

NESTING ECOLOGY OF DIAMONDBACK TERRAPINS (*Malaclemys terrapin*)
AT GATEWAY NATIONAL RECREATION AREA

THESIS

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ABSTRACT

The nesting ecology of diamondback terrapins (*Malaclemys terrapin*) was studied in 1998 and 1999 at Gateway National Recreation Area. I found populations of nesting terrapins at three different locations. Most of my research was conducted at the Jamaica Bay Wildlife Refuge. Female terrapins nested from early June through late July, and laid up to two clutches per season, depositing an average of 10.9 eggs per nest. Nesting activity increased with daily high temperature and high tide. The majority of females were captured when there was 25-75% cloud cover. The majority of nests were counted in shrub-land, mixed-grassland, and dune habitats, but nest density was highest on a man-made, sandy trail and also on beaches. Raccoons depredated 92.2% of terrapin nests. Only 5.2% of terrapin nests survived to produce hatchlings. I counted 1,319 and 1,840 depredated nests in 1998 and 1999, respectively, at the Refuge. I also found the carcasses of 23 female terrapins that were apparently killed by raccoons as they came on land to nest.

INTRODUCTION

The diamondback terrapin (*Malaclemys terrapin*) is an estuarine, emydid turtle that inhabits coastal regions along the Atlantic and Gulf coasts of North America, from Cape Cod, Massachusetts, to Corpus Christi Bay, Texas (Palmer and Cordes 1988). There are seven recognized subspecies, and the northernmost subspecies is the northern diamondback terrapin (*Malaclemys terrapin terrapin*). This subspecies is found from Cape Cod to Cape Hatteras, North Carolina (Ernst et al. 1994).

Significant individual variation is common among terrapins. The carapace ranges in color from gray or light brown to black and is characterized by concentric markings or ridges on the scutes (Ernst et al. 1994). Skin coloration varies from light gray with dark spots, to black without obvious spots. The plastron also varies in color from orange-yellow to green-gray and lacks distinguishing marks (Conant and Collins 1991).

Malaclemys exhibits extreme sexual dimorphism (Seigel 1984; Lovich and Gibbons 1990). Adult females range in size from 15 to 23 cm and adult males, from 10 to 14 cm, with females having wider heads, larger shells, and shorter tails than males (Ernst et al. 1994). Population sex ratios vary substantially (Hurd et al. 1979; Auger 1989; Lovich and Gibbons 1990; Roosenburg 1991; Morreale 1992) and biases as high as 4.4 males per female and 5 females per male have been reported in Louisiana (Cagle 1952) and Florida (Seigel 1984), respectively. A significant amount of research on sex ratios, growth, and reproduction has also been conducted using captive

specimens (Hildebrand and Hartsel 1926; Hildebrand 1929, 1933). These findings may have questionable scientific value when applied to wild populations (Cagle 1952; Seigel 1984; Zimmerman 1992; Ernst et al. 1994) and are not used in this paper.

Terrapins inhabit coastal marshes, tidal creeks, estuaries, bays, and coves (Palmer and Cordes 1988). These aquatic habitats usually contain *Spartina* sp., an important ecological component for terrapin populations (Burger and Montevecchi 1975; Hurd et al. 1979; Palmer and Cordes 1988; Morreale 1992). Terrapins primarily feed on invertebrates such as mollusks and crustaceans (Marganoff 1970; Tucker et al. 1995). Because of their locally high population densities, active foraging style, and significant predatory impact, terrapins may constitute an important component of estuarine food webs (Hurd et al. 1979). However, it may not be possible to analyze the true ecological significance of terrapins accurately, due in part to the population declines that have occurred throughout much of the species' range for more than a century.

Terrapins also use the marsh habitat to hibernate during winter. Individuals generally seek refuge in depressions at the bottom of salt marsh creeks, buried in the sides of creek banks or beneath undercut banks (Yearicks et al. 1981). In Virginia, hibernation was observed on a sand beach above the high tide line, away from the marsh (Lawler and Musick 1972).

Terrapins tend to follow an annual pattern of activity that includes (in chronological order): "initiation of feeding, mating, nesting, incubation, hatching [of eggs], emergence of hatchlings, cessation of feeding, hibernation" (Cook 1989a). In general, these activities tend to commence earlier, and last for greater periods of time in populations living at lower latitudes than in populations at higher latitudes (Cook 1989a).

Terrapins of all size classes are prey for numerous predators (Ernst et al. 1994). Adult terrapins are eaten by bald eagles (*Haliaeetus leucocephalus*) (Clark 1982), raccoons (*Procyon lotor*) (Seigel 1980a), gulls (*Larus* sp.) (Watkins-Colwell and Black 1997) and sea turtles, including Kemp's ridleys (*Lepidochelys kempi*), and loggerheads (*Caretta caretta*) (Frick 1997). Latham (1971) observed cold-shocked terrapins being eaten by both crows (*Corvus brachyrhynchos*) and opossums (*Didelphis virginiana*).

Predation on adult terrapins can significantly impact a population's ability to persist. Seigel (1980a, 1993) studied predation on East-coast terrapins of Florida (*M. t. tequesta*) at Merritt Island National Wildlife Refuge. He studied two terrapin populations, consisting of a combined estimate of 617 individuals (Seigel 1984). Between 1977 and 1978, raccoons were determined to have killed at least 10% of adult female terrapins as they came on land to nest (Seigel 1980a). Although terrapins of both sexes were preyed upon, the majority (86%) was adult females (Seigel 1980a). The scattered remains of additional old terrapin shells were also discovered, indicating that similar predation had occurred prior to the investigation. When Seigel returned to the site in 1992 and 1993, he found no more than a total of six terrapins per year (Seigel 1993). Predation on adult terrapins had apparently continued between 1979 and 1992, eventually decimating both populations at the study site. Predation on adults irrevocably removes reproductive females from the population, rather than eggs that are replaceable.

The nests and hatchlings of *M. terrapin* are known to fall prey to ghost crabs (*Ocypode quadrata*) (Zimmerman 1992), striped skunks (*Mephitis mephitis*) (Auger and Giovannone 1979), red foxes (*Vulpes vulpes*), raccoons, crows, and laughing gulls

(*Larus atricilla*) (Burger 1977). The roots from beachgrass (*Ammophila breviligulata*) (Auger and Giovannone 1979; Lazell and Auger 1981; Zimmerman 1992) and *Spartina* sp. (Roosenburg 1992) have also been shown to depredate terrapin nests. Other biotic causes of nest and hatchling mortality include fungal infections and maggots (Auger and Giovannone 1979). Abiotic causes of nest mortality include flooding of nests laid near the high-tide line (Roosenburg 1992) and wind erosion (Auger and Giovannone 1979). Developmental problems such as infertility, underdevelopment, and unexplained mortality of hatchlings further decrease success and survivorship (Burger 1977).

Egg survivorship, hatchling survivorship, and overall nest survivorship have been observed in several studies (Burger 1976, 1977; Auger and Giovannone 1979; Auger 1989; Roosenburg 1992; Zimmerman 1992). "Egg survivorship" is the ratio of eggs producing both viable (live) and non-viable (dead) hatchling, to the actual or estimated number of eggs contained in a sample. "Hatchling survivorship" is the ratio of eggs that produce only viable hatchlings to the total number of eggs contained in a sample. "Overall nest survivorship" is the ratio of successful nests to the total number of all nests in a sample. In this paper, a successful nest is defined as a nest that produces at least some hatchlings.

Nest predation has been studied at several different sites. Burger (1976, 1977) conducted extensive research on predation of terrapin nests at Little Beach Island, New Jersey, in 1973 and 1974. Burger found that predators destroyed 51% ($n = 37$) and 73% ($n = 200$) of nests, respectively. Mammalian predation occurred at night, and was predominantly caused by raccoons and red foxes. Avian predation occurred diurnally, and was caused by laughing gulls and crows. Roosenburg (1992) observed nest

predation at two beaches on the Patuxent River in Maryland from 1987 to 1991, and found that the average rate of nest predation was 83.5% at the first beach and 41.3% at the second beach. Predation at the first beach reached 95% in 1987 and 1988. Raccoons were the major nest predators.

Two distinct scenarios have been reported describing the method by which terrapin eggs are consumed by raccoons. In New Jersey, raccoons consumed eggs completely, shell included (Burger 1977). Burger also found that raccoons often left some eggs uneaten in the nests that they had raided. However, in Connecticut, Aresco (1996) reported that raccoons only partially consumed eggs, discarding the shells in neat piles adjacent to the nest. He also reported that no uneaten eggs were left in depredated nests.

The nesting ecology of terrapins appears to vary considerably throughout the species' range. Terrapins nest from April through July, and the time and duration of the nesting season varies, depending on location (Ernst et al. 1994). Terrapins tend to nest during fair weather, when cloud cover is minimal (Burger and Montevecchi 1975; Seigel 1979, 1980b; Zimmerman 1992). Nesting has also been observed nocturnally (Auger and Giovannone 1979; Roosenburg 1992; Wood and Herlands 1997), during rain (R. Wood, Wetlands Institute, pers. comm.), and soon after rain (Burger and Montevecchi 1975; Roosenburg 1992). Female terrapins prefer to nest in areas of flat or gently sloping topography (Burger and Montevecchi 1975). Females also seem to prefer nesting in sunny, sparsely vegetated areas (Burger and Montevecchi 1975; Roosenburg 1992; Zimmerman 1992). The preferred nesting substrate of terrapins is sand

(Roosenburg 1994). In Florida, terrapin nesting occurs between 28.0-36.0 °C, with a mean temperature of 31°C (Seigel 1979).

Distinct variation has been reported in terrapin nesting, hatchling, and clutch data from different latitudes and populations. Although characteristics such as the plastral length of adult females and mass of the total clutch did not vary significantly, other reproductive characteristics such as clutch size, hatchling size, incubation time, and length of nesting season did follow latitudinal trends (Zimmerman 1992). This variation may be a graded response to different environmental conditions such as temperature, resource availability, and nest site availability associated with latitudinally varying climates (Zimmerman 1992). Zimmerman suggests that terrapins living in cooler, temperate climates are subject to greater environmental unpredictability, and may produce more, smaller eggs to increase the probability of survivorship. In warmer, sub-tropical climates, the environmental conditions are generally more stable and predictable (Zimmerman 1992). Zimmerman suggests that terrapins in these climates place greater reproductive investment in fewer, larger eggs that will produce larger hatchlings of higher quality.

Mean clutch size has generally been found to be larger in northern and mid-Atlantic terrapin populations than in southern populations. Mean clutch size ranges from 14 in Massachusetts (Auger 1989) to 9.8 in New Jersey (Montevecchi and Burger 1975), to 13 in Maryland (Roosenburg 1991). In southern populations, mean clutch sizes of 6.9 have been reported from South Carolina (Zimmerman 1992) and 6.7 from Florida (Seigel 1980b).

Conversely, hatchling size generally increases with decreasing latitude. Mean plastron lengths have been reported at 24.4 mm in New Jersey (Burger 1977), 27.0 mm in Virginia (Reid 1955), 28.7 mm in South Carolina (Zimmerman 1992), and 27.9 mm in Florida (Seigel 1980b).

Incubation time is dependent on nest temperature, and is likely to be longer in cooler climates than in warmer climates (Zimmerman 1992). Incubation periods range from 87-146 (\bar{x} = 108) days in Massachusetts (Auger and Giovannone 1979), 61-104 (\bar{x} = 76) days in New Jersey (Burger 1977), and 52-59 (\bar{x} = 54.5) days in South Carolina (Zimmerman 1992).

The length of the nesting season appears to be longer in warmer climates than in cooler climates (Zimmerman 1992). The number of nesting days per season ranges from 34-44 days in New Jersey (Burger 1977), to 60 days in South Carolina (Zimmerman 1992) and 52-57 days in Florida (Seigel 1980b).

Variations in climate may also affect the number of clutches produced by individual females per year (clutch frequency). Female terrapins living at higher latitudes may produce fewer clutches per year due to the time constraints associated with a shorter nesting season and increased developmental time associated with colder nest temperatures (Zimmerman 1992). Zimmerman speculates that terrapins at lower latitudes may produce more clutches to counterbalance smaller clutches.

Terrapins from northern populations produce up to two clutches per year. In New Jersey, females were found to single clutch (Montevecchi and Burger 1975; Burger 1977), whereas double clutching was documented in Massachusetts (Auger and Giovannone 1979) and New York (Klemens 1993). In mid-Atlantic and southern

populations, female terrapins produce up to three clutches per year. Triple clutching was observed among terrapins in Maryland (Roosenburg 1991) and Florida (Seigel 1980b). In contrast, Zimmerman (1992) observed single clutching among female terrapins in South Carolina.

Although some characteristics of terrapin reproductive biology seem to follow distinct clinal trends, other characteristics vary without following any obvious clinal patterns. The nesting activity of terrapins appears to be influenced by tidal activity in New Jersey (Burger and Montevicchi 1975), Massachusetts (Auger and Giovannone 1979), and South Carolina (Zimmerman 1992). Terrapins from these populations appeared to prefer nesting at high tide. In Florida nesting activity was correlated with air temperature, as females preferred to nest close to the daily high temperature (Seigel 1980b). Roosenburg (1994) discussed behavioral nesting variation among terrapins from Massachusetts, New Jersey, Maryland, and Florida. Distinct nesting behaviors such as facial probing of sand and false nest digging occur in some populations and do not occur in others. In addition, characteristics such as daily time of nesting and the number of nests per hectare varied randomly.

Humans have commercially exploited terrapins throughout much of their range for more over a hundred years. Since the middle nineteenth century, diamondback terrapins were prized for their meat and considered a delicacy by dining connoisseurs. Terrapins were harvested and used primarily in soup, which led to the extirpation of many populations, especially those near cities (Ernst et al. 1994). By the early twentieth century, harvesting had taken such a toll on wild populations that the U.S. Bureau of Fisheries began captive breeding programs (Garber 1990). With the onset of World

War I and the enactment of prohibition, demand for terrapins began to vanish along with the champagne that often accompanied the meal (Marganoff 1970). Finally, the arrival of the Great Depression signified an end to the historic demand for terrapin meat (Wood and Herlands 1997).

In the New York metropolitan region, terrapins have been subjected to the intense pressures associated with human exploitation, activity, and development since the late nineteenth century (Garber 1990). Long Island terrapin populations were heavily exploited through the early part of the twentieth century because of their convenient proximity to New York City (Marganoff 1970). This proximity, coupled with the fact that Long Island terrapins were renowned as the premium terrapin on the market (Coker 1951), led to severe population declines (Marganoff 1970). In 1916, *M. terrapin* was described as “formerly common in the bays of Long Island, as elsewhere along the Atlantic coast, but now rather rare because it has been hunted...” (Murphy 1916). By the mid-1930s, terrapins had become so rare on Long Island that local naturalists considered the species extirpated from the area (Marganoff 1970; Garber 1990). There were no records of terrapin sightings anywhere on Long Island for the next three decades. In 1969, a local magazine published several articles on terrapin sightings that had occurred between 1962 and 1969 (Spagnoli and Marganoff 1975), and Latham (1971) reported numerous terrapin observations he had made from Orient, Long Island, between 1915 and 1957, confirming that terrapins had never completely vanished from the island. New York populations have slowly recovered (Morreale 1992). The recovery over the past five decades may have had additional support through the release of commercial terrapins (Spagnoli and Marganoff 1975; Garber

1990). Terrapins currently occur in coastal habitats along much of Long Island (Morreale 1992). Small populations also occur in the lower Hudson River (Simoes and Chambers 1998).

The New York Department of Environmental Conservation currently considers *M. terrapin* to be a "Special Concern Species." The New Jersey Department of Environmental Protection currently lists terrapins as a "Decreasing" species. Although terrapin populations have certainly rebounded since the early part of this century, their long-term status may be in jeopardy. Harvesting and collection continues in certain local areas, and terrapins also drown as by-catch in crab traps (Garber 1988; Cook 1989a; Wood 1997). Terrapins face the destruction and development of their estuarine habitats as well as their nesting habitats (Morreale 1992). Marshes are being dredged, filled, and altered, reducing the aquatic habitat crucial to terrapin survival. Lawns and bulkheads now replace many of the areas that were once the nesting beaches of terrapins in the New York metropolitan area. In urban regions such as Jamaica Bay, tide-borne debris such as plastic holders from six-packs and monofilament fishing line may pose a threat to nesting terrapins and hatchlings (Sadove et al. 1996).

