



Reexamining the Minimum Viable Population Concept for Long-Lived Species

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Abstract: For decades conservation biologists have proposed general rules of thumb for minimum viable population size (MVP); typically, they range from hundreds to thousands of individuals. These rules have shifted conservation resources away from small and fragmented populations. We examined whether iteroparous, long-lived species might constitute an exception to general MVP guidelines. On the basis of results from a 10-year capture-recapture study in eastern New York (U.S.A.), we developed a comprehensive demographic model for the globally threatened bog turtle (*Glyptemys mublenbergii*), which is designated as endangered by the IUCN in 2011. We assessed population viability across a wide range of initial abundances and carrying capacities. Not accounting for inbreeding, our results suggest that bog turtle colonies with as few as 15 breeding females have >90% probability of persisting for >100 years, provided vital rates and environmental variance remain at currently estimated levels. On the basis of our results, we suggest that MVP thresholds may be 1–2 orders of magnitude too high for many long-lived organisms. Consequently, protection of small and fragmented populations may constitute a viable conservation option for such species, especially in a regional or metapopulation context.

Keywords: Bayesian state-space modeling, capture-recapture, conservation triage, minimum viable population, population viability analysis (PVA), small population paradigm

Reexaminando el Concepto de Población Mínima Viable para Especies Longevas Resumen

Resumen: Durante décadas, los biólogos de la conservación han propuesto reglas generales básicas para el tamaño poblacional mínimo viable (TMV); típicamente, fluctúan entre cientos y miles de individuos. Estas reglas han desplazado recursos para poblaciones pequeñas y fragmentadas. Examinamos si especies iteróparas, longevas pueden constituir una excepción a las reglas generales del TMV. Con base en los resultados de un estudio de captura-recaptura durante 10 años en el este de Nueva York (E.U.A.), desarrollamos un modelo demográfico integral para la tortuga *Glyptemys mublenbergii* amenazada globalmente, considerada en peligro por la UICN (2011). Evaluamos la viabilidad poblacional de un amplio rango de abundancias iniciales y capacidades de carga. Sin considerar la endogamia, nuestros resultados sugieren que colonias de *G. mublenbergii* con tan solo 15 hembras reproductoras tiene >90% de probabilidad de persistir por >100 años, suponiendo que las tasas vitales y la variación ambiental permanecen en los niveles estimados actuales. Con base en nuestros resultados, sugerimos que los umbrales del TMV pueden ser 1–2 órdenes de magnitud más altos para muchos organismos longevas. Consecuentemente, la protección de poblaciones pequeñas y fragmentadas pueden constituir una opción de conservación para tales especies, especialmente en un contexto regional o metapoblacional.

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Palabras Clave: Análisis de viabilidad poblacional (AVP), captura-recaptura, categoría de conservación, modelo bayesiano estado-espacio, paradigma de la población pequeña, población mínima viable

Introduction

Current abundance plays a prominent role in classifying endangerment (Mace et al. 2008; Vie et al. 2008) because abundance data are widely available and relevant to population viability (Purvis et al. 2000; Clements et al. 2011). For years conservation biologists have proposed minimum abundance thresholds (minimum viable population [MVP]) below which populations have an unacceptable risk of extirpation (Shaffer 1981). Generic rule-of-thumb estimates for MVP are in demand due to the paucity of information for developing species-specific MVP estimates (Brook et al. 2011) and the utility of clear and simple guidelines in communicating conservation science to policy makers (Tear et al. 2005). Recently it has been suggested that MVP thresholds of thousands or even tens of thousands of individuals may be required to ensure long-term population persistence (Reed et al. 2003; Traill et al. 2007; Traill et al. 2010; but see Jamieson & Allendorf 2012). Although some conservation biologists caution against the use of generic MVP thresholds (e.g., Flather et al. 2011), efforts to generalize MVP thresholds across species continue to garner substantial attention (Traill et al. 2010; Bradshaw et al. 2011; Brook et al. 2011).

Conservation triage, in which management actions with low probability of success are bypassed in favor of less quixotic efforts, is a logical management response to populations that have fallen well below MVP thresholds (Traill et al. 2010; Clements et al. 2011). However, conservation triage may lead to irreversible loss of species or populations (Pimm 2000). In many cases, particularly for imperiled species relegated to small and fragmented populations, available habitat cannot feasibly support hundreds or thousands of individuals, even under ambitious habitat restoration scenarios. A broad policy of conservation triage informed by generic MVP estimates would presumably direct substantial conservation resources away from species occurring in small and fragmented populations. To reduce the risk of misguided triage of small yet viable populations, we investigated a potential exception to generic MVP rules of thumb.

