Estimating the consequences of multiple threats and management strategies for semi-aquatic turtles

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Summary

1. Roads are pervasive fixtures on most landscapes but are typically among many factors contributing to wildlife population declines. Addressing road mortality as part of larger conservation efforts is challenging because it can be difficult to measure *per capita* mortality from roads and other concurrent threats.

2. We used 4 years of mark–recapture–recovery data for diamondback terrapins *Malaclemys terrapin* on a causeway in Georgia, USA, to directly estimate threats of adult road mortality and nest predation, contrast the consequences to population growth using stage-based matrix models and make management recommendations to stabilize the population.

3. Mean estimated annual adult road mortality was 11·1% (range = 4·4–16·4%). Estimated annual nest predation was 61·9%. We estimated that the population was declining ($\lambda < 0.98$) in all scenarios where both threats were included. Variation in adult survival was the most influential (highest elasticity) contributor to population growth relative to other demographic rates; however, λ would remain below 1 with any nest predation rate exceeding our estimate even if actions to mitigate road mortality were 100% effective.

4. *Synthesis and applications.* Our study provides some of the first direct estimates of vehicle mortality rates and shows that mortality can remain sufficiently high among years to cause population declines. We also demonstrate that management actions focused on singular threats are inadequate for recovering populations. We conclude that integrated road and predator management is necessary to conserve turtle populations, and we suggest alternative strategies to compensate for some vehicle mortality and nest depredation.

Key-words: diamondback terrapin, *Malaclemys terrapin*, matrix model, nest predation, population growth rate, road mortality, roads

Introduction

Roads have become a pervasive fixture on most landscapes with ecological implications for many species. In the conterminous United States alone, 82% of all land area is within 1 km of the nearest roadway (Riitters & Wickham 2003). Multiple factors often contribute to wildlife population declines, and because roads are so pervasive, mitigating road threats may be more costly or less logistically feasible than other management activities. Therefore, there may be a tendency to prioritize management of other threats over the more challenging issue of road management. However, failing to address the negative impacts caused by roads may compromise the ability of any management efforts to stabilize or recover declining populations. Ultimately, pragmatic conservation of declining species should identify and address all threats, including road-associated threats, in an integrated management framework (Heppell, Crowder & Crouse 1996).

Roads can affect wildlife populations through mechanisms including the permanent loss of habitat and creating a barrier to movement that restricts a species access to complementary habitats (reviewed by Forman & Alexander 1998). The most direct effect of roads is wildlife–vehicle collisions (hereafter, road mortality), which can have relatively large impacts for a wide range of vertebrate taxa (reviewed by Fahrig & Rytwinski 2009). Species that appear particularly vulnerable to direct road mortality are those that make extensive overland movements or do not avoid or are attracted to roads (Forman & Alexander 1998; Gibbs & Shriver 2002; 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. For example, slight reductions (<3%) in adult survival in many long-lived turtle species have the largest impacts on population growth relative to other stages (Congdon, Dunham & van Loben Sels 1993; Heppell 1998; Enneson & Litzgus 2008), and road mortality, most commonly, impacts adults of these species as individuals complete movements related to breeding and nesting (Wood & Herlands 1997; Gibbs & Shriver 2002; Beaudry, Demaynadier & Hunter 2010). Despite the growing abundance of road ecology studies, surprisingly, few have directly estimated rates of mortality and projected those impacts on population viability (but see Mumme *et al.* 2000; Row, Blouin-Demers & Weatherhead 2007).

