SHORTER COMMUNICATIONS

Journal of Herpetology, Vol. 37, No. 1, pp. 178–182, 2003

Beach Selection in Nesting Pig-Nosed Turtles, *Carettochelys insculpta*

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Abstract.—**We investigated beach selection of nesting Pig-Nosed Turtles (*Carettochelys insculpta*) along a 63-km stretch of river for two years. We found 221 nests on 82 nesting beaches and identified 171 potential nesting beaches based on previously published criteria. Beaches with nests had a greater substrate moisture content and corresponding higher cohesive sand line (hereafter CSL) than beaches without nests. Beaches with nests also had a higher CSL than beaches with only crawls. Beach temperatures increased with a seasonal increase in air temperatures and were influenced by aspect and total angle of solar exposure. Turtles did not select beaches that were hotter or cooler, on average, than what was available, indicating that turtles were not manipulating offspring sex through choice of nesting beach.**

In oviparous animals, the choice of nest site can have a profound influence on embryonic development and survival by moderating the incubation environment (reviewed in Packard and Packard, 1988; Janzen, 1994; Wilson, 1998). Surviving offspring are also affected via the influence of incubation environment on phenotypes (Allsteadt and Lang, 1994; Shine and Harlow, 1996). In reptiles with temperature-dependent sex determination (TSD), one such phenotype is sex (Bull, 1980; Ewert and Nelson, 1991). Maternal nest site choice may influence hatchling sex in TSD species (Janzen, 1994; Roosenberg, 1996; but see Schwartzkopf and Brooks, 1987).

The Pig-Nosed Turtle, *Carettochelys insculpta*, is a beach-nesting turtle with TSD (Webb et al., 1986) that inhabits rivers and billabongs in northern Australia and New Guinea (Georges and Kennett, 1993; Georges and Rose, 1993). In theory, hatchling sex could be manipulated on two different spatial scales: by choosing a beach with a particular thermal profile (Vogt and Bull, 1984; Roosenberg, 1996), or by choosing among sites differing in thermal characteristics within a beach (Janzen, 1994; Janzen and Morjan, 2001).

We report on the broad scale option of choosing among beaches. We address the following questions: (1) What variation in thermal environment exists among beaches? (2) Do mothers select beaches with a particular thermal profile? (3) What physical factors (e.g., aspect, solar exposure) determine beach temperatures? (4) Do mothers select beaches randomly with respect to those factors? (5) Do mothers select beaches with a particular moisture content? We also examined beach attributes such as height above water and the presence of vegetation to better understand nest site choice in the species.

Materials and Methods

We studied the Pig-Nosed turtle (*Carettochelys insculpta*) in the Daly River, a spring-fed system characterized by shallow depths and clear water during the dry season and deep turbid water during the wet season. The climate is typical of the wet-dry tropics of northern Australia (Taylor and Tulloch, 1985) with a mean monthly rainfall less than 7 mm from May to September, rising to a peak monthly average of 284 mm in February (Stn 014139/014941, Oolloo, 1962–1985). *Carettochelys* nest in the dry season (Georges and Rose, 1993). Data were collected as part of a sex determination study, which spanned three dry seasons from 1996 to 1998. The study area was a 63-km stretch of the Daly between Dorisvale Crossing and Oolloo Crossing (14°04′40″S, 131°15′00″E), Northern Territory (NT).

We characterised all potential nesting beaches and surveyed for nests during two-day boat trips during the dry season (July to October). There were 11 trips in 1997 and nine trips in 1998. In both years, the trips were spread evenly over the nesting season. Our criteria for potential nesting beaches were based on prior knowledge of the species (Georges, 1992; Georges and Kennett, 1993; JSD and AG, unpubl. data). These criteria were sandy banks and beaches adjacent to the water, little or no vegetative cover, and a minimum height of 0.25 m above water. Each beach was mapped, and we measured aspect, slope, and solar exposure for each beach. We also recorded the presence of any vegetation both on the beach and in the water at the beach edge. To investigate whether turtles might prefer nesting near deeper water, we measured the water depth 2 m from the beach. Finally, for each beach, we estimated the maximum height in which a nest chamber could be constructed, based on the friability of the sand. We did this by attempting to construct a nest chamber by hand at 15 cm depth at the highest point on the beach. If we could not make a chamber (the sand fell in on itself because of low moisture content), we moved progressively lower and repeated the procedure until we were able to construct a chamber. We then measured the height above water of this ''cohesive sand line'' (hereafter CSL) with a level and metersticks.

