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# Orientation and swimming behavior of hatchling loggerhead turtles *Caretta caretta* L. during their offshore migration

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**Abstract:** Loggerhead turtle *Caretta caretta* L. hatchlings emerging from nests on the eastern coast of Florida swim offshore toward the Florida Current. Part of the trip is accomplished during an initial 20-h period of swimming (the "frenzy"); the remainder may take a day or more of oriented swimming. Swimming speeds are slower than those of green turtles *Chelonia mydas* L. Hatchlings are well oriented in an offshore direction when released into the ocean during the day or night. Completion of a crawl down the beach or a plunge into the surf are unnecessary for proper orientation. Immediately after entering the ocean at night, responses to light appear essential for oriented swimming. However, present hypotheses based upon phototropotaxis may not account for orientation later in the migration.

**Key words:** Sea turtle; Orientation; Migration; Swimming behavior

## INTRODUCTION

Sea turtle hatchlings typically emerge at night from underground nests located above the high tide level of oceanic beaches. After a brief crawl down the beach, they enter the surf and swim rapidly out to sea (Bustard, 1972; Carr, 1984). Newly emerged green turtle *Chelonia mydas* hatchlings, observed in captivity, exhibit an initial period of intensive swimming activity (the "frenzy" period) lasting from hours (Bennett, 1978) to days (Dalton, 1979). Field studies indicate that during the frenzy, hatchlings are strongly oriented offshore (Frick, 1976; Ireland *et al.*, 1978). Tests within circular water-filled arenas also show strong tendencies for green turtle (Van Rhijn, 1979) and Kemp's Ridley sea turtle *Lepidochelys kempi* G. (Wibbels, 1984) hatchlings to orient primarily in an offshore direction.

Because hatchlings are relatively defenseless, this oriented swimming activity is crucial to their survival. It quickly displaces them from shallow-water habitats, where predators are abundant (Hirth, 1971), to offshore waters where cover, such as *Sargassum* (Caldwell, 1968; Fletemeyer, 1978; Witham, 1983), food, and favorable currents for dispersal exist (Witham, 1976; Carr, 1986). Yet we know little about these critical first hours and most of our information is based upon green turtles.

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Loggerhead turtles *Caretta caretta* L. nest in great numbers along the eastern coast of Florida (Conley & Hoffman, 1986) but, in spite of their abundance, little is known concerning the duration of their swimming frenzy period, the open water speed at which hatchlings swim, or the stimuli essential for normal orientation. Our purpose in this study was to address these deficiencies and to determine whether some of the generalities documented from studies of green turtles also apply to loggerheads.

The following questions were central. First, what is the duration of the frenzy period and is it correlated, as in green turtles (Dalton, 1979), with distance to a presumed "goal"? Secondly, is the performance of a crawl and the plunge into the surf important for normal offshore orientation? Green turtles deprived of this experience are incapable of orienting when released away from land (Frick, 1976). Thirdly, is oriented swimming only associated with the frenzy or does it persist for a longer period? In green turtles held in tanks, tendency to orient persists for several weeks (Carr, 1965). Fourthly, how fast do hatchlings swim in the field and how does their swimming behavior compare to that of green turtles? Finally, because light appeared to be important to hatchling orientation, we asked "Could hatchlings maintain a compass heading while swimming in total darkness?"

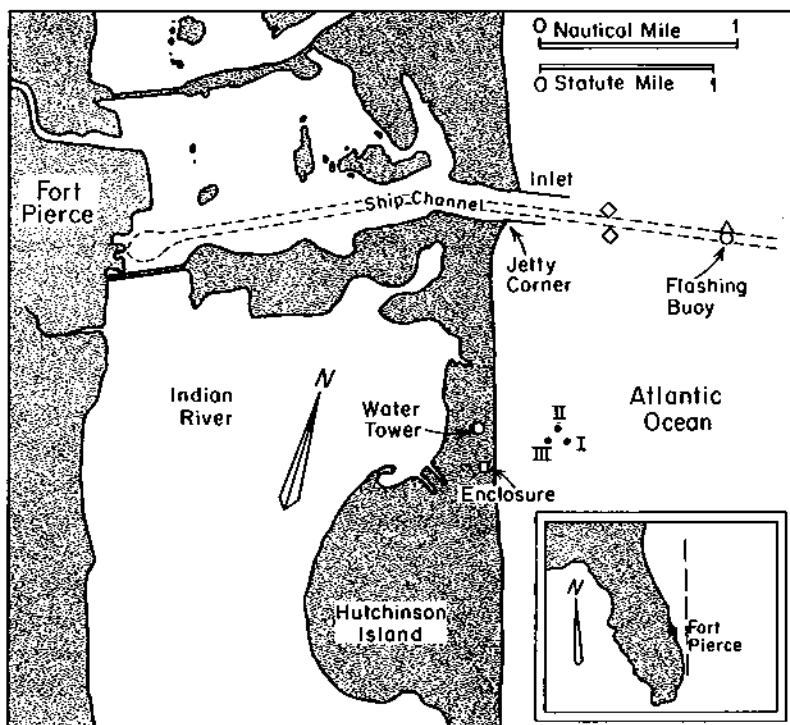


Fig. 1. Studies were carried out at Ft. Pierce, on the eastern coast of Florida (inset). Dashed line indicates approximate position of the Florida Current. Hatchlings were obtained from nests relocated within a screened enclosure. All diurnal field releases began  $\approx 30$  m offshore, in front of the enclosure. All nocturnal releases started the same distance from shore in front of the water tower. I-III, final positions reached by three hatchlings without harnesses, released during the day. These were calculated by triangulation, using the enclosure, jetty corner and flashing buoy as references.

## METHODS

All experiments and observations were conducted during July and August 1986 at Ft. Pierce, Florida (Fig. 1). Some hatchlings were captured as they emerged from natural nests; most of our subjects were from nests relocated to a fenced (40 × 5-m) enclosure, positioned ≈ 25 m above the spring high tides on an ENE-facing nesting beach. Fence meshing excluded mammalian predators, but permitted hatchlings to escape unassisted during their crawl to the ocean.

