



Integrated analysis for population estimation, management impact evaluation, and decision-making for a declining species



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ABSTRACT

A challenge for making conservation decisions is predicting how wildlife populations respond to multiple, concurrent threats and potential management strategies, usually under substantial uncertainty. Integrated modeling approaches can improve estimation of demographic rates necessary for making predictions, even for rare or cryptic species with sparse data, but their use in management applications is limited. We developed integrated models for a population of diamondback terrapins (*Malaclemys terrapin*) impacted by road-associated threats to (i) jointly estimate demographic rates from two mark-recapture datasets, while directly estimating road mortality and the impact of management actions deployed during the study; and (ii) project the population using population viability analysis under simulated management strategies to inform decision-making. Without management, population extirpation was nearly certain due to demographic impacts of road mortality, predators, and vegetation. Installation of novel flashing signage increased survival of terrapins that crossed roads by 30%. Signage, along with small roadside barriers installed during the study, increased population persistence probability, but the population was still predicted to decline. Management strategies that included actions targeting multiple threats and demographic rates resulted in the highest persistence probability, and roadside barriers, which increased adult survival, were predicted to increase persistence more than other actions. Our results support earlier findings showing mitigation of multiple threats is likely required to increase the viability of declining populations. Our approach illustrates how integrated models may be adapted to use limited data efficiently, represent system complexity, evaluate impacts of threats and management actions, and provide decision-relevant information for conservation of at-risk populations.

1. Introduction

Conservation management requires addressing problems involving complex interactions between social and ecological systems; multiple, concurrent threats to natural resources; and potential strategies whose outcomes are uncertain (Game et al., 2014). Concomitantly, ecological modeling can help infer and forecast system dynamics, upon which management decisions can be based. Modeling approaches that are realistic in the representation of context-specific processes and transparent in the treatment of key uncertainties are a means to robust conservation decisions (Schmolke et al., 2010).

Population viability analysis (PVA) is an effective tool for predicting outcomes of interest (e.g., population abundance, growth, persistence)

for wildlife species (Akçakaya and Sjögren-Gulve, 2000; Morris and Doak, 2002). PVAs are highly customizable to a species' life history (e.g., life stages, behavioral states) and context-specific factors that affect demographic rates on which predictions are based (Akçakaya and Sjögren-Gulve, 2000; Morris and Doak, 2002; Rhodes et al., 2011; Wilson et al., 2016). Modeling multiple, concurrent threats within a single PVA is crucial for decision-making, since factors not addressed may render targeted management actions ineffective (Heppell et al., 1996; Rhodes et al., 2011; Crawford et al., 2014a). PVAs also provide decision-relevant information via efficient evaluation of the sensitivity of model outcomes to changes in parameter values, including values estimated by expert opinion (Wade, 2002). Still, obtaining reliable predictions from PVAs remains challenging within many conservation

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contexts given multiple sources of parameter uncertainty. These issues magnify as PVAs are commonly applied to rare, declining, and cryptic species with sparse datasets. Population parameters (e.g., abundance, survival, productivity) are estimated from observation data; thus, uncertainty around parameter estimates inherently includes variation of demographic process as well as observation error that should be separated before making inferences (Clark and Bjørnstad, 2004). Overestimation of demographic rates and increases in uncertainty can occur for species with limited data or low detection (e.g., Zipkin et al., 2014). In some cases, there may be no current data on which to estimate parameters, such as for rare species or novel management actions, and PVAs may rely on expert elicitation associated with higher degrees of uncertainty (Krueger et al., 2012). Finally, the effectiveness of management strategies may be difficult to estimate for cryptic species or those with low productivity or delayed maturity because longer post-management periods are necessary to detect changes in population growth (Heppell et al., 1996; Moore et al., 2012; Tempel et al., 2014).

Novel modeling approaches have been developed to improve the accuracy of parameter estimates and population predictions associated with PVAs. First, an integrated model is a unified analysis that can leverage information contained in multiple, partial datasets to estimate shared demographic processes for a population (e.g., Wilson et al., 2016). Integrated models increase precision, ensure consistency of estimates across datasets, and reduce effects of potential bias of individual datasets (Schaub and Abadi, 2011). Examples of these frameworks include the joint live-dead encounter model for mark-recapture and dead-recovery data developed by Burnham (1993) and, more recently, integrated population models (IPMs) for the unified analysis of mark-recapture, population count, and other datasets (Schaub and Abadi, 2011). Second, recent PVA formulations have been developed to improve the accuracy of population predictions by formally incorporating uncertainty around parameter estimates while separately modeling annual stochasticity in population simulations (e.g., Moore et al., 2012; Shoemaker et al., 2013). These models have been constructed in Bayesian (e.g., Bayesian PVAs: Wade, 2002, Kéry and Schaub, 2012) and frequentist frameworks (e.g., McGowan et al., 2011), and we refer to this general class of models as robust PVAs. Robust PVAs reduce the risk of overestimating population outcomes, such as probability of persistence (McGowan et al., 2011), and have also been used to explicitly evaluate effects of management alternatives on population outcomes (Moore et al., 2012; Hegg et al., 2013; Servanty et al., 2014; Green and Bailey, 2015). To date, the application of integrated models to conservation issues is limited (Schaub and Abadi, 2011; Zipkin and Saunders, 2018). The application of robust PVAs to evaluate management actions is growing, but these efforts have not been coupled with integrated models for improved parameter estimation in the context of conservation decision-making (but see Hoyle and Maunder, 2004, Maunder, 2004, Lieury et al., 2015, Saunders et al., 2018). Here, we use integrated models and robust PVAs to estimate context-specific demographic rates, evaluate management actions, and predict population outcomes to inform decision-making for a declining species of conservation concern, the diamondback terrapin (*Malaclemys terrapin*).

Diamondback terrapins inhabit salt marshes along the Eastern and Gulf Coasts of the United States – regions experiencing the fastest annual increases in developed area, road density, and traffic loads (Baird, 2009). Multiple anthropogenic threats contribute to terrapin population declines, which has prompted many states to list the species as “of special concern” or a higher protection status (Roosenburg, 1991; Gibbons et al., 2001; Grosse et al., 2011; Crawford et al., 2014a; Chambers and Maerz, in press; Maerz et al. in press). Terrapins are frequent bycatch in commercial and recreational crab pot fisheries (Roosenburg et al., 1997; Grosse et al., 2011; Chambers and Maerz, in press), and in areas where roads fragment salt marsh, adult females are struck by vehicles while searching for elevated nesting habitat (Butler et al., 2006; Szerlag-Egger and McRobert, 2007; Crawford et al.,

2014b). Terrapins share characteristics with the majority of turtles (e.g., long-lived, delayed maturity, naturally high adult survival) that are likely to make populations susceptible to even low rates (3–10%) of additive mortality due to roads (Gibbs and Shriver, 2002; Steen and Gibbs, 2004; Butler et al., 2006; Maerz et al. in press). Human-subsidized predators, such as raccoons (*Procyon lotor*), contribute to high rates (50–90%) of nest mortality on roadsides and other developed areas (Crawford, 2015; Maerz et al. in press). The density of roadside vegetation can also influence terrapin demographic rates. Grosse et al. (2015) observed higher predation rates and higher proportions of male hatchlings for nests laid in planted hedgerows (commonly cedar and wax myrtle *Myrica cerifera*), relative to cleared, open areas along roadsides. Like many reptiles, terrapins exhibit environmental sex determination (ESD) where warmer incubation temperatures produce greater proportions of female offspring (Ewert et al., 1994). While existing management practices have targeted road mortality (Aresco, 2005) and predation (Munscher et al., 2012), vegetation management practices also have the potential to increase population growth (Maerz et al. in press).

The aim of this research was to apply an integrated analysis to evaluate the consequences of management strategies to inform decision-making within the context of road impacts on wildlife. We used a population of terrapins that nest on the causeway to Jekyll Island, Georgia, USA as a model system. Our specific objectives were (i) to develop an integrated model to jointly estimate demographic rates from two mark-recapture datasets, (ii) to directly estimate impacts of road mortality and management actions deployed during the study on demographic rates, and (iii) to incorporate estimates from this and other studies, as well as expert opinion, in a robust PVA to project population persistence under simulated management strategies. This work builds on previous research that estimated the effects of road-associated threats and identified management targets (Crawford et al., 2014a; Crawford et al., 2014b; Crawford et al., 2017; Grosse et al., 2015). It precedes research that will incorporate population persistence outcomes for each strategy in the context of other socioeconomic objectives for road management on Jekyll Island. Our approach, linking integrated models and robust PVAs in a unified analysis, is applicable across conservation contexts for using limited data efficiently, tailoring models to represent system complexity, and prioritizing threats and management actions that impact at-risk populations.

