Habitat Selection and Antipredator Behavior in Three Species of Hatchling Sea Turtles

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According to the "lost year" theory of sea turtle development, hatchlings swim offshore in a frenzy until they reach floating weed beds where they live in relative safety for the first few years of life. Direct observations of post hatchlings in nature have been rare, so we utilized very young captive hatchlings presented with open water or artificial weed bed habitats (Experiments 1 and 2). Loggerhead (*Caretta caretta*) and hawksbill (*Eretmochelys imbricata*) hatchlings congregated in the weed bed, but green (*Chelonia mydas*) hatchlings did not. Green hatchlings that were slightly older and presented with *sargassum* continuously did show more tendency to gather in the weeds, particularly at night (Experiment 3). The young green turtles oriented towards the open ocean and congregated in the end of the tank closest to the ocean and actively avoided weeds (Experiments 4 and 5). When hatchlings were given simulated predation experience the loggerheads and hawksbills remained immobile following prediction, but the greens actively swam away (Experiment 6 and 7). These results suggest that the lost year theory of sea turtle development must be refined to take into account species differences and that different species of post hatchlings in nature may be found in different microhabitats, and reacting differently to potential and actual threat of predation.

During their period of post hatchling development, marine turtles lead a pelagic existence, commonly referred to as the "lost year" (e.g., Witham, 1980). The current version of the lost year theory suggests that immediately after their nocturnal emergence from the nest the young turtles find the sea using visual cues provided by the relatively brighter sky over water than land (Mrosovsky, 1972). Hatchlings then swim in a frenzy for a period of time, perhaps 24 to 48 h. (Wyneken & Salmon, 1992), directly away from shore (Frick, 1976). The proximate mechanism for orientation toward the open ocean appears to involve the hatchling swimming directly into waves (Salmon & Lohmann, 1989; Wyneken, Salmon, & Lohmann, 1990; Lohmann & Lohmann 1992; 1994). Once the frenzy is over, the hatchlings are thought to drift with the currents using floating patches of *sargassum* for both protection and food (Carr, 1980, 1987; Carr & Meylan, 1980; Witham, 1980), although the relative safety of sargassum

has been questioned (Witham, 1988). A magnetic sense triggered by the initial orientation toward the sea at the time of emergence from the nest, is thought to keep the young turtle correctly oriented during this period (Lohmann & Lohmann, 1994, 1995, 2000), for a lengthy period, probably several years, until they appear in shallow waters as juveniles and subadults. The extended lost year has been the topic of considerable speculation, and empirical research (see Musick & Limpus, 1996, for a review of the literature). Only recently have systematic attempts to observe turtles during this period of pelagic development been undertaken (Witherington, 1994a, 1994b, 2002).

Anecdotal reports of sightings or other evidence of post hatchling sea turtles being associated with floating sargassum include discovery of loggerheads washed ashore partially entangled in sargassum (Witham, 1988) or showing sessile growths on their carapaces that were the same as that found in sargassum (Caldwell, 1968). Witham (1974) reported finding eight loggerhead and one green hatchling in the stomach of a fish caught near floating sargassum. Carr and Meylan (1980) reported seeing three green turtle hatchlings resting in sargassum after only a 10 min search for them. The observation was made while the authors were following a radio-fitted adult female turtle who paused near a line of sargassum mats.

Extensive attempts to locate hatchlings at convergence fronts with sargassum present have been undertaken by Witherington (1994a, 1994b, 2002). He reported finding large numbers of loggerhead hatchlings and post hatchlings in these areas. Green hatchlings might be expected to also be found in this habitat, but none were. Of course, the failure to find something may have been due to insufficient searching time. The failure to find green hatchlings could also be due to the fact that there are far fewer green turtle nests in Florida than there are loggerhead nests. In fact, taking into account the number of hatchlings of each species emerging from nests along the Florida coast, the failure to find a single green hatchling relative to the number of loggerhead hatchlings found occurs with a probability of less than 5% (Witherington, 2002).

Experiment 1

In order to evaluate the hypothesis that turtle hatchlings utilize sargassum and other floating debris found at convergence fronts as a preferred habitat, we provided three species of hatchlings with a series of test trials offering a choice between an artificial weed bed and open water under controlled conditions. The hatchlings were tested in groups in their home tank over the first few days post emergence from the nest. A habitat selection trial consisted of two parts, baseline and test. The rectangular-shaped home tank was divided into two areas. One area, consisting of 25% of the total surface area (i.e., a quadrant), was the part where an artificial weed bed was placed in the test trial. In the baseline trial the entire tank was open water, and the number of turtles in the prospective weed bed area was counted each minute for 15 min. Following the baseline, the weed bed was placed in the tank and again the number of turtles in the weed bed area was counted each minute for 15 min. Our hypothesis was that the turtles would be attracted to the weed bed and that there would be significantly more present in the weed bed area during the test trial than during the baseline trial.

We chose to use artificial weeds (plastic, like those found in pet store aquariums) rather than real sargassum in order to differentiate the choice of habitat from approach to food (e.g., Heatwole, 1977). However, we conducted some trials with real sargassum to evaluate its attractiveness as a habitat and a food source.

