MORTALITY AND MANAGEMENT: ASSESSING DIAMONDBACK TERRAPINS (MALACLEMYS TERRAPIN) ON THE JEKYLL ISLAND CAUSEWAY

by

BRIAN ANDREW CRAWFORD

(Under the Direction of John C. Maerz)

ABSTRACT

Conservation of declining species relies on identifying threats, predicting their impacts, and mitigating these risks with specific solutions. Diamondback terrapins (*Malaclemys terrapin*) are declining or of unknown status across the majority of their range due to multiple anthropogenic threats, including road mortality of adult females. This thesis assessed the patterns of road mortality on a heavily used causeway leading to Jekyll Island, Georgia and modeled terrapin population growth using current estimates of road mortality and nest predation. Terrapin-vehicle collisions were concentrated spatially and temporally based on predictable cues. We predicted substantial declines in the terrapin population near Jekyll Island given current threat levels. Population growth was most sensitive to changes in adult survival, so management should prioritize the reduction of road mortality. These results yield a firmer understanding of the characteristics and probable impacts of road mortality on terrapin populations and can influence mitigation strategies for this and other causeways.

INDEX WORDS: Diamondback terrapin, *Malaclemys terrapin*, Road mortality, Conservation management, Matrix model, Turtle

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DEDICATION

I would like to dedicate this thesis to my parents and my two sisters, Allison and Caitlin, for their incredible love and support that they have given me since before I can remember. I especially thank you, mom and dad, for being models of both compassion and intellect, as well as providing the family vacations, that inspired me to pursue a career in the study and stewardship of nature. This work is another step in my growth as a scientist, so I gratefully dedicate it to my friends at the Savannah River Ecology Lab, the Georgia Sea Turtle Center, and the Maerz Herpetology Lab that shaped my development and gave me the gift of experience – often "the most brutal [and effective] of teachers" (C.S. Lewis).

Lastly, I want to dedicate this work to two vehicles. First, my Altima, in which I drove 24,000 miles on the Jekyll Island Causeway through three summers – ironically, in the name of conservation. And finally, Kurt's 1971 Shasta camper that lost its life in protecting mine from a live oak branch on the Jekyll Island Campground on the morning of July 9th, 2009.

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CHAPTER 1

INTRODUCTION

Conservation management of declining species relies on identifying threats, predicting their impacts on a population, and mitigating these risks with specific solutions. Impacts of a single threat on a wide-ranging species are often dynamic in both space and time (Kristan III and Boarman 2003; Litvaitis and Tash 2008); thus, management is most successful when it is engineered to conditions at a finer, population-centric scale (Stahl et al. 2001; Wittingham et al. 2007; Beaudry et al. 2008). If a combination of spatial or temporal variables threatens a substantially large proportion of individuals in a population, declines and subsequent extirpations are expected (Congdon et al. 1993; Doak et al. 1994; Beaudry et al. 2010). In real-world cases where multiple threats occur in concert and mitigation resources are limited, management plans should focus on reversing those threats that will most likely hamper population recovery (Heppell et al. 1996). Developing solutions to ameliorate threat effects requires detailed knowledge of the threat process itself and the species' ecology and behavior.

Among extant species of turtles, over 42% are currently listed as threatened on the IUCN Red List (Baillie et al. 2004), and the majority of turtle species worldwide have felt negative impacts from anthropogenic threats including habitat development and fragmentation (Gibbons et al. 2000), commercial harvest (Seigel and Gibbons 1995), and road mortality (Wood and Herlands 1997; Aresco 2005; Steen et al. 2006). Turtles are relatively long-lived, and population stability is strongly governed by high annual adult survivorship that compensates for delayed sexual maturity and low yearly recruitment (Congdon et al. 1993; Heppell 1998), thereby making populations particularly vulnerable to threats that increase adult female mortality (Congdon et al. 1993).

Roads have gained increased attention as a pervasive ecological threat (reviewed by Fahrig and Rytwinski 2009), and road mortality represents a significant agent in declines of certain wildlife populations (Fahrig et al. 1995; Trombulak and Frissell 2000; Forman et al. 2003; Dodd et al. 2004; Andrews et al. 2007; Litvaitis and Tash 2008). For most turtle species, road mortality most commonly affects adults, especially females, which causes detrimental declines to populations (Gibbs and Shriver 2002; Aresco 2005; Steen et al. 2006; Beaudry et al. 2010). Adult turtles utilize complex habitat networks for migrating, mate-searching, nesting, and hibernating that often brings them across roadways in the process (Gibbs and Shriver 2002; Aresco 2005; Beaudry et al. 2008; Langen et al. 2009). Behaviorally, turtles demonstrate suboptimal responses to roads compared to other species – characterized by low road avoidance and the inability to elude oncoming traffic – resulting in vehicle strikes and subsequent mortalities (Gibbs and Shriver 2002; Fahrig and Rytwinski 2009). Furthermore, nesting females of some species show an attraction to open, elevated road banks (Aresco 2005; Szerlag-Egger and McRobert 2007) that increases time spent adjacent to roads and overall mortality (Forman et al. 2003).

The diamondback terrapin (*Malaclemys terrapin*) is the only North American species of turtle to exclusively inhabit brackish salt marshes along the U.S. East and Gulf Coasts. Terrapin populations are declining or of unknown status across the majority of their range due to chronic, human-induced threats, but certain populations remain locally abundant (Butler et al. 2006). Thus, we have the opportunity to assess the impacts of these threats on population growth and to develop conservation strategies before local extirpations occur. Anthropogenic factors threatening the species include habitat degradation (Seigel 1993; Gibbons et al. 2001), mortality in crab traps (Seigel and Gibbons 1995; Wood 1997; Dorcas et al. 2007; Grosse et al. 2009; Grosse et al. 2011), and road mortality of adults (Wood and Herlands 1997; Szerlag and McRobert 2006). In addition, nest predation by subsidized predators (e.g., raccoons; *Procyon lotor*) has become a well-documented concern for terrapin population viability that reduces egg survival and overall recruitment (Burger 1977; Feinberg and Burke 2003; Butler et al. 2004). While studies have begun to dissect each of these threats, the effects of road mortality on terrapin populations are still equivocal. For example, Grosse et al. (2009) found no measurable correlation between terrapin density and road density or proximity when sampling populations across the state of Georgia. However, the authors cautioned that substantial road mortality observed on certain high-traffic roads can likely cause local declines.

In fragmenting salt marsh habitat, roads provide attractive nesting sites for terrapins, characterized by elevated, open areas with little vegetation and ground cover (Szerlag-Egger and McRobert 2007); thus, roads represent a female-biased threat to terrapins. Roadsides also provide suitable habitat for predators of terrapin nests (e.g., *Procyon lotor*) to thrive (Burger 1977; Feinberg and Burke 2003). Female terrapins are known to have predictable nesting habits that might be used to anticipate spatial and temporal peaks of road mortality risk. For example, past research has shown nesting activity directly correlates with higher tide amplitudes (Burger and Montevecchi 1975; Feinberg and Burke 2003) and daily high temperatures (Seigel 1980; Feinberg and Burke 2003). Spatially, female terrapins nest more frequently in areas of maximum solar radiation and minimal ground vegetation – a behavior that may increase the number of female offspring due to environmental sex determination of this species (Roosenburg 1996). It is still unknown how additional habitat features, such as proximity to creeks, are associated with nest site selection. Without effective mitigation solutions that prevent wildlife-vehicle collisions and preserve habitat connectivity, models predict road mortality to cause rampant declines of turtle populations on a regional scale (Fahrig et al. 1995; Gibbs and Shriver 2002; Andrews et al. 2007; Litvaitis and Tash 2008; Langen et al. 2009; Beaudry et al. 2010). Although vehicle-induced mortality and nest predation have been proposed as contributors to terrapin population declines (Wood and Herlands 1997; Butler et al. 2006; Grosse et al. 2011), no formal models have been created to estimate the effects of these threats on population growth.

Matrix models are frequently used to project population growth where individuals are grouped by life-stages based on size or maturity (Lefkovich 1965; Caswell 1989). One strength of stage-based models is their ability to compare the relative effects of changing stage-specific vital rates (e.g., survival, fecundity) and identify factors that have the largest influence on future population growth (Caswell 1978; de Kroon et al. 1986; Caswell 1989). Individuals of most turtle species are easily grouped by life-stages (e.g., hatchlings, juveniles, adults) while more precise aging techniques are lacking. Likewise, conservation strategies have traditionally targeted specific stages, including the protection of nests, rearing or "headstarting" of hatchlings in captivity, and reducing adult mortality from habitat destruction, harvest, or wildlife-vehicle collisions. Thus, stage-based models of turtles have become an effective tool for developing conservation strategies that target stage-specific parameters and rank plans according to their expected benefit to population growth (Crowder et al. 1994; Escos et al. 1994; Heppell et al. 1994; Marschall and Crowder 1996; Enneson and Litzgus 2008).

Through studying a diamondback terrapin population in the southeastern United States, the purpose of this thesis is to identify the patterns and peaks of nesting activity that put adult females at risk of road mortality and to estimate the impacts of multiple threats on this population. Specifically, we build on past monitoring efforts (begun in 2007) of terrapins surrounding the Downing-Musgrove Causeway (Jekyll Island Causeway: JIC) leading to Jekyll Island, GA. In Chapter 2, we focus on the spatial and temporal peaks of nesting activity to determine where and when vehicle-terrapin collisions are most likely to occur on the JIC. We also explore the associations between certain environmental features and the locations of these crossing "hot spots" and "hot moments." In Chapter 3, we estimate per capita rates of road mortality and nest predation occurring on the JIC and incorporate these into a stage-based population model in order to assess population growth under current and potential scenarios. Because turtle populations cannot sustain high adult female mortality rates, determining hot spots and hot moments of nesting activity on a local scale can help target areas along causeways where management can be most effectively employed at specific times – ultimately reducing negative effects of these roads. Furthermore, our models will predict the population-level impacts of two major threats and simulate the effects of reducing each with targeted management efforts. Overall, we believe the results of our research will provide conservation strategies that will stabilize or grow the diamondback terrapin population of Jekyll Island, and the approach we employ can inform management research at similar sites where terrapin populations are threatened by roadways.

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CHAPTER 2

DEFINING HOT SPOTS AND HOT MOMENTS OF DIAMONDBACK TERRAPIN (*MALACLEMYS TERRAPIN*) ACTIVITY ALONG THE JEKYLL ISLAND CAUSEWAY

Introduction

The effective management of declining species relies heavily on targeting specific threats with specific solutions. A single threat acting on a wide-ranging species may fluctuate in how it impacts populations; thus, management has found the most success when it is engineered to conditions at a finer, localized scale (Stahl et al. 2001; Wittingham et al. 2007; Beaudry et al. 2008). Risk assessment takes into account the probability and frequency that 1) a threat occurs, 2) elements vary in both space and time, and 3) the ultimate consequences for a population (Rowe 1977; Holton 2004). Spatially, threat processes can be generalized across a large scale or occur at higher rates in specific areas – known as threat hot spots (e.g., Beaudry et al. 2008). Likewise, threat processes can change temporally to produce hot moments, which are specific times when the threat impacts the species at a higher rate (Beaudry et al. 2010). If a combination of spatial or temporal variables threatens a substantially large proportion of individuals in a population, declines and potential extirpation are expected (Congdon et al. 1993; Doak et al. 1994; Beaudry et al. 2010). Developing specific solutions to ameliorate the effects of hot spots and hot moments requires detailed knowledge of the threat process itself and the species' ecology and behavior.

Roads have gained increased attention as a pervasive ecological threat (reviewed by Fahrig and Rytwinski 2009), and road mortality represents a significant agent in declines of certain wildlife populations (Fahrig et al. 1995; Trombulak and Frissell 2000; Forman et al. 2003; Dodd et al. 2004;

Andrews et al. 2007; Litvaitis and Tash 2008). Road width, presence or absence of barriers, traffic speed and volume, and adjacent habitat types can impact rates of road mortality (Forman and Alexander 1998; Litvaitis and Tash 2008). The road-effect zone constitutes the maximum buffer area away from a road where substantial ecological impact still exists for an individual species, which is positively correlated with species mobility (Forman and Alexander 1998; Gibbs and Shriver 2002; Steen and Gibbs 2004). Thus, in addition to road characteristics, behavioral responses of species must be considered to predict the magnitude of risk imposed by roadways (reviewed by Fahrig and Rytwinski 2009). Types of behavioral responses to roads that determine an animal's susceptibility to vehicle-induced mortality include the animal's degree of avoidance of or attraction to roadways and the ability to move out of the path of a moving vehicle (Jaeger et al. 2005). Not surprisingly, vehicle mortality most likely affects slow-moving species that display no road avoidance or an inability to avoid oncoming cars (van Langevelde and Jaarsma 2004; Fahrig and Rytwinski 2009).

Turtles use complex habitat networks for migrating, mate-searching, nesting, and hibernating that often brings them across roadways (Gibbs and Shriver 2002; Aresco 2005a; Beaudry et al. 2008; Langen et al. 2009). Roads have had pervasively negative effects on the viability of reptiles and amphibians as a group (reviewed by Fahrig and Rytwinski 2009) and can be especially detrimental to the viability of some turtle populations (Gibbs and Shriver 2002). Turtles are relatively long-lived, and population stability is strongly governed by high annual adult survivorship that compensates for delayed sexual maturity and low yearly recruitment (Heppell 1998), thereby making populations particularly vulnerable to factors that increase adult female mortality (Congdon et al. 1993). Behaviorally, turtles demonstrate suboptimal responses to roads compared to other species – characterized by low road avoidance and the inability to elude oncoming traffic – resulting in vehicle strikes and subsequent mortalities (Gibbs and Shriver 2002; Fahrig and Rytwinski 2009). Furthermore, nesting females of some species show an attraction to open, elevated road banks (Aresco 2005a; Szerlag-Egger and McRobert

2007) that increases time spent adjacent to roads and overall mortality frequencies (Forman et al. 2003).

