

Movements, overwintering, and mortality of hatchling Diamond-backed Terrapins (*Malaclemys terrapin*) at Jamaica Bay, New York

K.A. Muldoon and R.L. Burke

Abstract: As with other turtles, the postemergent movements, overwintering behaviours, and survivorship of hatchling Diamond-backed Terrapins (*Malaclemys terrapin* (Schoepff, 1793)) are poorly known, but anecdotal reports suggest that they may spend more time on land than most aquatic turtles. We investigated this behaviour using drift fences with pitfall traps on the island of Ruler's Bar, Jamaica Bay, New York, fall 2006 to spring 2008. We captured 324 live hatchling Terrapins, 95 were recaptured at least once, and we found 43 dead. After emergence from nests in the fall, most hatchlings moved up-land away from the water; this pattern was reversed in the spring. Hatchling body sizes shrank during winter, probably owing to desiccation, and hatchlings were more likely to move on warmer days and days without precipitation. We recaptured some hatchlings on land as long as 9 months after emergence. As a result, hatchling *M. terrapin* were seen on land from April to December, well outside fall and spring during which they emerge from nests, and we found strong evidence that hatchling *M. terrapin* overwinter on land outside their nests. One important nest predator (raccoons, *Procyon lotor* (L., 1758)) was also an important hatchling predator, as were Norway rats (*Rattus norvegicus* (Berkenhout, 1769)). Future work should investigate the terrestrial microhabitats used by hatchling *M. terrapin*, and management should protect hatchlings during this life stage.

Key words: hatchling, turtle, overwinter, drift fence, movements, survival, freeze, terrestrial, Diamond-backed Terrapin, *Malaclemys terrapin*, raccoon, *Procyon lotor*, Norway rat, *Rattus norvegicus*.

Résumé : Si, comme pour d'autres tortues, les connaissances sur les mouvements post-émergents, les comportements hivernaux et la survie des bébés tortues à dos diamanté (*Malaclemys terrapin* (Schoepff, 1793)) sont limitées, des signalements anecdotiques suggèrent qu'ils passeraient plus de temps en milieu terrestre que la plupart des tortues aquatiques. Nous avons étudié ce comportement à l'aide de clôtures de déviation et de pièges à fosse, dans l'île de Ruler's Bar, dans la baie de la Jamaïque (État de New York), de l'automne 2006 au printemps 2008. Nous avons capturé 324 bébés tortues vivants, dont 95 ont été recapturés au moins une fois et 43 ont été retrouvés morts. Après l'émergence du nid à l'automne, la plupart des bébés se sont dirigés vers les terres, s'éloignant de l'eau; au printemps, ce déplacement s'inversait. La taille du corps des bébés a diminué durant l'hiver, probablement en raison de la dessiccation, et les bébés étaient plus susceptibles de se déplacer durant des jours plus chauds et sans précipitations. Des bébés ont été recapturés en milieu terrestre jusqu'à neuf mois après leur émergence. Ainsi, des bébés *M. terrapin* ont été observés sur terre d'avril à décembre, bien en dehors des périodes automnale et printanière durant lesquelles ils émergent du nid. Des observations probantes indiquent en outre qu'ils passeraient l'hiver sur terre, hors du nid. Un important prédateur de nids (le raton laveur, *Procyon lotor* (L., 1758)) s'est également avéré être un important prédateur de bébés, tout comme le rat surmulot (*Rattus norvegicus* (Berkenhout, 1769)). Des travaux futurs devraient se pencher sur les microhabitats terrestres utilisés par les bébés *M. terrapin*, et des efforts d'aménagement devraient être déployés pour protéger les bébés durant cette étape de leur cycle de vie.

Mots-clés : bébés, tortue, comportement hivernal, clôture de déviation, déplacements, survie, gel, terrestre, tortue à dos diamanté, *Malaclemys terrapin*, raton laveur, *Procyon lotor*, rat surmulot, *Rattus norvegicus*.

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Introduction

The ecology of hatchling turtles is poorly known, despite its importance to life-history models and management plans (Morafka 1994). This is primarily because turtle hatchlings typically occur in low densities, are inconspicuous, and until recently, radio-tracking technology was too large for use on

such small animals (i.e., <6 g). On land, turtle hatchlings are vulnerable to predation (Janzen et al. 2000), desiccation (Gregory 1982; Finkler et al. 2000; Kolbe and Janzen 2002), and thermal stress through either overheating or freezing (Dinkelacker et al. 2005a, 2005b; Baker et al. 2006). Nevertheless, hatchlings of some other members of the family Emydidae spend a considerable amount of time on land out-

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side the nest (e.g., Sliders, *Trachemys scripta* (Thunberg in Schoepff, 1792): Moll and Legler 1971; Blanding's Turtles, *Emys blandingii* Holbrook, 1838: Butler and Graham 1995; Standing et al. 1997; McNeil et al. 2000; Linck and Gillette 2009; Wood Turtles, *Glyptemys insculpta* (LeConte, 1829): Castellano et al. 2008; Walde et al. 2008; and Eastern Box Turtles, *Terrapene carolina* (L., 1758): Burke and Capitano 2012). Although emergence of turtle hatchlings from nests is influenced by a variety of factors (Costanzo et al. 2008), little is known about the environmental conditions that affect terrestrial movements after emergence.

Another feature of the ecology of hatchling turtles that is poorly known in temperate zone species is overwintering locations. Hatchlings of most aquatic turtle species emerge from their nests in the fall and move immediately to water (Ehrenfeld 1979; Ultsch 2006), where they are difficult to follow. This pattern is not ubiquitous; hatchlings of some aquatic species spend their first winter in the nest (Costanzo et al. 2008). Costanzo et al. (1995) therefore summarized aquatic turtle hatchling overwintering location options as (i) terrestrial hibernation in shallow nests, (ii) terrestrial hibernation deep underground (below the nest), and (iii) aquatic hibernation. The specific locations of hatchlings overwintering in water are known for very few species (Ultsch et al. 2007). Costanzo et al.'s (1995) three options do not include terrestrial hibernation at or near the ground surface outside the nest, as occurs in some *E. blandingii* (Butler and Graham 1995; Linck and Gillette 2009). Variation in overwintering patterns also exists both among and within species of Emydidae; overwintering patterns can even vary within a clutch (i.e., *T. scripta*: Costanzo et al. 2001; Northern Map Turtles, *Graptemys geographica* (LeSueur, 1817): Nagle et al. 2004).

