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The Spatial Ecology and Microhabitat Selection of the Pygmy Rattlesnake (*Sistrurus miliarius*) in Southwestern Missouri

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**THE SPATIAL ECOLOGY AND MICROHABITAT SELECTION OF THE
PYGMY RATTLESNAKE (*SISTRURUS MILLARIUS*) IN
SOUTHWESTERN MISSOURI**

A Master's Thesis

Presented to

The Graduate College of

Missouri State University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science, Biology

By

Dylan Wallace Maag

December 2017

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ABSTRACT

Despite a wide distribution throughout the southeastern United States, pygmy rattlesnakes (*Sistrurus miliarius*) have received less research attention than many other rattlesnake species. I captured a total of 33 *S. miliarius* at the Drury-Mincy Conservation Area (DMCA) and retained 14 large individuals (mostly gravid females) for a radio telemetry study. Snakes were primarily captured during evening road driving surveys and were encountered rarely with any other sampling technique. *Sistrurus miliarius* are widespread at DMCA where they were encountered in forest, savanna, and glade habitats. Snakes selected microhabitats with more vegetative cover and tree canopy closure than random sites while avoiding areas with sparse cover. All telemetrically monitored snakes were relatively sedentary and occupied very small (0–2.6 ha) home ranges. Reproductive status of females strongly affected activity with mean home range size of gravid females increasing five-fold following parturition. Births occurred in mid-August with maternal attendance observed for several litters for up to three days.

KEYWORDS: snake, rattlesnake, pigmy, pygmy, *Sistrurus miliarius*, home range, spatial ecology, movements, microhabitat, habitat, selection, mating, telemetry, radio, telemetry

This abstract is approved as to form and content

Brian D. Greene, PhD
Chairperson, Advisory Committee
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In the interest of academic freedom and the principle of free speech, approval of this thesis indicates the format is acceptable and meets the academic criteria for the discipline as determined by the faculty that constitute the thesis committee. The content and views expressed in this thesis are those of the student-scholar and are not endorsed by Missouri State University, its Graduate College, or its employees.

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TABLE OF CONTENTS

Introduction.....	1
Methods.....	5
Study site.....	5
Snake sampling and processing	6
Telemetry	6
Home ranges and movements	8
Microhabitat selection.....	9
Results	14
Snake captures	14
Body size.....	14
Telemetry	17
Movements.....	19
Home ranges	21
Microhabitat selection.....	23
Discussion	29
Movements and home range sizes	29
Habitat selection.....	32
Evidence of r-selected reproduction	34
Further questions.....	35
Literature Cited	36
Appendix—Home Ranges	43

LIST OF TABLES

Table 1. Structural variable definitions and sampling radii used to characterize microhabitat selection	10
Table 2. Summary of movement and home range data for 14 snakes radiotracked	18
Table 3. Top microhabitat models from the paired logistic regression	25
Table 4. Habitat selection results from averaging the top 24 models of the paired multiple logistic regression	27

LIST OF FIGURES

Figure 1. Capture locations of all <i>Sistrurus miliarius</i>	15
Figure 2. Mass vs Snout-Vent Length	16
Figure 3. Comparison of mean (± 1 SE) movement measures for seven gravid <i>Sistrurus miliarius</i> before and after parturition.....	20
Figure 4. Mean MCP sizes (± 1 SE) for seven gravid female <i>Sistrurus miliarius</i> monitored before and after parturition	22
Figure 5. Spearman correlations between home range size and number of days tracked, and snake SVL for 11 radiotracked snakes.....	24

INTRODUCTION

The use of space is a central component of animal ecology and considerable effort has been directed toward understanding sources of variation in home range size. In heterogeneous landscapes, the size of a home range and the time spent in different locations is strongly influenced by the dispersion of key resources such that space use and habitat selection are linked by movement responses (Van Moorter et al., 2016).

However, responses to resources may vary with body size (Schoener, 1968; Perry and Garland, 2002; Tucker et al., 2014), diet (Myerstrud et al., 2001), social factors (Gaulin and FitzGerald, 1988; Jetz et al., 2004), and energetic costs of movement (Slavenko et al., 2016). Despite these important influences, a substantial amount of variation in home range size may still be attributed to individual differences (Borger et al., 2006).

Disentangling a diverse collection of influences can complicate the understanding of space use by animals. The study of spatial patterns and habitat selection is facilitated in organisms such as snakes for which resource needs are easily identified and confounding social influences are mostly lacking (Gregory et al., 1987).

Spatial patterns and habitat selection of snakes are primarily explained by four key resource influences: prey availability, access to hibernacula, the thermal environment, and the distribution of mates. In some temperate environments, spatial segregation of hibernacula and foraging habitats can induce significant seasonal migrations (e.g. Gregory and Stewart, 1975). Snakes may also track prey densities across landscapes due to seasonal changes in prey distribution (e.g. Madsen and Shine, 1996) or exhibit numerical responses to discrete habitat patches with high prey densities

(Wittenberg, 2012). In cooler environments, gravid females often select discrete thermally favorable microhabitats that are spatially distinct from those used by males and non-gravid females (Blouin-Demers and Weatherhead, 2001; Crane and Greene, 2008). Adult males of many species exhibit consistently larger seasonal home range sizes and rates of movement than females as a consequence of searching for mates (Roth, 2005; Smith et al., 2009).

Radio telemetry has facilitated the growing body of literature on ecology and conservation of rattlesnakes (Beaman and Hayes, 2008) and has contributed to their characterization as model organisms (Beaupre and Duvall, 1998). In general, rattlesnakes are ambush foraging strategists with low energetic demands that typically exhibit low activity levels and reduced home range sizes compared to active foraging snakes (e.g. Secor, 1995). Rattlesnake studies have elucidated causes of movement patterns, including how prey distribution influences migration to foraging habitats (Duvall et al., 1990), the influence of the thermal environment on habitat selection by gravid females (Graves and Duvall, 1993; Harvey and Weatherhead, 2011), and the relationship between search patterns and mating success for males (Duvall and Schuett, 1997). Telemetry studies also have facilitated the acquisition of detailed quantitative information on foraging behavior and predator-prey interactions (Reinert et al., 1984; Clark, 2005; 2006a; b) and trailing behavior of neonates (Cobb et al., 2005).

The pygmy rattlesnake, *Sistrurus miliarius*, is a very small crotalid that inhabits coastal plains regions of the southeastern United States from North Carolina to eastern Texas. Its range extends northward into eastern Oklahoma and the Ozark Plateau of southern Missouri, which represents the northernmost range limit. *Sistrurus miliarius*

exhibit a fast life history relative to other crotalids, with attainment of sexual maturity estimated at 2–3 years (Messenger, 2010). In Florida, where *S. miliarius* is active all year (May et al., 1996), some females reproduce annually and have consistent patterns of reproductive life history traits (Farrell et al., 1995; Farrell et al., 2009). Parturition occurs mainly in August (Fleet and Kroll, 1978; Farrell et al., 1995; Messenger, 2010) and females often exhibit maternal attendance of their litters (Greene et al., 2002). Mating has been reported both in spring (Palmer and Braswell, 1995) and late summer or early fall (Montgomery and Schuett, 1989; May et al., 1996; Messenger, 2010). Information on spatial movement patterns of *S. miliarius* is limited to locality data from a mark-recapture study (Hudnall, 1979) and preliminary movement data from four telemetrically monitored snakes (Holder, 1988). *Sistrurus miliarius* reportedly occupy a diversity of habitat types including forests, xeric uplands, glades, and floodplains (Trauth et al., 2004; Gibbons and Dorcas, 2005) however, no quantitative assessment of habitat selection has ever been attempted.

I conducted a single-season radio telemetry study of 14 *S. miliarius* to characterize their movement patterns, home range sizes, and selection of microhabitat in a managed Ozark landscape. Because males are expected to engage in mate searching, I predicted movement frequencies and length, and possibly estimated home range sizes, to be male-biased. Pregnancy imposes physiological constraints on movement and habitat selection of viviparous snakes (Gregory et al., 1987; Reinert, 1993). Therefore, I also expected that gravid snakes would be more sedentary and more selective of available microhabitat features than males and non-gravid females. In addition to addressing spatial and habitat selection objectives, I also summarized incidental observations of

mating and parental care in monitored snakes. I hope that my data will provide some initial insight into the spatial patterns and habitat selection of *S. miliaris*, for which such information does not currently exist, and provide a basis for comparative studies in regions with contrasting environments.

METHODS

Study site

My field research was conducted 15 April through 15 November 2016 at the Drury and Mincy Conservation Areas (DMCA) in southwestern Missouri (494885.2E, 4047377.7N, Zone 15). The DMCA is an 809-ha tract that is owned and managed by the Missouri Department of Conservation (MDC). The Bull Shoals Field Station (BSFS), operated by Missouri State University, facilitates research activities at DMCA and coordinates such activities with MDC management objectives. The study area resides in the Springfield Plateau of the Ozarks which is characterized by a karst landscape with rolling terrain; elevation at DMCA ranges from 201–274 m above sea level. The DMCA experiences hot summers and short cold winters; mean minimum and maximum monthly temperatures range from -18.8–19.8 °C and 15.9–43.6 °C, respectively. Annual precipitation at DMCA averages 1092.2 mm and is distributed relatively evenly throughout the year (Bull Shoals Field Station, 2001–2015 averages).

The DMCA landscape is primarily a mixture of woodland and savanna with scattered limestone/dolomite glades. Two intermittent streams flow into Bull Shoals Reservoir which forms the eastern boundary of DMCA. A system of gravel roads provides access to 51 discrete wildlife food plots and 21 small temporary or permanent ponds. Much of the area is managed by prescribed burning to maintain an open understory and prevent woody plant encroachment onto glades. Upland forested areas are dominated by oaks (*Quercus spp.*) and hickories (*Carya spp.*), while riparian stream corridors contain mainly sycamore (*Platanus occidentalis*), sweetgum (*Liquidambar*

styraciflua), hackberry (*Celtis occidentalis*), and green ash (*Fraxinus pennsylvanica*), with an understory of buttonbush (*Cephalanthus occidentalis*), pawpaw (*Asimina triloba*), and Ohio buckeye (*Aesculus glabra*). Ozark glades are open, xeric habitats with thin soil and exposed bedrock outcrops dominated by warm-season grasses and other prairie herbs (Baskin and Baskin, 2000). A detailed description of plant species found at DMCA has been provided through recent botanical surveys (King et al., 2012).

