

Multi-scale Responses of Eastern Massasauga Rattlesnakes (*Sistrurus catenatus*) to Prescribed Fire

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ABSTRACT.—The eastern massasauga rattlesnake (*Sistrurus catenatus*) is a threatened species that occurs in habitats frequently targeted by prescribed burns. There have been reports of massasauga mortality as a result of prescribed fires, but little is known regarding the indirect effects of fire on this species. The objective of this study was to monitor massasaugas during a prescribed fire to assess direct and indirect effects. We initially implanted radio transmitters in 13 massasaugas inhabiting an area targeted for periodic prescribed fires and tracked them following a prescribed fire to determine burn related-mortality and behavioral influences. Data loggers, temperature sensitive paint, and measuring posts were used to record detailed fire data. Of the five snakes on the burn unit at the time, two died as a result of the fire. No differences were observed in daily movements and home range sizes between burn categories (in the burn, same site not in the burn and at a nearby unburned site). Snakes on and off the burn unit at the same site exhibited the same habitat preference for wetland habitats, whereas snakes at the control site preferred herbaceous areas. Slight differences were observed in microhabitat selection related to litter depth, surface light intensity, distance to water, and surface temperature. The snakes did not appear to alter their seasonal activities as a result of the prescribed fire. The results of this study suggest ways to minimize impacts from prescribed fires on massasauga populations.

INTRODUCTION

The eastern massasauga rattlesnake (*Sistrurus catenatus*), has experienced range-wide population declines and is a candidate for listing under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service, 2011). Its range encompasses the Midwestern United States throughout the Great Lakes Region and can be found in restricted populations in southern Ontario and as far east as New York and Pennsylvania (Szymanski, 1998; Johnson *et al.*, 2000). This species is listed as threatened, endangered, or of special concern throughout its

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remaining range. Habitat use for this species varies geographically, but common attributes include relatively open-canopy compared to surrounding area, presence of the water table near the surface, and adjoining upland and lowland areas with variable elevation (Szymanski, 1998; Johnson *et al.*, 2000). In Michigan massasaugas inhabit a wide variety of early successional wetland habitats and exhibit a preference for sedge dominated, emergent wetlands, particularly prairie fens (Lee and Legge, 2000; Moore and Gillingham, 2006; Bailey *et al.*, 2012).

One of the main threats to early successional massasauga habitat is encroachment of woody vegetation and exotic plant species (Durbian, 2006; Moore and Gillingham, 2006). These communities are frequently maintained using prescribed fires designed to slow the rate of woody vegetation succession and invasion by exotic plants. Other less cost effective methods of maintaining early successional plant communities include herbicide application, mowing, and manual removal of target species (Durbian, 2006). Prescribed fires implemented during the growing season are most effective at reducing woody vegetation (Lee *et al.*, 2005; reviewed in Knapp *et al.*, 2009). Because these effective burn times coincide with the massasauga's active season, preventing incidental harm as a result of management is a recurring issue facing land managers (Durbian and Lenhoff, 2004; Durbian, 2006). Vipers in general are considered to be very vulnerable to extinction because of their restricted distributions, susceptibility to habitat destruction, low reproductive rates and persecution (Greene and Campbell, 1992). Given massasaugas currently exist in small, disjunct populations throughout their range, loss of a few individuals from small populations can lead to drastic population declines (Seigel and Sheil, 1999). Fire-related mortality for this species has been reported (Durbian, 2006; Moore and Gillingham, 2006), but how prescribed fires indirectly affect massasaugas is unknown. Possible indirect effects of prescribed fires include altered prey base, increased surface temperatures and predation risk (Russell *et al.*, 1999). Reptile species tend not to conform well to generalized models predicting responses to fires (Driscoll and Henderson, 2008; Lindenmayer *et al.*, 2008). As such, it is necessary to obtain information on individual species' responses to fires to effectively guide habitat management efforts.

Of particular interest to land managers is how to conduct prescribed burns in areas known to contain massasaugas in a manner that will yield the desired management results with minimal impact on the massasaugas. The objective of this research was to determine direct and indirect effects from habitat alteration on massasaugas as a result of a prescribed fire. We examined responses of the massasaugas to prescribed fire by monitoring movements, home ranges and habitat use at three scales: microhabitat, macrohabitat and landscape-level. We evaluated the effects of a certain type of prescribed fire by monitoring fire behavior and gathering thermal data of the substrate and refugia.

METHODS

STUDY AREA

Field research for this study was conducted from April to November 2007 and 2008 at two sites on private property in Cass (41°57'N, 85°60'W) and Van Buren counties (42°10'N, 85°46'W; approximately 29 km apart), southwest Michigan. Total area at the two sites differed, but the areas occupied by massasaugas used for this study were approximately the same size (350 ha). The major habitat types within these sites were mixed hardwood swamps, scrub/shrub wetlands, herbaceous rangeland and upland deciduous forests. Dominant soil types include Oshtemo sandy loam and Sprinks loamy sand with Houghton and Adrian muck interspersed throughout (Natural Resources Conservation Service, 2000a, b). These

soils support rare prairie fen communities characterized by sedges (*Carex*, *Scirpus*), rushes (*Juncus*), grasses (*Andropogon*, *Bromus*, *Diarrhena*, *Panicum*, *Poa*, *Sorghastrum* and *Sparobolus*), cinquefoil (*Dasiphora fruticosa*), poison sumac (*Toxicodendron vernix*) and cattail (*Typha*).

