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ORIENTATION AND OPEN-SEA NAVIGATION IN SEA TURTLES

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Summary

Loggerhead sea turtle hatchlings (*Caretta caretta* L.) emerge from underground nests, scramble to the sea and begin a transoceanic migration by swimming away from their natal beach and into the open ocean. Evidence suggests that hatchlings sequentially use three different sets of cues to maintain orientation during their initial migration offshore. While on the beach, hatchlings find the ocean by crawling towards the lower, brighter seaward horizon and away from the dark, elevated silhouettes of vegetation and dunes. Upon entering the ocean, turtles initially orient seawards by swimming into waves, which can be detected as orbital movements from under water.

Laboratory experiments have demonstrated that turtles can transfer a course initiated on the basis of waves or visual cues to a course mediated by a magnetic compass. Thus, by setting a magnetic course on the basis of nearshore cues that indicate the seaward direction, hatchlings may continue on offshore headings after entering deep water beyond sight of land.

Sea turtles may use the earth's magnetic field not only as a cue for compass orientation but also as a source of world-wide positional information. Recent experiments have demonstrated that loggerheads can detect subtle differences in magnetic field inclination and intensity, two geomagnetic features that vary across the surface of the earth. Because most nesting beaches and oceanic regions are marked by a unique combination of these features, these findings raise the possibility that adult sea turtles navigate using a bicoordinate magnetic map.

Key words: orientation, navigation, waves, magnetic, magnetoreception, sea turtle, *Caretta caretta, Chelonia mydas.*

Introduction

The long-distance migrations of sea turtles involve some of the most remarkable feats of orientation and navigation in the animal kingdom. As hatchlings, turtles that have never before been in the ocean establish unerring courses towards the open sea as soon as they enter the water and then maintain their headings after swimming beyond sight of land. Adult turtles of several species migrate across hundreds or thousands of kilometers of open ocean to nest on their natal beaches, which are often isolated stretches of continental shores or tiny, remote islands. Such impressive feats are all the more astonishing in view of the fact that they are accomplished in an open-ocean environment devoid of visual landmarks and by marine animals whose poor eyesight above water (Ehrenfeld and Koch, 1967) probably precludes the use of star patterns and other celestial cues.

Like the hatchlings of other sea turtle species, loggerhead hatchlings (*Caretta caretta* L.) embark on a long-distance migration immediately after emerging from their nests. Hatchlings from the east coast of Florida, USA, migrate into the Gulf Stream current and the North Atlantic gyre (Carr, 1987). As the turtles grow, they remain in the gyre for a period of years before eventually returning to the southeastern United States coast (Carr, 1986). Later, as adults, the females migrate back to their natal beaches to nest (Bowen *et al.* 1993, 1994, 1995).

The initial offshore migration, in which hatchlings swim from the east coast of Florida to the Gulf Stream current, has provided a convenient starting point for investigating orientation mechanisms in sea turtles (Lohmann, 1992; Salmon and Wyneken, 1993). Analysis of this migration has not only revealed the cues that hatchlings use but has also provided insight into the sensory abilities that adults may have available for navigation. In this paper, we begin by summarizing the cues that guide the offshore migration of hatchlings and conclude with results suggesting that sea turtles use features of the earth's magnetic field in global position-finding and perhaps in navigation.

Orientation of hatchlings on the beach: finding the sea

Hatchlings nearly always emerge from their nests at night (Mrosovsky, 1968; Witherington *et al.* 1990). Once on the beach, turtles must reach the sea quickly to avoid terrestrial predators such as racoons, foxes and ghost crabs. Hatchlings usually begin to crawl seawards within a few seconds of emerging and continue on a straightline course until they enter the ocean. The course selected, however, is apparently not based on an innate preference for a specific direction. Turtles translocated from the east coast of Central America to the west coast, for example, crawled seawards in their new location (Carr and Ogren, 1960).

Debris that has washed ashore (e.g. seaweed and shells) and small irregularities in the beach surface often obstruct the view of hatchlings on the ground at the nest site, so that turtles must frequently ascertain the seaward direction without viewing the ocean directly. Visual cues are nevertheless indispensable for sea-finding. Hatchlings released on a beach with their eyes covered, for example, were disoriented and unable to find the water (Carr and Ogren, 1960; Mrosovsky and Shettleworth, 1968).

Because water reflects more moonlight and starlight than does land, the oceanic horizon at night is nearly always slightly brighter than the landward horizon. This finding, combined with evidence that hatchlings prefer brighter lights to dimmer ones (Mrosovsky and Shettleworth, 1968; Mrosovsky, 1972), led to the hypothesis that hatchlings locate the ocean by crawling towards the brightest horizon (Mrosovsky and Shettleworth, 1968).

Recent experiments, however, have suggested that this explanation is incomplete. When loggerhead hatchlings were tested in a circular arena in which one side had a low, dimly illuminated horizon and the other a higher, brighter horizon, the turtles consistently moved towards the lower, dimmer light (Salmon *et al.* 1992). The orientation of hatchlings thus appears to depend on both the brightness of the light and its elevation. Turtles may normally move seawards by crawling towards the lowest illuminated horizon and perhaps only choose the brightest in the special case in which horizon elevation is equal in all directions (Limpus, 1971; Salmon *et al.* 1992). Under natural conditions, crawling towards the lower and brighter horizon presumably leads turtles to the ocean, given (1) that most loggerhead nesting beaches slope gently down to the water, and (2) that the vegetation and dunes that line the inland border of most beaches raise the apparent elevation of the landward horizon (Limpus, 1971; Salmon *et al.* 1992; Witherington, 1992).

Waves as an orientation cue

Almost immediately after entering the ocean, hatchlings establish a course towards the open sea (Frick, 1976; Ireland *et al.* 1978; Salmon and Wyneken, 1987). Wave direction appears to be the primary orientation cue used by turtles as they swim away from the beach. Hatchlings tethered in floating orientation arenas (Salmon and Lohmann, 1989; Lohmann *et al.* 1990) and unrestrained turtles released directly into the ocean (Lohmann and Lohmann, 1992) all swam into approaching waves, even under unusual conditions when doing so resulted in orientation back towards land (Lohmann and Lohmann, 1992) (Fig. 1). On days when no waves were present, tethered loggerheads either adopted courses towards seemingly random directions or swam in circles (Salmon and Lohmann, 1989).