Automobiles also injure and kill terrapins. Cook (1989a) reported that 100-200 female terrapins were killed each year on a single "stretch of road, several miles in length" on Long Island, and Wood and Herlands (1997) recorded more than 4000 roadkills over seven years in Cape May, New Jersey.

A less obvious potential threat to local terrapin populations is the release of commercial stock. Murphy (1916) reported that during the heyday of the terrapin industry, Long Island was home to numerous holding and shipping pens. During that

time, quantities of southern terrapins were shipped to the region and kept in captivity, where some may have later escaped (Marganoff 1970). In addition to escapees, commercial terrapins may have been liberated into local waters after the demise of the industry (Spagnoli and Marganoff 1975). If introduced into wild populations, these once-captive terrapins from southern populations could have interbred with local terrapins, possibly contributing to the significant variation reported for terrapins on Long Island (Marganoff 1970).

Release of captive terrapins still continues, mostly during Asian religious ceremonies in which commercial terrapins from fish markets in New York City are released into local waters at rates as high as 100 turtles per month (Morreale 1992). Terrapins sold at such fish markets may come from the Carolinas, Virginia, Maryland, and southern New Jersey (Garber 1988). In addition to the release of terrapins for religious rituals, individuals purchased as pets may also be “liberated” into local waters (Garber 1990). Introduction of terrapins from other areas could lead to genetic mixing with local native populations, and may also introduce disease. Release of commercial terrapins could also skew population sex ratios, because terrapins sold commercially are generally large adult females (Morreale 1992).

Terrapin Research in Jamaica Bay

To date, no in-depth studies regarding *M. terrapin* nesting ecology and predation have been conducted in New York State, and few studies in any capacity have been conducted on terrapin populations in the vicinity of New York City and the Hudson River Bight. As a result, little is known about terrapin populations in this region.

One of the largest and most robust terrapin populations in New York State occurs in Jamaica Bay. Morreale (1992) assumed that Jamaica Bay supports thousands of terrapins because of the Bay's large size and productivity. Unfortunately, there is little available information regarding the history of terrapins in the Bay prior to the 1970s. Local fishermen reported that Jamaica Bay terrapins have descended from naturally occurring ancestors that had lived in the Bay (Garber 1988). Garber also suggests that a significant number of terrapins may have been released into the Bay from fish markets, possibly forming their own populations or mixing with terrapins native to Jamaica Bay to create modern-day population of subspecies hybrids.

Most of the scientific information regarding Jamaica Bay terrapins has been collected within the last several decades, after significant geophysical alterations to the Bay and surrounding areas were already made (see Methods and Materials). Basic observations of *M. terrapin* nesting and life history were conducted at the Jamaica Bay Wildlife Refuge, a part of Gateway National Recreation Area (Gateway NRA) by Cook (1989a). He observed nesting as early as the first week of June, and as late as the third week of July. The nesting season averaged 34 days, and females produced 11-18 (\bar{x} = 14.5) eggs per nest. The average time of incubation was 81 days (Cook 1989a). These data are concordant with the clinal variation described for the species by Zimmerman (1992). Cook (1989b) also reported "viable resident populations present" at three other parts of Gateway NRA including Sandy Hook, New Jersey, Staten Island, New York, and another site in Jamaica Bay outside the Wildlife Refuge.

In the early 1980s, terrapins had an overall egg survivorship rate of 93%, and nest predation was never observed at the Jamaica Bay Wildlife Refuge (R. Cook, NPS,

pers. comm.). During a large-scale survey of mammals conducted at the time, typical predators of turtle nests such as raccoons, red foxes, and striped skunks were not found or reported to occur at the Refuge (O'Connell 1980). Thus, in the absence of nest predators, Jamaica Bay terrapins were not subject to nest predation typical of most turtle populations elsewhere (R. Cook, NPS, pers. comm.).

Cook (1989a) credited the historically high overall nest-survivorship rates at the Jamaica Bay Wildlife Refuge to the extirpation of red foxes from the New York City region. He also assumed that raccoons, present in other parts of the city, were unable to colonize the man-made uplands created throughout much of Jamaica Bay, including the Refuge itself. Thus, this highly altered urban environment provided terrapins with unusually safe nesting conditions. Geographic factors also may have further reduced the likelihood of colonization by predators. Because the Jamaica Bay Wildlife Refuge is constituted solely of islands and marshes, it is physically isolated from the Long Island mainland (aside from a narrow bridge that extends from Long Island onto the main island of the Refuge, called Ruler's Bar Hassock).

Raccoons did not historically occur at the Refuge. On extremely rare occasions of no more than once per year (starting in the early 1980s), a dead raccoon was observed on the main road that runs through the Refuge. An event such as this occurred so rarely, that it was quite noteworthy (R. Cook, NPS, pers. comm.). During the early to mid 1990s, the frequency of raccoon sightings at the Wildlife Refuge began to increase (R. Cook, NPS, pers. comm.). Although the factors that had prevented natural raccoon colonization had not changed, it is thought that people began to release nuisance raccoons illegally from the mainland directly onto Ruler's Bar Hassock (D.

Riepe, NPS, pers. comm.). During this same period of time, depredated nests became a common sight, as did raccoons themselves. Although the demographic increase in raccoons was not documented, it was clear by 1995 that a significant threat to terrapins in Jamaica Bay Wildlife Refuge was developing (R. Cook, NPS, pers. comm.).

With the above situation in mind, combined with the overall lack of information regarding the nesting ecology of terrapins in the New York City metropolitan region, the primary objectives of this study were as follows:

- 1)** To locate nesting sites used by terrapins throughout Gateway National Recreation Area.

- 2)** To study and quantify current predation levels on *M. terrapin* nests at Jamaica Bay Wildlife Refuge. This included examining five upland islands within the Refuge for terrapin nesting, activity, and predation. Whereas one of these islands, Ruler's Bar Hassock, had been studied, the other islands in the Refuge had not. It is likely that they are too small and isolated to support raccoons (D. Avrin, R. Cook, NPS, pers. comm.). If terrapins are nesting on these islands at similar levels to Ruler's Bar Hassock, then they may provide sanctuary from nest predation, much as Ruler's Bar Hassock did before raccoons arrived.

- 3)** To observe and report the nesting behavior, ecology, and environmental preferences of *M. terrapin*, and the physical characteristics at the Jamaica Bay Wildlife Refuge.

METHODS AND MATERIALS

Description of Study Area

Gateway NRA is a large, federally operated, estuarine park managed by the National Park Service (NPS) (Figure 1). It is composed of three geographically separate units that contain a total of approximately 10,500 hectares of land and water that include more than 430 km of shoreline. Two units are located in New York State and the third in New Jersey. Every part of Gateway NRA interfaces with the Hudson River Bight, otherwise known as the New York-New Jersey Harbor Estuary. The Hudson River Bight is the southernmost part of the Hudson River watershed and the primary physical feature that unifies Gateway NRA.

Gateway NRA lies within the boundaries of one of the largest metropolitan complexes in the world, New York City. With the exception of the New Jersey unit, which is approximately 8 km south of the city border, all other parts of Gateway NRA are located within the city limits. The New York City metropolitan area contains an estimated twenty million people, and in 1996 Gateway NRA had approximately 6.4 million visitors. As the fifth most highly visited national site in the United States,

Gateway NRA has approximately the same number of visitors per year as Yosemite and Yellowstone National Parks combined.

I characterized the relevant areas of Gateway NRA into nine habitat types. Descriptions of the first seven habitat types were based on characterization schemes used by the NPS (National Park Service 1979; Venezia and Cook 1991), and the remaining two habitat descriptions come from my personal observation. The following habitat types are found within Gateway NRA and these terms are used throughout this report:

- 1) Salt Marsh – This habitat is predominated by low marsh cordgrass (*Spartina alterniflora*), the only species found below mid-tide level. At higher elevations in the marsh, plants such as glasswort (*Salicornia* sp.), sea lavender (*Limonium carolinianum*), salt-meadow cordgrass (*S. patens*), and salt hay (*Distichlis spicata*) are found. This habitat is normally subject to tidal and storm-driven flooding.
- 2) Reed Marsh – This habitat is found in both disturbed and non-disturbed areas of Gateway NRA. The common reed (*Phragmites australis*) dominates, and low shrubs may sometimes be interspersed. Disturbed reed marshes are generally found at landfill sites or areas that have been cleared, disturbed or flattened.
- 3) Beach – This habitat borders oceans and bays and is distinguished by exposed sand and flat beaches that lack vegetation.
- 4) Dune – Beach-paralleling dunes containing 20-50% vegetation characterize this habitat. Stabilizing grasses such as American beach grass (*Ammophila breviligulata*) are common. Seaside goldenrod (*Solidago sempervirens*) and mugwort (*Artemisia vulgaris*) are also found in this habitat.

- 5) Mixed Grasslands – This habitat characteristically contains denser vegetation, and is dominated by seaside goldenrod, switchgrass (*Panicum virgatum*), bluestem (*Andropogon virginicus*), and American beach grass. Vegetation coverage is 20-75%.
- 6) Shrub Land – This includes “open shrub-land” areas where grassland with 10-50% tree and shrub coverage occurs, and “Low Thicket” areas where low growing shrubs 50-250 cm tall generally dominate more than 50% of cover. Shrub species include bayberry (*Myrica pensylvanica*), beach plum (*Prunus maritima*), dwarf sumac (*Rhus copallinum*), and poison ivy (*Toxicodendron radicans*). Pockets of high thickets, grasslands, woodlands or reed marsh may be interspersed throughout.
- 7) Woodland – This habitat is characterized by deciduous and/or coniferous trees taller than 5 meters.
- 8) Terrapin Trail – This is a 590-meter sand trail that runs through the primary terrapin nesting area at Ruler’s Bar Hassock, the main island in Jamaica Bay Wildlife Refuge.
- 9) Main Trail – This trail encircles much of the western side of Ruler’s Bar Hassock. The section that runs through the primary terrapin nesting area is 1,730 meters long and covered with gravel.

The Three Units of Gateway NRA

1) Jamaica Bay/Breezy Point Unit (New York) – This unit encompasses 7,821 hectares of land and water in the Jamaica Bay. It is located in southern Queens and Kings counties, New York. This unit is often subdivided into three districts: “Wildlife Refuge,” “Breezy Point,” and “Jamaica Bay” (Figure 2).

Both the “Wildlife Refuge” and “Jamaica Bay” districts were significantly impacted over the past 120 years by extensive dredging and physical alteration to create shipping channels and John F. Kennedy International Airport (Black 1981). These alterations have increased the volume of water in the Bay yet reduced its overall surface area.

Most of the Bay's natural, small marsh islands were either consolidated into large upland islands or removed altogether, greatly decreasing the original number of islands (Black 1981). When alterations ceased in the 1950s, marshland that had once covered 10,115 hectares was reduced to approximately 5,260 hectares.

The Wildlife Refuge district, also known as the Jamaica Bay Wildlife Refuge (JBWR), is protected from development and managed by the NPS as a wildlife area (Figure 3). This unit is composed of scattered islands and marshes. There are five upland islands at JBWR, yet only Ruffle Bar was formed naturally (Black 1981). The main island of JBWR, Ruler's Bar Hassock, originally consisted of several neighboring marshes that did not contain uplands. Starting in 1910, developers began to connect and enlarge these marshes using fill obtained from dredging operations that were occurring in the Bay (Black 1981). By the 1930s most of the development of Ruler's Bar Hassock was complete, aside from two ponds that were added in the 1950s. Three additional upland islands, Canarsie Pol, Subway Island, and Little Egg Island, also were created in a similar manner at the time, bringing the total number of upland islands in the Refuge to five.

Ruler's Bar Hassock is the largest island in the Refuge and the only one accessible to the public. It contains a Visitor Center, research facilities, and two artificially created ponds. The only connection to Ruler's Bar from mainland Long Island is via the Cross Bay Boulevard Bridge. The dominant ecological communities at JBWR are salt marsh, reed marsh, beach, dune, mixed-grassland, shrub land, and woodland (pers. obs.).

Breezy Point, the second district within the Jamaica Bay/Breezy Point Unit, lies at the western end of the Rockaway peninsula, which faces the Atlantic Ocean to the south and Jamaica Bay to the north (Figure 2). This peninsula forms the northern "gate" leading into the Hudson River Bight, hence the name "Gateway." The dominant habitat

types include grassland, dune, and beach (National Park Service 1979). The Rockaway peninsula is an Atlantic barrier beach.

The remaining district, known as the Jamaica Bay district, was also heavily impacted and altered during the development of Jamaica Bay. This district, which is part of Long Island, borders the northwestern rim of Jamaica Bay (Figure 2). Most of the natural streams and marshes that once ran through this district have been turned into bulk-headed basins, and much of the current land areas have resulted from the development of extensive marshlands using fill (National Park Service 1979; Black 1981). This includes two closed landfills, a large pier, recreational facilities, seven dredged inlets, and an airfield. The current dominant ecological communities include beach, reed marsh, mixed-grassland, and scattered areas of shrub land (National Park Service 1979).

2) Staten Island Unit (New York) – Encompassing 1,204 hectares of land and water, this district is composed of several parks scattered along the eastern side of Staten Island, Richmond county, New York (Figure 1). This unit has also undergone significant development and disturbance (National Park Service 1979). It is dominated by beach, mixed-grassland, reed marsh, and woodland habitats (National Park Service 1979). A small area of beach, dune, and salt marsh habitat is located in Great Kills Harbor and is the only sheltered body of water in the unit.

3) Sandy Hook Unit (New Jersey) – This unit covers 1,758 hectares of land and water. Sandy Hook lies on a peninsula in Monmouth county, New Jersey, forming the southern “gate” to the Hudson River Bight (Figure 1). This largely undisturbed unit has several distinct ecosystems (National Park Service 1979). The eastern side of the peninsula faces the Atlantic Ocean and is dominated by extensive beach and dune habitats, typical of an Atlantic barrier beach (National Park Service 1979). The western side of

the peninsula faces the Hudson River Bight and has several coves and areas of well protected beach, salt marsh, dune, mixed-grassland, shrub land, and woodland.

Locating Nesting Areas

All feasible regions of Gateway NRA were physically surveyed for nesting evidence of *M. terrapin* from June through September 1998. In this study, “feasibility” was defined as an area’s potential to support *M. terrapin* nesting, based on three main physical criteria. The first criterion was availability of the sun-exposed, sparsely vegetated areas that terrapins seem to prefer for nesting (Roosenburg 1992; Zimmerman 1992), including small pockets of exposed areas surrounded by relatively denser vegetation as reported by Burger and Montevicchi (1975). Because densely shaded and densely vegetated areas are avoided by nesting terrapins (Roosenburg 1994), dense woodlands, high thickets, and reed marshes in Gateway NRA were not considered. The second criterion was nesting substrate availability. Roosenburg (1994) reported that terrapins prefer to nest in sandy soils composed of large particles because of increased gas diffusion and decreased water demand. Loose soil and gravel substrates were also reported to attract nesting terrapins at Gateway NRA (D. Taft, National Park Service, pers. comm.) and were considered as well. Substrates such as peat and mud were not considered. The third and final criterion was proximity to water. The maximum distance from water considered in this study, based on nesting evidence, was approximately 250 meters. In addition to these three physical criteria, historic terrapin occurrence data from Cook (1989b) were also used in determining site feasibility. Ocean-facing Atlantic beaches, shorelines stabilized with bulkheads, and landfills were considered non-feasible, and were not considered in this study.

Fourteen different locations met the required criteria and were surveyed in Gateway NRA. Each site was surveyed once in 1998. I searched for indications of

nesting activity including depredated nests, turtle egg shell fragments, dead adult female terrapins found in upland regions, hatchlings, false nests, and tracks leading inland from the water. Dead terrapins found directly on the beach (within two meters of the high tide line) were not used as indicators of nesting activity because they may have died elsewhere and been washed ashore.

