

Hot spots and hot moments of diamondback terrapin road-crossing activity

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Summary

1. Road mortality is a major component of human impacts on wildlife populations, and the pervasiveness of roads on the landscape presents a substantial challenge for managing those impacts. The feasibility of methods to reduce road mortality depends on the degree to which this threat is spatially or temporally concentrated, which can be based on habitat, human activities or species' ecology. Diamondback terrapins *Malaclemys terrapin* are a species of conservation concern across their range, and road mortality is a major threat contributing to local population declines.

2. We used intensive road surveys of the 8.7-km Downing-Musgrove Causeway to Jekyll Island, Georgia, USA, over 2 years to determine whether road activity and mortality was diffused or concentrated spatially (hot spots) or temporally (hot moments) in order to guide efficient management.

3. In 2009 and 2010, we documented 636 terrapin crossings that were temporally and spatially condensed. Temporally, there was a 70–80% chance of a terrapin occurring on the road within a 3-h period around the diurnal high tide and within the first 30 days of the ~75 day nesting season. Over the two nesting seasons, 52% of terrapin occurrences on the road occurred within the 3-h period around high tide. Spatially, 30% of terrapins were observed crossing in three hot spots that composed less than 10% of the length of the entire causeway, and the percentage of unvegetated high marsh was negatively associated with the number of terrapins that occurred on a section of road.

4. *Synthesis and applications.* Our results demonstrate that hot spots and hot moments can be identified for species at finer scales than those found by other studies and are related, strongly or weakly, to specific temporal processes or habitat features. We found patterns of road mortality, like most threats, can be diffused or concentrated; therefore, complementary management tools that focus on hot spots or moments and also address the more diffused component of road mortality will be required to reduce this threat for at-risk wildlife.

Key-words: diamondback terrapin, Georgia, hot moment, hot spot, *Malaclemys terrapin*, road mortality, roads, turtle

Introduction

The effective management of declining species relies heavily on targeting specific threats with specific solutions. For wide-ranging species that face wide-ranging threats such as roads, addressing such threats can appear daunting.

However pervasive, threats are likely to fluctuate in space and time such that the largest impacts are relatively localized. Thus, management regimes engineered to conditions at finer, localized scales are often more successful (Wittingham *et al.* 2007; Beaudry, Demaynadier & Hunter 2008). Localized risk assessment takes into account (i) the probability and frequency that a threat occurs, (ii) how threat levels vary in space and time, and (iii) the effect size of the threat on population growth (Holton 2004).

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Spatially, threat processes can be diffused across large scales or concentrated at higher rates in specific areas, referred to as hot spots (e.g. Beaudry, Demaynadier & Hunter 2008). Likewise, threat processes can be temporally diffused or more concentrated during specific times, referred to as hot moments, when the threat impacts the species at a higher rate (Beaudry, Demaynadier & Hunter 2010). Once a combination of spatial or temporal variables threatens more individuals than can be compensated for in a population, declines and potential extirpation are expected (Congdon, Dunham & van Loben Sels 1993; Beaudry, Demaynadier & Hunter 2010). Developing specific solutions to ameliorate hot spots and hot moments requires detailed knowledge of how threat processes are governed by the species' ecology and behaviour.

Wildlife–vehicle collisions (hereafter, road mortality) are a pervasive ecological threat known to cause declines of wildlife populations (Forman *et al.* 2003; Litvaitis & Tash 2008; Fahrig & Rytwinski 2009). Road mortality can be relatively high for a wide range of vertebrate taxa (reviewed by Fahrig & Rytwinski 2009). Species that appear particularly vulnerable to road mortality are those that make extensive overland movements, do not avoid or are attracted to roads (Gibbs & Shriver 2002; Forman *et al.* 2003; Jaeger *et al.* 2005). Species with low reproductive rates, naturally high adult survival or long generation times may also be particularly sensitive to even low levels of additive road mortality (Congdon, Dunham & van Loben Sels 1993; Steen & Gibbs 2004; Beaudry, Demaynadier & Hunter 2010). Among these species, road mortality can influence population demographics with respect to sex- and stage-specific survival (Haxton 2000; Mumme *et al.* 2000; Row, Blouin-Demers & Weatherhead 2007). Species and landscape characteristics may interact in ways that produce diffused or clustered patterns of mortality. Road mortality may be diffused for more 'nomadic' or widely dispersing species, while species that migrate between proximate complimentary habitats may exhibit hot spots of road mortality (Clevenger, Chruszcz & Gunson 2003; Forman *et al.* 2003; Fahrig & Rytwinski 2009). For example, hot spots are often associated with wetlands because wetlands are complementary habitats for many species that exhibit seasonal breeding migrations (Ashley & Robinson 1996; Beaudry, Demaynadier & Hunter 2008; Langen, Ogden & Schwarting 2009; Cureton & Deaton 2012). Species that exhibit hot spots of road mortality associated with migration are also likely to exhibit hot moments of road mortality during the breeding season or prior to overwintering when frequent overland movements occur (Grilo, Bissonette & Santos-Reis 2009; Beaudry, Demaynadier & Hunter 2010; Cureton & Deaton 2012). Seasonal peaks of road mortality can aid in targeted management; however, no studies have addressed finer temporal peaks in road mortality that might relate to daily activity patterns of animals or motorists. The ability to identify fine-scale characteristics of hot spots and hot moments would

