

**A STUDY OF TEMPERATURE-DEPENDENT SEX DETERMINATION IN THE
DIAMONDBACK TERRAPINS OF JAMAICA BAY**

A Final Report of the Tibor T. Polgar Fellowship Program

Amanda L. Widrig

Polgar Fellow

Department of Biology
Hofstra University
Hempstead, NY 11549

Project Advisor:

Russell L. Burke
Department of Biology
Hofstra University
Hempstead, NY 11549

Widrig, A. and R. Burke. 2006. A Study of Temperature-Dependent Sex Determination in the Diamondback Terrapins of Jamaica Bay. Section VI: 22 pp. *In* W.C. Nieder & J.R. Waldman (eds.), Final Reports of the Tibor T. Polgar Fellowship Program, 2005. Hudson River Foundation.

ABSTRACT

Nesting ecology and temperature-dependent sex determination were studied in diamondback terrapins *Malaclemys terrapin* at the Jamaica Bay Wildlife Refuge in Queens, New York. In 2005, the nesting season occurred from June 7th to July 28th. One hundred and seventy six females were documented coming onshore; 58% of these had been captured in previous years. Days with the largest number of terrapin captures usually followed days with long periods of rainfall. I placed temperature loggers in 136 nests, then protected the nests from predators and monitored them for hatching. Average nest depth was 149mm, mean clutch size was 13 eggs, and mean egg mass was 8.73g. The average time before the first hatchling emerged from the nests was 62 days, which is much sooner than previous studies have shown. Nest viability was also higher than previously documented; only 8.8% of nests failed to produce any hatchlings. Egg viability was lower than previously documented; only 63% of eggs produced hatchlings that emerged from the nest. Hatchling emergence chronology appeared to be dependent on temperature and rainfall, because more hatchlings emerged on very hot days and during or directly after large amounts of rainfall. Nest temperatures and hatchling sex ratios have yet to be analyzed and will not be discussed in this paper.

TABLE OF CONTENTS

Abstract.....	VI-2
List of Figures.....	VI-4
Introduction.....	VI-5
Methods.....	VI-9
Results.....	VI-11
Discussion.....	VI-16
Acknowledgements.....	VI-19
Literature Cited.....	VI-20

LIST OF FIGURES

- Figure 1. Relationship between the number of nests laid each day and the average daily temperatureVI-12
- Figure 2. Relationship between the number of nests laid each day and the amount of rainfall each day.....VI-13
- Figure 3. Distribution of nests throughout the seven main habitats.....VI-14
- Figure 4. Relationship between the number of hatchlings emerging each day and the average daily temperature.....VI-15
- Figure 5. Relationship between the number of hatchlings emerging each day and the amount of rainfall each day.....VI-15

INTRODUCTION

The northern diamondback terrapin *Malaclemys terrapin terrapin* is the only completely estuarine turtle in North America. Terrapins inhabit *Spartina* marshes and tidal creeks where they feed on mollusks, crabs and other crustaceans and invertebrates (Tucker et al. 1995). Although little is known about the aquatic ecology of *M. terrapin*, its nesting ecology has been well documented. In New York, the nesting season begins in late May and extends to early August (Feinberg and Burke 2003). Diamondback terrapins nest primarily on isolated sandy beaches and vegetated dunes. Females come ashore primarily along with high tides (Feinberg and Burke 2003) to seek out appropriate nest sites. Nesting activity increases with high tides and increased temperatures (Burger and Montevecchi 1975; Feinberg and Burke 2003). Adult terrapins are highly dimorphic and females are two to three times larger than males.

Many species of turtles, including terrapins, have temperature-dependent sex determination (TSD). In animals with TSD, sex is determined after fertilization by the incubation temperature that the embryo experiences during a short window of time called the thermosensitive period (Mrosovsky and Pieau 1991). There are two types of TSD found in turtles. In TSD I females are produced at warm temperatures and males are produced at cooler temperatures; TSD II is the exact opposite (Ewert et al. 2004). Diamondback terrapins exhibit TSD I (Rosenberg and Kelly 1996; Giambanco 2004), with 28°C being the pivotal temperature.

Research on TSD has increased dramatically in recent years. Survey work on 79 species of turtles has shown that 64 have TSD (Ewert et al. 2004). Nearly all TSD research has been done in laboratory settings where it is easier to determine the effect of

temperature on hatchlings incubated at constant temperatures. From these studies we have learned how controlled temperatures affect incubator-produced hatchlings. This is how TSD, in both its forms, was discovered in many turtle species. Also, it has been found that incubation time is negatively correlated with nest temperature, such that constantly warmer nests hatch faster than colder nests (Valenzuela et al. 1997). It has also been shown that hatchling size is negatively correlated with incubation temperature, such that constantly warmer temperatures produce smaller hatchlings (Giambanco 2004). These characteristics are important because reducing incubation duration may reduce predation risk; and hatchling size is related to locomotor performance and perhaps therefore survivorship (Ashmore and Janzen 2003). Hatchling sex of course can have tremendous implications for individual reproductive success and population sex ratios.