On the average, one emergence occurred in the enclosure every night. By dusk, a small depression was evident above any nest from which hatchlings would emerge that evening. Such areas were monitored by flashlight at 15–30-min intervals from dusk onward until hatchlings exposed their heads above the sand. Turtles captured and deprived of the crawling experience were used in field releases to test orientation capabilities (see below). Other turtles were allowed to crawl to the surf zone (requiring 7–12 min) and were used to measure locomotor activity in the laboratory. No more than eight subjects were transported in light-tight styrofoam coolers containing damp beach sand. Loggerhead hatchlings typically emerge at night (Demner, 1981). At the enclosure, most did so between 2100–0100. The majority of subjects used in frenzy activity experiments were swimming in our laboratory by midnight. Day 1, the first 24 h of swimming activity, arbitrarily began at midnight.

## MEASUREMENT OF FRENZY ACTIVITY

Hatchlings were transported ≈ 12 km to our laboratory at the Harbor Branch Oceanographic Institute where each was weighed (to the nearest 0.5 g) and fitted with a lycra nylon cloth harness (Fig. 2). A 10-cm long light monofilament line, attached to the harness, was used to connect each hatchling to a lever arm. The arm could freely rotate in any compass direction and pivoted within an opaque central post positioned in the middle of a circular sea water-filled orientation tank (fig. 3). Four peripheral contacts, 90° apart within the central post, were aligned by a compass to correspond to the cardinal directions. A "wiper" contact, attached to each lever arm, closed an electrical circuit of an event recorder (Esterline-Angus A620X) when a swimming hatchling pulled the lever down as it swam toward the tank periphery. The wiper touched two adjacent peripheral contacts when a hatchling oriented between cardinal directions (NE, SE, etc.). When hatchlings were inactive a counterweight caused each lever arm to pivot upward, lifting the wiper off the contacts to break the circuit. Thus, the system simultaneously measured hatchling activity and orientation to the nearest 45° (Fig. 3). All data were tallied from strip charts of the recorder, using a chart speed of 7.62 cm · h<sup>-1</sup>. Resolution was to the nearest 2 min.

Four tanks (blue plastic "kiddy-pools", 1.83 m in diameter and 20.3 cm deep) were located within a large (30 × 6 × 4.6-m high) greenhouse. Each was filled with ≈ 15 cm of sea water, elevated 25 cm above the floor and positioned in a N–S row adjacent to

the eastern side of the building. A black plastic curtain, extending from the floor to a height of 2 m, served to isolate the tanks from the remaining area of the greenhouse. To minimize overheating, one end of the greenhouse was equipped with a large exhaust fan which forced air cooled by evaporation through the building. Aluminum strips,



Fig. 2. Harnessed loggerhead subject. Note that the fore- and hind-limbs are unimpeded. Harness line clips to the lever arm.

2.31 cm wide and separated by a 1.27 cm space, spanned the length of the roof. These reduced light intensity and heat by reflection. Greenhouse air temperatures ranged from 23 (at night) to 35 °C on the hottest days. Water temperatures never exceeded 33 °C.

Four smaller (1.52 m in diameter  $\times$  19.0 cm deep) tanks, containing identical central posts and lever arms, were inverted, tan-colored fiberglass satellite dishes placed in each corner of an apartment sun-porch (3.05  $\times$  3.66  $\times$  2.44 m high). These were used to run more tests under normal or modified (total darkness) light conditions. The porch, which was surrounded by open windows on three sides, faced NE. An opened air-conditioning vent prevented air temperatures from exceeding 32 °C. A sliding glass door entry way

along the SW wall was covered with black plastic so that at night subjects were shielded from apartment lights. In tests to measure activity and orientation under total darkness, the windows were also covered. These experiments began < 1 h after turtles emerged (usually, by midnight) and continued until dawn.

For each turtle we measured activity (in min) as time spent in any one 45° sector · h<sup>-1</sup>. Subjects were left undisturbed except for brief inspections each morning.

