

MOVEMENTS AND HABITAT USE BY WESTERN RATSNAKES (*PANTHEROPHIS OBSOLETUS*) IN A FRAGMENTED MIDWESTERN LANDSCAPE

ANDREW D. GEORGE^{1,4}, FRANK R. THOMPSON III², AND JOHN FAABORG³

¹Department of Biology, Pittsburg State University, 1701 South Broadway Street, Pittsburg, Kansas 66762, USA

²U.S.D.A. Forest Service Northern Research Station, 202 ABNR Building, Columbia, Missouri 65211, USA

³Division of Biological Sciences, University of Missouri, 105 Tucker Hall, Columbia, Missouri 65211, USA

⁴Corresponding author; e-mail: adgeorge@pittstate.edu

Abstract.—North American ratsnakes (*Pantherophis* spp.) are regionally important predators whose behavior has previously been linked to habitat fragmentation and climate change. Ratsnakes are hypothesized to benefit from fragmentation that creates favorable microclimates, but previous studies have produced inconsistent results, potentially reflecting geographic variation or study design limitations. We used radiotelemetry and kernel-based home range estimators to evaluate the seasonal movements and habitat use of 53 Western Ratsnakes (*Pantherophis obsoletus*) in central Missouri, USA. Snakes frequently remained in the same location for several days at a time, and often returned to the same locations used previously, suggesting apparent spatial memory. Consistent with seasonal reproductive behavior, home range size and distance moved per day were greater for males than females during April–June, but not July–September. Resource utilization functions indicated a negative linear relationship between intensity of space use and distance to forest-field edges for males during the early period and for females during both the early and late periods. The spatial behavior of Western Ratsnakes was affected by sex, season, and vegetation density. Ratsnake use of edge habitats may explain increased avian predation rates near edges and in fragmented landscapes.

Key Words.—edge effects; habitat fragmentation; home range; spatial ecology; utilization distributions

INTRODUCTION

Movement patterns and space use are among the most fundamental aspects of animal ecology. The frequency and distance of movements, area traversed (i.e., home range), and habitats used reflect availability of food, water, access to mates, and shelter sites that may vary widely across landscapes and through time (Burt 1943; Bowler and Benton 2005). Movement patterns typically involve tradeoffs between access to resources and energy expenditures or predation risk. Thus, animal spatial ecology is closely linked to physiology, population dynamics, and species interactions (Tilman and Kareiva 1997). Knowledge of the spatial requirements of a species is also critical for habitat management and conservation planning (Winter and Faaborg 1999; Pe'er et al. 2014; Fauvellet et al. 2017).

Although the majority of spatial ecology literature has focused on mammals and birds, the miniaturization and automation of tracking technology, coupled with new analytical approaches, has increasingly allowed researchers to study movements of ectotherms, including secretive species such as snakes (Dorcas and Willson 2009; Kays et al. 2015; George et al. 2017). Some general spatial patterns have remained consistent between reptiles

and other terrestrial vertebrates. For example, space use increases with body size, and carnivores have larger home ranges than herbivores (Tamburello et al. 2015; Todd and Nowakowski 2021). Males often move longer distances or have larger home ranges than females (Gregory et al. 1987; Perry and Garland 2002). Within populations, home range size is related to habitat type or resource availability (Kapfer et al. 2010; Breiningner et al. 2011; Young et al. 2018). Despite these basic advances, the spatial ecology of most ectotherms remains poorly understood compared to endotherms, reflecting broader taxonomic biases (Rosenthal et al. 2017). Specific information regarding movement patterns and habitat use is needed, particularly for species facing conservation threats, or species that are model organisms for understanding ecosystem processes (Pittman et al. 2014; Fraser et al. 2018).

