Articles

Effects of Vegetation Structure and Artificial Nesting Habitats on Hatchling Sex Determination and Nest Survival of Diamondback Terrapins

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Abstract

It is often the case that multiple factors contribute to wildlife population declines such that management will require simultaneous, integrated interventions to stabilize and recover populations. Diamondback terrapins *Malaclemys terrapin* are a species of high conservation priority, and local populations can be threatened by multiple factors, including bycatch in commercial and recreational crab pots, vehicle strikes on coastal roads, nest depredation from subsidized and introduced predators, and terrestrial habitat alteration. Mitigation of just one of these factors will often be insufficient for recovering at-risk populations; thus, information to manage multiple threats is needed. We measured the effects of natural vegetation structure and constructed (artificial) nesting habitat on hatchling sex ratios and nest depredation for a declining terrapin population on Jekyll Island, Georgia. Nest temperatures were highest on constructed nesting mounds, intermediate in open grass areas, and coolest under the shrub-dominated hedgerows. Higher nest temperatures led to shorter incubation times for nests on mounds and open habitat, such that all surviving nests on nesting mounds and open areas produced female hatchlings. In contrast, surviving nests under hedge produced 85% male hatchlings. Raccoon *Procyon lotor* predation rates of simulated (chicken egg) nests were highest on nesting mounds (95.3%), followed by hedge (84.4%) and open habitats (45.2%). Our results demonstrate that vegetation management can positively affect both production of female hatchlings and nest survival. Artificial nest mounds were successful at producing female hatchlings, but we documented high predation of simulated (chicken egg) nests despite structures to exclude predators. Further modifications to nest boxes atop constructed nesting mounds are needed for these devices to effectively contribute to population management. We suggest the relatively low cost and maintenance associated with removing shrubs and trees can be a viable strategy to manage large areas of nesting habitat for the increased production of female turtles, and to reduce the impacts of subsidized predators.

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Introduction

In many cases there are multiple factors that contribute to wildlife population declines such that management will require simultaneous, integrated interventions to stabilize and recover populations. In the case of diamondback terrapins *Malaclemys terrapin* (Figure 1), populations are perceived to be declining due to multiple factors, including crab-trap mortality (Dorcas et al. 2007; Grosse et al. 2011), vehicle-induced mortality (Wood and Herlands 1997; Szerlag and McRobert 2006), high nest predation from subsidized and introduced predators (Feinberg and Burke 2003; Szerlag and McRobert 2006), and habitat degradation and alteration (Seigel 1993; Gibbons et al. 2001).

Numerous studies have shown that bycatch in crab pots is associated with local and regional declines in terrapin populations (Dorcas et al. 2007; Grosse et al. 2011; Chambers and Maerz, in review). In addition, terrapin populations are affected by a suite of factors, including high nest depredation and high mortality of gravid females along roads that bisect marsh habitats, both of which can independently and collectively contribute to terrapin population declines (Wood and Herlands 1997; Crawford et al. 2014a; Maerz et al. in review). Prior management strategies have focused on reducing bycatch rates (Grosse et al. 2011; Hart and Crowder 2011; Chambers and Maerz, in review) and road mortality (Crawford et al. 2014b). However, addressing those two threats may be insufficient to stabilize or recover some terrapin populations (Crawford et al. 2014a). Management interventions to address nest survival and performance are also needed as part of an integrated approach to terrapin management.

Major factors affecting terrapin nest success include loss and degradation of nesting habitats and high nest depredation by subsidized mammalian predators. Nesting habitat may be lost to bulkheading, constructing protective barriers to stabilize the shoreline (Roosenburg 1991, 1994; Winters 2013), and land conversion degraded by soil modification (Roosenburg 1994; Wnek 2010) and the succession of woody vegetation or invasive plants that increase shade (Roosenburg 1991; Wnek 2010). Like many turtles, terrapins exhibit temperature-dependent sex determination, with cooler incubation temperatures ($<28°C$) producing predominantly males and warmer temperatures ($>30°C$) producing predominantly females (Jeyasuria and Place 1997). Terrapins prefer to nest in areas of patchy, short vegetation; nests in open habitat develop faster and tend to produce a higher proportion of female hatchlings (Burger and Montevecchi 1975; Goodwin 1994; Roosenburg 1994; Feinberg and Burke 2003; Ner 2003; Scholz 2006; Hackney 2010). Dense vegetation shades nests, resulting in longer development times, higher egg mortality, and male-biased hatchling sex ratios (Wnek 2010). Mortality of terrapins on land, particularly nest and hatchling mortality, is clearly related to subsidized predator abundance. Roosenburg and Place (1995) found that shaded nests in dense grass had higher survival rates but produced almost 100% male hatchlings. Numerous studies show that raccoon *Procyon lotor* predation is the biggest determinant of terrapin nest success, and in many studies at sites with high raccoon densities throughout the species' range, raccoons routinely depredate as many as 95% of nests (Burger 1976, 1977; Roosenburg 1991; Goodwin 1994; Roosenburg and Place 1995; Feinberg and Burke 2003; Ner 2003; Butler et al. 2006; Munscher et al. 2012; Crawford et al. 2014a).

