



Research Article

Eastern Massasauga Demography and Extinction Risk under Prescribed-Fire Scenarios

ERIC T. HILEMAN,^{1,2} *Department of Biological Sciences, Northern Illinois University, DeKalb, IL 60115, USA*

RICHARD B. KING, *Department of Biological Sciences, Northern Illinois University, DeKalb, IL 60115, USA*

LISA J. FAUST, *Department of Conservation and Science, Lincoln Park Zoo, Chicago, IL 60614, USA*

ABSTRACT The use of poorly estimated or surrogate population parameter estimates to assess population viability may result in misleading predictions. Consequently, a critical first step to understanding population health and the effects of land management practices on threatened species is estimation of site-specific demographic parameters. A major threat to the eastern massasauga (*Sistrurus catenatus*) is habitat loss due to encroachment of woody vegetation and invasive species. Current land management practices require periodic burning or mowing to maintain habitat suitability. Although these methods improve habitat quality, they may also increase the risk of depredation due to reduced ground cover if burns are too extensive or cause mortality if conducted when snakes are active. We fitted contemporary capture–recapture and matrix models to an 8-year dataset to estimate population parameters for an eastern massasauga population near the range center of the species, where the largest number of eastern massasauga populations may still persist. From 2009 to 2016, we captured 826 eastern massasaugas 1,776 times. In general, annual survival increased with increasing age (age 0 = 0.38, age 1 = 0.65, age 2 = 0.67, age ≥ 3 females = 0.71, age ≥ 3 males = 0.66). Abundance estimates ranged from 84 to 140 adults and annual reproductive frequency was 0.44 (95% CI = 0.29–0.59). We simulated increased mortality due to prescribed burns during spring, fall, and late fall for 50 and 100 years. The baseline model, which incorporated current prescribed–fire practices, indicated a stable population with only a 0.2–0.6% probability of extinction over 100 years, suggesting that management practices at this site are sustainable if they remain unchanged. Simulations of conservative increases in mortality due to fire changed the probability of extinction little over 50 years ($\leq 0.7\%$) but increased probability of extinction up to 24.5% over 100 years in the most pessimistic prescribed–burn scenario. These prescribed–burn simulations may be comparable to burn regimes used at other eastern massasauga sites. The population parameters estimated here provide information needed for assessing range-wide population viability and investigating geographic variation in eastern massasauga demography. © 2018 The Wildlife Society.

KEY WORDS abundance, age-specific survival, eastern massasauga (*Sistrurus catenatus*), extinction, litter size, Michigan, prescribed fire, reproductive frequency.

Estimation of demographic parameters is an important first step to monitoring population health and predicting population responses to threats such as disease (Frick et al. 2010, Muths et al. 2011, Hileman et al. 2018), invasive species (Wiles et al. 2003, Diller et al. 2016, Hileman et al. 2017b), habitat loss (Lande 1988, McCluskey and Bender 2015), and climate change (Whitfield et al., 2007, Pomara et al. 2014, Lunn et al. 2016). Fortunately, advances in capture–recapture models (Williams et al. 2002, Kéry and

Schaub 2012, McCrea and Morgan 2014, Royle et al. 2014) and sampling technologies (Dorcas and Willson, 2009) have made it increasingly possible to obtain unbiased estimates of key demographic parameters. These parameter estimates are also necessary to establish a baseline model from which potential effects of land management practices (e.g., prescribed fire) on species and communities can be evaluated (Boulinier et al. 1998, Lyet et al. 2009, Russell et al. 2009). Prescribed fire is commonly used to reduce fuel loads, release soil nutrients, manage invasive species, and retard the encroachment of woody vegetation for species adapted to early successional habitat. Although the benefits of prescribed fire on flora are known, the long-term effects of fire on fauna populations and communities are poorly understood (Clarke 2008, Driscoll et al. 2010, Haslem et al. 2011).

Received: 22 August 2017; Accepted: 19 February 2018

¹E-mail: hileman.et@gmail.com

²Current affiliation: U.S. Geological Survey, Guam National Wildlife Refuge, Ritidian, Route 3A Spur Road, Yigo, Guam 96929.

Because of their physiology, most temperate squamates are dependent on early successional or otherwise open habitat for nearly all aspects of their life history (Peterson et al. 1993). For instance, the North American eastern massasauga rattlesnake (*Sistrurus catenatus*) depends on open wetland habitats for thermoregulation, feeding, mating, gestation, and parturition, and in some populations, even overwintering (Reinert and Kodrich 1982, Moore and Gillingham 2006, Bailey et al. 2012). Consequently, throughout its Great Lakes-centered distribution, a major threat to the eastern massasauga is habitat loss due to encroachment of woody vegetation and invasive species (Dovciak et al. 2014, Steen et al. 2015, U.S. Fish and Wildlife Service [USFWS] 2016). The eastern massasauga is a federally listed threatened species in the United States and Canada and current land management practices require periodic burning or mowing to maintain habitat suitability (Committee on the Status of Endangered Wildlife in Canada 2012, USFWS 2016). Although these methods improve habitat quality (Shoemaker and Gibbs 2010, Dovciak et al. 2014, Steen et al. 2015, Johnson et al. 2016a), they can also increase the risk of depredation due to reduced ground cover if burns are too extensive (Wilgers and Horne 2007, Shoemaker and Gibbs 2010) or cause mortality if conducted when snakes are active (Durbian 2006, Cross et al. 2015).

With few exceptions (Bailey et al. 2012, Jones et al. 2012), demographic estimates for the eastern massasauga are qualitative in nature (Faust et al. 2011) or based on quantitative data from populations near the northern (Middleton and Chu 2004, Jones et al. 2017), southern (Dreslik 2005, Aldridge et al. 2008, Dreslik et al. 2016), or eastern (Johnson et al. 2016b) range limits for the species. Although these studies yield valuable information, eastern massasaugas at these sites may exhibit climate-dependent life-history extremes (Hileman et al. 2017a), which highlights the need for equally detailed information from more centrally located populations where the largest number of eastern massasauga populations may still persist (Szymanski et al. 2015). Assessing population viability for centrally located populations using poorly estimated parameters or surrogate estimates from range extremes may result in misleading predictions (Patterson and Murray 2008, Hernández-Camacho et al. 2015). Consequently, for realistic and reliable predictions, unbiased, site-specific parameter estimates are needed.

The eastern massasauga population in Cass County, Michigan, USA, is near its range center and the area has climate conditions intermediate to those in southern Illinois, USA, (the southern edge of the range) and Ontario, Canada (the northern edge of the range). Thus, knowledge of the demography of this population will clarify geographic patterns of variation by providing information characteristic of more centrally located populations. In addition, from 2004 to 2016 the site has been actively managed using prescribed fire.

Our first objective was to use contemporary capture-recapture methods, matrix models, and captive parturition data to estimate key demographic parameters necessary for

robust predictive modeling. Our second objective was to use these parameter estimates to develop individual-based, stochastic population models to evaluate baseline population persistence and identify how simulated additional mortality due to prescribed fire during spring, fall, and late fall might affect population growth 50 and 100 years into the future if current conditions persist.

STUDY AREA

The study area was privately owned and managed and located within the Lake Michigan Basin in Cass County, Michigan, almost exactly at the center of the eastern massasauga range (Fig. 1). Receding glaciers shaped the topography of this 1,052-ha parcel 20,000 to 15,000 years ago, creating rolling hills and a valley system with numerous springs that fed into a kettle lake (~4 ha). The creek exiting this lake ran through a large flood plain basin, along with several smaller spring-fed tributaries. The basin area elevation is 244 m above sea level, and the terrain around the basin rises rapidly with the valley edges approximately 280 m above sea level (U.S. Geological Survey [USGS] National Elevation Dataset).

