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TEMPERATURE RELATIONSHIPS IN NESTS OF THE NORTHERN DIAMONDBACK TERRAPIN, *MALACLEMYS TERRAPIN TERRAPIN*

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ABSTRACT: Aspects of temperature relationships in nests of the northern diamondback terrapin, *Malaclemys terrapin terrapin*, were examined in New Jersey. Nest temperatures had a diel variation from 2–9° C with a daily low at 0600h and a high at 1500h. Nest tempertures lagged behind sand surface temperatures. Prolonged periods of rain depressed surface temperatures and lowered nest temperatures to the daily low. Two nests on north-facing slopes had a mean daily temperature for the 70 days of development of $\approx$ 1° C lower than two nests on south-facing slopes. Ten nests on south-facing slopes hatched in an average of 71 days vs. a mean of 79 days for 10 nests on north-facing slopes ($P < .001$). Metabolic heat was produced in nests. The mean difference in temperature between nests and the sand at the same depth was 2–12° C per day. Depth of nests influenced nest temperatures and developmental period of the eggs. Nest depth and developmental period for eggs were positively correlated. Eggs failed to develop in very shallow nests. Because monthly temperatures differ, nests initiated in June hatched in less time (74 days) than nests initiated in July (86 days).

MALACLEMYS TERRAPIN inhabit brackish waters off the Atlantic coast and nest in the adjacent sand dunes and barrier beaches. Information on wild terrapin is limited to size data (Cagle 1952), descriptive data on one individual hibernator (Lawler and Musich, 1972) quantitative data on nest site selection (Burger & Montevecchi 1975), egg success (Burger, *In press a*) and nest and egg sizes (Reid, 1955; Montevecchi and Burger, 1975).

In 1939, Cunningham observed that the rate of development of *M. t. terrapin* under pen conditions did not vary as a function of environmental temperature. Most other studies show that rate of development is correlated with temperature (Yntema 1960, 1964; Moorehouse 1933; Bustard and Greenham, 1968). In this paper, I present evidence that under field conditions nest temperatures vary, and that these variations affect the presence or absence of development as well as the rate of development of the eggs of *M. t. terrapin.*

METHODS

Research was conducted from June through August 1973 and June through September 1974 on *M. t. terrapin* nesting on Little Beach Island (39° 29′ N, 74°, 21′ W) Brigantine National Wildlife Refuge, New Jersey. Little Beach Island is a barrier beach containing sand dunes in all stages of succession, salt marsh, protected coves and upland areas of staghorn sumac *Rhus typhina*, poison ivy *Rhus toxicodendron*, and cherry *Prunus* sp. Two separate but continuous areas, 20 × 400 m, were examined. The cove transect contained high dunes with sparse ground cover. This area was bordered by *Spartina* marsh on one side and cherry-poison ivy-marsh elder on the other. The woods transect was farther from the cove and was bordered on both sides by low shrubs. Further description of the study area can be found in Burger & Montevecchi (1975).

During the egg laying period the study area was searched two to three times daily for digging turtles or signs of nests. Digging females were not disturbed until they had completed nesting. Nests were marked with stakes a third of a metre away from the nests in varying directions. All eggs were numbered with a permanent ink felt pen and replaced in nests. The marking of the eggs did not in itself effect nest success since the hatching rate in hatched nests with unmarked eggs (68% in 1973) was similar to that in hatched nests with marked eggs (70%). At the time of hatching I located some unmarked nests by looking for the emergence patterns of the hatchlings. In 20 such nests the hatching rate was 73% —thus digging up the nests did not appear to effect the hatching rate.

A field telethermometer was used weekly to probe for sand temperatures at nest depths 5 cm away from 30 randomly selected nests on slopes facing in all directions. This method was used to determine differences in sand temperature at nest depths as a function of the direction of the dune slope.

