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Spatial Ecology and Multi-Scale Habitat Selection by a Threatened Rattlesnake: The Eastern Massasauga (*Sistrurus catenatus catenatus*)

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Using radio telemetry and geographic information systems (GIS), we investigated movement patterns, home ranges, and habitat selection by Eastern Massasauga rattlesnakes from 2003 to 2004 at an 815-ha fen preserve located in southeastern Michigan, USA. We tested habitat selection on three different scales: microhabitat (by modeling differences in climatic and structural variables between snake-selected sites and random sites, using logistic regression), macrohabitat, and landscape-scale (both by compositional analysis comparing proportions of habitat types used versus proportions available). One hundred percent minimum convex polygon (MCP) home ranges averaged 1.3 ha, and daily movement rates averaged 6.9 m/d. Models predicted that snakes exhibit complex microhabitat selection based on multiple climatic and structural variables including soil temperatures, relative humidity, canopy cover, litter depth, and various vegetation parameters. Snakes actively establish home ranges in the broader landscape by selecting areas with disproportionate quantities of emergent wetland, scrub/shrub wetland, and lowland hardwood habitats. Upland hardwood and all human-altered landscapes were rarely used, even though they were available. This has potentially serious conservation implications. Encroachment of these types of landscapes into areas of suitable habitat could severely restrict movement and home range sizes of these snakes. Potential disruption of movement patterns and gene flow of remaining populations could be extremely detrimental to this species.

MOVEMENT enables many animals to carry out life's requisites. The patterns of spatial movement exhibited may reflect various elements of a species' ecology, such as the animal's needs at a particular point in time or the availability of resources (Gregory et al., 1987). Often, these elements are interwoven and ultimately determine that animal's use of a specific habitat within a broader, heterogeneous environmental landscape.

Use of a habitat presumably results from selection of that habitat, which may be evident on a number of different scales (Wiens, 1989). Johnson (1980) defined habitat selection as simply ''the process of choosing resources.'' Use is considered selective if an animal actively makes choices, thereby using certain habitats disproportionately to their availability (Ford and Burghardt, 1993; Garshelis, 2000). Habitat selection should be especially evident in ectothermic animals like snakes, whose unique temperature requirements, sensory adaptations, and limblessness may require them to select very specific microhabitats and microclimates within their environment.

Early habitat studies of snakes focused mainly on habitat correlations (i.e., the relationship between the distribution of an animal and specific environmental factors; Klopfer, 1969). These studies were rife with misinterpretations and often resulted in incorrect hypotheses regarding the basis of assumed habitat selection (Reinert, 1993). Quantitative studies of patterns of habitat use, which seek to explicate the causes or mechanisms of habitat selection, are becoming increasingly common among a broad range of taxa (Plummer, 1990; Theodoratus and Chiszar, 2000; Weller and Zabel, 2001).

Many snakes actively select certain fragments of their habitats (Burger and Zappalorti, 1988; Theodoratus and Chiszar, 2000; Blouin-Demers and Weatherhead, 2001). Habitat selection may be based on climatic cues such as water or moisture (Whitaker and Shine, 2002), chemical cues from prey or predators (Theodoratus and Chiszar, 2000), or structural cues, such as the physical arrangement of objects in space (Plummer, 1981; Burger and Zappalorti, 1988; McCoy and Bell, 1991). Because the scale(s) at which habitat selection occurs may be unknown or misperceived by the observer, it is important to investigate at multiple scales in order to accurately detect habitat selection (Wiens, 1989).

The goal of this study is to elucidate the movement patterns, potential habitat selection, and home range use by the threatened Eastern Massasauga (*Sistrurus catenatus catenatus*). Due primarily to habitat destruction and conversion, the geographic range of this rattlesnake has been severely restricted, and an estimated 50% of historical populations have been extirpated (Szymanski, 1998). Currently, the Eastern Massasauga is listed as endangered in Canada and has been a candidate species for listing under the U.S. Endangered Species Act since 1999. Individual states throughout the range of the Eastern Massasauga have listed *S. c. catenatus* as either threatened or endangered, with the exception of Michigan where it remains a species of special concern.

Under the broader context of applying new knowledge toward conservation of this species and its critical habitat, we addressed the following questions regarding habitat use by Eastern Massasaugas: What are the home range sizes and movement patterns? Are habitats actively selected? If so, at what scale(s), and based upon what variables?

