

Nesting Ecology and Predation of Diamondback Terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New York

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ABSTRACT.—We studied Diamondback Terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New York. We found evidence of nesting terrapins at three locations within the Recreation Area and focused our research on the islands of Jamaica Bay Wildlife Refuge. Female terrapins nested from early June through early August and oviposited at least two clutches per year. Mean clutch size was 10.9 eggs. Nesting activity increased with daily high temperature and high tide. The greatest number of terrapin nests was found in shrubland, dune, and mixed-grassland habitats, but nest densities were higher on a human-made sandy trail and on sandy beaches. We estimate that approximately 2053 nests were oviposited on the largest island in the refuge in 1999. In 1998 and 1999, we counted 1319 and 1840 depredated nests, respectively, throughout the refuge. Raccoons were introduced into Jamaica Bay Wildlife Refuge approximately 20 yr prior to this study. Raccoons depredated 92.2% of nests monitored on the largest island during the 1999 nesting season. We also found the carcasses of adult female terrapins that apparently were killed by raccoons as they came on land to nest. This terrapin population may be undergoing demographic changes as a result of the introduction of raccoons.

The Diamondback Terrapin, *Malaclemys terrapin*, is an estuarine emydid turtle that occurs along the Atlantic and Gulf coasts of North America, from Cape Cod, Massachusetts, to Corpus Christi Bay, Texas (Ernst and Bury, 1982). In New York, terrapin populations are scattered around Long Island, Staten Island, and the lower Hudson River north to Rockland, Putnam, and Orange Counties.

Terrapin nesting ecology varies widely. Variation in clutch size (Montevecchi and Burger, 1975; Auger, 1989; Roosenburg, 1991), clutch frequency (Burger, 1977; Cook, 1989; Roosenburg, 1991), and incubation time (Burger, 1977; Auger and Giovannone, 1979; Zimmerman 1992) have been documented in different terrapin populations. The time and duration of the nesting season also varies by location (Burger, 1977; Seigel, 1980a; Ernst et al., 1994). Terrapins have been reported to nest from April through July with a preference for nesting during the day in fair weather with minimal cloud cover (Burger and Montevecchi, 1975; Seigel, 1979, 1980a; Zimmerman, 1992). However, nesting also occurs nocturnally (Auger and Giovannone, 1979; Roosenburg, 1992, 1994; Wood and Herlands, 1997), during rain (R. Wood, pers. comm.), and soon after rain (Burger and Montevecchi, 1975; Roosenburg, 1992, 1994). Female terrapins prefer nesting in sunny,

sparsely vegetated areas (Burger and Montevecchi, 1975; Roosenburg, 1992, 1994; Zimmerman, 1992), and sand is the preferred nesting substrate (Roosenburg, 1994).

Variation in nest survivorship has been documented in different parts of this species' range (Burger 1976, 1977; Auger and Giovannone, 1979; Roosenburg, 1992). Eggs and hatchlings of *M. terrapin* are eaten by ghost crabs (*Ocypode quadrata*; Zimmerman, 1992), striped skunks (*Mephitis mephitis*; Auger and Giovannone, 1979), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), crows (*Corvus brachyrhynchos*), and laughing gulls (*Larus atricilla*; Burger, 1977). The roots from beachgrass (*Ammophila breviligulata*) and *Spartina* spp. also invade terrapin nests (Auger and Giovannone, 1979; Lazell and Auger, 1981; Roosenburg, 1992). Other biotic causes of nest and hatchling mortality include fungal infections and maggots (Auger and Giovannone, 1979). Abiotic causes of nest mortality include flooding and wind erosion (Auger and Giovannone, 1979; Roosenburg, 1992). Infertility, failed development, and unexplained mortality of hatchlings can further decrease survivorship (Burger, 1977). Predation upon adult terrapins has been observed (Seigel, 1980b; Clark, 1982; Watkins-Colwell and Black, 1997).

Terrapins are facing increased threats throughout their range (Ernst et al., 1994; Burke et al., 2000). Nevertheless, information on their status in the New York metropolitan area is very limited, threats to their survival have not been fully identified, and they continue to be sold illegally in many major cities (Burke et al., 2000;

