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NEST PREDATION AND HATCHLING SEX RATIO IN THE DIAMONDBACK TERRAPIN: IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

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Abstract: We report the effects of differential survivorship and environmental sex determination on the nesting habitat requirements of the diamondback terrapin (*Malaclemys terrapin*). Nesting beaches used by the diamondback terrapin covary in nesting density and predation, rate suggesting that nest predation is density-dependent. Additionally, we report the results of an experiment that manipulated nests on a single nesting beach for 2 years. These nests were placed in a variety of microhabitat types throughout the nesting seasons of 1989 and 1990. Of the 185 hatchlings that were produced from these nests, 184 were male and 1 was female as a result of environmental sex determination. The consequences of density-dependent predation and environmental sex determination strongly suggest that effective management or conservation of the terrapin includes the preservation of a wide variety of nesting habitats. Preserving only high-density or south-facing nesting areas could disrupt recruitment and alter population sex ratio.

INTRODUCTION

Habitats used for reproduction are essential to the successful existence of a species. Frequently, these habitats may be used for an extremely brief period during the life cycle of the organism; however, even partial destruction or alteration of these habitats could adversely affect population dynamics. Additionally, variation in the predation, resource, or biophysical environments among habitats used by a particular species frequently has differential effects on its population level processes (Dunham et al. 1989, Dunham 1993). We present evidence from the diamondback terrapin (*Malaclemys terrapin*) and illustrate how variation in the predation and biophysical environment can affect nesting success and sex ratio.

The diamondback terrapin, is an estuarine emydid turtle that ranges from the Gulf Coast of Texas to Cape Cod, Massachusetts. Though typically a coastal species restricted to the lagoons and embayments that lie behind the sand dunes of barrier islands in Chesapeake Bay terrapin populations penetrate far inland in the tributaries where estuarine conditions exist. Inland waters of the Bay

lack the elevated sand dunes that are used by terrapins for nesting in coastal populations; instead, terrapins nests on narrow isolated sandy beaches found on the fringes of salt marshes (Roosenburg 1994). The nesting areas in Chesapeake Bay vary considerably in size, elevation above high tide, orientation with respect to the sun, and distance from the water.

The diamondback terrapin has two unusual requirements for its reproduction. First, the terrapin is one of the few species that lives and feeds in the waters of the Bay, but must be able to transcend the intertidal zone to successfully reproduce. Failure to reach areas above the mean high tide frequently results in the death of developing embryos. Second, terrapins require a restricted range of thermal conditions on nesting beaches to ensure appropriate sex ratios because they exhibit environmental sex determination (ESD) as a species (Jeyasuria et al. 1994, Roosenburg and Kelley in press). ESD occurs in most species of turtles and all crocodylians (Bull 1980, 1983 Ewert and Nelson 1991; Janzen and Paukstis 1991).

Temperature is the primary environmental factor that influences sex in turtles, and when eggs are incubated at a constant temperature, there is a narrow threshold range (approximately 2° C) that produces mixed sex ratios. For terrapins, constant incubation temperatures of 28.5° C to 29.5° C produce mixed sex ratios. Ecologically, the most interesting consequences of ESD are that a nest placed in a particular nesting location usually results in offspring that are all the same sex (Bull 1985, Vogt and Bull, 1984).

METHODS

Since 1987 one of us (Roosenburg) has been conducting a detailed study of the nesting biology of the diamondback terrapin. Two nesting areas, Marsh Point Beach and Burton's Beach, located on the western shore of the Patuxent River approximately 8 km south of Benedict, Maryland, were monitored throughout the nesting season from 1987 to 1991. Marsh Point Beach is a small sandy strip that faces southeast and is approximately 0.20 hectare; Burton's Beach faces east-northeast and is approximately 0.25 hectare (Roosenburg 1994). (Further details of the methodology can be found in Roosenburg 1990, 1991, 1992). Briefly, all nests that were discovered were identified and monitored daily throughout the incubation period for predation.

To understand how the natural incubation environment affects sex determination, we conducted a series of experiments in which we placed artificial nests of terrapin eggs in different microhabitats on Burton's Beach. Eggs were collected from several different beaches along the Patuxent River, but away from the study site. The eggs were taken back to the laboratory, weighed and randomly assigned to experimental nests of 12 eggs each. During 1989 and 1990 three nests were placed in each of nine different microhabitat types. Microhabitat types were cross-classified according to exposure to direct solar radiation, in terms of sun (> 8 hrs), semishade (4-8 hrs), and shade (< 4 hrs), and to the amount of vegetation in the area, in terms of open (0 stems/0.25 m²), edge (1 - 50 stems/0.25m²), and vegetation, (> 50 stems/0.25 m²). We took advantage of natural variation in vegetation to manipulate the vegetation and we used artificial shade cloth (70% blockage) to manipulate the exposure. Our expectation was that warmer microhabitat types would produce females

while cooler sites would produce males.

