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Relation of Temperature, Moisture, Salinity, and Slope to Nest Site Selection in Loggerhead Sea Turtles

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Nest site selection in reptiles can affect the fitness of the parents through the survival of their offspring because environmental factors influence embryo survivorship, hatchling quality, and sex ratio. In sea turtles, nest site selection is influenced by selective forces that drive nest placement inland and those that drive nest placement seaward. Nests deposited close to the ocean have a greater likelihood of inundation and egg loss to erosion whereas nest placement farther inland results in greater likelihood of desiccation, hatchling misorientation, and predation on nesting females, eggs, and hatchlings. To evaluate the role of microhabitat cues in nest site selection in Loggerhead Sea Turtles (*Caretta caretta*), we assessed temperature, moisture, salinity (conductivity), and slope along the tracks of 45 female loggerheads during their beach ascent from the ocean to nest sites in the Archie Carr National Wildlife Refuge in Florida on the beach with the greatest density of loggerhead nesting in the Atlantic. Of the four environmental factors evaluated (slope, temperature, moisture, and salinity), slope appears to have the greatest influence on nest site selection, perhaps because it is associated with nest elevation. Our results refute the current hypothesis that an abrupt increase in temperature is used by loggerheads as a cue for excavating a nest. Moisture content and salinity of surface sand are potential cues but may not be reliable for nest site selection because they can vary substantially and rapidly in response to rainfall and changes in the water table. Sea turtles may use multiple cues for nest site selection either in series with a threshold that must be reached for each environmental factor before the turtle initiates nest excavation or integrated as specific patterns of associations.

SELECTION of a nest site is an adaptive trade-off between the cost of searching for a site (both in terms of energy and predation risk) and the reproductive benefits of selecting a site suitable for successful incubation. The position of the nest affects the fitness of parents through the survival of their offspring. In many oviparous reptiles, environmental factors influence embryo survivorship (Horrocks and Scott, 1991; Burger, 1993; Resetarits, 1996), hatchling size (Packard and Packard, 1988), performance (Janzen, 1993), growth (Joanen et al., 1987; McKnight and Gutzke, 1993; Bobyn and Brooks, 1994), behavior (Burger, 1989, 1990, 1991), and sex determination (Ewert and Nelson, 1991; Janzen and Paukstis, 1991; Spotila et al., 1994). Selection of nest sites can also influence probability of nest predation (Fowler, 1979; Horikoshi, 1992).

Nest site selection in sea turtles can be divided into three phases: beach selection, emergence of the female, and nest placement. Beach selection and emergence probably depend largely on offshore cues and beach characteristics. Mortimer (1982) determined that Green Turtles (*Chelonia mydas*) at Ascension Island tend to emerge on beaches with an accessible offshore approach. Provancha and Ehrhart (1987) suggested that offshore characteristics of beaches provide cues, such as slope, that Loggerhead Sea Turtles (*Caretta caretta*) use to select a stretch of nesting beach. Hawksbill Sea Turtles (*Eretmochelys imbricata*) in Barbados also seem to use slope as a cue for beach selection, tending to nest on those beaches with steep slopes and low wave energy (Horrocks and Scott, 1991). Once a turtle selects a beach, how she decides to emerge at a particular location along that beach is unknown. Some evidence suggests sea turtles use dune profile as a cue for emergence (Camhi, 1993).

Nest site selection in sea turtles is influenced by selective forces that drive nest placement inland and selective forces that drive nest placement seaward (Bjorndal and Bolten, 1992; Camhi, 1993). Placement of nests close to the sea increases the likelihood of inundation and egg loss to erosion whereas placement of nests farther inland increases the likelihood of desiccation, hatchling misorientation, and predation on nesting females, eggs, and hatchlings.