With the loss of suitable nesting habitat, terrapins may nest in suboptimal habitats, or concentrate nests into smaller areas, which can lead to higher nest predation rates (Roosenburg and Place 1995). In particular, vegetation cover may interact with predator abundance to affect terrapin nest success. Burger (1977) reports high mammalian depredation of terrapin nests in wooded shrub and edge habitats, and Hackney (2010) found that terrapin nests in shrub or edge habitats closer to marshes had a higher probability of being depredated compared with nests in open sandy areas farther from the marsh. The interactive effects of vegetation on terrapin hatchling sex ratios and nest predation have the potential to negatively impact terrapin populations, but afford a potential management intervention opportunity to reduce these threats and potentially compensate for other sources of mortality.

The objectives of this study were to measure the effects of vegetation structure and constructed nesting mounds on hatchling sex determination and nest survival of terrapins in the field. Specifically, we evaluated nest temperatures, hatchling sex ratios, and nest predation rates in areas of managed open grass versus dense shrub (hedgerows) where terrapins nested naturally. We also measured nest temperatures and hatchling sex ratios on constructed nesting mounds (Buhlmann and Osborn 2011) and measured nest predation rates in presumed predator-proof nest boxes on nesting mounds. We hypothesized that nests on artificial mounds and open grass areas would have higher incubation temperatures than those in shrub areas and, as a result, nests on the nest mounds and grassy habitat would produce a greater proportion of female hatchlings. In addition, we hypothesized that the presence of predator guards on nest mounds and the absence of shrub cover would result in higher nest survival of simulated nests.

Study Site

Jekyll Island is a 2,306-ha (5,698-acre) barrier island located in Glynn County, Georgia. Access to Jekyll Island is along an 8.7-km, paved causeway that bisects the marsh. The shoulder of the Downing–Musgrove Causeway (aka Jekyll Island Causeway: JIC) is a raised, dredge-spoil–deposited area, above the high tide line, that provides attractive nesting habitat for female diamondback terrapins. Female terrapins nest along the JIC from April to July, with individuals producing up to two clutches of 4–13 eggs (mean = 7 eggs) each year (Seigel 1980; Zimmerman 1989). A hedgerow of predominantly cedar *Juniperus virginiana* and wax myrtle *Morella cerifera* occurs along most of the causeway adjacent to the high marsh, and is managed to serve as a windbreak. However, the shrub layer has been removed along some

Figure 1. Adult diamondback terrapins *Malaclemys terrapin* in a tidal marsh near Jekyll Island, Georgia, USA. The photo on the left is an adult male and the photo on the right is an adult female of the same species captured in the same tidal creek, May 2010.

sections of the causeway, creating gaps maintained as short herbaceous (grassy) vegetation up to the high marsh. Between the hedgerow and road there is a parallel strip of maintained (mowed) short grass and other herbaceous plants. As a result, there are two general types of nesting habitat available for diamondback terrapins along the road shoulder: 1) open, regularly mowed, grassy habitat, and 2) shaded hedgerow. In 2009, we created a third habitat type by removing sections of the hedgerow and installing artificial nesting areas (mounds of sandy soil with large predator excluder cages on road shoulders; Figure 2; see Buhlmann and Osborn 2011) designed to allow terrapins access to the center of each nesting mound while excluding mammalian and avian predators. Preliminary monitoring demonstrated that female terrapins would nest on nest mounds and inside the caged areas (nest boxes) on the nest mounds.