Materials and Methods

Study site.—Field research was conducted from April to November 2003, and July to November 2004, at Ives Road Fen Preserve (IRFP), Lenawee County, Michigan, USA. This fen system is situated in the southern floodplain of the Raisin River. It lies along a moraine through which the river now flows, forming steep bluffs to the east dominated by shrubs and upland hardwoods. Abundant groundwater seeps flow eastward from these bluffs through the open fen and forested lowland floodplain to empty into the river. Alkaline springs and a mix of Kibbie/Lamson/Conover and Boyer/Fox/Wasepi soils (STATSGO, USDA Soil Conservation Service) support a rare prairie fen community, characterized primarily by sedge meadow vegetation including sedges (*Carex*), rushes (*Juncus, Scirpus*), grasses (*Sporobolus, Diarrhena, Andropogon, Sorghastrum*), goldenrod (*Solidago*), prairie Indian plantain (*Cacalia plantaginea*), cinquefoil (*Potentilla*), and poison sumac (*Toxicodendron vernix*). Interspersed throughout the fen are stands of cattail (*Typha*) monocultures. Calcium and magnesium bicarbonates have precipitated in areas to form marl flats that have resulted in accumulations of saturated peat.

Two hundred sixty-seven ha of this approximately 815-ha site are currently owned and actively managed by the Michigan Chapter of The Nature Conservancy. In the 1940's, ceramic drainage tiles were laid in order to make the site suitable for pasture or hayfield. The resultant hydrological alteration has facilitated the invasion of woody shrub species, most notably Glossy Buckthorn (*Rhamnus frangula*), which now exists in large fragmented patches throughout the site. Other potential threats to the site include invasion by herbaceous exotic flora (especially Purple Loosestrife, *Lythrum salicaria*, and Garlic Mustard, *Alliaria petiolata*), natural succession, fire suppression, and nutrient enrichment from nearby septic systems, a golf course, and croplands. Active management, concurrent with this study, included manual removal of invasive shrubs, herbicide application, annual rotations of prescriptive burning, tile removal, and drainage ditch filling.

Radiotelemetry.—Beginning in April 2003, following emergence from hibernacula, Eastern Massasaugas were located using intensive visual encounter surveys. All opportunistically encountered snakes were marked on-site by injecting subdermal passive integrated transponder (PIT) tags (AVID® MicroChip ID Systems, Folsom, Louisiana, USA). All snakes were weighed, sexed by cloacal probing (Schaefer, 1934), and snout–vent length (SVL) was measured using the squeezebox and cartometer technique (Quinn and Jones, 1974).

Snakes weighing greater than 100 g were implanted with temperature-sensitive radio transmitters (model SB-2, mass = 4–5 g, Holohil Systems Ltd., Carp, Ontario, Canada) following the general surgical methodology of Reinert and Cundall (1982), with the exception that the inhalation anesthetic isoflurane was used in place of halothane. To minimize the negative effects of transmitter implantation, transmitter weight was always <5% of the snake's body weight (Reinert, 1992; Hardy and Greene, 2000). Four females and five males were tracked in 2003, and seven different females were tracked in 2004.

Following a 48-h recovery period, rattlesnakes were returned to the fen, released at their points of initial capture, and relocated every 24–72 h (AVM Instruments LA-12Q receiver [Colfax, California, USA], 3 element Yagi antenna). Relocations were made between 0700–2100 h. Upon relocation, a series of quantitative climatic and structural habitat variables was recorded (Table 1; see James and Shugart, 1970, for specific methodology) and the locations were marked using a handheld GPS unit (Trimble© GeoExplorer 3, Trimble Navigation Limited).

From each snake relocation site, an associated random site at a random distance (4–100 m) and compass heading was located. We recorded the same suite of climatic and structural variables at the random sites and marked them with a GPS. Random sites were sampled no more than 15 min after their associated snake locations were sampled.

Movement and home range.—Location points were post-processed using differential correction (base files from Adrian, Michigan, USA; Trimble© GPS Pathfinder Office 2.80), bringing location pre-

TABLE 1. CLIMATIC AND STRUCTURAL HABITAT VARIABLES MEASURED AT EACH EASTERN MASSASAUGA LOCATION AND ASSOCIATED RANDOM LOCATION AT IRFP IN 2003 AND 2004.

