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Sea Turtles: Navigation and Orientation

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Sea Turtle Life History

Among the sea turtles, orientation and navigation have been studied most thoroughly in loggerhead (*Caretta caretta*) and green turtles (*Chelonia mydas*). These two species have similar life histories and are highly migratory. In the typical case, females lay clutches of 100–150 eggs and bury them in the sand of the nesting beach. After ∼ 2 months, the young turtles hatch below ground and slowly dig their way to the surface. The hatchlings emerge onto the surface of the sand, then scramble to the sea and migrate offshore, where they begin a prolonged period in the open sea, sometimes migrating across entire ocean basins. Later, juveniles recruit to various coastal feeding areas. Adults of most populations also exploit coastal feeding areas and then migrate from the feeding areas to the same breeding area in which they originally hatched.

Many of these migrations depend on the ability of turtles both to orient (i.e., maintain a course in a particular direction) and to navigate (i.e., to determine their position relative to their goal). The cues used for these tasks have been the focus of considerable research during the last 20 years.

Finding the Sea: Use of Visual Cues

When young turtles crawl from their nests, they almost immediately establish courses directly toward the sea. Recent research has confirmed the findings of studies published nearly a century ago: despite emerging at night, hatchlings use visual cues to set and maintain their courses to the sea. Apparently, the turtles are attentive to light levels near the horizon. They crawl toward low bright lights and veer away from dark silhouettes such as the outlines of vegetated dunes. The turtles ignore bright lights from overhead. The result is that, at night, turtles are drawn to the sea, which reflects starlight and moonlight far more than land does. Moreover, they are not often drawn to the brightest nighttime object, the moon, because it is too high in the sky overhead.

This reliance on light cues has undoubtedly served sea turtles well over the course of their 120 My history. On wilderness beaches, they are seldom misoriented toward the land. On beaches shared with modern humans, however, artificial lighting has been a serious problem. As development overtook the beaches of south Florida in the latter twentieth century, young turtles began crawling toward parking lots and tennis courts instead of toward the sea. Caught there at sunrise, the turtles often died from predation and desiccation before they could find their way back to the ocean. Happily, the understanding of their orientation mechanisms has informed conservation efforts throughout the world. In most populated areas, an effort is now made to reduce beach lighting on turtle nesting beaches and the incidence of misoriented hatchlings has declined.

The Offshore Migration

Migration by hatchlings in the ocean has been studied most thoroughly using loggerhead and green turtles from populations found along the Atlantic coast of Florida, USA. For these turtles, the first step of the migration is a journey from the beach out to the Gulf Stream current. This ‘offshore migration’ is accomplished during the first 2 or 3 days after emergence, when the turtles are nourished by yolk reserves and consequently do not feed. At this point in their lives, they are small swimming machines highly motivated to migrate.

Use of Wave Cues in the Ocean

When the ancestral turtles forsook the land and took up life in the sea, new orientation cues became available to them that their terrestrial brethren could not exploit. Among these is the information inherent in wave trains traveling across the ocean surface. The first indication that turtles might use wave cues came in studies of the offshore migration. Hatchlings in a floating orientation arena moored off the Florida coast swam in random directions when the ocean was still, but swam east when waves moved from the east toward the Florida shore. Subsequently, it was shown that when hatchlings first enter the water, they almost always swim into waves – even under unusual weather conditions when waves come from the landward direction.

Various anecdotal observations indicate that hatchlings cease swimming into waves after several hours in the ocean. These observations thus suggest that hatchlings use wave direction as an orientation cue only for a short time after entering the sea. Because waves in shallow water near the shore are refracted until they move nearly straight toward the shore, swimming into the oncoming waves would cause the turtles to orient straight toward the open ocean. This orientation allows turtles to avoid swimming parallel to the beach; instead, they head out to sea and quickly escape the nearshore, predator-filled waters.

