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Long-term demographic data are important for conserving populations of threatened and endangered species. Collecting data specific to the population of interest can improve conservation success by allowing managers to make informed decisions, evaluate the efficacy of habitat management, and assess extinction risk. Population viability analysis (PVA), a tool commonly used to estimate extinction risk in threatened populations, is most informative when precise, population-specific data are available. We used mark-recapture data spanning ten years (2008–2017) to estimate annual adult survival rates in a population of threatened Eastern Massasauga rattlesnakes (*Sistrurus catenatus*) in Barry County, Michigan. Using these survival estimates and ten additional parameter values obtained from our site and a nearby population, we modeled population viability over the next 100 years. We performed sensitivity analysis using Latin hypercube sampling, followed by logistic regression to assess the relative influence of model parameters on extinction risk. We estimated annual apparent survival rates of 0.79 (95% CI = 0.69–0.87) for adult males and 0.78 (95% CI = 0.69–0.85) for adult females, which are higher than expected given the population's locality. Results of our sensitivity analysis suggest that actions promoting high survival of adult females should be a management priority, followed by activities that facilitate high reproductive output and neonate survival. We recommend focusing future research and monitoring efforts on these parameters.

RECOVERY of threatened and endangered species is often contingent on having reliable population-level data. For instance, long-term demographic estimates specific to a focal population are important for making informed decisions, monitoring the impacts of management actions, and evaluating population extinction risk (White et al., 2002; Williams et al., 2002). However, precise and accurate estimates of demographic parameters such as vital rates and population size are generally difficult to obtain for many threatened and endangered species because of their low detectability (Williams et al., 2002).

Initial declines in population size that may lead to a species' threatened or endangered status generally arise from deterministic factors (e.g., habitat loss, over-exploitation; Lacy, 1993). However, once a population has declined in size it becomes more susceptible to stochastic processes, which can continue to damage the population even if the initial threat is mitigated. Probabilistic demographic events, including sex determination, birth, and mortality, have a greater impact in small populations because their outcomes exhibit higher variance when there are fewer individuals to act on (Shaffer, 1981; Engen et al., 1998). Environmental fluctuations can also add to the negative effects of demographic stochasticity (Caughley, 1994; Engen et al., 1998). Likewise, random genetic processes of inbreeding and drift are more likely to lead to reduced average fitness and adaptive potential in small populations (Wright, 1931; Lande, 1995; Frankham, 1996). Because these stochastic processes play such a large role in the fate of small populations, it can be important to account for them when assessing extinction risk.

Population viability analysis (PVA) is a common conservation tool used to estimate extinction risk in small populations by incorporating demographic, environmental, and genetic stochasticity into models of population dynamics (Boyce, 1992; Beissinger and McCullough, 2002). PVA can be an accurate tool for assessing extinction probability, particularly when long-term, population-specific data are available (Brook et al., 2000). However, uncertainty associated with parameter values and future environmental conditions usually precludes reliable projections (Beissinger and Westphal, 1998; Coulson et al., 2001; Ralls et al., 2002). In these cases, PVA may still be useful for predicting relative impacts of conservation efforts on population dynamics if the model adequately represents the system and biology of the species (Beissinger and Westphal, 1998). For example, PVA can be used to compare alternative management strategies by modeling their relative effects on extinction risk, population growth, or some other outcome (Beissinger and Westphal, 1998; Ralls et al., 2002; Hileman et al., 2018a). Additionally, exploring sensitivity of model output to parameter input (e.g., via incremental changes or using variation representative of parameter uncertainty) can reveal the relative importance of each factor to population persistence (Mills

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and Lindberg, 2002). Managers can use this relative importance to prioritize habitat management goals and direct future research and monitoring efforts to obtain precise estimates of the parameters deemed most important (Cross and Beissinger, 2001; Mills and Lindberg, 2002; Reed et al., 2002).

A classic case demonstrating the usefulness of sensitivity analysis involves reevaluating management priorities for the Loggerhead Sea Turtle (*Caretta caretta*; Crouse et al., 1987; Crowder et al., 1994). By examining the sensitivity of population growth to changes in various model parameters (e.g., stage-specific survival, fecundity, and growth rates), studies revealed that the existing conservation approach, which focused on protecting nests to increase egg success, was unlikely to result in this species' recovery (Crouse et al., 1987; Crowder et al., 1994). Instead, they found that mortality rates in older juveniles had a greater influence on population growth, shifting the focus of management efforts to preventing juvenile bycatch from trawl nets (Crouse et al., 1987; Crowder et al., 1994).

Often the factors expected to have the greatest impact on population persistence are those with the largest contribution to individual fitness and, consequently, population growth (Mills, 2012). In studies comparing the response of population growth rates to proportional changes in demographic parameters (i.e., elasticity analysis), survival rates were generally the most influential parameters in species with "slow" life history traits (i.e., long-lived, delayed sexual maturity, small broods; Heppell et al., 2000; Sæther and Bakke, 2000; Oli and Dobson, 2003). In contrast, reproductive parameters were more influential on population growth within species with "fast" life-history traits (i.e., short-lived, fast maturation, large broods).

