

MAGNETIC ORIENTATION BY HATCHLING LOGGERHEAD SEA TURTLES (*CARETTA CARETTA*)

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Summary

Laboratory experiments were conducted to test the ability of loggerhead sea turtle hatchlings (*Caretta caretta* L.) to orient using the magnetic field of the earth. Hatchlings were tethered to a rotatable lever-arm apparatus which tracked swimming orientation in complete darkness. Hatchlings tested in the earth's magnetic field were nonrandomly oriented with a mean angle of 42°; those tested under an earth-strength field with a reversed horizontal component were also nonrandomly oriented, but with a mean angle of 196°. The distributions under the two magnetic field conditions were significantly different, indicating that loggerhead sea turtle hatchlings can detect the magnetic field of the earth and use it as a cue in orientation.

Introduction

Sea turtle hatchlings emerge from underground nests on sandy oceanic beaches, scramble to the sea, and swim towards the open ocean in a migration lasting several days. Once in the water, hatchlings quickly establish well-oriented offshore headings that are maintained even when turtles swim beyond sight of land (Frick, 1976; Ireland *et al.* 1978). Hatchling loggerhead sea turtles (*Caretta caretta* L.) from nests along the southeastern coast of the United States eventually reach the Gulf Stream and the North Atlantic gyre, where they forage and take refuge in floating sargassum weed (Carr, 1986*a,b*).

Visual cues guide hatchlings from the nest to the ocean (reviewed by Hayes and Ireland, 1978; Mrosovsky and Kingsmill, 1985), but little is known about the orientation mechanisms used by turtles during the offshore migration. Recent field experiments have indicated that hatchlings detect the propagation direction of waves and oceanic swells and use this information as an orientation cue (Salmon and Lohmann, 1989). Additional sources of directional information, however, may simultaneously or subsequently be used by migrating turtles.

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Behavioral experiments have demonstrated that diverse organisms can derive directional information from the magnetic field of the earth. Among these are certain bacteria (Blakemore and Frankel, 1981), mollusks (Lohmann and Willows, 1987), arthropods (Walker and Bitterman, 1985; Lohmann, 1985), fish (Quinn, 1980; Quinn and Brannon, 1982), amphibians (Phillips, 1986), reptiles (Mathis and Moore, 1988), birds (Wiltchko and Wiltchko, 1988) and mammals (Mather and Baker, 1981). To determine whether loggerhead sea turtles can orient to the magnetic field of the earth, the orientation of hatchling loggerheads was monitored under two ambient magnetic field conditions. Results indicate that hatchlings possess a magnetic compass sense capable of functioning in the offshore migration.

Materials and methods

Animals

Hatchling loggerheads were obtained from a beach hatchery located about 30 km south of Fort Pierce, Florida, USA. The hatchery consisted of 123 nests relocated from local beaches unsafe for hatchlings. All nests were moved to the hatchery within 24 h of natural deposition, positioned in a row parallel to the sea about 10 m above the spring high tide line, and marked by a stake indicating the date that the eggs were laid. The hatchery beach faced east-northeast, typical of the shoreline in the area, and was commonly used by loggerheads as a nesting site.

Nests were examined daily. When a depression formed in the sand above a nest (indicating the eggs had hatched and emergence would probably occur that night), several hatchlings were removed, placed into a styrofoam cooler, and transported within 45 min to a laboratory at the Harbor Branch Oceanographic Institution.

Hatchlings were tested once on either their first, second or third night of captivity. Turtles kept in the laboratory for more than one night were maintained either in holding tanks filled with sea water or in styrofoam coolers containing damp sand or paper towels.

Measurement of orientation

In each trial a hatchling was placed inside a nylon-Lycra harness that encircled the turtle's carapace without impeding swimming (Salmon and Wyneken, 1987). The harness was connected by a short monofilament line to a lever arm, which was mounted on a 360° rheostat positioned on a post in the center of an inverted fiberglass satellite dish (Fig. 1). The dish was filled with sea water to a depth of 19.0 cm in the center. The lever-arm was free to rotate within the horizontal plane and could easily be pulled clockwise or counterclockwise by a swimming hatchling. The arm thus tracked the direction towards which the hatchling swam.