Methods

Terrapin collection and oviposition

We collected eggs from 19 live, gravid female diamondback terrapins (i.e., none were injured or road-killed animals) found on the JIC between 15 May and 4 July 2010. We transported females to the Georgia Sea Turtle Center, where we radiographed them to determine number of calcified eggs present (Gibbons and Greene 1979). We injected terrapins with 0.5 mL/kg intramuscular of calcium (Mader 2006). After 30 min, half of the females were either given 7.5 units/kg subcutaneous of oxytocin or a combination of 7.5 units/kg subcutaneous of oxytocin and 1.5 mg/kg of prostaglandin. We placed each individual in a large enclosure and observed her until she oviposited. If oviposition did not begin within 2 h, we administered a second dose of 7.5units/kg subcutaneous of oxytocin. We released each female terrapin back into the marsh most proximate to her capture location and within 24 h of capture. We measured and weighed all deposited eggs and held

Figure 2. View of the Jekyll Island Causeway (Glynn County, Georgia) and three associated nesting habitat types for diamondback terrapins: hedgerow and open habitats (top), and artificial nesting mound with a nest box (bottom), 2010.

them in vermiculite before transferring them to an experimental nest placed along the causeway.
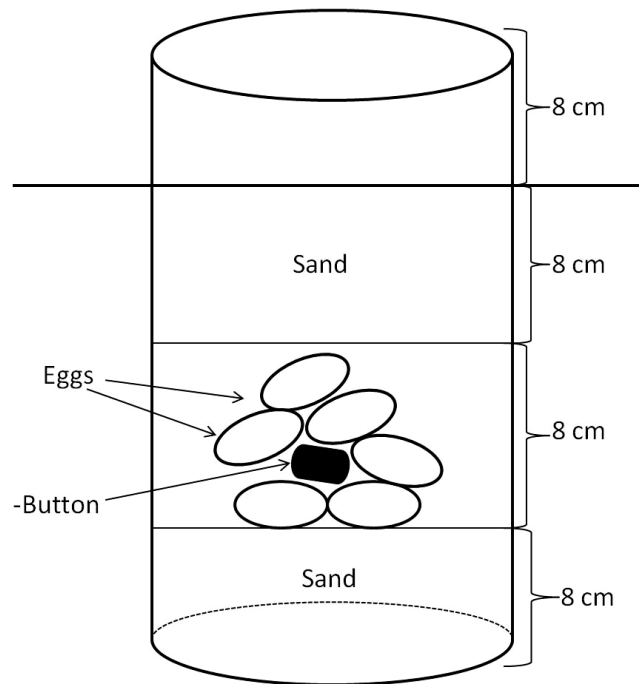
Experimental nests

We created 19 experimental nests along the JIC. We based the dimensions of our experimental nests on reports of natural nests (Burger 1976; Jeyasuria et al. 1994). We placed each clutch of eggs into one of the three randomly selected habitat treatments: open grass, hedgerows, or nest mounds. We established 15 nests (5/treatment) in May during the initial nesting peak, and 4 nests in late June during the window when many females nest a second time. All clutches were analyzed together taking into consideration temperature variations throughout the year.

Each experimental nest consisted of a "nest basket" constructed from a 30.5 × 45.7 cm piece of plastic hardware cloth with 1.02-cm mesh, to prevent nest predation. Each piece of hardware cloth was rolled into a 15.2-cm–diameter cylinder and connected with plastic zip ties. Additionally, we placed a 15.2 × 15.2 cm square on the bottom of each cylinder and secured it with plastic zip ties (Figure 3). We dug a 23-cm–deep hole in which we placed nest baskets, which we then filled with 7.6 cm of sand before adding terrapin eggs (Figure 3). We added each clutch of eggs within 24 h of collection, placing them carefully within the nest basket, 15.2 cm from the soil surface, taking care not to rotate eggs. Additionally, we coated Thermochron i-button data-loggers (model DS1922L-F5#) with Performix Plasti-Dip and added them to the center of each clutch to record hourly temperature during the incubation period (Table S1, *Supplemental Material*). Once eggs and data-loggers were appropriately placed within the nest basket, we added moist sand to cover the eggs and filled the hole surrounding the basket with soil removed during the initial excavation. We then placed a 15.2 × 15.2 cm square piece of plastic hardware cloth on the top of the exposed 7.6 cm of the nest basket, securing it with plastic zip ties to further protect each nest from predation.

All nests were allowed to incubate naturally up to 65 d between May and August 2010, after which all intact nests were excavated to collect hatchlings and any unhatched eggs (Table S2, *Supplemental Material*). We placed all viable, unhatched eggs in an incubator until hatching. Because sex determination occurs well before the 65-d mark, excavation presumably had no effect on hatchling sex (Jeyasuria and Place 1997). We reared hatchlings in captivity until they were approximately 9 mo old, at which time we weighed, measured, and determined sex based on secondary sex characteristics (head width and tail length). Using a laparoscopic surgical technique to visually inspect the reproductive tract (Hernandez-Divers et al. 2009), we confirmed sex in a subset of hatchlings (Table S3, *Supplemental Material*). We released all individuals back into small tidal creeks in the high marsh at locations near where their mothers were found, but away from the causeway.