The Eastern Massasauga (*Sistrurus catenatus*) is a federally listed, threatened rattlesnake (Environment Canada, 2012; U.S. Fish and Wildlife Service, 2016) with "moderate" life history traits in terms of its longevity and fecundity. Mean brood size across the species' distribution is approximately nine offspring (including stillbirths; Hileman et al., 2017), with females in most populations approximating biennial reproduction (Szymanski et al., 2015). Although longevity in the wild is unknown, records of longevity for captive *Sistrurus* spp. range from 11 to 20 years (Snider and Bowler, 1992). Range-wide population declines are primarily due to habitat loss and fragmentation caused by succession, invasive plant monocultures, agricultural conversion, urban development, and other modifications of wetland habitat (Dahl and Johnson, 1991; Szymanski, 1998; Szymanski et al., 2015). Additional threats, including human persecution (Szymanski, 1998) and road mortality (Shepard et al., 2008; Baker et al., 2016), have also contributed to declines in some localities. Most remaining Eastern Massasauga populations are relatively small and isolated (Szymanski, 1998; Chiucchi and Gibbs, 2010).

The geographic range of the Eastern Massasauga extends throughout the Midwest and Great Lakes regions of the United States and into southern Ontario, Canada (Harding, 1997). Survival rates, litter size, and other life-history and demographic parameters demonstrably vary across this range in response to environmental gradients, such as precipitation, temperature, and anthropogenic landscape modification (Aldridge et al., 2008; Jones et al., 2012; Pomara et al., 2014; Hileman et al., 2017). Therefore, obtaining data specific to the population of interest, or a similar population, is important for assessing population viability. Our objectives were to 1) provide estimates of survival valuable for monitoring a population of threatened rattlesnakes in southwestern Michigan, USA; 2) use this and other pertinent demographic data to estimate extinction probability over the next 100 years; and 3) determine the relative influence of model parameters on extinction probability to guide management and future research.

MATERIALS AND METHODS

Study site.—Our study was in Barry County, Michigan (Fig. 1) on a 277 ha privately owned parcel of land bisected by a single public dirt road. The study area is primarily composed of prairie fen, upland prairie, and old-field vegetation types surrounding a third-order stream and a small lake (~5 ha). The remainder of the parcel includes deciduous and coniferous forests, prairie, and developed sites and has trails open to the public. Open wetlands and adjacent uplands are actively managed to control invasive species and promote early successional communities. From 2003 to 2012, prescribed burns were conducted opportunistically in these areas, but with caution to avoid the Eastern Massasauga's active season (i.e., burns were typically conducted in March or December). Additional land management activities performed in the study area between 2003 and 2017 included mechanical removal of woody and invasive species, targeted herbicide application, and the introduction of biological control agents (i.e., *Galerucella calmariensis* to control invasive Purple Loosestrife).

Data collection.—We collected mark-recapture data during 2008, 2009, and 2011–2017. In all years, we primarily located snakes using visual encounter surveys, but also used drift fences and artificial cover objects as supplemental capture methods during 2015 and 2016 (Bartman et al., 2016). In 2008 and 2009, surveys were conducted in conjunction with a radio-telemetry study (Bailey et al., 2011, 2012), and 19 of the 21 individuals marked within our study area over these two years were surgically implanted with radio transmitters. Surveys associated with the telemetry study used two surveyors and spanned May through October, and we only included initial captures (i.e., captures made without radio tracking) in our mark-recapture data set. In 2011 and 2012, we conducted short-duration, high-effort mark-recapture surveys that included five days spanning 21–25 June 2011 and 12 days spanning 8–12 May, 19–23 June, and 7–8 August in 2012. These shorter surveys relied heavily on volunteer effort with up to 20 surveyors in the field at a time. For the remainder of the study period, surveys spanned a larger portion of the active season (approximately late April/early May through mid-July or August), and two to four people regularly conducted surveys aided by occasional volunteer assistance. For all years, we used handheld GPS units to record the locations of captured snakes.

After capturing a snake, we restrained it within a clear PVC tube and determined its sex via cloacal probing (Schaefer, 1934). For females, we used x-ray, ultrasound, or palpation to detect developing embryos, with palpation being the sole method from 2011–2017. To determine age class, we measured the snout-vent length (SVL) of each individual using a flexible measuring tape, either while it was restrained in the snake tube (2008 and 2009) or using a squeezebox (2011–2017; Quinn and Jones, 1974). We considered females to be adults if SVL was ≥ the smallest observed female with developing embryos at our study site (45.1 cm). We classified