Long-lived, iteroparous species may challenge the general rule that that viable populations must number in the thousands or tens of thousands of individuals. Evolutionary and genetic issues (e.g., inbreeding) notwithstanding (Jamieson & Allendorf 2012), environmental stochasticity (including catastrophic events) is generally considered the most important determinant of viability for small populations, and demographic stochasticity is thought to increase vulnerability at abundances ≤ 50 individuals (Lande 1993; Brook et al. 2006). However, populations of long-lived, iteroparous species may be relatively sta-

ble under typical sources of environmental stochasticity; reproductive adults can persist through harsh years and compensate with higher fecundity during favorable years and thus effectively smooth interannual changes in resource availability (e.g., Gaillard et al. 1998). Turtles are emblematic of this life-history pattern, characterized by iteroparity, very long generation times (often up to 20 or 30 years), and populations that are far more sensitive to long-term changes in adult survival rate than to short-term fluctuations in juvenile survival rate or fecundity (Jonsson & Ebenman 2001). Among the many threatened turtle species relegated to very small populations are the Burmese star tortoise (*Geochelone platynota*), Vietnamese pond turtle (*Mauremys annamensis*), Madagascan big-headed Turtle (*Erymnochelys madagascariensis*), and North American bog turtle (*Glyptemys mublenbergii*) (Turtle Conservation Coalition 2011).

We used a well-studied population of bog turtles as a case study to investigate a possible exception to previously published MVP rules of thumb. The bog turtle is a small, long-lived turtle that has declined precipitously over the past century and is listed as Threatened in the United States (USFWS 2001). Historically, bog turtle populations probably persisted in dynamically stable metapopulations whereby recolonization events compensated for extirpations (Rosenbaum et al. 2007). The decline of the bog turtle has been attributed to the loss of stable metapopulations via fragmentation and habitat loss (Carter et al. 1999). Most extant bog turtle populations are thought to comprise <50 individuals (Rosenbaum et al. 2007). Small population sizes and dispersal limitations raise concerns about vulnerability to demographic and environmental stochasticity (USFWS 2001). We built a comprehensive demographic model for bog turtles with long-term capture-recapture data and assessed MVP. Finally, we contrasted our MVP estimate for this species with general MVP rules of thumb. We hope our findings will promote critical assessment of the utility of general MVP thresholds for other threatened, long-lived species.

Methods

Study System

The bog turtle is a diminutive freshwater turtle of the eastern United States (adult carapace length 7.9–11.4 cm). Its home range varies from 0.05–2 ha. Nesting, feeding, and hibernation frequently occur within the same fen (USFWS 2001). The bog turtle (northern population) is listed as endangered by the International Union for Conservation

of Nature (IUCN 2012), as threatened under the U.S. Endangered Species Act (USFWS 2001), and is protected as an endangered or threatened species in many U.S. states (e.g., New York, Massachusetts, Connecticut). The bog turtle is considered one of the most imperiled turtle species globally (Turtle Conservation Coalition 2011).

The study region comprised a complex of swamps, fens, and wet meadows within the Taconic highlands extending from southeastern New York into southwestern Massachusetts. This valley supported >20 extant bog turtle colonies separated by distances ranging from hundreds of meters to tens of kilometers interspersed by a range of land-cover types and potential barriers to movement (e.g., ridges, streams, roads). Our focal fen complex (Fig. 1) was a network of approximately 11 calcareous fens near the center of the study region and supported some of the largest known bog turtle populations in New York (Jaycox & Breisch 2006).

Data Collection

During April and May of 2001 through 2007, systematic area-constrained surveys were conducted at each of 4 fens within the focal fen complex (sites WFP, EFP, CFP, and SHR) (Fig. 1) approximately 3 days/year by 3–6 experienced volunteers with the New York State Natural Heritage Program and the Endangered Species Unit of the New York State Department of Environmental Conservation (Jaycox & Breisch 2006). From 15 April through 15 July 2008 to 2010, the surveys were expanded to include all known occupied habitat patches within the focal fen complex for which landowner permission could be obtained (sites EMF, MRF, and BUL) (Fig. 1) and 2 fens within a complex approximately 20 km north of the focal fen complex (sites DSM and COL). During this second phase, surveys were conducted 5 days/week by 2–3 experienced researchers. All bog turtle habitat (fen and connected shallow wetlands) was visited during each survey bout. Survey duration for a single fen was 1–6 hours, depending on fen area and number of turtles encountered. One to 3 fens were surveyed during a typical survey day. Workers visually scanned an area to locate basking turtles and used tactile survey methods (muddling or sifting muck by hand) to locate individuals occupying underground retreats (Whitlock 2002). Ages of juvenile and young adult bog turtles were estimated on the basis of annulus count from the 4 largest plastral scutes, and gender was determined visually. All turtles with one or more full years of growth were assigned a unique identification code by notching marginal scutes. Due to practical and ethical concerns, hatchling turtles (with no discernable growth) were not assigned a unique code. Turtles were released at point of capture immediately after processing. Due to limited survey effort in 2001, we pooled survey data from 2001 and 2002 before analyses.