The habitat within the study area (~64.3 ha), bisected by the creek described above, consisted primarily of calcareous fen and marshes, dominated by graminoids (e.g., sedge [*Carex* spp.]), cattails (*Typha* spp.), and common reed (*Phragmites* spp.). Woody species included tamarack (*Larix laricina*), willow (*Salix* spp.), cinquefoil (*Dasiphora fruticosa*), and poison sumac (*Toxicodendron vernix*). Stands of beech (*Fagus* spp.) and maple (*Acer* spp.) forests with occasional pockets of oaks (*Quercus* spp.) surrounded the study site. At the time of the study, site management documented 31 reptile and amphibian species and >100 bird species on the property.

Climatic conditions within Cass County are intermediate for the eastern massasauga range based on 30-year annual

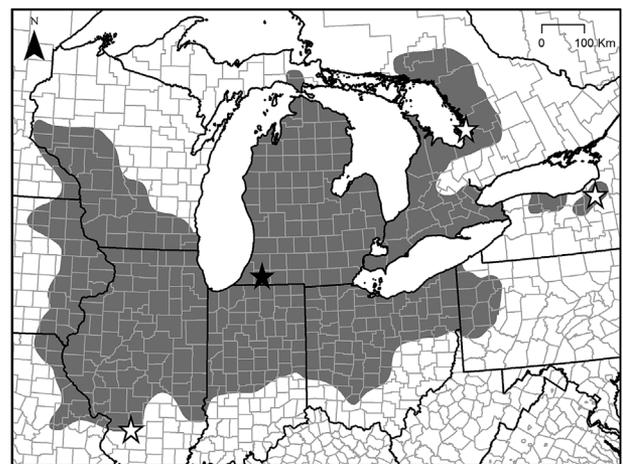


Figure 1. The approximate historical range of the eastern massasauga (gray shading, from <http://www.iucnredlist.org/>) and the current study area (black star) in Cass County, Michigan, USA, 2009–2016. White stars (clock-wise from the top) denote study sites with published, long-term demographic estimates from Beausoleil Island, Georgian Bay, Canada (Jones et al. 2017); Cicero, New York, USA (Johnson et al. 2016b); and Carlyle, Illinois, USA (Dreslik et al. 2016).

climate normals (Hileman et al. 2017a). For example, mean annual frost-free days, temperature, and precipitation were recorded as 175 days, 8.8 °C, and 1,034.8 mm at a weather station within 11.2 km of the study site. These same climatic variables ranged from 110 to 221 days, 4.8 °C to 12.6 °C, and 828.6 mm to 1,119.7 mm for 38 populations spanning the distribution for the species (Hileman et al. 2017a). Monthly air temperature (1.5 m above ground) and precipitation averages during the active season (Apr–Oct) ranged from 7.2 °C to 25.4 °C and 25.4 mm to 291.3 mm from 2009 to 2016 (Michigan State University 2017).

METHODS

In May 2009, the Association of Zoos and Aquariums' Eastern Massasauga Rattlesnake Species Survival Plan[®] (EMR SSP) initiated a 6-day per year multi-year capture–recapture study on a 40.1-ha plot (site A, Table 1). To increase snake encounter probabilities and acquire additional data on reproduction, ingress and egress phenology, neonate survival, and neonate scent-trailing behavior (Hileman et al. 2015), we substantially increased sampling effort and the number of survey days in 2010–2014 to include the entire active season (Table 1). This research was conducted under a Michigan Department of Natural Resources Scientific Collector's Permit and an approved Northern Illinois University's Institutional Animal Care and Use Committee Protocol (number LA10-001). From 2011 to 2016, a research easement agreement with a neighboring private landowner allowed expansion of survey areas to include an additional 24.2 ha of contiguous habitat along the opposite side of a bisecting creek (site B, Table 1). To reduce heterogeneity in captures, we employed multiple detection methods including visual surveys, drift fences, funnel traps, and cover objects made of carpet or plywood. We captured snakes using tongs and secure containers and recorded capture locations using handheld global positioning system (GPS) units. We transferred captured snakes to an on-site laboratory for processing.

We determined sex by probing and subcaudal scale counts (Schaefer 1934, Gregory 1983). Using a measuring tape, we recorded total length (cm) with a squeeze box (Quinn and Jones 1974). We recorded tail length (cm) directly while the upper body was safely restrained in a transparent polyvinyl chloride tube. We calculated snout-vent length (SVL, cm) via subtraction and recorded mass (g) using a digital scale. We determined sexual maturity by the presence of enlarged

follicles or embryos in females (detected via palpation) and by the presence of motile sperm in males (Mengden et al. 1980). We assessed female reproductive status (gravid, non-gravid) via palpation for enlarged follicles or developing embryos. We validated our palpation methods by comparing detection of embryos or slugs (unfertilized eggs) via palpation with hormone assays ($n = 8$) and observed production of neonates by wild-caught females held for captive parturition ($n = 35$).

Each year from 2011 to 2014 we maintained up to 10 gravid female eastern massasaugas in captivity until parturition at an on-site laboratory to obtain data on reproductive parameters and to increase the number of marked neonates. To minimize time in captivity, we collected gravid females as close to parturition as possible with the objective of releasing them within 3 weeks of capture. Housing and captive husbandry are described in Hileman (2016). We processed and released postpartum females and offspring at the site of capture within 48 hours of parturition.

We marked adults and juveniles using passive integrated transponders (PIT tags) injected subcutaneously (Gibbons and Andrews 2004). Neonates were uniquely marked on ventral and flank scales using high-heat medical cautery units (Winne et al. 2006) and with PIT tags upon recapture at a larger SVL. We collected blood samples via caudal veins from all individuals for genetic banking and for projects related to nutrition (Slater et al. 2017), plasma electrophoretic profiles (Allender et al. 2015), and multiple paternity (Stedman et al. 2016). Except for individuals held for captive parturition or recovering from radio-transmitter surgeries (for a concurrent egress phenology study), we released snakes at their place of capture within 24 hours.

We used Program MARK version 8.1 (White and Burnham 1999) and capture–recapture models to estimate adult abundance and survival using closed robust design (Kendall et al. 1997), reproductive transition probabilities using multistate models (Nichols et al. 1994), reproductive frequency using a matrix model (Schwartz and White 2008), and age-specific apparent survival using the Cormack–Jolly–Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965). Unless otherwise specified, we used May–August snake captures to build capture histories required for capture–recapture analyses. We stratified capture histories by sex, survey unit, and age class. We identified age classes by combining information on the size of known-aged individuals (e.g., offspring born to wild-caught females held captive until parturition) with plots of SVL versus day of year

Table 1. Eastern massasauga survey dates, survey units, and sampling effort (i.e., number of person-hours spent conducting visual surveys) per year Cass County, Michigan, USA, 2009–2016.

Year	Survey unit	Approximate sampling area (ha)	Survey dates	Sampling effort (hr)
2009	A	40.1	3–8 May	277
2010	A	40.1	3–10 May, 20 Jul–15 Oct	581
2011	A and B	64.3	8 Apr–15 Oct	895
2012	A and B	64.3	19 Mar–11 Oct	817
2013	A and B	64.3	7 Apr–16 Oct	932
2014	A and B	64.3	29 Mar–17 Oct	815
2015	A and B	64.3	29 Apr–2 May, 20–22 May, 24–26 June	481
2016	A and B	64.3	11–14 May	327

(Fig. 2). Captures for snakes implanted with radio-transmitters ($n = 10$) over the course of the study were included in individual capture histories only if they were encountered via methods other than radio-telemetry. Additionally, we censored (i.e., treated as known removals) the terminal captures of these individuals to avoid introducing bias from possible radio-transmitter-related mortalities.