We used three species of turtles, two endangered and one threatened. We explored the possibility that each species might exhibit different reactions to our test trials. Obviously, our test situation was not the same as the natural environment, but by comparing different species under equal conditions we can gain important clues about their behavior in natural conditions (e.g., Wyneken & Salmon, 1992). Our observation of green (*Chelonia mydas*), loggerhead (*Caretta caretta*) and hawksbill (*Eretmochelys imbricata*) hatchlings in captivity suggested to us that they might have different reactions to the habitat selection trial. The green hatchlings appeared more active and more oriented to the direction of the ocean in their tanks than did the loggerhead and hawksbill hatchlings. The loggerhead and hawksbill hatchlings appeared to spend much of their time in a "tucked" position with their foreflippers flattened over the carapace, occasionally flippering with their rear flippers, but often just floating. Selection of a weed bed habitat is more consistent with the relative inactivity of the loggerhead and hawksbill hatchlings; selection of an open water habitat is more compatible with the active swimming of the green hatchlings.

Method

Subjects. Hatchlings were randomly sampled from the complete clutch for participation in the experiment. Clutches came from nests in their original location and nests transplanted to a protected area. Two clutches of hawksbill turtles, Ns = 42 and 40, were used. Four clutches of loggerhead turtles, Ns = 50, 46, 44 and 46, were used. One clutch of green turtles, $N = 3$, were used. Each of the clutches appeared normal for their species in their general appearance and behavior. They were tested across the first five days post emergence depending on weather and other factors. All testing was done between 09:00 and 16:00 h (i.e., during daylight).

Apparatus. The living tanks for the turtles also served as the experimental situation. The tank measured 2.36 x 1.09 m and were 40 cm deep. They were located on a bluff above the beach, approximately 50 m from the high tide line. They were partially protected from the sun and rain by an unfinished "palapa" roof and a green canvas tarp. Sea water was circulated through the tanks when an electric pump was working and electricity was available, but during experimental trials the water to the tank being used was turned off. Water temperature was reasonably constant at 28°C and the air temperature ranged from 29-36°C. A video camera was used to tape most of the trials, and data were also taken by visually scanning and counting turtles as the trial occurred.

The artificial weed bed was made from plastic fern-like aquarium plants-each plant had several flat branching shoots. The branches were separated and their roots were stuck into a perforated flat sheet of plastic. The five flat plastic pieces (each 11.5 x 27 cm) with plastic weeds embedded in them were loosely wired together with gaps of about 5 cm between each segment. The whole weed bed was fastened to the tank so that the flat plastic bases were 5-8 cm below the water surface and the weeds extended to the surface and slightly above it from the bases.

An area equal to 25% of the total surface area of the tank was marked by stretching two pieces of string across the tank, above the water. One string was at the midpoint of the long side of the tank and the other was midway between the middle and the end. When the weed bed was added to the tank it was centered between the strings.

Procedure. Each habitat selection trial lasted for a little over 30 min. During the first 15 min., the number of hatchlings between the strings was counted every minute, on the minute. After this baseline, the weed bed was placed between the strings for the test condition. During this 15 min

test period, the number of hatchlings between the strings was counted each minute, on the minute. At the end of the test period the weed bed was removed from the tank. Total numbers of habitat selection trials were 9, 12, and 5 for the hawksbill, loggerhead and green hatchlings, respectively.

The research was conducted in cooperation with the Centro de Investigaciones de Quintana Roo (CIQRO) at their conservation research facility in Xcacel, Q. Roo, Mexico (see Zurita-Gutierrez, Herrera & Prezas, 1993, for a complete description of sea turtle activity in this area of Mexico). All turtles were released to the ocean some time after being in the experiment.

Statistical Analyses. Two kinds of statistical analyses were performed on the data. A sign test was used to compare the average number of hatchlings rounded to the nearest whole number between the strings under baseline and test conditions on the last 5 min of each condition. The binomial expansion was used to calculate the number of hatchlings that would be found in the marked area on the test trial under the null hypothesis assumption that the proportion of hatchlings found during the baseline is the appropriate probability value for the binomial expansion (e.g., Dwass, 1967). For example, loggerhead clutch 2 had a total of 46 hatchlings and on the baseline period on the first day postemergence there were an average of 7.68 hatchlings in the marked area (16.7% of the total, see Table 1). The binomial expansion with $N = 46$ and $p = 0.167$ predicts that between 3 (6.5%) to 12 (26%) turtles will be found in the marked area 95% of the time. Thus the finding of 22.8% of the clutch being present on the test trial was not significantly different from chance.

Results and Discussion

The main finding of this experiment was that the loggerhead and hawksbill hatchlings showed a strong affinity for the artificial weed bed habitat and the green turtles did not, almost to the point of showing avoidance of the weed bed. These differences in habitat preference showed no change across the first four days postemergence. These results are shown in summary form in Table 1.

Table 1
Percentage of Turtles Found in the Marked Area on Baseline (B) and Test (T) Periods as a Function of Post-emergence Day and Clutch.

