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# MITIGATING ROAD MORTALITY OF DIAMOND-BACKED TERRAPINS (*MALACLEMYS TERRAPIN*) WITH HYBRID BARRIERS AT CROSSING HOT SPOTS

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**Abstract.**—Roads represent a pervasive feature on most landscapes that can pose multiple threats to wildlife populations and substantial challenges for management. To be effective, management strategies must often target where threats are most concentrated. Road mortality and nest predation are well-documented threats to Diamond-backed Terrapins (*Malaclemys terrapin*) across the majority of their range, including the 8.7-km causeway to Jekyll Island, Georgia, USA, where both are predicted to contribute to population declines if left unmitigated. From 2009 to 2014, we used intensive road surveying to identify spatial peaks (hot spots) of terrapin crossing activity and road mortality and exploit these as targets for management. In 2011, we deployed a hybrid barrier composed of nest boxes, which were designed to prevent terrapins from accessing the road and mitigate nest predation, at one hot spot while leaving two other hot spots unmanaged. We evaluated the impact of the barrier on terrapin emergences on the causeway under a Before-After-Control-Impact (BACI) design, and a companion study evaluated the effects of nest boxes on nest predation rates. We estimated a 57% reduction in annual terrapin emergences at the barrier site compared to no measurable change at control hot spots. Our findings support the use of hybrid barriers for simultaneously addressing road mortality and nest predation for other terrapin populations at risk to these threats. Our approach highlights the need to design feasible but robust management strategies that target spatial peaks of road mortality while addressing additional threats contributing to population declines of terrapins and other species.

**Key Words.**—Before-After-Control-Impact (BACI); conservation management; nest predation; turtle; wildlife-vehicle collision

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## INTRODUCTION

As road networks and traffic volumes expand across most landscapes, ecologists have increasingly documented negative impacts on herpetofauna species (Fahrig and Rytwinski 2009; Andrews et al. 2015). These impacts include the destruction of viable habitat, impediment to movement, increased predation by species subsidized by human activities (e.g., Northern Raccoons; *Procyon lotor*), alteration of species behavior, and mortality from vehicles (reviewed by Forman and Alexander 1998; Trombulak and Frissell 2000; Forman et al. 2003). Roads present a complex challenge to wildlife managers for two reasons. First, multiple road-associated threats can contribute to population declines simultaneously (Forman et al. 2003; Litvaitis and Tash 2008; Fahrig and Rytwinski 2009), and failure to address any one threat may render management ineffective overall (Marschall and Crowder 1996; Rhodes et al.

2011; Crawford et al. 2014a). Second, the impacts of threats may be spatially or temporally diffuse making the design and implementation of management actions logistically difficult and expensive (Beaudry et al. 2008; Langen et al. 2009; Crawford et al. 2014b). Therefore, designing management strategies that address these challenges is essential for sustaining wildlife populations currently at risk to road threats.

Frequently, road ecology and management studies have focused on the most direct and ubiquitous road-associated threat, i.e., wildlife-vehicle collisions (hereafter referred to as road mortality), and have documented its impacts across herpetofauna taxa (reviewed by Fahrig and Rytwinski 2009; Andrews et al. 2015). Many species of herpetofauna share several life-history and behavioral traits that make them especially vulnerable to the effects of road mortality. Species that complete extensive overland movements, do not avoid or are attracted to roads, and have lower reproductive

rates and longer generation times are expected to be more susceptible because they will encounter roads more frequently and recover less quickly from road mortality (Gibbs and Shriver 2002; Forman et al. 2003; Jaeger et al. 2005; Rytwinski and Fahrig 2012). Many types of roadside barriers have been commonly used to reduce road mortality with mixed success (Clevenger et al. 2001; Dodd et al. 2004; Aresco 2005b; Glista et al. 2009; Andrews et al. 2015). Because barriers can be costly to install at large scales, it has been suggested that assessments identifying particular places (hot spots) where road mortality occurs most frequently could be used as management targets with potentially great effect on population growth (Beaudry et al. 2008; Langen et al. 2009; Cureton and Deaton 2012; Crawford et al. 2014b). Although barriers can yield direct benefits to a population by reducing road mortality, they may lead to negative effects over a longer term, including reductions in connectivity between individuals on opposite sides of a road and increases in predation rates if nests are concentrated near barriers (Glista et al. 2009; Langen 2012; Andrews et al. 2015). Barrier designs that include culverts to allow animals safe passage under roads have been successfully used to mitigate road mortality while maintaining population connectivity (Dodd et al. 2004; Aresco 2005b; Glista et al. 2009), but effective barrier designs have not been developed that mitigate nest predation.