Observing Nest Predation and Ecology

Nest predation and ecology were only studied at JBWR. Observations were conducted daily, from 1 June to 31 July, generally over 4-to 6-hour periods between 0700 to 2200 h. The daily observation period was adjusted according to daytime high tide, with the middle of the observation period timed to correspond with high tide. This was done to maximize the number of observed terrapins, because nesting activity was reported to increase with high tide (Burger and Montevecchi 1975, Auger and Giovannone 1979; Zimmerman 1992). On days with two daytime high tides, either the tide closer to the solar zenith was selected as the observed tide, or observations were conducted during both tides. Volunteer groups ranging from 2-10 individuals provided daily assistance with observations.

Nesting terrapins were observed from shore via 7 x 35 field binoculars as they emerged from the water. Observers were positioned slightly inland, where terrapins could be seen leaving the water. Where available, trees were used as natural blinds. Once a terrapin was located on land, an observer followed her at a distance of approximately 10 m. Observers watched the complete nesting event whenever possible, maintaining a reasonable distance, and then captured the female for additional data collection. Some nesting terrapins were also found using hourly walking sweeps, which were conducted along the shorelines and trails. In rare instances, disturbed soil patterns were used to locate recently laid nests. Various disturbed soil patterns were

used to locate significant numbers of terrapin nests by Burger (1977) and Roosenburg (1992), but this was difficult in Jamaica Bay due to the presence of dense vegetation.

After a nest was located, it was marked with surveyor's flags. Three flags were placed in an equilateral triangle around each nest, approximately 1 m from the nest center. Flags were placed at greater distances in areas where visitors could tamper with them (i.e. main trail, terrapin trail). Flags were never placed precisely above a nest in an effort to prevent predators from learning to associate flags with nests.

Approximately 3,180 m of feasible nesting shoreline and 22 hectares of nesting habitat were monitored at Ruler's Bar Hassock. In an effort to increase the efficiency of monitoring the hassock, I arbitrarily divided the nesting habitats into eight "study zones" (figures 4a, b). Because the study zones were arbitrarily delineated, their sizes varied among each other. The habitat types and physical characteristics of the study zones varied both within and among each other. Study zones were ranked and monitored with different levels of intensity (Table 1). Ranking was based upon the amount of nesting activity observed in each zone during preliminary observations conducted early in the 1998 nesting season. Those zones where nesting terrapins were usually observed at least once per day were categorized as "Primary" zones, and monitored consistently throughout the field day. Zones where nesting terrapins were observed 1-5 times per week were categorized as "Secondary" zones, and monitored at least once per day, but not consistently. The remaining zones, where nesting terrapins were observed less than once per week, were categorized as "Tertiary" zones, and monitored sporadically throughout the nesting season, once every 1-2 weeks.

1) Depredated Nest Counts (1998 & 1999) – Islands found to support nesting terrapin populations were surveyed for depredated nests. On Ruler's Bar Hassock, counts were conducted daily throughout the nesting seasons in both 1998 and 1999. On the smaller

islands found to contain active nesting areas during the initial 1998 nesting area surveys (discussed above), counts were only conducted once each year, on a single day in 1998 and 1999.

I conducted surveys alone and with the aid of volunteers, depending on the size and vegetation coverage of a site. In areas where visibility was limited by dense vegetation, volunteers were required. When alone, I surveyed sites by walking parallel transects 1-2 m apart, traversing the entire site. When volunteers were used, we spread out, 2-3 m apart and walked parallel transects together, in unison. In smaller, more confined areas, it was not necessary to walk transects while searching for nests because the entire site could be covered by foot.

For a hole to be considered a depredated nest, it was necessary that it be accompanied by eggshell evidence (unless the nest had been marked and monitored prior to disturbance). Eggshell evidence was required to differentiate true terrapin nests from aborted terrapin digs and holes dug by other animals. Predators were identified to species where possible, through direct observation, tracks, nest scars, and/or scat.

In 1999, habitat type designations (based on the descriptions presented earlier in this section) were recorded for depredated nests on Ruler's Bar Hassock. After depredated nests were discovered and counted, the eggshell fragments were removed and the nest scar covered to prevent them from being re-counted in the future.

The data collected during the 1998 and 1999 nest counts were used to design Geographic Information System (GIS) maps of depredated nest distribution throughout Ruler's Bar Hassock. Initially, in 1998, I intended to create GIS maps using the eight study zones I had established. Later during that nesting season, I further subdivided the study zones into 41 "polygons" so the resulting maps could present the distribution of depredated nests with greater specificity, precision, and detail. These polygons were again delineated arbitrarily, in the same manner as the study zones, and their size

varied among each other. The habitat types and physical characteristics of the polygons varied within and among each other.

In 1999, I was unable to conduct the fieldwork necessary for creating a second year of the detailed polygon maps. Therefore, I reverted back to collecting data using the more general study-zone system, rather than the polygon system. To allow for comparisons of the distribution of depredated nests between years, maps of the 1998 data were also presented by study zone.

The 1999 polygon maps and the 1998 and 1999 study-zone maps presented information in two different formats. One format presented "count data," which was the actual number of depredated nests recorded in each area. The second format presented normalized "density data," which was obtained by calculating the average number of depredated nests per square meter. This was done to eliminate the bias caused by comparing regions of varying size. GIS maps were designed using the ESRI Arcview program, version 3.2. All GIS data were mapped in the field at JBWR using Trimble Global Positioning System (GPS) equipment.

2) Adult Predation (1998 & 1999) – The result of predation on adult terrapins was observed at JBWR. On Ruler's Bar Hassock, surveys of dead adults were conducted daily throughout the nesting seasons in 1998 and 1999. Surveys for dead adults were also conducted on the other four upland islands in the Bay in 1998, during the initial surveys of nesting areas (discussed above). In 1999, I only surveyed those islands with active nesting areas when I returned for the counts of depredated nests. The surveys on these smaller upland islands were only conducted once each season, on a single day in 1998 and 1999. Carcasses found during this study were inspected for cause of death. Sex was recorded as "unknown" when the carapace was less than 140 mm and severe decomposition had occurred.

3) Nest Mortality Rates at Ruler's Bar Hassock (1998 & 1999) – Freshly laid terrapin nests were marked and monitored daily, through the end of September, unless they were depredated or disturbed earlier. All monitored depredated nests were examined for predator spoor, uneaten eggs, and method of egg consumption by raccoons. If a marked nest was raided and no eggshell fragments were left behind, it was assumed that raccoons had completely consumed the eggs as reported by Burger (1977).

4) Survivorship Rates at Ruler's Bar Hassock (1999 only) – This part of the study was conducted to provide information on egg and hatchling survivorship from a sample of nests that were protected from predators. The results from this section, along with the results from the nest mortality section were used to estimate survivorship. Survivorship results are presented in two different ways: 1) "Overall," which represents survivorship among a sample that includes both successful and unsuccessful nests, and 2) "Among successful nests," which represents survivorship among a sample of successful nests only.

Predator excluder devices similar to those employed by Auger (1989) were used to prevent predation. Excluders consisted of fifty-centimeter-square sheets of one-quarter-inch hardware cloth. The excluders were buried approximately 2 cm below the ground, and kept in place with 200-mm metal stakes anchored at each corner.

Predator excluders were removed after 40 days, which was considered sufficient time to reduce detection by predators sufficiently. Excluders were also removed so that hatchlings were not trapped or obstructed as they emerged. On the same day that excluders were removed, the top layer of sand was removed from the nest chambers, and top eggs in each nest were checked for developmental characteristics such as

swelling and texture changes. The eggs were viewed without removing them, and the top layer of sand was replaced immediately thereafter. Nests were monitored weekly after removal of the excluders, through the end of September, for signs of hatchling emergence. On 27 September, nests were completely exhumed and inspected for live and dead hatchlings, undeveloped eggs, and eggs affected by plant roots. If hatchlings had emerged prior to 27 September, then their eggshells (which exhibited distinct post-hatching characteristics) were used to count successful hatching events. Non-emerged hatchlings were removed from the nest chamber, measured, and then released into the nearest adjacent marsh.

All hatchlings that were recovered from successfully protected nests were measured for straight-line carapace and plastron length and width with a plastic ruler. Carapace length was measured from the anterior center of the nuchal scute to the juncture of the rear marginals. Carapace width was measured across the widest part of the carapace. Plastron length was measured from the anterior juncture of the gular scutes to the posterior juncture of the anal scutes. Plastron width was measured between the junctures of the left and right pectoral and humeral scutes.

One additional nest was incubated indoors and hatchlings were released within 48 h of hatching. These eggs were incubated in sand taken from the original nest to simulate the natural substrate condition, and kept in a plastic container that was partially submerged in water, at approximately 27°C. The sand was moistened every 3-5 days.

5) Clutch and Nesting Data from Ruler's Bar Hassock (1998 & 1999) – Female terrapins captured on land were uniquely marked in 1999 using the shell-notching method of Cagle (1939). Triangular files were used to notch marginal scutes to a depth of

approximately 8 mm. Notch marks enabled recaptured turtles to be identified, and were used in this study to discover if females at JBWR lay multiple clutches. Information such as behavior, the location, and time of capture was also recorded for all captured female terrapins. Those that were observed laying nests were recorded as “nesters,” and those that were found on land not nesting, were recorded as “disturbed.” If females were found to lay more than one clutch per season, their nest location information would be used to assess nest site fidelity.

Because I intended to ascertain “natural” predation rates, freshly laid nests were not unearthed as a means for calculating clutch size. Most data used to estimate mean clutch size came from counting the eggshells found around depredated nests. The only time that clutch size measurements were taken from intact, non-depredated nests was when the successfully protected nests used in survivorship rate calculations were opened, on 27 September. Clutch-size data from nests in 1998 were combined with the data from 1999 to calculate mean clutch size.

Temporal data, such as mean time of nesting events, hourly nesting levels, earliest and latest nesting dates, and time between nesting and predation for individual nests were recorded in 1999. To avoid sampling biases in this study, appropriate temporal observations are presented in standardized indices, such as the one used by Seigel (1979). Index values are calculated by dividing the number of turtles observed in a unit time by the total observer-hours during that time period. Non-indexed, hourly capture data are also presented for reference. The time of capture of each female terrapin was compared to tidal and temperature data to determine whether or not either or both of the two environmental factors influence nesting activity levels at JBWR.

6) Measurements of Female Terrapins at Ruler’s Bar Hassock (1999 only) – The straight-line plastron length of captured females was measured using a one-meter tape

measure. Plastron length was measured from the anterior juncture of the gular scutes to the posterior juncture of the anal scutes. Growth rings or “annuli” were counted from the most prominent carapacial scute and used to approximate the age of females.

7) Environmental Data (1999 only) – Climatic data such as air temperature and cloud cover were obtained from the National Climatic Data Center weather station at John F. Kennedy International Airport. Salinity and water temperature data were obtained from the NPS 1998 Water Quality Sampling Program (Ringenary 1998). These data come from weekly measurements that were made from 1 June-27 July 1998, in the Beach Channel section of Jamaica Bay. The NPS also provided information on tidal activity in Jamaica Bay.

* All results concluded in this paper are presented \pm 1 standard deviation and statistical tests are two-tailed unless otherwise stated.

RESULTS

Nesting Areas

Fourteen different areas in Gateway NRA were surveyed for *M. terrapin* nesting activity (figures 1,2,3). Evidence of terrapin nesting activity was found at two of the four locations reported to support viable populations in 1989 by Cook (1989b). A third, previously unreported terrapin population was found on Little Egg Island (Figure 3, Table 2). Nesting activity was only observed on two islands at JBWR: Ruler's Bar Hassock and Little Egg Island.

Nest Predation and Ecology

Counts of Depredated Nests – The combined total of depredated nests counted on Ruler's Bar Hassock and Little Egg Island was 1,319 in 1998, and 1,840 in 1999 (Table 3). The majority of depredated nests, 1,303 in 1998 and 1,822 in 1999, were found at Ruler's Bar Hassock, whereas only 16 nests in 1998 and 18 nests in 1999 were found on Little Egg Island.

At Ruler's Bar Hassock, raccoons appeared to be the primary nest predator based on tracks, scat, nest scars, eggshell evidence, and direct observation. I did not observe evidence of predation by any other mammalian or avian predators at Ruler's Bar Hassock. The vast majority of predation events were discovered post facto, but

raccoons were observed depredating nests on at least three different occasions, each between 1800 and 0600 h. During these occasions, as many as six raccoons were observed per night, usually in small groups of two to three individuals.

I also observed one incident of partial nest predation by plant roots. Two plant species were growing within approximately 30 cm of the nest, but I could not determine which, if either, of the species' roots contributed to predation of the eggs. Seven of nine eggs were penetrated, shriveled, and desiccated, possibly as a result of the roots absorbing the egg contents. The nearby plants were identified as tall wormwood (*Artemisia campestris caudata*), and bayberry (K. Krause, NPS, pers. comm.).

No nesting events were directly observed on Little Egg Island, and all nests there were located post facto. The evidence of nest predation on Little Egg Island was extremely different from what I observed at Ruler's Bar Hassock. Depredated nests were scattered about the island, and not concentrated near one another. In many cases, the top and middle eggs of nests were depredated, whereas the bottom eggs were intact, and the nest scars were different from ones left by raccoons at Ruler's Bar Hassock. Rats and mice may inhabit the island, but I did not observe any, nor did I find any evidence of their presence such as tracks or scat of small mammals around the nests.

Habitat Use and GIS Analysis – The habitats surrounding 1,459 depredated nests on Ruler's Bar Hassock were categorized in 1999, using the habitat classifications in the "Methods and Materials" section. Data from the dune and mixed-grassland habitat

types were combined because of difficulties in differentiating between the two habitat types in the field (Table 4, Figure 5).

GIS maps of the distribution of depredated nests at Ruler's Bar Hassock were prepared to show island-wide predation (figures 6a, 7a, 8a, 9a, 10a, 11a). Enlarged maps of the principal nesting areas are also presented with maps of the entire island, for greater detail (figures 6b, 7b, 8b, 9b, 10b, 11b).

1998 GIS Data (Polygons) – Count-data maps indicate that the greatest number of depredated nests ($n = 238$) was found in the large polygon adjacent to the terrapin trail, on the inland side (figures 6 a, b). This polygon is dominated by mixed-grassland and shrub-land habitats. Density-data maps indicate that the polygon with the highest relative density of depredated nests was the one that represented the terrapin trail (figures 7a, b).

1998 and 1999 GIS Data (Zones) – The 1998 count-data maps indicate that zone B had the greatest number of actual depredated nests (figures 8a, b). This zone contains both extensive grasslands and the terrapin trail. However, the density-data maps show that the relative nest densities were highest in zone E, which represented the western beach of Ruler's Bar Hassock (figures 9a, b).

Distributions of depredated nests in 1999 were extremely similar to distributions in 1998, aside from a few subtle differences. The 1999 count-data maps showed increased nesting in zone F, along the beach (figures 10a, b). The 1999 density-data

maps showed decreased nest density in zone A and increased nest densities in zones B and E (figures 11a, b).

Adult Predation – When bodies of dead adult terrapins were found ($n = 31$), they were visually inspected for cause of death (Table 5). Although I never observed predation on adult turtles directly, raccoons were presumed to have killed those terrapins that were found with severed rear limbs, punctured body cavities, and evisceration adjacent to the hindquarters, as seen in a Florida population (Seigel 1980a). Dead terrapins did not necessarily die in the year they were found. The shells of seven dead terrapins found between 1998 and 1999 were so weathered and decomposed that it was impossible to estimate when they had died. The most common cause of death among adult terrapins during this study was determined to be raccoon attack, based on the conditions described by Seigel (1980a). Turtles counted in the “possible raccoon attack” category were too severely decomposed to confirm raccoon attack, but evidence such as location (found in upland nesting areas) and physical condition (i.e. upside down) were indicative of raccoon attack during nesting. Three dead terrapins were found in non-nesting areas of JBWR other than Ruler’s Bar Hassock and Little Egg Marsh. The body cavities of these turtles were not punctured and limbs were not severed, indicating that they may have died of causes unrelated to predation, and subsequently washed ashore.

