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Population Ecology

Range-Wide Analysis of Eastern Massasauga Survivorship

PETER C. JONES,[1] *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*
ROBYN L. BAILEY, *Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA*
NICKOLAS D. BIESER, *Department of Biology, Indiana University-Purdue University Fort Wayne, Fort Wayne, IN 46805, USA*
KRISTIN BISSELL,[2] *Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA*
HENRY CAMPA, III, *Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA*
TRISHA CRABILL, *Ecological Services, U.S. Fish and Wildlife Service, Columbia, MO 65203, USA*
MATTHEW D. CROSS, *Department of Biology, Central Michigan University, Mt. Pleasant, MI 48859, USA*
BRETT A. DEGREGORIO, *Department of Biology, Indiana University-Purdue University Fort Wayne, Fort Wayne, IN 46805, USA*
MICHAEL J. DRESLIK, *Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, Champaign, IL 61820, USA*
FRANCIS E. DURBIAN,[3] *Squaw Creek National Wildlife Refuge, Mound City, MO 64470, USA*
DANIEL S. HARVEY, *Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana, IL 61801, USA*
SCOTT E. HECHT,[4] *Department of Biology, Indiana University-Purdue University Fort Wayne, Fort Wayne, IN 46805, USA*
BENJAMIN C. JELLEN, *Division of Science and Mathematics, McKendree University, Lebanon, IL 62254, USA*
GLENN JOHNSON,[5] *College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, USA*
BRUCE A. KINGSBURY, *Department of Biology, Indiana University-Purdue University Fort Wayne, Fort Wayne, IN 46805, USA*
MATTHEW J. KOWALSKI, *Pennsylvania Natural Heritage Program, Middletown, PA 17057, USA*
JAMES LEE, *Camp Shelby Field Office, The Nature Conservancy, Camp Shelby, MS 39407, USA*
JENNIFER V. MANNING, *Department of Biology, Indiana University-Purdue University Fort Wayne, Fort Wayne, IN 46805, USA*
JENNIFER A. MOORE, *Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA*
JULIE OAKES, *Seven Lakes State Park, Michigan Department of Natural Resources, Fenton, MI 48430, USA*
CHRISTOPHER A. PHILLIPS, *Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, Champaign, IL 61820, USA*
KENT A. PRIOR, *Parks Canada, Gatineau, QC, Canada K1A 0M5*
JEANINE M. REFSNIDER,[6] *Department of Biology, Indiana University-Purdue University Fort Wayne, Fort Wayne, IN 46805, USA*
JEREMY D. ROUSE, *Ontario Ministry of Natural Resources, Parry Sound, ON, Canada P2A 1S4*
JOSEPH R. SAGE, *Department of Biology, Indiana University-Purdue University Fort Wayne, Fort Wayne, IN 46805, USA*
RICHARD A. SEIGEL, *Department of Biological Sciences, Towson University, Towson, MD 21252, USA*
DONALD B. SHEPARD,[7] *Center for Biodiversity, Illinois Natural History Survey, Champaign, IL 61820, USA*
CHAD S. SMITH,[8] *Department of Biology, Indiana University-Purdue University Fort Wayne, Fort Wayne, IN 46805, USA*
TERRY J. VANDEWALLE, *Stantec, Independence, IA 50644, USA*
PATRICK J. WEATHERHEAD, *Program in Ecology, Evolution and Conservation Biology, University of Illinois at Urbana-Champaign, Champaign-Urbana, IL 61820, USA*
ANNE YAGI, *Ministry of Natural Resources, Vineland Station, ON, Canada L0R 2E0*

ABSTRACT Decisions affecting wildlife management and conservation policy of imperiled species are often aided by population models. Reliable population models require accurate estimates of vital rates and an understanding of how vital rates vary geographically. The eastern massasauga (*Sistrurus catenatus catenatus*) is a rattlesnake species found in the Great Lakes region of North America. Populations of the eastern massasauga are fragmented and only a few areas harbor multiple, sizable populations. Eastern massasauga

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[1] *E-mail: pjones2@niu.edu*

[2] *Present address: Waterloo Wildlife Office, Department of Natural Resources, 13578 Seymour Road, Grass Lake, MI 49240, USA.*

[3] *Present address: J. Clark Salyer National Wildlife Refuge, Upham, ND 58789, USA.*

[4] *Present address: 2395 Conservation Road, Campbellville, ON, Canada L0P 1B0.*

[5] *Present address: Department of Biology, State University of New York at Potsdam, Potsdam, NY 13676, USA.*

[6] *Present address: Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011, USA.*

[7] *Present address: Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN 55108, USA.*

[8] *Present address: Navajo Nation Department of Fish and Wildlife, Window Rock, AZ 86515, USA,*

research has typically focused on single populations or local metapopulations but results suggest that demographic parameters vary geographically. We used 21 radiotelemetry datasets comprising 499 telemetered snakes from 16 distinct locations throughout the range of the eastern massasauga to characterize geographic patterns of adult survival using the known-fate model in Program MARK. Annual adult survival ranged from 0.35 to 0.95 (mean = 0.67) and increased along a southwest to northeast geographic axis. Further analysis of 6 datasets indicated no consistent difference in survival between males and females. Our results provide a better understanding of the relationship between survivorship and geography for the eastern massasauga and suggest that such variation should be incorporated into population models as well as local and regional management plans. © 2012 The Wildlife Society.

KEY WORDS eastern massasauga, Great Lakes, radiotelemetry, rattlesnake, *Sistrurus catenatus catenatus*, survival rate.