All the data obtained so far are consistent with the hypothesis that hatchlings normally maintain a seaward orientation early in the offshore migration by using wave propagation direction as an orientation cue. Because waves and swells entering shallow, coastal areas are refracted until they approach a beach directly, swimming into waves reliably results in movement away from land and towards the open sea.

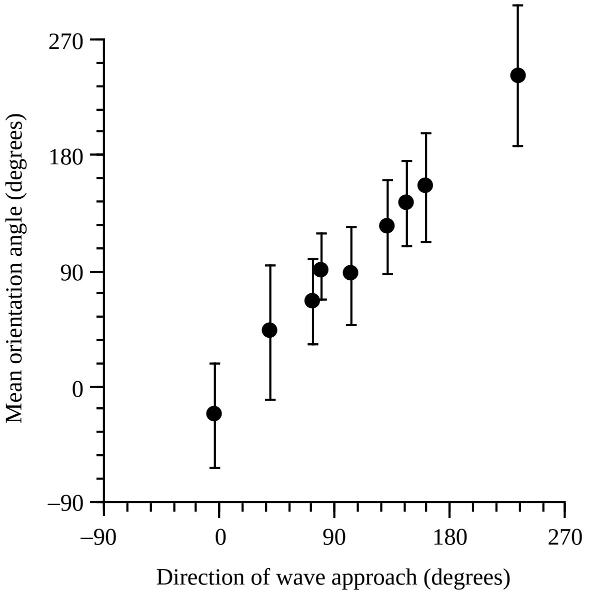

Fig. 1. A summary of experiments in which green turtle hatchlings were released at sea near the east coast of Florida, USA, on days when waves moved in various directions. Each data point represents the mean angle of orientation of a group of hatchlings plotted with respect to the angle of wave approach at the time of release. Hatchlings in each experiment swam into waves, even when doing so resulted in orientation towards directions other than offshore. Data from Lohmann and Lohmann (1992). Error bars indicate angular deviation.

Detecting waves while under water

The ability of hatchlings to detect wave direction while swimming under water at night suggests that turtles do not detect waves visually. Experiments in a wave tank have confirmed that visual cues are not necessary for wave orientation; turtles oriented to waves in the absence of visible light (Lohmann *et al.* 1990; Wyneken *et al.* 1990).

One way in which turtles might detect wave direction in darkness is to sense the orbital movements associated with wave propagation. Objects under water near the surface of the ocean describe a circular pattern of movement as waves pass above (Denny, 1988). In addition, the accelerations that occur in typical wave orbits exceed the threshold that the vertebrate inner ear can detect (Cook, 1984; Lohmann and Lohmann, 1992). We therefore hypothesized that turtles might determine their orientation relative to wave propagation direction by monitoring the sequence of accelerations they experience in the water column (Lohmann *et al.* 1995). For example, a turtle facing into approaching waves is accelerated upwards, then backwards, then downwards and forwards with each wave cycle, whereas a turtle oriented in the direction of wave movement would be accelerated upwards, forwards, downwards and then backwards (Fig. 2) (Cook, 1984;

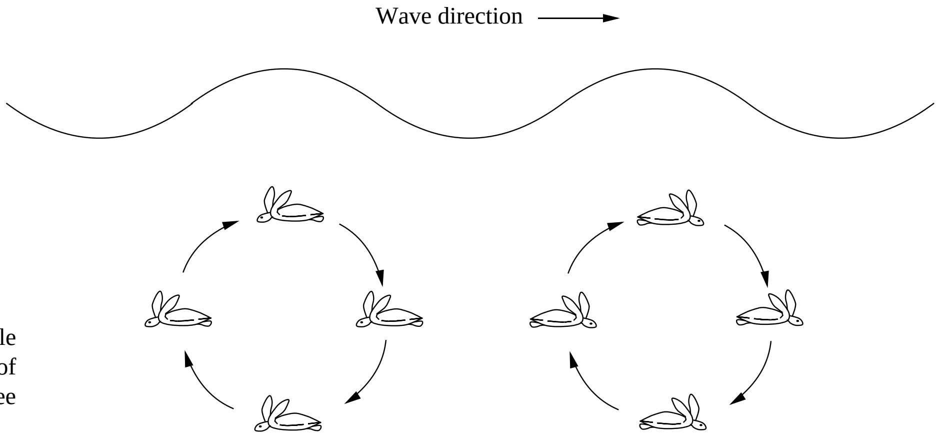

Fig. 2. The motion of a hatchling turtle swimming with and against the direction of wave propagation (Lohmann *et al.* 1995). See text for details.

Lohmann and Lohmann, 1992; Lohmann *et al.* 1995). The turtle would need only to distinguish between these two sequences to differentiate orientation against and with wave propagation direction.

To determine whether hatchlings might detect wave direction in this way, we constructed a wave motion simulator (Fig. 3) to reproduce in air the circular movements that a turtle would normally encounter while swimming beneath small oceanic waves (Lohmann *et al.* 1995). Because the swimming motor program in sea turtle hatchlings is activated when the ventral surface of the turtle fails to contact the substratum (Carr, 1963, 1981), it is possible to test the responses of turtles 'swimming' in air (Lohmann *et al.* 1995). Hatchlings suspended in air and subjected to orbital movements that simulated waves approaching from their right sides attempted to turn right, whereas movements that simulated waves from the left elicited left-turning behavior (Fig. 4) (Lohmann *et al.* 1995). Movements simulating waves from directly in front of the turtles elicited little turning in either direction.