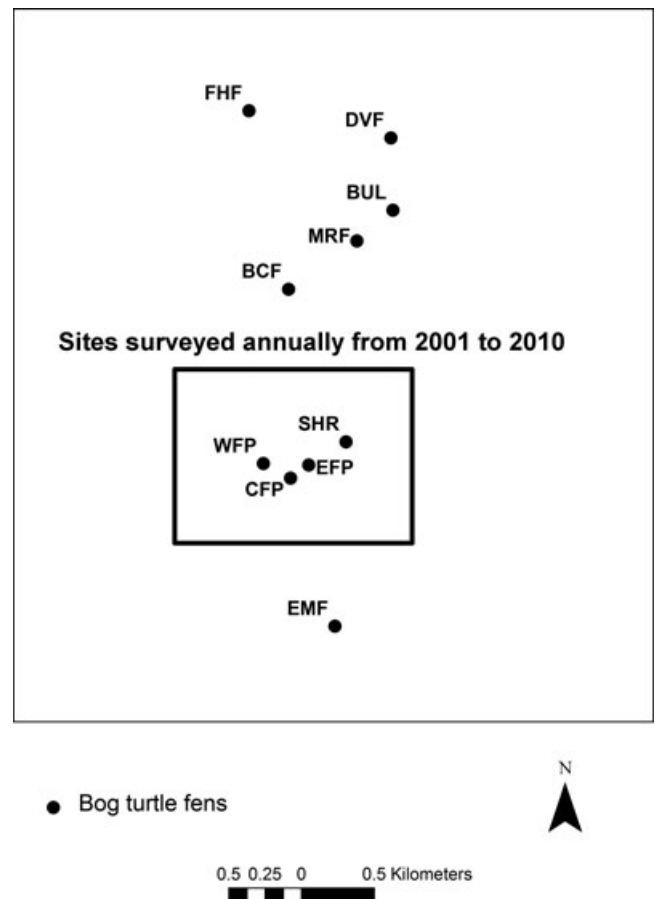


Figure 1. Schematic depiction of the study populations of bog turtles in southeastern New York State. The geographic configuration of the focal fen complex is illustrated (sites in rectangle, long-term study populations surveyed annually from 2001 to 2010; EMF, MRF, and BUL, sites surveyed only during the spring and summer of 2008–2009; DVF and FHF, not surveyed; BCF, surveyed extensively, but only 2 bog turtles were found). Two additional populations surveyed in 2008–2009 (COL and DSM) were approximately 20 km north of the fen complex pictured here.

Statistical Analyses

We used Bayesian closed-population models (assuming no entry or removal of individuals) to estimate abundance for all study populations. To accommodate random variation among individuals, we used the data-augmentation framework, in which an excess of hypothetical unobserved individuals (all-zero rows) was appended to the capture-history matrix. Under this framework, we inferred true population membership status on the basis of information on capture probability (Royle & Dorazio 2008). We fitted heterogeneity in capture probability across individuals, fen sites, and survey bouts with

logit-normal random intercept terms (Royle & Dorazio 2008). We estimated adult abundance for the 2008 – 2009 study period only, during which all study populations were simultaneously subject to intensive surveys. Juvenile turtles (<9 years old) were excluded from these abundance estimates because young turtles were more likely to violate closed-population assumptions over the 2-year period (abundance estimates derived from open-population models included adults and juveniles [see below]). We tested for a relation between abundance and fen area with standard linear regression. Fen area was estimated by digitizing polygons from orthorectified aerial photographs (New York State GIS Clearinghouse, 0.5-foot resolution) in ArcGIS 9.3.1 (ESRI Corporation, Redlands, California) following field inspection to adjust fen boundaries.

We used Bayesian open-population models (allowing for mortality and recruitment) to estimate abundance (adults and juveniles, excluding neonates) and demographic rates (survival and fecundity) for the 4 long-term study populations at the focal fen complex (Fig. 1). We modified open-population models from the data-augmented Schwarz–Arnason formulation (Jolly-Seber variant) of Royle and Dorazio (2008). We used a robust design framework to enhance estimation of survival and capture probabilities and assumed populations were closed within years and open to mortality and recruitment among years (Pollock et al. 1990). We modeled survival rates and probabilities of capture as logit-linear functions of years to maturity (e.g., 9 for a neonate turtle and 0 for an adult) and annual environmental variability in survival rate as a logit-normal random intercept. Entry of yearling individuals into each population was modeled under the data-augmentation framework. Total numbers of yearling recruits varied across time and across fen sites. Annual abundance, per capita fertility rate (average number of yearlings produced per mature female per year), final age distribution, and juvenile fraction (proportion of total abundance accounted for by juveniles under 9 years of age) were computed as derived parameters. Annual survival and fecundity estimates were stored for use in the population projection model (see below). We pooled fen sites CFP and EFP for the open-population analysis due to low abundance of turtles (insufficient data to model separately) and geographic proximity.

