided (e.g. Gould, 1982; Walker, 1998; Wallraff, 1999; Wallraff, 2005).

Structure of magnetic maps

Although magnetic maps are known to exist in some animals, little is known about their organization, capabilities and limitations. In examining these issues, it is important to recognize that different species use magnetic positional information in different ways; moreover, some animals, such as sea turtles, appear to use magnetic maps in different ways at different life history stages. In addition, a magnetic map should be viewed not as the totality of an animal's navigational ability, but as a single component of a large and integrated suite of mechanisms, each of which can be used or not used depending on circumstances and needs. Having a magnetic map does not compel an animal to use it in all situations, and an animal with such a map is likely to have sufficient alternatives that it may often navigate successfully without using magnetic cues at all. In the same way, possession of a GPS unit does not make its use imperative.

How then, should we envision magnetic maps? How are they organized, what are their capabilities, what magnetic element or elements are involved, and what magnetic navigational strategies do animals use? The answers to these questions are almost entirely unknown. Below we outline just a few possible ways that magnetic maps might be organized.

Bicoordinate magnetic maps

Historically, most discussion of magnetic maps has focused on the possibility that animals detect and exploit two different magnetic field elements, endowing them with a kind of bicoordinate map (e.g. Fig. 6) that enables them to determine their location relative to a goal. There is little doubt that this concept, first suggested more than a century ago (Viguiet, 1882), resonates deeply with researchers in the western world because it parallels so closely our own deeply ingrained spatial system of latitude and longitude. Indeed, there often seems to be an unstated expectation that, if animals exploit bicoordinate maps, then they must process and use them in much the same way that humans do. Animals are often assumed to have a mental image of the map, on which they can place themselves and their destination for the purpose of computing the most direct path between them, in much the same way that we place pins on locations on a paper map and draw a line between them.

This interpretation, however, imposes a rigid human concept of maps onto animals and also requires considerable cognitive

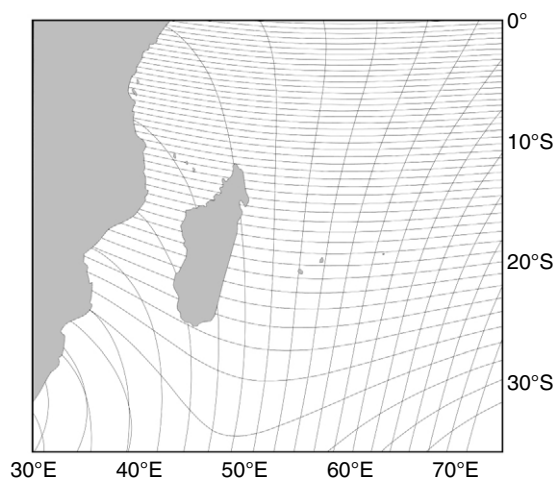


Fig. 6. Isoclinics (lines of equal magnetic inclination) and isodynamics (lines of equal magnetic field intensity) in the Indian Ocean, along the east coast of Africa. Isoclinics run approximately east–west in this region and are shown in 1° contours. Isodynamics run approximately north–south and are represented in 1000 nT increments. Thus, in this geographic area, the two sets of isolines form a nonorthogonal grid that birds, sea turtles, fish or other animals might, in principle, exploit as a kind of bicoordinate magnetic map. Whether any animal does this is not known. (Modified from Lohmann et al., 1999.) Isolines were derived for the year 1995 from the International Geomagnetic Reference Field (IGRF) 1995 model.

and computational skills. A more realistic alternative might be that animals treat a bicoordinate map as two separate magnetic gradients. For example, if an animal knows the magnetic inclination and intensity that exist in a target area and the isolines of these two magnetic parameters are not parallel in the geographic region, then the animal could approach the goal by using first one gradient and then the other in alternating succession. Such a strategy might produce a more meandering path than computing a straightline course, but no mental image and no unusual computational skills would be required.