Diamond-backed Terrapins (*Malaclemys terrapin*) inhabit salt marshes along the Eastern and Gulf Coasts of the United States, regions experiencing the fastest annual increases in both the densities and traffic loads of roads (Baird 2009). Terrapins are currently listed as state threatened or of special concern in numerous U.S. states including Georgia (Georgia Department of Natural Resources. 2015. Georgia State Wildlife Action Plan. <http://www.gadnr.org/cwcs/Documents/strategy.html>. [Accessed 15 May 2009]). Causeways that bisect coastal salt marshes impact terrapin populations in Georgia, as well as range-wide, through multiple mechanisms (Gibbons et al. 2001; Maerz et al. In press). Like many turtles, terrapins have habits and life-history traits that make them particularly vulnerable to road-associated threats (Gibbs and Shriver 2002; Aresco 2005b; Fahrig and Rytwinski 2009). Each summer, females complete nesting forays on land and show an attraction to open, elevated habitat, which can bring them across roads and result in mortalities (Wood and Herlands 1997; Butler et al. 2006; Szerlag-Egger and McRobert 2007; Crawford et al. 2014b). Nests laid on roadsides can experience high predation rates, especially from subsidized mesopredators (e.g., Northern Raccoons), that reduce recruitment (Feinberg and Burke 2003; Szerlag-Egger and McRobert 2007; Crawford et al. 2014a; Quinn et al. 2015). Similar to other long-lived turtle species,

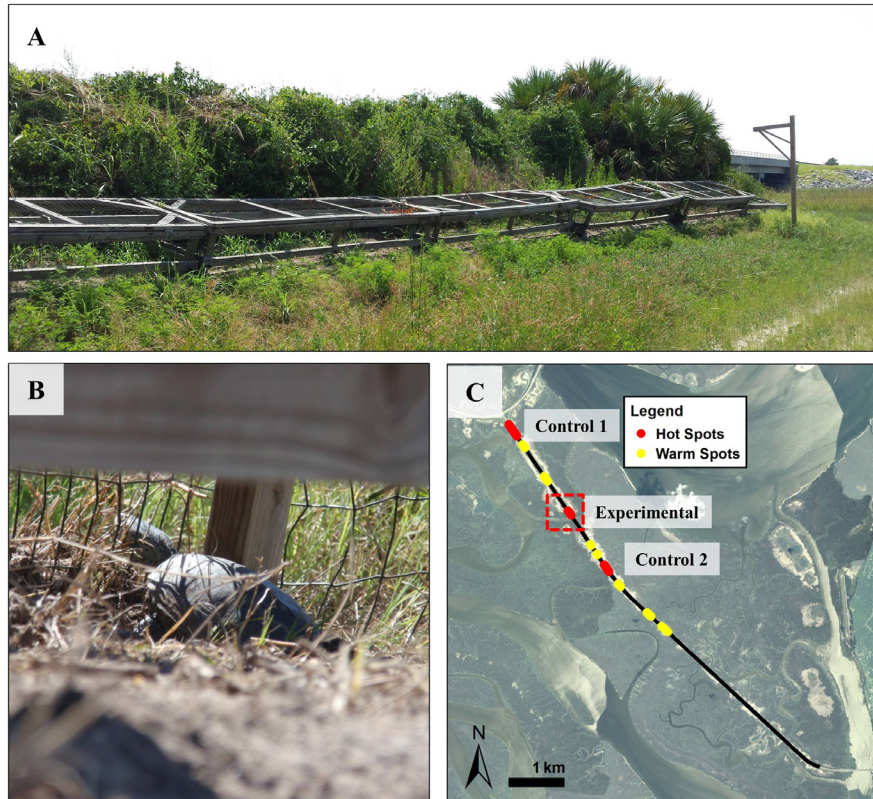
terrapin populations are most sensitive to reductions in adult survival, such as those caused by road mortality (Wood and Herlands 1997; Grosse et al. 2011), but nest predation rates can be sufficiently high to maintain population declines even when road mortality is reduced or eliminated (Crawford et al. 2014a).

To develop cost-effective management devices that mitigate road threats for at-risk wildlife populations, we designed a novel roadside barrier to reduce road mortality and nest predation for Diamond-backed Terrapins on the Jekyll Island Causeway, Jekyll Island, Georgia, USA. Previous studies showed that these two threats contribute to local population declines and population stability could not be achieved without management actions that addressed both (Crawford et al. 2014a). A companion study (Quinn et al. 2015) estimated the effects of the barrier on local nest predation rates. In the current study, we used a Before-After-Control-Impact design to experimentally estimate the effects of the barrier on terrapin emergences on the road.

## MATERIALS AND METHODS

**Study site description.**—The 8.7-km Downing-Musgrove Causeway (aka Jekyll Island Causeway: JIC) is the only road connecting the mainland with Jekyll Island (31.08°N, 81.47°W). The JIC is a high-speed (89 km/hr [55 mph]) state highway with average annual daily traffic of 3,440 vehicles/d that peaks from May through July, corresponding with increased summer tourism (Georgia Department of Transportation. 2014. Georgia's State Traffic and Report Statistics (STARS). <http://www.dot.state.ga.us/statistics/stars/Pages/GlynnTraffic.aspx>. [Accessed 19 Oct 2011]). Representative of many high-traffic coastal areas, the JIC is a regional hot spot of mortality where 100–400 adult female terrapins are struck and killed each year while attempting to cross the road to nest within the nesting season (late April to July; Crawford et al. 2014b). Early monitoring of the JIC revealed three concentrated hot spots of nesting activity and road mortality that were stationary across study years (2009–2010; Crawford et al. 2014b), which is likely a product of philopatry and nest site fidelity (Sheridan et al. 2010). These sites spanned < 10% of the JIC length, but 30% of terrapins observed during the study crossed within these segments.