The hatchling ecology of the Diamond-backed Terrapin (*Malaclemys terrapin* (Schoepff, 1793)) is particularly enigmatic. *Malaclemys terrapin* are medium-sized turtles that primarily inhabit estuarine smooth cordgrass (*Spartina alterniflora* Loisel.) marshes along the east and Gulf coasts of the United States. *Malaclemys terrapin* oviposit from May to August (Feinberg and Burke 2003; Ernst and Lovich 2009), generally within 100 m of shore; nests are usually laid in sandy areas and on vegetated dunes (Seigel 1980; Roosenburg 1994; Scholz 2007). Hatchlings emerge in the fall (August–September) and spring (April–May) (Scholz 2007). Nest and egg survivorship have been well studied (Burger 1976, 1977; Auger and Giovannone 1979; Lazell and Auger 1981; Roosenburg 1992; Roosenburg and Place 1995; Feinberg and Burke 2003; Butler et al. 2004; Ner and Burke 2008); egg mortality owing to predation is often very high. Little is known regarding the survivorship of hatchling *M. terrapin*, although their predators are diverse, e.g., ghost crabs (*Ocypode quadrata* (Fabricius, 1787)) (Arndt 1991, 1994; Zimmerman 1992; Butler et al. 2004), praying mantids (species unknown) (D. Reipe, unpublished data), Norway rats (*Rattus norvegicus* (Berkenhout, 1769)) (Draud et al. 2004), raccoons (*Procyon lotor* (L., 1758)) (Burger 1977; Butler et al. 2004; Rulison 2009), red fox (*Vulpes vulpes* (L., 1758)), Laughing Gulls (*Leucophaeus atricilla* (L., 1758)), and Black-crowned Night Herons (*Nycticorax nycticorax* (L., 1758)) (Burger 1976, 1977). Nothing is known about the environmental factors that influence terrestrial movements of hatchling *M. terrapin*, but anecdotal evidence suggests that

they spend a considerably larger fraction of posthatching time on land than do most aquatic turtles (Pitler 1985; Lovich et al. 1991; Roosenburg 1991). In addition to survivorship, little has been reported concerning the movements of hatchling *M. terrapin* after emergence, although Burger (1976) and Butler et al. (2004) reported on hatchling movement immediately after emergence, and Draud et al. (2004) reported on both hatchling terrestrial overwintering sites and predation by *R. norvegicus* after emergence.

Our primary goal was to test the hypothesis that hatchling *M. terrapin* routinely overwinter on land. Our hypothesis was based on (i) Draud et al.'s (2004) observation of predation by *R. norvegicus* on hatchlings emerging from terrestrial hibernacula in the spring; (ii) Baker et al.'s (2006) demonstration that hatchling *M. terrapin* are freeze tolerant, while at our study site (see below), hatchlings rarely overwinter in the nest (Ultsch 2006); (iii) Rulison's (2009) observation of remains of hatchling *M. terrapin* in the diets of *P. lotor* in early July, indicating that hatchlings were on land some 9 months after emergence; (iv) Pitler's (1985) observation of hatchling and juvenile *M. terrapin* under wrack (dried marine vegetation and other debris) lines in New Jersey, well outside the normal season of emergence; and (v) Kinneary's (2008) observation that hatchling *M. terrapin* readily feed on land, unlike most water turtles. Furthermore, we sought to identify the environmental factors associated with hatchling terrestrial movements (as demonstrated by Butler et al. 1995 and Keller et al. 1997), investigate whether overwintering on land might be advantageous, and identify important hatchling predators. We hypothesized that hatchlings would be more likely to move under conditions that minimized thermal stress, desiccation, and predation risk.

Materials and methods

Field site

Rulers Bar (RB) is a 458 ha island (40°36'58.68"N, 73°50'07.63"W) near the center of Jamaica Bay (JB). JB is divided evenly by the borders of Brooklyn and Queens boroughs, New York City, New York, USA, and has the largest population of Diamond-backed Terrapins in New York State (Feinberg and Burke 2003; R.L. Burke unpublished data). Over 95% of nests of western JB Diamond-backed Terrapins are laid on RB (Ner and Burke 2008). RB is located near the center of the range of the subspecies Northern Diamond-backed Terrapin (*Malaclemys terrapin terrapin* (Schoepff, 1793)).

RB is part of the Gateway National Recreation Area, managed by the National Park Service. From 1979 to 1992, National Park Service employees regularly recorded wildlife observations that they made while in the field. We examined all available National Park Service records for reports of hatchling Diamond-backed Terrapins. Search time was not recorded, so these data cannot be adjusted for search effort.

Hatchling captures

All work was carried out under permits from Hofstra University's Institutional Animal Care and Use Committee, as well as appropriate federal and state authorities. In fall 2006, spring and fall 2007, and spring 2008, we installed drift-fence lines near ocean shorelines, using 13 cm high alumi-

num flashing with metal stakes to anchor the flashing. We chose drift fences with pitfalls over radio telemetry because hatchling *M. terrapin* are small (some <3.7 g) and available transmitters with useful battery life were greater than the usual 10% mass limit for telemetry packages (Beaupre et al. 2004). We distributed the drift fences among six RB field locations with different habitat types (dune, light shrub, heavy shrub, gravel trail) where high levels of nesting activity of *M. terrapin* had occurred in previous years (R.L. Burke, unpublished data). Fences were positioned in arrays of two to four lines between nesting areas and ocean shorelines, through nesting areas parallel to shorelines, and parallel but upland from nesting areas. Fence-line length (mean = 7.8 m, range = 3.9–13.4 m) varied according to habitat patch size. We removed drift fences between sampling seasons except between spring 2007 and fall 2007. Dates of fence establishment varied among seasons and years, but for each season, all fence lines were installed at least 2 days before the first hatchling was captured at any fence. We adjusted the number of fence lines and traps each season to add new sites or make adjustments because of erosion and storm damage. The number of drift fences varied from 10–11 per season.

We buried pairs of pitfall traps made from plastic liter-sized milk containers along each side of each drift fence at 1 m intervals, and one pair at each end. The number of traps varied from 242–294 per season. We used two styles of pitfall traps: one made by cutting the milk containers in half transversely and using only the bottom half of the container, and the other by placing the container on its side and cutting a 5 cm × 7 cm rectangular hole on the top of the container. We cut four puncture holes in the bottom of each trap for drainage. We buried the traps into the substrate with the lip of the trap opening flush with the substrate surface and placed a thin layer of sand and dried plant material in each for refuge. We maintained fence lines and traps daily, removing sand that accumulated along the fences and in traps, trimming vegetation that abutted the fence by hand, and repositioning traps exposed by erosion.

We checked all pitfall traps daily, generally between the hours of 1200 and 2000, except in fall 2007 when we checked them until 2300. We photographed and measured carapace and plastron lengths and widths with Pittsburgh® digital calipers to the nearest 0.01 mm, and recorded locations (site, fence line, trap number, and side of the fence) of all hatchlings. Hatchlings caught in pitfalls were released under nearby vegetation on the opposite side of the fence. Hatchlings found walking along the fence line but not in a trap were processed and replaced at the capture site. We marked each hatchling with a unique identification number using a Sharpie® marker on its carapace and plastron. We recorded the date, location, and condition of hatchlings found dead and attempted to determine sources of mortality.

We measured the effects of air temperature and precipitation on the movements of hatchling *M. terrapin* using the number of hatchlings recaptured per trap-night as an index of activity. We limited most of our analyses in both seasons to recaptured individuals, so as not to confound our data with hatchling nest emergence patterns because at RB hatchling *M. terrapin* emerge in both fall (August and September) and spring (April and May) (Ultsch 2006; Scholz 2007). In addition, emergence of RB hatchling *M. terrapin* tends to oc-

cur synchronously among multiple nests (R.L. Burke, unpublished data), which would tend to obscure tests of any general relationship between environmental factors and terrestrial movements by hatchlings that had emerged previously.

Photograph identification

Because our marking system was not permanent, we also used photographic records of plastron patterns as a second method to identify recaptures. We compared all photographs from all hatchlings for the four field seasons to each other to test whether we failed to identify a previously caught hatchling as a recapture. For each hatchling photograph, we located an unusual pattern or design on its plastron and twice searched by eye all other photographs for the same pattern.

Predator surveys

We surveyed daily for predator tracks while checking traps and walking on the beach. We also monitored predator presence using powdered track plates and motion sensitive cameras (Long et al. 2008) along the drift-fence lines.