facilitate more targeted and efficient actions to reduce road mortality rates.

The diamondback terrapin *Malaclemys terrapin* is currently listed as state threatened or 'of special concern' in numerous states including Georgia (Georgia Department of Natural Resources 2005). Threats to terrapin populations include habitat degradation (Gibbons *et al.* 2001), mortality in crab traps (Dorcas, Willson & Gibbons 2007; Grosse *et al.* 2011), excessive predation by subsidized predators and road mortality (Wood & Herlands 1997; Szerlag-Egger & McRobert 2007). Like many turtles, terrapins have habits that make them particularly vulnerable to road mortality (Gibbs & Shriver 2002; Aresco 2005; reviewed by Fahrig & Rytwinski 2009). Females nest on land and show an attraction to open, elevated areas often near roads, resulting in vehicle strikes and subsequent mortalities (Szerlag-Egger & McRobert 2007). As a long-lived species, terrapin population stability is strongly dependent on high annual adult survivorship, and road mortality along coastal causeways can be sufficiently high to cause population declines (Wood & Herlands 1997; Grosse *et al.* 2011; Crawford *et al.* 2014). Owing to its association with nesting, road mortality is disproportionately female-biased and concentrated within the nesting season (late April to July: Grosse *et al.* 2011; Crawford *et al.* 2014). Although nocturnal nesting has been documented at some sites (Wood & Herlands 1997), females generally nest diurnally during weather with minimal cloud cover and high daily temperatures (Seigel 1980; Feinberg & Burke 2003), proximate to diurnal high tides (Burger & Montevecchi 1975) and during higher tide amplitudes (Burger & Montevecchi 1975; Feinberg & Burke 2003). Burger and Montevecchi (1975) also noted that there was no strong seasonal peak in nesting activity for their study area, but the number of nesting terrapins observed daily was higher towards the beginning of the season. Terrapins show a degree of nest site fidelity (Szerlag-Egger & McRobert 2007) and nest more frequently in areas of maximum solar radiation and minimal ground vegetation (Roosenburg 1996). These nesting habits of terrapins may yield finer-scale hot spots and hot moments of road mortality for targeted management.

The Downing-Musgrove Causeway to Jekyll Island, Georgia, USA, is currently an area of high terrapin road mortality. Each year since 2007, researchers have documented 100–400 adult females killed on the road during nesting forays (B. Crawford; GSTC, unpublished data), and the annual road mortality rate is estimated to cause moderate-to-high population declines (Crawford *et al.* 2014). Crawford *et al.* (2014), following Beaudry, Demaynadier & Hunter (2010), recommended that identifying hot spots or hot moments of terrapin road mortality at this site could lead to targeted management actions to reduce terrapin mortality. The objectives of this study were to (i) identify whether terrapin activity on the causeway was spatially (hot spots) or temporally (hot moments) predictable and (ii) identify whether particular

habitat features were associated with hot spots. We predicted that terrapin appearances on roads would peak earliest in the nesting season and proximate to the diurnal high tide and hot spots would be located where the roadside lacked vegetation cover, that is, more open areas, and was most proximate to creeks.