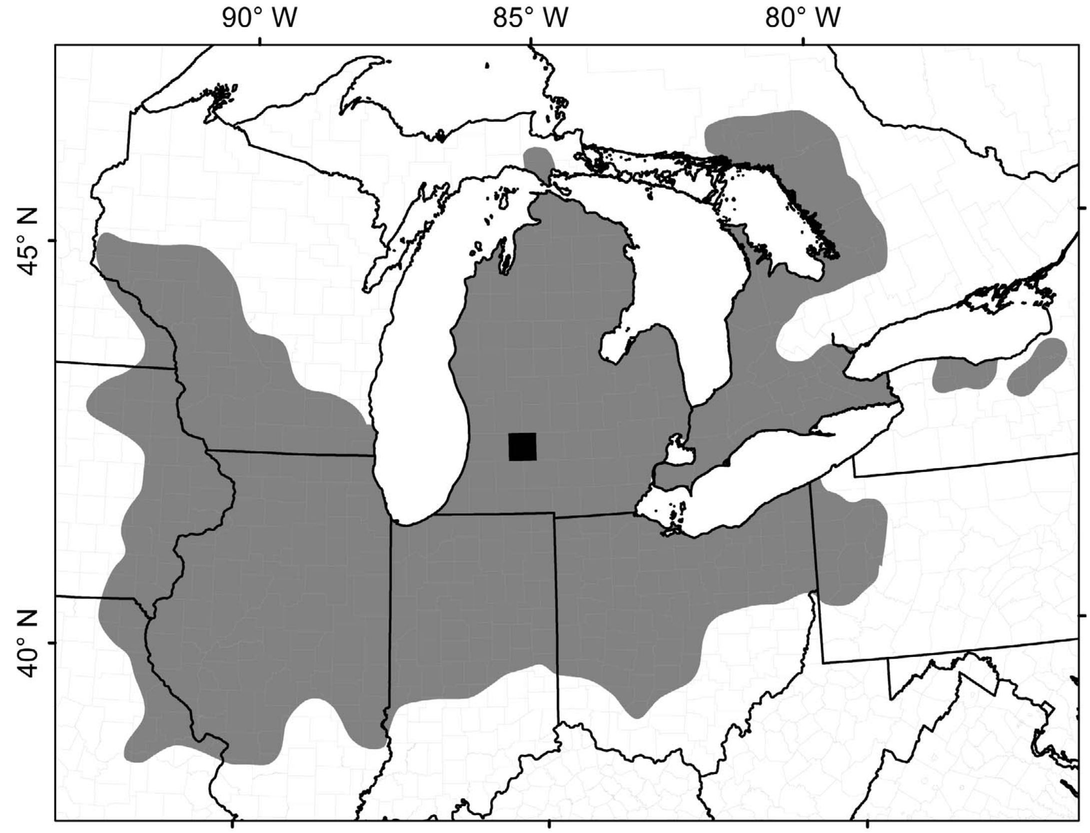

Fig. 1. Study site location in Barry County, Michigan (black) within the Eastern Massasauga's historical geographic range (gray). Reproduced with modifications from Jaeger et al. (2016) with permission granted by Collin P. Jaeger.

males as adults if SVL was $\geq$ the smallest observed male with motile sperm detected from cloacal smear at a nearby site (43.3 cm SVL; Richard B. King, pers. comm.). Upon first capture, we marked snakes with a subcutaneous passive integrated transponder (PIT) tag (Gibbons and Andrews, 2004). After processing, we released each snake at its capture location.

Survival analysis.—We used Cormack-Jolly-Seber models (Cormack, 1964; Jolly, 1965; Seber, 1965) implemented in Program MARK version 8.1 (White and Burnham, 1999) to estimate annual apparent survival of reproductively mature adults from 2008–2017. This parameter is termed "apparent" survival because it incorporates the confounded effects of mortality and permanent emigration. For this analysis, we allowed expansions but not contractions in the study area across years, as reductions to survey area may bias survival estimates low.

We included captures made between 1 May and 17 August of each survey year and created binary individual capture histories, which specified whether each snake was captured (1) or not captured (0) during each year. Three individuals that were part of the radio telemetry study in both 2008 and 2009 were treated as unavailable in 2009 by entering a "." in their capture history, as they were unlikely to be encountered by chance because their locations were generally known. Additionally, we treated two snakes with surgery-induced mortalities as known removals so these deaths would not influence survival estimates.

We included 16 models in our candidate set (Table 1), ranked models using Akaike's information criterion adjusted for small sample size (AIC_c), and generated model-averaged estimates of survival based on AIC_c weight (Akaike, 1973; Burnham and Anderson, 2002). In each model, we either treated survival probability (Φ) as constant or allowed it to differ between males and females. To account for potential effects of different survey methods on detection, we allowed recapture probabilities (p) to vary by survey type (i.e., radio-telemetry study vs. short-duration, high-effort mark-recapture vs. full-season mark-recapture), to vary by time (i.e., each year with a different recapture probability), or to be constant across all years. Because females tend to increase basking behavior when gravid, which may result in greater detection, we also modeled sex differences in recapture rates and included model variations that tested for additive vs. interactive effects between sex and time or sex and survey type. To test for overdispersion, we used a goodness-of-fit bootstrap procedure with 1,000 iterations on our global model: $\Phi(\text{sex})p(\text{sex*time})$.

As a *post hoc* analysis, we assessed whether transient snakes had a significant effect on apparent survival. Transient individuals are not part of the resident population, but pass through the study area (Pradel et al., 1997). Thus, if there is a significant effect of transience, our survival estimates may be biased low. A transience effect can be modeled by allowing survival probabilities to differ between the initial year after marking and subsequent years (Pradel et al., 1997; Jones et al., 2017). To assess whether this effect was significant, we used a likelihood ratio test, comparing our top ranked model to one that was identical except it included a transience effect. We considered a P-value < 0.05 to be significant.

