

Dispersal of Newly Emerged Diamond-Backed Terrapin (*Malaclemys terrapin*) Hatchlings at Jamaica Bay, New York

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ABSTRACT. – Overwintering behavior of diamond-backed terrapin (*Malaclemys terrapin*) hatchlings is highly unusual; a substantial percentage of hatchlings leave nests in the fall, travel overland, and rebury themselves on land farther from water. Many aspects of this behavior are poorly documented and conflicting. We tracked 81 newly emerged *M. terrapin* hatchlings from their nest sites in Jamaica Bay, New York, to their overwintering refugia and until spring/summer emergence. Hatchling *M. terrapin* used the wrack line only as short-term cover before moving upland and burying themselves in terrestrial refugia. Hatchling refugia depths were variable, up to 10 cm deep, with some vertical movement seasonally. Hatchlings selected winter refugia with relatively high levels of vegetative cover; in this way, overwintering sites differed substantially from temporary refugia. Hatchlings emerged from overwintering refugia between 17 March and 7 July following fall emergence. Our observations better characterize what may be a unique behavior among turtles, but any adaptive value remains obscure.

KEY WORDS. – *Malaclemys terrapin*; diamond-backed terrapin; hatchling; refugia; overwintering; terrestrial; desiccation; emergence

Neonate turtles face different ecological and physiological challenges than do adults, and most of what we know about neonates is based on laboratory studies (Costanzo et al. 2008). An example of both of these characteristics is the diamond-backed terrapin, *Malaclemys terrapin* (Schoepff 1793), which may be the only aquatic turtle in which the hatchlings routinely travel overland away from brackish water and overwinter on land outside the nest (Muldoon and Burke 2012). Females come ashore to nest between April and August (Ernst and Lovich 2009). In New York, *M. terrapin* nest from 3 June to 7 August, with an average clutch size of 12 eggs (Feinberg 2000; Feinberg and Burke 2003; R.L.B., unpubl. data, 1999–2010). Nests are laid above the high-water line in loose soil, in areas with high sunlight exposure, and in sites with more bare soil and less leaf litter than random sites (Roosenburg 1994; Scholz 2006). Shrubland, dune, and mixed grassland are preferred nesting habitats (Feinberg and Burke 2003).

Adult *M. terrapin* hibernate from mid- to late November to April–May in shallow marsh creeks and in the mud in the intertidal zone (Yearicks et al. 1981), but little is known regarding overwintering behavior of neonatal *M. terrapin* after they emerge from nests. The hatchlings either overwinter within nests or emerge from nests in the fall and overwinter elsewhere (Baker et al. 2006; Costanzo et al. 2008). Small numbers of fall-emergent hatchlings have been found in tidal wrack lines (the accumulated debris deposited by the highest recent tide), intertidal high marsh vegetation, tidal mudflats, and

dense vegetation (Pitler 1985; Lovich et al. 1991; Draud et al. 2004; Costanzo et al. 2008) and crossing nesting areas (Muldoon and Burke 2012). In New Jersey, *M. terrapin* hatchlings emerge from nests in both fall and spring (Baker et al. 2006); in New York, few overwinter in the nest (A.L. Scholz, A. Kanonik, and R.L. Burke, unpubl. data, 2004–2005, 2015; reviewed by Costanzo et al. 2008). This behavior results in pulses of hatchlings in nesting areas in both fall and spring (Muldoon and Burke 2012).

Overwintering on land, either in the nest or elsewhere, potentially exposes turtles at high latitudes to very low temperatures, and not surprisingly, some turtle neonates supercool extensively or are freeze tolerant (reviewed by Ultsch 2006; Costanzo et al. 2008). In laboratory trials, *M. terrapin* hatchlings survived freezing to -3.0°C for 3 d and up to 12 d at -2.5°C (Baker et al. 2006), which is more extreme than conditions experienced by conspecifics in natural nests (Baker et al. 2006). Hatchlings of 2 other emydid turtles, Blanding's turtles, *Emys blandingii* (Packard and Packard 1999), and ornate box turtles, *Terrapene ornata* (Costanzo et al. 1995), are similarly freeze tolerant; this characteristic is associated with turtles that overwinter on land (Ultsch 2006; Costanzo et al. 2008).

