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UNDERSTANDING THE INFLUENCE OF TIDE, TIME, AND WEATHER ON HOT SPOTS OF DIAMONDBACK TERRAPIN ROAD CROSSINGS AND THE MORTALITY OF TURTLES

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Abstract.—**Vehicle induced road mortality poses a serious threat to Diamondback Terrapin (*Malaclemys terrapin*) populations in coastal areas throughout their range, with disproportionate impacts on adult females. A greater understanding of the influence temporal and spatial factors have on road crossings and mortality is needed to improve management of this pervasive and persistent threat. From 2017–2020, we surveyed a 4.9 km road bisecting a saltmarsh in southern New Jersey, USA, for Diamondback Terrapin activity during daily surveys throughout the nesting season (May-July). For each Diamondback Terrapin encountered, we recorded vitality (live, dead, injured), GPS location, time, weather, tide gage height, and tidal stage. Crossing hot spots occurred mainly on the eastern end of the road closer to high density nesting locations, despite the presence of mitigation fencing. Gaps in mitigation fencing for driveways and roads likely compromised fence effectiveness. Crossings were influenced by tidal stage, with greater likelihood of encounters during high and falling tides. Cloud cover and time of day interacted to affect crossings. Under partly cloudy conditions, Diamondback Terrapin road crossings increased by 50.7% in mid-afternoon and decreased by 28.8% in late morning, suggesting a possible shift to later nesting. Together, these results will guide installation strategies and material choices for fencing and strategic placement of signage and timing of surveys for continued conservation efforts to mitigate areas of high mortality risk for Diamondback Terrapins.**

Key Words.—conservation; *Malaclemys terrapin;* nesting; turtles; road mortality

INTRODUCTION

Roads have long been recognized as a problem for wildlife, acting as barriers to movement, isolating populations physically and genetically, and creating a source of mortality from vehicle collisions that can impact local populations (Wilkins 1982; Rosen and Lowe 1994; Fahrig et al.1995; Shine et al. 2004). The impacts of road mortality can vary based on sex or age class, resulting in changes in the demographics and dynamics of affected wildlife populations (Steen and Gibbs 2004). Additionally, impacts of roads can be localized both spatially and temporally, resulting in so called hot spots and hot moments, places and periods of disproportionately high mortality (Crawford et al. 2014b). At the population level, species most at risk to adverse effects of roads are characterized by low reproductive rates, an attraction to roads for ecological or physiological reasons, and slow mobility (Fahrig and Rhytwinski 2009). Turtles fit these criteria and are known to be prone to population declines due to small decreases in adult survival (Congdon et al. 1993; Heppell 1998; Ennesson and Litzgus 2008). The sensitivity of turtle populations to perturbation in adult survival makes them susceptible to adverse impacts from roadways, and declines in turtle populations as a result of road impacts have been documented in several species (Haxton 2000; Gibbs and Shriver 2002; Steen and Gibbs 2004; Szerlag and McRobert 2006).

Diamondback Terrapins (*Malaclemys terrapin*; Fig. 1) reside exclusively in coastal, brackish water wetlands of the eastern U.S., from the Gulf Coast of Texas north to Cape Cod, Massachusetts (Lovich et al. 2018). While males remain largely in aquatic habitat, females leave the water multiple times in the nesting season to lay clutches of eggs in coastal uplands (Lovich et al. 2018). Historically, Diamondback Terrapin populations have been impacted by a wide range of conservation issues. Once harvested to

Figure 1. An adult female Diamondback Terrapin (*Malaclemys terrapin*) from New Jersey, USA. (Photographed by Amanda Lyons).

near extinction for human consumption (Hildebrand 1929), the species currently faces declines throughout much of its range (Seigel and Gibbons 1995; Gibbons et al. 2001) and is classified as Vulnerable by the International Union for Conservation of Nature (Roosenburg et al. 2019). Current threats to Diamondback Terrapin populations include habitat loss, illegal trade, bycatch in commercial crab traps, and road mortality (Wood and Herlands 1997; Grosse et al. 2011; Crawford et al. 2014a; Egger et al. 2016).

Though road mortality is a localized conservation concern throughout the range of the Diamondback Terrapin, it is a pervasive and persistent threat in coastal regions of southern New Jersey (Fig. 2), where development of barrier islands resulted in the construction of low-lying roads that bisect salt marshes (Wood and Herlands 1997). These coastal roads, paired with development of historic terrapin nesting sites and shoreline hardening, have dramatically altered nesting habitat availability and use. For nesting habitat, Diamondback Terrapins require elevated areas above tidal flooding range and prefer sparsely vegetated areas that receive a high degree of solar radiation, traits common in habitats along coastal roadways (Roosenburg 1996). As development reduced the availability of and access to historically used nesting habitat on barrier islands, Diamondback Terrapins adopted the shoulders of coastal roads for nesting (Wood and Herlands 1997; Szerlag and McRobert 2006). These roadsides have become important but risky areas for female Diamondback Terrapins during nesting, and the loss of adult females to vehicles can pose a serious threat to Diamondback Terrapin populations in the region.