These sites are managed using prescribed fire, manual removal, and chemical controls to maintain early successional wetland vegetation and to deter invasive species including glossy buckthorn (*Rhamnus alnus*), purple loosestrife (*Lythrum salicaria*), and garlic mustard (*Alliaria petiolata*). Current burn recommendations for areas known to contain massasaugas include, but are not limited to: burning early in the spring before emergence, burning on days when the snakes are likely to be inactive, only burn when ambient temperatures do not exceed 10 C and that wetlands not be burned after May 15th (Johnson *et al.*, 2000; Kingsbury, 2002). Sections of both sites had been burned in the past, with the most recent burns occurring 2 y before our study was conducted. Burns at these sites are on a rotational basis to mimic the frequency of natural fires and to avoid repeatedly burning areas before the vegetation and associated organisms have time to recover (McGowan-Stinski, 2004; McGowan-Stinski and Pearsall, 2004). Only the Van Buren site was burned during the course of this study. The two study sites were then split into three experimental groups: burned – the burn unit at the Van Buren county site, unburned – available area at the Van Buren county site that was not burned, and an unmodified reference site – the Cass county site.

FIRE PRESCRIPTION AND DATA COLLECTION

On 5 May, 2008, The Nature Conservancy (TNC) administered a prescribed burn to a 6.1 ha unit at the site in Van Buren Co. to mitigate the effects of woody encroachment and invasive species into the wetland. The burn prescription called for a backing fire with a very low rate of spread to maximize fuel consumption. This burn was representative of those typically used by TNC when managing their wetland sites.

In the months leading up to the burn, the unit was prepared by manually removing and chemically treating the stumps of glossy buckthorn stands and creating fire breaks around the perimeter of the burn unit. A total of 35 brush piles (approximately 2 m × 2 m × 1.5 m, or ½ t of fuel) created from the preparation process were stacked in the burn unit.

On the morning of the burn, all of the snakes at the Van Buren study site were located and their positions were marked with a flag. At this time snakes were assigned to one of the three experimental burn treatment groups; there was a total of five snakes on the burn unit, three off the unit, and five at the reference site. Two Tidbit® data loggers (Onset Computer Corporation, Pocasset, MA, U.S.A.) were placed in a hummock (level with the surface of the wetland, but under sphagnum) and in a burrow (approximately 10 cm below the surface) within 1 m of each snake in the burn unit. Data logger placement was representative of refugia used by the massasaugas at this site during their active season. During the 2 y of our study, 15.44% of our massasauga observations were of snakes under sphagnum hummocks, abandoned burrows, or holes in the peat and every massasauga we tracked was observed using these refugia at least once, if not multiple times throughout the active season. Additionally, three ceramic tiles painted with 14 ranges of Tempilaq G® temperature-sensitive paint (B.J. Wolfe Enterprises, Inc., Agoura Hills, CA, USA) ranging from 93.3–648.9 C were placed 0.3 m above ground level, on the litter and underneath the litter near the data loggers. To determine flame length and rate of spread around the snakes, four 3 m tall, height-marked stakes (metal conduit painted in alternating blue and white 0.5 m stripes) were placed at measured distances around the snakes within three meters of its location (Fig. 1). Following placement of the data loggers, ceramic tiles and stakes, the snakes were located again to make sure none of them had moved.