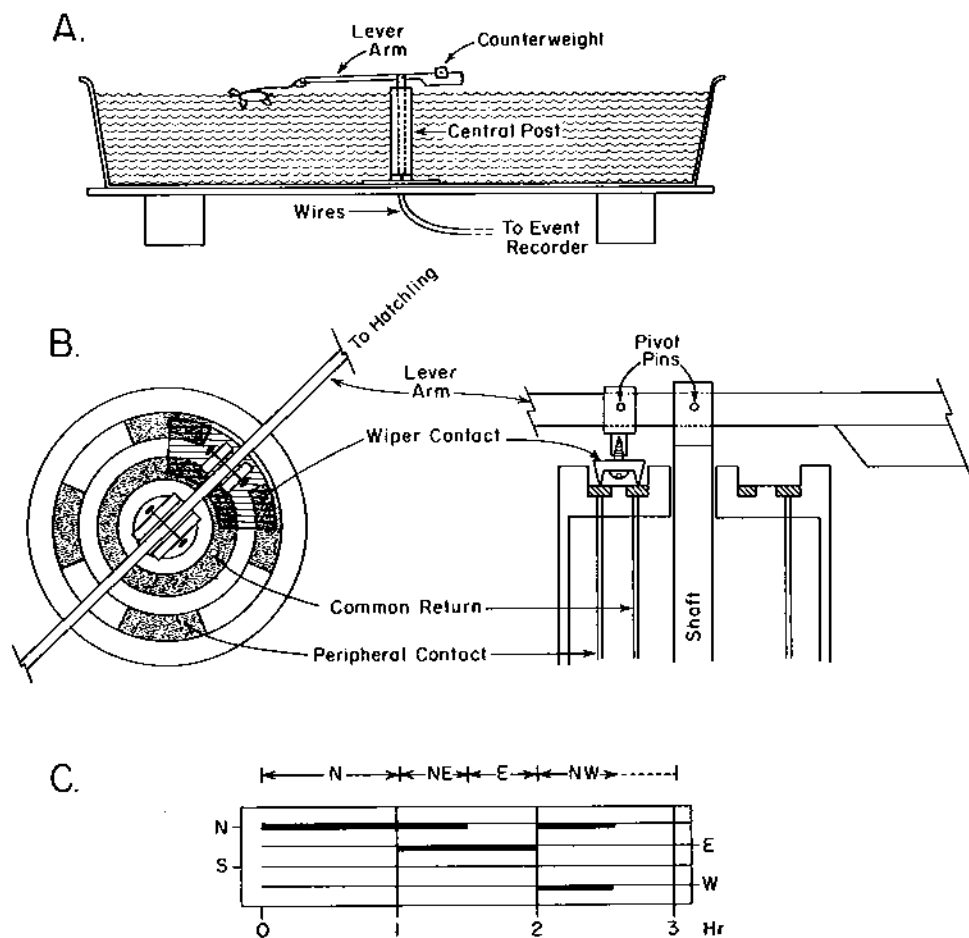


Fig. 3. (A) Schematic of a greenhouse pool, showing position of the hatchling, lever arm, and central post during swimming. Apartment tanks were water-filled satellite dishes bearing identical posts and arms. When the subject swims, it pulls down the lever arm; when inactive, a counterweight causes the arm to pivot upward. (B) Top (left) and sectional (right) view of the central post showing position of the peripheral, common return, and wiper contacts. Post is hollow opaque plastic. Shaft rests in a bottom depression and is free to rotate in any direction. Wiper contact makes a circuit when the turtle is swimming but is elevated by the counterweight to break the circuit when the hatchling rests. Screw adjusts wiper position under the lever arm. (C) Idealized record from the event recorder. Hatchling swims to the N during Hour 1, NE (30 min) then E in Hour 2, and NW (30 min) in Hour 3. It is inactive during the final 30 min.

When experiments ran > 2 days, hatchlings were fed raw fish or shrimp at random times, once daily. Tank water lost by evaporation was replaced with fresh water. At the completion of each experiment, tanks were drained, cleaned, and filled with new sea water (25–28 ppt).

Ambient light intensity levels in the greenhouse and apartment were measured in  $\mu\text{W} \cdot \text{cm}^{-2}$  by a photometer (Kahl Scientific Instruments 268WA10, uniform sensitivity between 460–650 nm) during both clear and overcast days. The turtles often responded to patterns of bright light reflected from the tank walls or other surfaces. These were measured with a wide-angle light meter placed upon the central post, then rotated horizontally to record the general direction of maximum light intensity.

All hatchlings swam in a characteristic manner: several seconds of underwater “powerstroking”, employing synchronous movements of only the front flippers, alternating with shorter periods of “dogpaddling” with all four flippers while on the surface. We timed 10 powerstroke and dogpaddle “cycles” shown by each of four loggerhead hatchlings < 30 min of their introduction into apartment tanks, using a stopwatch. We also counted the number of foreflipper movements shown during each bout of powerstroking. In late August, we obtained four green turtle hatchlings. These were used for identical measurements so that swimming temporal patterns could be compared between the species.

#### FIELD RELEASES

All hatchlings released in the ocean were captured at night as they emerged from their nests, then placed in light-tight coolers. Those used in night experiments were released < 2 h of capture. Day-time releases were carried out the following morning. Surface-water temperatures ranged from 26–29 °C.

Hatchlings released at night were taken in a small boat powered by outboard motor to < 30 m of shore in front of a large water tower (Fig. 1). This structure, with its dim red roof light, served as an easily observed reference point to begin releases. Each hatchling was fitted with a cloth harness to which was attached  $\approx 1.5$  m of light monofilament line. A small streamlined styrofoam float,  $\leq 6$  cm long, 1 cm thick, and 2 cm wide, was tied to the end of the line. To increase its visibility, strips of red light-reflecting tape were glued to its side and top surfaces. Observations began when a hatchling was released gently into the water while the boat moved slowly in broad circles. The hatchling faced any direction at the moment of release. Thereafter, the float and turtle were followed from behind at a distance of 6–10 m. At 5–15-min intervals, both the float and turtle were briefly illuminated by flashlight to estimate travel direction with a hand-bearing compass (Ritchie 100). Winds at night were light or nil; thus a sighting from the styrofoam float to the turtle’s head during the dogpaddle phase provided an accurate estimate of heading. After five readings were taken (20–40 min after the release), the hatchling was recaptured, its harness removed, and released. Mean direction of orientation was calculated according to Zar (1984).

Diurnal releases took place directly in front of the enclosure, again < 30 m of shore. The following differences from night releases warrant mention. Individuals were kept in coolers on the sun-porch, generally  $\leq 6$  turtles  $\cdot$  cooler $^{-1}$ . The cooler lid was open so subjects were exposed to a normal change in light cycle at dawn and to continuous light until release. Each turtle was followed for  $\leq 1$  h, with readings of swimming direction based upon a sight down the hatchling's midline during surface (dogpaddle) swimming. At the conclusion of the test, each hatchling was recaptured and held in the boat's live well. After all were tested, they were taken to the laboratory, held in a large aquarium, fed daily, then released within several weeks well offshore, usually near *Sargassum* matts.

We assumed that pulling floats affected swimming speed. Therefore, three non-harnessed subjects were followed to estimate how rapidly they could swim. Each was followed for 20–35 min, then recaptured. Final position offshore was recorded by triangulation using the water tower, jetty corner, and flashing channel buoy as compass references (Fig. 1). Finally, because hatchlings could see us during their dogpaddle phase, we followed them when not taking sights by continuous circling at distances of 6–10 m.

## RESULTS

### DURATION OF THE FRENZY PERIOD

Upon their introduction into the orientation tanks all hatchlings swam vigorously. Records for eight hatchlings, each of which had crawled down the beach before capture, indicated most (seven of eight subjects) swam nearly constantly throughout the first night and the day that followed, although occasionally some briefly paused (Fig. 4; Subjects I, II, VIII). After Day 1, activity levels were both lower and more diurnal in expression.

