

## Functional Autonomy of Land and Sea Orientation Systems in Sea Turtle Hatchlings

KENNETH J. LOHMANN<sup>1</sup>\*, MICHAEL SALMON<sup>2</sup>, AND JEANETTE WYNEKEN<sup>2</sup>

<sup>1</sup>*Neural and Behavioral Biology Program, University of Illinois, Urbana, Illinois 61801, and*

<sup>2</sup>*Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida 33431-0991*

Sea turtle hatchlings emerge from underground nests on oceanic beaches and immediately confront two separate problems in orientation. First they must locate the ocean and crawl to it; then they must orient offshore while they swim out to sea in a migration lasting several days.

Visual cues guide hatchlings from the nest to the sea (1, 2), but little is known about the cues used by turtles in the ocean. Nevertheless, the crawl across the beach has long been considered essential to swimming orientation because hatchlings released offshore without a crawl reportedly fail to orient seaward (3, 4). Here we report that hatchling leatherback (*Dermochelys coriacea*) and green (*Chelonia mydas*) sea turtles released offshore consistently swam toward approaching waves and oceanic swells. Wave tank experiments confirmed that swimming hatchlings oriented into waves. A crawl across the beach was not a prerequisite for wave orientation in either the field or lab, indicating that hatchling sea turtles possess two separate orientation systems, each based on different sensory cues and capable of functioning autonomously. The first guides hatchlings on land to the sea; the second, based on wave detection, functions during the ocean migration.

In five field experiments with green turtles and five others with leatherbacks, we monitored the swimming orientation of hatchlings released at various distances offshore near Fort Pierce, Florida. A total of 45 green turtle and 48 leatherback hatchlings were tested. All experiments were conducted between July and September in 1988 and 1989.

Hatchlings were obtained from nests deposited on beaches in the Fort Pierce area. Nests were checked daily

until a depression formed above the eggs (indicating the eggs had hatched and an emergence would probably occur that evening). We then carefully dug in the sand and removed hatchlings, placed them into styrofoam boxes, and transported them by motorboat to testing sites 2.0-30.0 km offshore. All turtles were tested and released within 48 h of capture.

Each turtle was placed into a nylon-lycra harness (5) tied by a short line to the side of a spherical, half-submerged floating buoy (Fig. 1A). The buoy was attached by another line to the submerged center of a floating cage (Fig. 1A). Swimming hatchlings exerted sufficient force to easily rotate the buoy. Markings on the buoy were clearly visible from the boat, enabling observers to determine the orientation of the buoy (and thus of the turtle) as the hatchling swam in place. Previous reports have indicated that migrating hatchlings do not change course or alter their behavior in response to nearby boats (3, 5, 6). In the present experiments, driving the boat around the cage at distances of 10-20 m also had no detectable effect on hatchling orientation.