2. Methods

2.1. Study area and population

We conducted research in conjunction with long-term monitoring efforts of the Georgia Sea Turtle Center (GSTC) on the 8.7-km Downing-Musgrove Causeway (aka Jekyll Island Causeway: JIC) to Jekyll Island, GA, USA (31.08°N, 81.47°W; Fig. 1). The JIC bisects a salt marsh peninsula consisting of a network of intertidal creeks and high marsh dominated by *Spartina* spp. We defined the population of interest for this study as terrapins inhabiting this peninsula and using JIC roadsides for nesting. The JIC represents a regional road mortality hot spot where 100–400 adult female terrapins are killed each summer while searching for roadside nesting habitat (Crawford et al., 2014b; GSTC, unpubl. data). Previous monitoring during terrapin nesting seasons revealed that crossing activity was concentrated spatially on road sections (hot spots) and temporally within a daily 3-h period around the scheduled diurnal high tide (Crawford et al., 2014b), and we exploited these peaks with two management actions. In 2011, we constructed a 22-m hybrid barrier composed of fencing and nest boxes at one hot spot and evaluated its effects on preventing terrapins from accessing the road (Crawford et al., 2017). Nest boxes consisted of elevated artificial mounds of sand with electrified cages on top, which were designed to allow terrapins access to the box while excluding mammalian and avian predators (see Buhlmann and Osborn, 2011; Quinn et al., 2015) and

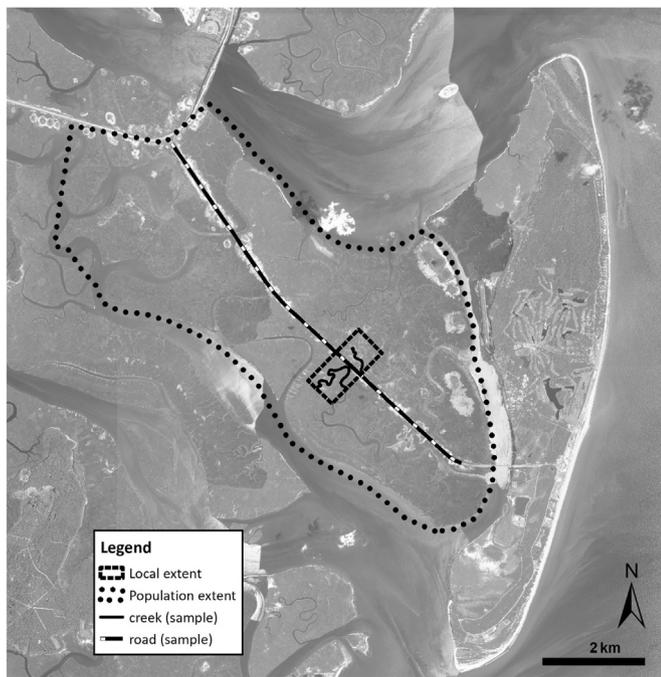


Fig. 1. Map of areas sampled for each dataset used to estimate parameters of the diamondback terrapin population inhabiting the salt marsh peninsula around the Jekyll Island Causeway, Jekyll Island, GA, USA. Robust Design mark-recapture data (CREEK) were collected at the local extent on a subset of the population; multistate recapture/recover live-dead data (ROAD) was collected at the population extent.

increase the percentage of female hatchlings (Grosse et al., 2015). In 2013, we collaborated with the Georgia Department of Transportation to install two terrapin crossing signs with flashing warning beacons (R829 Series Solar School Zone Flashing Beacons, Carmanah Technologies®, Victoria, British Columbia, Canada) to alert drivers entering a 6-km section of the JIC from either direction. We activated signs for 2 h per day during the temporal peak of terrapin crossing corresponding to the scheduled diurnal high tide (Crawford et al., 2014b), and we evaluate the effects of signs on terrapin survival below.

2.2. Data collection

We collected two datasets at different spatial scales from the terrapin population (Fig. 1) to develop the integrated model: (1) a mark-recapture dataset of adult male and female terrapins inhabiting two creeks adjacent to the JIC (hereafter, “CREEK”) collected at a local scale from 2010 to 2015, following Pollock’s Robust Design (Pollock, 1982), and (2) a multistate mark-recapture/recover live-dead dataset of adult nesting females on the JIC (hereafter, “ROAD”) collected at the population scale from 2009 to 2015, following a joint live-dead encounter design (Burnham, 1993).

At the local scale, we used a Robust mark-recapture design, seining creeks (following Dorcas et al., 2007) for three consecutive days (secondary periods) each April (primary periods; 18 total capture occasions). Captured animals were sexed based on body size, the position of the cloaca on the tail, and head allometry, and all unmarked animals were given a unique code by drilling or notching marginal scutes. We released all animals prior to the next sampling occasion.

At the larger population scale, we marked adult females attempting to nest on JIC roadsides for later encounter on the roadway as either live recaptures or dead recoveries. We conducted intensive road surveys of the JIC during each nesting season (1 May–15 July; Crawford et al., 2014b). Since both sides of the road are suitable nesting habitat, some terrapins will emerge from the marsh and nest on the proximate side

without attempting to cross the road. Alternatively, terrapins may attempt to cross, nest on the opposite roadside, and then attempt a return trip across the road. We recorded any terrapin observed on the road surface or within 1 m of the road and walking toward it as alive in the crossing state (denoted $F_{A,c}$) and we intervened by capturing these individuals before they could be struck by vehicles. We recognize our intervention likely affected individuals’ fates when vehicles were nearby. Therefore, the estimated effect of road mortality on survival rates for crossing females is likely conservative (see Results). If we observed a terrapin that nested on a roadside and attempted to return to the adjacent marsh without crossing the road, we recorded its state as non-crossing (denoted $F_{A,nc}$). We recorded any terrapin, dead or still alive, found struck by a vehicle on the road as state $F_{d,c}$. We processed and marked all uninjured terrapins using the same methods described above, and we released animals in nest boxes located roughly every mile on the side of the road the individual came from within 1 h of capture. We took injured or dead terrapins to the GSTC to confirm identity if marked and administer appropriate veterinary care.

2.3. Integrated model

We developed a state-space integrated model fitted in a Bayesian framework to leverage information from both datasets and jointly estimate parameters for adults in the population of interest. This approach parallels that of IPMs (Schaub and Abadi, 2011); however, unlike IPMs, we performed estimation and projection of the population in two separate steps instead of under a single model. Our motivation for this approach was to avoid lengthy computer processing time expected if we merged the estimation and projection models and still allow for the inclusion of complexity in the integrated and PVA models (see below). When describing the integrated and PVA models, we subscripted parameters to denote sex (M males; F females), stage class (E eggs; H hatchlings; J juveniles; A adults), and subclass for adult females (c crossing the road; nc not crossing; o outside the study area; d dead or struck by vehicle) where appropriate.

The integrated model consisted of two submodels with independent and shared parameters: (1) a Robust Design model was fit to the mark-recapture data (CREEK) and (2) a multistate parameterization of a Jolly-Seber model (Kéry and Schaub, 2012) was fit to the mark-recapture/recover live-dead data (ROAD) (Fig. 2). The parameters shared between submodels and informed by both datasets were adult female survival probability ($\phi_{F,A}$), entry (b_F), and site fidelity (γ_F). Following Kéry and Schaub (2012), the entry probability in our model represents the probability of entering the adult population either via local recruitment (juveniles that survive and mature to an adult stage) or immigration from another population. In the absence of other information, we assumed random temporary emigration in the population, irrespective of an animal’s previous availability state; therefore, we used the single parameter γ to represent site fidelity, which we defined as the probability of a terrapin being in the sampled area (i.e., in a creek at the local extent and using the JIC to nest at the population extent). This parameter should be consistent across datasets for the following reasons: (i) female terrapins complete temporary migrations from creeks to nesting areas prior to nesting (Tucker et al., 2001; Sheridan et al., 2010), (ii) we obtained Robust Design data from creeks adjacent to the JIC and sampled immediately prior to the nesting season each year, and (iii) the JIC is the largest and nearest nesting area within our population extent. Taken together, it is plausible that females would exhibit the same annual movement patterns related to nesting, exposing them to sampling in both datasets in the same year. We present the comprehensive development of each submodel in Appendix A but illustrate core components below.

We fit both submodels and the integrated model using a Bayesian framework with Markov chain Monte Carlo (MCMC) methods in Jags called from R (version 3.1.2, R Core Team, 2013) via the R2jags package (Su and Yajima, 2012). We assigned diffuse prior distributions

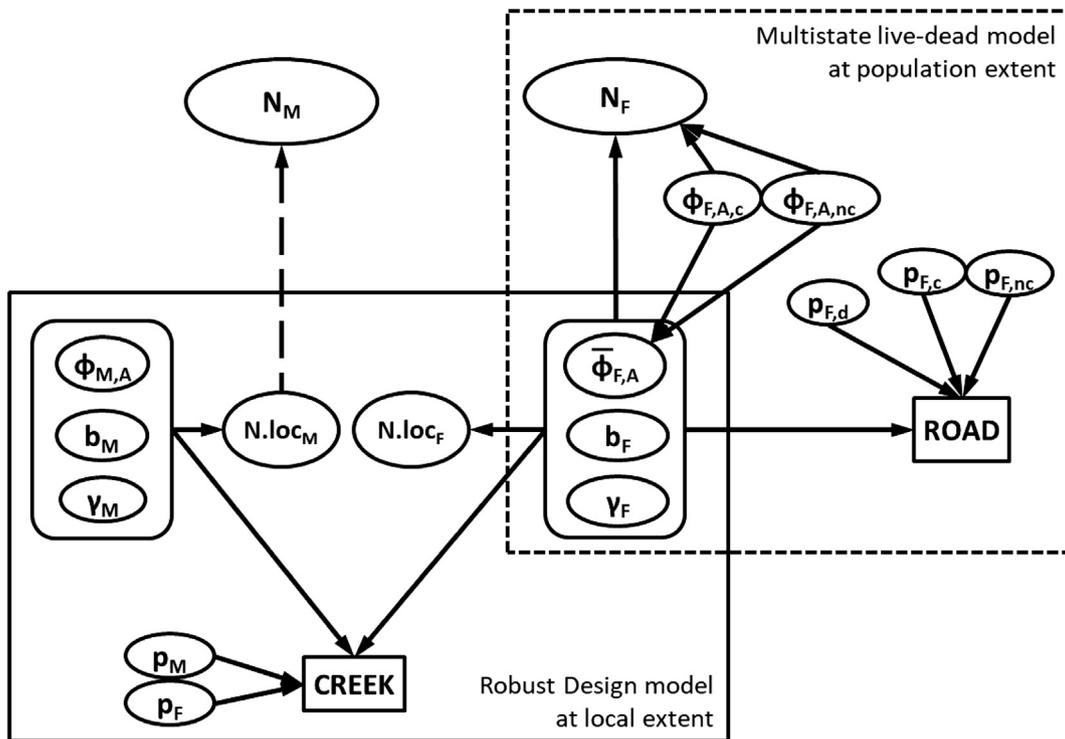


Fig. 2. Directed acyclic graph of the integrated model, showing demographic parameters that were independently or jointly estimated from separate capture-mark-recapture datasets. Estimated and derived parameters are represented by ovals and the data are represented by rectangles. Solid arrows represent dependencies between nodes that were implicit in the model; dashed arrow represents assumed dependences between local and population-level abundances that were used in the population viability analysis. Node notations: CREEK Robust Design mark-recapture data; ROAD recapture/recover live-dead data; ϕ survival; b entry; γ site fidelity; p capture probability; $N.loc$ abundance at local scale; N abundance at population scale. Subscript notations: M male; F female; A adult; c crossers; nc non-crossers; d dead or struck. Note that the priors are not shown on this graph.