All hatchlings that emerged were taken back to the laboratory, killed, dissected, and sexed based on the gross morphology. Females were identified by the presence of Muellerian ducts and the presence of a translucent ovary. Males were diagnosed by the presence of a small opaque testis and lack of or regressing Muellerian ducts (Yntema 1981).

RESULTS AND DISCUSSION

Marsh Point Beach had a greater number of nests than Burton's Beach during each of the 5 years of the study (figure 1). Predation rates of nests varied (30-94%) depending on the year and the beach (figure 2). Raccoons destroyed from 59% to 70% of the nests, followed by foxes (5-9%) and otters (1-3%) during the 5-year study. The predator could not be determined for 18-35% of the nests destroyed. Predation rates of terrapin nests were greater on Marsh Point Beach than Burton's Beach for each of the 5 years of the study (figure 2). These results suggest that predation may be density-dependent because Marsh Point, which has a higher density, had a much greater predation rate than Burton's Beach, the low-density nesting area. To corroborate the findings that predation rate may be positively correlated with nesting density, data of additional nesting areas are needed. As a consequence of the density-dependent predation, Burton's Beach produced 369 hatchlings over 5 years, compared to 30 hatchlings produced on Marsh Point Beach. The difference in recruitment between the two beaches suggests that sites that have low nesting densities may actually have a greater impact on the terrapin populations than similar sized beaches with higher nesting densities.

We do not know what the predation rates on terrapin nests have been over the evolutionary history of the species. However, anthropogenic causes have eliminated the natural predators of raccoons and foxes, increasing their density. Additionally, the collapse of the fur market owing to public opinion concerning the use of fur has further decreased mortality of turtle nest predators. Our study and others suggests that increasing raccoon and fox populations pose a serious threat to turtle populations (Congdon et al. 1993). The nest predator problem in Chesapeake Bay may be further exacerbated by the increased development of shoreline areas, reducing the trapping and hunting of raccoons and foxes that traditionally have taken place in rural areas. Raccoons, in particular, are opportunistic animals that appear to

thrive in suburban environments that are rapidly developing in waterfront areas. The combination of all these factors may result in historically high levels of predation on terrapin nests, shifting the burden of recruitment on nesting areas that may be marginal or somewhat less preferred for nesting.

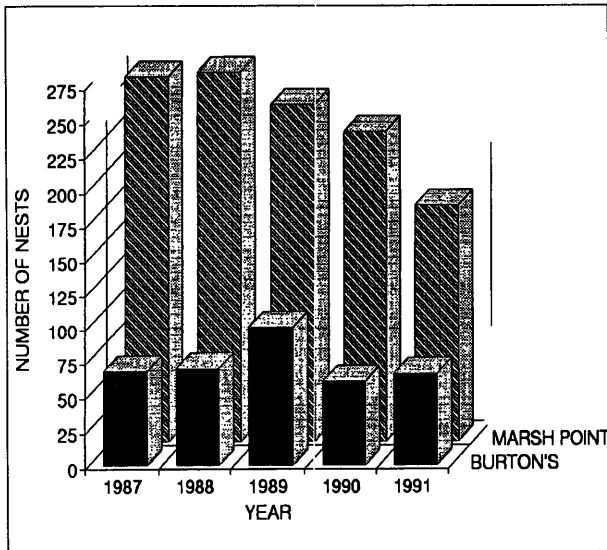


Figure 1. The number of nests found on the two nesting beaches during the 5-year study. Both beaches are almost equivalent in size (see text). Marsh Point Beach is a high-density nesting site, Burton's Beach is a low density site.

