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MOVEMENT AND MACROHABITAT SELECTION OF THE EASTERN MASSASAUGA IN A FEN HABITAT

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ABSTRACT: The eastern massasauga, *Sistrurus c. catenatus*, is a small rattlesnake threatened with extirpation throughout its range. Massasaugas occur in a variety of habitats and adequate knowledge of their natural history at local scales is essential for effective management. We used radiotelemetry to document patterns of movement and macrohabitat selection of massasaugas in a fen environment, an important, but understudied, habitat. Based on both 100% minimum convex polygons and 95% kernel density, seasonal home ranges of males were larger than those of non gravid females which, in turn, were larger than those of gravid females. Activity center estimations followed the same trend as the seasonal range estimations. Similarly, activity centers (50% kernel density) of males were larger than those of non gravid females which were larger than those of gravid females. Non gravid females and gravid females differed in their mean frequency of daily movement, distance moved per day and total distance moved in a season. Males also differed from gravid females in these three regards, but only differed from non gravid females in distance moved per day. Compositional analysis of both 100% MCPs and 95% kernel densities indicated a preference for emergent wetland vegetation by all individuals; however, wooded areas and meadows were used to a lesser extent.

Key words: Activity patterns; Compositional analysis; Eastern massasauga; Fens; Habitat selection; Kernel density; Movement; Reptile; *Sistrurus*; Statistical power

STUDIES of snake movement patterns and habitat use have benefited from the advancing technology of surgically implantable radio transmitters. Radio telemetry has helped to demonstrate how spatial ecology of snakes can be influenced by factors such as gender (e.g., Weatherhead and Hoysak, 1988), reproductive status (e.g., Graves and Duvall, 1993), and resource distribution (e.g., Roe et al., 2004). Information on how these factors effect spatial ecology is still limited in many taxa and habitat types, hindering our ability to understand how their influence varies both within and across populations.

Ecological differences between male and female snakes often result from divergent selective pressures on body size, from both natural (e.g., Pearson et al., 2002) and sexual selection (Shine, 2001). Sexual size dimorphism (SSD) often leads to differential prey use (e.g., Vincent et al., 2004) which can influence habitat use (Shine, 1986). SSD in the eastern massasauga rattlesnake is largely restricted to tail length differences (e.g., Seigel, 1986); males typically have longer tails to accommodate retraction of the hemipenes

(Klauber, 1997). It is unclear if tail length differences between genders results in any ecological differences. Anecdotal evidence exists that suggests the possibility of SSD in some massasauga populations (B. A. Kingsbury, personal observation).

Gender differences in mating behavior might also influence spatial needs (e.g., Walker, 2000). Rattlesnake mating systems are characterized as prolonged mate search polygyny (Duvall et al., 1992), where males search for relatively sedentary females. The magnitude of differential mating behavior on spatial use might depend on the predictability of (or proximity to) females in the landscape. Widely spaced or randomly dispersed females would force males to traverse larger areas to locate females than would be necessary if their locations were more predictable (Duvall et al., 1992).

Ecological differences between genders may result from reproductive status. Gravid female rattlesnakes often reduce activity (e.g., Ashton and Patton, 2001) and fast during most of gestation (e.g., Keenlyne and Beer, 1973). Gravid females may also utilize different habitats than non gravid females (and males), habitats that promote efficient embryological development (e.g., Graves and Duvall, 1993).

Studies of the eastern massasauga rattlesnake have demonstrated that this species'

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spatial ecology varies geographically and is influenced by gender (King, 1997; Weatherhead and Prior, 1992) and reproductive status (Johnson, 2000; King, 1997; but see Reinert and Kodrich, 1982). We predict male and nongravid female massasaugas in a small isolated wetland will exhibit similar activity patterns and utilize similar habitats. The existence of SSD other than tail length in a massasauga population has not been demonstrated and is unlikely in our population. Also, in a small isolated wetland females should be closer to males, and hence more predictable to locate, reducing mate searching distances. Conversely, we predict that gravid female massasaugas will exhibit reduced activity and will utilize different habitats, regardless of the size of the wetland, in accordance with gestation activities.