Variable	Description
tfif[a]	Soil temperature (°C) at 15 cm
tfive	Soil temperature (°C) at 5 cm
ts[a]	Temperature (°C) on soil surface
tamb	Shaded air temperature (°C) ~1.5 m above surface
liamb	Light intensity (lux) at 2 m above surface
ls[a]	Surface light intensity (lux)
rhamb	Relative humidity (%) at location 2 m above surface
rhs[a]	Relative humidity (%) on surface
cloud	Cloud cover (estimated rating 1–5)
ws[a]	Wind speed (km/h) 2 m above surface
bp[a]	Barometric pressure (mm Hg)
ld[a]	Litter depth (m)
gc[a]	Ground covered by litter or vegetation (%)
cc[a]	Canopy cover (%)
sv[a]	Vegetation covering site (%)
vh[a]	Maximum vegetation height (m)
wveg	Percent woody vegetation
hveg	Percent herbaceous vegetation
dci	Distance to nearest cover item (m)
dbrush	Distance to nearest brush (m)
dwtr	Distance to nearest water (m)
dwveg	Distance to nearest woody vegetation (≤15 cm diameter)
dost	Distance to nearest over story tree (≥15 cm diameter)

[a] Variables retained for candidate models.

cision to less than 1–3 m, and were subsequently entered into a geographic information system (GIS) as point coverages. Using the snake location points, 100% minimum convex polygon (MCP) home ranges were estimated using the Animal Movement Extension in ArcView© GIS 3.2a (Hooge and Eichenlaub, 1997). Minimum convex polygon home ranges are simply the smallest convex polygons that encompass all known locations for an animal (Mohr, 1947; Jennrich and Turner, 1969). There are many problems associated with MCPs (reviewed in White and Garrott, 1990). However, due to ease of measurement and use for comparison to previous studies, MCP estimates have been included.

Circular point statistics (Batschelet, 1981), which determine the significance of the direction of travel, and other statistics, such as average daily movement rates, were also calculated. Home ranges were estimated for all animals that were tracked for ≥60 d and with ≥15 marked relocations. Five snakes were not used due to depredations ($n = 3$) or insufficient relocations prior to overwintering ($n = 2$). Means are reported as ±1 SE unless otherwise noted.

Microhabitat selection.—Climatic data and structural habitat data were analyzed separately using conditional logistic regression for 1:1 matched pairs (proc logistic, no intercept model in SAS 9.1). This form of regression is preferred over traditional logistic regression, because instead of pooling all snake locations and all random locations, the program compares each snake location with its associated random location (Weller and Zabel, 2001; Compton et al., 2002). The models are therefore interpreted with respect to differences in habitat or climate instead of absolute measured values. This analysis was appropriate for this study because of the temporal (<15 min) and spatial (<100 m) proximity of each snake and associated random location.

To minimize the number of candidate variables, and simplify resultant models, a subset was chosen based on their lack of correlation with one another. Only the six least intercorrelated structural (*ld, sv, vh, gc, cc, dci*) and climatic variables (*tfif, ts, ls, ws, rhs, bp*; with correlation coefficients ≤0.70) were retained for multivariate candidate models (Table 1). All possible combinations of remaining variables were considered as candidate models. Akaike's Information Criterion (AIC), was used to rank models and select the most parsimonious microhabitat model (Burnham and Anderson, 1998; Anderson et al., 2000). The ratio of sample size (n) to estimated parameters (K) was high (n:K ≥ 40:1, $n = 238$, K = 6). Therefore, it was not necessary to use a modified criterion (Anderson and Burnham, 2002). Akaike's Information Criterion values were rescaled to Δ_i values for ease of interpretation and ranking, and Akaike weights (w_i) were calculated to give the approximate probability of each model being the best model in the set (Anderson and Burnham, 2002). The model with the lowest AIC value was considered to be the top model, and all models within two AIC values of the minimum were considered to be supported (Burnham and Anderson, 1998; Compton et al., 2002).

Macrohabitat selection.—A land cover dataset was created for the study site using the most recent available published aerial images (1998 NAPP, USGS, EROS Data Center) for Lenawee County. The aerial images were first scanned into digital format and ortho-rectified. Known locations had previously been marked (using a GPS) in a grid around the study site in order to reduce the margin of error to <3 m. The photos were then interpreted and classified and polygons were created for each land cover type based on the Michigan Resource Information System (MIRIS; Michigan Department of Natural Resources, 1978) mapping standards. Areas where the land cover types had changed since 1998 were field checked and re-interpreted if necessary.

