REFERENCES

TEMPERATURE DEPENDENT SEX DETERMINATION IN THE GREEN TURTLE (*CHELONIA MYDAS*): EFFECTS ON THE SEX RATIO ON A NATURAL NESTING BEACH

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ABSTRACT: Temperatures of natural nests of green turtles, *Chelonia mydas*, determined the sex of hatchlings at Tortuguero, Costa Rica. The beach could be divided into three distinct thermal zones: Zone 1—Low Beach, above high water mark up to sparse vegetation; Zone 2—Mid-Beach, area of sparsely vegetated sand up to dense jungle vegetation; Zone 3—High Beach, area of dense vegetation. At depths of 30 and 50 cm, sand temperatures in the High Beach were significantly lower than those in the Low Beach and Mid-Beach. Temperatures <28.5 C produced males and temperatures >30.3 C produced primarily females. Nests in the Low and Mid-Beach produced 72.0% and 87.0% female hatchlings while nests in the High Beach produced significantly fewer (7.4%) females. There were no seasonal trends in soil temperatures or sex ratios of hatchlings. The primary sex ratio computed for the entire beach for the 1977 nesting season was 67:33 female: male.

Key words: *Chelonia mydas*; Temperature dependent sex determination; Natural nests; Tortuguero; Costa Rica; Primary sex ratio; Sand temperatures

Sex determining mechanisms in reptiles were long assumed to be similar to those of other vertebrates. Charnier (1966), however, indicated that sexual differentiation in the lizard *Agama agama* is influenced by incubation temperatures of the eggs during embryogenesis. Higher temperatures result in all male animals and lower incubation temperatures yield all females. Subsequent studies both in the laboratory and field indicate a direct correlation between incubation temperature and sex of hatchlings of two European turtles (Pieau, 1972), snapping turtles (Wilhoft et al., 1983; Yntema, 1976), emydid turtles (Bull and Vogt, 1979), some kinosternids (Vogt, 1982), at least four species of sea turtles (Morreale et al., 1982; Mrosovsky et al., 1984*a*; Spotila et al., 1983; Yntema and Mrosovsky, 1980), and alligators (Ferguson and Joanen, 1982).

These studies all reported a range of incubation temperatures that produced males, a range of temperatures that yielded females, and an intermediate range of temperatures yielding both sexes. The response of alligators resembled lizards in that higher incubation temperatures produced males. To date, all studies of temperature dependent sex determination (TSD) in turtles have reported that higher incubation temperatures (30 C and above) produce females and lower temperatures (24–28 C) produce males. Most studies have also concluded that the critical or temperature sensitive stage in gonadogenesis occurs only during the middle third of incubation.

There have been several reviews on TSD in reptiles (Bull, 1980; Standora and Spotila, 1985; Vogt and Bull, 1982). Recent research has been aimed at modifying conservation programs (Morreale et al., 1982; Mrosovsky and Yntema, 1980), discovering the biochemical or genetic processes involved in TSD (for review see Standora and Spotila, 1985), and elucidating the effect of TSD on population sex ratios and other demographic features.

To study further the effect of TSD on turtles, we measured and calculated the hatchling sex ratio on the green turtle nesting beach at Tortuguero, Costa Rica for a single nesting season and compared

it to known sex ratios of other turtle populations. Studies on natural nests are needed in order to determine whether TSD occurs in the field and in order to understand its effect on natural populations.

MATERIALS AND METHODS

This study was conducted from July–September 1980 at Tortuguero, Costa Rica (Lat. 10°30′ N, Long. 83°30′ W), on a natural nesting beach of the green turtle, *Chelonia mydas*. Tortuguero is the major nesting ground for the green turtle in the Caribbean Sea. The beach is an unbroken strip of black volcanic sand extending 35 km along the Caribbean coast (Carr, 1967; Fowler, 1979; Richard and Hughes, 1972). The width of the beach varies with constant erosion and soil deposition. Portions of the sand are littered with logs, branches and other debris originating from rivers and along-shore currents. The seaward portion is distinguished by loose sand and debris with no foliage. Above this area grow sparse herbaceous vines and occasional grasses. Higher up, the beach is bordered by dense sea grape and cocoplum forming a boundary between the open beach and the dense vegetation which is dominated by coconut palm (Hirth, 1963).