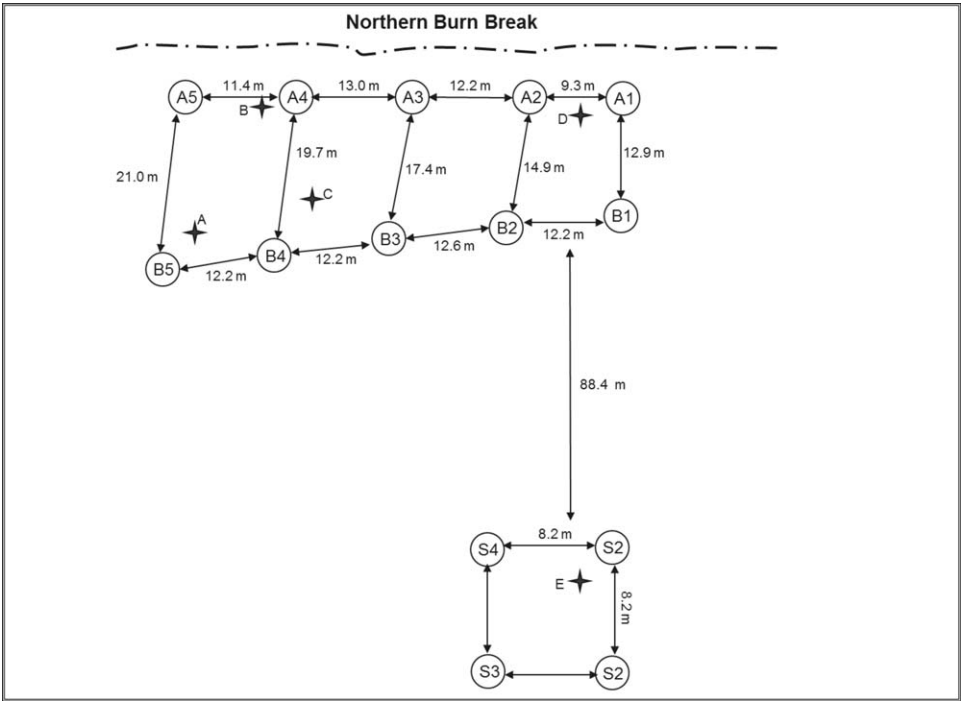


FIG. 1.—Schematic diagram of snakes (star) and fire survey posts (circles) in the burn unit at the Van Buren site. Scale is approximate

Immediately after the burn, snakes were located, their positions were marked and the distance moved was recorded. Researchers walked the burn unit to look for the carcasses of snakes and other animals. Carcasses were taken to a veterinarian to determine if fire was implicated as the direct cause of death.

CAPTURE AND TELEMETRY

Following emergence from overwintering sites (late April), eastern massasaugas were located in the study areas using visual encounter surveys and drift fences with funnel traps. A total of 13 massasaugas were implanted with transmitters in 2007 (Van Buren = 8; Cass = 5). Massasaugas were sexed via cloacal probing (Schafer, 1934), weighed and snout-vent length was measured using the squeezebox and cartometer technique (Quinn and Jones, 1974). Massasaugas that weighed more than 100 g were transported to a veterinarian (Kalamazoo, MI) for surgical implantation with a transmitter. Transmitter implant surgery followed the procedures described by Reinert and Cundall (1982), Weatherhead and Anderka (1984) and Fitzgerald and Vera (2006). Modifications to these procedures included the use of sevoflurane as an inhalant anesthetic through a small animal anesthetic machine, not refrigerating the snakes, implantation of the transmitters in the peritoneal cavity without cutting the ribs, dissolvable stitches and surgical glue to close the surgical site, use of a heating pad and administering antibiotics post-surgery. The transmitters used were 5 g or 9 g temperature sensitive models (SB-2 and SI-2, respectively, Holohil Systems Ltd., Carp, Ontario, Canada). During surgery we subcutaneously implanted the snakes with a Passive

TABLE 1.—Variables measured at paired massasauga locations within the two study sites following the prescribed burn in 2008

Variable	Description
tff	Soil temperature (C) at 15 cm
tfive	Soil temperature (C) at 5 cm
st ^b	Temperature (C) on the substrate surface
ta	Ambient air temperature (C) ~1.5 m above surface
hs ^b	Relative humidity (%) on the surface
ah	Relative humidity (%) 2 m above the surface
ld ^b	Litter depth (cm)
ws	Wind speed (km/h) 2 m above surface
cc	Cloud cover (estimated rating 1–5)
ls ^b	Surface light intensity (lux)
la	Light intensity (lux) at 2 m above surface
bp	Barometric pressure (mm Hg)
sv ^b	Vegetation covering the surface (%)
he ^b	Average vegetation height (m)
pw	Percent woody vegetation (%)
ph	Percent herbaceous vegetation (%)
dc	Distance to nearest cover item (m)
db ^b	Distance to nearest brush (m)
dww ^b	Distance to woody vegetation (≤ 15 cm diameter)
dos ^b	Distance to over story tree (≥ 15 cm diameter)
dw	Distance to water (m)

^b indicates variables that were retained for candidate models

Integrated Transponder (PIT tag; AVID® MicroChip ID Systems, Folsom, LA). The total weight of the transmitter and PIT tag was $<5\%$ of the snake's body weight (Hardy and Greene, 1999). We conducted capture, restraint and surgical procedures under Central Michigan University's Institutional Animal Care and Use Committee guidelines (IACUC Approval # 07-08). These procedures followed the regulations outlined by the Michigan Department of Natural Resources Scientific Collector's Permit (dates issued: April 2007 and April 2008).

Following surgery the snakes were allowed to recover for 2–3 d before releasing them at their initial capture location. It has been suggested transmitter implantation may influence snake behavior (Lentini *et al.*, 2011). Because transmitter implantation took place in 2007, we were able to monitor the snakes in our study prior to 2008 when the burn took place. During this monitoring period, all snakes were observed performing various normal behaviors (*i.e.*, feeding, mating, parturition, etc.), and successfully overwintered. No overwintering mortality was observed in our study.

Snakes were located every 2–4 d between 0700 h and 1230 h throughout their active season (May–October). The order and time of day each snake was tracked was randomized. Each time a snake was located, a series of environmental features (microhabitat) were measured (Table 1) and the location was recorded using a Global Positioning System (GPS) unit. For ease of comparison we used the same structural and environmental microhabitat variables as Moore and Gillingham, (2006). Microhabitat data were also measured at a random location, based on a random distance (3–100 m) and a random azimuth from the snake location. Random locations were sampled no more than 15 min after the associated snake locations were sampled. Analysis from data gathered during the 2007 season showed

the distance moved between subsequent locations was independent of the number of days between snake telemetry relocations (Kruskal-Wallis test, $\chi^2 = 8.0431$, $df = 6$, $P = 0.2350$; after Compton *et al.*, 2002).