Using this land cover dataset, all rattlesnake location points were classified based on the land cover/habitat type in which they occurred (ArcView GIS, ESRI 1992–2000). Compositional analysis (CA) was used to analyze habitat use versus availability and test for habitat selection at the home range level. This method is preferred because it considers individual animals as the sampling units and not the individual radio locations (Pendleton et al., 1998). Compositional analysis also allows testing for differences between different groups of animals (e.g., sex-age groups, different reproductive condition, etc.), and it yields rankings among habitat types (Aebischer et al., 1993; Garshelis, 2000).

For each snake, the proportions of habitat types used were determined by dividing the number of locations in each habitat type by the total number of locations for that animal. Since no universal definition of available habitat exists (Johnson, 1980; McClean et al., 1998), available habitat, at this scale, was defined as the proportion of each habitat type, classified by the land cover dataset, in each 100% MCP home range. Compositional analysis was performed in SAS 9.1 (bycomp.sas; Ott and Hovey, 1997) to examine data for disproportionate use. Habitat types that were available but not used by the animal (i.e., natural zeros) were replaced with small, non-zero proportions (0.0001) as suggested by Aebischer et al. (1993).

Landscape-level habitat selection.—Compositional analysis was also used to analyze habitat use and test for habitat selection at the level of the study site. An identical methodology as above was used with the exception of differing habitat availability. Available habitat was defined at this scale by buffering each radio location with a circle of radius equal to the greatest length of any 100% MCP home range (475 m). The contours created by these buffers were used to define the habitat available to that animal.

RESULTS

Movement.—From April 2003–October 2004, 16 snakes were tracked (one non-gravid female, ten gravid females, and five males) for durations ranging from 16 to 166 d. The number of snake relocations per individual ranged from three to 48 (mean = 28.6 ± 4.7), and all snakes were tracked from time of initial capture to either depredation or entrance into hibernacula (Table 2). Eastern Massasaugas at IRFP followed the general movement pattern of emergence from hibernacula in early to mid-April, then movement out of buckthorn dominated scrub/shrub or lowland hardwood floodplain to open and slightly higher elevation (approximately 5–15 m) emergent or scrub/shrub wetland during the summer months. Movement back to hibernacula in lowland hardwood floodplain occurred in early to mid-October (Fig. 1). Daily movement averaged 6.87 ± 1.14 m/d and ranged from 0.84–19.3 m/d. Movement rates differed significantly by season among males and females for the periods May–June ($n = 7$, t = 3.70, $P = 0.014$) and July–Aug ($n = 13$, t = 4.06, $P = 0.0019$; Fig. 2). No significant directionality to movements was found for any snake (Mean Rayleigh's Z = 0.88 ± 0.18, $P > 0.05$, $n = 16$).

Home ranges.—Minimum convex polygon home range sizes averaged 1.29 ± 0.37 ha and ranged in size from 0.25–4.52 ha, and length and width averaged 225.73 ± 32.63 m and 74.42 ± 10.89 m, respectively (Fig. 3). Mean MCP home ranges for males and females were 1.64 ± 0.73 ha ($n = 2$) and 1.21 ± 0.44 ha ($n = 9$), respectively (Table 3). Due to small male sample sizes, statistical comparisons between the sexes were not made.

Microhabitat selection.—From the climate analysis, the model that included all six variables ($y = 0.24\ tfif + -0.21\ ts + 0.028\ ws + -0.00019\ ls + 0.0729$

TABLE 2. SNOUT–VENT LENGTH (SVL), SEX, TRACKING DURATION, NUMBER OF RELOCATIONS, AND FATE OF EASTERN MASSASAUGAS TRACKED DURING TWO 180-D ACTIVE SEASONS IN 2003 AND 2004.

Snake ID	SVL (cm)	Sex	Tracking days	Relocations	Fate	Year
A	52	F	166	48	hibernated	2003–2004
B	61	F	105	39	depredated (bird)	2003
C	61	M	34	13	depredated (mammal)	2003
D	56	F	148	44	hibernated	2003
E	50	M	119	40	depredated (bird?)	2003
F	56	M	35	13	depredated (owl)	2003
G	55	M	95	26	hibernated	2003
H	48	F	67	13	hibernated	2003
I	51	M	22	3	hibernated	2003
J	60	F	71	17	hibernated	2004
K	54	F	63	15	hibernated	2004
L	57	F	63	16	hibernated	2004
M	57	F	16	4	depredated (mammal?)	2004
N	55	F	67	15	hibernated	2004
O	45	F	71	17	hibernated	2004
P	56	F	71	17	hibernated	2004

$rhs + 1.843\ bp$) was the top model selected by AIC to best explain the differences between snake and random locations. This model also had the highest probability of being the best model in the set (AIC = 310.9, $w_i = 0.6$). Only *tfif, ts,* and *rhs* were statistically significant in the analysis (Wald χ^2 $P < 0.05$). The next best model contained five climate variables and was supported by AIC ($y = 0.25\ tfif + -0.21\ ts + -0.00018\ ls + 0.070\ rhs + 1.86\ bp$; AIC = 312.4, $w_i = 0.3$), but was approximately half as likely, based on the Akaike weights, to be considered the best model in the set (Table 4).