Studies of nest placement in sea turtles have revealed a number of trends. On nesting beaches in Surinam shared by Leatherbacks (*Dermochelys coriacea*) and green turtles, leatherbacks tend to nest in open sand, whereas green turtles tend to nest in vegetated areas behind open sand (Whitmore and Dutton, 1985). Loggerhead nests in Greece also tend to be clumped near supra-littoral vegetation (Hays and Speakman, 1993). Hawksbill sea turtles change their crawl length on beaches with different slopes to clump their nests around a mean elevation of 1.2 m (Horrocks and Scott, 1991). Green turtles in Australia tended to nest on platforms of sand that were 1–3 m above the mean high-water line on beaches with lower salinities in surface sand and at nest depth (Johannes and Rimmer, 1984). In contrast, green turtles nesting at Ascension Island showed a wide tolerance to variation in sand color, grain size distribution, water content, pH, organic content, and calcium carbonate content (Stancyk and Ross, 1978).

Hays et al. (1995) modeled nest distribution of loggerheads nesting on a west Florida beach and concluded that nest placement was a product of each turtle crawling a random distance from the high-water line. Empirical evidence from other sites, however, does not support their model; Camhi (1993) found that environmental characteristics of loggerhead nest sites on a Georgia beach differed significantly from those of randomly chosen sites.

Little is known about proximate cues that sea turtles may use for nest site selection. Sea turtles in the genera *Caretta, Chelonia, Eretmochelys,* and *Lepidochelys* have a fixed behavior pattern before selecting nest sites that includes pressing their heads into the sand as they ascend the beach, perhaps to monitor microhabitat characteristics to assess potential nest sites (Hendrickson, 1958; Carr and Ogren, 1960; Carr et al., 1966). Sand characteristics that turtles may evaluate in this manner include temperature, moisture, and salinity. Studies have indicated that sea turtle nest sites are not randomly distributed according to available beach characteristics, but they do not indicate which characteristic or characteristics may be cues (Camhi, 1993; Hays and Speakman, 1993).

Our study evaluated temperature, moisture, conductivity (salinity), and slope as microhabitat cues for nest site selection by comparing these parameters at the nest site with those at sites along the track of a turtle as she ascends the beach to the nest site. Because sites along the track represent potential nest sites rejected by the female, environmental parameters that differ between nest sites and sites along the track may serve as cues in nest site selection.

We were particularly interested in testing the hypothesis that temperature was used as a microhabitat cue for nest site selection in loggerhead sea turtles. In turtles, temperature influences duration of embryogenesis and sex determination (Ewert and Nelson, 1991; Janzen and Paukstis, 1991; Ackerman, 1997). Turtles can influence duration of incubation (and thus length of exposure to nest predators) and sex of their hatchlings by selecting sites based on temperature (Janzen, 1994; Roosenburg, 1996). Stoneburner and Richardson (1981) reported that loggerheads nesting at three beaches (Cape Lookout National Seashore, North Carolina; Cumberland Island, Georgia; and Canaveral National Seashore, Florida) began nesting where surface sand temperature increased rapidly by 2.05–3.55 C on a water-to-dune axis. However, Camhi (1993) demonstrated that loggerhead sea turtles nesting on Cumberland Island, Georgia (one of the beaches on which Stoneburner and Richardson conducted their study) did not select nest sites in warmer or cooler patches of a heterogeneous beach. In addition, green turtles and hawksbills nesting at Tortuguero, Costa Rica, showed a varying nest distribution among different thermal zones of the beach (Bjorndal and Bolten, 1992). Lack of any consistent pattern of nest distribution among or within individual turtles suggests green turtles and hawksbills nesting at Tortuguero do not actively select nest sites based on temperature.

MATERIALS AND METHODS

Study site.—Data were collected between 13 June and 16 August 1996 in the Archie Carr National Wildlife Refuge near Melbourne Beach, Florida, (28°N, 80.5°W). Melbourne Beach is a high energy beach with a sloped berm and coarse-grained sand that includes broken shell. Erosional forces have left a steeply scarped foredune that prevents sea turtles from crawling into vegetated areas of the dune. The dominant flora are sea oats (*Uniola paniculata*), morning glory (*Ipomoea pes-caprae*), and saw palmetto (*Seronoa repens*). Witherington (1986) provided a detailed description of Melbourne Beach. The 2-km stretch of beach used in this study was located in a residential area that included single family homes, a restaurant, and a multistory condominium. The turtles had access to the full width of beach; no structures, such as sea walls, served as obstacles.