We used an information-theoretic approach and multi-model inference to evaluate multiple competing hypotheses for the observed data (Burnham and Anderson 2002, Anderson 2008). For model building, we *a priori* selected variables for a given candidate set that we believed to be important based on biology, sampling design, and available data. We then ran all possible model combinations from this subset (Doherty et al. 2012). We did not consider fully time-dependent global models for any of the candidate sets of models because data were sparse.

We assumed any overdispersion in the global model for a given analysis was due to unmodeled parameter heterogeneity rather than a lack of fit. We accounted for the unmodeled parameter heterogeneity using a variance inflation factor (\hat{c}) and the quasi-likelihood Akaike's Information Criterion corrected for sample size (QAIC_c; Anderson 2008). We estimated a variance inflation factor using the median \hat{c} method implemented in Program MARK version 8.1 (White and Burnham 1999). For model selection we used Akaike's Information Criterion adjusted for small sample size (AIC_c; Akaike 1973, Burnham and Anderson 2002). Unless the top-ranked model received $\geq 90\%$ model weight, we model-averaged across all models and used unconditional

standard errors to account for model uncertainty (Burnham and Anderson 2002).

Adult Survival and Abundance

We used the closed robust design model to estimate abundance and survival probabilities for adults (age ≥ 3 ; Kendall et al. 1997). The robust design model requires a 2-tiered sampling regime to estimate 5 fundamental parameter probabilities: survival (S), capture (p), recapture (c), emigration (γ'), and immigration (γ). Estimates of abundance are derived (Huggins 1989, 1991). Between primary occasions, the population is demographically open to mortality and migration. Within each primary occasion are ≥ 2 secondary occasions in which the population is treated as demographically and geographically closed. In our sampling design, we considered between-year samples as primary occasions and within-year samples as secondary occasions. Because the sampling area increased from 40.1 ha to 64.3 ha beginning in 2011, we excluded 2009 and 2010 so that changes in estimates of abundance across years would be meaningful. Using this sampling scheme resulted in 6 primary occasions and 24 secondary occasions. Years 2011–2014 each included 5 secondary occasions spanning May through August. Years 2015 and 2016 each included 2 secondary occasions, May and June. The terminal June 2016 occasion was fixed to zero. This dummy occasion (i.e., no sampling occurred) was included to meet the closed model requirements of ≥ 2 secondary sampling occasions per primary occasion.

We used Huggins closed-capture models during the secondary occasions because the Huggins model uses conditional likelihood and therefore allowed us to censor gravid females that were held in captivity for a single secondary sampling occasion (Huggins 1989, 1991). We censored individuals using dot notation within an individual's capture history, where animals were either captured (1), not captured (0), or unavailable (.) for a given occasion.

To reduce the number of possible candidate models, we employed a step-wise model-building strategy. We first considered 4 models that were identically parameterized for survival, capture, and recapture probabilities but differed in their parameterization of migration (Table 2). Survival varied by sex. Capture and recapture probabilities were treated as equal but varied through time by an interaction with sex. In our analysis, we treated emigration and immigration probabilities as nuisance parameters to account for male and female movement into and out of the study area between years. For females, these movement parameters can be interpreted as the products of migration and reproductive transition probabilities. Thus, they simultaneously account for movement and changes in reproductive status between years. For migration probabilities, we considered 4 primary movement models.

1. Random ($\gamma' = \gamma$). Movement between states (i.e., observable vs. unobservable) between time i and $i + 1$ is independent of the state at time i .
2. Markovian ($\gamma' \neq \gamma$). Movement between states between time i and $i + 1$ is dependent on the state at time $i - 1$.

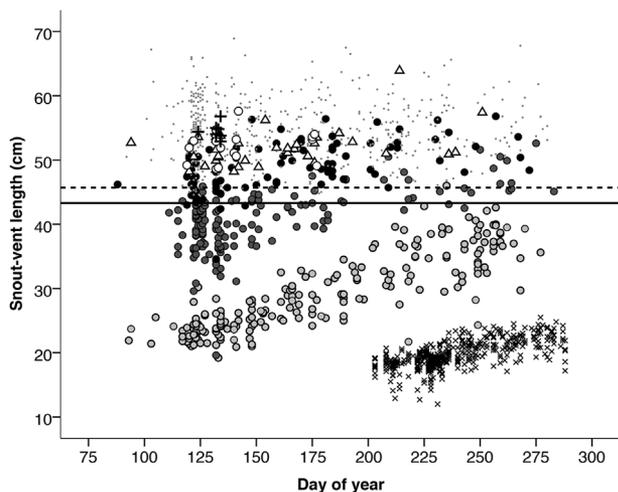


Figure 2. Snout-vent length versus day of year for eastern massasaugas captured 2009–2016 in Cass County, Michigan, USA. Two distinct age classes are evident: age 0 (young-of-the-year; \times) includes recently born animals prior to their first hibernation and age 1 (light gray circle) includes animals captured following their first hibernation but prior to their second hibernation. The remaining age classes are inferred from recaptures of known-age animals: age 2 (dark gray circle) includes animals captured following their second hibernation but prior to their third hibernation, age 3 (black circle), age 4 (hollow triangle), age 5 (hollow circle), and age 6 (+). Small gray dots identify older individuals and individuals of unknown age. Horizontal lines denote approximate size at sexual maturity for males (43.3 cm, solid line) and females (45.7 cm, dashed line).

Table 2. Four initial movement models considered in the closed-capture robust design analysis for adult eastern massasauga, Cass County, Michigan, USA, 2011–2016.

Model	QAIC _c ^a	ΔQAIC _c ^b	QAIC _c w_i^c	K^d	QDeviance ^e
Even flow	1,758.82	0.00	0.88	54	1,649.60
Random	1,763.62	4.81	0.08	54	1,654.41
Markovian	1,765.04	6.23	0.04	59	1,643.20
No movement	68,799.44	67,040.62	0.00	48	68,705.02

^a Models are ranked in ascending quasi-likelihood Akaike’s Information Criterion corrected for sample size (QAIC_c) order.

^b Difference between model i and the top-ranked model.

^c Adjusted model weight.

^d The number of parameters.

^e Adjusted difference in $-2\log(\mathcal{L})$ of the current model and the saturated model.

- Even flow ($\gamma'' = 1 - \gamma'$). Movement between states between time i and $i + 1$ are equal.
- No movement ($\gamma'' = 0, \gamma' = 1$). No movement between states.

We used the top-ranked migration parameterization from these 4 models to construct 47 additional models for the candidate set. We considered 2 models for survival, where survival was held constant or allowed to vary by sex. We included 4 additional migration parameters that treated immigration and emigration as equal and constant, or equal but allowed to vary by sex, time, or additive effects of sex and time. We considered 6 models for capture and recapture probabilities. We treated capture and recapture probabilities as unequal and varying by sex, or as equal and varying by sex, additive and interaction effects of sex and time, or additive and interaction effects of sex and sampling effort. We modeled sampling effort as an occasion-specific covariate and calculated it as the sum of per-person visual search hours for a given sampling period. We ran all combinations of these parameterizations. Including the 4 original migration models and a null model, this resulted in a candidate set of 52 models (Table S1, available online in Supporting Information). Because goodness-of-fit tests are not available for robust design models and because we considered only constrained-time models (i.e., no time dependence in survival), we evaluated the data for overdispersion using median \hat{c} by pooling data over the primary sampling occasions.