Population models are frequently used to inform wildlife management decisions and to set conservation policies. To provide reliable predictions of the probability of extinction and to forecast abundance, accurate estimates of vital rates (e.g., survival) and a population model with a sufficiently realistic structure are needed (Beissinger and Westphal 1998, Coulson et al. 2001, Ellner et al. 2002). Vital rates are especially challenging to estimate when rates vary geographically. For example, ectotherms are reliant on temperature for many physiological functions (Lillywhite 1987). Thus, geographic variation in demography and life history among populations is expected. Although the vital rates of ectotherms do vary (e.g., Wilson 1991, Blouin-Demers et al. 2002, Wilson and Cooke 2004, Sperry et al. 2010), the data necessary to estimate accurately the geographic variation in vital rates are often too labor-intensive and cost prohibitive to collect.

The eastern massasauga, *Sistrurus catenatus catenatus*, is afforded some level of protection (endangered, threatened, or special interest status) in every state or province in which it occurs (Szymanski 1998). It is a candidate species for listing under the United States Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 2010) and is listed as threatened under Canada's Federal Species at Risk Act (Environment Canada 2011). The eastern massasauga's range extends from eastern Iowa to western New York and from southern Illinois to southern Ontario (Conant and Collins 1998). Despite this large range, populations are highly fragmented and the majority appear to be declining (Szymanski 1998, Rouse and Willson 2002, U.S. Fish and Wildlife Service 2010). Because of the eastern massasauga's conservation status, state, provincial, and federal biologists have a strong interest in its demography to aid with habitat and population management decisions.

Of particular demographic interest is how eastern massasauga adult survival rates vary across its range. Although population viability analyses (PVA) were performed for several eastern massasauga populations showing some variation in survival on a geographic scale, empirical data on the magnitude of this variation is generally lacking (but see Aldridge et al. 2008 for an analysis of geographic variation in eastern massasauga fecundity). Our objectives were to estimate annual and active season adult survival and determine if survival vary geographically or shows sexual differentiation.

STUDY AREA

Researchers collected data at 16 different eastern massasauga population sites (Fig. 1). Typical eastern massasauga habitat consisted of both upland and wetland areas, but habitat used varied across the range (Reinert and Kodrich 1982, Weatherhead and Prior 1992, Johnson 1995, King 1999, Szymanski 1998, Harvey and Weatherhead 2006*b*). Detailed study area descriptions were described previously for each individual study (see citations in Table 2).

METHODS

Radiotelemetry datasets from participating investigators throughout the range of the eastern massasauga contained the release date of radio-implanted snakes, dates of relocation, sex, and fate (death, transmitter removal, or failure, lost from study). All studies used similar surgical techniques following methods described by Reinert and Cundall (1982), Weatherhead and Anderka (1984), Hardy and Greene (1999), and Fitzgerald and Vera (2006). Transmitter mass was <6% of individual snake mass in all cases. We excluded several datasets from analysis because of small sample size (Hallock 1991; Lentini 2008) or because the transmitters were force-fed instead of surgically implanted as in Reinert and Kodrich (1982). We used the known fate model within Program MARK (White and Burnham 1999) to estimate annual adult survival separately for each dataset. In contrast to more familiar Cormack–Jolly–Seber models, known fate models explicitly include mortalities in the encounter histories, and as a consequence, model performance depends on knowledge of the timing of mortality. To achieve this and to be consistent across datasets, we set relocation intervals (time between 2 successive relocation events) to 1 week for all analyses, thus we aggregated multiple relocations in a single week for an individual into a single relocation for that week. Any interval in which a snake was not relocated became a censored event. We excluded snakes whose deaths could be directly attributed to transmitter implantation from the analysis. We presumed all snakes to be adults based on body size (see citations in Table 1).

We censored mortalities directly attributable to human causes (e.g., road mortality, agriculture, construction, mowing, and prescribed burns) from the main analysis because our primary interest was in patterns of survival (e.g., geographic