for all fixed effect parameters and hyperparameters governing random effects in all models. For the integrated model, we generated three MCMC chains using 60,000 iterations where we retained the last 10,000 iterations without thinning (Link and Eaton, 2012), yielding a final set of 30,000 samples from posterior distributions of the parameters. We assessed convergence for all models by visually inspecting chain mixing in MCMC trace plots and posterior distribution plots for evidence of unimodality and by calculating the Brooks-Gelman-Rubin diagnostic (Brooks and Gelman, 1998), which compares within- and between-chain variance. We based parameter inferences on posterior means and 95% Bayesian credible intervals (BCIs; 2.5th–97.5th percentile of the distribution). Our R and JAGS code is in Appendix B.

2.3.1. Robust design model

We developed a Robust Design submodel to estimate demographic rates and derive local adult terrapin abundances for each sex g . Following Pollock (1982), we assumed the population was closed to mortality, recruitment, and emigration during the three-day secondary periods (u : days) but open between primary periods years (t : years), all individuals in a state shared the same capture or transition probabilities, and marks were retained and did not affect survival or behavior. Given low recapture rates in our study and the potential temporary movement of terrapins out of the sampling area, it is likely some individuals were in the population but not ever captured during the study. Therefore, we used data augmentation (Royle and Dorazio, 2012), which adds a large number of all-zero capture histories (representing pseudo-individuals) to the dataset. Following Kéry and Schaub (2012), our “superpopulation” model first assigned an inclusion state (w_i) for each individual i in the augmented dataset that is drawn from a Bernoulli trial with probability ψ_{CREEK} , where $w_i = 1$ if the individual is a member of the superpopulation and $w_i = 0$ otherwise. Thus, the superpopulation size represents the total number of

individuals that were alive and in the population at any time during the study. Next, we modeled the state history ($z_{i,t}$) for individuals describing if the individual was alive and in the population each year ($z_{i,t} = 1, 0$ otherwise) conditional on its state in the previous year ($z_{i,t-1}$). We used a Bernoulli trial with probability $\phi_{g,t}$ or $b_{g,t}$ given that the individual had ($z_{i,t-1} = 1$) or had not ($z_{i,t-1} = 0$) yet entered the population, respectively. We derived estimates for local abundance ($N.loc_{g,t}$) of males and females by summing the z states for all individuals in the superpopulation for each sex and each year. We modeled availability in the study area each year as a Bernoulli trial with probability $\gamma_{g,t}$. We modeled the observation process of capturing a terrapin each sampling occasion ($y_{i,u} = 1, 0$ otherwise), conditional on the individual being alive and in the local population as a Bernoulli trial with probability $p_{g,u}$. We found no evidence of behavioral effects from capture (see Appendix A) and set capture and recapture parameters equal.

We modeled survival as a logit-linear function of sex, year, and an effect of a management intervention (flashing signage) using the relationship

$$\text{logit}(\phi_{g,t}) = \mu_g + \varepsilon_{g,t} + \beta_{per} X_t \tag{1}$$

where estimated parameters were μ_g (sex-specific intercept), $\varepsilon_{g,t}$ (random year effect for each sex), and β_{per} (additive effect of management on survival), and X_t is a binary indicator variable that is 0 in years prior to management implementation and 1 in years post-management. The random year effect for each sex was drawn from a zero-centered normal distribution with variance parameter $\sigma_{\phi, g}^2$. We modeled the process of annual entry into the population as a vector of probabilities that summed to 1 using a Dirichlet distribution constructed from prior random variables drawn from a diffuse gamma distribution. We then re-expressed these as conditional entry probabilities, the probability of entry at year t given that the individual had not yet entered the population (see Kéry and Schaub, 2012), for each year and sex. We

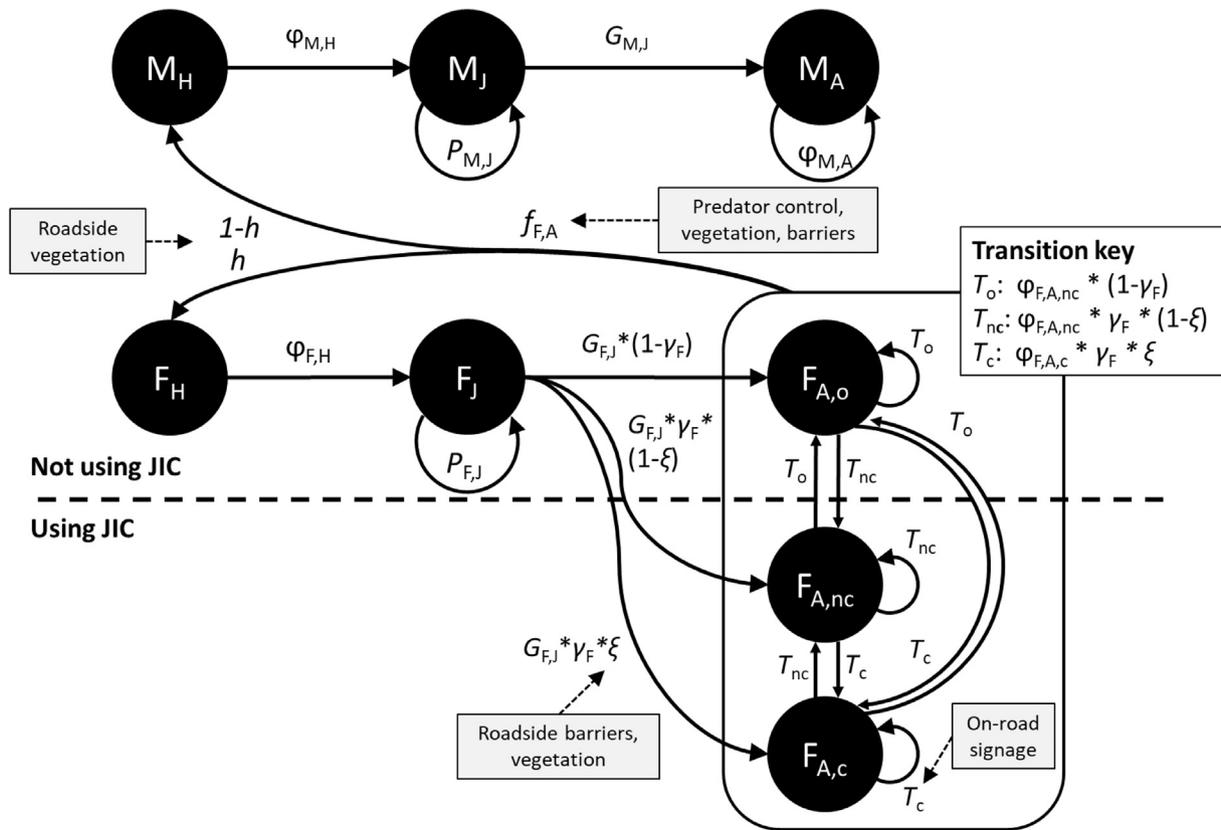


Fig. 3. Male (M) and female (F) three-stage model for projecting dynamics of a road-impacted diamondback terrapin population (adapted from Gilliland et al., 2014). Ovals represent life stages and states; grey rectangles represent management strategies expected to impact model parameters; symbols along arrows and in the transition key represent parameters described in Table 1. Subscript notations: M males; F females; H hatchlings; J juveniles; A adults; c crossing adults; nc non-crossing adults; o adults outside study area. The rounded rectangle contains all adult female states, and states below the dashed line represent individuals nesting on the JIC. Mortality states (e.g., $F_{d,c}$, $F_{d,o}$) and transitions to these states are not shown.

modeled site fidelity with a fixed sex effect and a random year effect drawn from a zero-centered normal distribution with variance parameter $\sigma_{y,g}^2$. Lastly, we modeled capture as a logit-linear function of the fixed effects of sex and tide amplitude β_{tide} (data obtained from <http://tidesandcurrents.noaa.gov>) and a random day effect drawn from a zero-centered normal distribution with variance parameter σ_U^2 . Tide amplitude may negatively affect detection since higher tides create wider, deeper creeks that increase the chance a terrapin can evade fixed-length seines used for sampling. See Appendix A for justification of parameter effect selection.