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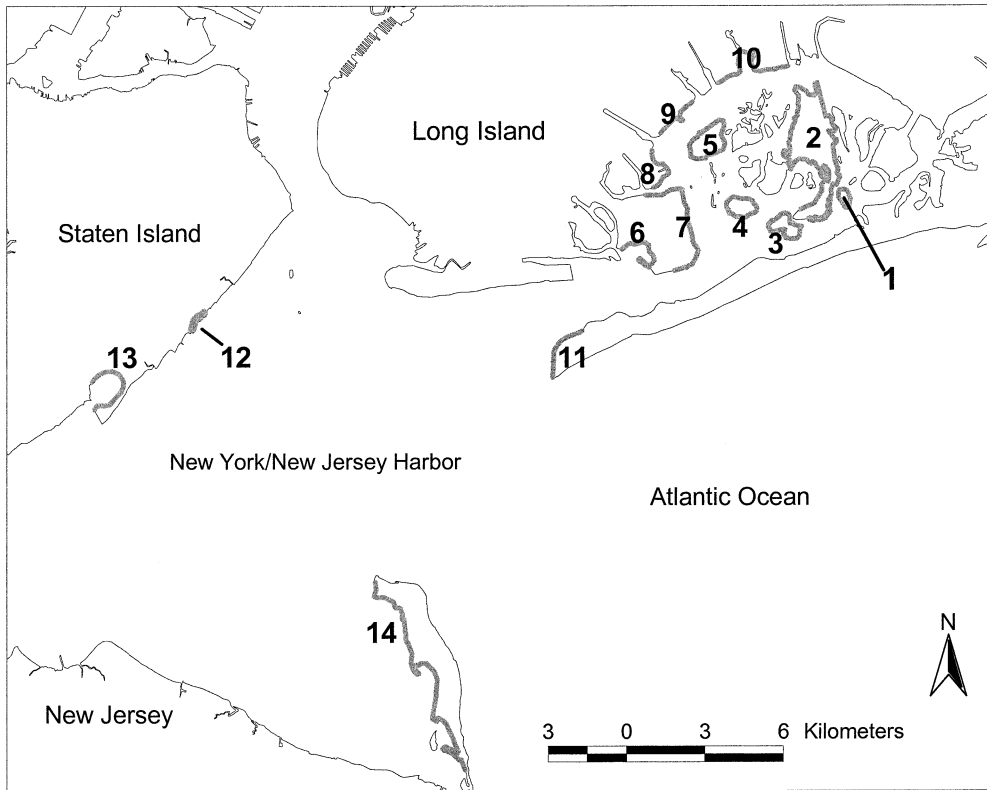


FIG. 1. Map of Gateway National Recreational Area (GNRA). 1 = Subway Island; 2 = Ruler's Bar Hassock; 3 = Little Egg Island; 4 = Ruffle Bar; 5 = Canarsie Pol; 6 = Dead Horse Bay; 7 = Floyd Bennett Field; 8 = Bergen Beach; 9 = Canarsie Pier; 10 = Spring Creek; 11 = Breezy Point; 12 = Miller Field; 13 = Great Kills Park; 14 = Sandy Hook.

RLB, pers. obs.). We sought to address the lack of information regarding terrapin nesting ecology in the New York metropolitan area, identify important nesting sites, and quantify current nest predation to develop a better understanding of their survival and recruitment. On a broader scale, we sought to obtain a greater understanding of how external factors such as predation and environmental conditions influence terrapin ecology and nesting behavior.

MATERIALS AND METHODS

Study Area.—Gateway National Recreation Area (GNRA) stretches across the mouth of the Hudson River from southwestern Long Island, New York to Sandy Hook, New Jersey (Fig. 1). Gateway is composed of 10,400 ha of land and water, including the 3,700 ha Jamaica Bay Wildlife Refuge (JBWR). JBWR and surrounding areas have been significantly altered over the past 120 yr by extensive dredging for land reclamation, shipping channels, and the creation of John F. Kennedy International Airport (JFK; Black, 1981). JBWR includes five upland islands: Ruler's Bar

Hassock (RBH, the largest island), Little Egg Island (LEI), Ruffle Bar, Canarsie Pol, and Subway Island.

Nesting Area Identification at GNRA.—In 1998, we identified all feasible nesting areas in GNRA based on three criteria. The first criterion was availability of sun-exposed, sparsely vegetated habitats; we also included small pockets of exposed areas surrounded by relatively dense vegetation as reported by Burger and Montevecchi (1975). The second criterion was the presence of sandy soils for nesting. We included mixed soils and gravel substrates because they attract nesting terrapins at GNRA (D. Taft, pers. comm.). The third criterion was proximity to water. Our preliminary surveys suggested the maximum distance from water used by terrapins was approximately 250 m. In addition to these criteria, we also reviewed historic terrapin data from GNRA. We considered ocean-facing beaches, bulkheaded shorelines, and landfill sites unfeasible.

We searched all feasible areas for evidence of nesting activity including depredated nests,

punctured turtle eggs and egg fragments, live or dead adult female terrapins found in uplands, hatchlings, false nests, and crawl trails leading inland from the water. Dead terrapins found on the beach were not used as indicators of nesting activity because they may have died elsewhere and washed ashore.