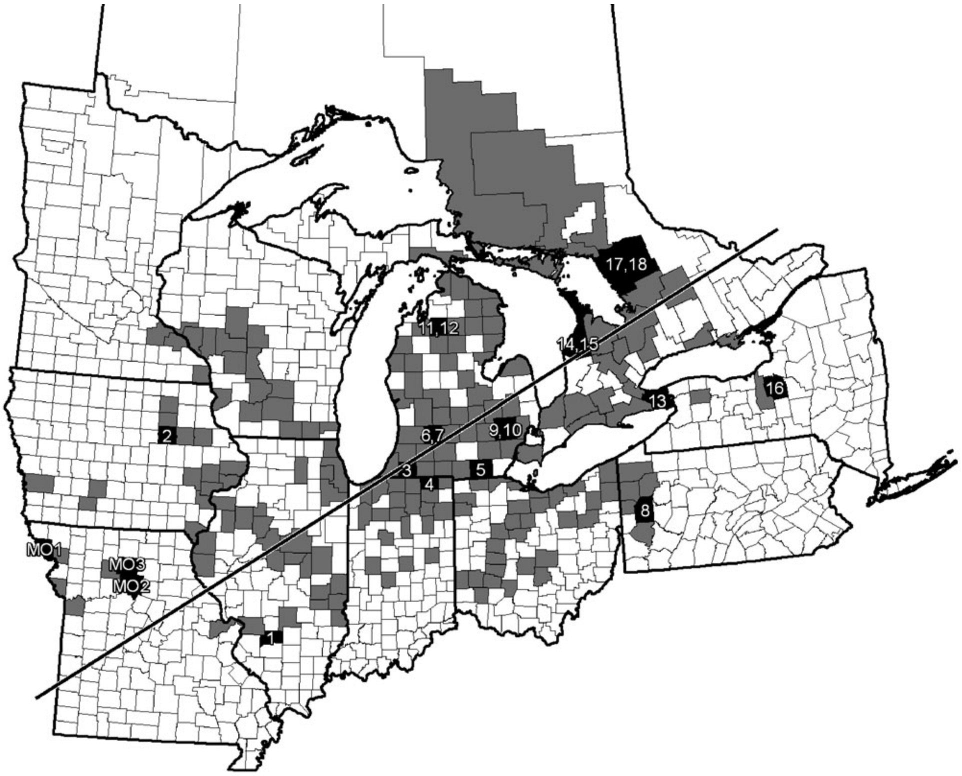

Figure 1. Range map for the eastern massasauga. Shaded counties represent the eastern massasauga's historic range. The line represents a southwest to northeast axis along which the eastern massasauga's range falls. The numbered counties in black correspond to the numbered datasets in Tables 2–5.

trends) exclusive of direct human causes. However, because of the magnitude of such human-caused mortality, we compared these results with those from an analysis in which such mortalities were not censored.

Because eastern massasaugas spend winter underground (Atkinson and Netting 1927), winter mortalities were not discovered until the following spring (when snakes failed to emerge) and may have occurred at any time during the winter period. The winter period also varied in length among studies (Table 2). For example, in southern Illinois (study 1) telemetry monitoring was conducted year-round but snakes were inactive from November to March (Dreslik 2005). In contrast, in Ontario (study 15) telemetry monitoring ended in October and resumed in May (Harvey and Weatherhead 2006*a*, *b*) yielding a quasi-winter of 6 months. We use the term quasi-winter to describe the time period during which regular radiotelemetry monitoring did not occur for a given study. The quasi-winter period varied among datasets because of differences both in the length of time snakes were inactive and in monitoring schedules but it did not vary within a dataset. As a result, the quasi-winter period for some studies included several weeks during which snakes may have been active. To deal with these issues, we modeled the quasi-winter period as a single time interval

Table 1. Eastern massasauga survival estimates and vital rate sources from studies published from 1999 to 2011.

Location	Annual adult survival	Vital rate source(s)	Study
Missouri	0.78	Population viability analysis (PVA) based on local population mark-recapture data, literature (mating system)	Seigel and Sheil (1999)
Ontario	0.69	PVA based on local population mark-recapture data, literature, expert opinion (parameter estimation limited by partial corruption of mark-recapture data)	Middleton and Chu (2004)
Ontario	0.69	PVA based on parameters from Middleton and Chu (2004), local spatial data	Brennan and Tischendorf (2004)
Ontario	0.69	PVA based on parameters from Middleton and Chu (2004) (parameter estimates were modified to achieve 2–3% annual growth rate)	Miller et al. (2005)
Michigan	0.66	PVA based on local population radiotelemetry, field data, literature (survival estimate did not include over-winter survival)	Bissell (2006)
Michigan	0.95	PVA based on local population radiotelemetry, field data, literature	Bailey (2010)
Various locations	0.70	Expert opinion	Faust et al. (2011)
Ontario	0.79	Local population radiotelemetry data	Harvey and Weatherhead (2006a)
Wisconsin	0.33	Local population radiotelemetry data	King (1999)

Table 2. Characteristics of eastern and western (Missouri) massasauga radiotelemetry datasets including location, study years, sample size, number of snake days (relative study size), number of censored mortalities, and source of datasets. The sample size values in parentheses represent the number of male and female snakes in the dataset, respectively. Snake days is equal to the cumulative number of days all snakes in a dataset were tracked, and quasi-winter weeks are the beginning and end week of the year for the quasi-winter period with the total number of weeks in the quasi-winter period in parentheses. The quasi-winter period was the period of time where regular radiotelemetry monitoring did not occur for a given study. Numbers assigned to each study correspond to locations shown in Figure 1.

