

Frenzy and Postfrenzy Swimming Activity in Loggerhead, Green, and Leatherback Hatchling Sea Turtles

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Sea turtle hatchlings emerge from subsurface nests on oceanic beaches, crawl to the ocean, and swim out to sea. Once in the water, hatchlings at first swim almost continuously (a period called the frenzy). In this laboratory study, we compared the duration and diel pattern of frenzy and postfrenzy swimming activity among loggerhead, green turtle, and leatherback hatchlings from beaches in southeastern Florida. The frenzy of all species lasted one day (24 h). After the frenzy, hatchlings continued to swim during the day. Green and loggerhead hatchlings eventually became inactive at night, but leatherback hatchlings typically swam between 15-45% of the dark period. Because the frenzy is temporally similar in all species, its function may also be the same: escape from shallow waters near shore. Postfrenzy differences in diel activity may reflect contrasts among species in foraging, predator avoidance, and energy conservation strategies.

SEA turtle hatchlings emerge from underground nests, crawl down to the ocean, and swim rapidly away from shore (Carr and Ogren, 1960; Bustard, 1972). After entering water, hatchlings undergo a period of hyperactive swimming (termed the "frenzy," Carr, 1962) during which they swim continuously (Deraniyagala, 1930, 1939).

Little is known about the species-specific length of the frenzy or how it compares across populations of a species. In Florida loggerhead sea turtles (*Caretta caretta* Linnaeus), the frenzy is characterized by nearly continuous swimming for the first 24 h (Salmon and Wyneken, 1987). After the frenzy (the "postfrenzy" period), loggerhead hatchlings swim only during the day and are inactive at night.

Bennett (1978) found that Florida green turtle (*Chelonia mydas* Linnaeus) hatchlings swam vigorously when they were first immersed in water. Activity levels declined within 10 h and showed no further change through 24 h. Dalton (1979) reported that green turtle hatchlings from Tortuguero, Costa Rica, had a three-day swimming frenzy whereas 66% of turtles from Ascension Island, South Atlantic Ocean, showed no frenzy period.

Variation in frenzy behavior might reflect species-specific and/or population-specific differences in frenzy function. Alternatively, differences could be an artifact of experimental design or handling. In this study, we compared frenzy and postfrenzy swimming activity in loggerhead, green, and leatherback (*Dermochelys coriacea* Vandelli) sea turtle hatchlings. All tur-

tles were treated identically and came from the same geographic location (southeastern Florida). Two primary questions were addressed: (1) How long does the frenzy period last in each species? (2) Are there differences in frenzy or postfrenzy swimming activity? We also discuss the biological implications of species-specific differences in postfrenzy swimming activity.

METHODS

Animals.—Hatchling leatherbacks were obtained from natural nests. Loggerhead and green turtles were captured from natural nests or from nests reburied within 24 h of deposition at safer locations on a nearby nesting beach. All nests were located on Hutchinson or North Hutchinson Island, Florida. Experiments with green turtles and leatherbacks were carried out in the summers of 1988 and 1989; loggerheads were studied in the summer of 1986.

Hatchlings were captured either as they emerged from nests or just prior to natural emergence. To capture turtles before they emerged, nests deposited on known dates were monitored for several days prior to expected emergence. When a depression appeared in the sand surface above the egg chamber, we dug down and removed four hatchlings. Only turtles at the top of the clutch and presumably in the process of digging to the surface were collected. Remaining hatchlings were covered with sand and left to emerge naturally. Captured subjects were placed in Styrofoam boxes, taken to our laboratory within 30 min, and held in a

dark room at ambient temperature. Each hatchling was weighed immediately before use in experiments.

Activity recordings began at midnight. Thereafter, hatchlings were left undisturbed except for brief inspections each morning and afternoon. On the third and subsequent days of swimming, hatchlings were fed either during the morning or the afternoon. Green turtles and loggerheads ate small pieces of raw shrimp or scallop; leatherback hatchlings were given live jellyfish (*Cassiopeia*). Feeding times varied each day and only briefly interrupted normal swimming activity.