Materials and methods

STUDY AREA AND SPECIES

We conducted this study in conjunction with long-term monitoring efforts of the Georgia Sea Turtle Center (GSTC), initiated in 2007, and focused on the 8.7-km Downing-Musgrove Causeway/Jekyll Island Causeway (JIC) from Rt. 17 to Jekyll Island, GA, USA (31.08°N, 81.47°W). The JIC was a state highway with average annual daily traffic (AADT) of 3460 vehicles day⁻¹ (Georgia Department of Transportation 2011) and a speed limit of 89 km h⁻¹ (55 miles h⁻¹) along the majority of the road. Although monthly averages were not available for the JIC, data from adjacent coastal highways showed that monthly traffic volumes peaked from May to July, corresponding with increased summer tourism (Georgia Department of Transportation 2011). The JIC bisected saltmarsh consisting of a network of intertidal creeks and high marsh dominated by *Spartina* sp. experiencing semi-diurnal tides 2–3 m in amplitude (Grosse *et al.* 2011). Several creeks were in proximity to or crossed under the causeway, and the edge of the road was regularly within 20 m of the high tide mark of the high marsh. Much of the area along roadsides was covered by densely vegetated hedgerows of cedars *Juniperus virginiana* and wax myrtles *Myrica cerifera* maintained as a wind break. The high marsh located within 150 m of the road contained large patches of unvegetated, sandy habitat.

FIELD METHODS

Starting in 2009, we conducted intensive road surveys to observe where and when terrapins emerged on the causeway between 1 May and 20 July. We included observations of dead and live terrapins that we saw on or about to cross the road in spatial and temporal analyses. One or two observers completed each survey by driving the length of the causeway and back and recorded the number of terrapins observed and minutes to the nearest scheduled high tide. We surveyed the JIC every 20–90 min generally between 08.00 and 20.00, with opportunistic surveys outside of this period. When a dead or injured terrapin was found after a survey gap of >30 min, we did not include that animal in temporal analyses. We marked each turtle's location with a hand-held global positioning system (GPS: Garmin International, Olathe, KS, USA). We sexed individuals, palpated females for eggs and uniquely marked live individuals by drilling marginal scutes. We returned turtles to nearby artificial nest mounds within 1 h of capture (*sensu* Buhlmann & Osborn 2011). We transported all injured or dead terrapins to the GSTC for treatment or euthanasia and to recover eggs for a head-start programme.

ANALYSIS OF HOT SPOTS

We used a moving window analysis in a geographic information system (ARCGIS 9.3; ESRI, Redlands, CA) to determine whether

there were aggregations (hot spots) of terrapin activity pooled from 2009 and 2010 on the JIC and identify habitat features that best predicted their locations. Beginning at one end of a route layer created for the causeway, and moving along the road in 1-m increments, the window counted terrapins and generated summary statistics for three habitat features within a specified window size. First, distances between the window's centre and the nearest creek on each side of the road was recorded (Fig. 1a). 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/>]). Percentage of hedge cover was calculated as a fraction of the total length of the window along the road's edge (Fig. 1b). The hedge layer was derived from field GPS locations marking each transition in hedge type. We ranked the fraction of hedge vegetation into three categories: full (dominated by wax myrtle), intermediate (sparse wax myrtle or short shrubs) and no hedge. Lastly, the moving window calculated the percentage of unvegetated area (sand and mud flat) in the high marsh within 150 m of the JIC. We isolated unvegetated area with an unsupervised classification of a 1-m resolution orthophotomosaic 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 colour bands available (R, G, B) with 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 field-collected data, this classification method was at least as accurate as a heads-up digitizing process and captured the feature of interest at a sufficient spatial scale.

Next, we overlaid terrapin GPS locations on the route and counted those within the window (Fig. 1c). Finally, an output layer containing every point analysed 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 (Fig. 1d).

We selected appropriate window sizes based on empirical data of terrapin movements. Since terrapins show some degree of both creek and nest site fidelity (Gibbons *et al.* 2001; Szerlag-Egger & McRobert 2007), it is plausible that females approach consistent nesting sites on roadsides from consistent locations in the saltmarsh. 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 generated by 100-m windows to map hot spots of terrapin crossing activity along the causeway. Based on breaks in a frequency histogram of these counts, we set two cut-off values to interpret aggregations: (i) a strict cut-off (higher terrapin counts observed at fewer areas of the road) was chosen to represent hot spots of crossing activity and (ii) a less