Study	State/Province	County	Years	*n* (M/F)	Snake days	Censored mortalities	Quasi-winter weeks	Citation; contributing authors
1	Illinois	Clinton	2000–2002	48 (27/21)	10,647	8	45–09 (16)	Dreslik (2005); MJD, BCJ, CAP, DBS
2	Iowa	Bremer	2002–2005	20 (13/7)	4,665	0	40–16 (28)	TJV
3	Michigan	Cass	2007–2008	22 (7/15)	3,654	2	40–16 (28)	Cross (2009)
4	Indiana	LaGrange	1999–2001	15 (5/8)	2876	2	36–20 (36)	BAK, JVM
5	Michigan	Lenawee	2003–2004	16 (5/11)	1,546	0	41–31 (42)	Moore and Gillingham (2006); JAM
6	Michigan	Barry (2004)	2004–2006	23 (4/21)	4,651	0	43–15 (24)	Bissell (2006), Bailey et al. (2011); KB, HC
7	Michigan	Barry (2008)	2008–2009	25 (8/17)	4,328	0	44–20 (21)	Bailey (2010), Bailey et al. (2011); RLB, HC
8	Pennsylvania	Butler	2005–2006	21 (6/15)	4,776	3	45–14 (21)	Jellen and Kowalski (2006); BCJ, MJK
9	Michigan	Oakland (2002)	2002–2007	47 (26/21)	22,878	2	44–19 (27)	Hecht (2007), Sage (2005); BAK, JRS, SEH, CSS
10	Michigan	Oakland (2003)	2003–2004	12 (5/7)	1,904	0	43–18 (27)	JO
11	Michigan	Kalkaska (2002)	2002–2004	28 (12/16)	8,760	1	43–19 (28)	BAK, JVM, JMR
12	Michigan	Kalkaska (2006)	2006–2008	32 (16/16)	12,042	0	43–19 (28)	Bieser (2008), DeGregorio (2008), DeGregorio et al. (2011), Smith (2009); NDB, BAD, BAK, CSS
13	Ontario	Welland	2000–2004	13 (7/6)	6,018	1	46–15 (21)	AY
14	Ontario	Bruce (1991)	1991	9[a]	808	0	N/A	Prior and Weatherhead (1994), Weatherhead and Prior (1992); KAP, PJW
15	Ontario	Bruce (2001)	2001–2004	34 (19/15)	12,917	0	42–20 (30)	Harvey and Weatherhead (2006*a*, *b*, 2010); DSH, PJW
16	New York	Onondaga	1989–1992	12[a]	5,373	2	45–17 (24)	Johnson (1995); GJ
17	Ontario	Parry Sound (1995)	1995–1998	29 (12/17)	14,306	2	42–17 (27)	JDR
18	Ontario	Parry Sound (2001)	2001–2005	33 (23/10)	14,418	4	41–19 (30)	Rouse (2006); JDR
MO1	Missouri	Holt	2002–2003	29 (16/13)	4,389	4	47–16 (21)	Durbian et al. (2008); JL, RAS
MO2	Missouri	Chariton	2002–2003	22 (17/4)[b]	4,622	1	46–13 (19)	Durbian et al. (2008); RAS
MO3	Missouri	Linn	2004	10 (5/5)	1,192	0	N/A	Durbian et al. (2008); TC, FED, RAS

[a] Dataset did not include data on snake sex.

[b] Dataset included 1 snake of unknown sex.

Table 3. Annual survival estimates with censored human-caused mortalities (uncensored human-caused mortalities) calculated from Program MARK known fate models for 18 eastern massasauga and 3 western (Missouri) massasauga radiotelemetry datasets. The active season survival rate is equal to the weekly active season survival rate raised to a power equal to the number of weeks in the active season. The annual survival rate is equal to the active season survival rate multiplied by the winter survival rate. The standard errors are listed for the annual survival rate with censored human-caused mortalities.

Study	Weekly active season survival	Active season survival	Quasi-winter survival	Annual survival	SE
1	0.9811	0.51	0.69	0.35 (0.26)	0.079
2	0.9747	0.55	0.88	0.49	0.105
3	0.9747	0.55	1.00	0.55 (0.47)	0.124
4	0.9892	0.85	0.89	0.76 (0.64)	0.124
5	0.9695	0.76	1.00	0.76	0.094
6	0.9828	0.63	1.00	0.63	0.104
7	0.9979	0.95	1.00	0.95	0.046
8	0.9954	0.87	1.00	0.87	0.085
9	0.9904	0.79	0.78	0.62 (0.60)	0.058
10	0.9737	0.53	1.00	0.53	0.151
11	0.9941	0.87	0.88	0.77 (0.70)	0.122
12	0.9956	0.90	0.86	0.78	0.063
13	0.9973	0.92	0.86	0.79 (0.72)	0.108
14	0.9835	0.65		[a]	0.066
15	0.9919	0.84	0.73	0.62	0.073
16	0.9976	0.94	0.82	0.77 (0.67)	0.120
17	0.9929	0.84	0.85	0.72 (0.66)	0.076
18	0.9950	0.90	0.71	0.64 (0.59)	0.073
MO1	0.9896	0.73	1.00	0.90 (0.73)	0.093
MO2	0.9915	0.76	1.00	0.76 (0.70)	0.120
MO3	0.9950	0.86		[a]	0.041

[a] Dataset did not allow for annual survival estimate.

within Program MARK. Thus, we estimated 2 parameters using Program MARK: weekly active season survival and quasi-winter survival. Although typical Cormack–Jolly–Seber survival estimation models necessitate goodness of fit testing, such tests are not possible with the known fate model (Cooch and White 2010). To determine whether survival differed between sexes, we chose 6 datasets with sample sizes of 10 or more for each sex (studies 1, 11, 12, 15, 18, and MO1; Table 2). For these datasets, we investigated 3 different models: season-only model, season and sex additive model, and season and sex interaction model. We compared models using Akaike's Information Criterion corrected for small sample sizes (AIC$_c$; Akaike 1973, Burnham and Anderson 2002).

For all models, the survival rate for time intervals in which no mortalities occurred was fixed at 1. We used the sine link function and second partial derivative method for variance estimation for each model. To calculate an annual adult survival rate, we raised the weekly active season survival estimates from Program MARK to a power equal to the number of intervals in the active season (number of weeks in the active season − 1) for that dataset and then multiplied by the winter survival rate. For example, a dataset with an active season of 26 weeks, weekly active season survival rate

Table 4. Program MARK model summaries for the sex (S), seasonal (W), sex and season additive (S + W), and sex-by-season interaction (S × W) effects analyses of 5 eastern massasauga and 1 western (Missouri) massasauga radiotelemetry datasets. We used Akaike's Information Criterion corrected for small sample sizes (AIC$_c$) to determine whether these studies had sex differences in survival.