**Experimental design and data collection.**—Using hot spots of road mortality as target areas for cost-effective management on the JIC, we designed a hybrid barrier to mitigate road mortality and nest predation of terrapins in partnership with the Georgia Sea Turtle Center (GSTC) and the Savannah River Ecology Lab of the University of Georgia. The hybrid barrier was composed of short fencing and six nest boxes placed



**FIGURE 1.** (A) The hybrid barrier composed of six nest boxes (22.9 m in total length). (B) A terrapin nesting inside the barrier after entering from the opening (foreground) on the marsh-facing side. Note the road-facing side of the boxes (background) is completely closed to prevent movement toward the road. (C) Concentrated areas of road mortality of Diamond-backed Terrapins (*Malaclemys terrapin*) on the Jekyll Island Causeway (Jekyll Island, Georgia, USA: Crawford et al. 2014b) that were used as Control and Experimental sites, with the dashed box indicating the hot spot where the hybrid barrier was placed in 2011. (Photographed by Brian Crawford).

side-by-side (Fig. 1A), which were placed atop an elevated, artificial mound of suitable nesting habitat (adapted from Buhlmann and Osborn 2011; Quinn et al. 2015). Each box included a horizontal opening (8.9-cm in height) at ground-level on the marsh-facing side but was completely closed on the road-facing side. This design allowed terrapins emerging from the marsh on nesting forays to enter boxes, prevented terrapins from continuing onto the road, and protected nests laid inside boxes from predators (Fig. 1B). There was a strip of open grass approximately 5 m in width between the barrier and pavement, so any individual crossing from the opposite roadside had access to suitable nesting habitat. The barrier (22.9 m in length) was placed on the south roadside at one hot spot (164 m in length) due to early observations that most terrapins emerged from the southern marsh at that section of the road and logistic constraints. See Quinn et al. (2015) for a detailed description of the barrier design.

We tested the effects of the hybrid barrier on terrapin emergence on the JIC using a Before-After-Control-Impact (BACI: Green 1979; Skalski and Robson 1992) design over six consecutive years (2009 to 2014). We

deployed the hybrid barrier prior to the nesting season in 2011 at one hot spot of terrapin activity (Experimental: Fig. 1C) while leaving two other hot spots unaltered (Control 1 and Control 2), which yielded two pre- and four post-intervention years for the analysis. We assumed independence among these sites because all pairwise distances between hot spots were > 1 km and terrapins exhibit nest site fidelity where most individuals attempt to cross the road to nest within 50–100 m from previous nesting locations (Szerlag-Egger and McRobert 2007; Crawford et al. 2014b). From 1 May to 20 July in each year of the study, we conducted intensive road surveys to record terrapin emergences on the causeway within the Experimental and Control sites as part of a long-term mark-recapture effort (see Crawford et al. 2014a). Relative to post-intervention (range, 288–360 surveys/y), sampling effort was higher pre-intervention (range, 571–881 surveys/y) to identify spatial and temporal peaks of activity and inform barrier placement (Crawford et al. 2014b). One or two observers completed each survey by driving the length of the causeway and back every 20–90 min generally between 0800 and 2000, with opportunistic surveys outside of this period.



We recorded the number of observed dead terrapins on the road and live terrapins on or about to cross the road. We recorded the location of each turtle with a handheld Global Positioning System (GPS: Garmin International, Olathe, Kansas, USA), and we included any individual observed within the known spatial extent of each hot spot (Crawford et al. 2014b) in the analysis. We only included turtles crossing from the south (barricaded) side of the road within the Experimental site, because only these individuals had the opportunity to encounter the barrier before potentially emerging on the road. We collected and processed turtles for the mark-recapture work and then returned individuals to artificial nest mounds within one hour of capture (sensu Buhlmann and Osborn 2011). We transported all injured or dead terrapins to the GSTC for treatment or euthanasia and to recover eggs for a head-start program.

**Estimation of barrier effects.**—To estimate the effect of barriers on preventing turtles from entering the road, we estimated the number of terrapins emerging on the road per year  $i$  at a site  $j$  ( $\lambda_{i,j}$ ) by fitting the following mixed model with a Poisson distribution, determined by the same mean and variance:

$$C_{i,j} \sim \text{Poisson}(\lambda_{i,j})$$

$$\log(\lambda_{i,j}) = \text{year}_i + \text{site}_j + \beta_j X_{i,j} + \varepsilon_{i,j}$$

$C_{i,j}$  represents the observed count of terrapins on or attempting to cross the road in year  $i$  at site  $j$ ,  $\text{year}_i$  is the random year effect,  $\text{site}_j$  is the fixed site effect, and  $\varepsilon_{i,j}$  is the residual error term.  $\beta_j$  is the vector of site-specific period (i.e., before-after) fixed effects, assumed to arise from a uniform prior distribution between -20 and 20, and  $X_{i,j} = 1$  in years after the barrier was installed versus 0 before intervention. To estimate the effect of the barrier while accounting for other sources of variation, we derived a treatment  $\times$  period interaction parameter using the formula

$$\frac{\beta_{\text{Control1}} + \beta_{\text{Control2}}}{2} - \beta_{\text{Experimental}}$$

Because the betas are estimates on the log scale of post-intervention effects, we estimated the percentage change in terrapin emergences on the road due to the treatment by exponentiating posterior estimates of  $\beta$  for Control sites (first taking the mean) and the Experimental site.