Studies have traditionally assessed the impact of road mortality using one of the two approaches, and while each has merit, neither can provide adequate estimates needed for the management. A number of studies document total numbers of animals struck on roads (Wood & Herlands 1997; Aresco 2005; Langen, Ogden & Schwarting 2009). This approach may be useful in identifying species, sexes or age classes vulnerable to road mortality but has biases (e.g. imperfect detection of road kills due to survey methodologies or scavengers) that limit demographic analyses (Langen *et al.* 2007). Another approach uses probability models to predict the frequency of road mortality and subsequent population responses (Litvaitis & Tash 2008). These studies typically employ the equation developed by Hels and Buchwald (2001) that incorporates road and animal characteristics to produce a mortality probability. Although using this methodology is often more tractable than exhaustive field surveys when investigating low-density species or expansive road networks (Gibbs & Shriver 2002; Beaudry, Demaynadier & Hunter 2010), several assumptions of the model may deviate from real-world conditions. For example, the model assumes no variation in driver behaviour, but drivers may intentionally avoid or target certain species on the road (e.g. Beckmann & Shine 2012). Row, Blouin-Demers and Weatherhead (2007) directly estimated road mortality by radiotracking >100 black ratsnakes *Pantherophis obsoletus* and found this rate to be half the rate estimated from the probability model. To our knowledge, Row, Blouin-Demers and Weatherhead (2007) is the only study to apply direct road mortality estimates to population effects; however, a limitation of that study is that effects of road mortality cannot be compared to other concurrent threats that may need management.

Through studying diamondback terrapins *Malaclemys terrapin* that nest on a causeway to Jekyll Island, Georgia, USA, our objectives were (i) to estimate and compare population responses to directly measured rates of road mortality and another well-documented threat – nest predation and (ii) to make conservation recommendations that will stabilize or grow this population. We used a mark-recover approach across 4 years to estimate *per capita* road mortality rates, as well as empirical and literature-based estimates of nest predation, and evaluated their relative impacts with population modelling. Additionally, we simulated the effects of producing female-biased sex ratios to augment population growth as a potential management solution. We expected that adult road mortality, compared to nest predation, would more negatively impact population growth rates and even a minimal rate of road mortality will lead to population declines.

Materials and methods

STUDY AREA AND SPECIES

We used the 8·7-km Downing-Musgrove Causeway to Jekyll Island, GA, USA (31·08°N, 81·47°W) as a model system for estimating multiple road-associated threats. The Downing-Musgrove Causeway (aka Jekyll Island Causeway: JIC) is a state highway with average annual daily traffic of 3440 vehicles day^{-1} (Georgia Department of Transportation 2011). Monthly traffic volumes for this and other coastal highways peak from May to July, corresponding to increased summer tourism. The JIC bisects a saltmarsh peninsula consisting of a network of intertidal creeks and high marsh dominated by *Spartina* spp.

Diamondback terrapins inhabit saltmarshes along the Eastern and Gulf Coasts of the United States – regions experiencing the fastest annual increases in both the densities and traffic loads of roads (Baird 2009). By fragmenting saltmarsh habitat, roadsides provide open, elevated nesting sites attractive to adult females, which are struck by vehicles while attempting to cross roads (Butler, Heinrich & Seigel 2006; Szerlag-Egger & McRobert 2007). Therefore, road mortality represents a female-biased threat for terrapins that is typically confined to summer nesting seasons (Wood & Herlands 1997; Szerlag-Egger & McRobert 2007). The JIC represents a regional road mortality hot spot where 100–400 terrapins are killed each summer (recorded since 2007; B. Crawford, GSTC, unpublished data). Terrapins share characteristics with the majority of turtles (described above) that are likely to make populations susceptible to even low rates (5–10%) of additive mortality due to roads (Butler, Heinrich & Seigel 2006). Additionally, subsidized predators such as raccoons *Procyon lotor* can cause high rates (50–90%) of egg mortality (Feinberg & Burke 2003; Szerlag-Egger & McRobert 2007; Munscher *et al.* 2012). Bycatch in commercial and recreational crab pots can increase juvenile and male mortality, leading to population declines (Hart 2005; Grosse *et al.* 2011), but we do not address the management of bycatch relative to road mortality (but see Hart 2005) because crabbing occurs infrequently at our study site; however, we do address the relative impacts of road mortality and nest depredation. We also address the potential to use vegetation management to manipulate hatchling terrapin sex ratios. Like many reptiles, terrapins exhibit environmental sex determination where warmer incubation temperatures produce greater proportions of female offspring (Ewert, Jackson & Nelson 1994).