Study	Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ weights	No. of parameters	Deviance
1	W	232.20	0.00	0.65	2	97.94
	S + W	234.20	2.00	0.24	3	97.93
	S × W	235.82	3.62	0.11	4	97.53
11	S × W	61.77	0.00	0.44	4	22.91
	W	62.60	0.83	0.29	2	25.75
	S + W	62.76	0.99	0.27	3	23.90
12	W	58.48	0.00	0.61	2	21.23
	S + W	60.01	1.53	0.28	3	20.74
	S × W	62.01	3.53	0.10	4	20.71
15	W	128.54	0.00	0.42	2	57.43
	S + W	128.82	0.28	0.37	3	55.70
	S × W	129.96	1.42	0.21	4	54.82
18	W	112.70	0.00	0.65	2	43.74
	S + W	114.63	1.93	0.24	3	43.67
	S × W	116.30	3.60	0.11	4	43.32
MO1	S + W	28.30	0.00	0.34	3	13.46
	S × W	28.30	0.00	0.34	4	13.46
	W	28.64	0.34	0.30	2	15.82

Table 5. Model-averaged estimates of male and female annual survival rate for 1 eastern massasauga and 1 western (Missouri) massasauga radiotelemetry datasets. The active season survival rate is equal to the weekly active season survival rate raised to a power equal to the number of weeks in the active season. The annual survival rate is equal to the active season survival rate multiplied by the winter survival rate.

Study	Sex	Weekly active season survival	Active season survival	Quasi-winter survival	Annual survival
11	Male	0.9893	0.95	0.95	0.90
	Female	0.9914	0.81	0.83	0.68
MO1	Male	0.9937	0.82	1.00	0.60
	Female	1.0000	1.00	1.00	1.00

of 0.98, and a winter survival rate of 0.88, the calculation for annual adult survival was $0.98^{25} \times 0.88 = 0.53$. We calculated standard errors for annual adult survival estimates via the Delta method (Seber 1982).

Although pooling all the datasets would provide a more detailed analysis of survival differences among populations, pooling data would require us to fix the quasi-winter interval in Program MARK across all datasets despite biologically relevant differences among sites. Homogenizing the quasi-winter period would also require additional censoring and assignment of some active season mortalities to the quasi-winter interval. As such, we chose not to analyze a pooled dataset.

The eastern massasauga's distribution follows a southwest to northeast axis (Fig. 1). To investigate possible trends along this axis, we computed the first principal component of latitude and longitude using principal component analysis. We then tested for a correlation between this principal component and annual and weekly active season survival. We calculated the harmonic mean survival rate for temporally separated survival estimates of 4 sites (studies 6 and 7, 9 and 10, 11 and 12, and 17 and 18 in Tables 2 and 5 and Fig. 1). To identify possible climatic correlates with this latitude–longitude axis, we obtained information on annual rainfall, mean summer temperature (average daily temperature in Jun, Jul, and Aug), and mean winter temperature (average daily temperature in Dec, Jan, and Feb) from WorldClimate (2010) and the National Climate Data and Information Archive of Canada (Environment Canada 2010) for weather stations near eastern massasauga radiotelemetry sites (within 5–60 km). These variables served as proxies for the suite of climatic variables (e.g., cooling degree days, heating degree days, 24-hr average temperature) that vary along the latitude–longitude axis and may influence eastern massasauga life history. We then generated the first principal component of climate and tested for a correlation with the latitude–longitude principal component. We chose not to compute correlations between active season and annual survival and climatic variables to avoid including many possibly correlated climate variables given the large number of climate variables that could be tested.

At the beginning of this project, we questioned whether the Missouri populations were eastern massasauga, western massasauga (*Sistrurus catenatus tergeminus*), or hybrids (Evans and Gloyd 1948). Subsequently, molecular genetic analyses have provided strong evidence that Missouri populations are in fact western massasaugas (Gibbs et al. 2010, Kubatko et al. 2011). Because of significant conservation concerns about these populations and their ecological similarities (Seigel et al. 1998, Szymanski 1998, Gibbs et al. 2010), we included them in our analyses of survival but not in tests for geographic patterns in survival within eastern massasaugas.

RESULTS

We analyzed 18 radiotelemetry datasets from 13 separate locations throughout the eastern massasauga's range and 3 western massasauga datasets from 3 locations in Missouri (Fig. 1, Table 2). Two datasets (studies 14 and MO3) provided only active season data. The number of snakes in each dataset varied from 9 to 48 comprising a total of 499 individuals across all datasets. Eleven datasets contained at least 1 human-caused mortality (range = 1–8). We recorded 197 snake mortalities across all datasets with 32 caused by humans (including construction activities, prescribed burn, mowing, plowing, and automobiles), which we censored in the primary survival estimation analyses. Of the remaining 165 mortalities, 67 were due to predation, 3 were due to illness, and 59 were due to unknown or unrecorded causes during the active season. The remaining 36 mortalities occurred during the quasi-winter period without definitive cause because most of these snakes failed to emerge.