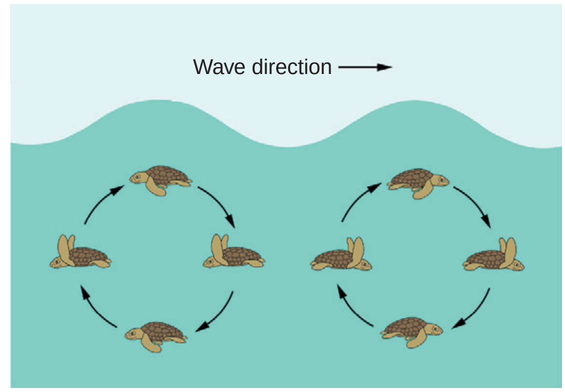

Figure 1 The motion of a hatching turtle swimming with and against the direction of wave propagation. For a hatchling oriented into waves (left), the sequence of accelerations during each wave cycle is upwards, backwards, downwards, and forwards. A turtle swimming with the waves (right) is accelerated upwards, forwards, downwards, and backwards. Modified from Lohmann KJ, Swartz AW, and Lohmann CMF (1995) Perception of ocean wave direction by sea turtles. *Journal of Experimental Biology* 198: 1079–1085.

Detection of Wave Direction

The direction of wave approach is fairly simple for a human to observe visually while standing high above the water in daylight hours. For a small turtle swimming below the surface of the water while migrating in the dark, the problem is more challenging. Under these conditions, wave direction cannot be seen from below, nor is the turtle able to raise its head high enough above the water to see the waves on the surface. In addition, as experiments in a laboratory wave tank demonstrated, turtles can swim into waves even in complete darkness.

Clearly, sight is not used by turtles to determine wave direction. Instead, it appears that turtles are able to monitor the accelerations that occur below the surface as waves pass overhead. Envision a waterlogged cork floating at a depth of a meter or so. When a wave passes through the ocean, the cork will describe a circle as it is accelerated around by the wave, eventually returning to its starting location (oceanographers refer to this as an orbital movement). Now, instead of a cork, imagine a turtle swimming at the same depth. Because the turtle provides its own forward accelerations, it is unlikely that its body will actually describe a circle, but it will feel the same accelerations that move a cork when a wave goes by. Moreover, the sequence of accelerations will appear to differ depending on how the turtle's body is oriented relative to the wave. For example, if the turtle is facing directly into the oncoming wave, the sequence will begin with the turtle perceiving an acceleration going up and back, then down and forward around to the starting point again. In contrast, a turtle swimming away from the wave would perceive a sequence in which it is accelerated upward and forward, then downward and backward around to the starting point (Figure 1).

The hypothesis that hatchling turtles could distinguish between such patterns of orbital movements was tested in experiments that took advantage of the unusual nature of sea turtles. First, turtles are air-breathing reptiles so can be removed from the water allowing all hydrodynamic cues to be eliminated. Second, when suspended in air with flippers no longer in contact with the substrate, hatchlings behave as if in water and attempt to swim. When the suspended turtles were moved in gentle circles similar to those found beneath waves (Figure 2), the turtles responded by attempting to turn in a way that would cause them to experience the same accelerations they would feel if swimming into a wave. For example, when a turtle was subjected to simulated waves from the right, the turtle tried to turn right. Thus, turtles sense wave direction by monitoring the sequence of accelerations they experience beneath waves.

Use of a Magnetic Compass Sense

In some parts of Florida, the Gulf Stream current flows very close to the coastline and turtles can reach it in a few hours; in other areas, the current is several days away. In either case, however, wave cues are insufficient to guide turtles all the way to the Gulf Stream, because the wave refraction zone, where waves proceed directly toward shore, is relatively narrow. Once turtles pass through this zone, waves are no longer a reliable orientation cue.