From the structural analysis, the model with the lowest AIC value was a five variable model ($y = 0.12\ ld + 0.013\ sv + 0.31\ vh + 0.0044\ gc + -0.021\ cc$; AIC = 327.6, $w_i = 0.2$), followed by a four variable model that had an AIC value very close to that of the top model ($y = 0.21\ ld + 0.016\ sv + 0.30\ vh + -0.021\ cc$; AIC = 327.9, $w_i = 0.2$; Table 4). We considered the top four models to be supported (i.e., are all within two AIC values of one another). Only *sv, vh,* and *cc* were statistically significant in the analysis (Wald χ^2 $P < 0.005$).

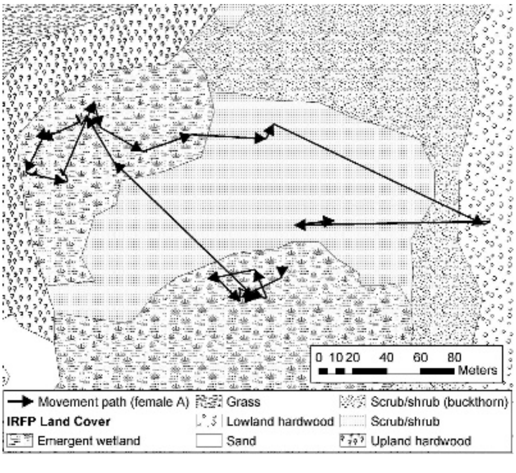

Fig. 1. The movement path of a female Eastern Massasauga at Ives Road Fen Preserve from April 2003 to April 2004. Arrows indicate direction of travel.

Macrohabitat selection.—Snake locations and MCP home range proportions were categorized as one of four different land cover types: upland, lowland, emergent, and scrub/shrub (Table 5). Because upland was not used by any animal and was available only in small proportions to three

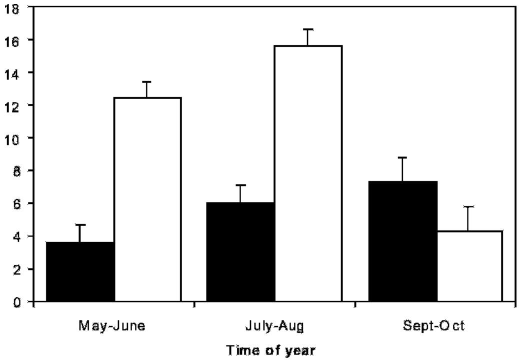

Fig. 2. Mean movement rate (+1 SE) for male (open bars) and female (closed bars) Eastern Massasaugas by time of year.

animals at this scale, it was removed from this analysis.

There was no significant overall non-random habitat use on the scale of radio locations versus MCP home ranges (Wilk's $\Lambda = 0.547$, df = 3, $P = 0.214$ by randomization). A ranking matrix ordered the habitat types in the following sequence of use: lowland > emergent > scrub/shrub.

Landscape-level habitat selection.—Non-random habitat use was significant at this scale (Wilk's $\Lambda = 0.000424$, df = 3, $P < 0.0001$ by randomization). A ranking matrix ordered the habitat types in the following order of use: emergent > scrub/shrub > lowland > agriculture > bare > upland > golf > grass > residential (Table 6). Residential was used significantly less than all other habitat types, and grass was used significantly less than the top five ranked habitats. Emergent was used significantly more than all but scrub/shrub and lowland, and lowland was used significantly more than all except emergent and scrub/shrub.