2.3.2. Multistate mark-recapture model

We developed a multistate Jolly-Seber submodel that combined data on recaptures of live individuals and recoveries of dead individuals on the road to estimate the influence of road crossing and management on survival and abundance of adult females in the JIC population. We considered individuals to be in one of six true states each year: not yet entered the population (NYE), alive and crossing the JIC ($F_{A,c}$), alive and not crossing the JIC ($F_{A,nc}$), alive and outside (i.e., not nesting on) the JIC ($F_{A,o}$), dead on the road ($F_{d,c}$), and dead elsewhere ($F_{d,o}$; $z_{i,t} = \{1: \text{NYE}, 2: F_{A,c}, 3: F_{A,nc}, 4: F_{A,o}, 5: F_{d,c}, 6: F_{d,o}\}$). We recorded individuals in the dataset as being in one of four observation states each year that were conditional on the true underlying states: $y_{i,t} = \{1: F_{A,c}, 2: F_{A,nc}, 3: F_{d,c}, 4: \text{not seen (NS)}\}$. We again assumed all individuals in a state shared the same capture or transition probabilities, and marks were retained and did not affect survival or behavior.

Using the same superpopulation approach as before, we fit the multistate submodel to the dataset augmented with capture histories of all NS states, and we assigned a latent inclusion state (w_i) for each individual in the augmented dataset that is drawn from a Bernoulli trial

with probability ψ_{ROAD} . We modeled the individual's state using a matrix of conditional probabilities of being in a particular state each year given its state in the previous year. Briefly, the parameters governing these state conditional probabilities were as follows: given that an individual has not entered the population before year t , it may enter with probability $b_{F,t}$; given its existence in the population, it may remain in the study area and use the JIC for nesting ($\gamma_{F,t}$); and given that it is nesting in the study area, it may cross the road with probability ξ and survive either having crossed the road ($\varphi_{F,A,c,t}$) or not crossed the road ($\varphi_{F,A,nc,t}$). We modeled the process of observing a terrapin in each sampling year, given that it is a member of the superpopulation, using a matrix of conditional probabilities, which included the probability of capturing a live terrapin, given that it was crossing ($p_{F,c}$) or not crossing ($p_{F,nc}$), and the probability of recovering an individual given that it died on the road ($p_{F,d}$). We considered any NYE, $F_{A,o}$, or $F_{d,o}$ individual as unobservable. The full matrices of conditional probabilities used in the state and observation models are presented in Appendix A. We derived annual estimates for adult female population size ($N_{F,t}$) by summing the z states for all individuals in the superpopulation that were alive ($F_{A,c}$, $F_{A,nc}$, or $F_{A,o}$) each year.

We modeled survival of females in the multistate dataset using all parameters in Eq. 1 with additional terms to estimate effects for crossing and non-crossing groups where

$$\text{logit}(\varphi_{g,t}) = \begin{cases} \mu_g + \varepsilon_{g,t} + \beta_{per}X_t + \beta_{cross} + \beta_{int}X_t & \text{for non-crossing females} \\ \mu_g + \varepsilon_{g,t} + \beta_{per}X_t - \beta_{cross} - \beta_{int}X_t & \text{for crossing females} \end{cases} \quad (2)$$

We included a zero-sum fixed effect (β_{cross}) for crossing where the same value was added to the survival of non-crossers and subtracted

Table 1

Parameter estimates used in a population viability analysis for diamondback terrapins. All survival rates are expressed annually, except where indicated.

Parameter	Value	SD	Description	Source
$\varphi_{F,H}$, $\varphi_{M,H}$	0.530	–	Survival of hatchlings (males and females)	Gilliand et al. (2014)
$\varphi_{F,J}$, $\varphi_{M,J}$	0.570	–	Survival of juveniles (males and females) ^a	Mitro (2003)
$\varphi_{M,A}$	0.680	0.082	Survival of adult males	Estimated, this study
$\varphi_{F,A}$	0.720	0.075	Survival of adult females (grand mean)	Estimated, this study
$\varphi_{F,A,c}$ (before)	0.235	0.069	Survival of crossing females before warning signage	Estimated, this study
$\varphi_{F,A,c}$ (after)	0.532	0.139	Survival of crossing females after warning signage	Estimated, this study
$\varphi_{F,A,nc}$	0.903	0.061	Survival of adult females not crossing roads	Estimated, this study
γ_M	0.865	0.138	Probability of adult males remaining in the study area	Estimated, this study
γ_F	0.683	0.135	Probability of adult females using causeway for nesting	Estimated, this study
ξ	0.531	0.033	Probability of adult females crossing the road	Estimated, this study
$b_{M,A}$	0.263	0.164	Probability of males entering the population	Estimated, this study
$b_{F,A}$	0.187	0.070	Probability of females entering the population	Estimated, this study
k	6.9	1.5	Mean clutch size ^b	Zimmerman (1992)
u	2	–	Mean clutch frequency per year	Roosenburg (1991)
φ_E	0.790	0.065	Natural survival of eggs (through nesting period)	Grosse et al. (2015)
ns_{hab}			Nest success by habitat type - the proportion of nests not depredated	
open	0.660	0.045	Open	Estimated, J.C.M., unpubl. data
hedges	0.495	0.051	Hedges	Estimated, J.C.M., unpubl. data
mounds	0.963	0.026	Mounds with electrified boxes	Quinn et al. (2015)
h_{hab}			Proportion of female hatchlings by habitat type	
open	1		Open	Grosse et al. (2015)
hedges	0.15		Hedges	Grosse et al. (2015)
mounds	1		Mounds with electrified boxes	Grosse et al. (2015)
Age_M	5		Age of first reproduction (males)	Lovich and Gibbons (1990)
Age_F	6		Age of first reproduction (females)	Lovich and Gibbons (1990)

^a Juvenile was a multi-year stage class, so annual survival (φ_J) was separated into sex-specific rates for surviving and remaining in the stage (P) or surviving and graduating to the adult stage class (G) in the population model (see text and Fig. 3).

^b Parameters k , u , ns_{hab} , φ_E , and $\varphi_{F,H}$ were used to calculate fertility (f).

from survival of crossers. We included a second zero-sum fixed effect (β_{int}) that was governed by the same indicator variable as β_{per} and added to the survival of non-crossers and subtracted from survival of crossers in years post-management. The interaction thus allowed the estimation of the impact of flashing signs on survival of crossing females relative to non-crossing females and to crossing females pre-installation.

2.4. PVA model

We constructed a stage-based, robust PVA model for the terrapin population (Fig. 3) using parameter estimates from this and other studies, and we predicted population growth and persistence probability under scenarios representing no management (baseline conditions), current management (flashing signs and a hybrid barrier at one crossing hot spot), and seven potential management strategies. We ran 1000 iterations of each scenario and projected the population for 50 years. To compare the consequences of scenarios, we estimated persistence probability as the proportion of iterations (out of 1000) that did not reach a quasi-extinction threshold of 50 individuals during the 50-year time horizon. We also estimated the mean population growth rate (λ) for each scenario by averaging the annual growth rates across the final 30 years of all iterations, where the annual growth rate was calculated as N_{t+1}/N_t . We discuss the construction of the baseline PVA model first, followed by alterations made to reflect management scenarios.

We expanded simple stage-based models (Morris and Doak, 2002) to represent dynamics realistic for the JIC terrapin population. We grouped individuals into six stage classes based on previous life history and population modeling studies (Lovich and Gibbons, 1990; Gilliland et al., 2014): female hatchlings (F_H ; age 1), female juveniles (F_J ; ages 2–5), female adults (F_A ; ages 6+), male hatchlings (M_H ; age 1), male juveniles (M_J ; ages 2–4), and male adults (M_A ; ages 5+). Since the juvenile stage lasted multiple years, we separated annual juvenile survival of each sex g into the probability of surviving and remaining a juvenile ($P_{J,g}$) and the probability of surviving and graduating to the adult stage ($G_{J,g}$), which were calculated using the number of years the

juvenile stage lasts for each sex (Caswell, 1989). We subdivided the adult female stage class into three subclasses used in the multistate model ($F_{A,c}$, $F_{A,nc}$, and $F_{A,o}$), and individuals' year-specific survival and transition probabilities depended on their crossing (c or nc) and site fidelity status on the JIC (Fig. 3). To model the processes of annual fertility (f) and hatchling sex-determination (h) that yielded the number of individuals that were hatched and survived to age 1, we specified the following sequential steps. Because habitat type (Grosse et al., 2015) and position along the JIC (J.C.M., unpubl. data) can influence nest survival, we assigned adult females that nested on the JIC into 100-m sections of the road using the proportion of terrapins observed in each section during road surveying. We then assigned females in each section to one of three habitats (hedge, open, or nest boxes) in proportion to the availability of each type in the section, which we calculated in a geographic information system (ARCGIS 10.1; ESRI, Redlands, CA). Nests survived (i.e., were not depredated) based on habitat-specific rates of nest success (ns_{hab}) that accounted for position, and we summed the surviving nests by habitat type. Eggs survived to produce new age 1 individuals with probability $\varphi_E * \varphi_H^{(3/4)}$, which represents the probability of surviving the 3-month period during the egg stage and the remaining $3/4$ of the year as a hatchling. Hatchlings were assigned a sex using habitat-specific hatchling sex ratios (h_{hab} ; the probability of a hatchling being female). We note that only adult females using the JIC contributed to recruitment of hatchlings each year; thus, we assumed individuals not using the JIC were either not breeding or nesting in an area outside the extent of our population of interest. We did not include a maximum age or density-dependent effects in this model.

