Journal of Herpetology, Vol. 50, No. 4, 534–540, 2016

Demography of a Small and Isolated Population of Eastern Massasauga Rattlesnakes (*Sistrurus catenatus*) Threatened by Vegetative Succession

Brent D. Johnson,[1,3] James P. Gibbs,[1] Kevin T. Shoemaker,[2] and Jonathan B. Cohen[1]

[1] *Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, New York, USA*
[2] *Department of Natural Resources and Environmental Science, University of Nevada, Reno, Reno, Nevada, USA*

Abstract.—**Reforestation of early successional vegetation types has been implicated in the decline and extirpation of snake species dependent on exposed basking sites. Consequently, basking-site improvement measures (e.g., brush clearing) are frequently proposed to conserve threatened and endangered snake populations; however, demographic response of snakes to vegetation manipulation is largely unknown. This study measured changes in reproductive fitness, survival, and abundance of females in an isolated population of endangered Eastern Massasauga Rattlesnakes (*Sistrurus catenatus*) in years before and after cutting of woody vegetation to create basking opportunities. We marked a total of 181 snakes from 2006 to 2014, over which time substantial vegetation was cleared in key gestation areas to increase availability of basking sites for gravid females. Reproductive cycles of females in this population appeared to be primarily biennial, with parturition dates strongly influenced by maximum daily summer temperatures. Estimated annual survival ($s = 0.78$, 95% confidence interval: 0.67–0.86) and number of gravid females (range = 9–46 individuals) showed no temporal trend, nor did body condition (mass relative to length) of gravid females. Our results imply that if a demographic response to basking-site manipulations occurs in Eastern Massasauga Rattlesnakes, it will significantly lag management intervention.**

Many snake species rely on early successional cover types for thermoregulation (Trani, 2002), and reforestation has been implicated in the decline or extirpation of many populations (Jäggi and Baur,1999; Smith and Stephens, 2003; Webb et al., 2005; Fitch, 2006). Although manipulation of vegetation to reduce canopy cover (e.g., mechanical cutting, burning, mowing) has been used as a management strategy for populations of threatened and endangered snakes (e.g., Johnson and Leopold, 1998; Pike et al., 2011), strong evidence that this practice can improve the conservation status of targeted snake populations remains scarce (Shoemaker et al., 2009). Bonnet et al. (2016), however, showed that clearing of forest cover increased the abundance of four snake species within six survey seasons at an urban park in France.

A convincing demonstration of conservation success requires evidence of a population-level response (Smallwood, 2001). For long-lived snake species, changes in the reproductive output of females may be the first measurable, short-term response to habitat management (Dorcas and Willson, 2009), yet carefully designed, long-term monitoring is required to detect a more direct population-level response, such as a change in population size, survival, or recruitment (Seigel et al., 1998; Renken et al., 2004; Dorcas and Willson, 2009). Ideally, monitoring begins several years in advance of habitat manipulation, and demographic estimates made before or concurrent with management efforts serve as valuable baselines (Smallwood et al., 1999; Smith, 2002). Comparison of baselines with future estimates can reveal positive impacts of habitat manipulation on a snake population, or unintended negative outcomes (Seigel, 1986; Setser and Cavitt, 2003; Durbian, 2006).

Manipulations within gestational habitats are intended to improve snake population viability by enhancing thermoregulatory opportunities for gravid females. Alteration of basking-site conditions can have important consequences for reproduction in a viviparous species because of its potential influence on gestation period length, fitness of offspring, frequency of stillbirths (Lourdais et al., 2004), and small-mammal prey abundance (Carey and Wilson, 2001; Crosswhite et al., 2004). Earlier parturition dates also may allow postpartum females more time to forage before hibernation (Charland and Gregory, 1990; Burger, 1991). Improved body condition of females resulting from increased year-round foraging opportunities can lead to greater reproductive output that manifests via larger brood sizes (Ford and Seigel, 1989) or reduced interbrood intervals (Macartney and Gregory, 1988). When direct measurements of female fecundity are not possible, changes in the gestation period length or body condition of females may serve as evidence for improved reproductive fitness.

Eastern Massasauga Rattlesnakes (EMRs, *Sistrurus catenatus* [*catenatus*], Rafinesque, 1818) are a candidate for federal listing as an endangered species (U.S. Fish and Wildlife Service, 2011). Threats to EMRs throughout their range include habitat loss and modification, natural succession in disturbed habitats, human persecution and collection, encroachment of invasive species, and road mortality (Szymanski, 1998). Cicero Swamp Wildlife Management Area ("Cicero Swamp") in New York (where this species is listed as Endangered) represents a northern and the easternmost occurrence of the species. Known gestation areas of gravid female EMRs at Cicero Swamp have undergone succession to tall (>1.5 m) woody plant communities within the past half-century (LeBlanc and Leopold, 1992). Shoemaker and Gibbs (2010) concluded that increasing canopy cover was limiting thermoregulatory opportunities for EMRs and suggested the cutting of shrub vegetation to <0.5 m height to allow the snakes to achieve higher body temperatures (>2°C). Following these recommendations, the New York State Department of Environmental Conservation (NYSDEC) cut shrub vegetation within known gestation areas in several subsequent years. These manipulations were intended to improve female EMR fitness and reproduction by increasing basking opportunities. Field surveys following initial management efforts recorded improved thermal properties, adequate crypsis potential, and increased presence of EMRs within manipulated sites relative to nearby uncut sites (Johnson, 2013).