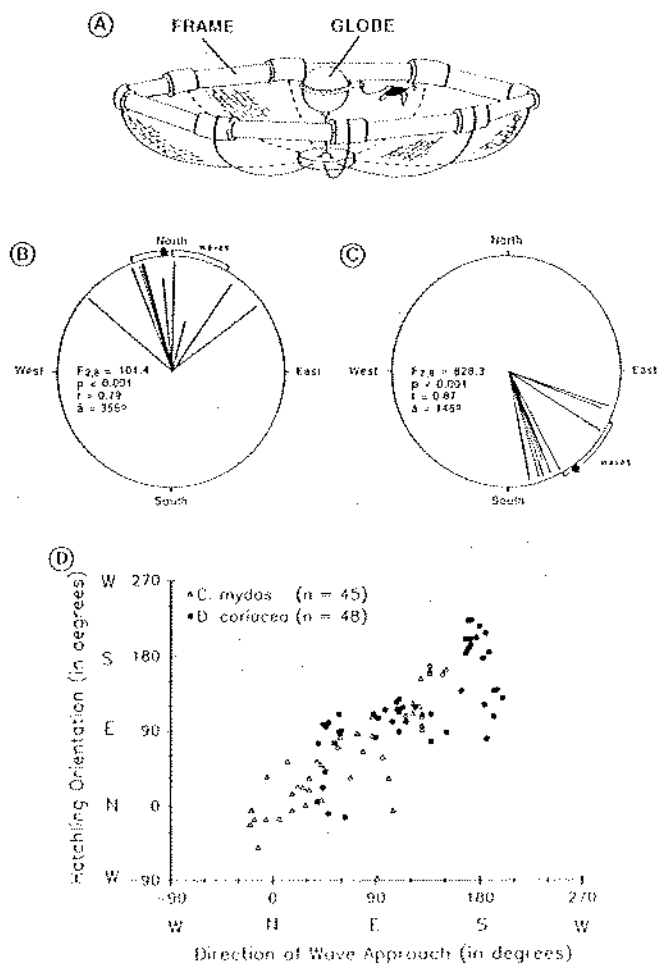
When released into the cage, harnessed hatchlings often dove or circled for their first few minutes in the water. After 2-5 min, nearly every hatchling established an essentially constant swimming course from which it only occasionally deviated. Once a turtle settled on its course (or 6 min elapsed), its orientation was determined once each minute for five minutes with a sighting compass. These five readings were used to calculate the mean angle and vector length for each hatchling, following standard procedures for circular statistics (7).

Hatchlings consistently oriented into approaching waves in all experiments, regardless of distance from shore. Data from two different green turtle experiments, in which waves approached from nearly opposite directions, are

Received 18 April 1990; accepted 20 July 1990.

\* Present address: Friday Harbor Laboratories, 620 University Road, Friday Harbor, Washington 98250.





**Figure 1.** Results of field experiments with the floating cage. (A) The floating orientation cage, globe, and tethered turtle. The cage was constructed of eight equal lengths of PVC pipe (5 cm diameter) fixed end to end to form an octagonal frame 1.12 m in diameter. The frame floated in the water so that only about 1 cm of its upper surface was exposed. Stainless steel supports converged on a baseplate 25 cm below the water. The hatchling was tethered to a buoyant globe anchored to the baseplate by a thin, nylon line. The turtle could thus swim in any direction, while markings on the globe enabled observers in a nearby boat to monitor its swimming orientation. The bottom of the cage was encased in a mesh net to exclude predators. A detailed description of the floating cage is provided elsewhere (6).

(B) Results from an experiment with green turtle hatchlings in which waves approached from approximately north. The range of wave directions during the experiment is indicated by marks outside the edge of the circle. The mean angle of orientation for each hatchling is indicated by a line originating at the circle center (7). Line length is proportional to mean vector length, with a line reaching the edge of the circle corresponding to  $r = 1$ . Long lines thus indicate consistent orientation toward a single direction throughout the test period; shorter lines indicate more directional variability.  $F$  and  $r$  values were calculated with the Hotelling test (7). The mean angle of the group ( $\bar{\alpha}$ ) is indicated by the large arrow outside of the circle. The coastline was approximately parallel to a line defined by the  $343^\circ$ – $163^\circ$  axis (westward, or to the left) but was not visible because we were 28–30 km from shore.

(C) A second experiment with green turtles in which waves approached from approximately southeast. Conventions as in (B).

(D) Summary of the five green turtle and five leatherback orientation experiments conducted 2.0–30.0 km from shore. Orientation of each hatchling is plotted as a function of direction of wave approach during the test. Direction of wave approach was defined as the mean direction of propagation for all wave types present. One or more of three wave types (swells, waves, and wind ripples) were present in all trials. Oceanic swells are generated by prevailing winds over large expanses of water in the open ocean; near Fort Pierce, swells consistently approach from  $70^\circ$ – $140^\circ$

shown in Figures 1B and C. These results are representative of responses shown by both species. The orientation angles of all hatchlings are plotted as a function of wave approach direction in Figure 1D. Jupp-Mardia circle-circle correlation analysis (7) indicated that wave direction and hatchling orientation were significantly ( $P < 0.001$  for each species) related.