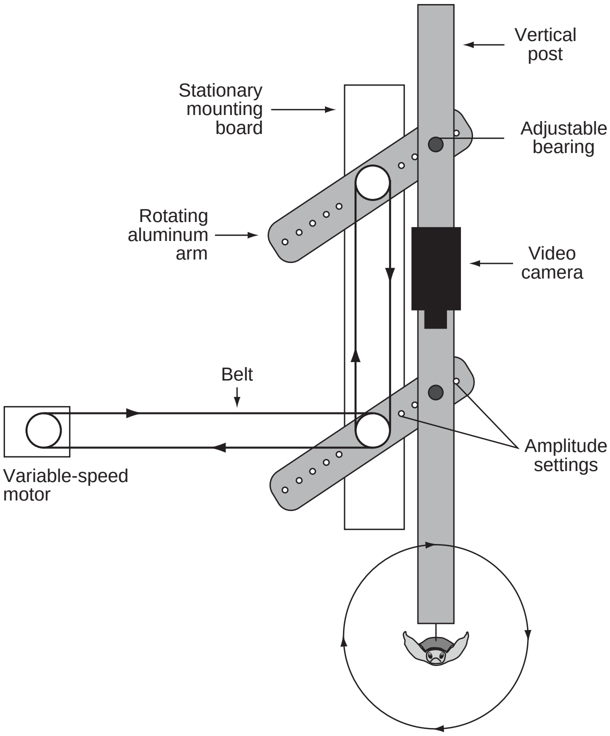

Figure 2 A machine designed to simulate wave motion by reproducing the sequence of accelerations that occur beneath a propagating wave. The responses of hatchling turtles to these simulated waves have been studied by placing turtles into cloth harnesses and subjecting them to orbital movements while they are suspended in air. Modified from Lohmann KJ, Swartz AW, and Lohmann CMF (1995) Perception of ocean wave direction by sea turtles. *Journal of Experimental Biology* 198: 1079–1085.

It seems likely that once beyond the wave refraction zone, turtles rely on their magnetic compass sense. Like other famous navigators (notably migratory birds and homing pigeons), turtles have the ability to sense Earth's magnetic field. This was demonstrated originally in a laboratory orientation arena (**Figure 3**) consisting of a pool of water in which a hatchling could be tethered. When the hatchling swam, it pulled a rotatable tracker arm. The tracker arm was in turn connected to electronics that recorded the direction toward which it was pointing and, by extension, the direction toward which the turtle swam.

The orientation arena was surrounded by a magnetic coil system which, when activated, reversed the magnetic field around the turtle. Thus, the turtle would perceive magnetic north in geographic south and so on. In initial experiments, turtles that swam in the unaltered Earth's field swam to geographic (and magnetic) northeast on average, while those in a reversed field swam to geographic southwest (which was now the new magnetic northeast). Thus, turtles could sense the magnetic field and use it to orient.

Subsequent work has shown that the direction turtles swim in such experiments is not the result of an innate directional preference. Rather, the turtles have the ability to acquire a magnetic preference based on other environmental cues such as the position of a light or the direction of waves. In nature, this flexible system presumably allows turtles to learn the direction of the open ocean from local cues. For example, after swimming eastward into waves, the Florida turtles on the east coast might acquire a directional preference for east and use the magnetic

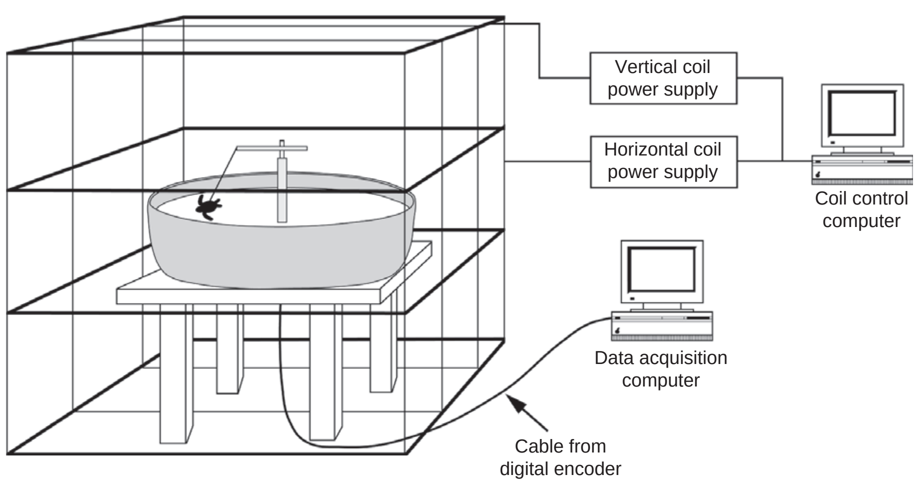

Figure 3 The orientation arena, coil system for generating earth-strength magnetic fields of different inclinations, data acquisition system and coil control system. Each hatchling was tethered to a rotatable arm mounted on a digital encoder (which was inside the central post of the orientation arena). The rotatable arm tracked the direction towards which the turtle swam in darkness. Signals from the digital encoder were relayed to the data acquisition computer. The coil control system regulated current running through the box-like magnetic coil system and was used to create specified magnetic fields inside the volume of the coil. Modified from Lohmann KJ and Lohmann CMF (1994) Detection of magnetic inclination angle by sea turtles: A possible mechanism for determining latitude. *Journal of Experimental Biology* 194: 23–32.

compass to maintain that course, whereas turtles on Florida's west coast might similarly set their magnetic compasses for west and then swim in that direction until reaching the Gulf Stream Current.