Turtles either terrestrially overwinter in the nest (TIN) or terrestrially overwinter outside the nest (TON). The TON strategy is known only in eastern box turtles (*Terrapene carolina*; Burke and Capitano 2011), perhaps *M. terrapin* (Draud et al. 2004; Muldoon and Burke 2012),

and *E. blandingii* (Paterson et al. 2014, also reviewed by Costanzo et al. 2008). Initial indications that *M. terrapin* hatchlings might not immediately escape to water, as do most aquatic turtles, came from Burger's (1976) study of *M. terrapin* hatchling behavior, which found that hatchlings always moved from their nests to nearby vegetation and not to nearby water. It is not known what habitat is utilized by hatchling *M. terrapin* overwintering terrestrially or what the adaptive significance of this behavior might be.

Because *M. terrapin* hatchlings have been found in tidal wrack lines, Roosenburg (in Costanzo et al. 2008) suggested this might be their overwintering habitat. Similarly, 9 laboratory-raised *M. terrapin* hatchlings released into the water in an estuary quickly sought refuge in the flotsam of the high-tide wrack line (Lovich et al. 1991). However, wrack lines would be environmentally challenging places to overwinter. Dunson and Mazzotti (1989) and A.M. Calichio (unpubl. data, 2014) found that *M. terrapin* hatchlings cannot survive long in even mildly salty conditions without access to freshwater, so even if *M. terrapin* hatchlings inhabit the wrack line, they must leave occasionally to avoid desiccation. Wrack lines would also provide little protection from extreme temperatures.

Other evidence indicated that some recently emerged *M. terrapin* hatchlings spend considerable amounts of time on land. Muldoon and Burke (2012) found strong evidence that at least some *M. terrapin* hatchlings in New York overwinter well above the tide (and wrack) line. Draud et al. (2004) noted depredated hatchling *M. terrapin* carcasses 0.5–35 m from the mean high-tide line during the period of spring emergence. Over a 3-yr period, Pitler (1985) found 12 juvenile *M. terrapin* that used beach surface debris as well as matted *Spartina* grass, dense low-lying vegetation, and a rock, all on well-drained ground about 91 m from the water edge at low tide. Diet analysis (King 2007) and feeding behavior (Kinneary 2008) of hatchling *M. terrapin* indicate they forage on prey from both aquatic and terrestrial habitats.

Determining which habitats *M. terrapin* hatchlings utilize after nest emergence would illuminate a poorly known aspect of the early life history of the species and may be associated with this species' unusual adaptation to brackish water environments. Thus, we considered 2 scenarios: 1) *M. terrapin* hatchlings regularly overwinter in the high-tide wrack line, a microhabitat that experiences dramatic temperature and moisture extremes but that might provide food (Lovich et al. 1991; Draud et al. 2004; King 2007), and 2) *M. terrapin* hatchlings regularly overwinter in unknown locations upland (sensu Muldoon and Burke 2012). Without knowing the microhabitat of possible upland refugia, we could make no predictions about their environmental conditions or feeding opportunities. However, Paterson et al. (2012) found that some *E. blandingii* hatchlings overwintered in open upland areas and others in marshes and swamps and that the hatchlings preferentially selected specific habitats and microhabitats as they

traveled to overwintering sites. Therefore, we sought to identify characteristics of both temporary refugia and overwintering refugia. Finally, hatchlings are seen terrestrially in 2 annual pulses, April–July and August–October (Muldoon and Burke 2012). We hypothesized that the first pulse would be consistent with dates for hatchlings leaving TON refugia. Costanzo et al. (2008) noted that the general lack of field data regarding neonate turtles is due in part to the difficulty associated with monitoring large numbers of nests and in locating hatchlings after they disperse from the nesting site. We worked in an area with exceptionally large numbers of *M. terrapin* nests and used a novel tracking method to follow hatchlings.

METHODS

Study Area. — Rulers Bar (RB; lat 48°36'58.68"N, long 73°50'07.63"W) is a 458-ha human-constructed island in Jamaica Bay Wildlife Refuge, part of Gateway National Recreation Area, and is administered by the National Park Service (NPS). At the time of this study, a 1730-m-long gravel trail encircled West Pond, an 18.21-ha mildly saline impoundment. The island is surrounded by tidal beachfront backed by dunes interspersed with *Spartina* marsh. The west beach usually had a substantial wrack line that abutted the dune edge and was fully inundated during peak high tides. Vegetation coverage from the dune top to the edge of West Pond varied from sparse ground cover to a full tree canopy. The NPS routinely cuts large sections of dune, grassland, and shrubland vegetation to a height of 4–5 cm up to 20 m from the trail edge. Ground cover varied from none to 100% and was composed of woody debris, forbs, leaf litter, rock, or combinations thereof.