None of the hatchlings used in these experiments crawled across the beach; all were taken directly from the nest to the testing site. Thus, turtles can clearly orient in the ocean without crawl experience. But hatchlings might still acquire directional information during the crawl that could alter their orientation while swimming. Turtles with crawl experience, for example, might use different orientation cues than those released offshore without a crawl, or the two groups might use the same guideposts in different ways.

To examine these possibilities, hatchlings with and without beach crawl experience were tested offshore in the floating cage on the night of their expected emergence. Hatchlings were removed from nests before sunset and placed into one of two styrofoam boxes. After sunset both boxes were transported to a nesting beach. The hatchlings in one box were released on dry sand at distances of 10–20 m from the edge of the water. They were permitted to crawl to the wet sand at the edge of the wave wash zone, then retrieved and placed into styrofoam coolers. The lid of the second box was removed during the time the first group was crawling, so that the turtles inside could crawl in the box with a view of the sky. Thus, turtles in both groups crawled, but only one group crawled across the beach.

The orientation of hatchlings with and without a beach crawl was statistically indistinguishable for both green turtles (Fig. 2A–B; Watson test,  $U^2 = 0.097$ ,  $P > 0.20$ ) and for leatherbacks (Fig. 2C–D;  $U^2 = 0.045$ ,  $P > 0.20$ ). Nearly all of the turtles swam in the general direction of approaching waves, suggesting that hatchlings released

(E–SE) during the summer and are largely unaffected by weather conditions near land. Waves generated by local wind patterns were often present and usually moved in directions similar (within  $80^\circ$ ) to those of swells. A few minutes after abrupt changes in wind direction, wind ripples 1–5 cm in height tracked the new wind direction, while larger "old" waves continued to track the previous wind direction. No trials were conducted under stormy conditions when the various wave types could not be clearly resolved or when waves (or swells) exceeded 1.5 m in height. The direction of each wave type was measured easily by sighting down the axis of wave propagation with a digital hand-bearing "Autohelm" compass. Because we had no a priori reason to consider one wave type more important than another, we calculated a mean direction of wave approach for this study. However, hatchlings may actually orient only to the largest waves present (regardless of type) while ignoring the others. For a detailed discussion of wave types, see (10).

Circle-circle correlation analysis (7) indicated that direction of wave approach and hatchling orientation were significantly related (see text). There was no evidence that responses varied with distance from shore.

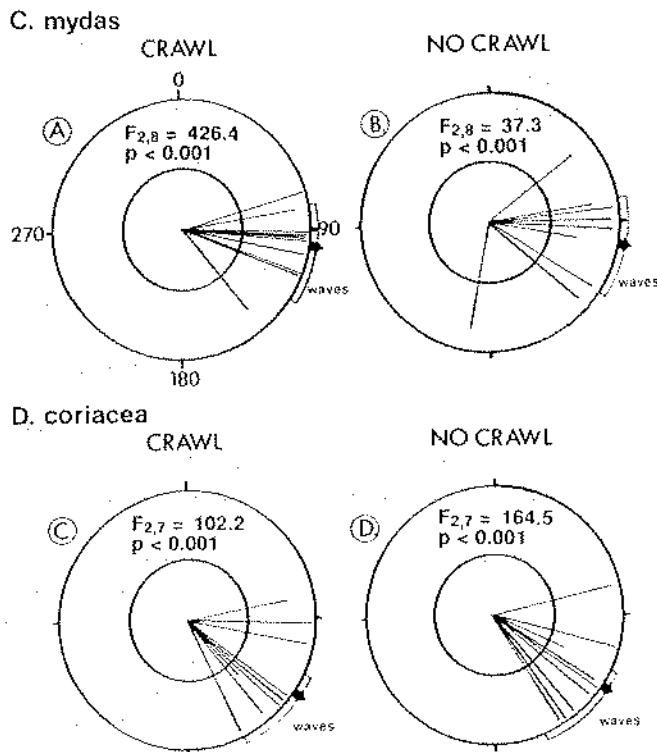


Figure 2. Results of offshore orientation experiments with hatchlings that had and had not crawled across a beach prior to testing.