The Gyre Migration of North American Loggerheads

Loggerhead turtle hatchlings from the eastern coast of North America migrate offshore and then spend several years in the North Atlantic Gyre. This circular current system flows north along the southeastern United States, arches eastward across the Atlantic, turns south along the northern coast of Africa, and then flows back west toward the Caribbean.

Because small turtles cannot swim fast enough to progress against the current, researchers initially speculated that the turtles drifted passively in the gyre during the many years of their pelagic existence. Recent evidence suggests, however, that the turtles actively guide themselves in the gyre and adjust position to help stay within its confines.

Positional Information in the Earth's Magnetic Field

Human navigators have long known that the Earth's magnetic field provides compass information and the use of a magnetic compass sense by turtles and many other animals is now well-documented. A novel finding that arose largely from work on turtle navigation is that animals can also use the magnetic field to help them determine their position relative to a goal or habitat boundary. The use of positional information is based on the detection of magnetic features that vary more or less regularly across the Earth's surface.

Sea turtles are capable of detecting at least two such features: (1) magnetic intensity or strength, which increases steadily as one moves from the magnetic equator toward the magnetic poles and (2) magnetic inclination angle, which is defined as the angle that magnetic field lines make with the surface of the Earth; this angle becomes steadily steeper as one moves from the magnetic equator toward the poles.

The ability to detect either of these features would theoretically allow a turtle to roughly approximate its latitude. Detecting both might provide turtles with some information about longitude as well, because, while both inclination and intensity vary with latitude, they do so independently. Thus, most locations within an ocean basin have unique combinations of intensity and inclination.

Use of Magnetic Positional Information by Hatchling Turtles: Staying Within the Gyre

In an initial study of magnetic positioning, hatchling turtles were placed into an orientation arena (**Figure 3**) and exposed to several magnetic fields that differed only in inclination; a subsequent study involved fields that differed only in intensity. The swimming orientation of turtles in these magnetic fields clearly demonstrated that the turtles could detect both inclination and intensity. Moreover, the responses, when considered in the context of the hatchling's migratory route, would have had the effect, in nature, of keeping turtle hatchlings from straying out of the gyre. For example, when exposed to an inclination found near the northern edge of the gyre, the turtles swam south, but at an inclination found near the southern border of the gyre, they swam northeast.

In subsequent studies, the coil system was used to produce specific combinations of inclination and intensity that exist at three actual locations around the gyre. In all the three cases, the turtles swam in directions that would keep them within the gyre and progressing along their migratory route (**Figure 4**). It thus appears that hatchlings

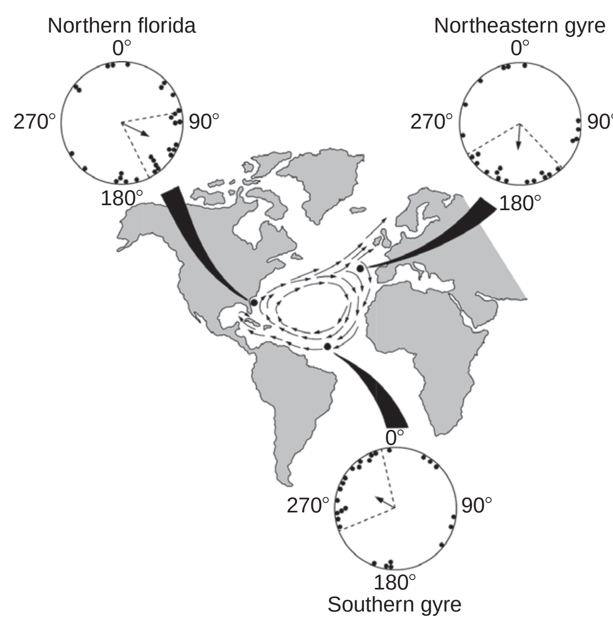

Figure 4 Orientation of hatchling loggerhead turtles in magnetic fields characteristic of three widely separated locations (marked by black dots on the map) along the migratory route. Generalized main currents of the North Atlantic gyre are represented on the map by arrows. In the orientation diagrams, 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. Dashed lines represent the 95% confidence interval for the mean angle. From Lohmann KJ, Cain SD, Dodge SA, and Lohman CMF (2001) Regional magnetic fields as navigational markers for sea turtles. *Science* 294: 364–366. Reprinted with permission from AAAS.

employ a sort of magnetic waymark navigation to circumnavigate the gyre. When they encounter a particular magnetic field, they use it as a waymark that triggers a directional response that keeps them within the appropriate habitat.