Due to their life-history characteristics as a long-lived species with high juvenile mortality, high adult survival is paramount to the stability of Diamondback Terrapin populations, and small decreases can contribute to population declines (Grosse et al. 2011; Crawford et al. 2014a). In particular, female Diamondback Terrapins take longer to reach maturity than males, about 8–13 y compared to 4–7 y, respectively, and their terrestrial nest seeking behavior puts them at greater risk of road mortality than males (Roosenburg 1991; Lovich et al. 2018). Studies of nesting behavior suggest that Diamondback Terrapins exhibit site fidelity and typically lay one to three clutches each nesting season (Feinberg and Burke 2003; Szerlag and McRobert 2007; Butler et al. 2018). As a result, Diamondback Terrapins that must cross a road to reach nesting habitat will not only have to cross again to return to the marsh after nesting but may venture onto the road multiple times per season to nest, compounding the risk of mortality.

Multiple strategies have been implemented to mitigate road mortality in Diamondback Terrapin populations throughout their range (Wood and Herlands 1997; Crawford et al. 2014b; Quinn et al. 2015; Reses et al. 2015). In southern New Jersey, The Wetlands Institute initiated a comprehensive conservation program in 1989 to monitor and mitigate the effects of roads on local Diamondback Terrapin populations (Wood and Herlands 1997). Since its inception, group personnel have conducted daily surveys of Diamondback Terrapin road crossings during the nesting season along approximately 61.2 km of roads spanning Atlantic barrier islands and marshes in Cape May County, New Jersey, USA. In addition to road surveys, personnel have employed several additional conservation strategies including mitigation fencing, conspicuous warning signs, and habitat enhancement, allowing for study of crossing activity and risk related to spatial, temporal, and road condition factors.

Another strategy for mitigating road mortality is the identification of likely periods of increased nesting activity when road mortality risk might be heightened. Diamondback Terrapins typically nest diurnally, though nocturnal nesting has been documented at some sites, including in southern New Jersey (Auger and Giovannone 1979; Roosenburg 1992; Wood and Herlands 1997). Peak nesting activity in this region correlates with tide height and is typically highest during diurnal high and recently falling tides, and at higher tidal amplitudes (Burger and Montevecchi 1975; Feinberg and Burke 2003).

We are less certain how known predictors of Diamondback Terrapin nesting activity correspond to spatial and temporal factors influencing when terrapins are most at risk on roads. A better understanding of

Figure 2. An adult female Diamondback Terrapin (*Malaclemys terrapin*) found along the road transect in New Jersey, USA. (Photographed by Addie Schlussel).

this nexus is critical to guide road mitigation efforts and the allocation of limited resources toward Diamondback Terrapin conservation. To this end, we initiated focused surveys on a section of our historically sampled transect known to have high rates of Diamondback Terrapin crossing activity and road casualties. Our goal was to identify the role of spatial and temporal factors on road crossing activity and casualties to inform continued conservation action for the Diamondback Terrapin.

Materials and Methods

Study area.—Our study focused on a 4.9 km length (Fig. 3) of our larger patrol route that bisects the Smooth Cordgrass (*Sporobolus alterniflorus*) dominated salt marshes between the Cape May peninsula mainland and a barrier island along the Atlantic coast of Cape May. The two-lane road is a main thoroughfare to local resort communities, and experiences seasonally heavy traffic, particularly during the months of June, July, and August that coincide with the local Diamondback Terrapin nesting season. The roadside is moderately developed, with over 100 houses and businesses along its length. Bulkheads, a form of shoreline hardening intended to reduce erosion, surround most developed properties along the road. These structures create a vertical barrier between the marsh and the developed property and depending on their height and condition can greatly impede or entirely restrict terrapin access to upland habitats at these locations (Wood and Herlands 1997). Undeveloped sections of the road are lined by narrow bands of grassy upland habitat, dominated by Groundsel Tree (*Baccharus halmifolia*), Marsh Elder (*Iva fructescens*), Eastern Red Cedar (*Juniperus virginiana*), Common Reed (*Phragmites australis*), and various grass species. The upland habitat slopes gradually to the adjacent saltmarsh across a height differential of approximately 1.5 m, allowing mature female Diamondback Terrapins easy passage from the marsh to the roadside during the nesting season (Wood and Herlands 1997). The pavement is 6.9 ± (standard deviation) 4.4 m from the edge of the saltmarsh, and the speed limit ranged from 35–50 mph during our study period. Four sections of undeveloped roadside, totaling approximately 1.4 km, are protected by 20.3 cm corrugated plastic tubing barriers installed and maintained since 2010 as a mitigation fence to prevent Diamondback Terrapins from entering the road and reduce road mortality (Fig. 4), while providing nesting habitat in the grassy upland area behind the barrier (Reses et al. 2015). The fencing is only placed along sections of the road where Diamondback Terrapin access can be restricted on both sides, either by fence installation or existing bulkheads. Otherwise, a Diamondback Terrapin crossing from an unprotected side could become trapped on the road and face greater risk of a vehicle strike.