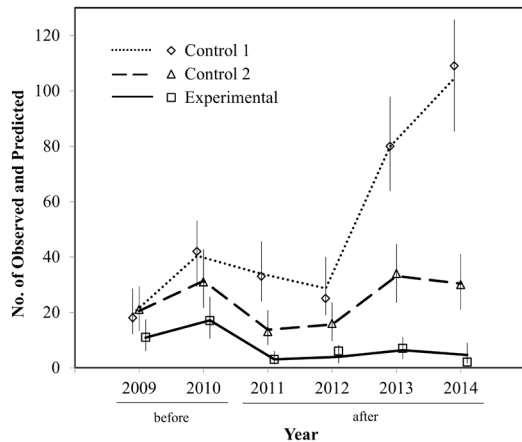
We included year as a random effect, assumed to arise from a zero-centered normal distribution with variance  $\sigma_Y^2$ , in our model because the annual number of females observed nesting in hot spots varied considerably throughout our 6-y study in a non-systematic pattern.

We included the fixed effect for site, assumed to arise from a uniform prior distribution between -20 and 20, because sites varied in length (Control 1 = 331 m; Control 2 = 310 m; Experimental = 162 m) and other roadside characteristics (e.g., vegetation composition) that could influence the number of terrapins observed using these areas each year to nest. Lastly, we included a residual random effect, assumed to arise from a zero-centered normal distribution with variance  $\sigma_E^2$ , to improve model fit and account for other unmeasured sources of variation.

We used a Bayesian mixed modeling approach using Markov chain Monte Carlo (MCMC) methods to estimate management impacts and fitted the model in WinBUGS 1.4.3 (Spiegelhalter et al. 2003) called from R (R Core Team 2013) via the R2WinBUGS package (Sturtz et al. 2005). We assigned  $U(\text{min} = -20, \text{max} = 20)$  diffuse prior distributions for all fixed effect parameters and  $U(\text{min} = 0, \text{max} = 5)$  distributions for hyperparameters governing random effects to represent lack of previous knowledge about management effects. We estimated posterior distributions using 600,000 iterations of three chains after discarding the first 400,000. We retained every 50<sup>th</sup> iteration to reduce autocorrelation among samples, which resulted in a total sample size of 12,000 from posterior distributions. We assessed convergence for the model by visually inspecting posterior distributions for evidence of unimodality, examining chain mixing in MCMC plots, examining effective sample size ( $> 5,000$  for all parameters), and calculating the Brooks-Gelman-Rubin statistic (Brooks and Gelman 1998), which compares within- and between-chain variance. We assessed goodness of fit with a Bayesian  $P$ -value (Kéry 2010): a statistic that compares the discrepancy between observed and simulated data predicted from the model, where model fit is interpreted as best with values near 0.5 and worst as values approach 0 or 1. A high degree of uncertainty existed in posterior estimates due to low sample size (annual counts across six years) and multiple sources of variation included in the model (see Results). Therefore, we based inferences of barrier effect sizes and direction on posterior medians and Bayesian credible intervals (BCIs) at the 90% (5<sup>th</sup>–95<sup>th</sup> percentiles of the distribution) and 95% (2.5<sup>th</sup>–97.5<sup>th</sup>) levels (e.g., Naidoo et al. 2016). We interpreted parameters as having ecologically important impacts when BCIs did not overlap 0.

## RESULTS

From 2009 to 2014, we observed 498 terrapins crossing (of which, 255 were struck by vehicles) within any of the three hot spots. The number of terrapins observed on the road varied considerably between sites and years but always fell within the 95% BCIs of the



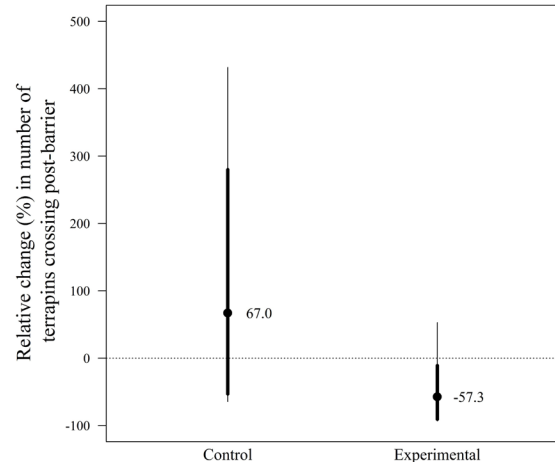
**FIGURE 2.** Annual number of Diamond-backed Terrapins (*Malaclemys terrapin*) observed (points) and predicted (lines: 95% Bayesian credible intervals) emerging on the road during surveys in Experimental and Control sites on the Jekyll Island Causeway (Jekyll Island, Georgia, USA) in periods before and after the installation of the hybrid barrier at the Experimental site.

estimated number of emergences ( $\lambda$ : Fig. 2). Relative to years before barrier installation, we observed fewer terrapins emerging on the road annually at the Experimental site and equal or more terrapins emerging at Control sites post-intervention.