Among all datasets, the earliest the active season began was week 10 (approx. mid-Mar), and except study 5, the latest it began was week 20 (approx. mid-May). The earliest the active season ended was week 35 (approx. the end of Aug) and the latest it ended was week 46 (approx. mid-Nov). For the analyses in which we censored human-caused mortalities, weekly active season survival averaged 0.99 (range = 0.97–1.00), cumulative active season survival averaged 0.77 (range = 0.51–0.95), and quasi-winter survival averaged 0.89 (range = 0.69–1.00; Table 3). Annual adult survival weighted by sample size averaged 0.67 (range = 0.35–0.95) for the 17 full-year datasets (Table 3, Fig. 2). Annual adult survival rates were 0.73 and 0.76 for the 2 full-year Missouri datasets (Table 3). Models that included sex as an additive or interactive effect had the smallest AIC_c for only 2 of 6 studies tested (studies 11 and MO1; Table 4). For the other studies, the season-only model was most parsimonious (Table 4) and models that included sex (resulting in an increase from 2 to 4 parameters) had little support ($\Delta AIC_c < 4$, Δdeviance < 3; Arnold 2010). Furthermore, model-averaged estimates of survival for studies 11 and MO1 did not show a consistent pattern; males had greater survival in study 11 and females had greater survival in study MO1 (Table 5). Consequently, we pooled sexes in all other analyses.

We generated 2 component variables for the latitude–longitude PCA, but only the first component variable had an eigenvalue >1 (1.685). The first component variable

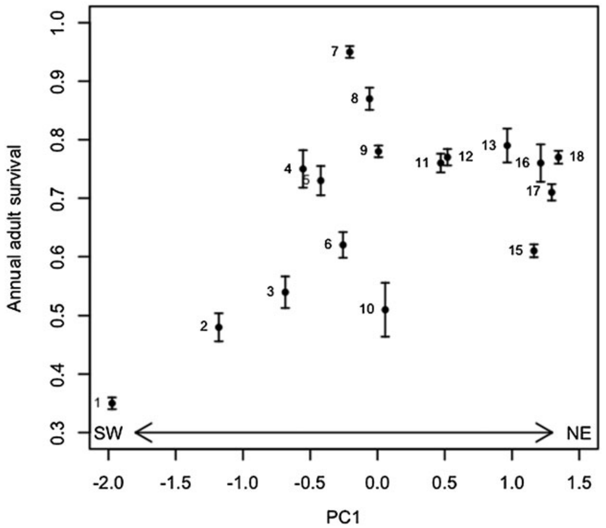

Figure 2. Association between eastern massasauga annual survival and geographic location along a southwest to northeast axis (PC1). Whiskers represent ±1 standard deviation. Numbers correspond to studies listed in Tables 2–5 and locations shown in Figure 1. Temporally separated survival estimates from 4 sites (studies 6 and 7, 9 and 10, 11 and 12, 17 and 18) were averaged prior to correlation analysis but are shown separately here.

explained 84% of the variation in geographic location among telemetry sites and included positive loadings of latitude (0.92) and longitude (0.92). Excluding human-caused mortalities, annual adult survival and weekly active season survival were positively correlated with the first principal component of latitude–longitude (annual survival: $r = 0.613$, df $= 13$, $P = 0.026$, Fig. 2; weekly active season survival: $r = 0.664$, df $= 13$, $P = 0.013$; Fig. 3). Given that this component represents a southwest to northeast axis, this correlation indicates that survival was lower in the southwest and higher in the northeast.

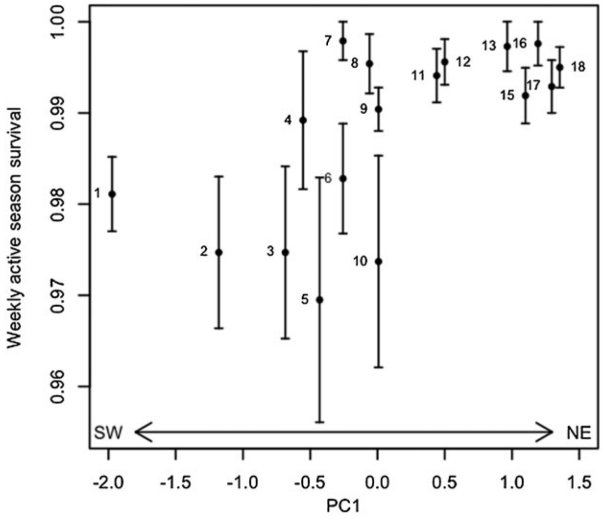

Figure 3. Association between eastern massasauga weekly active season survival and geographic location along a southwest to northeast axis (PC1). Numbers correspond to studies listed in Tables 2–5 and locations shown in Figure 1. Temporally separated survival estimates from 4 sites (studies 6 and 7, 9 and 10, 11 and 12, 17 and 18) were averaged prior to correlation analysis but are shown separately here.

We generated 3 component variables for the climate PCA, but only the first component variable had an eigenvalue >1 (2.042). The first component variable of climate included positive loadings of rainfall (0.78), summer mean temperature (0.83), and winter mean temperature (0.86) and explained 68% of the variation in climate among sites. The climate principal component was negatively correlated with the latitude–longitude principal component ($r = -0.56$, $P = 0.046$). Annual rainfall decreased from 984.5 mm to 745.2 mm, mean summer temperature decreased from 24.1° C to 19.4° C, and mean winter temperature decreased from −0.87° C to −6.67° C along this southwest to northeast axis.

When human-caused mortalities were not censored, mean annual adult survival weighted by sample size was 0.63 (range = 0.26–0.95) for the 17 full-year datasets (Table 3), and annual adult survival rates were 0.59 and 0.70 for the 2 full-year Missouri datasets (Table 3). Including human-caused mortalities resulted in a non-significant correlation between annual adult survival and latitude–longitude ($r = 0.422$, df $= 13$, $P = 0.150$), but the weekly active season survival and latitude–longitude correlation remained significant ($r = 0.561$, df $= 13$, $P = 0.046$).