Road surveys.—We conducted surveys of the 4.9 km transect during the Diamondback Terrapin nesting season, May-July, from 2017 to 2020. We initiated surveys for nest seeking terrapins by May 26 each year in advance of the first sighting of nesting

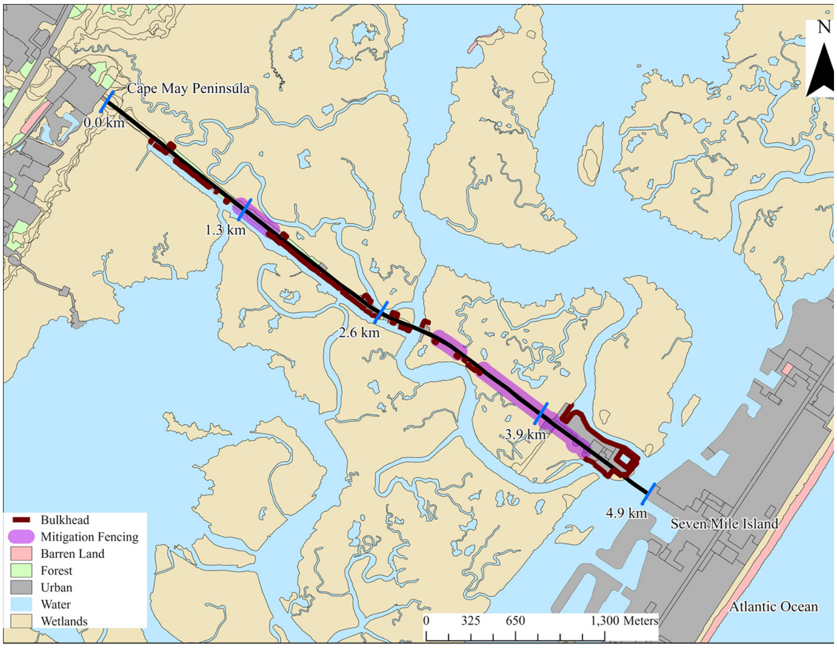

Figure 3. Land use cover map of the study area surveyed daily May-July 2017–2020 for Diamondback Terrapin (*Malaclemys terrapin*) activity. The 4.9-km road (bold black line) bisects salt marsh habitat and connects the more heavily developed mainland of Cape May Peninsula and Seven Mile Island in Cape May County, New Jersey, USA. Blue markers show distance along the road when viewed alongside Figure 5. (Data source: New Jersey Geographic Information Network, https://njogis-newjersey.opendata.arcgis.com/).

activity and ended daily surveys after nesting had concluded for the season. We defined the end of the nesting season as a period of three consecutive days with no observations of Diamondback Terrapins on the transect. We conducted road surveys five times per day between 0800–1800 in 2017–2019. In 2020, we reduced the number of surveys to four times per day due to decreased personnel. Depending on schedule logistics, we completed surveys as a single pass of the transect (4.9 km) or, when driven back and forth, as two passes (9.8 km). We adjusted tallies of terrapins encountered by distance to account for survey effort.

During surveys, we drove slowly along the transect, stopping for all Diamondback Terrapins observed. When we found a live, dead, or injured Diamondback Terrapin on the road, we recorded time, date, location, and sex. We determined the sex of all individuals by examining body size and the position of the cloaca on the tail. For dead individuals, we classified carcass condition based on visible injuries, desiccation status, and the presence or absence of eggs. We later measured intact plastron length at the laboratory for a subset of dead individuals collected for further study. We immediately released all live Diamondback Terrapins on the roadside in the direction they were crossing. We did not measure live Diamondback Terrapins on the roadside before their release to reduce time spent away from patrol activities and limit risk to survey personnel. We grouped dead and injured Diamondback Terrapins for analysis of vehicle casualties and grouped casualties and live encounters for analysis of total documented crossings.