Predation at JBWR.—In 1998 and 1999, we surveyed all suitable nesting areas on RBH (including 3180 m of shoreline and 22 ha of uplands) with the assistance of volunteer groups ranging from 2–10 people. We searched for depredated nests and dead terrapins from 1 June through 31 July and sporadically in August. We surveyed LEI, Ruffle Bar, Canarsie Pol, and Subway Island once in July 1998, and in July 1999, we resurveyed LEI and Ruffle Bar. These four islands were surveyed by walking parallel transects 2 m apart, traversing each entire island.

During depredated nest counts, we only counted holes that were accompanied by punctured eggs or egg fragments (unless we had previously observed oviposition). We identified predators to species when possible, using direct observation, tracks, nest scars, or scat. When punctured eggs were found complete and intact adjacent to depredated nests, we counted them for clutch size estimates (see Nesting Ecology in Materials and Methods). We removed depredated eggs and covered holes to prevent recounting them.

In 1999, we recorded the surrounding habitat type of depredated nests on RBH when time permitted, to compare nesting habitat selections. We calculated absolute values and a relative index that corrected for differences in habitat size by dividing the number of nests per habitat type by the total area of each habitat type. We used three habitat types from a National Park Service (NPS) characterization (National Park Service, 1979): beach (exposed sand and no vegetation); dune and mixed grassland (20–75% vegetation such as *A. breviligulata* and seaside goldenrod [*Solidago sempervirens*]); and shrubland (10–50% low-growing shrubs such as bayberry [*Myrica pensylvanica*] and beach plum [*Prunus maritima*]). We based two additional habitat types on our observations: Terrapin Trail (a 590-m sandy trail), and Main Trail (a 1730-m trail covered in gravel and mixed soils).

When we found adult terrapin carcasses, we inspected them for cause of death. We presumed a “probable raccoon attack” for those found with severed rear limbs, punctured body cavities, and evisceration adjacent to the hindquarters, as seen by Seigel (1980b) and RLB (pers. obs.). We presumed a “possible raccoon attack” when carcasses were too severely decomposed to confirm a raccoon attack, but evidence such as location (e.g., upland nesting areas) and physical condi-

tion (e.g., upside down) indicated raccoon attack during nesting. We recorded sex as “unknown” when a carcass had washed onshore, the carapace was less than 140 mm, and/or severe decomposition had occurred.

Nesting Ecology on Ruler’s Bar Hassock.—With the assistance of our volunteers, we searched all suitable nesting areas on RBH for nesting terrapins. The searches were conducted from 1 June through 31 July, and 5, 19, and 29 August 1999, over 4–6-h periods from 0700–2200 h. We adjusted the daily observation period according to daytime high tide by timing the middle of the period to correspond with high tide. We did this to maximize the number of terrapins observed based on reports of increased nesting activity associated with high tide (Burger and Montevecchi, 1975; Auger and Giovannone, 1979; Zimmerman, 1992). On days with two daytime high tides, we selected the tide closer to the solar zenith or conducted observations during both tides.

We observed nesting terrapins as they emerged from the water and inconspicuously followed them on their nesting forays. We also found some terrapins during walking surveys along the shorelines and trails. We recorded terrapins observed ovipositing as “nesters” and terrapins we disturbed or encountered prior or subsequent to nesting events as “incidentals.” Observers watched complete nesting events whenever possible and then captured the females. We uniquely marked females using the shell-notching method of Cagle (1939). In rare instances, we used disturbed soil patterns to find recently laid nests as did Burger (1977) and Roosenburg (1992), but dense vegetation made this difficult. The earliest and latest nesting dates were recorded based on direct observations of oviposition or depredated nests. In addition to our 1999 data, we collected supplemental field data on earliest and latest nesting in 2000.

We compared the time of capture for each female terrapin to tide, temperature, and cloud-cover to determine how environmental factors influence nesting activity. We obtained our data from the National Climatic Data Center weather station at JFK. We recorded absolute values and calculated relative indices by dividing the number of terrapins observed in a measured unit by the total number of observer-hours or overall hours during the study period.

Whenever we observed terrapins nesting, we marked the nests and monitored them for survivorship. We define “nest survivorship” as the percentage of nests in a sample that were not destroyed (e.g., depredated or flooded). We estimated nest survivorship by marking a sample of nests ($N = 77$) with three surveyor’s flags placed approximately 1 m from each nest in an

TABLE 1. Density of *Malaclemys terrapin* nests by habitat type.