Track data.—Only turtles intercepted as they ascended the beach and followed until initiation of oviposition were included in this study (n = 45). All nesting emergences were nocturnal events. To avoid including a turtle more than once, turtles were tagged after oviposition was completed with Monel metal tags that bear an identification number. After a turtle was located, we marked the water line with a stake and then waited in a prone position behind her. When the turtle began to dig a body pit, the first stage of nest preparation, we recorded the temperature of the sand 2 cm below the surface at her cloaca. Sand temperatures at nose positions of nest sites were not measured because movement near the turtle's head could have caused her to abort nesting and the sand was too disturbed by the time it was safe to measure temperature. All temperature measurements were taken with an Omega HH-25TC digital thermometer with a type-T thermocouple accurate to ±(0.4% + 0.6 C). The two thermocouples used to collect data were calibrated to an NBS-certified mercury thermometer, accurate to ± 0.01 C (serial number 7F7747, Parr Instrument Company, Moline, IL). We then returned to the stake, and, at 1.5-m intervals along the track, we measured temperature of sand 2 cm below the surface (our best estimate of the depth "sampled" by turtles) and immediately lateral to the track (i.e., sand within 2 cm of the track) to avoid sampling sand that the turtle had disturbed during her ascent. These measurements were recorded within 30 min of the turtle passing each sampling location. Temperature trials performed at 262 sampling sites from 23 additional turtle tracks not used in this study indicated there was no significant difference between sand temperatures in the track and immediately lateral to the track (t-test; $P = 0.46$) or between temperatures immediately lateral to the track compared to repeated measurements taken 15–30 min later (t-test; $P = 0.81$). Thus, these interval measures represent temperature of sand at 2 cm below the surface when the turtle crawled up the beach.

Slope was measured at the same 1.5-m intervals and at cloaca and nose positions of nest sites. A board, 1.5 m long, was placed perpendicular to the water line. A Brunton Cadet Pocket Transit with a protractor reading from −90° to +90° in 2° increments was placed on the board and used as a clinometer. Slope of each interval was recorded to the nearest degree.

We also collected sand samples at each interval and at cloaca and nose positions of nest sites for moisture and conductivity analyses. Samples were wrapped in plastic to avoid moisture loss in transit to the lab. Samples were weighed to the nearest 0.1 g and dried to a constant mass at 105–110 C. Moisture content was calculated as the ratio of water loss to dry mass multiplied by 100 (Head, 1992).

Electrical conductivity was used to estimate salinity. Conductivity was measured by mixing 50 g of dried sand with 50 ml of deionized water. The supernatant was decanted, and conductivity was measured using a digital conductivity meter (Fisher Scientific Company). Greater electrical conductivity values indicate higher salinity. Conductivity measurements were recorded as microsiemens for statistical analysis.

We measured track length (overall distance crawled by turtles, ± 5 cm), straight-line distance from water line to the nest as demarcated by the stake and nest site, and nest elevation. Nest elevation was calculated by multiplying the sine of overall slope (measured with an Abbney level accurate to within 2°) and the straight-line distance from water to nest. A straightness index was calculated for each track using the ratio of straight-line distance from water to nest to overall distance traversed by the turtle (Witherington, 1992; Johnson et al., 1996).

Hatching success.—Twenty-six of the 45 loggerhead nests included in this study were marked and monitored to determine hatching success as part of another study (Bouchard and Bjorndal, in press). Nests were excavated and inventoried 72 h after hatchlings left or after 65 days of incubation. Clutch size was estimated by summing hatched and unhatched eggs. Hatching success was the percentage of eggs that produced live hatchlings.