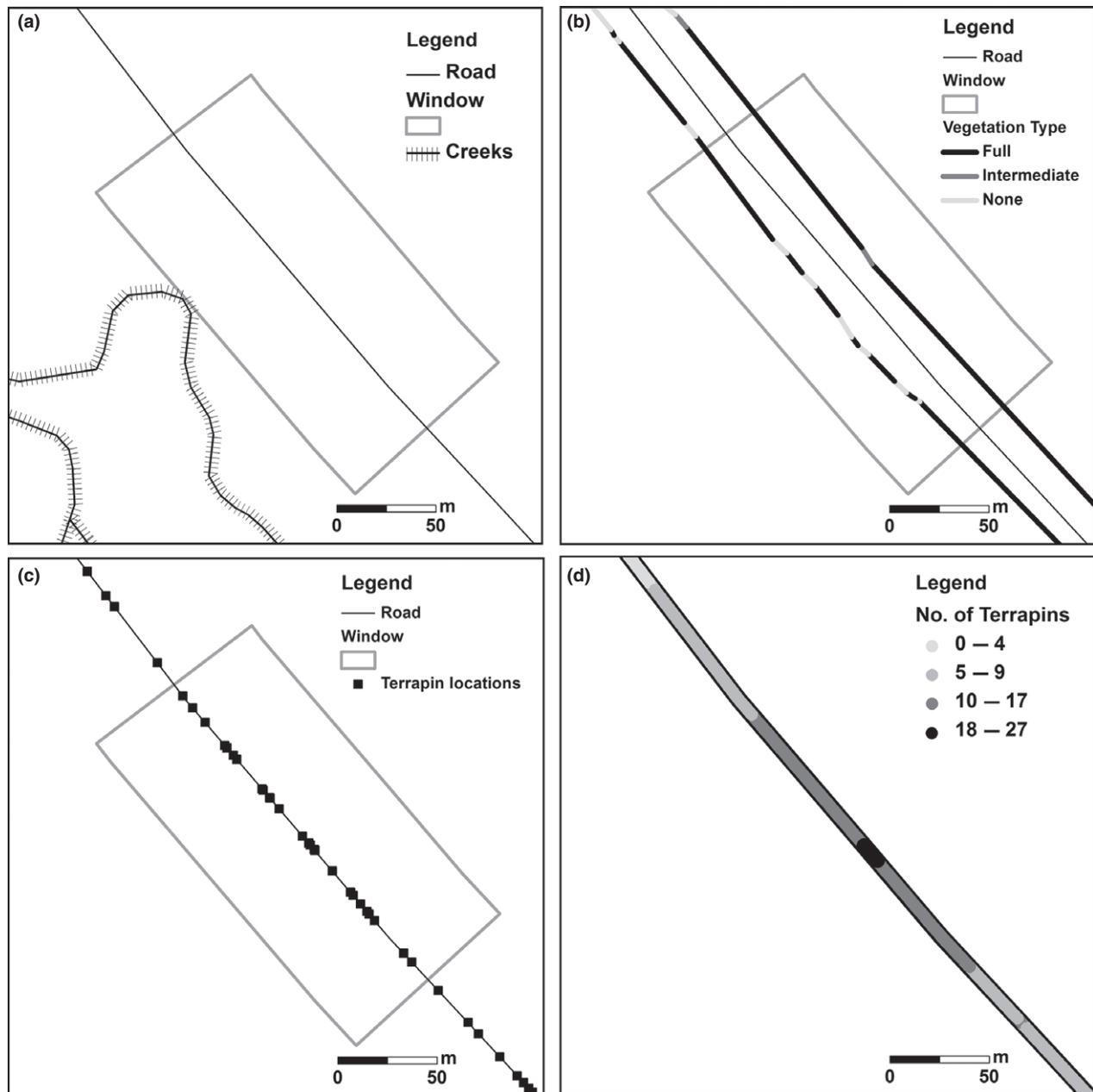


Fig. 1. Moving window analysis steps using ARCGIS 9: (a) calculate nearest distance from centre of window to creek, (b) calculate percentage of each vegetation type on both roadsides within window, (c) count terrapins observed within window and (d) generate distribution of terrapin crossings along causeway.

stringent cut-off (including lower terrapin counts observed at more areas of the road) represented minor spatial peaks, or ‘warm spots’, of terrapin crossing activity. We mapped hot and warm spots on the causeway based on these cut-offs and compared localized activity levels with the average amount of crossing activity seen along the entire causeway. Because we identified hot spots pooled from the 2009 and 2010 nesting seasons, we used a chi-squared contingency test to assess pattern consistency by comparing the number of terrapins observed for every 500-m section of the causeway between years. We used this greater length, so the expected number of terrapins in each section was >5.0 , conforming to test assumptions.