The results demonstrate that hatchling sea turtles can determine the propagation direction of ocean waves by monitoring orbital movements. Additional experiments with the wave simulator have revealed that loggerhead hatchlings

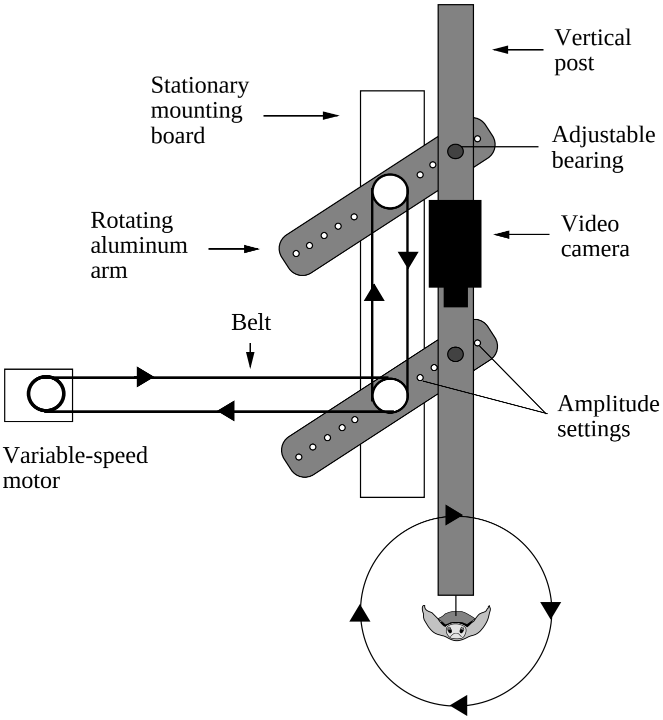

Fig. 3. Diagram of the wave motion simulator used to simulate the orbital movements that occur beneath small oceanic waves (Lohmann *et al.* 1995). A small, variable-speed motor turned a belt, which in turn drove two identical acrylic arms coupled by a second belt. As the arms rotated, they remained parallel to each other and moved a vertical post (with a hatchling attached to the bottom) through a series of circular movements.

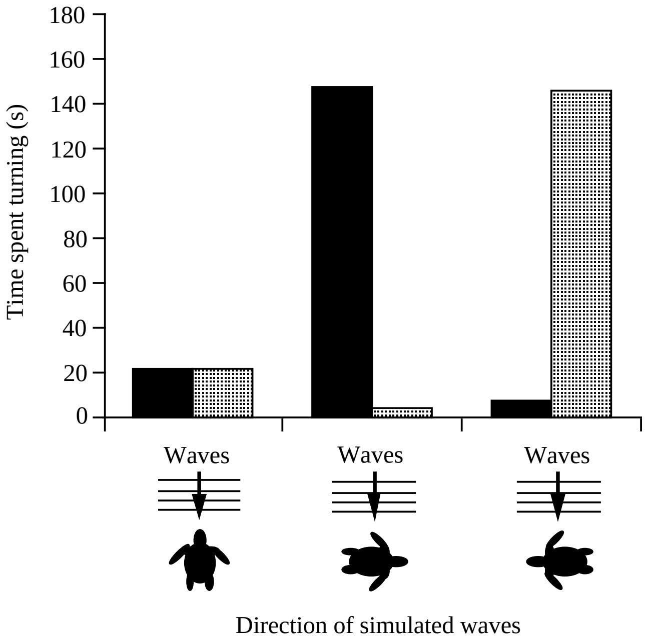

Fig. 4. Results from a wave simulator experiment in which loggerhead hatchlings were subjected to orbital movements simulating waves approaching from one of three directions (from the front, left or right). The black bars represent the time out of 180 s that hatchlings spent attempting to turn left, whereas the stippled bars indicate the time that hatchlings spent turning right. Data from Lohmann *et al.* (1995).

respond most strongly to ‘wave orbits’ with amplitudes and periods closely resembling those of typical waves that occur near the natal beach in Florida (Manning *et al.* 1996). Thus, hatchlings may be ‘tuned’ to recognize specific wave parameters at the time they enter the sea.

Orientation within and beyond the wave refraction zone

Hatchlings that have just entered the ocean appear to orient exclusively on the basis of waves; no evidence presently exists for the involvement of other directional cues at this early stage of the offshore migration. Loggerhead, green turtle (*Chelonia mydas*) and leatherback (*Dermochelys coriacea*) hatchlings tested in the ocean swam into waves both during the day and at night, within sight of shore and beyond, under sun, partial cloud cover, complete overcast, and without regard to whether waves moved in typical (shoreward) or atypical (seaward) directions (Salmon and Lohmann, 1989; Lohmann *et al.* 1990; Lohmann and Lohmann, 1992).

In shallow water near shore, waves refract until they approach a beach directly (Bascom, 1980); thus, orienting into waves leads turtles seawards (Lohmann and Lohmann, 1992). In deeper water farther from land, however, waves no longer provide a reliable indicator of offshore direction. Evidence suggests, however, that hatchlings may orient into waves for only a short time after entering the sea. Hatchling loggerheads tracked from a Florida beach into the open ocean swam into waves initially, but continued on the same seaward headings after entering offshore areas in which wave direction no longer coincided with their established courses (Witherington, 1995). The ability to maintain courses seemingly independent of wave direction suggests that hatchlings use one or more alternative sources of directional information to guide their movements after they have swum a short distance from land.

Magnetic orientation and acquisition of a magnetic directional preference

Several laboratory experiments (Fig. 5) have demonstrated that loggerhead and leatherback hatchlings can orient to the earth’s magnetic field (Lohmann, 1991; Lohmann and Lohmann, 1993; Light *et al.* 1993). Thus, one possibility is that magnetic compass orientation supplants wave orientation as hatchlings distance themselves from shore.