	Postemergence Day									
	1		2		3		4		5	
Clutch	B	T	B	T	B	T	B	T	B	T
H1 (*N*=42)	16.4	21.0	11.7	15.2	11.7 x	38.3	12.4 x	23.3		
H2 (*N*=40)	11.0 x	43.0	10.8 x	22.8	16.0 x	30.5	19.5	22.8	16.2 x	26.6
L1 (*N*=50)	23.3 x	56.0	16.7 x	46.9						
L2 (*N*=46)	16.7 x	22.8	13.7 x	41.1	17.6 x	37.6	15.0 x	45.7		
					14.9 x	45.7				
L3 (*N*=44)	27.1 x	38.3								
L4 (*N*=46)	20.4 x	31.1	17.4 x	29.3	18.4 x	42.9	17.1 x	30.9		
G1 (*N*=33)	11.9	5.8	17.1	20.0	10.0	10.3	4.8	1.3	19.1 x	9.7

Note. x=difference between B and T is significant at the 0.05 level using the sign test. Underline numbers are in the 0.025 probability region of the binominal expansion (see text).

As can be seen in Table 1, the number of hatchlings present during baseline was significantly fewer than the number present during the presence of the weeds on 6 of the 9 hawksbill trials and on 12 of the 12 loggerhead trials (using the sign test). One of the 5 trials for the green hatchlings showed a significant difference between the number of turtles present on baseline and test, but in this case there were significantly more turtles present during baseline than during the weeds present period.

The binomial expansion also supported the conclusion that there were more loggerhead and hawksbill hatchlings present during the presence of the weeds than would be expected by chance. As shown in Table 1, the artificial weed bed attracted significantly more turtles than expected by chance on 5 of 9 hawksbill trials and 11 of 12 loggerhead trials. The green hatchlings were not significantly different in baseline and the test period using the binomial test. Figure 1 shows the percentage of animals in the critical area for baseline and weeds present averaged across all trials.
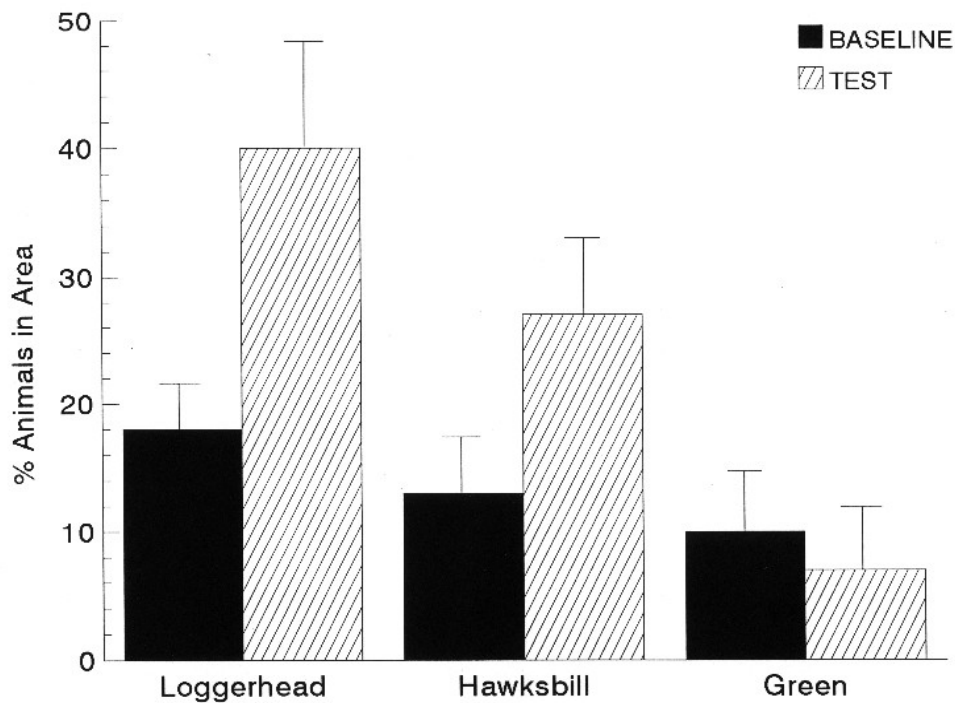

Figure 1. Mean percentage of turtles found in the marked area of the tank on baseline and test trials, averaged across all trials.

Both the loggerhead and hawksbill hatchlings were similar in behavior, usually entering the weed bed using a rear flipper kick with the fore flippers tucked against the carapace or simply drifting into the weed bed due to the slight movement of water in the trials caused by wind and the activity of other turtles. Once in the weed bed, they remained relatively motionless except for occasional breaths of air, which required that they move their head upward resulting in a counterbalancing movement of the rear flippers.

Experiment 2

We have had the opportunity to study multiple clutches of green hatchlings in previous years, but the timing of our presence and turtles nesting during Experiment 1 resulted in only one clutch of green hatchlings being available for study. Although this clutch seemed typical of other clutches we have observed, we felt it important to test additional clutches of green hatchlings to insure the generality of the results. Thus we returned to the study site in Xcacel the following year to replicate the experimental procedures on two additional clutches of green hatchlings.