DISCUSSION

Annual adult survival estimates for eastern massasaugas revealed substantial variation among populations. This variation remains regardless of whether or not we included human-caused mortalities. When we censored human-caused mortalities, variation in both annual and weekly active season survival rates followed a clinical gradient along a southwest–northeast axis. Admittedly, the observed extremes in annual adult survival rates (0.35, 0.95) may overestimate the true extent in variation along the gradient; major axis regression analysis suggests that variation in annual survival ranges from 0.39 to 0.87 from southwest to the northeast. When we did not censor human-caused mortalities, weekly active season survival was correlated significantly with the latitude–longitude axis.

Some of our results were derived from reanalysis of datasets that were previously used to generate survival estimates (study MO1, Seigel and Sheil 1999; study 6, Bissell 2006; study 15, Harvey and Weatherhead 2006*a*; study 7, Bailey et al. 2011), and our estimates both with and without human-caused mortalities are concordant with them (Tables 1 and 3). Our reanalysis ensured we used maximum likelihood methodology for all survival estimates and handled the seasonal issues (our quasi-winter period) in the same manner for all datasets. Our average adult annual survival estimates were also similar to the estimate of 0.65 from an analysis of a mark-recapture dataset of eastern massasaugas in Georgian Bay, Ontario (P. Jones, Northern Illinois University, unpublished data) and other previously calculated estimates of eastern massasauga survival (Tables 1 and 3). These previously published survival estimates did not exclude human-caused mortalities. Analyses of mark-recapture datasets for multiple populations throughout the eastern massasauga's range would be useful for confirming the trends in survival reported here.

Geographic Variation in Survival

Our analysis suggests that geographic variation in survival is associated with climate; we found a significant, negative correlation between the first component variable of the climate variables and the first component variable of the latitude–longitude axis. Possibly, geographic variation in survival is associated with the length of the active season with a longer active season providing more opportunity for mortality (e.g., predation). Warmer climates also increase the energy requirements of ectotherms, which may result in higher mortality (Homyack et al. 2011). Considering that this geographic axis also represents a climate gradient, climate likely affects eastern massasauga survival. Eastern massasaugas also exhibit latitudinal variation in other demographic and life history characteristics. For example, fecundity increases with latitude (Aldridge et al. 2008), and expert opinion suggests that age of maturation and longevity do as well (Faust et al. 2011).

When human-caused mortalities were uncensored, the correlation between annual adult survival and the latitude–longitude axis was not significant. This is not unexpected because human-caused mortalities are unlikely to follow the same geographic pattern as natural mortalities (in fact, the 2 datasets with the greatest number of human-caused mortalities, studies 1 and 17, are on opposite ends of the latitude–longitude axis). Roadkills and mortality due to management actions made up the majority of human-caused deaths. Given that road density and traffic as well as management actions are likely to vary among populations, removal of human-caused mortalities from the analysis was justified. The number of human-caused mortalities in these datasets (14% of all mortalities) was significant and represents a management concern (Shepard et al. 2008). Small reductions in adult survival can have large impacts on population growth and lead to increased extinction probabilities for small populations (Seigel and Sheil 1999). For example, a small number of additional roadkills per year could have strong negative impacts on small eastern massasauga populations.

Geographic patterns of body size (Bergmann's rule) and life history trait variation (Stearns 1984, Angilletta et al. 2004, Sears 2005, Kearney 2012) are often analyzed, but geographic patterns of survival have been examined less frequently. Although variation in life history traits are expected to cause variation in survival as observed here (Roff 1992, Stearns 1992), few studies provide empirical data on range-wide variation in survival. Among snakes, comparisons are often limited to a few geographically separated sites. Three populations of ratsnakes (in Texas, Illinois, and Ontario) had equal survival (Sperry et al. 2010); however, a comparison of life history traits between ratsnake populations in Maryland and Ontario demonstrated that growth rates decreased, whereas age of maturity and longevity increased in the Ontario population compared to the Maryland population (Blouin-Demers et al. 2002). However, we note that the species status of snakes in these 2 studies, all formerly *Elaphe obsoleta*, is unclear (see Burbrink et al. 2000, Burbrink 2001, Gibbs et al. 2006). Variation in survival among populations may also be related to habitat type and suitability. Two populations of the terrestrial gartersnake (*Thamnophis elegans*) exhibited large differences in multiple life history traits, including survival, because of differences in food availability in their respective habitats (Bronikowski and Arnold 1999). The degree to which variation in habitat quality or food availability contributes to variation in life history traits and survival among eastern massasauga populations warrants investigation.