DAILY MOVEMENT AND HOME RANGES

Daily movement was estimated in the field by measuring the straight-line distance between successive locations. The Animal Movement Extension in ArcView[®] GIS 3.2a (Hooge and Eichenlaub, 1997) was used to estimate 100% minimum convex polygons (MCP), fixed kernel home ranges and to conduct asymptote analysis. Asymptote analysis was used to determine the minimum number of relocations required to adequately describe a home range (Odum and Kuenzler, 1955). Minimum convex polygon home ranges are the minimum bounding polygons that encompass all of the known locations for a given animal (Jenrich and Turner, 1969). Kernel estimators are nonparametric home range estimators that produce an intensity distribution depicting the likelihood of finding the animal in question at a particular location within its home range (Worton, 1989). Kernel home ranges were created following the methods outlined by Row and Blouin-Demers (2006). This method involves using the area of the MCP to determine the area of the kernel as opposed to traditional methods of estimating kernel size such as least-squares cross-validation.

We used the Kruskal-Wallis procedure to test for differences in daily movement and MCP home range sizes for snakes that were on the burn unit, off the burn unit, and at the reference site. Due to the small sample size within each unit, statistical comparisons were not made between sexes. The gravid females in this study were depredated, leaving only males and non gravid females. Other studies have found that males and non gravid females exhibit similar movement patterns and habitat selection (Johnson, 2000; Marshall *et al.*, 2006), so we grouped these two classes for the purpose of analysis.

MACROHABITAT AND LANDSCAPE-LEVEL HABITAT

Aerial images [2008 National Agriculture Imagery Program (NAIP)] and land cover maps [2001 Integrated Forest Monitoring, Assessment, and Prescription (IFMAP)] were obtained for both counties (USDA Natural Resources Conservation Service, 1997 Natural Resources Inventory, Revised December 2000). These were examined simultaneously to determine where there were discrepancies between the two and the land cover map was adjusted accordingly. Using this updated land cover map, all rattlesnake location points were classified according to the land cover type in which they were found.

Macrohabitat, or third-order selection (Johnson, 1980), was defined as the area within the kernel home range. We conducted chi squared analyses to determine massasauga habitat preference (habitat use vs. availability) in each of the three experimental units, considering all habitats simultaneously (White and Garrott, 1990). Habitats were aggregated from the land use/land cover maps into the following categories: Herbaceous (herbaceous rangeland and pasture), Forest (deciduous, evergreen and mixed forest), and Wetland (woody and emergent wetlands).

Following chi squared analyses, Bonferroni confidence intervals were created to determine if certain habitat types were preferred or avoided by massasaugas, considering all habitats individually (Neu *et al.*, 1974; Beyers *et al.*, 1984; White and Garrot, 1990; Kapfer *et al.*, 2008). The Bonferroni confidence intervals were calculated using the Bonferroni z statistic and the proportion of snake habitat usage of each habitat type. Preference or avoidance was indicated by whether or not the expected proportion of habitat usage fell within the confidence interval.

The same methods were used to analyze habitat use at the landscape-level, or second-order selection (Johnson, 1980), with the exception of different habitat availability. Available habitat at the study sites was defined by buffering each location point with a circle of radius equal to the greatest length of any 100% MCP home range (Moore and Gillingham, 2006). Proportions of available habitat did not differ significantly between the two sites (Wilcoxon: $Z = 7.50$, $P = 0.4258$).

Where appropriate, data were log transformed to satisfy the assumptions of data distribution and heterogeneity of variances. Statistical analyses were conducted with JMP 10 and SAS 9.2 (SAS Institute, Cary, NC) statistical software. ArcGIS 9.3 (Environmental Systems Research Institute, Inc, Redlands, CA.) was used for GIS analysis. We used $\alpha = 0.05$ in all statistical tests.

MICROHABITAT ANALYSIS

Microhabitat variables (Table 1) were analyzed using conditional logistic regression (PROC LOGISTIC; SAS® 9.2) for 1:1 matched pairs. This method compares each snake location to its associated random point instead of pooling the snake locations and random locations (Compton *et al.*, 2002). The values from the random points are subtracted from the snake location points and are interpreted as the differences in habitat variables instead of absolute measured values (Compton *et al.*, 2002; Moore and Gillingham, 2006). Before conducting our analysis, we minimized the number of candidate variables by removing one variable from pairs of highly correlated (correlation coefficients ≥ 0.7) variables and biologically similar variables to reduce multicollinearity. Models were fit separately for each of the experimental units. All possible candidate models were tested with Akaike's Information Criterion (corrected for small sample size), AIC_c (Burnham and Anderson, 2002) to select and rank the most parsimonious model. The model with the lowest AIC_c and all models with AIC_c within four units of the lowest were considered to be supported (Burnham and Anderson, 2002). We used Nagelkerke's rescaled R^2 (Nagelkerke, 1991) to determine the best-approximating microhabitat model. We evaluated the ecological importance of each variable in the candidate models by summing the Akaike weights over our candidate models that included that variable (Burnham and Anderson, 2002).