The rheostat on which the lever-arm rested was part of a circuit containing a 3 V d.c. power source and a strip chart recorder in an adjacent room. Each orientation of the lever-arm resulted in a different resistance through the rheostat and a different voltage through the circuit. The chart recorder provided a continuous

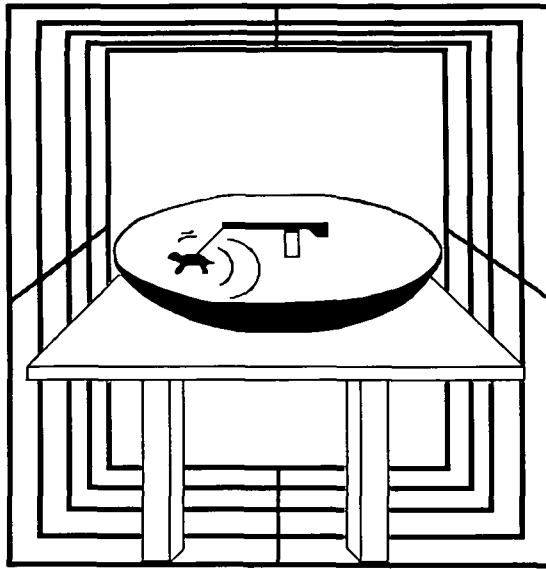


Fig. 1. The orientation apparatus. Hatchlings were tethered to a lever-arm mounted on a rheostat in the center of an inverted satellite dish 1.02 m in diameter (see text). The satellite dish was enclosed by a Rubens cube coil measuring 130 cm on each side.

record of the voltage output and thus of the movements and orientation of each turtle (accurate within 15°). Immediately before or after each experiment, the system was calibrated by obtaining chart recorder measurements for a series of known compass directions.

Altering the magnetic field

The satellite dish and supporting table were encircled by a Rubens cube coil (Rubens, 1945) measuring 130 cm on each side (Fig. 1). The coil was used to control the direction and intensity of the magnetic field around the satellite dish. When connected to a d.c. power source, the coil generated a field that was twice as strong as the horizontal component of the geomagnetic field and opposite in direction. The geomagnetic and imposed fields combined to produce a resultant horizontal field approximately equal in intensity to the geomagnetic horizontal component but opposite in direction. The vertical component of the earth's field was not altered. Thus, turtles could be exposed to a reversed magnetic field in which magnetic north was shifted 180° with respect to geomagnetic north.

Measurements with a Schonstedt single-axis digital fluxgate magnetometer (model DM 2220) indicated that, with the coil on, the horizontal component of the reversed field ranged from 0.23–0.26 Oe in the circular zone where turtles swam. Thus, the reversed field was not precisely uniform throughout the area occupied by the turtles; hatchlings circling the satellite dish with the coil on encountered slight variations in field intensity in the course of a single revolution. When

the coil was off, horizontal field intensity was a constant 0.26 Oe throughout the satellite dish.

Testing procedure

The coil, satellite dish and supporting table were positioned in the center of a light-tight room. Experiments began shortly after sunset and continued throughout the night, the time when virtually all hatchlings emerge from nests and enter the ocean (Mrosovsky, 1968; Demmer, 1981). All experiments were terminated by 05:45 h. One or two hatchlings were tested each night, and all experiments were conducted between July and October, 1988.

After each harnessed turtle had been released into the satellite dish, all lights in the room were turned off except for a dimly lit, frosted, spherical light bulb (General Electric 40 W no. 40G25/W) suspended just above water level on the east side of the orientation arena. The brightness of the bulb was controlled by a Powerstat[®] variable autotransformer (type 3PN116B from The Superior Electric Co., Bristol, Connecticut, USA) maintained at a setting of 30 units.