Snake sampling and processing

Sistrurus miliarius were captured during nighttime road surveys, cover board searches, and fortuitous encounters at DMCA. Collected snakes were individually marked with a PIT tag (Biomark, Boise, ID), sexed by manual eversion of hemipenes, if present, weighed (± 0.1 g), and measured for snout-vent length (SVL) and tail length using a squeeze box (Bertram and Larsen, 2004). I palpated the abdomens of females to detect enlarged ova or developing embryos for determination of reproductive status. All activities involving live animals in this study were approved by the Missouri State University Institutional Animal Care and Use Committee (IACUC) (Protocol #16-018).

Telemetry

Snakes retained for telemetry were transported to Missouri State University for surgical implantation of transmitters (model SB-2, 3.8 g, five-month battery life, Holohil Systems Ltd., Ontario, Canada,). Radio transmitters were coated in a 1:1 ratio of paraffin and beeswax (Lutterschmidt et al. 2012) and surgically implanted into snakes, after being anesthetized with isoflurane, using a composite of standard methods (Reinert and

Cundall, 1982; Hardy and Greene, 1999; 2000). Transmitters were always $\leq 5\%$ (range = 3–5%) of snake body mass. Because of the diminutive size of *S. miliarius* only larger adults were suitable for transmitter implants. Snakes of similar size but lower body condition than other implanted snakes were maintained in captivity and fed one mouse (*Mus musculus*) per week until a 5% transmitter mass threshold was achieved. Captive feeding was short-term (2–5 weeks) for all snakes involved. After surgery, snakes were individually caged and monitored for adverse reactions for 24–48 hours before being released at their original capture locations. To minimize possible behavioral bias associated with surgery, a seven-day post-release acclimation period was observed prior to initial data collection (Goode et al., 2008).

Snakes were tracked two to four times per week between 0800 and 1700 using a hand-held H-antenna and receiver (Telonics, TR-2 or Communications Specialist Inc. R-1000) until the snake entered hibernation, was found deceased, or the transmitter battery life expired. Upon locating a snake, a handheld Global Positioning System (GPS) device (eTrex, vista HCx, Garmin Ltd.) was used to record the Universal Transverse Mercator (UTM) coordinates of the location, at a precision of ± 3 m. Only snakes that were found concealed or in a coiled body posture were considered to have selected a location.

Snakes that appeared to be moving were relocated later the same day and their positions recorded after they assumed a sedentary posture. To minimize monitoring disturbance, snake-selected sites were flagged and dated to facilitate habitat measurements following the snake's departure.

Home ranges and movements

GPS coordinates and associated dates, were used to calculate home range estimates and quantify movement patterns. To facilitate comparisons, I calculated standard movement statistics of mean distance moved per day and mean distance per movement. Mean distance moved per relocation (the average distance traveled between the last known location and the current location of the snake), and frequency of movement (mean number of moves per day) also were calculated. All movements were measured as straight-line distances between successive points. To evaluate the potential influence of GPS measurement error on spatial calculations, I jittered each snake location by three meters 200 times. I then recalculated movement and home range estimates and compared those to estimates derived from original points. Because estimates with and without jittering were essentially identical, all calculations reported are based on raw data.

Spatial studies commonly use multiple home range estimation methods because each has contrasting strengths and weaknesses (Kernohan et al., 2001). The minimum convex polygon (MCP) method defines a home range as the minimum area enclosed by the outermost points occupied by an individual. While this method has important deficiencies (White and Garrott, 1990; Powell, 2000) it is the most commonly used home range estimator due to its historical prominence, simplicity of calculation, and ease of interpretation. Because the MCP does not provide critical information about how the area within a home range is used, many researchers advocate methods based on utilization distributions, especially the kernel estimator (Powell, 2000). However, accuracy of kernel estimates is hindered by low sample sizes (20–50 locations

recommended; Worton, 1987; Seaman et al., 1999) and autocorrelation of animal locations (Swihart and Slade, 1985; Hansteen et al., 1997). Because spatial patterns in my study were both autocorrelated, from repeated use of locations by snakes, and typically had marginal sample sizes for kernel estimation as a consequence of short transmitter battery life, I elected to report only MCP home range estimates with a three meter buffer to account for GPS error.

Microhabitat selection

I analyzed habitat selection at the microhabitat scale using a paired multiple logistic regression. This technique is increasingly favored in microhabitat selection studies because the practice of pairing animal-selected points with random points ensures that each random point is actually available to the animal and due to the frequent non-normality of the data (Press and Wilson, 1978). Once microhabitat variables were recorded at each snake location, a random location was generated by randomly picking a compass bearing and distance using Random Number (Saranomy, v. gpv1.0.10) (Cross and Petersen, 2001; Moore and Gillingham, 2006; Harvey and Weatherhead, 2006; Steen et al., 2010). I constrained the distance of the sampling radius for random points to 1–36m based on the 95% confidence interval of mean distance per move (1–36 m) from four *S. miliarius* previously radio tracked in Southwestern Missouri (Holder, 1988). The lower confidence limit was adjusted to 4 m to account for GPS measurement error (± 3 m).

To characterize the habitat, 22 structural variables were measured, counted, or estimated relative to the flagged location of each snake (Table 1). Each variable was

Table 1. Structural variable definitions and sampling radii used to characterize microhabitat selection of *Sistrurus miliarius* at Drury-Mincy Conservation Areas.

Variable	Definition	Sampling radius (m)
%CANCOV	% canopy closure	1
%USCOV	% understory closure	1
%VEG	% of total vegetation cover	1
%VEGS	%VEG that is 0-0.25 m tall	1
%VEGT	%VEG that is 0.25-1.00 m tall	1
%LOG	%Fallen log cover	1
#WSTEM	Woody stem density	1
HWS	Height of tallest woody stem (cm)	1
DLL	Depth of leaf litter (m)	1
%LEAF	% leaf litter cover	1
%ROCK	% rock cover	1
%WATER	% water coverage	1
%BARE	% Bare Ground coverage	1
DLOG	Distance to log ≥ 7.5 cm in diameter (m)	30
DIALOG	Max diameter of nearest log	30
DIAOS	Diameter at breast height of nearest overstory tree that is ≥ 7.5 cm DBH and > 2.0 m tall	30
DOS	Distance to nearest overstory tree that is ≥ 7.5 cm DBH and > 2.0 m tall	30
DUS	Distance to understory tree (m) that is < 7.5 cm DBH and > 2.0 m tall	30
DSHRUB	Distance to nearest shrub (m) that is < 2.0 m tall	30
MDR	Mean distance to nearest rocks (m) that were > 10.0 cm long	30
LROCK	Mean max length of rocks used in MDR (cm)	30
DRETREAT	Distance to nearest retreat site (m)	30

assigned a sampling radius that reflected its spatial variation at DMCA. Cover variables that would likely influence selection by snakes in close proximity were quantified within a 1 m² plot surrounding the snake location. Distance variables relating snake proximity to large structural features were evaluated within a 30 m radius. Any feature occurring beyond its respective sampling radius at a particular sampling point was considered to be unavailable to the snake at that location and received a value of zero. Identical measurement criteria were applied to data collected at random locations.

Telemetry studies attempt to make inferences from repeated measurements on a limited number of individuals. Under these circumstances it is important to ensure that the contribution of each individual to the data set is balanced, thus preventing an unusual individual from biasing results (Reinert, 1984). Some snakes remained at a single site for extended periods, especially when gravid, or returned to a single site on multiple occasions. While repeated use of sites represents non-independent events, it is likely that snakes re-used some sites disproportionately because of their biological importance (Row and Blouin-Demers, 2006a). I addressed such repeated use of single sites by adjusting the number of times a particular location was represented in the data set based on snake movement frequency. Since it was found that snakes moved on average once every five days, any string of relocations found within one meter of the same location was reduced by randomly deleting observations so that the location was only represented once in any five-day interval. Because snakes, on average, typically left any location after five days, failing to do so constitutes repeated selection of a single site by snakes.

Because the proximity of habitat features to a snake location should logically reflect selection of that feature (Wasko and Sasa, 2010), I adjusted distance variables by

subtracting each value from 30 m. This reformatted the data so that values of 30 mean that the snake was on top of, inside, or underneath the feature, whereas values of 1 would indicate maximal distances; values of 0 would be considered unavailable to the snake. Next, I reduced the number of candidate variables to be used in microhabitat modeling procedures by retaining only those variables with correlations < 0.70 (Harvey and Weatherhead, 2006; Moore and Gillingham, 2006; Martino et al., 2012). This reduced the number of variables from 22 to 13. The remaining variables were then standardized by subtracting each value from its respective mean and dividing by the standard deviation.

I evaluated microhabitat selection using multiple logistic regression. This method has the advantage of pairing each location selected by an animal with an associated spatially-relevant random location such that available habitat can be realistically estimated for each individual (Compton et al., 2002). This procedure generated candidate models with various combinations of variables which were evaluated and ranked with Akaike's Information Criterion (AIC) to determine which models best explained snake microhabitat selection (Burnham and Anderson, 1998).

Statistical analyses were conducted in R (v. 3.3.1). Home range estimates were generated using the MCP function in the *adehabitatHR* package (Calenge, 2006) and the *gBuffer* function to account for the three meters of GPS error. Home range figures were created in ArcGIS 10.5 (ESRI, 2016). Logistic regression was performed and evaluated with AIC by the function *dredge* from the package *MuMin* (Barton, 2016). The function *model.avg* was used on all models within two AIC units of the top model to generate

coefficient point estimates and their standard errors for the variables within those models.

All means are reported ± 1 SE and statistical significance was accepted at $\alpha = 0.05$.

RESULTS

Snake captures

From April to October of 2016, a total of 33 *S. miliarius* were captured ($n = 11$ males; 14 non-gravid females; 8 gravid females) (Figure 1). Most snakes ($n = 24$) were found during nightly two-hour road driving surveys, starting 30 minutes before sundown. Snakes were also found under coverboards ($n = 4$) and by fortuitous encounters ($n = 5$). All captures from coverboards occurred before June whereas road survey captures mainly occurred in summer ($n = 24$, 73% of *S. miliarius*). Encounter frequencies for *S. miliarius* were highest around glades ($n = 13$) and forests ($n = 13$) but also occurred in association within savannas ($n = 7$). Wildlife food plots and riparian corridors were the only habitat types where snakes were never encountered. Although most snakes were collected during road surveys and all home ranges were within 50 m of a roadside, traversal of roads was apparently uncommon; telemetered individuals collectively crossed roads only 13 times during the study.