If the magnetic compass does indeed function in the offshore migration, then turtles must inherit or acquire a magnetic directional preference that reliably leads them seawards (east to northeast from beaches along the Atlantic coast of Florida). During initial magnetic orientation experiments, hatchlings had been permitted to establish a course towards a dim light in the east before they were tested in darkness; these animals subsequently oriented east to northeast in the geomagnetic field (Lohmann, 1991; Light *et al.* 1993; Lohmann and Lohmann, 1993). To determine whether the initial course of the turtles influenced their subsequent magnetic orientation, we studied the orientation of turtles exposed to light from either magnetic east or west (Lohmann and Lohmann, 1994*a*). Hatchlings that had been exposed to light in the east oriented eastwards when tested in darkness, whereas those that had been exposed to light in the west swam approximately westwards (Fig. 6). Reversing the magnetic field resulted in a corresponding shift in orientation, indicating that the turtles were indeed orienting magnetically in the dark. Another group of turtles tested in darkness without prior exposure to light cues was not significantly oriented (Fig. 6).

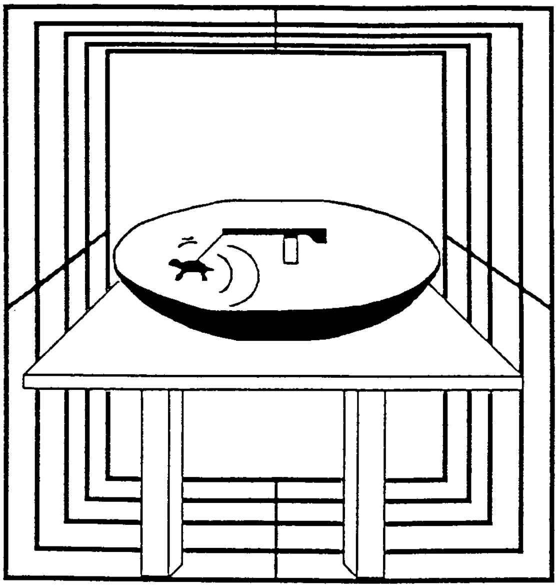

Fig. 5. The orientation apparatus used in initial magnetic orientation experiments (Lohmann, 1991; Lohmann and Lohmann, 1993). Hatchlings were placed into nylon–Lycra harnesses and tethered to a rotatable lever-arm mounted on an electronic tracking unit in the center of a circular arena filled with sea water. The arena was surrounded by a Rubens coil system (Rubens, 1945), so that the horizontal component of the earth’s field could be reversed.

These results indicate that the position of light cues, or perhaps just the experience of maintaining a course towards a specific direction, can influence subsequent magnetic orientation behavior. Moreover, because hatchlings without prior light exposure oriented randomly, the results suggest that turtles do not emerge from their nests with a preferred magnetic compass bearing, but instead must acquire one.

Although light cues play a critical role in the orientation of hatchlings on the beach (see above), turtles that enter the ocean under natural conditions initially orient into waves (Salmon and Lohmann, 1989; Lohmann and Lohmann, 1992) and appear to ignore visual cues (Salmon and Wyneken, 1990). Thus, if light cues are normally involved in setting the preferred magnetic direction, the process may occur during the beach crawl. To investigate whether hatchlings can set a magnetic course while crawling from their nests to the ocean, turtles were placed into one end of a short (4.1 m) runway with a dim light placed in the opposite end and permitted to crawl towards the light (K. J. Lohmann and C. M. F. Lohmann, unpublished data). As the hatchling finished the crawl, the light

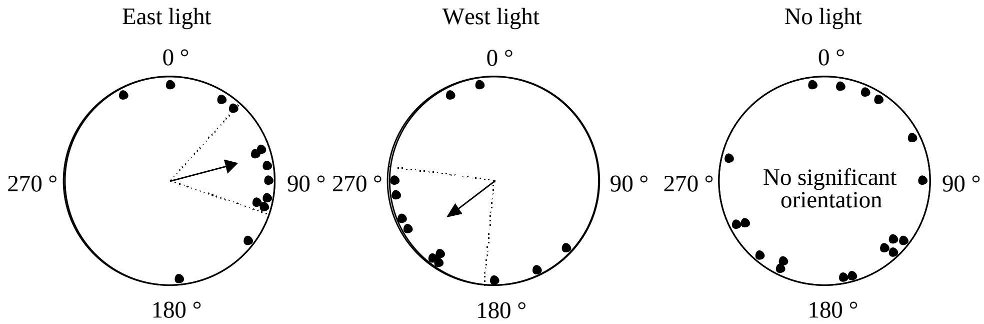

Fig. 6. Orientation of hatchlings swimming in complete darkness in the geomagnetic field after previous exposure to a light in the east (left-hand diagram), a light in the west (middle diagram) or no light (right-hand diagram). Each data point represents the mean angle of orientation for a single hatchling; arrows represent the mean angle of the group for the two significant distributions. Dotted lines represent 95 % confidence intervals for the mean. Turtles exposed to the east light subsequently swam approximately eastwards, whereas hatchlings exposed to the west light swam approximately westwards. Turtles that had not previously been exposed to light were not significantly oriented.

was extinguished and the turtle was transferred in darkness to a water-filled orientation arena, where its orientation was monitored.

Turtles that had crawled towards an east light subsequently swam eastwards in darkness, whereas hatchlings that had crawled west swam westwards. Reversing the magnetic field around the swimming hatchlings resulted in a reversal of orientation, demonstrating that the turtles were orienting to the earth's magnetic field. Other hatchlings placed into the runway in complete darkness and permitted to crawl with no light present were not significantly oriented. These results are consistent with the hypothesis that turtles emerge from their nests without an established directional preference; they may, however, acquire one while crawling a short distance across the beach.

Recent experiments have also demonstrated that hatchlings can establish a magnetic directional preference on the basis of wave cues (Goff *et al.* 1995). Loggerhead hatchlings that had never crawled across a beach were tethered inside a wave tank and allowed to establish a course into waves. The waves were then terminated, and hatchlings continued swimming in darkness under one of two magnetic field conditions while their orientation was monitored. Half of the turtles continued to swim in the local geomagnetic field. The other half were subjected to a field with a reversed vertical component, a treatment that has the same effect on the turtle magnetic compass as reversing the horizontal component (Light *et al.* 1993). Hatchlings that swam in the earth's field continued to swim in the direction from which waves had previously approached. Turtles tested in the reversed field, however, swam in the opposite direction. A third group of turtles that swam in darkness without previous exposure to waves was not significantly oriented. These results provide additional evidence that turtles do not inherit a magnetic preference for the offshore direction, but instead acquire one based on other directional cues.