We used radiotelemetry to investigate massasauga behavior and ecology in a small fen wetland. Specifically, we examined movement patterns with location data and quantified seasonal range using 95% kernel density (KD) and 100% minimum convex polygons (MCP), as well as activity center (50% KD) characteristics for males, nongravid females, and gravid females. We also quantified macrohabitat use using compositional analysis (Aebischer et al., 1993). To our knowledge, compositional analysis has never been performed with both MCP and KD in the same study. Such data could provide valuable insights into how these two statistical methods might influence interpretation of habitat use. We also address the issue of statistical power analyses in radio telemetry studies.

MATERIALS AND METHODS

Study Animal

The eastern massasauga rattlesnake (*Sistrurus c. catenatus*) is a federal candidate for listing as threatened under the Endangered Species Act of 1973 (Johnson et al., 2000), hence the urgency to obtain information on their spatial ecology, particularly in understudied habitats. Massasaugas use a variety of habitats including wet prairies (Seigel, 1986), sedge meadows and peatlands (Johnson, 2000), coniferous forests (Weatherhead and Prior, 1992), and meadows and old fields (Reinert and Kodrich, 1982; Smith, 1961;

Wright, 1941). Massasaugas also inhabit fens (Kingsbury, 1996), which occur in parts of the northeastern United States, the Great Lakes region, and much of Canada. This wetland type is characterized by nutrient and mineral-rich ground water which passes through glacial till and surfaces to create a continuous flow through the peatland (Casebere, 1997). Fen use by massasaugas has received relatively little attention thus far despite the fact fens may support some of the largest populations of massasaugas in parts of their range (e.g., Indiana, Casebere, 1997).

Study Site

Our study site was located in northeastern Indiana and consisted of open water, floating sedge mats (*Carex* spp.) and extensive patches of broad and narrow-leaved cattails (*Typhus* spp.). The study site was subdivided into macrohabitat types, based on major vegetational and hydrological features. The seven macrohabitat types were: Old field, agricultural field left fallow for several years, but currently undergoing prairie restoration efforts; Carex tussock, consists almost entirely of sedge tussocks (*Carex* spp.) and standing water; Cattail, dominated by cattails (*Typha* spp.) with some standing water and floating sedge mats; Shrub/scrub, dominated by *Rhus* spp., *Cornus* spp., with significant stands of *Populus* spp., *Larix* spp., and *Quercus* spp.; Shoreline, consists of a narrow band of habitat along the shore of the kettle lake which is dominated by rushes (*Juncus* spp.) and shrubby cinquefoil (*Potentilla fruticosa*); *Eupatorium* spp./*Solidago* spp., area thought to be previously cultivated, and dominated by these species; and Agriculture, a combination of hay fields, residential property and road-sides.

Radio Telemetry

We captured individuals from their spring emergence in 1999 through the 2002 field season (April through October). We began spring research with systematic searches for aggregations of crayfish burrows or expansions of sphagnum hummocks, both of which are known to support massasauga hibernacula (Johnson, 1995; Kingsbury, 1996; Maple and Orr, 1968; Seigel, 1986). Temperature-sensitive radio transmitters (Model SI-2T, Holohil Systems Inc., Carp, Ontario, 8.6 g,

20 months battery life at 20 C) were implanted intraperitoneally in selected individuals using a modification of the Weatherhead and Anderka (1984) method. We selected our subjects by striving to equalize the sex ratio, while including additional females that were gravid, and minimized transmitter weight to body weight ratios by selecting large adults (>200 g). Glass encapsulated passive integrated transponders (PIT tags, AVID®) were implanted subcutaneously in all captured individuals just anterior and lateral to the cloacal opening to facilitate permanent identification.