EMR mark–recapture efforts at Cicero Swamp occurred from 2006 to 2014, including years before (2006–2007) and concurrent

---

[3] Corresponding Author; Email: brent.d.johns@gmail.com

DOI: 10.1670/121

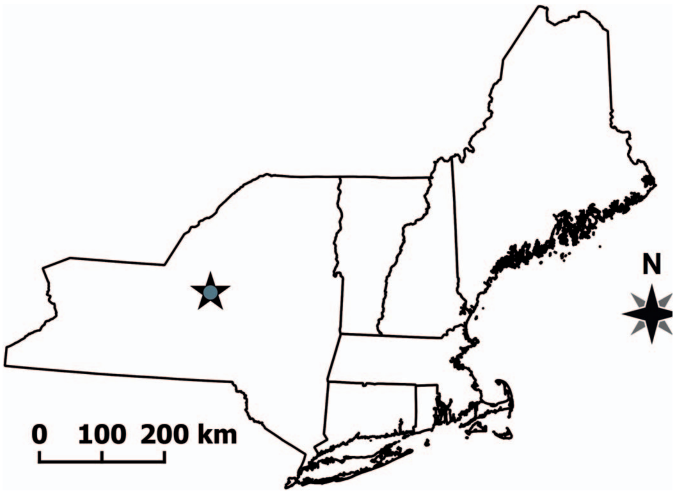

FIG 1. Approximate location of Cicero Swamp Wildlife Management Area, Cicero, New York, within the northeastern United States.

with (2008, 2011–2014) significant vegetation management. Our objectives were to use the resulting mark–recapture data to: 1) generate estimates of important demographic parameters for this endangered population and for EMRs generally, and 2) assess population-level response to basking-site manipulations in terms of the reproductive fitness, abundance, and survival of gravid female EMRs.

MATERIALS AND METHODS

Study Site.—Cicero Swamp Wildlife Management Area (43°8′N, 76°1′W; Fig. 1) is a 2,003-ha wetland complex managed by the NYSDEC. The core range of the EMR at the site, known as the "Burn Area," is a 37-ha shrub-dominated peatland (Johnson, 2000) that has undergone natural succession from herbaceous and low shrub vegetation to tall woody shrubs and forest since a 6-mo-long fire in 1892 burned away nearly 1 m of its peat layer (LeBlanc and Leopold, 1992). Current dominant shrub species include highbush blueberry (*Vaccinium corymbosum*), mountain holly (*Ilex mucronata*), and black chokeberry (*Aronia melanocarpa*). Primary tree species include black spruce (*Picea mariana)* and tamarack (*Larix laricina*) as well as red maple (*Acer rubrum*) and silver birch (*Betula pendula*). Gravid female EMRs occupy discrete areas throughout their gestation period that are located at the northern and southern edges of the Burn Area and that contain shorter vegetation and greater hummock-hollow definition than surrounding areas (Johnson, 1995; Shoemaker, 2007). Johnson (2000) speculated that nongravid females and males overwinter in these sites, but typically move into surrounding forests during each active season. During this study, NYSDEC cut shrub vegetation within the two gestation areas to ≤0.25-m height to generate: 1) 6 28-m^2 plots in 2008, 2) 32 100-m^2 plots in 2011, 3) 12 28-m^2 plots in 2012, 4) 7,900 m^2 of open area in 2013, and 5) 16,900 m^2 of open area in 2014. We surveyed snakes in the two gestation areas and considered only gravid female captures in most analyses because of limited recaptures of nongravid adults.

Field Methods.—Two or more experienced observers captured EMRs within gestation areas among a total of 64 survey periods during the years 2006–2014 (n = 11, 10, 1, 2, 4, 11, 10, 7, and 8 periods, respectively). Surveys occurred within the active season of EMRs, from June to August, primarily between 0830 and 1300 h. We marked newly captured adult EMRs with passive integrated transponder (PIT) tags (AVID Identification Systems, Inc., Norco, California) for permanent identification (Jemison et al., 1995). To measure snout–vent length (SVL) of each individual, we used a flexible measuring tape while holding the snake partially in a plastic snake tube. Individuals shorter than ca. 40 cm SVL were assumed to be juveniles, as we found no gravid females under this length. We determined sex using a cloacal probe and reproductive condition by palpating for oviductal eggs (Johnson, 1995). After placing each snake in a cloth bag, we measured its mass using a spring scale (Pesola® Medio-Line 41000; Pesola AG, Baar, Switzerland).

Data Analysis.—In all analyses, we assessed potential temporal changes in population parameters (as opposed to before/after responses to vegetation manipulations) given that extent of manipulated habitats increased throughout our study time frame. To determine if parturition dates occurred earlier in response to increasing summer basking opportunities (suggesting shortening of gestation periods), we calculated the 10th percentile of Julian dates of brood sightings for each year in which we found broods (2006, 2007, 2008, 2011, 2012, 2013, and 2014) and acquired an average maximum daily air temperature for each summer (June–August) from the archives of the Hancock International Airport weather station in Syracuse, New York (ca. 7 km from the study site). We evaluated the effects of year and average maximum daily air temperature on parturition dates using a generalized linear model (glm in R 3.1.1; R Core Team, 2012) with quasi-binomial error to account for overdispersion because of a low sample of years (n = 7). We determined statistical significance at $\alpha = 0.05$.

We evaluated body condition of adult female EMRs in response to survey year using generalized additive models (GAMs; mgcv package in R; Wood, 2001). GAMs controlled for the nonlinear relationship between mass and SVL while examining a possible influence of year (2006–2012) on body condition. We included reproductive status as a random effect because of higher mass expected among gravid females. We also included PIT number as a random effect to account for repeated measurements of individuals (Crawley, 2007).