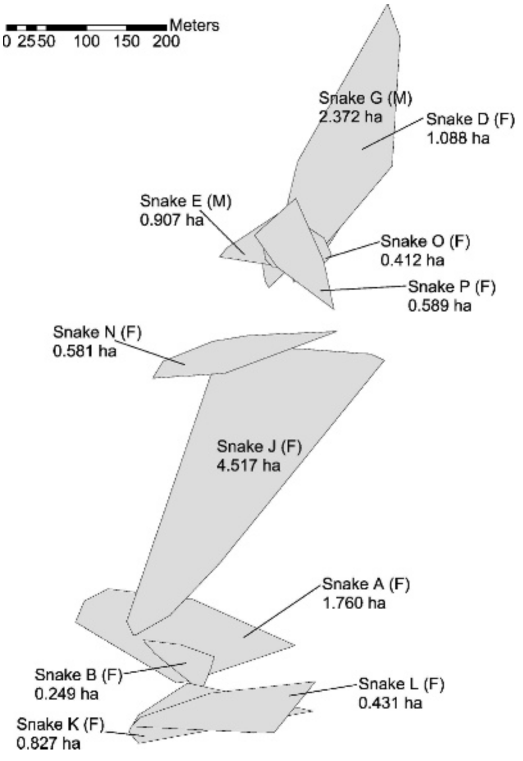

Fig. 3. All 100% minimum convex polygon home ranges for Eastern Massasaugas radiotracked at Ives Road Fen Preserve during 2003 and 2004 including snake ID, sex (M = male, F = female), and size.

TABLE 3. MOVEMENT STATISTICS AND 100% MINIMUM CONVEX POLYGON (MCP) HOME RANGE ESTIMATES FOR ALL SNAKES TRACKED AT IVES ROAD FEN PRESERVE FROM 2003–2004. "–" indicates insufficient number of relocations necessary to calculate home ranges; F = female, M = male.

Snake ID	Sex	Mean movement (m/d)	MCP home range (ha)
A	F	3.43	1.76
B	F	3.10	0.25
C	M	11.20	–
D	F	3.00	1.09
E	M	9.35	0.91
F	M	19.27	–
G	M	5.73	2.37
H	F	2.68	–
I	M	0.84	–
J	F	11.20	4.52
K	F	5.43	0.83
L	F	7.35	0.83
M	F	6.05	–
N	F	9.71	0.58
O	F	4.36	0.41
P	F	7.20	0.59
Total mean		6.87	1.29

DISCUSSION

Movement.—The average daily movement for Eastern Massasaugas at IRFP (6.87 ± 1.14 m/d) was less than all previous studies of these snakes. Weatherhead and Prior (1992) found that snakes at Bruce Penninsula National Park (BPNP), Ontario, averaged 56 m/d, and Johnson (2000) found that snakes moved an average of 19.5 m/d in peatland habitat in New York. The mean daily movement by snakes at IRFP was most similar to that of snakes at two disjunct study sites in Pennsylvania (9.1 m/d; Reinert and Kodrich, 1982). The relatively low average daily movement of snakes at IRFP could be a reflection of the high number of gravid females used in the analysis.

The greater daily distances moved by male Eastern Massasaugas from May to August can likely be attributed to two phenomena. First, because these snakes overwinter singly and are not in close proximity to females upon emergence, intensive mate searching is necessary (Gillingham, 1987). Increasing movement would therefore greatly increase a male's chance of encountering a female (Macartney et al., 1988). Although mating was not observed during this study, mating typically occurs from July–Sept (Keenlyne and Beer, 1973; Reinert, 1981; Johnson, 2000). Secondly, a reduction in movement by gravid females during August–September would further augment this difference.

TABLE 4. FIVE BEST CONDITIONAL LOGISTIC REGRESSION MODELS FOR CLIMATE AND STRUCTURE DATA FROM ALL EASTERN MASSASAUGAS TRACKED AT IVES ROAD FEN PRESERVE FROM 2003–2004. AIC = Akaike's Information Criterion, Δ_I = AIC rank, w_i = Akaike weights, *tfif* = soil temperature at 15 cm, *ts* = surface temperature, *ws* = wind speed, *ls* = surface light intensity, *rhs* = surface relative humidity, *bp* = barometric pressure, *ld* = litter depth, *sv* = surface vegetation, *vh* = vegetation height, *gc* = ground cover, *cc* = canopy cover, *dci* = distance to cover item.