The possibility of bicoordinate magnetic maps has been discussed in the context of several different animals (e.g. Lohmann and Lohmann, 1996; Phillips, 1996; Gould, 1998). Although the hypothesis remains viable, direct evidence that any animal uses this kind of map has not yet been obtained.

Single-coordinate magnetic maps

In many cases, seemingly difficult feats of navigation can potentially be accomplished with considerably less information than a bicoordinate map requires. Indeed, many specific target areas can be reached if an animal detects only a single magnetic parameter such as inclination or intensity.

The ability of sea turtles to return to specific feeding or nesting locations along continental coastlines is one instance of navigation that hypothetically could be accomplished using only one magnetic parameter (Lohmann and Lohmann, 1994; Lohmann et al., 1999). Many feeding grounds and most major sea turtle rookeries are located on continental coastlines aligned approximately north–south, whereas magnetic isolines in these

areas trend east–west (Fig. 7) (Lohmann et al., 1999). Thus, each area of coastline is marked by a unique inclination angle and intensity, two magnetic elements that hatchling loggerheads are known to detect (Lohmann and Lohmann, 1994; Lohmann and Lohmann, 1996).

If turtles learn the value of a single magnetic element (such as inclination angle or intensity) that exists at a particular coastal location, then returning from a considerable distance away might be relatively easy. The turtle might need only to find the continent, if it is not already there, and then swim north or south along the coastline until the target area is reached and recognized (Lohmann et al., 1999). Moreover, a turtle could determine whether to swim north or south along the coast by comparing the value of the crucial magnetic element at its present location to the remembered value at the target area.

Traveling along an isoline

Under favorable conditions, a single-coordinate strategy can hypothetically be used to locate almost any target area (Lohmann and Lohmann, 2006). To implement the strategy, the animal must know at least one magnetic element (such as intensity or inclination) that exists at the target, so that it can recognize the magnetic isoline on which the target lies. All that is then required is for the animal to adopt a heading that is sufficiently offset to one side or the other of the target so that, when the isoline is intersected, the animal knows which direction to travel along the isoline to intersect the target area (Fig. 8).

A similar strategy of ‘parallel sailing’ was used by mariners at a time when latitude, but not longitude, could be measured (Casey, 1993). Instead of steering directly toward a destination,

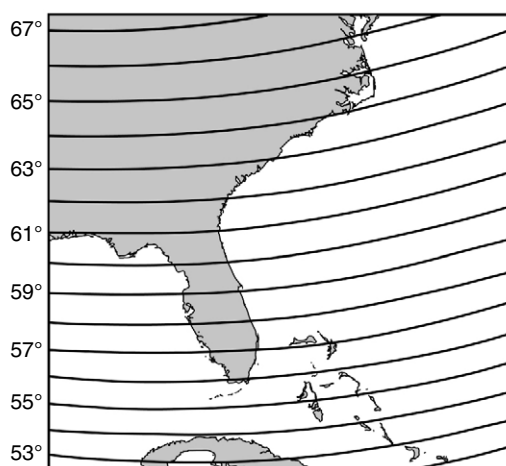


Fig. 7. Map of magnetic field inclination along the southeastern coast of the United States. The isolines represent isoclinics (lines of equal magnetic field inclination). In this part of the world the isoclinics trend east–west, while the coastline is aligned approximately north–south. As a result, each area of coastline along the eastern seaboard is marked by a unique inclination angle. A similar pattern exists for the isolines of total intensity. A sea turtle navigating along the east coast to a particular coastal feeding or nesting area might thus hypothetically do so by detecting a single magnetic element such as inclination or intensity (see text for details).