We used linear regression to evaluate three habitat features – distance to nearest creek, percentage of hedge vegetation on road-

sides and percentage of unvegetated area in the adjacent high marsh – as predictors of the number of terrapins crossing a section of causeway obtained at 1-m increments using 100-m windows. We evaluated relative fit of candidate models based on Akaike Information Criterion adjusted for small sample size (AIC_c ; Burnham & Anderson 2002). We calculated model-averaged coefficients and 95% confidence intervals for the confidence set ($\Delta AIC_c \leq 2$), where model-specific estimates are rescaled by each model’s Akaike weight (as described by Burnham & Anderson 2002). To allow for ease of interpretation, we scaled coefficients and confidence intervals, based on a t -statistic with $n-1$ degrees of freedom. The scalars corresponded to what we believed to be biologically relevant unit changes in the predictors (e.g. a 25% increase in roadside hedge cover). Lastly, we

evaluated the relative importance for each habitat variable by calculating the ΔAIC_c that resulted 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, Diniz-Filho & Bini 2006). For each set, we created candidate models with all possible combinations of the three habitat variables (resulting in seven models per set) where spatial variables were forced into every model to eliminate spatial autocorrelation in residuals (see Diniz-Filho, Rangel & Bini 2008). In the first set, we included a single spatial variable accounting for fine-scale autocorrelation in all 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, Diniz-Filho & Bini 2006). For the second set, we included the fine-scale autoregressive variable and a spatial variable accounting for broadscale trends in all models. We used the trend surface analysis in SAM to filter for broadscale spatial patterns in terrapin occurrence along the causeway to account for variation that is unexplained by measured explanatory variables (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 broadscale pattern likely existed in our data, including both spatial variables in a model set could cause multicollinearity and produce overfit models. Hence, we performed both sets of model selection in SAM and report results from each procedure.

ANALYSIS OF HOT MOMENTS

Based on prior associations between terrapin nesting activity and tide level (Burger & Montevecchi 1975; Feinberg & Burke 2003) as well as early observations in our study, we analysed seasonal trends and daily temporal patterns of activity on the JIC relative to the diurnal high tide. We grouped terrapin encounters during surveys into 30-min intervals relative to the scheduled high tide time. 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 fits 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 version 8.0; StatSoft, Tulsa, OK). Distance-weighted least-squares models provide regression estimates at a given value of X by attributing greater weight to closer data points within a defined neighbourhood and 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 min before and 60–90 min after) and then compared the distribution of activity relative to high tide between years using a chi-squared contingency test.

Results

During the 2009 and 2010 nesting seasons, we observed 234 and 402 terrapins, respectively, of which 137 (59%) and 210 (52%) were struck by vehicles again, respectively. We recaptured 40 females marked in 2009 in 2010, allowing us to estimate interannual capture distances. In 2010, 20 terrapins (50%) were captured on the road within 50 m of their 2009 capture location, and 32 (80%) were captured within 200 m of their original capture.

ANALYSIS OF HOT SPOTS

Terrapin activity was concentrated in three distinct hot spots and seven 'warm' spots. Hot spots were defined as areas on the causeway where 21–40 terrapins were observed per 100 m. The three hot spots only comprised a total of 803 m (10%) of the total causeway, yet 30% of all terrapins observed crossed the road within these segments. We estimated that 10–13 terrapins crossed per 100-m section of hot spot per nesting season, which was 5–6 times greater than the background rate of crossing (2 terrapins 100 m^{-1} per season) along the remainder of causeway. Additionally, there were seven areas totalling 1056 m (12%) of the causeway where 23% of all terrapins were observed crossing the road (rate = 6–7 terrapins 100 m^{-1} per season¹). Collectively, 53% of all terrapin crossings were localized to 22% of the causeway.