I computed a temperature index in the following manner. For each day the total number of 3-hour periods of 1° C were counted, parts of a 3-hour-1° C unit were added to the total (*refer to* Fig. 1). Thus, if from 0800h to 1100h, the temperature was 20° C, I added 20 to the total. This yields an index of temperature for each

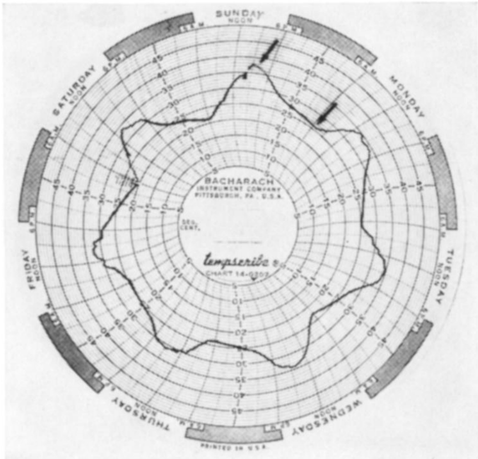

FIG. 1.—Graph showing temperatures in a *Malaclemys terrapin* nest for the week of 23 June 1974.

day which ranged over the 10-week period from 105 to 233. When divided by 8 these temperature indices yield the mean daily temperature in the nest. Thus if the temperature index is 210, the mean nest temperature is 26° C. Temp-scribe® temperature probes recorded the temperatures of nests under various conditions. Terrapin eggs lie in a hard-packed chamber surrounded by air and covered by sand (this study, Montevecchi and Burger 1975). Temperatures in four nests (two each on south- and north-facing slopes) were monitored from egg laying until hatching. At each nest the probe was placed at the bottom of the nest and a second probe was placed at the sand surface. Nests were selected that had equal nest depths (16 cm), and clutch sizes (eight eggs) and were initiated within 5 days of one another.

In two other nests, temperature probes were placed 5 cm away from the nests at the same depths as temperature probes located in these nests. This procedure was followed to examine for metabolic heat in the nests.

RESULTS

Daily Variations.—Sea turtles have little daily variation in the nest temperatures

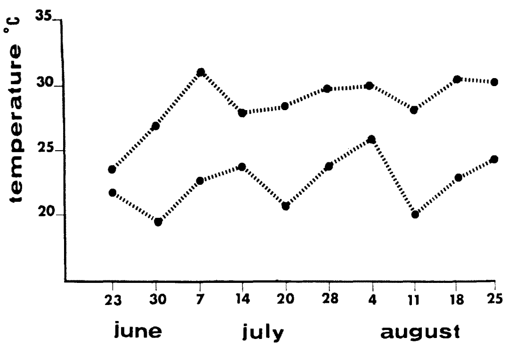

FIG. 2.—Mean high and low temperatures recorded at depths of turtle nests during the developmental period as a function of date.

(Carr and Hirth, 1961). *Malaclemys terrapin*, however, show a daily variation of from 2° C to 12° C, but temperatures at the surface vary from 0° to 30° C. The daily low is at 0600h and the daily high is 1500h (*see* Fig. 1). This is similar to, but lags slightly behind, the temperatures at the sand surface.

Nest temperatures were taken in 30 additional nests at 0600h (daily low) and 1500h (daily high) each Sunday for the 10 weeks of incubation. The probe of the telethermometer was inserted 5 cm to the right of the nest so as not to break the eggs. Except for the presence of metabolic heat in nests [see below] these temperatures approximate nest temperatures, and provide data on the range of variation. These temperatures were similar to those of the continuously recording probes. The high and low means for the 10-week period are shown in Fig. 2. The mean low ranged from 19° (SD = 1.2°) to 24° C (SD = 1.1°), and the mean high ranged from 23° (SD = ± 2.0°) to 31° C (SD = ± 1.9°).

Several environmental factors decreased surface temperature for short periods of time: brief showers, heavy cloud cover, and fog. Short variations in surface temperature did not normally cause changes in the daily temperature pattern of nests. Prolonged periods of rain caused long periods of decreased surface temperature which depressed nest temperature. All day rains result in little diel surface temperature variation and thus little nest variation in temperature. However, shorter periods of low sand surface temperatures did not result in as great a drop in nest temperatures.

Slope Difference.—Midday insolation on a 20° slope at New Jersey latitude is, on the average, 40% greater on south slopes than on north slopes (Smith 1966). Differences in temperature were measured directly with continuously recording probes and indirectly by comparison with sand temperatures.

Temperatures were measured at two nests each on the north-facing and south-facing slopes. The surface temperatures on the south-facing slope are higher for longer periods of time in the afternoon than they are on the north-facing slope. The nest temperatures are higher at the high and low periods on south-facing slopes than they are on north-facing slopes.