Ratsnakes (*Pantherophis* spp.) represent a group of large-bodied Colubrid snakes that are widespread in eastern North America (Burbrink 2001). Where they occur, ratsnakes are predominant predators of birds and small mammals, and their foraging behavior has been linked to prey productivity (Thompson and Burhans 2003; Cox et al. 2013; DeGregorio et al. 2015). Ratsnakes have also become model organisms for understanding the effects of global warming on ectotherm physiology, behavior, and

predator-prey interactions (Weatherhead et al. 2012; Cox et al. 2013; George et al. 2015). Considerable behavioral variation has been documented across the geographic range of ratsnakes, including latitudinal gradients in daily and seasonal activity patterns (Stake et al. 2005; Sperry et al. 2010; Howze et al. 2019). In some cases, this variation may reflect geographic and ecological differences among populations. Alternatively, apparent behavioral variation may reflect differences in study design or sampling limitations. For example, results from two telemetry studies of ratsnakes reported preference for forested habitats and avoidance of open habitats (Keller and Heske 2000; Carfagno and Weatherhead 2006). In contrast, the most comprehensive study of ratsnake habitat selection to date in terms of sampling design and modeling framework found strong seasonal preference for habitats that provide thermal heterogeneity, including fields and forest-field edges (George et al. 2017). An increase of edge habitat is a consequence of habitat fragmentation, and ratsnakes are frequent bird nest predators near forest-field edges and in old fields when compared to forest interiors (Thompson and Burhans 2003; Cox et al. 2012). Thus, evaluating ratsnake movement patterns and use of forest-field edges is particularly important for understanding effects of habitat fragmentation on ratsnakes and their prey.

We used radiotelemetry to study the spatial ecology of Western Ratsnakes (*Pantherophis obsoletus*; Fig. 1) in a system where they have been identified as important predators of nesting birds (Thompson and Burhans 2003; Cox et al. 2012). Our goal was to identify factors that affect movements and home range size, and to describe the habitat features used by snakes across their active season. We hypothesized that space use would reflect habitat selection and activity patterns previously identified in our study population (George et al. 2015, 2017), and



FIGURE 1. A Western Ratsnake (*Pantherophis obsoletus*) at Three Creeks Conservation Area in central Missouri, USA. (Photographed by Andrew George).

predict that home ranges will encompass forest-field edges and will be larger for males than females during the spring breeding period. In contrast to traditional point-based analyses, we used Utilization Distributions (UDs; Millspaugh et al. 2006) to model spatial variation in intensity of use across the home ranges of individual snakes. Thus, we considered ratsnake habitat use as a continuous and probabilistic surface instead of discrete categories (i.e., used versus unused). This approach permitted us to describe finer scale variation in home range composition than has been possible with previous studies of snake spatial ecology.

MATERIALS AND METHODS

Study area.—We studied Western Ratsnakes in central Missouri on the Thomas S. Baskett Wildlife Research and Education Center (38°44'N, 92°12'W) and on the Three Creeks Conservation Area (38°49'N, 92°17'W), which were 917 ha and 607 ha, respectively, and classified as Oak Woodland/Forest Hills within the Outer Ozark Border ecological subsection (Nigh and Schroeder 2002). Forests covered approximately 73% of the study area and were dominated by second-growth Mixed Oak-Hickory (*Quercus* spp., *Carya* spp.) Forest, with Sugar Maple (*Acer saccharum*) dominating the understory. Forests were interspersed with abandoned fields or early successional Red Cedar (*Juniperus virginiana*). Nest camera studies have identified the Western Ratsnake as the most frequent nest predator of multiple bird species in the region, including in our specific study areas (Thompson and Burhans 2003; Cox et al. 2012).

Radiotelemetry.—We used radiotelemetry to track 53 ratsnakes from 2010–2013. We captured snakes opportunistically by hand or using funnel traps and drift fences placed around hibernacula during spring emergence in March. We surgically implanted snakes with radio-transmitters (models R1530, R1535, R1680, R1655; Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) using standard methods (Reinert and Cundall 1982; Blouin-Demers et al. 2000). Transmitter mass ranged from 1.2 to 14 g and was always < 3% of the body mass. Using different transmitter models allowed us to maximize transmitter battery life in a variety of snake body sizes. We monitored snakes for 3 d in captivity after surgery and then released them in the same locations where they were captured.