ESTIMATING ROAD MORTALITY

We used a capture-mark-recover approach to estimate *per capita* road mortality of individuals that nest along the JIC during

summer nesting seasons (1 May–15 July) from 2009 to 2012. We drove along the JIC every 20–90 min between 08·00 and 20·00 each day during the study period. All uninjured terrapins found on the road were sexed based on body size, the position of the cloaca on the tail and head allometry, females were palpated for eggs, and unmarked animals were given a unique code by drilling or notching marginal scutes and returned to the marsh within 1 h of capture. Injured or dead terrapins were taken to the Georgia Sea Turtle Center to confirm identity if marked and to receive veterinary care. For uninjured terrapins discovered on the road with cars nearby, researchers intervened and captured animals before they could be struck. We recorded such animals as 'saved' and included any marked individuals from this group in our final estimates of annual road mortality rates. We estimated three rates of annual road mortality using data from consecutive seasons (2009–2010, 2010–2011 and 2011–2012) by calculating the proportion of marked individuals struck or saved during 1 year from the previous year's cohort. This approach assumes no other sources of annual mortality (all unrecovered turtles are alive); therefore, our estimates of *per capita* vehicle mortality are probably low. However, reports of natural annual mortality rates for terrapins and other turtle species are 85–90%, so the low bias is likely to be small. We also assumed perfect detection of mortalities since turtle carcasses can persist on roads for hours, and we performed multiple surveys per day.

ESTIMATING NEST PREDATION

We conducted walking surveys from 10 May to 1 July 2011 to estimate predation rates of known nests on the JIC. We repeatedly walked along nine transects, selected from observed hot spots of nesting activity, that ranged from 300 to 350 m in length. Surveys were carried out between 3 h before and 3 h after the scheduled high tide, coinciding with peaks of nesting activity (Crawford *et al.* 2014). We only intercepted females after observing nesting activity and palpated individuals to confirm that all eggs were deposited at that location. We marked the location of each nest by flagging shrubs 1–3 m away so as to not affect predation rates (Burke, Schneider & Dolinger 2005) and monitored nests daily for signs of predation within the first 10 days. We also checked nests with unknown fates each week after this period until 20 July. We could not measure predation rates for individual eggs because we did not excavate intact nests to count the number of eggs laid so as to not affect the likelihood of predation, and when nests were depredated, egg shells were often missing and presumed carried away by predators. We also did not account for eggs or clutches that failed but were not depredated (Feinberg & Burke 2003). Therefore, we assumed in our models that clutch sizes among nests were similar and used the proportion of non-depredated nests to total nests as an approximate estimate for egg survival.

POPULATION MODELLING

We constructed a females-only, stage matrix for a stable population (Lefkovitch 1965; Caswell 1989; Heppell 1998), relying on published demographic data (Table 1), and evaluated the effects of estimated annual road mortality and nest depredation. We parameterized our model with a 1-year time interval in Microsoft Office Excel 2007 to calculate the population growth rate (λ):

$$n(t + 1) = An(t)$$

where $n(t)$ is a vector of stage-specific abundances at time t and A is the population projection matrix that tracked individuals through three stages based on the following parameterization:

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

P_{ij} was the probability that an individual in class j survived and transitioned into stage i, and F was the reproductive output, or fertility, of individuals in the adult stage (Lefkovitch 1965; Morris & Doak 2002). Population growth rate was calculated as the dominant eigenvalue of the matrix using combinations of demographic rates that reflected three modelling scenarios: (i) baseline conditions without additional sources of mortality, (ii) current conditions using estimates of road mortality and nest predation from the JIC and (iii) potential conditions reflecting mitigation of one or both of these threats. Stage 1 was the hatchling stage, beginning when eggs hatch in late summer to early fall and ending the following year. We calculated the hatchling survival rate on the basis of all other model parameters that yielded a stable population. Stage 2 was the juvenile stage from ages 2 to 5. Although age of maturity varies latitudinally in female terrapins, we assumed females in this Georgia population mature at age 6, similar to individuals in South Carolina (Lovich & Gibbons 1990). We combined ages 6 and greater into Stage 3 representing adults. We did not include a maximum age in the model, so P_{33} equalled the annual adult survival rate. Fertility was calculated by multiplying mean clutch size, mean clutch frequency and the annual egg survival rate together. Since we used a female-only model, we also multiplied our fertility rate by the assumed proportion of female offspring to represent the number of female recruits (e.g. Enneson & Litzgus 2008). We assumed a baseline annual egg survival rate of 0·5, which is likely higher than most terrapin populations but falls within the range of reported rates (Burger 1977).