The temperature indices for every day from the day of initiation until the day of hatching for two nests on the north slope and two nests on the south slope were calculated and averaged for slope direction. The mean daily temperature for the south-facing slope surface was 23.3° C, and for the nest it was 21.8° C. The mean daily temperature for north slopes at the surface was 20.2° C, and for the nest it was 20.9° C. The nest temperatures averaged 0.9° C lower on north-facing slopes every day over the entire 70 day period. The two north-facing nests hatched in 76 and 75 days, while the two south-facing nests hatched in 73 and 72 days.

Temperature differences on north- and south-facing slopes were also measured by inserting temperature probes 5 cm away from each of 30 randomly selected nests at the high and low periods weekly during the 10-week incubation period. I then computed the mean high and low temperatures for each of the days, and computed the difference between the temperatures at each site and the mean for that period. These differences were summed as a function of

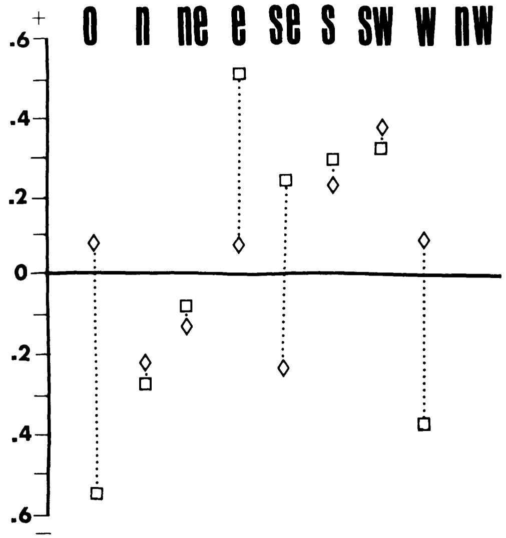

FIG. 3.—Mean differences of temperature at nest depth for the high (squares) and low (diamond) temperatures for the 10-week period as a function of the direction of slope of the nest. O = open, N = north, E = east, S = south, W = west.

slope directionality. The mean differences for the high and low sample times are shown in Fig. 3 as a function of slope direction. North and northeast slopes consistently had lower than mean temperatures and south and southeast slopes always had higher than mean temperatures. Flat areas, each, southeast and west-facing areas were not as consistent with regard to temperature.

The mean incubation period of 10 nests on north northeast-facing slopes was 79 ± 3 days compared to a mean incubation period in 10 nests on a south southwest-facing slope of 71 ± 3 days ($t = 5.86$, df = 18, $p < .001$). The mean incubation period for 10 nests on flat areas (73 ± 3 days) was significantly shorter than north northeast-facing slopes ($t = 46$, df = 18, $p < .001$) but was not significantly different from the incubation period on south southwest-facing slopes ($t = .813$, df = 18).

Metabolic Heat in Nests.—Hendrickson (1958) and Carr and Hirth (1961) showed that nest temperatures in sea turtles were greater than equivalent depth sand tem-

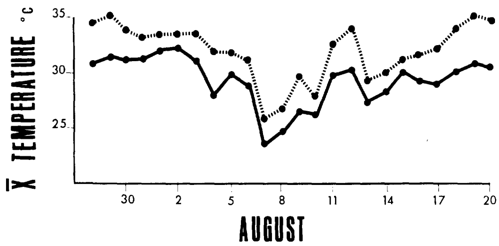

FIG. 4.—Mean nest temperatures in a nest (hatched line) compared to mean temperature at the same depth 5 cm away (solid line) for the last 3 weeks of the developmental period.

peratures. They proposed that the difference was caused by metabolic heat produced by the eggs. In this study I inserted a temperature probe in a nest and a second probe 5 cm away but at the same depth. The data were analyzed in the manner described previously. The mean temperatures for the nest and for 5 cm away are shown in Fig. 4 for the last 3 weeks of the incubation period. The mean difference in temperature between the two was 2°–7° C per day. The highs were higher and the lows were higher in the nest compared to that of the sand 5 cm away. No differences were noted among empty nests and fresh nests with eggs, and sand 5 cm away.

Temperature as a Function of Depth.—Temperatures were measured at several different depths, and temperature decreased as depth increased. If temperature has an effect on incubation time or on the development of eggs, then incubation time should vary as a function of depth. I used only nests hatched within 15 days of each other (1–15 September) to eliminate gross seasonal temperature differences. The depths of nests and the incubation period of the first egg to emerge from its shell in each of 36 nests was positively correlated ($r = .591$, df = 434, $p < .001$) (Fig. 5). Eggs in individual nests hatched over a 1 to 4-day period (Burger, *In press b*).