Because hatchling turtles in these studies had no prior experience in the ocean, these studies strongly suggest that the turtles emerge from their nests programmed to respond to particular magnetic fields by swimming in certain directions. The possibility that these responses are innate has interesting conservation implications, because it might be that populations of loggerheads from different ocean basins have different inherited responses. If so, then it might be very difficult to reestablish endangered or eradicated populations by bringing in stocks from other areas; these introduced stocks would not possess the correct responses for the local migratory route. The failure to reestablish a nesting population of green turtles in Bermuda with eggs and hatchlings from Costa Rica may be the result of this difficulty.

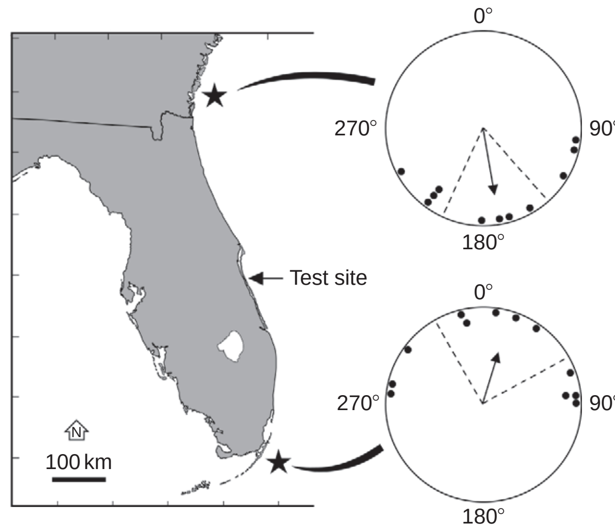

Figure 5 Evidence for a magnetic map in juvenile green turtles. Juvenile turtles were captured in feeding grounds near the test site in Florida, USA. Each turtle was exposed to a magnetic field that exists at one of two distant locations (represented by stars along the coastline). In the orientation diagrams, each dot represents the mean angle of a single turtle. The arrow in the center of each circle represents the mean angle of the group. Dashed lines represent the 95% confidence interval for the mean angle. Modified from Lohmann KJ, Lohmann CMF, Ehrhart LM, et al. (2004) Geomagnetic map used in sea turtle navigation. *Nature* 428: 909–910.

Use of Magnetic Positional Information by Coastal Juveniles: Finding Specific Feeding Sites

After spending several years in the North Atlantic Gyre, young juvenile loggerheads move into coastal areas of the eastern United States and establish neritic feeding areas, to which they show long-lasting fidelity. In the northern part of the loggerhead range, for example, feeding sites are used seasonally. Tag returns indicate that the same individuals return to the same sites in successive years, even after migrating hundreds of kilometers in the interim. In other areas, turtles have been displaced from harbors to allow for dredging and other human activities, and the same turtles have subsequently returned to those areas.

These returns suggest an ability to navigate back to specific locations. Additionally, it seems unlikely that use of specific feeding sites is genetically programmed; rather, one would expect site selection on the basis of local conditions (i.e., food abundance and availability of shelter) that can easily change in response to storms. Thus, fidelity to particular feeding sites is unlikely to be based on innate responses. Instead, it appears that juvenile turtles learn the locations of their favored sites and can return to them from long distances.

The process of long-distance navigation in the ocean probably consists of two basic steps. To reach a specific site, turtles must first use long-range cues to guide themselves across the ocean and arrive in the general area. Then short-range cues might be used to identify the exact location. In sea turtles, the short-range cues have not been studied extensively, though visual, olfactory, auditory, and even wave cues are all possibilities. For the long-range cues, evidence suggests that sea turtles use magnetic maps based on inclination and intensity.