Statistical analyses.—All descriptive statistics, principal component analyses (PCA), correlations, and linear regressions were performed with Statistical Package for Social Sciences (SPSS) version 7.0. Track data were analyzed with SPSS using general linear model (GLM) repeated measures with simple and repeated contrasts. Simple contrasts compared the mean of each interval to a reference site; nose position of nest sites was the reference site for every characteristic except temperature for which cloaca position was the reference site. Repeated contrasts compared the mean of each interval to the mean of the previous interval. For each nesting crawl, the nose and cloaca positions at the nest site and the nine preceding 1.5-m intervals leading from the water to the nest were used. The temperature dataset started with cloaca positions of nest sites and used nine preceding intervals. Nine preceding intervals were used because most tracks had at least that number of sites; only nine nesting crawls with fewer than nine sites preceding the nest had to be excluded from the analysis. GLM repeated measures were also used to compare changes in temperature, moisture, conductivity, and slope between adjacent interval samples (Wood,

Table 1. Correlations (Spearman's Rank) for Sites Along 45 Loggerhead Sea Turtle Nesting Crawls at Melbourne Beach, Florida. Numbers in parentheses are sample size.

	Distance from dune	Temperature	Moisture	Conductivity
Track sites				
Temperature	−0.323**	1.00		
	(639)			
Moisture	0.582**	−0.541**	1.00	
	(640)	(639)		
Conductivity	0.394**	0.037	0.413**	1.00
	(640)	(639)	(640)	
Slope	−0.005	−0.061	0.107**	0.139**
	(640)	(638)	(639)	(639)
Cloaca positions at nest sites				
Temperature	−0.103	1.00		
	(45)			
Moisture	−0.201	−0.507**	1.00	
	(45)	(45)		
Conductivity	0.013	0.335*	−0.404*	1.00
	(45)	(45)	(45)	
Slope	0.045	−0.039	−0.050	−0.063
	(44)	(44)	(44)	(44)
Nose positions at nest sites				
Moisture	−0.004	—	1.00	
	(37)			
Conductivity	0.151	—	−0.451**	1.00
	(37)		(37)	
Slope	0.134	—	0.228	−0.184
	(36)		(36)	(36)

* Correlation is significant at the 0.05 level; ** Correlation is significant at the 0.01 level.

1998), but because no meaningful relationships were revealed, those results are not presented here. Moisture content of sand and hatching success, both of which were expressed as percentages, were arcsine transformed for analyses. All *P*-values were compared to an alpha level of 0.05.

Results

Beach gradients.—Loggerheads nesting at Melbourne Beach tended to crawl nearly perpendicular from the edge of the water. The mean straightness index of nesting tracks was 0.914 (SD = 0.081, range = 0.651–1.0, n = 45; 1.0 = straight). Therefore, nesting crawls can be used as transects to characterize gradients on the beach and evaluate correlations between environmental parameters along the axis from ocean to dune (Table 1, Figs. 1–2).

Average temperatures at sites along a loggerhead track were significantly lower near water (Fig. 1). Slope increased significantly near the water line, remained relatively constant at midbeach, and again increased significantly near nests (Fig. 1). Moisture and conductivity were both significantly higher near the water line and decreased closer to nest sites (Fig. 2).

Physical attributes of nest sites.—Mean track length (distance traveled to the nest from water line at time of female emergence) was 23.5 m (SD = 5.6, range = 11.8–34.8, n = 45). Mean straight-line distance from nest to water line at time of female emergence was 21.4 m (SD = 5.5, range = 11.1–34.0, n = 45). Mean distance from dune to cloaca position of nest site was 2.2 m (SD = 3.0, range = 0–12.3, n = 45), and mean distance from dune to nose position of nest site was 1.4 m (SD = 2.5, range = 0–11.3, n = 37). Mean nest elevation was 3.2 m (SD = 0.7, range = 2.1–5.6, n = 42). The mean overall slope of the beach from the water line to nest site was 9° (SD = 2, range = 5–13, n = 42). Correlations among environmental factors at nest sites are presented in Table 1.