Method

We had one clutch of green hatchlings that was 13 days postemergence $(N = 51)$ and the other was 4 days postemergence $(N = 50)$. In addition, a clutch of loggerheads of 14 days postemergence $(N = 51)$ was also tested. The artificial weed bed was not the same as the one used in Experiment 1, but it was as similar as possible to it, as were the baseline and testing procedures.

Results

The results of the habitat selection trials confirm what we found in Experiment 1. The percentage of green hatchlings in the marked area was low on both baseline (8% and 6%) and test trials (4.8% and 7.8%) and the differences were not statistically significant. The percentage of loggerheads in the weed bed area was 10% during baseline and 39% during the test, a significant difference using the sign test and binomial expansion.

Experiment 3

The hypothesis that hatchling sea turtles should associate with sargassum is compelling because the food and protection afforded by the weeds. It is therefore surprising that the green hatchlings show little interest, and even avoidance of weeds. For this reason we decided to repeat our experiments under somewhat different, but conceptually similar, conditions. We decided to use real floating weeds (sargassum) taken from the ocean rather than artificial weeds in order to maximize the potential attractiveness of the weed bed habitat.

Method

These observations were carried out at Xcaret, Mexico, about 20 Km from our previous study site. There were two 3 m x 2 m tanks and they contained 104 and 119 green turtles, 21-28 days post hatch during the experiments. Once a supply of sargassum was obtained from the ocean, one tank was provisioned with weeds (experimental tank) and one was not (control tank). The weeds were confined to the middle one-third of the tank by pieces of wood and plastic mesh. The turtles were observed a total of 16 times over a 4 day period at various day and night times. The number of turtles in the sargassum were counted and the number in the comparable area of the control tank were also counted. An animal was classified as inactive if it remained motionless for more than 5 s during a counting trial.

Results and Discussion

Observations of the two tanks revealed a common pattern of behavior in each. With no special manipulation, but routine feeding twice a day, the hatchlings were generally active and swimming during daylight hours and less active and a majority of the turtles were motionless at night.

The number of turtles in the area of sargassum was greater at night than during the day. The percentage of turtles in the sargassum was 28.3% (SEM = 5.6) during morning hours, and 42.3% (7.8) in the afternoon hours.   Of these percentages, 48.2% (6.3) of the turtles were inactive. In the control tank 16.3% (3.9) of the turtles were found in the middle third (in open tanks turtles have a tendency to be found in corners) during the morning hours and 21.5% (4.3) in the afternoon hours. Only one or two turtles were classified as inactive in the control tank in contrast to the experimental tank.

Night time observations resulted in 76.3% (4.9) of the turtles being found in the sargassum, and virtually all of them were inactive. The 23.7% of turtles not in the sargassum were generally active with a few exceptions. The turtles in the control tank were also inactive at night, but the percentage was 68.3% (5.1), somewhat lower than the turtles in the experimental tank. The inactive turtles in the control tank tended to drift to the edge of the and so there were only 14.1% (3.1) found in the middle section at night.

This experiment demonstrates that the addition of sargassum to the captive green turtle hatchlings tank can result in the turtles using the sargassum for a resting place both at night, and to a lesser degree, during daylight. The utilization of weeds of any sort as a resting place is in contrast to the effect of artificial and real weeds found in Experiments 1 and 2. Several factors may account for the differences between experiments. First, the turtles in this experiment were older than those in the other experiments, and also had spent more time in captivity. Either age or time in captivity could cause a shift in habitat preference. Second, in this experiment the sargassum was continually present, while in the previous experiments it was placed in the tank for 15 min periods only. Habitation to the presence of the weeds may have made their utilization as a resting habitat more likely.   Third, the weeds were present at night, the primary period of inactivity/sleeping. Turtles of this age float on the surface during sleep (while adult turtles who submerge for sleep), thus rendering weeds a relatively safe place providing some degree of cover.

Experiment 4

The fact that the green hatchlings did not select the weed bed as a preferred habitat in the first few postemergence days suggests that either they prefer open water or simply that their habitat selection preferences are undifferentiated at this very early stage of development. Our observations of the green hatchlings suggested that during daylight hours they were orienting and showing a "habitat preference" consisting of swimming toward the open ocean even though the sea was not visible to them. Carr (1965) provided a photograph of hatchling green turtles swimming freely in a round tank, almost all of them oriented toward the sea. He suggested the mechanism the hatchlings used to orient

toward the sea was the perceived difference in the light coming from the seaward direction as compared to the landward. Extensive documentation of visual guidance of hatchlings' orientation is consistent with Carr's speculation (e.g., Mrosovsky, 1972).

In order to evaluate further the green hatchlings tendency to orient and swim according to the location of open ocean and to avoid artificial weeds, we conducted a series of experimental trials. For each trial, the hatchlings were gently gathered together in a net, leaving them in the water at all times. The net was moved to a particular position in the tank and the hatchlings were released. We measured where individuals went when released, how quickly they went and how long they stayed. We varied the release point and the location of the tank relative to overhead conditions (partial roof or open sky). Individuals were given a temporary distinctive white mark on the carapace (a letter or number) so we could identify individual turtles.

Method

Subjects. The subjects were the same clutch of green turtles described in Experiment 1 and the trials for this experiment were conducted when they were 6-16 days postemergence.