The dim light was provided for three reasons. First, healthy hatchlings swim towards light sources in the laboratory (Salmon and Wyneken, 1987). The response of each hatchling to the light source thus served to verify that the turtle was developmentally and behaviorally competent to establish and maintain an oriented course; the few hatchlings that failed to orient to the light source were replaced with other turtles. Second, hatchlings entering the sea on dark beaches near Fort Pierce encounter a dim glow of light along the eastern (seaward) horizon because the ocean reflects more light from the night sky than does the land. The presence of light in the east thus approximately simulated the natural condition. Finally, light cues may play a role in calibrating the magnetic compass (see Discussion). In most trials (27 of 32), turtles were exposed to the east light for 60–120 min; five turtles were exposed to the light for longer periods (125–245 min).

Once the light had been turned off each hatchling was permitted to swim in complete darkness for 90–180 min. Half the turtles ($N=16$) swam in the unaltered magnetic field of the earth. The remaining turtles ($N=16$) were tested under identical conditions, except that during the dark period the horizontal component of the earth's field was reversed by turning on the Rubens coil. The chart recorder provided a continuous record of the orientation of each hatchling throughout the experiment.

Oriented swimming periods and circling behavior

Preliminary observations indicated that, in complete darkness, hatchling swimming behavior varied from rapid, apparently random circling of the satellite dish to consistent swimming towards a single direction. Nearly all movement patterns could be assigned to one of two categories, here termed circling and oriented swimming.

During circling, a turtle typically swam towards the perimeter of the tank, but its

orientation gradually shifted clockwise or counterclockwise. Over time, this lateral displacement resulted in a series of circles around the perimeter of the satellite dish. Circling could be slow or fast, with the course of the turtle changing by $1-8^{\circ}\text{s}^{-1}$. Hatchlings occasionally reversed direction; in all cases, however, circling was characterized by continuous movement around the central post. While circling, hatchlings thus demonstrated no directional preferences, but instead spent virtually identical amounts of time swimming towards all directions.

In contrast, turtles engaged in oriented swimming greatly reduced lateral movement, sometimes maintaining an essentially constant course towards a specific direction for several (usually 3–10) minutes. Several such periods often occurred during an hour, but they were nearly always interspersed with longer intervals of circling. On the basis of preliminary observations, oriented swimming periods were arbitrarily defined as intervals of 3 min or longer during which a turtle remained in the same 90° sector of the satellite dish.

Orientation analysis and statistics

While circling, turtles spent equal amounts of time in each part of the tank and did not show directional preferences. Analyses were therefore based only on periods of oriented swimming.

Chart records were analyzed beginning at the point in each trial when the turtle had completed its first circle around the satellite dish in complete darkness. Orientation was then determined to the nearest 45° (e.g. $N=0^{\circ}$, $NE=45^{\circ}$, $E=90^{\circ}$) for each subsequent 1-min interval on the chart record for the duration of the experiment. Chart record marks exactly between two 45° directions were assigned a value halfway between the two (e.g. a mark precisely between N and NE was recorded as 22.5°).

The record was then analyzed for oriented swimming periods. Because these periods were defined as intervals of 3 min or longer during which a turtle remained in the same 90° sector, a sequence on the chart record had to satisfy two criteria to qualify. First, four or more consecutive 1-min readings had to vary by 90° or less. Second, the turtle could not have circled the dish between readings.

Each oriented swimming period ended when the turtle left the 90° sector it had been in. The hatchling could then begin a new oriented swimming period; however, turtles nearly always circled the satellite dish for 5 min or longer before once more establishing such a course.

A mean angle for each oriented swimming period was then calculated using standard procedures for circular statistics (Batschelet, 1981). Each mean was based upon all consecutive 1-min readings that occurred before the turtle left the 90° sector (four or more readings). Oriented swimming period means were then used to calculate the final mean angle for each hatchling. This angle represented the average direction towards which the turtle swam during its oriented swimming periods. Those few hatchlings (4 of 32) which circled continuously or nearly so (i.e. had three or fewer oriented swimming periods during the entire dark period) were replaced with other turtles.