Distance from the dune, moisture, and conductivity were not significantly different be-

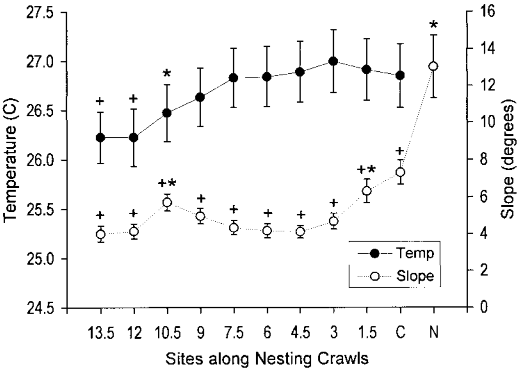

Fig. 1. Mean temperatures (C) and slopes (angular degrees) for sites along the nesting crawls of loggerheads at Melbourne Beach, Florida. For sites along crawls, numbers represent meters from nest site; the letters "C" and "N" refer to cloaca and nose positions of nest sites, respectively. Vertical bars represent one standard error, asterisks (*) indicate sites that were significantly different from the adjacent site closer to the water (GLM, repeated contrasts; $P < 0.05$), plus symbols (+) indicate sites that were significantly different from the cloaca position for temperature and the nose position for slope (GLM, simple contrasts; $P < 0.05$).

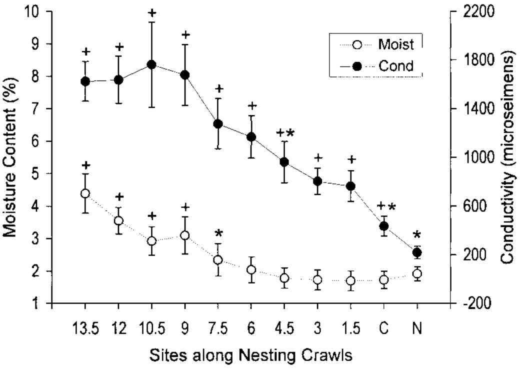

Fig. 2. Mean moisture content (%) and conductivity (microsiemens) values for sites along the nesting crawls of loggerheads at Melbourne Beach, Florida. For sites along crawls, numbers represent meters from nest site; the letters "C" and "N" refer to cloaca and nose positions of nest sites, respectively. Vertical bars represent one standard error, asterisks (*) indicate sites that were significantly different from the adjacent site closer to the water (GLM, repeated contrasts; $P < 0.05$), plus symbols (+) indicate sites that were significantly different from the nose position (GLM, simple contrasts; $P < 0.05$).

tween cloaca and nose positions of nest sites (one-way ANOVAs and Bonferroni posthoc multiple comparison tests, $P > 0.05$). Only the slopes at cloaca and nose locations of nest sites were significantly different (one-way ANOVA and Bonferroni posthoc multiple comparison test, $P < 0.02$). Temperature was not measured for nose positions of nest sites.

Hatching success was not correlated with temperature, moisture, or conductivity at nest sites. The correlation between hatching success and nest elevation was not significant for all nests ($P = 0.275$, df = 23), but the relationship approached significance ($P = 0.059$, $r^2 = 0.23$, df = 15) when depredated nests were removed. When depredated nests were removed from the analysis, inundation by tides or storm wash, the factor against which nest elevation would be expected to protect, was the major mortality factor. Slope at cloacal positions of nest sites was the only factor that had a significant relationship with hatching success ($P = 0.01$, $r^2 = 0.25$, df = 24).

Comparisons among track sites and nest sites.— Track (nonnest) sites were significantly different from nest sites for mean distance from the dune, mean temperature, mean moisture, mean conductivity, and mean slope (one-way ANOVAs and Bonferroni posthoc multiple comparison tests, $P \leq 0.02$). A factor loading plot from principal component analysis showed how distance, temperature, moisture, conductivity, and slope were related in a two-dimensional space (Fig. 3). Qualitative associations among distance, temperature, moisture, conductivity, and slope are different for track sites and nest sites. For track sites, moisture, conductivity, distance, and, to a lesser extent, temperature were associated along the first factor axis (Fig. 3). As distance from the dune increased, moisture and conductivity increased, whereas temperature de-