Nest Mortality Rates – A total of 81 unprotected nests were monitored from the time of oviposition, during the nesting seasons of 1998 ($n = 4$) and 1999 ($n = 77$). Predation accounted for the loss of all four nests in 1998. In 1999, predation accounted for the

loss of 92.2% of unprotected nests, whereas flooding accounted for the loss of 2.6% of nests (Table 6). Among the remaining non-predated nests ($n = 4$), nest survivorship was assumed to be 100% (see Survivorship Rates), but could not be confirmed because I was unable to determine egg survivorship and hatchling survivorship among these nests. This was due to the fact that I avoided marking their precise locations to deter predators from learning to associate flags with terrapin nests. The 1999 nest mortality results were used to estimate the overall number of nests oviposited at Ruler's Bar Hassock based on the following formula from Burger (1977):

$$N_2 = \frac{(N_1) (P_1)}{P_2}$$

P_1 = number of unprotected, depredated, marked nests (71)

P_2 = number of depredated nests on Ruler's Bar Hassock (1822)

N_1 = total unprotected marked nests (77)

N_2 = total number of unmarked nests on Ruler's Bar Hassock = 1976

Estimated Overall Number Nests at Ruler's Bar Hassock: **$N_1 + N_2 = 2053$**

Examination of the monitored depredated nests also yielded information on the consumption methods used by raccoons on terrapin eggs. I never found uneaten eggs in raccoon-depredated nests at Ruler's Bar Hassock. The results were more variable regarding the way terrapins dealt with eggs that they had eaten. There appeared to be a distinct mid-season shift in the way raccoons consumed eggs. During the first half of the nesting season (3 June-28 June), raccoons almost always left eggshells in conspicuous mounds within a few centimeters of the depredated nest. During the

second half of the nesting season (28 June-23 July), the eggs from many nests were completely consumed with little or no eggshell evidence left behind. This behavioral shift was quantified among all monitored depredated nests in 1999, including the 71 unprotected depredated nests and 2 protected depredated nests (Table 7). An additional unmonitored depredated nest was also included in this calculation. I originally found this nest by following the crawl trail left behind by a female, but I could not determine its exact location until I found it depredated the next day. There was significant difference in the way that nests were predated between the first half and the second half of the nesting season ($\chi^2 = 14.90$, d.f. = 1, $P = 0.00003$). Further evidence of a shift in raccoon egg consumption behavior comes from qualitative observations I made during the counts of depredated nests at Ruler's Bar Hassock in 1998 and 1999. An unusual and distinct change in the composition of raccoon scat occurred throughout Ruler's Bar Hassock in both years. In the beginning of the nesting season, raccoon scat was dark brown. Starting gradually in early July, I began to observe raccoon scat laden with visible quantities of terrapin eggshell fragments. By the end of the nesting season nearly all the raccoon scat I observed throughout the island appeared white and contained large quantities of eggshell fragments.

Survivorship Rates and Hatchling Data – Five nests were protected using predator excluders. All five nests were successfully protected during the entire time that the excluders were in place. Excluders were removed after 40 days so that hatchlings would not be trapped or obstructed as they emerged. Two nests were completely depredated after their excluders were removed, before hatching occurred, and could not

be used in egg and hatchling survivorship calculations (Table 6). One of these depredated nests contained the carcass of a dead hatchling, indicating that at least some developmental success had occurred, and that the nest contents were not completely consumed by the predator.

The three surviving protected nests were exhumed and inspected 70, 69, and 64 days after oviposition, on 27 September 1999. Each of these nests produced at least some hatchlings. All successful eggs had completely developed into hatchlings. Hatchling survivorship in these nests was 22% (2 hatchlings from 9 eggs), 46% (6 hatchlings from 13 eggs), and 85% (11 hatchlings from 13 eggs), respectively (Table 8). In the third nest, 12 hatchlings were produced, and egg survivorship was 93%, but one hatchling had died.

All hatchlings were still in the first and third nests at the time of exhumation, and they might have overwintered if undisturbed. The six hatchlings from the second nest had all emerged prior to exhumation. Only unsuccessful eggs and eggshells left behind by the emerged hatchlings were recovered from this nest. The plastrons and carapaces of the 13 viable hatchlings found in the first and third nests were measured, and results are presented in Table 9.

The terrapin nest that was incubated indoors had 39% hatchling survivorship ($n = 13$). Hatchlings emerged over a three-day period, 46 to 48 days after oviposition on the beach. Five eggs produced viable hatchlings, four eggs contained partially developed embryos, and the remaining four eggs were undeveloped. No significant difference in hatchling survivorship was found between the naturally incubated nests and the

artificially incubated nest ($\chi^2 = 0.42$, d.f. = 1, $P = 0.33$). Nevertheless, the artificially incubated nest was not used in calculations pertaining to natural survivorship.

The three surviving protected nests were located in different habitat types. The nest with the highest hatchling survivorship (85%) was located on the terrapin trail. The nest with the lowest hatchling survivorship (22%) was located in shrub land, and most of the eggs were penetrated by plant rootlets. The two viable hatchlings in this nest had slightly deformed shells and tails that may have resulted from developmental interference caused by the rootlets. The remaining nest (46% hatchling survivorship) was located directly on the beach, less than 2 m from the high tide line and was occasionally inundated by water during extreme high tide. Average egg survivorship among these successful nests was 57%. Because one hatchling was found dead, average hatchling survivorship among these nests (54%) was slightly lower (Table 8).

A key component in estimating island-wide egg and hatchling survivorship is hatching data from a sample of surviving nests. I applied the egg and hatchling survivorship results above to the data on unprotected monitored nests from the previous section to estimate island-wide survivorship (Table 10). Because at least some hatchlings were produced in all non-depredated protected nests as well as in the depredated nest containing the dead hatchling, the same rate of nesting success was assumed for the surviving unprotected nests. Therefore, out of 77 total were assumed to have produced at least some hatchlings.

The estimates of overall survivorship on Ruler's Bar Hassock were derived using observed nesting and predation data. The total number of eggs (22,378) was estimated by multiplying 2,053 (the total number of nests estimated at Ruler's Bar Hassock) by the

mean clutch size at Ruler's Bar Hassock (10.9 eggs/nest). An estimate of 107 successful nests island-wide was derived by calculating 5.2% of 2,053 total nests. Successful nests were estimated to contain 1,166 eggs by multiplying 107 nests by 10.9 eggs per nest. Overall egg survivorship and overall hatchling survivorship were estimated on Ruler's Bar Hassock, by calculating 57% and 54% of 1,166 eggs, respectively.

I did not record the exact number of incubation days for the three natural nests. Thus, incubation time was presented as the range of days between checking the eggs in the nest (29 August, the day the excluder panels were removed) and final exhumation (27 September).

Clutch and Nesting Data – Unique shell notches were made on 133 adult female terrapins in 1999. Six of these were recaptured later in the season, in the same nesting areas upon which they were originally captured (Table 11). These turtles apparently returned to land to lay second clutches. The mean number of days between the first and second date of capture was 17.5 ± 1.39 days (range = 15-19). No terrapins were captured three times.

There was no significant difference in mean clutch size calculated by counting depredated nest eggshells ($n = 42$) versus counting whole eggs in the nest ($n = 3$) (one-tailed $t = 0.56$, d.f. = 43, $P = 0.18$), so these data were combined. A one-tailed t-test was used because animals, waves, wind, and visitors all could have conceivably removed the eggshell evidence adjacent to the depredated nests, whereas underground nests were protected from these variables. The overall mean clutch size calculated

from nests in 1998 ($n = 30$) and 1999 ($n = 15$) was 10.9 ± 3.53 eggs per nest (range = 3-18) (Figure 12). It is worthwhile to mention that one depredated nest appeared to contain 29 eggs. The reliability of this number was treated with extreme caution due to the unusually high number of eggs. Because this nest was found after oviposition and depredation, it was possible that the 29 eggs may have actually been the combined remains of two adjacent nests. Therefore, the data from this nest were not included in calculations; however, I am fairly certain that the 29 eggs were from a single nest.

In 1999, terrapins at JBWR nested from 3 June to 23 July, a 51-day nesting season. The average time of nest completion, from start to finish (including digging, oviposition and covering of the nest), was 24.8 ± 6.94 min ($n = 28$, range = 13-47). The average nesting time for females discovered in progress, from discovery to finish, was 13.7 ± 7.36 min ($n = 40$, range = 2-28). The difference in mean nesting time between these two groups was significant based on a one-tailed t-test ($t = 6.37$, d.f. = 66, $P < 0.0001$).

Overall, the greatest number of terrapins captured per hour was between 1100-1200 h (Figure 13a). Based on an hourly activity index that corrects for monitoring effort, the probability of finding terrapins was greatest between 2000-2100 h (Figure 13b).

The greatest number of terrapins captured on a single day was 13 June 1999 (Figure 14a). Based on a daily season index that corrects for monitoring effort, three distinct activity peaks occurred during the 1999-nesting season. The earliest time I observed a nest at JBWR being oviposited was 0930 hours, and the latest nest, at 2115 hours.

The time between nesting and predation was recorded in one-day intervals, for 70 depredated nest (Figure 15). Seventy-one percent of predation occurred in the twenty-four-hour period immediately following oviposition. The greatest time between oviposition and depredation observed at Ruler's Bar Hassock was seven days.

There was a significant correlation between terrapin captures and high tide ($r = +0.75$, d.f. = 22, $P < 0.001$) (Figure 16a). There was also a significant correlation between terrapin captures and daily high temperature ($r = +0.72$, d.f. = 26, $P < 0.001$) (Figure 16b). The greatest difference between time of capture and daily high temperature was 7 h, as shown in Figure 16b.

During the nesting season, female terrapins usually congregated in the waters surrounding Ruler's Bar Hassock. During this time, I commonly observed groups of 5-15 females per day moving along the shorelines of zones E and F, intermittently stopping to observe the beach and adjacent land areas. The size and frequency of these groups decreased as the nesting season progressed. I usually observed terrapin groups within 2-3 hours of high tide, and they tended to occur more during the hours of the rising tide rather than the falling tide. Usually, 1-5 of these females eventually moved to the edge of the water and visually surveyed the beach. These terrapins frequently retreated into the water after surveying the beach, often repeating the cycle multiple times before actually making their final approach to land or returning to the Bay. All but one of the terrapins I observed acting this way entered the nesting area on gently sloping shoreline. One female climbed a steep rock jetty to get to a flat sand embankment approximately 3 m above the water.

Once on land, female terrapins immediately began to search for nesting sites. The roundtrip journey from the water to the nest and back again ranged from approximately 30 to 50 min, but one female searched for 120 min before nesting.

Nesting terrapins at JBWR facially probed the ground before selecting a nest site. Digging behavior often followed this. After digging, females would either complete the nest or abort it and move to a different location. Nests were aborted after varying levels of excavation effort, from slight surface scratches to completely excavated nest chambers. The mean number of these “test” digs, when observed, was 1.92 ± 1.91 digs ($n = 24$, range = 1-10) per terrapin. Nine terrapins that aborted their digs returned to the water without nesting.

An interesting behavior was observed among terrapins encountered in grassy areas. Upon approach by humans, females “hid” themselves under mats of dried grass, making them extremely difficult to find. These females, revealed only after intense probing, were found motionless under grass patches, often within a meter’s distance of where we began searching.

Measurements of Nesting Female Terrapins – There was no significant difference in plastron length between nesters and disturbed females ($d = 0.06$, d.f. = 122, $P > 0.05$); therefore, data from the two groups were combined. The mean plastron length of females at JBWR was 172.9 ± 8.63 mm ($n = 124$, range = 145-198). I added the plastron-length data from JBWR to data from New Jersey, South Carolina and Florida that Zimmerman (1992) compared, and performed an ANOVA similar to his. There was significant variation of plastron length after adding the JBWR data (One way ANOVA,

$F_{(3,494)} = 100.6$, $P < 0.05$). Pairwise comparisons were then performed between the four sites using a Dunn-Sidak test (Table 12). Mean plastron length was significantly larger at JBWR than at the other three sites.

The mean number of growth rings did not differ significantly between nesters and disturbed females ($t = 0.38$, d.f. = 58, $P = 0.70$), therefore data from the two groups were combined. The mean number of growth rings was 9.42 ± 1.46 ($n = 60$, range = 7-13).

Extensive variation in skin color, shell color, and patterning was common among captured females. Due to the uncertain origins of the population of terrapins in Jamaica Bay, the observed variation might indicate significant genetic diversity within the population. Several females with deformed shells were observed as well. One female terrapin was missing the anterior half of its plastron, and the anterior region of its carapace was warped. Two other females were found with fewer than normal scutes.

Environmental Data – Mean air temperature at time of capture was lower for nesters than for disturbed females ($t = 2.3$, d.f. = 101, $P = 0.03$). Mean air temperature at time of capture for nesters was 25.4 ± 3.15 °C (range = 19.4-35.0 °C). Mean air temperature at time of capture for disturbed females was 27.7 ± 4.71 °C (range = 20.6-35.0 °C). More terrapins were captured between 23.1-25.0 °C than between any other temperature interval (Figure 17).

The overall mean air temperature during the 1999 nesting season (3 June-23 July) was 23.5 ± 6.85 °C (range = 17.2-32.8). Seasonal mean water temperature and salinity were calculated from 1998 data, because 1999 data were not available. The

mean water temperature was 21.3 ± 2.91 °C (range = 16.8-26.0) and the mean salinity was 19.0 ± 1.06 parts per thousand (range = 17.3-20.5).

In this study, cloud cover was divided into five categories: clear (0-25%), partly sunny (25-50%), partly cloudy (50-75%), overcast (75-100%) and rain (100% with precipitation). There was a significant difference between the level of cloud cover in which nesting females and disturbed females were captured ($\chi^2 = 15.3$, d.f. = 2, $P = 0.0005$), and data for the two groups are presented separately. Only one nesting female was captured during “rain,” so her cloud cover category was combined with nesting females in the “overcast” category for analysis. Only one disturbed female was captured in the “clear” category, and she was combined with disturbed females captured in the “partly sunny” category for analysis. Disturbed female terrapins were captured most frequently in partly cloudy conditions (67%, Figure 18a), and nesting females were captured most frequently in partly sunny (37%) and partly cloudy (36%) conditions (Figure 18b).

As my assistants and I improved our terrapin stalking skills during the 1999 nesting season, the number of females that were disturbed decreased. By 1 July, capture of disturbed females ceased (figures 14a,b).

DISCUSSION

Nesting Areas

Nesting populations of terrapins were found at three locations in Gateway NRA: Sandy Hook, Ruler’s Bar Hassock and Little Egg Island. Floyd Bennett Field and Great

Kills Park do not appear to support nesting terrapin populations. I did not observe any evidence indicating terrapin nesting activity at either of these locales during this study. I thoroughly surveyed both sites in 1998, and Park Service officials provided additional monitoring during the study. Officials at Great Kills Park did report a single dead terrapin in 1999, but the body was discarded and no information on sex or cause of death was provided.

Floyd Bennett Field and Great Kills Park were considered to support “viable resident populations” in the 1980s by Cook (1989b). Floyd Bennett Field was considered to support a population based on occasional observations of nesting terrapins and hatchlings “over the years” (R. Cook, NPS, pers. comm.). Great Kills Park was considered to support a population based on records of nesting terrapins and hatchlings (R. Cook, NPS, pers. comm.). Although both sites contain upland nesting habitat (i.e. beaches, dunes, and grassland), the aquatic habitats may be insufficient for sustaining terrapin populations. Both sites lack ample *Spartina* marsh, and have been dredged, bulkheaded, filled, and developed to a state that seems unfavorable to terrapins.

Although terrapins have occasionally been observed and reported at Floyd Bennett Field and Great Kills Park, I do not believe that either site is capable of supporting an independent population of terrapins. Instead, I suspect that the terrapins observed at these sites were actually migrant individuals that came from populations located elsewhere. The hatchlings observed and reported at these sites may have hatched from nests laid by migrant females, or they may have hatched elsewhere and drifted in the water to these sites.