All individuals were relocated three times per week, on average, using a Telonics TR-4 or TR-3 receiver and hand-held "H" antennas (Telonics Inc., Mesa, Arizona). Telemetry locations were plotted by triangulation to known points, angle and distance to a known point, or geographical positioning system (GPS). GPS was available only late in 2000 and for most of 2001 and 2002. Because of the variability in the error of estimated position by the GPS, it was generally used to estimate a single location, which could then be used as a reference for subsequent movements. In rare instances dense undergrowth, and/or canopy cover limited satellite signal receiving capabilities; in these cases used a short series of angles and distances to known points to estimate animal location.

Regardless of the position-collection method used, our objective was to obtain universal transverse mercator (UTM) coordinates, which we then plotted on a geographically referenced aerial photograph of the study site with the aid of the Arc View (ESRI Inc.) geographical information system (GIS) application. These points were then used to estimate the habitat use of individuals in this population.

Spatial Ecology

Seasonal ranges and activity centers.—Seasonal range is defined as the area of the study site used by an individual during the activity season. Two methods were used to characterize seasonal range. The 100% minimum convex polygon (MCP) method describes the area used by enclosing all observations within a polygon, with no concavities in its form (Jennrich and Turner, 1969). We also calculated seasonal range using 95% isopleth kernel density (KD)

estimates (Worton, 1989). The KD method is a nonparametric estimator of an animal's home range and is constructed using a probabilistic distribution of spatial use (Worton, 1989). We used the fixed kernel method and least squares cross-validation to select the smoothing parameter (h) to reduce bias in area estimates (Seaman and Powell, 1996). Despite increased popularity of the KD approach to delineate seasonal ranges, it is seldom performed in conjunction with older methods (e.g., MCP). Because many methods (if not all) of estimating area usage have limitations, we calculated two seasonal range estimators (Harris et al., 1990).

Activity centers are simply those areas of the seasonal range where individuals concentrate use. Activity centers are not necessarily singular and central in nature, and may thus be separated by extensive, rarely visited areas. We used 50% isopleth probabilities (50% KD) for delineation of activity centers (e.g., Secor, 1994; Tiebout and Cary, 1987).

We estimated spatial movements only for animals tracked at least 70 days within a season. For individuals tracked over multiple seasons, we randomly selected a single year to include in spatial analyses to avoid pseudoreplication. All seasonal ranges, activity centers, and movement parameters were estimated from the Animal Movements extension within Arc View (ESRI Inc.). All statistical procedures were performed using SPSS (v11.0, Claritus Inc. 2001). Area estimations for MCPs, 95% and 50% KD were tested for normality using Kolmogorov-Smirnov tests. Homoscedasticity was evaluated using Levene's tests and residual plots. We employed General Linear Models (ANOVA) to evaluate seasonal range and activity center areas among the three categories of study animals. Tukey's honestly significant difference (HSD) post hoc tests provided pair-wise comparisons. Initially, year was a factor in all seasonal range and activity center ANOVA models; however, it was non-significant in all cases and hence eliminated (all $F > 0.9$, all $P > 0.09$). Multi-nodal activity centers were common and we used a Fisher's Exact Test to compare numbers of activity centers among snake categories. Number of activity centers for each individual was categorically defined for analysis as one activity center or two or more. MCP, KD, 50% KD,