The pivotal experiment on magnetic maps was performed in Melbourne Beach, Florida, using juvenile green turtles with feeding sites roughly 100 m from the shore. These turtles were collected, brought to an onshore facility a few kilometers away, and placed in an orientation arena similar to that used for hatchlings except that it was much larger to accommodate the significantly larger size of the juveniles. When in the arena, the turtles were exposed to one of two magnetic fields: either the inclination and intensity of a location ~340 km to the north of the test site or the inclination and intensity of a location ~340 km south of the test site. Turtles exposed to the northern field swam south, whereas those exposed to the southern field swam north (**Figure 5**). Because the only difference between the two treatments was the magnetic field in the arena, the turtles were clearly detecting and responding to those fields. Moreover, the turtles behaved as if they had been displaced and were attempting to return to their feeding areas, apparently using magnetic positional information to determine whether they were north or south of their goal.

These results suggest that juvenile turtles have what is, in essence, a magnetic map. They have the ability to detect and remember magnetic features of their feeding grounds and have learned how these features vary across the surface of the Earth. When presented with a new set of magnetic features replicating a new location, they can determine where they are relative to their goal.

Use of Magnetic Positional Information by Adult Sea Turtles: Natal Homing

Like the juvenile turtles, adult turtles show fidelity to specific feeding sites. Males regularly migrate between these sites and courtship sites. Females migrate between feeding sites, courtship sites, and nesting beaches. Tagging studies indicate that females display fidelity to specific nesting beaches, sometimes returning to nest within just a few kilometers of their nest sites from previous years.

Recent genetic studies have confirmed an even more surprising ability. Apparently, sea turtles tend to nest in the same regions in which they themselves hatched. This behavior of natal homing is so strong that, for example, the population of loggerheads that nests in south Florida is genetically distinct from that nesting in north Florida.

How turtles accomplish natal homing is not known. It appears, however, that the task can be considered a special instance of long-distance ocean navigation. Thus, the turtle may first use long-range cues to navigate into the general location of the natal beach, and then use local, short-range cues to identify the appropriate nesting site. It seems likely that the initial long-range step is accomplished magnetically, and shorter-range navigation relies on other cues.

Recent evidence indicating the use of magnetic cues by adult turtles involves an experiment in which female turtles were displaced away from an island nesting beach. Some individuals were fitted with magnets that disrupted the ambient magnetic field and their homing ability was compared with controls fitted with nonmagnetic brass bars. The magnetically disrupted turtles found the nesting beach but took longer to do so and followed far less direct routes than controls. These results suggest that magnetic cues are indeed used by swimming turtles to find their nesting beach – but how do the turtles know which nesting beach is theirs?

The unique challenge in natal homing is that a turtle must quickly acquire, at a very young age, sufficient information that it can recognize its home region and return to it years later. One possible way that turtles might accomplish this task involves imprinting on the magnetic features of the natal area. If hatchlings detect and memorize the magnetic features of their home area – perhaps during the offshore migration, or even while in the nest – then as adults, turtles can potentially use their magnetic map sense to locate the general region of the natal beach.

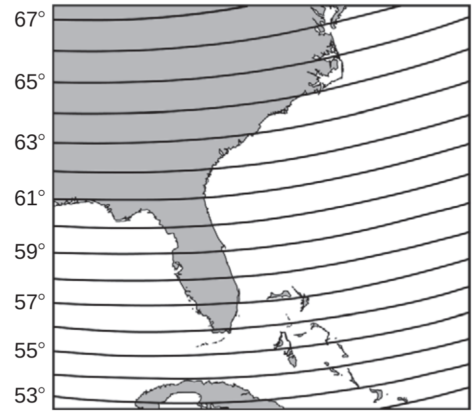

Figure 6 Diagram of southeastern United States with isoclinics (lines of equal magnetic inclination). The scale on the right shows the inclination angles in degrees. Each isoclinic intersects the Atlantic coastline only once; thus each area of coast is marked by a unique inclination angle.

Many major nesting beaches are located on continental shorelines aligned approximately north to south and in geographic areas where magnetic intensity and inclination also vary in a north–south direction. In such regions, different areas along the coastlines have unique magnetic signatures (Figure 6). A turtle could theoretically swim along the coastline until it finds a remembered magnetic intensity or inclination, or perhaps combination of the two, and then search until appropriate nesting habitat is discovered.