Predation of simulated turtle nests

Using store-bought chicken eggs to simulate turtle nests, we estimated habitat-specific predation rates on

Figure 3. Diagram of the nest basket used for each of the 19 experimental diamondback terrapin *Malaclemys terrapin* nests in the three habitat types (hedgerow, open, and artificial nesting mound with a nest box) on the Jekyll Island Causeway (Glynn County, Georgia), May–August, 2010.

the JIC. We placed a nest, consisting of a single chicken egg not protected by caging, in one of the three habitat types on JIC road shoulders. In each habitat type, we placed four nests within a 300-m transect along the roadside. We replicated this design spatially across four 300-m transects and then temporally across four time periods (approx. 2 wk apart) spanning the majority of the terrapin nesting season at our site (sample unit = nest; total *N* = 192; Table S2, *Supplemental Material*). Because we suspected raccoons were entering nest boxes, we placed two simulated chicken egg nests inside each of four nest boxes during the latter two time periods to also estimate predation rates within the nest boxes (*N* = 16). For each nest, we dug a chamber 8–10 cm in depth, buried a single egg, and poured approximately 250 mL of scented water obtained from aquaria containing captive *M. terrapin* over the nest to mimic the release of bladder water by the female at the time of nesting (see Marchand and Litvaitis 2004b; Foley et al. 2012). We spaced nests in the latter three time periods ≥3 m from any previous nest location, and we marked the location of each nest with a handheld Global Positioning System unit and a small flag marker placed 2 m from the nest. Other studies report that up to 98% of depredated terrapin nests were taken within the first 48 h of nesting events (Burger 1977; Goodwin 1994; Butler et al. 2004; Munscher et al. 2012), so we monitored simulated nests daily for 11 d for evidence of predation. After day 11, we excavated all nondepredated nests to confirm whether chicken eggs were still intact. We wore latex gloves

during all phases of the experiment to limit human scent left at simulated nests.

Statistical analyses

We investigated the effects of time period, habitat type, and the habitat × time interaction on nest temperature using a factorial analysis of variance with nest temperature as the dependent variable. We performed these statistical analyses in STATISTICA v8.0 (StatSoft, Inc., Tulsa, Oklahoma). We conducted generalized linear models with a logit-link function in R (R Development Core Team 2014) to determine the influence of habitat type and time period on the probability of nest predation. We originally included transect as a random effect in the mixed model, but the variance estimate was zero, which indicated low between-transect variability; therefore, we removed this factor from the model. The unit of analysis was the fate (depredated or not) of an individual nest, and we assumed independence between nests. This assumption was likely met in the open and hedge treatment groups where distances between nests were >50 m. However, nests on mounds were approximately 4 m apart and likely subjected to similar predation risks as adjacent nests. Because nesting habitat on artificial mounds is inherently more confined than natural habitats, we proceeded with the analysis to assess predation risk associated with these management devices. We first tested the full model, including habitat type, time period, habitat × time interaction, and transect as predictor variables and dropped nonsignificant factors (α = 0.05) in a backward stepwise procedure using likelihood-ratio tests. We performed post hoc Wald's tests to make pairwise comparisons between levels within significant factors using the reduced model.

Results

Experimental nest fates, temperatures, and hatchling sex

Of 19 experimental terrapin nests, 4 nests hatched in the field within 65 d, and 12 nests were excavated after 65 d and hatched in captivity, and 3 nests were poached (presumably by humans) during the course of the study. Three of the four nests that hatched in the field had been placed on constructed nest mounds and hatched in 52, 55, and 62 d for an average of 56 d. The fourth nest to hatch in the field had been placed in the open grass habitat and hatched in 52 d. The hatching success for the nests that hatched naturally and those that were transported back to the laboratory were 88% and 71%, respectively. Nest success by habitat type was 44% for the artificial nest mounds, 100% for the shrub hedge, and 83% for the open grass habitat. Overall, 79% of all eggs hatched successfully.