Age-Specific Apparent Survival

We used the CJS model to estimate age-specific annual apparent survival for ages 0, 1, and 2 using 2009–2016 data (Cormack 1964, Jolly 1965, Seber 1965). The CJS model uses conditional likelihood to estimate 2 fundamental parameters: apparent survival (ϕ) and recapture probability (\hat{p}). Survival is considered apparent because the CJS model assumes that emigration is permanent and is therefore indistinguishable from mortality (Seber 1982, Pollock et al. 1990). Because our closed-capture robust design models explicitly accounted for temporary migration in estimation of adult survival, and because adult apparent survival probabilities can influence the apparent survival probabilities of younger individuals, we fixed CJS adult apparent survival estimates to the values resulting from the robust design analysis. We also used May–September as our sampling

occasion length to ensure sufficient captures of age 0 and age 1 individuals. To confirm that using the fixed adult estimates from the robust design analysis did not bias CJS estimates, we compared model-averaged estimates of age 0 through age 2 that resulted from using fixed adult estimates to those that included adult estimates generated by the CJS model. Similarly, we compared apparent survival estimates resulting from May–September pooled occasions versus the May–August pooled occasions. Model-averaged parameter estimates were largely congruent for all 4 comparisons. Therefore, we report the model-averaged, age-specific annual apparent survival estimates for ages 0, 1, and 2 that resulted from using unfixed adult parameters and the more inclusive dataset (May–Sep).

For our global model, we allowed apparent survival to vary by age (age 0, 1, 2, and ≥ 3) and sex in adults (age ≥ 3). Recapture probabilities varied by an interaction between sex and time in adults and by age and time for age 0 through age 2. We considered 4 models for apparent survival and 17 models for recapture probabilities, all of which were nested within the global model. Models varied in their treatment of time, sampling effort, sex (in adults), and number of age classes (2, 3, or 4 age classes). In the reduced age models for apparent survival, age 1 and age 2 were constrained to share apparent survival probabilities. In the reduced age models for recapture probabilities, adult males were constrained to share recapture probabilities with animals of age 1 and age 2. We modeled all permutations of these parameterizations. Including additive and interactive effects and a null model resulted in a candidate set of 69 models (Table S2, available online in Supporting Information).

Reproductive Transition Probabilities and Reproductive Frequency

We used a multistate generalization of the CJS model to estimate transition probabilities between gravid and non-gravid states for adult females captured between 2009 and 2016 (Arnason 1972, 1973; Brownie et al. 1993; Schwarz et al. 1993; Nichols et al. 1994). This model assumes a first-order Markov process. In other words, the transition probabilities at time $t + 1$ are assumed to be dependent on the state at time t . All individuals were assigned a state for a given capture year. State variables included 2 observable states, gravid (G) and non-gravid (N), and 1 unobservable state (0). We censored 6 observations where reproductive

status was unknown using dot notation (.). We did not consider fully time-dependent effects because of small sample size but included a state by sampling effort interaction effect on recapture probabilities. Our global model allowed apparent survival to vary by state, recapture probabilities to vary by an interaction with state and sampling effort, and transition probabilities (Ψ) to vary by state. We modeled all permutations of these parameterizations, including models where state or time was held constant, resulting in a candidate set of 20 models (Table S3, available online in Supporting Information).

To estimate reproductive frequency, we incorporated the transition probabilities resulting from the multistate modeling described above into the following matrix equation:

$$[1 \ 0] \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}^k \quad (1)$$

The row vector represents an adult gravid female. The 2×2 matrix includes 4 transition probabilities: the probability of a gravid female in year (t) being non-gravid (a_{11}) or becoming gravid again (a_{12}) in year $t+1$ and the probability of a non-gravid female in year (t) becoming gravid (a_{21}) or staying non-gravid (a_{22}) in year $t+1$. We determined the number of years (k) required to reach a stable-state reproductive frequency iteratively (Schwartz and White 2008) using R version 3.3.1 (R Core Team 2016) and the R packages matrix (Bates and Maechler 2016) and expm (Goulet et al. 2015). We approximated the variance for reproductive frequency using the delta method (Seber 1982).

Population Viability Under Various Prescribed-Fire Regimes

To evaluate population persistence and explore the effects of different prescribed-fire regimes on population trajectories,

we used Vortex 10.2.8.0 (Lacy and Pollak 2015) to construct an individual-based demographically and environmentally stochastic model that incorporated our population-specific parameter estimates. For our baseline model, we set the initial population size (N_0) to 294 because this resulted in a stable age distribution that included 135 adults, the estimated adult population size in 2016 resulting from the closed-capture robust design analysis. To avoid projections that were unrealistically pessimistic, we allowed populations to “. . . grow away from the absorbing state of extinction” (White 2000:322) by setting carrying capacity (K) to $1.5N_0$ and $2N_0$ (i.e., 1.5 and 2 times the initial population size, $K=441$ and $K=588$ individuals; Miller 2006). In the absence of fire, K should logically decrease as a function of suitable habitat size. Thus, as suitable habitat decreases because of encroachment of woody vegetation, K should also decrease. We held K constant over the simulated years to mimic the positive effect of prescribed fire in maintaining K by preventing habitat shrinkage from succession. Because of uncertainty in K , we used both values of K ($1.5N_0$ and $2N_0$) to evaluate model sensitivity to the parameter. We defined extinction as when only 1 sex remained in the population. Values used for age at first reproduction, sex ratio at birth, percent adult females breeding each year, mean and maximum litter size, and age-specific mortality came from our demographic analyses (Table 3).

During the course of the study (2009–2016), prescribed burns occurred within the study site or in neighboring contiguous habitat in 6 of the 8 survey years. In the 6 years prescribed fires took place, 1–3 non-overlapping habitat burns were conducted annually with an average burn covering 22.5 ± 15.1 (SD) ha (range = 1.6–35.6 ha). Burns occurred 21 March–12 April and 26 October–9 November and were scheduled to avoid the active season and thus

Table 3. Eastern massasauga parameter estimates and associated environmental variation (EV) used in the baseline population viability model using Program Vortex, Cass County, Michigan, USA, 2009–2016.

Parameter	Value (EV)	Source
Breeding system	Polygynous	Duvall et al. (1992), Stedman et al. (2016)
Age of first reproduction	3	This study.
Max. lifespan	15	Unknown in wild, 20 years in captivity (Harding 1997); western massasauga, <i>Sistrurus tergeminus</i> (Snider and Bowler 1992).
Max. age of reproduction	15	Unknown. Captive animals ~15 years old have reproduced in captivity (Miller 2006).
Inbreeding depression?	No	Data unavailable.
Annual % adult females reproducing	44.0 (7.7)	This study. Environmental variation estimated using the delta method (Seber 1982).
Density-dependent reproduction?	No	Data unavailable.
Max. litter size	16	This study.
\bar{x} litter size	7.60 (0.54)	This study. Environmental variation estimated using bootstrapping with replacement ($n = 10,000$).
Sex ratio at birth (% males)	47.3	This study.
% annual mortality		This study. Process variance calculated as 11% of the total variance for each mortality estimate (Jones et al. 2017).
Age 0–1	62.2 (0.7)	
Age 1–2	34.7 (0.7)	
Age 2–3	32.7 (0.7)	
Age ≥ 3 males	33.8 (1.0)	
Age ≥ 3 females	28.6 (0.5)	
Harvest	No	This study. Harvest due to the effects of prescribed fire is built into the parameter estimates.
Initial population size (N_0)	294	This study. Based on the size required, assuming a stable age distribution, to produce 135 adults, which is the estimated adult population size from 2016.
Carrying capacity (K)	441, 588	$K = 1.5 N_0$ and $K = 2 N_0$ (Miller 2006)

minimize eastern massasauga mortality. Although we never encountered eastern massasauga carcasses during post-burn walkthroughs at this site, we expect that some mortality occurred, either as a direct result of fire or as an indirect effect of increased depredation due to decreased ground cover. However, the data were insufficient to model prescribed-burn effects explicitly using the capture–recapture data. Given that the parameter estimates included 6 burn years and our baseline model incorporates these parameter estimates, any effects of the current prescribed–fire regime on mortality or detection probabilities from this site are built into the baseline model.