Habitat type	Number depredated nests	Area (m ²)	Nests/m ²
Beach	129	50,512	0.0026
Dune/Mixed Grasslands	469	50,851	0.0092
Shrubland	485	119,593	0.0040
Terrapin Trail	254	945	0.269
Main Trail	122	5190	0.0235
Total	1459	227,091	0.0064

equilateral triangle. We monitored them daily through September and recorded the length of time between oviposition and depredation. We examined all monitored depredated nests for predator spoor, uneaten eggs, and egg remains. If a marked nest was disturbed and no eggshell fragments were found, we assumed that predators had completely consumed the eggs within the nest.

We monitored another sample of nests ($N = 5$) for hatchling development using predator excluders (Auger, 1989). Excluders consisted of 50-cm² sheets of one-quarter-inch hardware cloth. We buried excluders approximately 2 cm below the surface and anchored them with 200-mm metal stakes. After 40 days, we removed the excluders so that hatchlings would not be obstructed if they attempted to emerge. We then excavated the top eggs in each nest to check developmental characteristics such as swelling and texture changes. We examined the eggs without removing them and then re-covered them. We continued monitoring these nests weekly for signs of hatchling emergence through the end of September. Two of the nests were depredated after the predator excluders were removed. We excavated and inspected the remaining three nests on 27 September 1999. Where hatchlings had emerged prior to 27 September, we counted eggshells in the nest. We removed nonemerged hatchlings from the nest chamber and released them into an adjacent marsh. Because our data were gathered from excavated nests, the results should not be interpreted as emergence data.

We calculated mean clutch size by counting punctured eggs adjacent to depredated nests. We generally did not dig up marked nests to determine clutch size because we did not want to bias predators. The only time we took clutch size measurements from intact, nondepredated nests was when we excavated the successfully protected nests, and in one additional instance, when we counted the eggs of an intact nest that was laid below the high-tide line, before it flooded.

We present all results in this paper as ± 1 SD, and statistical tests are two tailed, unless otherwise noted.

RESULTS

Nesting Area Identification at GNRA.—We determined that 14 different areas in GNRA were feasible for nesting by *M. terrapin* (Fig. 1), but we found evidence of nesting in only three areas: RBH, LEI, and Sandy Hook. Nesting areas were generally sparsely vegetated sandy uplands with *Spartina* marshes nearby.

Predation at JBWR.—We found a combined total of 1319 depredated nests in 1998 and 1840 nests in 1999 on RBH and LEI. Eggshells did not persist between years, and we are confident that our numbers accurately represent the reported year class. Of the 3159 depredated nests counted during this study, 98.9% were found on RBH where raccoons were the primary nest predators. We saw no evidence of predation by other animals on RBH. We never found uneaten eggs in depredated nests. We discovered nearly all predation events post factum, but we did observe raccoons depredating nests on three occasions between 1800 and 0600 h. We saw as many as six raccoons per night in the nesting area, and they were usually in groups of two or three individuals.

One of our protected nests was invaded by plant roots. Seven of nine eggs were penetrated, shriveled, and desiccated. Nearby plants were tall wormwood (*Artemisia campestris caudata*) and bayberry, but we could not determine which, if either, of the species' roots were involved.

We found depredated nests ($N = 34$) on LEI but did not observe nesting there. In three cases, the top and middle eggs of nests were depredated, yet the bottom eggs were intact. In all cases, the nest scars were different from those left by raccoons on RBH.

We categorized the habitat surrounding 1459 (80.1%) depredated nests on RBH. We observed significant differences in the absolute and relative number of depredated nests found in each habitat type (Table 1; absolute comparison: χ^2 goodness-of-fit test = 447, $df = 4$, $P < 0.001$; relative comparison: χ^2 goodness-of-fit test = 10,644, $df = 4$, $P < 0.001$). The greatest absolute number of depredated nests was in dune and mixed grassland habitat and shrubland habitat. The Terrapin Trail and Main Trail had the highest relative depredated nest densities.

It appeared that the way raccoons ate eggs on RBH varied seasonally. During the first half of the 1999 nesting season, raccoons usually left depredated eggs in conspicuous mounds within a few centimeters of depredated nests. During the second half of the nesting season, the number of nests that were consumed with little or no

