Nest Site Selection in the Terrapin *Malaclemys terrapin*

JOANNA BURGER AND WILLIAM A. MONTEVECCHI

Northern diamondback terrapins nesting in sand dunes on Little Beach Island, Brigantine, New Jersey were studied during June and July 1973 to determine the factors affecting the timing of egg laying and the selection of nest sites. One to three censuses were taken daily over a transect 800 m long and 18 m wide at various times of the day. Turtles were found laying from 10 June through 23 July, between the daylight hours of 0700 h to 1900 h. There was no correlation between the time of day and the number of turtles on the nesting area. There was, however, a high positive correlation between the number of turtles in the census area and the height of the tide. Beaching at high tide decreases the time the turtle is exposed to predation, thermal stress and desiccation, decreases the distance the turtle must walk to reach the nesting area, and increases the turtle's chance of nesting above high tide.

The nesting area of diamondback terrapins is an old, vegetated dune near a cove and behind the barrier beach. Within the study area the turtles preferred to nest in the high dune area compared to available low dune and flat sand areas. However, specific nest sites were on low slopes in areas of low vegetation cover. Nesting in a vegetated area provides a stable substrate, while placing the nest away from the vegetation reduces the number of roots encountered while digging. We suggest that the choice of high dune areas functions to promote laying well above the high tide. Nesting on low slopes within the high dune area minimizes the problems of digging on a steep incline and reduces erosion around nests.

FEW detailed studies have been made on the behavioral ecology of nest site selection in any species of turtles. Authors have noted that sea turtles nest on sand beaches, over banks (Bustard and Greenham, 1969) or on the tops of dunes (Limpus, 1971). In this study we examined a population of northern diamondback terrapins, *Malaclemys terrapin terrapin*, Schoepff nesting on sand dunes in New Jersey to determine the factors affecting the timing of egg laying, and the selection of nest sites.

Diamondback terrapins inhabit brackish waters off the Atlantic coast and nest on adjacent sand dunes and barrier beaches. Little is known of their breeding biology and behavior in the wild (Carr, 1952). Information on wild diamondback terrapins is limited to size data (Cagle, 1952; Schwartz, 1955) and to descriptive data on one nest (Redi, 1955) and on one hibernator (Lawler and Musick, 1972).

In the early 1900's diamondback terrapins were raised for market (Coker, 1906, 1920; Hay, 1917). Data obtained from captives includes clutch and egg size (Burns and Williams, 1972), growth, sex ratios and longevity (Hildebrand, 1932; Allen and Littleford, 1955) and other life history information (Coker, 1920).

STUDY AREA

Field work was conducted during June and July 1973 on Little Beach Island (39° 28′ N, 74° 21′ W), Brigantine National Wildlife Refuge, New Jersey. Little Beach is ideal for an examination of nest site selection since it is undisturbed by man. Much of the salt marsh-sand dune habitat along the Atlantic coast has been filled in and developed by man, apparently decreasing the available habitat for diamondback terrapins.

Little Beach Island is a barrier beach with dunes in all stages of succession from recently formed, steep unvegetated dunes through gentle dunes covered with grasses and bayberry.

The study area was located on the inland side of the island and borders a cove (Fig. 1). Salt marsh, dominated by *Spartina alterniflora*, separates the cove from the dune area. Tides regularly inundate the marsh and come to within 15 m of the dunes. The study area was