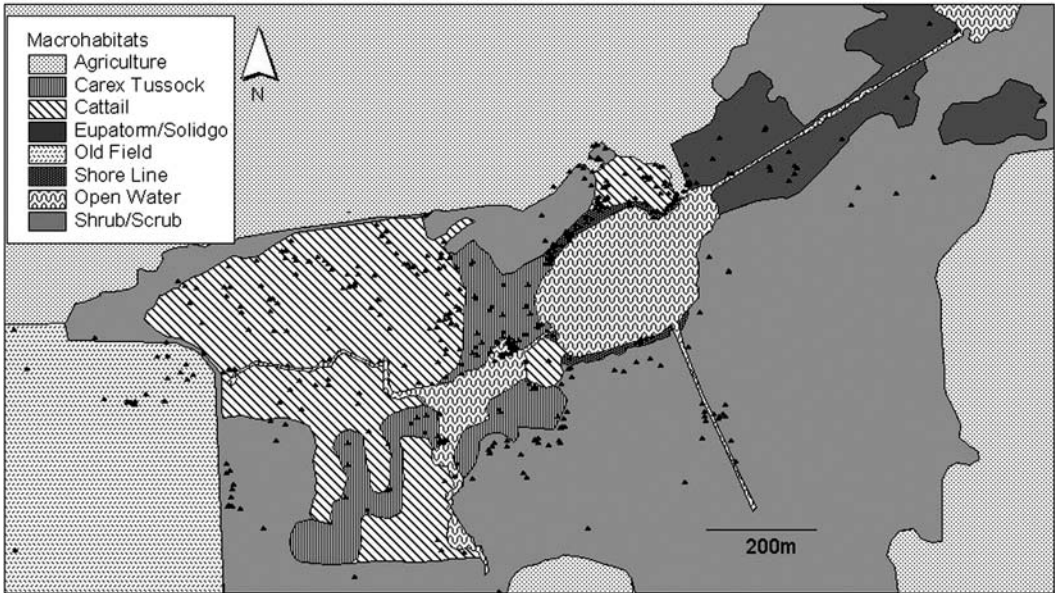


FIG. 1.—Macrohabitat composition of Cline Fen. Black triangles represent all snake locations across all four years of the study. A single triangle may represent more than one location if an individual did not move between successive sightings. 381 total triangles; 2.6% agriculture, 6.6% old field, 7.3% *Eupatorium/Solidago*, 15.5% sedge tussocks, 16.5% shoreline, 21.8% shrub/scrub, 29.7% cattails. See text for more complete description of habitat.

distance moved per day, and total distance moved per season were \log_{10} transformed to meet normality and homoscedasticity assumptions of ANOVA. Alpha equaled 0.05.

Movement parameters.—We characterized individual movements in several ways. Mean frequency of movement equaled the number of successive relocations exceeding 5 m. This distance was selected to distinguish between smaller, local adjustments in position, from larger scale shifts to new areas. Movement per day (m) is the total distance traversed divided by the total number of days tracked. Range length (m) is the distance measured between the two most distant location points within the seasonal range, and total distance moved (m) is the sum of all successive movements. Movements per unit time are likely underestimates of actual distances traveled, but provide relative indices. We analyzed movement patterns using GLM and Tukey's HSD. Movement patterns did not differ across years and were pooled for analyses ($F_{12,32} = 2.02$, $P = 0.06$). Repeated measures ANOVA was employed to compare nongravid females and gravid females in their patterns of seasonal movement which were estimated by the

distance (m) moved between successive locations averaged in 10 Julian day increments.

Habitat selection.—We delineated macrohabitat availability by fitting a rectangle around all of the seasonal ranges used at the study site (Fig. 1). Proportions of macrohabitat types available at the site level and at the seasonal range level were quantified with aerial photographs using Arc View (ESRI, Inc.). In addition, extensive ground truthing ensured the accuracy of inferences made about macrohabitat coverage. The available macrohabitat encompassed 84.8 ha (including 4.18 ha of open water). The most abundant macrohabitat type was Shrub/scrub, comprising 36.1% of the study site. The proportions of the other macrohabitat types were as follows: Agriculture (35.7%), Cattail (10.7%), Old field (9.3%), Sedge tussocks (3.5%), *Eupatorium/Solidago* (4.4%), and Shoreline (0.4%) (Fig. 1). The only macrohabitat massasaugas did not use was open water, hence it was excluded from the analyses because it would simply always be ranked last.

We performed compositional analysis (Aebischer et al., 1993) to assess macrohabitat selection because it uses individuals as the

sampling unit instead of pooling radio locations across individuals. Compositional analysis also considers all available habitats simultaneously. Because proportions must sum to one, however, an animal's avoidance of one habitat may seem to indicate a preference for another.