Quantitative analyses revealed all turtles swam most persistently through Day 1, beginning on the night of their emergence (Fig. 5). Greenhouse turtles, for example, averaged 20.69 h of swimming while apartment subjects averaged 19.10 h of activity out of a possible 24 h. By the end of Day 2, activity levels for both groups had fallen significantly (by 5 h for apartment hatchlings;  $t = 3.56$ ,  $df = 20$ ,  $P < 0.005$ ; by 7 h for greenhouse hatchlings;  $t = 4.36$ ,  $df = 26$ ,  $P < 0.001$ ). From Day 2 onward, within-group means showed no statistically significant differences. Hatchlings in both groups averaged 6–13 h of swimming per day. While activity values for apartment turtles were consistently lower than greenhouse subjects, means did not differ significantly (by a  $t$  test) largely because of the extreme variation in activity within apartment turtles.

Light intensity levels in the greenhouse reached their peak values ( $3.80 \mu\text{W} \cdot \text{cm}^{-2}$ ) between 0900–1030. By mid-afternoon, levels were reduced by roof shades and ranged at  $2.0$ – $2.30 \mu\text{W} \cdot \text{cm}^{-2}$  on sunny days. Apartment light levels were brightest between 0900–0930 h, when sunlight into the room was direct. They ranged at

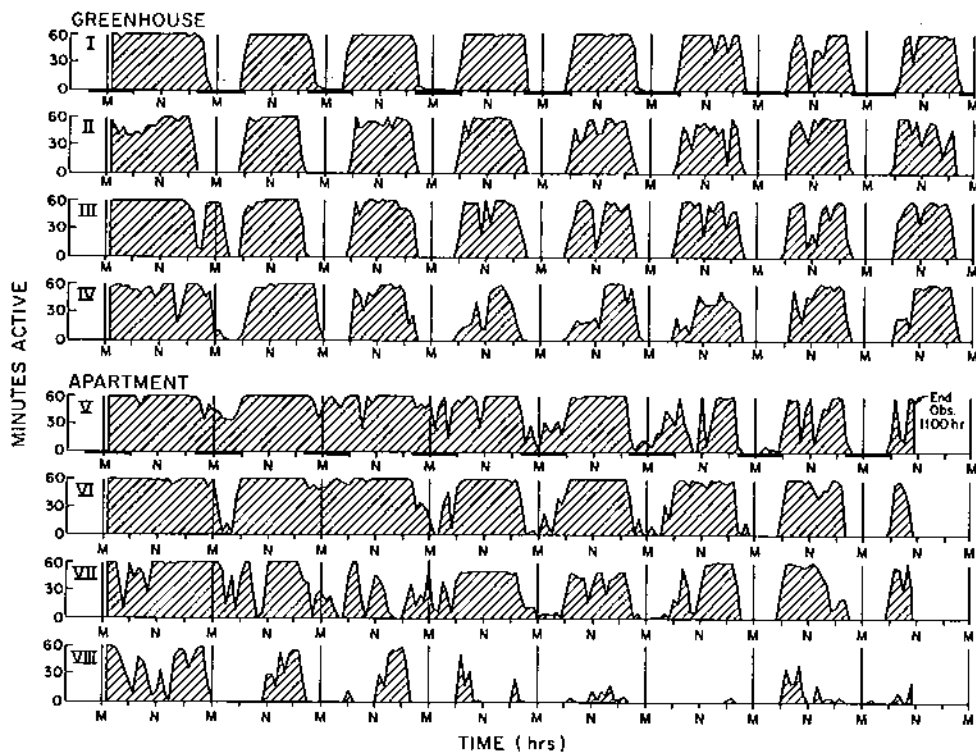


Fig. 4. Activity records for four greenhouse (above, 13–20 July) and four apartment (below, 13–19 July) subjects from two different nests. M, midnight; N, noon. Black bars indicate dark period for all turtles. Records begin at 0100 on the night of emergence (Day 1). Note most turtles show high levels of swimming through Day 1. On subsequent days, swimming occurs primarily during the day.

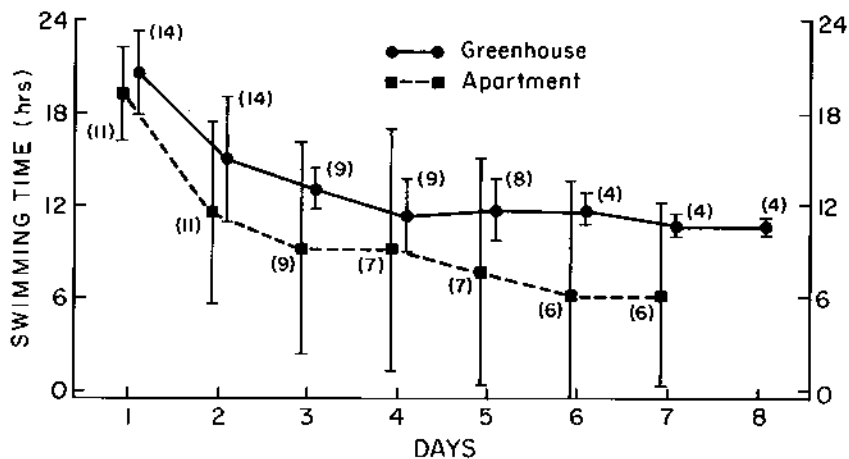


Fig. 5. Summary (mean  $\pm$  SD) of activity data for all greenhouse and apartment hatchlings. Values in parentheses are the sample size.

1.50–1.72  $\mu\text{W} \cdot \text{cm}^{-2}$  on clear days. Thereafter, the room was illuminated only by reflected light which ranged from 0.40  $\mu\text{W} \cdot \text{cm}^{-2}$  at noon to 0.17  $\mu\text{W} \cdot \text{cm}^{-2}$  at 1750 on clear days. Frequent afternoon thunderstorms, especially in late July and August, often reduced light levels in both the greenhouse and apartment to less than half these values.

