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Orientation by hatchling loggerhead sea turtles *Caretta caretta* L. in a wave tank

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Abstract: Within minutes after emerging from underground nests, sea turtle hatchlings *Caretta caretta* L. locate and crawl to the ocean, enter the surf, then maintain oriented courses that lead them out to sea even after they no longer detect land. The cues hatchlings use, while the subject of some speculation, were unknown. Recent field studies show that hatchlings orient toward surface waves. Our experiments, conducted in a wave tank, demonstrate that loggerhead sea turtle hatchlings maintain headings toward oncoming waves. The response does not depend upon visual cues as it persists in the absence of visible light.

Key words: *Caretta caretta*; Orientation; Sea turtle; Wave orientation; Wave tank

INTRODUCTION

Each summer and fall loggerhead sea turtle hatchlings *Caretta caretta* L. emerge from underground nests located on ocean beaches. Emergence usually occurs at night (Hendrickson, 1958; Mrosovsky 1968; Witherington et al., in press). Evidence suggests that hatchlings from Florida's east coast beaches migrate to the Gulf Stream where they find refuge within floating sargassum weed (Carr, 1986a).

Light cues from the seaward horizon are thought to guide hatchlings from the nest to the ocean (reviewed by Hayes & Ireland, 1978; Mrosovsky & Kingsmill, 1985). However, little is known about the orientation mechanisms used by hatchling turtles once they enter the sea. Turtles continue to swim toward the open sea, even when distant lights make the shoreward horizon brighter (Hayes & Ireland, 1978; Salmon & Lohmann, 1989). Thus differences in horizon brightness, thought to be critical for guiding hatchlings from the nest to the sea, appear unlikely to guide swimming turtles offshore (Frick, 1976).

Witham (1980) proposed that hatchlings might establish and maintain seaward bearings using wave cues. Recent field experiments indicate that loggerhead hatchlings consistently swim toward approaching waves and swells (Salmon & Lohmann, 1989).

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These field experiments provided correlations between turtle headings and surface wave direction under field conditions.

In the present study we report on orientation by loggerhead hatchlings in a wave tank where wave parameters and other conditions could be rigorously controlled.

METHODS

ANIMALS

Loggerhead hatchlings (*n* = 87) were collected from 12 nests relocated to an on-the-beach hatchery 17 km south of the Fort Pierce Inlet, Florida, USA. All hatchlings were obtained from nests between 1600 and 1900, several hours before their evening emergence. They were immediately placed in a covered styrofoam box and brought to the laboratory where they were held for experiments run the same night.

WAVE TANK

Experiments were conducted using a wave tank (Fig. 1) located in a large windowless room at the Florida Institute of Technology, Melbourne, Florida. The tank (9.07 m in length, 0.93 m high, and 0.6 m wide) was constructed of glass and supported by an external steel frame. A paddle at one end produced waves and was driven by an external DC motor (Dayton 3/4 hp, model 2M169C). A sloping plywood platform (4.88 m long) at the opposite end of the tank absorbed wave energy and minimized wave reflection. The tank was filled with freshwater to a depth of 0.5 m. We observed no differences in hatchling behavior when tested in fresh- or saltwater.

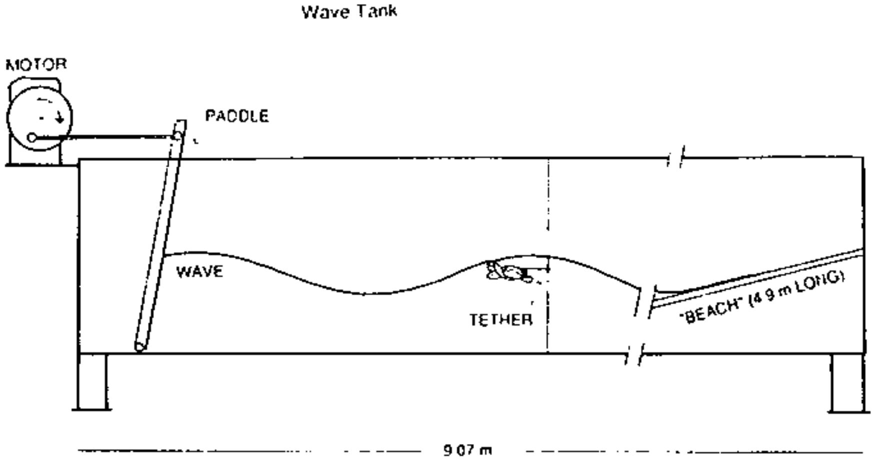

Fig. 1. Wave tank showing tethering system for turtle. Hatchling wears a nylon-lycra harness tethered by a short line to a longer, vertically oriented axis positioned between tank walls. Hatchlings can swim in any direction without touching walls and can dive and surface at will.