We modeled alternative scenarios to simulate the effects of additional spring, fall, and late fall prescribed–burn mortality (as might occur with a less conservative use of prescribed fire) at varying levels of burn intensity using Vortex’s harvest functions. For each season, we specified which age classes were available and thus vulnerable to prescribed–fire harvest for a given burn scenario. For instance, in spring, males and females of age classes 1, 2, and ≥ 3 are vulnerable to prescribed fire, whereas neonates are not yet born. In fall, because parturition typically occurs in July or August, neonates (age 0) and individuals of age classes 1, 2, and ≥ 3 are vulnerable to prescribed fire. In late fall (Oct), neonates ingress on average 7.5 days after the rest of the population based on the last date of observation in the field (E. T. Hileman, Northern Illinois University, personal observation). Therefore, for the late fall prescribed–burn scenario only neonates were considered vulnerable to prescribed fire. Prescribed–fire harvest of neonates in fall and late fall was implemented by having harvest occur before age in the sequence of events for a Vortex year (Lacy et al. 2017).

For each of the temporal burn scenarios, we considered 3 levels of severity where the available population was subjected to both the baseline model’s built-in prescribed–fire mortality and an additional biennial harvest mortality using a linear density-dependent function:

$$\frac{N_t}{K} \times \text{Poisson}(x) \quad (2)$$

where N_t is the population size at time t , K is the carrying capacity, and x is the mean number of individuals at risk of prescribed fire for a given sex and age. For biological realism, we included zero in the Poisson distribution so that some burn years resulted in no mortality. For a given burn scenario, x was fixed for each available sex and age class to achieve the specified mean individual mortalities (i.e., low = 5, medium = 10, or high = 20) when the population was equal to K . When N_t was $< K$, mean mortalities declined linearly as a function of the population size at time t . For example, at the initial population size $N_0 = 294$ with $K = 2N_0$, mean harvest would be 2.5, 5, or 10 individuals for the low, medium, and high burn harvest scenarios, respectively. We simulated baseline and biennial spring, fall, and late fall prescribed–burn scenarios at low, medium, and high harvest levels for 50 and 100 years and $K = 1.5N_0$ or $2N_0$ using 1,000 iterations per scenario (40 scenarios in total).

RESULTS

From 2009 to 2016, 826 eastern massasaugas were captured 1,776 times. Animals of known age spanned 0–6 years (Fig. 2). Based on estimated age at first capture and last known observation, 1 individual, who was also gravid, was ≥ 10 , 2 were ≥ 9 , 2 others were ≥ 8 , and 3 were ≥ 7 years old. Mean litter size based on captive-born neonates (i.e., age 0) was 7.6 ± 3.2 (SD), with litters ranging from 2 to 16 individuals ($n = 35$ litters). Bootstrapping these data using sampling with replacement ($n = 10,000$) resulted in a mean litter size estimate for the population of 7.6 ± 0.54 (SE; 95% CI = 6.6–8.7; R package, Boot). Snout-vent length at birth was similar between males ($\bar{x} = 18.4$ cm ± 1.2 [SD], $n = 112$) and females ($\bar{x} = 18.7$ cm ± 1.3 , $n = 147$); mass was the same for males and females ($\bar{x} = 11$ g ± 2 , $n = 112$ and $n = 145$). Sex ratio of captive-born offspring was significantly different than 0.50 (proportion male = 112/259, 0.433, 95% CI = 0.371–0.496, $P = 0.03$, binomial test). However, no bias in sex ratio was evident when we pooled captive-born and wild-born neonates (proportion male = 199/421, 0.473, 95% CI = 0.424–0.522, $P = 0.28$, binomial test).

Adult Survival and Abundance

We estimated a variance inflation factor of 1.21 for the capture–recapture data pooled over the primary sampling occasions using median \hat{c} . Thus, we assumed latent heterogeneity was present and adjusted for overdispersion using the quasi-likelihood QAIC_c. Based on the initial 4 movement models, we found strong evidence for equal immigration and emigration probabilities; the even flow model received most of the model weight (QAIC_c $w_i = 0.88$; Table 2). For the full candidate set of 52 models, the top-ranked model (QAIC_c $w_i = 0.30$; Table S1) treated survival as constant, immigration and emigration probabilities as equal but varying by an additive effect of sex and time, and capture and recapture probabilities as equal but varying by an additive effect of sex and sampling effort. Accounting for movement, model-averaged annual adult survival was 0.66 ± 0.09 (SE; 95% CI = 0.47–0.81) for males and 0.71 ± 0.05 (95% CI = 0.61–0.80) for females. From 2011 to 2016, abundance estimates ranged from 84 to 140 adults (Table 4; Fig. 3). However, confidence intervals broadly overlapped in all years. Based on overlapping confidence intervals, estimates of sex-specific abundance were indistinguishable between sexes and across years.

Age-Specific Apparent Survival

Using median \hat{c} , we estimated a variance inflation factor of 1.09, which indicated only modest overdispersion for the global model. Of the 69 models considered, the top 9 garnered $>95\%$ of the QAIC_c model weight (Table S2). For apparent survival, the top-ranked model (QAIC_c $w_i = 0.23$) included 3 groups: adults (no sex effect), age 2 and age 1 treated as equal, and age 0. Recapture probabilities also included 3 groups: an additive effect of adult females and time; adult males, age 2, and age 1 all treated as equal and varying across years by an additive effect of time; and an additive effect of age 0 and time. Annual estimates of apparent survival for adult males and females overlapped

Table 4. Adult eastern massasauga abundance (\hat{N}) for combined survey units A and B resulting from the robust design analysis, Cass County, Michigan, USA, 2011–2016. We provide the number of unique adult snakes captured per year (M_{t+1}). We calculated estimates of standard error for the combined adults using the delta method.

Group	Year	M_{t+1}	\hat{N}	SE	95% CI
Males	2011	19	32	9	23–63
	2012	28	64	20	41–128
	2013	32	79	24	51–152
	2014	15	43	21	23–117
	2015	10	56	42	20–221
	2016	28	96	62	43–342
Females	2011	35	54	10	42–85
	2012	41	45	3	42–55
	2013	55	61	3	57–72
	2014	36	41	3	38–52
	2015	29	46	9	35–76
	2016	31	40	12	32–99
Combined adults	2011	54	86	14	68–124
	2012	69	110	20	85–171
	2013	87	140	24	110–211
	2014	51	84	21	62–154
	2015	39	102	43	58–250
	2016	59	135	64	77–377

with adult male and female survival estimates from the closed-capture robust design analysis (Table 5).

Model averaging resulted in adult apparent survival estimates that had smaller point estimates (and narrower 95% CIs) than those generated from the closed-capture robust design analysis. Point estimates of apparent survival increased with increasing age from age 0 to age 2 but declined slightly in adult males (Table 5). However, confidence intervals broadly overlapped between all age classes except for age 0, which were significantly lower than all other age classes (Table 5).