Depth influences the development or nondevelopment in an absolute sense. The nest depth of nests having all eggs develop ($\bar{x} = 182 \pm 20.0$ mm, $n = 20$) was significantly greater than the nest depth in which

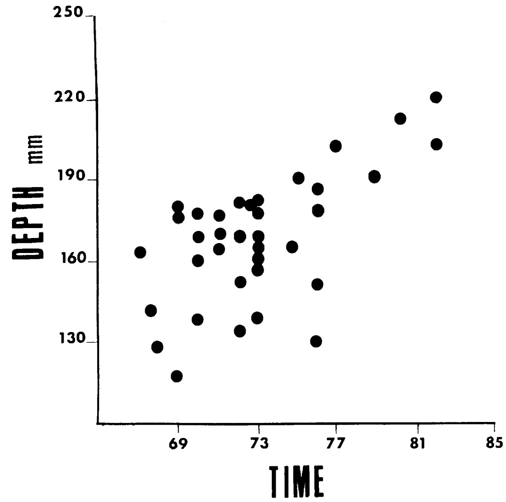

FIG. 5.—Age in days at hatching for the first eggs to hatch in nests of *Malaclemys terrapin* as a function of nest depth.

TABLE 1.—Development of eggs as a function of depth, in *Malaclemys terrapin*. Note that nests having all eggs undeveloped were significantly shallower than those in which all eggs hatched. NS = not significant.

Condition of eggs	Mean depth (mm) ($\pm$ SD)	Range
A All eggs undeveloped	125 $\pm$ 18.3	110–155
B Top eggs undeveloped	143 $\pm$ 12.7	120–160
C Bottom eggs undeveloped	187 $\pm$ 16.2	170–220
D All eggs developed	182 $\pm$ 20.8	155–220

t values and significance

	A	B	C	D
A		2.31	7.17	5.81
B	$p < .02$		4.64	4.09
C	$p < .005$	$p < .001$		.07
D	$p < .005$	$p < .01$	NS	

no eggs hatched ($\bar{x} = 125 \pm 18.3$ mm, $n = 11$) ($t = 5.81$, df = 29, $p < .005$) (Table 1). In 5 nests having a mean depth of 143 $\pm$ 12.7 mm, the top eggs did not hatch, and in 11 nests having a mean depth of 187 $\pm$ 16 mm the bottom eggs did not hatch. In all nests in which eggs did not hatch, embryos were partially developed and then died. In a few nests some eggs did not develop and appeared infertile; these were not considered in this analysis. Thus, it appears that shallow nests are exposed to high temperatures and do not develop properly and very deep nests may also experience low temperature stress. Deep nests may also experience O_2 and moisture deficits. Since all eggs were removed when they were marked, their order was mixed and bottom eggs were not laid first. Nest depth is not related to the size of the nesting female. Clutch size, but not egg size, is correlated with the size of the female (Montevecchi and Burger, 1975).

Seasonality and Incubation Time.—The eggs of *M. terrapin* are laid from 9 June through 12 July, and nests are exposed to different temperature regimes and amount of sunlight as a function of the season. For example, a clutch laid 9 June would be exposed to the prevailing temperatures of June, July, and August; and a clutch laid 12 July would be exposed to the prevailing temperatures of July, August, September. If air temperature influences development, then incubation time would be different if the mean temperatures in June were different from those in September. In 1974, September was much cooler than June. The mean incubation period of the nests initiated in June ($\bar{x} = 74.5$ days $\pm$ 3.4) was significantly shorter than the incubation period of nests initiated in July ($\bar{x} = 86.0$ days $\pm$ 15.2) ($t = 3.29$, df = 38, $p < .001$). The mean nest depths for these two samples were not significantly different ($t = .06$, df = 38).

For eggs laid on the same date at the same nest depth, there was a negative correlation between incubation time and egg length (–.548) and egg width (–.492).

These data indicate a diel variation in nest temperature; a difference in mean temperatures on north- and south-facing slopes, and a difference in temperature as a function of nest depth. Incubation time was positively correlated with depth and influenced by slope and seasonality. Eggs in nests that were very shallow did not develop and nests that were slightly deeper had the top eggs fail to develop.