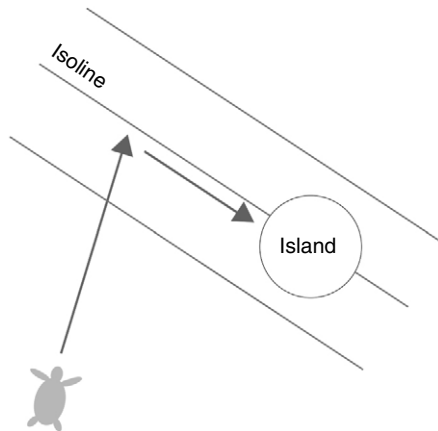


Fig. 8. A possible strategy for locating a specific target area using a single magnetic element such as inclination or intensity, illustrated here with an example of a sea turtle using the strategy to approach an oceanic island. The turtle needs to 'know' the value of one magnetic element at the target and might also need some minimal information about the pattern of isolines in the region. Instead of attempting to steer directly toward the island, the animal swims on a path that is deliberately offset from the target by enough that the turtle will arrive at the appropriate magnetic isoline on a known side of the target. In this example, the turtle adopts a course that takes it well west of the island. Thus, when it arrives at the appropriate isoline, it knows to turn right and swim along the isoline toward the southeast rather than turning left and following the isoline northwest. Because the isoline intersects the target, the turtle locates the goal.

a ship's navigator would chart a course that would cause the ship to arrive at the appropriate latitude either significantly east or west of the target. The ship would then sail along the latitude in the appropriate direction until the destination was reached.

A somewhat similar strategy was proposed to explain how some migratory birds relocate specific areas at the end of a long migration (Mouritsen, 2003). According to this hypothesis, birds migrate north or south until arriving at a particular latitude (as indicated by magnetic or other cues), and then search east and west until the target area is found. This idea can be modified easily to include a deliberate offset; thus, a bird might bias its path so that it arrives at an area that is unambiguously east or west of the goal, and then search along the isoline in the opposite direction to locate the target area. Whether the strategy is used is not known.

Magnetic waymark navigation

Most discussions of magnetic maps have focused on local or regional patterns of isolines, with the expectation that an animal learns the pattern of variation in an area and uses this to assess its position. Yet the responses of hatchling sea turtles and young pied flycatchers to magnetic fields along a migratory route demonstrate that it is possible for evolution to couple directional movements to a regional magnetic field that serves, in effect, as a navigational marker. This suggests the possibility of a fundamentally different magnetic navigational strategy. Instead of learning the pattern of magnetic isolines or the magnetic gradient of an area, an animal might instead respond to specific

fields by orienting in directions that help it advance toward a specific target area or, alternatively, toward another geographic area marked by another field, which in turn elicits a directional response that guides the animal through the next segment of the migration.

The responses of young turtles (Lohmann et al., 2001) and birds (Beck and Wiltschko, 1988) to regional magnetic fields are presumably inherited, inasmuch as the animals responded to the fields the first time they encountered them. Nevertheless, crucial associations between specific fields and particular directions of travel might also be learned in some cases. An interesting possibility is that as animals mature and gain migratory experience, they might learn to recognize magnetic fields associated with a limited number of important locations along their migratory route, including those where changes in migratory direction are required. In effect, the migration might eventually be carried out as a sequence of learned steps, with