The mixed effects model showed adequate convergence based on MCMC mixing of chains and Brooks-Gelman-Rubin statistics  $< 1.1$  for all parameters. The Bayesian  $P$ -value was 0.431 indicating the model adequately fit the data. Posterior estimates revealed strong support of a treatment  $\times$  period interaction based on 90% and 95% BCIs that did not overlap 0. There was a negative period (before-after) effect for the Experimental site (the 90% BCI, but not the 95% BCI, was less than 0) and no effects for Control sites (Table 1). When comparing the percentage change in terrapin emergence from pre- and post-intervention periods, the model predicted a 57.3% median reduction in terrapins on the road at the Experimental site after the barrier was installed (the upper 90% BCI, but not the 95% interval, was less than 0) while there was no directional change of terrapin emergences at Control sites (Fig. 3). We interpreted this estimated effect as the proportion of turtles prevented from entering the road due to the hybrid barrier.

## DISCUSSION

Our results demonstrate that a novel, hybrid roadside barrier reduced the number of terrapins accessing the road, and our work adds to previous studies that have successfully used barriers to reduce vehicle strikes for at-risk herpetofauna populations (Dodd et al. 2004; Aresco



**FIGURE 3.** Relative median percentage change in Diamond-backed Terrapin (*Malaclemys terrapin*) emergences on the road at Control and Experimental sites following the installation of a hybrid barrier on Jekyll Island, Georgia, USA. Thick and thin bars indicate 90% and 95% Bayesian credible intervals, respectively.

2005b; Andrews et al. 2015). Although the number of terrapin emergences varied substantially by site and year, we found strong evidence that the barrier was effective, as indicated by the treatment  $\times$  period interaction effect. In years following the installation of the barrier, we estimated a 57% reduction in terrapin emergences on the road at the Experimental site while detecting no measurable change at Control sites. Preliminary observations at the Experimental site revealed that most terrapins approached the road from a concentrated area in the marsh where a creek comes in proximity to the road, and we strategically placed the barrier to intercept individuals using this route. The barrier caused a reduction in terrapins crossing the road even though it did not span the entire hot spot (22.9 of 164 m). By having our barrier substantially shorter than the crossing hot spot, we could confirm that no new hot spots of road crossing formed near the ends of the barrier, which has been observed in other barrier studies (e.g., Clevenger et al. 2001). Although it is possible that some of the individuals observed on the road post-intervention may have skirted the barrier after encountering it first, many terrapins were observed nesting in the boxes during the years of our study. Quinn et al. (2015) systematically monitored nest boxes in 2013 and observed 41 instances of nesting in the boxes; we observed seven individuals on the road at the Experimental site that year. These results indicate that the barrier effectively lowered the risk of road mortality and increased survival of intercepted individuals, and extending the barrier to span a larger portion of the hot spot would, almost certainly, result in few terrapins accessing the road. Additionally, extending hybrid barriers at coastal road hot spots is not

**TABLE 1.** Parameter estimates (medians and 90% and 95% Bayesian credible intervals) for the barrier effects model predicting the number of terrapin emergences on the Jekyll Island Causeway, Jekyll Island, Georgia, USA. Posterior parameter estimates that do not overlap zero are interpreted as ecologically important.

Model and parameter	Symbol	Median Estimate	Lower 95%	Lower 90%	Upper 90%	Upper 95%
Treatment $\times$ period interaction	--	1.44	0.39	0.58	2.30	2.51
Site-specific period effects	$\beta_{\text{Control1}}$	0.65	-0.70	-0.43	1.82	2.17
	$\beta_{\text{Control2}}$	-0.18	-1.51	-1.25	1.02	1.38
	$\beta_{\text{Experimental}}$	-1.18	-2.68	-2.38	-0.12	0.43
Site fixed effects	$\text{site}_{\text{Control1}}$	3.32	2.09	2.35	4.21	4.43
	$\text{site}_{\text{Control2}}$	3.21	1.99	2.25	4.10	4.31
	$\text{site}_{\text{Experimental}}$	2.59	1.34	1.60	3.49	3.74
Year random effect	$\sigma_Y^2$	0.52	0.07	0.12	0.52	1.77
Residual random effect	$\sigma_E^2$	0.32	0.05	0.08	0.68	0.78

expected to negatively impact population connectivity because terrapins exhibit high site fidelity to tidal creeks (Gibbons et al. 2001) and those individuals that do disperse could access areas across a road by crossing at adjacent, un-barricaded sites or using tidal creeks that pass under roads (e.g., the Experimental site in our study).