Depredated Nest Counts

Predation by raccoons is occurring at high levels at Ruler's Bar Hassock, yet the size of this raccoon population is still unknown. Size estimates of the raccoon population will be necessary for the development of management plans in the future. The number of depredated nests counted on this island increased significantly from 1,303 in 1998 to 1,822 in 1999, and this may indicate increasing levels of annual predation, and increasing numbers of raccoons. The results from the depredated nest counts are conservative. Hundreds of additional holes were found without eggshell evidence. Although it is likely that some of these holes were real terrapin nests, they were not counted because of the possibility that they resulted from other, non-predation causes such as aborted terrapin digs, raccoons, or other animals. Because 26% of nests monitored during the second half of the 1999 nesting season contained no eggshell evidence after depredation, it is likely that a portion of the uncounted holes were terrapin nests that had been consumed in this manner.

My data show that egg consumption methods used by raccoons vary during the nesting season. Although I do not have enough data to test this idea, I believe that in June, when a greater number of terrapins are nesting, raccoons have the luxury of eating the highly nutritious inner contents of the terrapin egg without consuming the shell. However, as the nesting season continues through July, egg availability decreases because fewer nests are being oviposited. Late in the nesting season, raccoons may become less selective and eat the eggs entirely.

There are other possible explanations for the decrease in eggshell evidence. Waves, wind, and erosion may remove evidence from depredated nests. Tampering and trampling by visitors certainly could have reduced or eliminated eggshell evidence near depredated nests on the trails. Predation by animals other than raccoons is another possibility, but seems unlikely. Although feral cats and dogs are occasionally seen at Ruler's Bar Hassock, there were no reports of predation on terrapin nests by these species, and I did not witness any such event. Red foxes have been extirpated throughout the Jamaica Bay/Breezy Point unit. Avian predation has never been observed or reported at Ruler's Bar Hassock, and may be limited by the constant daily flow of visitors during daylight hours, when avian predation typically occurs (Burger 1977). Rats and mice are common throughout JBWR, but very little is known about their interactions with terrapins and their nests. Based on the overall paucity of reports of rat and mouse predation on terrapin nests, it is unlikely these mammals pose a significant threat to terrapin nests.

Root predation may also be a source of significant nest mortality at JBWR. Beach grasses have shown the ability to obtain nutrients from terrapin nests (Stegmann et al. 1988). At JBWR, plant species such as tall wormwood, bayberry and beach grass may absorb nutrients from terrapin eggs. Because many depredated nests were found in dune, mixed-grassland, and shrub-land habitats with plants growing nearby, root predation may affect a significant percentage of nests not depredated by raccoons. It may be difficult to determine the true impact of root predation because of its inconspicuous nature. I suggest that further research into root predation be conducted

in nesting areas that are vegetated, using a larger sample of protected nests than were used in this study.

Habitat Use and GIS Analysis

My data indicate that shrub land, and the combined dune and mixed-grassland habitats contained the greatest overall number of depredated nests at Ruler's Bar Hassock (Figure 5). These habitats are sparsely vegetated, with plenty of available sunlight, similar to the habitat selections of nesting terrapins studied by Burger and Montevecchi (1975), Roosenburg (1992), and Zimmerman (1992).

The GIS maps used in this study present information on nest distributions in two distinct ways, "count data" and "density data." The results are quite different. GIS analysis of the count data showed that the most actual nests were oviposited in the large, sparsely vegetated shrub land and mixed-grassland habitats on the western side of Ruler's Bar Hassock. On the other hand, GIS analysis of density data showed that nest density was highest in small, narrow, non-vegetated habitats such as the terrapin trail and the beaches on the western side of Ruler's Bar Hassock. Density maps eliminate area biases, so that smaller areas (i.e. terrapin trail, beach) can be readily compared to larger ones (i.e. shrub land, grassland), regardless of the actual number of nests within. Valuable information can be gained from both types of maps, and the end results seem to indicate that terrapins at JBWR use multiple nesting habitats. A possible explanation for the higher overall nesting in sparsely vegetated habitats might be that these habitats simply cover more area than non-vegetated habitats.

The terrapin trail is a key nesting area and major corridor used by female terrapins in transit to the uplands of zone B. In addition to the high density of nests observed there, nests on the terrapin trail may also have increased hatchling survivorship. When considering hatchling survivorship from the three successful protected nests, the most successful nest (85% survivorship) was located on the terrapin trail. Although a sample size of three nests is far too small to draw conclusions, it is possible that survivorship varies by habitat. Roosenburg (1992) found that hatchling survivorship varied among habitats. I suggest further studies, with larger sample sizes, to see if survivorship varies among different habitats at JBWR.

In 1999, the four unprotected, monitored nests that survived were located in zone A, on or immediately adjacent to the main gravel trail. This was an unusual site for nesting because the substrate consisted of gravel that was continually compacted by the constant flow of visitors, making digging very difficult. Only 35 nests were observed within the gravel section of the main trail, yet all surviving nests were laid on or immediately adjacent to it. Scent-based hunting may have been difficult for raccoons on the main trail, due to the constant flow of park visitors. There were also two “errant” nests that park officials reported during this study, oviposited on the lawn of the JBWR Visitor Center. Unfortunately, I could not properly monitor these nests due to high levels of human activity. Roosenburg (1994) also observed nesting in similar “precarious” locations.

Roosenburg (1992) suggests that predation of terrapin nests might be density dependent. If this is the case, a possible drawback to high densities of nests in an area as narrow and confined as the terrapin trail or beach, is that concentrated nesting may

facilitate raccoon predation. On the other hand, terrapins that nest in areas of low nest density, such as the secondary and tertiary study zones, may experience less predation than reported in this study. Because I focused my efforts in areas of high nesting activity, I suggest that further investigation on predation rates be conducted in areas of lower overall nesting activity. Terrapins that select unusual nesting sites such as those laid on the main trail and Visitor Center lawn may also benefit from reduced predation due to the unpredictable, isolated nature of their nests. The extent to which this occurs at JBWR is unknown.

Further comparison and investigation of terrapin nesting ecology at Ruler's Bar Hassock and Little Egg Island is needed. Only 16 and 18 depredated nests were found on Little Egg Island in 1998 and 1999, respectively, far less than on Ruler's Bar Hassock. An explanation for the disparity between the number of nests counted on these two islands requires further investigation. Little Egg Island is substantially smaller than Ruler's Bar Hassock, but regardless of size, depredated nests were far less concentrated on Little Egg Island than in areas of comparable size and habitat on Ruler's Bar Hassock. Unfortunately, my research on Little Egg Island was limited. Because the nest detection techniques I used there were only suitable for finding depredated nests, I cannot estimate the total number of nests laid on Little Egg Island. If large numbers of nests are laid on Little Egg Island each year, then it might be a safe nesting haven compared to Ruler's Bar Hassock. Alternatively, if only a small number of nests are laid on Little Egg Island each year, then Ruler's Bar Hassock represents the main nesting area at JBWR. If this is the case, with the current predation situation in mind, the entire JBWR terrapin population may be in jeopardy.

Avian predators appeared to be the primary source of nest predation on Little Egg Island. This island is apparently too small and isolated to support raccoons, and they have not been observed there (R. Cook, D. Avrin, NPS, pers. comm.). Therefore, predation was likely the result of another species of predator. Because avian predators hunt visually and do not locate nests using scent (Harris 1980), it should be fairly easy to monitor unprotected nests on this island and to differentiate between avian predators that hunt visually and scent based mammalian predators.

The pattern of predation on Little Egg Island seems congruent to Burger's (1977) observations of gull predation. Little Egg Island hosts large breeding colonies of great black-backed gulls (*Larus marinus*) and herring gulls (*Larus argentatus*) (D. Riepe, NPS, pers. comm.). Fish crows (*Corvus ossifragus*) have also been reported on Little Egg Island but are far less common than gulls, and I did not observe any. Burger (1977) reported that gulls depredate nests diurnally and take only a portion of the eggs contained in each nest. This was the condition of most of the nests I found on Little Egg Island.

Adult Predation

Aside from the pressure placed on terrapin nests and hatchlings by raccoons, additional pressure on this terrapin population was caused by predation on adult turtles. The removal of adult females can have severe repercussions on a population's ability to persist, because reproductive adults are the source of recruitment. If the source of recruitment is removed, then a population will collapse. For example, an entire

population of terrapins in Florida vanished due to predation on adults (Seigel 1993). If the number of adult, female terrapins attacked by raccoons is increasing each year at Ruler's Bar Hassock, then the population may face an accelerated decline. However, it is important to note that the increased number of dead adults found at JBWR in 1999 relative to those found in 1998 does not necessarily indicate an actual increase between years. A substantial number of the turtles found in 1999 were old, and may have been dead for more than a year. An increase in volunteers, and improved search techniques in 1999, may have simply led to the discovery of dead adults that were present, but not seen in 1998.

Although the adult terrapin population at JBWR still appears to be large (Morreale 1992), an adult population decline might not be evident for years after a dramatic reduction in recruitment. For example, if recruitment of new terrapins (hatchlings) ceased, it would take years before enough adult females died to notice a drop in the population. If recruitment of new hatchlings has declined at JBWR as much as it appears in recent years, the noticeable effects on the overall population may not yet be evident.

Although raccoons were assumed to have killed adult terrapins found with broken limbs and puncture wounds, no actual predation on adults was observed. Conclusions of raccoon predation were based on Seigel's (1980a) description of terrapins killed by raccoons in Florida. Although the evidence almost certainly indicates raccoon attack, it is possible that the broken limbs and puncture wounds found on the dead terrapins were caused by scavenging raccoons that found terrapins already dead. Other possible scavengers at JBWR may have included gulls, crows, rats, and mice.

Nest Mortality and Survivorship

Studies of nest mortality and survivorship have been conducted at various locations throughout the range of the terrapin. Comparisons of results from such studies are presented along with data from this study (Table 10). The overall nest survivorship and overall egg survivorship results from Jamaica Bay are quite similar to the results from Roosenburg's (1992) research in Maryland. The Jamaica Bay and Maryland populations are the largest two populations presented in Table 10, and both seem to have experienced extremely low overall survivorship of nests and overall survivorship of eggs. However, egg survivorship and hatchling survivorship among successful nests at JBWR appear normal when compared to results from the other studies.

The results from this study show that predation accounted for the loss of 92.2% of unprotected, monitored nests, and also contributed to low overall survivorship rates for nests, eggs and hatchlings. Roosenburg (1992) suggested that nests oviposited within the first ten days of the nesting season may have a survival advantage resulting from the "lag time" predators experience at the start of a new nesting season. If this occurs on Ruler's Bar Hassock, then nests that are not detected by predators would also go undetected by researchers that rely on evidence of depredated nests as well. If early-season nests such as these were missed in this study, then the overall survivorship rates of nests, eggs and hatchlings may be greater than reported. Therefore, in future studies at JBWR, I suggest that researchers search beaches for the crawl marks left behind by nesting terrapins and also search for nesting females.

Starting the field season early, by 15 May, should permit researchers to locate the first terrapin nests laid in the new nesting season with greater certainty. This will enable the researchers to determine if a seasonal nesting advantage occurs at JBWR.

In 1999, nests laid within what was assumed to be the first ten days of the nesting season on Ruler's Bar Hassock were predated ($n = 9$) or flooded ($n = 1$). Although this may indicate that there is no advantage to nesting early in the season at JBWR, the nesting season may have started earlier than 3 June (when I observed the first nesting female and depredated nest), and resulting nests may have had an undetected advantage.

In addition to suggesting an earlier start to future field seasons, I also suggest further investigation of mortality and survivorship of nests throughout the nesting season. In future studies it will be important to obtain data on hatchling survivorship from unprotected, monitored nests in addition to protected nests. Unprotected nests should be marked and monitored with greater precision than the method I employed using triangulated flags. Although triangulating flags around nests may have prevented a raccoon learning bias, this practice ultimately compromised access to the surviving unprotected nests later in the season for survivorship analysis. I suggest the use of a single inconspicuous marker such as a piece of metal-hanger wire, directly above the nest to solve this problem.

Survivorship varied dramatically among the protected nests in this study, but the sample size was too small ($n = 3$) to assess differences statistically among habitats. Habitat type and nest location may have also affected hatchling behavior. Two nests contained all their hatchlings when exhumed in the fall, whereas the hatchlings from the

third nest had all emerged and left the nest. The nest from which hatchlings had emerged was located directly on a sandy beach, and was exposed to sunlight for the greatest amount of time per day. Therefore, development of eggs inside this nest may have been accelerated by higher temperature. The two nests from which hatchlings had not emerged were located in areas where the daily amount of sunlight was less, due to the surrounding vegetation. In future studies, measurement of underground nest temperatures may elucidate the cause of this variation in post-hatchling behavior. A larger sample of nests, from all habitat types, should also be protected with raccoon-excluder devices to compare hatchling survivorship and behavior accurately among habitats.

Hatchlings in the three successful protected nests all hatched within 70 days of oviposition. This is a substantially shorter developmental time than reported from other sites in the region. Cook (1989a) reported that the mean incubation time for terrapin eggs in Jamaica Bay was 81 days. In New Jersey, Burger (1977) reported incubation between 61 and 104 days ($\bar{x} = 76$), and in Massachusetts, Auger and Giovannone (1979) reported an incubation period of 87 to 148 days ($\bar{x} = 108$).

When comparing the results of regional studies on nest incubation, it is important to consider the small sample size used in my study, and the biases that may have resulted. It should also be noted that nests in my study were unearthed, whereas Cook (1989a) and Auger and Giovannone (1979) allowed hatchlings to emerge by themselves, presumably increasing the incubation period. Yearly variation in incubation temperatures and habitat characteristics also may have led to accelerated development of nests in this study.

Clutch and Nesting Data

Double clutching occurs at JBWR. Only one terrapin was actually observed to nest twice, yet I assume that all six recaptured females nested on or near both dates of capture. This assumption is based on the mean 17-day (range = 15-19) interval between recaptures at JBWR. In Rye, New York, terrapins double clutched on 17-day intervals (Klemens 1993). Therefore, based on the interval of recaptures, it is likely that all six terrapins double clutched. Additional support of this assumption comes from the fact that the six terrapins were captured in upland habitats. Use of upland habitats by terrapins is apparently restricted to nesting (Palmer and Cordes 1988). Observations of terrapins leaving their aquatic habitats to bask on mud flats have been reported (Ernst et al. 1994), but there are no reports, of which I am aware, of female terrapins traversing significant distances in upland habitats for non-nesting purposes. Auger and Giovannone (1979) reported that female terrapins made “non-nesting journeys” onto the beach, but also reported that these females were disturbed by “commotion”, which seems to indicate that the females intended to nest before they were disturbed. As the number of females receiving shell notch identifications at JBWR increases, it will become easier to determine the extent of multiple clutching in Jamaica Bay.

Zimmerman (1992) discussed clinal variation among terrapins and nesting ecology. The mean clutch size and hatchling plastral length measured at Ruler's Bar Hassock both seem to fit into the northern clinal scheme (Table 13). Surprisingly, the length of nesting season did not fit into the clinal scheme proposed by Zimmerman (1992). The 51-day nesting season at JBWR was substantially longer than the 34-to

44-day nesting seasons reported by Burger (1977) in New Jersey. The nesting season at JBWR was similar to the 52-to 57-day nesting season reported by Seigel (1980b). It is possible that this discrepancy was caused by yearly temperature fluctuations.

The annual index of nesting activity (Figure 14b) shows three seasonal activity peaks. These activity peaks may represent three pulses of nesting. Because the time intervals between peaks are 17-20 days apart, these peaks might represent multiple-clutch trends throughout the population. Because there are three peaks rather than two, terrapins at JBWR may in fact triple clutch, although triple clutching has only been reported as far north as Maryland (Roosenburg 1992). There is also the possibility that the three activity peaks represent two different groups of double-clutching females, or one group of single-clutching females and one group of double-clutching females.