Recently, researchers have begun to test the effects of incubation temperature on nests in the field in order to understand the biological relevance of this phenomenon. In the field the temperatures of the nests are not constant and can vary in complex ways. It is possible that characteristics such as hatchling size and sex may have much more complex relationships with incubation temperature under the varying temperature regimes commonly experienced in the field. There have been some recent studies on TSD in the field on a few species of turtles (e.g., the painted turtle *Chrysemys picta* [Janzen 1994, 2002; Morjan 2003], the striped mud turtle *Kinosternon baurii* [Wilson 1998] and the giant river turtle *Podocnemis expansa* [Valenzuela 2001]). Because of TSD, the local micro-habitat environment determines offspring sex and, therefore, many different fine-scale abiotic and biotic factors can influence offspring sex ratio in a population. In order to better understand how TSD affects turtles, it is necessary to look

at different species at different geographic localities to see how TSD affects each population.

One of the most critical aspects of TSD is nest placement. Nest-site selection can have a direct impact on nest conditions such as nest temperature and predation risk. Nest-site selection for turtles with TSD has been studied for only a few species (Janzen 1994; Wilson 1998; Kolbe and Janzen 2002; Valenzuela 2001). Even fewer studies have been documented using diamondback terrapins (Roosenberg 1996; Burger and Monevecchi 1975; Burke and Wojakowski, unpubl. data), but these have demonstrated that under some circumstances terrapins actively choose specific nest conditions non-randomly.

From these few studies of nest-site selection in turtles it is evident that the environment where the nest is laid can greatly affect the sex ratio of the hatchlings. Nests with more overhead vegetation cover are more likely to produce males and nests in more direct sunlight with less overhead cover are more likely to produce females (Janzen 1994; Wilson 1998; Valenzuela 2001). Nests placed closer to water are also more likely to produce males (Morjan 2003), as do deeper nests compared to shallower nests (Wilson 1998; Valenzuela 2001).

Very little is known of how females choose nest sites and why, but it is generally presumed that females choose nest sites so as to increase their own fitness by influencing the sex ratio of their offspring. Some researchers hypothesize that substrate temperature cues the female to nest in a certain area. Others hypothesize that the amount of overhead cover and direct sunlight are what the female uses when determining a nest site (Janzen 1994). Little work has been carried out to test these hypotheses.

Furthermore, the adaptive basis for a female choosing to produce one offspring sex rather than the other is also unclear. It seems unlikely that females can assess their population's current sex ratio and plan accordingly for the future. One of the most widely accepted hypotheses to explain the existence of TSD is that by Charnov and Bull (1977), which states that TSD is favored when certain incubation conditions confer fitness advantages to one sex more than the other. In this way sex is determined when the egg comes into contact with conditions that benefit the sex who will perform better in that environment. Roosenberg (1996) proposed that maternal condition determines nest site choice. His theory was based on the observation that larger females lay larger eggs and the size of the egg determines where the nest will be laid, in that larger eggs are laid in nests that will receive warmer, female-producing temperatures and smaller eggs are laid in nests that receive cooler, male-producing temperatures. This theory has been supported using *M. terrapin* (Roosenberg 1996) but not supported using *C. picta* (Janzen and Morjan 2002; Morjan and Janzen 2003).

One of the reasons studies testing these hypotheses are rare is that under most circumstances it is difficult to find fresh, non-predated turtle nests in sufficient numbers and density to carry out robust studies. In addition, until recently it was necessary to kill hatchlings to sex them, and killing large numbers of hatchlings is usually unacceptable. Unlike adults, hatchling turtles are not obviously dimorphic. Recently, it was discovered that subtle morphological differences exist between the male and female hatchlings in some turtle species, so it may be possible to sex terrapins upon emergence from the nest (Burke et al. unpubl.; Valenzuela et al. 2004). Geometric morphometric sex identification is based on the fact that there are subtle shell shape differences between

male and female turtles in species that have sexual dimorphism (Valenzuela et. al 2004). This technique has been used to correctly identify sex in painted turtles (*Chrysemys picta*) that were two weeks post-emergence and South American river turtles (*Podocnemis expansa*) that were two months post-emergence.

The purpose of my research is to answer several questions about how temperature sex determination and nest-site choice is affecting a terrapin population, on a scale much larger than has been accomplished in any other turtle study. Also, I hope to determine the best way to sex hatchlings in the field without having to kill them.