Population viability analysis.—We used Vortex v. 10.2.6.0 (Lacy and Pollak, 2016) to assess the probability of popula-

Table 1. Model selection results for estimating apparent survival (Φ) in adult Eastern Massasauga rattlesnakes from 2008–2017 in Barry County, Michigan. Models are ranked in order of AIC_c weight (w_i), where K indicates the number of parameters, (p) indicates recapture probability, (.) is a constant, (*) indicates an interaction term, and (+) indicates an additive term.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Φ(.) p(sex*time)	449.32	0.00	0.32	17	91.11
Φ(.) p(time)	449.55	0.22	0.28	9	109.28
Φ(.) p(sex+time)	451.13	1.81	0.13	10	108.68
Φ(sex) p(sex*time)	451.23	1.91	0.12	18	90.69
Φ(sex) p(time)	451.44	2.12	0.11	10	108.99
Φ(sex) p(sex+time)	453.31	3.98	0.04	11	108.67
Φ(.) p(survey type)	471.80	22.48	0.00	4	142.13
Φ(sex) p(survey type)	473.36	24.04	0.00	5	141.61
Φ(.) p(sex+survey type)	473.48	24.16	0.00	5	141.73
Φ(sex) p(sex+survey type)	475.41	26.09	0.00	6	141.56
Φ(.) p(sex*survey type)	477.32	28.00	0.00	7	141.34
Φ(sex) p(sex*survey type)	479.22	29.90	0.00	8	141.11
Φ(.) p(.)	479.41	30.09	0.00	2	153.86
Φ(sex) p(.)	480.88	31.56	0.00	3	153.28
Φ(.) p(sex)	481.24	31.91	0.00	3	153.63
Φ(sex) p(sex)	482.95	33.63	0.00	4	153.28

tion extinction within the next 100 years under current conditions at our study site. Vortex incorporates environmental, demographic, and genetic stochasticity, with probabilistic events (e.g., mortality, sex determination) occurring at the individual level and the fate of each individual is tracked through time (Lacy and Pollak, 2016). The majority of (i.e., 12 out of 17) parameter values used in our model were derived from data collected at our site or from a population located approximately 86 km away in Cass County, Michigan (Hileman et al., 2018a). The parameter values we obtained from other sources are either unlikely to vary among populations (i.e., reproductive system, maximum age of reproduction, sex ratio at birth, and percent of adult males in the breeding pool) or likely to have limited influence on PVA outcomes (i.e., maximum lifespan) due to interactions with other parameters (i.e., survival rates; described in greater detail below).

We calculated adult mortality rates (1–survival) from the survival analysis in this study. A mean litter size of 7 (SD = 2.9) viable offspring was also determined using data from our site (Bailey, 2010). We set an initial population size of 284 and a carrying capacity of 569 based on adult abundance estimated for our study site (148 individuals) and its upper 95% confidence interval (CI) limit (295 individuals), respectively (Bradke et al., in press), which we extrapolated to total population size by assuming a stable age distribution (Hileman et al., 2018a). Mortality estimates of sub-adult age classes, mean percent of adult females breeding each year (and associated environmental variation, EV), and age at first reproduction were set at values reported from the Cass County site (Hileman et al., 2018a; Table 2). We estimated environmental variation for mortality rates by taking 11% of total variance associated with each respective survival estimate (Jones et al., 2017; Hileman et al., 2018a). Maximum age of reproduction and maximum lifespan are unknown for wild populations; however, Western Massasaugas (*Sistrurus tergeminus*) can live up to 20 years in captivity (Snider and Bowler, 1992) and reproductive senescence is not evident in captive individuals (Miller, 2006). We recognize that animals likely have shorter lifespans in the wild than in captivity. Therefore, to put a reasonable restraint on these parameters, but allow mortality rates to be the principle determinant of longevity, we limited lifespan and reproduction to a maximum age of 15 years. We did not include inbreeding effects in our model, because the inbreeding coefficient (F_{IS}) calculated for our site using 2015 DNA samples was approximately zero (0.010; Bradke et al., in press). Additionally, we set the EV correlation between survival and reproduction at zero to avoid assigning an arbitrary value. Remaining parameters were set based on life history data from the literature (Table 2).

Finally, we used actual allele frequencies for 16 microsatellite loci so that we could track changes in genetic diversity. These frequencies were calculated in GenAlEx v 6.503 (Peakall and Smouse, 2006, 2012) for 75 individuals sampled at our site between 2013 and 2015. Loci, methods of DNA extraction, and protocol for PCR amplification and microsatellite genotyping are described in Bradke et al. (in press). We ran 10,000 iterations of the Vortex simulation and specified that population extinction occurred when only individuals of one sex remained.

Sensitivity analysis.—To evaluate the relative effects of each model parameter's uncertainty on extinction risk, we used Latin hypercube sampling (LHS) in Vortex followed by logistic regression in R v 3.3.2 (R Core Team, 2016). Latin hypercube sampling takes incremental samples from the range of uncertainty designated for each parameter (Lacy et al., 2017). Random combinations of these incremental parameter values are generated to create unique scenarios within the overall space of parameter uncertainty (Lacy et al., 2017). Consequently, this technique can generate high coverage of the parameter space using fewer samples than a strictly random sampling approach, while including interactions between model parameters that cannot occur in a single-factor sensitivity analysis.