An aluminum rod was placed across the top of the wave tank 2.2 m away from the paddle. A nylon line tied to the rod was tightly fastened to a flat weight resting on the tank bottom, forming a vertical axis between the tank side walls. To attach turtles to this axis, each hatchling was placed in a nylon-lycra harness (Salmon & Wyneken, 1987). Another short (10 cm long) line was used to tether the harness to the nylon axis (Fig. 1). This arrangement allowed the hatchling to dive, surface and swim in any direction without contacting the sides of the tank.

A circular frame, wedged between the tank walls above the turtle, was marked in 10° increments with 0° toward the paddle, 180° away from the paddle, and the 90°/270° axis to the right and left sides of the tank, respectively. The vertical nylon line passed through the center of the frame opening. The turtle's orientation to the nearest 5° was determined by sighting its swimming direction from above, relative to the frame markings.

PROCEDURE AND TREATMENTS

All experiments were conducted between 1930 and 0430, when most hatchlings enter the ocean and swim offshore (Witherington et al., in press). Each turtle was released in the tank facing 90° to the right of the heading faced by the preceding animal upon its release in the tank. Hatchlings were first "screened" by exposing them to a dim (15 W) light for 2 min. The light was suspended against the outside of the tank, just above water level. Hatchlings typically will swim toward light sources under laboratory conditions (Salmon & Wyneken, 1987). We used this response to determine if individuals were developmentally and motivationally competent to orient. Only seven of the 87 screened animals failed to commence swimming or show a phototaxis, and so were excluded from experiments.

After screening, the turtles were exposed to the following treatments while swimming in the absence of light. In the "silent" treatment, hatchlings swam in the tank with the motor driving the paddle turned off. This treatment controlled for the possibility that hatchlings could respond to unanticipated orientation cues.

In the "motor" treatment, hatchlings swam in the tank with the motor running but the paddle disconnected from the drive mechanism. This procedure controlled for the possibility that hatchlings might obtain orientation cues from sounds or vibrations generated by the motor while waves were produced.

In the experimental ("wave") treatment, the waves generated (3 cm peak to trough, 2 m in wavelength, 44 waves $\cdot$ min^{-1}) were within the range commonly observed under field conditions. In the field, hatchlings respond to wind ripples, minimally 1 cm in height, and continue to respond to waves up to 1 m in height (Salmon & Lohmann, 1989). No observations were made when waves exceeded 1 m.

Two sets of experiments were conducted using two separate groups of hatchlings. In the first set, hatchling orientation was observed by briefly (1–2 s) illuminating each turtle from above with a dim flashlight. The light beam was focused on an area slightly larger than the turtle's body. In the second set of experiments turtles were illuminated by a Kodak darkroom light equipped with a 40-W incandescent bulb and covered by an Edmund Scientific IR-transmitting filter (No. 8247–29–1). The orientation of this group of hatchlings was observed with a night-vision scope (Star Tron MK 202). In both sets of experiments, one of us determined the turtle's orientation every 30 s over a 5-min period while another, behind an opaque screen, timed the intervals and recorded the data. All observation periods were preceded by a 2-min exposure to the treatment without recording data (an acclimation period).

Experiments using visible light flashes

Following screening, each turtle in this set was exposed to one, two or all three of the treatments. When hatchlings were exposed to two or three treatments, the exposure sequence was varied. Turtles were used in more than one test because limited numbers of animals were available when we had access to the tank. A total of 26 hatchlings were used in this set of experiments. Sample sizes for treatments were as follows: silent, $n = 8$; motor, $n = 10$; and waves, $n = 15$.

Experiments using IR light

The first set of experiments demonstrated that hatchlings could orient using wave cues. However, turtles might have detected waves visually during brief light flashes. To determine if hatchlings could orient to waves in the absence of visible light, we repeated the experiments under IR illumination with a second group of hatchlings ($n = 54$, $18 \cdot \text{treatment}^{-1}$). After initial screening, each hatchling was exposed to only one treatment. Over the several evenings needed to complete these tests, we exposed the same number of turtles to each treatment. As a result, individuals from several clutches contributed equally to the data in each treatment category.