We estimated the effects of the hybrid barrier using counts of emergences that did not account for differences in detection and must consider this when interpreting our results. However, influences of detection on our results were likely minimal. We can reasonably assume detection of individuals was consistent across sites. Sampling effort was equal across sites (i.e., we drove through all sites during each road survey), which influenced our ability to detect live and dead terrapins. Also traffic load and risk of a terrapin-vehicle collision was equal across sites, which influenced our ability to detect dead terrapins, because all vehicles entering the JIC from one end drive through all three hot spots (i.e., there are no intersecting roads or pull-off areas between sites). Detection may have varied across years because sampling effort varied between years and was higher in the pre-intervention relative to post-intervention period. We accounted for this annual variation in sampling with the random year effect in the model when estimating effects attributable to the barrier. In fact, we recorded the highest number of terrapins on the road in the last two years of the study (2013 and 2014). The effect of the barrier was especially noticeable in 2013 and 2014 as we observed more terrapins emerging at Control sites, relative to the pre-intervention period, while the number of emergences at the Experimental site remained lower than years before the barrier was installed. This lends support that the hybrid barrier resulted in a measurable reduction in terrapin emergences on the road at the Experimental site even during years of higher nesting activity.

The hybrid barrier was designed to increase several terrapin demographic rates that could have complementary effects for reducing multiple road-associated threats, which have not been addressed by other designs. The current study demonstrated the utility of the barrier in reducing the risk of road mortality that should increase adult survival. Two companion studies examined the potential effects of the barrier on nest predation and hatchling sex ratio (Grosse et al. 2015; Quinn et al. 2015). A major concern for managers when considering the use of conventional barriers for mitigating road mortality is that these structures will attract or concentrate predators (e.g., raccoons), resulting in increased predation rates of adults and nests (Aresco 2005b; Andrews et al. 2015). Camera monitoring of nest boxes in 2013 showed no predation events of adult females on the nest mounds or in the boxes (Daniel Quinn, pers. comm.). Quinn et al. (2015) showed that our hybrid barrier significantly reduced the risk of predation for nests laid inside boxes. We emphasize that they observed a low (7%) predation rate inside boxes only after the barrier was outfitted with an electric wire that deterred mesopredators but did not come in contact with terrapins using boxes. When boxes were not electrified, predators entered them via the horizontal gap designed for turtles and depredated 100% of monitored nests. Additionally, terrapins have temperature dependent sex determination, and Grosse et al. (2015) found that nests laid in the mounds inside the hybrid barrier experienced high temperatures and produced 100% female hatchlings. Therefore, coupling hybrid barriers with nesting mounds is a means to increase recruitment of females into populations that are experiencing the female-biased threat of road mortality. Crawford et al. (2014a) predicted that a stable terrapin population on Jekyll Island could be achieved by moderately reducing road mortality and nest predation while increasing the percentage of females produced.

Collectively, these findings support the use of hybrid barriers for mitigating multiple road-associated threats for terrapin populations and other turtle species when hot spots exist.

Hybrid barriers, as components of broader conservation strategies, are applicable to other road-impacted terrapin populations across the species range, as well as to other conservation contexts. We suggest that hybrid barriers can be a viable tool for terrapins and other species of freshwater turtles that nest on roadsides (Aresco 2005a). Although costs were reasonable for testing the barrier at a single site in our study, deploying hybrid barriers across larger spatial scales will require more considerable funds for construction and maintenance, which can include replacement of materials every 3–5 y and annual removal of ground vegetation on artificial nest mounds. Studies have identified specific roads as regional hot spots of mortality for terrapins across their range (Butler et al. 2006; Maerz et al. *In press*) and freshwater turtles (Aresco 2005b; Beaudry et al. 2008; Langen et al. 2009; Cureton and Deaton 2012), but cost-effective implementation of barriers requires that managers identify hot spots at a finer resolution via monitoring of roads and roadsides and using these as targets (Langen et al. 2007; Langen et al. 2009; Crawford et al. 2014b). Although we deployed the barrier at a hot spot of terrapin activity adjacent to a tidal creek, Crawford et al. (2014b) found that distance to creek was not a reliable predictor for where hot spots occurred on a road. Therefore, site-specific monitoring can inform barrier placement when consistent, concentrated peaks of terrapin activity are identified.

The approach used in our study provides a model for designing and deploying road management that is not only cost-effective, but also robust for addressing multiple threats simultaneously that are contributing to population declines. Our study echoes previous conservation studies calling for focus on complementary management actions to address multiple threats and ensure the viability of declining populations, and that failure to address any one threat may undermine the effectiveness of broader strategies (Marschall and Crowder 1996; Rhodes et al. 2011; Crawford et al. 2014a). It is important to note that we found evidence that barriers reduced road crossings at one hot spot and can be effective when applied at other sites, but terrapins continued to be struck on the road in other areas. Because road mortality and other threats to species inhabiting road-fragmented landscapes may be spatially diffuse, managers could explore coupling the use of hybrid barriers at hot spots with complementary actions, such as predator removal (e.g., Munscher et al. 2012) or road signage (e.g., Sullivan et al. 2004), implemented across broader scales. Forthcoming studies will determine management efforts needed to stabilize the terrapin