Reproductive Transition Probabilities and Reproductive Frequency

We estimated a variance inflation factor of 1.11 for the global model using median \hat{c} . The top-ranked model (QAIC_c, w_i

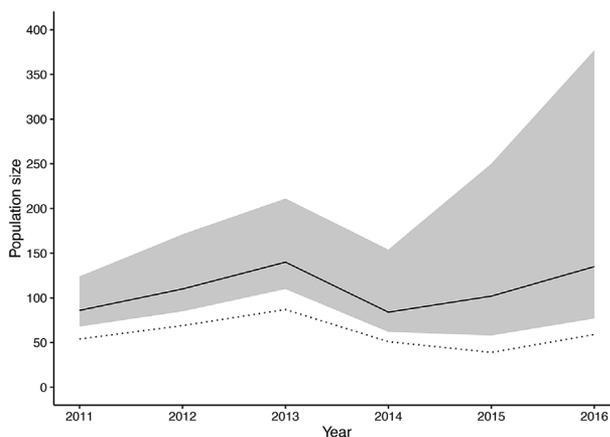


Figure 3. Eastern massasauga adult abundance estimates (solid black line) in 2011–2016, Cass County, Michigan, USA, resulting from the closed-capture robust design analysis. Gray shaded area represents the 95% confidence intervals. The dotted line represents the minimum number of individuals known alive per year.

Table 5. Eastern massasauga age-specific annual survival based on Cormack-Jolly-Seber apparent survival (ϕ) or robust design survival (S) probabilities for Cass County, Michigan, USA, 2009–2016.

Age class	Estimate	SE	95% CI
Age ≥ 3 male	0.66 ^S (0.59 ^{ϕ})	0.09 (0.06)	0.47–0.81 (0.46–0.71)
Age ≥ 3 female	0.71 ^S (0.65 ^{ϕ})	0.05 (0.04)	0.61–0.80 (0.57–0.73)
Age 2	0.67 ^{ϕ}	0.07	0.53–0.79
Age 1	0.65 ^{ϕ}	0.06	0.52–0.77
Age 0	0.38 ^{ϕ}	0.06	0.27–0.50

= 0.34) allowed apparent survival, recapture, and transition probabilities to vary by state (i.e., gravid vs. non-gravid; Table S3). Model averaging resulted in gravid females that had larger point estimates for annual apparent survival (0.75 ± 13 [SE]; 95% CI = 0.45–0.92) than non-gravid females (0.59 ± 07 ; 95% CI = 0.45–0.72), but confidence intervals for the 2 estimates overlapped. Across years, recapture probabilities for gravid females were significantly higher than those of non-gravid individuals (Fig. 4). Gravid females had a 0.98 ± 0.02 (SE; 95% CI = 0.90–1.00) probability of transitioning to non-gravid the next year. Thus, the probability of being gravid 2 years in a row was only 0.02 ± 0.02 (95% CI = 0.00–0.10). Non-gravid females had a 0.77 ± 0.08 (95% CI = 0.58–0.89) probability of transitioning to gravid the next year, or a 0.23 ± 0.08 (95% CI = 0.11–0.42) probability of remaining non-gravid for 2 years in a row. Using these transition probabilities resulted in a stable-state reproductive frequency of 0.44 ± 0.08 (95% CI = 0.29–0.59) after 33 years.

Population Viability Under Various Prescribed-Fire Regimes

For the baseline model, the deterministic intrinsic rate of population increase, $r = 0.0020$, indicated modest population growth. Including demographic and environmental

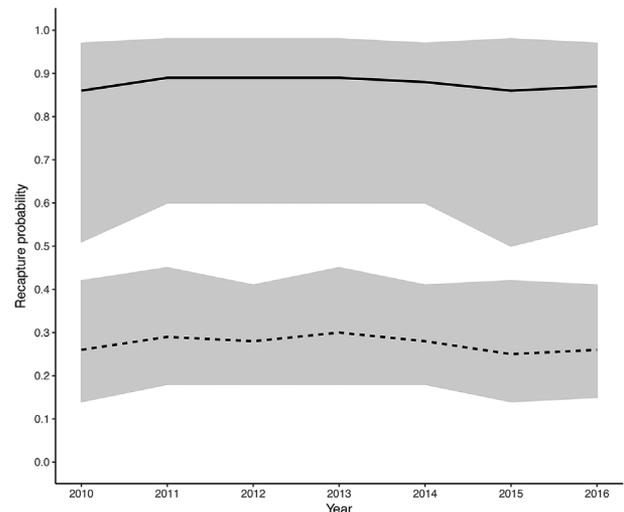


Figure 4. Eastern massasauga annual recapture probabilities (p) for gravid (solid line) and non-gravid (dashed line) females, Cass County, Michigan, USA, 2009–2016. Gray shaded areas represent the 95% confidence intervals.

stochasticity for the 50-year baseline model scenarios reduced r only slightly (-0.0002 ± 0.0928 [SD], $K=1.5 N_0$; -0.0005 ± 0.0938 , $K=2N_0$) and resulted in a zero probability of extinction for the $2K$ settings. The probability of extinction was low (≤ 0.007) for all 50-year prescribed-burn scenarios regardless of season (spring, fall, late fall) or burn severity (low, medium, high settings).

Increasing the baseline model projection to 100 years resulted in little change to r (-0.0003 , -0.0006) or the probability of extinction (0.002, 0.006) for $K=1.5 N_0$ and $K=2 N_0$, respectively (Table 6). Depending on the burn season and severity, additional mortality due to prescribed fire over 100 years decreased r (-0.0032 to -0.0277) and increased the probability of extinction (0.009–0.245), with mean time to extinction ranging 80.1–88.3 years (Table 6). The highest probability of extinction for $K=1.5 N_0$ and $K=2 N_0$ was with fall burns (0.245, 0.130), followed by spring burns (0.201, 0.111), and late fall burns (0.075, 0.034; Table 6). Final population size at year 100 decreased from N_0 an average of 25.2–83.2% from fall burns, 19.7–78.2% from spring burns, and 12.1–62.9% from late fall burns depending on harvest severity and carrying capacity setting, with the high harvest setting resulting in the most pessimistic trajectories (Fig. 5).

DISCUSSION

Land management practices that require burning or mowing to maintain habitat suitability require careful planning. This is particularly true for sites hosting species sensitive to disturbance such as the federally threatened eastern massasauga (Durbian 2006, Cross et al. 2015, USFWS 2016). Using contemporary capture–recapture and matrix models, we estimated key population parameters needed for reliable prospective modeling and evaluation of population viability under various prescribed-burn management scenarios. Our study represents the most complete population demographic analysis to date for this species. To our knowledge, this article provides the first published estimates of eastern massasauga age-specific survival from birth to adulthood and reproductive frequency corrected for

state-specific (gravid and non-gravid) recapture probabilities. Such estimates are essential for reliable prospective modeling and conservation planning for the species.

Survival

Our closed robust design estimates of adult annual survival for males (0.66; 95% CI = 0.47–0.81) and females (0.71; 95% CI = 0.61–0.80) fall within the range of adult survival estimates for the species (0.35–0.95; Jones et al. 2012, Johnson et al. 2016b). Sex-specific adult annual survival has been reported for only a few eastern massasauga populations: males (0.90) and females (0.68) in Kalkaska, Michigan (Jones et al. 2012); males (0.74, 95% CI = 0.67–0.80) and females (0.73, 95% CI = 0.64–0.80) in Georgian Bay, Ontario (Jones et al. 2017); and females (0.78, 95% CI = 0.67–0.86) in Cicero, New York, USA (Johnson et al. 2016b). The adult female survival estimate for Cass County is most similar to those reported in Kalkaska, Michigan, and Georgian Bay, Ontario. However, our adult male estimate is lower than those reported for either of these sites. Adult males travel greater distances than females (Rouse et al. 2011). Some males may have left the survey area during the study resulting in a slightly lower point estimate of survival. Jones et al. (2017) reported evidence for adult emigration, which is not permitted in CJS models. They corrected for this violation by modeling emigration as a transient effect in first encounter for apparent survival in males and females. The robust design model we used allows for temporary emigration between primary occasions (yrs), but it does not permit permanent emigration. If we compare our CJS top-ranked model that includes a sex effect in survival (Table S2, model 2) with a model that includes a first capture transient effect in male survival, the model that includes the transient effect is rejected, suggesting permanent emigration is not a factor ($\chi^2_1 = 0.429$, $P = 0.51$, likelihood ratio test).