Body size

The body sizes of 32 *S. miliarius* captured in this study ranged from 171 – 415 mm SVL (mean = 327.8 ± 10.6 mm) and 6.9–111.1 g in mass (mean = 53.8 ± 4.63 g). Body sizes of adult snakes (SVL > 300 mm) were similar between sexes for SVL (females: mean = 357.0 ± 6.48 mm, $n = 14$; males: mean = 363.8 ± 9.85 mm, $n = 8$) and mass (females: mean = 68.4 ± 5.54 g; males: mean = 61.4 ± 6.01 g) (Figure 2). Tail lengths of adult males (mean = 55.6 ± 1.78 mm) were longer, and represented

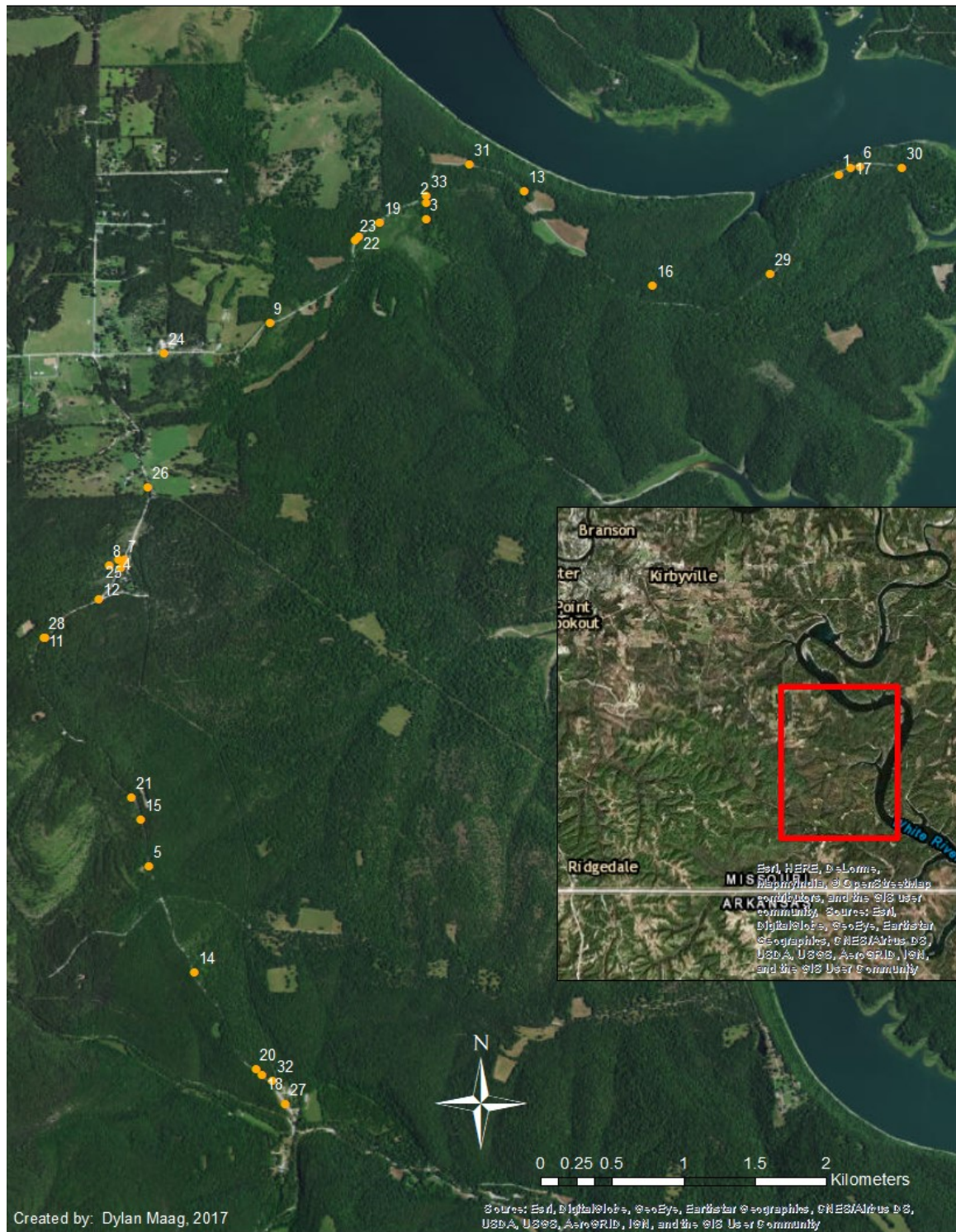


Figure 1. Capture locations of 33 *Sistrurus miliarius* at Drury-Mincy Conservation Areas in 2016.

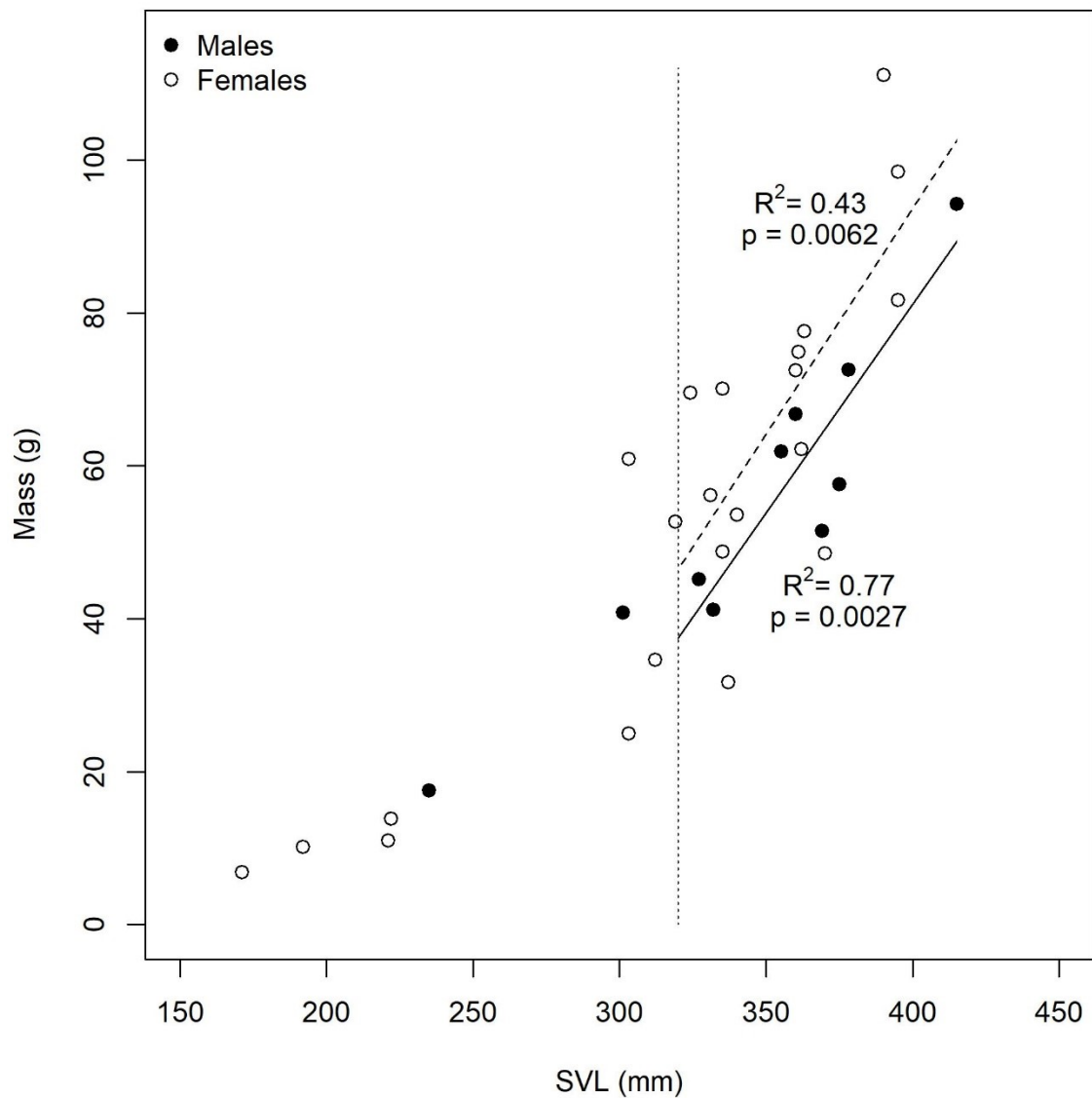


Figure 2. Mass-length relationship for 32 *Sistrurus miliarius* captured at Drury-Mincy Conservation Areas in 2016. Comparative linear regressions provided for adult male ($n = 8$) and female ($n = 14$) snakes. The dotted line indicates the SVL of the smallest gravid female.

significantly greater proportions of SVL (Welch's t-test, $T = 7.28$, $df = 19.8$, $P < 0.0001$), than adult female tail lengths (mean = 43.8 ± 1.31 mm).

Telemetry

Fourteen *S. miliarius* (8 gravid females; 3 non-gravid females; 3 males) were implanted with radio transmitters and tracked during July–October 2016, yielding 397 telemetry locations. Eight snakes died during the study, three from apparent predation and five from undetermined causes. Tracking of three additional snakes ceased due to transmitter battery failure before the end of the activity season. Three snakes were tracked into hibernation. Three of the snakes that died were excluded from analyses because the duration of observation was too brief (< 10 d) to contribute meaningful information. I included data for the remaining five non-surviving snakes which were each tracked for a minimum of 43 days (mean: 76.8 d). Thus, analyses were based on 386 telemetry locations of 11 snakes that were tracked for a mean duration of 96.6 ± 10.9 d (range: 43–150) and were relocated a mean of 40.6 ± 6.30 times (range: 11–77) (Table 2).

Tracking duration varied among snake categories because gravid females tended to be captured earlier in the activity season than males. The overall mean tracking duration for gravid females ($n = 7$) was 115.1 ± 11.6 d, including 55.3 ± 9.04 d before and 57.5 ± 9.96 d after parturition. Tracking during gravid and non-gravid intervals yielded corresponding means of 29.7 ± 5.65 and 14.9 ± 2.22 relocations. Non-gravid females ($n = 2$) were tracked, on average, 47.3 ± 22.0 d, yielding an average of 14.3 ± 5.93 relocations per snake. Lastly, males ($n = 2$) were tracked, on average, 43.0 ± 19.6 d,

Table 2. Summary of movement and home range data for 14 *Sistrurus miliarius* radiotracked at the Drury-Mincy Conservation Areas during 2016. SVLs and masses were taken at initial capture. Means are reported (± 1 SE). Died (U) fates are snakes that died from undetermined causes. Abbreviations: Repro = Reproductive and Reloc = Number of relocations.