This study was confined to a 1-km stretch of beach beginning 0.8 km south of the Tortuguero River mouth and continuing southward past the Green Turtle Station. The average width of this stretch of beach was approximately 50 m from high water mark to the jungle.

Fowler (1979) described four zones on the beach. Zone 1 included the seaward portion of the beach frequently washed by surf. Zone 2 included the beach above the high water mark up to the sparsely vegetated mid-beach portion. Zone 3 included the mid-beach up to the dense jungle vegetation. Zone 4 began at the border vegetation and extended into the jungle. Fowler showed that turtles utilize all four of these zones for nest sites.

To determine whether these zones represent different temperature regimes, we recorded thermal profiles (depths of 0, 20, and 50 cm) at 10-m intervals along four transects of the beach, from the surf line up to and including the first 20 m of dense vegetation. Based on these measurements, three temperature regimes were apparent: Low Beach, Mid-Beach, and High Beach (corresponding to Fowler's zones 2, 3, and 4, respectively). We subsequently monitored temperatures in these zones throughout the study with thermal profile probes consisting of a series of eight thermocouples buried at depths of 0, 5, 10, 20, 30, 50, 75, and 100 cm. We used 24-gauge Cu-Cn thermocouples and a BAT-12 thermocouple meter (Bailey Instruments) for all temperature measurements. We placed a profile probe in each of the three thermal zones and a fourth in a heavily shaded coconut palm area of the jungle. Daily measurements provided a complete thermal account of the beach at different depths and in different zones. To determine the amount of temperature fluctuations in a single day, soil temperatures were monitored at either 2- or 3-h intervals for complete 24-h cycles for various days throughout the study.

Once the process of egg deposition commences in green turtles, the animal becomes oblivious to external stimuli, making it possible to manipulate both the turtle and the eggs (Carr, 1967). Thus, while eggs were being laid in the egg chamber, we were able to insert a thermocouple wire at the approximate center of the clutch. This allowed turtles to cover the nests naturally and, more importantly, enabled monitoring of nest temperature with minimal disturbance to the eggs.

To protect the study nests from predation (Fowler, 1979), we buried a cylindrical enclosure of ¼-inch hardware cloth 120 cm high, to a depth of approximately 70 cm, which surrounded the nest without impairing normal thermal flow into and out of the nest. We placed a control thermocouple in the sand 2 m from each nest at a depth equivalent to that of the center of the nest.

We monitored a total of 49 natural nests in the study area. Low Beach contained seven study nests, Mid-Beach contained 29 study nests, and High Beach had 13 study nests. In addition to the natural nests, we constructed an artificial hatchery, trans-
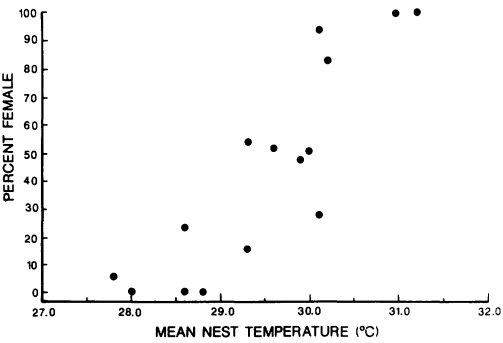
FIG. 1.—Relationship of temperatures during middle third of development of natural nests of *C. mydas* to the percentage of female hatchlings produced at Tortuguero, Costa Rica during the 1980 nesting season.

TABLE 1.—Spatial and temporal positioning of 15 natural green turtle nests on the beach at Tortuguero in 1980. Nest locations represent three distinct thermal regimes. The proportion of females is reported for each nest.