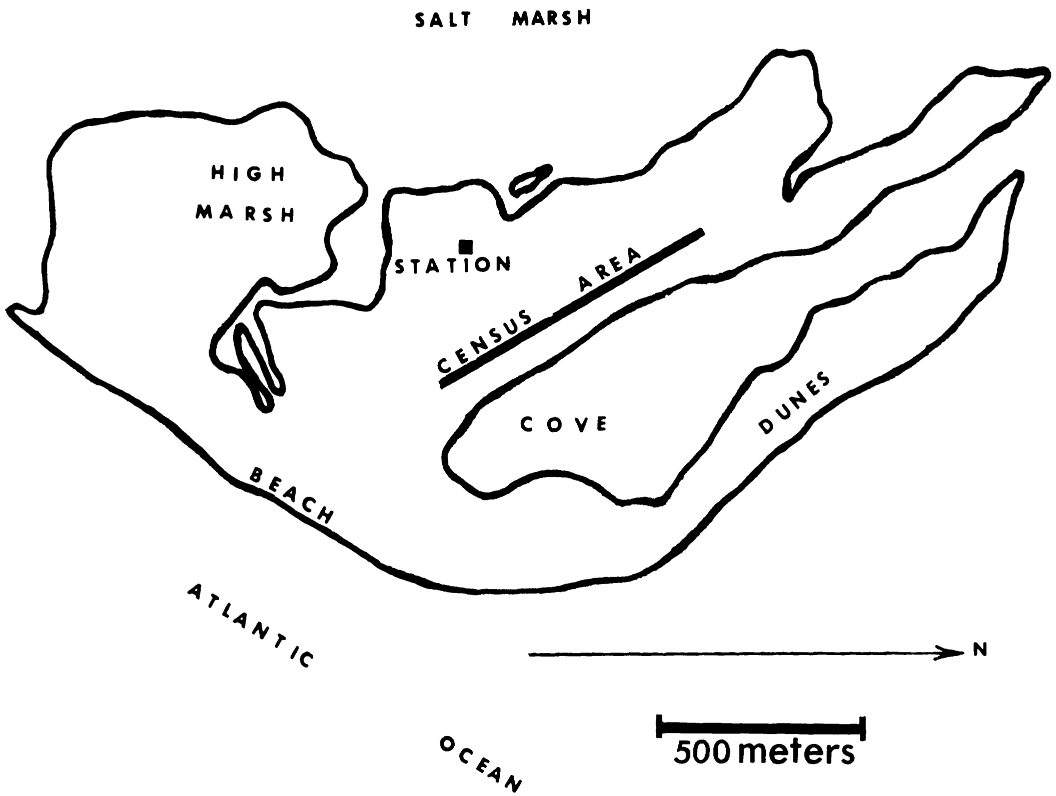

Fig. 1. Map of Little Beach Island, New Jersey showing study area.

800 m long and 18 m wide. It contained approximately equal areas of low flat sand dunes and high dunes. Vegetation on the area was primarily beach grass *Ammophilia breviligulata* Fern., bayberry *Myrica pensylvanica*, heather *Calluna vulgaris*, *Salicornia* sp., and marsh elder *Iva frutescens* var. oraria.

Methods

Most of the sand dune areas on Little Beach Island were searched during the study season for such evidence of turtle use as tracks, holes, predated eggs, and the presence of turtles. The study area was censused one to three times per day between 0600 and 2300 hrs from early June to early August. Censusing consisted of walking an 800 m transect in a 45 min period and recording the following data: time of day, number of hours since low tide, direction of the tide, size, location and activity of all turtles. The turtles encountered on a census were either searching for nest sites, in the process of nesting, or walking back to the sea. The location of 40 nesting turtles was noted, and subsequently the following data were taken at nests: type of area (flat or high dune), slope at nest site, distance from the closest vegetation, species of closest vegetation, percent cover in a one meter plot around the nest, diameter and depth of the nest, and the number and size of the eggs. The first five parameters were also measured at 100 randomly-chosen plots within the census area for statistical comparison.

During censuses most turtles were marked with washable ink on the plastron so that they would remain marked for the time they were on land. These markings were not worn off by abrasion while the turtle searched for a nest site since diamondback terrapins walk with their bodies elevated above the ground. Turtles marked during one census were never seen on the succeeding census that same day. Thus turtles counted on one census were not counted on another census later in the day. The behavior of the turtles was also observed sufficiently to establish that they come up on the dune area, dig, lay and cover the eggs, and then return to the cove within an hour.

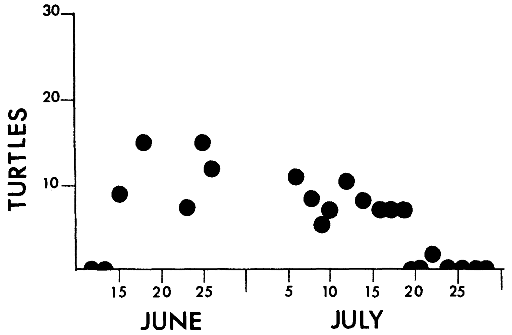

Fig. 2. Number of turtles in census area at tide time of ½ to 2 during June and July 1973.