Not all nesting beaches are continental; some cases of turtle navigation involve navigation to remote, island nesting sites. It is interesting to note that these may be special cases of the more general process. For instance, a Brazilian population of green turtles nests on tiny Ascension Island, some 2000 km away from the Brazilian coast. To all appearances, gravid females find the 8-km long island with amazing pinpoint accuracy, far more accurate than what one would expect using a magnetic map. In this case, it seems likely that turtles use magnetic map information to arrive in the area of Ascension and then use local cues to find a nesting beach. Because the only suitable beaches in the area are the beaches of Ascension, all of the turtles eventually find and nest on the same tiny piece of land.

One difficulty with the hypothesis of magnetic imprinting of natal homing information is its potential vulnerability to problems with magnetic drift (secular variation). The magnetic field changes slightly each year and most species take 10–40 years to reach maturity; during this time, the field in the natal areas may change. If they relied solely on magnetic fields to find their nesting beaches, turtles might arrive many kilometers from their goals. Recent calculations suggest, however, that turtles in many geographic areas arrive within a region where short-range cues are available for use in identifying appropriate nesting sites. Kemp's ridley turtles, for example, nest in large aggregations on a 160 km beach near Rancho Nuevo, Mexico. If a turtle imprinted on the magnetic inclination at the center of that beach, calculations show that it would return to a location several kilometers away but usually within the limits of the nesting beach.

Future Directions

During the past two decades, tremendous progress has been made in unraveling the mechanisms that underlie orientation and navigation in sea turtles. Many questions remain unanswered. How do sea turtles sense the magnetic field? Do hatchlings indeed imprint on the magnetic field of their home beaches? What local cues are used to identify precise locations? What population differences exist? Nonetheless, the rapid progress in this field has provided a window into the world of one of the most remarkable animal navigators.

See also: Magnetic Orientation in Migratory Songbirds; Pigeon Homing as a Model Case of Goal-Oriented Navigation.

Further Reading

Bolten AB and Witherington BE (eds.) (2003) *Loggerhead Sea Turtles.* Washington, DC: Smithsonian Institution Press.
Carr AF (1979) *The Windward Road: Adventures of a Naturalist on Remote Caribbean Shores.* Tallahassee, FL: University Presses of Florida.
Carr AF (1986) *The Sea Turtle – So Excellent a Fishe.* Austin, TX: University of Texas Press.
Johnsen S and Lohmann KJ (2005) The physics and neurobiology of magnetoreception. *Nature Reviews Neuroscience* 6: 703–712.
Lohmann CMF and Lohmann KJ (2006) Quick guide to sea turtles. *Current Biology* 16(18): R784–R786.
Lohmann KJ, Cain SD, Dodge SA, and Lohmann CMF (2001) Regional magnetic fields as navigational markers for sea turtles. *Science* 294: 364–366.
Lohmann KJ and Lohmann CMF (1994) Detection of magnetic inclination angle by sea turtles: A possible mechanism for determining latitude. *Journal of Experimental Biology* 194: 23–32.
Lohmann KJ, Lohmann CMF, Ehrhart LM, et al. (2004) Geomagnetic map used in sea turtle navigation. *Nature* 428: 909–910.
Lohmann KJ, Lohmann CMF, and Endres CS (2008) The sensory ecology of ocean navigation. *Journal of Experimental Biology* 211: 1719–1728.
Lohmann KJ, Putman NF, and Lohmann CMF (2008) Geomagnetic imprinting: A unifying hypothesis of natal homing in salmon and sea turtles. *Proceedings of the National Academy of Sciences of the United States of America* 105: 19096–19101.
Lohmann KJ, Swartz AW, and Lohmann CMF (1995) Perception of ocean wave direction by sea turtles. *Journal of Experimental Biology* 198: 1079–1085.
Luschi P, Benhamou S, Girard C, et al. (2007) Marine turtles use geomagnetic cues during open-sea homing. *Current Biology* 17(2): 126–133.
Lutz PL and Musick J (eds.) (1997) *The Biology of Sea Turtles.* Boca Raton, FL: CRC Press.
Putman NF and Lohmann KJ (2008) Compatibility of magnetic imprinting and secular variation. *Current Biology* 18(14): R596–R597.
Spotila JR (2004) *Sea Turtles: A Complete Guide to Their Biology, Behavior, and Conservation.* Baltimore, MD: Johns Hopkins University Press.

Relevant Websites

http://www.unc.edu/depts/oceanweb/turtles/ – Sea Turtle Navigation.
http://www.seaturtle.org – Global Sea Turtle Network.