Statistical analysis

The number of hatchlings per day was calculated using the total number of hatchlings that fell into each trap per day (hand captures were excluded) divided by the number of traps open the previous 24 h during the active season (from the date of the first capture to that of the last capture for that season). We compared carapace and plastron lengths of individuals recaptured between seasons using one-tailed (because we expected them to grow) Wilcoxon rank-sum tests for paired data. We compared carapace and plastron lengths of individuals captured in fall 2006 with those captured in fall 2007, and similarly compared individuals captured in spring 2007 with those captured in spring 2008, using two-tailed Student's *t* tests.

We used local weather data (daily low, mean, and high air temperatures, and daily rainfall) recorded at a weather station located at John F. Kennedy International Airport (4 km NE from the study site) collected by the US National Weather Service. We compared the daily minimum, mean, and high temperatures for fall activity seasons (combined 2006 and 2007) and spring activity seasons (combined 2007 and 2008) using two-tailed Student's *t* tests. We combined hatchling capture data from both fall seasons into a single fall data set, and both spring seasons into a single spring data set, and tested for possible effects of environmental conditions on hatchling movements three ways. We used recaptures only to avoid inflation of our data because of newly emerged hatchlings. First, we used regression analysis to compare the number of hatchlings captured per day with the daily low, daily mean, and daily high air temperatures for each season and for both seasons combined. Second, we compared the temperatures (daily minimum, mean, and maximum) on days when we had at least one recapture with days on which there were no recaptures, using two-tailed Student's *t* tests. Third, for each seasonal data set, we divided the daily precipitation data into the smallest possible precipitation intervals (i.e., number of days) that resulted in a minimum of five hatchling recaptures in each interval, predicted the random probability of hatchling captures based on the number of days in each interval and the total number of hatchlings captured, and

compared these predictions with observed data using χ^2 tests. Values are reported as mean \pm SD, unless otherwise specified.

Results

Capture–recapture rates

We captured 324 hatchling *M. terrapin* (dead and alive) and made 433 recaptures (dead and alive) in the four field seasons (fall 2006, spring 2007, fall 2008, and spring 2008) (Figs. 1–4) combined. Ninety-five hatchlings were recaptured at least once within the same season as their first capture. National Park Service employees found 228 terrestrial hatchling *M. terrapin* on RB from 1979 to 1992. Terrestrial hatchlings were found every month of the year except January, February, and March (Fig. 5).

Interseasonal comparisons of body size

The number of hatchling *M. terrapin* captured in pitfall traps per day during the active seasons varied; in general, we captured fewer in 2006–2007 (fall 2006: 1.32 ± 1.81 hatchlings captured/day; spring 2007: 0.88 ± 1.07 hatchlings captured/day) than in 2007–2008 (fall 2007: 2.63 ± 3.50 hatchlings captured/day; spring 2008: 2.37 ± 2.92 hatchlings captured/day). Hatchlings captured in fall 2006 were significantly larger in plastron length than those captured in spring 2007 ($t_{[58]} = 4.15$, $P = 0.0001$), but not in carapace length ($t_{[38]} = 1.89$, $P = 0.06$). Hatchlings captured in fall 2007 were not significantly different in plastron length than those captured in spring 2008 ($t_{[145]} = 1.59$, $P = 0.11$), but those captured in fall 2007 were significantly larger in carapace length than those captured in spring 2008 ($t_{[124]} = 2.81$, $P = 0.006$).

We captured 18 hatchling *M. terrapin* in fall seasons (2006 and 2007 combined) that we recaptured in the subsequent spring. The length of time between these fall captures and spring recaptures ranged from 183 to 276 days (226 ± 27.4 days). In the spring, 4 of these 18 were found upland (farther from water) from their fall capture sites; 9 were found near the same location as in fall, and 5 were found closer to water than their fall locations. Two of those that moved upland traveled at least 85 m from fall capture location to spring recapture location.

Eight of the 18 hatchlings that we caught in both the fall (2006 and 2007 combined) and subsequent spring decreased in carapace length from fall to spring, losing 0.35%–3.6% of their fall length. We failed to measure 5 of the 18. Four were unchanged in carapace size, and one grew 1.4% in carapace length. Ten of the 13 hatchlings decreased in plastron size, losing 0.4%–10% of their fall length. Three hatchlings grew in plastron length, gaining 0.85%–8.6% of their fall length. Overall, the fall–spring recaptures had significantly smaller carapace lengths (Wilcoxon rank-sum test, $W_+ = 40.50$, $P = 0.014$) and smaller plastron lengths ($W_+ = 72$, $P = 0.034$) in spring compared with the previous fall, that is, they shrank over the winter.

Intraseasonal movements

In fall 2006, 26 hatchling *M. terrapin* captured in pitfall traps were recaptured later that fall having moved away from the shoreline and 21 were recaptured closer to the shoreline (this difference was not significant, $\chi^2_{[1]} = 0.53$, $P = 0.46$) (Fig. 6). In fall 2007, significantly more (85 of 138) hatch-

lings captured in pitfall traps were recaptured later that fall having moved away from the shoreline than moving towards the shoreline ($\chi^2_{[1]} = 12.58$, $P = 0.0004$) (Fig. 6). In spring 2007, significantly more (16 of 19) hatchlings captured in pitfall traps were recaptured having moved towards the shoreline ($\chi^2_{[1]} = 7.2$, $P = 0.007$) than away from the shoreline (Fig. 6). Again in spring 2008, significantly more (45 of 67) hatchlings captured in pitfall were recaptured having moved towards the shoreline ($\chi^2_{[1]} = 8.4$, $P = 0.004$) than away from the shoreline (Fig. 6).

The longest time a hatchling remained on land between recaptures within a fall season was 61 days. The longest time a hatchling remained on land within either spring season was 17 days. The longest time between recaptures of the same hatchling was 276 days from fall to spring.

Hatchling activity patterns and environmental conditions

Daily minimum, mean, and maximum temperatures were higher in the fall activity seasons than in the spring activity seasons ($t_{[188]} = 5.40$, $P < 0.001$; $t_{[164]} = 3.93$, $P < 0.001$; and $t_{[144]} = 2.44$, $P = 0.016$, respectively). We found no significant relationships between any temperature variable and the number of recaptures per trap-night using regression analysis (all $P > 0.08$). However, in both fall seasons combined, days in which hatchlings were recaptured had higher mean temperatures and higher minimum temperatures ($t_{[60]} = 2.05$, $P = 0.044$ and $t_{[60]} = 2.03$, $P = 0.046$, respectively), but not maximum temperatures ($t_{[60]} = 1.94$, $P = 0.057$). In contrast, in the combined spring data, we found that the temperature on days in which recaptured hatchlings were captured were not different (minimum, mean, or maximum) from the temperature on days without captures (all $P > 0.116$).

Precipitation affected hatchling movement in both fall and spring seasons. In fall seasons, hatchlings moved on days with no precipitation, and on days with very heavy precipitation (>6.10 mm rain), in relatively greater proportion than the occurrence of these events ($\chi^2_{[2]} = 6.74$, $P = 0.034$). In spring seasons, hatchlings moved on days with no precipitation and less on days with heavy precipitation (>1.8 mm rain) in relatively greater proportion than the occurrence of these events ($\chi^2_{[2]} = 7.44$, $P = 0.024$).

Hatchling predation and predators

We found 43 dead hatchling *M. terrapin* during the four field seasons combined (Figs. 1–4). All dead hatchlings were dead less than 24 h, the time between our previous trap check and our return the next day. We found 26 dead hatchlings in traps and 17 dead hatchlings on wrack lines or sand. Twenty-six (60%) of the dead hatchlings were missing limbs or heads, or punctured and disemboweled through either the carapace or plastron.