METHODS

Study Site. Jamaica Bay Wildlife Refuge (JBWR) is a 3662 ha estuarine wildlife refuge located at the southwestern corner of Long Island, New York, in Jamaica Bay. The refuge is in the boroughs of Queens and Brooklyn, and consists of one large island, Ruler's Bar Hassock (RBH, 520 ha), and several smaller islands. JBWR is part of Gateway National Recreation Area (GNRA), a large, federally-operated estuarine park managed by the National Park Service. GNRA is geographically located in the Hudson-Raritan Estuary, otherwise known as the New York-New Jersey Harbor Estuary.

Although terrapin numbers are declining throughout their range (Wood and Herlands 1997), the JBWR population is still impressively large. Feinberg and Burke (2003) reported more than 2000 nests are laid there annually. Due to its size and the fact that the turtles are protected from commercial and recreational collection, JBWR is an excellent study site.

Nesting Ecology. In June and July of 2005 we observed female terrapins nesting at the JBWR. Females were allowed to finish nesting and were then processed. Processing an animal included measuring its carapace and plastron length, noting any abnormalities and giving each animal a unique PIT-tag in front of their back-right foot, if not previously tagged. Females also received a scute notch denoting what year they were caught, if not previously marked. The females were then released back into the water.

Nest Excavation. All nests were excavated on the day they were oviposited. The eggs were counted and each egg was weighed. Nest depth was measured and then the eggs were placed back into the nest in the opposite order of which they were taken out. One I-button temperature logger was placed on the bottom of the nest and another on the top of the nest. These temperature loggers recorded the temperature of the nest every hour with 0.5° accuracy.

Nest Characteristics. For each nest found, measurements were made to determine the nest habitat. I measured % bare ground, % grass, % succulent plants and % litter for a 1m area around each nest. I also measured % cover directly over the nest using a spherical densiometer. The measurements were repeated for four random points around each nest; random points were chosen using handmade spinners. Basic habitat type was recorded, using seven different habitat categories: beach, dune, gravel trail, mixed grass, mixed shrubs, terrapin trail and next-to-main trail.

Nest Protection. Nests were then protected from egg predators. Nest protection consisted of a circular cage made from ½ inch hardware cloth measuring 60 cm deep with a diameter of 45 cm. These cages were placed 10 cm into the ground around the nest and then staked into the ground.

Hatchlings. Nests were monitored daily until emergence. If hatchlings never emerged, the nest was excavated when it was 105 days old. Upon emergence hatchlings were collected and taken back to the laboratory at Hofstra University. In the lab, carapace length, plastron length, tail length, anal width and carapace height were measured. Abnormalities were also identified. These measurements will be used to attempt to sex the hatchlings using a multivariate technique developed for gopher tortoises *Gopherus polyphemus* and desert tortoises *Gopherus agassizii* (Burke et al., 1994). Hatchlings were housed separately in 16-ounce deli containers with about 2.5 cm of water in the bottom. They were fed twice a week a diet of frozen bloodworms, frozen *Mysis* shrimp and Reptomin turtle sticks. A day after each feeding each hatchling's water was changed. Two weeks post-hatching, a digital photograph was taken of each hatchling's carapace and plastron; these were digitized using the TPSDig computer software program. The digitized landmarks are then analyzed using TPSRelw to determine whether there are differences in shell shape between the sexes. Then discriminate analysis is used to assign sex to hatchlings.

RESULTS

Female terrapins began nesting in 2005 on June 7th and ended on July 28th, a nesting season of 52 days. There were 176 females captured during this time, of which 58% (N=102) were recaptures from previous years. Females had an average carapace length of 20.0cm and an average plastron length of 17.5cm. Scute abnormalities were observed in 31% (N=54) and one or more barnacles on the carapaces of 37% (N=66). The frequency of barnacles on carapaces decreased during the summer: in June 43% (N=36) had at least one barnacle whereas in July only 33% (N=30) had barnacles. The

greatest number of female terrapins caught and processed in one day was on July 9th (N=18). The earliest a female was observed nesting was 8:19am and the latest was 17:28pm. Figure 1 shows the relationship between average temperature and the number of females captured each day.