Compositional analysis was conducted at two levels using MCPs and at three levels using KDs. "Seasonal range selection" is a comparison of the composition of seasonal range relative to the composition of the study site, and comparable to Johnson's (1980) second-order selection. This analysis provides information about the choices an animal makes about the area it will utilize in the context of available habitat. "Activity site selection" is an examination of the composition of relocation sites relative to seasonal range composition (Johnson's third-order selection). This analysis provides insights about how an animal positions itself within its seasonal range. Kernel densities allow for an additional level of analysis that fits between Johnson's (1980) second and third-order selection. "Activity center selection" is a comparison of the macrohabitat found within the 50% KD to that available at the study site. Using both MCPs and KDs provides a qualitative comparison of these two approaches in delineating home ranges and activity centers.

Compositional analyses were performed using the Resource Selection program (Leban, 1999). When overall use of macrohabitats was nonrandom ($P < 0.05$), macrohabitats were ranked in order of preference and two-tailed t -tests ($P < 0.05$) were used to determine which rankings differed significantly (after Bonferroni corrections for multiple tests). We used MANOVA to compare the logarithmically transformed differences (which retain linearity, Aitchison, 1989) of the proportions of one macrohabitat (e.g., individual MCP) to another (e.g., study site). MANOVAs indicated no significant effects of year (all $P > 0.11$) or any significant interactions (all $P > 0.12$) in any of the macrohabitat use models.

RESULTS

Spatial Ecology

Emergence from hibernation occurred typically in mid-April but could be as early as late

March. After emergence, massasaugas moved to basking areas within a few meters of their hibernacula and remained there (i.e., within 10–30 m) for approximately a week. During the subsequent two weeks, males and nongravid females migrated 200 m to 600 m away from their hibernacula to habitats where they established activity centers. Gravid females remained near their hibernacula until parturition in late July or early August and then moved to other locations, presumably to forage.

Seasonal range.—Seasonal range estimates ranged from 0.18–15.8 ha (MCP) and from 0.15–24.48 ha (KD). Study animal categories differed in seasonal range area for both MCP and KD ($F_{2,23} = 11.27$, $P < 0.000$; $F_{2,23} = 26.29$, $P < 0.000$, respectively). Male seasonal ranges did not differ from those of nongravid females (MCP and KD, $P = 0.15$); however, the seasonal range sizes (MCP and KD) of both males and nongravid females differed from those of gravid females (all $P < 0.02$). The KD estimates of seasonal range were larger than MCP estimates (two-tailed paired-sample t -test; $t = -2.68$, $df = 25$, $P = 0.013$).

Activity center estimations ranged from 0.04–5.5 ha and varied significantly between categories ($F_{2,15} = 23.22$, $P < 0.001$). Activity center area followed the same trend as the seasonal range estimations. Males had larger activity centers than nongravid females ($P = 0.04$). The incidence of multi-nodal activity centers was unequal among the three categories of snakes. All eight gravid females had only one activity center. In contrast, both males and nongravid females often had multiple activity centers (for males: 3 with 1 activity center, 6 with 2; for females: 3 with 1 activity center, 4 with 2, and 2 with 3). Males and nongravid females did not differ in number of centers (Fisher's Exact Test; $P = 1.00$), but when combined these groups had more activity centers than gravid females (Fisher's Exact Test; $P = 0.002$).

Movement parameters.—The three categories of snakes differed in movement patterns ($\lambda = 0.24$, $F_{8,42} = 5.23$, $P < 0.001$). Males consistently had the largest values for all movement parameters examined; movement parameters of nongravid females were consistently larger than those of gravid females (Table 1).

TABLE 1.—Movement parameter estimates, two estimates of seasonal range area, 100% MCP and 95% KD, and activity center area (50% KD) for male, nongravid female, and gravid female *Sistrurus c. catenatus* tracked continuously for at least 70 days within a season. Mean (SE). Difference in letters indicates statistical significance ($\alpha = 0.05$).