The six recaptured terrapins in this study were found on the same beach where they had originally been found earlier in the season. Due to the small sample size ($n = 6$), conclusions of nest site fidelity should be discussed with caution. If terrapins indeed return to the same nesting area repeatedly, they may be under exceptionally high risk of predation. Consistently returning to nesting sites that are heavily patrolled by raccoons could drastically reduce the success of such terrapins, and all subsequent nests would be threatened. On the other hand, if terrapins vary their nest sites without any coordinated fidelity, then individual terrapins might lay successful nests from time to time, if they occasionally nest in areas of low predation.

The highest level of nesting activity occurred on 13 June 1999. This event was truly noteworthy because nesting terrapins came on land constantly throughout the day, even at low tide. This intense burst of activity appears to have started a day earlier on

12 June, and peaked on 13 June. Both days were characterized by periods of rain, high humidity, and overcast skies. The increase in activity may have been a response to below normal temperatures on 11 June, the coldest day during the 1999-nesting season.

The greatest numbers of nesting terrapins were observed between 1100-1200 hours. The results from the hourly index of terrapin activity showed that the greatest number of terrapins captured per unit time occurred during the interval of 2000-2100 hours. Although the probability of finding terrapins was greatest between 2000-2100 hours, based on the results of the hourly activity index, only four terrapins were actually captured during that time interval.

The step-by-step nesting behaviors of terrapins at JBWR are similar to those reported by Burger (1977). Although general nesting behaviors such as digging technique and the sequence of digging events do not seem to vary among terrapin populations, specific behavior such as the duration of nesting events, facial probing of the ground, and test digging do vary among populations (Auger and Giovannone 1979; Roosenburg 1994). The "hiding" behavior of females encountered in the mixed-grasslands of Ruler's Bar Hassock is a previously unreported behavior that might be a defensive response to sight-based predators.

One of the biggest problems I faced in studying terrapins was the effect that assistants and I had on the females we encountered. We undoubtedly disturbed and altered the behavior of terrapins at times during this project. It was nearly impossible to avoid such problems when conducting this research, and it is important to mention other situations in which human disturbance may have influenced certain results.

The loss of two protected nests in the survivorship study was likely caused by human disturbance. After being protected for 40 days, I removed the excluders and checked the nests underground for progress. Burger (1977) examined the progress of developing nests daily by digging into the nest, without increased predation. Thus, I unearthed the first two nests in a manner similar to Burger. After considering the higher level of nest predation on Ruler's Bar Hassock relative to predation at Burger's study site, I took greater care with the remaining three nests. The first two nests were later depredated, and the remaining three were not, leading me to believe that the predator detected my scent and/or the scent of the eggs in the disturbed soil. A similar situation occurred with one unprotected, monitored nest that was located adjacent to the terrapin trail in shrub-land habitat. The nest was discovered and marked by my assistants. After six days, I was surprised that a nest located in an area of high predation had not been depredated. As a result, I removed the top layer of sand above the nest to confirm that my assistants had accurately located the nest. Upon removal of the top layer of sand, I found the nest intact, and then covered it back up. When I returned a day later to monitor the nest, it had been depredated, probably as a result of my scent and/or the scent of the eggs. Because this nest had survived undetected by raccoons for six days, I presume that if it had not been disturbed, it would have survived and represented the only non-predated, unprotected nest monitored in Zone B.

Human disturbance also may have influenced the duration of nesting events and the number of aborted nests that terrapins were observed to have dug. It is likely that female terrapins were cautious and nested at a slower pace when they detected human observers. One terrapin that took two hours to select a site before nesting (see Results)

may have simply taken longer because it was threatened by the observer. Although we tried to remain as inconspicuous as possible, terrapins often detected our presence. Human disturbance may have led to an increase in the number of nests that female terrapins aborted. In nine such cases, females actually abandoned their efforts altogether, without nesting, and returned to the water. Many additional terrapins were disturbed and fled to the water when we accidentally surprised them while walking along the winding trails.

The use of elevated observation decks with blinds might reduce disturbance of nesting females, while enabling researchers to locate nests and capture females only after their nesting is complete. Burger (1977) and Roosenburg (1992) located nests after oviposition, by recognizing cover-up patterns above the nests. I was unable to take advantage of this technique at JBWR because the crawl trails created by nesting females could only be followed for a short distance from the shoreline. Once terrapins entered vegetated areas (which was usually the case at Ruler's Bar Hassock) the crawl trails became impossible to follow.

It is still unknown whether or not night nesting occurs at JBWR. Because nighttime observations are difficult and tedious, I suggest implementing a method used by Roosenburg (1992) in the future. He raked the beaches that terrapins used to approach nesting areas at the end of the field day, and checked for terrapin crawl marks the following morning. Although this might not enable researchers to locate nests precisely at JBWR, it would at least provide the necessary evidence to determine if nocturnal nesting occurs.

Characteristics of Nesting Female Terrapins

Considerable variation in skin color, shell color, and patterning was observed among female terrapins captured during this study. Such phenotypic variation is commonly reported from populations throughout the species' range, yet, without any standardized way of defining variation, it is difficult to compare populations. I suggest the genetic makeup of New York terrapins be compared to terrapins from other parts of their range, to determine their genetic diversity and relatedness. I also suggest the development of a standardized system for categorizing the different patterns and colors often reported within and among terrapin populations. This might allow researchers to obtain a greater understanding of the causes of such variation, and allow them to determine the extent to which terrapin variation differs within and among different populations and subspecies.

The age of terrapins at JBWR was estimated by counting annuli. Age estimates made using this method should be taken with extreme caution, because as shell length increased, annuli appeared to become smoother, and subsequently less countable at JBWR. Therefore, if this is the case, then the annuli of larger, presumably older terrapins cannot be counted, and older turtles will be left out, leading to inaccurate age estimates.

The mean plastron length of adult, female terrapins at JBWR was 15-18 mm larger than that of female terrapins in New Jersey, South Carolina or Florida. Zimmerman (1992) found that the plastron lengths of adult females did not vary on a latitudinal basis. Therefore, one would expect that this discrepancy might be the result of differences in measurement technique or measurement error, but the difference is so

large (15-18 mm greater than other populations) as to make these explanations implausible. It appears then, that female terrapins at JBWR are larger, on average, than females at these other populations. This may be associated with the high levels of nest predation occurring at JBWR. If recruitment of new terrapins has decreased significantly as a result of predation, then adult females at JBWR may be older and larger than females in populations with less nest predation and consistent recruitment of younger nesting females. Assuming that the high levels of raccoon predation at JBWR started within the last 10 years, and that the minimum age of first reproduction for female terrapins is 8 years (based on terrapins in Maryland, [Roosenburg 1991]), then a reduction in recruitment should be noticeable by now. This might explain why adult, female terrapins at JBWR appear to be larger than terrapins from other populations.

Environmental Factors

Terrapin nesting activity at JBWR is influenced by tidal activity and air temperature. The number of observed terrapins was greatest when high tide and daily high temperatures coincided. Terrapins did not nest when air temperature exceeded 35°C. In Florida, the maximum observed air temperature during nesting was 36°C (Seigel 1979). Thus, nesting activity appears to cease when air temperatures exceed a threshold of 35-36 °C, regardless of climate or latitude. Although this threshold appears to be extremely similar in New York and Florida, terrapins at JBWR nested at a mean air temperature nearly 6°C less than terrapins studied by Seigel (1979) in Florida.

On average, disturbed terrapins were encountered more commonly during periods of higher temperature and greater cloud cover than nesters. Cloud cover and

air temperature may influence the level of disturbance tolerated by nesting terrapins at JBWR, but the cloud cover results pertaining to disturbed terrapins may have been biased by the tremendous influx of female terrapins on 13 June 1999 (Figure 14a). All disturbed terrapins captured on that day ($n = 37$) were located during partly cloudy skies. Because the 37 females captured on 13 June represent 63% of all disturbed females captured during the season ($n = 59$), they may have skewed the overall results for disturbed terrapins towards partly cloudy conditions.

It does not appear that data on air temperature for disturbed terrapins were influenced by the terrapin influx on 13 June. Although air temperature on 13 June averaged 25.3°C among disturbed captures, the air temperature throughout the season averaged 27.7°C among disturbed captures, a difference of 2°C.

The seasonal mean air temperature, water temperature, and salinity data provided in this paper are meant to give an approximation of the general environmental conditions experienced during a typical nesting season by terrapins living in Jamaica Bay, New York. These data should not be used in specific analyses of the results from 1999. It is also important to use caution when comparing disturbed females and nesters. As my assistants and I became more skilled at tracking female terrapins, the number of “disturbed” terrapins quickly declined, and after 30 June 1999, all captured terrapins were nesters. Therefore the two groups were not equally represented throughout the season.

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Table 1 – Area and monitoring level of the eight zones on Ruler’s Bar Hassock. Primary zones were monitored consistently throughout each day of the nesting season. Secondary zones were monitored daily, but not consistently. Tertiary zones were monitored sporadically throughout the nesting season (once every 1-2 weeks).

Zone	Area (m²)	Monitoring Intensity
A	20,357	Secondary
B	44,152	Primary
C	15,581	Secondary
D	77,993	Tertiary
E	4,937	Primary
F	2,126	Primary
G	6,005	Tertiary
H	49,807	Tertiary

Table 2 – Results of park-wide surveys of nesting beaches. Fourteen sites were surveyed for nesting activity. These results are compared to results from 1989.

SHU = Sandy Hook unit. SIU = Staten Island unit. JB/BPU = Jamaica

Bay/Breezy Point unit. YES = terrapin populations present. NO = terrapin populations not found at site.

Site Number	Site	Cook (1989b)	Feinberg (this study)
1	Sandy Hook (SHU)	YES	YES
2	Great Kills Park (SIU)	YES	NO
3	Miller Field (SIU)	NO	NO
4	Breezy Point Tip (JB/BPU)	NO	NO
5	Dead Horse Bay (JB/BPU)	NO	NO
6	Floyd Bennett Field (JB/BPU)	YES	NO
7	Bergen Beach (JB/BPU)	NO	NO
8	Canarsie Pier Area (JB/BPU)	NO	NO
9	Spring Creek (JB/BPU)	NO	NO
10	Canarsie Pol (JB/BPU)	NO	NO
11	Ruffle Bar (JB/BPU)	NO	NO
12	Little Egg Island (JB/BPU)	NO	YES
13	Subway Island (JB/BPU)	NO	NO
14	Ruler's Bar Hassock (JB/BPU)	YES	YES

Table 3 – Results from depredated nest counts. Totals from both 1998 and 1999 are given for the Ruler's Bar Hassock zones and Little Egg Island.

ZONE	1998 NEST NUMBERS	1999 NEST NUMBERS
A	248	179
B	437	808
C	224	198
D	110	194
E	50	67
F	46	145
G	62	55
H	126	151
Additional nests found outside of zones	0	25
RULER'S BAR TOTAL	1,303	1,822
LITTLE EGG ISLAND	16	18
JBWR TOTAL	1,319	1,840

Table 4 – Number of depredated nests by habitat type at JBWR ($n = 1,459$). Numbers are presented for individual study areas and refuge-wide totals. (g) = gravel substrate on trail. (s) = sand or dirt substrate on trail.

HABITAT TYPE	ZONE A	ZONE B	ZONE C	ZONE D	ZONE E	ZONE F	ZONE G	ZONE H	Additional Nests	LITTLE EGG ISLAND	TOTAL
BEACH		3	1		34	87	4				129
DUNES/MIXED GRASSLAND	14	177	32	25	10	28	45	120		18	469
SHRUBLAND	110	195	68	89			6	9	8		485
WOODLAND			0								0
TERRAPIN TRAIL (SAND)		231	1					22			254
MAIN TRAIL (GRAVEL & SAND)	16(g)	1(g)	19(g)	69(s)					17(s)		122

Table 5 – Numbers and presumed cause of death for dead *M. terrapin* found during this study.

Condition/Cause of Death	Females	Males	Unknown Sex
Found in 1998			
Probable Raccoon Attack	6	0	0
Possible Raccoon Attack (partially decomposed)	2	0	1
Unknown/Natural Causes (good condition-no puncture wounds)	0	1	0
Dead on Road	1	0	0
Subtotal (1998)	9	1	1
Found in 1999			
Definite Raccoon Attack	11	0	0
Possible Raccoon Attack (partially decomposed)	4	0	3
Unknown/Natural Causes (good condition-no puncture wounds)	1	1	0
Dead on Road	0	0	0
Subtotal (1999)	16	1	3
Totals (1998+1999) <i>n</i> = 31	25	2	4

Table 6 – Results of nest monitoring on Ruler’s Bar Hassock. Unprotected nests were monitored in 1998 ($n = 4$) and 1999 ($n = 77$). This table also presents results from additional nests that were protected with predator excluder devices in 1999 ($n = 5$). Fractions in the 1999 protected-nest results represent partial nest survival.

Nest Status of Unprotected Nests ($n = 81$)	1998	Percent	1999	Percent
Depredated	4	100%	71	92.2%
Flooded	0	0	2	2.6%
Uneaten	0	0	4	5.2%
Destroyed Nests (Predation + Flooding)	4	100	73	94.8%
Unprotected Subtotal	4	100%	77	100%

Nest Status of Protected Nests ($n = 5$)	1998		1999	
Depredated	0		2	
Root Predation	0		0.8	
Uneaten	0		2.2	
Protected Subtotal	0		5	
TOTAL NESTS OBSERVED Protected + Unprotected (Destroyed Nests)	4		82	

Table 7 – Method of raccoon predation observed among sample of depredated nests in 1999 ($n = 74$)

Condition of Predated Nests (1999)	Before 1 July	% of Nests Consumed	After 1 July	% of Nests Consumed
Eggshells piled next to nests, as reported by Aresco (1996)	47		16	
Eggs completely consumed, as reported by Burger (1977)	1		10	
Totals	48	2.08%	26	38.5%

Table 8 – Survivorship among non-predated protected nests ($n = 3$). Incubation time is presented as the range of days between the last inspection of the pre-hatched eggs and final exhumation, when hatchlings were found. A = total hatchling percentage based on all hatchlings found in nest (live and dead). B = Successful hatchling percentage based on live hatchlings only. Results from the artificially incubated nest are also included. The column called “other” refers to eggs accidentally destroyed during inspection.

Nest	Habitat	Incubation Time	Total # Eggs	Root Predated Eggs	Undeveloped Eggs	Partially Developed Eggs	Dead Hatchlings	Other	Viable Hatchlings	% Success
1	Shrub Land	42-70 days	9	7	0	0	0	0	2	22
2	Beach	41-69 days	13	0	6	0	0	1	6	46
3	Terrapin Trail	36-64 days	13	0	1	0	1	0	11	85
SUB-TOTAL	Nests 1-3		35	7	7	0	1	1	19	A = 57% B = 54%
4	Indoors	46 to 48 days	13	0	4	4	0	0	5	39
TOTAL	Nests 1-4		48	7	11	4	1	1	24	A = 52% B = 50%

Table 9 – Measurements of hatchling terrapins, showing mean, range, and standard deviation. Hatchlings from two of the surviving protected nests ($n = 11, 2$) were measured.

Measurements	Range (mm)	Mean (mm)	Standard Deviation
Plastron Length	21.5 – 24	23.1	0.961
Plastron Width	14 – 17	15.7	0.947
Carapace Length	25 – 27	26.4	0.682
Carapace Width	20 – 25	23.4	1.277

Table 10 – Survivorship data from wild populations of *M. terrapin*. * = Estimated value based on reported mean clutch sizes. † = Estimated value based on 1999 nest monitoring data, mean clutch size, and predation observations.