Hot spots of terrapin road crossings were spatially consistent between years and showed predictable but weak relationships with measured habitat features. The locations of terrapin hot spots did not differ between 2009 and 2010 ($\chi^2 = 9.57$, d.f. = 16, $P > 0.5$). The locations of hot spots were similar regardless of whether we conducted our analysis at 50-, 100- or 200-m window sizes, though the distance around these centres increased with window size. We used results from the 100-m window size to analyse and delimit the cores of hot spots to smaller, more manageable lengths of road while accounting for interannual variation in terrapin movements to nest sites. Distance between the road and the nearest creek ranged from 0 [bridge overpass] to 361 m (mean = 174 m). Mean roadside shrub coverage per 100 m of road ranged from 0 to 100% (mean = 77%), and mean vegetation coverage of the high marsh per 100 m of road ranged from 48% to 99% (mean = 80%). The saturated model with all habitat variables ranked among the best models in both model sets (Table 1). The percentage of unvegetated high marsh (areas of exposed mud flat) along a 100-m section of road was negatively associated with the number of terrapins observed on the road (Table 2), with a Drop-1 Importance value 5.5 and 2.5 times greater than the next most influential habitat feature in the first and second model sets, respectively. Scaled model-averaged estimates of all three habitat features changed in magnitude between the two model sets, and estimates for distance to creek and percentage 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. Based on 95% confidence intervals of the first model set, we estimated that a 25% increase in the percentage vegetation cover in the high marsh was associated with an increase of 2–3 terrapin crossings per 100-m section or road. Comparatively, a 25% decrease in roadside hedge cover or a 100-m increase in the distance between the road and a tidal creek was associated with increases of less than 1 terrapin per 100 m of road (Table 2).

ANALYSIS OF HOT MOMENTS

We observed one or more terrapins during 347 surveys (32%) between 06 May to 12 July and between 07.30 and 21.30 in both years. Terrapins were observed on the road throughout the nesting season; however, within the nesting season, the probability of terrapin occurrence on the road peaked 10–20 days into the nesting season and declined steadily over the remaining 60 days (Fig. 2). This probability also peaked around the scheduled diurnal high tide and declined with increases in time before or following the scheduled diurnal high tide (Fig. 2). Together, these seasonal and daily patterns produced a distinct hot moment of terrapin road activity. Between the first 10–20 days of the nesting season, there was a 70–80% chance of a terrapin occurring on the road within the 3 h of the scheduled diurnal high tide. Over the entire nesting season, 52% of all terrapins on the road were observed within a 3-h period spanning 30 min before to 150 min after the scheduled diurnal high tide, and 69% were observed within a 5-h period (90 min before to 210 min after high tide; Fig. 3). The distribution of terrapin

activity relative to the high tide did not differ between 2009 and 2010 ($\chi^2 = 18.74$, d.f. = 12, $P > 0.5$).

Discussion

Previous studies have demonstrated condensed patterns of road mortality at relatively broad spatial and temporal scales and have advocated that such broad hot spots or hot moments could improve management for road mortality (Grilo, Bissonette & Santos-Reis 2009; Beaudry, Demaynadier & Hunter 2010; Cureton & Deaton 2012). Our results demonstrate that even finer-scale hot spots and hot moments can be identified and related, strongly or weakly, to specific habitat features or temporal processes. At a minimum, identifying the scale at which road mortality threats are condensed will inform the types and scales of management actions needed to achieve meaningful mitigation.

Realistically, most threats occur in a combination of concentrated and diffused patterns across a given area (e.g. Beaudry, Demaynadier & Hunter 2008; Cureton & Deaton 2012). We found that 30% of terrapin road crossings occurred within three sections that comprised only 10% of the entire road; however, 22% of terrapin crossing were distributed among 'warm' spots and 48% were distributed among the remaining 78% of the causeway. During the time of this study, we estimated that road mortality reduced survival of adult female terrapins along the JIC between 4% and 16% annually, that this rate is almost certainly causing the population to decline and that road mortality would need to be reduced below 3% to stabilize the population (Crawford *et al.* 2014). Actions such as the installation of fencing at hot spots could maximally reduce annual road mortality by 30%, which is

Table 1. Linear regression models predicting abundance of terrapins in 100-m windows along the Jekyll Island Causeway in Georgia, USA

Model	Log-likelihood	<i>K</i>	AIC_c	ΔAIC_c	W_i
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	<0.001
Marsh	−2053.869	3	4095.738	23.912	<0.001
Hedge	−2089.253	3	4166.506	94.679	<0.001
Creek + Hedge	−2091.466	4	4166.932	95.106	<0.001
Creek	−2098.646	3	4185.291	113.465	<0.001
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	<0.001

Creek, distance to creek; Marsh, percentage unvegetated high marsh in window; Hedge, percentage vegetation of hedges on road shoulders in window; *K*, no. of parameters; AIC_c , Akaike Information Criterion; ΔAIC_c , difference in AIC_c from the best model; w_i , Akaike wt.