For our age-specific apparent survival analysis, we treated within-year captures between May and September as demographically and geographically closed. We assumed all additions (except for births, which we included for age 0

Table 6. Eastern massasauga prescribed-burn simulation results for Cass County, Michigan, USA, using Program Vortex and data collected 2009–2016. Each scenario included 1,000 simulations. Initial population size (N_0) was 294. Deterministic rate of increase was 0.0020. Harvest due to the effects of prescribed fire occurred at a biennial frequency and was density dependent so that a maximum of 5 (low), 10 (medium), or 20 (high) individuals were removed from the population when carrying capacity (K) = $1.5 N_0$ and $K = 2 N_0$. Different male and female groups were vulnerable to harvest in spring (age 1, age 2, age ≥ 3 ; 6 groups), fall (age 0, age 1, age 2, age ≥ 3 ; 8 groups), and late fall (age 0; 2 groups). We present the stochastic rate of increase (Stoch- r), the probability of extinction (PE), and the mean time to extinction in years (\bar{x} TE).

100-year scenarios	Harvest	$K = 1.5 N_0$				$K = 2 N_0$			
		Stoch- r	SD	PE	\bar{x} TE	Stoch- r	SD	PE	\bar{x} TE
Baseline		–0.0003	0.0967	0.002	96.5	–0.0006	0.0964	0.006	87.7
Spring	Low	–0.0064	0.1079	0.015	87.7	–0.0050	0.1037	0.016	81.0
	Medium	–0.0120	0.1211	0.044	83.0	–0.0092	0.1135	0.027	84.9
	High	–0.0245	0.1543	0.201	82.6	–0.0184	0.1359	0.111	81.9
Fall	Low	–0.0074	0.1094	0.019	80.1	–0.0056	0.1060	0.014	83.2
	Medium	–0.0132	0.1231	0.051	85.7	–0.0101	0.1139	0.029	85.3
	High	–0.0277	0.1631	0.245	83.3	–0.0206	0.1412	0.130	83.4
Late fall	Low	–0.0041	0.1027	0.009	86.8	–0.0032	0.0998	0.003	82.7
	Medium	–0.0079	0.1108	0.015	85.7	–0.0055	0.1057	0.009	88.3
	High	–0.0156	0.1305	0.075	85.4	–0.0110	0.1185	0.034	82.3

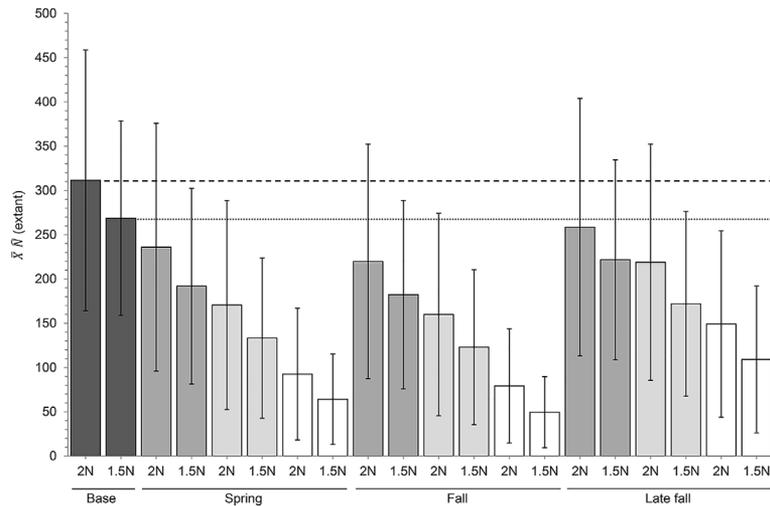


Figure 5. Eastern massasauga mean population size (\pm SD) of remaining extant populations from 1,000 simulations after 100 years for Cass County, Michigan, USA. We show the base model (dark gray), and low- (medium gray), medium- (light gray), and high-intensity (white) prescribed-fire settings for both of the carrying capacity (K) settings calculated based on initial population size (N_0): $K = 2N_0$ and $K = 1.5N_0$. The dashed line indicates the mean extant population size for the base model in 100 years for $K = 2N_0$. The dotted line indicates the mean extant population size for the base model in 100 years for $K = 1.5N_0$.

apparent survival) and subtractions to the population occurred during the interval between sampling occasions. The CJS model assumes sampling is instantaneous (Williams et al. 2002). Thus, our survival estimates apply to the midpoint of 1 sampling occasion to the midpoint of the next occasion (Pollock and Alipizar-Jara 2005). Longer sampling occasions like we used here can induce heterogeneity in apparent survival (and recapture probabilities) between individuals (Williams et al. 2002). Given that adult eastern massasaugas have reportedly high active-season survival (Bailey et al. 2011, Jones et al. 2012), the assumption of little to no mortality during May–September (or May–Aug for the robust design analysis) is reasonable. It is unknown if this assumption is reasonably approximated for younger age classes; however, heterogeneity in apparent survival does not generally result in biased estimation of this parameter (Pollock and Alipizar-Jara 2005).

We know of no other estimates of juvenile eastern massasauga survival, and comparable likelihood-based survival estimates for other juvenile viperids are scant (Diller and Wallace 2002, Altwegg et al. 2005, Brown et al. 2007, Brown 2008). Reported annual survival estimates for neonate meadow vipers (*Vipera ursinii ursinii*; 0.48 ± 0.11 [SE]) and European asp vipers (*Vipera aspis*; age 0 [~ 0.25 – 0.70], age 1 [~ 0.40 – 0.70], and age 2 [~ 0.57 – 0.70]) are similar to ours (Table 5; Altwegg et al. 2005, Baron et al. 2010). Not surprisingly, reported annual survival estimates for the substantially larger timber rattlesnake (*Crotalus horridus*) were higher for neonates (age 0 = 0.53 – 0.77) and juveniles (age 1–3 = 0.84 – 0.99 ; Brown et al. 2007, Brown 2008; see Diller and Wallace 2002 for comparable survival estimates that decline over time from a postulated handling effect. Note that we modified the age-specific naming conventions used in Altwegg et al. 2005, Brown et al. 2007, and Brown 2008 to conform to our own).

Reproductive Frequency

We estimated reproductive frequency by incorporating reproductive transition probabilities from the multistate model into a matrix model rather than using the reproductive proportion from uncorrected count data (i.e., $\frac{\text{gravid females}}{\text{total females}}$), as is common practice in herpetological research (Seigel and Ford 1987, Brown 1991, Holycross and Goldberg 2001, Martin 2002; see Bonnet and Naulleau 1996 for use of corrected counts, Schuett et al. 2011 for radio-telemetry methods, and Brown 2016 for direct observation). This resulted in an annual reproductive frequency of 0.44 (95% CI = 0.29 – 0.59), which is significantly smaller than the estimate that results when a weighted (by yr) average of the reproductive proportion method is used (0.62).