In our sensitivity analysis, we included potential inbreeding effects by varying lethal equivalents from 0–6.29 per individual, with percent due to recessive lethal alleles constant at 50% (Lacy et al., 2017). Here, the upper bound represents the estimated average lethal equivalents affecting fecundity and age 0–1 survival in a meta-analysis of wild species (O'Grady et al., 2006). We allowed mean litter size to vary ± one neonate from our baseline value (i.e., 6–8

Table 2. Parameter values included in Eastern Massasauga population viability analysis conducted in the Vortex program. SD represents standard deviation and EV represents SD due to environmental variation.

Parameter	Value	Source or justification
Inbreeding depression	None	Low F_{IS} value reported for this study site (Bradke et al., in press)
Reproductive system	Polygynous	Duvall et al., 1992
Age of first reproduction (both sexes)	3	Hileman et al., 2018a
Maximum lifespan	15	Up to 20 years in captivity (Snider and Bowler, 1992), but likely shorter for wild individuals (Miller, 2006)
Maximum age of reproduction	15	Unknown, but reproductive senescence not apparent in captive individuals (Miller, 2006)
Maximum broods per year	1	Bailey, 2010
Mean litter size (SD)	7 (2.9)	Bailey, 2010
Sex ratio at birth	0.5	Keenlyne and Beer, 1973
Mean % of adult females breeding/ year (EV)	44.0 (7.7)	Hileman et al., 2018a
% of adult males in breeding pool	100	Miller, 2006
Annual % mortality		
Age 0–1 both sexes (EV)	62.2 (0.7)	Hileman et al., 2018a (EV = 11% of total variance; Jones et al., 2017)
Age 1–2 both sexes (EV)	34.7 (0.7)	Hileman et al., 2018a (EV = 11% of total variance; Jones et al., 2017)
Age 2–3 both sexes (EV)	32.7 (0.7)	Hileman et al., 2018a (EV = 11% of total variance; Jones et al., 2017)
Adult males (EV)	21.1 (0.5)	This study (EV = 11% of total variance; Jones et al., 2017)
Adult females (EV)	21.8 (0.5)	This study (EV = 11% of total variance; Jones et al., 2017)
Initial population size	284	Extrapolated adult abundance estimate (148; Bradke et al., in press) to total population, assuming stable age distribution (Hileman et al., 2018a)
Carrying capacity	569	Extrapolated upper 95% CI of adult abundance estimate (295; Bradke et al., in press), assuming stable age distribution (Hileman et al., 2018a)

offspring), based on rounding the standard error of the sample mean to the nearest whole individual. We varied initial population size from 198–569 individuals based on upper and lower 95% CI bounds of the adult abundance estimate for our study site (102 and 295 individuals, respectively; Bradke et al., in press), which we extrapolated by assuming a stable age distribution. We set our uncertainty range for carrying capacity at 284–854 individuals (i.e., baseline initial population value to 150% baseline carrying capacity). We allowed mean annual percent of adult females breeding and mortality rates specific to each sex and age class to vary within ±0.05 of their respective baseline estimates. We maintained all additional parameters at the values specified in our baseline PVA (Table 2) and ran 3,000 samples with ten iterations each for 100 years, producing 30,000 observations of 3,000 unique scenarios.

We generated simple logistic regression models using our LHS output, where the binary response variable indicated whether a population went extinct and each explanatory variable was one of the 13 model parameters varied for sensitivity testing. Since all parameters fluctuated simultaneously and their values were combined randomly during LHS, we were able to assess their relative influence while accounting for interactions, but without building interactions into our models (Cross and Beissinger, 2001). To assess the relative importance of each explanatory variable on population extinction risk, we compared their standardized regression coefficients (Cross and Beissinger, 2001).

RESULTS

Survival.—Our apparent survival analysis included 270 captures of 169 unique adults (72 males and 97 females), spanning 2008–2017. Overdispersion was not evident based on the goodness-of-fit bootstrap procedure ($P = 0.59$), so we did not adjust the variance inflation factor (i.e., $\hat{c}$) in program MARK. Our model averaged apparent survival estimate was 0.79 (95% CI = 0.69–0.87) for males and 0.78 (95% CI = 0.69–0.85) for females. The top ranked model, receiving 32% of AIC_c weight (Table 1), supported equal survival rates for males and females and included an interaction effect between time and sex on recapture probability. The likelihood ratio test did not support a transience effect on survival ($\chi^2 = 1.404$, df = 1, $P = 0.24$).

Population viability and sensitivity analysis.—Our baseline PVA yielded a 0% probability of extinction over the next 100 years. The mean stochastic growth rate (r = 0.0185, SD = 0.0769) was slightly lower than the deterministic growth rate (r = 0.0199), and the mean population size at year 100 was 534.55 (SD = 45.16). At the beginning of the simulation (year zero), expected heterozygosity (H_e) was 0.69 (SD = 0.0032), observed heterozygosity (H_o) was 0.69 (SD = 0.0062), and mean number of alleles (N_a) was 7.55 (SD = 0.03). We observed reductions in all three measurements by year 100 ($H_e = 0.65$, SD = 0.018; $H_o = 0.65$, SD = 0.019; $N_a = 6.18$, SD = 0.24).