STATISTICAL PROCEDURES

Standard circular statistical procedures (Zar, 1984) were used to calculate (1) a single mean angle for each animal based upon its 10 consecutive headings, and (2) a second-order mean angle for all animals used in one treatment. A Hotelling one-sample test was then used to determine if turtles in a given treatment were significantly oriented. The Watson U^2 test was used to compare similar treatments in the two sets of experiments. This analysis allowed us to determine (1) if flashes of visible light, or (2) if multiple testing of individuals in the "light flash" experiments affected turtle orientation behavior.

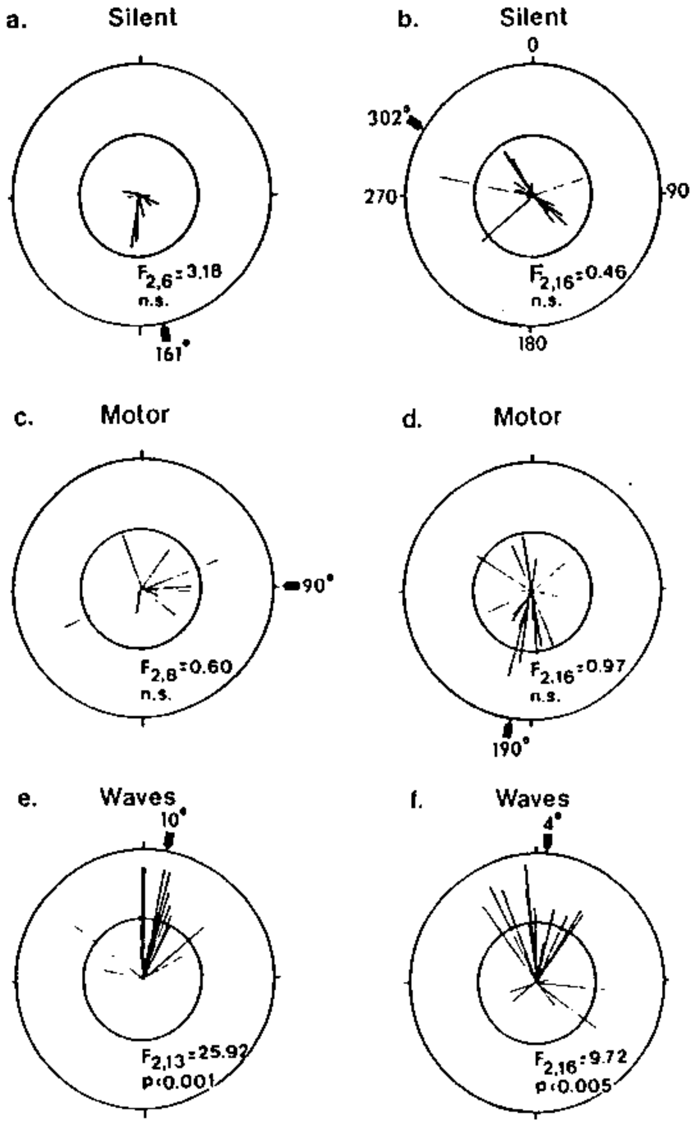

Fig. 2. Orientation of subjects in three treatments. Left circles (a, c, e): hatchlings whose orientation was observed during visible light flashes; right circles (b, d, f): hatchlings whose orientation was observed under IR light. For each diagram, 0° is toward paddle generating waves; 180° is away from paddle. Paddle's geomagnetic orientation relative to vertical axis was approximately east (83°).

Arrow outside each circle indicates mean (second order) angle for all subjects in that treatment. Each hatchling's mean orientation is indicated by a line, originating at center of circle. Line length is proportional to r value which varies from 0 (center of circle) to 1 (border of outer circle). Inner circle: r value = 0.5.

RESULTS

SILENT TREATMENT

In both sets of experiments individuals tended to circle continuously. Neither the eight hatchlings monitored by flashlight nor the 18 tested under IR light were significantly oriented (Fig. 2a, Hotelling $F_{2,6} = 3.18$, NS; Fig. 2b, Hotelling $F_{2,16} = 0.46$, NS). The two experiments (IR light vs. flashes of visible light) did not differ significantly (Watson $U^2 = 0.1675$).

