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

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Abstract.—Understanding use of space and habitat are central to animal ecology and provide insight into resource selection patterns. Despite a wide distribution throughout the southeastern U.S., research on Pygmy Rattlesnakes (*Sistrurus miliarius*) has been largely restricted to Florida populations. We studied *S. miliarius* in a managed forest landscape on a state conservation area in the Ozarks of southwestern Missouri, near their northern range limit, during 2016 and 2017. We captured 54 *S. miliarius*, primarily during evening road driving surveys, and used 19 (six males and 13 females: nine gravid, four nongravid) for a radiotelemetry study. Telemetered snakes were relatively sedentary, making short, infrequent movements that resulted in small home range estimates (range, < 0.001–2.6 ha). Reproductive status of females strongly affected activity with mean movement distances and home range sizes of gravid females increasing five-fold following parturition. We encountered *S. miliarius* in all available habitat types, suggesting that habitat selection was mainly occurring at the microhabitat scale. Snakes were very secretive but typically concealed themselves within vegetation (89% of observations) or beneath surface cover (8.5% observations) rather than underground. Snakes selected microhabitats with more vegetative cover and woody debris, and less leaf litter, than random sites. The ability of *S. miliarius* to use a variety of habitat types suggests that it is well adapted to the Ozarks landscape. Our study presents novel information to a growing body of knowledge on *S. miliarius* ecology that should lead to comparative studies in different geographic regions.

Key Words.—habitat; home range; Logistic Regression; movements; radiotelemetry; reptile; snake; viper

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). 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) and metabolic rates (Todd and Nowakowski 2021), although variation between body size and resources are less prominent in snakes than other vertebrates (Todd and Nowakowski 2021). In addition to these important influences, a substantial amount of variation in home range size may still be attributed to individual differences (Borger et al. 2006). Snakes are an optimal group to study factors on space use and habitat selection because resource needs are well known and confounding social influences are mostly lacking (Gregory et al. 1987).

Variation in spatial patterns and habitat selection of temperate snakes is generally explained by a combination of dispersion and availability of prey, hibernacula, thermal refugia, and mates. For example, spatial segregation of hibernacula and foraging habitats can induce lengthy seasonal migrations in some temperate environments (e.g., Gregory and Stewart 1975). Snakes may track prey densities across landscapes as they change with season (e.g., Madsen and Shine 1996) or exhibit aggregative 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 higher rates of movement than females as a consequence of searching for mates (Roth 2005; Smith et al. 2009; Fiedler et al. 2021; Todd and Nowakowski 2021).

As rattlesnakes are model organisms for radiotelemetry studies (Beaupre and Duvall 1998), there is breadth of literature on ecology and conservation of rattlesnakes (Beaman and Hayes

2008). Rattlesnakes generally 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; Todd and Nowakowski 2021). 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 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 small crotalid that inhabits the coastal plains regions of the southeastern U.S. 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. Individuals exhibit a fast life history relative to other crotalids, with attainment of sexual maturity estimated at 3–4 y in Florida (Rowe et al. 2002) and 2–3 y in North Carolina (Messenger 2010). In Florida, where *S. miliarius* is active all year (May et al. 1996), some females reproduce annually from late summer through early winter (Montgomery and Schuett 1989; May et al. 1996; Messenger 2010; Lind et al. 2018). 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). Information on spatial patterns of *S. miliarius* is limited to locality data from two mark-recapture studies (Hudnall 1979; Jemison et al. 1995) and preliminary movement data from four snakes monitored through radiotelemetry (Holder 1988). *Sistrurus miliarius* has been qualitatively reported to occupy forests, xeric uplands, glades, and floodplains (Trauth et al. 2004; Gibbons and Dorcas 2005), yet no quantitative assessment of habitat selection has been attempted, most likely due to limited detection probabilities and technological limitations due to the diminutive size of the species.

We conducted a two-season radiotelemetry study of *S. miliarius* to characterize their movement patterns, home range sizes, and microhabitat selection in a managed Ozark landscape. Because males are expected to engage in mate searching, we predicted movement frequencies and length, and home range sizes, to be more frequent, longer, and larger than those of females. Pregnancy imposes physiological constraints on movement and habitat selection of viviparous snakes (Gregory et al.

1987; Reinert 1993). Therefore, we also expected that gravid snakes would be more sedentary than males and nongravid females. Our data provide insight into the spatial patterns and habitat selection of *S. miliarius* and provide a basis for comparative studies in regions with contrasting environments.

MATERIALS AND METHODS

Study site.—We conducted field research from 15 April to 15 November 2016 and 26 March to 14 November 2017 at the Drury and Mincy Conservation Areas (DMCA) in southwestern Missouri, USA (36.57°N, -93.06°W, WGS 84). The DMCA is an 809-ha tract that is owned and managed by the Missouri Department of Conservation. The study area is in the Springfield Plateau of the Ozarks, which is characterized by a karst landscape with rolling terrain. Southwest Missouri experiences hot summers and short, cold winters; monthly mean minimum and maximum temperatures for each month of 2016 and 2017 range from -4.4° to 20.6° C and 6.1°–31.5° C, respectively. Annual precipitation was 98.4 cm for 2016 and 130.8 cm for 2017 (<https://www.ncdc.noaa.gov/data-access/land-based-station-data>). The DMCA landscape consists of Oak-Hickory Woodland and savanna with scattered limestone/dolomite glades, where warm season grasses and prairie herbs grow on thin soil surrounding exposed bedrock (Baskin and Baskin 2000). Much of the area is managed by prescribed burning to maintain an open understory and prevent woody plant encroachment onto 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. A detailed description of plant species at DMCA is provided in King et al. (2012).

