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Nesting Success and Barrier Breaching: Assessing the Effectiveness of Roadway Fencing in Diamondback Terrapins (*Malaclemys terrapin*)

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Abstract.—**Roads can adversely affect animal populations by impacting nesting behavior, causing roadway mortality, and fragmenting habitat. Fences have frequently been implemented to combat road mortality, but at the expense of changing patterns of nesting behavior and increasing population fragmentation. We studied the effectiveness of barrier fences that were installed to reduce road mortality in Diamondback Terrapins (*Malaclemys terrapin*) seeking nesting habitat along two causeways in coastal southern New Jersey. To determine whether the barriers limited roadway access, we surveyed the ground within five-meters of the fences for evidence of Diamondback Terrapin nest holes in relation to the barrier, indicating whether nesting activity occurred on the marsh side of the fence or on the road side. As a second direct measure of effectiveness, we created a corrugated tubing arena and documented Diamondback Terrapin escape success to examine barrier breaching. Fences were generally effective in restricting Diamondback Terrapin movement: we found far fewer road-side nests ($n = 39$) than marsh-side nests ($n = 521$), as well as a spatial clustering of road-side nests near the free ends of the fence at one field site. Additionally, the barrier breaching success was positively correlated with gap size between the fence and the ground ($P < 0.001$), irrespective of body size, indicating that diligent fence maintenance is imperative. Given Diamondback Terrapins' high probability of road mortality and population sensitivity to female mortality, we conclude that fences are currently essential in their conservation and may warrant greater consideration in the field of turtle conservation, particularly in species with nesting movements that intersect with roads.**

Key Words.—*barrier fence; habitat fragmentation; gravid females; road mortality; turtle; wetlands conservation*

Introduction

With land development and road networks constantly expanding in the United States, road construction has likely contributed to significant population declines in mammals, birds, amphibians, and reptiles (Ashley and Robinson 1996; Gibbs and Shriver 2002). Roads affect populations by impacting nesting behavior, fragmenting habitat, and causing direct road mortality due to vehicle collisions (Dodd et al. 2004). Once limited by topography, roads can now expand into previously undeveloped habitats and threaten an ever-increasing number of species (Ashley and Robinson 1996) due to the interconnectedness of wildlife, roads, and adjacent habitat (Andrews et al. 2008).

Many amphibians and reptiles are particularly vulnerable to environmental changes associated with roads (Andrews et al. 2008), as they often exhibit low roadway avoidance, low travel speed, extensive overland movements (Crawford et al. 2014a), and population sensitivity to female mortality, characterized by life history traits including long life spans, delayed sexual maturity, and low annual recruitment rates (Gibbs and Shriver 2002). Long-lived turtle populations, for example, are constrained in their ability to deal with additive annual mortality due to anthropogenic impacts, and studies indicate that only 2–3% additive annual mortality is more than most turtle species can cope with to maintain population stability (Congdon et al. 1993, 1994). Amphibians and reptiles encounter roads while searching for food, water, and breeding or nesting sites, and road mortality rates are often high (Ashley and Robinson 1996; Szerlag and McRobert 2006). Franz and Scudder (unpubl. report) examined road morality of snakes along a 3 km segment of U.S. Highway 441 in Florida and reported a mortality rate of 90.4% (Andrews et al. 2008). Seasonal peaks in turtle road mortality are often correlated with the migration of nesting females, hatchling dispersal, and the movement between wetland habitats (Ashley and Robinson 1996; Andrews et al. 2008). Major spikes in road mortality have been documented during nesting season in Western Painted Turtles (*Chrysemys picta*) in Montana (Fowle 1996), Snapping Turtles (*Chelydra serpentina*) in central Ontario (Haxton 2000), and Diamondback Terrapins (*Malaclemys terrapin*) in southern New Jersey (Wood and Herlands 1997).

For the last few decades, biologists and engineers have developed a number of potential solutions to the problem of roadway access and mortality of dispersing or nesting animals (Dodd et al. 2004). A common mitigation strategy is the installation of fence-culvert systems to prevent roadway access and facilitate dispersal (Aresco 2003; Dodd et al. 2004). Dodd et al. (2004) assessed the effectiveness of a fence-culvert system built on a section of highway in Alachua County, Florida and found that snake, turtle, and alligator mortality decreased dramatically post-construction. To alleviate impacts of a highway constructed through the center of a French population of Hermann's Tortoises (*Testudo hermanni*), Guyot and Clobert (1997) built a fence-culvert system and reported low road mortality and population stability post-installation. Aresco (2003) installed temporary barrier fences along U.S. Highway 27 in Lake Jackson, Florida, and reported that road mortality of turtles was almost completely eliminated after installation.

Barrier fences are used to restrict access to roads, thus reducing road mortality in species whose terrestrial movements intersect with roads. Barrier effectiveness is often defined by the extent to which barriers reduce road mortality or prevent animals from accessing the road (Aresco 2003; Dodd et al. 2004). The most direct measure of barrier effectiveness is documenting road kills. However, road kills are highly ephemeral and difficult to measure accurately as predators, scavengers, and cars can remove this form of evidence within hours, especially for small animals. In species that encounter roads when searching for nesting habitat, such as turtles, an alternative, longer-lasting metric of barrier efficacy involves measuring nesting characteristics in relation to the fence. When the land on both sides of the barrier is equivalent in terms of area, moisture, substrate, and vegetation, the location of the nest (i.e., habitat-side of the barrier or road-side of the barrier) is an important metric to assess barrier effectiveness, as the distribution should be equal if the fence is ineffective.

The status of the observed nests (i.e., whether the nest has been predated or attempted before abandonment) is another useful metric of barrier effectiveness. Diamondback Terrapins are a species of estuarine, emydid turtle whose populations have been impacted by roadways, and barriers have been installed to reduce roadway mortality. For many turtles including Diamondback Terrapins, successfully laid nests are often difficult to detect due to their cryptic concealment, but predation on turtle nests is extremely high in most turtle populations (Spencer 2002), making depredated nests a useful indicator of nesting activity. Butler et al. (2004) monitored daily nesting by Diamondback Terrapins for two summers and found 81.9% (in 1997) and 86.5%

(in 2000) of nests were depredated. Feinberg and Burke (2003) similarly recorded Diamondback Terrapin nest predation of 92.2%, providing support for depredated nests being a good measure of egg-laying activity and making a reasonable proxy for successful nests resulting in hatchlings. While depredated nests represent a high percentage of successfully laid nests, nest abandonment before egg-laying can be as common as completing a nest (Roosenburg 1994), so additional documentation of abandoned nests gives a more complete picture of female movement during this critical nesting phase. Further, directly observing animals' barrier breaching success (i.e., whether an animal is able to pass over or under a barrier) when faced with a fence is another useful metric to assess barrier effectiveness, providing better understanding of the conditions under which fences are likely to be breached by females of different body sizes. This pairing of nest observations with behavioral tests can thus provide robust, inclusive estimates of general fence effectiveness for adult females, which is especially important in species with sensitive life history traits like turtles.