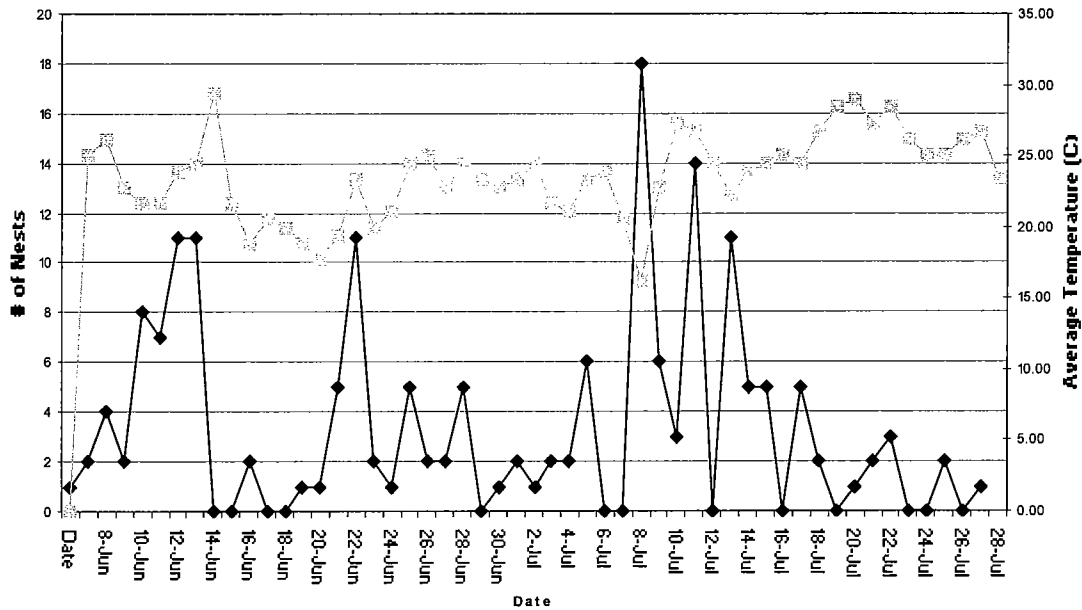


Figure 1. The amount of nests created each day of the nesting season along with the average temperature of each day. Number of nests is shown in squares and average temperature is shown in diamonds.

Figure 2 shows the relationship between the daily rainfall and the amount of females captured each day. Six females were documented nesting twice. The average time between consecutive clutches was 19.67 ± 5.7 days (range = 15-31).

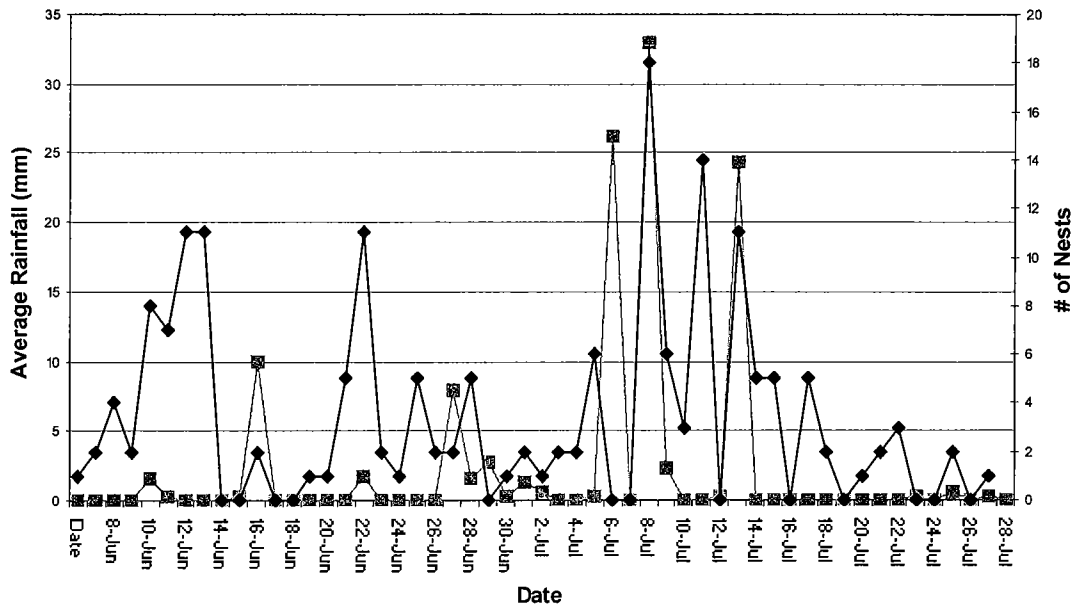


Figure 2. The number of nests created each day of the nesting season and the amount of rainfall for each day. Number of nests is shown in diamonds and the average daily rainfall is shown in squares.

Of the 176 females captured, 136 resulted in usable nests that we could protect with predator excluders. Those 136 nests amounted to 1,793 eggs being protected. Figure 3 shows how many nests were oviposited in each of the seven different habitat areas. The nesting distribution among the habitat areas was 32% dune, 20% mixed grasses, 16% terrapin trail, 13% gravel trail, 10% mixed shrubs, 5% next-to-the main trail and 4% beach. Although nests were protected at the day of oviposition, four nests were completely predated by raccoons.