Procyon lotor were common in all trapping areas. We observed *P. lotor*, mostly during the evening, while they were preying on nests of *M. terrapin*, foraging, and walking alongside active fence lines in every field season. We regularly observed tracks of *P. lotor* alongside fence lines. Video recordings, pictures from motion-sensitive cameras, and track plates all showed that *P. lotor* were often present and active in known hatchling areas. We also observed tracks of *R. norvegicus* on nearby beaches. We regularly saw birds that may

Fig. 1. The frequency of newly captured, recaptured, and dead hatchling Diamond-backed Terrapins (*Malaclemys terrapin*) in Fall 2006. New captures are indicated in black, recaptures in white, and dead hatchlings in gray.

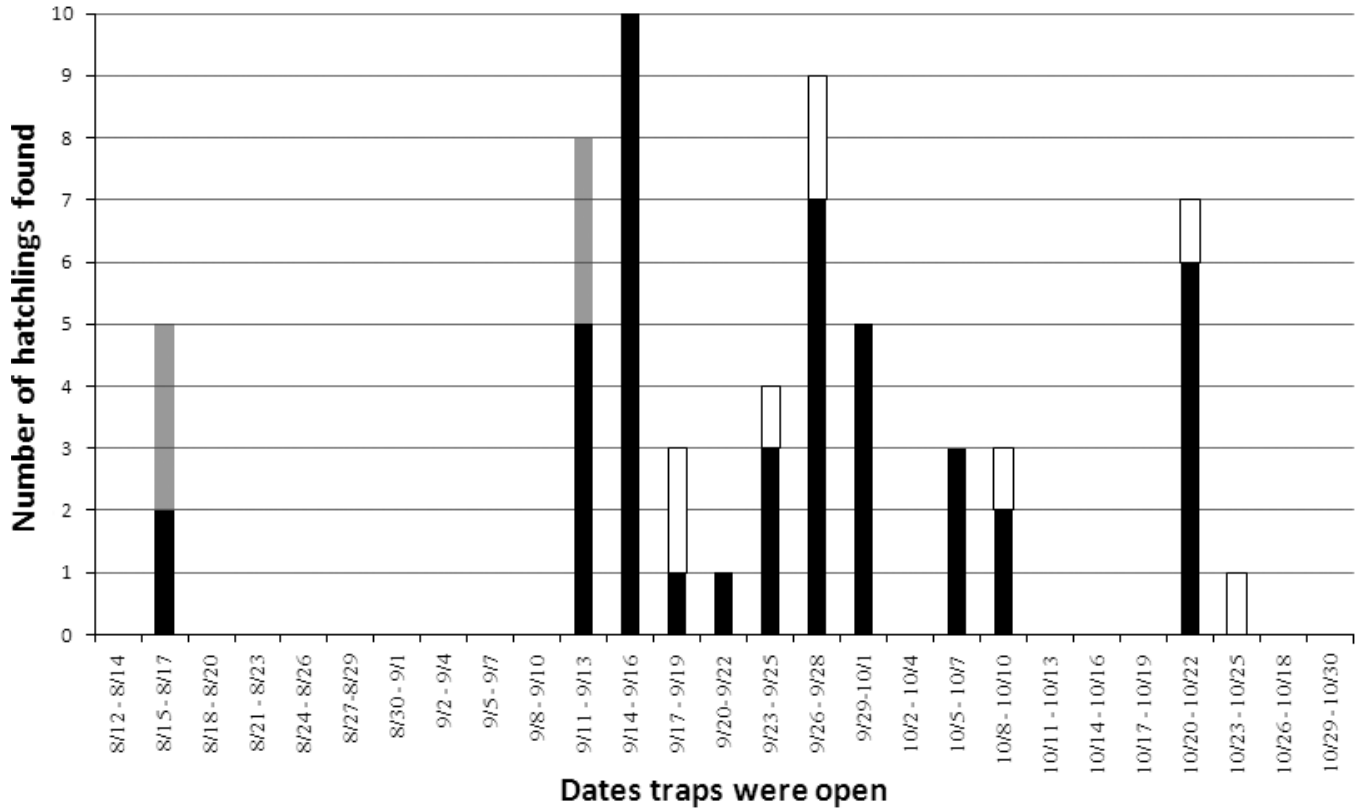
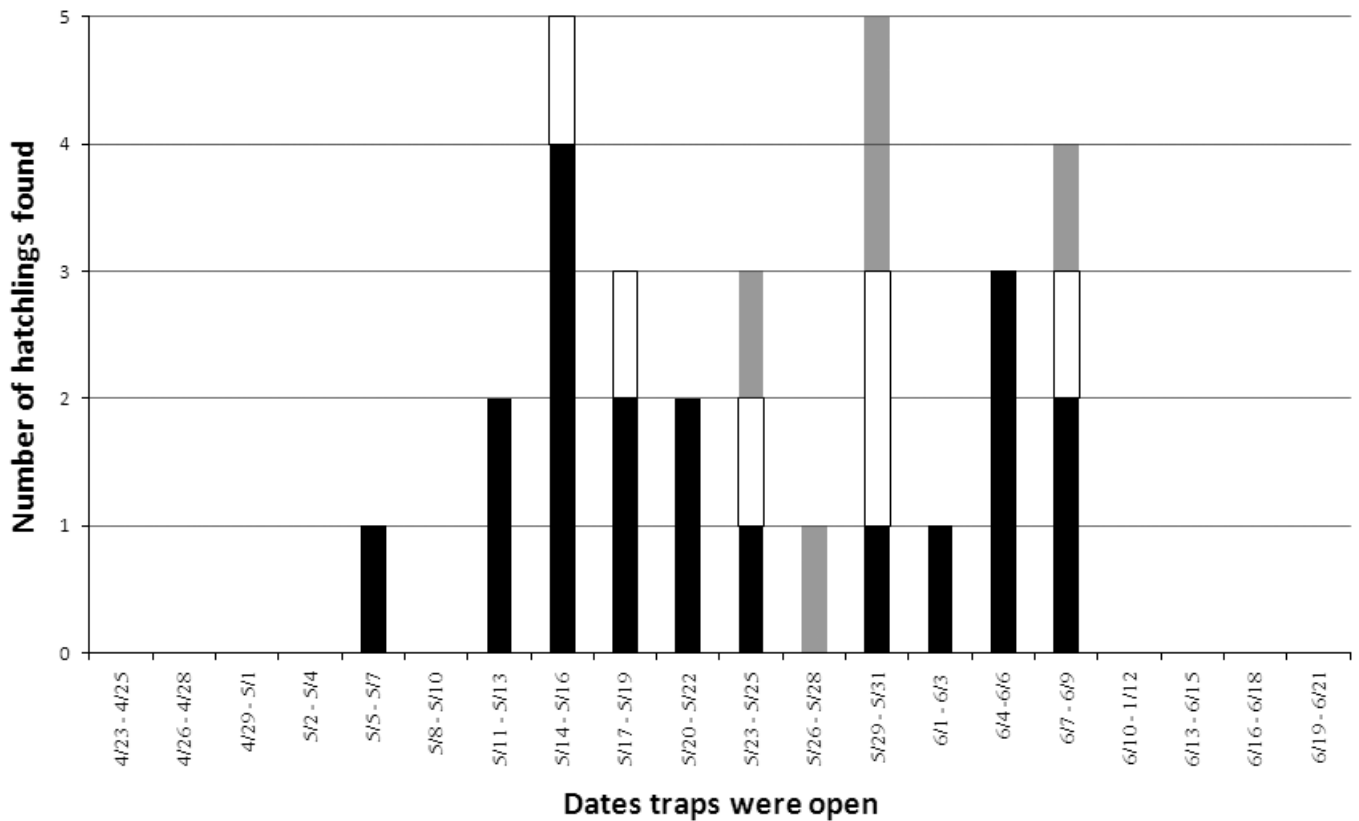
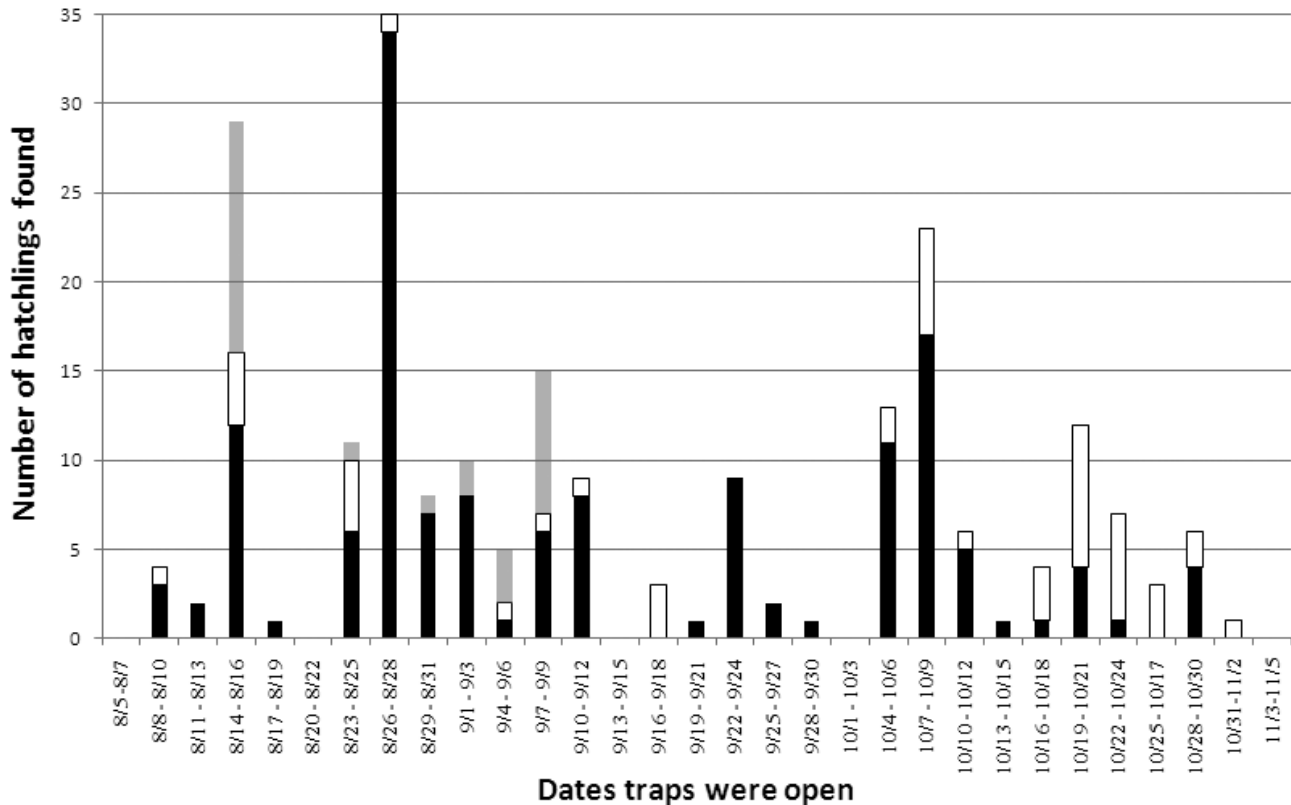