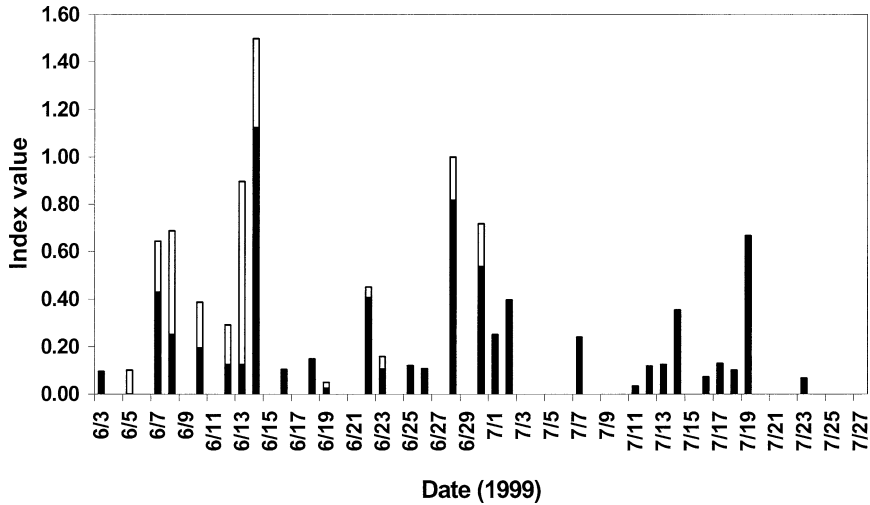


FIG. 2. Index of total daily captures. Black bars represent “nesters” that were observed nesting and then captured ($N = 85$). White bars represent “incidental” females ($N = 59$).

eggshell evidence left behind increased. Additionally, our observations of raccoon scat in 1998 and 1999 provide further support of a change in the way raccoons consumed eggs. In the beginning of the 1998 and 1999 nesting seasons, raccoon scat in the nesting areas was typically dark brown. Starting gradually in early July, we observed some raccoon scat with visible quantities of terrapin eggshell fragments. By the end of both nesting seasons, nearly all the raccoon scat we observed was white and contained large quantities of eggshell fragments.

We found 28 adult terrapin carcasses on RBH during our study. In 1998, we found eight females (six probable raccoon attacks, two possible raccoon attacks) and one terrapin of unknown sex (possible raccoon attack). In 1999, we found the carcasses of 15 female terrapins (11 probable raccoon attacks, four possible raccoon attacks), one male (unknown/natural causes), and three terrapins of unknown sex (possible raccoon attacks). Predation appears to have been the primary cause of mortality, but we never observed predation on adults.

Nesting Ecology on Ruler’s Bar Hassock.—In 1999, terrapins nested from 3 June through 23 July, a 51-day nesting season. In 2000, terrapins nested from 9 June through 4 August, a 57-day nesting season. The earliest time we observed nesting was 0930 h; the latest was 2115 h. The average time of nesting was 24.8 ± 6.9 min (range 13–47, $N = 28$).

We found no significant difference in mean clutch size between depredated eggs ($N = 41$) and whole eggs from nondepredated nests ($N = 4$; one-tailed Mann-Whitney U -test = 62.5, $P = 0.45$); thus, we combined the data. We used a one-

tailed test because animals, waves, wind, and visitors could have removed eggshells from depredated nests whereas nondepredated nests were protected from those influences. The overall mean clutch size was 10.9 ± 3.5 eggs per nest ($N = 45$, range 3–18). One depredated nest appeared to contain 29 eggs, but we are skeptical of this large number. It may have been the remains of two adjacent nests; thus, we did not include it in our calculations.

We marked 133 adult female terrapins captured on land in 1999. Six of these were recaptured, all in the same general areas of initial capture. One of these was observed to nest twice during the nesting season. A second turtle was gravid and disturbed during a nesting attempt on 13 June 2003 and observed nesting on 2 July 2003, 19 days later. Two other turtles were recaptured moving toward the water from uplands 17 days after they were originally observed nesting. The remaining two recaptures were gravid or nested on at least one of their dates of capture. The mean number of days between the first and second capture for all six terrapins was 17.5 ± 1.39 days (range 15–19). We did not capture any terrapins more than twice in a year.

The greatest number of terrapins captured on a single day ($N = 43$) occurred on 13 June 1999. When we corrected for the total number of search hours each day, we found three distinct activity peaks during that nesting season (Fig. 2).

Although we found nesting turtles at all times, from low to high tide, and from dawn to dusk, we found significant correlations between the number of terrapin captures per hour and increased tide level ($r = 0.74$, $df = 100$, $P < 0.001$) and between the number of terrapin

TABLE 2. Relative number of *Malaclemys terrapin* nests oviposited under different cloud cover regimes.