Apparatus. The tanks were the same as described in Experiment 1. One tank was used for all except 2 of the 12 trials. The "standard" tank was located in the southeast corner of the facility and was the most exposed to the sky of all the tanks. The other tank that was used was located between two other tanks on the west side of the facility. The west location resulted in much of the overhead view, particularly to the east or seaward direction, being obscured by the palapa and tarp roof. Both tanks were oriented in the same direction so any geomagnetic cues were the same in both tanks. The eastern-most, or seaward, 30 cm and western-most, or landward, 30 cm of the tank were marked by a string stretched across the width of the tank.

Procedure. All 33 turtles were gathered in a fisherman's type landing net and released simultaneously. The release point was one variable we manipulated. For a "standard trial" they were released in the landward end of the tank, the latency of an individual to arrive in the seaward area was recorded for 10 min (600s maximum latency). The presence of each turtle in the marked area was recorded by noting the number or letter of each hatchling in the area during a scan at each minute for the first 5 min. This dependent variable will be referred to as the "asymptote" and consists of a score ranging from 0 to 5 depending on how many times the turtle was present on each minute scan of the marked area. We also scanned the marked area and recorded the individuals that were present prior to the start of a trial. These data we will refer to as "baseline."
On three trials the turtles were released in the middle of the tank. The latency to arrive in the seaward end and the landward end were recorded and their presence were also recorded (a "midrelease" trial).
For a "backward trial" the hatchlings were released in the seaward end of the tank, the latency and asymptote measures were taken for the landward area. All trials were conducted in the southeast tank except where noted.
The order and conditions for trials were as follows: Trial 1, first standard trial; Trial 2, standard trial, but in the west tank; Trial 3, standard trial, also in the west tank; Trial 4, first midrelease trial; Trial 5, second midrelease trial; Trial 6, second standard trial; Trial 7, first backward trial; Trial 8, third midrelease trial; Trial 9, third standard trial; Trial 10, fourth standard trial. Trials were conducted on 8 of 11 consecutive days. All trials were conducted between 09:35 and 11:20 h.

Statistical Analyses. The latency to arrive in the seaward vs. landward marked area for each subject was compared using a dependent *t*-test with significance level at .01 to adjust for the multiple comparisons between trials and minimize Type I errors. The same procedure was used to compare asymptotic scores. In addition, a correlation matrix of latencies and asymptotes were

constructed. It would be expected that the correlations should be negative-shorter latencies to arrive, more likely to be present during asymptote.

Results and Discussion

Midrelease Trials. On Trials 4, 5, and 8 the hatchlings were released in the middle of the tank and data were recorded at each end of the tank. The mean latency to appear at the seaward end of the tank was lower than the landward end. At asymptote there were more hatchlings in the seaward end than the landward end. Statistically, the difference in latencies were significant on trials 4, $t(31) = 3.12$ (81 vs. 260 s) and 8, $t(31) = 2.81$ (101 vs. 186 s), but not 5, $t(31) = 1.40$ (118 vs. 146 s). The asymptotic differences were significant on all three trials. On average, the turtles were observed in the seaward end of the tank for 3 of the 5 min, but were in the landward end on 0.4 of the 5 min. It is interesting that when the latency difference failed to reach the conventional significance level (Trial 5), the sky was cloudy and overcast, a condition known to reduce hatchling ability to use the sky for orientation (Carr, 1980).

The correlations between latency to arrive at one end of the tank and the number of times the turtle was found at that end of the tank at asymptote was expected to be negative. The correlations for arrival latency and number of times present in the seaward and landward ends of the tank were, respectively, -0.41 and -0.48 on Trial 4, 0.31 and 0.12 on Trial 5, and -0.45 and -0.25 on Trial 8. Once again Trial 5 was conducted under cloudy conditions and produced different effects than Trials 4 and 8.
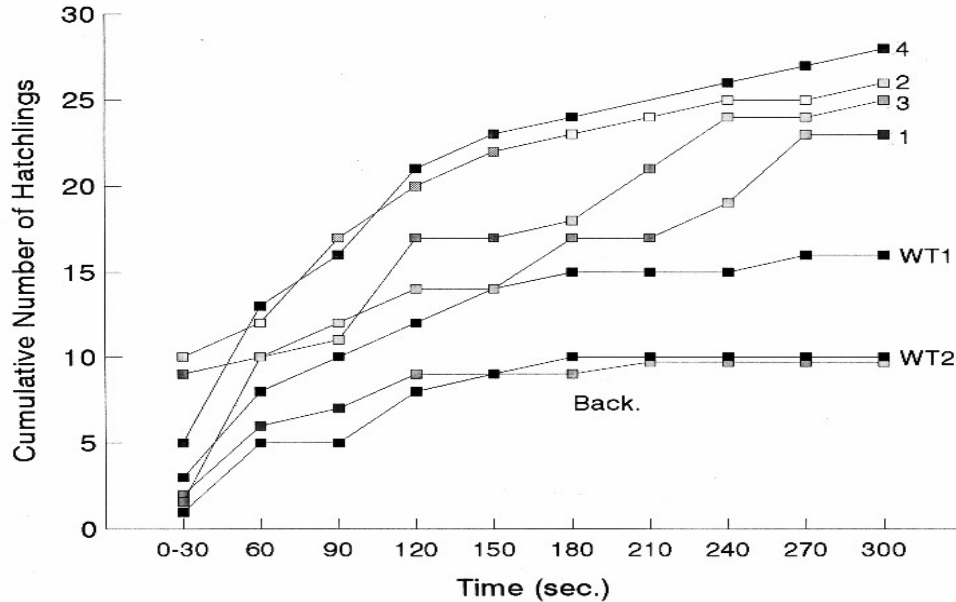