Snake I.D.	SVL (mm)	Mass (g)	Repro Status	Track Days	Reloc	\bar{X} /Day (m)	\bar{X} /Move (m)	\bar{X} /Reloc (m)	Freq of Movement (moves/d)	100% MCP (ha)	Fate
1	335	70.1	Gravid	75	53	4.5 (1.85)	16.9 (3.60)	9.1 (2.68)	0.27	0.61	Died (U)
			Non-Gravid	63	16	12.0 (3.85)	50.3 (7.91)	47.1 (7.91)	0.24	1.48	
2	363	77.6	Gravid	75	37	1.8 (0.77)	8.1 (1.63)	3.7 (1.12)	0.23	0.08	Battery failure
			Non-Gravid	75	17	4.9 (2.46)	28.8 (5.92)	22.0 (5.34)	0.17	0.28	
4	395	81.7	Gravid	71	35	3.3 (1.34)	13.1 (2.67)	6.7 (1.94)	0.25	0.42	Battery failure
			Non-Gravid	74	20	13.3 (4.49)	54.6 (9.10)	49.1 (8.86)	0.24	2.63	
7	361	74.9	Gravid	71	36	3.3 (1.37)	11.3 (2.53)	6.6 (1.96)	0.30	0.33	Battery failure
			Non-Gravid	37	7	5.6 (6.54)	52.3 (19.91)	29.9 (16.26)	0.11	0.41	
8	327	45.2	Male	77	22	4.8 (2.01)	24.6 (4.55)	16.8 (3.85)	0.20	0.53	Hibernated
9	395	98.5	Gravid	48	24	0.3 (0.16)	2.3 (0.42)	0.7 (0.23)	0.15	0.01	Depredated (Bird)
			Non-Gravid	18	6	9.7 (11.40)	43.8 (24.19)	29.2 (21.64)	0.22	0.26	
10	335	48.8	Non-Gravid	79	23	6.3 (4.21)	33.3 (9.71)	21.7 (8.02)	0.19	0.95	Depredated (Bird)
12	331	56.2	Gravid	8	3	N/A	N/A	N/A	N/A	N/A	Died (U)
18	324	69.6	Gravid	30	15	0.3 (0.46)	9.4 (2.52)	0.6 (0.67)	0.03	0	Hibernated
			Non-Gravid	76	19	5.6 (3.87)	27.8 (8.61)	23.4 (8.12)	0.20	1.10	
21	360	66.8	Male	9	5	N/A	N/A	N/A	N/A	N/A	Depredated (Mammal)
23	360	72.5	Non-Gravid	5	3	N/A	N/A	N/A	N/A	N/A	Died (U)
24	390	111.1	Gravid	17	9	0.7 (0.36)	2.6 (0.67)	1.5 (0.53)	0.29	0.008	Hibernated
			Non-Gravid	76	19	5.3 (2.42)	25.4 (5.29)	21.5 (4.99)	0.21	1.13	
25	362	62.2	Non-Gravid	58	17	1.3 (0.84)	8.7 (2.15)	4.6 (1.61)	0.16	0.07	Died (U)
27	415	94.3	Male	43	11	15.5 (15.6)	110.8 (42.02)	60.4 (32.54)	0.14	2.20	Died (U)

yielding an average of 12.7 ± 4.98 relocations per snake.

Occasionally telemetrically monitored snakes were observed engaging in reproductive activities. Parturition for all gravid snakes occurred 11–25 August and five of these individuals were observed with their young after parturition for up to three days. Four post-partum females were also observed mating or with one or more males from late August to early October. One non-gravid female (#25), was observed in association with a male in late September. Neither of the male snakes that I tracked were observed interacting with any females.

Movements

Overall, *Sistrurus miliarius* moved infrequently (0.199 ± 0.012 moves/d) and over relatively short distances per move (mean: 31.6 ± 8.27 m), resulting in low mean movement rates (distance/day: 5.95 ± 1.15 m; distance/relocation: 18.7 ± 4.55 m). Reproductive status strongly affected the movements of females. Mean distances moved by gestating females per day (2.06 ± 0.633 m), per movement (9.10 ± 2.01 m), and per relocation (4.13 ± 1.28 m) all increased significantly (Wilcoxon Signed Rank tests, all $V = 28$, $n = 7$, $P = 0.0156$) to 8.09 ± 1.33 m, 40.4 ± 4.80 m, and 31.7 ± 4.42 m after parturition, respectively (Figure 3A, B, and C). However, mean movement frequency (moves/d) was not significantly affected by reproductive status (gravid: 0.217 ± 0.036 ; post-partum: 0.200 ± 0.018 ; Wilcoxon Signed Rank test, $V = 10$, $n = 7$, $P = 0.578$; Figure 3D), indicating that the magnitude of movements, but not the rate, increased after parturition.

For non-gravid females, mean distances moved per day (3.84 ± 2.49 m), per

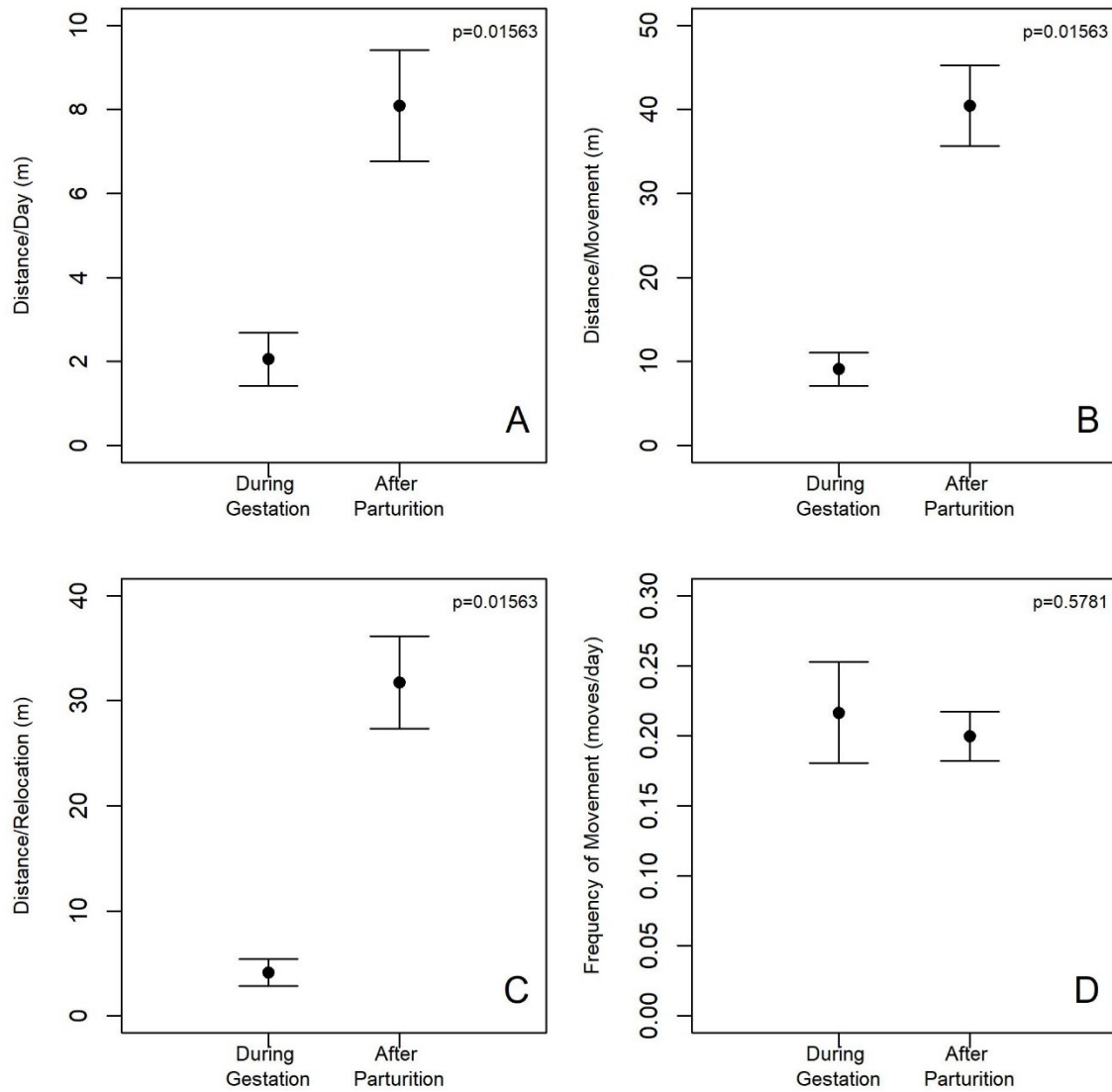


Figure 3. Comparison of mean (± 1 SE) movement measures for seven gravid *Sistrurus miliarius* before and after parturition, including (A) daily distance moved, (B) distance per movement, (C) distance per relocation, and (D) movement frequency. Means were compared with the Wilcoxon-Signed Rank test.

movement (21.0 ± 12.3 m), and per relocation (13.2 ± 8.55 m) were roughly one-third of the corresponding values for males (daily distance: 10.1 ± 5.33 m, movement distance: 67.7 ± 43.1 m, relocation distance: 38.6 ± 21.8 m). However, movement frequencies were similar for both groups (non-gravid female: 0.173 ± 0.017 moves/d, male: 0.167 ± 0.028 moves/d), suggesting that males moved greater distances than non-gravid females but not more often. Because of the small sample sizes ($n = 2$ for both non-gravid females and males) no statistical comparisons were attempted.

There was a shift in the sampling regime from three to four times a week in the summer to one to two times a week during the fall. To assess whether this change in monitoring frequency affected movement estimates, I made paired comparisons of mean relocation distances for six snakes (two gravid females after parturition, two non-gravid females, and two males) tracked during both periods and found no significant difference (Wilcoxon Signed Rank test, $V = 6$, $n = 6$, $P = 0.438$).

Home ranges

Area use was also substantially affected by reproductive status of females (Figure 4). Mean MCPs of gestating snakes (0.20 ± 0.092 ha) increased to 1.04 ± 0.320 ha after giving birth ($n = 7$, Wilcoxon Signed Rank test, $V = 28$, $n = 7$, $P = 0.015$).