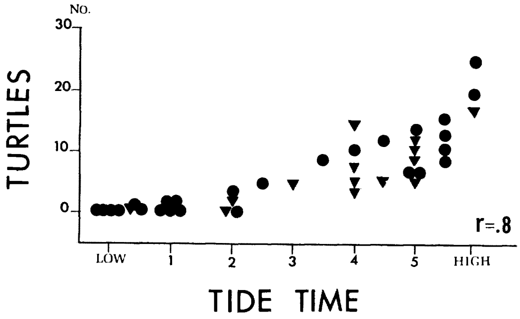

Fig. 3. Number of turtles in census area as a function of tide time. Low tide time is 0, and high tide time is 6. A value of 2 equals 2 hours before or 2 hours after low tide. Circles represent a rising tide; triangles a falling tide.

Results

Timing of Nesting

Seasonal and daily. Turtles were observed in the census area from 10 June through 23 July although the greatest number was observed from 15 June through 18 July. Since there was a correlation between tide and the number of turtles observed on the dunes (see below), only those censuses taken around high tide were analyzed for seasonal timing of egg laying. Fig. 2 indicates that there was no sharp seasonal peak in the numbers of turtles on the dunes.

No correlation ($r = -.07$, d.f. = 38, N.S.) was found between the hour of the day and the number of turtles in the census area during daylight. No turtle was observed on the dunes from 0600 to 0700 hrs, and only 1 turtle was observed from 1900 to 2300 hrs. Censuses taken at 0600 hr revealed no evidence that turtles had been on the dunes during the previous night.

Tidal. The time of low tide was recorded for every census. For the purpose of analysis, the tide time of a census was defined as the number of hours from low tide. Low tide was designated as zero, and high tide was designated as six since it is approximately six hours from low to high tide. A rising tide was designated as +, and a falling tide as –. Thus, if a census was taken three hours before low tide it was recorded as –3, if taken three hours after low tide it was + 3. Fig. 3 shows the correlation of the numerical value of tide time with the number of turtles on the sand dune area during each census. There was a high positive correlation between tide time (thus height of the tide) and the number of turtles on the nesting area ($r = +.80$, d.f. = 38, $p < .001$).

On nine of the censuses taken, we recorded the direction that 51 turtles were walking as they were entering and leaving the sea near the census area. This sample does not include those turtles that were searching for nest sites or nesting within the study area. Fig. 4 shows the relationship between the number of turtles observed and the tide times with respect to those turtles moving in a seaward direction and those turtles moving inland. Just before high tide turtles were walking inland ($r = 1.0$, d.f. = 1, $p < .001$), whereas just after high tide the turtles were walking toward the cove ($r = .99$, d.f. = 1, $p < .001$).

Other factors. No turtles were observed on the dunes during heavy or prolonged rains, even during high tides. However, if the rains stopped and the sun shown near high tide, the number of turtles observed on the dunes was

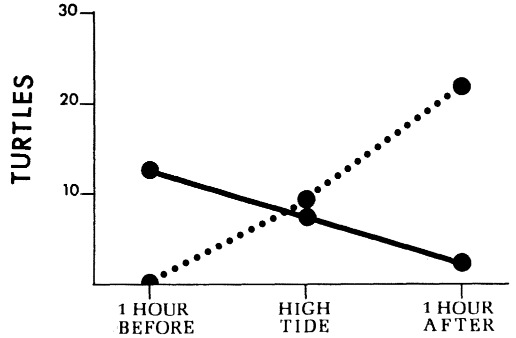

Fig. 4. Direction of movement of turtles entering and leaving the study area as a function of tide time. The solid lines represent the turtles facing inward, and the dotted line represents turtles facing the cove.

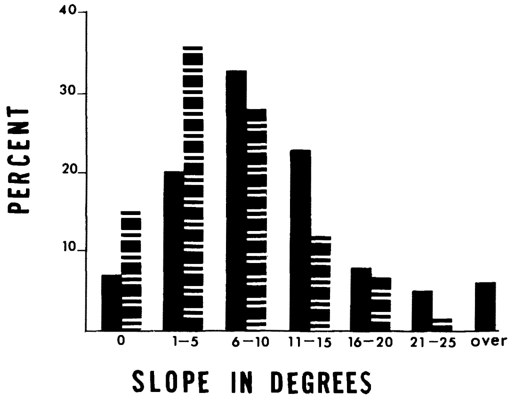

Fig. 5. Variation in slope in random plots (solid area) compared to turtle nest sites (hatched area).

often higher than at the same tide time on the previous rainless day. For example, on 25 June it rained from noon to 1500 hrs, and at 1530 hrs the sun shown and 16 turtles were recorded, whereas 7 turtles were recorded on 23 June and 10 turtles were recorded on 26 June at the same tide time.