Snake sampling and processing.—We captured *S. miliarius* individuals during nighttime road surveys, coverboard checks, and fortuitous encounters. We used corrugated steel coverboards (0.5 × 1.5 m) arranged in transects at five locations where *S. miliarius* had been observed previously. We marked snakes individually with a PIT tag (HPT12 134.2 KHz; Biomark, Boise, Idaho, USA), determined their sexed by manual eversion of hemipenes of males, weighed them (± 0.1 g), and measured their snout-vent lengths (SVL) and tail lengths using a squeeze box (Bertram and Larsen 2004). We determined the reproductive status of females by palpating their abdomens to detect enlarged ova or developing embryos.

Telemetry.—We transported snakes retained for telemetry to Missouri State University for surgical

implantation of transmitters (2016: model SB-2, 3.8 g, 5-mo battery life; 2017: model PD-2, 2.5 g, helical antenna, 4-mo battery life; Holohil Systems Ltd., Ontario, Canada). We coated transmitters in a 1:1 ratio of paraffin and beeswax (Lutterschmidt et al. 2012) and surgically implanted them into snakes that were anesthetized with isoflurane, using a composite of standard methods (Reinert and Cundall 1982; Hardy and Greene 1999, 2000). Because of the small size of *S. miliarius*, relatively few individuals were large enough to carry transmitters. We attempted to limit the metabolic cost of transmitter mass on snakes by ensuring that transmitter to snake mass ratios did not exceed 5% (Reinert 1992).

We maintained four snakes (one gravid female, one non-gravid female, and two males), similar in SVL but of lower body condition than other implanted snakes, in captivity and fed one mouse (*Mus musculus*) per week until a 5% transmitter to body mass ratio was achieved. This supplemental feeding of sufficiently large (in SVL) but thinner snakes allowed us to make transmitter influence consistent across our sample while not creating unnaturally fat subjects. Captive maintenance of supplementally fed snakes was generally brief (3–4 weeks for three snakes and seven weeks for the fourth) and involved 2–6 feedings. To ensure that mass changes of supplementally fed snakes were caused by tissue mass gain, we allowed 7 d for gut clearance and confirmed absence of feces by abdominal palpation. After surgeries, we individually caged and monitored snakes for adverse reactions for 24–48 h before being release at their original capture locations; none of the snakes showed any sign of necrosis or infection at the surgery site. To minimize post-surgical behavioral bias, we observed a 7-d acclimation period prior to data collection (Goode et al. 2008). We implanted gravid snakes also with transmitters at least a month before parturition occurred to minimize the effect of clutch mass on the overall mass of the snake.

We tracked snakes 2–4 times per week between 0800 and 1700 using a hand-held H-antenna (TR-2, Telonics, Mesa, Arizona, USA) and receiver (R-1000, Communications Specialist, Inc. Orange, California, USA) until they entered hibernation, were found dead, or the transmitter failed. Upon locating a snake, we recorded UTM coordinates with a handheld Global Positioning System (GPS) device (eTrex, vista HCx, Garmin Ltd., Olathe, Kansas, USA) at a precision of ± 3 m. We only considered snakes that we found concealed or in a coiled body posture to have selected a location. We re-tracked snakes that appeared to be moving later the same day and we recorded their positions after they assumed a sedentary posture. To minimize monitoring disturbance, we flagged snake-selected sites and returned to complete habitat measurements following

the departure of the snake. We typically characterized snake-selected sites within a week of occupancy; however, the sedentary behavior of gravid females sometimes delayed habitat measurements up to seven weeks. All such delays occurred during summer when vegetation structure was stable.

Movements and home ranges.—We used GPS coordinates and straight-line distances between successive points to calculate home range estimates and quantify movement patterns. To facilitate comparisons, we calculated standard movement statistics of mean distance moved per day and mean distance per movement (Reinert 1992). We also calculated mean distance moved per tracking event (average distance traveled between successive tracking events), and frequency of movement (mean number of moves per day). To adjust for GPS measurement error on spatial calculations, we jittered each snake location 200 times for the 2016 season by 3 m. Because movement and home range estimates from jittered points were essentially identical to those derived from original points, we ceased jittering after 2016 and report only calculations based on raw data.

It is generally recommended that multiple home range estimation methods be used in spatial studies, and that kernel estimators be included because they allow identification of core activity areas (Kernohan et al. 2001). We elected to report only Minimum Convex Polygon (MCP) estimates, however, because our sample sizes were insufficient or marginal for Kernel Analyses (Seaman et al. 1999). We also desired to make general comparisons with previous studies for which only MCP estimates were provided. The MCP method has been criticized for including unused habitats within home range areas; this was not true for our study except for road surfaces that snakes crossed, which contributed trivially to the overall home range size estimates.

Microhabitat selection.—To characterize the habitat structure, we measured, counted, or estimated 22 variables within circular plots, using sampling radii scaled to the spatial variation of each variable (Appendix Table 1). We quantified cover variables that would likely influence selection by snakes in close proximity within a 1-m² plot surrounding the snake location. We evaluated distance variables relating snake proximity to large structural features within a 30-m radius. We considered any feature occurring beyond its respective sampling radius unavailable to the snake at that location and received a value of zero. To facilitate interpretation of snake selection of distance variables, we transformed each value by subtracting from 30 so that larger values would indicate proximity of a feature (Wasko and Sasa 2010).

We evaluated microhabitat selection using matched-pairs Logistic Regression. This method pairs each

location selected by an animal with a random location, providing an assessment of available habitat that is both spatially and temporally relevant (Compton et al. 2002; Moore and Gillingham 2006). We determined random locations using a random number generator to select a compass bearing and distance from a given snake location (Cross and Petersen 2001; Harvey and Weatherhead 2006; Steen et al. 2010). Initially we constrained the distance of the random point sampling radius to 1–36 m, based on the 95% confidence interval of mean distance per move from four *S. miliarius* individuals tracked by Holder (1988). In 2017 we adjusted random point sampling radii to 19–51 m after including movement data for 11 snakes we tracked in 2016. After 2016, we also reduced the number of candidate variables used in microhabitat analyses by removing highly correlated ($r > 0.7$) variables (Harvey and Weatherhead 2006; Moore and Gillingham 2006; Martino et al. 2012) and limited 2017 data collection to the 13 variables retained. Prior to analyses, we standardized each variable by calculating Z-scores.