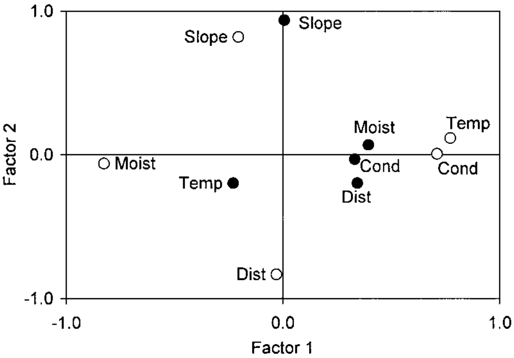

Fig. 3. Factor loading plot from principal component analysis for distance from the dune (dist), temperature (temp), moisture content (moist), conductivity (cond), and slope for track sites (closed circles) and nest sites (open circles) along 45 loggerhead nesting crawls at Melbourne Beach, Florida.

creased. Slope loaded strongly on the second factor axis and was not noticeably associated with other environmental variables.

The factor plot for nest sites showed different relationships among environmental variables (Fig. 3). Distance from the dune was negatively associated with slope at nest sites, but neither was associated with other variables. Moisture was inversely related to temperature and conductivity. In contrast to track sites, a decrease in moisture content was accompanied by increases in temperature and conductivity.

To evaluate quantitative differences in track sites and nest sites, GLM repeated measures were performed. For temperature, only sites 12.0 and 13.5 m from nest sites were significantly different from nest sites (simple contrasts, $P \leq 0.006$; Fig. 1). These sites were cooler than nest sites and probably reflect the influence of waves washing ashore. Mean temperature at sites 10.5 m from the nest were significantly higher than previous sites 12.0 m away from nests (repeated contrasts, $P = 0.004$). Temperature was relatively constant for track sites within 7.5 m of nest sites.

Mean slopes at all sites were significantly lower than mean slopes at nose position of nest sites (simple contrasts, $P < 0.001$; Fig. 1). Repeated contrasts supported this relationship; nose position of nest sites had a mean slope significantly higher than that of cloaca positions of nest sites, and sites 1.5 m away from nests had a significantly higher mean slope than sites 3 m from nests ($P \leq 0.033$).

For moisture, means of sites 9–13.5 m away from nest sites were significantly higher than mean moisture at nest sites (simple contrasts, $P \leq 0.042$; Fig. 2). Only sites 7.5 m away from nest sites were significantly different from previous sites (repeated contrasts, $P = 0.049$).

All track sites had a mean conductivity that was significantly higher than the mean at nose positions of nest sites (simple contrasts, $P \leq 0.006$; Fig. 2). In addition, mean conductivity at cloaca positions of nest sites was significantly lower than the mean at previous sites 1.5 m away, and mean conductivity was significantly lower at sites 4.5 m away from nest sites than sites 6.0 m away (repeated contrasts, $P \leq 0.007$).

DISCUSSION

Nest site selection.—On dynamic beaches where the primary mortality factor for incubating eggs is beach erosion and environmental characteristics such as slope, temperature, moisture, and salinity provide little information about potential nest success, turtles seem to scatter nests on population and individual levels (Mrosovsky, 1983; Eckert, 1987; Bjorndal and Bolten, 1992). In these unpredictable environments, scattering nests along the water-to-dune axis may maximize reproductive success (Eckert, 1987; Tucker, 1990; Bjorndal and Bolten, 1992). On more stable beaches where environmental characteristics may provide more information about nest survival, a more structured nesting strategy may develop (Eckert, 1987). Where clumped nest distributions persist, sea turtles must alter crawl lengths during different tidal cycles to reach the same area of beach. Loggerhead turtles clump nests near supra-littoral vegetation on the west coast of Florida (Hays et al., 1995) and on the island of Cephalonia, Greece (Hays and Speakman, 1993), near the toe of the foredune in Georgia (Camhi, 1993), and 2.2 m in front of the dune at Melbourne Beach, Florida (this study).

To reach the appropriate area for nesting, sea turtles that clump their nests in a particular zone probably use environmental information to assess their position on the beach. At Melbourne Beach, gradients of temperature, moisture, salinity, and slope run along the beach perpendicular to the water line. To sample efficiently the available nesting environment, an emerging female need only crawl along the water to dune axis. Loggerheads at Melbourne appear to use this strategy. The 45 nesting emergences examined had a mean straightness index of 0.914 (1.0 = straight path).