We inferred the reproductive frequency (e.g., annual, biennial) and estimated annual survival of adult females using Pollock's robust design models (Pollock, 1982; Kendall and Nichols, 1995; Kendall et al., 1995, 1997) in Program MARK 6.1 (White and Burnham, 1999) that incorporated primary (between-year) and secondary (within-year) capture periods. Closed-capture parameterization (Otis et al., 1978) within robust design models provided estimates for within-season first capture probability (p) and recapture probability (c), and allowed us to derive seasonal abundance estimates for gravid females (N). Our use of robust design models included the assumption that gestation areas harbored closed populations of gravid females within each active season as we captured many gravid females multiple times within these areas. Because closed-capture models typically require two survey periods but only one survey period occurred at Cicero Swamp in 2008, we added a false second survey period for that year with corresponding p and c values fixed at zero (W. Kendall, pers. comm.). We also modeled within-season capture probabilities (p and c) as constant rather than time-varying, because the number of parameters required to estimate all survey periods independently was beyond the scope of our data set. Annual emigration probability (γ'') during between-year intervals represented the probability of females remaining nongravid (and therefore unavailable for capture) after those years in which we observed

TABLE 1. Influence of year and average maximum daily temperature on parturition dates of female Eastern Massasauga Rattlesnakes at Cicero Swamp, New York from 2006 to 2014. A generalized linear model with quasi-binomial error was used to assess correlation between temperatures and dates for years 2006–2014 (2009 and 2010 not included).

Coefficients	Estimate	SE	*t*	*P*
Intercept	1.38	10.25	0.14	0.90
Average maximum daily temperature (°C)	−0.03	0.01	−2.98	0.04
Year	<0.01	0.01	0.13	0.91

them in gravid condition (Kendall et al., 1997). Likewise, estimated reimmigration probability ($1 - \gamma'$) indicated the probability that a female would re-enter the pool of gravid individuals (i.e., become available for capture). We used robust design models to test for symmetrical annual transition rates into and out of the reproductive population ($\gamma'' = 1 - \gamma'$), which would indicate biennial reproduction if both rates were estimated close to 1, and to test for differences in the survival of adult females (φ) among survey years as a possible response to habitat manipulations. Additionally, we included models with p and c values estimated both separately and together as a single parameter for each survey season to test for a possible behavioral response of EMRs to their initial capture (and marking with a PIT tag for newly caught individuals) within a given season.

Because goodness-of-fit tests are not available for robust design models in Program MARK, we conducted a c-hat ($\hat{c}$) sensitivity analysis (increasing $\hat{c}$ to 1.5, 2.0, and 3.0) to evaluate the robustness of our conclusions to possible overdispersion (Cooch and White, 2006). Although this approach did not allow for estimation of a $\hat{c}$ value specific to our data, it served as a pragmatic evaluation of our use of models with large numbers of parameters and allowed for better comparison of the different models in our candidate list (e.g., for a similar approach see Anthony et al., 2006; McGowan et al., 2011). We selected a best model from our candidate list on the basis of our sensitivity analysis results and corrected quasi-Akaike's information criterion ($QAIC_c$; Burnham and Anderson, 2002).

RESULTS

Among nine survey seasons, we marked 143 female and 38 male adult EMRs in the Burn Area and surrounding habitats. We determined 101 of the females to be gravid and within gestation areas in at least one season ($n = 19, 9, 11, 1, 26, 25, 13,$ and 39 gravid females for each year from 2006 to 2013, respectively), with recaptures of these females occurring each year from 2008 to 2014 ($n = 5, 1, 12, 4, 8, 16,$ and 6 gravid females, respectively).

Julian date corresponding with first broods encountered correlated with average maximum daily temperature for the given summer ($P = 0.04$, $n = 7$; Table 1), occurring ~10.0 days earlier per 1°C increase, but not with the survey year ($P = 0.91$). Mean (±SD) SVL of adult females measured among all years ($n = 172$) was 54.2 ± 6.0 cm. Mass–length relationships of females did not differ among survey years 2006–2012 (Table 2).

Ranking of our robust design models varied somewhat across different values of $\hat{c}$, but overall inferences changed very little. Only one model retained high support ($\Delta QAIC_c < 2.0$) among all $\hat{c}$ values (Appendix 1). This model included estimates of constant survival (φ) among seasons, differing emigration and reimmigration rates ($\gamma'' \neq 1 - \gamma'$), and equal probabilities of first capture and recapture for each survey season ($p = c$). A similar model with differing probabilities of first capture and recapture ($p \neq c$) had high support only at a $\hat{c}$ value of 1.0, and this model provided comparable estimates of survival, emigration, reimmigration, and abundance. Models with time-varying survival generally remained lower ranking. The model with fewest parameters (equal emigration and reimmigration [$\gamma'' = 1 - \gamma'$] and equal probabilities of first capture and recapture [$p = c$]) achieved a higher ranking with increasing $\hat{c}$, but failed to gain high support ($\Delta QAIC_c < 2.0$). In conclusion, larger values of $\hat{c}$ resulted in support for only one model, and we used this model to obtain all demographic estimates presented hereafter while assuming a moderate level of overdispersion in our data ($\hat{c} = 2.0$).

EMR capture probabilities varied among years, trending higher after the creation of small-scale basking plots (2010–2012) but lower again after the creation of larger-scale vegetation clearings (2013–2014; Fig. 2). Annual emigration probability was estimated at 0.99 (95% confidence interval [CI] = 0.86–1.00), indicating that nearly all females left gestation areas in years subsequent to when we captured them; however, the annual reimmigration probability estimate (0.71; 95% CI = 0.44–0.88) suggests that not all nongravid females become gravid in their next year. Seven percent of recaptures of gravid females occurred in consecutive years, 65% in 2-yr intervals, 15% in 3-yr intervals, and 13% in intervals of ≥4 yr.