With few exceptions, we tracked snakes in a rotating order a minimum of 4 d/week during the morning, afternoon, evening, and after dark, from April through September using a handheld receiver and antenna (models R410, R2000, 13562, 13863; Advanced Telemetry Systems, Inc.). We always tracked snakes to actual locations, i.e., we never used triangulation. Each

time a snake was located, we recorded GPS coordinates, behavioral observations (e.g., moving, basking, or hidden), and whether the snake was in a new location, the same location as the previous location, or had returned to an earlier location. We also recorded the substrate that the snake was in and the height above ground of the snake. We classified heights as high (> 3 m), low (> 0 but ≤ 3 m), or ground (≤ 0 m). We classified substrates as building/hay, ground, tree/snag, or coarse woody debris. Building/hay was included as a single category because snakes regularly used hay bales stacked next to barns. Coarse woody debris included stumps, logs, and brush. We calculated the proportion of locations for each individual that fell within class levels of each variable and calculated the mean and standard error of these proportions across individuals by sex, by month, and in total.

Data analysis.—To characterize ratsnake activity and space use, we estimated the home range for each individual across each year and within two time periods: early (April–June) and late (July–September). Minimum convex polygons (MCP) are the most widely used method for estimating home range area in herpetofauna, but MCPs do not account for continuous spatial variation in use within the home range (Kernohan et al. 2001). Kernel Density Estimators (KDE) are a robust alternative to MCPs that can be used to relate intensity or probability of use (i.e., the UD) to underlying resources (Marzluff et al. 2004, Millspaugh et al. 2006). KDEs require selection of a smoothing factor (h) but commonly used methods for h -factor selection, such as least squares cross validation or the reference method, may result in erroneous home range estimates for animals that move infrequently or that reuse locations (Row and Blouin-Demers 2006). Therefore, following Row and Blouin-Demers (2006), we first generated MCPs for each ratsnake and then adjusted KDE h -factors until the area of the 95% probability contour of the KDE matched the area of the MCP.

We used Linear Mixed Models within an information theoretic framework to evaluate the effects of sex, snout-vent length (SVL), and time period on ratsnake seasonal home range size and distance moved per day (Burnham and Anderson 2002). Distance per day calculations were based on Euclidian distance and only included sequential locations taken < 48 h apart. Calculations from longer time steps may be biased due to increasingly non-linear trajectories (George et al. 2015). For each response variable, we fit a set of 14 *a priori* candidate models that included combinations of additive and two-way interaction terms for each predictor variable, a global model with all predictor variables, and a null model with only the intercept. To account for non-independence of repeated estimates from individual snakes within and among years, all models included random intercepts for year nested by snake. We ranked models using Akaike

Information Criterion corrected for small sample size (AIC_c) and model weights. We based inference on models with $\Delta AIC_c < 2$ and assessed overall model fit by calculating the conditional R^2 (Burnham and Anderson 2002; Nakagawa and Schielzeth 2013).

To evaluate habitat use, we generated Resource Utilization Functions (RUF) that related space use within the 95% UD contours of individual snakes to fine-scale vegetation characteristics including canopy density (height > 3 m), understory density (height > 1 m but ≤ 3 m), and distance to the nearest forest-field edge (Marzluff et al. 2004; Millspaugh et al. 2006). We constructed the RUFs by fitting linear models with log-transformed UD cell values as the response variable and the three LiDAR-derived habitat rasters as additive predictor variables for each snake in each time period and then averaged model coefficients across time period and sex. We calculated standard errors and 95% confidence intervals across model coefficients; thus, population-level estimates did not incorporate intra-individual variation (Millspaugh et al. 2006). We also calculated the proportion of each home range by volume of the 95% UD that encompassed forest, edge, and open habitats. We classified edge using a 15-m buffer from forest boundaries. Habitat rasters were derived from 2009 LiDAR data downloaded from the Missouri Spatial Data Information Service (<http://www.msdis.missouri.edu>; George et al. 2017). We performed all analyses using program R version 4.1.0 and with packages nlme and adehabitatHR (Calenge 2006; Pinheiro et al. 2021; R Core Team 2021).