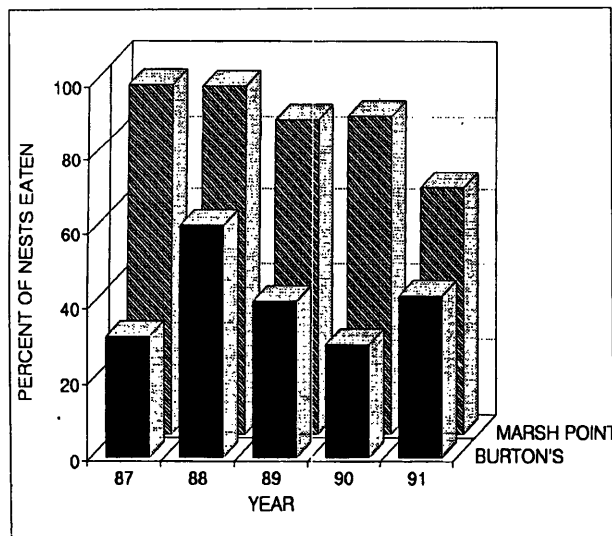


Figure 2. The percentage of nests destroyed during the 5 years of the study for both beaches. Predation was greater on Marsh Point during each of the 5 years of the study suggesting that predation of terrapin nests may be density dependent.

The interesting question remains, Why do terrapins continue to nest in areas with high predation rates? We offer two hypotheses. The first hypothesis is predator satiation—saturating a beach with eggs may provide enough food to satiate the predators and ensure that some terrapins are left to hatch before the predators can discover them, analogous to the masting phenomenon observed in many trees. Unfortunately, the increases in predator populations may result in the inability of terrapins to satiate the predators. The second hypothesis suggests that nest site fidelity observed in terrapins (Roosenburg 1990) constrains terrapins to nesting on particular beaches and that naturally fluctuating levels of predator populations in certain years produce a high number of terrapin offspring on high-density beaches when predation is low.

Our experimental nests produced 185 hatchlings from 648 eggs. Of these 185 hatchlings, 63 resulted from nests that were placed in warmer microhabitats that were anticipated to produce a high proportion of females. Contrary to our expectations, 184 of the 185 hatchlings were male and 1 was a female. This result suggested that there may be qualitative differences among beaches with regard to the sex ratio of the recruits that are produced on these beaches. Because the majority of the microhabitat types that we chose were cooler sites (Roosenburg 1992), we expected a male bias in our sex ratio. However, the sex ratio bias we observed was far greater than we anticipated. Vogt and Bull (1984) observed variation in sex ratios of nests owing to microhabitat differences; however the hatchling sex ratio of their nesting areas was female-biased.

Two likely explanations exist for the biased sex ratio we observed. First, nests were planted at times that resulted in the temperature-sensitive stage occurring when it was too cool to produce females. This explanation, however is unlikely because nest, were planted in both warm and cool microhabitats throughout the summer, and the likelihood is low that they all would incur only male producing temperatures based on the ambient climatic conditions during the time of sex determination. The second explanation is that the beach that was used for the experiment has certain properties that constrain it to being a male-producing beach.

There are two physical features of nesting beaches that might have an overriding effect on the microclimatology of a nesting area. First, orientation of the nesting beach with regard to the sun (e.g., beaches that face to the south) may

be warmer beaches compared to beaches that face to the north. The solar flux that impinges on an object is a function of the cosine of the angle created by the "normal" (a line extending perpendicular from the surface) and the angle of the sun's rays (figure 3 [Gates 1980]). As the angle created by the normal and the sun's rays decrease, the solar flux owing to solar radiation increases (figure 3). Thus, beaches that face to the south have a smaller angle and are likely to have warmer sand temperatures than beaches that face to the north (figure 3). The beach used in our experiment faced east-northeast. Although it was exposed to direct sunlight, the angle of the incoming solar radiation may not have warmed the sand as much as on beaches that faced to the south where the angle may have been less acute throughout the day.

Second, elevation of the nesting area above mean high tide could affect temperatures of the nest. Terrapins usually nest within 10 m of the water's edge. The proximity of the nest to the water indicates that the subterranean water level under the nest is determined by the rise and fall of the tide. Nests on beaches with less elevation are cooler than nests at higher elevation simply by decreasing the length of the thermal gradient