We altered baseline population parameters using observed *per capita* rates of road mortality and nest predation, both independently and then in concert. We iteratively used low, high and

Table 1. Parameters used for baseline conditions for stage-classified population models of diamondback terrapins on the Jekyll Island Causeway, GA

Parameter	Value	Sources
Hatchling survival	0·253	Derived from entering other parameters and solving for $\lambda = 1·0$
Juvenile survival	0·570	Mitro (2003), Hart (2005)
Adult survival	0·887	Mitro (2003), Hart (2005)
Age at maturity (females)	6	Lovich & 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

mean estimates of road mortality obtained from this study to model reductions in annual adult survival. We reset adult survival and modelled population responses given low and high nest survival rates (15% and 50%, respectively) reported in other studies (Burger 1977; Munscher *et al.* 2012) as well as our estimate of nest predation on the JIC. Lastly, we estimated λ by varying both road and nest mortality at low, average and high levels.

We conducted additional modelling scenarios to contrast the effects of road mortality and nest predation and inform management strategies. We systematically altered vital rates from baseline levels to estimate decreases in egg and adult survival rates that the population could tolerate before falling below a threshold for short-term persistence (λ = 0·98). Next, we estimated reductions to either road mortality or nest predation needed to raise λ to this threshold, given current mortality rates on the JIC. Finally, we modelled the potential to stabilize the terrapin population (λ = 1·0) through combinations of three management goals: (i) reduce adult road mortality, (ii) reduce nest predation and (iii) increase the proportion of female hatchlings.

SENSITIVITY AND ELASTICITY ANALYSIS

We used CSIRO PopTools (Greg Hood, http://www.poptools.org/) to calculate transition probabilities between life 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 proportional contribution of each demographic parameter in the model (i.e. adult survival, fertility) to λ (de Kroon *et al.* 1986). Elasticity values sum to 1·0, which allows for direct comparisons between matrix elements (e.g. adult survival versus fertility) and identification of population vulnerability to stage-specific threats (de Kroon *et al.* 1986; Crouse, Crowder & Caswell 1987; Caswell 1989). We 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

Between 2009 and 2012, we observed 613 adult female terrapins struck and killed on the JIC (annual mortalities ranged from 104 to 221). We marked 387 live adult females attempting to cross and nest on JIC roadsides and, of these, recovered 36 struck or 'saved' individuals (Table 2). Mean estimated road mortality rate was 11·1%, but annual estimates varied from 4·4% to 16·4% (Table 2). We observed 21 nesting events in 2011, and 13 (61·9%) of those nests were depredated within the first 7 days. We did not observe the predation of any nest after 7 days.

POPULATION MODELLING

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). Among scenarios where only one threat was modelled, λ ranged from 0·981, given our observed egg survival rate on the JIC, to 0·902, given our highest estimate of annual adult road mortality. When both threats acted in concert across the range of current rates, λ ranged from 0·810 to 0·971. Model projections resulted in a λ of 0·908 given our mean estimates of current threats on the JIC.

We estimated that the JIC terrapin population could tolerate larger decreases in nest survival than adult survival (12·4% and 3·1%, respectively) from baseline rates before λ fell below 0·98. Using the average rates of current threats on the JIC, model projections showed that reducing adult mortality by 10·9% was needed to achieve short-term population persistence (λ = 0·98) if nest predation was left unmanaged. Alternatively, reducing nest predation by 44·2% was necessary if road mortality was left unmanaged. No increase in the proportion of female hatchlings was capable of producing a stable population (λ = 1·0) with current rates of road mortality and nest depredation (Table 4); however, a stable population could be achieved using a combined approach for management that moderately reduced road mortality and nest predation while increasing the percentage of females produced.