Our sensitivity analysis indicated that variation in adult female mortality has the strongest influence on extinction probability, with mean litter size, percent of adult females breeding each year, and age 0–1 female mortality also conveying a relatively strong influence (Table 3; Fig. 2). Male mortality rates were least important among the parameters examined (Table 3).

DISCUSSION

Few published studies on threatened snakes have used population viability analysis to inform conservation efforts, likely due to a usual shortage of demographic data (Dorcas and Wilson, 2009). In this study, we used mark-recapture data spanning ten years to estimate survival rates and conducted a PVA for a population of federally threatened rattlesnakes, with the majority of parameter values derived

Table 3. Sensitivity analysis of model parameters used in Eastern Massasauga population viability analysis. Range indicates the minimum and maximum values specified for Latin hypercube sampling in Vortex. The relative influence of each parameter on population extinction risk was determined using simple logistic regression and is indicated by its standardized regression coefficient (α_n/SE_n).

Parameter	Range	α_n/SE_n
Adult female mortality (%)	16.8–26.8	53.4
Mean litter size	6–8	−39.4
Mean adult females breeding/yr (%)	39–49	−36.5
Age 0–1 female mortality (%)	57.2–67.2	35.1
Age 1–2 female mortality (%)	29.7–39.7	23.0
Age 2–3 female mortality (%)	27.7–37.7	22.7
Lethal equivalents (per individual)	0–6.29	15.9
Initial population size	198–569	−12.8
Carrying capacity	284–854	−6.5
Adult male mortality (%)	16.1–26.1	3.5
Age 0–1 male mortality (%)	57.2–67.2	2.0
Age 1–2 male mortality (%)	29.7–39.7	1.7
Age 2–3 male mortality (%)	27.7–37.7	0.9

from data collected at our site or a relatively close population, approximately 86 km away. Our results indicate that under our model of population dynamics and current environmental conditions, this population is likely to persist over the next 100 years. However, as is typical of PVAs, this model only accounts for known threats and processes currently affecting the population and, therefore, may underestimate extinction risk (Boyce, 1992; Ludwig, 1999; Beissinger and McCullough, 2002).

Density-dependent processes and threats related to climate change and disease are some of the factors not considered in our PVA that may be significant now or in the future. For instance, flooding and drought are strong predictors of variation in adult survival rates across the Eastern Massasauga's range (Pomara et al., 2014). As climate change intensifies, these catastrophes are more likely to influence the trajectory of this population. Additionally, the fungal pathogen *Ophidiomyces ophiodiicola*, which causes snake fungal disease (Allender et al., 2015), was recently confirmed in our study population (Allender et al., 2016), although estimated prevalence of the fungus was low in 2016 (0.03, 95% CI = 0.00–0.19; Hileman et al., 2018b). Because the influence of environmental conditions on snake fungal disease dynamics is unknown, it is difficult to predict future impacts (Lorch et al., 2016). Furthermore, while extinction probability for our baseline PVA was 0%, we still observed a slight loss in mean genetic diversity, with the most notable change being a decrease in mean number of alleles from 7.55 (SD = 0.03) to 6.18 (SD = 0.24). We cannot translate these results to a loss in adaptive potential, but a link between genetic diversity and evolutionary potential has been made in other studies (England et al., 2003; Swindell and Bouzat, 2005; Reed, 2008). Lowered adaptive potential could reduce the population's ability to respond to threats like disease or climate change. This reduction in response, combined with this species' limited ability to disperse to adjacent areas with suitable habitat, often in landscapes fragmented with development and/or agriculture, could easily create a very different scenario than our results demonstrate.

Despite the inherent uncertainty associated with PVAs, sensitivity testing can still help guide management decision-making, research, and monitoring efforts. Following the approach of Cross and Beissinger (2001), we used a global sensitivity analysis and logistic regression to determine the relative effects of model parameters on extinction risk. In this analysis, all parameter values varied simultaneously, allowing for interactions among them. This method improves model realism compared to the single-factor analyses more commonly used in PVAs, where each parameter is varied individually across its specified range of values while other