Category	Frequency of movement (%) ¹	Distance moved/day (m)	Range length (m)	Days tracked	Total distance moved (m)	100% MCP (ha)	95% KD (ha)	50% KD (ha)
Males (n = 9)	78.11 (5.18) a	15.13 (1.85) a	417.49 (69.70) a	109.78 (7.13) a	1653.01 (238.93) a	7.32 (1.44) a	12.53 (2.31) a	2.41 (0.55) a
Nongravid females (n = 9)	72.78 (5.85) a	10.11 (1.05) a	317.57 (54.18) a	111.22 (7.14) a	1183.53 (175.16) a	3.36 (0.68) a	5.24 (0.71) a	0.88 (0.22) a
Gravid females (n = 8)	48.38 (5.18) b	6.17 (1.06) b	276.17 (62.72) b	96.25 (6.25) a	636.88 (132.94) b	1.40 (0.51) b	1.03 (0.40) b	0.17 (0.08) b

¹ Index of movement, defined by successive movements >5 m.

Movement varied as a function of time of season (Wilk's Lambda = 0.442, $F_{8,23} = 3.6$, $P = 0.007$), and by snake category (gravid versus nongravid female) (Wilk's Lambda = 0.551, $F_{8,23} = 2.3$, $P = 0.05$). Early in the season, both gravid and nongravid females made large movements to either gestation or foraging sites, respectively. Throughout the middle of the season, gravid females moved significantly less than nongravid females did (Fig. 2). Movement of postpartum females, however, were similar to those of nongravid females (Fig. 2).

Habitat selection.—Proportions of the macrohabitats used within the MCP seasonal ranges were non-random relative to the available macrohabitat ($\lambda = 0.06$, $df = 6$, $\chi^2 = 73.43$, $P < 0.001$). MCP seasonal range selection indicated that Shoreline had significantly greater relative use followed by

Cattail, Sedge tussocks, Shrub/scrub (which was significantly different than *Eupatorium/Solidago*), Old field and Agriculture. MANOVA revealed no significant effects of snake category on the composition of macrohabitat in the seasonal ranges ($\lambda = 0.23$, $F_{12,18} = 1.26$, $P = 0.32$).

Proportions of the macrohabitats within the KD seasonal ranges were also non-random relative to the available macrohabitat ($\lambda = 0.07$, $df = 6$, $\chi^2 = 67.97$, $P < 0.001$). KD seasonal range selection indicated that Shoreline had the greatest relative use followed by Cattail, Sedge tussocks, Shrub/scrub (which was significantly different than Agriculture), *Eupatorium/Solidago*, and Old field. In contrast to the MCP analysis, MANOVA of KD seasonal ranges revealed a significant effect of snake category ($\lambda = 0.13$, $F_{12,18} = 2.74$, $P = 0.03$). Gravid females utilized significantly more Shoreline macrohabitat than either nongravid females ($P = 0.001$) or males ($P = 0.001$).

Composition of relocation sites relative to MCP seasonal range composition was non-random ($\lambda = 0.46$, $df = 6$, $\chi^2 = 20.23$, $P < 0.05$). Old field had greater relative use than *Eupatorium/Solidago* followed by Sedge tussocks, Agriculture, Shoreline, Cattail, and Shrub/scrub; however, there were no statistically significant differences among the rankings.

Composition of relocation sites relative to KD seasonal range composition was non-random ($\lambda = 0.30$, $df = 6$, $\chi^2 = 31.53$, $P < 0.001$). Compositional analysis indicated that *Eupatorium/Solidago* had greater relative use than Shoreline followed by Sedge tussocks,

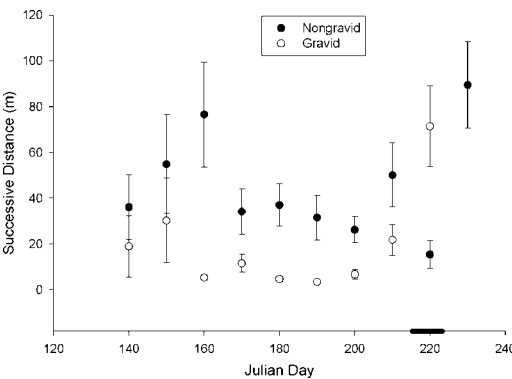


FIG. 2.—The successive distance (m) between locations averaged across 10 Julian day increments (\pm SE) for nongravid (n = 9) and gravid females (n = 8). The black bar on the X-axis represents the period of parturition dates.