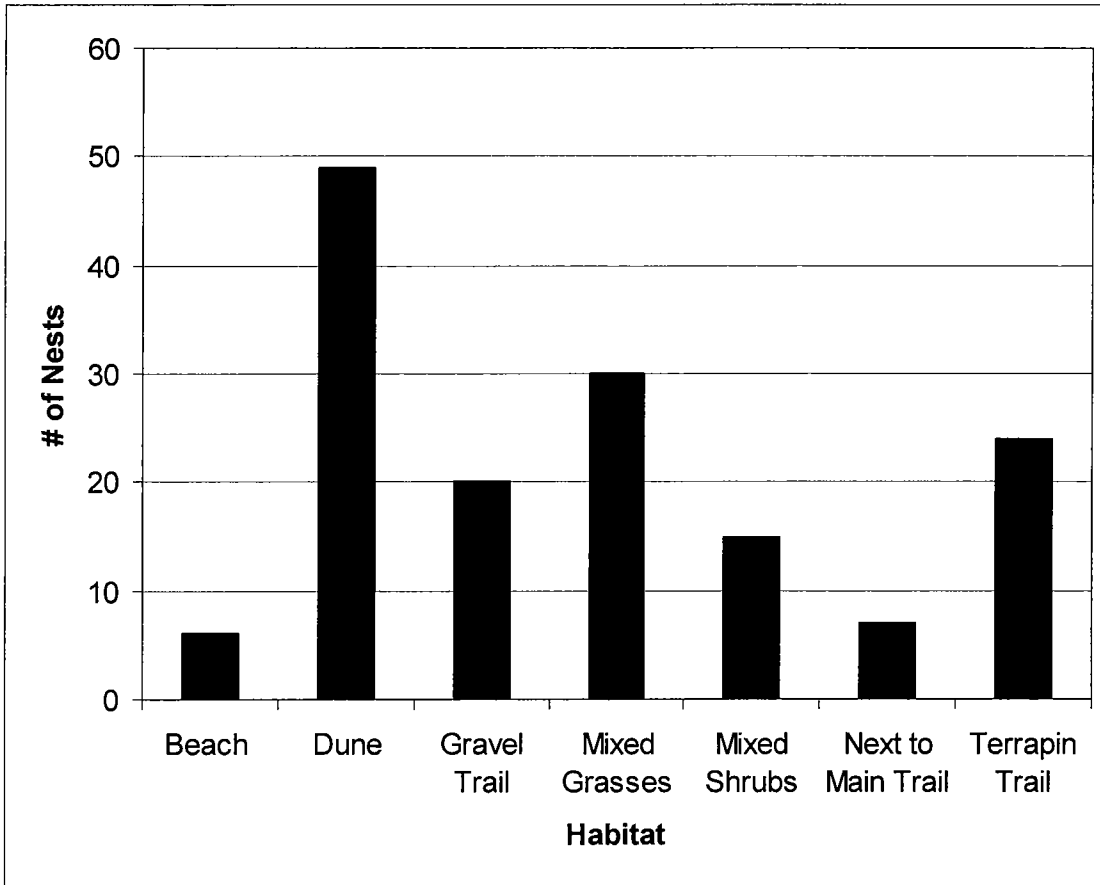


Figure 3. The distribution of nests in each of the seven habitat categories.

Average depth of the nest measured from the bottom of the nest to the ground surface was $149 \pm 22\text{mm}$ (range = 95-200). Average depth of the nest measured from the top of the nest to the ground surface was $98 \pm 23\text{mm}$ (range = 39-150). Mean clutch size was 13 ± 2.9 eggs (range = 4-21). Mean egg mass was $8.73 \pm 1.14\text{g}$ (range = 4.70-11.73).

Figure 4 shows the relationship between the number of hatchlings emerging each day and the average temperature of each day. Figure 5 shows the relationship between the number of hatchlings emerging each day and the average rainfall of each day.