We also came to expect fewer turtles for a given tide time on cloudy days.

Nest Site Selection

Most sand dune and beach areas of Little Beach Island were searched widely for evidence of nesting use by turtles. No turtles, tracks, nest holes or predated eggs were found in unvegetated dune areas. Little evidence of turtle use was found on sparsely vegetated dunes or on dunes exposed to the sea. Some of the dunes facing seaward were heavily vegetated, but these were also not used by the turtles.

The sand dune area used for nesting by the turtles is an old sand dune area which is present on the U. S. Geological Survey maps of Brigantine from 1894. In 1894 the study area was exposed to the sea, but since that time a sand spit has formed on the north side of the island, forming a cove and separating the study area from the ocean (Fig. 1). New dunes are presently being formed on the ocean side of the island.

Since the area used by diamondback terrapins for nesting is 0.8 km long and parallels the cove, turtles approaching the study area enter directly from the cove upon crossing the salt marsh. Turtles that entered the flat sand area usually turned abruptly and walked relatively rapidly parallel to the cove until they reached the high dunes where they nested. Other turtles entered the high dunes directly, and these individuals usually nested there. Daily censuses involving over 200 turtles showed that 70% of the turtles observed in the study area searching for nests, nesting, or leaving, were on the high dune area, even though 50% of the study area was comprised of low sand dunes.

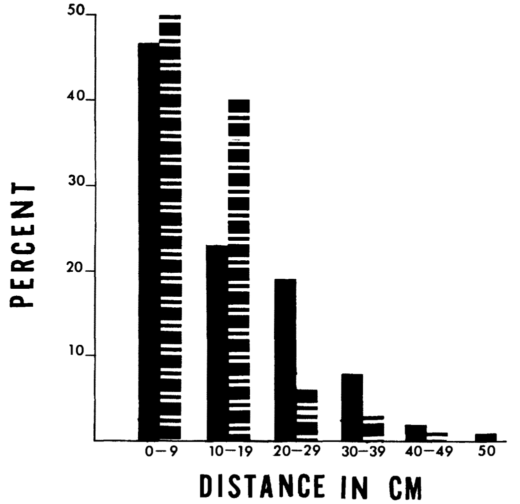

Fig. 6. Distance to the nearest vegetation of random plots (solid areas) compared to turtle nest sites (hatched areas).

Turtles observed selecting nest sites did not appear to sniff the sand as has been reported for sea turtles (Carr and Ogren, 1960; Carr and Hirth, 1962; Carr, Hirth and Ogren, 1966), but walked with a slow steady gait until they stopped to dig. While digging turtles faced up the incline. Since dunes provide inclines in all directions digging turtles faced in all directions relative to the cove and sea. Turtles observed during this phase dug only one hole, and deposited eggs in that hole. Only when disturbed did they abandon nests.

The nest site preferences of diamondback terrapins were determined by comparing actual nest sites to randomly chosen points with respect to the several parameters discussed below.

Dune type. Half of the study area, and 56% of the random points were in the high dune area, while 88% of the nests were in these dunes. Thus, turtles preferred to nest in the higher dune areas. These data for nesting agree with the census data from the same area pertaining to "searching" turtles.