Old field, Shrub/scrub, Cattail, and finally Agriculture. MANOVA indicated a significant effect of snake category ($\lambda = 0.07$, $F_{12,18} = 4.10$, $P = 0.004$). Post hoc tests revealed that gravid females use significantly less Cattail than nongravid females ($P = 0.003$) but not less than males ($P = 0.07$), and that males and nongravid females did not differ from each other ($P = 0.25$). In addition, gravid females used marginally less *Eupatorium/Solidago* than nongravid females ($P = 0.046$) but not less than males ($P = 0.84$), and males and nongravid females did not differ ($P = 0.11$).

Compositional analysis of "activity center selection" indicated that proportion of macrohabitats found within activity centers was nonrandom relative to the available macrohabitat ($\lambda = 0.10$, $df = 6$, $\chi^2 = 59.16$, $P < 0.001$). Shoreline had greater relative use than Cattail followed by Sedge tussocks, Shrub/scrub, *Eupatorium/Solidago*, Old field, and Agriculture.

DISCUSSION

Spatial Use and Patterns of Activity

Our results supported the prediction of little difference in the spatial ecology of male and nongravid female massasaugas in a small fen, regardless of the method used to estimate seasonal ranges. The only significant difference in seasonal range area obtained was between gravid females and both males and nongravid females. This result was not influenced by differential tracking periods (Table 1), or a consequence of SSD in the radio-tracked sample (GLM, $F_{1,16} = 0.243$, $P = 0.629$). Reinert and Kodrich (1982) and Johnson (2000) also found no significant difference in seasonal range area between males and nongravid females, but Weatherhead and Prior (1992) and King (1997) did find differences. Weatherhead and Prior (1992) did not distinguish between nongravid and gravid females, however. Pooling females, regardless of their reproductive status, might influence interpretation of gender effects because gravid females are sessile during gestation (Johnson, 2000; King, 1997; this study; but see Reinert and Kodrich, 1982).

A lack of significant difference in the spatial ecology between male and nongravid female massasaugas likely reflects several factors.

First, size dimorphism beyond tail length was not evident in our population (GLM, $F_{1,40} = 0.14$, $P = 0.91$), nor in any other massasauga population (e.g., Seigel, 1986). Given the similarity in the size of males and females they likely feed on the same rodent species, thus occupying the same habitats. Second, sexual differences in mating season activity were negligible. Although females remained relatively stationary during the breeding season (early August) and some males did make large movements (e.g., several hundred meters) during this same time period, these behavioral differences were not evident in the size of their seasonal ranges, rather in estimates of their daily activity (Table 1). Additionally, male-male competition was observed (J. Marshall, personal observation), a situation expected to be rare if female locations are largely unpredictable (Duvall et al., 1992). Finally, small sample sizes may limit statistical power, and thus our ability to detect a difference. Statistical power is a function of the magnitude of the difference between groups (i.e., effect size), difference within groups (i.e., variance), and sample size (Cohen, 1988). With a small effect size (i.e., 0.2), as defined by Cohen (1988), we would need to track more than 50 individuals of each sex to obtain a power of 0.8 (sufficient statistical power rule-of-thumb, 2×1 ANOVA, Cohen, 1988). Even with a medium effect size (i.e., 0.5) we would still need to track ca. 20 individuals of each sex. Clearly, our sample size is insufficient to detect a difference between males and nongravid females when a small to modest effect size is expected. Therefore, we must acknowledge the possibility that a difference exists in male and nongravid female spatial ecology we could not detect.