Jamaica Bay tides mix ocean water and freshwater twice daily. Average salinity toward the center of the bay varied from 23 to 27 parts per thousand (ppt; Gordon et al. 2002), but nearshore and in *Spartina* marshes, high-tide salinities were between 28 and 30 ppt, and low-tide salinities were 31–32 ppt (A.M. Calichio, unpubl. data, 2014).

Jamaica Bay contains the largest *M. terrapin* population in New York. An estimated 2053 *M. terrapin* nests were laid at RB in 1999 (Feinberg and Burke 2003), and 95% of *M. terrapin* nests found in western Jamaica Bay are laid on RB (Ner and Burke 2008).

Passive Integrated Transponder Tag Insertion. — We located hatchlings after they left their nests by using radio-frequency identification (passive integrated transponder [PIT]) tags. Most hatchlings were captured at nest sites located as part of a larger ongoing, long-term study of *M. terrapin* ecology. Female *M. terrapin* were observed nesting in June and July, and after completion of oviposition and nest covering, the nests were protected from predation by wire-mesh enclosures. During the hatchling emergence period (August–October), nests were checked at least once per day. Emerged hatchlings were

removed from enclosures and tagged (see below). On 19 and 20 December 2009 and on 19 March 2011, about 15 m of wrack line was manually searched for newly emerged *M. terrapin* hatchlings.

In 2009, 2010, and 2011, we inserted 9×2.12 -mm (0.067-g) PIT tags (Biomark, TX148511B) intraperitoneally into 60, 36, and 251 (respectively) *M. terrapin* newly emerged from nests (Duncan 2013). Hatchlings were observed a minimum of 20 min and up to 24 hrs postinsertion and then released within 1 m of capture sites or nests (Duncan 2013). Whenever possible, hatchlings were inconspicuously observed from a distance of > 10 m when released to observe their general direction of movement and to identify potential refugia.

Hatchling Searches. — After hatchling releases, area searches were conducted with a Biomark FS2001 Reader and portable antenna. The reader was worn in a chest harness, and the attached antenna was mounted on a handle and waved a few centimeters over or in direct contact with the ground much like a metal detector. Conducted on average 1 d/wk from the date of nest emergence until 1 March, searches were generally concentrated on potential cover such as wrack lines, under dense vegetation, and areas of leafy and woody debris. Failure to locate particular individuals was followed by a more methodical grid search centered on the release point (Duncan 2013).

Refugia Locations. — If a hatchling moved from a location and was found elsewhere, the previous site was considered a temporary refugium. At each temporary and overwintering refugium, we noted the distance from nest site. Percent ground cover, grass, forb, bush, mature tree, and canopy cover were visually estimated to the nearest 10% for circular areas with a 1-m radius immediately surrounding each refugium. Heights for tree, bush, grass, and forb were estimated within the same 1-m radius.

Refugia were checked periodically throughout the winter until the following July, even when no PIT tag signal was detected, in case hatchlings had been buried too deeply for detection, and then moved back within the range of the reader. Hatchlings were considered to have left their refugia if, after 1 March, their signals could not be located despite multiple attempts over 2 wk in the areas where they had been previously located.

Excavation of Refugia. — After 1 July, the year after nest emergence, refugia with PIT signals were thought to either have dead hatchlings or be the result of hatchlings shedding their tags. These sites were excavated carefully by hand to recover tags or hatchling remains.

Three refugia were chosen randomly in 2012 to measure the depth of hatchlings; these were excavated just deep enough to partially expose the hatchlings. Depth was quickly measured and soil replaced. One hatchling was checked twice (23 March 2012 and 6 April 2012) when the ground surface was apparently disturbed after the first excavation, possibly by a predator.

Statistical Analysis. — Logistic regression was used to compare temporary and overwintering refugia for the 10 habitat characteristics measured over the area within 1 m (% ground cover, % grass, grass height, % bush, bush height, % tree, tree height, % forb cover, forb height, and canopy height). Logistic regression was also used to compare the same 10 habitat characteristics within 1 m of sites where hatchlings successfully overwintered with sites where they buried themselves but did not successfully overwinter (apparently died).

RESULTS

Hatchling Locations. — Three hundred forty-one *M. terrapin* hatchlings were captured when they emerged from their nests. Hatchlings were implanted with PIT tags and released at their nests. Six additional hatchlings were found during a wrack line search on 21 September 2009, implanted with PIT tags, and returned to their capture sites. Of these 347 hatchlings, 205 (59%) were never located again. Of the 142 found at least once more after tagging, 81 were buried in overwintering refugia until spring, when they likely emerged. Of these 81, 77 were found in only 1 location where they overwintered, 3 were located in 2 separate refugia (a temporary, later abandoned refugium and a successful overwintering refugium) each, and 1 settled in an overwintering refugium after abandoning 2 temporary sites. These successful overwintering refugia averaged 5.91 m (SD ± 7.04 , range = 0.1–47; Fig. 1) from the original nest sites.