Maximum nest temperatures and diel variation varied among the three habitats in relation to vegetation effects on nest shading. Maximum nest temperatures at each habitat were 47.1°C, 35.7°C, and 32.2°C on nest mounds, in open grassy areas, and underneath the hedgerows, respectively. Maximum diel temperature fluctuations were 17.0°C, 5.5°C, and 3.8°C on nest
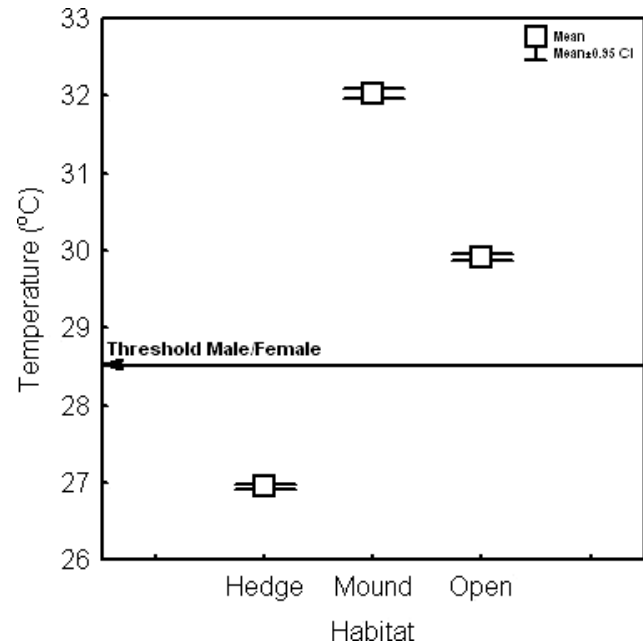
Figure 4. Mean nest incubation temperature and 95% confidence interval for experimental diamondback terrapin *Malaclemys terrapin* nests placed in each habitat type across the 65-d incubation period, occurring May–August, 2010 on the Jekyll Island Causeway (Glynn County, Georgia). Arrow represents the pivotal temperature at which sex ratios are 50:50 male:female (Jeyasuria et al. 1994).

mounds, in open grass areas, and underneath the hedgerows, respectively. Across the entire nesting season, mean incubation temperature was 32.0°C, 29.9°C, and 26.9°C on nest mounds, in open grass areas, and underneath the hedgerows, respectively (Figure 4). Mean incubation temperature was statistically different among nesting locations (MS = 456.4, $F_{2,15}$ = 63.81, P = <0.001). Mean weekly nest temperatures showed similar increases across the nesting season among the three habitats (MS = 18.3, $F_{10,150}$ = 12.28, P = <0.001), but the differences in mean temperature remained relatively constant among the three nesting habitat types (Figure 5; MS = 2.0, $F_{20,150}$ = 1.31, P = 0.178). Weekly mean temperatures never exceeded 35°C in any habitat, which is the lethal temperature reported for terrapin embryos (Cunningham et al. 1939; Butler et al. 2006); however, nests on nest mounds experienced 7 wk in which mean temperatures were above 32°C (Figure 5), which is the temperature at which scute anomalies can become more prevalent (Herlands et al. 2004).

In total, we collected and raised 104 hatchling terrapins to 9 mo of age. Laparoscopic surgery of a subset of individuals (N = 44) verified that we accurately determined the sex of all (100%) hatchlings using noninvasive assessments of head width and tail length (i.e., head size, tail length, distance to cloaca from shell; T. Norton, personal communication). As a result, we feel confident in the determination of sex of all 104 hatchlings assigned based on external characteristics. The proportion of hatchlings that were female was 100%
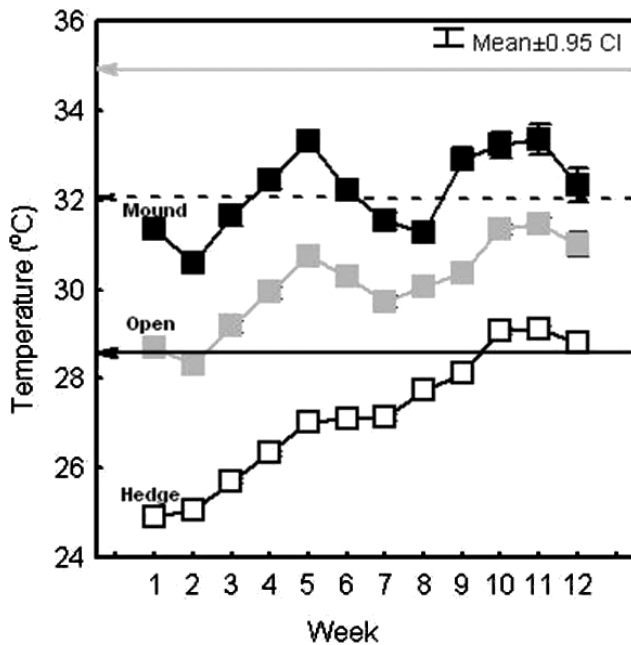
Figure 5. Weekly average incubation temperatures and 95% confidence interval for experimental diamondback terrapin *Malaclemys terrapin* nests placed in three habitat types along the Jekyll Island Causeway, Georgia, May–August, 2010. The straight solid black line represents the pivotal temperature at which sex ratios are 50:50 male:female (Jeyasuria et al. 1994). The straight dotted line at 32°C represents the threshold at which scute anomalies are more prevalent in diamondback terrapin hatchlings (Herlands et al. 2004). The straight solid gray line at 35°C represents the threshold at which terrapin embryos do not survive (Cunningham et al. 1939; Butler et al. 2006).

from nest mounds and grassy habitats, and only 15% from hedgerows.