We recorded all data on a mobile phone or tablet using customized forms in Epicollect5 (https://five.epicollect.net). We recorded time of day and tide for each turtle encounter, and spatial coordinates of each encounter using the GPS function of the handheld device. We obtained weather data from local weather stations (KNJAVALO20, KNJAVALO2, KNJSTONE3, between 0.9–6.3 km from the transect) and categorized cloud cover at the time of survey as: clear (0–25% cloud cover), partly cloudy (25–75% cloud cover), and overcast or raining (75–100% cloud cover). We did not conduct surveys during periods of heavy rain. We obtained tide gage height values from a USGS water gage located at the eastern extent of the survey transect (USGS 01411360 Great Channel) to derive tidal stage.

Spatial analyses.—We analyzed road crossing and casualty data separately using Siriema 2.0 (https://github.com/nerf-ufrgs/siriema). Prior to analysis, we excluded all GPS locations with a location error > 30 m. In Siriema, we used Ripley's K-function,

Figure 4. Corrugated plastic tubing barriers installed along portions of the road transect in Cape May County, New Jersey, USA. (Photographed by Addie Schlussel).

modified to account for bi-dimensionality of the road, to test for significant spatial clustering or dispersion of crossing and casualty events along the road (Coelho et al. 2008). Ripley's K-function measures statistically significant spatial dispersion and clustering of events at multiple scales across a given line or area to determine the scales at which significant spatial aggregations occur (Coelho et al. 2012).

We also used Siriema to determine the number of events within a 30 m circle centered on each road crossing or casualty event and then multiplied this sum by a correction factor based on the road length within each circle. We selected a 30 m radius based on the length of the road, the accuracy of location data we collected, and to generate results at a scale that would be useful in assessing our current mitigation approaches and informing future mitigation efforts. Once we evaluated all observed events at this initial scale, we calculated aggregation intensity. We repeated this process at increasing scales until the radius of the circle was equivalent to the road length (https://www.ufrgs.br/siriema), resulting in calculation of aggregation intensity across multiple scales. We ran 1,000 simulations to reduce the risk of Type 1 error (Grabarnik et al. 2011) when determining the significance of spatial clustering of events (Lutterschmidt et al. 2019).

To determine the location of specific areas with significant clustering of road crossing and casualty events (hot spots), we used the 2D Hot Spot Identification analysis in Siriema 2.0 (Coelho et al. 2012). For this analysis we divided the road into 150 sections 32 m in length. In the analysis, a circle of 30 m radius passed over each crossing or casualty event, summing all events contained in the circle (https://www.ufrgs.br/siriema). We then multiplied this sum by a correction factor to account for the length of the road within the circle and repeated this for each event, giving an aggregation intensity value for each road segment (Coelho et al. 2012; https://www.ufrgs.br/siriema). We considered road segments with aggregation intensity values above the 90% upper confidence interval significant hot spots of crossing activity and casualties. Conversely, aggregation intensity values below the 90% lower confidence interval indicated significant cold spots of crossing activity and casualties.

To examine the influence of road attributes at hot and cold spots, we measured the linear distance from the central point of each road segment to the nearest creek edge (ArcGIS; Esri, Redlands, California, USA.). For each road segment, we also determined the presence or absence of mitigation fencing at adjacent roadsides, the presence or absence of bulkhead within that segment, and the presence or absence of urban habitat features, such as buildings, driveways, or road intersections, as an indicator of development. We used Logistic Regression to examine the relationship of these attributes and the locations of hot and cold spots of terrapin crossing events (JMP 15.2.1 2019, SAS Institute Inc., Cary, North Carolina, USA).

Temporal and environmental factor analyses.—The sample of Diamondback Terrapin encounters used for the temporal and environmental factor analyses was restricted to those occurring within our main survey window, 0800–1800. In most cases we were unable to determine the exact time of death for casualties encountered. We limited our sample for temporal analyses to terrapins recently killed by omitting from further analyses 235 dead terrapins that were desiccated, or classified as dry and flat, when encountered. We divided the survey window into five equal 2-h time classes designated mid-morning (0800–1000), late morning (1000–1200), early afternoon (1200–1400), mid-afternoon (1400–1600), and late afternoon (1600–1800) and tallied the number of encounters for each time class. For each 2-h period, we determined the time of nearest high and nearest low tide and then assigned each time class a tidal stage, using the dominant tidal stage over the 2-h period. We classified tide into six stages, each approximately 2 h: low (low tide ± 1 h), high (high tide ± 1 h), rising and falling low (low + about 2 h, low - about 2 h), rising and falling high (high + about 2 h, high - about 2 h).