Estimated annual survival for adult female EMRs at Cicero Swamp did not vary among survey years and was 0.78 (95% CI = 0.67–0.86). Among years of highest surveying intensity (2006–2007, 2009–2014), estimated abundance of gravid females averaged 20 individuals (range = 9–41 individuals; Fig. 3). Because of high rates of emigration and reimmigration from and to the gestation areas, those years with higher abundance of

TABLE 2. Influences on body condition of adult female Eastern Massasauga Rattlesnakes at Cicero Swamp, New York from 2006 to 2013. A generalized additive model controlled for mass and length (SVL) relationship, reproductive status, and PIT numbers (identification [ID]) of snakes while testing the effects of habitat manipulations occurring in years 2008 and 2011–2013. Deviance explained for female body mass equals 73.6% ($n = 184$).

	Parametric coefficients				Nonlinear effects		
Parameter	Estimate	SE	*t*	*P*	df	*F*	*P*
Intercept	3,417.66	3,129.00	1.09	0.28	—	—	—
Year (2006–2013)	−1.58	1.56	−1.02	0.31	—	—	—
SVL (cm)	—	—	—	—	8.01	35.47	<0.01
Gravid (yes vs. no)	—	—	—	—	1.00	38.35	<0.01
ID	—	—	—	—	119.00	0.12	0.12

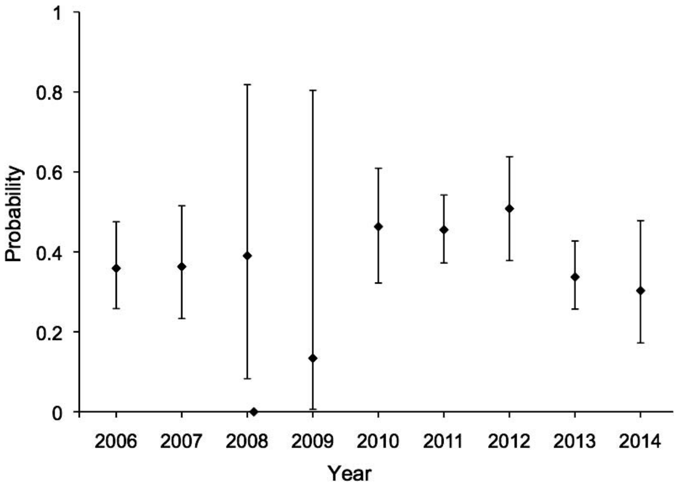

FIG 2. Estimates of within-season capture probabilities for gravid female Eastern Massasauga Rattlesnakes of Cicero Swamp, New York with 95% confidence bars. Values were obtained from a Pollock's robust design model incorporating closed capture estimation. Two capture probability (*p*) estimates are shown for 2008 representing two survey periods, with the second fixed at zero, as it did not actually occur. Shrub cutting in gestation areas began in 2008.

gravid females generally were preceded by years of lower abundance, with the exception of high abundance in both 2010 and 2011.

DISCUSSION

We detected no change in the reproductive fitness, survival, or abundance of adult female EMRs at Cicero Swamp over time in response to substantial manipulation of gestation habitat. That we observed no demographic response of the population in subsequent years is possibly because of a lagged response time for most population-level traits of this long-lived species (Dorcas and Willson, 2009). Imprecision of estimates because of small sample size (necessarily limited in this small population of endangered snakes) and environmental stochasticity also may not have enabled detection of modest changes in reproductive fitness or survival that might have occurred.

Despite finding no evidence of improved reproductive fitness in adult female EMRs in response to habitat manipulations, the negative correlation we observed between ambient temperatures and parturition dates is in accordance with a known effect of temperature on gestation period length for viviparous snakes (Charland and Gregory, 1990; Burger, 1991). That parturition dates occur earlier for EMRs at Cicero Swamp as ambient temperatures increase is noteworthy because it suggests reduced thermal constraints on the population (that is, a lengthening active season). Climate change is expected to cause dramatic phenological shifts among terrestrial ectotherms at mid- to high latitudes within the next century via changes in performance that could either improve or reduce fitness (Deutsch et al., 2008). Although earlier parturition dates may benefit both female snakes and their neonates by allowing them more foraging time before hibernation (Charland and Gregory, 1990; Burger, 1991), higher temperatures also may extend active seasons and thereby decrease survival rates by increasing time exposed to associated threats (e.g., predation; Harvey and Weatherhead, 2010; Jones et al., 2012).

Body condition of nongravid adult EMRs before habitat manipulations (2006–2007) was above average in comparison with other EMR populations (Gibbs and Chiucchi, 2012), and no change in the body condition of females after habitat manipulations indicated no improvement in foraging opportunities for gravid or postpartum females. Improved quality of basking sites for gravid snakes could potentially increase the size of their broods (O'Donnell and Arnold, 2005) and the size and fitness of their neonates (Shine, 1995; Lourdais et al., 2004); however, our study lacked an adequate sample of broods to evaluate these possibilities.