Using the proportion of gravid females as a proxy for reproductive frequency will yield biased estimates if significant differences in detection probabilities exist between gravid and non-gravid females (Bonnet and Naulleau 1996). The method we used explicitly accounted for this source of bias by modeling reproductive state-specific recapture probabilities. Had we used the positively biased estimate of 0.62 rather than our reproductive frequency estimate of 0.44, it would have resulted in unrealistically optimistic projections. For example, if we consider our most pessimistic burn simulation (i.e., the 100-yr high intensity fall prescribed-burn scenario, $K = 1.5N_0$) but with reproductive frequency = 0.62, r increases to 0.046 (vs. -0.028), probability of extinction decreases to 0.00 (vs. 0.25), and mean final population size increases to 434 (vs. 50), only 6 individuals shy of carrying capacity. Similarly, if we use the same 100-year high intensity fall prescribed-burn scenario but with reproductive frequency = 0.42, a surrogate estimate from a New York population (discussed below), r decreases to -0.039 , probability of extinction increases to 0.52, and final population size decreases to just 32. These stark

examples serve to highlight the importance of using unbiased, population-specific estimates in population viability analyses. If population-specific parameter estimates are unavailable, we recommend cautious use of parameter estimates from demographically similar populations (Hernández-Camacho et al. 2015).

To reproduce, female eastern massasaugas must gain adequate capital in the form of energetic reserves that can sustain them through follicular and embryonic development, parturition (Van Dyke and Beaupre 2011), and maternal attendance (Hileman et al. 2015). Our transition probability estimates provide strong evidence for this reproductive cost in eastern massasaugas. For example, we estimated that 0.98 (95% CI = 0.90–1.00) of gravid females transition to a non-gravid state the next year, but only 0.77 (95% CI = 0.58–0.89) of non-gravid females transition back to a gravid state the following year. If reproduction incurred no cost above what is spent from biennial reproduction, these transition probabilities should be approximately equal (rather than skewed toward gravid females transitioning to non-gravid states). Our results indicate that for some individuals (0.23), ≥ 2 years are required to recover from the reproductive expenditures before another episode of reproduction is possible.

Reproduction transition probabilities have been previously estimated for the European meadow viper (*Vipera ursinii esinii*) using Arnason-Schwartz models (Baron et al. 2013) and for the eastern massasauga using robust design models (Johnson et al. 2016b). However, neither study extended the transition probabilities to matrix models to explicitly estimate reproductive frequency. For a New York eastern massasauga population (Johnson et al. 2016b), combining a matrix approach with their transition probabilities (modeled as annual emigration of non-gravid females and re-immigration of gravid females) results in an annual reproductive frequency estimate of 0.42, which is similar to our estimate of 0.44. The transition probability resulting from Johnson et al. (2016b) corroborates our finding that reproductive cost in eastern massasaugas is paid, in part, by reduced frequency of reproduction.

Population Viability Under Various Prescribed-Fire Regimes

The baseline model in our population viability analysis incorporated the effects of recent prescribed-fire practices by its inclusion of parameters estimated from 2009 to 2016 data, which included 6 prescribed-burn years (2010, 2012–2016). Spring prescribed burns at this site occurred between 21 March and 12 April and only if soil temperatures at 10 cm depth were below 7.8 °C. Thus, it is probable that most burns occurred while snakes were still underground. Similarly, fall burns occurred late in the season between 26 October and 9 November after most snakes had likely ingressed. Our results suggest that current burn practices (i.e., the baseline model) will not have an appreciable negative impact on the population 50 or 100 years into the future if prescribed-fire management practices and demographic parameters remain unchanged (Table 6 and Fig. 5). Our findings also

suggest that modest increases in burn-related mortality are likely to have little effect on the probability of extinction over the next 50 years but noticeable effects over 100 years. Increases in burn-related mortality above that in the baseline model are projected to result in (slightly) negative population growth and declining population size that increase the probability of extinction over time.

Although all of our models provided biological realism by including population-specific demographic and environmental stochasticity, and reasonable prescribed-burn scenarios, some model simplification was necessary. For instance, because they are unknown and difficult to estimate, we excluded genetic stochasticity and catastrophic events, 2 important sources of uncertainty in population dynamics and population persistence (Shaffer 1981). In addition, we assumed the probability of harvest was equal across sexes and age groups present. Last, our prescribed-fire simulation models did not include spatial factors, such as prescribed-fire events occurring near hibernacula during egress or ingress when a larger number of individuals may be susceptible to mortality than we considered in our models. This was an intentional omission to maintain a tractable number of models and because we agree with the recommendations of Cross et al. (2015) that hibernacula should be identified and avoided prior to conducting prescribed burns during these sensitive phenological events.

Several factors contribute to determining the timing of prescribed burns (e.g., temperature, relative humidity, dew point, wind speed, available fuel loads; Weir 2009). To focus on the effects that increased mortality and timing of burns had on population persistence, we did not model these important pre-burn considerations. Still, to minimize eastern massasauga mortality, prescribed fires should be conducted pre-emergence or post-ingress (Johnson 2000, Kingsbury 2002, Durbian 2006, Cross et al. 2015). If a prescribed burn is conducted while snakes are active, late fall burns may have the smallest effect on the population, provided the timing of the burn can be calibrated so that only neonates are vulnerable. This could be achieved by having experienced individuals conduct visual surveys of the proposed site in advance of the prescribed burn.

By halting the encroachment of woody vegetation, prescribed fire prevents shrinkage of suitable habitat and thereby helps to maintain eastern massasauga carrying capacity. Thus, prescribed fire can bolster population persistence as long as collateral mortality is minimized and does not result in long-term negative population growth. Our results suggest that current prescribed-fire practices in Cass County will be sustainable 100 years into the future if prescribed-fire management practices remain unchanged and current conditions persist.

MANAGEMENT IMPLICATIONS

We modeled prescribed-burn scenarios assuming varying levels of management-caused mortality, which may be comparable to burn regimes used at other eastern massasauga sites. The prescribed-fire projection models we constructed incorporated site-specific parameter estimates from a

population that appears to be healthy and where poaching and road mortality are likely negligible. Eastern massasauga population parameters are known to vary geographically (Aldridge et al. 2008, Jones et al. 2012, Hileman et al. 2017a) and road mortality in this species has been documented elsewhere (Choquette and Valliant 2016) and may even be a primary source of mortality for some populations (Shepard et al. 2008, Baker et al. 2016). Thus, caution is warranted in extrapolating the results from this study to other managed eastern massasauga populations. Acknowledging these limitations, our results may help inform prescribed-fire management for populations similar in demography, habitat size, and habitat structure. In addition, the population parameters estimated here provide vital information for assessing range-wide population viability and investigating geographic variation in eastern massasauga demography.

ACKNOWLEDGMENTS

We thank M. C. McCuiston, J. Suseland, and the Edward Lowe Foundation staff; field technicians D. R. Bradke, J. Vecchiet, D. M. Delaney, J. J. Knapp; G. C. White, R. C. Lacy, P. S. Miller, and C. N. von Ende for their input on specific aspects of our analyses. We thank the many EMR SSP members and volunteers, especially J. M. Adamski, T. Archer, K. Bekker, C. Berg, D. Boehm, D. Bowman, G. M. Brink, J. M. Earnhardt, A. Eckstein, P. M. Felski, D. Ferri, B. Flanagan, T. Goniea, J. A. Grow, B. C. Harrison, J. J. Hileman, C. P. Jaeger, J. Jundt, R. E. Junge, B. Krzyzanowski, A. M. Lentini, T. Long, M. Madden, D. Malone, D. Messman, D. Mulkerin, S. E. Netherton, S. Ostman, D. Pelc, M. Redmer, R. Santymire, K. Schad, A. Snider, K. Sprague, and R. Vos. We thank M. Goode and 2 anonymous reviewers for helpful comments. U.S. Fish and Wildlife Service, Edward Lowe Foundation, Columbus Zoo and Aquarium, EMR SSP, Fort Wayne Children's Zoo, Potawatomi Zoo, Lincoln Park Zoo, and Northern Illinois University provided funding.

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Associate Editor: Matt Goode.

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