We adjusted the total sample of live encounters and recent casualties by the number of survey passes during each time class. We analyzed temporal and environmental factors using Generalized Linear Mixed Models (GLMM) with a Poisson distribution and log link function. We used total precipitation accumulation for the prior date and the categorical variable cloud cover as two weather variables of interest. The full model included season day as a squared term due to an apparent non-linear relationship with crossing activity, time class, tidal stage, cloud cover, and precipitation, as well as a suite of two-way interactions of season day squared, time class, tidal stage, cloud cover, and precipitation as fixed effects, and year as a random effect. We used stepwise backward selection approach to remove non-significant interaction effects ($P < 0.10$). Data are presented as mean, standard error, with $P \leq 0.05$ unless otherwise stated.

RESULTS

Road surveys.—From 2017–2020, we encountered and recorded location data for 1,065 Diamondback Terrapins on the transect during 1,254 road surveys, including 315 live individuals and 750 casualties. The mean number of Diamondback Terrapins encountered across years was 266.2 ± 14.2 (Table 1). Of the Diamondback Terrapins encountered, 1,062 (99.7%) were adult females, one was a juvenile of indeterminate sex, and two were adults of unknown sex. Of the collected casualties that were intact for measurement, plastron length was 15.7 ± 0.28 cm (n = 9). In total, we determined that 199 Diamondback Terrapins recovered on roads as casualties were gravid at the time of vehicle collision, with 49.8 ± 2.8 gravid individuals found as casualties annually, though only a portion of carcasses were in a condition to be assessed. The nesting season began on 26 May 2018, 27 May 2017 and 2019, and 7 June 2020 and ended between 22–24 July in all years.

Spatial analyses.—We identified and removed as outliers points with GPS location errors > 30 m (n = 19) and erroneous points that fell outside the road edge on visual inspection (n = 4). Following removal of 23 outliers, we included 305 live encounters and 737 casualties for spatial analysis (n = 1,042). We found significant clustering of terrapin crossing and casualty events at most scales examined. Clustering was apparent for crossing events at scales up to 4.6 km and for casualty events at scales between 0.03 and 4.5 km.

Examining these aggregations further, we found that both significant hot and cold spots of crossing and casualty events existed along the road, with high intensity hot spots concentrated towards the eastern end of the road (Fig. 5, Appendix Figure). Hot spots of crossing activity occurred sporadically along the road starting 2.0 km east of the mainland, while hot spots of casualty events occurred farther east, starting at approx. 2.6 km. In both cases, the most intense hot

TABLE 1. Length of season (days) and the number of live Diamondback Terrapins (*Malaclemys terrapin*) and casualties encountered along a 4.9-km coastal road transect in Cape May County, New Jersey, USA from May through July 2017–2020. The abbreviation SE = standard error.

Year	Length of Season	Live	Casualties	Total Encounters	Gravid Casualties
2017	56	65	241	306	53
2018	59	81	182	263	54
2019	56	90	180	270	52
2020	46	79	147	226	40
Total	217	236	603	1065	199
Mean	54.2	78.8	187.5	266.2	49.8
SE	2.4	4.5	17.0	14.2	2.8