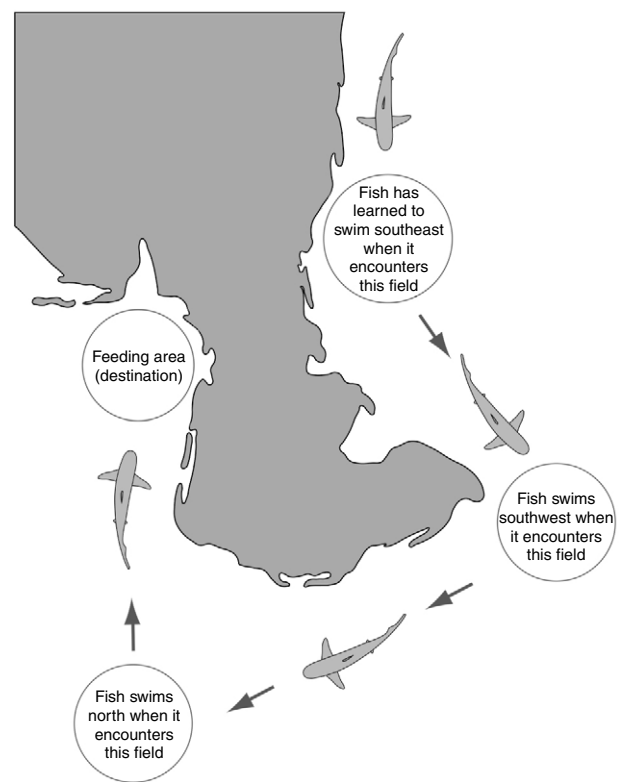


Fig. 9. Strategy for traveling along a complex migratory route using magnetic waymark navigation. In this hypothetical example, a migratory shark has learned to return to a feeding area on the west side of a peninsula. It began life with the ability to perceive magnetic inclination and intensity, as young sea turtles do (Lohmann and Lohmann, 1994; Lohmann and Lohmann, 1996), but as it gained migratory experience, it learned that the easiest way to complete its route is to ignore the regional pattern of isolines and instead change direction at several crucial locations, each marked by a distinctive magnetic field. Eventually, the shark learns to associate each magnetic waymark with a direction of swimming, and the migration is completed as a series of sequential steps, with each magnetic waymark triggering the appropriate direction for the next segment. (In reality, whether sharks can derive positional information from the Earth's field is not known.)

each magnetic waymark triggering the appropriate direction for the next segment of the journey until the goal is reached (Fig. 9). The idea has some parallels in the insect navigation literature, inasmuch as ants and bees can learn to associate compass directions with visual landmarks under some conditions (Collett et al., 1998; Menzel et al., 1998; Giurfa and Capaldi, 1999).

Magnetic maps and secular variation

A potential complication for all strategies of magnetic map navigation is that the Earth's field is not static but instead changes gradually over time. This change in field elements, known as secular variation (Skiles, 1985), means that the magnetic field that exists at a given location will not necessarily remain exactly the same over the life span of a long-lived animal. Similarly, the pattern of isolines throughout a given geographic region gradually changes.

It has been argued that functionally useful responses to specific regional fields, such as those reported in young flycatchers (Beck and Wiltschko, 1988) and sea turtles (Lohmann et al., 2001), are unlikely to evolve because of secular variation (Courtilot et al., 1997). This argument, however, overlooks the evolutionary processes that sculpt behavior as environments change. Although the Earth's field changes over time, strong selective pressure presumably acts to ensure a continuous match between the responses of animals and the fields that mark critical locations in migratory routes at any point in time (Lohmann and Lohmann, 1998; Lohmann et al., 1999; Lohmann et al., 2001). For example, under present conditions in the North Atlantic, natural selection presumably removes from the population those young Florida turtles that stray out of the warm-water 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 while turtles with slightly different responses that enhance the likelihood of survival under the new conditions will persist. Only the genes of the surviving turtles will be passed on, and in this way, the responses of hatchlings may evolve rapidly in parallel with the continuously changing field.

Because numerous factors are involved, the effect that secular variation might have on magnetic map navigation is a complex matter that defies easy answers (Lohmann and Lohmann, 1998; Lohmann et al., 1999; Lohmann and Lohmann, 2003). Secular variation varies greatly among different parts of the world, and whether the drift in field elements poses a problem for an animal in a given situation depends in part on the navigational strategy used, the length of time that the animal lives, and whether the animal inherits magnetic positional information or constantly learns and updates it (Lohmann et al., 1999). The fact that several animals possess functional magnetic maps demonstrates that such potential complications do not prevent animals from exploiting magnetic positional information, yet whether secular variation imposes significant constraints on magnetic navigation in some species or in some parts of the world remains unknown.

No universal magnetic map?

The various hypothetical strategies of magnetic map navigation outlined in the paper are intended to stimulate

thought and represent only a few of many possibilities. The ideas are not mutually exclusive, and it is possible that animals, particularly those that live for many years and range over large geographic areas, are pragmatic and opportunistic in the navigational strategies that they adopt, relying on whatever works to complete a given navigational task in a particular situation and geographic area.