Intraspecific patterns of habitat selection in snakes can vary with sexual dimorphism (Shine 1986) and reproductive condition of females (Reinert 1993). When such factors are suspected to be influential, it is common to evaluate habitat selection of groups separately; however, *S. miliarius* exhibits minimal sexual dimorphism in body size (Bishop et al. 1996; May and Farrell 2012) and, although reproductive condition of females significantly influenced spatial patterns, we did not observe any obvious disparity in use of habitat structure between gravid females and other monitored snakes. Therefore, we evaluated habitat selection for a pooled sample rather than attempting to characterize subcategories.

Logistic Regression assumes independence of observations, which is not feasible in radiotelemetry studies where repeated measurements are obtained from a limited number of subjects. Under such circumstances it is important to ensure that the results are not biased toward individuals with higher proportional representation. Because contributions were relatively balanced across individuals (median = 5.8%; max = 12.4%) we treated each snake location as an independent observation (Row and Blouin-Demers 2006; Blouin-Demers et al. 2007; Wasko and Sasa 2010). Moreover, some snakes occupied individual sites for extended periods, especially when gravid. To minimize the impact of repeated site use on habitat selection inferences, we rarefied the data using the mean movement frequency for all snakes, so that we only used sites used consecutively by an individual snake in analyses once per 5-d interval. Sites occupied by the same snake in separate 5-d intervals were treated as independent selection events.

Prior to evaluating candidate models, we conducted preliminary univariate analyses on each of the 13 remaining habitat variables and identified three variables that were not helpful in discriminating between snake-selected and available sites ($P > 0.25$). We used the remaining 10 variables to generate candidate models, which were ranked and evaluated with Akaike Information Criterion (AIC) to select the most parsimonious microhabitat models (Burnham and Anderson 1998). We considered all models within two AIC units of the lowest score to be supported (Burnham and Anderson 1998). We tested the contribution of each variable to the best supported models using Z-scores of the estimated coefficients (β) and interpreted the influence of each variable on habitat selection as an n -unit increase in each habitat variable that results in an e^{β} change in the odds ratio.

We conducted statistical analyses in R, v. 3.3.1 (R Core Team 2021). We generated home range estimates using the MCP function in the adehabitatHR package (Calenge 2006) and the gBuffer function to account for the 3 m of GPS error. We performed Wilcoxon Signed-rank Tests to compare the means between pre- and post-partum females in their movements and home range sizes due to the inability to achieve normality through transformations. To determine if the sampling duration or size of the snakes were biasing the home range sizes, we tested both against the estimated home range sizes using Spearman's Correlations. We performed matched-pairs Logistic Regression that we 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. We report all means ± 1 standard error and we used $\alpha = 0.05$.

RESULTS

Snake captures.—From April–October of 2016 and March–October of 2017, we observed 55 *S. miliarius* ($n = 21$ males; 23 nongravid females; 10 gravid females; one unidentified), 18 of which were juveniles. Most snakes ($n = 44$; 80%) were found during nightly 2-h summer road driving surveys, starting 30 min before sundown throughout the sampling periods. We found the remaining snakes under coverboards in April and May ($n = 5$) and by fortuitous encounters ($n = 6$). We encountered only one snake (male, #32) while tracking a transmitted animal. Encounter frequencies for *S. miliarius* were highest around forests ($n = 29$) but also occurred in association within glades ($n = 15$), savannas ($n = 8$), and food plots ($n = 3$). Because all captures near roads happened when the snake was crossing the road, we did not use road edge as a macrohabitat type.

No snakes showed any obvious clinical signs of snake fungal disease.

Telemetry.—Of the 54 *S. miliarius* we captured, only 14 *S. miliarius* individuals (eight gravid females; three nongravid females; three males) in 2016 and six individuals (one gravid female; two nongravid females; three males) in 2017 were large enough to be implanted with radio transmitters. We tracked snakes during July–October 2016, yielding 397 telemetry locations, and July–November 2017, yielding 121 telemetry locations, respectively. These snakes were captured in or crossing the road adjacent to all available macrohabitat types except for food plots. Ten snakes died in the field during the study, four of which from apparent predation due to direct observation of the predator, or which we inferred from a damaged transmitter with no snake carcass, or because we found a bare transmitter that had been rapidly displaced an unusually long distance (~2 km) from the last known position of the snake. Six snakes died from undetermined causes with an undamaged transmitter. Of these, there was one instance of a partial snake carcass where we could speculate suture failure, but it was unclear, and the rest of the remains were incomplete. Mortality was similar across snake categories with gravid females exhibiting the fewest losses (44.4%), followed by males (50%) and nongravid females (60%). Mortality of gravid females did not seem to be related to body size based on initial masses of survivors and non-survivors. Of the 10 snakes that survived their monitoring periods, three exceeded transmitter battery life during the activity season, another eventually occupied an inaccessible cliff face until battery life expired, and we tracked six into hibernacula. We excluded from analyses five of the snakes that died because the duration of observation was too brief (≤ 13 d) to contribute meaningful information. We included data for the remaining five non-surviving snakes, which were each tracked for a minimum of 43 d (mean = 76.8 d). Thus, we based analyses on 491 telemetry locations of 15 snakes that were tracked for a mean duration of 92.3 ± 8.80 d (range, 41–150 d) and that we tracked for a mean of 37.8 ± 4.87 times (range, 11–77; Appendix 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 was 115.1 ± 11.6 d ($n = 7$), including 55.3 ± 9.0 d before and 57.5 ± 9.9 d after parturition. Tracking during gravid and nongravid intervals yielded corresponding means of 29.7 ± 5.6 and 14.9 ± 2.2 tracking events, respectively. We tracked nongravid females ($n = 4$), on average, 65.8 ± 10.1 d, yielding an average of 24.1 ± 4.4 tracking events per snake. Lastly, we tracked males ($n = 4$), on average,

79.0 ± 13.5 d, yielding an average of 26.5 ± 6.4 tracking events per snake.