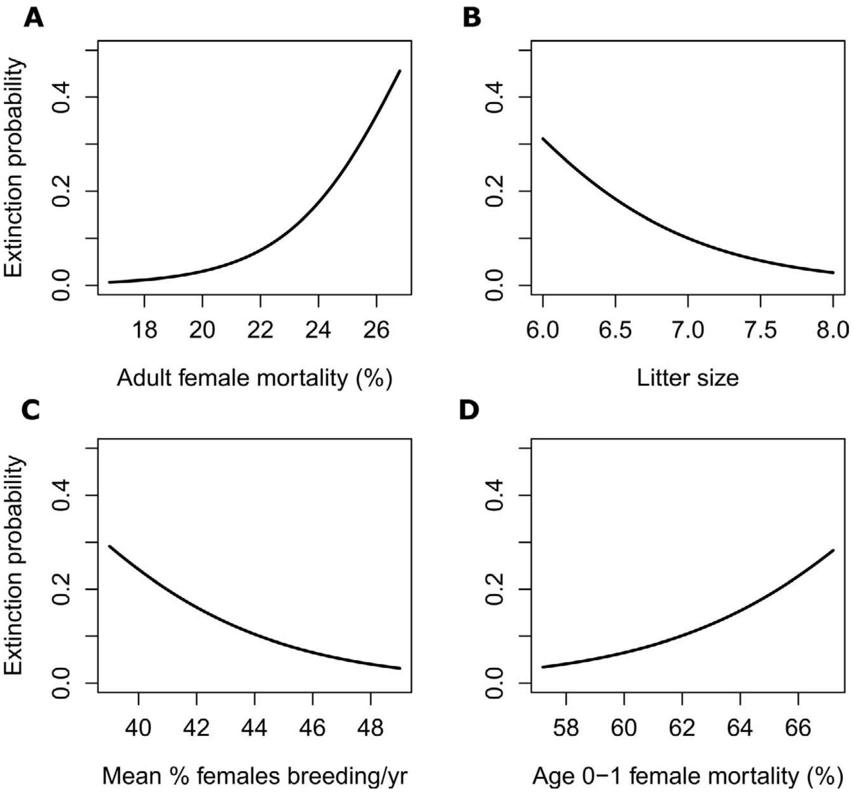

Fig. 2. Global sensitivity analysis of model parameters used in an Eastern Massasauga population viability analysis, Barry County, Michigan. We modeled the results from Latin hypercube sampling using simple logistic regression to evaluate the relative influence of each parameter on extinction probability. The top four parameters were (A) adult female mortality, (B) litter size, (C) mean percent of females breeding/year, and (D) mortality of the 0–1 age class.

parameters are held constant (Fieberg and Jenkins, 2005; Cariboni et al., 2007). Of the model parameters tested, standardized regression coefficients indicated that variation in adult female mortality had the strongest impact on population persistence with mean litter size, percent of adult females breeding each year, and age 0–1 female mortality also relatively important. These results are consistent with Miller (2006) who found high sensitivity to uncertainty in the same four factors in his PVA of Eastern Massasaugas in the Bruce Peninsula, Ontario. On the other hand, our results differ slightly from Baker (2016) who found that reproductive rates, including percent breeding females, litter size, and offspring sex ratio were most important for predicting extinction probability in Clinton County, Illinois. We did not consider model sensitivity to offspring sex ratio in this study because we have no reason to believe the probability of producing male versus female offspring differs from 1:1.

Results of our sensitivity analysis suggest that actions promoting high survival of adult females should be a management priority, followed by activities that facilitate high reproductive output and neonate survival. However, it is also important to consider the capacity for management actions to achieve each of these goals (Manlik et al., 2016, 2018). In other words, managers should take into account the feasibility of decreasing adult female mortality rates versus the feasibility of attaining changes in other parameters when making decisions. For example, adult survival in this population is already relatively high (Jones et al., 2012; discussed below), but mean litter size is relatively low compared to other populations (Aldridge et al., 2008; Hileman et al., 2017; but note that most litter sizes in the literature include nonviable offspring). Thus, it may be more feasible to increase mean litter size than adult female survival in this case (Manlik et al., 2018).

Habitat management that reduces resource limitations could enhance fecundity through increased reproductive frequency, brood size, or offspring viability (Ford and Seigel, 1989; Naulleau and Bonnet, 1996; Shine and Bonnet, 2009). Additionally, adult survival rates in snakes have been linked to prey abundance (Forsman and Lindell, 1997; Sperry and Weatherhead, 2008; Olson et al., 2015). This highlights the importance of providing a variety of early successional vegetation types with structural diversity that would support diverse small mammal communities. Obtaining or maintaining such habitat would likely require planned habitat management interventions.

We also recommend conducting land management activities that facilitate basking in gravid females as a means to increase reproductive output, as well as neonate and adult survival. Because Eastern Massasaugas are viviparous, they require specialized habitat to increase body temperatures for embryogenesis (Foster et al., 2009). Maintaining suitable gestation habitat may result in healthier offspring or earlier parturition, which provides more time for mother and offspring to forage and increase body reserves prior to ingress (Charland and Gregory, 1990; Burger, 1991; Lourdais et al., 2004). In a previous study conducted at our site, gravid females demonstrated a preference for early to mid-successional uplands, so maintaining these vegetation types and connectivity between wetlands and uplands is likely important (Foster et al., 2009). Although available vegetation types differ widely at sites supporting Eastern Massasaugas, maintaining areas with low canopy cover and high mean soil temperatures, in general, is supported by studies throughout the species' range (Reinert and Kodrich, 1982; Harvey and Weatherhead, 2006; Foster et al., 2009). Small scale habitat manipulations have also been recommended for creating or maintaining basking sites in known gestation areas. Plots of $\leq$100 m^2 where woody plants were cut to heights of $\leq$25 cm were used for basking more often than plots that were left uncut in a New York population, and authors of this study recommended cutting every three years during months when snakes are inactive (Johnson et al., 2016a).