Cloud cover	Number of nests	Total number of hourly cloud-cover observations	Nests/cloud-cover observation
Clear (0–25%)	10	680	0.555
Partly sunny (25–50%)	32	94	0.077
Partly cloudy (50–75%)	31	201	0.164
Overcast (75–100%)	13	249	0.203

captures per hour and daily high temperature ($r = 0.72$, $df = 100$, $P < 0.001$). Mean air temperature at time of capture for nesters was $25.4 \pm 3.2^\circ\text{C}$ ($N = 78$, range 19.4 – 35.0°C). Mean air temperature for incidentals was $27.7 \pm 4.7^\circ\text{C}$ ($N = 25$, range 20.6 – 35.0°C). This difference is significant ($t = 2.3$, $df = 101$, $P = 0.03$). The cloud-cover regime during the 1999 study period was 56% clear, 20% partly sunny, 16% partly cloudy, and 8% overcast. Of the 86 nesters we observed in total, 15% nested in rainy or overcast conditions (75–100% cloud cover), 36% nested in partly cloudy conditions (50–75% cloud cover), 37% nested in partly sunny conditions (25–50% cloud cover), and 12% nested in clear conditions (0–25% cloud cover). Both absolute and relative differences were significant (absolute comparison: χ^2 goodness-of-fit test = 18.84, $df = 3$, $P < 0.001$; relative comparison: χ^2 goodness-of-fit test = 148.84, $df = 3$, $P < 0.001$). The absolute and relative numbers of nests found in each cloud-cover regime are presented in Table 2.

We estimated that nest survivorship among our sample of unprotected nests was 5.2% ($N = 77$). Predation accounted for the loss of 92.2% of nests and flooding accounted for a 2.6% loss. The time between nesting and predation was recorded in one-day intervals for 70 depredated nests. Seventy-one percent of predation occurred in the 24-h period following oviposition (Fig. 3). The greatest time between oviposition and depredation was seven days.

We used our nest survivorship data to estimate the total number of nests laid on RBH based on Burger's (1977) use of the Lincoln-Peterson index (Brower et al., 1998):

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

where P_1 = number of unprotected, depredated, marked nests (71), P_2 = number of unmarked, depredated nests on RBH (1822), N_1 = total unprotected marked nests (77), and N_2 = total number of unmarked nests on RBH = 1976. Thus, we estimate the total number of nests laid

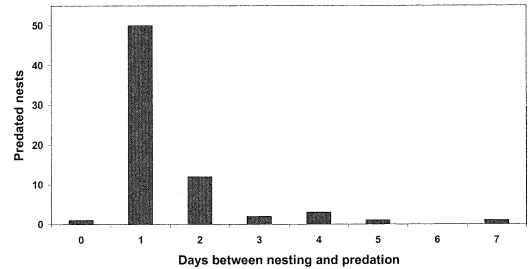


FIG. 3. Time (in days) between oviposition and depredation by raccoons on Ruler's Bar Hassock ($N = 70$).

at RBH ($N_1 + N_2$) in 1999 = 2053 (95% CI = 1615–2491) and the total number of eggs laid on RBH to be 22,378, calculated by multiplying 2053 (estimated total nests on RBH) by 10.9 (mean clutch size).

The three successfully protected nests used to monitor hatchling development were excavated 70, 69, and 64 days after oviposition. Each nest contained some live hatchlings. Two of nine eggs in Nest 1 (22%) produced live hatchling, six of the 13 eggs in Nest 2 (46%) produced live hatchlings, and 12 of the 13 eggs (92%) in Nest 3 produced hatchlings, but one was dead. Additionally, eggs within the two depredated protected nests (see Materials and Methods) were developing normally prior to depredation, and a hatchling carcass was found in one of them after depredation indicating some hatchling production in that nest as well. Hatchlings from Nest 1 and Nest 3 were still present at the time of excavation. All six live hatchlings from Nest 2 had emerged, with only the unsuccessful eggs and posthatch eggshells remaining. Although we did not study nest emergence, our observations from Nest 2 suggest that the hatchlings emerged within 69 days of oviposition.

Only four (5.2%) of the 77 monitored unprotected nests survived predation and flooding. We could not determine the success of the eggs in these nests because we were unable to determine their precise locations within our marking flags, even though we originally observed oviposition of all four nests. Nevertheless, we assumed that at least some hatchlings were produced in all four surviving nests based on the data from our protected nests. Therefore, we estimate that there were 107 successful nests on RBH (5.2% of 2053 nests) and that successful nests contained 1166 eggs (107 nests \times 10.9 eggs/nest).

DISCUSSION

Nesting Area Identification at GNRA.—Although 14 areas at GNRA appeared feasible as terrapin nesting areas, only three definitively

proved so. Nesting had not been previously recorded on LEI. The 11 other areas contained suitable upland habitat (e.g., beaches, dunes, and grasslands) similar to the three confirmed sites, but nearby aquatic habitats may have been insufficient for sustaining terrapin populations. Most of these sites lacked ample *Spartina* marsh, and have been dredged, bulkheaded, filled, and substantially developed. We did not find nesting evidence at Floyd Bennett Field or Great Kills Park, two areas where Cook (pers. comm.) reported occasional observations of nesting terrapins and hatchlings in the 1980s although a NPS official reported a dead terrapin at Great Kills Park in 1999.