Slope. Although the turtles preferred nesting on the high dune areas, they selected flat

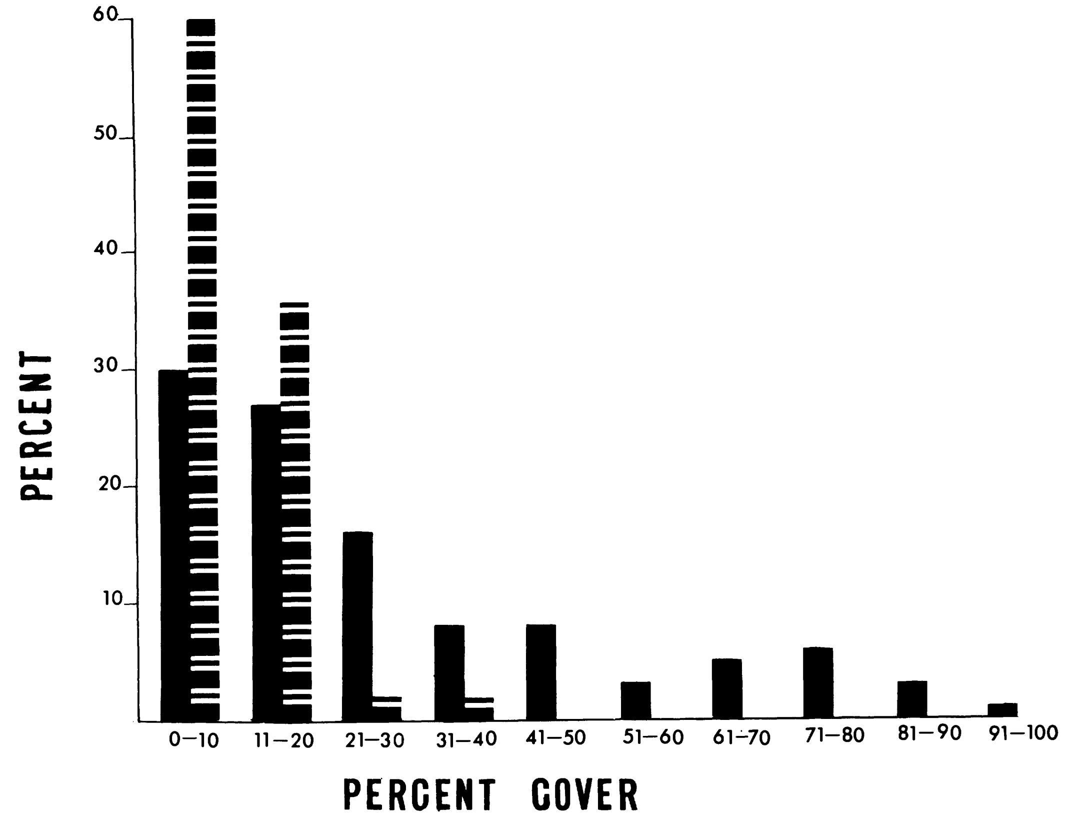

Fig. 7. Cover of random plots (solid area) compared to turtle nest sites (hatched areas).

locations within these areas for their nests (Fig. 5). The mean slope of random plots over the whole study area was 11.7 degrees (S.D. = 8, range = 0–52). However, in the high dune areas where 88% of the nests were located, the mean slope of the random points was 18.1 ± 9.8. The mean slope of the turtle nests was 7.2 (S.D. = 6.0, range =0–24). A student's t test shows that the turtles selection of slope is significantly different from the random samples ($t = 4.2$, d.f. = 138, $p < .001$).

Vegetation. Beach grass was the closest vegetation to the center of the random plots 76% of the time, while it was the closest vegetation to turtle nests 80% of the time. Thus, there appears to be no selection on the part of the turtles for nesting in close proximity to particular species of vegetation.

Turtles nested less than 20 cm from the closest vegetation ($\bar{x} = 11.2$, S.D. = 8.3, range = 0–41). Although the random points were often farther from vegetation ($\bar{x} = 18.2$, S.D. = 16.3, range = 0–50), these differences are not significantly different ($t = .4$, d.f. = 138, $p > .5$) (Fig. 6).

Available cover ranged from zero to 100% ($\bar{x} = 25$, S.D. = 25.6). The turtles selected areas of less than 20% cover for nesting (Fig. 7, $\bar{x} = 8.2$, S.D. = 6.4, range = 0–36). The cover selected by the turtles is significantly different from random ($t = 4.7$, d.f. = 138, $p < .001$).

Discussion

Diamondback terrapins are members of the Emydidae. However, since most other emydines nest in terrestrial and freshwater situations, it is most relevant to compare the behavioral ecology of these terrapins to chelonians that also nest in a marine shore situation.