Diamondback Terrapin populations have experienced declines range-wide due to various human activities including road development (Dorcas et al. 2007; Grosse et al. 2011). Roads have contributed to population declines of Diamondback Terrapins due to their low travel speed, population sensitivity to female mortality, and nesting activity that incorporates terrestrial movement. Diamondback Terrapins are the only turtle species in the world exclusively adapted to brackish water coastal salt marshes (Ernst and Barbour 1989; Wood and Herlands 1997), and coastal salt marshes in the United States have been heavily impacted by industrial and real estate development over the past century (Wood and Herlands 1997). Along the Atlantic coast of New Jersey, Diamondback Terrapins' natural nesting habitat (sand dunes on barrier beach islands) has largely disappeared due to human encroachment. There has been considerable alteration of both the mainland and barrier beach island sides of the marshes, so while some of the salt marsh has been preserved, natural Diamondback Terrapin nesting sites on sand dunes above the high tide line have largely been destroyed (Wood and Herlands 1997) or rendered inaccessible by bulkheading. This development has forced Diamondback Terrapins to seek alternative nesting habitat along the embankments of the heavily trafficked causeways that cross salt marshes (Wood 1997), as they must lay their eggs above the high tide line (Roosenburg and Place 1994; Butler et al. 2004). The upper slopes of these embankments create a suitable nesting habitat for Diamondback Terrapins seeking high ground. Nesting alongside heavily trafficked roads results in substantial roadway access, use, and mortality within some parts of their range during their six-week nesting season from mid-May to late-July (Wood and Herlands 1997; Hoden and Able 2003).

Over 10,000 Diamondback Terrapin road kills were documented between 1989 and 2011 in Cape May County, New Jersey (Daniel McLaughlin, unpubl. data). Since 2004, both scientists and community volunteers have attempted to combat this source of Diamondback Terrapin mortality by developing and installing various types of barrier fences designed to restrict females seeking nesting habitat to the marsh side of the barriers. The barrier installation techniques and materials have been refined over the years, first using silt, then plastic mesh, and now plastic corrugated tubing. Corrugated tubing is currently favored because it is relatively less conspicuous, easy to install, and more durable than previous fence materials. Over 12,000 feet of barrier fences have been installed along the coast of southern New Jersey (Daniel McLaughlin, unpubl. data).

The primary objective of our study was to assess Diamondback Terrapin barrier effectiveness, defined as the degree to which the fences limited roadway access. To determine barrier effectiveness, we first surveyed the ground adjacent to the fences for evidence of nest holes in relation to

Figure 1. Map of two study sites in New Jersey, USA. Atlantic County and Cape May County are outlined in red on the inset state map. Source: "New Jersey." 39° 13'22.52"N and 74° 44'45.12" W. Google Earth. 9 April 2013, 15 July 2014.

the barrier, indicating whether nesting activity occurred on the marsh side of the fence or on the road side. As a second measure of effectiveness, we created a corrugated tubing arena and documented Diamondback Terrapin escape success to determine the likelihood of barrier breaching. We hypothesized that if the barriers were effective, we would find more nests on the marsh side of the barriers, and escape success would increase with gap size between the ground and the fence. Determining barrier effectiveness is critical to understanding how barriers impact adult female nesting behavior, ensuring that our conservation efforts and resources are being properly allocated, and identifying opportunities for improvement in barrier design to better protect the species in those parts of its range where road kills during nesting season are a significant problem.

Materials and Methods

Study species.—Diamondback Terrapins (*Malaclemys terrapin*) are estuarine, emydid turtles whose range is several thousands of miles long but limited in width to coastal habitat, extending along the Atlantic Coast from Cape Cod, Massachusetts, to southernmost Florida and around the Gulf Coast to Texas (Ernst et al. 1994; Wood and Herlands 1997). Within this range seven subspecies are recognized (Wood and Herlands 1997). We focused our study on a population of the northernmost subspecies, the Northern Diamondback Terrapin (*Malaclemys terrapin terrapin*), which is found from Massachusetts to North Carolina (Wood and Herlands 1997).

Study site.—We studied two sections of roadway that connect the mainland to coastal barrier islands on the Atlantic Coast of southern New Jersey. We chose Stone Harbor Boulevard (SHB), Cape May County (39.06°N, 74.77°W) and the Margate Causeway (MC), Atlantic County (39.34°N, 74.54°W) as representative of the many causeways in the area that cross salt marshes and have Diamondback Terrapins nesting on their embankments. We surveyed a 589-m section of the SHB and a 623-m section of the MC (Fig. 1). Both causeways cross salt marshes dominated mainly by Saltmarsh Cordgrass (*Spartina alterniflora*) and Saltmeadow Cordgrass (*Spartina patens*). Embankments alongside the causeways range in width from less than 1 m to 10 m in parts of the MC. Crabgrass (*Digitaria sanguinalis*) and other vegetation cover the sandy embankments.