Figure 2. The cumulative number of turtles (each individual was counted only once) arriving in the seaward (landward for the backward trial) end of the tank across time. Trials 1, 2, 3 and 4 were Standard Trials, WT1 and 2 were conducted in the West tank.

Standard Trials versus Backward Trial. The latency to arrive in the seaward end on the 4 standard trials was less than the latency to arrive in the

landward end on the backward trial, the difference being significant on each of the four standard trials compared to the backward trial (overall mean = 109 s for the standard trials and 368 s for the backward trial). The asymptotic number of turtles present in the seaward end on standard trials was also significantly greater than the number present in the landward end on the backward trial in all four comparisons (overall mean = 3.70 for the standard trials, and 0.60 for the backward trial). Correlations between the latency to arrive in the seaward end and the asymptotic number of observations of the turtle in that end were generally negative, but reached statistical significance only on Trial 9, rs = -0.26, -0.28, -0.60 and 0.06, respectively.

Standard Trials vs Standard Trials in the West Tank. There were two trials conducted in the west tank where the sky to the seaward end was mostly obscured by overhead structures. Comparison of the two trials in the obstructed overhead view west tank to the four standard trials in the southeast (open) tank showed that the latency to arrive in the seaward end was greater in the west tank than the southeast tank in all cases. The differences were significant on all four comparisons of the first standard trials in the west tank (Trial 2), and on standard Trials 6 and 10 and west Trial 3. Similarly, the asymptotic number of turtles present in the seaward end was greater in the southeast tank (standard trial) than the west tank, in each case, but only 3 of the 8 possible comparisons reached an acceptable significance level.

Figure 2 shows the effects in a somewhat different way. The cumulative number of hatchlings arriving at the seaward end of the tank across time for the four standard trials and the two standard trials in the west tank are plotted. It also shows the cumulative number of hatchlings arriving at the landward end of the tank on the backward trial.

Experiment 5

In order to evaluate whether active green turtles avoid weed beds or are simply neutral with respect to them, we decided to use the clear preference for orientation toward the seaward part of their tank as a means of evaluating the avoidance/neutrality of artificial weeds. To do this we conducted trials like those in Experiment 4, but we added artificial weeds near the seaward end of the tank between the time the turtles were gathered up for the start of the trial and when they were released. If the green turtle hatchlings avoid the artificial weeds we would expect fewer to be in the seaward end of the tank when weeds are present then when they are not.

Method

Once again, the tank in the southeast part (most open to the sky) of the study area was used to conduct the trials. The trial consisted of counting the number of hatchlings in the seaward end of the tank for 15 min, once each minute, then gently gathering them in the net for release in the landward end of the tank. The weed bed was placed in the seaward end close to, but not against the tank wall, before the hatchlings were released.

The number of hatchlings in the seaward end was counted once each minute for 15 min (30 min on one trial). A clutch of green hatchlings (N = 51) was given two trials, one at 13 days post-

emergence and the other at 15 days. On the second trial the test period was extended to 30 min. In addition, one clutch of loggerhead hatchlings ($N = 54$) was given a trial for comparison to the green hatchlings. The loggerheads were 14 days postemergence at the time of the test.

Results and Discussion

The green hatchlings again showed their aversion to an artificial weed bed. There were significantly fewer green hatchlings in the seaward end of the tank on the test than on the baseline for both trials ($p < 0.01$ using the sign test). On the other hand, there were more loggerheads in the seaward end on the test than on the baseline ($p < 0.01$), once again confirming their affinity for the artificial weeds. Moreover, the behavior of the two species was different when in the seaward end with the weeds present. The loggerheads were predominantly resting and mostly immobile. The greens, on the other hand, were actively swimming between the weeds and the end wall of the tank, oriented toward the ocean.

The results of Experiments 4 and 5 show that green hatchlings have a strong open sky-open ocean swimming orientation well past the early frenzy period of development. Their orientation is not determined by extraneous factors such as being gathered together in a net and swimming to escape from the net since midtank release and the "backward" trial effectively rule out the net escape as a primary explanation of their behavior. At this stage of development, the green hatchlings seem to have an aversion to artificial objects placed in their immediate vicinity. Whether this aversion would occur to different kinds of objects, both artificial and natural and how it might change across developmental time (e.g., Experiment 3) should be of some importance in forming a more well-developed description of the natural history of this species.