The model used a 1-year time step and advanced individuals in each life stage through stochastic processes of survival, reproduction, and transition among stage classes using appropriate distributions (i.e., Binomial, Multinomial, Poisson) and demographic rates estimated from the integrated model or obtained from the literature (Table 1). We allowed certain demographic rates to vary between iterations and/or years while keeping other rates constant. We used the same initial stage abundances for all iterations. We set the initial abundance of adult female subclasses as the mean annual abundances estimated from the

integrated model. To calculate the initial abundance of adult males at the population scale, we assumed the ratio of males to females estimated at the local (creek) scale was equivalent to the sex ratio at the population (JIC) scale, and multiplied the local ratio by the estimated total female population abundance. We calculated initial abundances for all other stage classes using the adult male and female abundances and the stable stage distribution found in another terrapin population (Gilliand et al., 2014). We accounted for uncertainty due to parameter estimation and stochastic, year-to-year variation (Wade, 2002; Moore et al., 2012). For each PVA model iteration, we drew a single sample from posterior distributions in the integrated model, with replacement, and used estimates for adult survival rates representing baseline conditions (i.e., survival in years before JIC management was initiated) and a standard deviation of temporal variability in survival for M_A , $F_{A,c}$, and $F_{A,nc}$ stages. For a given draw, we retrieved the full complement of simulated quantities from a single MCMC iteration thus preserving correlations among parameters in the PVA. The sampled parameter values for each iteration defined probability distributions from which stochastic survival rates were drawn each year in the simulation. We sampled mean values of ξ and γ_F from their posterior distributions for each year of each iteration of the baseline model. We kept all other demographic rates constant across iterations and years. We acknowledge this approach did not fully account for the uncertainty of all parameters in the PVA model, but we explored the sensitivity of model predictions to incremental changes of all parameters (see *Sensitivity analysis*). This approach still allowed us to account for uncertainty around parameters estimated in this study and likely reduced further imprecision of model predictions that enabled easier comparison among management scenarios to inform decision-making.

We altered parameters in the baseline PVA model to simulate current management actions and seven alternative strategies. Given the multiple road-associated threats impacting this and other terrapin populations, management strategies were composed of different combinations of actions representing four types of management expected to affect model parameters (Fig. 3). Current management actions (the “status quo” strategy) consisted of the on-road flashing signs and the hybrid nest box barrier at one crossing hot spot. The seven alternative strategies included, in addition to status quo actions, one or more of the following three management actions: (1) hybrid barriers at two other hot spots of crossing identified on the JIC (Crawford et al., 2014b), (2) intensive removal of mesomammal predators to increase nest success (e.g., Munscher et al., 2012), and (3) roadside vegetation management to increase nest success and proportion of female hatchlings (Grosse et al., 2015). With input from local managers, we defined the vegetation management strategy as clearcutting hedges along an additional 12% (2.0/17.4 linear km) of JIC roadsides to create open nesting habitat. We obtained estimates for management effects from this and other empirical studies or expert elicitation of 12 terrapin research professionals. For current and potential strategies that included flashing signage, we used the mean $\varphi_{F,A,c}$ estimated in years post-management from the integrated model, and we employed the same procedures of sampling from posterior distributions to account for parameter uncertainty and stochasticity. We incorporated estimates from previous studies for the effects of hybrid barriers on proportion of terrapins crossing (Crawford et al., 2017), hybrid barriers on nest success (Quinn et al., 2015), hybrid barriers on proportion of hatchlings born female (Grosse et al., 2015), and vegetation management on nest success (J.C.M., unpubl. data) and hatchling sex ratios (Grosse et al., 2015). Finally, we used expert opinion to estimate the effects of predator management on nest success and all interactive effects among management actions. See Appendix A for further details about incorporating management effects into PVA model scenarios and Appendix B for our R code for the PVA model.

2.5. Sensitivity analysis

Predictions, and their precision, from the robust PVA are affected by the collective parametric uncertainty and temporal variation of model parameters, but we further explored the sensitivity of mean population growth rate and persistence to variation of individual demographic rates. We systematically increased and decreased baseline means of the following demographic parameters one at a time by 5% with all other parameters unaltered: annual survival of each life stage and adult female subclass, γ_F , ξ , and each parameter used to calculate fertility. Varying demographic rates by 5% represented small, realistic changes to parameters (less than the standard deviation for most estimates) and allowed for direct comparison of model outcomes. We estimated the change in mean λ resulting from 1000 runs of each model perturbation, relative to the baseline model. We also estimated sensitivity of persistence under each management strategy by replacing mean estimates of management effects with the lower and upper 90% confidence intervals around estimates obtained from expert opinion, in turn, while keeping all other rates unaltered.

3. Results

The Robust Design dataset included adult males (294 encounters of 194 individuals) and females (68 encounters of 56 individuals). Since we only captured 33 terrapins (with 7 total recaptures) from one of the creeks during the study period, we combined data from both creeks for analysis. Annual captures ranged from 4 to 100 individual males and 2 to 21 females. The multistate dataset contained 2307 encounters ($F_{A,c}$: 1065 [46.2%]; $F_{A,nc}$: 227 [9.8%]; $F_{d,c}$: 1015 [44.0%]) of 1984 individuals. The annual number of terrapins observed in any state on the JIC ranged from 171 to 448; the annual number found dead on the road ranged from 81 to 196. Across all study years, we marked 1076 individual females (crossing or not crossing) and collected 1015 struck and killed females on the JIC (107 marked, 908 unmarked).

At the local scale, we estimated a mean (95% BCI) annual abundance of 207 (125–303) males and 53 (33–80) females, yielding an estimated mean sex ratio of 80% males to 20% females. At the population scale, the mean female annual abundance was 1684 (881–2760), which included individuals outside the sampled area but alive in the population extent. An estimated 1265 (788–1918) females used the JIC for nesting (individuals in $F_{A,c}$, $F_{A,nc}$, $F_{d,c}$ states) each year, on average. We present posterior mean estimates and 95% BCIs for target parameters used in PVA models in Table 1. The estimated mean survival rate was similar for males and females with overlapping BCIs. Female survival showed an interaction between crossing status and management period (Fig. 4). Survival of crossing females was lower than non-crossing females in years pre- and post-management, but mean crossing female survival increased from 23.5% pre- to 53.2% post-management implementation while survival of non-crossing females remained similar. See Appendix A (Table A.2) for posterior estimates of additional parameters.

PVA simulations under baseline (no management) conditions predicted a declining population in 50 years (Fig. 5a) with the lowest persistence probability (Fig. 5b) among all scenarios. Current management conditions (status quo scenario [SQ]) increased λ and persistence probability, but the population was still predicted to decline. Mean estimates of λ from the seven alternative management scenarios ranged from 0.91 to 0.93, and persistence probability ranged from 0.59 to 0.77. Among scenarios that considered adding only one action to status quo actions, additional roadside barriers increased persistence probability more than predator or vegetation management. The scenario where all three actions were used in combination resulted in the highest persistence probability. Sensitivity analysis revealed that λ was influenced most by proportional changes to adult female survival, followed by juvenile female survival and probability of crossing the road. Population growth was influenced least by changes to female site

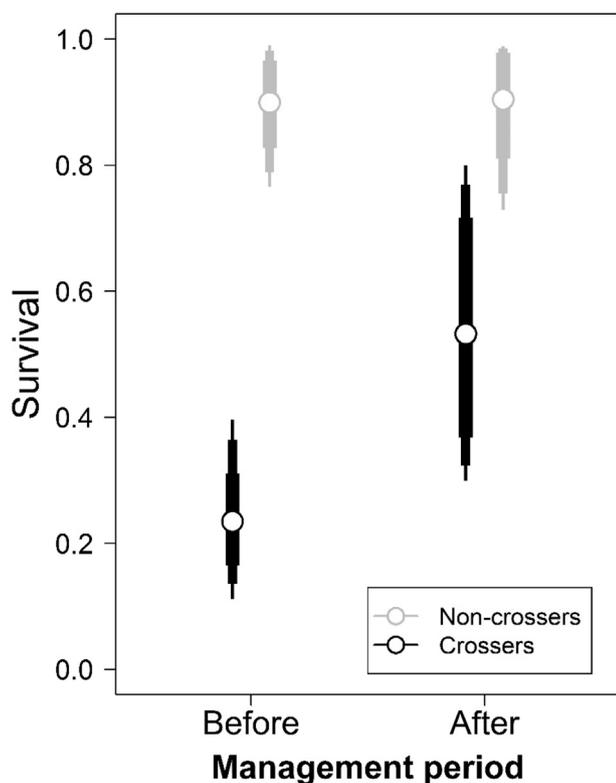


Fig. 4. Effects of road crossing status (crosser vs non-crosser) and management period (before vs after installation of flashing signage) on mean (\pm 75% [thick bars], 90% and 95% [thin bars] BCI) annual survival for adult female diamondback terrapins on Jekyll Island, GA.

fidelity and juvenile and adult male survival (Table A.4). Persistence estimates and ranks of management strategies were relatively insensitive to uncertainty around experts' estimates of management effects (Table A.5).