RESULTS

We tracked 36 male and 17 female Western Ratsnakes in 2010–2013. We captured and measured an additional 18 males and seven females but did not implant them with radio-transmitters. Mean body mass for males was $543.7 \pm$ (standard error) 42.1 g (range, 73–1,285 g). Mean body mass for females was 473.0 ± 33.9 g (range, 284–967 g). Mean snout-vent length for males was 112.8 ± 2.7 cm (range, 62–157 cm) and for females was 109.5 ± 2.0 cm (range, 97–132 cm). We obtained 55.0 ± 7.9 locations per snake from eight snakes in 2010, 32.9 ± 12.7 locations from 22 snakes in 2011, 61.9 ± 16.7 locations per snake from 41 snakes in 2012, and 42.1 ± 11.8 locations per snake from 22 snakes in 2013 for a total of 4,615 locations. We tracked 33 snakes for at least 2 y, and we tracked seven snakes for at least 3 y. All other snakes were only tracked in 1 y.

We did not see ratsnakes at most locations, but we saw males twice as frequently as females during the early period (Fig. 2). We located both sexes most frequently on or near the ground, but we found snakes on elevated locations approximately 40% of the time during the early period and 20% of the time during the late period (Fig.

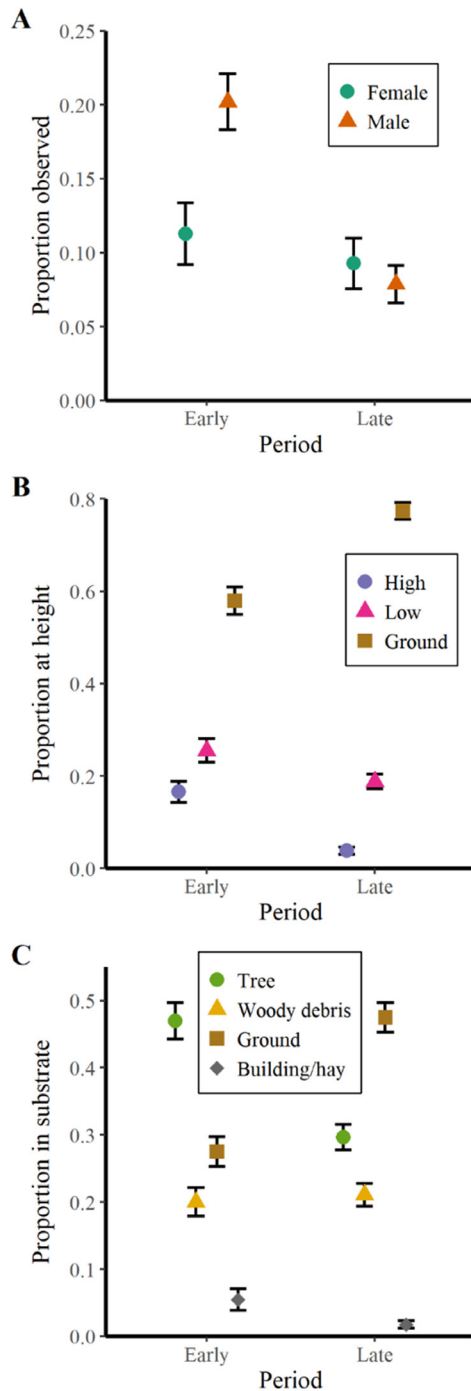


FIGURE 2. Mean (\pm standard error) proportion of locations in which 36 male and 17 female Western Ratsnakes (*Pantherophis obsoletus*) (A) were visually observed; (B) used high (> 3 m), low (> 0 but ≤ 3 m), or ground (≤ 0 m) heights; and (C) used trees, woody debris, ground, or buildings or hay during the early (April-June) and late (July-September) time periods in central Missouri, USA, 2010–2013. Proportions were first calculated by individual snake and then averaged within time periods.