Field survey: nest census.—We surveyed the north and south sides of the two roads, both previously fenced with 15.24-cm diameter corrugated tubing staked in place at ground level, for evidence of Diamondback Terrapin nesting activity. We installed fences on the embankments such that the microhabitat characteristics and the total area of searchable nesting habitat on both sides were qualitatively similar based on visual observations. We observed no noticeable difference in plant assemblage or moisture gradient. Preliminary data comparing fenced and unfenced roadways suggest that the distribution of nests across the strip of land between the road and the marsh is uniform (data not shown). During 2011, we surveyed both sides of each road once a week from 17 June through 8 July. Based on the results from 2011, we refined our methods and sampled less frequently, but more intensively, in 2012 by surveying both sides of each road twice between 7 June and 4 July. During every survey, we documented Diamondback Terrapin nest holes by walking along the marsh side of the fence in one direction and on the road side in the other direction to ensure that all nest holes were recorded. We randomly selected which end of the fence to begin each survey on. One individual (H. Reses) completed all surveys to control for observer bias. For each nest hole, we recorded the road name, whether it was on the north or south side of the road, whether it was on the marsh side or road side of the corrugated tubing barrier,

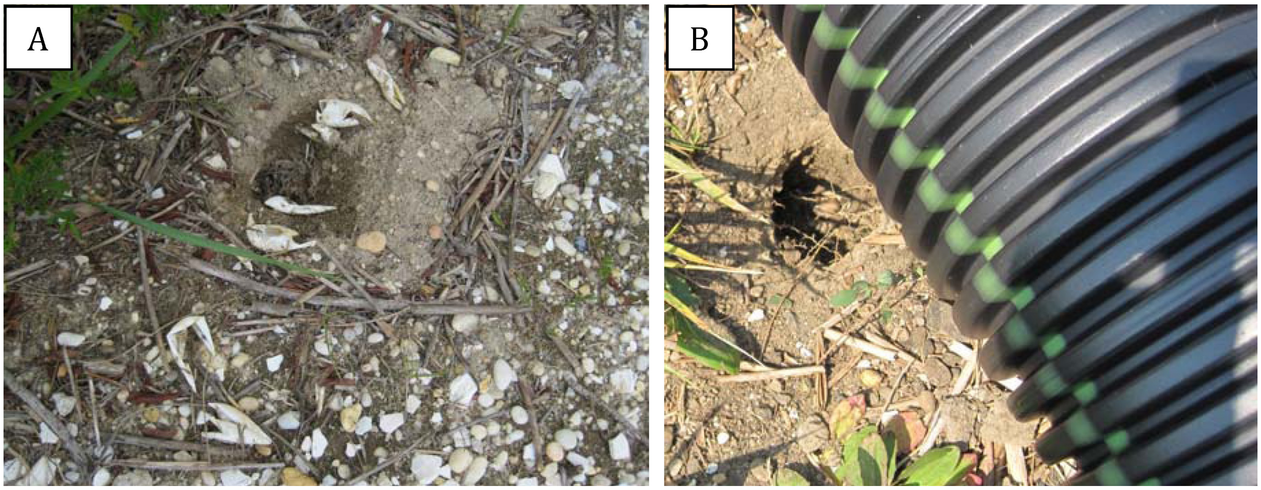

Figure 2. Depredated and abandoned Diamondback Terrapin (*Malaclemys terrapin*) nests reflect nesting activity by indicating where Diamondback Terrapins chose to lay eggs. Depredated nests (a) are identified by eggshells scattered nearby a shallow circular excavation. Abandoned nests (b) appear as shallow, circular excavations.

GPS location (using a Magellan Triton), and the distance (in meters, to the nearest centimeter) from the corrugated tubing. We used a 10-m rolling tape measure to record the straight-line minimum distance (to the nearest centimeter), and we flattened vegetation that was in the way to measure more accurately.

Field survey: predation.—Depredated and abandoned nests reflect nesting activity as they indicate where Diamondback Terrapins attempted to nest. Both depredated (Fig. 2a) and abandoned (Fig. 2b) nests appear as shallow, circular excavations approximately 4–6 cm in diameter and 10–15 cm in depth. Abandoned nests may be smaller if they were not completed before abandonment. Terrapin nest holes are distinguishable from other depressions in the ground as they curve to the side at the base of the hole, forming a 'J' shape. We identified nests depredated by common mammalian predators (e.g., Skunks, *Mephitis mephitis*; Red Foxes, *Vulpes vulpes*) by eggshells scattered nearby. We estimated the number of eggs per depredated nest by piecing together the eggshells, which were often broken into halves or thirds of the original whole eggs. However, some predators (e.g., Raccoons, *Procyon lotor*; Fish Crows, *Corvus ossifragus*) may eat eggs whole and leave little or no evidence of their predation. There is no definitive way to recognize this type of predation, so we counted holes without eggshells as abandoned nests. To prevent double counting of nests, we filled in each hole after recording it and collected all depredated eggshells. Nests do not remain visible for more than one season, as rain and flooding fill in the holes and wash away old eggshells.

Arena experiment.—Diamondback Terrapins can occasionally reach the road side of the barriers by crawling underneath the corrugated tubing in areas where gaps have formed. Gaps may be formed where corrugated tubing spans ground depressions, or they may result from vegetation growing upwards underneath the corrugated tubing. To understand how such gaps influence barrier effectiveness, we built a five-m oval arena of corrugated tubing and raised a section of the tubing to various heights (0–8 cm). We placed adult female Diamondback Terrapins (n = 40 individuals; 74 trials) individually in the arena and observed the number of Diamondback Terrapins that escaped through the gap within 10 min. We measured the height of the Diamondback Terrapins and recorded gravidity. We assessed gravidity by holding the female on her side, placing fingers in the area just in front of her hind limbs, and palpating the oviducts for shelled eggs. We tested only adult females, as males do not typically emerge from the safety of the salt marsh. This experiment was run for three consecutive summers during June and July. In 2010 and 2011, the arena was placed on a flat area of grass and we tested a range of gap sizes: 0, 2.5, 3.8, 6.4, and 7.6 cm. Based on these results, we also tested gaps of 5.1 cm in 2012 to complement the sizes evaluated in previous years. We tested each individual for one or two gap sizes, so gap size and location within the arena were randomly selected for each trial. We considered each trial to be independent.

Data analysis.—We plotted all of the nest locations on Google earth images using R package 'Google Maps' (R version 2.15.2). We combined the two years of field survey data (n = 560) and three years of arena experiment data (n = 40 individuals; 74 trials) for analysis. We tested the field survey results, specifically whether the nest holes were on the marsh side or the road side of the fence, for normality and homogeneity of variance using SAS 9.3 (SAS Institute 2011). We evaluated the effect of marsh vs. road side of fence, north vs. south side of causeway, and site, as well as the interactions among these variables, on the number of depredated and abandoned nests using chi-square analysis in R for each comparison. We calculated mean road length by summing the distances on both sides of the road and dividing by two for both study sites: (MC: [540.6 + 623.3]/2 = 581.9 m; SHB: [575.3 + 589.2]/2 = 582.2 m). Because mean road length was similar between sites, we used raw nest counts for subsequent analyses.