Occasionally we observed snakes, monitored through radiotelemetry, engaging in reproductive activities. Parturition for all gravid snakes occurred 11–25 August 2016 and we observed five of these individuals with their young after parturition for up to 3 d. We also observed four post-partum females mating or with one or more males from late August to early October 2016. We observed three nongravid females in association with a male in September 2016 (#25) and 2017 (#2 and #4). None of the male snakes that we tracked were observed interacting with females.

Movements and home ranges.—Overall, *S. miliarius* moved infrequently (0.22 ± 0.01 moves/day) and over relatively short distances per move (mean = 30.7 ± 6.1 m), resulting in low mean movement rates (distance/day: 6.5 ± 0.9 m; distance/tracking event: 19.6 ± 3.44 m). Reproductive status strongly affected the movements of females. Mean distances moved by gestating females per day (2.1 ± 0.6 m), per movement (9.1 ± 2.0 m), and per tracking event (4.1 ± 1.3 m) all increased (all $V = 28$, $df = 7$, $P = 0.016$) to 8.1 ± 1.3 m, 40.4 ± 4.8 m, and 31.7 ± 4.4 m after parturition, respectively (Fig. 1). Mean movement frequency (moves/day), however, was not affected by reproductive status (gravid: 0.22 ± 0.04 ; post-partum: 0.20 ± 0.02 ; $V = 10$, $df = 7$, $P = 0.578$; Fig. 1), indicating that the magnitude of movements, but not the rate, increased after parturition.

For non-gravid females, mean distances moved per day (5.3 ± 1.5 m), per movement (23.3 ± 6.0 m), and per tracking event (15.4 ± 4.3 m) were roughly one-half of the corresponding values for males (mean distances moved per day: 9.9 ± 2.3 m, mean distance per movement: 49.5 ± 20.7 m, mean distance per tracking event: 32.4 ± 9.9 m; Fig. 1). Movement frequencies, however, were similar for all groups (gravid female: 0.22 ± 0.04 ; post-partum female: 0.20 ± 0.02 ; nongravid female: 0.22 ± 0.03 moves/day, male: 0.24 ± 0.04 moves/day; Fig. 1), suggesting that males moved greater distances than non-gravid females but not more often. Because of the small sample sizes ($n = 4$ for both non-gravid females and males), we did not attempt statistical comparisons.

During 2016, we shifted the sampling regime from 3–4 times a week in the summer to 1–2 times a week during the fall. To assess whether this change in monitoring frequency affected movement estimates, we made paired comparisons of mean distances per tracking event for six snakes (two gravid females after parturition, two non-gravid females, and two males) tracked during both sampling periods, and found no significant difference ($V = 6$, $df = 6$, $P = 0.438$). A single female (snake #2) we monitored in both seasons

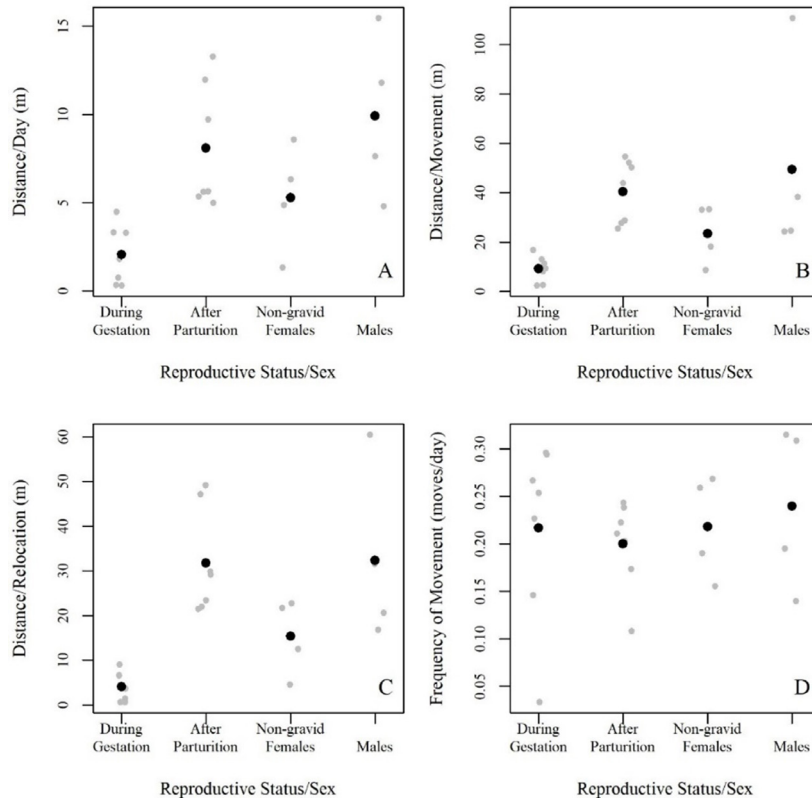


FIGURE 1. Comparison of (A) daily distance moved, (B) distance per movement, (C) distance per tracking event, and (D) movement frequency for 15 (four male, four non-gravid female, and seven gravid female) Pygmy Rattlesnakes (*Sistrurus miliarius*) at Drury-Mincy Conservation Areas, Missouri, USA, 2016–2017.

had a much larger MCP estimate in 2017 (1.89 ha) than in her non-gravid portion of 2016 (0.28 ha).

Area use was substantially affected by reproductive status of females (Appendix Table 2). Mean MCPs of gestating snakes (0.20 ± 0.09 ha) increased to 1.04 ± 0.32 ha after giving birth ($n = 7$; $V = 28$, $df = 7$, $P = 0.016$). Comparatively, the mean home range sizes of nongravid females and males were 0.76 ± 0.43 ha and 1.35 ± 0.50 ha, respectively (Fig. 2). Variation in home range sizes was not explained by snake SVL ($r = 0.21$, $F_{1,13} = 0.57$, $P = 0.462$) or number of days tracked ($r = 0.44$, $F_{1,13} = 3.08$, $P = 0.103$).