Fig. 2. The frequency of newly captured, recaptured, and dead hatchling Diamond-backed Terrapins (*Malaclemys terrapin*) in Spring 2007. New captures are indicated in black, recaptures in white, and dead hatchlings in gray.



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Fig. 3. The frequency of newly captured, recaptured, and dead hatchling Diamond-backed Terrapins (*Malaclemys terrapin*) in Fall 2007. New captures are indicated in black, recaptures in white, and dead hatchlings in gray.



have been predators of hatchling *M. terrapin* (e.g., *L. atricilla*; Herring Gulls (*Larus argentatus* Pontoppidan, 1763); Ring-Billed Gulls (*Larus delawarensis* Ord, 1815); Great Blue Herons (*Ardea herodias* L., 1758); *N. nycticorax*; Yellow-Crown Night Herons (*Nyctanassa violacea* (L., 1758)); Fish Crows (*Corvus ossifragus* Wilson, 1812)) in the study area; however, we never witnessed avian predation on hatchling *M. terrapin*.

Discussion

Capture rate patterns

We caught more hatchling *M. terrapin*, both initial captures and recaptures, in fall 2006 and 2007 than in either spring sampling season. This is probably because most hatchlings emerged from their nests in the fall rather than spring, and with placement of drift fences near nesting areas, we captured hatchlings as they emerged and moved away from nests. This is the same pattern observed by National Park Service personnel (Fig. 5). Hatchling *M. terrapin* rarely overwinter in the nest at RB (Ultsch 2006), but this pattern may be different at different locations (Baker et al. 2006). In the spring seasons, there also may have been fewer hatchlings owing to overwintering mortality and (or) they may have dispersed so they evaded our drift fences. We found the greatest numbers of hatchlings in all four field seasons in the same areas that had the highest density of nests of *M. terrapin* at RB (R.L. Burke, unpublished data).