To assess barrier efficacy and test whether nests on the road side of the fence were closer to the free ends of the fenced sections than marsh-side nests, we used Monte Carlo simulations in R to compare the observed and expected distributions of road-side nest distances. We converted each nest coordinate from decimal degrees to UTM using a batch conversion worksheet in MS Excel (Available at: http//www.uwgb.edu, [Accessed 27 September 2013]). For each site independently, we used the UTM coordinate of each nest to calculate the shortest straight-line distance in meters between each nest and its nearest fence-end to generate an observed distribution of distances for the road side of the fence. To create a test statistic representing this distribution, we calculated the median distance within this observed distribution. We then resampled (100,000 repetitions) the full distribution of distances for each site to generate expected distributions of marsh-side distances with the same number of nests as the observed road-side distributions (n = 14 for SHB, n = 20 for MC) and similarly calculated the median for each simulated distribution. We analyzed the arena experiment using logistic regression to measure proportional breaching success vs. gap size and Diamondback Terrapin height. All statistical tests were performed using R, and we assessed significance at $P < 0.05$.

Results

Field survey: nest census.—We first assessed whether there was variation among sites and years to ensure that Diamondback Terrapin nesting behavior was similar across these variables. We found a significantly greater number of nests on the SHB than on the MC ($\chi^2 = 146.1$, df = 1, $P < 0.001$). In terms of year, there was a weaker, yet significant effect, with slightly more nests found in 2012 than 2011 ($\chi^2 = 4.83$, df = 1, $P = 0.028$). We found no interaction between year and site ($\chi^2 = 5.03$, df = 1, $P = 0.249$). Because site effect is more biologically relevant and has a stronger statistical effect, we only considered site differences in the subsequent analyses and combined the 2011 and 2012 data.

Orientation (north vs. south side of road) played no role in nesting activity ($\chi^2 = 0.714$, df

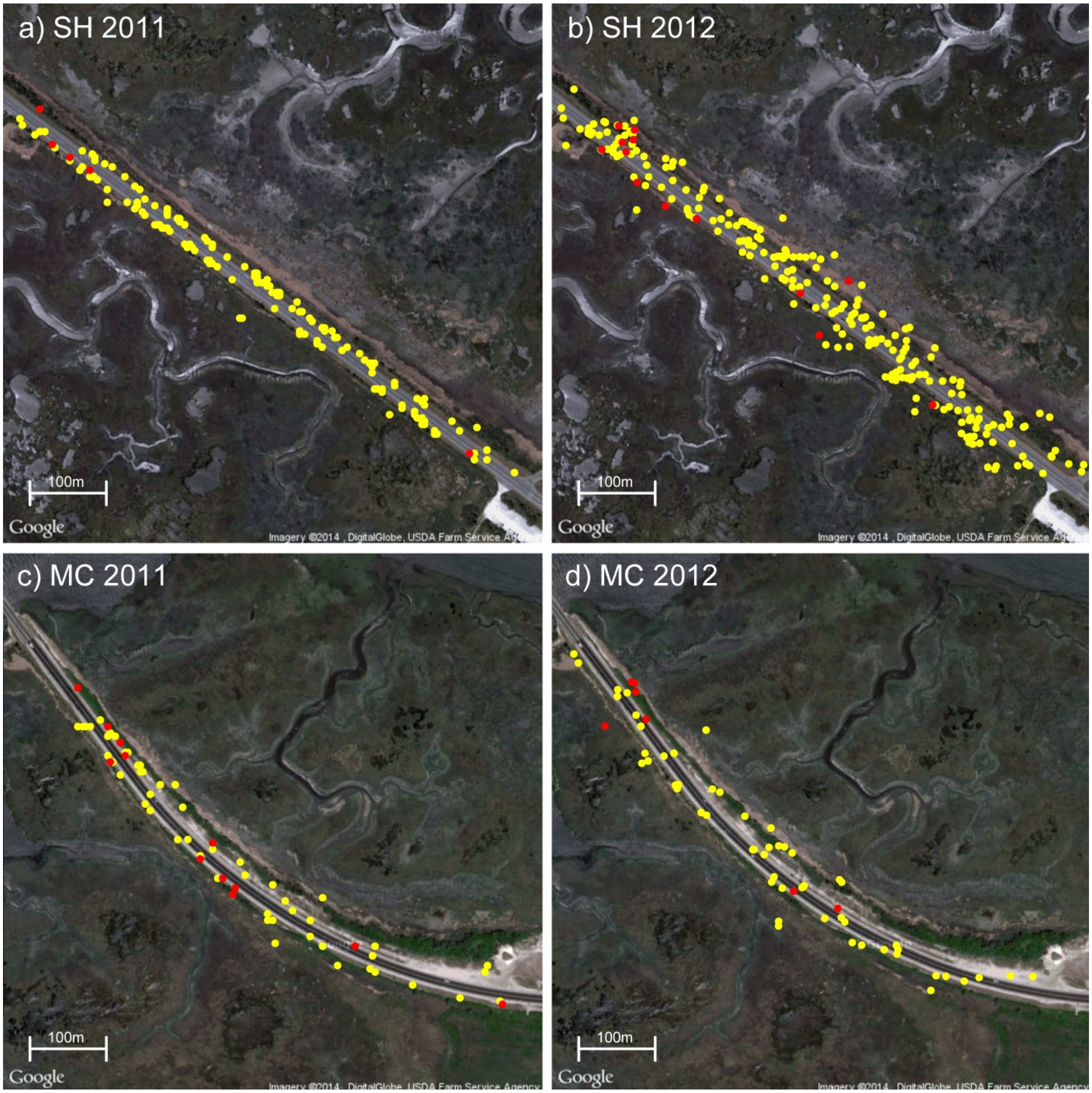

Figure 3. Distribution of Diamondback Terrapin (*Malaclemys terrapin*) nests on Stone Harbor Boulevard in 2011 (a) and 2012 (b) and Margate Causeway in 2011 (c) and 2012 (d). Note that there are far more marsh-side nests (yellow circles) than road-side nests (red circles). Points are randomly jittered along both axes in (b) and (d) to allow the display of overlapping data. Source: "Stone Harbor Boulevard." 39°3'46.8" N and 74°46'33.6" W. Google Earth January 1, 2013. July 16, 2014. Source: "Margate Causeway." 39°20'20.91" N and 74°31'7.43" W. Google Earth 1 January 2013, 16 July 2014.