4. Discussion

There are few studies to date that used joint analyses, such as integrated population models, of multiple data sources to explore the conservation status and management targets for a population (Rhodes et al., 2011; Tempel et al., 2014; Lieury et al., 2015; Wilson et al., 2016; Saunders et al., 2018). Our work contributes an example of applying integrated modeling and robust PVA approaches for rigorous parameter estimation, population prediction, and management strategy evaluation for improved conservation decision-making. Conducting an integrated analysis for diamondback terrapins around Jekyll Island revealed findings essential for guiding management decisions: (i) the population is predicted to decline due to current impacts of road-associated threats on demographic rates, and (ii) current and potential management strategies varied in their expected outcomes, which allows for the prioritization of actions when seeking desired thresholds of population growth and persistence. Population outcomes (e.g., persistence probability), often used as criteria for evaluating management or policy decisions, hinge on the accuracy and precision of parameters used in predictive models. Although we did not estimate parameters separately with each dataset and compare them with estimates from the integrated model, we saw evidence of a gain in precision between estimates for male and females. There was a higher degree of uncertainty around male demographic rates, which we estimated using only the CREEK dataset, than female demographic rates, which were informed by both datasets. Integrated models represent a valuable tool for future conservation efforts that can efficiently use available data, which is often

limited for species of conservation concern, to reduce uncertainty and bias around parameter estimates. Numerous integrated models have been developed recently that can be adapted to various types of data, limitations of sampling designs, and context-specific demographic processes (reviewed in Schaub and Abadi, 2011; Zipkin and Saunders, 2018), and several online resources and code for developing integrated models have become available (e.g., <http://www.vogelwarte.ch/de/projekte/publikationen/bpa/>). Furthermore, robust PVAs formally account for remaining parametric uncertainty, which is important for producing unbiased predictions (Wade, 2002; Moore et al., 2012) to be used in a broader decision-making framework.

Integrated and PVA models usually require several assumptions that should be considered when interpreting results. In our integrated model, the extent to which survival, site fidelity, or entry are shared and consistent parameters between local- and population-scale datasets may have influenced parameter uncertainty. We ensured consistency of female survival across datasets by parameterizing this rate with a grand mean that was informed by both datasets and incorporating additional terms to estimate survival of crossing and non-crossing females with road survey data. In the absence of other information, we can assume that annual entry into the population is proportional to those of local creeks. A related, implicit assumption is that the subpopulation sampled at the local (creek) scale was representative of all terrapins within the population (JIC) scale. A limitation of our study was that we could only sample two creeks, due to logistical constraints, to draw inferences at the local scale and inform inferences at the population scale. We have no evidence that sampled creeks differed from others within the population extent; habitat characteristics were uniform across the population extent, and we observed no additional threats occurring in sampled or nearby creeks. Although we observed adequate interval widths of posterior estimates, sampling additional creeks in the future may reduce parameter uncertainty further. Despite being unable to test these assumptions at the present, we can rely on the integrated modeling approach to reduce potential biases of individual datasets. To simplify the PVA model, we used a mean fertility rate for all adult females; although, many turtle species lay larger and more frequent clutches as females increase in age and size (Congdon and van Loben Sels, 1993). Given that females that cross the road and survive likely repeat this behavior in subsequent years, road mortality may remove older females and reduce the mean fertility rate in road-impacted populations. Thus, we acknowledge literature-derived fertility rates used in this study could lead to overestimates of population growth and persistence. However, population growth was less sensitive to changes in parameters used to calculate fertility rates relative to effects of threats and management on other stages, especially adults (see Table A.4).

Our integrated analysis advances previous modeling efforts for diamondback terrapins and provides novel insights into their population dynamics while also corroborating previous demographic estimates. Terrapins are well-studied as a species of conservation concern. Still, estimating certain demographic rates has remained challenging given cryptic life stages (e.g., hatchlings) and dynamic movement through complex habitats that limit rates of detection, as well as long generation times that require longer study durations to measure population trends. In our study, estimates of survival for non-crossing adult females likely represent natural survival rates, consistent with previous estimates (0.83–0.94: Mitro, 2003, Hart, 2005), since no other direct female-specific threats are apparent in our study site. Mean male survival was slightly lower and more imprecise than previous estimates (0.79–0.90: Tucker et al., 2001, Hart, 2005). We estimated higher site fidelity for males than females, which is consistent with findings that females were more likely to move between tidal creeks, presumably related to upland nesting movements (Gibbons et al., 2001; Tucker et al., 2001; Sheridan et al., 2010; Maerz et al. in press). For females, site fidelity was still high (0.683), which is consistent with previous findings that female terrapins exhibit high fidelity to nesting sites

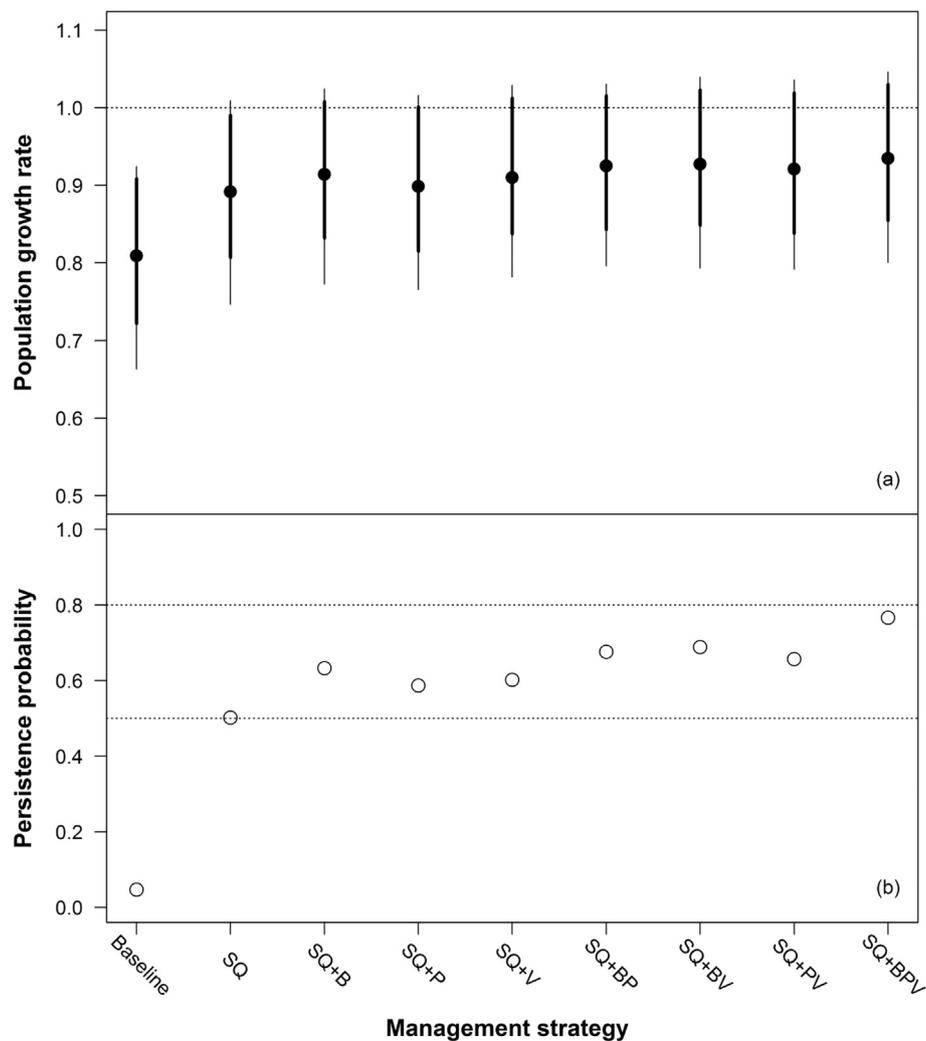


Fig. 5. Simulation outcomes (a: mean population growth rate λ with 90% [thick bars] and 95% [thin bars] BCI; b: mean persistence probability) for a 50-year projection of the diamondback terrapin population on Jekyll Island, GA under baseline (no management), status quo (SQ), and seven alternative management scenarios. Notations: B barriers at two additional crossing hot spots; P predator management; V vegetation management.

between years with few individuals dispersing to additional nesting areas (Szerlag-Egger and McRobert, 2007; Sheridan et al., 2010; Crawford et al., 2014b). No study has estimated recruitment rates for terrapins, and we were only able to estimate entry probabilities, which combined processes of immigration and within-population recruitment. Since estimated λ was sensitive to juvenile survival and recruitment into the adult stage class, developing sampling and modeling techniques for differentiating local recruitment from immigration will inform future models of population dynamics.

Despite extensive work in the field of road ecology, evaluating population-level impacts of roads on wildlife remains challenging. Previous road mortality studies have assessed impacts using naïve counts of dead individuals (e.g., Langen et al., 2007), predictive spatial models for wildlife-vehicle collisions based on species and road characteristics (e.g., Hels and Buchwald, 2001), survival estimates from limited mark-recapture or radio-telemetry (e.g., Row et al., 2007), or indirect indicators (e.g., population density, sex ratio) of road mortality in sites of varying road densities (e.g., Steen and Gibbs, 2004; Grosse et al., 2011). While each approach has merit for assessing road impacts to populations under practical sampling constraints, all are limited in their ability to estimate population consequences that are robust to important biases or assumptions (e.g., imperfect detection: Langen et al., 2007, Crawford et al., 2014a). This is the first study to advance these approaches by employing multistate models, or any joint analysis

(e.g., joint live-dead encounter model: Burnham, 1993), to directly estimate the impacts of road mortality on demographic rates. We found empirical evidence that, when road threats were left unmitigated, mortality on the JIC significantly reduced per-capita survival of crossing females relative to non-crossers and caused severe population declines. Furthermore, estimated survival of crossing females is likely conservatively high since researchers intervened to capture live terrapins found on the road that may have otherwise been struck by vehicles. The multistate model allowed for separate estimation of two processes that contribute to the cumulative impact of road mortality on local populations: the portion of the population exposed to the risk of road mortality and the magnitude of that risk (i.e., the degree to which survival is reduced when crossing). Disentangling these processes was essential for our PVA as we modeled the effects of two common road management actions designed to either (1) prevent individuals from crossing the road (i.e., barriers) or (2) increase survival of crossing individuals by targeting driver awareness (i.e., warning signage). Although obtaining multi-year mark-recapture datasets will be difficult in many contexts, our study demonstrates how these data can be used to develop context-specific estimates of road effects on populations needed to guide future research and management. Datasets requiring less effort (e.g., presence-absence data, population counts) can still be combined in integrated models to improve the precision of demographic estimates when mark-recapture data is (Schaub and Abadi,

2011) or is not available (Zipkin et al., 2014).