At the completion of all experiments, the mean angles of turtles swimming in the geomagnetic and reversed fields were analyzed to determine whether: (1) each group was significantly oriented in a preferred direction, and (2) the distributions of mean angles under the two field conditions differed significantly. Because different turtles had different numbers of oriented swimming periods, analyses were based on hatchling mean directions without regard to individual vector lengths (Batschelet, 1978).

Results

No difference was observed between the orientation of turtles kept in coolers and those allowed to swim in holding tanks before testing. Similarly, the length of captivity before testing (0, 1 or 2 days), the length of the dark period (90–180 min) and the period of exposure to dim eastern light (60–245 min) had no apparent effect on turtle orientation (Tables 1 and 2). The data thus provided no justification for separating hatchlings other than on the basis of magnetic field conditions during testing.

The mean angles for the 16 turtles tested in the geomagnetic field are plotted in Fig. 2A. Turtles were nonrandomly oriented ($r=0.73$, $Z=8.53$, $P<0.001$) with a mean angle of 42° . Mean angles for the 16 turtles tested in the reversed field are shown in Fig. 2B. Reversed-field turtles also were nonrandomly oriented ($r=0.50$, $Z=4.00$, $P<0.05$), but with a mean angle of 196° . The distributions of orientation angles under the two field conditions were significantly different (Watson test, $U^2=0.6206$, $P<0.001$), indicating that the magnetic field conditions influenced the orientation of the turtles. In addition, the angular deviation of orientation angles in the geomagnetic field was significantly smaller than that in the reversed field ($P<0.05$, Walraff's modified Wilcoxon–Mann–Whitney U -test; Batschelet, 1981), indicating that orientation angles in the reversed field were more dispersed.

Discussion

When tested in complete darkness under geomagnetic or reversed-field conditions, tethered loggerhead hatchlings demonstrated statistically nonrandom directional preferences. The mean angle of turtles tested in the magnetic field of the earth was 42° (Fig. 2A), whereas the mean angle for the reversed field group was 196° (Fig. 2B). Thus, when the ambient magnetic field was shifted by 180° , the group mean angle showed a corresponding shift of 154° . The distributions in the two fields were significantly different, indicating that the orientation of loggerhead hatchlings is influenced by ambient earth-strength magnetic fields.

Previous attempts to demonstrate magnetic field detection by sea turtles have relied upon conditioning experiments. These have been unsuccessful (Lemkau, 1976) or have yielded ambiguous results (Perry *et al.* 1985). In these earlier studies, however, turtles were required to respond to a briefly imposed magnetic field by pressing paddles or keys within seconds after a stimulus was presented; in

Table 1. Summary of trials and results in the geomagnetic field

Turtle	Time with east light (min)	Time in dark (min)	Number of oriented swimming periods	Time of oriented swimming (min)	Time spent in oriented swimming (%)	Hatching Rayleigh <i>r</i> value	Mean angle (degrees)
1	265	119	4	113	95.0	0.57	50
2	80	89	7	23	25.8	0.04	294
3	115	90	6	69	76.7	0.64	40
4	80	150	8	64	42.7	0.37	44
5	95	136	7	27	19.9	0.48	46
6	81	92	8	59	64.1	0.22	8
7	140	90	9	44	48.9	0.35	291
8	85	93	9	65	69.9	0.18	1
9	140	91	6	19	20.9	0.48	42
10	80	152	8	25	16.5	0.23	82
11	80	90	6	21	23.3	0.13	77
12	80	120	7	29	24.2	0.50	87
13	66	90	12	51	56.7	0.30	38
14	129	180	10	102	56.7	0.14	35
15	93	121	6	19	15.7	0.42	83
16	90	102	5	18	17.6	0.37	70

Time with east light indicates the length of time at beginning of each trial during which the light in magnetic east remained on.

Time in dark indicates the length of time the turtle was monitored in complete darkness, beginning with the point at which it completed its first full circle.

Oriented swimming periods were intervals of 3 min or longer during which a turtle remained in the same 90° sector (see text).