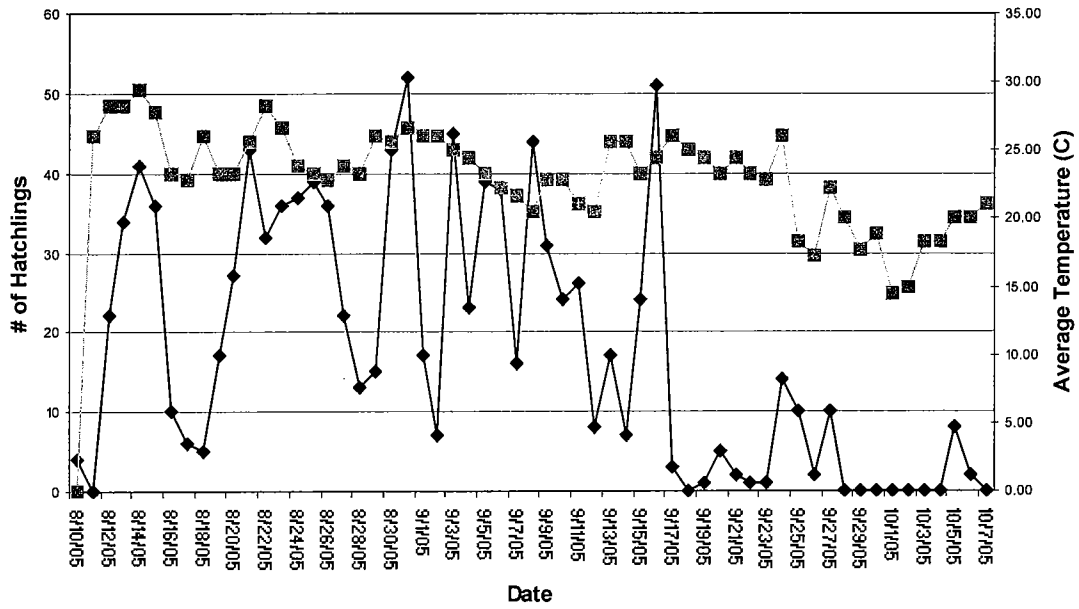


Figure 4. The number of hatchlings that emerged each day is shown in diamonds and the average temperature each day is shown in squares.

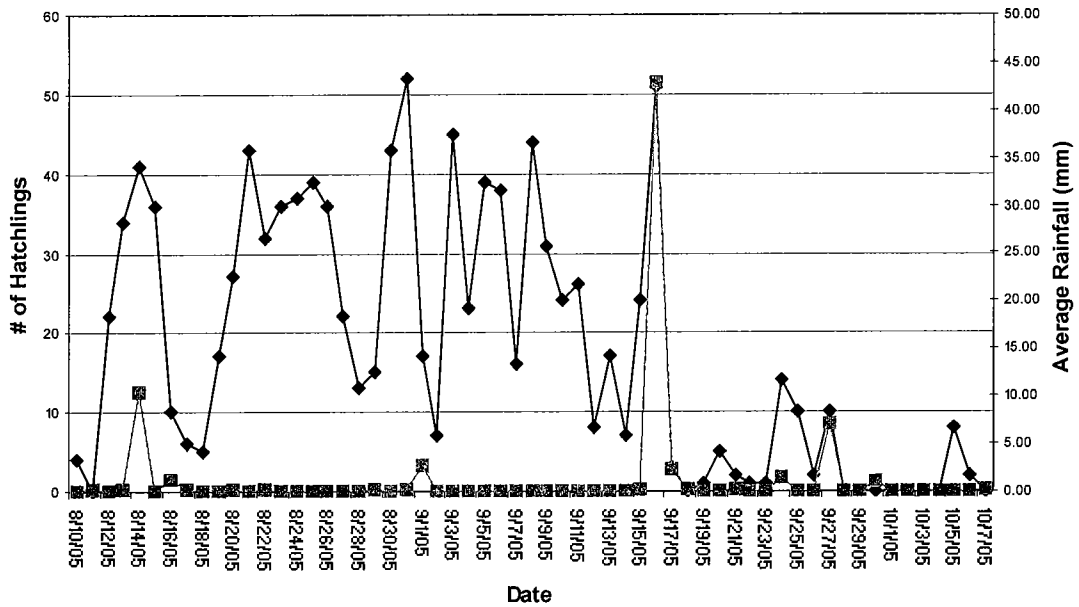


Figure 5. Average rainfall for each day is shown in squares and the amount of hatchlings that emerged each day is shown in diamonds.

Two nests survived being repeatedly flooded during high tide. Of the 1,724 eggs that were protected, 4.8% (N=82) were root predated, 20% (N = 350) were apparently infertile, 1% (N = 19) were found emerged from the egg but dead in the nest and 5.1% (N = 88) were found dead-pipped (hatchling had broken the shell but failed to emerge from the shell). Egg viability, the number of eggs that produced hatchlings that emerged from the nest successfully was 63% (N = 1087). The mean number of days before the first hatchling emerged was 62 ± 8.6 days (range = 50-95). Social hatches, where all the hatchlings in the nest emerge on the same day, were not common this year. Only 5.5% (N=7) of the nests had social hatches. Only 8.8% (N=12) of the nests so far have failed to hatch any emergents at all.

Temperature logger data and hatchling sex ratios have yet to be analyzed and will not be reported at this time.