We estimated parameters with Markov-Chain Monte Carlo (MCMC) in WinBUGS (version 1.4) (Lunn et al. 2000) via the R2WinBUGS package in R (Sturtz et al. 2005; R Development Core Team 2012). Uninformative uniform prior probability distributions were assigned to all parameters (Supporting Information). We discarded the initial 10,000 MCMC samples as a burn-in. We performed a further 20,000 MCMC iterations and saved every 10th iteration to reduce serial autocorrelation among samples (Bolker 2008). We tested for convergence of the Markov chains to the stationary posterior distribution with the

Gelman–Rubin diagnostic (Bolker 2008). We summarized posterior distributions for all parameters with the mean of all MCMC samples as a point estimate and the 2.5 and 97.5 percentiles of the MCMC samples as a 95% credible interval (Bolker 2008). Our R and WinBUGS code and a detailed description of the statistical model are in Supporting Information.

Projection Modeling

We constructed a simple, individual-based projection model of bog turtle population dynamics. We sampled input parameters directly from the open-population model described above. We modeled production of yearlings with a Poisson distribution (Burgman et al. 1993), the mean of which was the product of previous-year female abundance and expected per capita fertility rate (Eq. 1). Annual survival of each individual was modeled as a Bernoulli trial with probability equal to the expected age-appropriate survival rate. To model environmentally driven variation in fecundity and (age-specific) survival rates, we sampled, with replacement, year-specific survival and fertility rates from the open-population capture-recapture analysis. We contrasted the magnitude of environmental variability within our study period with annual environmental variance over the past century using climate records for the past 100 years downloaded from the PRISM database (Daly et al. 2002).

Lacking information on density dependence in vital rates or population growth rate for this species, we conservatively assumed no compensatory density dependence for any demographic process at or below initial abundance values. To constrain abundance near initial values, we introduced a logistic density-dependence formulation for yearling production that affected only populations at or above initial abundance levels:

$$\begin{cases} \text{yearlings}_t = N_adult_{t-1} \times \text{fertility}_t \\ \quad \times \left(1 - \frac{N_{t-1}}{2 \cdot N_0}\right) & \{N_{t-1} \geq N_0\} \\ \text{yearlings}_t = N_adult_{t-1} \times \text{fertility}_t & \{N_{t-1} < N_0\} \end{cases} \quad (1)$$

where N_adult_t is adult female abundance at year t , fertility_t is expected number of female offspring produced per adult female at year t , N_t is total female abundance (including juveniles) at year t , and N_0 is initial abundance. Because mean fertility values below current estimated levels tended to result in below-replacement growth, the net result of this method was to set a soft abundance ceiling (or carrying capacity) approximately equal to initial abundance.

We took parameter values for projection models directly from the open-population capture-recapture results. We treated each multivariate MCMC sample as an independent draw from the joint posterior probability