= 1, P = 0.398) when considering all data. Both site and orientation were analyzed together using chi-square, and we found that there was no effect (χ^2 = 1.19, df = 1, P = 0.275). When analyzing within site, orientation did not impact nesting activity on either road (MC: χ^2 = 2.11, df = 1, P = 0.146; SHB: χ^2 = 0.021, df = 1, P = 0.884).

When considering all data, we found a significantly greater number of nests on the marsh side of the corrugated tubing barriers than on the road side (χ^2 = 414.9, df = 1, P < 0.001). When analyzing within site, both roads had significantly more nests on the marsh side of the barriers than on the road side (MC: χ^2 = 68.68, df = 1, P < 0.001; SHB: χ^2 = 350.4, df = 1, P < 0.001; Fig. 3). We separated the dataset by site in order to look at the effect of each road. Chi-square analysis of both site and fence side revealed a significantly greater number of road-side nests on the MC than on the SHB (χ^2 = 14.79, df = 1, P < 0.001). We found that on the SHB, road-side nests were closer to the fence-ends than expected by chance (P < 0.001), but we found no such spatial effect on the MC (P = 0.131; Fig. 4).

Field survey: predation.—There was a site effect on predation such that nests on the SHB were more often depredated than those on the MC (χ^2 = 15.09, df = 1, P < 0.001). Within-site analyses revealed that there was more abandonment than predation on the MC (χ^2 = 12.27, df = 1, P < 0.001; Fig. 5a) but marginally more predation than abandonment on the SHB (χ^2 = 3.60, df = 1, P = 0.058; Fig. 5b). We found a year effect on predation, such that predation was more common in 2011 than in 2012 (χ^2 = 9.289, df = 1, P = 0.002). We found an interaction between year and predation such that predation was higher in 2011 than 2012 across sites (χ^2 = 9.290, df = 1, P = 0.002). However, within-site analyses showed evidence of an interaction effect with trends in opposite directions; the effect was significant on the MC (χ^2 = 14.43, df = 1, P < 0.001; Fig 5a) but only marginally significant on the SHB (χ^2 = 3.304, df = 1, P = 0.069; Fig. 5b).

When all data were considered simultaneously, we found that predation and fence-side (marsh vs. road) were not related (χ^2 = 1.0389, df = 1, P = 0.308). Similarly, neither within-site analysis showed an interaction between predation and fence side (MC: χ^2 = 0.573, df = 1, P = 0.449; SHB: χ^2 = 2.170, df = 1, P = 0.141).

Arena experiment.—Diamondback Terrapins typically crawled straight to the barrier, attempted to climb over the tubing, and then proceeded to walk along the inner circumference of the tubing, occasionally attempting to crawl over or under it. The only way Diamondback Terrapins were able to breach the barrier was by crawling underneath (Fig. 6). We fit a logistic regression to the data and found that increasing gap size below the fence was correlated with increasing escape success (Z = 4.373, df = 73, P < 0.001; Fig. 7). Gaps of 6.4 cm and 7.6 cm allowed all but one individual to escape. We found that gravidity of the Diamondback Terrapin did not impact escape success (Z = 1.227, df = 73, P = 0.220). Carapace length, used as an estimate of size, was not correlated with escape success (Z = 0.623, df = 56, P = 0.533).

Discussion

We found that the fences were effective in reducing Diamondback Terrapins' road access, but efficacy depended on microenvironmental factors and was not constant within or between sites. These results have important implications for understanding the ecological tradeoffs associated with fences and recommendations for the management of Diamondback Terrapins and other wetlands species. Our constructed barrier fences were highly effective in restricting nest-seeking Diamondback Terrapins to the marsh side of the barriers, and therefore substantially decreased roadway access and subsequent road mortality. Given that Diamondback Terrapins emerge from