Table 2. 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 for the Jekyll Island Causeway in Georgia, USA

Variable	Coefficient	Std error	Unit change	Scaled coefficient.	Scaled 95 lower	Scaled 95 upper	Drop-1 importance*
Composite of models with pure autoregressive spatial variable							
Constant	1.356	0.376					
Creek	0.006	0.001	100 m	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	100 m	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

*Values taken from ΔAIC_c that occurs when dropping the specific variable from the saturated model.

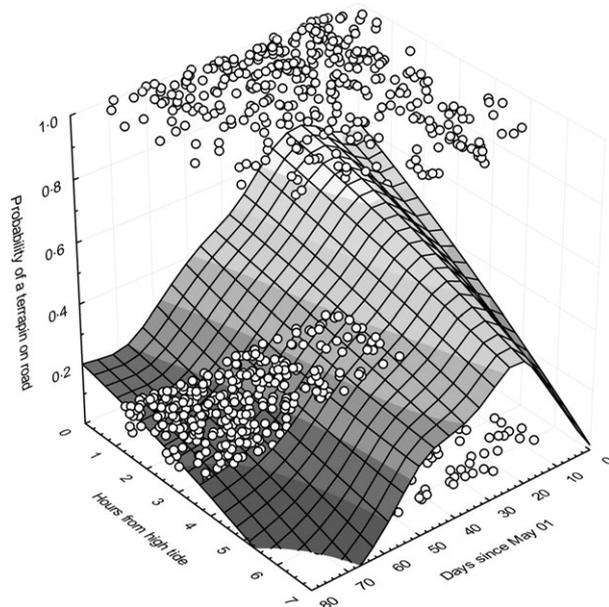


Fig. 2. Probability of observing a terrapin on the Jekyll Island Causeway during a survey relative to hours to the scheduled high tide (0 = high tide, 7 = low tide) and day of the nesting season (0 = 1 May, 80 = 20 July). Shadings indicate 10% probability intervals.

likely to be inadequate to prevent population declines except in years when road mortality outside hot spots is at its lowest. Therefore, complementary management tools to address the more diffused component of road mortality will be required, although highly effective reductions in mortality within hot spots would reduce the need to fully mitigate more diffused mortality.

We propose that management strategies that take advantage of hot moments of terrapin road crossings offer a means to complement management of hot spots. We found that terrapin activity peaked in the early portion of the nesting season and was strongly related to the diurnal high tide. Similar temporal patterns of nesting have been reported in other parts of the species range (Burger &

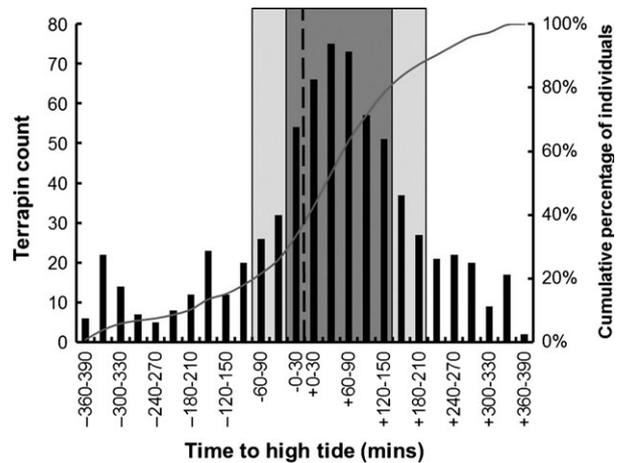


Fig. 3. Terrapin activity relative to high tide (dotted line). Dark grey zone contains 52.4% of all terrapins seen nesting near the causeway in a 3-h window. Dark and light grey zones contain 69.4% of all observations in a 5-h window.

Montevecchi 1975; Feinberg & Burke 2003), and other turtle species and wildlife are likely to show temporal predictability related to season, time of day or weather (Ashley & Robinson 1996; Clevenger, Chruszcz & Gunson 2003; Aresco 2005; Cureton & Deaton 2012). Nesting during high tide may be adaptive if it reduces the distance that terrapins must travel between the water and nesting habitat, which should decrease the risk of thermal stress or predation. Though our hot moment appears shifted towards the falling tide, we note that we used scheduled high tides for the Jekyll Island Marina, but the tide level in creeks adjacent to the causeway peaked and remained high for up to 90 min after the scheduled high tide. Local tidal schedules are known months in advance and therefore can be used to target peak periods of road mortality risk.