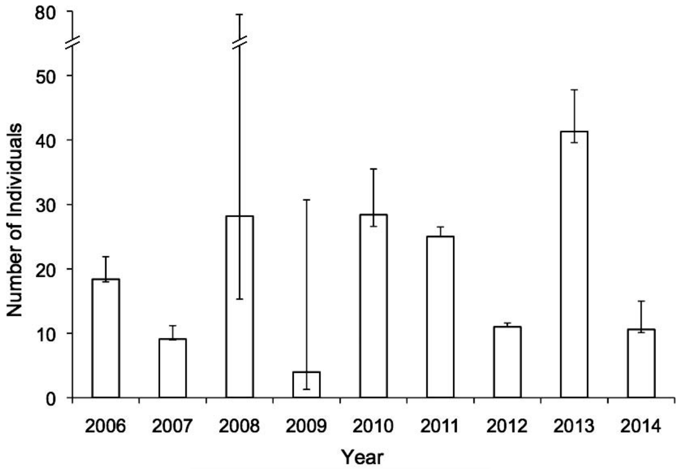

FIG 3. Estimated abundance of gravid female Eastern Massasauga Rattlesnakes in gestation areas of Cicero Swamp, New York with 95% confidence bars. Values were derived from a Pollock's robust design model incorporating closed capture estimation. Shrub cutting in gestation areas began in 2008.

Biennial reproductive cycles appear to occur among the majority of adult female EMRs at Cicero Swamp. Estimated annual emigration from each gestation area was very high (0.99), indicating that nearly all females are nongravid, and therefore outside of either gestation area, in seasons subsequent to those in which they were gravid. Despite low support for "even flow" models in which we set reimmigration equal to emigration, estimated immigration remained fairly high (0.71), indicating that biennial reproduction occurs among most, but not all, females. Some females may actually experience triennial reproductive cycles, making biennial reproduction a general trend rather than a rule for the population. Biennial reproduction has been recorded among female EMRs in Pennsylvania (Reinert, 1981) and Missouri (Seigel, 1986). Triennial reproductive cycles have not been suggested for any population of the species, but have been recorded among northern populations of Timber Rattlesnakes (*Crotalus horridus;* Brown, 1991; Martin, 1993). Biennial or triennial reproductive cycles may occur more often than annual cycles among rattlesnake populations in locations with cool climates and low prey abundance (Klauber, 1972). Low abundance of small-mammal prey within the Burn Area at Cicero Swamp is likely why male and nongravid female EMRs spend each active season in adjacent forest areas (Johnson, 1995).

Average annual survival of adult females (0.78) from 2006 to 2014 was similar to that previously estimated for all adults at Cicero Swamp on the basis of a small sample of radiotracked individuals (n =12; estimate = 0.77 ± 0.12 SE; Johnson, 1995, in Jones et al., 2012) and above a predicted range-wide trend for the species (i.e., 0.67; Jones et al., 2012). It also is similar to annual survival estimated for adult EMRs in Missouri (Seigel and Sheil, 1999; Jones et al., 2012), Ontario, Michigan, and

Indiana (Jones et al., 2012). Annual adult survival generally increases along a SW-NE axis across populations, which corresponds to a gradient of decreasing ambient temperatures (Jones et al., 2012). Cooler temperatures may reduce active-season length and associated mortality risks (e.g., predation) for EMRs. Accordingly, active-season survival (0.94) was estimated to be higher than overwinter survival (0.82) for EMRs at Cicero Swamp by Jones et al. (2012). Similarly, active-season survival was reported to be 0.95 at a population site in southwestern Michigan (Bailey et al., 2011).

Estimated abundances of gravid females within gestation areas were virtually the same as raw counts among years of highest survey intensity (2007, 2011, and 2012). Alternating years of high and low abundance provide further evidence of biennial reproduction in this EMR population. At most, we estimated 41 gravid females to be within gestation areas in a single year, suggesting a maximum adult population of 164 individuals when assuming a 1:1 ratio of gravid females to nongravid females, because of biennial reproduction, and a 1:1 ratio of females to males (Seigel, 1986). At an average of 20 females found gravid each year (excluding low-intensity survey years, 2008 and 2009), however, the actual adult population size may be closer to 80 individuals. This number of individuals is far lower than the effective population size recently estimated for Cicero Swamp ($N_e = 400$) and for several other EMR sites via comparisons of temporal change in genetic diversity (Gibbs and Chiucchi, 2012), suggesting a recent population collapse or errors in assumptions of genetic methods for estimating effective population size.

Efforts to monitor EMR populations have used both radiotelemetry (e.g., Johnson, 1995; Parent and Weatherhead, 2000; Durbian, 2006; Bailey et al., 2011) and long-term mark–recapture surveys (e.g., Seigel et al., 1998; Parent and Weatherhead, 2000; Seigel and Pilgrim, 2002; Aldridge et al., 2008). Compared with radiotelemetry, mark–recapture methods incur lower costs and allow for substantially larger samples of individuals to be studied over longer time periods (but can be limited by low detection rates that lead to low precision of demographic estimates). Furthermore, if mark–recapture surveys are conducted over long (ideally, multigenerational) timescales, these methods can produce a comprehensive description of the processes driving population dynamics, including precise estimates of temporal process variance (White and Burnham, 1999). Ultimately, these estimates may be incorporated into simulation models for evaluating population viability and ranking management alternatives (White et al., 2002).

Although we did not detect demographic effects of habitat manipulations, the results of this study should serve as important baselines for future studies (Smallwood et al., 1999) and planning of conservation efforts at Cicero Swamp. To our knowledge, robust design models have rarely been used to estimate demographic rates and population dynamics of snakes. One exception was a study that assessed the possibility of a population decline for Golden Lancehead Pitvipers (*Bothrops insularis*) in southern Brazil by estimating survival, capture probability, temporary emigration, and abundance from a 9-yr data set (Guimarães et al., 2014). Continued monitoring in a robust design framework holds promise for understanding the complexity of population dynamics, including breeding periodicity, and for adaptively managing populations of EMRs at Cicero Swamp and other critical snake habitats.