RESULTS

FIRE DATA

The prescribed burn followed the outlined burn prescription and met the burn unit resource and treatment objectives. The wind was from the northwest and the fire moved westerly through the unit with an average flame length of 1.37 m and a rate of spread of 0.024 m/sec (Table 2). The fire briefly changed from a backing to a flanking fire (increased height, intensity, and speed) as it passed over one of the snakes due to a temporary wind shift. The burn lasted for approximately 3 h and when it was completed, approximately 95% of the designated unit had been burned. The data loggers recorded maximum temperatures of 35 C. Flame temperatures from the ceramic tiles were between 93.3 C and 148 C.

The visual survey of the burn unit found a burned, but still alive, eastern box turtle (*Terrapene carolina carolina*) and several bird nests, but no snakes. One crew member heard a rattle from a non transmitted snake but was unable to visually locate the snake. Within a week of the burn the emaciated carcasses of a neonate massasauga and a brown snake (*Storeria dekayi dekayi*) were found in the burn unit. No new adult massasaugas were found following the burn, however four new neonates were found in the burn unit.

TABLE 2.—Fire data observations for snakes, survey poles and ceramic tiles within the burn unit (Fig. 1)

Observation point	Average flame length (m)	Max. flame length (m)	Fire behavior	Fire direction
Pole B1	0.61	1.07	Backing	NNW
Pole B2	0.61	1.07	Backing	WNW
Pole A1	0.76	1.22	Backing	WNW
Snake D	1.07	1.37	Backing/Flanking	NNW
Pole A2	0.30	0.46	Backing	NW
Pole B3	0.61	1.22	Backing	WNW
Pole A3	0.46	0.61	Backing	NW
Snake C	0.46	0.76	Backing	NNW
Pole B4	0.46	0.76	Backing	NNW
Pole A4	0.61	1.22	Backing	W
Snake B	0.76	1.07	Backing	NNW
Snake A	0.06	0.91	Backing	NNW
Pole B5	0.46	0.76	Backing	NW
Pole A5	0.46	0.61	Backing	W
Pole S1	0.30	0.61	Backing	W
Pole S2	0.61	1.22	Backing	W
Pole S3	0.91	1.52	Backing	W
Pole S4	0.76	1.22	Backing	W

MASSASAUGA RESPONSES

Two of the snakes from the Cass County site were depredated. Of the five snakes on the burn unit, two of the snakes were killed during the burn. One snake was within 0.5 m of a brush pile before the burn and sought refuge there where it was burned as the fire consumed the brush pile. The other snake fled 18.3 m in the opposite direction of the fire and was overtaken by the fire as it fled. The remaining three snakes sought refuge in hummocks or burrows and survived the fire. Necropsy of the two dead massasaugas ruled out health complications as a cause of death and indicated that their deaths were a direct result of the fire.

DAILY MOVEMENT AND HOME RANGES

Daily movements for snakes on the burn unit ($n = 3$), off the burn unit ($n = 3$), and at the reference site ($n = 3$) averaged 8.58 ± 3.76 (SD) m/d, 5.76 ± 2.79 (SD) m/d and 7.47 ± 2.55 (SD) m/d, respectively. Mean MCP home range sizes for snakes on the burn unit, off the burn unit and at the reference sites averaged 4.58 ± 4.65 (SD) ha, 1.97 ± 1.54 (SD) ha and 1.57 ± 1.03 (SD) ha, respectively. Daily movements and MCP home ranges did not differ between experimental units ($\chi^2_2 = 0.3556$, $P = 0.8371$; $\chi^2_2 = 1.1556$, $P = 0.5611$, respectively).

MACROHABITAT AND LANDSCAPE-LEVEL HABITAT SELECTION

Chi square analysis revealed that habitat use at the macrohabitat scale differed from availability for all three of the experimental units (burn: $\chi^2_2 = 37.59$, $P \leq 0.001$; non burn: $\chi^2_2 = 41.84$, $P \leq 0.05$; reference: $\chi^2_2 = 24.92$, $P = 0.032$). At the landscape scale, habitat use differed from availability for all three experimental units (burn: $\chi^2_2 = 116.87$, $P \leq 0.001$; non burn: $\chi^2_2 = 41.84$, $P \leq 0.001$; reference: $\chi^2_2 = 24.92$, $P \leq 0.001$). At both scales Bonferroni confidence intervals indicated that snakes on and off of the burn unit at the

TABLE 3.—Habitat selection in eastern massasauga rattlesnakes in Cass and Van Buren counties, Michigan, as determined by using the method of Neu *et al.* (1974) to compare habitat proportions used by the snakes to proportions habitat available within the homerange and within the landscape. P = preferred, A = avoided, N = neutral

Macrohabitat			
Habitat	Burn unit ^a	Off unit ^a	Reference ^a
Grassland	A	A	P
Forest	A	A	A
Wetland	P	P	A
Landscape			
Habitat	Burn unit ^a	Off unit ^a	Reference ^a
Grassland	A	A	P
Forest	A	A	A
Wetland	P	P	A

^a A “P” indicates significantly more of the habitat was used than available (*i.e.*, selection for the habitat). An “A” indicates significantly less habitat was used than was available (*i.e.*, avoidance)

same site preferred wetlands and avoided grasslands and forests; snakes at the reference site preferred grasslands and avoided forests and wetlands (Table 3).