Nest location (zone)		% female	Depth to top of nest (cm)	Dates corresponding to middle third of incubation
High Beach		6	40	14 Aug.–17 Aug.
(3)		0	55	14 Aug.–30 Aug.
		24	—	10 Aug.–28 Aug.
		0	—	9 Aug.–25 Aug.
		0	40	12 Aug.–29 Aug.
		16	38	9 Aug.–27 Aug.
	$\bar{x}$	7.6		
Mid-Beach		53	—	9 Aug.–25 Aug.
(2)		47	48	10 Aug.–27 Aug.
		50	—	9 Aug.–25 Aug.
		94	40	8 Aug.–24 Aug.
		100	35	5 Sept.–21 Sept.
		100	65	9 Aug.–26 Aug.
	$\bar{x}$	74.0		
Low Beach		52	62	20 Aug.–4 Sept.
(1)		28	63	9 Aug.–26 Aug.
		83	50	9 Aug.—26 Aug.
	$\bar{x}$	54.3		

planted 20 nests into it, and exposed them to various levels of sunlight (Morreale et al., 1982). We measured sand and nest temperatures at least once each day, and at several times during the study, we monitored temperatures every 3 h over a 24-h period to measure the extent of diurnal fluctuations.

A few days prior to hatching (based upon expected incubation period), we uncovered nests and removed 20 eggs from each clutch using a random numbers table and replaced the remainder of the clutch to complete their normal development. This sample size was large enough to allow the statistical analysis to be sensitive to minor differences in sex ratios among the nests while minimizing the number of animals used. In some cases, hatchlings emerged before the predicted date necessitating collection of hatchlings from the screen enclosures surrounding the nest. We mixed the hatchlings in a bucket, randomly removed 20 turtles, and released the rest into the surf at night.

Specimens were killed by cardiac injection of 0.1 ml of euthanasia solution (T61, National Laboratories Corp.). Death was instantaneous. We dissected out kidneys with attached gonads, stored them in 10% neutral buffered formalin, and transported them back to the USA for sex determination by histological analysis (Spotila et al., 1983). Criteria for determining sex were the same as those reported by Ynte-

ma and Mrosovsky (1980) and Miller and Limpus (1981).

RESULTS

Incubation temperatures had a direct effect on the sex of *C. mydas* eggs incubated in both natural and hatchery nests at Tortuguero, Costa Rica. Comparison of sex ratios for the Tortuguero green turtle eggs with mean incubation temperatures for different time periods or fractions of embryonic development (tenths, weeks, quarters, thirds, and halves) suggested that the critical period for sex determination occurred during the middle third of development. In general, temperatures >30.3 C during the critical period produced females and temperatures <28.5 C generated males (Fig. 1).

Destruction of natural nests by humans and nesting turtles accounted for considerable losses on the beach (approximately 33%). Some of the turtles from nests that hatched early (warm nests) had to be released due to an unexpected delay in the arrival of preservative. Thus, at the com-
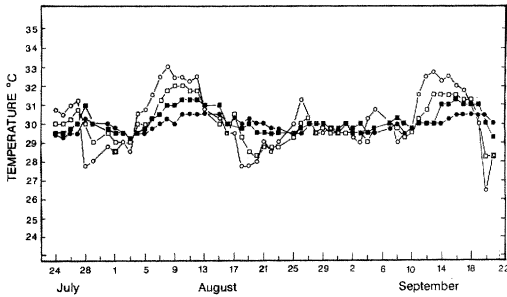
FIG. 2.—Seasonal variation in sand temperature at different depths in the Mid-Beach zone (2) at Tortuguero, Costa Rica in 1980. Closed circles represent temperature at a depth of 1 m, closed squares are for temperature at a depth of 75 cm, open squares are for a depth of 50 cm, and open circles are for a depth of 30 cm. There was no seasonal trend upward or downward for temperature at any of these sand depths. Increases were associated with sunny periods and decreases with rainy periods and/or storms. Temperatures at nest depths (50–75 cm) seldom dropped below 29 C.
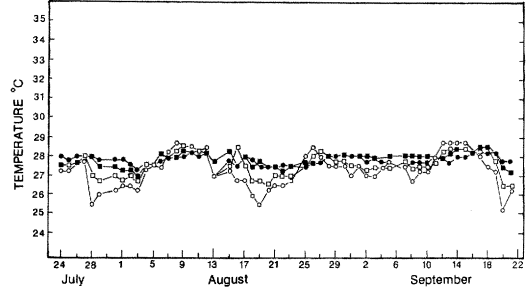