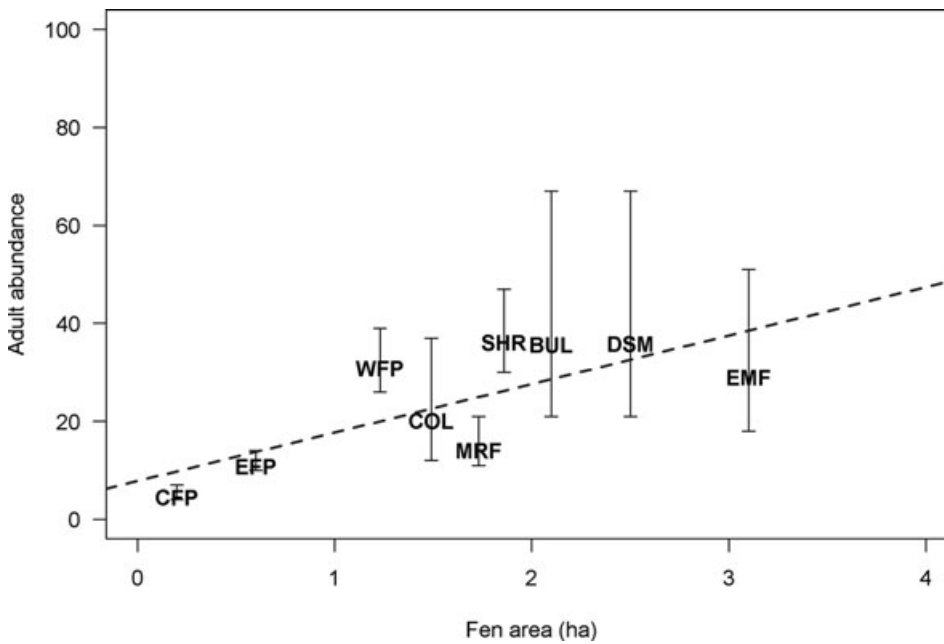


Figure 2. Adult abundance estimates (age < 9) for 9 bog turtle populations in southeastern New York from 2008 to 2010. The dotted line illustrates the linear relation between abundance and fen area.

distribution of all vital-rate parameters (Wade 2002). We sampled parameter values for projection models once per iteration (i.e., a 100-year simulation run) and held them constant within iterations (Wade 2002). Populations were considered functionally extirpated after reaching a quasi-extinction threshold of 2 adult females or fewer at any point during the simulation (approximating the smallest known extant bog turtle populations [e.g., population CFP from Fig. 2]), although all simulations were allowed to run to completion. We estimated extirpation probability as the proportion of simulation runs ($n = 1000$) reaching the quasi-extinction threshold at least once during the 100-year duration. To evaluate the effect of demographic and environmental stochasticity on the viability of very small bog turtle populations and to assess MVP size for bog turtles, we ran projection models for 4 hypothetical initial population sizes: 6, 10, 20, and 30. Initial age distributions varied among iterations and were drawn from the posterior distribution of final-year ages estimated from the capture-recapture analyses. All simulation models were female-only because we presumed females were the limiting sex (Pearse & Avise 2001). A more detailed description of the projection model and the R code are in Supporting Information.

Results

From 2001 to 2010, 554 capture records were compiled for 148 distinct bog turtles at the 4 long-term study populations (sites SHR, WFP, and EFP). From 2008 to 2010, an additional 154 captures of 102 distinct bog turtles were recorded at 3 additional fen sites within the focal fen complex and 2 additional sites outside the complex

(Fig. 1). No bog turtles were recaptured outside their original population of capture. Sex ratios of captures were female biased. There were 408 female capture records (149 distinct individuals) and 256 male capture records (84 distinct individuals). We determined that bog turtles reached sexual maturity at 9 years of age (consistent with Ernst 1977) because gravid females were never observed with fewer than 9 annuli and growth rates declined markedly thereafter.

Mean adult abundance estimates for populations within the focal fen complex from 2008 to 2009 varied from 5 (site CFP) to 38 adult turtles (site SHR) (Fig. 2). Mean capture probability was 0.24/survey bout, and the among-population standard deviation for capture probability was 0.55 on the logit scale (resulting in capture probabilities of 0.20–0.45 among study populations). Estimated standard deviation for capture probability among survey bouts and among individuals was 0.25 and 0.45 on the logit scale, respectively. Abundance estimates correlated strongly with estimated fen area (Fig. 2) ($R^2 = 0.546$, $p = 0.023$). On the basis of linear regression ($n = 7.85 + 9.89 \times \text{area}$), expected abundance was approximately 20 adult turtles for a 1-ha fen and approximately 60 adult turtles for a 5-ha fen.

Age-specific survival rates varied from 0.48 (95% credible interval 0.39 to 0.55) for yearling bog turtles to 0.96 (95% credible interval 0.94 to 0.97) for mature bog turtles (age ≥ 9) (Fig. 3b). Year-to-year coefficient of variation (CV) in survival was approximately 0.15 for young juveniles and 0.02 for adults. Mean capture probability per survey varied from 0.02 for yearling bog turtles to 0.19 for mature bog turtles (Fig. 3a). Annual abundance estimates for all 3 long-term study populations were stable, and temporal variation in abundance was