MICROHABITAT ANALYSIS

The least correlated variables retained for multivariate analysis were surface temperature (*ts*), surface light intensity (*ls*), relative humidity on the surface (*hs*), litter depth (*ld*), vegetation covering the surface (*sv*), average vegetation height (*he*), distance to nearest brush (*db*), distance to water (*dw*), and distance to overstory tree (*dos*) (Table 1).

For the microhabitat analysis of snakes on the burn unit, the top model selected by AIC_c to best explain the differences between the snake locations and the random points contained *ts*, *ls*, *dw* and *dos* (Table 4). Competing models contained the following additional variables: *sv* and *he*. Of the variables present in these models, *ts* and *dw* were the significant variables (Wald χ^2 $P \leq 0.05$) and had relative importance values of 1.0.

The top model for snakes off the burn unit, at the same site contained the variables *ts*, *ld* and *dw* (Table 4). The top competing models also contained *ls* and *db*. Of the variables present in the top models, *ld*, *ls* and *dw* were significant (Wald χ^2 $P \leq 0.05$) with *dw* having the highest relative importance (1.0).

The top model for snakes at the reference site contained the variables *ls*, *he*, *db* and *dw* (Table 4). Supporting models contained *ts*, *sv*, *dos*, *hs* and *ld*. None of the variables were significant (Wald χ^2 $P \geq 0.05$), but *ls*, *db*, and *dw* had relative importance values of 1.0. The variables *sv*, *dos*, and *he* had similarly high importance values (0.84, 0.84, and 0.92, respectively).

DISCUSSION

Our results showed direct effects from prescribed fires can be a significant source of mortality in massasaugas. However, massasaugas in our study did not appear to alter daily movement, home range sizes, and habitat use as a result of the fire. Massasaugas within each of our experimental units selected macro- and microhabitat characteristics that favor thermoregulation (surface temperature, light intensity, surface vegetation, etc.).

TABLE 4.—Treatment unit, variables, Akiake’s Information Criterion corrected for small sample sizes (AIC_c), difference of AIC_c between the model with the lowest AIC_c (ΔAIC_c), model weights (w_i) and Nagelkerke’s R^2 for the best conditional logistic regression models for environmental data from eastern massasaugas within the treatment units

Unit	Model ^b	AIC_c	ΔAIC_c	w_i	R^2
Burn	$ts + ls + dw + dos$	29.089	0.000	0.243	0.776
	$ts + sv + he + dw$	29.157	0.068	0.235	0.775
	$ts + ls + dw$	29.177	0.088	0.233	0.739
	$ts + dw + dos$	29.790	0.701	0.171	0.738
	$ts + sv + dw + dos$	30.553	1.464	0.117	0.754
Non burn	$ts + ld + dw$	31.512	0.000	0.299	0.746
	$ls + ld + dw$	31.918	0.406	0.244	0.741
	$ls + db + dw$	32.717	1.205	0.164	0.730
	$ts + ls + ld + dw$	32.850	1.338	0.153	0.761
	$ts + ld + db + dw$	33.050	1.538	0.139	0.768
Reference	$ls + sv + he + db + dw + dos$	19.558	0.000	0.525	0.873
	$ls + ld_{sv} + he + db + dw + dos$	21.917	2.359	0.162	0.872
	$ls + hs + sv + he + db + dw + dos$	22.076	2.518	0.149	0.957
	$ls + he + db + dw$	23.253	3.694	0.083	0.960
	$ts + ls + db + dw$	23.298	3.739	0.081	0.962

^b ts = surface temperature, ls = surface light intensity, dw = distance to water, dos = distance to overstory tree, sv = vegetation covering the surface, he = average vegetation height, ls = surface light intensity, ld = litter depth, db = distance to brush, hs = surface humidity

The fire data gathered was representative of a prescribed burn typically carried out by TNC in a wetland habitat (J. McGowan-Stinski, Michigan Chapter of the Nature Conservancy, pers. observ.). Data loggers revealed that refugia provided adequate protection from and kept temperatures below critical thermal maximum, approximately 40 C. Critical thermal maximum can be lethal because of possible cardio-respiratory stress, acid-base imbalance, and disruption of protein and enzyme function (Lillywhite, 1987). The effectiveness of these refugia is further supported by the survival of the snake that was in the fire when it switched from a backing to a flanking fire. Most studies that look at burn mortality fail to take into account those animals that sought shelter underground and may have perished there. Smith *et al.* (2001) reported many rattlesnakes in their study fled underground where mortality is often impossible to determine. Inhalation of hot or toxic gasses produced by the fire has been suggested as a source of mortality for snakes that have fled underground (Durbian, 2006). The three snakes in our study that survived the burn did so by seeking refuge underground and appeared unaffected by hot or toxic gasses even with a fire that had a low rate of spread and long residence time (0.024 m/sec). In the case of the wetland habitats in our study, refugia appear to be abundant enough to provide snakes with ample protection during prescribed fires, should they use them. Prescribed fires in plant communities where refugia may be less abundant, such as upland prairies, may cause more direct mortality than in wetland habitats.