#### ORIENTATION UNDER LABORATORY CONDITIONS

All hatchlings, whether kept in the apartment or the greenhouse, were oriented toward a compass direction during part or most of Day 1. Most apartment subjects, for example, were strongly attracted toward the NE windows, either in response to distant street lights (at night), sunlight (in the morning) or diffuse light (in the afternoon). Greenhouse turtles showed more behavioral variation, probably because they were exposed to more variable lighting conditions (Fig. 6). For example, preferences for

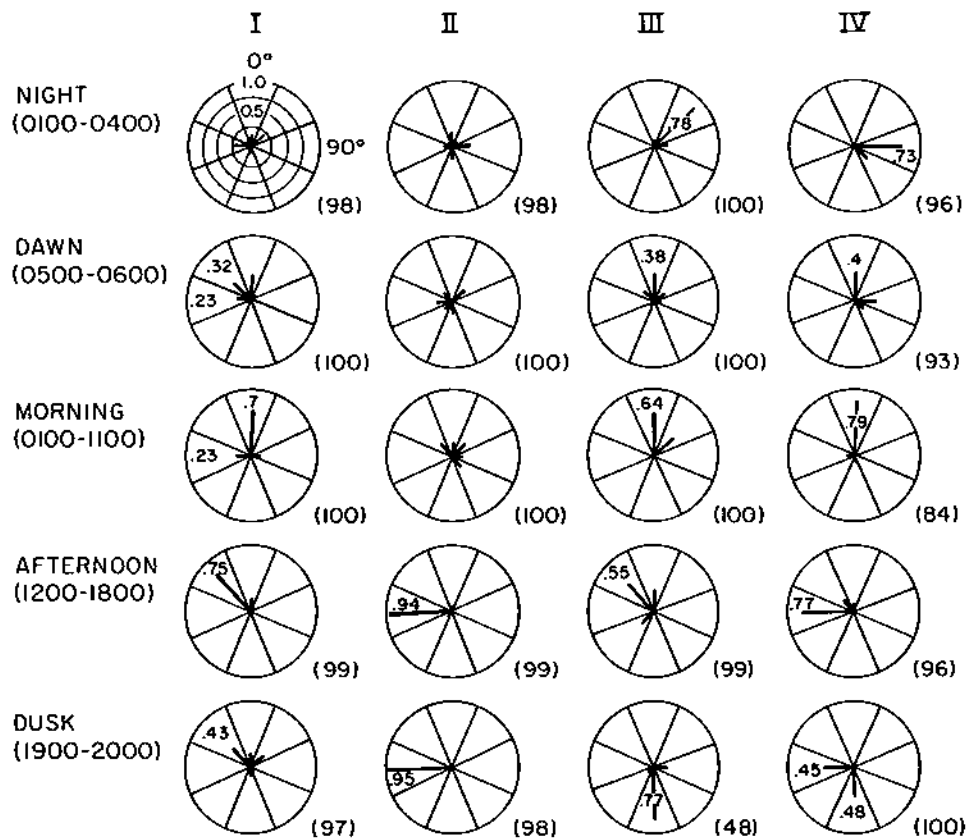


Fig. 6. Activity patterns shown by four greenhouse turtles through Day 1, beginning at night and continuing through dusk (1900–2000). Each circle is subdivided into eight 45° sectors, representing the analyzed compass directions. 0°, N; 90°, E. Bar length within a sector indicates the percentage of time swimming in that direction. Value in parentheses is the percentage of total time (e.g., 4 h at night; 2 h at dawn) the hatchling was active.

particular directions might (Hatchlings III, IV) or might not (Hatchlings I, II) change dramatically throughout the day. Diurnal patterns also varied. Hatchling I was strongly oriented in the morning and afternoon while Hatchling II showed its strongest directional preferences in the afternoon and at dusk.

All turtles showed periods of orientation that lasted well past Day 1 of swimming (Fig. 7). In the greenhouse, bright patches of light to which hatchlings were exposed

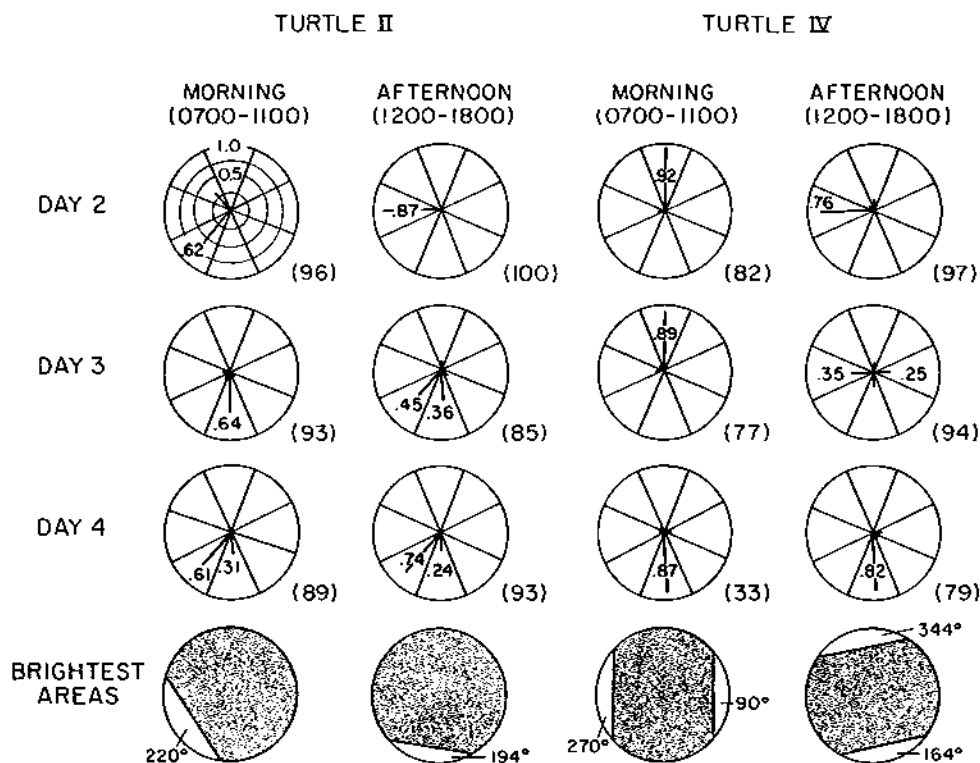


Fig. 7. Activity patterns of Hatchlings II and IV (from Fig. 6) over Days 2-4. Format as in Fig. 6 except for bottom circles which show direction(s) of brightest horizontally reflected light (as measured by a light meter). These could come from one side (Hatchling II) or both sides (Hatchling IV) of the orientation tank.

often changed in direction from the morning to the afternoon. These changes were correlated with variation in directional responses of the hatchlings which shifted from headings approximately toward patches (e.g., most responses of Hatchling II) to those between patches located on opposite sides of the tanks (most responses of Hatchling IV). Headings for individual turtles were also inconsistent from one day to the next.