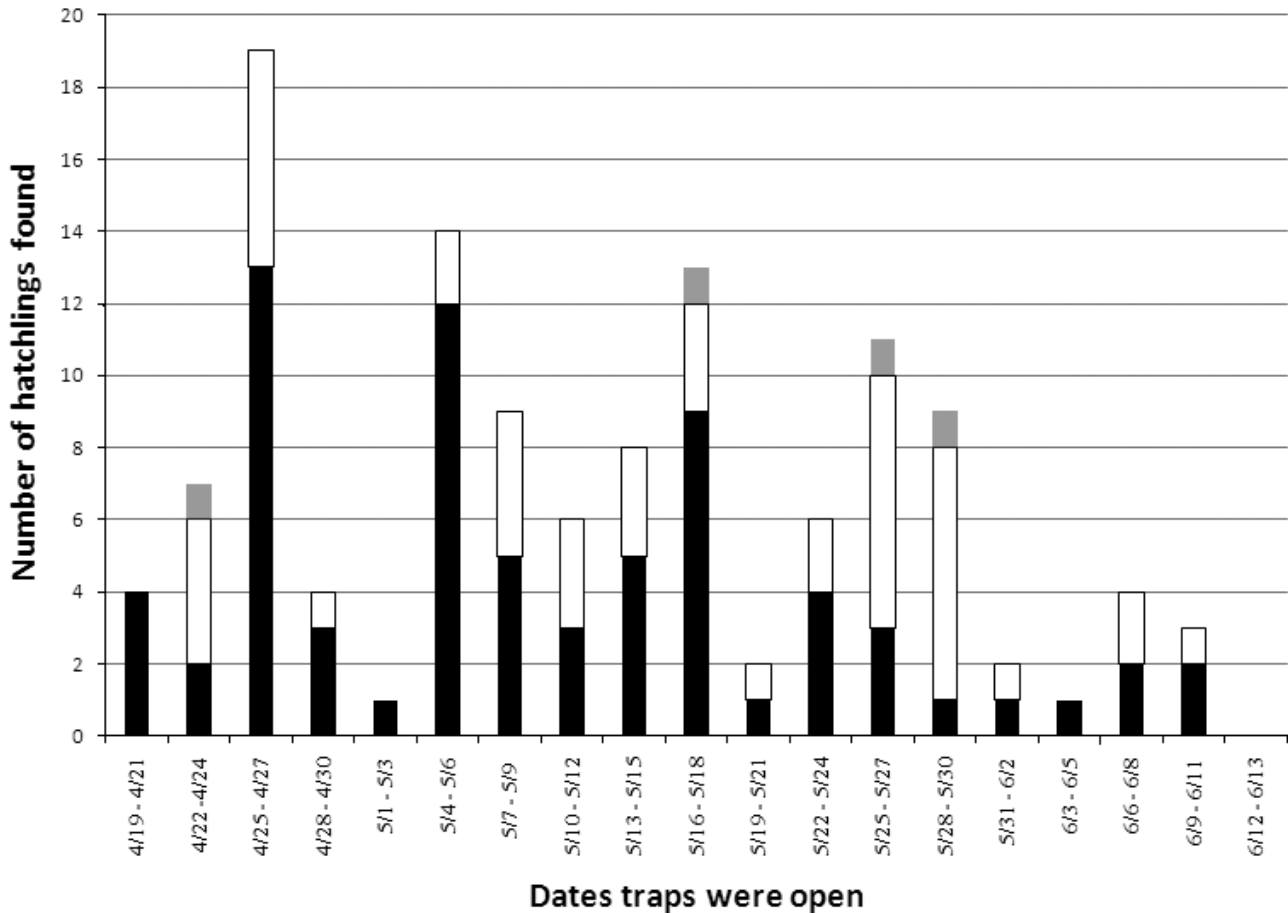
Postemergent movement patterns

We found that RB hatchling *M. terrapin* had a consistent

pattern: in the fall, substantial numbers of hatchlings (55%–64%) moved away from water, whereas in spring, most (68%–80%) moved towards water (Fig. 6). Similarly Roosenburg et al. (2009) reported hatchling *M. terrapin* captured from natural nests and released into the water in September and October returned to land and sought higher ground. Butler et al. (2004) found that 93% ($n = 172$) of crawl trails of postemergent *M. terrapin* headed in the direction of terrestrial vegetation or an adjacent salt marsh and not to the nearby open water. Draud et al. (2004) radio-tracked eight hatchling *M. terrapin* that remained on land after hatching at least through October. Burger (1976) found that hatchling *M. terrapin*, both in laboratory and field conditions, moved up or along unvegetated slopes to vegetation as a refuge, regardless of direction. Lovich et al. (1991) also found that hatchling *M. terrapin* avoided open water and burrowed into wrack. However, none of these studies tracked a substantial number of naturally incubated hatchling *M. terrapin* over a significant period of time; therefore, it has been unclear whether their results were artifacts of manipulation, small samples, or temporary microhabitat choices.

Hatchlings of most aquatic Emydidae move towards water after emergence (Anderson 1958, Ehrenfeld 1979) and subsequently are found in shallow water (Hart 1983; Pluto and Bellis 1986; Buhlmann and Vaughan 1991; Congdon et al. 1992). Although this life-history stage is poorly studied in many species, some freshwater Emydidae do not move directly to water but spend considerable time on land before arriving at water (Moll and Legler 1971; Castellano et al. 2008; Linck and Gillette 2009). The combination of data

Fig. 4. The frequency of newly captured, recaptured, and dead hatchling Diamond-backed Terrapins (*Malaclemys terrapin*) in Spring 2008. New captures are indicated in black, recaptures in white, and dead hatchlings in gray.



from previous studies and our data provide strong evidence that hatchling *M. terrapin* often do not move directly to water after fall emergence from their nests.

Overwintering behaviour

Our seasonal movement data and the fact that we recaptured 18 hatchling *M. terrapin* on land in spring that we had initially caught on land in the previous fall is the strongest evidence yet that hatchling *M. terrapin* regularly overwinter terrestrially outside the nest (TON). We suspect this is an underestimate of the number of hatchling *M. terrapin* that TON, because others might easily have circumvented our drift fences or were predated on land. It is not clear what selective advantages may accrue with TON relative to overwintering in the proven safety of overwintering in the nest (TIN), but in 2011, 6 of 35 RB nests of *M. terrapin* containing hatchlings were destroyed by a powerful hurricane (R.L. Burke, unpublished data), whereas other hatchlings that had already emerged and moved upland were safe. Hurricanes occur regularly along the US Atlantic coast during the incubation and emergence seasons of *M. terrapin*, and may be an important selective force. A possible disadvantage of TON is greater exposure to predation, both while moving and while in overwintering sites. Terrestrial movements from the nest may also increase the risk of desiccation (Kolbe and Janzen 2002). Although TON probably occurs throughout tortoises, among Emydidae, TON is known only in some populations

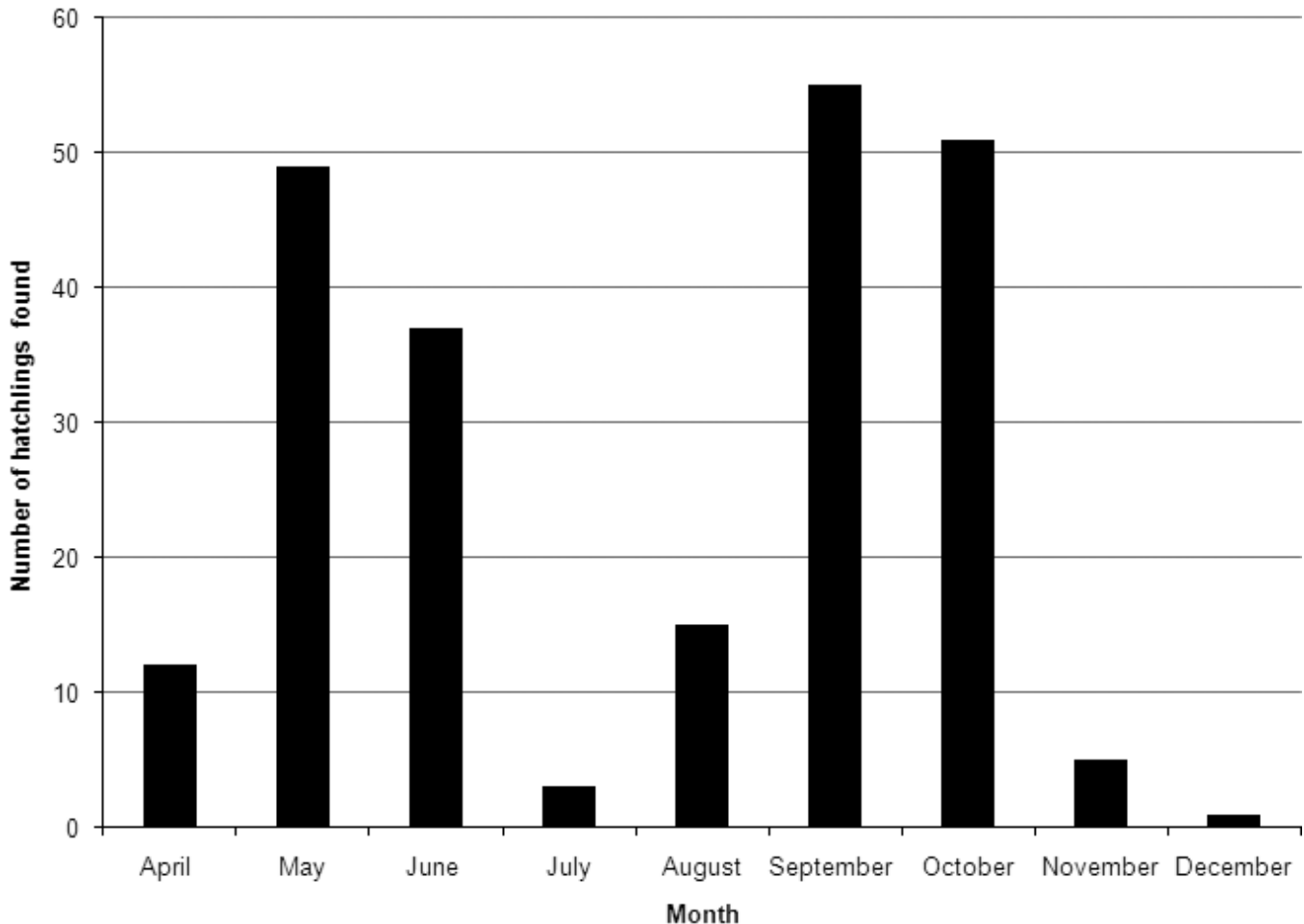
of *T. carolina* (Burke and Capitano 2012) and may occur in *E. blandingii* (Butler and Graham 1995; Linck and Gillette 2009).