The responses of snakes during the fire and the resulting mortality are similar to what was observed by Durbian (2006). While both of our studies consist of relatively small sample sizes, when the observed mortality is extrapolated to the whole population, the sustainability of massasauga populations in areas subjected to prescribed burns becomes an issue. Since

TABLE 5.—Daily movement and home ranges for massasaugas across their range (1 - Weatherhead and Prior, 1992; 2 - Reinert and Kordich, 1982; 3 - Johnson, 2000; 4 - King, 1997; 5-9 - Durbian *et al.*, 2008; 10 - Marshall *et al.*, 2006; 11 - Moore and Gillingham, 2006; 12 - Bissell, 2006)

Location	Distance moved m/d	100% MCP (ha)
1. Bruce Peninsula, Ontario	56.0	25.0
2. W. Pennsylvania	9.1	1.0
3. Cicero Swamp, NY	19.5	26.2
4. Wisconsin	100.5	21.2
5. Monroe, Co., WI	—	2.4
6. Juneau, Co., WI	—	135.8
7. Pershing State Park, MO	—	11.9
8. Swan Lake National Wildlife Refuge, MO	—	7.4
9. Squaw Creek, MO (2008)	—	17.1
10. N.E. Indiana	10.5	4.0
11. S.E. Michigan	6.9	1.3
12. S.W. Michigan	11.8	2.5

mortality of a few adults and juveniles can lead to eventual population declines (Seigel and Sheil, 1999), prescribed fires, when added to other sources of mortality, could potentially have profound impacts on remaining populations. Population demographics, especially density estimates, are unknown for many of the extant populations, of which many are considered small and fragmented (Johnson *et al.*, 2000). It is therefore important to minimize management-related mortality (Durbian, 2006). In terms of habitat and ecosystem management though, the mortality that results from fire is possibly outweighed by the benefits of the increase in habitat heterogeneity and maintenance of required habitat resources (Brennan *et al.*, 1998; Russell *et al.*, 1999). As such, to better understand the appropriateness of prescribed fires as a management tool for massasauga habitat, detailed studies of individual populations and their dynamics are needed. However, it may be more appropriate to err on the side of caution when implementing prescribed fire (*e.g.*, minimize direct mortality) given the imperiled status of this species and the inherent challenges of detailed population studies.

The daily movements for snakes in this study were smaller than what has been reported in other studies (Table 5). Minimum convex polygon home ranges were smaller than other studies (Table 5) but were most similar to those found in southern Michigan (Bissell, 2006; Moore and Gillingham, 2006), northeastern Indiana (Marshall *et al.*, 2006) and Monroe Co., Wisconsin (Durbian *et al.*, 2008). The lack of differences between daily movements and home range sizes could indicate that at least from the aspect of these characteristics, massasaugas do not immediately alter their movements in response to fires and as a result, do not alter their home range sizes. The small home ranges observed for massasaugas at our study sites suggest that the ecological needs regulating distribution and abundance of individuals can be met within a relatively small area (Anderson and Gutzwiller, 2005; Fuller *et al.*, 2005).

Snakes in our study exhibited preference for wetland and grassland habitats at the macrohabitat and landscape scales. Selection of wetland habitats is well documented for this species, as is avoidance of upland and forested areas (Johnson, 2000; Marshall *et al.*, 2006; Moore and Gillingham, 2006; Bailey *et al.*, 2011). Preference for grassland habitat at the reference site was similar to what was reported by Harvey and Weatherhead (2006), although comparisons to their study may be unfair because their sample size was

significantly larger. The preference for grasslands observed in the reference site snakes was driven by the two non gravid females at that site spending the whole active season in an upland prairie adjacent to the wetland.

Microhabitat models suggest massasaugas at the study locations are selecting sites that favor thermoregulation. Snakes on the burn unit tended to prefer areas with lower surface temperatures, a relatively close proximity to water and to a lesser extent, lower surface light intensity, and surface vegetation compared to what was available. Overall, snakes from both of these treatment units selected similar microhabitat characteristics and subtle differences can most likely be attributed to variance among individuals. Snakes at the reference site selected similar microhabitat variables but had more complex models explaining the differences between snake locations and random points. Microhabitat variables promoting thermoregulation and available retreat sites at both sites were similar to those observed by Moore and Gillingham (2006) and Harvey and Weatherhead (2006). Some geographic habitat variation is expected (Johnson, 2000) and differences between our experimental units and study sites could be due to individual selection differences that are exacerbated by the small sample size within each experimental unit. As discussed previously, like macrohabitat usage, microhabitat selection at the reference site may have been driven by the two females that spent the active season in an upland prairie.