DISCUSSION

Most aspects of the 2005 nesting season were consistent with other studies done in New Jersey (Burger 1977) and at the JBWR (Feinberg and Burke 2003). Female recapture rate increased this year from 48% in 2004 (Widrig unpubl.) to 58% in 2005. Figure 1 shows that the days with the most female terrapins captured occurred on days or following days with a substantial amount of rain. Average clutch size from 2004 was 13 eggs (Widrig unpubl.). This is consistent with this year's average of 13 eggs. Feinberg and Burke (2003) found an average clutch size from 1999 to be 10.9 eggs, slightly

smaller than the 2005 data. Giambanco (2004) also found a slightly lower clutch size in 2000 and 20001, 12.1 eggs and 11.6 eggs, respectively.

Nest viability observed this season (91.2%) was much higher than some studies and consistent with other studies. A viable nest is defined here as a nest that produced at least one hatchling. Burger (1977) found the viability of nests in New Jersey to be 69% and Feinberg (2000) found the viability of nests at JBWR in 1999 to be 57%. My observed nest viability was 1/3 times greater than that found six years ago. This could be due to the fact that I collected data from a much larger sample size than either of the two previous studies. Giambanco (2003) found that nest viability was 95% (N=67) in both 2000 and 2001. Widrig (unpubl.) found the nest viability was 93% (N=131/141) in 2004. The discrepancy between the two consecutive years, 2004 and 2005, is most likely due to the difference in temperatures between the two years.

Egg viability, the number of eggs that produced live hatchlings, for 2005 was 63% (N=1087/1724). This is lower than found in previous studies. Ner (2003) found the egg viability at Little Egg Island and Ruffle Bar (other islands in Jamaica Bay) to be 96.9% (N=63/65) in 2000 and 95% (N=57/60) in 2001. Giambanco (2004) found the egg viability was 88.6% (N=639/721) in 2000 and 86.5% (N=624/721) in 2001 at Ruler's Bar Hassock. Widrig (unpubl.) found that in 2004 the egg viability was 78.8% (N=1562/1856), and might have been much higher if seven nests had not been washed away during tropical storm Jean. The low egg viability in 2005 may be explained by the warmer temperatures that summer, but the temperature logger data must be analyzed before I can determine the true cause of the lower nest and egg viability.

The time to first hatchling emergence for each nest this summer was also much quicker than in 2004. In 2004 the average time to first emergence was 85 days (Wojakowski unpubl.). This year the average was 62 days, almost two weeks earlier. Previous studies on terrapins have shown that the average incubation time for nests in New Jersey was 76 days (Burger 1977), 108 days in Massachusetts (Auger and Giovannone 1979) and 54.5 days in South Carolina (Zimmerman 1992). My 2005 results are closer to the results from South Carolina than the results from last year. This is almost certainly due to the abnormally warm summer and early fall experienced on Long Island in 2005. There were 16 days (five in a row in August) where the temperature was over 32°C. As demonstrated in Figure 4, more hatchlings that emerged during the beginning of the season emerged on days where the temperature was higher than previous days. The extreme warm temperatures and, possibly, the high humidity appear to be the cause of the short incubation period, but the temperature data must be analyzed before I can draw any firm conclusions. Figure 5 also shows that rainfall could be affecting emergence time. The days where the most amount of hatchlings emerged later in the season are days in which there was a substantial amount of rainfall. The rainfall could be acting as a cue for the hatchlings to emerge from the nest.

Because the temperature data and hatchling sex ratios have yet to be analyzed there are still many core questions of my project that I am unable to answer in this paper.

ACKNOWLEDGEMENTS

I would like to thank the Tibor T. Polgar Fellowship Program for this support, which enabled me to afford so many temperature loggers. Chris Olinjynk of the NPS was very helpful with equipment set up and removal. My advisor, Dr. Russell Burke, was very helpful both in the field and while writing this paper. Asma Madad helped considerably by assisting in the sexing of the hatchlings. Eric Rulison also helped considerably by watching my terrapins, nests and hatchlings while I was away. Also I would like to thank all of my volunteers without which I would never be able to have such a large sample size of nests.