One possible benefit of TON over TIN is the opportunity to feed and grow. For example, Castellano et al. (2008) and Tuttle and Carroll (2005) observed hatchling *G. insculpta* feeding on land soon after emerging from nests in the fall, and Kinneary (2008) found that hatchling *M. terrapin* fed on land, unlike most aquatic turtles. Contrary to our expectations, most of hatchling *M. terrapin* with appropriate recapture data were either unchanged or decreased in size; we detected significant decreases in both plastron and carapace lengths. Without presenting data, Hay (1917) also reported that hatchling *M. terrapin* were lighter and smaller in the spring than they were when newly emerged in the fall. In contrast, TIN seems more favourable for hatchling growth than TON. Roosenburg and Sullivan (2006) found hatchling *M. terrapin* that overwintered in the nest did not differ in plastron length from fall emerged hatchlings, and DePari (1996) reported that in *C. picta*, TIN resulted in increased hatchling sizes.

The body size shrinkage that we observed may have been due to desiccation, instead of or in addition to metabolism of food reserves. Such shrinkage has been reported in tortoises: hatchling Agassiz's Desert Tortoise (*Gopherus agassizii* (Cooper, 1861)) shrank dramatically during a long drought (K.J. Field, personal communication; as cited in Field et al.

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Fig. 5. The frequency of hatchling Diamond-backed Terrapins (*Malaclemys terrapin*) observed by National Park Service employees by month from 1979 to 1992.



2007); however, the shrinkage was reversed with access to water. Loehr et al. (2007) found that straight carapace length, shell height, and shell volume, as well as shell width and plastron length, of both juvenile and adult Speckled Padloper Tortoises (*Homopus signatus* (Gmelin, 1789)) also shrank. Although shrinking occurred in all 4 years of Loehr et al.'s (2007) study, the greatest number of shrinking individuals was during a drought.

Surviving winter conditions

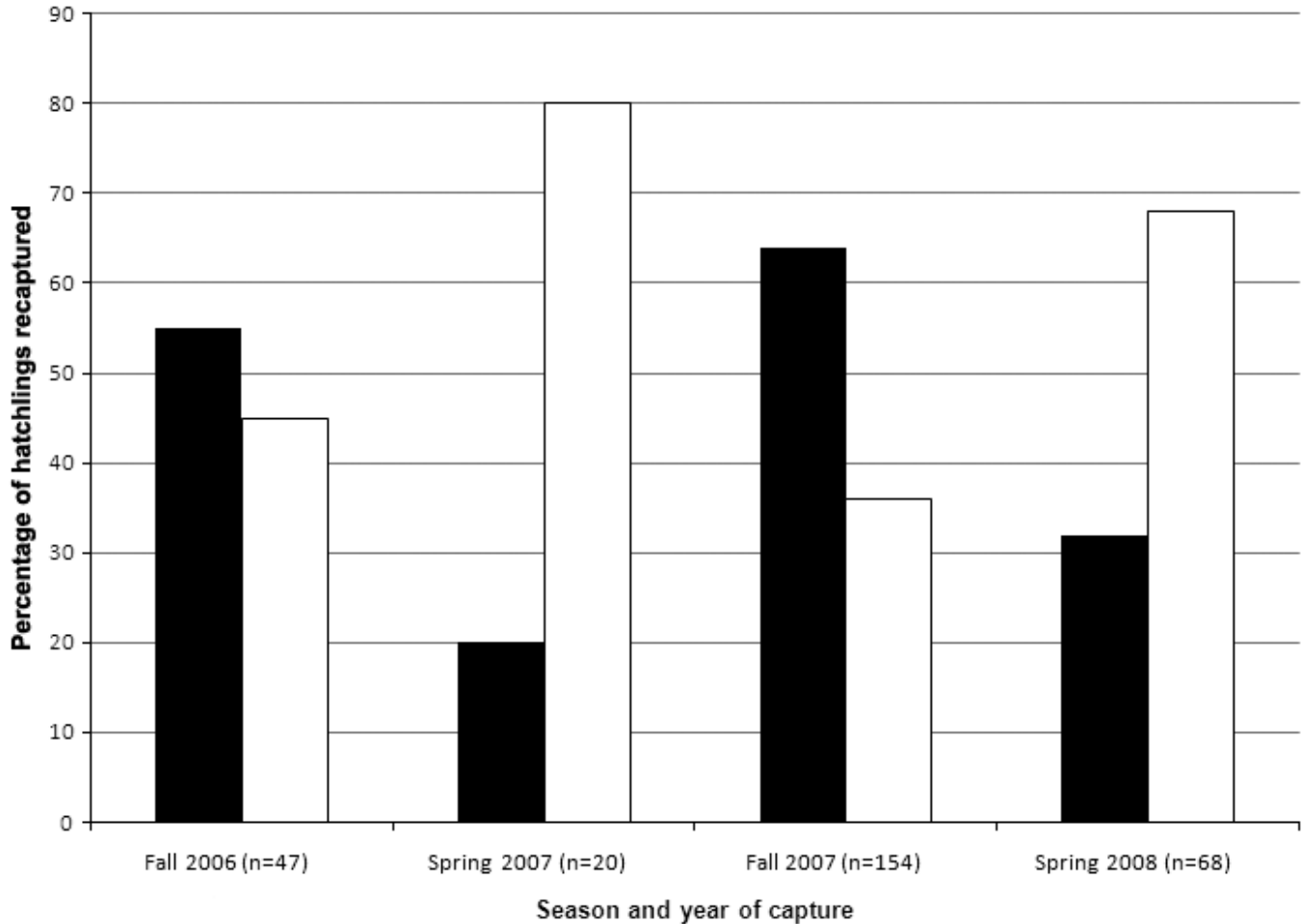
Hatchling *M. terrapin* appear to be adapted to terrestrial overwintering in temperate zones because they can both supercool and tolerate freezing, depending on specific conditions. While frozen, hatchling *M. terrapin* survived exposure to -2.5 °C for at least 7 days, but none were able to survive after being frozen at -2.5 °C for 12 days (Baker et al. 2006). Hatchling *M. terrapin* also can supercool; in the absence of ice-nucleating agents, hatchling *M. terrapin* remained unfrozen to -15 °C (Baker et al. 2006). However, hatchling *M. terrapin* are highly susceptible to inoculation from ice or ice-nucleating agents in the environment (Baker et al. 2006) and this can reduce supercooling capability by 8–10 °C and force freezing (Costanzo et al. 2000, 2003). Packard and Packard (2003) suggested that for freeze tolerance to be a successful overwintering strategy, hatchlings must not be exposed to

temperatures below -3 °C for more than 24 h. During winter 2006, we found the coldest RB air temperature was -13 °C and mean minimum air temperatures reached -6 , -8 , -9 , and -10 °C for periods of 2–6 days. Unfortunately, we are unable to report the temperatures experienced by overwintering hatchling *M. terrapin*. We observed that RB hatchlings moved towards upland vegetated habitats with thin leaf litter layers over sandy soils, but the relationship between air temperature and ground temperature is unknown.