Table 2. Adult female diamondback terrapins marked and recovered as mortalities the following year to yield interannual road mortality rates on the Jekyll Island Causeway, GA

| Year | New marked individuals | Road 'mortality' recaps in next season | | | Interannual mortality rate | Threat level |
		Struck	Saved	Total		
2009	110	10	8	18	0·164	High
2010	205	4	5	9	0·044	Low
2011	72	4	5	9	0·125	Mid
					0·111	Mean

Table 3. Projected population growth rates (λ) for diamondback terrapins nesting near the Jekyll Island Causeway given low, average and high estimates of road mortality and nest predation occurring separately and concurrently

	Threat		
Threat level	Nest predation	Road mortality	Both
Low	1·000	0·971	0·971
Average	0·981	0·935	0·908
High	0·933	0·902	0·810

Table 4. Sex ratios (in % females) needed in conjunction with the management of road mortality and nest predation to produce a stable population ($\lambda = 1\cdot0$) of diamondback terrapins on the Jekyll Island Causeway, GA

Road mortality	Nest predation	% females needed
Current average (11%)	Current (62%)	Impossible
Reduce to 8%	Reduce to 50%	85·4
Reduce to 5%	Reduce to 20%	51·5

Sensitivity was highest for juveniles survival to adulthood (0·884), followed by annual adult survival (0·683). Elasticity was 4·8 times higher for adult survival (0·564) than juvenile survival to adulthood (0·119), which was the next highest elasticity. The ranks of these values did not change with variation in sensitivity and elasticity among scenarios. Similarly, proportional changes in adult survival resulted in greater changes in λ compared to all other vital rates (Fig. 1).
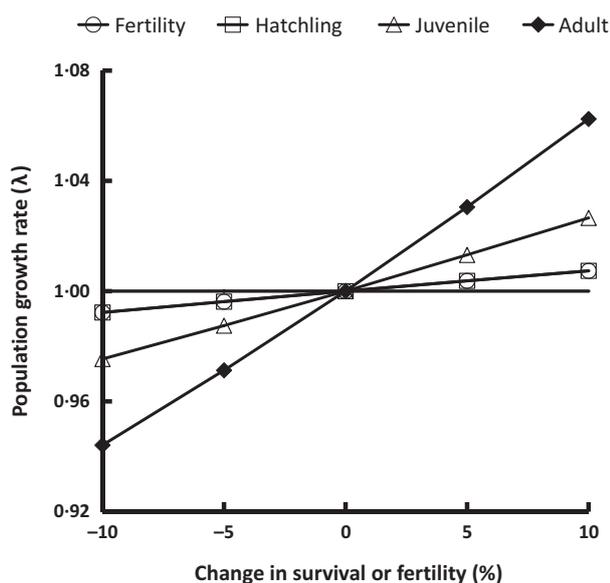
Fig. 1. Population growth rate (λ) versus percentage change in stage-specific survival rates and fertility from the stable baseline model ($\lambda = 1\cdot0$) for diamondback terrapins nesting near the Jekyll Island Causeway, GA.

Discussion

Through directly estimating rates of road mortality and nest predation of diamondback terrapins, our study provides a model for ranking multiple threats to species inhabiting road-fragmented landscapes, predicting population responses and prioritizing management goals. The results of our study lend additional, empirical support to hypotheses that roads in general, and road mortality specifically, can reduce population viability among wildlife including birds and mammals (Benítez-López, Alkemade & Verweij 2010), amphibians (Hels & Buchwald 2001) and reptiles (Gibbs & Shriver 2002; Row, Blouin-Demers & Weatherhead 2007; Beaudry, Demaynadier & Hunter 2010). However, this study is only the second to directly measure *per capita* road mortality and estimate the effect on population growth (Row, Blouin-Demers & Weatherhead 2007) and the first to simultaneously address concurrent, empirically measured threats. With more than 100 adult females killed on the JIC annually, our estimate of road mortality may appear surprisingly low; however, it is generally well above levels sufficient to cause population declines. Though we do not have long-term data to demonstrate a declining terrapin population on the JIC, our estimates of road mortality and nest predation suggest it is highly improbable that the population is stable or growing. These findings are consistent with other turtle demography studies, indicating that harvest of 3–5% of the adult female population is sufficient to cause populations to decline (Crouse, Crowder & Caswell 1987; Congdon, Dunham & van Loben Sels 1993; Enneson & Litzgus 2008). Therefore, we conclude that the terrapin population on the JIC is very likely to be declining due to road mortality, as well as nest depredation, and that both threats must be addressed to stabilize or recover the population.