Under laboratory conditions, then, a magnetic directional preference can be established in at least three different ways: by swimming towards a light source, by crawling towards a light source and by swimming into waves. Taken together, the results suggest that the experience of maintaining a course, either on land or in water, may be sufficient to set the magnetic compass. Under natural conditions, hatchlings crawl across the beach towards the brighter, lower horizon of the open sea, then continue offshore by orienting into approaching waves. Thus, one possible interpretation of our laboratory experiments is that the seaward course turtles initiate while crossing the beach and swimming away from land is subsequently transferred to the magnetic compass as the hatchlings enter the open ocean.

Summary of orientation mechanisms during the offshore migration

Evidence suggests that hatchling loggerheads from the east coast of Florida rely on three distinct types of orientation cues during their migration from the natal beach to the Gulf Stream (Fig. 7). These cues appear to be used sequentially at different stages of the migration.

On the beach, hatchlings crawl seawards by orienting towards the lower, brighter, oceanic horizon. Once in the ocean, turtles initially swim offshore by orienting into waves, apparently without regard to visual cues that guided their movements on land. By the time hatchlings swim beyond the wave refraction zone, they have probably transferred the initial seaward heading to their magnetic compasses, enabling them to maintain offshore courses long after swimming beyond sight of land.

Navigation in the open ocean and adult migrations

Although the orientation mechanisms just described may suffice to guide hatchling Florida loggerheads from their natal beach to the Gulf Stream, the offshore migration is just the first step in a much longer transoceanic journey. Young turtles evidently remain in the North Atlantic gyre for several years, during which time they cross to the east side of the Atlantic before returning to the southeastern United States coast as subadults (Carr, 1986, 1987). Recent analyses of mitochondrial DNA from nesting loggerheads has provided strong evidence that adult females eventually return to nest on or near the same beaches where they themselves emerged as hatchlings (Bowen *et al.* 1993, 1994, 1995).

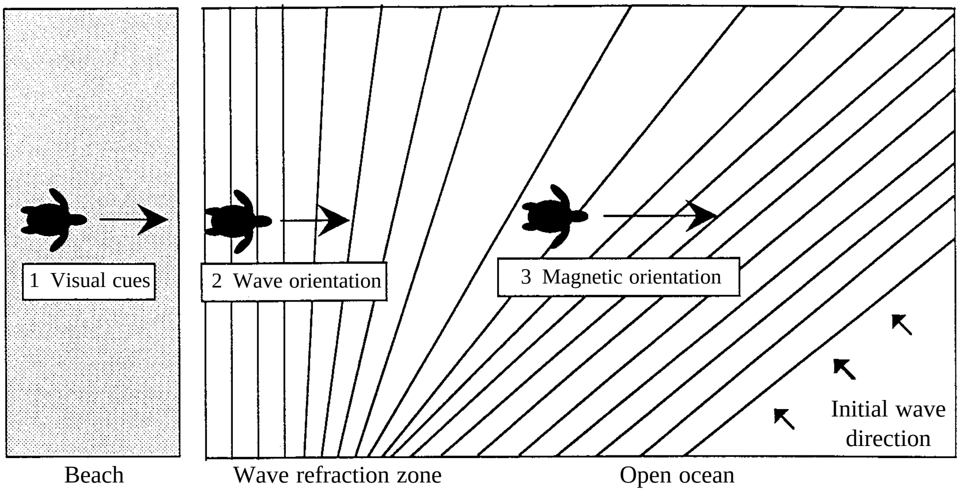

Fig. 7. Diagram summarizing the orientation cues hypothesized to guide hatchling Florida loggerheads from their nests to the Gulf Stream current. The beach is to the left and progressively deeper water to the right. Lines represent oceanic waves moving towards the beach; as they enter shallow coastal areas, waves refract until they approach the beach directly. Visual cues guide hatchlings from their nests to the sea. Near shore, turtles swim into refracted waves, which provide a reliable cue for swimming seawards. In deeper water, waves no longer provide a consistent cue for offshore orientation, and hatchlings are hypothesized to transfer their seaward courses to their magnetic compasses.

The ability to return to a specific nesting beach from hundreds or thousands of kilometers away after years in the open ocean is not uncommon among sea turtles. Green turtles that nest on tiny Ascension Island, for example, regularly migrate between their nesting beach and Brazilian feeding grounds, a straightline distance of more than 2000 km (Carr, 1975). Kemp's ridley turtles (*Lepidochelys kempi*) throughout the Atlantic, Caribbean and Gulf of Mexico converge from hundreds or thousands of kilometers away to nest along a single, isolated beach in Mexico (Carr, 1963, 1984). And loggerheads that nest in Japan apparently traverse the entire Pacific Ocean to Baja California before returning to their natal beaches to nest (Bowen *et al.* 1995). Such precise targeting of specific destinations from immense distances is difficult to explain without hypothesizing an ability to determine geographic position relative to the goal (Gould, 1985; Salmon and Wyneken, 1993; Papi *et al.* 1995).

Detection of inclination angle by hatchling Florida loggerhead turtles

Although hatchling loggerheads do not migrate to a destination as specific as a single nesting beach, they may still benefit from an ability to approximate their position within the ocean. For example, straying beyond the latitudinal extremes of the North Atlantic gyre can be fatal for young turtles. As the northern edge of the gyre approaches Portugal, the east-flowing current abruptly 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). Similarly, hatchlings that venture south of the gyre risk being swept into the south Atlantic current system and carried far from their normal range.

In principle, the ability to detect the earth's magnetic field might assist young turtles in remaining within the North Atlantic gyre, if they can detect parameters of the field that vary latitudinally. Among several geomagnetic features that vary across the surface of the earth, field line inclination is the most consistently correlated with latitude (Skiles, 1985). As a first step towards determining whether loggerheads can derive positional information from features of the earth's field, we studied the orientation behavior of hatchlings tested under earth-strength fields with different field line inclinations (Lohmann and Lohmann, 1994*b*).