Current management actions increased the probability of persistence, relative to the baseline scenario, but additional actions were needed to further increase population outcomes. All management scenarios had overlapping and uncertain estimates of population growth due to parametric uncertainty and complexity of the PVA, but predicting population persistence offers a means to compare strategies for conservation decision-making. The best-performing strategy included all four types of management actions (Fig. 5), which complementarily targeted multiple threats, stage classes, and demographic rates. These results support previous conservation studies showing mitigation of multiple threats was required to ensure the viability of declining populations (Rhodes et al., 2011; Crawford et al., 2014a; Saunders et al., 2018). It is not surprising that additional roadside barriers resulted in higher probabilities of persistence since the PVA model was sensitive to changes in the probability of a nesting female crossing the road. The probability of crossing was closely linked with adult female survival – the most sensitive model parameter – since non-crossing terrapins survived at a significantly higher rate than those exposed to vehicle mortality. Thus, small changes in probability of crossing were accompanied by large changes in survival. Management strategies that prevent turtles from accessing the road should more efficiently increase population growth than strategies directly targeting survival of females on the road. Population outcomes have been found to be most sensitive to changes in adult survival in numerous elasticity analyses for long-lived reptiles (e.g., Crouse et al., 1987; Heppell, 1998). An important finding of our study was that flashing warning signage, the first-ever of its kind to target turtles, was associated with significant increases in survival of crossing individuals. Previous studies have found static warning signage to be ineffective (e.g., Putman, 1997), presumably due to driver habituation to signage during periods when signs are present in the absence of animal crossing activity. Alternatively, we implemented signs to flash around concentrated peaks (~2 h per day around daily high tide events) of terrapin activity to avoid driver habituation. Terrapins reliably use high tide as a cue for nesting migrations (Feinberg and Burke, 2003; Crawford et al., 2014b), so these devices can be deployed in areas of frequent road mortality throughout the species range. Signs may be a viable component of broader management strategies for terrapins and other species that demonstrate predictable and concentrated patterns of road-crossing activity. In addition to managing for adult terrapins, predator management has yielded increases in egg survival and recruitment (e.g., Munscher et al., 2012), and Grosse et al. (2015) proposed managing roadside vegetation (i.e., clear-cutting hedges) as an additional means to increase these parameters. Although each management action considered in this study increased population outcomes, the terrapin population was approaching stability but still expected to decline ($\lambda < 1.0$), on average, under the strategy that included all actions. Thus, we expect the use of additional or more intensive actions (i.e., constructing barriers that extend beyond crossing hot spots) would be needed to further increase persistence and stabilize the terrapin population on the JIC. Although our study focused on managing terrestrial threats, terrapin populations are frequently impacted by mortality in crab pots (Roosenburg et al., 1997; Grosse et al., 2011; Chambers and Maerz, in press), and both terrestrial and aquatic threats and management could be evaluated within a single study in the future.

Our work highlights the use of integrated models and robust PVAs to inform conservation decisions while overcoming challenges of limited data and low detection that are often associated with cryptic, rare, and at-risk species. Because conservation practitioners (e.g., U.S. Fish & Wildlife Service, State wildlife agencies) are often required to make management decisions for these species, linking integrated models with robust PVAs is a means to use data efficiently, determine parameters to which population outcomes are most sensitive, and assess the risk associated with potential strategies, including doing nothing. On Jekyll Island, our findings give impetus for increased local management to

meet population objectives, given that the diamondback terrapin population on Jekyll Island is currently declining due to road-associated threats and additional strategies were predicted to increase population persistence. Specifically, actions that prevent terrapins crossing at hot spots of activity complemented with on-road signage to further increase adult female survival and predator and vegetation removal to increase recruitment are expected to maximize population persistence. For other at-risk terrapin populations, future studies could better address sampling challenges and inform management decisions by collecting complementary datasets to be analyzed within an integrated framework. Multiple sampling methods have been tested or are in developmental phases for terrapins, including the use of modified crab traps (Roosenburg et al., 1997), photographic mark-resighting using drones, or presence-absence surveys using citizen science programs, which could each yield informative datasets. Our approach could be adapted for numerous other at-risk species needing status assessments and management decisions. For example, studies focused on cryptic pond-breeding anurans could incorporate productivity data from egg mass counts with occupancy data from call surveys in an integrated model and robust PVA to estimate demographic rates and persistence. Prior to implementing any management strategy, tradeoffs of other socio-economic objectives (e.g., cost, driver safety, road aesthetics) may be vital to consider in specific decision-making contexts. Accompanying implementation of management strategies with monitoring will allow local managers to better understand impacts of their effects, and this is especially important for novel actions such as flashing signs and vegetation clearing. Monitoring data could inform estimates of management effects originally obtained from expert opinion, and site-specific PVAs may be updated iteratively as part of an adaptive management framework.

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References

- Akçakaya, H.R., Sjögren-Gulve, P., 2000. Population viability analyses in conservation planning: an overview. *Ecol. Bull.* 48, 9–21.
- Aresco, M.J., 2005. Mitigation measures to reduce highway mortality of turtles and other