Comparatively, the mean home range sizes of non-gravid females and males were 0.50 ± 0.439 ha and 1.36 ± 0.834 ha, respectively. Variation in home range sizes was not explained by snake SVL (Spearman's, $r = 0.16$, $P = 0.63$) or number of days tracked ($r = 0.21$, $P = 0.52$), suggesting that snakes were tracked long enough to achieve stable home

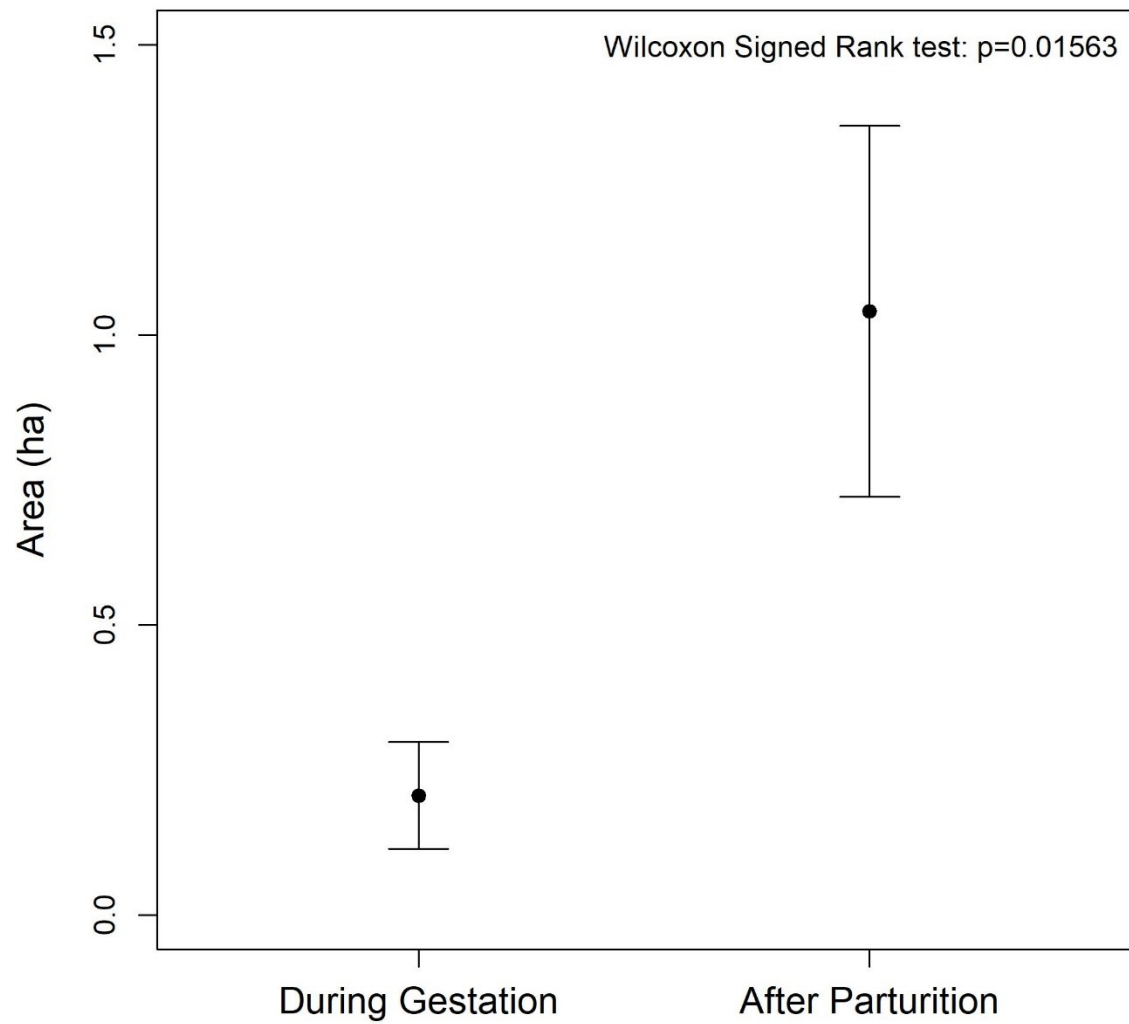


Figure 4. Mean MCP sizes (± 1 SE) for seven gravid female *Sistrurus miliarius* monitored before and after parturition.

range estimates (Figure 5). Home range size estimates for individual snakes are reported in table 2 and graphically depicted in the appendix.

Microhabitat selection

Sistrurus miliarius were typically located on the surface within or surrounded by ground-level vegetation (88.8% of all locations). Less frequently, snakes selected underground refuges (2.8%), or surface locations in association with rocks (6.0%) or logs (2.5%).

I characterized the microhabitat at 262 snake locations (24 male and 238 female) and 262 paired random locations. Of the microhabitat variables measured, nine (%LOG, %ROCK, DLL, %WATER, %VEGS, %VEGT, #WSTEM, HWS, and DOS) were excluded from the logistic regression due to high intercorrelation ($r > 0.70$) with one or more other variables. The remaining 13 variables were used to create a global multiple logistic regression model with only first order interaction terms. From this global model, a total of 8191 other models of different combinations of variables were constructed. This result yielded 23 candidate models within two AIC units of the top model (Table 3).

Of the 13 variables included in the top 24 models, only five (%CANCOV, DIALOG, DRETREAT, DSHRUB, and %LEAF) were contained in all of them. The variables DLOG and %BARE were found in 22 and 20 models, respectively. The remaining six variables were included in 14 or fewer models, suggesting that they were less important in explaining habitat selection by snakes (Table 4). Based on the interpretation of the variables that contributed significantly to top models, *S. miliarius* selected sites with closed canopy cover close to retreat sites, small logs, and shrubs.

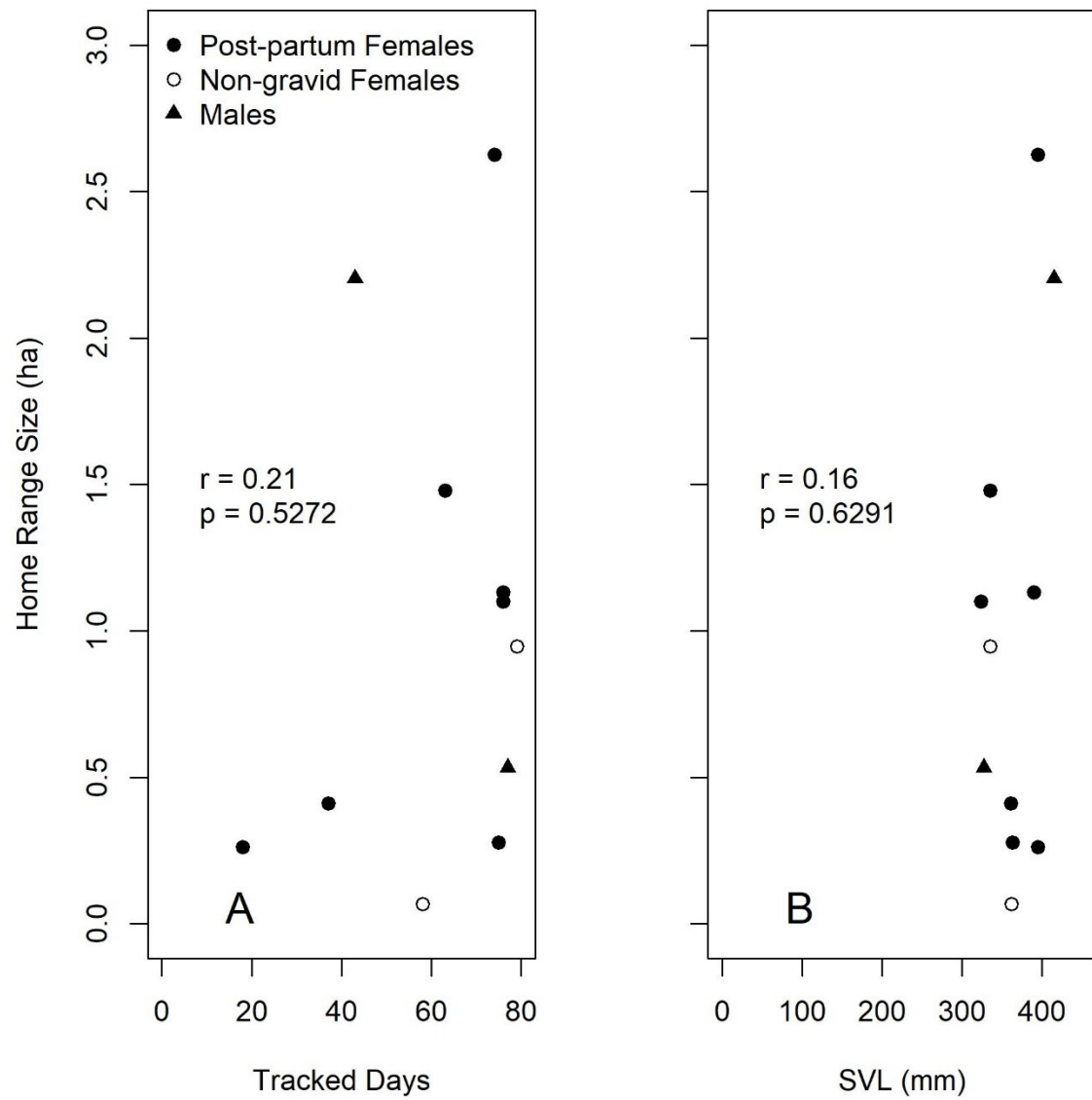


Figure 5. Spearman correlations between home range size and (A) number of days tracked, and (B) snake SVL for 11 *Sistrurus miliarius* tracked at Drury-Mincy Conservation Areas.

Table 3. Top microhabitat models from the paired logistic regression (First 12 models).