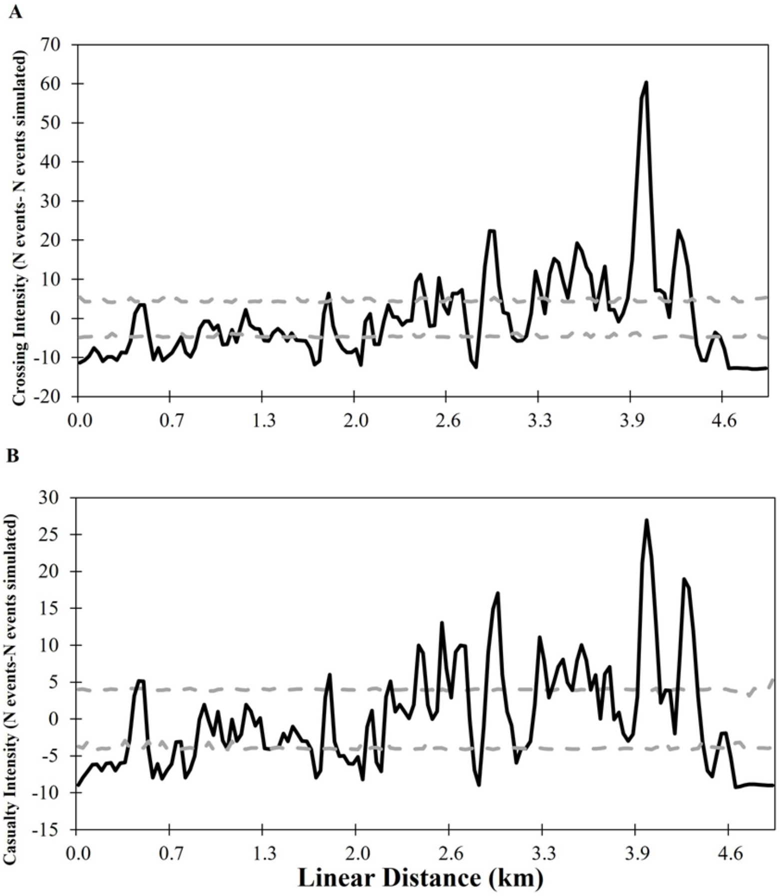

Figure 5. Aggregation intensity (black line) with upper and lower confidence intervals (gray lines) for Diamondback Terrapin (*Malaclemys terrapin*) road crossing events (A) and casualty events (B) encountered along a 4.9 km coastal road transect in Cape May County, New Jersey, USA, from May through July 2017–2020. Transect starts at mainland of Cape May Peninsula (0.0 km) and ends at Seven Mile Island (4.6 km) in Cape May County, New Jersey, USA. Areas where intensity is higher than the upper confidence interval are hot spots of crossing activity or casualties, and areas where the black line falls below the lower confidence interval indicate areas of significant dispersion, or cold spots.

spots occurred around 3.9 km east of the mainland (Fig. 5). Cold spots of both crossings and casualties occurred mainly toward the western end of the road, and the most intense cold spots occurred closest to the mainland from 0.0–2.8 km, with additional intense cold spots occurring from 4.6–4.9 km close to and on a bridge (Fig. 5, Appendix Figure).

While we identified some areas with mitigation fencing as cold spots of terrapin crossing activity and casualties, the easternmost areas of the road where fencing was installed still experienced high levels of crossing activity and casualties and were identified as hot spots (Fig. 5, Appendix Figure). Analysis of road attributes at hot and cold spots of terrapin crossing activity supported Siriema results ($X^2 = 44.0$, df = 4, $P < 0.001$). Compared to areas without fencing, the road segments with fencing had 70.0 times the odds of being a crossing hot spot ($X^2 = 15.4$, $P < 0.001$). Odds of a crossing hot spot were 35.0 times more likely in developed segments versus undeveloped segments ($X^2 = 9.4$, $P = 0.002$). There was a significant but weaker relationship with bulkhead presence ($X^2 = 3.7$, $P = 0.054$), with crossing hot spots 3.8 times more likely in areas without bulkheads compared to areas with them. Creek proximity did not affect the probability of hot or cold spots ($X^2 = 0.2$, $P = 0.630$).

Temporal and environmental factor analyses.—We used an adjusted total of 529 live encounters and recent casualties observed during 346 occasions (Table 1) to analyze effects of temporal and environmental factors on crossing activity (Appendix Table). Tidal stage ($F_{5,319.6} = 2.39$, $P = 0.038$) was the only main effect to significantly affect terrapin activity on roads. During high and falling high tides, terrapins were 18.5% and 16.1% more likely

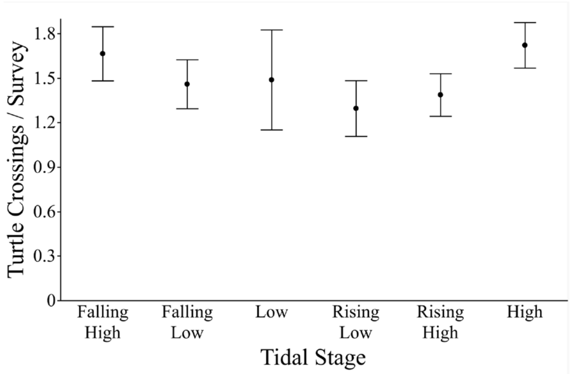

Figure 6. The mean (± standard error) number of Diamondback Terrapin (*Malaclemys terrapin*) road crossings by survey categorized by tidal stage in Cape May County, New Jersey, USA, 2017–2020.

to be encountered on the road, respectively, and 21.3% less likely to be encountered during rising low tide (Fig. 6). The effects of time category and cloud cover interacted to significantly affect terrapin activity ($F_{8,319.5} = 3.46$, $P < 0.001$; Fig. 7). Under partly cloudy conditions, the likelihood of terrapin encounters increased by 50.7% during mid-afternoon and decreased by 28.8% during late morning. There was a moderately significant interaction of the effect of cloud cover on terrapin encounters across season day squared ($F_{2,320.8} = 2.60$, $P = 0.076$), with a greater rate of change on partly cloudy surveys compared to clear or overcast and raining surveys.