(A) Results of green turtle hatchlings that crawled across the beach. Inner circle indicates  $r$  value of 0.5 (outer circle still corresponds to  $r = 1.0$ ). All other conventions as in Figure 1B. Mean angle for the group is  $99^\circ$ .

(B) Results of green turtle hatchlings deprived of a beach crawl. Conventions as in Figure 2A. Mean angle for the group is  $100^\circ$ .

(C) Results of leatherback hatchlings that crawled across the beach. Conventions as in Figure 2A. Mean angle for the group is  $124^\circ$ .

(D) Results of leatherback hatchlings deprived of a beach crawl. Conventions as in Figure 2A. Mean angle for the group is  $124^\circ$ .

offshore orient toward waves regardless of whether they first experienced a beach crawl.

To study the relationship between turtle orientation and waves more rigorously, we monitored the orientation of hatchlings swimming in a wave tank. Under dim light, each turtle was tethered to a central post (made of nylon fishing line strung vertically from the bottom of the tank to a rod across the top). Thus, hatchlings could swim in any direction in the wave tank but could not contact the sides.

All lights were then turned off except for a single infrared source [a Kodak darkroom light with a 40 W bulb covered by an Edmunds infrared transmitting filter (#8247-29-1)]. After a 5-min acclimation period, an observer using a night vision scope recorded the orientation of each hatchling at 30-s intervals for 5 min; these measurements were used to calculate the mean angle and vector for each turtle (7). One group of hatchlings (for each species) was tested with the wave tank motor off so that

no waves were generated and the room was silent. A second group was tested with the motor running but the drive disconnected so that hatchlings were exposed to motor sounds and vibrations, but not to waves. The third group was tested with the motor on and the drive engaged so that waves were generated.

Results for green turtles and leatherbacks were qualitatively identical. Neither species was significantly oriented in the absence of waves (Fig. 3). When waves were present, however, the hatchlings oriented toward the direction of wave approach (Fig. 3). These experiments confirmed that hatchling sea turtles can use waves as an orientation cue, even in the absence of visible light.

Our results suggest that sea turtle hatchlings sequentially employ two separate orientation systems, each based on different cues. While on the beach, hatchlings find the sea by seeking out bright, open horizons (1, 2). Our field and wave tank experiments provide evidence that hatchlings released in the ocean orient by swimming toward waves. Because sea-finding orientation is not a prerequisite for wave orientation, the land and sea orientation systems can function independently.

Our results do not demonstrate, however, that the two systems never interact under natural conditions. Immediately after entering the sea, for example, hatchlings might use visual cues to establish an offshore course. Later, when visual contact with land is lost, hatchlings could maintain their orientation by swimming at a fixed angle relative to waves. Visual cues experienced during either the beach crawl or near land might also be critical for hatchlings that emerge on nesting beaches surrounded by exceedingly calm seas. Additional experiments are required to determine whether the land and sea orientation systems are completely independent under all conditions, or if they interact in some way as hatchlings migrate away from land.

During daylight hours, especially near shore, local winds can generate waves which induce hatchlings to swim in directions other than directly offshore (Fig. 1D). However, Florida sea turtle hatchlings nearly always emerge from nests and enter the sea shortly after dark (8, 9). Oceanic swells, produced by prevailing easterly winds, are the prevalent waves during this time (10). The swells move toward the Florida coast, where the propagation direction becomes oriented perpendicular to the shore as waves enter shallow water and approach a beach (11). Wave propagation direction thus provides a consistent, reliable cue for offshore orientation during the time hatchlings usually enter the ocean.