Nest dispersion. There does not seem to be a mechanism for nest dispersion since two of the 40 turtles observed digging dug up and destroyed recently laid eggs of a conspecific. The Amazonian turtle *Podocnemis expansa* had also been reported to dig up the nests of conspecifics (Vanzolini, 1967); similar behavior has been thought to regulate population size in the green turtle (Bustard and Tognetti, 1969).

Bustard and Greenham (1969) suggested that some populations of the green sea turtle (*Chelonia mydas*, in Australia) beach after dusk around the time of high tide. Quantitative data relevant to a correlation or lack of correlation between high tide and the number of turtles nesting are lacking. In this study we have shown a high positive correlation between the tide height and nesting. There are several possible adaptive reasons for turtles beaching during high tide: the overland distance to the nesting area is reduced, the area of marsh grass walked over is reduced, the time out of the water is reduced, and the chances of nesting above high tide are increased.

Beaching at high tide decreases the distance a turtle had to walk in our study area by 50%. Presumably this also reduces the time the animal is exposed to predation, desiccation, and possible thermal stress, and reduces the energy cost to the animal.

Beaching at high tide might also insure nesting above high tide in those areas where other cues (*i.e.* slope or vegetation) are not available. For example, in a gently sloping sand beach without a discrete break between sea and dunes turtles might be less apt to lay above the high tide line if they came ashore at low tide. Traveling an additional distance at high tide would be more likely to insure that the nest is placed above the highest spring tides.

The nesting grounds selected were on a heavily vegetated dune area approximately 150 m from a cove on the inland side of Little Beach Island. This choice of a vegetated area away from the constant winds of the sea is advantageous because the soil is stabilized. Erosion, by either wind or rain, might tend to uncover nests in some cases, or bury them in others. Partially uncovered nests might be more exposed to predation, desiccation and thermal stress, whereas hatchlings in nests that have been covered by drifting sand might not be able to reach the surface.

Although the turtles selected vegetated dunes on which to nest, the actual nest site was in an area of low cover. Digging would be facilitated by digging in areas with few roots.

Diamondback terrapins in this study seemed to prefer nesting in the high dunes. We suggest that selection for high dunes insures that turtles nest above the highest tides. Merely walking a finite distance would not insure this since high spring tides and storm tides inundate some of the sand areas of the island. However, if a turtle has walked up and over a dune it is more likely to be above the high tide. Nesting on the tops of banks or dunes has been reported for sea turtles (Bustard and Greenham, 1969; Limpus, 1971), and may serve a similar function. Bustard and Greenham (1969) report that green sea turtle eggs failed to develop when inundated by high tide.

The nest was placed on a spot with a low slope even though the turtles in this study selected high dunes in which to nest. Flat areas may be easier for digging and laying as the turtle elevates its body with extended front legs, and lowers the body into the nesting hole at about a 30 to 40 degree angle with the ground surface. This position would be difficult to maintain on a steep slope. Moreover, steep slopes would have more erosion, thus exposing the eggs to possible thermal stress etc.

In summary, selection of nesting sites in the diamondback terrapin seems to involve a general preference for vegetated, high dunes, and a specific nest site perference of low vegetation cover on gentle slopes. The general preferences brings the turtle to an area above the high tide, in an area within minimum erosion. Specific nest site preferences result in the turtle digging in open areas with few roots, gentle slopes, and lower erosion. Beaching during high tide increases the turtle's chances of nesting above high tides, and decreases the time and distance covered in nesting.

Acknowledgments

We would like to thank David W. Ehrenfeld, Phillip J. Regal and George Zug for help in the preparation of the manuscript.

We also thank the U. S. Fish and Wildlife Service for permission to work on the island, and the manager and staff of Brigantine National Wildlife Refuge for hospitality and cooperation.

This research was supported by Grant number MH 16727 to C. G. Beer from the U. S. Public Health Service, and by an Alfred P. Sloan Foundation Grant to D. A. Lehrman. This constitutes contribution number 171 from the Institute of Animal Behavior, Rutgers University.