LITERATURE CITED

- Auger, P. J. and P. Giovannone. 1979. On the fringe of existence: Diamondback terrapins at Sandy Neck. *Cape Naturalist* 8:44-58.
- Ashmore, G. M. and F. J. Janzen. 2003. Phenotypic variation in smooth softshell turtles (*Apalone mutica*) from eggs in constant versus fluctuating temperatures. *Oecologia* 134:182-188.
- Burger, J. 1977. Determinants of hatching success in diamondback terrapin, *Malaclemys terrapin*. *American Midland Naturalist* 97(2):444-464.
- Burger, J. and W. A. Montevecchi. 1975. Nest site selection in the terrapin *Malaclemys terrapin*. *Copeia* 1975:113-119.
- Burke, R. L., E. L. Jacobson, M. J. Griffith and L. J. Guillette. 1994. Non-invasive sex identification of juvenile gopher and desert tortoises (genus *Gopherus*). *Amphibia-Reptilia* 15:183-189.
- Charnov, E. L. and J. J. Bull. 1977. When is sex environmentally determined? *Nature* 266:828-830.
- Ewert, M. A., R. E. Hatcher and J. M. Goode. 2004. Sex determination and ontogeny in *Malacochersus tornieri*, the Pancake Tortoise. *Journal of Herpetology* 38:291-295.
- Feinberg, J. A. 2000. Nesting Ecology of Diamondback Terrapins (*Malaclemys terrapin*) at Gateway National Recreational Area. M.S. Thesis. Hofstra University, Hempstead, NY.
- Feinberg, J. A. and R. L. Burke. 2003. Nesting ecology of diamondback terrapins (*Malaclemys terrapin*) at Gateway National Recreational Area. *Journal of Herpetology* 37:517-526.
- Giambanco, M. 2004. Comparison of viability rates, hatchling survivorship, and sex ratios of laboratory-and -field incubated nests of the estuarine, emydid turtle, *Malaclemys terrapin*. M.S. Thesis. Hofstra University, Hempstead, NY.
- Janzen, F. J. 1994. Vegetation cover predicts the sex ratio of hatchling turtles in natural nests. *Ecology* 75:1593-1599.
- Janzen, F. J. and C. L. Morjan. 2002. Egg size, incubation temperature, and posthatchling growth in painted turtles (*Chrysemys picta*). *Journal of Herpetology* 36:308-311.

- Kolbe, J. J. and F. J. Janzen. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology* 83:269-281.
- Morjan, C. L. 2003. Variation in nesting patterns affecting nest temperatures in two populations of painted turtles (*Chrysemys picta*) with temperature-dependent sex determination. *Behavioral Ecology and Sociobiology* 53: 254-261.
- Morjan, C. L. and F. J. Janzen. 2003. Nest temperature is not related to egg size in a turtle with temperature-dependent sex determination. *Copeia* 2003:366-372.
- Mrosovsky, N., and C. Pieau. 1991. Transitional range of temperature, pivotal temperatures and thermosensitive stages for sex determination in reptiles. *Amphibia-Reptilia* 12:169-179.
- Ner, S. 2003. Distribution and predation of diamondback terrapin nests at six upland islands of Jamaica Bay Unit and Sandy Hook Unit, Gateway National Recreation Area. M.S. Thesis. Hofstra University, Hempstead, NY.
- Roosenburg, W. M. 1996. Maternal condition and nest site choice: An alternative for the maintenance of environmental sex determination? *American Zoology* 36:157-168.
- Roosenburg, W. M. and K. C. Kelley. 1996. The effect of egg size and incubation temperature on growth in the turtle, *Malaclemys terrapin*. *Journal of Herpetology* 30:198-204.
- Tucker, A. D., N. N. Fitzsimmons and J. W. Gibbons. 1995. Resource partitioning by the estuarine turtle *Malaclemys terrapin*: trophic, spatial, and temporal foraging constraints. *Herpetologica* 51(2): 67-181.
- Valenzuela, N. D. 2001. Constant, shift, and natural temperature effects on sex determination in *Podocnemis expansa* turtles. *Ecology* 82:3010-3024.
- Valenzuela, N. D., R. Botero and E. Martinez. 1997. Field study of sex determination in *Podocnemis expansa* from Columbian Amazonia. *Herpetologica* 53:390-398.
- Valenzuela, N., D. C. Adams, R. M. Bowden and A. C. Gauger. 2004. Geometric morphometric sex estimation for hatchling turtles: A powerful alternative for detecting subtle sexual shape dimorphism. *Copeia* 2004:735-742.
- Wilson, D. S. 1998. Nest-site selection: Microhabitat variation and its effects on the survival of turtle embryos. *Ecology* 79:1884-1892.
- Wood, R. C. and R. Herlands. 1997. Turtles and tires: The impact of roadkills on northern diamondback terrapin, *Malaclemys terrapin terrapin*, population on Cape May Peninsula, southern New Jersey, USA. *Proceedings: Conservation*,

Restoration and Management of Tortoises and Turtles-An International Conference. Pp. 46-53.

Zimmerman, T. D. 1992. Latitudinal reproductive variation of the salt marsh turtle, the diamondback terrapin (*Malaclemys terrapin*). Unpublished M.S. thesis. University of Charleston, South Carolina.