Time of oriented swimming refers to the total time spent in oriented swimming periods; time spent in oriented swimming (%) indicates time spent in oriented swimming out of time in complete darkness.

Mean angle and *r* values were calculated using standard procedures for circular statistics (Batschelet, 1981); however, no statistical procedure exists to evaluate whether an individual turtle was 'oriented' because repeated oriented swimming periods by the same turtle are not statistically independent.

Table 2. *Summary of trials and results in the reversed field*

Turtle	Time with east light (min)	Time in dark (min)	Number of oriented swimming periods	Time of oriented swimming (min)	Time spent in oriented swimming (%)	Hatching Rayleigh r value	Mean angle (degrees)
1	150	157	17	72	45.9	0.20	186
2	91	159	4	15	9.4	0.08	229
3	95	174	8	27	15.5	0.42	117
4	144	176	10	34	19.3	0.19	276
5	104	164	6	20	12.2	0.50	274
6	92	152	8	32	21.1	0.72	313
7	95	138	4	14	10.1	0.45	199
8	95	90	9	33	36.7	0.22	165
9	100	180	4	12	6.7	0.37	245
10	94	90	5	21	23.3	0.24	262
11	96	180	17	62	34.4	0.26	133
12	89	180	7	29	16.1	0.49	160
13	95	180	5	22	12.2	0.50	99
14	125	170	11	38	22.4	0.23	148
15	95	180	4	84	46.7	0.44	143
16	92	180	11	95	52.8	0.17	231

Conventions as in Table 1.

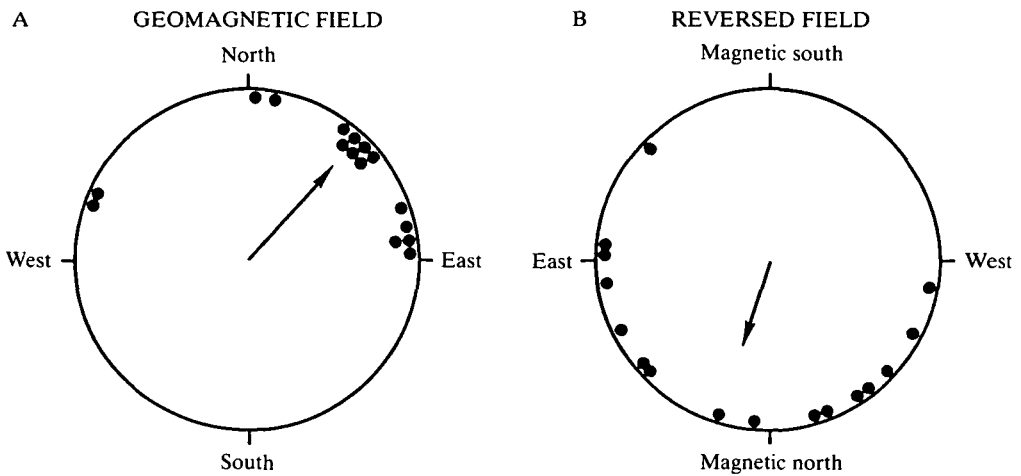


Fig. 2. (A) Results of hatchlings tested in the geomagnetic field. Each data point represents the mean angle of a single hatchling. The arrow indicates the group mean angle and vector. Turtles were significantly oriented (mean angle = 42° , $r=0.73$, $Z=8.53$, $P<0.001$, Rayleigh test). (B) Results in the reversed field. Turtles were significantly oriented (mean angle 196° , $r=0.50$, $Z=4.00$, $P<0.05$, Rayleigh test).

addition, all turtles tested were at least 1 year old. In contrast, the present experiments examined the unconditioned responses of hatchling loggerheads during the first few days after emergence, when turtles are strongly motivated to orient and swim. Moreover, hatchlings were tested in an earth-strength field that remained essentially constant for 1.5 h or more after the light was turned off. These conditions more closely approximate those under which migrating turtles may utilize magnetic cues naturally.