The diamondback terrapin (*Malaclemys terrapin*) is currently listed as a "species of special concern" in the state of Georgia (Georgia Department of Natural Resources 2005). Anthropogenic factors threatening the species include habitat degradation (Seigel 1993; Gibbons et al. 2001), mortality in crab traps (Seigel and Gibbons 1995; Wood 1997; Dorcas et al. 2007; Grosse et al. 2011), and road mortality (Szerlag and McRobert 2006). Across large spatial scales, the impact of road networks on terrapin populations is ambiguous, but vehicle-induced mortality in specific areas, such as along causeways to barrier islands, has been identified as a contributor to population declines (Wood and Herlands 1997; Grosse et al. 2011). Causeways provide a unique case where animals are attracted to characteristics of the road itself. By creating elevated habitat through salt marshes, causeways provide attractive nesting sites for terrapins (Szerlag-Egger and McRobert 2007); therefore, roads likely represent a female-biased threat to terrapins. Mortality of nesting females is particularly detrimental to turtle population growth (e.g., Congdon et al. 1993). Female-biased mortality can result in skewed sex-ratios that limit the effective population size causing long-term declines and even extirpation (Doak et al. 1994; Mitro 2003; Aresco 2005a).

Female terrapins are known to have predictable nesting habits that might be used to anticipate periods of high road mortality risk. Females have been reported to nest diurnally from April through July, with seasonal peaks in activity varying across geographic region, in weather with minimal cloud cover (Seigel 1980; Zimmerman 1992; Feinberg and Burke 2003); though, terrapins may occasionally nest at night and during rain events (Feinberg and Burke 2003). Nesting activity has also been found to directly correlate with higher tide amplitudes (Burger and Montevecchi 1975; Feinberg and Burke 2003) and daily high temperatures (Seigel 1980; Feinberg and Burke 2003). Terrapins can nest more than once per season (Feinberg and Burke 2003; Szerlag-Egger and McRobert 2007) and show a degree of nest site fidelity (Szerlag-Egger and McRobert 2007), so females may repeatedly cross roadways to nest, increasing their risk to road mortality. Spatially, female terrapins nest more frequently in areas of maximum solar radiation and minimal ground vegetation – a behavior that may increase the number of female offspring due to environmental sex determination of this species (Roosenburg 1996). Past studies assessing road mortality hot spots in other systems have found a direct correlation between crossing frequency of turtles and the proximity of surrounding aquatic habitats for a given section of roadway (Beaudry et al. 2008; Langen et al. 2009). Although it has not been directly studied with terrapins, hot spots may exist on a causeway where surrounding habitat features, such as proximity to tidal creeks, minimize the thermal stress and distance a nest-searching female must walk to reach a suitable nesting site (Burger and Montevecchi 1975; Feinberg and Burke 2003).

Using the Downing-Musgrove Causeway to Jekyll Island, Georgia as a case study, we set out to 1) determine whether terrapin activity on the causeway was spatially (hot spots) or temporally (hot moments) predictable, and 2) determine whether particular habitat features were associated with hot spots. Given past research on factors associated with peaks in road mortality for turtles and specific nesting habits of terrapins, we predicted that hot moments of terrapin road mortality are centered on diurnal high tides and hot spots are located where roadsides lack vegetation cover and are proximate to creeks.

Methods

Site Description

We conducted this study in conjunction with long-term monitoring efforts of the Georgia Sea Turtle Center (GSTC), initiated in 2007. Through past and present monitoring, we focused on the Downing Musgrove Causeway from Rt. 17 to Jekyll Island, GA, USA (31°N, 81°W). The Downing-Musgrove Causeway (Jekyll Island Causeway: JIC) is characterized as a state highway with average annual daily traffic (AADT) of 3,460 vehicles/day (Georgia Department of Transportation 2009) with a speed limit of 89 km/hr (55 mi/hr) along the majority of the road. Although monthly averages were not available for the JIC, data from adjacent coastal highways show that monthly traffic volumes for March through August are greater than yearly averages, corresponding with increased summer tourism, and peak from May through July (Georgia Department of Transportation 2009). The JIC bisects 8.7 km of salt marsh consisting of a network of intertidal creeks and high marsh dominated by *Spartina sp*. Several creeks come in proximity to or cross under the causeway, and the edge of the road is regularly within 20 m of the high-tide mark of the high marsh. The slope up from the marsh to the road provides attractive nesting habitat for females terrapins, which nest above the high tide line to prevent egg inundation (Aresco 2005a; Brennessel 2006). Much of the area along roadsides is covered by densely vegetated hedgerows of cedars and wax myrtles (*Myrica cerifera*) maintained as a wind break. While viewing a georeferenced map of the JIC and surrounding landscape, we noticed the high marsh located within 150 m of the road contained large patches of unvegetated, sandy habitat.

Field Methods

Since 2007, researchers documented 100-400 adult female terrapins killed during nesting forays by vehicle strikes on the JIC (B. Crawford; GSTC, unpublished data). Starting in 2009, we conducted intensive road surveys to obtain real-time (within 20 min) observations of when and where terrapins emerged on the causeway between 1 May and 20 July. One or two observers completed road surveys by patrolling the causeway in a vehicle while scanning the road and shoulders for terrapins. For each survey, we recorded the date and hours to the nearest high tide along with number of terrapins observed. Initially, we completed a full survey of the JIC every 20 – 30 minutes beginning just before dawn and ending just after dusk. Occasionally we waited up to 2 hours between surveys, and we also completed some opportunistic nighttime surveys. When a dead or injured terrapin was found after a survey gap of >30 min, we did not include that animal in our hot moments analysis. Dusk surveys allowed us to “clear” the JIC of any dead or injured turtles, such that we could assume a terrapin found during a dawn survey was struck during the night. For every terrapin found, we noted the location on a data sheet and marked it with a handheld Global Positioning System (GPS: Garmin International, Olathe, Kansas, USA). We sexed, palpated for eggs, measured (carapace length, plastron length, shell width and depth, and head width), weighed (g), and gave a unique code by drilling or notching marginal scutes to any terrapin intercepted alive and uninjured. We also recorded the time each turtle was found on the road, and the direction it was heading when intercepted or struck. We assumed that turtles with eggs were heading from their aquatic habitat toward their desired nesting area, and turtles without eggs were returning from their nesting habitat toward their aquatic habitat. We returned turtles to the side of the road they originally came from (opposite side of road from nest site) within 1 hr of capture to a nearby artificial nest mound, designed after similar management devices (Buhlmann and Osborn 2011). We transported all injured or killed terrapins to the Georgia Sea Turtle Center for examination, treatment or euthanasia, and recovering of eggs for a head start program. All methods were conducted in accordance with the recommendations for humane treatment of these animals for research and have been approved by the University of Georgia Institution Animal Care and Use Committee (Animal Use Protocol #: A2009 10-189, expires November 24, 2012).

Analysis of Hot Spots

We used a geographic information system (ArcGIS 9.3; ESRI, Redlands, CA) to determine whether there were predictable hot spots of terrapin activity on the JIC. First, we created a route layer along the causeway, and terrapin GPS locations were snapped to the nearest point on the route for later analysis. We represented tidal creeks with a polyline layer generated in September 2009 and obtained from the National Hydrology Dataset (available online [http://nhd.usgs.gov/]). Next, we ranked the degree of hedge vegetation along each side of the causeway into 3 categories: full hedge (dominated by wax myrtle), intermediate hedge (sparse wax myrtle or short shrubs), and no hedge. We took manual

GPS locations at each transition in hedge type along the JIC, and then we added that information as a hedge layer in our GIS analysis. Lastly, we calculated the percent of unvegetated area (sand and mud flat) in the high marsh within 150 m of the road. To calculate unvegetated area, we performed an unsupervised classification of a 1-m resolution orthophoto mosaic for Glynn County, GA from the National Agriculture Imagery Program (2009; obtained from Georgia GIS Clearinghouse, data available online [http://data.georgiaspatial.org/]) using the isodata clustering algorithm available in ArcToolbox on the three colorbands available (R, G, B), using 20 classes. Unvegetated areas were sufficiently distinct from all other areas based on the RGB spectral signature that we were able to select the classes falling in unvegetated areas by visual inspection and reclassify the raster as “unvegetated” and “other.” Although we did not perform an error analysis with ground-truth data, this classification method was at least as accurate as a head-up digitizing process and captured the feature of interest at a sufficient spatial scale.

We used a moving window analysis, beginning at one end of the route layer and moving sequentially along the road in 1-m increments, to count number of terrapins and generate summary statistics for environmental variables of interest within a specified window size. First, distances between the window’s center and the nearest creek on each side of the road were recorded (Fig 2.1, A). Within the window, percent of each hedge type was recorded on both sides of the road (Fig 2.1, B) and percent of unvegetated high marsh habitat was calculated. Next, all terrapins observed on the section of road within the window were counted (Fig 2.1, C). Finally, an output layer containing every point analyzed along the causeway was generated, along with the summary statistics for each variable of interest. We displayed this layer by number of animals observed in a window using the Natural Breaks (Jenks) method provided in ArcGIS as a classification choice to visually represent the distribution of terrapin-crossing hot spots along the causeway (Fig 2.1, D).

We selected appropriate window sizes based on empirical data of terrapin movements across the causeway. Since terrapins show some degree of both creek and nest site fidelity (Gibbons et al.

2001; Szerlag-Egger and McRobert 2007), it is plausible that females approach the road from consistent locations in the salt marsh and identify suitable nesting sites at a relatively fine scale. For our purposes of identifying habitat features that affect terrapin crossing, window size should account for variation in terrapin movements to nesting sites as they relate to the surrounding landscape. Therefore, we estimated this variation in our data set using inter-recapture distances from GPS locations of recaptured turtles (n = 40; see results) and chose appropriate window sizes of 50, 100, and 200 m to evaluate terrapin occurrence and habitat features at scales that likely encompass variation in movement and nest-site selection.

We used the terrapin counts at each meter generated by the 100-m window analysis to map aggregations (hot spots) of terrapin crossing activity along the causeway. We constructed a histogram to evaluate the frequencies of terrapin counts observed per 100-m window. Next, we set two cutoff values to interpret aggregations: 1) a strict cutoff (higher terrapin counts observed at fewer areas of the road) was chosen to represent hot spots of crossing activity, and 2) a less stringent cutoff (including lower terrapin counts observed at more areas of the road) represented minor spatial peaks, or warm spots, of terrapin crossing activity. Using the locations where terrapin counts were taken from, we were able to map hot and warm spots on the causeway based on these cutoffs and compare localized activity levels with the average amount of crossing activity seen along the entire causeway. Because our analyses used data pooled between the 2009 and 2010 nesting seasons, we used a chi-squared contingency test to compare the consistency of terrapin activity patterns. Specifically, we compared the number of terrapins observed for every 500-m section of the causeway in 2009 and 2010. We used this larger length so the expected value of terrapins in each section was > 5.0, abiding with test assumptions.

For the next phase of analysis, we used linear regression to evaluate 3 habitat features – distance to nearest creek, percent of hedge vegetation on roadsides, and percent of unvegetated area in the adjacent high marsh – as predictors of the number of terrapin crossings observed on a section of causeway from data obtained at the optimal 100-m window scale. Although this data was obtained for windows centered at every meter along the causeway, this resulted in too many points (8610) for the software to calculate a spatial weights matrix (below). Thus, we selected one point every 10 m to reduce the dataset to 861 points. We used an information-theoretic approach to evaluate relative fit of candidate models based on Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). We also computed the ΔAIC_c of each model *i* (i.e. $\Delta AIC_i = AIC_i -$ minAIC), and adhered to guidelines that a $\Delta AIC_c > 7$ indicated a poorly fitting model while $\Delta AIC_c \leq 2$ corresponded to models equivalent to the best model (Burnham and Anderson 2002). The relative fit of each candidate model was further assessed by calculating Akaike weights w_i (Burnham and Anderson 2002), which can range from 0 to 1, with the best-fitting candidate model having the greatest Akaike weight. To evaluate the effect of individual habitat variables on terrapin crossing, we used a multi-model inference to incorporate model uncertainty. This approach averages the estimated coefficients and standard errors of each variable across all models in which they are present after rescaling these estimates based on each model's Akaike weight (as described by Burnham and Anderson 2002). To allow for ease of interpretation and to evaluate the precision of the parameters, we scaled parameter coefficients and the upper and lower 95% confidence intervals, based on a *t*-statistic with *n*-1 degrees of freedom, of the model-averaged estimates. The scalars corresponded to what we believed to be biologically relevant unit changes in the predictors (e.g. a 5% increase in roadside hedge cover). Lastly, we evaluated the relative importance for each habitat variable by calculating the ΔAIC_c that results from removing each from the saturated model ("Drop-1 Importance").

In order to account for our spatially autocorrelated data, we applied the procedures described above to two sets of linear regression models generated in the Spatial Analysis for Macroecology 3.0 (SAM) software (Rangel et al. 2006). For each set, SAM's model selection module allowed us to create candidate models with all possible combinations of the 3 habitat variables (resulting in 7 models per set) where spatial variables were forced into every model to eliminate spatial autocorrelation in residuals (see Diniz-Filho et al. 2008). In the first set, a single spatial variable, which accounted for fine-scale autocorrelation, was included in all candidate models. This spatial variable was a pure autoregressive term generated using SAM given by $\rho \mathbf{W} y$, where $\mathbf{W}$ is the connectivity matrix, y is terrapins observed and ρ is the autoregressive coefficient estimate by a first-order autoregressive model (Rangel et al. 2006). For the second set, a spatial variable accounting for broad-scale trends was applied, in addition to the previously described fine-scale autoregressive term, to all candidate models. Prior to model selection, we noticed terrapins were more abundant along the northwest compared to the southeast portion of the causeway. We used the trend surface analysis in SAM to filter for broad-scale spatial patterns in terrapin occurrence, as it has been shown to account for broad-scale spatially structured variation in a response variable that is unexplained by measured explanatory variables (Legendre and Legendre 1998; Lichstein et al. 2002).

We calculated correlations between all explanatory and spatial variables, and only the two spatial variables were highly correlated (Pearson's $r = 0.724$). While fine-scale autocorrelation and a broad-scale pattern likely existed in our data, including both spatial variables in a model set could cause multicollinearity and produce overfit models. Thus, instead of choosing to ignore broad scale trends due to the correlation with local spatial structure, we performed the two sets of model selection in SAM and report results from each procedure: first with the local autoregressive term, and second, with both local and trend terms.