Acknowledgments.—Funding was provided by the Society of Wetland Scientists, Western New York Herpetological Society, Edna Bailey Sussman Foundation, and the NYSDEC through a grant obtained from the U.S. Fish and Wildlife Service Great Lakes Restoration Initiative. The NYSDEC granted access and support to use their property. Field assistance was provided by T. Bell, T. Cunningham, C. Radell, A. Robillard, L. Brown, A. Viscito, and K. Olson. Valuable suggestions were made by T. Bell, D. Leopold, P. Ducey, and G. Johnson. Field methods were approved by the State University of New York College of Environmental Science and Forestry Institutional Animal Care and Use Committee Protocol #120303.

LITERATURE CITED

Aldridge, R. D., B. C. Jellen, M. C. Allender, M. J. Dreslik, D. B. Shepard, J. M. Cox, and C. A. Phillips. 2008. Reproductive biology of the massasauga (*Sistrurus catenatus*) from south-central Illinois. Pp. 403–412 in W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.), The Biology of Rattlesnakes. Loma Linda University Press, USA.

Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, et al. 2006. Status and trends in demography of northern spotted owls, 1985–2003. Wildlife Monographs 163:1–48.

Bailey, R. L., H. Campa III, T. M. Harrison, and K. Bissell. 2011. Survival of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) in Michigan. Herpetologica 67:167–173.

Bonnet, X., S. Lecq, J. L. Lassay, J. M. Ballouard, C. Barbraud, J. Souchet, S. J. Mullin, and G. Provost. 2016. Forest management bolsters native snake populations in urban parks. Biological Conservation 193:1–8.

Brown, W. S. 1991. Female reproductive ecology in a northern population of the timber rattlesnake, *Crotalus horridus*. Herpetologica 47:101–115.

Burger, J. 1991. Effects of incubation temperature on behavior of hatchling pine snakes: implications for reptilian distribution. Behavioral Ecology and Sociobiology 28:297–303.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. 2nd ed. Springer-Verlag, USA.

Carey, A. B., and S. M. Wilson. 2001. Induced spatial heterogeneity in forest canopies: responses of small mammals. Journal of Wildlife Management 65:1014–1027.

Charland, M. B., and P. T. Gregory. 1990. The influence of female reproductive status on thermoregulation in a viviparous snake, *Crotalus viridis*. Copeia 1990:1089–1098.

Cooch, E., and G. White. 2006. Program MARK: a gentle introduction. Available at http://www.phidot.org/software/mark/docs/book. Archived by WebCite at http://www.webcitation.org/6brWgkbKL on 27 September 2015.

Crawley, M. J. 2007. The R Book. John Wiley & Sons, UK.

Crosswhite, D. L., S. F. Fox, and R. E. Thill. 2004. Herpetological habitat relations in the Ouachita Mountains, Arkansas. Pp. 273–282 in J. M. Guldin (ed.), Ouachita and Ozark Mountains Symposium: Ecosystem Management Research. Gen. Tech. Rep. SRS-74. U.S. Department of Agriculture, USA.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences of the United States of America 105: 6668–6672.

Dorcas, M. E., and J. D. Willson. 2009. Innovative methods for studies of snake ecology and conservation. Pp. 5–37 in S. J. Mullin and R. A. Seigel (eds.), Snakes: Ecology and Conservation. Cornell University Press, USA.

Durbian, F. E. 2006. Effects on mowing and summer burning on the massasauga (*Sistrurus catenatus*). American Midland Naturalist 155: 329–334.

Fitch, H. S. 2006. Ecological succession on a natural area in northeastern Kansas from 1948 to 2006. Herpetological Conservation and Biology 1:1–5.

Ford, N. B., and R. A. Seigel. 1989. Relationships among body size, clutch size, and egg size in three species of oviparous snakes. Herpetologica 45:75–83.

Gibbs, H. L., and J. E. Chiucchi. 2012. Inbreeding, body condition, and heterozygosity–fitness correlations in isolated populations of the endangered eastern massasauga rattlesnake (*Sistrurus c. catenatus*). Conservation Genetics 13:1133–1143.

Guimarães, M., R. Munguìa-Steyer, P. F. Doherty Jr., M. Martins, and R. J. Sawaya. 2014. Population dynamics of the critically endangered golden lancehead pitviper, *Bothrops insularis*: stability or decline? PLoS One 9:e95203.

Harvey, D. S., and P. J. Weatherhead. 2010. Habitat selection as the mechanism for thermoregulation in a northern population of massasauga rattlesnakes (*Sistrurus catenatus*). Ecoscience 17:411–419.

Jäggi, C., and B. Baur. 1999. Overgrowing forest as a possible cause for the local extinction of *Vipera aspis* in the northern Swiss Jura mountains. Amphibia-Reptilia 20:25–34.

Jemison, S. C., L. A. Bishop, P. G. May, and T. M. Farrell. 1995. The impact of PIT-tags on growth and movement of the rattlesnake, *Sistrurus miliarius*. Journal of Herpetology 29:129–132.

Johnson, B. D. 2013. Management and Status of an Endangered Massasauga Rattlesnake Population in New York State. M.S. Thesis, State University of New York, USA.

Johnson, G. 1995. Spatial Ecology, Habitat Preferences, and Habitat Management of the Eastern Massasauga, *Sistrurus c. catenatus*, in a New York Weakly Minerotrophic Peatland. Ph. D. diss., State University of New York, USA.

Johnson, G. 2000. Spatial ecology of the eastern massasauga (*Sistrurus c. catenatus*) in a New York peatland. Journal of Herpetology 34:186–192.

Johnson, G., and D. J. Leopold. 1998. Habitat management for the eastern massasauga in a central New York peatland. Journal of Wildlife Management 62:84–97.