Predation at JBWR.—We detected high levels of predation by raccoons at RBH. Despite similar search efforts in both years, the number of depredated nests on RBH increased from 1303 in 1998 to 1822 in 1999. This may indicate an increase in predation, improved proficiency in our nest detection, increased nesting, or some combination of these. We also found that the rate of nest predation dropped off rapidly after 24 h, indicating that raccoons likely use a transient indicator, probably scent, to locate terrapin nests.

During the early 1980s, Cook (1989, pers. comm.) studied terrapin nesting ecology on RBH. He never observed nest predation and hatching success was 93% ($N = 8$), but this estimate may be suspect because of low sample size. None of the typical predators of turtle nests (raccoons, foxes, skunks) were present on RBH (O'Connell, 1980). In the mid-1980s, raccoons began to colonize RBH but were observed only rarely, dead on roads (R. Cook, pers. comm.). Raccoon sightings remained uncommon until the early to mid-1990s when sightings began to increase (R. Cook, pers. comm.). NPS officials attribute this to an increase in the number of nuisance raccoons that were captured by humans and illegally released on RBH (D. Riepe, pers. comm.). Subsequently, depredated terrapin nests and raccoons have both become common on RBH (R. Cook, pers. comm.). Avian predation has never been reported on RBH and may be limited by the constant daily flow of visitors during daylight hours when avian predation typically occurs (Burger, 1977).

We observed nest invasion by roots. Many nests were found in dune, mixed grassland, and shrubland habitats with plants growing nearby. Roots may represent a significant source of egg mortality exclusive of animal predators. Beach grasses can obtain nutrients from terrapin nests (Lazell and Auger, 1981; Stegmann et al., 1988). It was difficult to determine the full extent and impact of roots because of their inconspicuous nature.

We found that shrubland habitat and dune and mixed-grassland habitat contained the greatest number of depredated nests on RBH. These habitats were similar to those studied by Burger and Montevecchi (1975), Roosenburg (1992), and Zimmerman (1992) in that they were sparsely vegetated, contained loose sand, and received substantial sunlight. Although the Terrapin Trail represents a small area relative to other habitats, it is also a key nesting area (Table 1) as well as a major corridor for nesting terrapins. The trail's sandy soil and minimal vegetation is ideal for nesting terrapins. Moderate pedestrian use of this trail is common outside the nesting season and may benefit terrapins by inhibiting plant growth and maintaining high-quality nesting habitat. Nesting also was observed in marginal habitats. Thirty-six depredated nests were oviposited on gravel sections of the Main Trail, which is extremely compacted and difficult to excavate.

Far fewer depredated nests were found on LEI than on RBH. We were unable to estimate the total number of nests on LEI because we only surveyed LEI for depredated nests. Raccoons have not been observed on LEI, and the island's lack of fresh water, small size, and isolation may preclude it from supporting raccoon populations (R. Cook, D. Avrin, pers. comm.). The pattern of predation on LEI was more consistent with Burger's (1977) observation of avian predation where gulls only took a few eggs from each nest. LEI hosts large breeding colonies of great black-backed gulls (*Larus marinus*) and herring gulls (*Larus argentatus*). Burger (1977) reported that raccoons also occasionally left eggs intact within raided nests, but they only left two or three eggs per nest. We suspect that avian predators are the primary nest predators on LEI because we found greater numbers of intact eggs in depredated nests.

We observed what appears to be a qualitative seasonal shift in the way raccoons consumed eggs on RBH. Early in the season, raccoons generally displayed the behavior described by Aresco (1996) in that they only consumed the contents of eggs while discarding the shells adjacent to the nest. Later in the season, raccoons displayed the behavior described by Burger (1977) in that they consumed eggs completely, shells included. If this behavior is common, then our estimate of the total number of depredated nests may be conservative because our depredated nest counts only considered nests accompanied by eggshell evidence.

Roosenburg (1992) suggested that nests laid within the first 10 days of the nesting season may have a survival advantage because of a "lag time" that exists before predators start to detect nests. The first nests we observed each season

were depredated nests. Thus, if such a lag time exists on RBH, we might have missed a number of nondepredated nests laid at the start of the season and nest survivorship rates may be higher than we report.

Like eggs and hatchlings, adult terrapins are vulnerable to predators, and the death of substantial numbers of adult females can have severe impacts on population persistence (Hep-pell, 1998). Seigel (1980b) studied two terrapin populations comprising more than 600 turtles. Raccoons killed at least 10% of adult female terrapins as they came on land to nest. Although terrapins of both sexes were killed, the majority were adult females (86%). The scattered remains of additional old terrapin shells were also discovered, indicating that similar predation had occurred prior to Seigel's investigation. During a resurvey in 1992 and 1993, Seigel (1993) found no more than six terrapins per year because of a severe population crash caused by raccoons.