Discussion

Yntema (1960, 1964), working with *Chelydra serpentina*, in a laboratory showed that eggs develop at a rate of one somite per day at 20° C, and five somites per day at 30° C. At 30° C, eggs required 60 days to hatch and at 22° C they required 2 to 4 weeks longer to hatch. Similar results have been found for sea turtles (Moorehouse, 1933; Bustard and Greenham, 1968). Cunningham (1939) performed a series of experiments that showed the rate of development of *M. terrapin* eggs does not fluctuate with environmental temperature, and that the development rate is constant through a wide range of temperature. He set up four conditions: (1) outdoor pens with normal environmental conditions: eggs hatched in 61–68 days, no diel temperature variations; (2) indoor pens with constant high temperature (37° C): eggs failed to develop; (3) indoor pens with constant medium temperature: eggs hatched in 61–68 days; (4) indoor pens at room temperature (18–33° C): eggs hatched in 61–68 days (Cunningham et al., 1939). My results differ from the foregoing in several ways. There was a diel variation of 2 to 12° C in nests. Secondly, under field conditions the incubation period varied from 65–104 days. Cunningham and his co-workers worked in North Carolina, where mean nest temperatures were surely higher. At hatching, Cunningham removed the eggs from the nest and reset them on a bed of sand covered with wet towelling. Such disturbance of the eggs may shorten the incubation time. I found that nests disturbed by predators a week before normal hatching time, hatched shortly thereafter. For example, one nest partially predator-disturbed at 64 days hatched at 65 days. Moving of the eggs near to hatching time may have contributed to the synchrony Cunningham observed. Thirdly, in his experiments with high temperatures the temperature never exceeded 40° C yet the eggs failed to develop. New Jersey *M. terrapin* nests regularly approached 45° C and the eggs hatched. However such high nest temperatures were not sustained for more than an hour in any given day.

Temperature relationships in nests of other turtle species have been examined. No diel variation in nests has been noted for sea turtles (Hendrickson 1958, Carr and Hirth 1961, Bustard & Greenham 1968) that nest in Malaya, Costa Rica, and Australia. Diel variations have been found for the *Chrysemys scripta* nesting in the southern United States (Cagle 1937), and in Louisiana (Cagle 1950). The effect of temperature on development can be inferred from natural experiments (as in this study) or shown by laboratory experiments (*see above*). Very high temperatures are lethal (Cunningham 1939, Cagle 1950), high temperatures decrease incubation period (Yntema 1934, Moorehouse 1933, Bustard and Greenham, 1968; this study), and low temperatures increase incubation time. The effect of very low temperatures is unknown (Cagle 1950), although Cunningham (1939) reported that at 49° C development of *M. terrapin* was inhibited. Cagle (1950) maintained *C. scripta* eggs at 10° C for 2 weeks and none survived but the lethal effects could not be positively attributed to the low temperature.

The metabolic heat produced by developing eggs in the nest chamber results in a nest temperature significantly above that of the surface sand (Hendrickson 1958, Carr and Hirth 1961, Bustard and Greenham, 1968). These studies were of *Chelonia mydas* and showed a mean difference of 5.9° C in Australia (Bustard and Greenham, 1968) and 2.3° C in Ascension Island (Carr and Hirth, 1961).

In the present study, I found a mean temperature difference of 2–7° C between the nest and sand 5 cm from the nest. These temperature differences were produced by metabolic heat alone, since I found no difference in temperature among (1) a nest with freshly laid eggs, (2) an empty nest, and (3) the sand temperatures

5 cm from a nest. Mean clutch size for *C. mydas* is 104 (Hendrickson, 1958). Thus, I expect that a nest of 104 *C. mydas* eggs would generate more metabolic heat than a nest of 10 eggs of *M. terrapin.* Secondly, nests having a diel variation in temperature might be expected to produce less metabolic heat during the low point in the diel variation, thus lowering the mean temperature difference due to metabolic heat.

It has been shown that larger gull eggs take significantly longer to hatch than smaller eggs (Parsons, 1972). However, in some birds eggs are continuously incubated and the temperature remains relatively constant. In this study, large eggs laid on the same day as small eggs hatched in less time. I believe this is due to reduced heat loss during the cold period of the day because of a lower surface:volume ratio in the larger eggs.

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