population on Jekyll Island by predicting terrapin population-level responses (via a population viability analysis: PVA) to different strategies that vary in the spatial extent at which barriers are deployed (e.g., at hot spots vs. JIC-wide) and the inclusion of complementary actions (e.g., predator removal, roadside vegetation management, and on-road signage). Conducting PVAs requires considerable demographic information that does not exist for many species and sites, and managers are often faced with acting before this information is fully known. We suggest that hybrid barriers improve upon previous designs and represent a cost-effective option for managers to consider in contexts where road mortality is spatially-concentrated and nest predation is a concern. Ultimately, we will consider the predicted impacts of management to terrapins alongside other socioeconomic objectives (e.g., driver satisfaction, safety, and project costs) in a decision-making framework, and we encourage managers to adopt this approach in order to identify optimal, publicly acceptable solutions for managing road impacts on herpetofauna.

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## LITERATURE CITED

- Andrews, K.M., P. Nanjappa, and S.P.D. Riley. 2015. Roads and Ecological Infrastructure: Concepts and Applications for Small Animals. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Aresco, M.J. 2005a. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. *Biological Conservation* 123:37–44.



- Aresco, M.J. 2005b. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. *Journal of Wildlife Management* 69:549–560.
- Baird, R.C. 2009. Coastal urbanization: the challenge of management lag. *Management of Environmental Quality: An International Journal* 20:371–382.
- Beaudry, F., P.G. Demaynadier, and M.L. Hunter. 2008. Identifying road mortality threat at multiple spatial scales for semi-aquatic turtles. *Biological Conservation* 141:2550–2563.
- Brooks, S.P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7:434–455.
- Buhlmann, K.A., and C.P. Osborn. 2011. Use of an artificial nesting mound by Wood Turtles (*Glyptemys insculpta*): a tool for turtle conservation. *Northeastern Naturalist* 18:315–334.
- Butler, J., G. Heinrich, and R. Seigel. 2006. Third workshop on the ecology, status, and conservation of Diamondback Terrapins (*Malaclemys terrapin*): results and recommendations. *Chelonian Conservation and Biology* 5:331–334.
- Clevenger, A.P., B. Chruszcz, and K.E. Gunson. 2001. Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin* 29:646–653.
- Crawford, B.A., J.C. Maerz, N.P. Nibbelink, K.A. Buhlmann, and T.M. Norton. 2014a. Estimating the consequences of multiple threats and management strategies for semi-aquatic turtles. *Journal of Applied Ecology* 51:359–366.
- Crawford, B.A., J.C. Maerz, N.P. Nibbelink, K.A. Buhlmann, T.M. Norton, and S.E. Albeke. 2014b. Hot spots and hot moments of Diamondback Terrapin road-crossing activity. *Journal of Applied Ecology* 51:367–375.
- Cureton, J.C., and R. Deaton. 2012. Hot moments and hot spots: identifying factors explaining temporal and spatial variation in turtle road mortality. *Journal of Wildlife Management* 76:1047–1052.
- Dodd, C.K., W.J. Barichivich, and L.L. Smith. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. *Biological Conservation* 118:619–631.
- Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* 14:21 <http://www.ecologyandsociety.org/vol14/iss1/art21/>.
- Feinberg, J.A., and R.L. Burke. 2003. Nesting ecology and predation of Diamondback Terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New York. *Journal of Herpetology* 37:517–526.
- Forman, R.T.T., D. Sperling, J.A. Bissonette, A.P. Clevenger, C.D. Cutshall, V.H. Dale, L. Fahrig, R. France, C.R. Goldman, K. Heanue, et al. 2003. *Road Ecology: Science and Solutions*. Island Press, Washington D.C., USA.
- Forman, R.T.T., and L.E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207–231.
- Gibbons, J.W., J.E. Lovich, A.D. Tucker, N.N. Fitzsimmons, and J.L. Greene. 2001. Demographic and ecological factors affecting conservation and management of the Diamondback Terrapin (*Malaclemys terrapin*) in South Carolina. *Chelonian Conservation and Biology* 4:66–74.
- Gibbs, J.P., and W.G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. *Conservation Biology* 16:1647–1652.
- Glista, D.J., T.L. DeVault, and J.A. DeWoody. 2009. A review of mitigation measures for reducing wildlife mortality on roadways. *Landscape and Urban Planning* 91:1–7.
- Green, R.H. 1979. *Sampling Design and Statistical Methods for Environmental Biologists*. Wiley Interscience, Chichester, UK.
- Grosse, A.M., B.A. Crawford, J.C. Maerz, K.A. Buhlmann, T.M. Norton, S.M. Kaylor, and T.D. Tuberville. 2015. Effects of vegetation structure and artificial nesting habitats on hatchling sex determination and nest survival of Diamondback Terrapins. *Journal of Fish and Wildlife Management* 6:19–28.
- Grosse, A.M., J.C. Maerz, J. Hepinstall-Cymerman, and M.E. Dorcas. 2011. Effects of roads and crabbing pressures on Diamondback Terrapin populations in coastal Georgia. *Journal of Wildlife Management* 75:762–770.
- Jaeger, J.A.G., J. Bowman, J. Brennan, L. Fahrig, D. Bert, J. Bouchard, N. Charbonneau, K. Frank, B. Gruber, and K.T. von Toschanowitz. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling* 185:329–348.
- Kéry, M. 2010. *Introduction to WinBUGS for Ecologists: Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses*. Academic Press, Burlington, Massachusetts, USA.
- Langen, T.A. 2012. Design considerations and effectiveness of fencing for turtles: three case studies along northeastern New York State highways. Pp. 545–556 *In* *Proceedings of the 2011 International Conference on Ecology and Transportation*. Wagner, P.J., D. Nelson, and E. Murray (Eds.). Center for Transportation and the Environment, North Carolina State University, Raleigh, North Carolina, USA.
- Langen, T.A., A. Machniak, E.K. Crowe, C. Mangan, D.F. Marker, N. Liddle, and B. Roden. 2007. Methodologies for surveying herpetofauna mortality