Authority	Overall Nest Survivorship		Overall Survivorship			Survivorship Among Successful Nests		
	Total Nests	Successful Nests	Total Eggs	Egg Survivorship	Hatchling Survivorship	Total Eggs	Egg Survivorship	Hatchling Survivorship
UNPROTECTED NESTS								
Burger, 1977 (1973 Data)	37	31 (84%)	360	141 (39%)				
Burger, 1977 (1974 Data)	200	51 (25%)	1,746	307 (18%)				
Burger, 1976, 1977 (1974 Data)	100	36 (36%)	883	207 (23%)	157 (18%)	298	207 (70%)	157 (53%)
Auger & Giovannone, 1979	55		550*		85 (15%)			
Roosenburg, 1992	1,539	51 (3.3%)	20,007*	307 (1.5%)		652	307 (47%)	
PROTECTED NESTS								
Auger, 1989		10				141	123 (87%)	
Zimmerman, 1992		5				48	18 (38%)	15 (31%)
Feinberg, This Study (1999 Data)		3				35	20 (57%)	19 (54%)
JBWR POPULATION ESTIMATE								
Feinberg, This Study (1999 Data)	2,053†	107† (5.2%)	22,378†	665† (2.97% †)	630† (2.82% †)	1,166†	665† (57%)	630† (54%)

Table 11 – Female terrapins recaptured in 1999. All turtles were captured in uplands, away from the bay. The result of the encounter is presented. For turtles listed as “disturbed,” nesting was not observed.

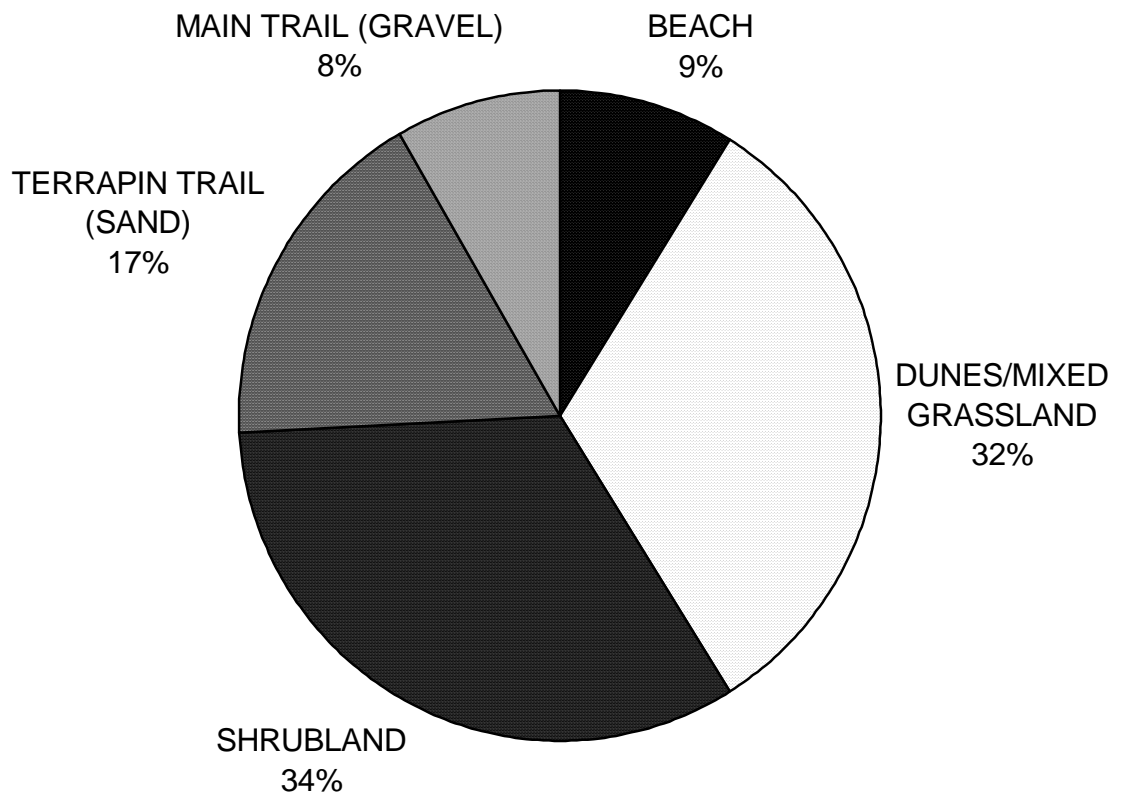
TERRAPIN IDENTIFICATION NUMBER	DATE OF FIRST CAPTURE	STATUS OF TERRAPIN CAPTURE	DATE OF SECOND CAPTURE	STATUS OF TERRAPIN CAPTURE
11R9L	6/12/99	Nesting Observed	6/30/99	Disturbed
12R1L2L	6/13/99	Disturbed	6/28/99	Disturbed
1R1L2L	6/13/99	Disturbed	7/1/99	Nesting Observed
1R10L	6/14/99	Nesting Observed	7/2/99	Nesting Observed
3R1L	6/13/99	Nesting Observed	6/30/99	Disturbed
8R10L	6/13/99	Disturbed	7/2/99	Nesting Observed

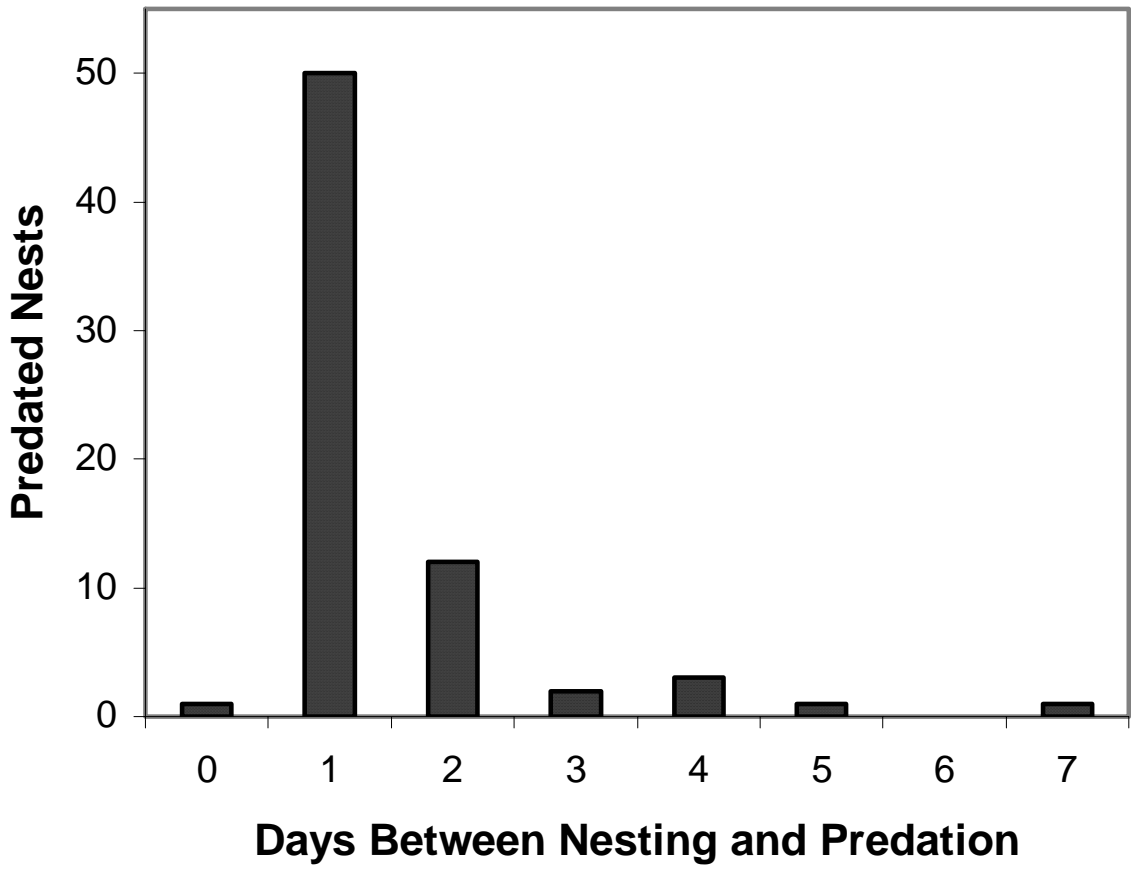
Table 12 – Dunn-Sidak comparison between plastral lengths of female terrapins from New York (this study), New Jersey (Montevecchi and Burger 1975), Florida (Seigel 1984), and South Carolina (Zimmerman 1992). The critical value based on $t_{0.0086,494}$ was 2.641. * = significantly different. NS = not significantly different. n = sample size. s = standard deviation.

Site Location	Mean Plastron Length (mm)	n	s	Calculated value of t	Significance
New York (NY)	172.9	124	8.6	NY vs. NJ = 16.09	$P < 0.001$ (*)
				NY vs. FL = 14.21	$P < 0.001$ (*)
New Jersey (NJ)	154.4	221	9.9	NY vs. SC = 8.55	$P < 0.001$ (*)
				NJ vs. FL = 0.34	$P > 0.50$ (NS)
Florida (FL)	154	113	10.0	NJ vs. SC = 1.48	$P > 0.10$ (NS)
				FL vs. SC = 1.60	$P > 0.10$ (NS)
South Carolina (SC)	157	40	12.1		

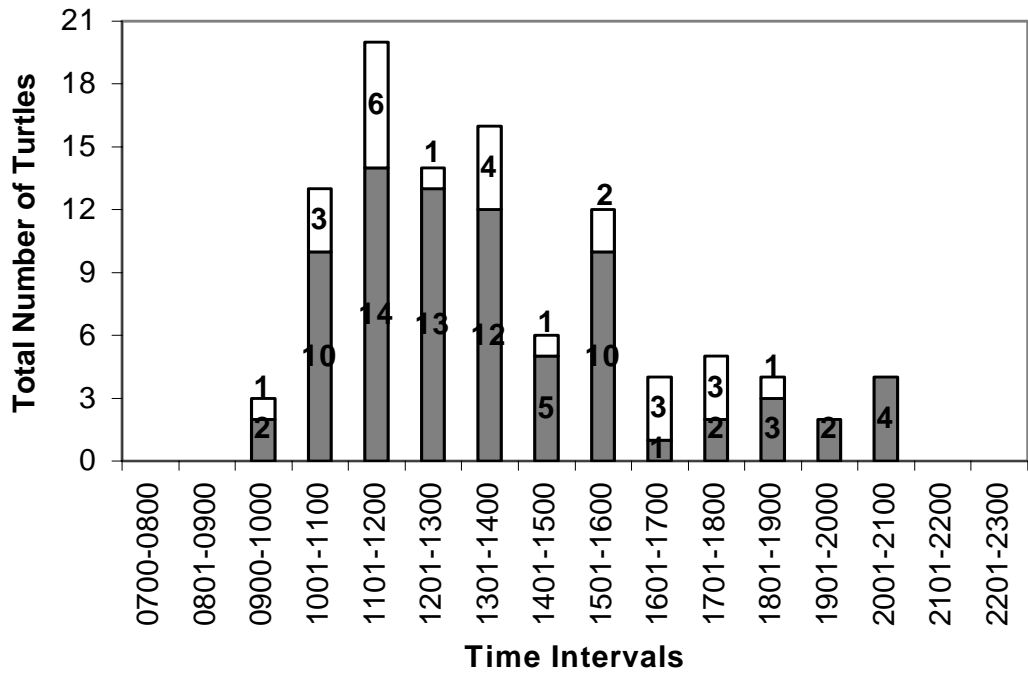
Table 13 – Mean lengths of hatchling plastrons and clutch sizes of *M. terrapin* populations in New York (this study), New Jersey (Burger 1977), South Carolina (Zimmerman 1992), and Florida (Seigel 1980b).

Location	Latitude	Mean Hatchling Plastron Length (mm)	Mean Clutch Size (eggs)
New York	40°37'N 73°50'W	23.1	10.9
New Jersey	39°29'N 74°21'W	24.4	9.2
South Carolina	32°35'N 80°08'W	28.3	6.9
Florida	28°35'N 80°40'W	27.9	6.7