- herpetofauna at a North Florida lake. *J. Wildl. Manag.* 69, 549–560.
- Baird, R.C., 2009. Coastal urbanization: the challenge of management lag. *Manag. Environ. Qual.* 20, 371–382.
- Brooks, S.P., Gelman, A., 1998. General methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Stat.* 7, 434–455.
- Buhlmann, K.A., Osborn, C.P., 2011. Use of an artificial nesting mound by wood turtles (*Glyptemys insculpta*): a tool for turtle conservation. *Northeast. Nat.* 18, 315–334.
- Burnham, K., 1993. A Theory for Combined Analysis of Ring Recovery and Recapture Data. In: Lebreton, J., North, P. (Eds.), *Marked Individuals in the Study of Bird Population*. Birkhauser Verlag, Basel, Switzerland, pp. 199–213.
- Butler, J., Heinrich, G., Seigel, R., 2006. Third workshop on the ecology, status, and conservation of diamondback terrapins (*Malaclemys terrapin*): results and recommendations. In: *Chelonian Conservation and Biology*. 5. pp. 331–334.
- Caswell, H., 1989. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, U.S.A.
- Chambers, R.M., Maerz, J.C., 2018. Terrapin bycatch in the blue crab fishery. In: Roosenburg, W.M., Kennedy, V.S. (Eds.), *Ecology and Conservation of the Diamondback Terrapin*. Johns Hopkins University Press, Baltimore, MD (in press).
- Clark, J.S., Bjørnstad, O.N., 2004. Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology* 85, 3140–3150.
- Congdon, J.D., van Loben Sels, R.C., 1993. Relationships of reproductive traits and body size with attainment of sexual maturity and age in Blanding's turtles (*Emydoidea blandingi*). *J. Evol. Biol.* 6, 547–557.
- Crawford, B.A., 2015. Lessons from terrapin mortality and management on the Jekyll Island Causeway, Georgia, USA. In: *Roads and Ecological Infrastructure: Concepts and Applications for Small Animals*. Johns Hopkins University Press, Baltimore, MD, pp. 140–145.
- Crawford, B.A., Maerz, J.C., Nibbelink, N.P., Buhlmann, K.A., Norton, T.M., 2014a. Estimating the consequences of multiple threats and management strategies for semi-aquatic turtles. *J. Appl. Ecol.* 51, 359–366.
- Crawford, B.A., Maerz, J.C., Nibbelink, N.P., Buhlmann, K.A., Norton, T.M., Albeke, S.E., 2014b. Hot spots and hot moments of diamondback terrapin road-crossing activity. *J. Appl. Ecol.* 51, 367–375.
- Crawford, B.A., Moore, C.T., Norton, T.M., Maerz, J.C., 2017. Mitigating road mortality of diamondback terrapins (*Malaclemys terrapin*) with hybrid barriers at crossing hot spots. *Herpetol. Conserv. Biol.* 12, 202–211.
- Crouse, D.T., Crowder, L.B., Caswell, H., 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68, 1412–1423.
- Dorcas, M.E., Willson, J.D., Gibbons, J.W., 2007. Crab trapping causes population decline and demographic changes in diamondback terrapins over two decades. *Biol. Conserv.* 137, 334–340.
- Ewert, M.A., Jackson, D.R., Nelson, C.E., 1994. Patterns of temperature dependent sex determination in turtles. *J. Exp. Zool.* 270, 3–15.
- Feinberg, J.A., Burke, R.L., 2003. Nesting ecology and predation of diamondback terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New York. *J. Herpetol.* 37, 517–526.
- Game, E.T., Meijaard, E., Sheil, D., McDonald-Madden, E., 2014. Conservation in a wicked complex world: challenges and solutions. *Conserv. Lett.* 7, 271–277.
- Gibbons, J.W., Lovich, J.E., Tucker, A.D., Fitzsimmons, N.N., Greene, J.L., 2001. Demographic and ecological factors affecting conservation and management of the diamondback terrapin (*Malaclemys terrapin*) in South Carolina. In: *Chelonian Conservation and Biology*. 4. pp. 66–74.
- Gibbs, J.P., Shriver, W.G., 2002. Estimating the effects of road mortality on turtle populations. *Conserv. Biol.* 16, 1647–1652.
- Gilliand, S.C., Chambers, R.M., LaMar, M.D., 2014. Modeling the effects of crab potting and road traffic on a population of diamondback terrapins. In: *Proceedings of the Symposium on BEER 1:1*.
- Green, A.W., Bailey, L.L., 2015. Using Bayesian population viability analysis to define relevant conservation objectives. *PLoS One* 10, e0144786.
- Grosse, A.M., Maerz, J.C., Hepinstall-Cymerman, J., Dorcas, M.E., 2011. Effects of roads and crabbing pressures on diamondback terrapin populations in coastal Georgia. *J. Wildl. Manag.* 75, 762–770.
- Grosse, A.M., Crawford, B.A., Maerz, J.C., Buhlmann, K.A., Norton, T.M., Kaylor, M., Tuberville, T.D., 2015. Effects of vegetation structure and artificial nesting habitats on hatchling sex determination and nest survival of diamondback terrapins. *J. Fish Wildl. Manag.* 6, 19–28.
- Hart, K.M., 2005. *Population Biology of Diamondback Terrapins (Malaclemys terrapin): Defining and Reducing Threats across their Geographic Range* (PhD dissertation). Duke University, Durham, NC.
- Hegg, D., MacKenzie, D.I., Jamieson, I.G., 2013. Use of Bayesian population viability analysis to assess multiple management decisions in the recovery programme for the endangered takahe *Porphyrio hochstetteri*. *Oryx* 47, 144–152.
- Hels, T., Buchwald, E., 2001. The effect of road kills on amphibian populations. *Biol. Conserv.* 99, 331–340.
- Heppell, S.S., 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998, 367–375.
- Heppell, S.S., Crowder, L.B., Crouse, D.T., 1996. Models to evaluate headstarting as a management tool for long-lived turtles. *Ecol. Appl.* 6, 556–565.
- Hoyle, S.D., Maunder, M.N., 2004. A Bayesian integrated population dynamics model to analyze data for protected species. *Anim. Biodivers. Conserv.* 27, 247–266.
- Kéry, M., Schaub, M., 2012. *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*. Academic Press, Oxford, UK.
- Krueger, T., Page, T., Hubacek, K., Smith, L., Hiscock, K., 2012. The role of expert opinion in environmental modelling. *Environ. Model. Softw.* 36, 4–18.
- Langen, T.A., Machniak, A., Crowe, E.K., Mangan, C., Marker, D.F., Liddle, N., Roden, B., 2007. Methodologies for surveying herpetofauna mortality on rural highways. *J. Wildl. Manag.* 71, 1361–1368.
- Lieury, N., Gallardo, M., Ponchon, C., Besnard, A., Millon, A., 2015. Relative contribution of local demography and immigration in the recovery of a geographically-isolated population of the endangered Egyptian vulture. *Biol. Conserv.* 19, 349–356.
- Link, W.A., Eaton, M.J., 2012. On thinning of chains in MCMC. *Methods Ecol. Evol.* 3, 112–115.
- Lovich, J.E., Gibbons, J.W., 1990. Age at maturity influences adult sex-ratio in the turtle *Malaclemys terrapin*. *Oikos* 59, 126–134.
- Maerz, J.C., Seigel, R.A., Crawford, B.A., 2018. Terrapin conservation: mitigating habitat loss, road mortality, and subsidized predators. In: Roosenburg, W.M., Kennedy, V.S. (Eds.), *Ecology and Conservation of the Diamondback Terrapin*. Johns Hopkins University Press, Baltimore, MD (in press).
- Maunder, M.N., 2004. Population viability analysis based on combining Bayesian, integrated, and hierarchical analyses. *Acta Oecol.* 26, 85–94.
- McGowan, C.P., Runge, M.C., Larson, M.A., 2011. Incorporating parametric uncertainty into population viability analysis models. *Biol. Conserv.* 144, 1400–1408.
- Mitro, M.G., 2003. Demography and viability analyses of a diamondback terrapin population. *Can. J. Zool.-Revue Canadienne De Zoologie* 81, 716–726.
- Moore, C.T., Converse, S.J., Folk, M.J., Runge, M.C., Nesbitt, S.A., 2012. Evaluating release alternatives for a long-lived bird species under uncertainty about long-term demographic rates. *J. Ornithol.* 152, 339–353.
- Morris, W.F., Doak, D.F., 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland, Massachusetts.
- Munscher, E.C., Kuhns, E.H., Cox, C.A., Butler, J.A., 2012. Decreased nest mortality for the Carolina diamondback terrapin (*Malaclemys terrapin centrata*) following removal of raccoons (*Procyon lotor*) from a nesting beach in northeastern Florida. *Herpetol. Conserv. Biol.* 7, 176–184.
- Pollock, K.H., 1982. A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manag.* 752–757.
- Putman, R.J., 1997. Deer and road traffic accidents: options for management. *J. Environ. Manag.* 51, 43–57.
- Quinn, D.P., Kaylor, M., Norton, T.M., Buhlmann, K.A., 2015. Nesting mounds with protective boxes and an electric wire as tools to mitigate diamond-backed terrapin (*Malaclemys terrapin*) nest predation. *Herpetol. Conserv. Biol.* 10, 969–977.
- R Core Team, 2013. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rhodes, J.R., Ng, C.F., de Villiers, D.L., Preece, H.J., McAlpine, C.A., Possingham, H.P., 2011. Using integrated population modelling to quantify the implications of multiple threatening processes for a rapidly declining population. *Biol. Conserv.* 144, 1081–1088.
- Roosenburg, W.M., 1991. The diamondback terrapin: Population dynamics, habitat requirements, and opportunities for conservation. In: *New Perspectives in the Chesapeake System: A Research and Management Partnership. Proceedings of a Conference*. CRC Publishing, pp. 227–234.
- Roosenburg, W.M., Cresko, W., Modesitte, M., Robbins, M.B., 1997. Diamondback terrapin (*Malaclemys terrapin*) mortality in crab pots. *Conserv. Biol.* 11, 1166–1172.
- Row, J.R., Blouin-Demers, G., Weatherhead, P.J., 2007. Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). *Biol. Conserv.* 137, 117–124.
- Royle, J.A., Dorazio, R.M., 2012. Parameter-expanded data augmentation for Bayesian analysis of capture-recapture models. *J. Ornithol.* 152, 521–537.
- Saunders, S.P., Cuthbert, F.J., Zipkin, E.F., 2018. Evaluating population viability and efficacy of conservation management using integrated population models. *J. Appl. Ecol.* <http://dx.doi.org/10.1111/1365-2664.13080>.
- Schaub, M., Abadi, F., 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J. Ornithol.* 152, 227–237.
- Schmolke, A., Thorbek, P., DeAngelis, D.L., Grimm, V., 2010. Ecological models supporting environmental decision making: a strategy for the future. *Trends Ecol. Evol.* 25, 479–486.
- Servanty, S., Converse, S.J., Bailey, L.L., 2014. Demography of a reintroduced population: moving toward management models for an endangered species, the whooping crane. *Ecol. Appl.* 24, 927–937.
- Sheridan, C.M., Spotila, J.R., Bien, W.F., Avery, H.W., 2010. Sex-biased dispersal and natal philopatry in the diamondback terrapin, *Malaclemys terrapin*. *Mol. Ecol.* 19, 5497–5510.
- Shoemaker, K.T., Breisch, A.R., Jaycox, J.W., Gibbs, J.P., 2013. Reexamining the minimum viable population concept for long-lived species. *Conserv. Biol.* 27, 542–551.
- Steen, D.A., Gibbs, J.P., 2004. Effects of roads on the structure of freshwater turtle populations. *Conserv. Biol.* 18, 1143–1148.
- Su, Y.-S., Yajima, M., 2012. R2jags: A Package for Running Jags from R.
- Szerlag-Egger, S., McRobert, S.P., 2007. Northern diamondback terrapin occurrence, movement, and nesting activity along a salt marsh access road. In: *Chelonian Conservation and Biology*. 6. pp. 295–301.
- Tempel, D.J., Peery, M., Gutiérrez, R., 2014. Using integrated population models to improve conservation monitoring: California spotted owls as a case study. *Ecol. Model.* 289, 86–95.
- Tucker, A.D., Gibbons, J.W., Greene, J.L., 2001. Estimates of adult survival and migration for diamondback terrapins: conservation insight from local extirpation within a metapopulation. *Can. J. Zool.* 79, 2199–2209.
- Wade, P.R., 2002. Bayesian population viability analysis. In: Beissinger, S.R., McCullough, D.R. (Eds.), *Population Viability Analysis*. University of Chicago Press, Chicago, IL, pp. 213–238.
- Wilson, S., Gil-Weir, K.C., Clark, R.G., Robertson, G.J., Bidwell, M.T., 2016. Integrated population modeling to assess demographic variation and contributions to population growth for endangered whooping cranes. *Biol. Conserv.* 197, 1–7.
- Zimmerman, T.D., 1992. *Latitudinal Reproductive Variation of the Salt Marsh Turtle, the Diamondback Terrapin (Malaclemys terrapin)* (MS thesis). University of Charleston, Charleston, SC.
- Zipkin, E.F., Saunders, S.P., 2018. Synthesizing multiple data types for biological conservation using integrated population models. *Biol. Conserv.* 217, 240–250.
- Zipkin, E.F., Thorson, J.T., See, K., Lynch, H.J., Grant, E.H.C., Kanno, Y., Chandler, R.B., Letcher, B.H., Royle, J.A., 2014. Modeling structured population dynamics using data from unmarked individuals. *Ecology* 95, 22–29.