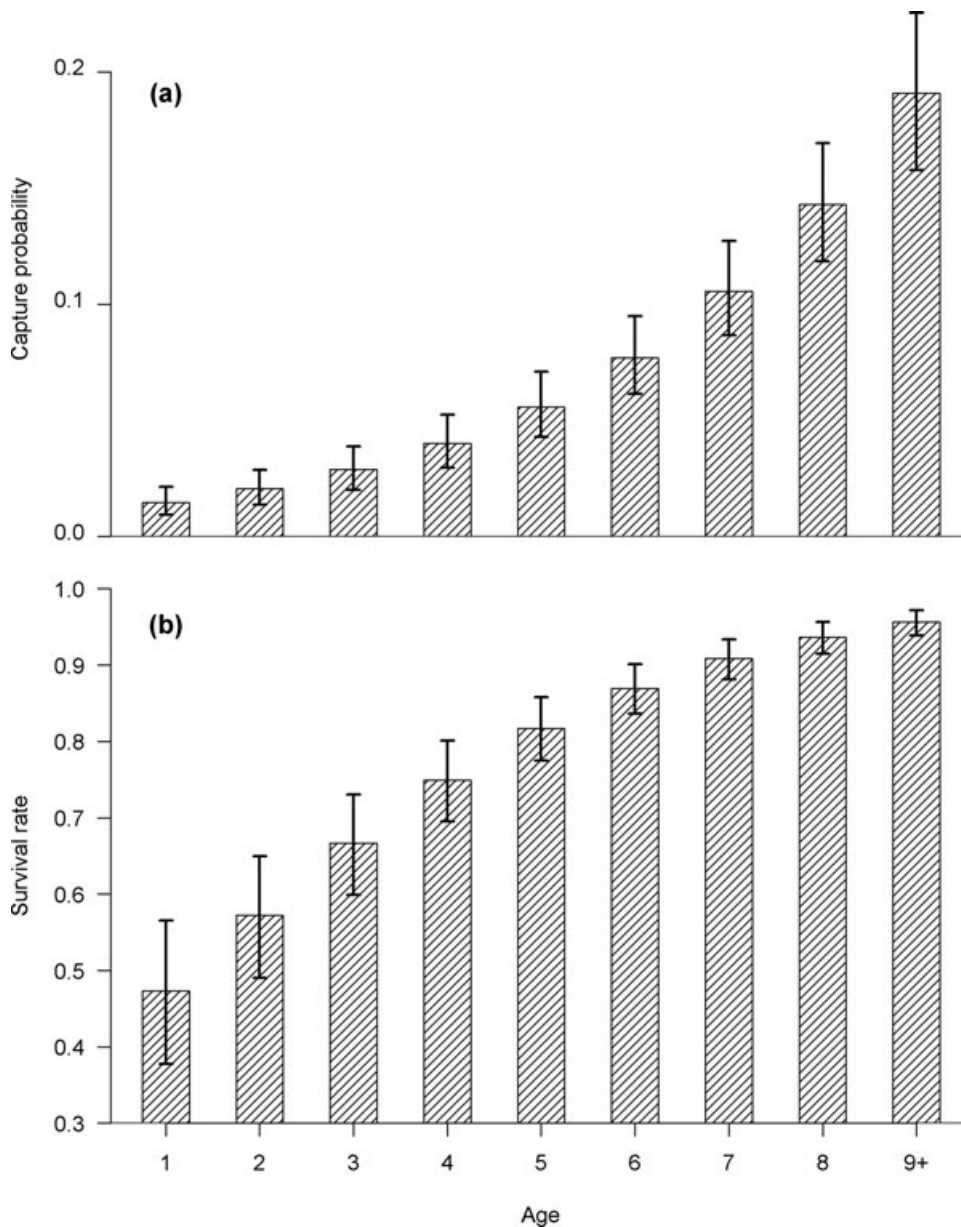


Figure 3. Mean age-specific (a) capture probabilities per survey bout (1–5 bouts per year), and (b) annual survival for bog turtles in southeastern New York. Point estimates (bar heights) are posterior means, and error bars are 95% credible intervals. With survey effort concentrated in the spring (beginning of the growing season), age (x-axis) is best interpreted in terms of growing seasons (e.g., age 1 turtles are those just beginning their second growing season, and age 9+ turtles are those that have completed 9 or more growing seasons [all adult turtles]).

moderate; expected abundance at the most temporally variable study population, WFP, varied from 70 to 89 total individuals (adults and juveniles, excluding neonates). Estimated absolute production of yearling turtles varied from 10/year (site EFP and CFP) to 25/year (site SHR) at the focal fen complex. Mean per capita fertility (yearling production) was estimated at approximately 0.97 yearling turtles produced per female turtle per year and varied from year to year (average CV of 0.28). Assuming mean clutch size of 3.5 (Whitlock 2002) and clutch frequency of 0.85 (K.T.S., unpublished data), first-year survival rate (from laying through first overwintering) was back calculated at approximately 0.33 (per capita yearling production divided by expected annual per capita egg production). The proportion of new adult recruits entering each population averaged 0.047 during the study pe-

riod, approximately offsetting the expected annual 0.040 mortality rate during the study period. Estimated juvenile fraction was 0.58 (0.47 to 0.65) for the entire metapopulation.