We used a compass to measure aspect, and a clinometer to measure slope and solar exposure. We de-

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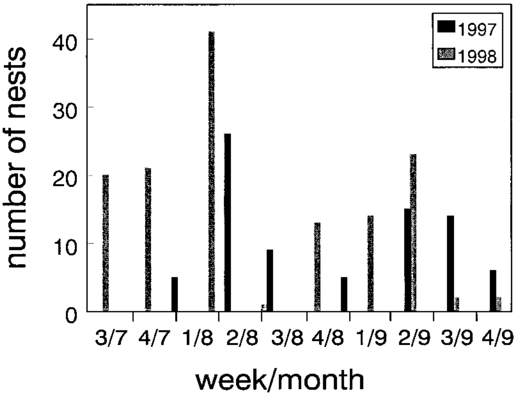

FIG. 1. Temporal variation in number of *Carettochelys insculpta* nests found during 63-km trips along the Daly River in 1997 and 1998. Note the bimodal distributions.

fined solar exposure as the total angle of exposure received by each beach, as dictated by treelines in the directions of sunrise and sunset. Aspect was coded symmetrically about due south to facilitate statistical analyses.

To estimate the relative thermal environment of each beach, we took spot sand temperatures 1 m above water at 50 cm depth. Although *C. insculpta* nests at depths of 10–25 cm, at 50 cm there is little diel variation in sand temperature (unpubl. data), allowing rapid assessment of thermal profiles of beaches without confoundment of time of day measured. This allowed us to gather large amounts of data over tens of kilometers of river within a day. We measured beach temperatures twice in 1997 and five times in 1998. To determine the relative range of sand temperatures on beaches, we also placed minimum-maximum thermometers 1 m above water at 16 cm depth on 33 beaches. These thermometers measured temperatures from 5–14 September 1998.

To estimate sand moisture for each beach, we collected approximately 500–700 g of substrate in plastic containers with lids. Substrate samples were weighed, oven-dried at 105°C for 48 h, and reweighed as dry samples.

We located nests by noting tracks in the sand and by searching each beach using a probe made of spring steel (Blake, 1974). We counted crawls and attempted nest excavations (conical pits) on each beach each trip. Upon discovery, each suspected nest was excavated for confirmation. At the end of the nesting season, beaches were classified as those with nests, those with crawls but no nests, and those without crawls or nests. Although we undoubtedly missed a few nests, we were confident in placing beaches into these categories, because crawls remain visible for longer than the survey interval (rainfall is rare during the nesting season). We avoided double-counting crawls by raking beaches each after each visit. We avoided double-counting nests by marking each nest site with a wooden stake or by removing eggs (for concurrent experiments).

All analyses were single factor ANOVA or linear regression with a significance level of 0.05. Where necessary, data were transformed prior to analyses.

RESULTS

Number of Beaches and Nests.—A total of 117 beaches in 1997 and 54 beaches in 1998 were designated as potential nesting beaches along the same 63-km stretch. We found 90 nests on 40 beaches in 1997 and 131 nests on 42 beaches in 1998. Turtles began nesting mid-July in 1998 and late July in 1997 (Fig. 1). In both years nesting ended in late September.

Beach Selection.—Beaches with nests were similar to beaches without nests with respect to temperature, height, aspect, and water depth at approach (Table 1). However, beaches with nests had higher moisture content and a higher CSL than beaches without nests (Ta-

TABLE 1. Comparison of physical attributes between beaches with nests and beaches without nests. CSL = cohesive sand line. Beach temperatures were spot temperatures taken at 50 cm depth. Data are means ± 1 SD (*N*). Significance is based on single-factor ANOVA. * denotes significant at 0.05, ** = 0.01.