After the first winter

Although we detected significant movement of hatchling *M. terrapin* towards water each spring, we did not recapture all hatchlings that we observed moving in the opposite direction in previous fall seasons. Some may have stayed on land later in the spring. National Park Service personnel observed terrestrially active hatchlings nearly year-round, suggesting that some hatchlings stay on land after their first winter. Rulison (2009) found hatchling *M. terrapin* remains in the seats of a RB *P. lotor* in July, and because RB *P. lotor* are mostly terrestrial foragers (R.L. Burke, personal observation), this suggests that the hatchling *M. terrapin* was on land long after emergence. Pitler (1985) found 12 juvenile *M. terrapin* (lengths 25–75 mm) in New Jersey from May to October, hiding under surface debris and vegetation as much as 91 m

Fig. 6. The percentages of hatchling Diamond-backed Terrapins (*Malaclemys terrapin*) caught each season moving away from the shoreline (black bars) and moving towards the shoreline (white bars).



from water’s edge. Four of these were found in June and five in July, outside the normal periods for either fall or spring emergence. Similarly, we recaptured one hatchling *M. terrapin* on land 9 months after fall emergence. These observations indicate that some *M. terrapin* may remain on land past their first spring.

Environmental conditions and hatchling activity patterns

We found that hatchlings were more likely to move on days with relatively high minimum and mean (but not maximum) air temperatures in the fall seasons (as did Keller et al. (1997) for Spur-thighed Tortoises (*Testudo graeca* L., 1758), but we found no such movement patterns in spring seasons. We cannot explain this result, but the weather data that we used were collected with temperature sensors approximately 154 cm from the ground, which probably differs from conditions experienced by hatchlings. The effects of temperature may also be modified by moisture and sunlight.

In contrast to our hypothesis, we found that hatchling *M. terrapin* traveled most commonly on days with no precipitation. Terrestrial movements by hatchling *G. insculpta* were more likely to occur during rainy weather, suggesting that rainfall may help hatchlings minimize desiccation during movement (Tuttle and Carroll 2005). It is possible that RB substrate conditions are damp enough to make desiccation

unlikely throughout most of the activity season. We found numerous hatchlings resting under wrack in all four field seasons. Wrack lines can retain moisture during the day and maintain heat during evening, provide food resources, and offer protection from predators (Pitler 1985; Lovich et al. 1991). However, wrack lines at RB are highly transient and could not provide stable long-term refuges.

Mortality owing to predation

Two of the predators (*O. quadrata* and *V. vulpes*) reported to eat hatchling *M. terrapin* elsewhere (Burger 1976, 1977; Arndt 1991, 1994; Zimmerman 1992; Butler et al. 2004) do not occur on RB. *Procyon lotor* are major predators of eggs of *M. terrapin* at RB and elsewhere through their range (Burger 1977; Roosenburg and Place 1995; Feinberg and Burke 2003; Butler et al. 2004), but predation by *P. lotor* on hatchling *M. terrapin* has only been reported by Rulison (2009). We did not observe *P. lotor* predating hatchling *M. terrapin* at RB, but they probably ate hatchling *M. terrapin* whole and did not leave carcasses. We frequently observed tracks of *P. lotor* close to drift fences and it is possible that they removed some hatchlings from our pitfall traps.

Non-native *R. norvegicus* are terrestrial predators of hatchling *M. terrapin* elsewhere (Draud et al. 2004), and *R. norvegicus* were trapped at RB by Rulison (2009). Draud et al.’s

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(2004) descriptions of predation by *R. norvegicus* on carcasses of hatchling *M. terrapin* matched 26 (60%) of the dead hatchling *M. terrapin* that we found. *Rattus norvegicus* are relatively recent invaders of habitat of *M. terrapin* and may be dramatically reducing hatchling survivorship. Although *R. norvegicus* are widespread and abundant in the United States, *R. norvegicus* eradication from islands such as RB is achievable (Howald et al. 2007).

Leucophaeus atricilla and *N. nyctiora* predate hatchling *M. terrapin* elsewhere (Burger 1976), and Red-Winged Blackbirds (*Agelaius phoeniceus* (L., 1766)) and Common Grackles (*Quiscalus quiscula* (L., 1758)) also predate young turtles (Janzen et al. 2000). All four species occur at RB but we never saw these birds near our equipment or foraging in areas where we knew hatchlings were present. They may only be important predators when hatchlings are congregated as they are emerging from nests.

The early life-history stages for turtles are characterized by high mortality (Wilbur and Morin 1988, but see Pike et al. 2008), especially owing to predation. However, far less is known about predation on turtle hatchlings than predation on eggs and nests. It is difficult to determine the cause of death of turtle hatchlings found in the field (e.g., Butler and Sowell 1996), as many predators leave similar signs, or no carcass at all, and one predator may kill a hatchling and another may scavenge it. DNA scatology (Dalén et al. 2004; Gompper et al. 2006) will probably be necessary to confirm most predators of turtle hatchlings. Iverson's (1991) multispecies comparison found that turtle hatchlings in terrestrial environments had generally lower predation rates than those in aquatic environments. Nearshore marine habitats, such as those available to hatchling *M. terrapin*, may be high predation-risk environments (Whelan and Wyneken 2007). If some hatchling *M. terrapin* choose terrestrial habitats and others choose aquatic habitats, they would provide an excellent opportunity to evaluate Iverson's (1991) conclusions within a single species.

Limitations of drift fences and pit falls

Drift fences with pit falls are used commonly to survey herpetofauna (e.g., Dodd 1991; Kolbe and Janzen 2002; Todd et al. 2007). Drift fences are less reliable if target species routinely climb over or under fences. Hay (1917) reported that hatchling *M. terrapin* are capable of climbing over a concrete wall 91 cm; we saw hatchlings attempt to climb our 13 cm aluminum flashing strips without success. We also made sure that all drift fences were securely pushed into the sand to prevent hatchlings from crawling underneath, but we may have underestimated hatchling movements.

Management implications

Many turtle conservation programs devote considerable resources to nest protection, which may greatly increase egg survival. However, hatchling survivorship and habitat selection are poorly known in nearly all turtle species. Our study shows that hatchling *M. terrapin* overwinter on land near their nests, where they are exposed to a suite of terrestrial predators. It is unclear whether increasing egg survival would increase recruitment into the adult population, it may instead simply provide more hatchlings for terrestrial predators. We suggest that conservation programs of *M. terrapin* should include more research devoted to understanding sources of

mortality while on land, management of overwintering habitat and terrestrial predators such as *P. lotor* and *R. norvegicus*, and should determine whether avian predators are important on a site-by-site basis.

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