If sea turtles use these gradients as proximate cues for nest site selection, it is not clear whether they select unique patches within a heterogeneous environment or whether all sites within a few meters of the dune are acceptable for nesting. That is, is the accuracy of the nest site selection process calibrated to select a particular site on the beach or to select a zone in which any site will have a high probability of incubating a successful nest? Camhi (1993) determined that nest sites were significantly different from randomly chosen sites on a loggerhead nesting beach in Georgia. Her randomly chosen sites included beach habitats, such as the fore and back slopes of the dune, that are not often utilized by nesting turtles. To address the question of whether loggerheads select particular sites or a zone of similar sites, the approach used by Camhi (1993) should be repeated to compare nest sites with randomly chosen sites within the zone where nests are usually clumped. If nest sites are different from randomly chosen sites within this zone, then that would suggest that sea turtles have a finely tuned ability to use environmental information to select unique patches for egg deposition. If nest sites are not different from randomly chosen sites, then sea turtles probably use environmental information on a broader scale to select a zone with the highest probability of nest survival but not necessarily a unique site within that zone.

Temperature as environmental cue.—Our results do not support the hypothesis that an abrupt increase in temperature is used as a cue for excavating a nest. In contrast to the work of Stoneburner and Richardson (1981) and consistent with the work of Camhi (1993), there were no significant differences between temperatures of nest sites and temperatures of track sites except for sites 12.0 m and 13.5 m from the nest. Because the study by Stoneburner and Richardson (1981) has been cited in theoretical literature on maternal effects on hatchling phenotype (e.g., Bernardo, 1996), it is important to note that their results are not consistent with those of our study and other studies. As has been suggested elsewhere (Hays et al., 1995), the abrupt increase in surface sand temperature that Stoneburner and Richardson (1981) reported was almost certainly an artifact of sampling warmer subsurface sand that had been exposed by the digging sea turtles (Moran et al., in press). This conclusion is the only reasonable explanation for the fact that the abrupt temperature increase was only found directly behind the nesting turtle and not along other gradients on the same beaches.

Moisture as environmental cue.—A sea turtle may be able to influence fitness of her hatchlings by selecting nest sites with a particular moisture content. Although too much moisture is detrimental, a certain amount of moisture is needed to maintain the integrity of the nest chamber and support embryogenesis. Moisture may affect hatchling size (Packard and Packard, 1988; Brooks et al., 1991) and hatchling performance (Miller et al., 1987; Janzen, 1993) in oviparous reptiles. Green turtle clutch survival at Ascension Island is lowest in the driest substrata (Mortimer, 1990). Hatching success for loggerheads nesting in Florida is highest in nests with a moisture content of 25% (McGehee, 1990). High levels of inundation from sea water or excessive rain are lethal for developing loggerhead embryos (Ragotzkie, 1959; Kraemer and Bell, 1980).

Although moisture is critical, moisture content was probably not used as a cue for nesting because only sites 7.5 m from nest sites were significantly different from previous sites. Moisture content of surface sand may be an unreliable proximate cue for nest site selection because it varies rapidly with rainfall. A strong correlation between moisture content at the surface and moisture content at nest depth is unlikely. Grant and Beasley (1996) reported that moisture content at nest depth (50 cm) from the high tide line to nest location on Topsail Island, North Carolina, remained relatively constant from 6 m beyond the high tide line to nests.

Salinity as environmental cue.—Salinity (conductivity) has also been suggested as a cue for nest site selection (Mortimer, 1990). Johannes and Rimmer (1984) reported that beaches in Australia where green turtles nest have lower salt content in surface sand than do beaches where turtles do not nest. Mortimer (1990) found that clutch survival of green turtles at Ascension Island was negatively correlated with salinity. Salinity could indicate the position of the mean high tide line or the most recent high tide. The farther a nest is placed above the high tide line, the less likely it is to be inundated by seasonal tidal fluctuations and storm surges.