Microhabitat selection.—Because each home range included only one habitat type, we evaluated habitat selection only at the microhabitat scale. We characterized the microhabitat at 348 snake locations (73 male and 275 female) and their paired random points. We excluded nine variables (%LOG, %ROCK, DLL, %WATER, %VEGS, %VEGT, #WSTEM, HWS, and DOS; see Appendix Table 1 for description of variables) from consideration due to high correlation ($r > 0.70$) with one or more other variables, and three

additional variables (%USCOV, LROCK, and MDR) that were unlikely to influence habitat selection ($P > 0.25$) based on univariate tests. We used the remaining 10 variables to create a group of candidate models,

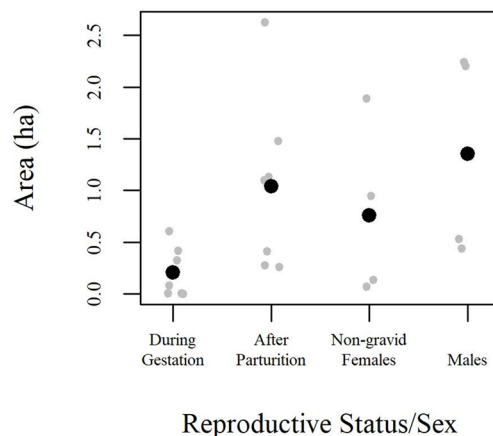


FIGURE 2. Estimated Minimum Convex Polygon sizes for 15 (four male, four non-gravid female, and seven gravid female) Pygmy Rattlesnakes (*Sistrurus miliarius*) at Drury-Mincy Conservation Areas, Missouri, USA, 2016–2017.

TABLE 1. Model averaged estimates for all variables included in the top 10 microhabitat selection models for Pygmy Rattlesnakes (*Sistrurus miliarius*) at Drury-Mincy Conservation Areas, Missouri, USA, 2016–2017, derived from matched-pairs logistic regression. Variable abbreviations are explained in Appendix Table 1. The abbreviation SE = standard error.

Variable	# of Models including	Estimate (± 1 SE)	Z-value	P-value
%BARE	10	-0.037 (0.012)	3.225	0.001
DIALOG	10	-0.056 (0.020)	2.806	0.005
DRETREAT	10	0.483 (0.066)	7.241	< 0.001
DSHRUB	10	0.400 (0.121)	3.290	0.001
%LEAF	10	-0.038 (0.008)	4.971	< 0.001
DLOG	8	0.094 (0.048)	1.935	0.052
DUS	6	0.057 (0.036)	1.574	0.115
DIAOS	3	0.010 (0.010)	1.060	0.289
%VEG	2	-0.005 (0.007)	0.669	0.503
%CANCOV	2	-0.003 (0.005)	0.665	0.506

which included 10 models within two AIC units of the top model (Appendix Table 3).

Five of the remaining 10 predictor variables were included in all top models (%BARE, DIALOG, DRETREAT, DSHRUB, and %LEAF) and were each importantly related to snake habitat selection (all $P < 0.005$; Table 1). The remaining five variables were included in eight or fewer models and had coefficients not significantly different from zero (Table 1). Odds ratios of the five influential variables in the top models suggest that *S. miliarius* selected sites close to retreat sites with small logs and shrubs (Table 2). A 1-cm increase in the diameter of a log decreased the selection probability of that site by 6%, while 1-m decrease in the distance to a retreat site or shrub increased their selection probabilities by 63% and 49%, respectively. Snakes also selected substrates with more vegetative cover than random sites while avoiding substrates containing mostly leaf litter or bare earth. A 10% increase in leaf litter or bare earth substrate coverage decreased the probability of selection by 32% and 31%, respectively.

The six snakes that we tracked into the fall selected hibernacula within or immediately adjacent to their MCP areas. These hibernacula were associated with a variety of structural surface features, including a dead tree stump, a rock ledge, and various mammal burrows. Snakes arrived at hibernacula by mid to late October but were sometimes observed on the surface in early November. We observed one telemetered snake at a hibernaculum with another individual.

DISCUSSION

Our study provides the first telemetry-based home range estimates for *S. miliarius* and our results suggest

TABLE 2. Coefficients and odds ratios for variables contributing significantly to the top microhabitat selection model for Pygmy Rattlesnakes, *Sistrurus miliarius*, at Drury-Mincy Conservation Areas, Missouri, USA, 2016–2017. Variable abbreviations are explained in Appendix Table 1. The abbreviations Co = coefficient and SE = standard error.

Variable	Co	SE	Increase or decrease	Odds ratio	95% CI
%BARE	-0.037	0.011	10%	0.691	(0.675, 0.706)
DIALOG	-0.057	0.020	1 cm	0.944	(0.908, 0.982)
DRETREAT	0.486	0.066	-1 m	1.626	(1.428, 1.853)
DSHRUB	0.398	0.124	-1 m	1.489	(1.168, 1.899)
%LEAF	-0.038	0.007	10%	0.683	(0.673, 0.693)

that *S. miliarius* at DMCA is a macrohabitat generalist that uses all habitat types containing dense vegetative cover at ground level. Consistent with response to high resource abundance, 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 3–5 fold following parturition. Although our sample size is relatively small ($n = 15$), we believe that our results provide a base level of knowledge about the ecology of this species to assist in further studies and management. Our study also begins to fill a geographic gap in the literature for this species with its focus on a population found at the northwestern boundary of the range of the species.