Discussion

Road mortality is a major threat to wildlife populations and is a persistent and increasing threat for Diamondback Terrapin populations along the Atlantic coast of southern New Jersey. Over the course of our 4-y study, over 70% of terrapins we encountered on roads had been killed by vehicles, a proportion that remains relatively consistent from year to year. The vast majority of terrapins encountered were reproductively mature females traveling to or from nesting habitat. This disproportionate impact of vehicle casualties on adult female terrapins may affect the sex ratio and age structure of the local population, as found in studies of this and other turtle species (Aresco 2005; Avissar 2006; Steen et al. 2006; Crawford et al. 2014a; Reid and Peery 2014). Furthermore, because continual additive loss of reproductively mature individuals can contribute to population declines in long-lived species such as Diamondback Terrapins, and because female terrapins reach maturity at a slower rate than males, the number of road casualties we observed during this study is cause for concern (Congdon et al. 1993; Ennesson and Litzgus 2008; Crawford et al. 2014a). Our results suggest impacts from roads on Diamondback Terrapin populations warrant continued study and increased mitigation to curtail losses.

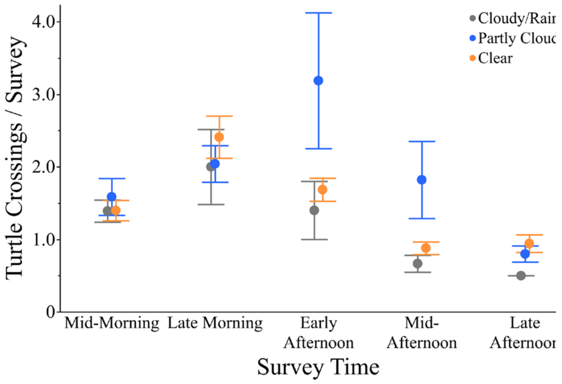

Figure 7. The mean number (± standard error) of Diamondback Terrapin (*Malaclemys terrapin*) road crossings by survey time of day and cloud cover in Cape May County, New Jersey, USA, May through July 2017–2020. Time of day for each survey was classified as mid-morning (0800–1000), late morning (1000–1200), early afternoon (1200–1400), mid-afternoon (1400–1600), and late afternoon (1600–1800). We categorized cloud cover at the time of survey as: clear (0–25% cloud cover), partly cloudy (25–75% cloud cover), and overcast or raining (75–100% cloud cover).

The most intense hot spots were concentrated along the eastern end of the road near heavily used nesting areas for Diamondback Terrapins. This section of road is bordered by urban development, a factor that likely contributes to increased crossing probability. Urbanization in this region has degraded or destroyed sandy nesting habitat typically preferred by Diamondback Terrapins (Wood and Herlands 1997), and nest-seeking females may cross the road in search of more suitable nesting habitat. Additionally, the places where mitigation fencing ends in this area are associated with urban features such as intersections and driveways. Intersections could also lead to increased vehicle traffic and heightened risk of vehicle strikes in an area where crossing activity is already high, resulting in the high-intensity mortality hot spots that we observed during our study. We did not examine traffic patterns as a variable; however, we anticipate that traffic density positively correlates with road casualty events for terrapins (Szerlag and McRobert 2006).

Mitigation fencing is intended to function as a barrier to terrapin movement and reduce crossing activity, but our results indicate that the probability of crossing hot spots increased in segments of roads with mitigation fencing. We must interpret these results with care, however, because fencing was placed prior to this study in areas identified to experience high crossing activity. Despite the use of fencing, these areas continued to be hot spots for crossings and casualties during our study. We cannot determine from this study whether fencing reduced the intensity of previously existing hot spots post-installation; however, it is possible fencing inadvertently contributed to hot spots of crossing activity due to fence-end effects (Clevenger et al. 2001). Gaps in road mitigation fencing can reduce fence effectiveness and may lead to increased abundance of wildlife found on mitigated roadways (Baxter-Gilbert et al. 2015; Markle et al. 2017). The numerous gaps in fencing for intersections and driveways along our transect may act to funnel terrapins into the road, increasing the likelihood of crossing and casualty hot spots, especially if terrapins become trapped by fencing once they have entered the road (Baxter-Gilbert et al. 2015). As a result, fence-end effects may explain the association of hot spots of crossing activity with our mitigation fence. Despite potential fence-end effects, our previous studies have shown that corrugated pipe fence installed at our site can reduce crossings by more than 80% if properly maintained (Reses et al. 2015). With this in mind, a precautionary approach prevents us from removing the fencing without further evidence to suggest harm to the population. Installing a new design of fencing that is more resilient and positioned in a way to minimize fence-end effects may help further reduce road impacts on turtle populations (Shortridge et al. 2025).

In contrast to the influence of mitigation fencing, bulkhead presence moderately reduced the likelihood of terrapin crossing activity. Bulkheads present a permanent and nearly insurmountable barrier that may cause terrapins to seek alternative routes to nesting habitat (Winters et al. 2015) or new locations altogether. On our transect, gaps between bulkheads and the prevalence of bulkheads on only one side of the road still allowed Diamondback Terrapins access to the upland and road, which may explain the weak effect of bulkhead presence in our models of hot spot occurrence. Bulkheads are becoming increasingly widespread to protect coastal communities from the effects of sea level rise with required and recommended heights increasing in coastal communities. Therefore, future work is important for understanding the impact shoreline hardening may have on terrapin access to nesting and road crossing activity and for identifying mitigation opportunities.