Literature Cited

Allen, J. F., and R. A. Littleford. 1955. Observations on the feeding habits and growth of

immature diamondback terrapins. Herpetologica 11:77–80.
BURNS, T. A., AND K. L. WILLIAMS. 1972. Notes on the reproductive habits of *Malaclemys terrapin pileata*. J. Herp., 6:237–238.
BUSTARD, H. R., AND P. GREENHAM. 1969. Nesting behavior of the green sea turtle on a Great Barrier Reef island. Herpetologica 25:93–102.
———, AND K. P. TOGNETTI. 1969. Green sea turtles: a discrete simulation of density-dependent population regulation. Science 163:939–941.
CAGLE, F. R. 1952. A Louisiana terrapin population (*Malaclemys*). Copeia 1952:74–79.
CARR, A. 1952. Handbook of turtles. Ithaca, New York. Comstock Publ. Assoc.
———, AND L. OGREN. 1960. The ecology and migrations of sea turtles, 4. The green turtle in the Caribbean Sea. Bull. Amer. Mus. Nat. Hist., 121:1–48.
———, AND H. HIRTH. 1962. The ecology and migrations of sea turtles, 5. Comparative features of isolated green turtle colonies. Amer. Mus. Novitates 2091:1–42.
———, ——— AND L. OGREN. 1966. The ecology and migrations of sea turtles, 6. The hawksbill turtle in the Caribbean Sea. *Ibid.* 2248:1–29.
COKER, R. E. 1906. The cultivation of the diamondback terrapin. N. C. Geol. Survey Bull. 14:1–69.
———. 1920. The diamond-back terrapin: past, present, and future. Scientific Monthly: 171–186.
HAY, W. P. 1917. Artificial propagation of the diamond-back terrapin. U. S. Bur. Fish. Econ. Cir. 5.
HILDEBRAND, S. F. 1932. Growth of diamond-back terrapins. Zoologica 9:551–564.
LAWLER, A. R., AND J. A. MUSICK. 1972. Sand beach hibernation by a northern diamondback terrapin, *Malaclemys terrapin terrapin* (Schoepff). Copeia 1972:389–90.
LIMPUS, C. J. 1971. The flatback turtle, *Chelonia depressa* Garman in southeast Queensland, Australia. Herpetologica 27:431–446.
REID, G. K., JR. 1955. Reproduction and development in the northern diamondback terrapin, *Malaclemys terrapin terrapin*. Copeia 1955:310–311.
SCHWARTZ, A. 1955. The diamondback terrapin (*Malaclemys terrapin*) of peninsular Florida. Proc. Biol. Soc. Wash. 68:157–164.
VANZOLINI, P. E. 1967. Notes on the nesting behaviour of Podocnemis expansa in the Amazon Valley (Testudines, Pelomedusidae). Papeis avulsos de Zoologia. 20:191–215.

INSTITUTE OF ANIMAL BEHAVIOR, RUTGERS UNIVERSITY, 101 WARREN STREET, NEWARK, NEW JERSEY. PRESENT ADDRESS (JB): BIOLOGY DEPARTMENT, LIVINGSTON COLLEGE, RUTGERS UNIVERSITY, NEW BRUNSWICK, NEW JERSEY 08903.

Osmotic and Ionic Composition of the Polypteroid *Erpetoichthys calabaris*

PETER L. LUTZ

The polypteroid *Erpetoichthys calabaris* is noteworthy in having one of the most dilute plasmas of any vertebrate (198.9 mOsm) distinguishing it physiologically from the fresh water teleosts (300 mOsm). In ion regulation, plasma sodium would appear to have a 1:1 relationship with plasma chloride which contrasts with the more restricted sodium excursion range found in some teleosts and other vertebrates, and in muscle, the chloride space of *Erpetoichthys* is much larger than that typical of teleosts (17.9% *Erpetoichthys*, 10% teleosts). Nevertheless, the relative ionic composition of plasma of both groups shows some important similarities and both have a very similar intracellular ionic composition.

POLYPTERUS and *Erpetoichthys* are the only living representatives of an ancient group of fish, the Polyterini, that is found as far back as the late Cretaceous. There is some disagreement as to their exact phylogenetic position, with some authors placing them in the Paleoniscoids, the Devonian stem order of the Actinopterygians (Moy-Thomas, 1939; Berg, 1958; Romer, 1968), while others have them in a separate group, the Brachyopterygians (Jarvik, 1968; Lehman, 1966). Nevertheless most authorities agree that they are of peculiar importance and the retention of many primitive features has caused them to be referred to as "living fossils" (Lagler et al., 1962).

As one might expect, their comparative morphology and structure has received wide attention (Orvig, 1968). Very little, however,