- on rural highways. *Journal of Wildlife Management* 71:1361–1368.
- Langen, T.A., K.M. Ogden, and L.L. Schwarting. 2009. Predicting hot spots of herpetofauna road mortality along highway networks. *Journal of Wildlife Management* 73:104–114.
- Litvaitis, J. A. and J. P. Tash. 2008. An approach toward understanding wildlife-vehicle collisions. *Environmental Management* 42:688–697.
- Maerz, J.C., R.A. Seigel, and B.A. Crawford. In press. Terrapin conservation: mitigating habitat loss, road mortality, and subsidized predators *In Ecology and Conservation of the Diamondback Terrapin*. Roosenburg, W.M., and V.S. Kennedy (Eds.). Johns Hopkins University Press, Baltimore, Maryland, USA.
- Marschall, E.A., and L. B. Crowder. 1996. Assessing population responses to multiple anthropogenic effects: a case study with Brook Trout. *Ecological Applications* 6:152–167.
- Munscher, E.C., E.H. Kuhns, C.A. Cox, and J.A. Butler. 2012. Decreased nest mortality for the Carolina Diamondback Terrapin (*Malaclemys terrapin centrata*) following removal of Raccoons (*Procyon lotor*) from a nesting beach in northeastern Florida. *Herpetological Conservation and Biology* 7:176–184.
- Naidoo R., B. Fisher, A. Manica, and A. Balmford. 2016. Estimating economic losses to tourism in Africa from the illegal killing of elephants. *Nature Communications* 7:13379.
- Quinn, D.P., S.M. Kaylor, T.M. Norton, and K.A. Buhlmann. 2015. Nesting mounds with protective boxes and an electric wire as tools to mitigate Diamond-backed Terrapin (*Malaclemys terrapin*) nest predation. *Herpetological Conservation and Biology* 10:969–977.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
- Rhodes, J.R., C.F. Ng, D.L. de Villiers, H.J. Preece, C.A. McAlpine, and H.P. Possingham. 2011. Using integrated population modelling to quantify the implications of multiple threatening processes for a rapidly declining population. *Biological Conservation* 144:1081–1088.
- Rytwinski, T., and L. Fahrig. 2012. Do species life history traits explain population responses to roads? A meta-analysis. *Biological Conservation* 147:87–98.
- Sheridan, C.M., J.R. Spotila, W.F. Bien, and H.W. Avery. 2010. Sex-biased dispersal and natal philopatry in the Diamondback Terrapin, *Malaclemys terrapin*. *Molecular Ecology* 19:5497–5510.
- Skalski, J.R., and D.S. Robson. 1992. Techniques in Wildlife Investigations: Design and Analysis of Capture Data. Academic Press, New York, New York, USA.
- Spiegelhalter, D., A. Thomas, N. Best, and D. Lunn. 2003. WinBUGS Version 1.4 User Manual. MRC Biostatistics Unit, Cambridge, UK.
- Sturtz, S., U. Ligges, and A.E. Gelman. 2005. R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software* 12:1–16.
- Sullivan, T.L., A.F. Williams, T.A. Messmer, L.A. Hellinga, and S.Y. Kyrychenko. 2004. Effectiveness of temporary warning signs in reducing deer-vehicle collisions during Mule Deer migrations. *Wildlife Society Bulletin* 32:907–915.
- Szerlag-Egger, S., and S.P. McRobert. 2007. Northern Diamondback Terrapin occurrence, movement, and nesting activity along a salt marsh access road. *Chelonian Conservation and Biology* 6:295–301.
- Trombulak, S.C., and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- Wood, R., and R. Herlands. 1997. Turtles and tires: the impact of roadkills on northern Diamondback Terrapin, *Malaclemys terrapin terrapin*, populations on the Cape May Peninsula, southern New Jersey, USA. Pp 46–53 *In Conservation, Restoration, and Management of Tortoises and Turtles - An International Conference*. J. Van Abbema. Turtle and Tortoise Society, New York, New York, USA.



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