Twelve hatchlings (four each from three nests) showed no evidence they could remain oriented under total darkness. However, when darkness was preceded by dim reflected light, hatchlings showed orientation until the light stimulus was removed (Fig. 8).

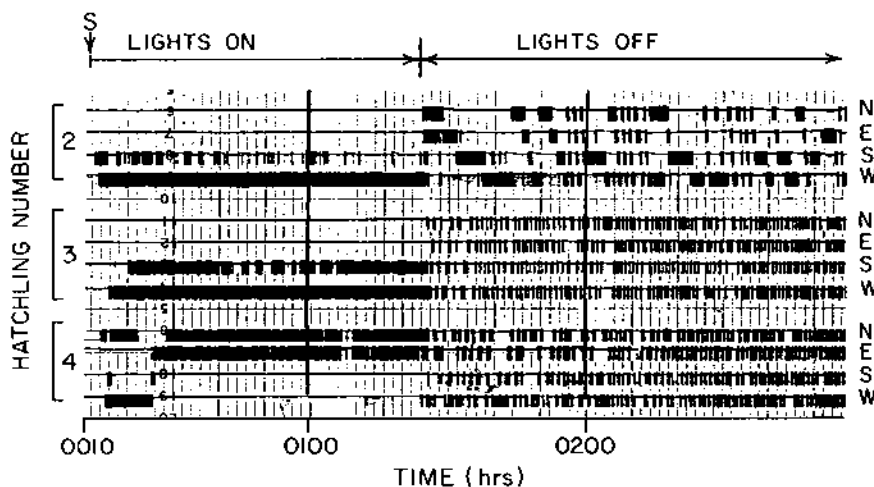


Fig. 8. Record for three hatchlings in the apartment pools on the night they emerged. Initially (at S), the subjects were dimly illuminated (until 0123); each orients toward the brightest reflected light around their tank. Thereafter, they were in total darkness. In the absence of light, they continuously turn slowly (Hatchling II) or rapidly (Hatchlings III and IV).

#### TEMPORAL PATTERNS OF SWIMMING BEHAVIOR

Four loggerheads, all from a single nest, were used to time swimming behavior within the first 30 min after they were placed into water (Table I). All subjects cycled through relatively long periods of powerstroking (mean of 11.53 s) while submerged just under the surface, followed by relatively short periods of dogpaddling (2.81 s) with the head

TABLE I

Temporal patterns of swimming shown by four green and four loggerhead hatchlings within 30 min of their first swimming experience. Values are mean  $\pm$  SD and the range;  $n = 40$  observations ( $10 \cdot \text{hatchling}^{-1} \cdot \text{behavior}^{-1}$ ).

Species	Powerstroke duration (s)	Dogpaddle duration (s)	Foreflipper strokes $\cdot$ powerstroke bout <sup>-1</sup>	Stroke rate (no $\cdot$ s <sup>-1</sup> )
<i>Chelonia mydas</i>	4.51 $\pm$ 1.15 2.55-7.38	1.87 $\pm$ 0.93 0.73-5.28	11.80 $\pm$ 3.48 5-19	2.59 $\pm$ 0.20 1.96-2.85
<i>Caretta caretta</i>	11.53 $\pm$ 5.55 3.15-22.79	2.81 $\pm$ 0.63 1.92-4.09	20.41 $\pm$ 9.04 5-39	1.79 $\pm$ 0.20 1.40-2.49
<i>t</i> statistic	7.83	5.27	5.61	17.99
$P_{(6 \text{ df})} <$	0.001	0.002	0.002	0.001

and much of the carapace protruding above the surface. There was considerable variation among siblings in the number of foreflipper strokes during bouts of powerstroking (range of 5–39 for all turtles; mean of  $20.41 \cdot \text{bout}^{-1}$ ). The stroke rate was fairly constant at  $\approx 1.8 \cdot \text{s}^{-1}$ .