Recording was continuous for six days (144 h) for green and leatherback hatchlings; for loggerheads, recording lasted for two to eight days. At the completion of recordings, hatchlings were taken several km offshore and released. Pools were drained, cleaned, and filled with new seawater before a new group of hatchlings was tested.

Measurement of swimming activity.—The apparatus used to record swimming activity was described by Salmon and Wyneken (1987). Each turtle's activity, inactivity, and heading were recorded as it swam within a circular pool (1.8 m diameter and 0.2 m deep) filled with seawater. A hollow, opaque post, rising above water level, was fixed in the center of each pool. The post housed a shaft attached to a lever arm at its top. The lever arm was free to rotate horizontally just above water level. A hatchling was attached by a lycra-nylon harness and a short piece of monofilament line to the end of the lever arm. It could swim freely in any direction, dive, or surface but could not contact the tank sides or bottom. Hatchlings swam toward the tank periphery, pulling the lever arm down to complete a circuit to a recorder. A counterweight caused the lever arm to elevate slightly, breaking the circuit when turtles were inactive. Data records were stored on an event recorder.

Four pools, located in a greenhouse or an outdoor screened porch, were used concurrently. Hatchlings were exposed to natural changes in lighting and to normal fluctuations in air temperature. Green turtle and leatherback hatchling records were obtained at both locations. Data for hatchling loggerheads were only collected from the greenhouse.

Data analyses.—"Total swimming time" was the number of min (± 2 min/h) spent swimming by

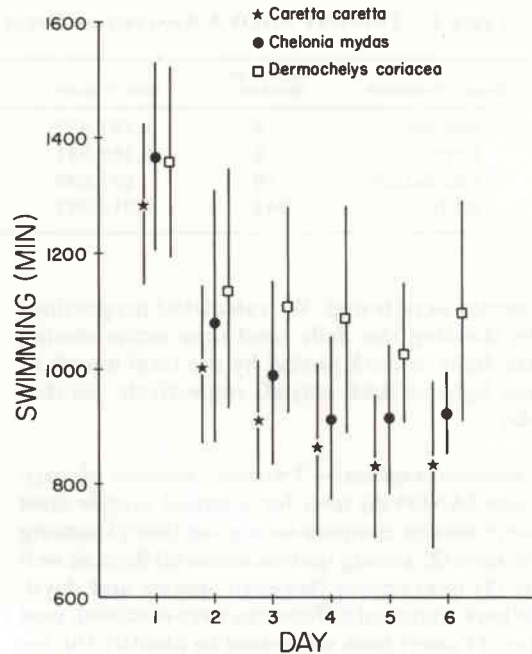


Fig. 1. Total swimming activity in min (mean \pm 1 standard deviation) by loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*) and green turtle (*Chelonia mydas*) hatchlings for each of their first six days in the water. One day (24 h) = 1440 min.

each turtle per day for the duration of the experiment. Consecutive days of experiments always began at midnight and ended at 23:59 h. Records were kept of total swimming time during the light and dark periods of each day. Hatchling headings are not reported here, but the data were used as criteria to ensure we were measuring normal hatchling activity (oriented swimming behavior). After the frenzy was over, hatchlings usually became active about one-half h before sunrise (as soon as the sky started to lighten). They swam at least until one-half h after sunset (when the sky darkened), then became relatively inactive. The light period was defined as extending from 0.5 h before sunrise until 0.5 h after sunset. The dark period consisted of the remainder of each day (24 h minus the light period). Proportions of time spent active during each photophase were calculated to eliminate potential effects of day length change upon activity comparisons. Leatherbacks nest between March and July, green turtles between June and September, and loggerheads between May and September. As a consequence, the light period varied as much as 30 min when different

TABLE 1. TWO-WAY ANOVA ANALYSIS OF TOTAL SWIMMING TIME FOR ALL SPECIES ACROSS SIX DAYS.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F	P
Species	2	1,131,812	565,906	17.23	<0.0001
Days	5	5,162,531	1,032,506	31.44	<0.0001
Interaction	10	281,638	28,164	0.86	n.s.
Within	244	8,011,942	32,836		

species were tested. We calculated proportions by dividing the daily total time active during the light or dark period by the total length of the light or dark period, respectively, on that day.