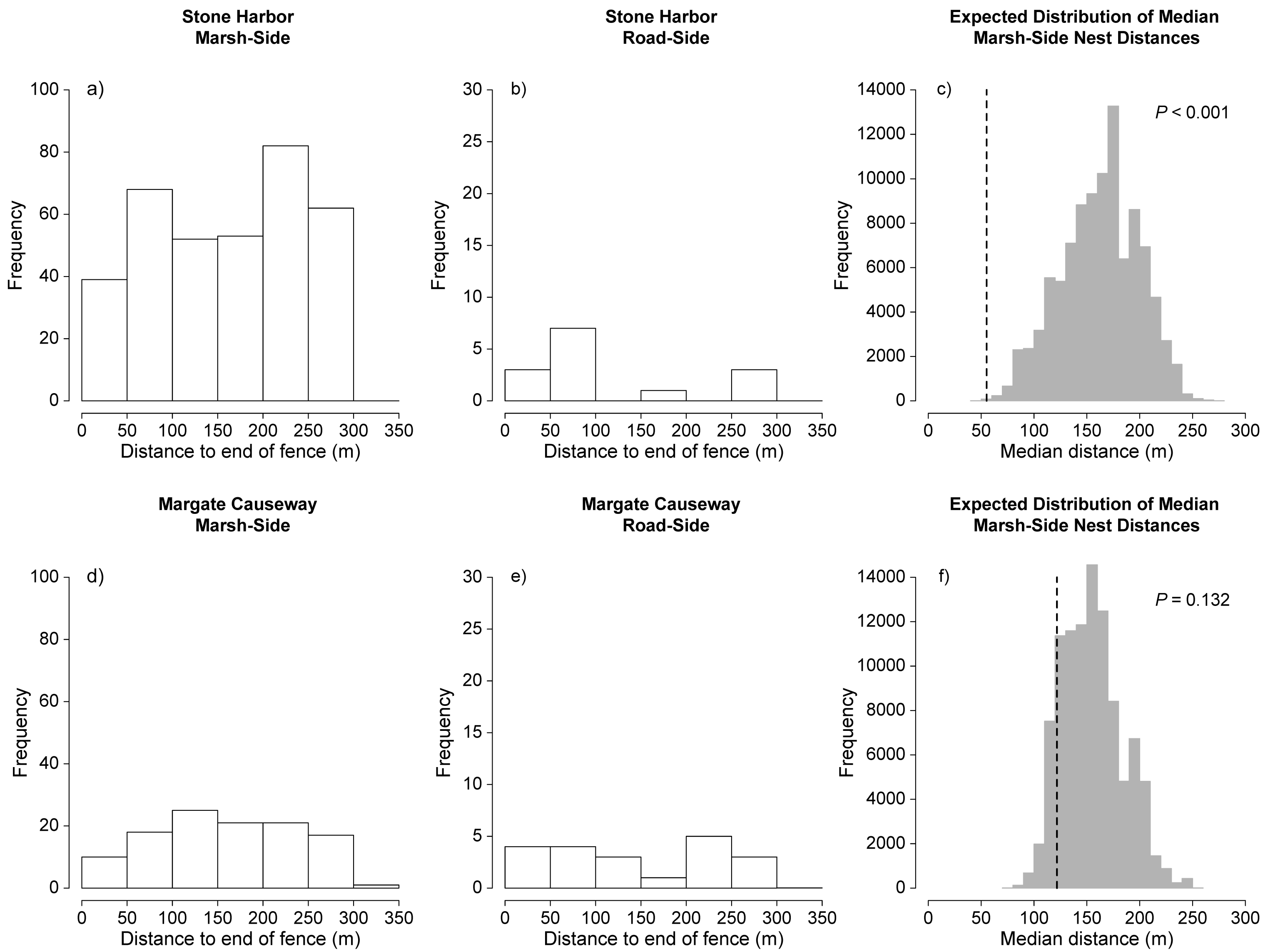

FIGURE 4. Straight-line distance to the free-ends of the fence on both roads. Distribution of Stone Harbor Boulevard marsh-side Diamondback Terrapin (*Malaclemys terrapin*) nests (a) and road-side Diamondback Terrapin nests (b) used to generate the expected distribution of marsh-side nest distances through Monte Carlo resampling (c). Distribution of Margate Causeway marsh-side nests (d) and road-side nests (e) used to generate the expected distribution of marsh-side nests as above (f). The vertical dashed lines in (c) and (f) represent the observed median road-side nest distance to the closest free end of the fence for each study site respectively for comparison to the simulated distributions of nest distances.

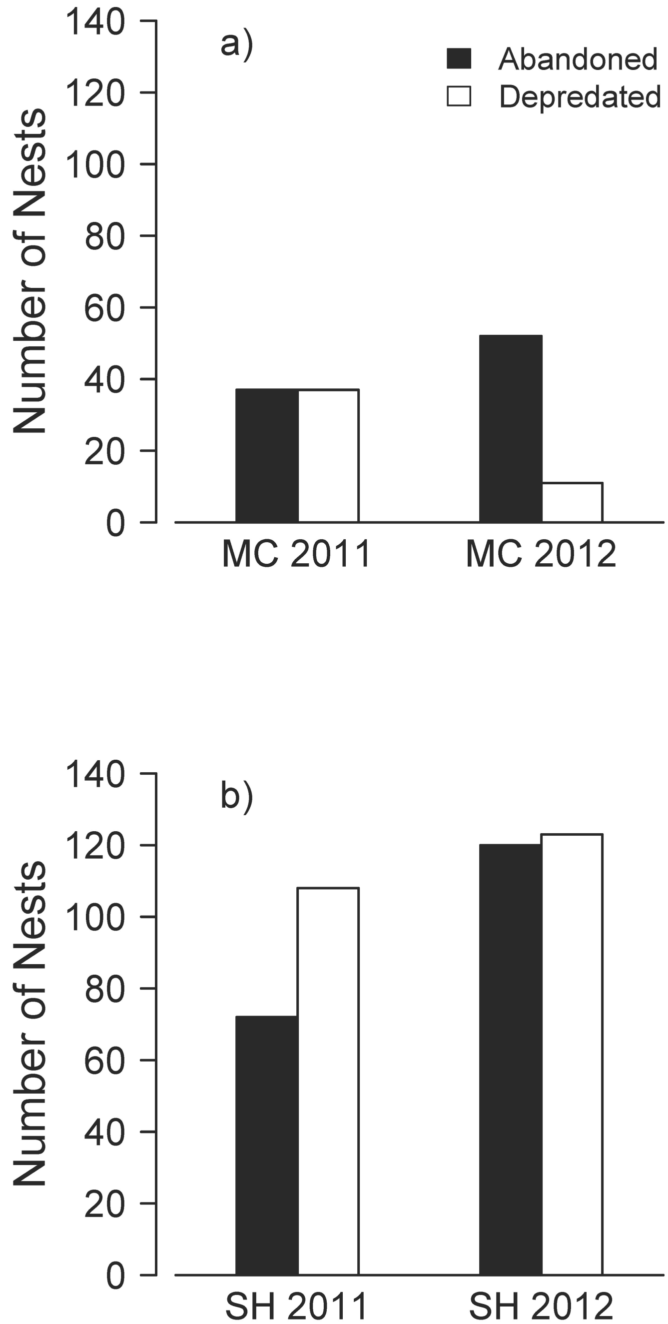

Figure 5. Number of depredated and abandoned Diamondback Terrapin (*Malaclemys terrapin*) nests on the Margate Causeway in 2011 and 2012 (a) and on Stone Harbor Boulevard in 2011 and 2012 (b).

the marsh, it is evident that the fences had an effect on roadway access and available nesting habitat; if the fences had no effect we would expect to find equal numbers of nests on both sides of the barrier.

Fences have been reported to work especially well in reducing mortality of turtles as compared with various animal groups (William Barichivich and C. Kenneth Dodd, unpubl. report; Aresco 2003). However, fence usage is often controversial because there are ecological tradeoffs associated with fences, as they may create barriers to dispersal, migration, and gene flow (Aresco 2003; Hayward and Kerley 2009). Fragmentation may be especially detrimental to Diamondback Terrapin populations due to their high site fidelity (Gibbons et al. 2001). Barriers to dispersal could further limit gene flow in species that already have restricted migration. It is important to consider the effects of fragmentation and roadway mortality on Diamondback Terrapins, despite only nest-seeking females being directly affected, as both anthropogenic impacts could have significant population-wide consequences; population model analyses for several long-lived turtle species indicate that an annual loss of only a few hundred subadult and adult female turtles can have a profound impact on population dynamics (Heppell et al. 1996).