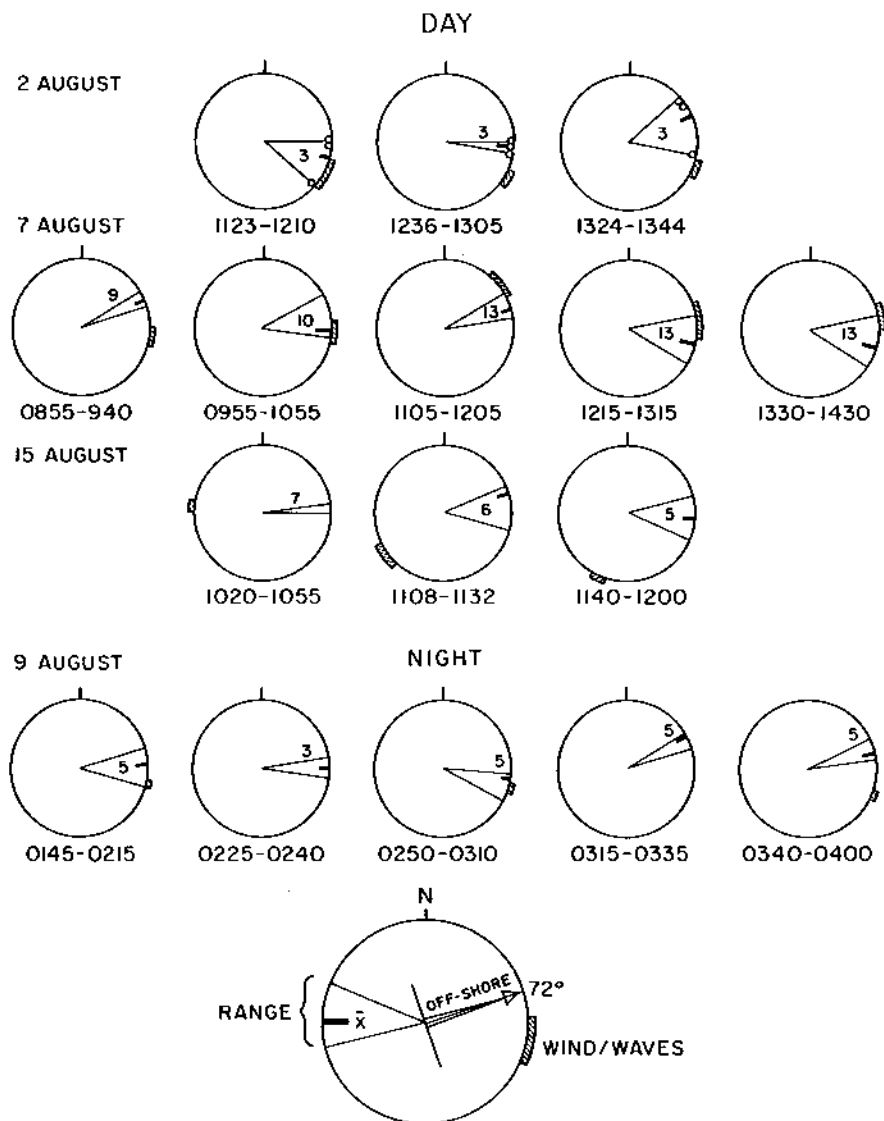


Fig. 9. Results of field releases carried out during the day (2, 7 and 15 August) and at night (9 August). Each circle shows the range and mean of compass readings for that hatchling at 5–15-min intervals during the swim and the time span of observations (below the circle). Values within circle are the number of readings, shown individually only for the 2 August releases (small circles). Hatched area to outside is the range of wave (and wind) direction, determined when hatchling headings were measured. In some cases, there was no wind and waves consisted of gentle swells (e.g., some night releases). All subjects are generally oriented in an offshore ( $72^\circ$ ) direction.

Four green turtle sibs also showed similar powerstroke-dogpaddle cycles but these differed significantly from loggerheads in their temporal features (Table I). Both the powerstroke and dogpaddle phases were shorter in duration while the number of strokes per powerstroke bout was only 11.8. However, the stroke rate in this species was considerably faster ( $2.59 \cdot \text{s}^{-1}$ ) than in loggerheads.

#### OFFSHORE ORIENTATION

All hatchlings released in the field, whether during the day or at night, oriented away from shore. After an initial prolonged dive following release, hatchlings surfaced, briefly circled as if "looking about to get their bearings", and began swimming in an E-NE direction (Fig. 9). Orientation appeared unaffected by wind or wave direction which, on most days, was from the NE, E, or SE. Hatchlings also oriented offshore on 15 August when winds came from the W and SW or when released at night when there was no wind and waves consisted of gentle swells. The absence of a harness did not affect orientation preferences. Three unharnessed hatchlings (15 August) showed no obvious differences in orientation behavior from harnessed subjects.

#### SWIMMING SPEED IN THE FIELD

Three hatchlings without harnesses were followed during the day on 15 August. They were swept northward from their starting point (30 m offshore, directly in front of the enclosure; Fig. 1) by strong along-shore currents. Their swimming distances, measured perpendicular from shore (minus 30 m), were: Turtle I, 457 m in 20 min; II, 549 m in 24 min; and III, 640 m in 35 min. Their individual average speeds ( $\text{m} \cdot \text{min}^{-1}$ ) were 22.85, 22.88, and 18.29 (average of  $21.34 \pm 2.64 \text{ m} \cdot \text{min}^{-1}$  for all three subjects).

### DISCUSSION

#### SWIMMING SPEED AND BEHAVIOR

Frick (1976) observed that swimming green turtle hatchlings cycled between "dives" and "surface-paddling while breathing." These correspond to our powerstroking-dogpaddling cycles. Her range (5–10 s) for dive duration was greater than ours (2.55–7.38 s, Table I) but her values were rough estimates. We do not know why temporal patterns of powerstroking and dogpaddling durations should be so different in loggerhead and green turtle hatchlings.

There are few data on the speeds achieved by hatchlings in the field during the frenzy period. Green turtle hatchlings ( $n = 24$ ) released off Bermuda averaged  $1.57 \text{ km} \cdot \text{h}^{-1}$  ( $26.17 \text{ m} \cdot \text{min}^{-1}$ ) when tracked over distances of 0.60–6.48 km (Frick, 1976). Ireland *et al.* (1978) reported a range of  $0.8\text{--}3.2 \text{ km} \cdot \text{h}^{-1}$  ( $\bar{x} = 1.1 \text{ km} \cdot \text{h}^{-1}$ ) for green turtle hatchlings pulling light floats. It is likely that doing so slowed their subjects.

Our three unharnessed loggerhead hatchlings swam more slowly ( $18.3\text{--}22.9 \text{ m} \cdot \text{min}^{-1}$ ) than Frick's green turtles. Florida loggerhead hatchlings

( $n = 169$  from 12 nests) are smaller in size (straight-line carapace lengths of 41–48 mm) and weight (15–21 g) than Florida green turtles (49–55 mm; 21.5–28 g;  $n = 31$  from 4 nests). They also do not move their foreflippers as rapidly when swimming (Table 1). Other, more subtle aspects of body shape (streamlining; the generation of lifting vs. dragging forces during swimming) also suggest that green turtle hatchlings should be capable of more rapid swimming speeds than loggerheads (Wyneken, in prep.).

O'Hara's (1980) laboratory study is the only other that measured swimming speeds of loggerheads during their frenzy. Speeds were measured in a long (8.2-m) tank in which hatchlings released at one end swam toward a light stimulus placed at the opposite end. Estimates were based upon repeated measures of fastest locomotion (which occurred during Laps 7–10) and ranged between 23 and 30  $\text{cm} \cdot \text{s}^{-1}$  ( $1218 \text{ m} \cdot \text{min}^{-1}$ ) at 25.6–33 °C. It is difficult to compare his results with ours because his subjects were attracted to different stimuli and had to stop, reverse direction, then accelerate repeatedly while we measured distances achieved during continuous swimming. Our combined results, however, are consistent with the hypothesis that loggerhead hatchlings do not swim as rapidly as green turtle hatchlings.