In order to use hot spots as a management focus, they must be spatially predictable or, once identified, temporally stable. We did not identify landscape characteristics that could be used to predict hot spots with a high level of confidence. The amount of unvegetated high marsh was a

modest, negative predictor of where terrapins occurred on the road. Terrapins feed in vegetated areas of high marsh while these areas are inundated at high tide, so terrapins may naturally be aggregated in areas with a higher percentage of vegetation cover in the high marsh. In addition, moving across exposed marsh habitat may increase thermal stress and predation risk. Surprisingly, distance to nearest creek was a weak predictor of where terrapins occurred on the road. Terrapins have been observed to travel over 1 km from tidal creeks to nest sites (Gibbons *et al.* 2001; Szerlag-Egger & McRobert 2007). All portions of our study causeway were within 370 m of a creek, and high tides inundated marsh even closer to the road. Though other studies have demonstrated that females will preferentially nest in open areas (Burger & Montevecchi 1975; Roosenburg 1996; Szerlag-Egger & McRobert 2007), we found that percentage of shrub cover also had a small and imprecise relationship to terrapin occurrence on roads. We routinely observed terrapins moving through, resting and nesting under hedges. Additional research into characteristics of a causeway itself or terrapin behaviour may improve our ability to predict likely hot spots.

Though we only have data for two consecutive years, our results indicate that hot spots are temporally stable. The stability of terrapin hot spots appears related to their high nest site fidelity. We recaptured a large portion (50%) of nesting females within 50 m of their capture location from the previous year. Szerlag-Egger and McRobert (2007) also report nest site fidelity in terrapins along coastal roadsides over 2 years, and Gibbons *et al.* (2001) reported high site fidelity by terrapins within tidal creeks over a 16-year period in South Carolina. Therefore, we believe that hot spots are likely to be stable for moderate time periods.

CONCLUSIONS AND RECOMMENDATIONS

Without effective mitigation, road mortality will contribute to wildlife population declines and extirpations at local and regional scales (Gibbs & Shriver 2002; Litvaitis & Tash 2008; Fahrig & Rytwinski 2009; Langen, Ogden & Schwarting 2009; Beaudry, Demaynadier & Hunter 2010). While prior studies identified more general hot spots and hot moments of mortality over coarser spatial and temporal scales, our approach identified fine-scale hot spots and hot moments of mortality. We also demonstrate that while some component of road mortality is condensed in time or space, a modest component is likely to remain diffuse. As a result, complementary actions that exploit hot spots of road mortality married with actions to address hot moments of mortality over wider spatial scales will be required. Our results would suggest that, when hot spots appear temporally stable, targeted low-cost measures such as fencing or reduced speed zones may be effective at eliminating mortality (Forman *et al.* 2003; Aresco 2005; Litvaitis & Tash 2008). Further, when paired with information on peak periods of road activity,

actions to significantly mitigate road mortality may be more feasible. For example, wildlife signage may potentially reduce both concentrated and diffused road mortality; however, efforts using signage have not proven effective (e.g. Putman 1997). Signage may be ineffective because signs are present outside periods of road mortality, causing drivers to habituate to the signage, and because signs do not alert drivers when the probability of encountering wildlife on the road is high. Hot spots and hot moments of wildlife occurrences on roads are analogous to school crossings for children. School zones use flashing signs timed to the periods when children are likely to be crossing roads to alert motorists. In the case of terrapins, we propose that signage equipped with flashing lights programmed to seasonal and daily [diurnal high tide] peaks in terrapin activity could reduce road mortality within hot spots and over the more diffused portions of the JIC. Complementary management actions, particularly reduced speed zones, the installation of barriers and the use of flashing traffic signage, will require considerable collaboration with government agencies, but we believe such actions can create solutions that will have a meaningful effect on reducing road mortality.

Acknowledgements

Funding for this research was provided by a State Wildlife Grant to J.C.M. from the Georgia Department of Natural Resources, Coastal Resources Division, by the Daniel B. Warnell School of Forestry and Natural Resources, University of Georgia and Jekyll Island Foundation through an assistantship to B.A.C. We thank GSTC staff and volunteers for their assistance throughout the project – especially M. Kaylor, A. Grosse, S. Diltz, L. Rodriguez and D. Quinn. We thank associates at the Savannah River Ecology Laboratory and the Jekyll Island Authority for their continued collaborations. 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 24 November 2012).

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Received 7 July 2013; accepted 19 November 2013

Handling Editor: Christopher Dickman