Hatchlings in the Wrack Line. — Nine hatchlings marked at their nests moved toward the water from their nests and hid in the wrack line. None of the hatchlings found in the wrack line were detected in the wrack line past 11 October. The maximum amount of time hatchlings were known to use the wrack line was 19 d. Eight hatchlings found in the wrack line were detected there only once, on the same day as tagging and release. One hatchling was found twice in the wrack line, having moved to a new location the day after it had been tagged and released. One hatchling left its temporary refugium in the wrack line for a different temporary refugium 8 d after it was initially tagged and released.

Spring Emergence. — Hatchlings generally left their winter refugia in late spring, although the timing varied considerably both within and among years. In 2010, hatchlings left their refugia between 25 April and 2 July ($n = 6$, mean date 19 May, SD ± 34.4 d); in 2011, the analogous dates were 9 April–13 May ($n = 8$, mean date 25 Apr ± 15.1 d); and in 2012, they were 17 March–12 May ($n = 67$, mean date 14 Apr ± 11.0 d; Fig. 2).

Depth of Refugia. — Twelve PIT tags that had been implanted in hatchlings were later recovered buried in overwintering refugia or on the ground surface. These tags were either expelled from hatchlings or from dead hatchlings. Three tags recovered in refugia on 22 July 2010 were found buried with hatchling remains; the cause

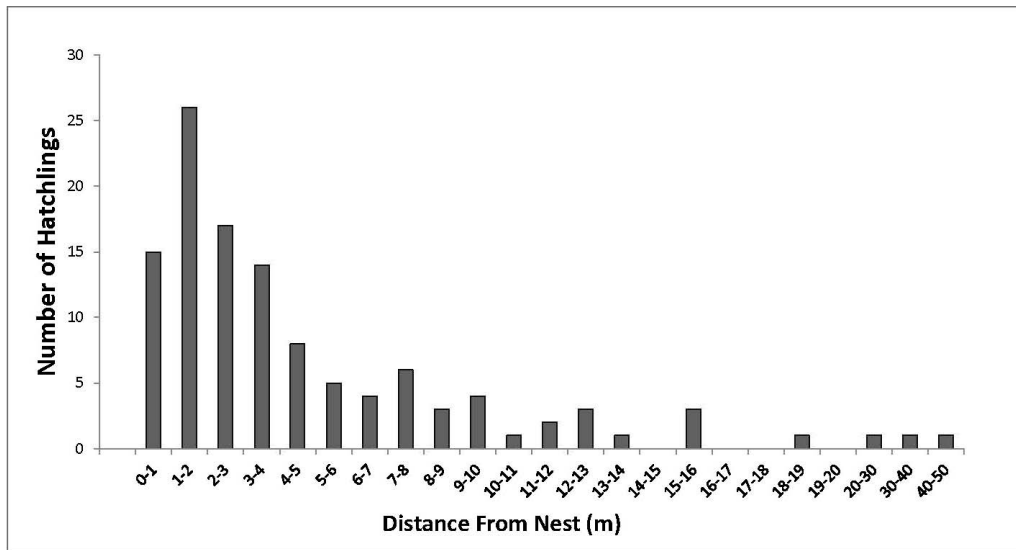


Figure 1. Distance (m) of *Malaclemys terrapin* hatchling refugia from natal nest sites, 2009–2011 ($n = 81$), on Rulers Bar, Jamaica Bay Wildlife Refuge.

of mortality could not be determined. Of these, 1 was found within 5 cm of the surface, 1 was 5–10 cm deep, and 1 was 8–10 cm deep. One of the 9 tags recovered without hatchling remains was found on the ground surface, and 8 were found below the surface.

Hatchlings excavated in their refugia ($n = 4$) were found up to 6 cm below the surface. One hatchling was checked twice; the first time it was 6 cm deep and the second time 3–4 cm deep. After the initial exhumation, a disturbance of the exact site up to a few centimeters below the surface indicated possible evidence of predator activity; despite a signal from the PIT, it had moved upward 2–3 cm and horizontally 3–4 cm, wedging itself

within a root system, apparently in response to disturbance.