Since these trials were all conducted outdoors with no control over weather, wind, temperature, and so on, we had to conduct trials under a variety of circumstances to determine what environmental characteristics controlled the hatchlings orientation. Both the natural occurrence of an overcast day and the imposition of an overhead cover implicate that the open sky provides the most effective stimulus for controlling the green hatchling's orientation. Wind was reasonably constant on all trials, varying only modestly in intensity from one trial to another. Geomagnetic stimuli, while probably important in later hatchling orientation (Lohmann & Lohmann, 1994, 1995) and in adult migrations, do not appear to be as important for hatchling orientation under these conditions as visual stimuli, since geomagnetic stimuli were present on the trials conducted in the west tank, yet the hatchling's orientation toward the ocean was substantially reduced.

Experiment 6

The habitat an animal selects to be in is often an important determiner of how an animal avoids predation. The fact that loggerhead hatchlings show a habitat preference for weeds, but green hatchlings, at least early in development during daylight, show an aversion to weeds, suggests that the species may also differ in their antipredator behavior.

Fleeing, freezing, and fighting are three behavioral adjustments commonly observed as antipredator behavior in a variety of species (e.g., Bolles, 1970). For a

hatchling sea turtle, fighting is not an option but fleeing in the form of active escape and freezing (closely related to tonic immobility or death feigning, Gallup, 1998) are vaiable options. Observations of hatchling turtles swimming away from their natal beach in Florida show that when threatened or attacked by an aquatic predator green hatchlings continue swimming, but loggerheads often become immobile, assuming a "tuck" position (Wyneken, Goff, & Glenn, 1994).

In this experiment, we tested the response of loggerhead, hawksbill and green hatchlings to a simulated predatory attack. We simply picked up an individual turtle and placed it back in the water and recorded its reaction.

Method

The same tanks as described in the previous experiments were used for this one. A wire mesh cage divided into 12 compartments was placed in one tank. Each of 12 compartments measured approximately 12 x 20 cm in two rows of 6. Subjects were removed from their living tank, placed in a dry plastic box, transported to the experimental tank and placed in one of the compartments. This took between 10 to 50 s. A stop watch started when the subject was put into the compartment and the time taken for it to begin swimming was recorded. A group of 12 green (10 days posthatch), 12 hawksbill (9 days posthatch) and 12 loggerhead (10 days posthatch) were tested on four consecutive days and the average time to swim across the 4 days was computed. The maximum duration of the trial was 600 s.

Results and Discussion

The average time to begin swimming following the simulated predation of being picked up and transported was 325.40 s for the loggerheads, 89.50 s for the hawksbills, and 1.8 sec for the greens. These differences were significant using an analysis of variance, $F(2, 33) = 13.24$, $p < 0.001$. The loggerheads and hawksbills that spent long periods being immobile were generally in a tuck posture with both fore and hind flippers folder against and underneath the carapace. When they were initially put back in water some of the loggerheads and hawksbills assumed a posture where the fore flippers were extended directly forward of their body, but usually with 10-15 s they gradually brought their fore flippers back to the tuck position. With only rare exceptions, the green hatchlings began swimming immediately on being placed in the water. Indeed, although we did not systematically record it, the greens typically struggled while in the hand of the experimenter, while the loggerheads and hawksbills typically were immobile during handling. The tendency to flee from potential predation must be particularly strong in green hatchlings since no real escape is possible in the confined test chamber, a fact that often results in defensive behaviors to fit the situation (Bolles, 1970), such as the immobility shown by the loggerheads.

Experiment 7

Observation of loggerhead hatchlings reveal that they spend a significant amount of time in an immobile posture, floating with flippers tucked to the carapace. In this experiment, we began a trial with the hatchling floating immobilized for at least 5 s. The hatchling was then either observed with no other manipulation (e.g., a sham trial), touched gently on the carapace, picked up for 3 s and placed back in the water, or picked up and turned over for three seconds and

placed back in the water (right side up). These different manipulations were hypothesized to represent increasing levels of simulated predation, or predator imminence, which may affect the topography of defensive behavior (Fanselow & Lester, 1988). In Experiment 6, all hatchlings were handled so there was no baseline of immobility. So while the loggerheads showed relatively long periods of immobility following simulated predation, these periods may be less, or not different than would have occurred if no simulated predation took place. This experiment provides an evaluation of this hypotheses and provides an additional comparison between species in antipredator behavior.

Method

A total of 46 loggerhead and 29 green hatchlings, 6-11 days post hatch, were used. Each species occupied one tank as previously described. Each loggerhead turtle was tested in all four conditions: sham, touch, 3 s hold, and 3 s turnover. Each turtle was marked with a letter or number for individual identification using white magic markers applied to its carapace. A predetermined sequence of turtles and trial types were used so that each turtle was tested once in each trial type per day and each of the four trials within a day were separated by all the other turtles within the tank having one trial of their own. This allowed us to counterbalance the order of trials across turtles, and to maximize the intertrial interval. They were given 3 consecutive days of testing.

Two or three experimenters carried out the trials and a scheduling/recording experimenter kept track of the schedule of subjects and trial types and recorded the latency to swim data provided by the experimenter who carried out the trial. At the start of a trial, the experimenter located the turtle and waited for it to be immobile for 5 s before starting the trial. On a sham trial, the experimenter merely started a stopwatch and watched the turtle and recorded the time until it became active. On a touch trial, the experimenter gently touched the carapace of the turtle, again recording the time until the turtle became active after the touch. On the hold and turnover trials, the experimenter picked up the turtle between their thumb and index finger and held it out of the water for 3 s (hold) or held it out and turned it upside down for 3 s (turnover) before placing it back in the water and recording the time until the turtle became active.