Jaeger and Fahrig (2004) used a simulation model to determine whether fences enhance or reduce the effect of roads on population persistence in various species, and they reported that fence effects depend on an animal's degree of roadway avoidance and its probability of roadway mortality upon entering the road. For species with high traffic mortality rates, fences generally enhance population persistence, especially when populations faced additional sources of anthropogenically induced mortality. In our study area and throughout their range, Diamondback Terrapins qualify as a species with a high likelihood of roadway mortality, low road avoidance, and multiple sources of mortality. Therefore, the model indicates that fences would likely enhance population persistence of Diamondback Terrapins despite the fragmentation tradeoff. In combination with our finding that fences are highly effective in restricting nest-seeking Diamondback Terrapin movement, we are confident that fences are currently necessary in maintaining Diamondback Terrapin populations in southern New Jersey.

Given that turtles' life history traits limit populations' ability to absorb the loss of sexually mature adults (Brooks et al. 1991), fences that restrict the movement of nesting or dispersing individuals may warrant greater consideration in the field of turtle conservation, despite the barrier-induced fragmentation effects. Many other Diamondback Terrapin populations and turtle species may benefit from the installation of barriers. Szerlag and McRobert (2006) found that Diamondback Terrapin road mortality rates correlate positively with increasing traffic volume on Great Bay Boulevard in Tuckerton, New Jersey, indicating that barriers that prevent roadway access could enhance population stability. Other species, including Montana populations of the Western Painted Turtle (*Chrysemys picta bellii*; Fowle 1996), may similarly experience positive population-wide effects via fence installation.

Our results also indicate that fence effects and ecological tradeoffs depend upon site differences and local conditions. Across sites, the fences were effective in reducing overall road access, but barrier breaching varied within and between sites due to microenvironmental factors including elevation, flooding, and vegetation. Barrier breaching was more common on the MC, as roadside nests represented a greater proportion of total nests than the SHB nests. Margate Causeway had lower elevation (4 m) than SHB (6 m), higher flooding, and dense vegetation growth along its embankments (pers. obs.). Vegetation can create gaps beneath the fence and provide Diamondback Terrapins with a bridge over the fence. Further, MC fences were newer than SHB fences, and it has been observed that corrugated tubing barrier effectiveness increases with time, barring damage, as the fences sink into the ground and kill

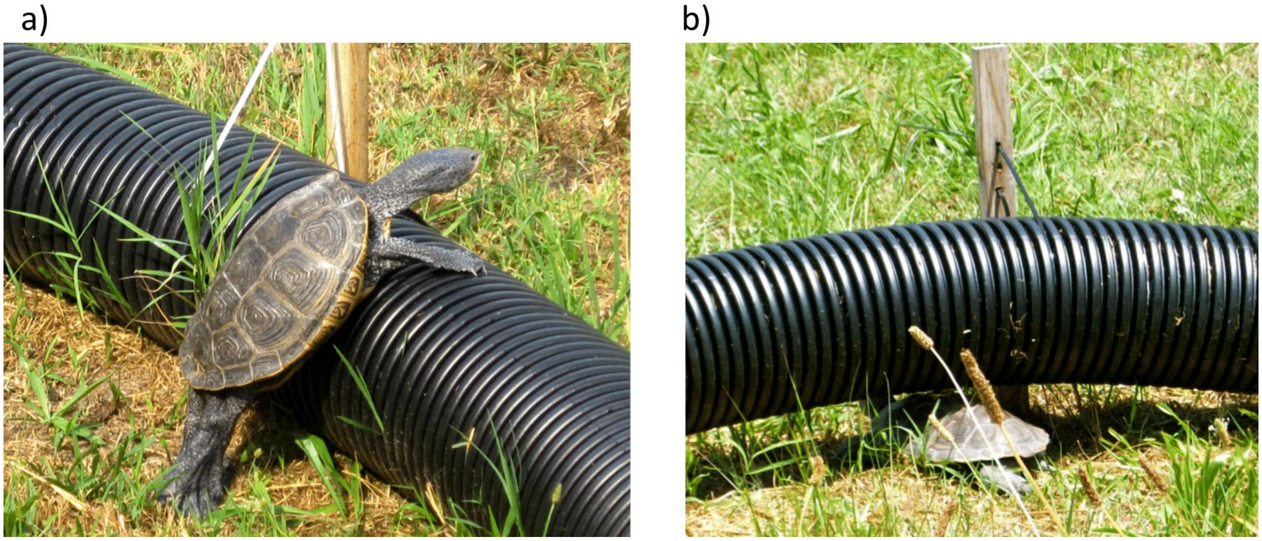

Figure 6. A Diamondback Terrapin (*Malaclemys terrapin*) attempting to crawl over the barrier tubing (a) and a Diamondback Terrapin successfully breaching the barrier via crawling under the tubing (b). Note that vegetation can push the tubing upwards to create these gaps.

the vegetation underneath. New fences are light and sit on top of live vegetation, making it much easier for Diamondback Terrapins to crawl beneath (pers. obs.). Fence effectiveness and subsequent ecological tradeoffs depended heavily on local conditions, so management plans and maintenance should be carefully tailored to complement microenvironmental conditions.

These findings were supported by our arena experiment results, which demonstrated that barrier breaching success was positively correlated with gap size between the bottom of the fence and the ground surface, irrespective of body size. Gravidity did not impact escape success, so gravid and non-gravid females were equally likely to breach the barriers. This unexpected result is encouraging, as our efforts to target adult females for protection are not being hindered by gravid female determination to overcome the barriers. Examining female body size and gravidity in relation to barrier behavior was a novel approach.

Predation and spatial placement of nests in relation to the barrier also depended on local conditions. Because there was a spatial clustering of road-side nests near the free-end of one SHB fence, this suggests that the SHB fence was even more effective than the road-side nest counts indicated, as Diamondback Terrapins likely accessed this road-side area by walking around the fence-end or emerging from the marsh in an unfenced section and walking to the fenced zone. This pattern was not found on the MC, as road-side nests were more evenly scattered throughout the fence. The MC study site was a small island, so accessing the road from beyond fenced sections was not possible. Predation patterns also varied between sites, likely caused by microenvironmental differences in elevation, flooding, vegetation, predator behavior, or some combination of factors. Fence-related effects often depend on local conditions, so it may not be possible to draw certain generalizations across sites.