With the complexities of mitigation fencing in our study area and the permanence of bulkhead, a better understanding of temporal and environmental cues may provide the best opportunity for reducing the threat of roadways to terrapins in southern New Jersey. Tide appears well established in its importance as a factor influencing the timing of nesting activity (Burger and Montevecchi 1975; Auger and Giovannone 1979; Crawford et al. 2014b), and it was an important factor in predicting periods when crossing activity was most likely in our study. Diamondback Terrapins may elect to nest during higher tides to reduce overland distance traveled, as well as risk of predation and desiccation. Simultaneously, nesting during and following higher tides may help ensure Diamondback Terrapins nest in areas above the reach of high water, decreasing the risk that nests are destroyed by flooding (Burger and Montevecchi 1975). We attribute the increased probability of road crossings that we observed during falling tides to a combination of individuals beginning the nesting process later in the tide cycle and individuals returning to the marsh, crossing the road a second time.

Cloud cover and time of day interacted to influence terrapin road crossing activity during the nesting season, a finding supported by several studies of terrapin road ecology and nesting activity throughout the range of the species (Burger and Montevecchi 1975; Seigel 1980; Feinberg and Burke 2003; Szerlag and McRobert 2006). Overall, we found that the chances of encountering Diamondback Terrapins on the road increased during surveys conducted in mid-afternoon and decreased in late morning on partly cloudy days. Though it was not included in our study due to a correlation with season day, differences in ambient temperature may help to explain this interaction. Ambient temperature has been shown to correlate with nesting activity (Seigel 1980; Feinberg and Burke 2003) and may suppress activity when temperatures exceed 35° C (Feinberg and Burke 2003). By nesting during times of partial cloud cover, terrapins may avoid temperature extremes that could occur during overcast or clear conditions (Feinberg and Burke 2003). Early afternoon surveys on partially cloudy days yielded the highest number of crossings overall. Under partially cloudy conditions, optimal nesting temperatures could be reached later in the day and thus shift road encounters from late morning to mid-afternoon as our results indicate.

Interestingly, although we did see a decreased probability of crossing activity during cloudy or rainy conditions, the timing of peak crossing probability under these conditions did not differ from the pattern observed during clear days. Possibly, differences in temperatures at a given time of day during overcast or clear conditions are not large enough to trigger a temporal shift in terrapin nesting behavior, while temperature may vary more widely during partly cloudy conditions.

Our results have several important implications for the conservation of terrapins locally, regionally, and rangewide. This study has increased our understanding of the influence of landscape features on terrapin road crossing activity, while simultaneously identifying where and when crossing activity is most likely to occur. Additionally, our results underscore the complex nature of road impacts, exposing potential shortcomings of current mitigation efforts along the road. Though mitigation fencing is a valuable tool that has been effective in reducing mortality at this and other locations, it is not a perfect solution (Aresco 2005; Reses et al. 2015). While gaps in fencing are necessary in some locations, managers must implement mitigation fencing properly for it to be effective and not exacerbate road mortality (Baxter-Gilbert et al. 2015; Markle et al. 2017). Options to reduce risks posed by fencing gaps include bending ends of the fencing at gaps towards interior habitat to guide wildlife away from the road or toward safe crossing locations (Harman et al. 2023) and installing fencing with design features that allow wildlife to exit the road if they bypass the fence. Roads are permanent structures, and road mortality is a long-term conservation issue that must be addressed with long-term and permanent solutions whenever possible (Baxter-Gilbert et al. 2015). Although we have so far been unable to install more durable fencing at the study site, testing and installing fencing that requires less maintenance will be a goal of our future work, and durability should be of primary concern when implementing road mitigation fencing.

With mitigation fencing already installed along the majority of areas of high crossing activity, to further reduce the impacts of road mortality, we must combine improved mitigation fencing with additional approaches, in particular in areas where gaps limit fence effectiveness. Researchers have installed dynamic signs along coastal roads that automatically change to indicate periods of increased terrapin activity and more effectively warn drivers (Crawford et al. 2014b). Our results identifying the times and conditions during which crossing activity is most likely are an important step toward implementation of similar signage. Finally, in areas where gaps in fencing exist, road surveys timed around the tide cycle would help to maximize conservation impact, particularly on days where the tide is high in the late morning or early afternoon. Our results, combined with continued work to examine the impacts of additional factors such as vehicle traffic and temperature on terrapin road mortality and crossing activity, will help us further understand and more effectively address this pervasive conservation issue.

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