FIG. 3.—Seasonal variation in sand temperature at different depths in the High Beach zone (3) at Tortuguero, Costa Rica in 1980. See Fig. 2 for symbols. There was no seasonal trend upward or downward for temperature at any of these sand depths. Temperatures at nest depth remained well below 29 C and did not exhibit much fluctuation throughout the entire period.

pletion of the study, there were 33 natural and 20 hatchery nests for which complete thermal records were available. Of these 53 nests, sex ratios could be analyzed from 15 natural nests (Table 1) and 19 hatchery nests.

There was a highly significant difference in the temperatures of the three thermal zones on the beach (one-way ANOVA, df = 2,165, $P < 0.0001$). Mid-Beach temperatures were the highest (Fig. 2) and High Beach temperatures were the lowest (Fig. 3). A Duncan's Multiple Range Test indicated that temperatures in all three zones were significantly different at depths of 100 and 75 cm ($P < 0.05$). At depths of 50 and 30 cm, temperatures in the High Beach were significantly different from those of the Low Beach and Mid-Beach ($P < 0.05$). There was more variation in temperatures at 10 and 20 cm, but temperatures at these depths did not affect turtle nests.

There was no seasonal trend in the soil temperatures of any of the zones (Figs. 2–4). Short-term fluctuations were due to changes in local meteorological conditions. Extended sunny dry periods, such as those from 5–13 August and 11–15 September, resulted in a substantial increase

in temperatures at all depths in the Low and Mid-Beach zones and a slight increase in the heavily shaded High Beach. Likewise, extended rainy periods on 28 July–2 August and 17–22 August resulted in lower temperatures in all three zones. Temperature fluctuations at shallower depths were more extreme in all three zones. Although Mid-Beach and Low Beach were both open, unshaded beach zones, Low Beach was near the sea, and lower temperatures there may have been a result of the presence of ground water.

The 24-h thermal profiles showed minimal temperature differences at all depths associated with natural nests. Temperatures at the shallowest of these depths did not fluctuate by more than 1.5 C during a 24-h period, even for the profile (Mid-Beach) with the most extreme fluctuations.

There was a significant difference in the percentages of females from the nests in all three zones (arcsin transformation ANOVA: df = 2,661, $P < 0.001$). Further analysis (Tukey's HSD Test) showed there was a significant difference between the High Beach ($\bar{x} = 7.6\%$ female, range = 0–24%, $n = 6$) and the other two zones ($P < 0.05$). However, there was no significant difference between the Low Beach ($\bar{x} = 54.3\%$ female, range = 28–83%, $n = 3$) and Mid-Beach ($\bar{x} = 74.0\%$ female, range = 47–100%, $n = 6$) (Table 1). Nest temper-
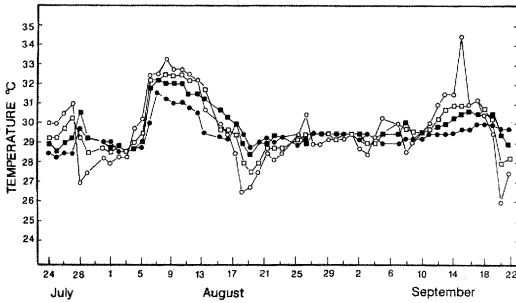
FIG. 4.—Seasonal variation in sand temperature at different depths in the Low Beach zone (1) at Tortuguero, Costa Rica in 1980. See Fig. 2 for symbols. There was no seasonal trend upward or downward for temperature at any of these sand depths. Increases were associated with sunny periods and decreases with rainy periods and/or storms. Temperatures at nest depths (50–75 cm) seldom dropped below 29 C.

atures below 28.5 C produced nearly 100% males and nest temperatures exceeding 30.3 C produced nearly 100% females.