Analysis of Hot Moments

Based on prior associations between terrapin nesting activity and tide level (Burger and Montevecchi 1975; Feinberg and Burke 2003) as well as early observations in our study, we analyzed daily temporal patterns of terrapin activity on the JIC relative to the peak of the diurnal high tide. We grouped terrapin encounters during surveys into 30-min intervals preceding, during, and following the peak of the diurnal high tide. Initially, we used standard logistic regression and other nonlinear models to evaluate associations between day of the nesting season (0 = 1 May) and hours to the nearest high tide with the likelihood of observing at least one terrapin on the road during a survey. However, the pattern of terrapin presence with respect to explanatory variables fit poorly to any conventional function. Therefore, we fitted a distance-weighted least-squares model with a stiffness of 0.25 to the likelihood of terrapin presence during a survey relative to the two temporal predictors (STATISTICA v.8.0; StatSoft, Tulsa, OK). Distance-weighted least-squares models have been used to explore fine-scale patterns that do not fit standard regression models (Cleveland 1993). We assessed the temporal consistency of activity between 2009 and 2010 with respect to high tide. We summed terrapin counts for 30-min intervals equidistant to the time of high tide (e.g., 60-90 mins before and 60-90 mins after) and then compared the distribution of activity relative to high tide between years using a chi-squared contingency test.

Results

We observed 234 terrapins during 2009 and 402 during the 2010 nesting season (total = 636), all adult females, on the causeway. We recaptured 40 females marked in 2009 in 2010, allowing us to evaluate inter-annual capture distances. In 2010, 20 female terrapins (50%) were captured within 50 m, and 32 females (80%) captured within 200 m, of their original capture location (Fig 2.2).

Analysis of Hot Spots

Along the JIC, terrapin activity was concentrated in 3 discrete hot spots and 7 warm spots (Table 2.1). Using all observations from 2009 and 2010 in the 100-m moving window analysis, we identified hot spots on the causeway where counts ranged from 21 to 40 terrapins. Nearly 30% of all terrapins observed during surveys were located inside the hot spots we delimited, and these zones encompassed less than 10% (803 m) of total causeway length. The rates of terrapin crossings in the 3 hot spots (range

= 9.6 to 12.9 terrapins/100m/season) were 4.4 to 5.9 times greater than the background rate of crossing along the entire causeway (2.2 terrapins/100m/season). A more modest cutoff where counts ranged from 15 to 20 terrapins was chosen to delimit warm spots. Taken together, 22% of terrapins were seen crossing within warm spots of activity, which covered 12% of total causeway length (1056 m) and had intermediate rates of terrapin crossings (range = 5.8 to 7.3 terrapins/100m/season) compared to hot spots and the baseline for the entire causeway.

The spatial distribution of terrapin activity along the causeway did not differ between 2009 and 2010 (χ^2 = 9.57, df = 16, p > 0.5; Fig 2.3). We found consistent locations of spatial peaks in terrapin activity between analyses at 50, 100, and 200-m window sizes. Specifically, the centers of hot spots generated at these different scales were identical, but the distance around these centers included in hot spot ranges increased with window size. Therefore, we used results from the 100-m window size to identify and analyze hot spots. Analysis at this scale delimited the cores of hot spots to smaller, and ultimately more manageable, lengths of road than the 200-m scale while still accounting for expected variations in individual terrapin movements more than the 50-m scale.

The moving window analysis showed that points along the causeway were a mean distance of 174.4 m from the nearest creek (range = 0 to 361 m). Roadsides in a 100-m section of the JIC were covered with a mean of 76.6% hedge vegetation (range = 0 to 100%). Lastly, the adjacent high marsh in a 100-m section of the JIC consisted of 19.5% unvegetated habitat on average (range = 0.2 to 52.3%). Although habitat composition varied at the 3 hot spots, each was within 284 m from the nearest creek, composed of predominantly open roadsides (percent hedge < 45%), and adjacent to vegetated marsh (percent unvegetated high marsh < 20%).

Distance to nearest creek, percent hedge vegetation, and percent of unvegetated high marsh were all weakly associated with hot spots of terrapin activity on the causeway. The saturated model, containing all three habitat features, performed equivalently well in both model sets that included different fixed spatial variables, ranking as the best model or within ΔAIC_c of 2 of the best model (Table 2.2; Burnham and Anderson 2002). The remaining candidate models in both sets predicted terrapin abundance on the causeway relatively poorly compared to the best model ($\Delta AIC_c > 7$). The percent of unvegetated high marsh (mud flats and sand) along a section of road had the greatest, negative effect on the number of terrapins observed on the road regardless of spatial variables included in the model set (Table 2.3). The Drop-1 Importance value for the high marsh variable was 5.5 times greater (=95.11/17.14) in the first set of models and 2.5 times greater (=11.73/4.62) in the second set compared to the next most influential habitat feature. Scaled model-averaged estimates of all three habitat features changed in magnitude between the two model sets, and estimates for distance to creek and percent of roadside hedge in the second set were small and imprecise with confidence intervals that included 0. However, the relative importance of each habitat feature did not differ. Using 95% confidence intervals of the first model set, a 25% increase in unvegetated high marsh area was associated with a relatively large reduction of 1.7 to 2.5 terrapin crossings per 100-m section, a 25% increase in hedge cover was associated with a reduction of only 0.13 to 0.5 terrapins, and a 100-m reduction in distance to nearest tidal creek was associated with an increase of crossings by 0.3 to 0.9 terrapins (Table 2.3).

Analysis of Hot Moments

We observed one or more terrapins during 347 surveys (32%) from 6 May to 12 July and between 730 and 2130 hrs. We found daily hot moments of terrapin nesting forays concentrated around the peak of the diurnal high tide. Relative to tide, 52.4% of all terrapins were observed within a 3-hr period (30 mins before to 150 mins after the peak diurnal high tide), and 69.4% were seen within a 5-hr period (90 mins before to 210 mins after high tide; Fig 2.4). The distance-weighted least-squares model of terrapin presence on the JIC showed a skewed peak where terrapins were most likely to be observed during a survey early in the nesting season (15 May to 25 May; Fig 2.5). Terrapins were always more likely to be on the road at high tide compared to low tide, but there was an interaction between time to high tide and day of the season. Comparing high versus low tide respectively, the probability of observing a terrapin on the road ranged from 60% to 0% prior to the seasonal peak, 70% to 45% during the seasonal peak, and 20% to 0% late in the season. The distribution of terrapin activity did not differ with respect to proximity to the time of high tide between 2009 and 2010 ($\chi^2 = 18.74$, df = 12, $p > 0.5$).

Discussion

We identified peaks in terrapin crossing activity that serve as a starting point for threat-specific conservation measures. Spatially, terrapin activity was disproportionally concentrated in 3 hot spots on the JIC. In addition, regression models supported relationships between terrapin activity levels in these areas and unvegetated high marsh, distance to nearest creek, and roadside hedge cover, which are features suspected to influence terrapin nest site choice; however, we caution that relationships between these variables and the number of terrapins observed crossing the road was modest to weak. Temporally, terrapins were more likely to be active along the road early in the nesting season (late May) and proximate to daily high tides. We observed patterns of activity along the causeway that showed hot spots and hot moments of potential vehicle mortality that were consistent between our two study seasons.

Roads have become a pervasive human footprint in the United States with inherent impacts on wildlife populations (Fahrig and Rytwinski 2009). While it may be unrealistic to mitigate the effects of roads across entire networks, defining local peaks of wildlife mortality will help prioritize the best sites and periods for conservation measures. Regionally, causeways (roads bisecting two aquatic habitats) were strongly associated with roadkill hot spots of many freshwater turtle species in the northeastern US that complete regular or seasonal movements between habitats (Langen et al. 2009), and some of the highest rates of turtle and other herpetofauna vehicle mortality have been reported along a >1-km causeway in Florida (Aresco 2005b). Extensive coastal causeways have been well-documented sites for terrapin mortalities (Szerlag and McRobert 2006; Grosse et al. 2011), including two roads in Cape May, New Jersey (totaling 11.5 km in distance) where the highest rate of vehicle-terrapin collisions were observed over 4 years (Wood and Herlands 1997). A major finding of our study was that, across the 8.7-km JIC, terrapins crossed in three hot spots (totaling 0.8 km) at a disproportionately high rate. Although the coastline of Georgia is relatively rural, mortality on high-traffic causeways is suspected to lead to localized declines in terrapin populations (Grosse et al. 2011). However, coastal marshland throughout the northeastern US is typically more developed with higher road densities, which may cause widespread impacts to terrapins (Wood and Herlands 1997). For roads that bisect extended areas of aquatic habitats and are implicated in declines of nearby wildlife populations, using our, or a similar, approach of delimiting hot spots at a finer scale is a crucial step in evaluating the threat of wildlife-vehicle collisions and prioritizing sites for management.

We identified spatial peaks of terrapin nesting activity using data from all turtles that were struck by vehicles or rescued alive during nesting forays. We expect in the near term for traffic volumes, and the risk they pose, to stay spatially consistent across our study area since there are no major intersecting roads, and only one establishment (the Jekyll Island Welcome Center), for cars to enter or exit this section of the causeway. Assuming that the risk of road mortality should not vary spatially, we believe that the degree of crossing activity should be proportional to the degree of expected road mortality at a specific site on the causeway. To test this assumption, we ran a moving window analysis *ad hoc* using a set of locations only including vehicle-stricken terrapins, and found hot and warm spots of road mortality consistent with those representing crossing activity. Therefore, implementing management devices at the hot spots of crossing activity found in this study should be the first step in reducing the impact of road mortality on this terrapin population.

We found all three habitat features (distance to nearest creek, percent of unvegetated high marsh, and percent of roadside hedge) were associated with hot spots, but each feature's effect on terrapin crossing activity was marginal. Despite the difference in the treatment of spatial correlation (local autocorrelation alone vs. autocorrelation + trend), all habitat features were included among the best-fitting models. The amount of surrounding unvegetated high marsh had the greatest (negative) effect on terrapin activity of the variables considered. In general, fewer terrapins crossed 100-m sections of the causeway where the adjacent high marsh was composed of larger, unvegetated patches (reduction of 1.7 – 2.5 terrapins for every 25% increase in unvegetated high marsh). Terrapin life-history traits and physiological needs may explain this relationship. We hypothesize that moving across bare marsh habitat exposes terrapins to increased risk of predation and thermal stress. This would result in hot spots around areas of dense high marsh vegetation that provide cover from predators and the sun.

The percent of roadside hedge and distance to nearest creek had small effects on terrapin activity on the causeway. Between the two model sets, there was a change in the direction of the effect that roadside hedge had on the number of terrapin crossings at a given section of causeway. However, the effect of hedge was minimal in both scenarios, which is indicated by small coefficients and importance values. Even sections of roadside with full hedges had ample open area between the hedgerow and the pavement for terrapins to nest. Terrapins were observed moving through, resting, and nesting under hedges (pers. obs.) suggesting these are not barriers to movement and may provide suitable habitat for nesting. Similarly, the distance between a location on the road and the nearest creek did not substantially affect terrapin crossing frequency. Terrapins have been observed to travel over 1 km to find nest sites (Gibbons et al. 2001; Szerlag-Egger and McRobert 2007). No position along our study area of the causeway was greater than 370 m from the nearest creek – well within the movement range previously observed for terrapins. Also, high tides periodically flooded portions of high marsh that extended from creeks to the base of road banks. Thus, it is likely that these landscape characteristics of the marsh surrounding the JIC do not spatially restrain nesting females and account for the minimal effect that distance to a creek had on crossing activity at a given location.

Hot moments of potential vehicle mortality were highly synchronized with the diurnal high tide. Terrapin activity on the road peaked during the 3-hr period spanning from 30 mins before the scheduled high tide to 150 mins after. Our measure of terrapin activity during hot moments is likely conservative, since only a portion of turtles crossing simultaneously could be observed due to logistic constraints of our survey techniques. The greatest number of terrapins was seen between 30 and 90 mins after the scheduled high tide, but we noted that the tide level in creeks adjacent to the causeway remained high during this period. The timing of management strategies on the JIC should focus on the period of elevated risk found in our study relative to the schedule of diurnal high tides, which are known months in advance. We expect terrapins to synchronize nesting forays with high tides across their geographic range, so local tidal schedules should be consulted when defining and mitigating hot moments of road mortality.

Terrapins may nest earlier in the summer and proximate to diurnal high tides to reduce physiological risks. Burger and Motevecchi (1975) also found that that the numbers of terrapins nesting was positively correlated with proximity to the diurnal high tide. Nesting during high tide may be adaptive if it reduces the distance terrapins must travel between the water and nesting habitat, which should decrease the risk of predation or thermal stress (Burger and Montevecchi 1975; Feinberg and Burke 2003). We also observed a seasonal peak of terrapin activity on the JIC during the early half of the nesting season between 15 May and 25 May. This pattern of nesting activity, skewed earlier in the season, is consistent with studies of terrapins across the US Atlantic coast; however, season length varies geographically. Northern terrapin populations tend to have shorter nesting seasons, lasting from June to July with the a peak of activity in the first 20 days (New Jersey: Burger and Montevecchi 1975; Wood and Herlands 1997), while terrapins in northern Florida nested from late April to mid-August with a peak of activity in May (Butler et al. 2004). Climatic differences and physiological constraints may allow courtship and nesting activities to begin earlier in populations at southern latitudes (Seigel 1980).

Using hot spots or hot moments to manage for road impacts on wildlife requires that hot spots be temporally stable. In the case of terrapins, we found that 50% of females were found on the road within 50 m of their capture location from the previous year. Similarly, Szerlag-Egger and McRobert (2007) found that 40% of female terrapins captured on a road in New Jersey were recaptured within 50 m of their capture location the previous year (30% were recaptured within 25 m). These results suggest high inter-annual nest site fidelity that should lead to consistent hot spot locations between years. Admittedly, both studies only have two consecutive years of data, so we cannot address whether hot spots are stable over longer time periods; however, Gibbons et al. (2001) reported high site fidelity by terrapins within tidal creeks over a 16-year period in South Carolina.