#	Model	df	log Likelihood	AIC	ΔAIC	Weight
640	%BARE+%CANCOV+%DIALOG+DIAOS+ DLOG+DRETREAT+DSHRUB+%LEAF	9	-274.22	566.44	0.00	0.0218
632	%BARE+%CANCOV+%DIALOG+DLOG+ DRETREAT+DSHRUB+%LEAF	8	-275.22	566.45	0.01	0.0217
4736	%BARE+%CANCOV+%DIALOG+DIAOS+DLOG+ DRETREAT+DSHRUB+%LEAF+%VEG	10	-273.37	566.73	0.29	0.0189
631	%CANCOV+%DIALOG+DLOG+ DRETREAT+DSHRUB+%LEAF	7	-276.42	566.83	0.39	0.0180
4728	%BARE+%CANCOV+%DIALOG+DLOG+ DRETREAT+DSHRUB+%LEAF+%VEG	9	-274.52	567.03	0.59	0.0163
639	%CANCOV+%DIALOG+DIAOS+ DLOG+DRETREAT+DSHRUB+%LEAF	8	-275.58	567.15	0.71	0.0153
2680	%BARE+%CANCOV+%DIALOG+DLOG+ DRETREAT+DSHRUB+%LEAF+%USCOV	9	-274.81	567.62	1.18	0.0121
2679	%CANCOV+%DIALOG+DLOG+DRETREAT+ DSHRUB+%LEAF+%USCOV	8	-275.90	567.80	1.36	0.0111
2688	%BARE+%CANCOV+%DIALOG+DIAOS+DLOG+ DRETREAT+DSHRUB+%LEAF+%USCOV	10	-273.92	567.84	1.39	0.0109
4976	%BARE+%CANCOV+%DIALOG+DIAOS+ DRETREAT+DSHRUB+DUS+%LEAF+%VEG	10	-273.93	567.85	1.41	0.0108
896	%BARE+%CANCOV+%DIALOG+DIAOS+DLOG+ DRETREAT+DSHRUB+DUS+%LEAF	10	-273.95	567.91	1.46	0.0105
6784	%BARE+%CANCOV+%DIALOG+DIAOS+DLOG+ DRETREAT+DSHRUB+%LEAF+%USCOV+%VEG	11	-273.06	568.11	1.67	0.0095

Table 3 continued. Top microhabitat models from the paired logistic regression (Last 12 models and the cumulative weight of all 24).

#	Model	df	log Likelihood	AIC	ΔAIC	Weight
5760	%BARE+%CANCOV+%DIALOG+DIAOS+DLOG+ DRETREAT+DSHRUB+%LEAF+LROCK+%VEG	11	-273.06	568.12	1.68	0.0094
4992	%BARE+%CANCOV+%DIALOG+DIAOS+DLOG+ DRETREAT+DSHRUB+DUS+%LEAF+%VEG	11	-273.07	568.14	1.70	0.0093
6776	%BARE+%CANCOV+%DIALOG+DLOG+DRETREAT+ DSHRUB+%LEAF+%USCOV+%VEG	10	-274.09	568.17	1.73	0.0092
760	%BARE+%CANCOV+%DIALOG+DLOG+ DRETREAT+DSHRUB+MDR+%LEAF	9	-275.11	568.21	1.77	0.0090
4720	%BARE+%CANCOV+%DIALOG+DIAOS+ DRETREAT+DSHRUB+%LEAF+%VEG	9	-275.11	568.22	1.78	0.0090
4864	%BARE+%CANCOV+%DIALOG+DIAOS+DLOG+ DRETREAT+DSHRUB+MDR+%LEAF+%VEG	11	-273.13	568.26	1.81	0.0088
888	%BARE+%CANCOV+%DIALOG+DLOG+ DRETREAT+DSHRUB+DUS+%LEAF	9	-275.15	568.30	1.85	0.0086
768	%BARE+%CANCOV+%DIALOG+DIAOS+DLOG+ DRETREAT+DSHRUB+MDR+%LEAF	10	-274.16	568.31	1.87	0.0086
2687	%CANCOV+%DIALOG+DIAOS+DLOG+ DRETREAT+DSHRUB+%LEAF+%USCOV	9	-275.17	568.34	1.90	0.0084
1664	%BARE+%CANCOV+%DIALOG+DIAOS+DLOG+ DRETREAT+DSHRUB+%LEAF+LROCK	10	-274.17	568.34	1.90	0.0084
1656	%BARE+%CANCOV+%DIALOG+DLOG+ DRETREAT+DSHRUB+%LEAF+LROCK	9	-275.19	568.37	1.93	0.0083
4856	%BARE+%CANCOV+%DIALOG+DLOG+DRETREAT+ DSHRUB+MDR+%LEAF+%VEG	10	-274.19	568.39	1.94	0.0083
Total weight of top models:						0.2820

Table 4. Habitat selection results from averaging the top 24 models of the paired multiple logistic regression. Bold text signifies important variables based on the second and fifth columns.

Variable	# of Models Including	Estimate (± 1 SE)	z-value	P-value
%CANCOV	24	0.0081 (0.0033)	2.439	0.0147
DIALOG	24	-0.0510 (0. 0157)	3.247	0.0012
DRETREAT	24	0.3776 (0. 0495)	7.618	< 0.0001
DSHRUB	24	0.2911 (0. 1170)	2.482	0.0131
%LEAF	24	-0.0212 (0. 0063)	3.344	0.0008
DLOG	22	0.0666 (0. 0380)	1.75	0.0802
%BARE	20	-0.0128 (0. 0103)	1.238	0.2157
DIAOS	14	0.0071 (0. 0092)	0.775	0.4384
%VEG	10	-0.0032 (0. 0055)	0.581	0.5611
%USCOV	6	-0.0011 (0. 0035)	0.322	0.7475
DUS	4	0.0036 (0. 0148)	0.243	0.8082
MDR	4	-0.0031 (0. 0176)	0.174	0.8619
LROCK	3	-0.0002 (0. 0012)	0.131	0.8958

Snakes also avoided leaf litter and bare earth covering the substrate in favor of sites with vegetation cover.

DISCUSSION

Sistrurus miliarius were encountered in nearly all habitat types at DMCA and appear to be macrohabitat generalists that will use all habitat types that include dense vegetative cover at ground level. Perhaps due to high prey availability and an apparent abundance of suitable hibernacula, movements of *S. miliarius* were infrequent and short, resulting in very small home range estimates relative to those reported in many previous rattlesnake studies. Reproductive status was a substantial source of variation for spatial patterns of females with movements and use of space increasing three-to five-fold following parturition. Fortuitous observations on the timing of mating and parturition of telemetered females were consistent with reports from populations with year-round activity (Farrell et al., 1995).

Movements and home range sizes

Home range estimates for *S. miliarius* at DMCA were on the low end of values reported for other small rattlesnakes. Elucidating possible explanations for home range size values for snakes requires an understanding of the spacing and availability of key resources (Macartney et al., 1988). For *Sistrurus miliarius*, insight into resource influences may be provided by home range studies of the congeneric and similarly-sized massasauga rattlesnake (*S. catenatus*), which has been studied extensively throughout its range and exhibits interpopulational MCP sizes that vary over two orders of magnitude. The high variability in home range size estimates among *S. catenatus* studies appears to be explained by differences in resource distribution and habitat structure. Habitat

configuration was implicated as the main factor explaining differences among five *S. catenatus* populations in Missouri and Wisconsin where mean MCP sizes varied from 2.4 ha, where only a single small basking area was available, to 135.8 ha, where multiple open habitat patches were widely dispersed (Durbian et al., 2008). The mean MCP for a Colorado population of *S. catenatus*, where snakes migrated approximately 2 km between hibernacula and summer foraging habitats, was approximately 42 ha (Wastell and MacKessy, 2011). In contrast, the MCP sizes reported for *S. catenatus* occupying open meadows and fen habitats where prey, hibernacula, and basking sites all occur in close proximity (Moore and Gillingham, 2006), were very similar to values of *S. miliarius* at DMCA. In my study, all *S. miliarius* tracked into the fall hibernated within, or in very close proximity to, their summer home ranges, and experienced high densities of small mammal prey (T. Remick, personal communication).

The sensitivity of the MCP estimator to increasing sample size may provide another explanation for the small home range size estimates observed for *Sistrurus miliarius*. The small body sizes of *S. miliarius* constrained transmitter size and battery life, which ultimately limited the duration of monitoring in my study. Because MCP estimates may progressively increase as spatial locations accumulate (White and Garrott, 1990), failing to monitor individuals for an entire activity season could lead to underestimation of home range sizes (Stone and Baird, 2002). However, if *Sistrurus miliarius* continued to occupy new areas throughout the activity season, home range size should be positively correlated with monitoring duration, which was not the case (Figure 5a). Thus, it appears that snakes were monitored for sufficient time to provide reliable home range estimates.

The MCP estimator has historically been prominent in snake spatial ecology studies. This method has been criticized for its tendency to include areas never used by monitored individuals, resulting in mischaracterization of home range size (Powell, 2000). *Sistrurus miliarius* at DMCA generally stayed within a single habitat type and, with the exception of roads, did not include areas that were unusable by these snakes. Therefore, it appears that the MCP method provided accurate estimates of home range size for telemetered snakes (Row and Blouin-Demers, 2006b).

Populations at the periphery of a species' distribution often exhibit different abundances, life history patterns, and demographic performance (e.g. population growth rate) compared to core populations (Lawton, 1993). Some North American snake populations at northern latitudes have larger home ranges than southern populations of the same species. This pattern has been suggested to result from challenging thermal environments with few hibernacula and wider dispersion of thermally favorable microhabitats in colder climates (DeGregorio et al., 2011; Martino et al., 2012). The *Sistrurus miliarius* population at DMCA lies on the northernmost edge of the species' range in a cooler thermal environment than most other locations in its geographic range. Snakes at this site appear to hibernate within their home ranges and likely experience favorable environmental temperatures of habitats during most of the activity season. Therefore, it is unlikely that range-wide variation in home range size would be influenced by thermal differences between Missouri and more southern locations.

Aspects of the reproductive biology of pit vipers commonly result in sexually distinct spatial patterns. Gravid pit vipers often occupy small home ranges centered on discrete thermally favorable microhabitats during gestation (Gregory et al., 1987; Reinert,

1993), which may result in different spatial patterns between gravid and non-gravid females (Crane and Greene, 2008). However, gestational constraints on movement may vanish after parturition, resulting in strong within-season differences in movements and area use for reproductive females (Privital et al., 2002). All of the aforementioned patterns appear consistent with *S. miliarius* spatial patterns at DMCA. Gravid females exhibited fidelity to specific locations during pregnancy and significantly increased their home range sizes in late summer following parturition. Male crotalids often have the largest home ranges in their respective populations (e.g. Weatherhead and Prior, 1992; Roth 2005; Durbian et al., 2008) as a consequence of mate searching activities (Duvall and Schuett, 1997). However, home range sizes of male *S. miliarius* at DMCA were within the range of the females' home range values. Whether this was a consequence of the small number of males tracked, or limited movement of males, cannot be determined without additional sampling.