Refugia Site Analysis. — The habitat characteristics (% ground cover, % grass, grass height, % bush, bush height, % tree, tree height, % forb cover, forb height, and canopy height) within 1 m of sites where hatchlings successfully overwintered ($n = 58$) differed significantly from those of sites where they buried themselves but did not successfully overwinter (apparently died, $n = 10$; $\chi^2_{10} = 19.3$, $p = 0.037$). The logistic regression model explained 46% (Nagelkerke R^2) of the variance in overwintering success and correctly classified 88% of the cases. None of the variables individually contributed significantly to the model (all $p \geq 0.09$; Table 1).

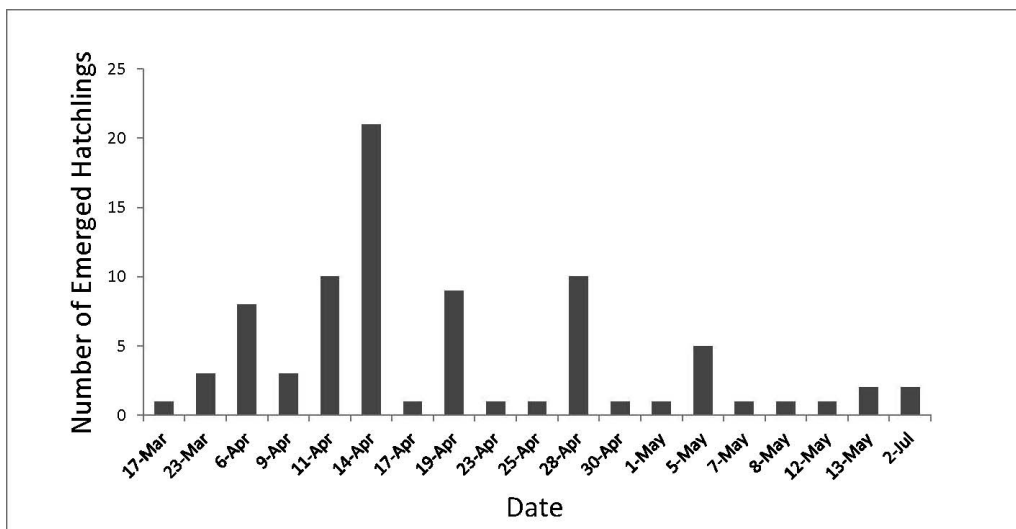


Figure 2. Dates of *Malaclemys terrapin* hatchling emergence from successful overwintering refugia, 2010–2012, on Rulers Bar, Jamaica Bay Wildlife Refuge. Hatchlings generally emerged from refugia from early April to mid-May ($n = 81$).

Table 1. Logistic regression results: comparison of successful refugia (overwinter survival) versus unsuccessful refugia (apparently did not survive).

	B	SE	Wald	df	<i>p</i>	Exp(B)
% Ground cover	0.064	0.043	2.172	1	0.141	1.066
% Grass	-0.031	0.032	0.939	1	0.332	0.970
Grass height	34.943	25.053	1.945	1	0.163	1.499E+15
% Bush	-0.011	0.024	0.207	1	0.649	0.989
Bush height	-0.584	0.810	0.520	1	0.471	0.558
% Tree	-0.034	0.030	1.232	1	0.267	0.967
Tree height	-0.848	0.770	1.216	1	0.270	0.428
% Forb cover	-0.008	0.020	0.157	1	0.692	0.992
Forb height	8.699	5.124	2.882	1	0.090	5999.352
Canopy height	1.527	1.054	2.098	1	0.148	4.604
Constant	-5.833	4.388	1.767	1	0.184	0.003

Logistic regression used to compare the same 10 habitat characteristics within 1 m of temporary refugia ($n = 45$) with overwintering refugia ($n = 68$) indicated that the differences were statistically significant ($\chi^2_{10} = 35.6$, $p < 0.001$). The model explained 38% (Nagelkerke R^2) of the variance in success and correctly classified 77% of the cases. Two variables (% ground cover and % forb cover) were individually significant contributors to the model; all other variables had $p \geq 0.077$ (Table 2). Temporary refugia had lower ground cover ($\bar{x} = 76.9$, $SD \pm 35.0$) and lower forb cover ($\bar{x} = 7.8 \pm 12.8$) than overwintering refugia ($\bar{x} = 97.1 \pm 11.7$ and 18.4 ± 27.9 , respectively).