Population Projection Models

Annual temperature variability over the study period (CV = 0.045, in °C) mirrored the variability over the last 100 years (CV = 0.046), and annual variation in precipitation over the study period (CV = 0.083) underrepresented that of the past century (CV = 0.166). Extirpation risk for a hypothetical bog turtle population with initial population size of 6 females of all ages was estimated at 0.51. Extirpation risk was substantially lower when starting population size was set at 10 females (0.20) and

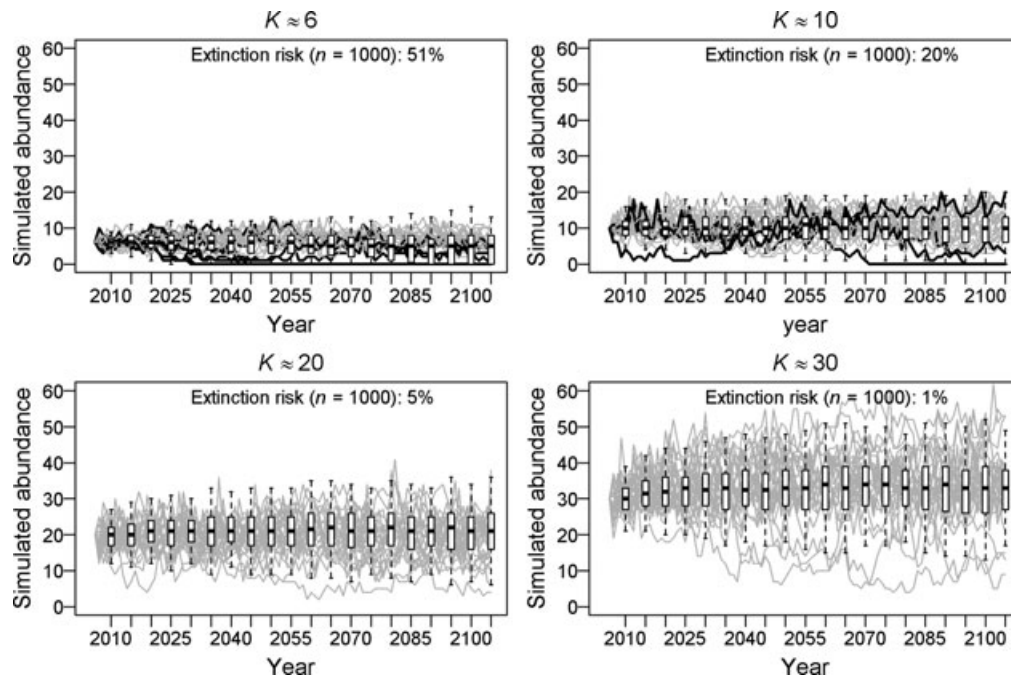


Figure 4. Simulated population trajectories for 4 hypothetical populations of bog turtle in which initial abundance (K) varied so we could assess the viability of small populations. Initial abundance ranged from 6 to 30 individuals. For each iteration ($n = 1000$), vital-rate parameters were sampled from the joint posterior distribution derived from capture-recapture analysis. To illustrate variation within and among simulations, every 40th trajectory is depicted (gray lines, trajectories that remained above the quasi-extinction threshold; black lines, trajectories that reached or fell below the quasi-extinction threshold at least once during the 100-year simulation run; all simulations ran to completion) (see Methods for model details).

decreased to 0.05 with a starting population size of 20 and to 0.01 at an initial population size of 30 (Fig. 4). Generation time for bog turtles (mean age of reproductive individuals), computed with the R package “popbio” with mean survival rate and fecundity parameter estimates entered as a projection matrix, was estimated at 27.5 years.

Discussion

In contrast to the small-population paradigm (Caughley 1994), our results suggest that some populations of <50 individuals are likely to persist for periods of a century or more, provided vital rates and environmental variance remain at currently estimated levels. Insofar as small populations of some threatened species with low vagility and patchy or fragmented habitat may not be at severe risk of extirpation, we re-examine the small-population paradigm for long lived species such as the bog turtle. In particular, suggested MVP thresholds (e.g., Reed et al. 2003; Traill et al. 2007) may be an order of magnitude too high for long-lived organisms, although some such estimates also account for deleterious genetic effects and loss of evolutionary potential, which we did not consider here (Jamieson & Allendorf 2012). Therefore, we caution

against using general MVP thresholds and abundance-based criteria such as the SAFE index (Clements et al. 2011) as a basis for conservation triage decisions. For species such as the bog turtle, a systematic policy of preserving very small populations may best serve long-term conservation goals by providing critical insurance reservoirs that contribute to species-level resilience to catastrophic events and other stochastic threats (Lindsey et al. 2005).