Hatchlings exposed to a field with an inclination angle matching that of the natal beach swam eastwards, as they normally do during their offshore migration. In contrast, those subjected to an inclination angle found on the northern boundary of the North Atlantic gyre swam south-southwest (Fig. 8). Hatchlings exposed to an inclination angle found near the southern boundary of the gyre swam in a northeasterly direction (Fig. 8), and those exposed to inclination angles that they do not normally encounter, or to a field inclination found well within the northern and southern extremes of the gyre, were not significantly oriented. These results demonstrate that sea turtles can distinguish between different magnetic

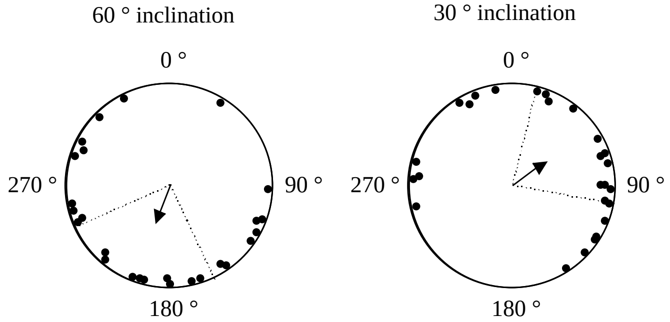

Fig. 8. Orientation of hatchlings tested in magnetic fields of the same intensity but different inclinations. Conventions as in Fig. 6. Turtles exposed to a 60 ° inclination angle (found near the northern edge of the North Atlantic gyre) were significantly oriented towards the south-southwest, whereas those exposed to a 30 ° inclination angle (found near the southern border of the gyre) swam in a northeasterly direction.

inclination angles and perhaps derive from them an approximation of latitude.

Detection of field intensity

A second feature of the earth's field that varies with latitude is field strength or intensity. Recent experiments have demonstrated that loggerhead hatchlings can also perceive differences in field intensity that occur over their migratory range (K. J. Lohmann and C. M. F. Lohmann, unpublished data).

In the same apparatus used in the inclination angle study (Lohmann and Lohmann, 1994*b*), loggerhead hatchlings were exposed to field intensities that they normally encounter during their first months in the sea. In all trials, the inclination angle of the field was kept constant. Turtles tested in a field of 52 000 nT (a field 10.6 % stronger than that of the natal beach field, and one that hatchlings first encounter near South Carolina, USA) swam eastwards. Those exposed to a 43 000 nT field (a field 8.5 % weaker than that of the natal beach field, and one first encountered on the eastern side of the Atlantic near Portugal) swam westwards.

These results demonstrate that hatchlings can distinguish between field intensities that occur in different locations along their migratory route. Moreover, because eastward orientation near South Carolina and westward orientation near the coast of Portugal would both function to keep hatchlings within the confines of the gyre, the results are consistent with the hypothesis that turtles use field intensity to assess their global position.

Do sea turtles have a bicoordinate magnetic map?

That sea turtles have the ability to derive at least some positional information from features of the earth's magnetic field now seems clear. At a minimum, such information appears likely to provide turtles with an estimate of latitude and perhaps to assist them in remaining within the borders of the North Atlantic gyre (Lohmann and Lohmann, 1994*b*). The ability of hatchlings to detect both inclination and intensity, however, raises the possibility that turtles may be able to pinpoint their global position by relying solely on geomagnetic cues.

The issue of whether certain animals can determine their global position by detecting features of the earth's magnetic field has been debated for more than a century (Viguier, 1882; Baker, 1984; Gould, 1985). For an animal to determine its location using magnetic parameters alone, two conditions must almost certainly be fulfilled: (1) the animal must be able to perceive (at a minimum) two distinct features of the earth's field, and (2) these parameters must vary in somewhat different directions across the earth's surface (or at least over the range of the animal's movements), so that a grid is formed and position-finding is feasible.

Given that loggerheads can detect differences in field inclination and intensity which match those they encounter while migrating, the basic sensory requirements for a bicoordinate magnetic map sense appear to be fulfilled in sea turtles. Inspection of magnetic features in the North Atlantic and other regions in which long-distance turtle migrations have been documented also suggests that a crude map based on inclination and intensity is theoretically possible (K. J. Lohmann and C. M. F. Lohmann, unpublished data). Over most oceanic regions, isoclinics (lines of equal inclination angle) and isodynamics (lines of equal field intensity) are not precisely parallel; thus, the two intersect and form a non-orthogonal grid, in which most locations along a given migratory route are defined by unique combinations of inclination and intensity.

In discussing the possibility of magnetic maps, it is perhaps important to distinguish between the migrations of hatchlings and adults. Because hatchlings do not migrate to isolated targets such as nesting beaches, it is difficult to assess whether they possess the same navigational abilities that adults have. Although hatchlings might conceivably inherit a map of magnetic features found throughout their migratory range, it is not necessary to invoke such an explanation to account for the orientation responses observed so far. Florida loggerhead hatchlings, for example, might begin their migration programmed only to swim in certain directions if and when they encounter a few specific magnetic features that mark critical boundaries of the gyre system. Such programmed responses might function to keep turtles within a favorable oceanic region without requiring an ability to fix position relative to a goal.

The long-distance migrations of adults to specific nesting beaches, however, appear to require a more sophisticated navigational system that probably includes an ability to assess position (Salmon and Wyneken, 1994; Papi *et al.* 1995; Papi and Luschi, 1996). Given that hatchlings can detect magnetic field inclination and intensity, one possibility is that turtles learn the local gradients of these two features and eventually, as adults, develop a large-scale bicoordinate magnetic map for use in long-distance migrations.