Management implications

Without effective mitigation solutions that prevent wildlife-vehicle collisions and preserve habitat connectivity, landscape models predict road mortality to cause rampant declines of turtle populations on a regional scale (Fahrig et al. 1995; Gibbs and Shriver 2002; Andrews et al. 2007; Litvaitis and Tash 2008; Langen et al. 2009; Beaudry et al. 2010). Since the impacts of road mortality are suspected to significantly reduce the viability of certain terrapin populations, a crucial first step in effective reduction of a threat is to assess its patterns and identify its peaks on a local scale. The results of this study can be used to develop management strategies that effectively reduce vehicle mortality on the JIC by targeting peaks of activity and inform management research at similar sites where terrapin populations are threatened by roadways. The synchrony of hot moments and hot spots observed here offers a reliable basis for targeted strategies to reduce road mortality. Although the patterns were stable over 2 years, locations of hot spots may shift over longer periods. We caution against employing permanent management devices (e.g., ecopassages or concrete barriers) before the long-term stability of hot spots is known. However, year-to-year consistency still provides managers with specific targets to effectively employ low-cost, adjustable measures such as fencing and signage. Although wildlife signage has not been an effective conservation measure when employed year-round (Putman 1997; Tanner and Perry 2007), establishing temporary signs, coupled with flashing lights (similar to school zones) deployed around daily high tides, may reduce vehicle-turtle collisions during these hot moments of activity. Fencing along the JIC at identified hot and warm spots could directly limit terrapin movement across the road while still providing access to suitable nesting habitat on the proximate road bank. Although all 3 habitat features may influence terrapin activity on the JIC, the composition of habitat at each hot spot varied. Direct studies of terrapin behavior and movements through these habitat types are necessary before we can use these features to predict and prioritize hot spots of road mortality at other sites. Examining characteristics of a causeway itself may be the next step in mitigating some of its pressure on the population. Road width, presence or absence of barriers, traffic volume, and vehicle speed can each impact rates of road mortality (Forman and Alexander 1998). Most of these traits can be altered (e.g., speed limits) and may provide additional management solutions that will reduce mortality.

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Table 2.1. Metrics of hot and warm spots of crossing activity along Jekyll Island Causeway in 2009 and 2010.

	Hot Spot No.	Length (m)	% of Causeway	No. of Terps	% of Total Terps	No. Terps/100m/ season
Entire Causeway	-	8710	-	636	-	3.7
Hot Spots	1	331	3.8	75	11.8	11.3
	2	162	1.9	31	4.9	9.6
	3	310	3.6	80	12.6	12.9
Subtotal		803	9.2	186	29.2	
Warm Spots	4	133	1.5	19	3.0	7.1
	5	130	1.5	19	3.0	7.3
	6	125	1.4	16	2.5	6.4
	7	140	1.6	20	3.1	7.1
	8	190	2.2	27	4.2	7.1
	9	156	1.8	18	2.8	5.8
	10	182	2.1	25	3.9	6.9
Subtotal		1056	12.1	144	22.6	
Grand Total		1859	21.3	330	51.9	

Table 2.2. Linear regression models predicting abundance of terrapins in 100-m windows along the Jekyll Island Causeway in Georgia, USA.

Model[a]	**Log-likelihood**	***K***[b]	**AIC$_c$**[b]	**ΔAIC$_c$**[b]	**W$_i$**[b]
Models with fixed pure autoregressive effects					
Creek+Marsh+Hedge	-2045.914	5	4071.827	0	0.986
Creek+Marsh	-2048.210	4	4080.42	8.594	0.013
Marsh+Hedge	-2052.481	4	4088.962	17.135	<.001
Marsh	-2053.869	3	4095.738	23.912	<.001
Hedge	-2089.253	3	4166.506	94.679	<.001
Creek+Hedge	-2091.466	4	4166.932	95.106	<.001
Creek	-2098.646	3	4185.291	113.465	<.001
Models with Fixed trend surface analysis and pure autoregressive effects					
Creek+Marsh	-1859.556	5	3699.111	0	0.61
Creek+Marsh+Hedge	-1862.249	6	3700.497	1.386	0.305
Marsh	-1860.076	4	3704.151	5.04	0.049
Marsh+Hedge	-1862.559	5	3705.117	6.006	0.03
Creek	-1863.283	4	3710.566	11.455	0.002
Hedge	-1863.300	4	3710.599	11.488	0.002
Creek+Hedge	-1866.112	5	3712.223	13.112	<.001

[a] Creek = distance to creek, Marsh = percent unvegetated high marsh in window, Hedge = percent vegetation of hedges on road shoulders in window

[b] *K* = no. of parameters, AIC$_c$ = Akaike's Information Criterion, ΔAIC$_c$ = difference in AIC$_c$ from the best model, and w$_i$ = Akaike wt.

Table 2.3. Model-averaged estimates for linear models of terrapin crossings per 100 m of road, biologically-relevant unit changes, rescaled estimates, upper and lower 95% confidence limits, and variable importance.

Variable	Coeff.	Std Error	Unit Change	Scaled Coeff.	Scaled 95Lower	Scaled 95Upper	Drop-1 Importance[a]
Composite of models with pure autoregressive spatial variable							
Constant	1.356	0.376					
Creek	0.006	0.001	100m	0.60	0.30	0.90	17.14
Marsh	-0.082	0.008	25%	-2.05	-2.45	-1.65	95.11
Hedge	-0.012	0.004	25%	-0.30	-0.48	-0.13	8.59
Composite of models with trend surface and pure autoregressive spatial variables							
Constant	3.51	0.277					
Creek	0.003	0.001	100m	0.30	0	0.50	4.62
Marsh	-0.025	0.007	25%	-0.63	-0.98	-0.28	11.73
Hedge	0.003	0.001	25%	0.075	0	0.50	1.39

[a] Values taken from ΔAIC_c that occurs when dropping the specific variable from the saturated model

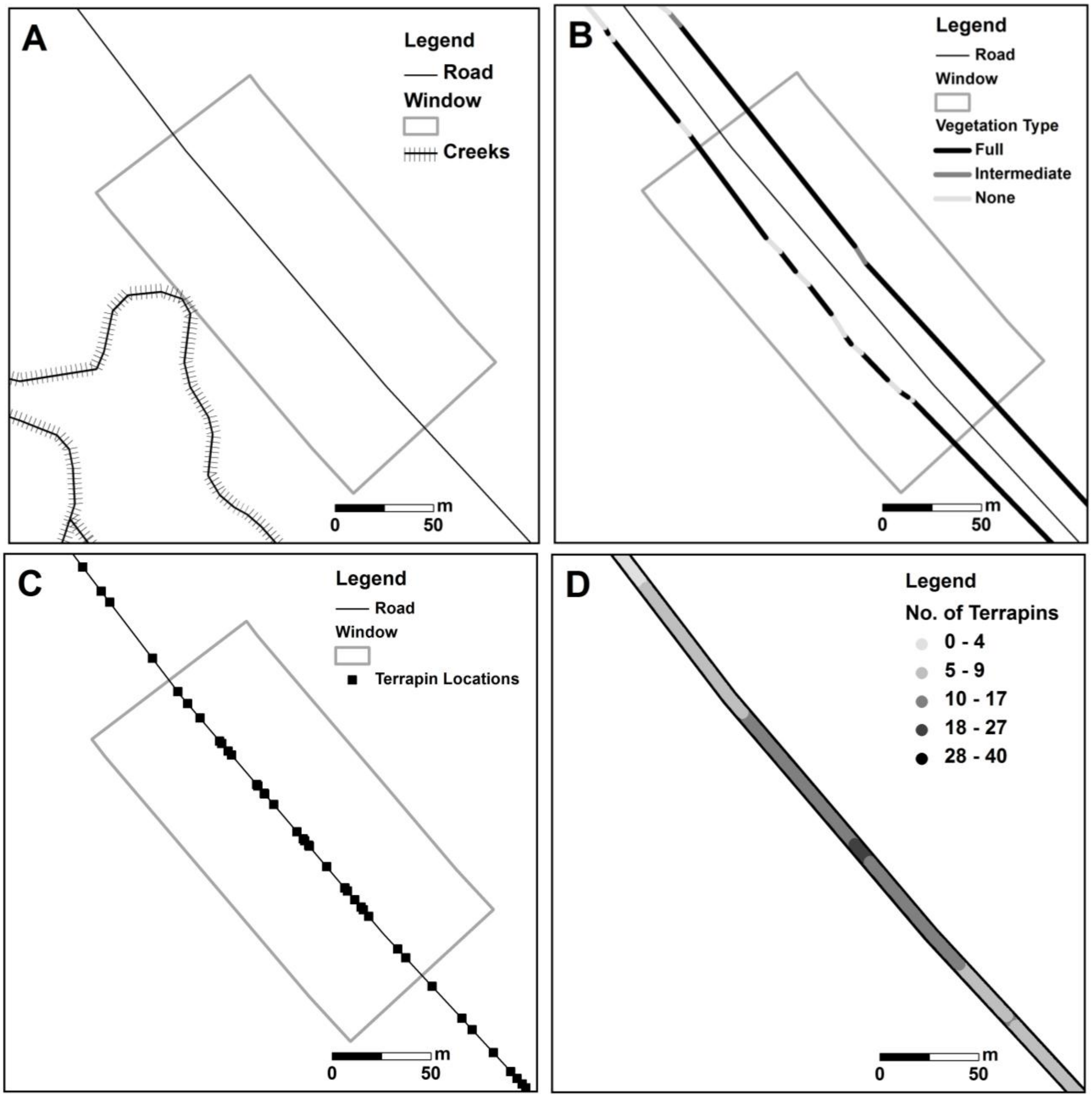

Fig 2.1: Moving window analysis steps using ArcGIS 9: A) calculate nearest distance from center of window to creek, B) calculate percentage of each vegetation type on both roadsides within window, C) count terrapins observed within window, and D) generate distribution of terrapin crossings along causeway.

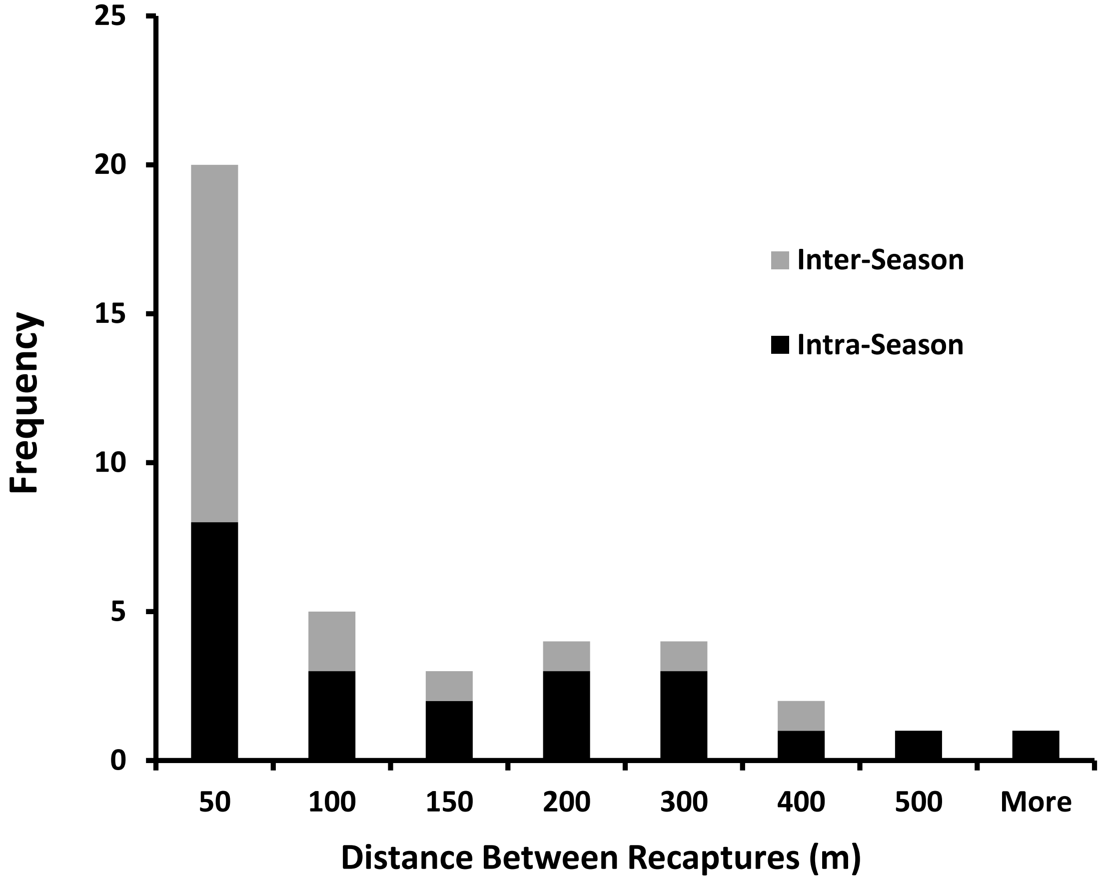

Fig 2.2: Frequency of inter-capture distances observed for all terrapin recaptures (n = 40). Intra-season recaptures indicate terrapins that were located twice within a single season. Inter-season recaptures indicate terrapins that were located in 2009 and 2010.

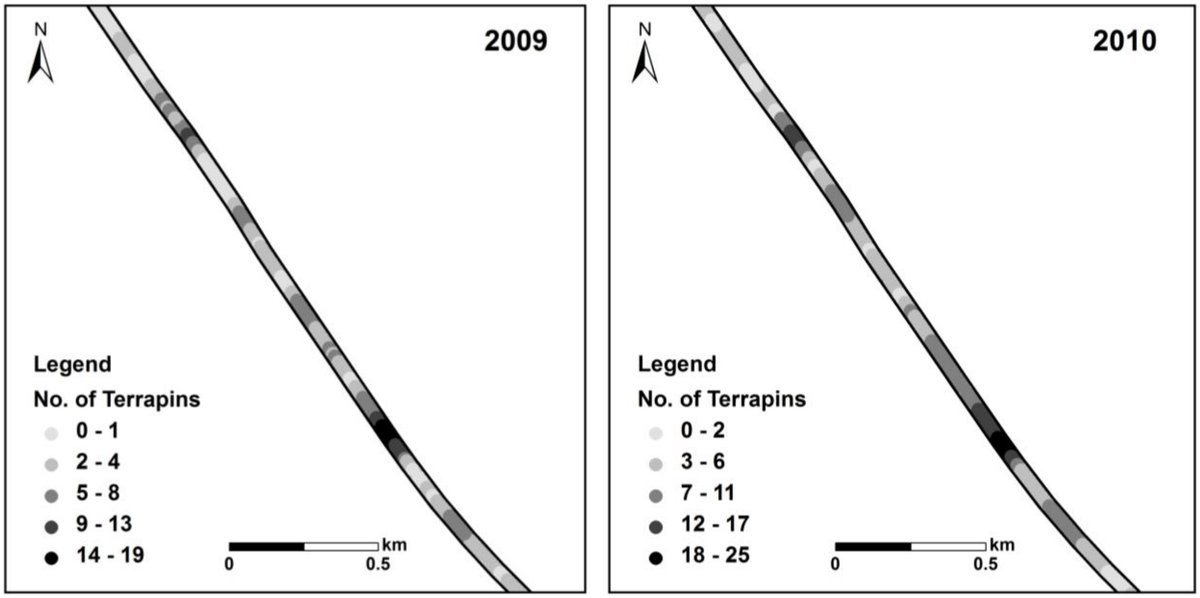

Fig 2.3: Year-to-year comparison of terrapin crossing activity along a portion of the Jekyll Island Causeway. Terrapin counts indicate the number of terrapins seen crossing within 50 m from point on road. Dark sections represent hot spots of activity that remained consistent between seasons.