We are among the first to infer temporal process variance in survival rate and recruitment rates for a turtle species—information that is critical for projecting population dynamics (Kendall 1998). However, our 10-year survey period spanned a fraction of a bog turtle generation (approximately 20–30 years). consequently, we may have underestimated process variance and may have failed to capture the effects of catastrophic events such as drought. The degree to which we underestimated environmental stochasticity can be loosely inferred for our study site from long-term climate records in the PRISM database (Daly et al. 2002). We found that annual precipitation (but not temperature) during the past century occasionally reached highs and lows not encountered during the study period, which indicates the absolute risk metrics derived from our population projection models should be interpreted cautiously. Nonetheless, our

results from 10 years of study strongly suggest that a single population with 10–15 females can contribute substantially to the overall security of the species. To the extent that stochastic events are uncorrelated among populations, increased environmental stochasticity should only enhance the importance of such populations for maintaining metapopulation viability (Akçakaya 2000).

In populations of long-lived species, the presence of tenacious adults can mask below-replacement recruitment rates for years or decades and result in apparently persistent but functionally extirpated populations (e.g., Gerlach 2008). However, juveniles of long-lived reptile species are often encountered too infrequently to develop effective recruitment estimates. This information gap remains one of the largest obstacles to understanding the demography of reptile populations (Pike et al. 2008) and other long-lived species such as large cats (Karanth & Nichols 1998). Furthermore, simple recruitment metrics (e.g., fraction of juveniles in a sample) may underrepresent true recruitment rates. It may be possible to correct for this bias, and thereby develop accurate metrics for rapid assessment of recruitment success, by estimating age-specific capture probabilities across several study populations (e.g., Fig. 3a). For example, sampling a bog turtle population with a true juvenile fraction of 0.55 (characteristic of stable populations in this study) should result in a sample juvenile fraction of approximately 0.23 after correcting for low juvenile capture probability. However, development of a reliable rapid assessment metric for bog turtle recruitment should incorporate results from outside the single fen complex sampled for this study.

Failure to account for parameter uncertainty can also bias extinction risk estimates (Ellner & Fieberg 2003). In population viability analyses (PVA) in which stochastic environmental fluctuations are modeled explicitly, extinction risk estimates may be overestimated if sampling variation is conflated with environmental variation (Dennis et al. 2006). Although such biases have sometimes been dismissed as conservative (e.g., Brook et al. 2006), overestimation of extirpation risk is clearly not conservative if results are being used to justify triage of small populations. The conventional treatment of parameter uncertainty in MVP studies derived from PVA involves one-at-a-time perturbation of parameter values for each of a set of uncertain parameters (local sensitivity analysis; Saltelli et al. 2004), which may overestimate population-level risk if strong correlations exist in parameter space. However, by using Bayesian PVA methods, which samples multidimensional parameter space in proportion to plausibility (Wade 2002), we were able to conclude that bog turtle populations in our study region can persist as stable populations with as few as 15–20 females across nearly the entire range of plausible parameter values. This result underscores the need for explicit treatment of (correlated) multivariate parameter

uncertainty in PVA, especially when estimating absolute metrics of extirpation risk (e.g., MVP thresholds).

We caution that the bog turtle may be atypical of the vast majority of species affected by habitat fragmentation. In fact, the bog turtle and other similar wetland turtles may be naturally adapted for persistence in small population units. In many parts of its range, bog turtle habitat (Carter et al. 1999; Whitlock 2002) is naturally patchy; individual patches may be smaller than 1 ha (Bedford & Godwin 2003). On the basis of the relation between fen area and adult abundance (Fig. 2), it is plausible that fens supporting < 50 adult individuals represent a historical norm for the bog turtle. Paleocological studies (e.g., Nicholson & Vitt 1990) and simulation models of landscape processes such as beaver (*Castor canadensis*) impoundment, wildfires, and forest succession may help elucidate historical patch sizes for long-lived wetland species like the bog turtle. Furthermore, it is possible that deleterious genetic effects such as inbreeding depression may be more severe in species not evolutionarily habituated to small and fragmented habitats, potentially due to purging of deleterious alleles (Laws & Jamieson 2010).

Caution must be used when extrapolating our results to other long-lived species because life-history strategies vary substantially among long-lived organisms, even among chelonians (Hellgren et al. 2000; Willemsen & Hailey 2001). More research is needed to clarify the range of successful life-history strategies that enable long-lived organisms to persist as small populations. Nonetheless, our study improves the conservation outlook for long-lived species widely believed to be in peril, has major implications for projecting costs to achieve recovery objectives (management targets for abundance may be lowered in some cases), and should serve as a cautionary note against applying generic MVP estimates to triage of small yet viable populations.

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New York College of Environmental Science and Forestry Institutional Animal Care and Use Committee.

Supporting Information

A detailed model description and table of parameter estimates (Appendix S1) and R and WinBUGS code (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries should be directed to the corresponding author.

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