Attribute	Beaches with nests	Beaches without nests	Significance
Temperature (°C)			
1997	29.4 ± 2.09 (35)	28.9 ± 2.50 (72)	$F_{1,106} = 1.35, P = 0.248$
1998	28.1 ± 1.77 (26)	28.6 ± 2.18 (8)	$F_{1,33} = 0.41, P = 0.525$
Substrate moisture (%)			
1998	6.1 ± 4.51 (21)	3.0 ± 3.39 (13)	$F_{1,33} = 4.51, P = 0.042$*
Height (m)			
1997	2.37 ± 1.466 (40)	2.02 ± 1.214 (73)	$F_{1,112} = 1.88, P = 0.173$
Aspect (coded)			
1997	20.0 ± 10.85 (40)	19.0 ± 10.91 (40)	$F_{1,79} = 0.20, P = 0.660$
CSL height (cm)			
1997	89.2 ± 63.44 (38)	60.6 ± 36.75 (75)	$F_{1,112} = 9.19, P = 0.003$**
Water depth at approach (m)			
1997	0.98 ± 0.424 (36)	0.98 ± 0.488 (67)	$F_{1,102} = 0.00, P = 0.988$

TABLE 2. Comparison of physical attributes between beaches containing *Carettochelys insculpta* nests and beaches containing only crawls. CSL = cohesive sand line. Data are means ± 1 SD (N). Significance is based on single-factor ANOVA. ** denotes significance at 0.001.

Attribute	Beaches with nests	Beaches with crawls only	Significance
Temperature (°C)			
1997	29.4 ± 2.09 (35)	29.6 ± 2.36 (32)	$F_{1,66} = 0.06$, $P = 0.812$
Height (m)			
1997	2.37 ± 1.466 (40)	2.08 ± 1.328 (37)	$F_{1,76} = 0.84$, $P = 0.363$
Aspect (coded)			
1997	20.0 ± 10.85 (40)	20.9 ± 11.28 (34)	$F_{1,73} = 0.11$, $P = 0.741$
Total angle of solar exposure (°)			
1997	131 ± 20.9 (38)	129 ± 23.3 (33)	$F_{1,70} = 0.30$, $P = 0.587$
CSL height (cm)			
1997	89.2 ± 63.44 (38)	66.6 ± 40.76 (35)	$F_{1,72} = 3.21$, $P = 0.077$

ble 1). Percent substrate moisture (arcsine transformed) was not significantly positively related to minimum beach temperature ($F = 1.33$, df = 1,23, $P = 0.261$, $r^2 = 0.057$) or maximum beach temperature ($F = 1.04$, df = 1, 23, $P = 0.319$, $r^2 = 0.045$).

Although not specifically quantified, beaches with submergent vegetation fringing most of the beach edge were not crawled upon by nesting turtles. This was corroborated by observations of the lack of turtle crawls in areas with such vegetation within a nesting beach. It was also evident that beaches < 0.25 cm above water were not nested upon.

We found 35 beaches with only crawls in 1997, and eight with only crawls in 1998. Beaches with nests had a higher CSL than beaches with only crawls (Table 2). Other comparisons between beaches with nests and beaches with only crawls revealed no significant differences in beach temperature at 50 cm, maximum height, aspect, or solar exposure (Table 2).

Beaches selected by nesting turtles comprised four basic types: trapped sand around logs (22 = 47%), sandy banks (13 = 28%), large sandbars along river bends (8 = 17%), and rocky areas with trapped sand (4 = 8%). Beaches ranged in size from a few square meters to large sandbars > 300 m in length. All types are formed during wet season flooding, and most beaches are ephemeral among years (unpubl. data).

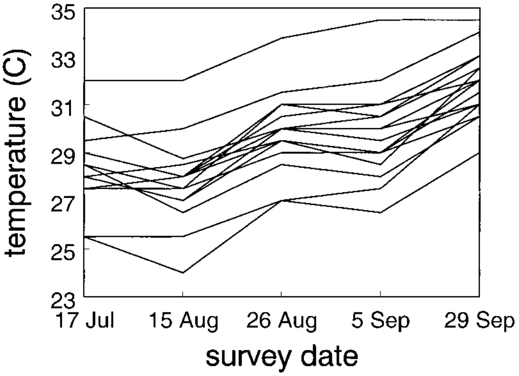

FIG. 2. Seasonal increase in beach temperatures with the onset of spring. Lines connect samples of the same location on the same beach. Samples were spot temperatures taken 1 m above water, at 50 cm depth in the substrate.