Jones, P. C., R. B. King, R. L. Bailey, N. D. Bieser, K. Bissell, H. Campa III, T. Crabill, M. D. Cross, B. A. DeGregorio, M. J. Dreslik, et al. 2012. Range-wide analysis of eastern massasauga survivorship. Journal of Wildlife Management 76:1576–1586.

Kendall, W. L., and J. D. Nichols. 1995. On the use of secondary capture–recapture samples to estimate temporary emigration and breeding proportions. Journal of Applied Statistics 22:751–762.

Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture–recapture estimation of demographic parameters. Biometrics 51:293–308.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578.

Klauber, L. M. 1972. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind. 2nd ed. University of California Press, USA.

LeBlanc, C. M., and D. J. Leopold. 1992. Demography and age structure of a central New York shrub-carr 94 years after fire. Bulletin of the Torrey Botanical Club 119:50–64.

Lourdais, O., R. Shine, X. Bonnet, M. Guillon, and G. Naulleau. 2004. Climate affects embryonic development in a viviparous snake, *Vipera aspis*. Oikos 104:551–560.

Macartney, J. M., and P. T. Gregory. 1988. Reproductive biology of female rattlesnakes (*Crotalus viridis*) in British Columbia. Copeia 1988:47–57.

Martin, W. H. 1993. Reproduction of the timber rattlesnake (*Crotalus horridus*) in the Appalachian Mountains. Journal of Herpetology 27: 133–143.

McGowan, C. P., J. E. Hines, J. D. Nichols, J. E. Lyons, D. R. Smith, K. S. Kalasz, L. J. Niles, A. D. Dey, N. A. Clark, P. W. Atkinson, et al. 2011. Demographic consequences of migratory stopover: linking red knot survival to horseshoe crab spawning abundance. Ecosphere 2:art69.

O'Donnell, R. P., and S. J. Arnold. 2005. Evidence for selection on thermoregulation: effects of temperature on embryo mortality in the garter snake *Thamnophis elegans*. Copeia 2005:930–934.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:3–135.

Parent, C., and P. J. Weatherhead. 2000. Behavioral and life history responses of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. Oecologia 125:170–178.

Pike, D. A., J. K. Webb, and R. Shine. 2011. Removing forest canopy cover restores a reptile assemblage. Ecological Applications 21:274–280.

Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752–757.

Rafinesque, C. S. 1818. Further account of discoveries in natural history in the western states. American Monthly Magazine Critical Review 4:39–42.

R Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Austria. Available at http://www.R-project.org. Archived by WebCite at http://www.webcitation.org/6ZkuIvTjh on 3 July 2015.

Reinert, H. K. 1981. Reproduction by the massasauga (*Sistrurus catenatus catenatus*). American Midland Naturalist 105:393–395.

Renken, R. B., W. K. Gram, D. K. Fantz, S. C. Richter, T. J. Miller, K. B. Ricke, B. Russell, and X. Wang. 2004. Effects of forest management on amphibians and reptiles in Missouri Ozark Forests. Conservation Biology 18:174–188.

Seigel, R. A. 1986. Ecology and conservation of an endangered rattlesnake, *Sistrurus catenatus*, in Missouri, USA. Biological Conservation 35:333–346.

Seigel, R. A., and M. A. Pilgrim. 2002. Long-term changes in movement patterns of massasaugas (*Sistrurus catenatus*). Pp. 405–412 in G. W. Shuett, M. Höggren, M. E. Douglas, and H. W. Greene (eds.), Biology of the Vipers. Eagle Mountain Publishing, USA.

Seigel, R. A., and C. A. Sheil. 1999. Population viability analysis: applications for the conservation of massasaugas. Pp. 17–22 in B. Johnson and M. Wright (eds.), Second International Symposium and Workshop on the Conservation of the Eastern Massasauga Rattlesnake, *Sistrurus catenatus catenatus*: Population and Habitat Management Issues in Urban, Bog, Prairie, and Forested Ecosystems. Toronto Zoo, Canada.

Seigel, R. A., C. A. Sheil, and S. Doody. 1998. Changes in a population of endangered rattlesnake *Sistrurus catenatus* following a severe flood. Biological Conservation 83:127–131.

Setser, K., and J. F. Cavitt. 2003. Effects of burning on snakes in Kansas, USA, tallgrass prairie. Natural Areas Journal 23:315–319.

Shine, R. 1995. A new hypothesis for the evolution of viviparity in reptiles. American Naturalist 145:809–823.

Shoemaker, K. T. 2007. Habitat Manipulation as a Viable Strategy for the Conservation of the Massasauga Rattlesnake in New York State. M.S. Thesis, State University of New York, USA.

Shoemaker, K. T., and J.P. Gibbs. 2010. Evaluating basking-habitat deficiency in the threatened eastern massasauga rattlesnake. Journal of Wildlife Management 74:504–513.

Shoemaker, K. T., G. Johnson, and K. A. Prior. 2009. Habitat manipulation as a viable conservation strategy. Pp. 221–243 in S. J. Mullin and R. A. Seigel (eds.), Snakes: Ecology and Conservation. Cornell University Press, USA.

Smallwood, K. S. 2001. Linking habitat restoration to meaningful units of animal demography. Restoration Ecology 9:253–261.

Smallwood, K. S., J. Beyea, and M. L. Morrison. 1999. Using the best scientific data for endangered species conservation. Environmental Management 24:421–435.

Smith, B. E., and N. T. Stephens. 2003. Conservation assessment of the pale milk snake in the Black Hills National Forest, South Dakota and Wyoming. USDA Forest Service.

Smith, E. P. 2002. BACI design. Encyclopedia of Environmetrics 1:141–148.

Szymanski, J. 1998. Status Assessment for the Eastern Massasauga (*Sistrurus c. catenatus*) 1998. U.S. D.I. Fish and Wildlife Service, Endangered Species Division, USA.