Predation of simulated turtle nests

Of 208 simulated chicken egg nests, 157 (75.4%) were depredated within the 11-d monitoring period. The majority (58.0%) of nest predation events occurred within 24 h of nest placement on the JIC, with only 5.7% of predation occurring after 5 d. Mean ($\pm$ SE) nest predation rates were 45.2% $\pm$ 6.3% in open grassy areas,

84.4% $\pm$ 5.4% in hedgerows, and 95.3% $\pm$ 2.6% on artificial nest mounds. The mean predation rate of nests placed inside nest boxes was 81.3% $\pm$ 2.9%. Predation rate was significantly affected by habitat type and time (likelihood-ratio tests [LRT], $\chi^2_2 = 48.08$, $P < 0.001$ and $\chi^2_3 = 31.80$, $P < 0.001$, respectively), while the habitat $\times$ time interaction and transect had nonsignificant effects (LRT, $\chi^2_6 < 2.47$, $P > 0.871$) and were dropped from the final model. Nests were significantly more likely to be depredated in hedgerows and on nest mounds relative to open habitats, and nest predation rates significantly increased in later time periods across habitat types (Table 1; Figure 6).

Discussion

Our results show that habitat affects both terrapin nest temperatures and associated hatchling sex ratio, but also nest depredation rates. Open grass areas had high nest temperatures that remained below levels that might induce embryonic mortality or deformities, but still yielded all female hatchlings. In addition, nest predation rates were significantly lower in open grass habitats. In contrast, hedgerows had relatively high nest depredation and significantly reduced mean nest temperatures that resulted in 85% of surviving eggs producing male terrapins. Constructed nest mounds had the highest nest temperatures, which resulted in the production of 100% female hatchlings; however, terrapin embryos on those mounds experienced up to 7 wk of nest temperatures above levels reported to cause scute abnormalities, and 95% of simulated chicken egg nests on constructed nest mounds were depredated. Therefore if we take all of our habitat-specific estimates, the probability that a terrapin egg laid in open grass hatched successfully as a female terrapin was 0.43. In contrast, the probability that a terrapin egg hatched successfully as a female was an order of magnitude lower for shrub habitats (0.02) or artificial nest mounds (0.04).

Other studies have reported interactions between vegetation cover effects on terrapin nest predation and hatchling sex ratios (Roosenburg and Place 1995), and our results are consistent with other studies that link higher nest depredation (particularly by raccoons), longer development times, and increased male-biased

Table 1. Generalized linear model (logit-link, binomial distribution) estimates and odds ratios for habitat type (open, hedgerow, or nest mound) and time period effects on predation rates of simulated chicken egg nests on the Jekyll Island Causeway, Georgia, during May–July 2011.

Variable	β	SE	z	Odds ratios Estimate[a]	95% CIs	
Intercept (Open, Time 1)	−3.063	0.682	−4.49*	0.17[A]	0.06	0.43
Hedgerows	2.438	0.522	4.67*	11.33[B]	4.33	33.65
Nest mounds	3.898	0.723	5.39*	47.59[B]	13.42	237.53
Time 2	0.733	0.551	1.33	2.08[AB]	0.72	6.36
Time 3	2.093	0.63	3.32*	8.11[ABC]	2.50	30.12
Time 4	3.399	0.784	4.33*	29.94[C]	7.29	166.67