DISCUSSION

Sex determination in the green turtle under natural conditions is dependent on the temperature at which the eggs are incubated (Fig. 1). The temperatures of the nests at Tortuguero were relatively stable throughout the 9-wk study during the summer of 1980. The combination of relatively small fluctuations of the tropical coastal climate, the fine grained hard packed volcanic sand, and the depth of the nests contributed greatly to the stability of nest temperatures. The frequent rains throughout this period were, for the most part, of short duration. The few extended rainy periods affected both air temperature and open beach sand temperatures at nest depth (Figs. 2, 4). The temperatures of the nests in the vegetation were relatively unaffected by the air and sand surface temperature changes (Fig. 4).

This beach provided a variety of sites with different thermal characteristics. These were represented by the three thermal zones (Figs. 2–4), and these three zones represented significantly different temperature regimes. The temperature of

the nest was thus affected by the zone utilized as a nest site.

Our data suggest that the pivotal temperature for Tortuguero green turtles is between 28.5 and 30.3 C. This range is similar to those reported for other sea turtles by Miller and Limpus (1981), Mrosovsky et al. (1984b), and Yntema and Mrosovsky (1980, 1982) and for freshwater turtles by Bull and Vogt (1979), Pieau (1972), Vogt and Bull (1982), and Yntema (1976, 1979). In general, pivotal temperatures range from 28–30 C.

During the nesting season of 1980, nests in the vegetation (High Beach) produced predominantly males while Low and Mid-Beach nests produced mostly females (Table 1). The similarity of sex ratios in the Low Beach and Mid-Beach was due to nest temperatures exceeding the pivotal temperature of this species. In other seasons, it is conceivable that slightly cooler temperatures could alter the sex ratios in the Low Beach by lowering nest temperatures to within the pivotal range. This would increase the number of males in the Low Beach nests but would not affect the Mid-Beach nests, which would still exhibit temperatures above pivotal.

In order to extend our study to account for seasonal effects on sex determination, we developed a model to predict sex ratios for nests with known temperatures. We used the 15 natural and 19 hatchery nests from which the sex ratios were determined. For nests with temperatures between 28.5 and 30.3 C, the relationship between incubation temperature and percentage female was best described by an exponential curve. For the calculation, we set all values of 0 = 1. The equation was of the form $y = ae^{bx}$, where $a = 1.36 \times 10^{-25}$, $b = 2.05$ and $r = 0.73$ (see fig. 1 in Standora and Spotila, 1985). Using this model, we calculated sex ratios for the remaining natural nests from which only temperature data were obtained. When these 19 nests are included, the value for the six nests in the Low Beach increases to 72.0% female and that for 20 nests in the Mid-Beach increases to 87.0% female. The value for seven nests in the High

Beach remains similar at 7.4% female. These combined values are more representative of the actual sex ratio values for the three zones. Many of the nests that were not represented in the original predictions were early hatching nests with shorter incubation periods and higher nest temperatures. These nests would have higher percentages of females (Miller and Limpus, 1981; Standora and Spotila, 1985; Yntema, 1979). When this group is added to the analysis, the mean values of percent females in the Low and Mid-Beach increase. A one-way ANOVA with Tukey's HSD Test of these revised values reveals the same results as shown previously. Hence, for management purposes (i.e., sex determination), the beach can be divided into two zones: (1) open beach—83.5% female, and (2) vegetation—7.4% female.

Fowler's study (1979) of numbers and survival rates for green turtle nests at Tortuguero yielded estimates of the relative numbers of nests laid in each zone (Fowler, personal communication). By combining the data from our 1980 study (sex ratios by zone) with Fowler's data (nest frequency by zone), we estimated a hatchling sex ratio for the entire nesting ground.