Basis of directional preference

The mean angles for most turtles (14 of 16) tested in the earth's magnetic field were between magnetic north and east (Fig. 2A). The reason for this directional preference is not known. Swimming towards the northeast from beaches at Fort Pierce, however, would displace turtles out to sea and towards the Gulf Stream, their presumed destination (Carr, 1986a).

A northeastward orientation preference could be based upon processes that occur either before or after hatchlings leave the nest. Upon emerging from eggs, turtles may already possess a preference for orienting towards magnetic northeast when other cues are absent. Alternatively, hatchlings could calibrate a magnetic compass on a directional reference available to them from inside the nest. They might, for example, determine the direction of the ocean from the sounds of breaking waves, the vibrations waves generate or other, as yet unidentified, cues. Calibration might thus have been completed before hatchlings were taken to the laboratory.

Another possibility is that the magnetic compass was calibrated on the basis of light cues provided at the beginning of each experiment. Each hatchling was exposed to a light in magnetic east for at least 1 h before it swam in the dark. The light was provided, in part, to simulate the brighter seaward horizon hatchlings encounter in the east when they enter the sea on darkened beaches in the Fort Pierce area. Because turtles were provided with this eastern light, the results are not incompatible with the hypothesis that the magnetic compass is calibrated on light cues. An analogous process, in which one compass system is calibrated or learned with respect to an independent source of directional information, is thought to occur in some birds soon after hatching (Alerstam and Högstedt, 1983).

Dispersion in orientation data

Although groups of hatchlings tested under both geomagnetic and reversed-field conditions were significantly oriented, the orientation angles of turtles tested in the reversed field were significantly more dispersed than those of hatchlings tested in the earth's field. Several factors could have contributed to the increased dispersion in the reversed field. First, the intensity of the reversed field was not precisely uniform throughout the satellite dish; circling turtles were exposed to variations in field intensity that conceivably could have affected the orientation response. No such variations were present in geomagnetic field tests. Second, the intensity of the reversed field decreased slightly (about 2–5 %) over the course of experiments as the wires of the coil became warm, the coil resistance increased and the current through the coil decreased. This change could also conceivably affect orientation adversely. A third possibility is that the rapid 180° field shift at the beginning of the dark period in reversed-field experiments affected hatchlings. Turtles tested in the earth's field were not subjected to any such reversal. None of these possibilities, however, alters the interpretation that earth-strength magnetic fields influenced the orientation of the turtles.

Physiological mechanisms

The physiological mechanisms that enable animals to detect the magnetic field of the earth have not been determined (reviewed by Lohmann and Willows, 1989). Ferrimagnetic material has been detected in several animals known to orient to magnetic fields (reviewed in Kirschvink *et al.* 1985), and such material has been hypothesized to provide the physical basis for the magnetic sense (Kirschvink, 1982). Magnetic material has been detected in hatchling, juvenile and adult green sea turtles (Perry *et al.* 1985). However, direct neurophysiological evidence implicating ferrimagnetic particles in the transduction process for the magnetic sense has not been obtained for any animal.

Several transduction mechanisms that do not involve ferrimagnetic material have also been proposed. Among these is the hypothesis that detection of magnetic fields occurs in photopigments of the eye through a transduction process requiring light (Leask, 1977). Some electrophysiological responses to magnetic fields in the nervous systems of birds cannot be elicited in darkness, suggesting that

light may indeed be necessary for some animals to detect or process geomagnetic cues (reviewed by Semm and Beason, 1990; Wiltschko and Wiltschko, 1988). In the present experiments, however, loggerhead sea turtle hatchlings oriented to magnetic fields in complete darkness. Light is therefore not required for magnetic field detection by loggerhead turtles. The transduction mechanisms underlying the magnetic sense in sea turtles, however, remain unknown.