The pattern of variation in magnetic field elements differs greatly among different geographic areas and may profoundly affect what an animal can do with magnetic maps. In some parts of the world, the four magnetic elements shown in Fig. 1 vary in similar directions over the surface of the Earth. In others, the gradients of inclination and intensity are oriented almost perpendicularly (e.g. Fig. 6), so that each location is marked by a unique magnetic field (Lohmann and Lohmann, 1996; Lohmann et al., 1999). Thus, in some areas, an animal might be able to determine position in only one dimension (for example, whether it is north or south of a goal), whereas in others, it might be able to assess its position relative to the goal when on any side of a target area.

A useful parallel can perhaps be drawn between an animal's ability to perceive magnetic fields and our own ability to perceive visual cues. Although nearly all humans possess the physiological ability to perceive visual landmarks, the exact landmarks that we use each day, and the strategies of visual navigation that we employ, are profoundly affected by our experience and what is available in our environment. In the same way, the exact magnetic features that are useful in magnetic maps and the strategies that are followed might differ greatly among different geographic areas. A search for a universal strategy of magnetic map navigation among animals, or even a set of consistent rules within a species, may be as fruitless as a search for a universal set of visual landmarks used by all humans. In each case, what is inherited may be the sensory ability, and exactly how it is used in navigation may depend upon local conditions.

Unraveling the mystery of how magnetic maps are organized, and how animals exploit magnetic positional information to guide their movements, will be a challenging undertaking. Nevertheless, the effort appears likely to provide considerable insight into the age-old enigma of how animals find their way in the world.

We thank Sönke Johnsen and John Wang for stimulating discussions. The research was supported by a grant from the National Science Foundation (IOB-0344387).

References

- Avens, L. and Lohmann, K. J.** (2004). Navigation and seasonal migratory orientation in juvenile sea turtles. *J. Exp. Biol.* **207**, 1771-1778.
- Avens, L., Braun-McNeill, J., Epperly, S. and Lohmann, K. J.** (2003). Site fidelity and homing behavior in juvenile loggerhead sea turtles (*Caretta caretta*). *Mar. Biol.* **143**, 211-220.
- Beck, W. and Wiltschko, W.** (1988). Magnetic factors control the migratory direction of pied flycatchers (*Ficedula hypoleuca* Pallas). *Acta Congr. int. Ornithol.* **19**, 1955-1962.
- Bennett, A. T.** (1996). Do animals have cognitive maps? *J. Exp. Biol.* **199**, 219-224.
- Boles, L. C. and Lohmann, K. J.** (2003). True navigation and magnetic maps in spiny lobsters. *Nature* **421**, 60-63.
- Bolten, A. B.** (2003). Active swimmers – passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic System. In *Loggerhead Sea Turtles* (ed.