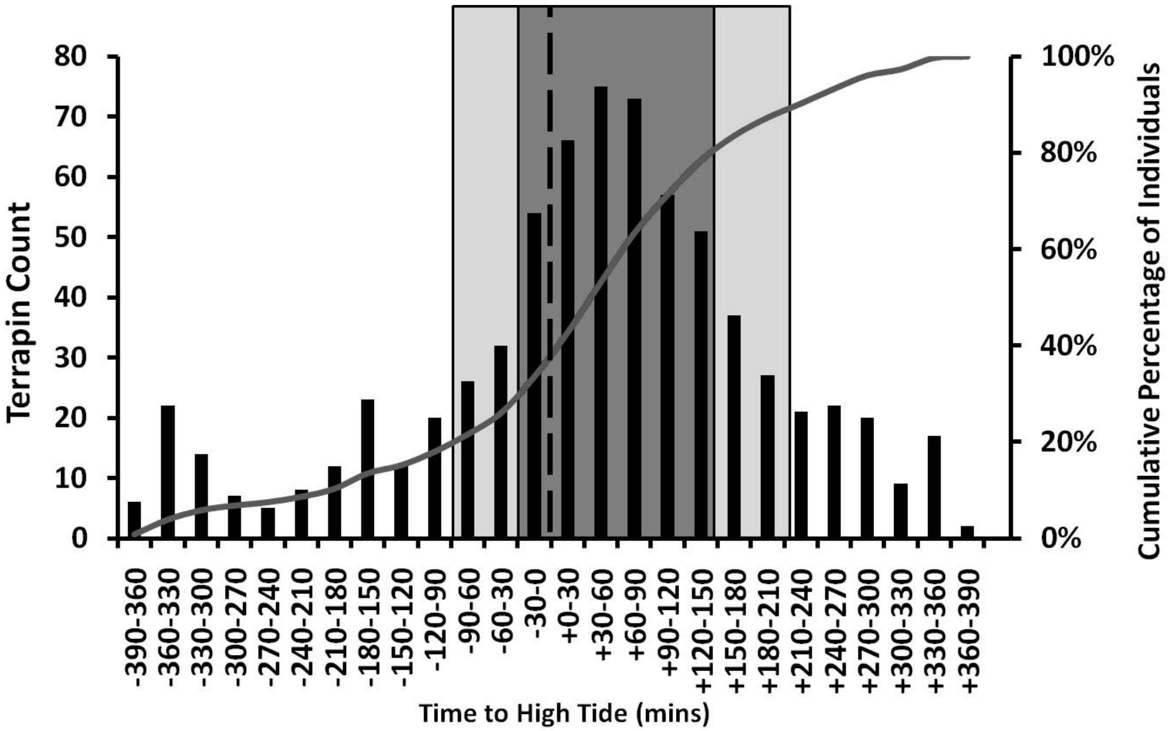

Fig 2.4: Hot moments of terrapin activity relative to high tide (dotted line). Dark grey zone contains 52.4% of all terrapins seen nesting near the causeway in a 3-hr window. Dark and light grey zones contain 69.4% of all observations in a 5-hr window.

Terrapin activity relative to high tide (dotted line). Dark grey zone contains 52.4% of all terrapins seen nesting near the causeway in a 3-hr window. Dark and light grey zones contain 69.4% of all observations in a 5-hr window

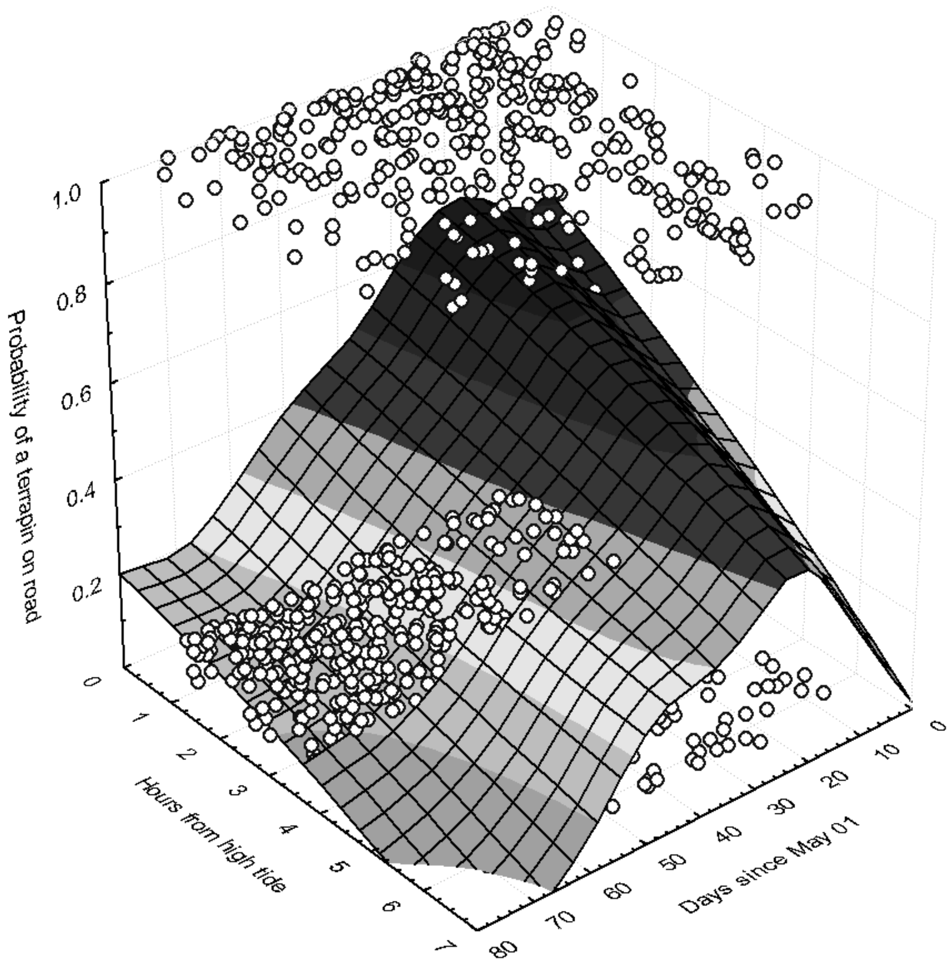

Fig 2.5: Probability of observing a terrapin on the Jekyll Island Causeway during a survey relative to hours to the scheduled high tide (0 = high tide) and day of the nesting season (0 = 1 May).

CHAPTER 3

ESTIMATING THE IMPACTS OF MULTIPLE THREATS AND MANAGEMENT STRATEGIES ON A DECLINING POPULATION OF DIAMONDBACK TERRAPINS

Introduction

Conservation management of declining species hinges on identifying threats and predicting their impacts. In real-world cases where multiple threats occur in concert and mitigation resources are limited, management plans should focus on reversing those threats that will most likely hamper population recovery (Heppell et al. 1996). Among extant species of turtles, over 42% are currently listed as threatened on the IUCN Red List (Baillie et al. 2004), and the majority of turtle species have felt negative impacts from a range of anthropogenic threats (Gibbons et al. 2000). Turtles are relatively long-lived, and population stability is strongly governed by high annual adult survivorship that compensates for delayed sexual maturity and low yearly recruitment (Heppell 1998), thereby making populations particularly vulnerable to threats that increase additive adult female mortality (Congdon et al. 1993). Conversely, changes in fertility rates of turtle species have less dramatic effects on population growth (Heppell 1998). For turtles, conservation strategies have traditionally targeted specific stages, including the protection of nests, rearing or "headstarting" of hatchlings in captivity, or reducing adult mortality from habitat destruction, harvest, or wildlife-vehicle collisions.

Diamondback terrapins (Malaclemys terrapin) inhabit salt marshes along the Atlantic and Gulf coasts of the United States and are declining or of unknown status across the majority of their range due to human-induced threats, but certain populations remain locally abundant (Butler et al. 2006). Thus, we have the opportunity to estimate the impacts of these threats on population growth and develop conservation strategies before local extirpations occur. Anthropogenic factors threatening the species include habitat degradation (Seigel 1993; Gibbons et al. 2001), mortality in crab traps (Seigel and Gibbons 1995; Wood 1997; Dorcas et al. 2007; Grosse et al. 2009; Grosse et al. 2011), and road mortality of adults (Wood and Herlands 1997; Szerlag and McRobert 2006). In addition, nest predation by subsidized predators (e.g., raccoons; Procyon lotor) has become a well-documented concern for terrapin population viability that reduces egg survival and overall recruitment (Burger 1977; Feinberg and Burke 2003; Butler et al. 2004). Within the state of Georgia the diamondback terrapin is currently listed as a “species of special concern” (Georgia Department of Natural Resources 2005), and road mortality and nest predation were identified as substantial threats to populations (Butler et al. 2006). By fragmenting salt marsh habitat, roadsides provide attractive nesting sites characterized by elevated, open areas with little vegetation and ground cover (Szerlag-Egger and McRobert 2007); thus, roads likely represent a female-biased threat to adult terrapins. Mortality of nesting females is particularly detrimental to turtle population viability (e.g., Congdon et al. 1993), and female-biased mortality can result in skewed sex ratios that limit the effective population size causing long-term declines and even extirpation (Doak et al. 1994; Mitro 2003; Aresco 2005a). Without effective mitigation solutions that prevent wildlife-vehicle collisions, models predict road mortality to cause rampant declines of turtle populations on a regional scale (Fahrig et al. 1995; Gibbs and Shriver 2002; Andrews et al. 2007; Litvaitis and Tash 2008; Langen et al. 2009; Beaudry et al. 2010). Although vehicle-induced mortality and nest predation have been proposed as contributors to terrapin population declines (Wood and Herlands 1997; Butler et al. 2006; Grosse et al. 2011), no formal models have been created to estimate the effects of these threats on population growth.

Matrix models are frequently used to project population growth where individuals are grouped by age, as in the Leslie matrix, or by life-stages based on size or maturity (Lefkovich 1965; Caswell 1989). Matrix models have recently been used to examine population persistence for a diverse array of taxa, including mammals (Lubben et al. 2008), birds (Marschall and Crowder 1996; Kesler and Haig 2007), plants (Silvertown et al. 1996; Osunkoya 2003; Jimenez-Sierra et al. 2007), and reptiles (Doak et al. 1994; Heppell 1998; Webb et al. 2002; Enneson and Litzgus 2008). One strength of stage-based models lies in their ability to measure stage-specific sensitivities, or elasticities, that identify factors that have the largest influence on future population growth (Caswell 1978; de Kroon et al. 1986; Caswell 1989). Thus, stage-based models have become an effective tool for developing conservation strategies that target those parameters (e.g., survival, fecundity) of a particular stage and ranking plans according to their expected benefit to population growth (Crowder et al. 1994; Escos et al. 1994; Heppell et al. 1994; Marschall and Crowder 1996; Enneson and Litzgus 2008). Stage-based models, opposed to age-based, are especially appropriate for most turtle species where accurate aging techniques are lacking. Instead, life-stages of eggs, hatchlings, juveniles, and adults can be easily defined for turtles. These models demand estimates of annual survival and fertility for each stage, and accurate demographic rates are sparse for iteroparous, long-lived species such as turtles with cryptic early life-stages (Iverson 1991). Still, population models have been effectively used to evaluate relative changes in population growth caused by anthropogenic threats and potential management strategies on a variety of species of freshwater turtles (Congdon et al. 1993; Enneson and Litzgus 2008; Beaudry et al. 2010), tortoises (Doak et al. 1994), and sea turtles (Crouse et al. 1987; Crowder et al. 1994; Heppell et al. 1996).

Through studying female diamondback terrapins that nest on a causeway leading to Jekyll Island, Georgia, USA, our objectives were 1) to estimate per capita rates of road mortality and nest predation, 2) to use stage-based population models that incorporate these rates to compare population growth under current and potential scenarios, and 3) to make conservation recommendations that will stabilize or grow this population. As an additional exercise, we simulated the effects of producing female-biased sex ratios to augment population growth as a potential management solution. We expected that even minimal rates of adult road mortality will lead to population declines and that adult road mortality, compared to nest predation, will cause a larger reduction in the population growth rate. Our ultimate goal was to estimate the impacts of both threats on local terrapins and simulate the effects of reducing each with targeted management efforts.

Methods

Study Site

This study was conducted in conjunction with the long-term monitoring efforts of the Georgia Sea Turtle Center (GSTC), initiated in 2007. Past and present monitoring has focused on the 8.7-km Downing-Musgrove Causeway to Jekyll Island, GA, USA (31.08°N, 81.47°W). The Downing-Musgrove Causeway (Jekyll Island Causeway: JIC) is characterized as a state highway with average annual daily traffic (AADT) of 3,460 vehicles/day (Georgia Department of Transportation 2009) with a speed limit of 89 km/hr (55 mph) along the majority of the road. The JIC bisects a peninsula of salt marsh roughly 32-km^2 in area consisting of a network of intertidal creeks and high marsh dominated by *Spartina spp*. Several creeks come in proximity to or cross under the causeway, and the edge of the road is regularly within 20 m of the high-tide mark of the marsh.

Our study modeled population growth rates for female terrapins that nest on the JIC. This group likely includes terrapins inhabiting the salt marsh peninsula surrounding the JIC; however, we acknowledge that terrapins may travel from farther distances to nest on the causeway. Female terrapins cross the causeway to nest above the high tide line on the grassy, elevated shoulders to prevent egg inundation (Aresco 2005a; Brennessel 2006), and the JIC represents most of the suitable nesting habitat in the surrounding landscape. Each year (recorded since 2007), 100-400 adult terrapins are struck and killed on the JIC, of which > 98% are females that annually nest along road banks from early May through mid-July (B. Crawford; GSTC, unpublished data). In addition to road mortality, nest predation has been frequently documented on roadsides of the JIC (K. Holcomb, unpublished data). Past studies have identified raccoons (*Procyon lotor*), American crows (*Corvus branchyrhynchos*), boat-tailed grackles (*Quiscalus major*), and fire ants (*Solenopsisi nvicta*) as key predators that most commonly raid terrapin nests within 24 hours of egg-laying (Burger 1977; Feinberg and Burke 2003; Butler et al. 2004).