Climate models	AIC	Δ_i	w_i
tfif + ts + ws + ls + rhs + bp	310.877	0.000	0.620
tfif + ts + ls + rhs + bp	312.423	1.546	0.286
tfif + ws + ls + rhs + bp	316.643	5.766	0.035
tfif + ts + ws + rhs + bp	317.383	6.506	0.024
tfif + ls + rhs + bp	318.306	7.429	0.015
Structure models			
ld + sv + vh + gc + cc	327.583	0.000	0.260
ld + sv + vh + cc	327.906	0.323	0.221
ld + sv + vh + gc + cc + dci	328.331	0.748	0.179
sv + vh + gc + cc + dci	329.535	1.952	0.098
sv + vh + cc	329.98	2.397	0.078

Home ranges.—Home ranges at IRFP, like daily movement rates, were much smaller than home ranges of Eastern Massasaugas in two of three previous telemetric studies of these snakes. They were, however, very similar to home range sizes from the third study in western Pennsylvania (Reinert and Kodrich, 1982). There are many possible explanations for the large discrepancies between this and the previous studies. First, because study durations were highly variable, it is possible that increasing durations would result in larger home ranges and a relatively equal number of relocations among these studies would have strengthened comparisons. It has been suggested that MCP home range sizes will increase indefinitely with an increasing number of relocations (White and Garrott, 1990), and too few relocations could result in an underestimation (Stone and Baird, 2002). Since the BPNP study durations were much smaller and home range sizes were more than 20 times greater, there should be no reason to suspect that home range sizes at IRFP are a gross underestimate. Secondly, Johnson (2000) and Weatherhead and Prior (1992) suggested that the reduced home ranges of the Pennsylvania snakes may have been an artifact of reduced movement due to induced thermophily or a simulated meal, because the Pennsylvania snakes were force-fed transmitters (Reinert and Cundall, 1982; Reinert and Kodrich, 1982). This is not the most likely explanation because we surgically implanted transmitters into snakes at IRFP, and home range sizes in this study were comparable to those in Pennsylvania.

The most compelling explanation for the high degree of variability among these studies lies in differing habitat structure and resource availability. Resources are most likely readily available and densest in the open canopied wet meadow and fen habitats of Reinert and Kodrich's (1982)

TABLE 5. LAND COVER TYPES AND DESCRIPTIONS AT IVES ROAD FEN PRESERVE, BASED ON THE MICHIGAN RESOURCE INFORMATION SYSTEM (MIRIS) MAPPING CLASSIFICATION.

Land cover type	Description
Agriculture	Agricultural areas including pasture and cropland (active agriculture)
Grass	Open grassy areas including maintained residential lawns
Emergent	Emergent wetland dominated by sedges, grasses, rushes, reeds, and few cattails
Bare Ground	Bare ground including gravel and sand pits, and open water
Residential	Residential areas including homes and farms
Upland	Upland hardwood dominated by sugar and red maple, elm, beech, birch, red, and white oak
Lowland	Lowland hardwood (highly variable) but typically dominated by black ash, elm, red maple, and cottonwood
Scrub/shrub	Shrub/scrub wetland dominated by native shrubs and low woody plants (including cinquefoil, sumac, dogwood) and non-native shrubs (glossy buckthorn) <5 m tall
Golf	Golf course

TABLE 6. RANKING MATRIX COMPARING PROPORTIONAL HABITAT USE OF MINIMUM CONVEX POLYGON HOME RANGES VERSUS PROPORTION AVAILABLE TO INDIVIDUAL EASTERN MASSASAUGAS IN THE STUDY AREA. Higher rank indicates higher disproportionate use. A triple sign represents significant deviation from random use at $P < 0.05$.

	Habitat type									
Habitat type	Emergent	Scrub/ shrub	Lowland	Agriculture	Bare ground	Upland	Golf	Grass	Residential	
Emergent		+	+	+++	+++	+++	+++	+++	+++	8
Scrub/shrub	-		+	+++	+++	+++	+++	+++	+++	7
Lowland	-	-		+++	+++	+++	+++	+++	+++	6
Agriculture	—	—	—		+++	+	+	+++	+++	5
Bare ground	—	—	—	—		+	+	+++	+++	4
Upland	—	—	—	-	-		+	+	+++	3
Golf	—	—	—	-	-	-		+	+++	2
Grass	—	—	—	—	—	-	-		+++	1
Residential	—	—	—	—	—	—	—	—		0

Pennsylvania sites and IRFP. Crayfish burrows (hibernacula), small mammals, and basking sites are all located in relatively close proximity at IRFP, and snakes were observed feeding, giving birth, and actively thermoregulating in the same general vicinity. Wetland composed only a small portion of the BPNP study site; snakes would therefore have to travel greater distances to get to these vital habitats. In addition, Johnson (2000) stated that small mammals may be limited in the New York peatland.