Magnetic orientation in the ocean

Although the results indicate that hatchling loggerheads can detect the magnetic field of the earth, they do not demonstrate that magnetic orientation is actually used in the offshore migration. Recent field experiments suggest that alternative directional cues take precedence over magnetic cues in the early phases of the migration. Loggerhead hatchlings released between 0.7 and 13 nautical miles from shore, for example, consistently swam towards approaching waves (Salmon and Lohmann, 1989). On days when unusual wind conditions generated waves that moved away from shore, hatchlings reversed their normal seaward orientation and swam towards the beach. If turtles were relying entirely upon magnetic orientation, they presumably would not have reversed swimming direction in response to a reversal in the direction of wave approach. However, the magnetic compass could conceivably supplant orientation to waves at a subsequent point in the migration, or it might continuously function as a 'back-up' system for use when waves and/or other cues are absent.

The ability to detect magnetic fields could be used not only in compass orientation but also in more complex navigational feats. Sea turtles are known to undergo migrations between nesting beaches and feeding grounds separated in some cases by thousands of kilometers (Carr, 1967). How such navigation is accomplished has not been determined. By virtue of magnetoreception, however, turtles could potentially detect several parameters of local magnetic fields that could be used as components of a map sense (Gould, 1985). Some geomagnetic parameters, such as field line inclination (dip angle), horizontal field intensity and vertical field intensity, vary with latitude (Skiles, 1985). Any of these could be used as one component of a map for determining location with respect to a goal (e.g. a nesting beach). Turtles might also have the ability to detect and remember parameters of localized magnetic anomalies unique to specific sites such as feeding, mating, or nesting grounds.

In addition, the north-south 'stripes' of maximum and minimum magnetic intensity detectable over large regions of the open ocean are thought to be used by some cetaceans in migratory navigation (Kirschvink *et al.* 1986). Whales and dolphins often strand at sites where magnetic minima intersect land, suggesting that some marine mammals follow paths of magnetic minima during migrations (Kirschvink *et al.* 1986). Sea turtles may also derive directional information from such magnetic pathways during their long migrations.

The results of the present study suggest that further investigations of orientation by sea turtle hatchlings may prove rewarding. Since hatchlings begin a migration

immediately after emerging from their nests and will orient to several cues, such as magnetic fields, waves (Salmon and Lohmann, 1989) and light (Mrosovsky, 1978), they may provide a useful system for studying the ontogeny of directional preferences, the use of magnetic field detection in migratory navigation and the integration and use of multiple directional cues.

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References

- ALERSTAM, T. AND HÖGSTEDT, G. (1983). The role of the geomagnetic field in the development of birds' compass sense. *Nature* **306**, 463–465.
- BATSCHULET, E. (1978). Second-order statistical analysis of directions. In *Animal Migration, Navigation, and Homing* (ed. K. Schmidt-Koenig and W. T. Keeton), pp. 3–24. New York: Springer-Verlag.
- BATSCHULET, E. (1981). *Circular Statistics in Biology*. London: Academic Press.
- BLAKEMORE, R. AND FRANKEL, R. B. (1981). Magnetic navigation in bacteria. *Scient. Am.* **245**, 58–65.
- CARR, A. (1967). *So Excellent a Fish*. New York: Natural History Press.
- CARR, A. (1986a). Rips, FADS, and little loggerheads. *Bioscience* **36**, 92–100.
- CARR, A. (1986b). New perspectives on the pelagic stage of sea turtle development. *NOAA Tech. Memorandum NMFS-SEFC-190*.
- DEMME, R. J. (1981). The hatching and emergence of loggerhead turtle (*Caretta caretta*) hatchlings. Unpublished MS thesis, University of Central Florida, Orlando, Florida, USA.
- 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.
- FRICK, J. (1976). Orientation and behaviour of hatchling green sea turtles (*Chelonia mydas*) in the sea. *Anim. Behav.* **24**, 849–857.
- HAYES, W. N. AND IRELAND, L. C. (1978). Visually guided behavior of turtles. In *The Behavior of Fish and Other Aquatic Organisms* (ed. D. I. Mostofsky), pp. 281–317. New York: Academic Press.
- 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.
- KIRSCHVINK, J. L. (1982). Birds, bees, and magnetism. *Trends Neurosci.* **5**, 160–167.
- KIRSCHVINK, J. L., DIZON, A. E. AND WESTPHAL, J. A. (1986). Evidence from strandings for geomagnetic sensitivity in cetaceans. *J. exp. Biol.* **120**, 1–24.
- KIRSCHVINK, J. L., JONES, D. S. AND MACFADDEN, B. J. (eds) (1985). *Magnetite Biomineralization and Magnetoreception in Organisms*. New York: Plenum Press.
- LEASK, M. J. M. (1977). A physicochemical mechanism for magnetic field detection by migrating birds and homing pigeons. *Nature* **267**, 144–145.
- LEMKAU, P. J. (1976). An attempt to condition the green sea turtle, *Chelonia mydas*, to magnetic fields. MS thesis, University of Rhode Island, Kingston, Rhode Island, USA.