Estimating Threats

We estimated two threats to terrapins that have been observed on the JIC: road mortality and nest predation. First, we used a capture-mark-recover approach to estimate annual rates of terrapin mortality due to vehicle strikes. Intensive road surveys were conducted from 1 May through 20 July in 2009, 2010, and 2011 to monitor the fates of nesting females crossing the causeway. Road surveys were completed by one or two observers patrolling in a vehicle while scanning the road and shoulders for terrapins. Surveys occurred throughout daylight hours from 0830 to 2000 between 20 and 120 mins apart, but a few opportunistic surveys were conducted outside of this period. For every terrapin found, we recorded location with a handheld Global Positioning System (GPS: Garmin International, Olathe, Kansas, USA) and recorded time of observation, condition and direction of the animal, and its code if it was a recapture. All alive and uninjured terrapins were sexed based on position of the cloaca on the tail and head allometry, palpated for eggs, measured (carapace length, plastron length, shell width and depth, and head width), weighed (g), and uniquely coded by drilling or notching marginal scutes. Turtles were returned on the side of the road they originally came from within 1 hr of capture. For live terrapins discovered on or about to cross the road with cars nearby, researchers intervened and captured animals before they could be struck. To account for this alteration in fates of terrapins, we recorded such animals as “saved” and included these individuals that were marked in our final estimates of annual road mortality rates. All dead and injured terrapins were examined for scute marks and taken to the GSTC for necessary care. Using our mark-recover data, we derived two estimates for annual road mortality rates using data from consecutive seasons (2009-2010 and 2010-2011). Each estimate was calculated by dividing the number of recaptured-recovered individuals that were struck or saved during one summer by the total number of individuals marked the previous summer. Since the two estimates of annual adult mortality produced by this method differed by >10% (see Results), we used them to represent low and high levels of road mortality and took their mean to estimate an average level of annual mortality from year to year.

In addition to road surveys, walking surveys were conducted from 10 May to 1 July 2011 to observe nesting activity along roadsides of the JIC and to monitor the fate of nests. Nine transects were selected based on hot spots of nesting activity observed from road surveys in the previous two summers (B. Crawford, GSTC; unpublished data) and ranged from 300 to 350 m in length. Surveys were completed between 3 hrs before and 3 hrs after the scheduled high tide, coinciding with peaks of nesting activity observed on the JIC (B. Crawford, GSTC; unpublished data), but opportunistic sightings outside of this period were included in the final dataset. Each transect was surveyed once per week. A survey consisted of a researcher walking along the north and south roadsides of a transect area, midway between the road and the marsh line, searching for nesting terrapins. In order to not disturb the nesting process of females, the only turtles captured prior to nesting were those attempting to cross the road. We recorded the location and behavior of each animal, and once captured, we checked for marginal scute marks and palpated females that had finished nesting to confirm all eggs were deposited at that location. We marked the location of each confirmed nest by flagging the shrub-line perpendicular to the road (1-3 m from the nest site) – a marking method that has been shown to not affect predation rates on terrapin nests (Burke et al. 2005) – and monitored nests daily for signs of predation. We did not excavate intact nests to count the number of eggs laid so as to not affect egg survival or predation rates. We excavated depredated nests and never found intact eggs. Additionally, egg shells were often missing (presumed carried away by predators) at depredated nest sites, so an accurate measure of surviving and depredated eggs was not possible. Thus, we assumed that clutch sizes among nests were similar and used the proportion of surviving nests as an approximate estimate for egg survival on the JIC; however, we acknowledge this method overestimates egg survival and does not account for other factors such as infertility, arrested development, and invasion by roots (Feinberg and Burke 2003).

Population Modeling

We constructed and parameterized a deterministic, stage-classified Lefkovitch population model, with a 1-year time interval, that was used to calculate finite rates of population growth (λ) for diamondback terrapins near the Jekyll Island Causeway: $n(t + 1) = An(t)$

where n(t) is a vector of stage-specific abundances at time t and A is the population projection matrix. Deterministic models, including ours, contain numerous assumptions: a closed population, density-independence, no environmental or demographic stochasticity, and uniformity of individuals in each stage regardless of age. Natural conditions do not often reflect these assumptions, but deterministic models have been successfully used for straightforward comparisons of population growth under different scenarios in turtle populations with limited demographic data (Heppell et al. 2000; Enneson and Litzgus 2008), including 2 studies of diamondback terrapin populations (Mitro 2003; Hart 2005).

Our modeling framework was built and run in spreadsheet software (Microsoft® Office Excel® 2007), and the user-friendly environment provides future opportunities for biologists of government organizations (e.g., Department of Natural Resources) to use this model to test additional management scenarios. This was a female-only model that tracked individuals throughout their life-cycle based on elements in matrix A including stage-specific survival, transition, and reproduction rates between years. Parameters were used to reflect 3 modeling scenarios: 1) baseline conditions without additional sources of mortality, 2) current population conditions using a range of estimates of road mortality and nest predation from the JIC, and 3) potential population conditions reflecting reductions to one or both of these threats.

We used a 3-stage projection matrix (*A*) with the following parameterization:

$$A = \begin{bmatrix} 0 & 0 & F \\ P_{21} & P_{22} & 0 \\ 0 & P_{32} & P_{33} \end{bmatrix}$$

P_{ij} is the probability that an individual in class j survives and transitions into stage i and *F* is the reproductive output, or fertility, of individuals in the adult stage (Lefkovitch 1965; Morris and Doak 2002). The population growth rate (λ) is calculated as the dominant eigenvalue of the matrix using parameters based on stage-specific annual survival rates of three stages for diamondback terrapins (Table 3.1). Stage 1 is the hatchling stage, beginning when eggs hatch in late summer to early fall and ending the following year, and stage 2 is the juvenile stage from ages 2 to 5. Age of maturity varies geographically in female terrapins and has been observed at 4-5 years in Florida (Seigel 1984) and 6 years in South Carolina (Lovich and Gibbons 1990). Therefore, we assumed an age of maturity of 6 years for this population of terrapins in Georgia, and combined ages 6 and greater into stage 3 representing adults. Similar to other population models on long-lived turtle species, we did not include a maximum age in the model, so P_{33} is equal to the annual adult survival rate. Baseline reproductive output (*F*) or fertility of adult females was calculated by multiplying mean clutch size, mean clutch frequency, sex ratio, and the annual egg survival rate together.

Parameterizing the baseline population

Baseline estimates of model parameters for annual adult, juvenile, and hatchling survival rates, as well as life history and demographic parameters used to estimate reproductive output (*F*) were gleaned from the literature (Table 3.1). Precise estimates of many life history and demographic rates for diamondback terrapins are still lacking or highly variable for 3 reasons: 1) hatchling and juvenile terrapins are difficult to sample and estimate survival rates in the wild, 2) studies have been conducted across the terrapin's range, and differences of reproductive estimates could be attributed to latitudinal variation in age at maturity, clutch size, and clutch frequency (Zimmerman 1992; Roosenburg and

Dunham 1997), and 3) most terrapin studies focus on declining populations where anthropogenic threats impact survival rates (e.g., Tucker et al. 2001; Hart 2005). In building our baseline model to represent a terrapin population located in Georgia under pristine conditions, we acknowledged sources of variation when choosing parameters to use from the literature. To estimate fertility, we used reproductive values (clutch size, frequency, and age of maturity) from studied populations that were geographically closest. Following previous terrapin population models, we assumed a 1:1 sex ratio (Mitro 2003; Hart 2005) and an annual egg survival rate of 0.5. While this baseline egg survival rate is likely higher than most terrapin populations, similar values have been effectively used in models of terrapin (Hart 2005) and other turtle populations in the same family (Emydidae: Congdon et al. 1993; Enneson and Litzgus 2008). To obtain a high but reasonable rate of annual adult survival that may exist under pristine conditions, we averaged the two highest estimates from the literature (Mitro 2003; Ernst and Lovich 2009). Next, we used the same value for juvenile survival employed in two previous terrapin models (Mitro 2003; Hart 2005). Lastly, little is known about the life history of hatchling terrapins, although studies have used variable estimates of survival (Mitro 2003; Hart 2005). Therefore, we estimated this parameter by entering all other parameters into our model and using the Solver function, an Excel add-in, to identify the value for hatchling survival that yielded $\lambda = 1.0$.

Parameterizing current and potential threat levels to the population

We altered baseline population parameters to simulate the effects of road mortality and nest predation, independently and then in concert, that we documented on the JIC. First, we used field-derived estimates of road mortality to simulate reductions in annual adult survival. After estimating inter-season road mortality rates from mark-recover data, we subtracted low, average, and high levels of adult mortality iteratively from the baseline adult survival rate to simulate a range of likely scenarios. Next, we reset adult survival to baseline conditions and replaced the egg survival term included in the fertility rate with nest survival based on a range of predation rates. Estimates of predation rates affecting nest survival are highly variable between sites and years, ranging from 41% to 88% in the literature (Burger 1977; Roosenburg 1992; Feinberg and Burke 2003; Butler et al. 2004)**.** To account for this uncertainty, we modeled population growth under scenarios of low and high nest predation (50% and 15% nest survival, respectively) that encompassed a wide range of potential values seen in other studies. Lastly, we modeled population growth using the current estimate of nest predation rates based on the proportion of marked nests that survived on the JIC in 2011. We simulated the effects of 3 levels of nest predation alone, the effects of 3 levels of road mortality alone, and finally the effects of both threats acting together at low, average, and high levels and calculated the resulting λ for each scenario.

Using the baseline model parameters, we plotted adult vs. nest survival rates that would result in population growth rates of 0.95, 0.98, 1.0, 1.02, and 1.05 to serve as a reference point of management needed to stabilize or grow the population. Then we represented the current ranges of survival rates for these stages given rates of egg predation and adult road mortality observed in this and other studies, and denoted the average levels of nest survival and adult survival observed in this study on the JIC.

We estimated the stage-specific threats of road mortality and nest predation in two additional ways by systematically altering vital rates to produce desired population growth rates. First, we used all baseline values for vital rates and calculating egg and adult survival rates, in turn, that resulted in an acceptably declining population that would persist in the short-term (λ = 0.98). This was taken to represent the maximum reduction of survival for a particular life-stage that the population could tolerate. Second, we explored the degree of management needed, given the current average estimates for threats on the JIC, for each threat that would result in a stable (λ = 1.0) or increasing (λ = 1.02) population.

Sensitivity and Elasticity analysis

We used a CSIRO program called PopTools (Greg Hood, http://www.dwe.csiro.au/vbc/poptools/), an Excel add-in, to calculate transition probabilities between stages and perform sensitivity and elasticity analyses. Sensitivity values represent the absolute changes to λ given an absolute change in a particular matrix element, whereas elasticity measures the relative contribution of each demographic parameter in the model (e.g., adult survival, fertility) to λ (de Kroon et al. 2000). Elasticity values sum to 1.0 (de Kroon et al. 1986), which allows for direct comparisons between parameters. Likewise, elasticity analysis has been used to measure the vulnerability of a population to threats that affect stage-specific vital rates (Crouse et al. 1987; Caswell 1989; de Kroon et al. 2000; Heppell et al. 2000; Gerber and Heppell 2004). Thus, elasticity analysis can identify the sources of mortality where management effort should be focused. We also compared changes in λ given proportional changes of survival rates for egg, hatchling, juvenile, and adult stages, ranging from -10% to +10%, while all other parameters were held at baseline values.

Results

Estimating threats

We estimated an inter-season road mortality rate for adult female terrapins of 16.4% (high threat level) between 2009 and 2010 and 4.4% (low threat level) between 2010 and 2011 based on the proportion of marked turtles dead or saved on the JIC (Table 3.2). The average rate of road mortality, given these 2 estimates, was 10.4%. Each walking transect was surveyed 9 times during the nesting season of 2011. Fewer females were active on the JIC in 2011 compared to previous summers, and we observed only 21 nesting events. Thirteen of 21 marked nests (61.9%) were depredated in the summer of 2011, yielding an estimated nest survival rate of 0.381. Of the 13, most nests (76.9%) were raided overnight and all but one were depredated within four days of laying.

Population modeling

The baseline projection matrix *A* for the study population of diamondback terrapins was:

$$A = \begin{bmatrix} 0 & 0 & 3.45 \\ 0.253 & 0.428 & 0 \\ 0 & 0.142 & 0.887 \end{bmatrix}$$

Altering baseline parameters by reducing stage-specific survival rates due to current threats of the JIC resulted in negative population growth for all scenarios (Table 3.3; Fig 3.1). Among scenarios where only one threat was simulated in the model, population growth ranged from the most optimistic case when nest survival was reduced by the nest predation rate observed on the JIC in 2011 ($\lambda = 0.981$) to the most dire case when adult survival was reduced by the high estimate of road mortality ($\lambda = 0.902$). In scenarios when each threat acted independently on the population at similar levels (i.e. low level of road mortality or nest predation), road mortality caused larger reductions in λ (Table 3.3). When both threats acted in concert on the population across a range of current rates, we predicted λ to range from 0.810 to 0.971 (Table 3.3; Fig 3.1; denoted by the box). Model projections resulted in a λ of 0.912 given our best estimates of current threats on the JIC (Table 3.3; Fig 3.1; denoted by the X).

Starting with baseline values for all parameters, the population tolerated larger decreases in nest survival compared to adult survival before population growth fell under an acceptable threshold ($\lambda = 0.98$; Table 3.4a). Using the average rates of current threats on the JIC, adult survival of 0.914 (a 14.3% increase from the current estimate) or nest survival of 0.960 (a 60.3% increase from the current estimate) was needed in order to stabilize the population (Table 3.4b). Adult survival of 0.941 (a 20.2% increase) was needed to produce a population growth rate of 1.02, and no rate of nest survival was able to produce a growing population while average rates of road mortality occurred (Table 3.4b).