The 50% mortality rate, 57% for 2016 and 33% for 2017, in our study raises concerns over whether mortality is truly this high, is perhaps a consequence of our methodology, or is a byproduct of the small sample size of individuals. Mortality rates in pitviper telemetry studies often involve mortality rates of 33–40% for the duration of studies (Danou 1997; Bissell 2006; Sutton et al. 2017; Delisle et al. 2019). Because most losses occurred in gravid females, we wondered if the combination of pregnancy, stress associated with surgery, and metabolic costs of pregnancy resulted in disproportionately high mortality in this subgroup. Gravid females, however, also were the category with the highest frequency in our sample and their survival rate (56%) was greater than other subgroups (non-gravid females 40% and males 50%). Additionally, all surviving snakes appeared to remain healthy throughout our study as evidenced by maintenance of healthy body weights, and absence of surgical necrosis, while successfully foraging, mating, and giving birth. Thus, we suggest that despite impacts of transmitter burden

that are inherent in telemetry studies (Weatherhead and Blouin-Demers 2004), our data still provide insight into the typical behavior of *S. miliarius*.

The high mortality rate that we observed for *S. miliarius* may be realistic for this very small pitviper. High mortality is consistent with the fast life history of this species, exemplified by its rapid maturity and high reproductive effort (Farrell et al. 1995). Apparent annual survival of the diminutive Namaqua Dwarf Adder (*Bitis schneideri*) was estimated by mark-recapture to vary from 39–56% and was attributed to high predation pressure (Maritz and Alexander 2012). Many snake deaths in our study were also a consequence of predation (42%).

Movements and home ranges.—Home range estimates for *S. miliarius* at DMCA were low relative to values reported for other small rattlesnakes, presumably reflecting spatial concentration of key resources (Macartney et al. 1988). Understanding how resource distribution influences *S. miliarius* spatial patterns can be inferred from studies of Massasaugas (*Sistrurus catenatus*) where MCP size varies among populations across two orders of magnitude. For example, a meta-analysis of spatial patterns among Midwestern *S. catenatus* populations revealed mean MCP estimates varying from 2.4 ha to 135.8 ha based on the availability and dispersion of basking habitats (Durbian et al. 2008). Wastell and MacKessy (2011) reported a mean MCP of 42 ha for a Colorado population of *S. catenatus*, where snakes migrated approximately 2 km between hibernacula and summer foraging habitats. In contrast, the MCP sizes reported for *S. catenatus* occupying open meadows and fen habitats where prey, hibernacula, and basking sites all occur close together (Moore and Gillingham 2006), were very similar to values of *S. miliarius* at DMCA. In our study, all *S. miliarius* tracked into the fall hibernated within, or in very close proximity to, their summer home ranges. Additionally, small mammal surveys concurrent with our studies revealed moderate to high densities of small mammal prey during this period (Beasley and Maher 2019).

Increases in resource availability, derived from supplemental feeding experiments (Wasko and Sasa 2012; Glaudas and Alexander 2017) and from resource hotspots (DeSantis et al. 2019) are consistently associated with reduced area use in pitvipers, raising concerns about whether our supplemental feeding practice may have negatively biased results. The relative MCP sizes of our four supplementally fed snakes varied inconsistently with values of non-fed snakes within the same category. The MCP areas of both supplementally fed males were approximately 20% those of two non-fed males. In contrast, MCPs of individual nongravid and gravid females were among the higher values in

their respective categories. Given the small sample sizes in all categories, the apparent contradictory response among fed snakes, and the inherent variability in individual spatial responses, it is difficult for us to determine whether differences observed in our study were attributed to feeding or simply represent random variation.

The sensitivity of the MCP estimator to increasing sample size may provide another explanation for the small home range size estimates observed for *S. miliarius*. The small body sizes of *S. miliarius* constrained transmitter size and battery life, which ultimately limited the duration of monitoring in this 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). If *S. miliarius* continued to occupy new areas throughout the activity season, however, home range size should be positively correlated with monitoring duration, which was not the case in our study along with the SVL of the snakes. Thus, it appears that we monitored snakes for sufficient time to provide reliable home range estimates.

The MCP estimator has been prominent historically in snake spatial ecology studies but has been criticized for mischaracterization of home range sizes because of its tendency to include areas never used by monitored individuals (Powell 2000). *Sistrurus miliarius* individuals at DMCA generally stayed within a single habitat type and, except for roads, did not include areas that were unusable (open water and gravel parking lots). Therefore, it appears that MCPs suitably characterized home range sizes for our telemetered snakes. Further, when we compared an additional method that allowed for a flexible kernel-based estimate with low sample sizes using the 2016 data, we found that area estimates were similar to the MCP estimates.

Our prediction that reproductive status would influence spatial patterns and activity of females was generally supported. Gravid females exhibited fidelity to specific locations during pregnancy and significantly increased their home range sizes following parturition. These results are consistent with expectations for gravid pitvipers in temperate regions to occupy small home ranges centered on favorable microhabitats (Gregory et al. 1987; Reinert 1993). The dramatic increase in movements and area use for postpartum reproductive females in our study corroborate the general pattern that physiological constraints imposed by gestation promote sedentary behavior (Reinert 1993). In contrast, the frequency of movement of females did not change with reproductive status, but was consistently low across all snake categories, perhaps reflecting relative inactivity of ambush foraging strategists (Reinert et al. 1984; Webb

and Shine 1997). Small shuttling movements between different basking sites a few meters away from one another, however, could have gone unnoticed due to the tracking regime.

We also predicted that home ranges and movement rates of male *S. miliarius* at DMCA would exceed those of females because of the mate searching activities typical of male pitvipers; however, mean movement distances and home range sizes of males were only marginally larger than those for females. In *S. catenatus*, some studies have reported significant differences in movement parameters with males moving more frequently and/or longer distances (e.g., Weatherhead and Prior 1992; Durbian et al. 2008; DeGregorio et al. 2011), while others found no differences between sexes (Reinert and Kodrich 1982; Wastell and Mackessey 2011), which likely reflects differences in the spatial distribution and density of receptive females (Duvall et al. 1992). Encounter rates of receptive females by mate searching males could be relatively high for *S. miliarius* given the high population densities reported in the species (May et al. 1996) and the capacity for annual reproduction of females (Farrell et al. 1995; Farrell et al. 2009). That we observed nearly all our telemetered females that survived until mating season engaged in mating activity suggests that males were locating females easily at DMCA. Inferences regarding spatial patterns of male *S. miliarius* in our study, however, should be viewed cautiously because our male sample included only four individuals with high individual variation.