Several marine molluscs (12, 13) and crustaceans (14, 15) can orient using waves or wave surge in shallow water near shore. Sea turtle hatchlings, however, continued to

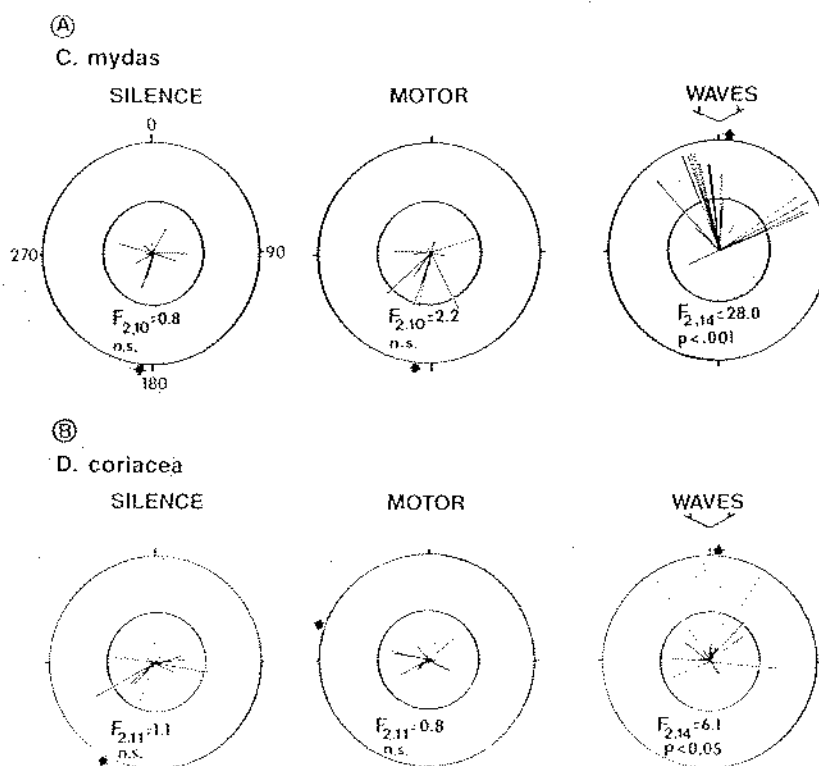


Figure 3. Results of the wave tank experiments: A. Results of green turtle hatchlings; B. Results of leatherback hatchlings. All conventions follow those in Figure 2A. For each species, "Silence" indicates results of hatchlings tested with the wave tank motor off; "Motor" indicates the motor was on but the drive was disconnected so no waves were produced; "Waves" indicates results of hatchlings tested when waves were generated (waves approached from 0° top of the diagram). Each species was significantly oriented only when waves were present. The mean angles in the two wave groups (far right, upper and lower) were directed almost straight toward the direction of wave approach.

**WAVE TANK.** The wave tank, located at the Florida Institute of Technology in Melbourne, Florida, was 9.1 m in length, 0.9 m high, and 0.6 m in width. It was filled with water to a depth of 0.5 m. A paddle at one end was driven by a DC motor. A sloping plywood platform 4.9 m in length at the opposite end absorbed wave energy and minimized wave reflection. Hatchlings were tethered (see text) so they could swim in any direction while an observer watched with a night vision scope through a circular opening in a styrofoam sheet wedged across the top of the tank. The styrofoam was marked in 5° increments providing a reference for determining orientation. Throughout the experiments we alternated between trials under the three treatments described in the text (silence, motor, waves) in semi-random order (blocks of 1–3 trials under one condition were followed by similar blocks of trials under the other two conditions). Each hatchling was tested only once under one of the three conditions.

Waves generated in green turtle experiments were 5 cm peak-to-pough in height (frequency, about 40 waves/min); waves in leatherback experiments were 2–3 cm in height, also at 40 waves/min. We have observed waves of these approximate heights and frequencies at sea on calm days during the summer at Fort Pierce. Natural waves during the summer are only occasionally smaller than this and are often considerably (2–50 times) larger.

swim toward waves even when out of sight of land (beyond about 18 km from shore), indicating that wave propagation direction can be used by animals as a cue for orientation in the open ocean. This cue might well be used by other long-distance ocean migrants such as fish and cetaceans.