The migration of Ascension Island green turtles provides one intriguing example of how a bicoordinate magnetic map based on inclination and intensity might, in principle, permit navigation over a large oceanic region. Off the coast of Brazil, isoclinics and isodynamics form nonorthogonal gradients (Fig. 9); Ascension Island and all points along the way (perhaps excepting occasional areas with strong, local anomalies) are defined by unique combinations of these two features. If Ascension Island hatchlings learn the magnetic features of their natal beach and subsequently learn the gradients of field inclination and intensity, navigating back to the vicinity of the island years later might be possible. Indeed, a magnetic map would not necessarily need to guide a turtle precisely to the island, but only to bring it close enough so that chemical odorants (Grassman, 1993) or other cues would enable it to pinpoint its final goal.

If such a magnetic map exists at all in turtles, it might range from a system that provides only a crude estimate of global

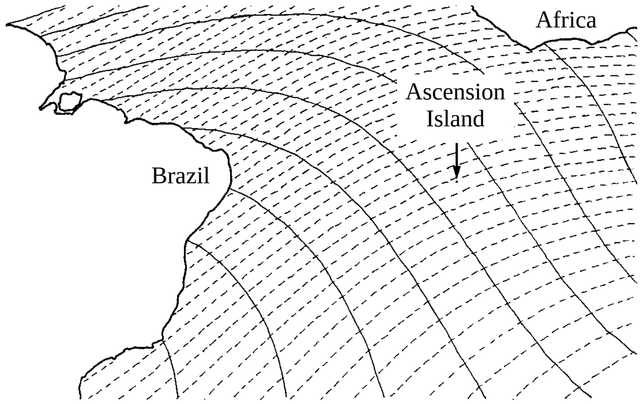

Fig. 9. Isoclinics (dashed lines) and isodynamics (solid lines) in the oceanic region surrounding Ascension Island. Adjacent isoclinics differ by 2° and adjacent isodynamics by 1000 nT. The two geomagnetic features form a non-orthogonal grid that might, in principle, provide Ascension Island turtles with a bicoordinate position-finding system as they migrate between Ascension Island and the Brazilian coast. Data from U.S. Defense Mapping Agency Hydrographic/Topographic Center (1985*a*,*b*).

position to a highly developed sensory system capable of pinpointing a specific beach. The resolution would depend to a large extent on the sensitivity of the turtles to the two parameters which, at present, is entirely unknown. It is interesting to note, however, that bees may detect intensity differences of as little as 260 nT, and perhaps as small as about 26 nT (Walker and Bitterman, 1989). A sensitivity of approximately 10–20 nT has been inferred for birds (Gould, 1985). If turtles have similar abilities to discriminate intensity and can also detect inclination angle with great exactitude, a highly accurate system is at least theoretically possible.

Although such speculation is inviting, whether turtles do indeed use a bicoordinate magnetic map sense during long-distance migrations remains to be determined. At present, the open-ocean navigational abilities of sea turtles remain an enduring mystery of behavioral biology.

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References

Baker, R. R. (1984). *Bird Navigation: The Solution of a Mystery?* London: Hodder and Stoughton.

Bascom, W. (1980). *Waves and Beaches*. New York: Anchor Press Doubleday.

Bowen, B. W., Abreu-Grobois, F. A., Balazs, G. H., Kamezaki, N., Limpus, C. J. and Ferl, R. J. (1995). Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proc. natn. Acad. Sci. U.S.A.* **92**, 3731–3734.

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

Bowen, B. W., Kamezaki, N., Limpus, C. J., Hughes, G. R., Meylan, A. B. and Avise, J. C. (1994). Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. *Evolution* **48(6)**, 1820–1828.

Carr, A. (1963). Panspecific reproductive convergence in *Lepidochelys kempi*. *Ergebn. Biol.* **26**, 298–303.

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

Carr, A. (1981). Notes on the behavioral ecology of sea turtles. In *Biology and Conservation of Sea Turtles* (ed. K. A. Bjorndal), pp. 19–26. Washington, DC: Smithsonian Institution Press.

Carr, A. (1984). *The Sea Turtle: So Excellent a Fishe*. Austin, TX: 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. *Cons. Biol.* **1**, 103–121.

Carr, A. and Ogren, L. (1960). The ecology and migrations of sea turtles. 4. The green turtle in the Caribbean Sea. *Bull. Am. Mus. nat. Hist.* **121**, 7–48.

Cook, P. H. (1984). Directional information from surface swell: some possibilities. In *Mechanisms of Migration in Fishes* (ed. J. D. McLeave, G. P. Arnold, J. J. Dodson and W. H. Neill), pp. 79–101. New York: Plenum Press.

Denny, M. W. (1988). *Biology and the Mechanics of the Wave-swept Environment*. Princeton, NJ: Princeton University Press.

Ehrenfeld, D. W. and 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. *Anim. Behav.* **24**, 849–857.

Goff, M. D., Salmon, M. and Lohmann, K. J. (1995). The magnetic compass of loggerhead sea turtle hatchlings: calibration by surface waves. In *Proceedings of the Fifteenth Annual Sea Turtle Workshop on Sea Turtle Biology and Conservation*. NOAA Technical Memorandum (in press).

Gould, J. L. (1985). Are animal maps magnetic? In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L. Kirschvink, D. S. Jones and B. J. MacFadden), pp. 257–268. New York: Plenum Press.

Grassman, M. (1993). Chemosensory orientation behavior in juvenile sea turtles. *Brain Behav. Evol.* **41**, 224–228.

Ireland, L. C., Frick, J. A. and Wingate, D. B. (1978). Nighttime orientation of hatchling green turtles (*Chelonia mydas*) in open ocean. In *Animal Migration, Navigation and Homing* (ed. K. Schmidt-Koenig and W. T. Keeton), pp. 420–429. New York: Springer-Verlag.

Light, P., Salmon, M. and Lohmann, K. J. (1993). Geomagnetic orientation of loggerhead sea turtles: evidence for an inclination compass. *J. exp. Biol.* **182**, 1–10.

Limpus, C. J. (1971). Sea turtle ocean finding behaviour. *Search* **2**, 385–387.

LOHMANN, K. J. (1991). Magnetic orientation by hatchling loggerhead sea turtles (*Caretta caretta*). *J. exp. Biol.* **155**, 37–49.