Habitat selection.—We found *S. miliarius* within all major habitat types at DMCA, and the home range of each snake included only one macrohabitat, suggesting little macrohabitat selection at the home range scale. This observation supports descriptions of the species as a macrohabitat generalist that occupies diverse environments ranging from upland hardwood forests and sandhills to floodplains and marshes (Mount 1975; Gibbons and Dorcas 2005). We confirmed that glades are an important habitat type for *S. miliarius* in Ozarks landscapes (Briggler and Johnson 2017) but found no evidence for them being glade specialists. Lack of habitat selection at the landscape level has been suggested to occur when preferred microhabitat features are available within multiple macrohabitats (e.g., Harvey and Weatherhead 2006). Our analysis is consistent with this interpretation in that *S. miliarius* did not select habitats based on canopy cover or distance to trees, explaining why both forested and open habitats were occupied. Instead, selection involved variables at the microhabitat scale related to surface cover. If this inference is correct, parallel studies would be of great interest to determine if the high diversity of habitats used

by *S. miliarius* throughout its range can be explained by selection for structural habitat components common to superficially dissimilar environments (Reinert 1993).

Sistrurus miliarius appears to select microhabitats based on a few structural variables that reflect an affiliation with surface cover. Telemetered snakes were typically close to retreat sites that included more shrubs and woody debris, and less leaf litter cover, than available at random sites. Unlike many snakes that are typically concealed underground (e.g., Gardiner et al. 2015; Richardson et al. 2006; Wund et al. 2007), *S. miliarius* rarely occupied subterranean refuges. Instead, snakes mainly remained on the surface within vegetative structure rather than other available shelter. Interestingly, rocks were not used more frequently than expected by their availability at DMCA despite suggestions based on visual encounters that *S. miliarius* is associated with rocky structure (Briggler and Johnson 2017). It is likely that visual detection bias distorts the understanding of habitat selection patterns for cryptic snake species, emphasizing the importance of radiotelemetry in informing habitat selection studies (Burger and Zappolorti 1988; Wasko and Sasa 2010).

Microhabitat selection patterns of *S. miliarius* and *S. catenatus* appear to involve similar responses to structural features. Analyses of an array of microhabitat variables indicate that both species typically associate with refuges involving ground level vegetation. The importance of shrubs as microhabitat cover is particularly interesting because of their 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 shrub cover may facilitate thermoregulation, it likely also provides cover from predators; at least four of our 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).

We conclude that *S. miliarius* primarily occupies forest and glade habitats in Ozarks landscapes and moves relatively infrequently within small home ranges. Home range size and extent of movement were considerably reduced in gravid individuals relative to other snakes and dramatically increased following parturition. This change in spatial pattern, however, did not appear to involve a concurrent change in habitat use as gravid individuals did not obviously select different habitat structure than other snakes. Given the apparently wide range of habitats and environmental conditions occupied within their geographic range, *S. miliarius* may be an excellent species to evaluate habitat selection processes at the landscape level. Comparative studies may be particularly interesting given various environmental

contrasts between DMCA, at the northern known distribution of *S. miliarius*, and most locations within the range of the species (Reinert 1993; DeGregorio et al. 2011, 2018). Thus, parallel studies on populations from different landscapes, climates, and latitudes would be of great interest.

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Herpetological Conservation and Biology



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APPENDICES

APPENDIX TABLE 1. Structural variable descriptions and sampling radii used to characterize microhabitat selection of the Pygmy Rattlesnake (*Sistrurus miliarius*) at Drury-Mincy Conservation Areas, Missouri, USA.

Variable	Description	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 (cm) of tallest woody stem	1
DLL	Depth (cm) of leaf litter within 1 m ²	1
%LEAF	% Leaf litter cover	1
%ROCK	% Rock cover	1
%WATER	% Water coverage	1
%BARE	% Bare ground coverage	1
DLOG	Distance (m) to log ≥ 7.5 cm in diameter	30
DIALOG	Max diameter (cm) of nearest log	30
DIAOS	Diameter (cm) at breast height of nearest overstory tree ≥ 7.5 cm DBH and > 2.0 m tall	30
DOS	Distance (m) to nearest overstory tree ≥ 7.5 cm DBH and > 2.0 m tall	30
DUS	Distance (m) to understory tree < 7.5 cm DBH and > 2.0 m tall	30
DSHRUB	Distance (m) to nearest shrub < 2.0 m tall	30
MDR	Mean distance (m) to nearest rocks > 10.0 cm long	30
LROCK	Mean max length (cm) of rocks used in MDR	30
DRETREAT	Distance (m) to nearest retreat site. Retreats were defined as any structure that could conceal a snake (e.g., mammal burrow, thick vegetation, large fallen logs, mammal middens). In other words, the only way for the research to see the snake is to destroy the feature that it is using for concealment (e.g., dig up the burrow, cut away the vegetation, remove the log, destroy the midden).	30

APPENDIX TABLE 2. Home range and movement summary for the Pygmy Rattlesnake (*Sistrurus miliarius*) implanted with radio transmitters at the at Drury-Mincy Conservation Areas, Missouri, USA, during 2016–2017. Abbreviations are F = female, M = male, G = gravid, SVL = snout-vent length, Loc = number of locations occupied, Dist = distance, D = days, MCP = Minimum Convex Polygon, Unk = unknown, Depredated (b) = depredated by bird of prey, and Depredated (m) = depredated by mammalian predator/scavenger. Individuals denoted by an asterisk (*) were supplementally fed prior to transmitter implantation. Distances are reported as meters per day, per move, and among locations. Means are reported (\pm 1 standard error).