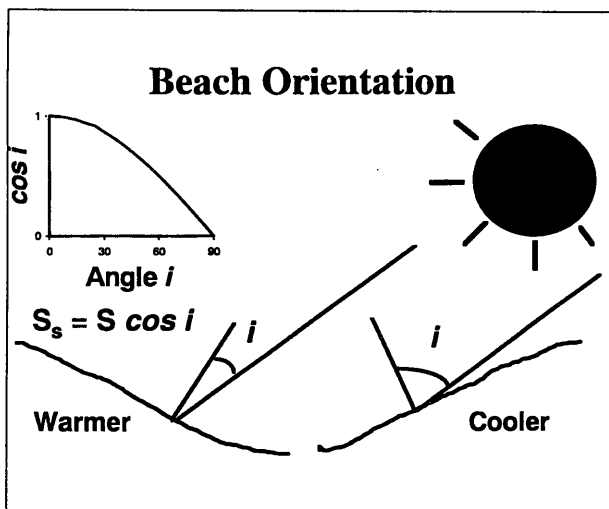


Figure 3. The relationship between the angle of a nesting site and the solar flux on that site. The solar flux is a function of the cosine of the angle i determined by the "normal" of the surface and the sun's ray. Beaches facing to the south decrease the angle i and thus receive a greater heat load than do beaches facing to the north. Thus, north-facing beaches may be predominately male-producing while south-facing beaches may be predominately female producing.

between the water and the nest (figure 4). Thus, nesting areas well above mean high tide are likely to be warmer than beaches with less elevation. Conversely, nests that are on higher beaches may be buffered from the cooling via a greater distance from the high tide. Burton's Beach has comparatively less elevation than some of the other nesting areas we have observed along the Patuxent River.

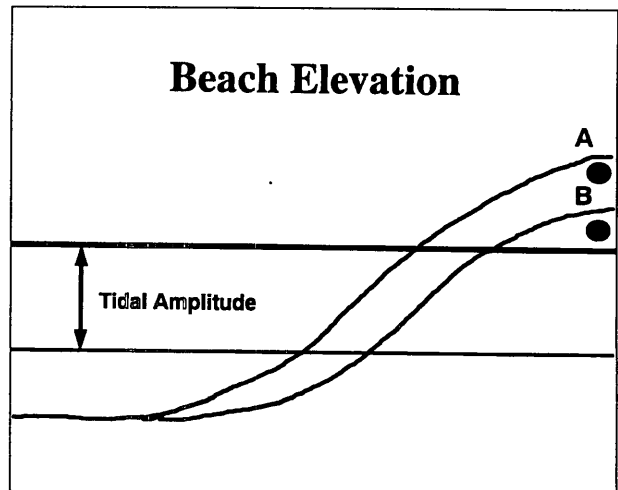


Figure 4. Relationship between the subterranean water level determined by the tide and the elevation of the beach. Beaches with lower elevation decrease the length of the thermal gradient and thus are likely to have lower temperatures than beaches with greater elevation. A represents a nest on a high (warmer) elevation beach and B represents a nest on a low (cooler) elevation beach.

CONCLUSIONS

Biased sex ratios of recruits and density-dependent predation have interesting consequences for the management and conservation of terrapin populations. First, our findings indicate that nesting areas that are not as heavily used by females may play an important role in maintaining populations. Second, environmental sex determination may result in certain beaches that produce mostly males and other beaches that produce mostly females. Though our data do not unequivocally demonstrate that this is the case, they do suggest that there are nesting areas that contribute differentially to the different sexes. Currently, there is a need to understand the ecological consequences of ESD in terrapins and in other reptiles that exhibit this peculiar form of sex determination, particularly as it relates to management and conservation.

A management strategy for terrapins within the Bay needs to consider the possibility that some beaches may be important for producing females while other beaches may be important for producing males. Elimination of certain beaches through bulkheading or other forms of shoreline development could ultimately have an impact on the sex ratio of local populations. Additionally, shoreline manipulation that may affect the elevation of the available nesting area might also affect the sex ratio of the recruits on a particular nesting beach.

Preservation of a few high-density nesting areas in locations where terrapins are known to occur may not be sufficient to maintain local populations. As historical nesting sites are eliminated by bulkheading or predator populations continue to increase, there are two consequences that can impinge on terrapin populations. First, terrapin populations can decrease because females are forced to nest in marginal habitats where nest survivorship is low (Roosenburg 1992). Combined with large or increasing predator populations, the number of recruits entering a population may be dramatically reduced. The second consequence is the alteration of the sex ratio. Beaches targeted for preservation may be biased in the sex ratio of recruits resulting in an unbalanced adult sex ratio. The importance of our findings to management considerations of terrapins and other species with ESD is far reaching. Further work is needed to determine the interaction between, and the elevation, orientation, and sex ratio of nesting areas to adequately describe critical attributes of nesting beaches. Until this information is available, preserving areas where nesting occurs represents the only logical choice. Similarly, preserving only high-density nesting areas may not adequately maintain viable terrapin populations or balanced sex ratios.

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