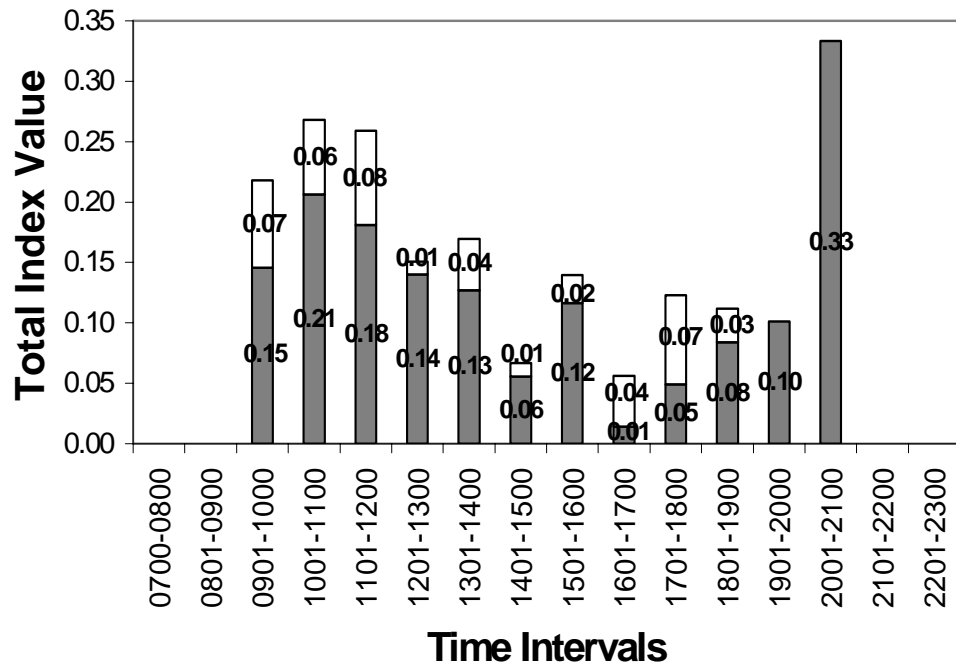




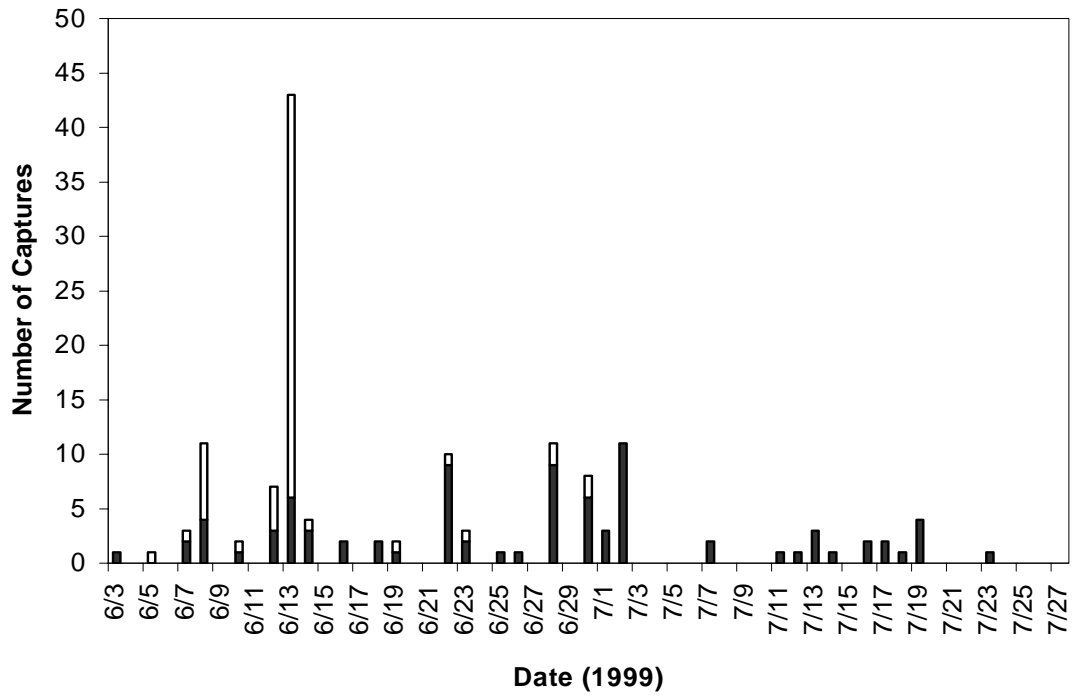
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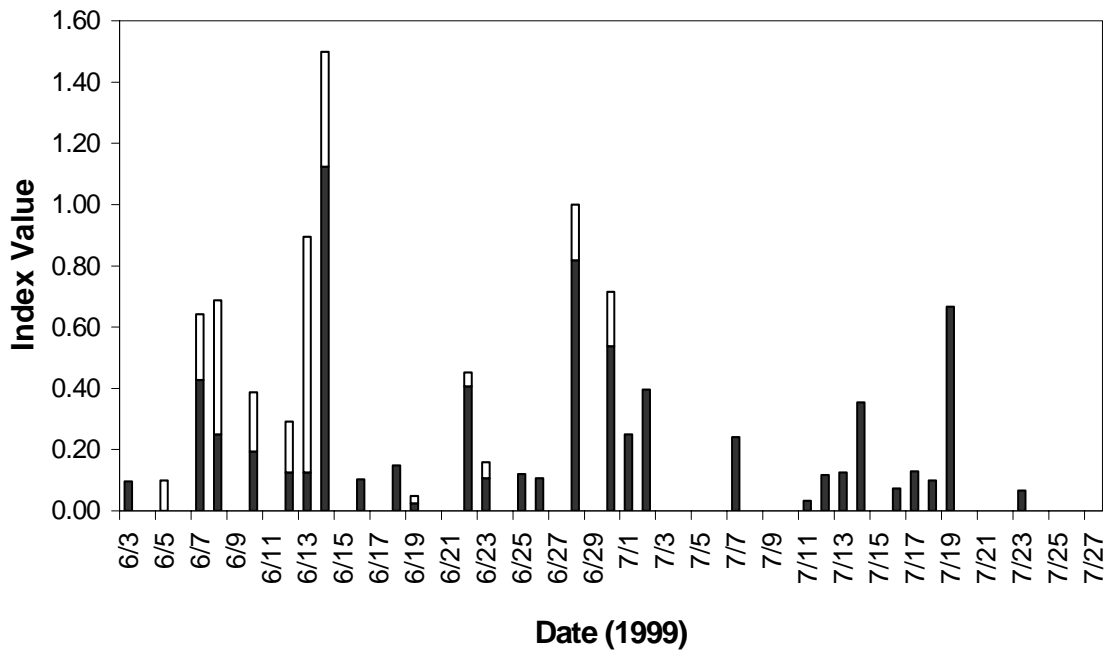
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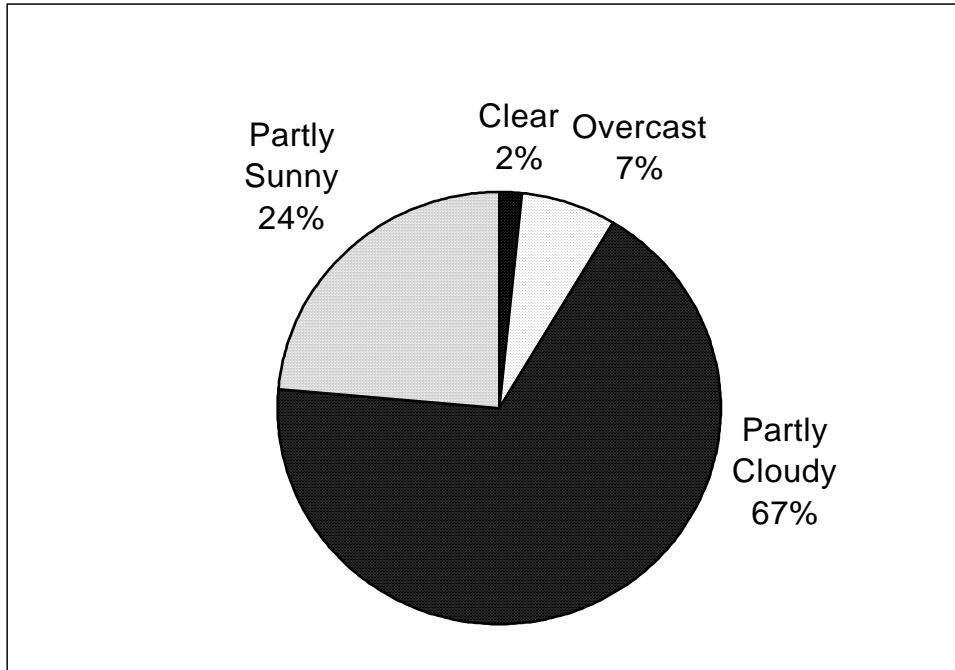
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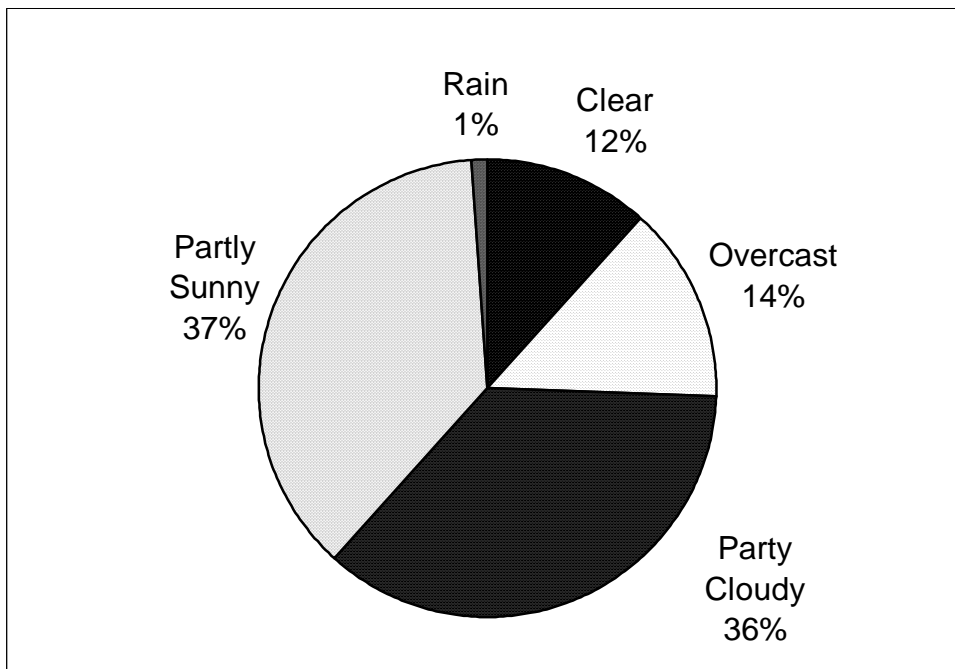
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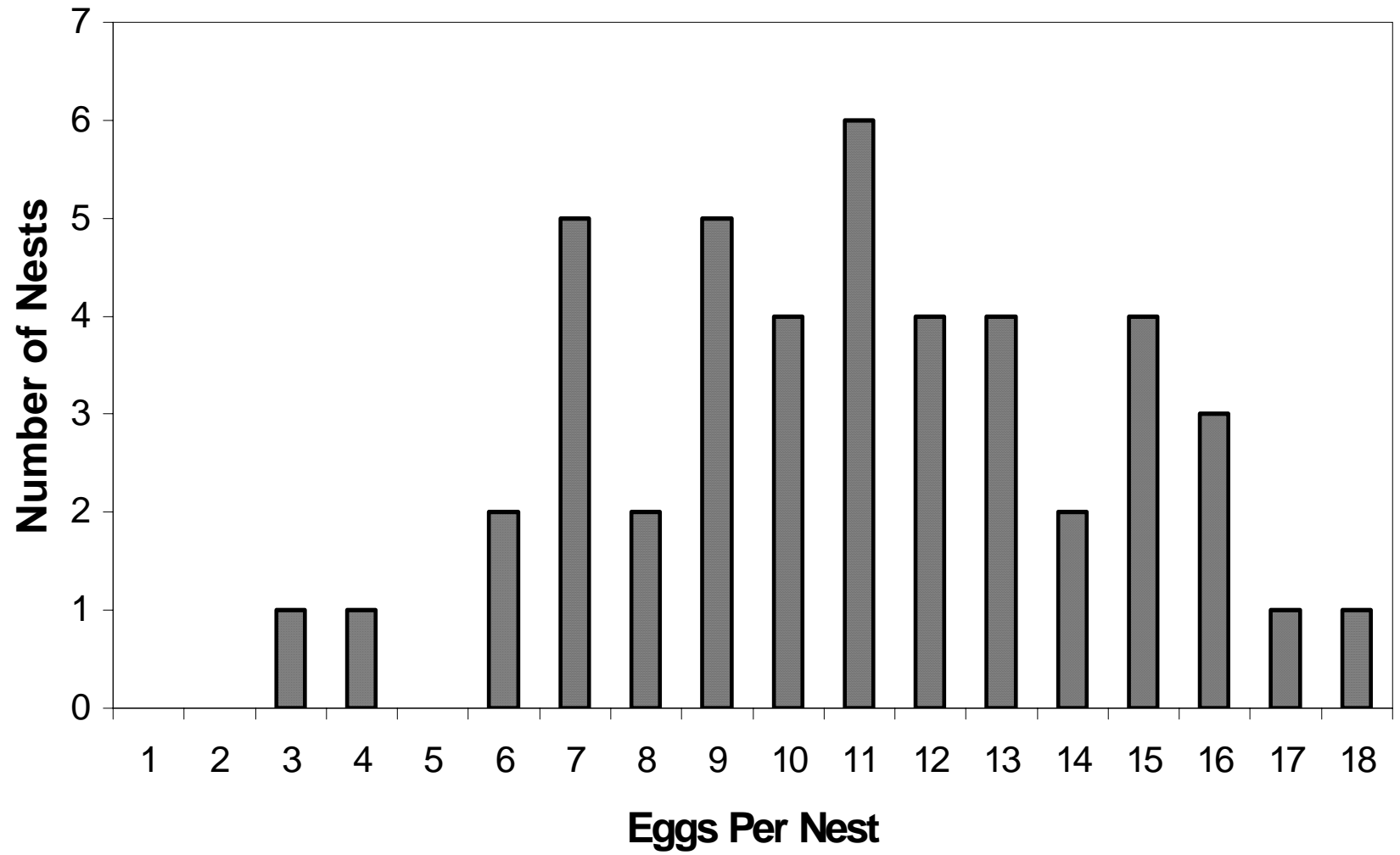


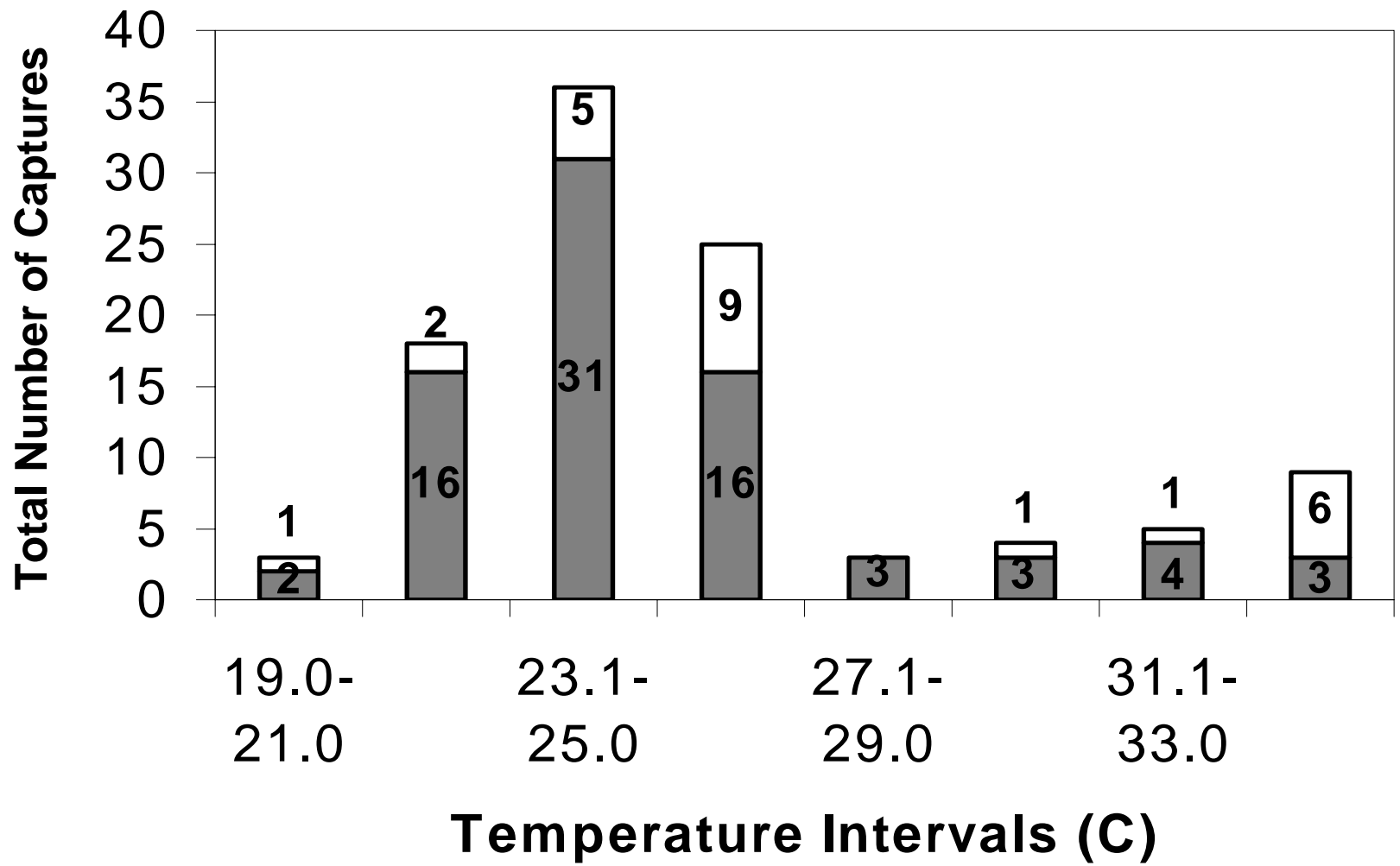
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b

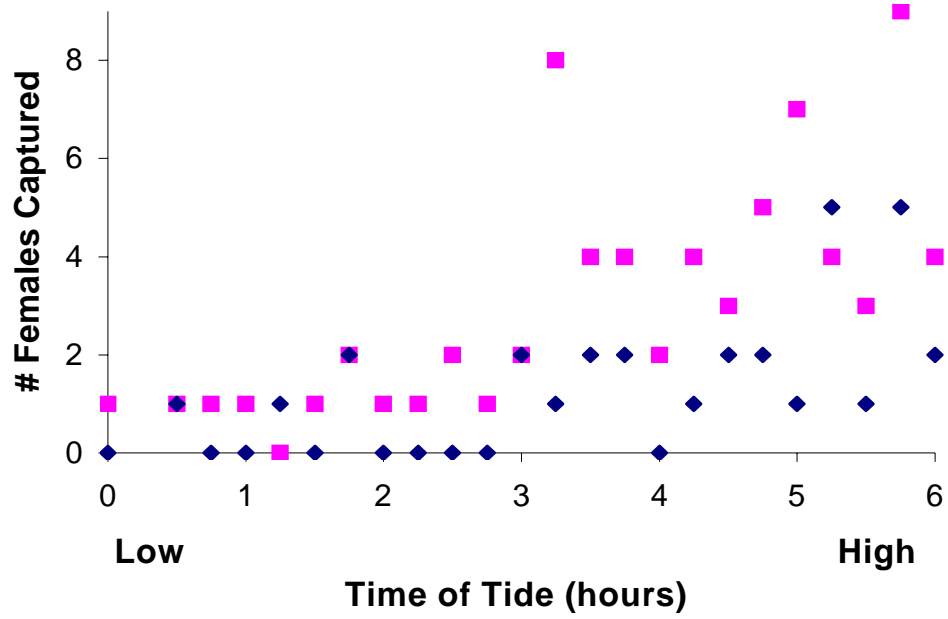






a

$r = 0.75, p < 0.001$



b

$r = 0.72, p < 0.001$