Snake	Year	SVL (mm)	Sex	Days tracked	Loc	Dist/day (m)	Dist/move (m)	Dist/loc (m)	Moves/d	MCP (ha)	Fate
Females During Gestation											
1*	2016	355	F(G)	75	53	4.5(1.9)	16.9(3.6)	9.1 (2.7)	0.27	0.61	Died (unk)
2	2016	363	F(G)	75	37	1.8(0.8)	8.1(1.6)	3.7(1.1)	0.23	0.08	Lost signal
4	2016	395	F(G)	71	35	3.3(1.3)	13.1(2.7)	6.7(1.9)	0.25	0.42	Lost signal
7	2016	361	F(G)	71	36	3.3(1.47)	11.3(2.5)	6.6(1.9)	0.30	0.33	Lost signal
9	2016	395	F(G)	48	24	0.3(0.2)	2.3(0.4)	0.7(0.2)	0.15	0.01	Depredated (b)
12	2016	331	F(G)	8	3	N/A	N/A	N/A	N/A	N/A	Died (unk)
18	2016	324	F(G)	30	15	0.3(0.5)	9.4(2.5)	0.6(0.7)	0.03	< 0.001	Hibernated
24	2016	390	F(G)	17	9	0.7(0.4)	2.6(0.7)	1.5(0.5)	0.29	0.008	Hibernated
39	2017	379	F(G)	13	6	N/A	N/A	N/A	N/A	N/A	Died (unk)
Females After Parturition											
1*	2016	335	F	63	16	12.0(3.9)	50.3(7.9)	47.1(7.9)	0.24	1.48	Died (unk)
2	2016	363	F	75	17	4.9(2.5)	28.8(5.9)	22.0(5.3)	0.17	0.28	Lost signal
4	2016	395	F	74	20	13.3(4.5)	54.6(9.1)	49.1(8.9)	0.24	2.63	Lost signal
7	2016	361	F	37	7	5.6(6.5)	52.3(19.9)	29.9(16.3)	0.11	0.41	Lost signal
9	2016	395	F	18	6	9.7(11.4)	43.8(24.2)	29.2(21.6)	0.22	0.26	Depredated (b)
18	2016	324	F	76	19	5.6(3.9)	27.8(8.6)	23.4(8.1)	0.20	1.10	Hibernated
24	2016	390	F	76	19	5.3(2.4)	25.4(5.3)	21.5(5.0)	0.21	1.13	Hibernated
Non-gravid Females											
2	2017	363	F	85	32	8.6(2.9)	33.1(5.9)	22.8(4.9)	0.26	1.89	Hibernated
10*	2016	335	F	79	23	6.3(4.20)	33.3(9.7)	21.7(8.0)	0.19	0.95	Depredated (b)
23	2016	360	F	5	3	N/A	N/A	N/A	N/A	N/A	Died (unk)
25	2016	362	F	58	17	1.3(0.8)	8.7(2.2)	4.6(1.6)	0.16	0.07	Died (unk)
40	2017	372	F	41	16	4.9(2.7)	18.2(5.1)	12.5(4.4)	0.27	0.13	Lost signal
Males											
8*	2016	327	M	77	22	4.8(2.0)	24.6(4.6)	16.8(3.9)	0.20	0.53	Hibernated
21	2016	360	M	9	5	N/A	N/A	N/A	N/A	N/A	Depredated (m)
27	2016	415	M	43	11	15.5(15.6)	110.8(42.0)	60.4(32.5)	0.14	2.20	Died (unk)
34*	2017	312	M	89	33	7.6(2.1)	24.3(3.8)	20.6(3.6)	0.31	0.44	Hibernated
42	2017	393	M	107	40	11.8(4.2)	38.3(7.5)	31.6(6.9)	0.31	2.24	Hibernated
48	2017	348	M	0	0	N/A	N/A	N/A	N/A	N/A	Depredated (<i>Lampropeltis holbrooki</i>)

APPENDIX TABLE 3. Top candidate models explaining microhabitat selection by the Pygmy Rattlesnake (*Sistrurus miliarius*) at Drury/Mincy Conservation Area in Southwestern Missouri, USA. Variable abbreviations are explained in Appendix Table 1.

Model	df	Log likelihood	AIC	Δ AIC	Weight
%BARE+%DIALOG+DLOG+DRETREAT+DSHRUB+DUS+%LEAF	7	-119.93	253.9	0.00	0.167
%BARE+%DIALOG+DLOG+DRETREAT+DSHRUB+%LEAF	6	-120.93	253.9	0.01	0.167
%BARE+%DIALOG+DIAOS+DLOG+DRETREAT+DSHRUB+DUS+%LEAF	8	-119.29	254.6	0.72	0.117
%BARE+%DIALOG+DIAOS+DLOG+DRETREAT+DSHRUB+%LEAF	7	-120.50	255.0	1.14	0.095
%BARE+%DIALOG+DRETREAT+DSHRUB+DUS+%LEAF	6	-121.67	255.3	1.48	0.080
%BARE+%CANCOV+%DIALOG+DLOG+DRETREAT+DSHRUB+DUS+%LEAF	8	-119.68	255.4	1.50	0.079
%BARE+%DIALOG+DLOG+DRETREAT+DSHRUB+DUS+%LEAF+%VEG	8	-119.69	255.4	1.53	0.078
%BARE+%DIALOG+DLOG+DRETREAT+DSHRUB+%LEAF+%VEG	7	-120.72	255.4	1.57	0.076
%BARE+%CANCOV+%DIALOG+DLOG+DRETREAT+DSHRUB+%LEAF	7	-120.74	255.5	1.61	0.075
%BARE+%DIALOG+DRETREAT+DSHRUB+DUS+%LEAF	7	-120.86	255.7	1.85	0.066