A key assumption of our model that is pertinent to the relative importance of different threats and establishing management targets is that road mortality and egg mortality are additive. We do not have estimates of rates of other natural or anthropogenic sources of adult or egg mortality, nor are we able to compare adult survival rates along the JIC with survival rates from similar populations where road mortality is largely absent. As a result, we cannot test the assumption of additive mortality. However, demographic compensation has never been observed in turtle populations while it has for other long-lived taxa such as mammals (e.g. Hadley *et al.* 2006). It is possible that the process of nesting, regardless of the presence of roads, is naturally associated with female mortality. 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 1 year may die before the following nesting season, which would result in underestimates of annual road mortality given our mark-recover approach. Lastly, our results may underestimate road mortality rates if struck terrapins crawled or were taken off the road by scavengers before they could be detected. However, Langen *et al.* (2007) reported that turtle carcasses persist on roads for days, so the frequency of our surveys (every 20–90 min) maximized detection and the accuracy of derived mortality rates. Despite uncertainty in these rates, we can draw on the greater accuracy of directly measuring road mortality, relative to other approaches, and the ability of stage-based models to target life stages most important for management.

The use of population models to evaluate threats and management strategies depends on the accuracy of baseline demographic rates and estimates of threat effects on these rates. A limitation of elasticity analysis is that we lack measures of the variation in demographic rates for different life stages related to different threats or compensatory demographic responses to changes in mortality rates at other life stages (e.g. density-dependent demographic rates). Even for relatively well-studied taxa such as turtles, we have persistent knowledge gaps of life-history and demographic data of cryptic life stages (e.g. hatchlings and juveniles; Lovich & Gibbons 1990; Congdon, Dunham & van Loben Sels 1993; Pike *et al.* 2008). Terrapins have an expansive range across the Eastern and Gulf Coasts, and certain demographic rates vary considerably between distant populations (Zimmerman 1992). However, we used published rates in our baseline model that were derived from populations in Georgia or adjacent states whenever available (e.g. female age of maturity estimated in populations from SC; Lovich & Gibbons 1990). Despite potential demographic differences between these populations and the Jekyll Island population, we reiterate that adult survival ranked highest in elasticity (and therefore, in management priority) across all scenarios where we varied (i) adult survival by a range of road mortality rates estimated at our study site and (ii) egg survival by a range of values estimated in our or other published studies. We lack information on possible juvenile survival rates. If juvenile survival rates on JIC are higher or more variable than the single value we used in our model, this would reduce the elasticity of adult survival rate and potentially increase the relative importance of factors affecting other life stages similar to findings of Hart (2005). Mortality related to bycatch, which disproportionately affects smaller terrapins, could alter juvenile survival rates (Hart 2005; Dorcas, Willson & Gibbons 2007) and has been linked to reduced terrapin abundance both within our study region (Grosse *et al.* 2011) and range wide (Butler, Heinrich & Seigel 2006). While terrapin bycatch in crab pots was not an issue at our study site, it is an additional factor that may need to be addressed as part of a comprehensive terrapin management plan in the future or at other sites. Again, this would illustrate that a singular management focus is likely inadequate for most wildlife populations and a failure to address any one threat could compromise all other management efforts.