LOHMANN, K. J. (1992). How sea turtles navigate. *Scient. Am.* **266**, 100–106.

LOHMANN, K. J. AND LOHMANN, C. M. F. (1992). Orientation to oceanic waves by green turtle hatchlings. *J. exp. Biol.* **171**, 1–13.

LOHMANN, K. J. AND LOHMANN, C. M. F. (1993). A light-independent magnetic compass in the leatherback sea turtle. *Biol. Bull. mar. biol. Lab., Woods Hole* **185**, 149–151.

LOHMANN, K. J. AND LOHMANN, C. M. F. (1994*a*). Acquisition of magnetic directional preference in hatchling loggerhead sea turtles. *J. exp. Biol.* **190**, 1–8.

LOHMANN, K. J. AND LOHMANN, C. M. F. (1994*b*). Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *J. exp. Biol.* **194**, 23–32.

LOHMANN, K. J., SALMON, M. AND WYNEKEN, J. (1990). Functional autonomy of land and sea orientation systems in sea turtle hatchlings. *Biol. Bull. mar. biol. Lab., Woods Hole* **179**, 214–218.

LOHMANN, K. J., SWARTZ, A. W. AND LOHMANN, C. M. F. (1995). Perception of ocean wave direction by sea turtles. *J. exp. Biol.* **198**, 1079–1085.

MANNING, E. L., CATE, H. S. AND LOHMANN, K. J. (1996). Discrimination of ocean wave features by hatchling sea turtles. *Mar. Biol.* (in press).

MROSOVSKY, N. (1968). Nocturnal emergence of sea turtles: control by thermal inhibition of activity. *Nature* **220**, 1338–1339.

MROSOVSKY, N. (1972). The water-finding ability of sea turtles. Behavioral studies and physiological speculations. *Brain Behav. Evol.* **5**, 202–225.

MROSOVSKY, N. AND SHETTLEWORTH, S. J. (1968). Wavelength preferences and brightness cues in the water finding behavior of sea turtles. *Behaviour* **32**, 211–257.

PAPI, F., LIEW, H. C., LUSCHI, P. AND CHAN, E. H. (1995). Long-range migratory travel of a green turtle tracked by satellite: evidence for navigational ability in the open sea. *Mar. Biol.* **122**, 171–175.

PAPI, F. AND LUSCHI, P. (1996). Pinpointing 'Isla Meta': the case of sea turtles and albatrosses. *J. exp. Biol.* **199**, 65–71.

RUBENS, S. M. (1945). Cube-surface coil for producing a uniform magnetic field. *Rev. scient. Instrum.* **16**, 243–245.

SALMON, M. AND LOHMANN, K. J. (1989). Orientation cues used by hatchling loggerhead sea turtles (*Caretta caretta*) during their offshore migration. *Ethol.* **83**, 215–228.

SALMON, M. AND WYNEKEN, J. (1987). Orientation and swimming behavior of hatchling loggerhead turtles (*Caretta caretta* L.) during their offshore migration. *J. exp. mar. Biol. Ecol.* **109**, 137–153.

SALMON, M. AND WYNEKEN, J. (1990). Do swimming loggerhead sea turtles (*Caretta caretta* L.) use light cues for offshore orientation? *Mar. Behav. Physiol.* **17**, 233–246.

SALMON, M. AND WYNEKEN, J. (1993). Orientation by hatchling sea turtles. In: *Orientation and Navigation: Birds, Humans and Other Animals.* 1993 Royal Institute of Navigation International Conference, Paper 35. Oxford: RIN.

SALMON, M. AND WYNEKEN, J. (1994). Orientation by hatchling sea turtles: mechanisms and implications. *Herpetol. nat. Hist.* **2**, 13–24.

SALMON, M., WYNEKEN, J., FRITZ, E. AND LUCAS, M. (1992). Seafinding by hatchling sea turtles: role of brightness, silhouette and beach slope as orientation cues. *Behaviour* **122**, 56–77.

SKILES, D. D. (1985). The geomagnetic field: its nature, history and biological relevance. In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L. Kirschvink, D. S. Jones and B. J. MacFadden), pp. 43–102. New York: Plenum Press.

U.S. DEFENSE MAPPING AGENCY HYDROGRAPHIC/TOPOGRAPHIC CENTER (1985*a*). *Magnetic Inclination or Dip. Epoch 1985.0* (map). U.S. Government Printing Office.

U.S. DEFENSE MAPPING AGENCY HYDROGRAPHIC/TOPOGRAPHIC CENTER (1985*b*). *Total Intensity of the Earth's Magnetic Field* (map). U.S. Government Printing Office.

VIGUIER, C. (1882). Le sens de l'orientation et ses organes chez les animaux et chez l'homme. *Rev. phil. France Etranger* **14**, 1–36.

WALKER, M. M. AND BITTERMAN, M. E. (1989). Honeybees can be trained to respond to very small changes in geomagnetic field intensity. *J. exp. Biol.* **145**, 489–494.

WITHERINGTON, B. E. (1992). Sea-finding behavior and the use of photic orientation cues by hatchling sea turtles. PhD dissertation, University of Florida, Gainesville, Florida, USA.

WITHERINGTON, B. E. (1995). Observations of hatchling loggerhead turtles during the first few days of the lost year(s). In *Proceedings of the Twelfth Annual Sea Turtle Workshop on Sea Turtle Biology and Conservation* (compilers J. I. Richardson and T. H. Richardson), pp. 154–157. NOAA Technical Memorandum NMFS-SEFSC-361.

WITHERINGTON, B. E., BJORNDAL, K. A. AND MCCABE, C. M. (1990). Temporal pattern of nocturnal emergence of loggerhead turtle hatchlings from natural nests. *Copeia* **4**, 1165–1168.

WYNEKEN, J., SALMON, M. AND LOHMANN, K. J. (1990). Orientation by hatchling loggerhead sea turtles *Caretta caretta* L. in a wave tank. *J. exp. mar. Biol. Ecol.* **139**, 43–50.