Movement of nongravid snakes within their seasonal ranges consisted of short duration (i.e., several days) movements to activity centers where they remained for extended periods (i.e., weeks or months). Movements within activity centers were short forays punctuated by periods of little activity, typical of an ambush forager. Conversely, and as we predicted, gravid females were sedentary in behavior. The sedentary behavior of gravid females was further indicated by their use of smaller and fewer activity centers than nongravid females. Gravid female activity largely

was restricted to shifting between basking locations or to and from overnight refugia. Other authors also have observed reduced movement in gravid female pit-vipers (e.g., Ashton and Patton, 2001; Brown et al., 1982; Reinert and Zappalorti, 1988; Secor, 1994; Viitanen, 1967). During gestation, gravid females regulate their body temperature to facilitate embryo development (e.g., Graves and Duvall, 1993; Naulleau, 1979; Prival et al., 2002). Consistent with this interpretation, postpartum females resumed activity levels similar to those of nongravid females. Presumably this increase in movement reflected foraging forays, not mating activity, as no postpartum females were seen being courted or copulating, nor were any females gravid in consecutive seasons.

Although fall monitoring was less frequent than during the summer, ingress (toward hibernacula) movements by all study snakes appeared to be similar to that of egress (away from hibernacula). All study snakes returned relatively quickly to areas within 50 m of their hibernacula, and reused the same general habitat corridor utilized for egress. Individuals returned to these areas by late September and were relatively inactive until their hibernacula entrance by mid October.

Habitat Use

Eastern massasaugas preferentially included emergent wetland vegetation in their seasonal ranges and activity centers with the lake shore (Shoreline) habitat being ranked highest. Compositional analysis of KD seasonal ranges indicated that gravid females utilized more Shoreline habitat than nongravid females. Within days of emergence from hibernation, gravid females moved to locations along the lakeshore, where they established gestation sites until early August. Vegetation along the shore was generally shorter than in other areas of the site but remained adjacent to taller vegetation (J. Marshall, unpublished data). Shorter vegetation may be more desirable for thermoregulation; whereas taller vegetation may provide better cover. Shoreline also had several man-made structures (e.g., old boats and a boat dock) that gravid females utilize for basking, refuge, and parturition. Finally, the Shoreline habitat comprised only a small

amount of the study site (0.4%) and compositional analysis is susceptible to bias when habitat availability is low (Pendleton et al., 1998).

Compositional analysis of activity site (i.e., locations within the seasonal range) indicated that eastern massasaugas, regardless of gender or reproductive condition, generally used some habitats in greater or lesser proportion than their availability within their seasonal ranges. However, habitat rank depended on the method used for delineating seasonal range. For instance, the MCP method ranked Old Field the highest, but the KD method ranked Old Field fourth with *Eupatorium/Solidago* ranked first. The discrepancy between the two methods was not evident when using seasonal range data, however; thus pattern differences detected by the two methods may depend on spatial scale.

Additionally, some differences in KD habitat analysis existed between categories of snakes. Gravid females utilized less Cattail compared to nongravid females, and nongravid females utilized more *Eupatorium/Solidago* habitat compared to gravid females. These differences were not apparent with the MCP method.

The average seasonal range size across all individuals was 4.03 ha, an area one-fifth that of conspecifics that reside in Bruce Peninsula National Park Ontario (25 ha, Weatherhead and Prior, 1992) and at Cicero Swamp New York (26.2 ha, Johnson, 2000). This population of eastern massasaugas was similar to those in Western Pennsylvania (Reinert and Kodrich, 1982); those individuals ranged just over 1.0 ha. Johnson (2000) speculated that smaller seasonal ranges in the Reinert and Kodrich (1982) study reflected at least in part, the methodology (i.e., force-fed transmitters and or short tracking periods). In this study, small seasonal ranges may more likely be a result of the ability of individuals to meet all their life requisites (e.g., foraging, mating etc.) within the fallow field and wet meadow habitats, which are contained in a relatively small area (<100 ha). Within these habitats, Marshall (2002) observed mating activity (e.g., courting and copulation), an abundance of crayfish burrows used for hibernation, gestation and parturition by females, and foraging. Marshall (2002) also noted that *Microtus pennsylvanicus*, the primary prey of massasauga popula-

tions in Wisconsin and Missouri (Keenlyne and Beer, 1973; Seigel, 1986, respectively), were most abundant in the wet meadow habitat. These habitats also were centrally located in the study area eliminating the need to traverse across expanses of inhospitable habitat, which might enlarge otherwise small seasonal ranges.

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