Habitat selection

Sistrurus miliarius were found throughout the major habitat types at DMCA, suggesting little selection by snakes at the landscape scale. This result is consistent with the species being described as a habitat generalist that inhabits habitats ranging from upland hardwood areas and sand hills to lowland floodplain environments and marshes (Mount, 1975; Gibbons and Dorcas, 2005). In addition to forests, *S. miliarius* is also associated with glades in the Missouri Ozarks (Johnson, 2000). Despite the apparent lack of habitat selection at the landscape level, multiple logistic regression analysis indicated that snakes were actively selecting microhabitat features. This pattern likely means that

many macrohabitat categories contain suitable microhabitats (Harvey and Weatherhead, 2006). If so, parallel studies of habitat selection would be of great interest to determine if the high diversity of habitats used by *S. miliarius* throughout its range can be explained by snake selection for structural habitat components common to apparently dissimilar environments (Reinert, 1993).

Sistrurus miliarius appear to select microhabitats based on a small number of structural variables. Telemetered snakes were typically located beneath a closed canopy of shrubs in close proximity to a retreat site. These sites had more small logs and branches and less leaf litter cover than available at random sites. Interestingly, rocks were not used more or less frequently than expected by their availability at DMCA, despite suggestions that *S. miliarius* is associated with rocky structure (Johnson, 2000). It is likely that visual detection bias distorts the understanding of habitat selection patterns for cryptic snake species (Wasko and Sasa, 2010), emphasizing the benefit of radio telemetry in informing habitat selection studies (Burger and Zappalorti, 1988).

In contrast to spatial pattern comparisons, there are striking similarities in habitat selection patterns between *S. miliarius* and *S. catenatus*. Both species use a variety of habitat types at the landscape level but exhibit strong selection for microhabitats involving dense ground-level vegetation. My results, and with those from two *S. catenatus* habitat studies all revealed that snakes chose microhabitats with high canopy cover and dense surface vegetation (Harvey and Weatherhead, 2006; Moore and Gillingham, 2006). The importance of shrubs as microhabitat cover is particularly interesting because of its prominence as a preferred microhabitat feature in three very different environments: southern Missouri (this study), Ontario, Canada (Harvey and

Weatherhead, 2006) and Colorado (Wastell and Mackessey, 2011). While selection of shrub cover may facilitate thermoregulation, it likely also provides cover from predators; at least three of my snakes were likely lost to predators and high depredation losses have been reported for *S. catenatus* in other studies (Harvey and Weatherhead, 2006; Moore and Gillingham, 2006; Durbian et al., 2008).

Evidence of r-selected reproduction

Sistrurus miliarius have been suggested to follow a more r-selected life history strategy than other crotalid species as exemplified by their small body size, rapid growth, and early maturity (Seigel and Ford, 1987; Farrell et al., 1995; Messenger, 2010; May and Farrell, 2012). If the high mortality rates observed in my study are typical for *S. miliarius*, selection pressure for compensatory reproductive effort should result in evidence of higher offspring production than expected for rattlesnakes in general. Specific observations from my study are consistent with this pattern and compatible with data from other populations. For example, four of the tracked gravid females were observed mating and/or consorting with male conspecifics within a few weeks after giving birth, suggesting the potential for an annual reproductive pattern, as has been reported in Florida (Farrell et al., 1995). Moreover, the absence of significant male-biased sexual size dimorphism in *S. miliarius* (this study; Bishop et al., 1996), is consistent with the presence of balanced selection pressures for increased body size in both sexes, conveying a mating advantage to large males (Shine, 1978) and a fecundity advantage to larger females (Seigel and Ford, 1987).

Further questions

As is typical in research, many more questions are generated than answered. More data are needed to determine if patterns reported here are typical of this population. Specifically, are the small home range sizes, short movements, and apparent annual reproduction events representative of the DMCA *S. miliarius* population or are these observations artifacts of the high prey density of 2016? In addition, in order to achieve this study's original objectives, more snakes must be monitored to make comparisons of the spatial ecology and microhabitat selection of *S. miliarius* of groups differing in reproductive status and sex. In addition to improving documentation of the spatial patterns and habitat selection of *S. miliarius* at DMCA, parallel studies on populations from different landscapes and climates would be of great interest.

LITERATURE CITED

- BARTON, K. 2016. MuMIn: Multi-model inference. R package version 1.15.6.
<https://CRAN.R-project.org/package=MuMIn>
- BASKIN, J. M., AND C. C. BASKIN. 2000. Vegetation of limestone and dolomite glades in the Ozarks and Midwest regions of the United States. *Annals of the Missouri Botanical Garden* 87:286–294.
- BEAMAN, K. R., AND W. K. HAYES. 2008. Rattlesnakes: research trends and annotated checklist, p. 5–16. *In*: Biology of the Rattlesnakes. W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.). Loma Linda University Press, Loma Linda, California.
- BEAUPRE, S. J., AND D. J. DUVALL. 1998. Integrative biology of rattlesnakes. *BioScience* 48:531–538.
- BERTRAM, N., AND K. W. LARSEN. 2004. Putting the squeeze on venomous snakes: accuracy and precision of length measurements taken with the “Squeeze box”. *Herpetological Review* 35:235–238.
- BISHOP, L. A., T. M. FARRELL, AND P. G. MAY. 1996. Sexual dimorphism in a Florida population of the rattlesnake *Sistrurus miliarius*. *Herpetologica* 52:360–364.
- BLOUIN-DEMERS, G., AND P. J. WEATHERHEAD. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 82:2882–2896.
- BORGER, L., N. FRANCONI, G. DE MICHELE, A. L. GANTZ, F. MESCHI, A. MANICA, S. LOVARI, AND T. COULSON. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75:1393–1405.
- BURGER, J., AND R. T. ZAPPALORLI. 1988. Habitat use in free-ranging pine snakes, *Pituophis melanoleucus*, in New Jersey Pine Barrens. *Herpetologica* 44:48–55.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model Selection and Multimodel Inference: A Practical Information—Theoretic Approach. Springer-Verlag, New York, New York.
- CALENGE, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.

- CLARK, R. W. 2005. Pursuit-deterrent communication between prey animals and timber rattlesnakes (*Crotalus horridus*): the response of snakes to harassment displays. *Behavioral Ecology and Sociobiology* 59:258–261.
- CLARK, R. W. 2006a. Strike-induced chemosensory searching by timber rattlesnakes during natural predation events. *Ethology* 112:1089–1094.
- CLARK, R. W. 2006b. Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. *Copeia* 2006:181–187.
- COBB, V. A., J. J. GREEN, T. WORRALL, J. PRUETT, AND B. GLORIOSO. 2005. Initial den location behavior in a litter of *Crotalus horridus* (Timber Rattlesnakes). *Southeastern Naturalist* 4:723–730.
- COMPTON, B. W., J. M. RHYMER, AND M. MCCOLLOUGH. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* 83:833–843.
- CRANE, A. L., AND B. D. GREENE. 2008. The effect of reproductive condition on thermoregulation in female *Agkistrodon piscivorus* near the Northwestern range limit. *Herpetologica* 64:156–167.
- CROSS, C. L., AND C. E. PETERSEN. 2001. Modeling snake microhabitat from radiotelemetry studies using polytomous logistic regression. *Journal of Herpetology* 35:590–597.
- DEGREGORIO, B. A., J. V. MANNING, N. BIESER, AND B. A. KINGSBURY. 2011. The spatial ecology of the eastern massasauga (*Sistrurus c. catenatus*) in Northern Michigan. *Herpetologica* 67:71–79.
- DURBIAN, F. E., R. S. KING, T. CRABILL, H. LAMBERT-DOHERTY, AND R. A. SEIGEL. 2008. Massasauga home range patterns in the Midwest. *The Journal of Wildlife Management* 72:754–759.
- DUVALL D., M. J. GOODE, W. K. HAYES, J. K. LEONHARDT, AND D. G. BROWN. 1990. Prairie rattlesnake vernal migration: Field experimental analyses and survival value. *National Geographic Research* 6:457–469.
- DUVALL D., AND G.W. SCHUETT. 1997. Straight-line movement and competitive mate searching in prairie rattlesnakes (*Crotalus viridis viridis*). *Animal Behavior* 54:329–334.
- FARRELL, T. M., P. G. MAY, AND M. A. PILGRIM. 1995. Reproduction in the rattlesnake, *Sistrurus miliarius barbouri*, in central Florida. *Journal of Herpetology* 29:21–27.

- FARRELL, T. M., P. G. MAY, AND M. A. PILGRIM. 2009. Repeatability of female reproductive traits in pigmy rattlesnakes (*Sistrurus miliarius*). *Journal of Herpetology* 43:332–335.
- FLEET, R. R., AND J. C. KROLL. 1978. Litter size and parturition behavior in *Sistrurus miliarius streckeri*. *Herpetological Review* 9:11.
- GAULIN, S. J. C., AND R. W. FITZGERALD. 1988. Home range size as a predictor of mating systems in *Microtus*. *Journal of Mammalogy* 69:311–319.
- GIBBONS, W., AND M. DORCAS. 2005. *Snakes of the Southeast*. University of Georgia Press, Athens, GA.
- GOODE, M., J. J. SMITH, AND M. AMARELLO. 2008. Seasonal and annual variation in home range and movements of tiger rattlesnakes (*Crotalus tigris*) in the Sonoran Desert of Arizona, p. 327–334. *In: Biology of the Rattlesnakes*. W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.). Loma Linda University Press, Loma Linda, California.
- GRAVES, B. M., AND D. DUVAL. 1993. Reproduction, rookery use, and thermoregulation in free-ranging, pregnant *Crotalus v. viridis*. *Journal of Herpetology* 27: 33–41.
- GREENE, H. W., P. G. MAY, D. L. HARDY SR., J. M. SCITURRO, AND T. M. FARRELL. 2002. Parental behavior by vipers, pp. 179–205. *In: Biology of the Vipers*. G. W. Schuett, M. Hoggren, M. E. Douglas, and H. W. Greene (eds.). Eagle Mountain Publishing, Eagle Mountain, UT.
- GREGORY, P. T., J. M. MACARTNEY, AND K. W. LARSEN. 1987. Spatial patterns and movements pp. 336–395. *In: Snakes: Ecology and Evolutionary Biology*. R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.). Macmillan Publ., New York.
- GREGORY, P. T., AND K. W. STEWART. 1975. Long-distance dispersal and feeding strategy of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake of Manitoba. *Canadian Journal of Zoology* 53:238–245.
- HANSTEEN, T. L., H. P. ANREASSEN, AND R. M. IMS. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. *Journal of Wildlife Management* 61:280–290.
- HARDY, D. L., AND H. W. GREENE. 1999. Surgery on rattlesnakes in the field for implantation of transmitters. *Sonoran Herpetologist* 12:25–27.
- HARDY, D. L., AND H. W. GREENE. 2000. Inhalation anesthesia of rattlesnakes in the field for processing and transmitter implantation. *Sonoran Herpetologist* 13:110–114.