Nesting Ecology on Ruler's Bar Hassock.—The 51 (1999) and 57 day (2000) nesting seasons we observed at JBWR are substantially longer than the 34- to 44-day nesting seasons reported in New Jersey (Burger, 1977) or the 34-day nesting season reported previously at JBWR (Cook, 1989). The nesting season we report is similar to the 52- to 57-day nesting season in Florida (Seigel, 1980a) and the 60-day nesting season in South Carolina (Zimmerman, 1992). Our report of a nest on 4 August 2000 is one of the latest reported nesting dates for this species. Late nesting may be influenced by annual weather variation. The 2000 nesting season was characterized by several extended periods of overcast skies and cool temperatures that may have temporarily suppressed nesting.

The mean clutch size we report (10.9 eggs/clutch) is smaller than the 14.5 eggs/clutch ($N = 10$) reported by Cook (1989, pers. comm.) at JBWR. This difference may be caused by our greater sampling effort. We are confident that the methodology we used to estimate clutch-size was reliable. We used extreme care when counting depredated eggs to avoid miscounts and Giambanco (2003) reported a similar mean clutch size of 11.8 eggs/nest ($N = 69$) in a subsequent study of whole eggs within nests at JBWR.

We conclude that some terrapins lay two clutches/yr at JBWR. One turtle nested twice and several others exhibited reproductive conditions on both dates of capture. Our mean-recapture interval was 17.5 days, which closely corresponds to the 17-day interesting interval for terrapins in Rye, New York (Klemens, 1993). Additionally, Auger and Giovannone (1979) reported two clutches/year from a terrapin population in Massachusetts, 150-km north of JBWR where temperatures are cooler.

There was a direct correlation between higher tide levels and the number of terrapins observed on land. Burger and Montevecchi (1975), Auger and Giovannone (1979), and Zimmerman (1992) reported similar findings. Our observations also indicated that onshore migrations of terrapins increased in association with daily high temperature. Likewise, Seigel (1980a) reported a similar association between temperature and nesting terrapins.

Terrapins did not nest when air temperature exceeded 35°C. In Florida, the maximum observed air temperature during nesting was 36°C (Seigel, 1979). Although the maximum nesting threshold is similar in New York and Florida, terrapins at JBWR nest at a mean temperature nearly 6°C lower than terrapins in Florida. Terrapins were more likely to nest under 25–75% cloud cover than either 0–25% or 75–100% cloud cover, perhaps because of the temperature extremes associated with very low or very high cloud cover. The extent to which terrapins nest at night at JBWR is still unknown, although four turtles started nesting between 2000 and 2030 h and continued nesting past sunset.

We conservatively estimated that approximately 2053 nests were laid on RBH in 1999, making this the largest nesting site reported in New York and one of the largest reported anywhere. Many factors may contribute to the large terrapin population at RBH including protection from commercial collection (for terrapins and their prey), large expanses of productive *Spartina* marshes (Tanacredi and Badger, 1995), and low nest predation rates prior to the recent colonization of RBH by raccoons.

We estimate that approximately 22,378 eggs were laid on RBH in 1999 but only 1166 in successful nests. Thus, most eggs do not survive and remain onshore. Bouchard and Bjorndal (2000) demonstrated that Loggerhead Seaturtles contributed significant quantities of nutrients in the form of eggs and eggshells, to a beach ecosystem in Florida. We conclude the same is true of terrapins at JBWR. Ricklefs and Burger (1977) estimated that on average terrapin eggs contain approximately 64.9 kJ/egg. Therefore, the terrapins that nest on RBH bring about 707 kJ/nest from marine ecosystems into terrestrial ecosystems each year, or approximately 1,450,000 kJ overall. More than 92% of this energy was consumed by raccoons quickly after eggs were laid, resulting in a much larger percentage of egg nutrients going to predators than found by Bouchard and Bjorndal (2000). The large amount of rapidly decomposing raccoon scat observed in terrapin nesting areas suggests that some of the ingested nutrients may be made available rapidly to nearby plants.

This paper documents current nesting areas, nesting ecology, and predation of Diamondback Terrapins in one of the largest and most densely populated urban areas in the country. Although typical threats such as development, commercial harvesting, and by-catch are limited in this federally-protected area, raccoons have been introduced onto RBH and may pose the greatest threat to this terrapin population. We suspect that raccoon predation on terrapin eggs and adults may detrimentally affect the long-term success of this population. Although beyond the scope of this paper, management strategies and community awareness programs aimed at preventing future raccoon introductions may be necessary to ensure the survival of Diamondback Terrapins at JBWR.

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