- A. B. Bolten and B. E. Witherington), pp. 63-78. Washington, DC: Smithsonian Books.
- Bolten, A. B., Bjørndal, K. A., Martins, H. R., Dellinger, T., Bischoff, M. J., Encalada, S. E. and Bowen, B. W.** (1998). Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. *Ecol. Appl.* **8**, 1-7.
- Casey, E. S.** (1993). *Getting Back into Place: Toward a Renewed Understanding of the Place-World*. Bloomington, IN: Indiana University Press.
- Collett, M., Collett, T. S., Bisch, S. and Wehner, R.** (1998). Local and global vectors in desert ant navigation. *Nature* **394**, 269-272.
- Courtilot, V., Hulot, G., Alexandrescu, M., leMouë, J.-L. and Kirschvink, J. L.** (1997). Sensitivity and evolution of sea turtle magnetoreception: observations, modelling and constraints from geomagnetic secular variation. *Terra Nova* **9**, 203-207.
- Creaser, E. P. and Travis, D.** (1950). Evidence of a homing instinct in the Bermuda spiny lobster. *Science* **112**, 169-170.
- Dennis, T. E., Rayner, M. J. and Walker, M. M.** (2007). Evidence that pigeons orient to geomagnetic intensity during homing. *Proc. Biol. Soc.* **274**, 1153-1158.
- Fischer, J. H., Freake, M. J., Borland, S. C. and Phillips, J. B.** (2001). Evidence for the use of magnetic map information by an amphibian. *Anim. Behav.* **62**, 1-10.
- Fischer, J. H., Munro, U. and Phillips, J. B.** (2003). Magnetic navigation by an avian migrant? In *Avian Migration* (ed. P. Berthold, E. Gwinner, and E. Sonnenschein), pp. 423-432. Berlin: Springer-Verlag.
- Fleissner, G., Holtkamp-Rötzler, E., Hanzlik, M., Winkhofer, M., Fleissner, G., Peterson, N. and Wiltchko, W.** (2003). Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. *J. Comp. Neurol.* **458**, 350-360.
- Fransson, T., Jakobsson, S., Johansson, P., Kullberg, C. and Lind, J.** (2001). Magnetic cues trigger extensive refueling. *Nature* **414**, 35-36.
- Freake, M. J., Muheim, R. and Phillips, J. B.** (2006). Magnetic maps in animals: a theory comes of age? *Quart. Rev. Biol.* **81**, 327-347.
- Giurfa, M. and Capaldi, E. A.** (1999). Vectors, routes, and maps: new discoveries about navigation in insects. *Trends Neurosci.* **22**, 237-242.
- Gould, J. L.** (1982). The map sense of pigeons. *Nature* **296**, 205-211.
- Gould, J. L.** (1998). Sensory bases of navigation. *Curr. Biol.* **8**, R731-R738.
- Herrnkind, W. F.** (1980). Spiny lobsters: patterns of movement. In *Biology and Management of Lobsters. Vol. 1. Physiology and Behavior* (ed. J. S. Cobb and B. F. Phillips), pp. 349-407. New York: Academic Press.
- Herrnkind, W. F. and McLean, R.** (1971). Field studies of homing, mass emigration and orientation in the spiny lobster, *Panulirus argus*. *Ann. N. Y. Acad. Sci.* **188**, 359-377.
- Ireland, L. C.** (1980). Homing behavior of juvenile green turtles, *Chelonia mydas*. In *A Handbook for Biotelemetry and Radio Tracking* (ed. J. Amlaner and D. S. MacDonald) pp. 761-764. Oxford: Pergamon Press.
- Johnsen, S. and Lohmann, K. J.** (2005). The physics and neurobiology of magnetoreception. *Nature Rev. Neurosci.* **6**, 703-712.
- Keeton, W. T., Larkin, T. S. and Windson, D. M.** (1974). Normal fluctuations in the earth's magnetic field influence pigeon orientation. *J. Comp. Physiol. A* **95**, 95-103.
- Kullberg, C., Lind, J., Fransson, T., Jakobsson, S. and Vallin, A.** (2003). Magnetic cues and time of season affect fuel deposition in migratory thrush nightingales (*Luscinia luscinia*). *Proc. R. Soc. Lond.* **270**, 373-378.
- Lohmann, K. J. and Lohmann, C. M. F.** (1994). Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *J. Exp. Biol.* **194**, 23-32.
- Lohmann, K. J. and Lohmann, C. M. F.** (1996). Detection of magnetic field intensity by sea turtles. *Nature* **380**, 59-61.
- Lohmann, K. J. and Lohmann, C. M. F.** (1998). Migratory guidance mechanisms in marine turtles. *J. Avian Biol.* **29**, 585-596.