- HARVEY, D. S., AND P. J. WEATHERHEAD. 2006. A test of the hierarchical model of habitat selection using eastern massasauga rattlesnakes (*Sistrurus c. catenatus*). *Biological Conservation* 130:206–216.
- HARVEY, D. S., AND P. J. WEATHERHEAD. 2011. Thermal ecology of massasauga rattlesnakes (*Sistrurus catenatus*) near their northern range limit. *Canadian Journal of Zoology* 89:60–68.
- HOLDER, T. L. 1988. Movement and life history aspects of the pygmy rattlesnake in southwest Missouri. Unpubl. M.Sc. thesis, Southwest Missouri State University, Springfield, Missouri.
- HUDNALL, J. A. 1979. Surface activity and horizontal movements in a marked population of *Sistrurus miliarius barbouri*. *Bulletin of the Maryland Herpetological Society* 15:134–138.
- JETZ, W., C. CARBONE, J. FULFORD, AND J. H. BROWN. 2004. The scaling of animal space use. *Science* 306:266–268.
- JOHNSON, G. 2000. Spatial ecology of the eastern massasauga (*Sistrurus c. catenatus*) in a New York peatland. *Journal of Herpetology* 34:186–192.
- KERNOHAN, B. J., R. A. GITZEN, AND J. J. MILLSPAUGH. 2001. Analysis of animal space use and movements, pp. 126–166. *In*: *Radio-Tracking and Animal Populations*. J. J. Millspaugh and J. M. Marzluff, (eds.). Academic Press, San Diego, California, U.S.A.
- KING, S. H., J. MOODY, P. L. REDFEARN, JR., J. L. KEENE, AND L. M. BOWE. 2012. Plants of the Bull Shoals Field Station, Taney County, Missouri. *Missouriensis* 31:19–43.
- LAWTON, J. H. 1993. Range, population abundance and conservation. *Trends in Ecology and Evolution* 8:409–413.
- LUTTERSCHMIDT, W. I., A. J. SMITH, E. J. TIVADOR III, AND H. K. REINERT. 2012. Diagnostic classification of connective tissue encapsulating transmitters and data acquisition units: evidence for not modifying a classic surgical implantation method. *Herpetological Review* 43:381–385.
- MACARTNEY, J. M., P. T., GREGORY, AND K. W. LARSEN. 1988. A tabular survey of data on movements and home ranges of snakes. *Journal of Herpetology* 22:61–73.
- MADSEN, T. W., AND R. SHINE. 1996. Seasonal migration of predators and prey: pythons and rats in tropical Australia. *Ecology* 77:149–156.

- MARTINO, J. A., R. G. POULIN, D. L. PARKER, AND C. M. SOMERS. 2012. Habitat selection by grassland snakes at Northern range limits: implication for conservation. *Journal of Wildlife Management* 76:759–767.
- MAY, P. G., AND T. M. FARRELL. 2012. Growth patterns of dusky pygmy rattlesnakes (*Sistrurus miliarius barbouti*) from Central Florida. *Herpetological Monographs* 26:58–79.
- MAY, P. G., T. M. FARRELL, S. T. HEULETT, M. A. PILGRIM, L. A. BISHOP, D. J. SPENCE, A. M. RABATSKY, M. G. CAMPBELL, A. D. AYCRIGG, AND W. E. RICHARDSON II. 1996. Seasonal abundance and activity of a rattlesnake (*Sistrurus miliarius barbaui*) in Central Florida. *Copeia* 1996:389–401.
- MESSENGER, K. R. 2010. Growth and age at reproductive maturity of the Carolina pigmy rattlesnake, *Sistrurus m. miliarius* (Reptilia: Serpentes). Unpubl. M.Sc. thesis, Marshall University, Huntington, West Virginia.
- MONTGOMERY, W. B., AND G. W. SCHUETT. 1989. Autumnal mating with subsequent production of offspring in the rattlesnake *Sistrurus miliarius streckeri*. *Bulletin of the Chicago Herpetological Society* 24:205–207.
- MOORE, J. A., AND J. C. GILLINGHAM. 2006. Spatial ecology and multi-scale habitat selection by a threatened rattlesnake: the eastern massasauga (*Sistrurus catenatus catenatus*). *Copeia* 2006:742–751.
- MOUNT, R.H. 1975. The Reptiles and Amphibians of Alabama. Auburn University, Auburn, AL.
- MYERSTRUD, A., F. J. PEREZ-BARBERIA, AND I. J. GORDON. 2001. The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oecologia* 127:30–39.
- PALMER, W. M., AND A. L. BRASWELL. 1995. Reptiles of North Carolina. Chapel Hill. University of North Carolina Press.
- PERRY, G., AND T. GARLAND. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. *Ecology* 83:1870–1885.
- POWELL, R.A. 2000. Animal home ranges and territories and home range estimators, pp. 65–110. *In: Research Techniques in Animal Ecology: Controversies and Consequences*. L. B and T. Fuller (eds.). Columbia University Press, New York, New York.
- PRESS, S. J., AND S. WILSON. 1978. Choosing between logistic regression and discriminant analysis. *Journal of the American Statistical Association* 73:699–705.

- PRIVITAL, D. B., M. J. GOODE, D. E. SWANN, C. R. SCHWALBE, and M. J. SCHROFF. 2002. Natural history of a northern population of twin-spotted rattlesnakes, *Crotalus pricei*. *Journal of Herpetology* 36:598–607.
- REINERT, H. K. 1984. Habitat variation within sympatric snake populations. *Ecology* 65:1673–1682.
- REINERT, H. K. 1993. Habitat selection in Snakes, pp. 201–240. *In: Snakes: Ecology and Behavior*. R. A. Siegel and J. T. Collins (eds.). McGraw-Hill, New York.
- REINERT, H. K., AND D. CUNDALL. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702–705.
- REINERT, H. K., D. CUNDALL, and L. M. BUSHAR. 1984. Foraging behavior of the timber rattlesnake, *Crotalus horridus*. *Copeia* 1984:976–981.
- ROTH, E. D. 2005. Spatial ecology of a cottonmouth (*Agkistrodon piscivorus*) population in East Texas. *Journal of Herpetology* 39:312–315.
- ROW, J. R., AND G. BLOUIN-DEMERS. 2006a. Thermal quality influences habitat selection at multiple spatial scales in milksnakes. *Ecoscience* 13:443–450.
- ROW, J. R., AND G. BLOUIN-DEMERS. 2006b. Kernels are not accurate estimators of home range size for herpetofauna. *Copeia* 2006 797–802.
- SEAMAN, D. E., J. J. MILLSPAUGH, B. J. KERNOHAN, G. C. BRUNDIGE, K. J. RAEDEKE, AND R. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- SCHOENER, T. W. 1968. Sizes of feeding territories among birds. *Ecology* 49:123–141.
- SECOR, S. M. 1995. Ecological aspects of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Herpetological Monographs* 9:169–186.
- SEIGEL, R. A., AND N. B. FORD. 1987. Reproductive ecology, pp. 210–252. *In: Snakes: Ecology and Evolutionary Biology*. R. A. Siegel, J. T. Collins, and S. S. Novak (eds.). Macmillan Publ., New York.
- SHINE, R. 1978. Sexual size dimorphism and male combat in snakes. *Oecologia* 33:269–277.
- SLAVENKO, A., Y. ITESCU, F. IHLOW, AND S. MEIRI. 2016. Home is where the shell is: predicting turtle home range sizes. *Journal of Animal Ecology* 85:106–114.

- SMITH, C. F., G. W. SCHUETT, R. L. EARLEY, AND K. SCHWENK. 2009. The spatial and reproductive ecology of the copperhead (*Agkistrodon contortrix*) at the Northeastern extreme of its range. *Herpetological Monographs* 23:45–73.
- STEEN, D. A., J. M. LINEHAN, AND L. L. SMITH. 2010. Multiscale habitat selection and refuge use of common kingsnakes, *Lampropeltis getula*, in Southwestern Georgia. *Copeia* 2010:227–231.
- STONE, P. A., AND T. A. BAIRD. 2002. Estimating lizard home range: the Rose Model revisited. *Journal of Herpetology* 36:427–436.
- SWIHART, R. K., AND N. A. SLADE. 1985. Influence of sampling interval on estimates of home-range size. *The Journal of Wildlife Management* 49:1019–1025.
- TRAUTH, S. E., H. W. ROBISON, AND M. V. PLUMMER. 2004. *The Amphibians and Reptiles of Arkansas*. University of Arkansas Press, Fayetteville.
- TUCKER, M. A., T. J. ORD, AND T. L. ROGERS. 2014. Evolutionary predictors of mammalian home range size: body mass, diet, and the environment. *Global Ecology and Biogeography* 23:1105–1114.
- VAN MOORTER, B., C. M. ROLANDSEN, M. BASILLE, AND J. M. GAILLARD. 2016. Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology* 85:21–31.
- WASKO, D. K., AND M. SASA. 2010. Habitat selection of the terciopelo (Serpentes: Viperidae: *Bothrops asper*) in a lowland rainforest in Costa Rica. *Herpetologica* 66:148–158.
- WASTELL, A. R., AND S. P. MACKESSY. 2011. Spatial ecology and factors influencing movement patterns of desert massasauga rattlesnakes (*Sistrurus catenatus eswardsii*) in Southwestern Colorado. *Copeia* 2011:29–37.
- WEATHERHEAD, P. J., AND K. A. PRIOR. 1992. Preliminary observations of habitat use and movements of the eastern massasauga rattlesnake (*Sistrurus c. catenatus*). *Journal of Herpetology* 26:447–452.
- WHITE, G. C., AND R. A. GARROTT. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, Inc., San Diego, California.
- WITTENBERG, R. D. 2012. Foraging ecology of the timber rattlesnake (*Crotalus horridus*) in a fragmented agricultural landscape. *Herpetological Conservation and Biology* 7:449–461.
- WORTON, B. J. 1987. A review of models of home range for animal movement. *Ecological Modelling* 38:277–298.

APPENDIX—HOME RANGES