Statistical analyses.—Two-way analysis of variance (ANOVA) tests for unequal sample sizes were used to compare swimming time (1) among all days (2) among species across all days, as well as (3) interactions (between species and days). Where statistical differences were obtained, post hoc (Tukey) tests were used to identify the responsible samples. Proportions were analyzed using nonparametric (Kruskal-Wallis) tests. Where statistical differences were found, nonparametric ("Tukey-type") multiple comparisons tests (Zar, 1984) were used to identify the samples involved.

RESULTS

Animals.—Sixteen green turtles were collected from four nests, 26 leatherbacks from eight nests, and 15 loggerheads from five nests. Hatchling weight (g) was (mean \pm 1 SD) 24.9 ± 2.1 for green turtles, 42.5 ± 3.0 for leatherbacks, and 19.2 ± 1.0 for loggerheads.

Activity patterns within species.—Hatchlings swam almost continuously during the first 24 h in the pools (Fig. 1). Thereafter, total activity declined. There were significant differences in total time spent swimming across days as well as among species. However, there were no significant interactions between species and days (Table 1). Tukey tests indicated that swimming time during Day 1 was significantly greater than on all other days. Levels of swimming activity between Day 2 and Day 6 failed to change with the exception of green turtle hatchlings (Day 2 vs Day 4, see below).

All species showed high levels of activity during the light period across all days when the data were analyzed as proportions of activity during the light and dark periods (Fig. 2). Di-

urnal swimming proportions failed to change significantly (Kruskal-Wallis Hc: *C. caretta* = 0.65, $n = 63$ light periods, n.s.; *Ch. mydas* = 5.03, $n = 80$, n.s.; *D. coriacea* = 4.69, $n = 119$, n.s.).

The proportion of the time spent active during the dark period declined significantly after Day 1 (green and leatherback hatchlings) and Day 2 (loggerhead hatchlings). Proportions of the dark period spent active did not significantly decline in leatherback hatchlings after Day 2. In green turtle hatchlings, proportions of the nocturnal period spent active after Day 1 remained statistically indistinguishable except for one evening (Day 4) when they were significantly less active. Proportions of nocturnal activity remained statistically indistinguishable in loggerheads between Day 2 and Day 5. No loggerheads showed any nocturnal swimming activity by Day 6. Day 6 differed significantly from Day 2 in loggerhead hatchlings.

Differences among species.—Tukey comparisons among species showed that total swimming time each day did not differ through Day 2. However, significant differences were apparent after Day 2. Hatchling leatherbacks were significantly more active than loggerheads from Day 3 through Day 6. Differences between leatherback and green turtle hatchlings were only apparent on Day 4 (nocturnal activity) when the latter showed a decline in activity. Loggerhead and green turtle hatchlings did not differ significantly in total swimming time.

Similar trends were apparent when proportions of activity during the dark periods were analyzed (Table 2). Species showed significant differences from one another after Day 2. From Day 3 to Day 6, hatchling leatherbacks swam 15–45% of the night (Fig. 2), which was significantly more than loggerheads. Differences between leatherback and green turtles were evident on one night (Day 4, Fig. 2). Significant differences between green turtles and loggerheads occurred on only one night (Day 6) when loggerhead hatchlings had completely ceased