- LOHMANN, K. J. (1985). Geomagnetic field detection by the western Atlantic spiny lobster, *Panulirus argus*. *Mar. Behav. Physiol.* **12**, 1–17.
- LOHMANN, K. J. AND WILLOWS, A. O. D. (1987). Lunar-modulated geomagnetic orientation by a marine mollusk. *Science* **235**, 331–334.
- LOHMANN, K. J. AND WILLOWS, A. O. D. (1989). Magnetic field detection and its neurobiological mechanisms. *Neuroscience Year* (Supplement 1 to the *Encyclopedia of Neuroscience*), pp. 94–97. Boston: Birkhauser.
- MATHER, J. G. AND BAKER, R. R. (1981). Magnetic sense of direction in woodmice for route-based navigation. *Nature* **291**, 152–155.
- MATHIS, A. AND MOORE, F. R. (1988). Geomagnetism and the homeward orientation of the box turtle *Terrapene carolina*. *Ethology* **78**, 265–274.
- MROSOVSKY, N. (1968). Nocturnal emergence of sea turtles: control by thermal inhibition of activity. *Nature* **220**, 1338–1339.
- MROSOVSKY, N. (1978). Orientation mechanisms of marine turtles. In *Animal Migration, Navigation, and Homing* (ed. K. Schmidt-Koenig and W. T. Keeton), pp. 413–419. New York: Springer-Verlag.
- MROSOVSKY, N. AND KINGSMILL, S. F. (1985). How turtles find the sea. *Z. Tierpsychol.* **67**, 237–265.
- PERRY, A., BAUER, G. B. AND DIZON, A. E. (1985). Magnetoreception and biomineralization of magnetite in amphibians and reptiles. In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L. Kirschvink, D. S. Jones and B. J. MacFadden), pp. 439–453. New York: Plenum Press.
- PHILLIPS, J. B. (1986). Two magnetoreception pathways in a migratory salamander. *Science* **233**, 765–767.
- QUINN, T. P. (1980). Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *J. comp. Physiol. A* **137**, 243–248.
- QUINN, T. P. AND BRANNON, E. L. (1982). The use of celestial and magnetic cues by orienting sockeye salmon smolts. *J. comp. Physiol. A* **147**, 547–552.
- RUBENS, S. M. (1945). Cube-surface coil for producing a uniform magnetic field. *Rev. Sci. Instrum.* **16**, 243–245.
- SALMON, M. AND LOHMANN, K. J. (1989). Orientation cues used by hatchling loggerhead sea turtles (*Caretta caretta* L.) during their offshore migration. *Ethology* **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.
- SEMM, P. AND BEASON, R. C. (1990). Sensory basis of bird orientation. *Experientia* **46**, 372–378.
- 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.
- WALKER, M. M. AND BITTERMAN, M. E. (1985). Conditioned responding to magnetic fields by honey bees. *J. comp. Physiol. A* **157**, 67–71.
- WILTSCHKO, W. AND WILTSCHKO, R. (1988). Magnetic orientation in birds. In *Current Ornithology*, vol. 5 (ed. R. F. Johnston), pp. 67–121. New York: Plenum Press.