During the 1977 nesting season, Fowler reported that 71% of the nests laid on the beach were in our Low and Mid-Beach (open beach) and 20% were laid in the High Beach (vegetation). The remaining 9% were laid below the high water mark where hatching success was very low. These are essentially "doomed nests" (Mrosovsky, personal communication). Thus, our Low and Mid-Beach contained 78% and High Beach contained 22% of the viable nests, and hatching success rate did not differ significantly among these zones. Assuming the same nesting distribution on the beach in 1980, then Low Beach and Mid-Beach would produce 0.78 × 0.835 (65% female) and High Beach would yield 0.22 × 0.074 (2% female). The percentages of males would be 0.78 × 0.17 (13% male) from Low and Mid-Beach and 0.22 × 0.93 (20% male) from the High Beach. Thus, the hatchling

sex ratio on the nesting beach for one season was approximately 33% male to 67% female.

At Tortuguero, sand temperatures throughout the nesting season showed no trend (Figs. 2–4); thus there was no seasonal change in sex ratio. The beach was diverse in vegetative structure, and nests from different zones experienced different temperatures, therefore producing different sex ratios. On the barrier islands of South Carolina and Georgia, nesting beaches are homogeneous in structure, hence reducing importance of spatial variables on the temperature–sex relationship (Mrosovsky et al., 1984*b*). For a 6-yr period, early and late nests of loggerhead turtles (*Caretta caretta*) produced mostly males. The majority of the nests, however, were laid during the middle of the season when temperatures were highest and a predominance of females resulted. Thus, the cumulative sex ratio was 1:1. In Suriname, Mrosovsky et al. (1984*a*) reported similar findings for both green and leatherback turtles (*Dermochelys coriacea*). There was little vegetation on the beaches, but the extended nesting seasons at this latitude resulted in seasonal trends in temperatures. Nests developing in drier months produced more females and those in wetter, cooler months produced males. Again the cumulative sex ratios approximated 1:1.

On nesting beaches of the southern Great Barrier Reef in Australia, Limpus et al. (1983) reported that loggerhead nests on the mainland produced a female biased sex ratio while those on a nearby island produced mostly males. Green turtles nested primarily on the island where the beach on the cooler side produced a male : female sex ratio of 2.4:1, and the warmer beach produced a female biased ratio of approximately 1:1.7. Although there was no temporal variability reported during the nesting season, it was evident that spatial variability of nesting patterns in both species resulted in highly different sex ratio values on different beaches in this region.

Nesting map turtles (*Graptemys pseu-*

dogeographica, G. geographica, and G. pulchra) on the Mississippi River (Vogt and Bull, 1984) utilized four nesting beaches which produced significantly different sex ratios in one season. In addition, sex ratios changed from nearly all females to mostly males from the beginning to the end of the season. This combination of both temporal and spatial variation of nests resulted in heavily female biased sex ratios for all three species of map turtles in one season.

Since sex in most turtles that have been studied is determined by temperature of incubation, environmental factors can directly affect sex ratios in a natural setting. Temperature dependent sex determination in turtles produces a variety of hatchling sex ratios when spatial and temporal environmental characteristics vary at a nest site. It is possible that environmental variables, which are partially stochastic, may balance out their effects over long periods of time, thus balancing out sex ratios. There is also a possibility that a nesting turtle may attempt to adjust the sex of its offspring through nest site selection. However, any nesting strategy that could predict environmental variables and assess future values of sex of offspring would necessarily be complex. In addition, the stochastic nature of the environment would make this, at best, an imprecise mechanism.

It is not known how skewed hatchling sex ratios affect the adult sex ratio. Turtles have long generation times and individuals can reproduce for many years. Many turtles also nest more than once in a single season. These characteristics increase the probability that an individual will encounter a diversity of situations in which to nest in a lifetime. While this added complexity does not preclude the evolution of an offspring sex adjustment strategy, it decreases the probability. Alternatively, a turtle's longevity and continued reproduction over many years enhances the probability of producing mixed sex ratios. A more parsimonious strategy for a nesting turtle would place emphasis on providing the highest opportunity for survivorship of the offspring rather than attempting to adjust for or produce a predetermined sex ratio.

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