* $P < 0.001$.
[a] Letters indicate significant differences ($P < 0.05$) in predation rates between levels within the same factor (e.g., Open and Hedgerows, Time 1 and 4).
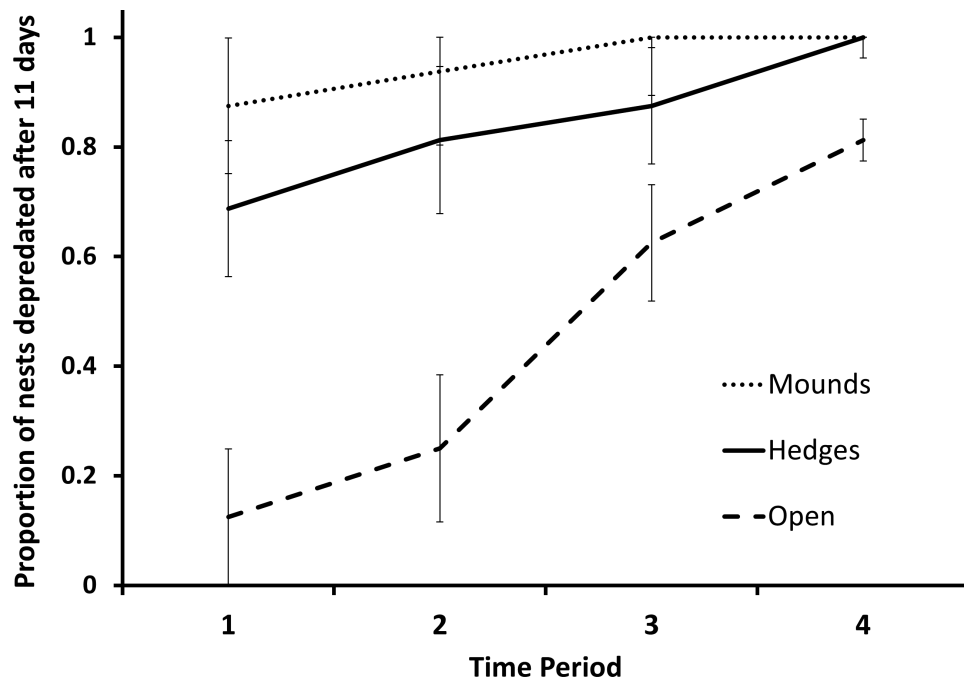
Figure 6. Mean predation rates (±SE) of plots with chicken egg (simulated diamondback terrapin *Malaclemys terrapin* nests (N = 48) in three habitats on the Jekyll Island Causeway, Georgia, during May–July 2011.

hatchling sex ratios to increased shrub and tree cover around nesting areas (Burger and Montevecchi 1975; Goodwin 1994; Roosenburg 1994; Feinberg and Burke 2003; Ner 2003; Scholz 2006; Hackney 2010; Wnek 2010). Collectively, these studies illustrate an important threat to terrapin populations as well as a potential area of management opportunity.

High predation on nests and hatchlings is a well-documented threat to terrapins and other turtle species (Feinberg and Burke 2003; Butler et al. 2006; Munscher et al. 2012). Munscher et al. (2012) demonstrated that raccoon removal could dramatically improve nest survival. However, high nest predation returned within 1 y of following cessation of raccoon control. Thus, raccoon control can be effective but requires sustained effort. Our results suggest that terrapin nest survival can be moderately high in open grass habitats in areas of high raccoon abundance, and suggest that the removal of shrub and tree vegetation around nesting areas could be an effective long-term management strategy for reducing raccoon predation. Also, removal of shrub cover for raccoons on the narrow causeway may reduce raccoon abundance. Maintaining or restoring open-grass nesting habitats should increase the production of female hatchlings, which is critical to the growth and recovery of turtle populations (Congdon et al. 1994; Mitro 2003; Crawford et al. 2014a). We also suggest that creating grass-dominated nesting habitats to increase the production of female hatchlings can be an important tool within an integrated management framework to offset other factors such as roads that cause high adult female mortality. For example, adult female mortality on the JIC ranges from 4 to 16% annually, which is sufficient to cause the population to decline (Crawford et al.

2014a). Crawford et al. (2014a) estimate that increasing nest success to 50% and the proportion of female hatchlings to 85% could stabilize the population when coupled with modest decreases in road mortality.

The results of our study suggest that maintaining and expanding open-grass nesting habitat could achieve both of these management targets, and in combination with efforts to reduce road mortality, could restore and sustain terrapin populations along the JIC. However, further study is warranted, because of the remaining concern that female terrapins on nesting forays will walk through the narrow grass-dominated areas on the roadsides and access the roadways, which they pre-sumably perceive as higher, well-drained areas. Discour-aging terrapin access to the roadway by intercepting them on their nesting foray was the initial intent of the constructed nest mounds. Reducing female terrapin road mortality must still remain a priority to prevent further population declines.