Our results also revealed an additional limitation to using indirect models to estimate road mortality rates. Our study shows that rates can vary by 400% among years. Admittedly, some of the variation in our estimates may be related to the assumption that background adult mortality was low and constant among years. The degree to which this assumption is untrue would create variation and error in our estimation of mortality rates, but we currently have no estimates of natural adult mortality among years at our study site. The probability model created by Hels and Buchwald (2001) has several assumptions that currently limit the ability to predict interannual variability in road mortality. Other studies have noted that this model cannot address driver and animal behaviour (Gibbs & Shriver 2002). Driver reactions could reduce or increase road mortality rates, and animal responses to an oncoming vehicle, such as stopping and pulling into its shell, would also affect road mortality rates. We suggest that interannual variability in road mortality rates of terrapins is related to variable daily traffic loads relative to when terrapins emerge on to roads. Vehicle traffic on the JIC is highest on weekends and when the weather is attractive for tourists. Terrapins are most likely to emerge onto roads proximate to diurnal high tides (Crawford *et al.* 2014). When conditions that are attractive to turtles and tourists align more frequently during a year, road mortality rates can be particularly high. It is possible that traffic patterns and driver behaviours could be modelled with established patterns of terrapin activity to create a more robust estimator of road mortality; however, until then, direct measures of road mortality are needed.

Our study demonstrates both the importance of assessing multiple threats concurrently, but also how the failure to assess and address some challenging threats such as road mortality will inevitably cause other management efforts to fail. Our estimates and models suggest that it is highly likely that the terrapin population near the JIC will decline even at our lowest estimated road mortality rate and that it is improbable to stabilize or grow the population without addressing road mortality. Therefore, reducing annual road mortality to below 3% must be a required component of management for terrapins. However, our study also suggests that nothing short of complete elimination of additive road mortality would be sufficient to stabilize or grow the terrapin population given our estimated nest predation rate. Moreover, we note that few studies report lower nest predation rates, but many studies report similar or much higher (up to 90%) rates (Feinberg & Burke 2003; Munscher *et al.* 2012). Higher predation rates than the one we estimated would mean that any management to reduce road mortality would be insufficient to stabilize the JIC terrapin population without also addressing nest predation.

Fortunately, management options for several terrapin threats are available to facilitate integrated management plans. Raccoon removal was shown to reduce nest depredation from a pre-removal rate of 76–80% to a post-removal rate of 17% (Munscher *et al.* 2012), and bycatch reduction devices are effective at significantly reducing or eliminating terrapin bycatch in crab pots (Roosenburg & Green 2000; Hart & Crowder 2011). Fewer strategies have been developed or evaluated for reducing road mortality. Barriers to prevent animals from crossing roads and signs to alert drivers to the potential presence of animals on roads have been used with mixed success (Clevenger, Chruszcz & Gunson 2001; Sullivan *et al.* 2004; Aresco 2005). However, it has been suggested that assessments identifying particular places (hot spots) or times (hot moments) when threats most likely occur could be used to target these measures to affect driver behaviours with potentially great effect (Sullivan *et al.* 2004; Beaudry, Demaynadier & Hunter 2010). We also examined the potential to manipulate hatchling sex ratio as an indirect way to compensate for elevated mortality rates. Our models show that no manipulation of sex ratio would be sufficient to compensate for current levels of road mortality or nest depredation; however, increasing the proportion of female hatchlings in conjunction with modest reductions in road mortality and nest predation could stabilize the population. Vegetation management might be a means to manipulate hatchling sex ratio. Roosenburg and Place (1994) advocated for attention to thermal nesting habitat management for terrapins as a means to manage population demography, though they did not specifically address vegetation management. Creating more open nesting habitat by removing shrubby vegetation could increase nest temperatures, which should increase the proportion of female hatchlings. Roosenburg (1996) also found that terrapins tend to deposit larger eggs in areas with more open vegetation, which can increase survivorship and decrease the age of first reproduction for female hatchlings. Vegetation management could affect nest survival through effects on soil moisture or predator foraging success, so further evaluation will be needed for this potential management tool.

Roads are an increasingly pervasive feature of the landscape, and managing the impacts of roads on wildlife is daunting in its scale and complexity. However, the challenge of managing road impacts cannot justify failing to address them. As our study demonstrates, failing to account for even small rates of road mortality could render other management activities ineffective. Further, a singular focus on managing road impacts or any threat in isolation is likely to be ineffective. An integrated approach to managing threats posed by roads and other factors is almost certainly required for effective conservation, and such an approach creates greater flexibility by identifying compensatory actions when certain threats cannot be addressed directly.

Acknowledgements

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