Trani, M. K. 2002. Chapter 5: Maintaining species in the South. Pp. 113–150 in D. N. Wear and J G. Greis (eds.), Southern Forest Resource Assessment Draft Report. USDA Forest Service, Southern Research Station.

U.S. Fish and Wildlife Service. 2011. Species Assessment and Listing Priority Assignment Form (*Sistrurus catenatus*).

Webb, J. K, R. Shine, and R. M. Pringle. 2005. Canopy removal restores habitat quality for an endangered snake in a fire suppressed landscape. Copeia 2005:894–900.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement:120–138.

White, G. C., A. B. Franklin, and T. M. Shenk. 2002. Estimating parameters of PVA models from data on marked animals. Pp. 169–190 in S. R. Beissinger and D. R. McCullough (eds.), Population Viability Analysis. University of Chicago Press, USA.

Wood, S. N. 2001. mgcv: GAMs and generalized ridge regression for R. R News 1:20–25.

Accepted: 18 April 2016.

APPENDIX 1

Candidate models and selection criteria for Pollock's robust design models estimating demographic parameters of gravid female Eastern Massasauga Rattlesnakes at Cicero Swamp, New York, 2006–2014. Parameters include survival (φ), emigration (γ''), reimmigration (γ'), and capture (p) and recapture (c) probabilities for each year. No goodness-of-fit test was available, so we tested for sensitivity of model rankings to changes in $\hat{c}$.

TABLE A1. Candidate model rankings when $\hat{c}$ is equal to 1.0.

Model	ΔAIC_c	Weight	Number of parameters	Deviance
$\{\varphi(.)\ \gamma''(.)\ \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	0.00	0.68	22	1,382.35
$\{\varphi(.)\ \gamma''(.)\ \gamma'(.)\ p\ (\text{year}) = c(\text{year})\}$	1.58	0.31	13	1,403.45
$\{\varphi(t)\ \gamma''(.)\ \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	7.84	0.01	29	1,374.43
$\{\varphi(t)\ \gamma''(.)\ \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	12.15	0.00	20	1,398.90
$\{\varphi(.)\ \gamma''(.) = \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	15.29	0.00	21	1,399.85
$\{\varphi(.)\ \gamma''(.) = \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	19.62	0.00	12	1,423.61
$\{\varphi(t)\ \gamma''(.) = \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	23.43	0.00	28	1,392.31
$\{\varphi(t)\ \gamma''(.) = \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	28.63	0.00	19	1,417.57

TABLE A2. Candidate model rankings when $\hat{c}$ is equal to 1.5.

Model	ΔQAIC_c	Weight	Number of parameters	Deviance
$\{\varphi(.)\ \gamma''(.)\ \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	0.00	0.93	13	935.63
$\{\varphi(.)\ \gamma''(.)\ \gamma'(.)\ p\ (\text{year})\ c(\text{year})\}$	5.46	0.06	22	921.57
$\{\varphi(.)\ \gamma''(.) = \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	11.32	0.00	12	949.07
$\{\varphi(t)\ \gamma''(.)\ \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	12.09	0.00	20	932.60
$\{\varphi(.)\ \gamma''(.) = \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	14.92	0.00	21	933.23
$\{\varphi(t)\ \gamma''(.)\ \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	15.94	0.00	29	916.29
$\{\varphi(t)\ \gamma''(.) = \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	22.34	0.00	19	945.05
$\{\varphi(t)\ \gamma''(.) = \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	25.57	0.00	28	928.20

TABLE A3. Candidate model rankings when $\hat{c}$ is equal to 2.0.

Model	ΔQAIC_c	Weight	Number of parameters	Deviance
$\{\varphi(.)\ \gamma''(.)\ \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	0.00	0.97	13	701.72
$\{\varphi(.)\ \gamma''(.) = \gamma'(.)\ p\ (\text{year}) = c(\text{year})\}$	7.96	0.02	12	711.81
$\{\varphi(.)\ \gamma''(.)\ \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	8.97	0.01	22	691.17
$\{\varphi(t)\ \gamma''(.)\ \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	12.84	0.00	20	699.45
$\{\varphi(.)\ \gamma''(.) = \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	15.52	0.00	21	699.93
$\{\varphi(t)\ \gamma''(.) = \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	19.99	0.00	19	708.79
$\{\varphi(t)\ \gamma''(.)\ \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	20.78	0.00	29	687.22
$\{\varphi(t)\ \gamma''(.) = \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	27.43	0.00	28	696.15

TABLE A4. Candidate model rankings when $\hat{c}$ is equal to 3.0.

Model	ΔQAIC_c	Weight	Number of parameters	Deviance
$\{\varphi(.)\ \gamma''(.)\ \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	0.00	0.91	13	467.82
$\{\varphi(.)\ \gamma''(.) = \gamma'(.)\ p\ (\text{year}) = c(\text{year})\}$	4.60	0.09	12	474.54
$\{\varphi(.)\ \gamma''(.)\ \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	12.49	0.00	22	460.78
$\{\varphi(t)\ \gamma''(.)\ \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	13.60	0.00	20	466.30
$\{\varphi(.)\ \gamma''(.) = \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	16.12	0.00	21	466.62
$\{\varphi(t)\ \gamma''(.) = \gamma'(.)\ p(\text{year}) = c(\text{year})\}$	17.63	0.00	19	472.52
$\{\varphi(t)\ \gamma''(.)\ \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	25.61	0.00	29	458.14
$\{\varphi(t)\ \gamma''(.) = \gamma'(.)\ p(\text{year})\ c(\text{year})\}$	29.29	0.00	28	464.10