Changes in conductivity corresponded to changes in moisture levels and may indicate the position of the most recent high tide (Fig. 2). Conductivity could be used as a nest site selection cue because nose and cloaca positions of nest sites differed significantly from track sites in mean conductivity. However, like moisture, conductivity would seem to be an unreliable cue for nest site selection because it is a highly variable factor that changes with rainfall and water table fluctuations. In addition, the concentrated salt solutions secreted by sea turtles from lachrymal glands (Lutz, 1997) probably would interfere with the ability of sea turtles to monitor sand salinity.

Slope as environmental cue.—Slope has been suggested as a cue for nest site selection in hawksbill sea turtles (Horrocks and Scott, 1991). Painted Turtles, *Chrysemys picta*, nested significantly more often on slopes in Ontario, Canada (Schwarzkopf and Brooks, 1987). In our study, mean slopes of all sites were significantly different from mean slope at nose positions of nest sites. The beach topography had three significant increases in slope, one 10.5 m away from the nest, one 1.5 m from the nest, and one between the cloaca and nose positions of the nest site (Fig. 1). The first change occurred where waves wash ashore and alter the slope of sand through erosional effects. The second and third changes may serve as cues for nest site selection.

Slope may be an important cue because it reflects changes in beach elevation. A change to a higher slope could indicate that the turtle has reached an elevation that increases the probability of hatching success for her nest. Horrocks and Scott (1991) found that nest elevation was positively correlated with hatching success for hawksbill sea turtles in Barbados. In our study, nest elevation was not correlated with hatching success, but our sample size was small, and variation in nest elevation among those nests was limited. Slope at cloacal positions of nest sites was the only factor that had a significant relationship with hatching success.

Caution should be exercised when using hatching success data to evaluate environmental cues for nest site selection. First, in this study, sample size is small. Second, in many nesting seasons, hatching success may not correlate with the cues that are used in nest site selection. The relationship between hatching success and the cues employed by nesting turtles to select nest sites may well be disguised by sources of egg mortality that are unpredictable (e.g., hurricanes) or that have been introduced relatively recently by human activities (e.g., feral predators; Fowler, 1979).

Multiple environmental cues.—The above discussion considers each environmental factor separately, but sea turtles may use multiple cues for nest site selection. All four factors—temperature, moisture, salinity, and slope—may be important for nest placement. For example, each factor could have a threshold that must be reached before a turtle initiates nest excavation. Temperature may be the first threshold crossed. When sea turtles emerge from the sea, they may continue to ascend the beach if sand temperature is at least 21.2 C (the lowest temperature of a track sample in our study; the actual threshold may well be lower). The threshold for moisture and salinity might be the most recent high-tide line, the position where moisture content and salinity drop substantially. Once female turtles have passed thresholds for temperature, moisture, and salinity, an increase in slope may be the final proximate cue that initiates digging. This sequential threshold hypothesis would explain why loggerhead sea turtles rarely stop to nest in the swash zone where they first encounter an increased slope that is significantly different from the previous site.

Another possibility is that sea turtles integrate environmental information to use as a cue for nest site selection. According to PCA, temperature, moisture, conductivity, and slope are associated with each other in different ways at track sites and nest sites (Fig. 3). For example, at track sites, temperature is associated negatively with moisture and conductivity, whereas at nest sites, temperature is associated negatively with moisture but positively with conductivity. A sea turtle could integrate this information and select sites based on specific patterns of associations or where associations of environmental factors change.

Conclusion.—The environmental factor that appears to have the greatest influence on nest placement at Melbourne Beach is slope. Slope increased significantly at nest sites, and steeper slopes usually indicate an area of the beach with higher elevation and thus higher probability of nest survival. Temperature, specifically a sudden increase in temperature, is not a cue for nest site selection at Melbourne Beach, the most important loggerhead sea turtle nesting beach in the Atlantic. Moisture and salinity cannot be ruled out as proximate cues but are susceptible to daily and seasonal variation and may not be reliable cues for nest placement. The different associations of environmental factors at track sites and nest sites may be used as cues for nest site selection. Sea turtles may also use sequential thresholds in which a threshold of each environmental factor is reached before nesting is initiated.

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