#### FRENZY DURATION AND SIGNIFICANCE

The frenzy of hatchlings is characterized by energetic and almost continuous swimming during the first few hours or days in water (Carr, 1984). It is indeed sufficiently different from the behavior shown by hatchlings only a few days later to qualify as a "specialized" response evolved for displacement of individuals in space (Dingle, 1980). During the frenzy, green turtle hatchlings usually do not feed (Dalton, 1979) and, at least for several hours are strongly oriented in an offshore direction (Hendrickson, 1958; Frick, 1976; Ireland *et al.*, 1978). Our field and laboratory observations upon loggerheads suggest they also conform to these general patterns. Hatchlings are strongly oriented offshore during their first hour in water (Fig. 9) and swim almost continuously during the first 24 h (Fig. 5). None of our hatchlings accepted food until they had been swimming for  $\geq 3$  days, about the same length of time as for green turtles (Dalton, 1979).

Dalton (1979) documented that the frenzy varied in duration between green turtle populations. She attributed this variation to differences in the distance separating nesting beaches from offshore currents favorable to dispersal. For example, six hatchlings from Ascension Island, tested in the laboratory, showed no frenzy while 11 others showed only a 1-h frenzy immediately after they were placed in the water. Ascension Island lies within the Equatorial Current which sweeps hatchlings toward feeding grounds along the Brazilian shoreline (Carr, 1965). Dalton proposed that only a brief frenzy was necessary to gain immediate entry into the current. In contrast, Tortuguero (Costa Rican) hatchlings showed 3–9-h periods of frenzied swimming over two ("large" hatchlings) or three ("small" hatchlings) days. Small and large hatchlings in Tortuguero are hypothesized to be the progeny of adults feeding to the north

(Nicaragua) and south, respectively, of Costa Rica. Dalton suggested that differences between their frenzy could be related to the longer and varying distances between shore and offshore currents appropriate for their displacement.

There is good evidence that both green (Witham, 1976) and loggerhead (Carr, 1986) hatchlings emerging from nests on the eastern coast of Florida eventually enter the Florida Current. Could hatchlings from Ft. Pierce reach the Florida Current within their 20-h frenzy period? We think it unlikely. The distance separating the western border of the Florida Current and the eastern coast of Florida varies with latitude, largely because the coastline slants to the NNW while the current proceeds due N (Fig. 1; Stommel, 1972; Pickard, 1979). At Ft. Pierce, the border of the current is usually no farther than 30 km from shore (Anon., 1975-1980). At the initial swimming speeds we recorded ( $18-23 \text{ m} \cdot \text{min}^{-1}$ ), and assuming a 20-h frenzy (Fig. 5), a hatchling could swim 22-28 km from shore. Actual distances achieved are probably considerably less because (1) swimming speeds are likely to decrease toward the end of the frenzy (Bennett, 1978), and (2) hatchlings might encounter summer squalls or surface currents which slow forward progress or displace them off-course, adding time and distance to the journey.

The design of our system (Fig. 3) allowed us to simultaneously measure both activity and orientation, processes that co-occur when hatchlings migrate offshore. The laboratory data, while admittedly recorded under unnatural circumstances (within a greenhouse and sun-porch), nevertheless suggest that tendencies to orient do not diminish after the frenzy period (Fig. 7). These results are consistent with the following hypothesis: the frenzy displaces hatchlings some distance offshore, but not sufficiently far to gain entry into the Florida Current. But subsequent days of oriented swimming probably enable hatchlings to complete the migration. Indeed, postfrenzy-oriented movement may be an adaptive component of behavior precisely because it can be used to counter the uncertainties of conditions (both hydrographic and climatic) under which the journey must be made.

#### ORIENTATION

Our field releases showed that loggerhead hatchlings can determine which direction is away from shore, both during the day and at night, without experiencing either a crawl or a plunge through the surf. These tests were carried out to complement and clarify similar experiments with green turtles done by Frick (1976). Her subjects were similarly deprived but, in addition, were released 5 km from shore and presumably, could not detect cues associated with land. Their subsequent disoriented behavior (circling, diving at nearly a vertical angle) was difficult to causally interpret because all three factors (no crawl; no contact with the surf; no contact with land) could, alone or in combination, have contributed to their lack of directionality. Our results suggest that neither the crawl nor the plunge through the surf are essential experiences for offshore orientation in loggerheads, at least when the hatchlings are released on clear days or nights.

Our field releases also suggest that wave orientation may not be a primary cue either because even when waves came from the SW (15 August releases), or consisted only of gentle swells (some night releases), hatchlings were oriented in an offshore direction. However, wave orientation could be used as a supplementary clue, especially near shore, as at shallow depths waves are normally parallel to the beach. One of three hatchlings released 15 August swam briefly into the waves and towards shore. However after several seconds, it turned 180° and headed out to sea.

Our results do not allow us to specify which cues are essential for orientation during the early stage of nocturnal frenzied swimming. But the data all strongly point to the importance of light as hatchlings tested under total darkness are disoriented (Fig. 8). What remains to be specified are the sources of light involved, their essential features both in space and in time, and the mechanisms involved in shaping the response. It is clear that a tropotaxis in response to differences in brightness between the landward and seaward horizon is used when hatchlings seek the ocean from their nest (Ehrenfeld, 1968; Mrosovsky & Shettleworth, 1968; Mrosovsky & Kingsmill, 1985). Such stimuli may also guide swimming hatchlings at least for several hours, i.e., as long as brightness differences are still visible.

However, once hatchlings swim sufficiently far from shore brightness differences are either unavailable or not used. This, at least, seems the most plausible explanation for the failure of green turtle hatchlings to orient when released only 5 km from land (Frick, 1976). We hypothesize that under normal circumstances, another compass mechanism must begin to guide loggerhead hatchlings to the Florida Current and green turtle hatchlings out to sea (where is not known). The specific nature of this compass is also unknown but it may depend upon a reference established during a previous period of tropotactic orientation. An analogous situation is well-known for some birds. Night-migrating warblers, for example, use stellar or magnetic compasses but can continue on their northward flight past the dark period by detecting polarized light from the dawn sun (Moore, 1986). We plan further experiments to identify the open sea compass (or compasses) used by hatchlings and to determine if it is set by the direction of brightness differences closer to shore.

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