Size of the burn is an important aspect contributing to the potential effects of fires on massasaugas. The burn in our study accounted for approximately 11% of the available habitat at the study site (not including an additional 24–40 ha of suitable habitat outside the study site on private property). Burning in smaller patches, as in our study, helps maintain the spatial heterogeneity of the landscape by creating a mosaic of habitats and should therefore minimize the negative side effects of the fire (Renken *et al.*, 2004; Schurbon and Fauth, 2003). In addition burning smaller patches that do not account for the whole study site will likely reduce the impacts of mortality on small populations. Wetland burns are inherently patchy, but in habitats with more uniform fuel, burning during seasons with increased humidity and fuel moisture could create the desired patchiness while maintaining favorable fire effects.

Conducting prescribed burns at different times of year may be beneficial to massasaugas. Many organisms that live in ecosystems supporting fire regimes have evolved in fire-adapted communities and should, themselves, be behaviorally fire-adapted (Means and Campbell, 1981). The results from our study indicate that while prescribed fires are a potential source of mortality, massasaugas do not appear to alter their active season movements in response to fire and may therefore be a behaviorally fire-adapted species. The current burn recommendations (Johnson *et al.*, 2000; Kingsbury, 2002) are designed to limit massasauga mortality by burning during times of year when massasaugas are less likely to be active (*i.e.*, before spring egress from or after fall ingress to overwintering sites). Burns that take place during the growing season are ultimately more effective in controlling for woody encroachment (Streng *et al.*, 1993; Brennan *et al.*, 1998; Sparks *et al.*, 1999; Schurbon and Fauth, 2003). Fires that take place during the lightning season or the growing season are more representative of when fires would naturally occur since winter fires are rare (Means *et al.*, 2004). If massasaugas are behaviorally fire-adapted, burning during natural or historic times may be more beneficial to them from fire-avoidance and habitat management standpoints.

Brush piles in burn units represent a potential source of significant massasauga mortality. Brush piles attract a variety of species, including small mammals (Swihart and Slade, 1985), which in turn may attract snakes. In addition to attracting prey, brush piles function as thermal refugia for snakes (Sperry and Weatherhead, 2010) and as basking sites.

Massasaugas in our study were frequently found in or near brush piles suggesting that accounting for fire-related brush pile mortality should be a component of conservation and management plans. However, if active management is occurring at a site, brush piles may be a one time or rare source of mortality.

Altered prey base following a prescribed fire may also influence massasauga behavior. Erwin and Stasiak (1979) reported a large number of rodent nests had been destroyed during a prescribed burn. Keyser *et al.* (2004) found reduced small mammal abundance in burned versus unburned forests. Elimination of prey through prescribed burns has been implicated as a factor contributing to Louisiana pine snake (*Pituophis melanoleucus ruthveni*) declines (Rudolph and Burgdorf, 1997). Adult massasaugas feed primarily on rodents and tend to favor voles (*Microtus spp.*; Wright, 1941; Seigel, 1986), if these prey become less abundant following a burn, the snakes might not encounter enough prey to build up sufficient fat reserves required for overwintering. We recommend long-term monitoring of snakes and prey following prescribed fires to further address these possible indirect effects.

There are several caveats to consider before making management decisions based on mortality and habitat use observed in this study. Great care should be taken when using the results of this study as a model for massasauga responses outside of wetlands and in different locations throughout their range. It is important to note that the results of this study are specific to a wetland habitat and represent data gathered over a short period of time on a small number of individuals. Massasaugas will likely respond differently to burns in upland sites or even different geographic locations. With the amount of seasonal and geographic variation in habitat use observed in massasaugas it is possible that subsequent seasons would find different movement and habitat use patterns. Furthermore, both of our study sites have had units burned in the past and we could be seeing the effects of previous fires. For instance the Van Buren site has seen a 50% increase in available wetland habitat since it was first burned (J. McGowan-Stinski, pers. observ.). To date a long-term study on massasauga responses to fires is lacking so it is difficult to determine the duration of the effects of habitat alteration by burning on habitat use.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Given the effectiveness and ecological benefits of prescribed fires, it is unlikely that this method of maintaining early successional habitat critical to massasaugas will be abandoned as a management technique. Nor should it be as fire is an important ecological process necessary for many communities. If managers wish to reduce fire-related mortality entirely, then the current burn recommendations for massasauga habitat (Johnson *et al.*, 2000; Kingsbury, 2002) should be adequate. When management goals require the use of burns outside of the recommended season, based on the results of our study, there are several measures that can be taken to minimize the direct impacts on massasaugas. First, burns should be patchy to leave suitable refugia available to the snakes. Second, if at all possible, brush piles should be removed from the burn unit, created outside of designated burn areas, broken up before a burn or be burned during the winter months. Finally, burns should not be conducted within close proximity to overwintering sites during ingress/egress. If it is necessary to conduct burns during these times, we recommend potential overwintering sites be identified prior to a burn and be excluded from the burn unit.

In spite of the evidence presented here suggesting that movements and seasonal activities are not affected by prescribed fires, great care should still be taken when conducting burns during the massasaugas' active season. In light of the potential effects of mortality on long-term survival of massasauga populations, management would be best geared toward reducing mortality and focus on indirect effects secondarily. Burn prescriptions that take

the species' habitat use and activity patterns into account could minimize the impacts fires have on these snakes, but will ultimately be site-dependent.

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