Sensitivity was highest for the matrix element representing the probability of juveniles surviving and transitioning into the adult stage-class (0.884), followed by the parameter for adult survival (0.683). Elasticity, representing the proportional change in λ given a proportional change of a parameter, was highest for adult survival (0.564), which was 4.8 times greater than the next highest elasticity value (0.119) attributed to the probability of juveniles surviving and transitioning into the adult stage-class. While absolute sensitivity and elasticity values varied as parameters changed in each scenario, the ranks of these values did not change, with elasticity always being highest for annual adult survival. Similarly, proportional changes in adult survival resulted in greater changes in λ compared to other vital rates (Fig 3.2). Changes in adult survival by -10, -5, +5, and +10% resulted in changes in λ of -5.6, -2.9, +3.1, and +6.2%, respectively. Proportional changes in all other vital rates resulted in smaller changes in λ: -2.5, -1.3, +1.3, and +2.7% (juvenile survival); and -0.8, -0.4, +0.4, and +0.7% (fertility and hatchling survival).

Discussion

The results of our matrix model indicate that, under current conditions of the Jekyll Island Causeway, the population of nesting female diamondback terrapins will decline in the absence of conservation actions. Population persistence is mostly dependent on high adult survival compared to other demographic rates. Considering only the threat of adult mortality from vehicle strikes at current levels on the JIC, the population is experiencing negative growth ($0.902 \le \lambda \le 0.971$). Although nest predation is an additional threat leading to population decline, nest survival would need to be raised to 96% (from the current rate of 38%) in order to achieve positive population growth as long as road mortality is still occurring at the average rate observed on the causeway. If road mortality occurs at a higher than average rate, no degree of nest protection will result in a sustainable population. Thus, reducing the rate of road mortality on adult female terrapins should be the priority for future management plans while improving nest success should be a secondary action.

Road mortality represents a major threat to numerous turtle species as well as a hazard to drivers; thus, conservation plans for areas such as the JIC should prioritize efforts to reduce wildlife-vehicle collisions. The findings of our study add to the growing body of evidence that roads can cause significant declines and alter the structure in turtle populations (Haxton 2000; Gibbs and Shriver 2002; Steen and Gibbs 2004; Aresco 2005a; Gibbs and Steen 2005; Beaudry et al. 2010; Patrick and Gibbs 2010). Roughly 98% of mortalities seen on the JIC during our study were adult females, implicating road mortality as a substantially stage- and sex-biased threat to local terrapins. With the exception of a few species (e.g., loggerhead sea turtles; Crouse et al. 1987), demographic analysis of most turtle populations have attributed adult survival rates as having the highest elasticity values and the greatest impacts on population growth (Doak et al. 1994; Heppell 1998; Enneson and Litzgus 2008). Across all scenarios run in our model, relative elasticities stayed the same, and our results support the trend among turtle species with annual adult survival ranking highest. Increasing adult survival (i.e., reducing road mortality) resulted in the largest change in population growth compared to proportional increases of survival or fertility in any other stage-class (Fig 3.2). Based on perturbations of our model, reducing adult survival by as little as 3.1% could result in unacceptable declines in this terrapin population (Table 3.4a). This finding was consistent with demographic analyses of other long-lived turtle species where anthropogenic sources of mortality are considered additive (Crouse et al. 1987; Congdon et al. 1993; Enneson and Litzgus 2008; Beaudry et al. 2010). We assumed road mortality to be additive to background rates; however, little is known regarding the timing of natural mortality events for terrapins. It is possible that the process of nesting, regardless of the presence of roads, is associated with mortality of adult females. Under these conditions, vehicle mortality of nesting females may be partially compensatory (removing those individuals from the population that would have died anyways), which would cause our model to underestimate adult survival and population growth rate. Alternatively, natural mortality events could occur outside of the nesting season (e.g., increased mortality during overwintering). In this case, a portion of animals marked on the JIC one year may die before nesting the next year, which would result in underestimates of per capita annual road mortality given our mark-recover approach. Additionally, we used the two inter-season estimates as low and high rates of annual road mortality, but we do not know the consistency of rates from year to year based on 3 years of data. However, we believe our estimates provide reference points, based on empirical data, for assessing current risks and developing mitigation strategies through population models. Despite these uncertainties, even the lowest estimate of annual adult mortality due to vehicle strikes on the JIC (4.4%) exceeds the amount a population could likely tolerate, and a reduction of adult survival by the highest estimate of road mortality (16.4%) would cause declines to be more rapid. Conversely, mitigating adult mortality should be the priority for conservation strategies, and even small increases in adult survival should augment the population.

Extensive coastal causeways have been well-documented sites for terrapin mortalities throughout their range (Szerlag and McRobert 2006; Grosse et al. 2011). The coastline of Georgia is relatively rural with extensive, undeveloped marsh, but mortality on high-traffic causeways like the JIC is suspected to lead to localized declines in terrapin populations (Grosse et al. 2011). However, these effects may not lead to broader declines across Georgia. Comparatively, mortality on coastal roads throughout the northeastern US may lead to widespread, regional declines of terrapin populations, where marshland is typically narrower and more developed with higher road densities (Wood and Herlands 1997). For example, the highest rate of vehicle-terrapin collisions was observed over 4 years on a network of roads in Cape May, New Jersey, USA (Wood and Herlands 1997).

Although reducing adult survival from road mortality was the main driver of population declines among model scenarios, the additional threat of nest predation to nest survival exacerbated declines in the diamondback terrapin population near the JIC. For example, the population's growth rate was 0.902 when a high level of road mortality was the only threat considered, but λ was reduced to 0.810 when a high level of nest predation was added to the scenario. Given current threat levels on the JIC, adult survival would have to increase by at least 13% in order to stabilize the terrapin population if nest predation remains unmitigated. Comparatively, a 60% increase in nest survival is necessary to stabilize the population if road mortality persists at current rates. Either scenario presents a likely implausible goal for management. Logically, protecting adults from road mortality will not result in positive population growth if extreme egg mortality from predators still occurs, and troublingly, egg predation rates exceeding 97% have been reported in certain terrapin populations (Roosenburg 1990). Thus, increasing recruitment rates by reducing nest predation should be considered an integral step, secondary to reducing road mortality, in conservation measures for this population.

Based on the range of scenarios we have modeled, we suggest that nest survival rates on the JIC need be increased by 60% to stabilize the population. Fortunately, we believe this is tenable with management actions. Conservation efforts of endangered sea turtle species have used predator control as a direct and effective method that reduced nest predation in certain areas by as much as 67-100% compared to years when predators were left unchecked (e.g., Engeman et al. 2003; Garmestani and Percival 2005). Similar success may be achieved by culling raccoons, the primary predators of terrapin nests, on the JIC. Artificial nesting mounds were constructed and placed on roadsides of the JIC in 2009 as an alternative strategy to increase terrapin nest success, which each consisted of an open, elevated mound of dirt and sand with a caged box that allowed terrapins access to the mound's top while excluding nest predators (see Buhlmann and Osborn 2011). Opportunistic sightings provided evidence that some terrapins nested inside these boxes, but more intense monitoring during the nesting season is necessary to measure the frequency at which terrapins are using these devices and estimate their impact on nest success of the population as a whole.

Most turtle species including terrapins have environmental sex determination (ESD) based on the incubation temperature of a developing embryo (Janzen and Paukstis 1991), which offers additional management options to increase female recruitment on the JIC. Diamondback terrapin embryos incubated at warmer nest temperatures produce females while male offspring are produced under cooler conditions (Ewert et al. 1994). Like many reptiles, growth of terrapin populations is largely female-driven since the number of reproductive females directly relates to recruitment (Girondot and Pieau 1996). Therefore, in female-only models of species with ESD, the recruitment of new females into a population can be achieved by increasing the fertility rate in two ways: increasing overall nest survival or changing the sex ratio to be female-biased. Our baseline conditions assumed a 1:1 sex ratio in our model, but ESD of diamondback terrapins allows for alternative management solutions that can manipulate the population’s sex ratio. Females generally prefer nesting in open areas with minimal ground and canopy cover (Roosenburg 1996; Szerlag-Egger and McRobert 2007), but individuals also nest underneath shady shrub areas (pers. obs.). On the JIC, the artificial nest mounds represent a third potential habitat type for nesting. In a pilot study of hatchlings produced from nests in different habitat types on the JIC, we found that nest temperatures in open habitat and on artificial mounds were sufficiently high and produced a strongly female-biased sex ratio of surviving offspring. In contrast, nests under roadside hedges were cooler resulting in strongly male-biased offspring (A. Grosse, GSTC; unpublished data). Since ESD in terrapins allows for sex ratios to deviate from the 1:1 value used in our baseline model, we simulated achieving a stable population through combinations of 3 management strategies: 1) reduce adult road mortality, 2) increase nest survival, and 3) increasing the percent of female hatchlings produced (Fig 3.3; Table 3.5). While reducing road mortality is most essential to population viability, management plans that combine all 3 factors would not have to remove any one threat entirely – a likely impossible task given limited time, funding, and resources. For example, a stable population could be reached with a moderate reduction (50%) of the current rate of road mortality, a moderate reduction of nest predation that results in 50% nest survival, and a sex ratio producing 73% females (Table 3.5).

Management implications

Although the terrapin population near the JIC is likely declining due to multiple threats, reducing the rate of road mortality should have the greatest positive effect on population growth. Without effective mitigation solutions that prevent wildlife-vehicle collisions, models predict road mortality to cause rampant declines of turtle populations on a regional scale (Fahrig et al. 1995; Gibbs and Shriver 2002; Andrews et al. 2007; Litvaitis and Tash 2008; Langen et al. 2009; Beaudry et al. 2010). Terrapin nesting activity on the JIC is highly concentrated around daily high tides and spatially clustered into 10 discrete areas where >50% of terrapins were seen crossing (B. Crawford, GSTC; unpublished data). These "hot spots" and "hot moments" represent the most important targets for management of road mortality. Viable solutions include fencing of hot spots to prevent turtle crossings (Jaeger and Fahrig 2004; Aresco 2005b) or employing flashing warning signage around daily high tides that could increase driver awareness. However, reducing adult mortality will not stabilize the population if nest predation rates are sufficiently high, so practices that increase recruitment through nest survival, such as culling of primary nest predators (e.g., raccoons), nest-capping, and creating predator-excluding artificial nesting mounds, should be employed secondarily to ensure population viability. Lastly, an opportunity exists for management strategies to increase recruitment, specifically of female hatchlings, by manipulating sex ratios of nests laid on the JIC. Habitat modification (e.g., clear-cutting of roadside hedges to create more open nesting habitat) or creating more artificial nesting mounds on the JIC, in conjunction with fencing, could expand warmer nesting areas that increase the number of female hatchlings entering the population. Manipulating sex ratios has been discussed as a management tool for declining turtle species and employed using incubation and headstarting techniques in captivity (Vogt 1994). However, management plans to alter sex ratios of nests in situ have not been attempted to our knowledge. Although adult survival impacts population growth more than the fertility rate, these strategies have the elegance of mitigating a female-biased threat (adult road mortality) with a female-biased solution and should be included in larger conservation plans.

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Table 3.1. Parameters used for baseline conditions for stage-classified population models of diamondback terrapins on the Jekyll Island Causeway.

Parameter	**Value**	**Source**
Hatchling survival	0.253	derived from entering other parameters and solving for λ = 1.0
Juvenile survival	0.570	Mitro 2003; Hart 2005
Adult survival	0.887	derived from Ernst and Lovich 2009; Mitro 2003
Age at maturity (females)	6	Lovich and Gibbons 1990
Mean clutch size	6.9	Zimmerman 1992
Mean clutch frequency	2	Roosenburg and Dunham 1997; this study
Egg survival	0.500	Assumed by Hart 2005
Proportion of female offspring	0.500	Assumed by Mitro 2003; Hart 2005
Fertility	3.450	derived from above estimates

Table 3.2. Adult female diamondback terrapins marked and recovered as mortalities the following year to yield inter-season road mortality rates on the Jekyll Island Causeway, GA.

Year	Terps marked that year still alive after season	Road mortality recaps in next season			Inter-season mort. rate	Threat level
		Struck	Saved	Total		
2009	110	10	8	18	0.164	High
2010	205	4	5	9	0.044	Low
2011	72	-	-	-	0.104	Average

Table 3.3. Projected population growth (λ) for a diamondback terrapin population under a range of likely conditions near the Jekyll Island Causeway, GA.

Threat	**Survival rates**	**Population growth rate (λ)**
Nest predation	nest	
Low (baseline)	0.500	1.000
JIC	0.381	0.981
High	0.150	0.933
Road mortality	adult	
Low	0.843	0.971
average	0.783	0.935
High	0.723	0.902
Both	adult, nest	
low, low	0.843, 0.500	0.971
JIC, average	0.783, 0.381	0.912
high, high	0.723, 0.150	0.810

Table 3.4. Changes in stage-specific survival rates needed to meet targets of population growth (λ) for diamondback terrapins on the Jekyll Island Causeway when other parameters are held constant in a stage-based matrix model. Under baseline conditions, decreases in survival rates that result in acceptable decline for short-term population persistence ($\lambda = 0.98$; a). Under current conditions of road mortality and nest predation, increases in survival rates needed for a stable ($\lambda = 1.0$) and increasing ($\lambda = 1.02$) population (b).

(a) Stage	**Starting value**	**Value resulting in: $\lambda=0.98$**	**% change resulting in: $\lambda=0.98$**
Nest survival	0.5	0.376	-0.124
Adult survival	0.887	0.856	-0.031

(b) Stage	**Starting value**	**Value resulting in:**		**% change resulting in:**	
		$\lambda=1.0$	**$\lambda=1.02$**	**$\lambda=1.0$**	**$\lambda=1.02$**
Nest survival	0.381	0.960	none	+0.603	none
Adult survival	0.783	0.914	0.941	+0.131	+0.158

Table 3.5. Sex ratios (in % females) needed in conjunction with management of road mortality and nest predation to produce a stable population (λ = 1.0) of diamondback terrapins on the Jekyll Island Causeway.