DISCUSSION

Neonate turtles at high latitudes employ a wide range of strategies to survive their first winter (Ultsch 2006; Costanzo et al. 2008). The strategy of diamond-backed terrapins (*M. terrapin*) is among the most unusual. They may be the only aquatic turtles in which a substantial percentage of the hatchlings leave nests in the fall, travel overland farther from water, and rebury themselves on land elsewhere. This behavior is unlike TON in the terrestrial emydid *T. carolina*, which do not bury themselves (Burke and Capitano 2011), and unlike TON in the aquatic emydid *E. blandingii*, which travel toward aquatic habitats and overwinter in moist soils (Linck and Gillette 2009; Paterson et al. 2012, 2014).

Among other characteristics, the TON strategy requires an ability to tolerate extreme cold temperatures. The ability of hatchling *M. terrapin* to survive whole body freezing is not unusual, as it is also known in 5 other high-latitude emydids (Baker et al. 2003; A.M. Calichio and R.L. Burke, unpubl. data, 2014–2015). In addition to the ability to survive freezing, in the absence of ice nucleators *M. terrapin* hatchlings can also supercool, resisting inoculative freezing even when cooled to $\sim 15^\circ\text{C}$ below their equilibrium freezing/melting point (Baker et al. 2006). This resistance to freezing is exceptional because it is lower than that of any of 8 other high-latitude turtle species (Costanzo et al. 2001). Northern map turtles (*Graptemys geographica*), the out-group species of the sister taxon of *Malaclemys*, may lack freeze tolerance but share the ability to supercool substantially (Baker et al. 2003). These 2 traits should be tested in more *Graptemys* to explore evolution of overwintering strategies in this clade, especially in comparison to *Malaclemys*. Nest depths (~ 12 cm deep; Baker et al. 2003) for *G. geographica* are shallower than for *M. terrapin* at RB (~ 15 cm; Scholz 2006); thus, *M. terrapin* are probably exposed to less extreme temperatures than *G. geographica*. However, *G. geographica* hatchlings have not been observed to use TON strategies as reported here for *M. terrapin*.

Use of the Wrack Line. — Although they use wrack lines occasionally in the fall, these sites are unimportant for *M. terrapin* hatchlings overwintering at RB. No hatchlings from nests more than 5 m from the wrack line were found in

Table 2. Logistic regression results: comparison of temporary refugia versus overwintering refugia.

	B	SE	Wald	df	<i>p</i>	Exp(B)
% Ground cover	0.038	0.018	4.436	1	0.035	1.039
% Grass	0.019	0.011	3.132	1	0.077	1.020
Grass height	-1.681	1.194	1.982	1	0.159	0.186
% Bush	0.010	0.011	0.829	1	0.363	1.011
Bush height	-0.434	0.612	0.502	1	0.479	0.648
% Tree	-0.023	0.021	1.293	1	0.255	0.977
Tree height	0.234	0.496	0.222	1	0.638	1.263
% Forb cover	0.042	0.017	6.167	1	0.013	1.043
Forb height	0.335	0.519	0.417	1	0.518	1.398
Canopy height	0.593	0.540	1.206	1	0.272	1.810
Constant	-4.583	1.740	6.934	1	0.008	0.010

the wrack line, which suggests that hatchlings may use the wrack line only when it is the closest cover. Burger (1976) found that emerging *M. terrapin* hatchlings preferred to move toward vegetation and, if an incline was present, preferred movement downslope; wrack lines are downslope from most RB *M. terrapin* nests. However, we often observed hatchlings climbing the dune face from their nest sites away from a substantial wrack line.

Of the 15 hatchlings that took refuge within the wrack line, 7 could not be found again more than 24 hrs later. They may have been depredated; raccoon tracks and evidence of raccoon foraging were abundant around the wrack line after hatchlings were found. There is some evidence that raccoons prey on hatchlings either after emergence (Rulison et al. 2012) or within the nest after emergence has begun (Burger 1977).

Spring Emergence. — Muldoon and Burke (2012) reported 2 separate pulses of *M. terrapin* hatchling sightings annually over 14 yrs: the first in April–July, peaking May–June, and the second in August–October. The phenology of the April–July pulse is consistent with the dates during which we detected hatchling emergence from overwintering refugia in 2010–2012 (Fig. 2). The possibility that the spring pulse of sightings could be hatchlings utilizing the TON strategy rather than of those emerging after overwintering in their nests (i.e., TIN) is consistent with the findings of Scholz (2006). She found that, of 120 observed RB *M. terrapin* nests in 2004, 114 had only autumn emergence, 4 had partial autumn emergence, and 2 had only spring emergence (Scholz 2006). We suggest that the assumption that turtle neonates found on land in the spring likely overwintered in their nest (e.g., Lovich et al. 2014) should be reexamined, as TON is a viable alternative explanation.