It is a concern that barriers could force Diamondback Terrapins to concentrate eggs along the fence, making it easier for predators to find nests, and therefore increasing predation rates. We found that fence side and predation were not related, so fences did not seem to be altering predator behavior. Over time, however, predators may learn to walk along the fence if there are higher concentrations of eggs there, so fencing techniques may need to be modified in the

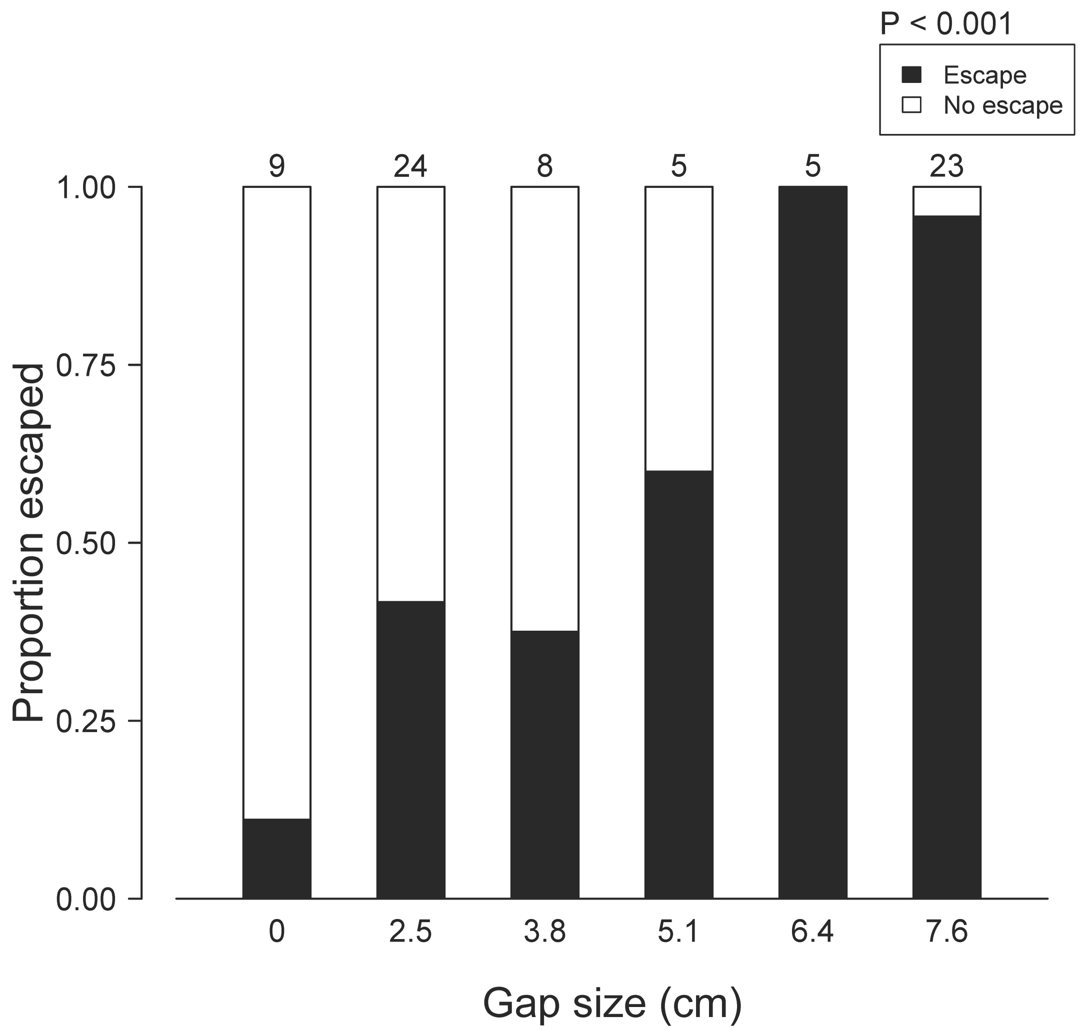

Figure 7. Diamondback Terrapin (*Malaclemys terrapin*) escape success increases with size of gap beneath the fence. Black sections of bars represent successful Diamondback Terrapin escape. White sections of bars represent Diamondback Terrapin escape failure. Number of trials at a given size class is at the top of each bar.

future to prevent this assisted predation. Furthermore, we were unable to definitively differentiate between abandoned and predated nests due to specific seasonal predator feeding habits, so our results are likely an underestimate of actual nest predation at our study sites. Few studies report predation rates lower than 90%, indicating that management to reduce road mortality may be insufficient to stabilize Diamondback Terrapin populations without also addressing nest predation (Crawford et al. 2014a). Fortunately, integrated management options are available and may be more effective (Crawford et al. 2014b). For example, Raccoon removal was shown to reduce nest predation from 76-80% (pre-removal) to 17% (post-removal) (Munscher et al. 2012).

Based on the results of our study, we offer a few basic recommendations for the conservation of Diamondback Terrapins (or other marshland specialists) subject to road mortality. Our study demonstrates that significant decreases in roadway access can be achieved through simple, low-cost management practices. Corrugated tubing fences have a measurable impact and are relatively easy, inexpensive, and fast to install. In order to optimize fence effectiveness, maintenance of the fence, vegetation, and ground is imperative during nesting season. This can be accomplished via vegetation management, filling gaps beneath fences with sediment, and regularly replacing broken fence stakes. New approaches should be investigated, including strategies to weigh down the fences, more permanently attach fences to the ground, and modify the fence-ends to prevent the spatial clustering of road-side nests near fence-ends, as seen on the SHB.

Given the limited funding available in conservation management, efficient use of resources is critical (James et al. 1999). Management of wetlands species, specifically dual-environment species, can be difficult, and conservation plans must be designed within the context of how microenvironmental characteristics differ and how the species uses its multiple habitats (Pressey 1994; Law and Dickman 1998). If regional populations are to persist, management plans must accommodate the nesting migration and local movements of turtles and other species (Gibbs and Amato 2000; Gibbs and Shriver 2002). By focusing our study on terrestrial nesting activity, we show that fences can effectively address the problem of female-biased roadway access, and subsequent mortality, in this semi-aquatic species. Protecting adult females in species with sensitive life history traits can have significant population-wide consequences (Wilbur and Morin 1988), so fences that reduce mortality of adult females represent an efficient use of conservation resources. Our results are encouraging and may be useful in situations dealing with complex habitat usage, as often is found in wetlands systems. Targeted protection of adult females could significantly help long-lived species cope with additive mortality.

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