Road mortality	**Nest survival**	**% females needed**
Current average	Current (38%)	impossible
	50%	96.0
	75%	64.0
Reduce by 30%	Current (38%)	impossible
	50%	82.1
	75%	54.8
Reduce by 50%	Current (38%)	95.8
	50%	72.9
	75%	48.6

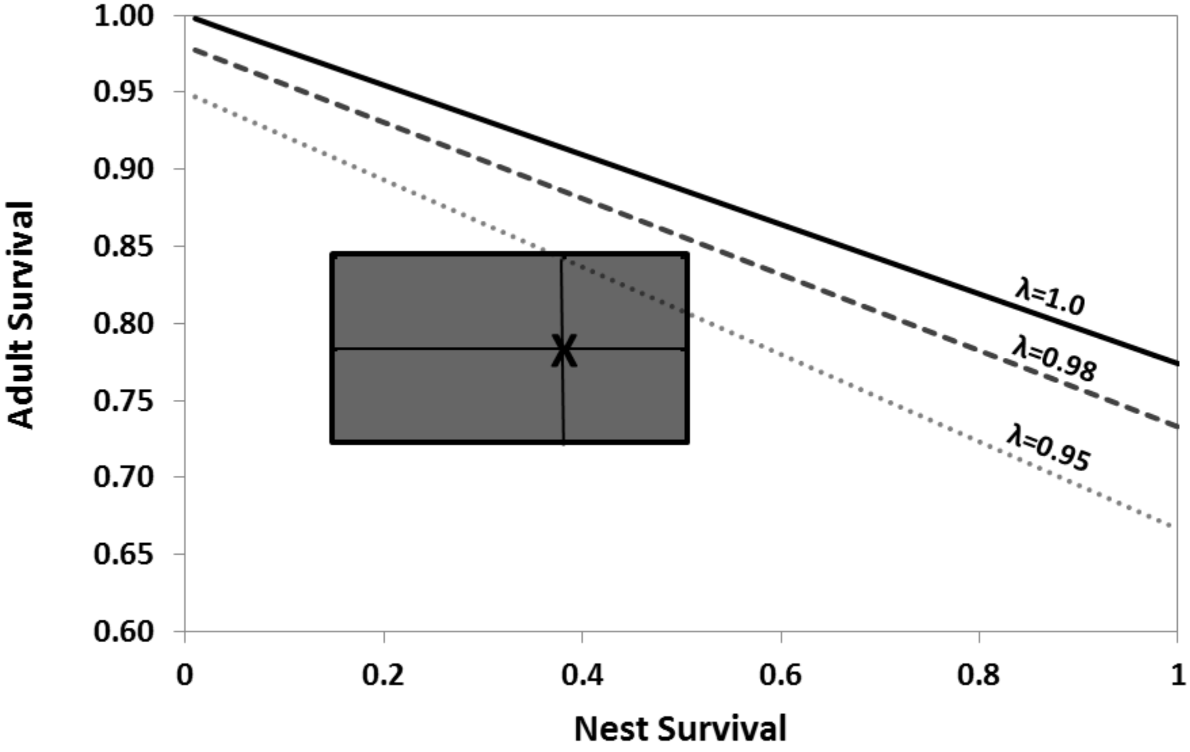

Figure 3.1. Projected population growth rates (λ) given adult and nest survival rates for a population of diamondback terrapins. The shaded box encompasses a range of nest survival rates seen in past studies and adult survival rates under low and high levels of road mortality. The X denotes average survival estimates from this study given current threats on the Jekyll Island Causeway.

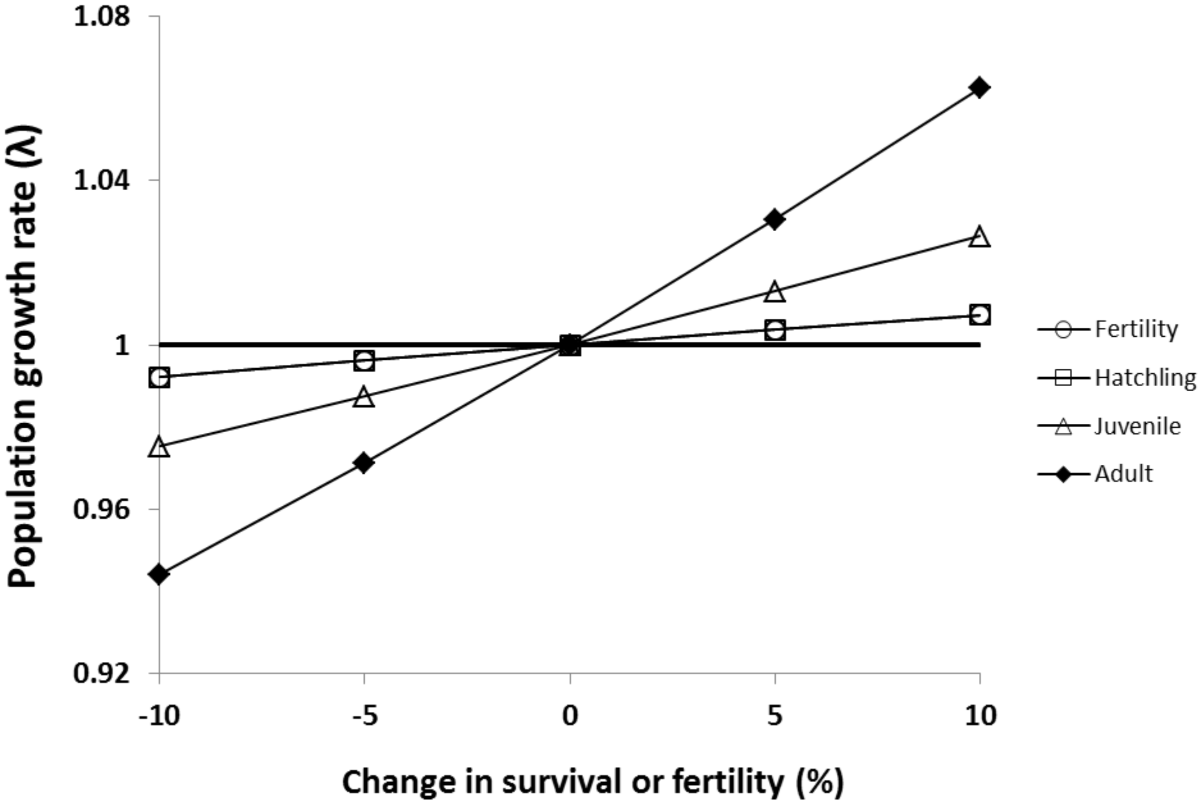

Figure 3.2. Population growth rate (λ) versus percent change in stage-specific survival rates and fertility from the stable baseline model (λ = 1.0) for diamondback terrapins nesting near the Jekyll Island Causeway, GA.

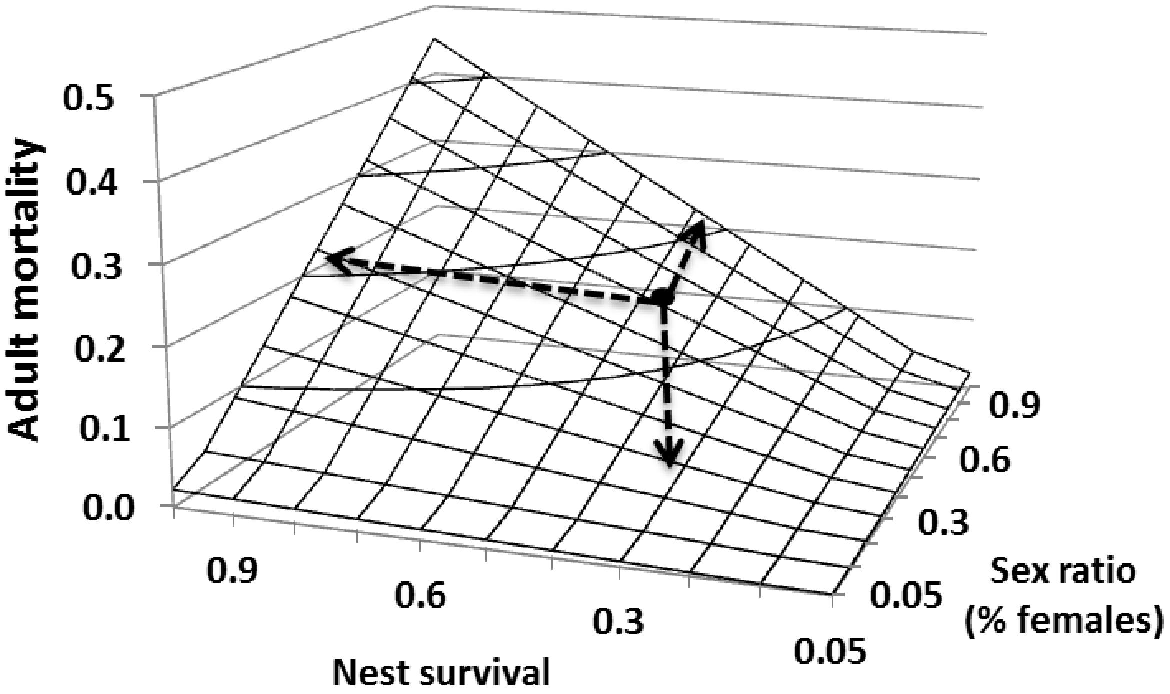

Figure 3.3. Combinations of adult mortality, nest survival, and % female offspring that yield a stable population (λ = 1.0) of diamondback terrapins. The reference point indicates average current estimates for the 3 parameters on the Jekyll Island Causeway, and dashed lines indicate how each parameter must change to reach a stable population if the others are held at current levels.

CHAPTER 4

CONCLUSION

Diamondback terrapin populations are currently facing multiple, pervasive, human-induced threats. While previous research has documented many of these threats, our understanding of how they impact terrapins and how management can mitigate risks remains insufficient. Given that terrapin populations are still locally abundant but predominantly declining, we have the opportunity to assess these threats and intervene before local extirpations occur. The purpose of this thesis was to examine the dynamics and impacts of road mortality that occur at a local scale to identify where, when, and to what degree management is needed to stabilize or grow a population of terrapins. While our study focused on one location (the Jekyll Island Causeway), our methodology and conclusions can certainly inform management at other sites where road mortality occurs.

In the first half of this research, we identified discrete hot spots and hot moments of terrapin nesting activity and road mortality on the JIC. Through methodologies of intensive road surveying and a unique moving-window spatial analysis, we obtained an accurate, fine-scale assessment of the threat of road mortality that will yield targeted management plans. Additionally, our results indicated that the amount of unvegetated high marsh, and to a lesser degree the proximity to creeks and amount of roadside hedge vegetation, is correlated with terrapin crossing activity at a particular location on the road. Peaks of terrapin activity were concentrated around diurnal high tides and were located at three specific sections of the JIC. Furthermore, the consistency of these peaks between years of our study is encouraging because future management plans can be based on the predictability of these patterns. Female terrapins likely use high tide as a temporal cue for nesting that results in less thermal stress from being out of water and higher nest survival from depositing eggs above the high tide line. Life history and physiological traits such as these likely account for the consistent hot moments of activity seen across years. The observed fidelity of terrapins to specific nesting locations on the roadside, often within 50 meters of previous nesting events, is a likely basis for the year-to-year consistency of hot spots of crossing activity.

In the second half of this research, stage-based matrix models predicted substantial declines for terrapin populations given current levels of road mortality and nest predation observed on the JIC. The findings of our study add to the growing body of evidence that roads can cause substantial population declines – even when mortality rates are minimal. Similar to other studies, we found that reductions in adult survival caused the greatest reduction in population growth rate compared to relative changes in egg, hatchling, or juvenile survival rates. This supports the conclusion that population persistence in the majority of turtle species relies on high adult survival compared to other demographic rates. Although reduced adult survival due to road mortality was the main driver of population declines among model scenarios, the additional threat of nest predation to egg survival exacerbated these declines. While the rates of nest success from other studies are highly variable, our findings indicate that the threat of nest predation can sufficiently limit recruitment and cause declines in terrapin populations. Thus, increasing nest success via predator removal or other strategies should be secondary, but still necessary, to improve the growth rate and ensure stability for these terrapin populations.

Without effective management solutions that prevent wildlife-vehicle collisions, substantial declines are imminent for the terrapin population near the JIC, based on the results of this thesis, and declines are expected at other sites where high-traffic roads bisect salt marshes. Our research has yielded a firm understanding of the characteristics and potential impacts of road mortality on the JIC that should directly influence mitigation strategies. The predictable hot spots and hot moments of crossing activity observed in this study serve as specific targets for management that reduces mortalities and maximizes the benefit to the population. Two viable, and relatively low-cost, methods of reducing adult mortality on the JIC are 1) placing fencing along hot spots that prevents terrapin movement across the road and 2) deploying wildlife signage, coupled with flashing lights (similar to school zones), around daily high tides during the nesting season to increase driver awareness. In the second half of this study, we showed that reducing adult road mortality should be the priority for management, but mitigating this one threat will not stabilize the population if nest predation rates are sufficiently high. Thus, practices that increase recruitment through egg survival, such as culling of primary nest predators (i.e., raccoons) or nest-capping, should be employed secondarily to ensure population viability. Currently, we are using an alternative strategy to increase terrapin nest success and recruitment that involves modifying artificial nesting mounds on JIC roadsides to provide attractive nesting habitat to adult females, reduce predation with protective cages, and potentially produce a female-biased sex ratio of hatchlings.

Further research into the effects of road mortality on terrapin populations is integral for conservation strategies on both regional and local scales. Long-term population monitoring will provide a direct assessment of the impacts of any anthropogenic threat and subsequent management actions. We began a monitoring effort of terrapin populations surrounding the JIC during this study, but continued surveys are necessary to model changes in population growth from threats and future management. Habitat features of roadsides and surrounding marsh could potentially be used to predict the locations of hot spots. There was high variability of habitat features associated with spatial peaks in our analysis, so direct studies focused on habitat use and behavior of female terrapins while on nesting forays could enhance our ability to use habitat features to predict the locations of road mortality hot spots along other causeways. While we have opportunistically observed many terrapins nesting on the artificial nest mounds, more intense monitoring of the use of these devices is necessary to estimate their impact on nest success of the population. Finally, there is an opportunity to research another potential management strategy to increase recruitment of females. This strategy can be used to alter sex ratios of hatchlings by manipulating temperatures in different nesting habitats surrounding the JIC. Future research into the effects of habitat modification (e.g., clear-cutting of roadside hedges to create more open nesting habitat) or building artificial nesting mounds could inform novel, alternative management strategies that increase recruitment in declining terrapin populations. Ultimately, we feel that cost-effective conservation solutions can be achieved by predicting the impact of roads on population growth and identifying hot spots and hot moments of risk, and this approach used in our study should be employed on other roads where wildlife-vehicle collisions are suspected to impact local populations.