Mortality and PIT Tag Loss. — Most of the hatchlings we tagged were never seen again. They may have been depredated and removed, or they may have moved beyond our tracking abilities. Paterson et al. (2012, 2014) used radiotelemetry to track *E. blandingii* and wood turtle (*Glyptemys insculpta*) hatchlings; 24% and 38%, respectively, of these hatchlings were similarly lost from their study. The tags we used were probably more physically robust than radio transmitters but were detectable over a much smaller spatial range.

Our study was vulnerable to possible mortality caused by PIT tag insertion and to PIT tag loss, but we consider these to be unlikely. In spite of care to sanitize instruments and tags, insertions were conducted under field conditions, and infections may have occurred. Three studies report PIT tag retention in emydid turtles. Runyon and Meylan (2005) found that, of 28 pit-tagged adult pond sliders (*Trachemys scripta*), 8 Florida cooters (*Pseudemys floridana*), and 3 Florida redbelly turtles (*Pseudemys nelsoni*), only 1 tag was lost in the first month, and that was probably due to poor tag placement. Postimplant recaptures showed tags still in place as long as 50 mo after initial insertion. Six of 7 recaptured subadult PIT-tagged *T.*

scripta retained their tags at least 16 mo, and 3 retained tags a minimum of 24 mo (Buhlmann and Tuberville 1998). Only 1 study has tested tag retention in hatchling turtles; of 8 hatchling painted turtles (*Chrysemys picta*) with tags inserted in peritoneal cavities, 2 tags were partially expelled and had to be reinserted within the first 10 d (Rowe and Kelly 2005). Thus, some or all of the 9 tags we recovered without hatchling remains may have been expelled. However, the 3 tagged hatchlings we found with partial remains may have died because of predation, desiccation, or another source of mortality, possibly including factors associated with PIT tags and insertion.

Refugia Depth and Seasonal Movement Within Refugia. — Refugia depth for hatchling *M. terrapin* may vary over the winter, and hatchlings may burrow deeper into hibernacula beyond the range of the antenna system we used. According to the manufacturer (Biomark), the antenna can scan through wood, soil, and water, although the signal is influenced by metals and other electronics, and the read range of the antenna at highest power is optimal when a tag is oriented vertically. The effective read range of the portable antenna with a 2.4-m cable is 9.4 cm deep with the tag at a parallel orientation and 26.7 cm when the tag is oriented perpendicularly (Anonymous 2011). During the 2011–2012 field seasons, 2 hatchlings were located on 9 October and 27 December, respectively. Despite frequent attempts to detect their PIT again at the same locations, signals for both hatchlings were not detected again until 14 April, which is well within the range of known emergence dates from refugia in 2012. The hatchlings were alive all winter and appear to have been buried beyond the scanner detection range, then moved back toward the surface in the spring. Hatchling refugia may extend to depths up to and perhaps greater than 10 cm. This hypothesis is further supported by hatchling remains recovered after burial up to 10 cm deep.

Movement from the Nest. — Overwintering refugia for hatchling *M. terrapin* were usually close to natal nest sites (Fig. 1); 51% overall were < 5 m from the natal nest site, and 59% of successful overwintering refugia were < 5 m from the natal nest site. One possible explanation for this result could be that, as hatchlings traveled farther from nests, we were more likely to lose them despite intensive searches. Another possibility is that *M. terrapin* hatchlings generally do not disperse far from their nests in their search for overwintering sites. Paterson et al. (2014) considered the hypothesis that turtle hatchlings (*E. blandingii* and *G. insculpta*) may leave their nests and overwinter elsewhere to lower the risk of predation and to minimize thermal extremes because ideal incubation conditions may not match ideal overwintering conditions. Nearly all nest predation at Jamaica Bay occurs in the first few days after oviposition (Feinberg and Burke 2003), but *M. terrapin* nests elsewhere often face predation by canids during the fall hatchling emergence season (R.L.B., *pers. obs.*). Thus, leaving the nest may minimize the second round of predation.