Beach Temperatures and Their Determinants.—Maximum (8 = 33.4 ± 2.63 SD°C) and minimum (8 = 25.6 ± 2.04 SD°C) beach temperatures were obtained for 33 beaches in 1998. Maximum and minimum temperatures were not related to solar exposure (Max. $F = 0.71$, df = 1,29, $P = 0.407$, $r^2 = 0.025$; Min. $F = 0.01$, df = 1,29, $P = 0.937$, $r^2 = 0.000$). Both maximum and minimum temperatures were generally positively related to temperatures taken at 50 cm depth (Max. $F = 4.13$, df = 1,32, $P = 0.051$, $r^2 = 0.118$; Min. $F = 6.77$, df = 1,32, $P = 0.014$, $r^2 = 0.179$).

Beach temperatures taken at 50 cm depth increased seasonally with the onset of spring (Fig. 2; $F = 32.21$, df = 4, 144, $P < 0.001$). Aspect, arbitrarily divided into 60°-intervals, significantly influenced 50 cm beach temperature ($F = 3.66$, df = 5, 108, $P = 0.004$), with north-facing beaches exhibiting the warmest temperatures (Fig. 3). Solar exposure significantly positively influenced 50 cm beach temperatures in 1997 ($F = 8.35$, df = 1, 108, $P = 0.005$, $r^2 = 0.072$) but not in 1998, although the result approached significance ($F = 3.58$, df = 1,28, $P = 0.069$, $r^2 = 0.117$). Aspect did not influence solar exposure ($F = 1.60$, df = 1,112, $P = 0.209$, $r^2 = 0.014$).

DISCUSSION

Beach Selection.—Generally, beaches used by nesting *C. insculpta* in the present study agreed closely with previous observations (Georges, 1992; Georges and Rose, 1993). Turtles nested on beaches and banks largely free of vegetation. However, nesting was not always restricted to clean fine sand, as previously reported (Georges, 1992). Although most nest sites were predominately sandy, turtles nested in a variety of substrate types ranging from gravel to loamy sand.

Turtles avoided nesting on the lowest elevation beaches; the lowest maximum height of a nesting beach in the study was 0.47 m. However, turtles often

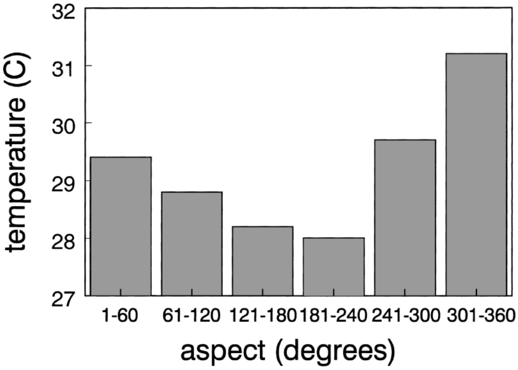

FIG. 3. Influence of aspect, or direction of the slope of the beach, on beach temperature. Temperatures were taken 1 m above water at 50 cm depth.

crawled onto these beaches. This reluctance to nest is consistent with flood mortality quantified for lower in nests for the species (Doody et al., 2001; JSD and AG, unpubl. data) and for other riverine turtle species (Doody, 1995; Plummer, 1976; Roze, 1964). Turtles also avoided nesting on beaches that were dominated by submergent vegetation (e.g., *Valisneria*) along the beach edge. In general, turtles did not crawl onto the beach when the submerged edge was not sandy. Observations of turtles ''sniffing'' the sand prior to crawling on the beach to nest at night (JSD, pers. obs.) suggests that *C. insculpta* use underwater cues to choose a potential nesting beach. This is in contrast to nest site choice in the more visually oriented freshwater crocodile (*Crocodylus johnstoni*) at the site, which locates sandy areas some distance from the water's edge and disconnected from it (pers. obs.).