The high degree of geographic and intrapopulation variability is not unique to Eastern Massasaugas. Macartney et al. (1988) suggested that there is probably no characteristic home range or movement pattern for any snake species. This emphasizes the need for multiple studies of the same species, in different geographic locales, in order to attempt to understand an overall pattern if one truly exists (Seigel, 1986; Weatherhead and Prior, 1992). Management decisions can then be made based on individual knowledge of local populations.

Habitat selection.—Eastern Massasaugas at IRFP clearly exhibit a complex, hierarchical habitat selection process based on different habitat scales (Reinert, 1993). Home ranges are established within the broad landscape by actively selecting areas with wetland habitat composed of emergent vegetation (e.g., bryophytes–*Sphagnum*, sedges–*Carex*, rushes–*Juncus, Scirpus*, grasses–*Sporobolus, Andropogon, Sorghastrum*, goldenrod–*Solidago*, prairie Indian plantain–*Cacalia plantaginea*), scrub/shrub habitat dominated by short, woody vegetation (e.g., cinquefoil–*Potentilla*, poison sumac–*Toxicodendron vernix*) and wet lowland hardwood habitat. The habitat types selected most closely resemble those in the Pennsylvania study (Reinert and Kodrich, 1982), with the exception of a greater preference for lowland hardwood habitat (which likely reflects use based on locations of hibernacula).

Further encroachment of human-altered landscapes (e.g., golf courses, residential areas, roads) could severely limit habitat use, home range sizes, and movement rates of Eastern Massasaugas (Plummer, 1981; Madsen, 1984; Gregory et al., 1987). There are anecdotal accounts of rattlesnakes commonly found on the golf course and crossing roads adjacent to IRFP in the past (R. Hyatt, pers. comm.). Massasaugas were never found, dead or alive, on the road adjacent to IRFP, and telemetered snakes never entered the golf course or adjacent residential areas. This provides some evidence for decreases in movement rates of Massasaugas at IRFP over recent time. These human-altered landscapes could potentially serve as barriers to migration. Parent and Weatherhead (2000) found that Massasaugas decreased movement with increasing exposure to human disturbance. There may be behavioral plasticity of movement in snakes exposed to human disturbance, or selection pressure for decreased movement from increased human-induced mortality on highly mobile animals. Both would result in avoidance of human-altered landscapes, decreased movement, and deflated home ranges (Bonnet et al., 1999).

Microhabitat models indicate that Eastern Massasaugas behaviorally thermoregulate by selecting sites with cooler surface temperatures, warmer sub-surface temperatures, and lower light intensity than are available. High humidity and, to a lesser extent, higher barometric pressure and wind speed, also appear to be important. By selecting these microclimatic conditions, snakes are likely able to avoid temperature extremes and dessication, thereby maintaining normal physiological processes. Sub-surface temperatures may reflect temperatures in retreat burrows (crayfish or small mammal burrows) that are regularly used by these snakes, and temperatures in these burrows may differ substantially from surface temperatures, thus enhancing efficient thermoregulation (Huey, 1982; Webb and Shine, 1998).

Microhabitat selection also appears to be based upon a number of structural variables. During the summer months, snakes are most often selecting open-canopied microhabitats with a high percentage of surface vegetation, a deep litter layer, and ample ground cover. Although snakes predominantly selected sites with taller vegetation (0.5–1.5 m) than was available on average, it is evident that dense stands of shrubs >5 m (e.g., invasive glossy buckthorn) may be avoided during these months.

Conservation and management implications.—Natural succession, or invasion by exotic woody shrubs, may pose significant threats to suitable Massasauga habitat. Prescriptive burning appears to be successful in slowing the rate of succession and controlling invasive flora. However, there has been some burn mortality of Massasaugas at IRFP, and burning off large areas of ground cover could hinder thermoregulation and expose these snakes to increased predation. Prescribed burns should be carried out before emergence in the spring, or on cool days when snakes are unlikely to be above ground (Seigel, 1986; Johnson and Leopold, 1998). Also, hydrological alteration during late fall or winter could severely affect overwintering success of these snakes. Although they may be able to withstand brief periods of flooding (Seigel et al., 1998), exposing them to lethally low temperatures by draining hibernacula could prove fatal.

Since Eastern Massasaugas use different habitat types at different times of the year, it is important to maintain the contiguity of these habitat types. Fragmenting habitats by imposing anthropogenic barriers between, for instance, hibernacula and summer ranges, could severely impact these populations.

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