MOTOR TREATMENT

Neither the 10 turtles that were monitored with flashes of visible light nor the 18 observed under IR light were significantly oriented (Fig. 2c, Hotelling $F_{2,8} = 0.6$, NS; Fig. 2d, Hotelling $F_{2,16} = 0.97$, NS). There were also no statistically significant differences between the two methods of data collection (Watson $U^2 = 0.0748$, NS).

WAVE TREATMENT

Nine of 15 hatchlings monitored by flashlight held relatively constant courses toward waves (Fig. 2e) while six turtles showed more variable headings. The group was strongly oriented toward the waves with a mean angle of 10° (Hotelling $F_{2,13} = 25.92$, $P < 0.001$).

Thirteen of the 18 hatchlings monitored under IR light consistently swam into the waves. The remaining five hatchlings either circled continuously or held several course headings. As a group the hatchlings were significantly oriented toward the waves (Fig. 2f, mean angle = 4°; Hotelling $F_{2,16} = 9.72$; $P < 0.005$). The two methods of data collection did not differ statistically (Watson $U^2 = 0.1675$, NS).

DISCUSSION

These experiments demonstrate that loggerhead hatchlings, when they first enter the water, are strongly predisposed to orient toward surface waves. This response does not depend upon observing the waves visually. Even when turtles are tested under IR illumination (which no vertebrate can detect with photoreceptors), they continue to swim toward approaching waves.

There were no statistically significant differences between "light flash" and IR light treatment groups. This result indicates that neither repeated testing nor exposure to flashes of visible light alter response patterns shown by experimental and control groups.

In experiments conducted on the ocean (Salmon & Lohmann, 1989), hatchlings oriented toward approaching waves or swells. When both waves and swells were present and approached from somewhat different directions, hatchlings selected courses which averaged between the two sources of surface stimuli. Orientation responses to the relatively uniform surface waves generated under laboratory conditions appeared weaker (although still statistically significant) than those observed in the field. Further analyses will be required to determine why. One possibility is that the amplitude, wavelength or frequency of the tank-generated waves was not optimal for the orientation response. Another is that under natural conditions, hatchlings use both mechanical and visual cues to detect surface waves but can continue to orient toward waves when light is absent. Low levels of light are always present over the ocean at night, even when the sky is cloud-covered. These permit a human observer, and presumably a turtle, to see approaching waves even on the darkest evenings. A third possibility is that other cues, yet to be identified, might enhance the ability of hatchlings to respond to waves.

Several species of invertebrates are known to utilize wave surge cues for underwater orientation. Among these are the horseshoe crab *Limulus* (Rudloe & Herrnkind, 1976), the blue crab *Callinectes* (Nishimoto & Herrnkind, 1978), the snail *Littorina* (Gendron, 1977), the sea hare *Aplysia* (Hamilton & Russell, 1982), and the spiny lobster *Panulirus* (Walton & Herrnkind, 1977; Herrnkind, 1980). In some instances, these responses also persist when tests are conducted in wave tanks (Gendron, 1977; Nishimoto & Herrnkind, 1978; Rudloe & Herrnkind, 1980).

This study provides conclusive evidence that a marine vertebrate can use surface waves as an orientation cue. Field releases showed correlations between hatchling heading and wave propagation direction in the open ocean (20–25 km from shore; Salmon & Lohmann, 1989). Cook (1984) suggested that salmonid fishes might gain valuable spatial information from surface waves during their open sea migrations. He also suggested that fish close to the surface might use accelerations to determine wave propagation direction. It is clear that hatchlings can discriminate the direction of wave propagation but how they do so remains unknown.

Oceanic swells are produced by prevailing wind belts (Bascom, 1980). These, in turn, are specific to particular latitudes. Thus orientation with respect to surface waves can be a potentially important cue for any open sea migrant. Loggerhead hatchlings migrating from the east coast of Florida encounter waves and swells generated by prevailing winds from the east or southeast (Anonymous, 1988). By swimming toward them hatchlings should eventually reach the Gulf Stream, their presumed goal (Carr, 1986a,b). Further studies are needed to determine how long hatchlings continue to respond to surface waves produced by prevailing winds, and if they use these stimuli to gain latitudinal, as well as directional information.

The possibility exists that wave cues are also used by juvenile and adult loggerhead sea turtles during their seasonal, as well as breeding, movements. While the spatial movement patterns shown during migration by older turtles are becoming better understood (Dodd, 1988), the cues employed to guide them remain almost a complete mystery.

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