How did turtles choose a nesting beach? Our results indicated that turtles chose beaches randomly with respect to aspect, height (but see above), temperature, and water depth at approach (Table 1). However, two related attributes we quantified differed between beaches with nests and other beach types. Beaches with nests had a greater substrate moisture content and corresponding higher CSL than the other beach types (Fig. 1). Apparently, turtles could not excavate a nest chamber above the CSL because of loose substrate consistency causing sand to fall in on itself. For example, in 1998, we found 20 beaches without nests that had numerous ($N > 5$) crawls and attempted nest constructions (conical pits in sand with looses consistency). Similarly, in 1997 we found 59 crawls and 30 such pits on one beach late in the nesting season. Turtles could only nest at low elevations below the CSL on beaches with low substrate moisture. Turtles apparently avoided nesting on these beaches because of the higher probability of nest flooding (Doody et al., 2001; JSD and AG, unpubl. data). In riverine turtles such as *C. insculpta*, height of the nest site may be the primary determinant of reproductive success caused by flooding (Roze, 1964; Plummer, 1976; Doody, 1995). In *C. insculpta*, this apparent selection from below is countered by the constraint of cohesive sand above, given that the species does not exhibit body-pitting like other beach-nesting reptile species (e.g., the crocodile *C. johnstoni*, sea turtles, the freshwater turtle *Podocnemis expansa*). Dry sand constraining nest site choice has also been reported in a population of sea turtles (Mortimer and Carr, 1987).

Although substrate moisture was higher on beaches with nests than on beaches without nests, further data are needed to determine whether substrate moisture was inherently important to nesting turtles, over and above the constraint imposed by cohesive sand. Comparisons of other attributes between beaches with nests and beaches with only crawls revealed that turtles were not selecting beaches according to those attributes once they exited the water (Table 2).

Determinants of Beach Temperatures.—Relative beach temperatures, as estimated with spot samples at 50 cm depth, increased with season (Fig. 2). This increase was associated with an increase in air temperatures with the onset of spring (Doody et al., 2001). This temporal effect influences timing of nesting, embryonic survival, and hatchling sex (unpubl. data), because *C. insculpta* have an extended nesting period (Fig. 1). The primary spatial determinant of beach temperature measured in the present study was aspect or direction of the slope of the beach. North-facing beaches exhibited the hottest temperatures (Fig. 3). In general, the total angle of solar exposure, measured between shading treelines at sunrise and sunset directions, positively influenced beach temperatures. These findings are similar to those of Janzen (1994), who found that vegetational cover, as influenced by aspect and solar exposure, predicted hatchling sex ratio in painted turtles (*Chrysemys picta*). Similarly, aspect of nest sites influenced incubation period in the turtle *Malaclemys terrapin* (Burger, 1976).

Implications for Manipulating Offspring Sex.—A concurrent study of movements revealed that gravid *C. insculpta* occupied linear home ranges averaging 8.6 km in length (Doody et al., 2002). Given the meandering path of the river, and the density of potential nesting beaches per river kilometer (0.86–1.86), female home ranges would include beaches spanning the full range of available temperature profiles. If turtles were manipulating offspring sex, as suggested for the turtle *Malaclemys terrapin* (Roosenberg, 1996), nests would be biased toward hotter or cooler beaches. However, turtles nested on beaches with temperatures covering the full thermal range of what was available. Thus, although we did not determine offspring sex, if *C. insculpta* mothers were manipulating sex through nest site choice, they were not doing so on an among-beach scale. It is possible that *C. insculpta* manipulate offspring sex on a finer scale, by nesting in spots with a particular thermal profile within beaches (Janzen, 1994; Janzen and Morjan, 2001).

Acknowledgments.—We thank the following people for assistance in the field: R. Alderman, K. Beggs, B. Christiensen, L. Hateley, D. Hunter, J. Kirby, B. Kropp, I. Longo, M. Pauza, A. Pepper, O. Price, H. Puckey, R. Sims, and M. Welsh. We thank the Northern Terrirory Parks and Wildlife Commission for logistical support. We thank C. K. Dodd Jr., R. Sims, and two anonymous reviewers for improving the manuscript. This work was funded by a Large ARC Grant awarded to AG for sex determination research.

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Accepted: 1 April 2002.