Fourteen of the *M. terrapin* hatchlings we tracked (17% of tracked hatchlings) moved extensively and overwintered > 10 m upland from their nest sites. It is unclear why *M. terrapin* hatchlings leave their nests to overwinter terrestrially elsewhere. TIN may be associated with numerous risks and benefits (Costanzo et al. 2008; Muldoon and Burke 2012), all of which appear just as likely to occur in the overwintering refugia chosen by *M. terrapin* hatchlings (TON). Two are especially relevant here. First, Costanzo et al. (2004) found that large groups of sibling *C. picta* hatchlings overwintering in the nest had higher survival than small groups, a conclusion that makes the observation that *M. terrapin* leave their siblings and overwinter alone difficult to explain. Second, Costanzo et al. (2008) suggested that overwintering in the nest might be energetically advantageous compared with overwintering in water because the colder conditions in the nest could result in lower metabolic demands. Overwintering *M. terrapin* hatchlings that we excavated were at shallower depths (1–6 cm) than the average nest depth in RB, so perhaps they left nests for shallower, colder overwintering refugia. However, it seems they could more easily remain in the nest and dig upward in the substrate. Although King (2007) showed that some *M. terrapin* hatchlings feed in *Spartina* marshes as early as the spring after hatching, we saw no direct or indirect evidence of foraging or feeding in the fall-emerged hatchlings. Paterson et al. (2014) similarly saw no evidence of foraging by hatchling *E. blandingii* or *G. insculpta* as they moved to overwintering sites and presumed these turtles were only metabolizing yolk reserves. Clearly, more research, especially comparing conditions of TON and TIN, would be valuable.

Refugia Site Selection. — Successful hatchling overwintering refugia had a higher frequency of grass, forb, bush, and tree cover than unsuccessful overwintering refugia. The most important criterion for a successful overwintering refugium may be greater percentage of ground cover. Movement from temporary to permanent refugia may reflect searching for an aspect of substrate cover necessary for successful overwintering. Paterson et al. (2012) suggested that overwintering turtle hatchlings select sites that minimize risks of predation and desiccation. They found that *E. blandingii* and *G. insculpta* showed microhabitat and macrohabitat preferences as they traveled to specific overwintering habitat types.

Hatchling *M. terrapin* may select refugia based on a suite of aboveground environmental factors; clearly, some sort of vegetative cover is important at a refugium. Vegetative cover is also important to *M. terrapin* nest-site choice and hatching success at Jamaica Bay but in the opposite direction—females choose nest sites with little vegetation, and hatching success is highest in sites with little or no vegetation (Scholz 2006). Movement away from the nest may be an attempt to shift from optimal incubation sites to optimal overwintering sites (sensu Spencer and Janzen 2014). This hypothesis would imply that TON refugia likely differ from nest sites but is weakened by our finding that most hatchlings overwintered only short distances from their

nest sites. This result may be due to differences in ground cover within a few meters of the natal nest.

Desiccation may be an important source of morbidity and mortality for hatchling turtles on land (reviewed by Muldoon and Burke 2012), especially for those overwintering on land. Costanzo et al. (2001) showed that desiccation resistance varied dramatically among hatchlings of 8 other high-latitude turtle species and that those species that overwintered terrestrially were both more resistant to inoculative freezing and generally more desiccation resistant than those that typically overwintered in water. Costanzo et al. (2001) therefore predicted that resistance to inoculative freezing and desiccation are highly correlated. In contrast, although *M. terrapin* is highly resistant to inoculative freezing (Baker et al. 2006), we predict that they are not also particularly desiccation resistant. We suggest that hatchling *M. terrapin* utilize the TON strategy to find refugia with relatively high moisture content to avoid desiccation. Similarly, Linck and Gillette (2009) noted that *E. blandingii* hatchlings chose overwintering sites on the edge of wetlands in damp soil, again perhaps to minimize desiccation. Further, *E. blandingii* were found not to be resistant to evaporative water loss and were freeze tolerant rather than having the ability to supercool (Dinkelacker et al. 2004). The authors offer that hatchling hibernacula must be found in moist microenvironments where water loss is minimal. These strategies warrant further investigation, especially in *M. terrapin*.

ACKNOWLEDGMENTS

All procedures were approved by Hofstra University's Institutional Care and Use Committee. We thank Biomark, Inc., for the generous loan of equipment during the early field trial stage of this project. For financial support, we are indebted to the National Park Service's Jamaica Bay Institute, the American Museum of Natural History Lerner Gray Fund for Marine Research, and the South Shore Audubon Society. We were assisted in data collection by the diamond-backed terrapin research team, especially Alex Kanonik, Shahriar Caesar Rahman, and Nathaniel Stanek. We thank Ronald Samo, Darrel Frost, Chris Raxworthy, E. Bernstein, Angelo Soto-Centeno, Fred Janzen, and anonymous reviewers for very helpful editorial comments.

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Received: 4 February 2016

Revised and Accepted: 13 June 2016

Handling Editor: Peter V. Lindeman