Despite the importance of suitable basking habitat, management conducted to maintain basking areas should be cautious to limit direct mortality by scheduling prescribed burns to avoid the active season (Johnson et al., 2000; Cross et al., 2015; Hileman et al., 2018a) or by incorporating alternative methods such as cutting to remove woody vegetation (e.g., Johnson et al., 2016a) to reduce the frequency of burns. Leaving sufficient cover for crypsis from predators (i.e., dense groundcover and retreat sites interspersed through basking areas) is also recommended to minimize indirect mortality and can be an important factor in basking site selection for this species (Shoemaker and Gibbs, 2010). If habitat management is not conducted cautiously with these potential sources of mortality in mind, costs associated with reduced female survival could outweigh any benefits gained. For example, re-running the baseline PVA with a 0.05 higher rate of adult female mortality increases the probability of population extinction from 0% to approximately 10%, demonstrating the importance of this parameter.

The same parameters identified as important management targets can also be the focus of research and monitoring. Adult female survival was estimated in the current study but should continue to be monitored over time. Fortunately, adult females tend to be the easiest class to observe due to increased basking behavior while gravid (Bonnet and Naulleau, 1996), so this is also a practical goal. Litter sizes should also be monitored by ultrasound or captive parturition. If captive parturition is used we recommend collecting gravid females as close to parturition as possible to minimize any effects of captivity on litter size. Other methods of monitoring such as palpation or x-ray can include nonviable embryos, and litter observations in the field are likely to be underestimates (Bissell, 2006; Bailey, 2010). We suggest directing future research at the Barry County site to obtain estimates of reproductive frequency and neonate survival because we used surrogate estimates from the Cass County site that might not be representative of our population. Multistate Cormack-Jolly-Seber models can be used to estimate female reproductive frequency if reliable records of reproductive status are kept (Hileman et al., 2018a). To estimate neonate survival, mark-recapture surveys should extend past parturition, which generally occurs in late July and throughout August (Bailey et al., 2012). Research on predation and diet in this age class could also inform how management might increase neonate survival rates.

Our apparent survival estimates are among the few generated for Eastern Massasaugas using relatively long-term mark-recapture data, rather than short-term telemetry data (but see Johnson et al., 2016b; Jones et al., 2017; Hileman et al., 2018a). In addition to allowing for studies of longer duration, mark-recapture methods generally produce a larger sample size than telemetry studies, yielding estimates that are more representative of the population. Our survival rates of 0.79 and 0.78 for adult males and females, respectively, are higher than the mean estimate of 0.67 from a meta-analysis of telemetry data by Jones et al. (2012), who found that survival increased across the southwest to northeast range distribution of the species. Based on our population's location at approximately the center of the species' range, we would expect survival to be closer to this mean, or perhaps below it since human-induced mortalities were censored out of the Jones et al. (2012) dataset. However, a telemetry-based estimate of active season survival at our site from 2008–2009 was also exceptionally high (i.e., 0.95; Bailey et al., 2011). These results may reflect high quality habitat at our site (Bailey et al., 2011). Additionally, despite a public dirt road that bisects suitable massasauga habitat, few road mortalities were observed over the course of this study (Bailey et al., 2011; pers. obs.), compared to other massasauga populations (e.g., Shepard et al., 2008; Baker et al., 2016). Higher road mortality at other sites may be due to habitat fragmentation that requires snakes to cross roads to obtain basic resources (e.g., food, mates, overwintering sites; Shepard et al., 2008; Baker et al., 2016), while our site is relatively unfragmented aside from the single road. Furthermore, managers at our site are very cautious in limiting prescribed burns conducted within massasauga habitat to pre-spring emergence or post-fall ingress, potentially avoiding burn mortalities observed at other sites (e.g., Durbian, 2006; Moore and Gillingham, 2006; Cross et al., 2015). Finally, private ownership and regular presence of staff near the study area may deter illegal collection.

Although our estimates are for apparent survival, we believe they approximate true survival, since we did not detect a transience effect that would indicate a significant number of nonresident individuals (i.e., emigrants) in our sample. Expansions in our study area over time may have also reduced the effects of emigration from the study area, as individuals on the edge are more likely to be encountered across years with study area increases. The markedly high survival estimates for our population corroborate a limited effect of emigration.

Similar to previous Eastern Massasauga mark-recapture studies in Michigan and Ontario, we did not detect a difference in the survival rates of males and females (Jones et al., 2017; Hileman et al., 2018a). While our top ranked model supported an interaction effect between time and sex on capture rates, there was only weak support for the interaction (AIC_c weight = 0.32), as the second ranked model, with only a time effect on capture rates, received similar support (AIC_c weight = 0.28; Table 1). This time effect on capture rates may relate to differences in surveyor effort or environmental conditions across years.

The relatively long-term survival estimates provided in our study may serve as a comparison to others throughout this species' range and provide useful information for the focal population. It may also be informative to compare the relative importance of model parameters here with other localities range-wide. Identifying trends in parameter sensitivity could help natural resource managers across the species' range better plan and implement habitat management activities to improve conservation efforts.

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