For the green hatchlings, it was not feasible to use all four trial types because the 5 s immobility criterion used to start a trial was difficult to satisfy since green hatchlings are rarely inactive for 5 s. For this reason, the green hatchlings received only sham and hold trials, again counterbalanced between subjects.

Results and Discussion

Preliminary analysis evaluating differences between days showed some variability, but it was not significant, so the latency to begin swimming was averaged across days for each subject and trial type. The green hatchlings usually swam away after being held for 3 s out of the water ($M = 2.55$ s). They continued to be immobile on the sham trial 14.88 s. The differences were significant using a repeated measures t-test (t (28) = 2.76, $p < 0.05$). Thus, the green hatchlings show an active fleeing from the source of simulated predation. Their response was often both vigorous swimming and diving. In contrast to the green hatchlings, the loggerheads showed an increase in the time spent being immobile. For the sham, touch, hold and turnover trials, the mean latencies to begin swimming were 41.30, 53.90, 85.30 and 68.20 s, respectively. The differences in latencies were significant, $F(3,42) = 14.88$, $p < 0.01$, and comparisons using Tukey's HSD method showed that the sham differed from both the hold and turnover conditions ($p < 0.05$), but not the touch condition. Thus, green and loggerhead hatchlings

show opposite responses to simulated predation, greens fleeing and loggerheads becoming immobile.

General Discussion

The general picture that emerges from this series of studies is that green turtle hatchlings have a much different way of behaving than loggerhead and hawksbill turtles, who seem to be similar in their patterns of response. Hatchling green sea turtles orient toward open ocean, avoid artificial weed during daylight hours, and actively swim away from a simulated predatory event. Hatchling loggerhead sea turtles congregate in artificial weed beds, floating without movement in them, and respond with inactivity to a simulated predatory event. We had limited opportunity to evaluate hatchling hawksbill sea turtles, but when we were able to include them in an experiment, they generally resembled the behavior of the loggerheads. We have consistently observed other differences between the green hatchlings and loggerhead and hawksbill hatchlings, some of the differences being important for understanding early development, while others may be a by product of being held in captivity with numerous conspecifics being present. Clearly protection of these endangered species will require the preservation of floating weed beds in the offshore environment near nesting beaches. The affinity of the loggerheads and hawksbills for such weed beds seems undeniable, and it seems highly likely that the greens are in close proximity to weeds since they are an abundant source of food and a likely resting place at night. Such weed beds occur at points of convergence of ocean currents, and so should be the focus of observation and protection of conservationists.

One of the most obvious differences between green and loggerhead-hawksbill hatchlings is the difference in coloration. The green hatchlings have a very dark carapace and a white plastron; the classic countershading of an open water, surface dwelling species that helps avoid detection from above and below. The darkness and whiteness does not vary to any noticeable extent. In fact the whiteness of the plastron is so dramatic that the local people in Mexico refer to the green turtle as "blanca," which is Spanish for white. Both loggerheads and hawksbills are more uniformly brown, with the carapace usually appearing a little darker than the plastron. There is a good deal of individual variation in the darkness of coloration, particularly in loggerheads, ranging from tan to dark brown. Coloration of this sort is consistent with hiding in weeds and other floating material, rather than an open water habitat.

Another obvious difference between species is the overall activity levels. Both loggerhead and hawksbill hatchlings spend significant amounts of time floating in a tuck position, while green hatchlings are usually actively swimming during daylight hours. In Experiment 7 we waited for the hatchlings to be inactive for 5 s before starting a trial. This required a long wait for the green hatchlings, and so they were used in only two conditions of the experiment while the loggerheads were in four conditions.

The morphology of the flippers and body are also consistent with the view that green hatchling seek open water and actively escape from predators, while the other two species use immobility and associate with cover to avoid predation. The flipper length of green hatchlings is greater than the other two species in the early

developmental phase (at least the first few months posthatch). For example, we measured the flipper length of 10 day posthatch turtles of each species, and the mean length was 4.41 cm. for the greens, 3.34 cm. for the loggerheads, and 3.14 cm. for the hawksbills. There was no overlap in the distributions of flipper lengths for the green and other two species. The greens were also bigger overall at this stage of development with a straight line carapace length of 5.65 cm, compared to 4.67 and 4.62 cm for loggerhead and hawksbill, respectively. To put these on a relative scale we divided the flipper length by body length, and the greens show a higher ratio at 0.78 as compared to 0.72 and 0.68. Thus the flipper power of the green turtle is greater than the other two species, consistent with the conclusion that they are a more open water-active escape species (see also, Wyneken, 1997).

In conclusion, our data from the experiments described above and our observations of the turtles in their tanks suggest that the beginning of the lost year is spent in different ways for different species. The choice of habitat is consistent with observations made in the natural habitat (Witherington, 2002) for green and loggerheads, lending support to the conclusion that our observations in captivity generalize to the real world of sea turtles.

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