Comparison to Other Vipers

Adult survival among vipers is generally high. Parker and Plummer's (1987) "late-maturing temperate viperids" group, based on estimates from 6 viper populations, had an average annual adult survival of 0.77. As a member of that group, the eastern massasauga has a lower mean survival of 0.67. However, the analyses summarized by Parker and Plummer (1987) preceded maximum likelihood techniques, so direct comparisons are difficult to make. Few examples of likelihood-based survival estimates exist for other viper species, and they vary significantly. Timber rattlesnakes (*Crotalus horridus*; Brown et al. 2007), cottonmouths (*Agkistrodon piscivorus*; Koons et al. 2009), and asp vipers (*Vipera aspis aspis*; Flatt et al. 1997) had greater annual adult survival rates (0.96, 0.79, and 0.75, respectively) whereas the northern Pacific rattlesnake (*Crotalus oreganus oreganus*; Diller and Wallace 2002) had a lesser annual adult survival rate (0.55) compared to the average annual survival rate we found for eastern massasaugas. Although not a viper, the tiger snake (*Notechis scutatus*) is a venomous, sit-and-wait predator, and it had a greater annual survival rate (0.78) than our eastern massasauga average survival estimate (Bonnet et al. 2011). Annual adult survival estimates from the Missouri studies (0.90 and 0.76) were greater than the average survival of the other studies, but were well within the range of estimates. An annual survival estimate was not possible with the third Missouri study, but its active season survival estimate was high compared to other studies.

Survival Differences Between Sexes

We observed differences in survival between the sexes in just 2 of 6 studies, and in these 2, the direction of the difference was not consistent; in study 11, male survival was greater and in study MO1 female survival was greater. The magnitude of the difference between male and female survival was large for both studies although female survival for MO1 was likely inaccurate as no female deaths occurred during that study (Table 5). The other 4 studies with sex effect analysis found no evidence of a difference in survival between sexes. For Texas ratsnakes (*Pantherophis obsoletus*), males had greater survival than females because of increased female activity following oviposition (Sperry and Weatherhead 2009). In Ontario, however, survival rates of male and female ratsnakes did not differ, nor did their behaviors associated with mortality (Weatherhead et al. 2012). A trend toward greater male survival was found in the viviparous European adder

(*Vipera berus*; Madsen and Shine 1993). After bearing young, females were emaciated and needed to forage, leading to increased exposure to predators (Madsen and Shine 1993). Among other viviparous snakes, females tend to have greater survival than males (aquatic gartersnakes [*Thamnophis atratus*], Lind et al. 2005; red-sided gartersnakes [*Thamnophis sirtalis parietalis*], Shine et al. 2001; plains gartersnakes [*Thamnophis radix*], Stanford and King 2004). From these differences, sex-biased mortality appears to vary among snake species and populations. Survival differences between sexes may also be related to habitat selection, which differs based on reproductive status (Dreslik 2005, Bissell 2006, Bailey 2010). However, confidently documenting differences in survival among sexes and reproductive states requires larger sample sizes than were available.

Transmitter Effects on Survival

The effects of surgically implanted transmitters are not well studied for snakes (Murray and Fuller 2000). Lentini et al. (2011) found that 11 of 12 captive eastern massasaugas implanted with transmitters had negative clinical reactions, but no deaths occurred as a consequence. In a field study, implanted transmitters in ratsnakes had negative effects on growth (mass but not length) and relative clutch mass but ambiguous results for survival (Weatherhead and Blouin-Demers 2004). Another field study on Texas ratsnakes found no effects of implanted transmitters on body condition or hematological characteristics except for equivocal evidence of reduced white blood cell count (Sperry et al. 2009). Surgical implantation methods in the above studies were similar to those listed earlier.

Judging the effects of transmitters on survival in this study is complex. Other than a few individuals (3) that exhibited complications immediately following surgery (and were excluded from analysis), mortality directly resulting from transmitter implantation was not observed. For example, post hoc examination of our data suggests no difference in weekly mortality rates during the first versus the second 6 weeks following release (mean weekly mortality = 0.016 vs. 0.017). Such a difference might be expected if mortality directly increased during recovery from surgery. However, we cannot exclude the possibility that transmitter implantation was an indirect cause of mortality (e.g., through increased depredation or winter mortality). In addition, several python species are capable of expelling surgically implanted transmitters unless those transmitters are anchored to the ribcage (Bryant et al. 2010). In most studies analyzed here, however, transmitters were anchored. We do caution that indirect mortality effects and rare instances of transmitter expulsion may have negatively biased our survival estimates.

MANAGEMENT IMPLICATIONS

The large variation in adult survival among eastern massasauga populations has implications for conservation planning and management. Populations in which we observed lesser annual adult survival may also be smaller or decreasing in abundance and thus might require more aggressive management strategies. As noted above, geographic patterns in demography and life history extend beyond survival for the eastern massasauga. These differences could be incorporated into population model sensitivity analyses to identify which vital rates most strongly affect population persistence, thus guiding management decisions and actions. For example, the population viability analysis of Middleton and Chu (2004) showed greatly increased risk of extinction when adult eastern massasauga mortality exceeded 30%. Eight of our survival estimates were below 70%, which puts them at high risk of extinction according to Middleton and Chu (2004). As this and other studies have shown, however, substantial variation exists in the demographic characteristics of the eastern massasauga across its range. Because the PVA of Middleton and Chu (2004) was parameterized with data from Canadian eastern massasauga populations, its results may not be accurate for a population in Indiana or Illinois. This discrepancy highlights the need for more data from multiple eastern massasauga populations across the species' distribution. These new datasets could then be used to parameterize more accurate PVAs for local populations.

Eastern massasaugas demonstrate substantial variation in survival across their range. Our analyses suggest variation in survival may be due to climate or some correlate of climate (e.g., length of active season, habitat suitability). Because the geographic trend in eastern massasauga survival indicates reduced survival in warmer climates, climate change has the potential to strongly and negatively affect this species. Further investigations into common causes of mortality and possible behavioral or physiological mechanisms for coping with climate change are necessary for the conservation of this imperiled snake species.

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