We posit that higher predation rates of simulated nests within the hedgerows and on nest mounds occurred for two reasons. First, nest mounds were placed in areas of high historical nesting densities (T. Norton, personal communication) and current hot spots of nesting activity (Crawford et al. 2014b), which is consistent with other studies that report higher predation rates in habitats with higher nest densities (e.g., Roosenburg and Place 1995; Feinberg and Burke 2003; Marchand and Litvaitis 2004a). Terrapins show high nest fidelity between years (Goodwin 1994; Sheridan 2010; Crawford et al. 2014b), and predators may learn to target these areas. Secondly, hedgerows form extended corridors for predator move-ment, particularly along roadways, and constructed nest mounds in the study were initially placed in small gaps

along the hedgerows. The nest boxes placed on top of the artificial nest mounds were intended to provide nest protection from predators. However, raccoons at our study site demonstrated the ability to squeeze through the box opening and depredate terrapin nests. We followed the nest box design of Buhlmann and Osborn (2011), which was successful at improving nest survival for other turtle species. Nonetheless, the effectiveness of nest boxes on artificial nest mounds remains unclear, but the nest boxes have undergone structural modification to ensure they are effectively excluding potential predators. If modified successfully, artificial nesting habitat with predator exclusion structures could be an effective tool for improving nest success at hotspots of terrapin nesting and road mortality (see Crawford et al. 2014b).

We caution that our advocacy for increasing open, grassy habitat must consider other factors that could degrade nesting habitat quality for terrapins. Management activities to remove shrubs or trees must not substantially change the soil composition or increase the potential for erosion within the nesting area. Terrapins nest in sandy soils with large particle size that improves gas diffusion and has a lower water potential, which reduces hydric constraints on developing embryos (Roosenburg 1994; Wnek 2010). Activities that increase organic content of soils or compact the soils would likely reduce terrapin egg survival (Wnek 2010). In addition, to avoid killing or disturbing nesting females, mowing to maintain open, grassy habitats should not occur during the nesting season. Care should also be taken to manage the types of herbaceous plants that replace shrubs and trees in restored habitats. The dense planting of either grasses to control erosion or of invasive plants are both known to increase terrapin nest failure (Roosenburg 1991; Wnek 2010). Some plant species have roots that can infiltrate and kill terrapin eggs (Lazell and Auger 1981), and dense grasses can reduce soil moisture potential, resulting in higher egg-failure rates. The creation of open-grass–dominated areas suitable for nesting should include clump grasses with open sandy areas in between.

In conclusion, we demonstrated that vegetation management around terrapin nesting habitat interacts to affect both nest predation rates and hatchling sex ratio. Both the intentional planting of shrubs and trees as hedgerows or windbreaks along causeways and the unintentional succession of woody plants are common scenarios in developed coastal areas, and may be contributing to terrapin population declines by creating male-biased hatchling sex ratios and facilitating subsidized predators. If conducted properly and in concert with methods to reduce road mortality, the maintenance and restoration of open grassy nesting areas can be a highly feasible and effective component of an integrated management plan to restore and sustain terrapin populations.

Supplemental Material

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Table S1. Diamondback terrapin nest temperatures data-file characteristics (from 2010 data-loggers on the Jekyll Island Causeway, Georgia). Variables are the date and time of each logged temperature, the habitat of each nest, the temperature of each nest (in °C), and the week of incubation for each nest.

Found at DOI: http://dx.doi.org/10.3996/082014-JFWM-063.S1 (2549 KB XLS).

Table S2. Predation of simulated diamondback terrapin nests data-file characteristics (from 2011 on the Jekyll Island Causeway, Georgia). Variables are time period that simulated nests were constructed May–July 2011 where 1 = 16 May 2011; 2 = 2 June 2011; 3 = 14 June 2011; 4 = 27 June 2011. Transect number refers to one of the four transects of simulated nests constructed at each time period. Habitat type refers to the four habitats where simulated nests were constructed: O = Open, H = Hedge, M = Mound, B = Inside box on mound. Other variables include the nest ID of each nest within each transect, the side of the road where each nest was located: N = North, S = South, whether or not each nest was depredated: 1 = yes, 2 = no, the date each nest was depredated, and the number of days after construction that each nest was depredated.

Found at DOI: http://dx.doi.org/10.3996/082014-JFWM-063.S2 (40 KB XLS).

Table S3. Diamondback terrapin experimental nest data-file characteristics (from 2010 on the Jekyll Island Causeway, Georgia). Variables are the ID for each individual nest, the habitat of each nest, the number of eggs buried with each nest, the date each nest was buried, the date each nest was removed, the number of incubation days, and whether or not the nest hatched naturally.

Found at DOI: http://dx.doi.org/10.3996/082014-JFWM-063.S3 (19 KB XLS).

Table S4. Diamondback terrapin hatchling sex data-file characteristics (from 2010 on the Jekyll Island Causeway, Georgia). Variables are the ID for each hatchling, the sex of each hatchling, the date each hatchling sex was determined, and whether or not an endoscopy procedure was conducted on each individual hatchling.

Found at DOI: http://dx.doi.org/10.3996/082014-JFWM-063.S4 (24 KB XLS).

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