The responses of the hatchlings reported here must be viewed as the earliest manifestations of a sophisticated orientation system, one that allows these animals as adults to complete migrations between nesting sites and feeding grounds located hundreds or thousands of kilometers apart (16, 17). Further ontogenetic analysis may provide

insight into how an orientation system that initially guides hatchlings offshore develops into one that provides adults with the ability to complete complex navigational tasks.

#### Acknowledgments

We thank M. Flaherty, J. Norton, and T. H. Frazzetta for technical assistance, B. Dally and the Florida Institute of Technology for the use of the wave tank, E. Martin and R. Ernest for locating turtle nests, C. M. F. Lohmann for critically reading the manuscript, and the Harbor Branch Oceanographic Institution for providing lab and

tank space. Supported by NIH grant MH18412-01 (post-doctoral training grant, Univ. of Illinois) and NSF grant BNS-87-07173. Research was conducted under Florida DNR special permit TP 073.

### Literature Cited

1. Mrosovsky, N. 1978. Orientation mechanisms of marine turtles. Pp. 413-419 in *Animal Migration, Navigation, and Homing*. K. Schmidt-Koenig and W. T. Keeton, eds. Springer-Verlag, Berlin.
2. Limpus, C. 1971. Sea turtle ocean finding behaviour. *Search* 2(10): 385-387.
3. Frick, J. 1976. Orientation and behaviour of hatchling green sea turtles (*Chelonia mydas*) in the sea. *Anim. Behav.* 24: 849-857.
4. Mrosovsky, N. 1983. *Conserving Sea Turtles*. British Herpetological Society, London.
5. Salmon, M., and J. Wyneken. 1987. Orientation and swimming behavior of hatchling loggerhead turtles *Caretta caretta* L. during their offshore migration. *J. Exp. Mar. Biol. Ecol.* 109: 137-153.
6. Salmon, M., and K. J. Lohmann. 1989. Orientation cues used by hatchling loggerhead sea turtles (*Caretta caretta* L.) during their offshore migration. *Ethology* 83: 215-228.
7. Batschelet, E. 1981. *Circular Statistics in Biology*. Academic Press, London.
8. Bustard, R. 1973. *Sea Turtles: Natural History and Conservation*. Taplinger Publ., New York.
9. Demmer, R. J. 1981. *The Hatching and Emergence of Loggerhead Turtle (*Caretta caretta*) Hatchlings*. M.S. thesis, Univ. Central Florida, Orlando, Florida.
10. Bascom, W. 1980. *Waves and Beaches*. Anchor Press Doubleday, New York.
11. Denny, M. W. 1988. *Biology and the Mechanics of the Wave-Swept Environment*. Princeton University Press, Princeton, New Jersey.
12. Gendron, R. P. 1977. Habitat selection and migratory behaviour of the intertidal gastropod *Littorina littorea* (L.). *J. Anim. Ecol.* 46: 79-92.
13. Hamilton, P. V., and B. J. Russell. 1982. Field experiments on the sense organs and directional cues involved in offshore-oriented swimming by *Aplysia brasiliana* (Rang) (Mollusca: Gastropoda). *J. Exp. Mar. Biol. Ecol.* 56: 123-143.
14. Walton, A., and W. Herrnkind. 1977. Hydrodynamic orientation of spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): wave surge and unidirectional currents. Proceedings of the Annual Northeastern Mtg. of the Animal Behavior Soc. 1977 Plenary Papers. Memorial University of Newfoundland, Marine Sci. Res. Lab. Tech. Report No. 20: 184-211.
15. Nishimoto, R. T., and W. F. Herrnkind. 1978. Directional orientation in blue crabs, *Callinectes sapidus* Rathburn: escape responses and influence of wave direction. *J. Exp. Mar. Biol. Ecol.* 33: 93-112.
16. Carr, A. 1965. The navigation of the green turtle. *Sci. Am.* 212(5): 78-86.
17. Carr, A. 1984. *The Sea Turtle. So Excellent a Fish*. University of Texas Press, Austin.