- Lohmann, K. J. and Lohmann, C. M. F.** (2003). Orientation mechanisms of hatchling loggerheads. In *Loggerhead Sea Turtles* (ed. A. B. Bolten and B. E. Witherington), pp. 44-62. Washington, DC: Smithsonian Books.
- Lohmann, K. J. and Lohmann, C. M. F.** (2006). Sea turtles, lobsters, and oceanic magnetic maps. *Mar. Freshw. Behav. Physiol.* **39**, 49-64.
- Lohmann, K. J., Hester, J. T. and Lohmann, C. M. F.** (1999). Long-distance navigation in sea turtles. *Ethol. Ecol. Evol.* **11**, 1-23.
- Lohmann, K. J., Cain, S. D., Dodge, S. A. and Lohmann, C. M. F.** (2001). Regional magnetic fields as navigational markers for sea turtles. *Science* **294**, 364-366.
- Lohmann, K. J., Lohmann, C. M. F., Ehrhart, L. M., Bagley, D. A. and Swing, T.** (2004). Geomagnetic map used in sea-turtle navigation. *Nature* **428**, 909-910.
- Menzel, R., Geiger, K., Joerges, J., Müller, U. and Chittka, L.** (1998). Bees travel novel homeward routes by integrating separately acquired vector memories. *Anim. Behav.* **55**, 139-152.
- Mouritsen, H.** (2001). Navigation in birds and other animals. *Image Vis. Comput.* **19**, 713-731.
- Mouritsen, H.** (2003). Spatiotemporal orientation strategies of long distance migrants. In *Avian Migration* (ed. P. Berthold, E. Gwinner, and E. Sonnenschein), pp. 493-513. Berlin: Springer-Verlag.
- Munro, U., Munro, J. A., Phillips, J. B., Wiltchko, R. and Wiltchko, W.** (1997). Evidence for a magnetite-based navigational 'map' in birds. *Naturwissenschaften* **84**, 26-28.
- Musick, J. A. and Limpus, C. J.** (1997). Habitat utilization and migration in juvenile sea turtles. In *The Biology of Sea Turtles* (ed. P. L. Lutz and J. A. Musick), pp. 137-163. Boca Raton: CRC Press, Inc.
- Phillips, J. B.** (1996). Magnetic navigation. *J. Theor. Biol.* **180**, 309-319.
- Phillips, J. B., Freake, M. J., Fischer, J. H. and Borland, C. S.** (2002). Behavioral titration of a magnetic map coordinate. *J. Comp. Physiol. A* **188**, 157-160.
- Sears, C. J., Bowen, B. W., Chapman, R. W., Galloway, S. B., Hopkins-Murphy, S. R. and 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. *Mar. Biol.* **123**, 869-874.
- Semm, P. and Beason, R. C.** (1990). Responses to small magnetic variations by the trigeminal system of the bobolink. *Brain Res. Bull.* **25**, 735-740.
- Skiles, D. D.** (1985). The geomagnetic field: its nature, history, and biological relevance. In *Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism* (ed. J. L. Kirschvink, D. S. Jones and B. J. MacFadden), pp. 43-102. New York and London: Plenum Press.
- Viguié, C.** (1882). Le sens de l'orientation et ses organes chez les animaux et chez l'homme. *Rev. Phil. France Etranger* **14**, 1-36.
- Walcott, C.** (1978). Anomalies in the earth's magnetic field increase the scatter of pigeon's vanishing bearings. In *Animal Migration, Navigation, and Homing* (ed. K. Schmidt-Koenig and W. T. Keeton), pp. 143-151. Berlin: Springer-Verlag.
- Walcott, C.** (1996). Pigeon homing: observations, experiments and confusions. *J. Exp. Biol.* **199**, 21-27.
- Walker, M. M.** (1998). On a wing and a vector: a model for magnetic navigation by homing pigeons. *J. Theor. Biol.* **192**, 341-349.
- Wallraff, H. G.** (1999). The magnetic map of homing pigeons: an evergreen phantom. *J. Theor. Biol.* **197**, 265-269.
- Wallraff, H. G.** (2005). *Avian Navigation: Pigeon Homing as a Paradigm*. Berlin: Springer.
- Wiltchko, R. and Wiltchko, W.** (1995). *Magnetic Orientation in Animals*. Berlin: Springer.
- Wiltchko, R. and Wiltchko, W.** (2003). Avian navigation: from historical to modern concepts. *Anim. Behav.* **65**, 257-272.
- Wiltchko, W. and Wiltchko, R.** (2005). Magnetic orientation and magnetoreception in birds and other animals. *J. Comp. Physiol. A* **191**, 675-693.