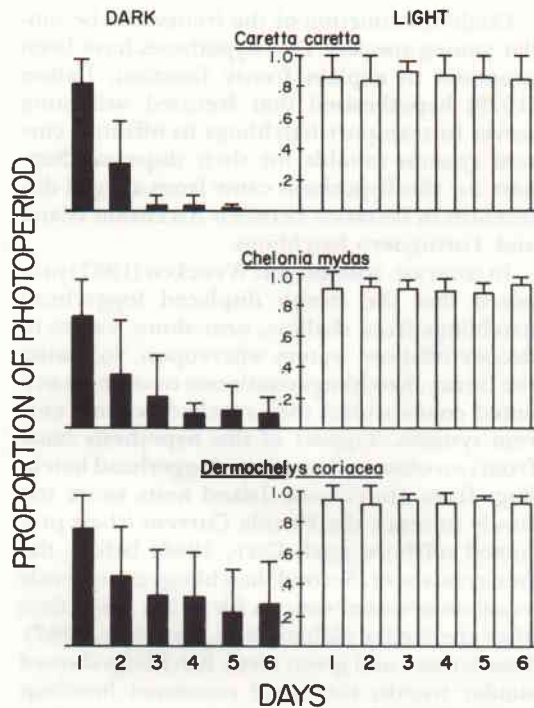


Fig. 2. The proportions (mean \pm 1 standard deviation) of the dark (left, filled bars) and light (right, open bars) periods that each species spent swimming on each of the six days of the experiment. Note all species persist in diurnal swimming activity but that, after Day 1, levels of nocturnal swimming activity decrease.

nocturnal activity. There were no differences in the proportions of the light hours spent active.

DISCUSSION

Loggerhead, green, and leatherback sea turtle hatchlings showed grossly similar patterns of locomotor activity in the first six days of swim-

ing. The hatchlings swam almost continuously during their first 24 h in the pools. Subsequently, there was a decrease in swimming activity as they became less active at night. However, the species differed in levels of nocturnal activity which was highest in leatherbacks and lowest in loggerheads.

Behavioral measurements.—Bennett (1978) and Dalton (1979) reported that green turtle hatchlings typically swam vigorously during their first few h in the water. However, in other respects, the patterns of activity they described differed from ours. The variation may result largely from differences in methodologies and/or criteria used to measure swimming behavior.

Bennett utilized an array of photocells lining the bottom of a square tank to detect green turtle movements. This system had several limitations when used to record hatchling activity. Constant illumination was required; thus turtles were deprived of a light-dark cycle. Additionally, individuals from the same clutch were tested on consecutive days because only one turtle's behavior could be monitored at a time. Thus, some were not placed in the tank until two weeks after hatching. Swimming was only monitored for short periods (24 h), which our results suggest is insufficient to detect behavioral changes.

Dalton's turtles were exposed to natural photoperiods over six to seven days of testing. Hatchlings swam in a narrow circular runway with screen walls. Movement was detected by paddles suspended in the water adjacent to the screen. The apparatus responded to water displacements generated by all turtle movements, including movements that may not have been "powerstroke" swimming, characteristic of rapid locomotion in open water. Dalton's frenzy measurements came from hatchlings tested five to 10 days after they hatched. Older hatchlings showed no frenzy, suggesting that age-related

TABLE 2. PROPORTIONS OF THE DARK PERIOD SPENT SWIMMING AMONG SPECIES. Hc = Kruskal-Wallis test statistic corrected for tied ranks; Q = nonparametric multiple comparison statistic.

Comparison	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
All species	n.s.	n.s.	Hc = 11.58 $P < .01$	Hc = 20.00 $P < .001$	Hc = 7.93 $P < .05$	Hc = 15.66 $P < .001$
Leatherback vs Loggerhead	n.s.	n.s.	Q = 3.72 $P < .001$	Q = 4.10 $P < .001$	Q = 2.80 $P < .02$	Q = 3.86 $P < .001$
Leatherback vs Green Turtle	n.s.	n.s.	n.s.	Q = 3.02 $P < .001$	n.s.	n.s.
Green Turtle vs Loggerhead	n.s.	n.s.	n.s.	n.s.	n.s.	Q = 2.78 $P < .02$