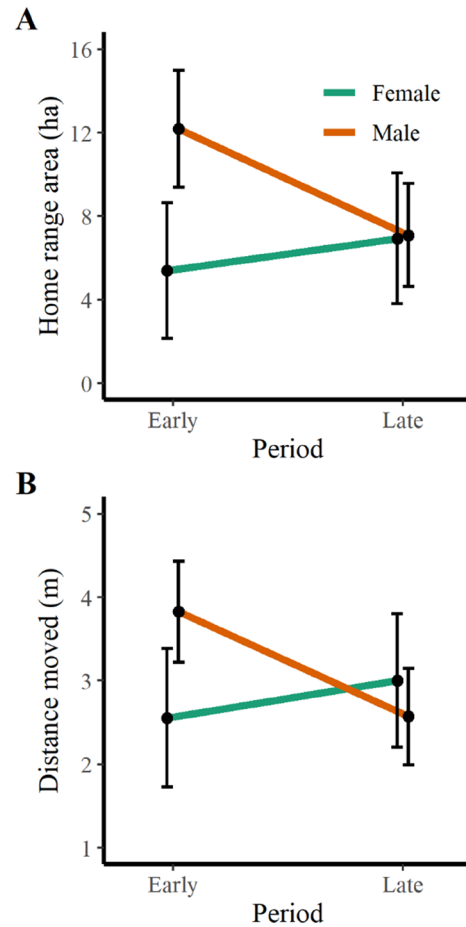


FIGURE 3. Predictions for the best-supported models showing the effects time period and sex on (A) home range size and (B) distance moved per day for Western Ratsnakes (*Pantherophis obsoletus*) in central Missouri, USA, 2010–2013. Error bars represent 95% confidence intervals.

2). Snakes used trees most frequently during the early period and ground habitats most frequently in the late period (Fig. 2). We frequently found multiple individuals together in the same location early in the season, and they often remained in the same location for several days at a time and frequently returned to the same locations they used previously.

Annual home range area (95% UD contour) was 15.68 ± 1.84 ha for males and 16.94 ± 2.90 ha for females and core area (50% UD contour) was 3.00 ± 0.35 ha for males and 3.28 ± 0.59 ha for females. The best supported models for both home range and distance moved per day included interactions between sex and time period (Tables 1 and 2). Home range size and distance moved per day were greater for males than females during the early period. Male space use decreased from the early period to the late period when home range size and distance moved per day were similar between males and females (Fig 3).

TABLE 1. Model-selection results from the five best-ranked *a priori* candidate models of the effects of time period, sex, and snout-vent length (SVL) on home range size and distance moved per day for Western Ratsnakes (*Pantherophis obsoletus*) in central Missouri, USA, 2010–2013. The null (intercept-only) model is also included for comparison. K represents the number of fixed and random variables in the model, w_i represents the relative model weight, and R^2_c represents the conditional coefficient of determination.

Response	Model	K	ΔAIC_c	w_i	R^2_c
Home range	Time period \times sex	5	0.00	0.88	0.45
	SVL + time period \times sex	6	4.34	0.10	0.44
	Time period + sex	4	9.47	0.01	0.33
	Sex + time period \times SVL	6	12.67	0.00	0.41
	Sex	3	12.83	0.00	0.29
	Null	2	16.30	0.00	0.29
Distance moved	Time period \times sex	5	0.00	0.77	0.32
	Time period	3	4.34	0.09	0.16
	Null	2	5.28	0.05	0.02
	Time period + sex	4	5.63	0.05	0.16
	Sex	3	6.54	0.03	0.02
	SVL + time period \times sex	6	8.25	0.01	0.34

Home range composition varied among snakes, but nearly all individuals used forests or forest-field edges more than open habitats during both the early and late time periods (Fig 4). RUFs indicated that ratsnake space use declined with distance to edges for both males and females during the early period and females during the late period (Table 3). Space use was negatively related to understory cover for males during the early period. Models did not detect population-level relationships between ratsnake space use and canopy density (Table 3).

DISCUSSION

A basic understanding of spatial ecology of any species remains a fundamental goal for targeted conservation actions. We evaluated the movements and habitat use of Western Ratsnakes in the central portion of their geographic range, in study sites where their

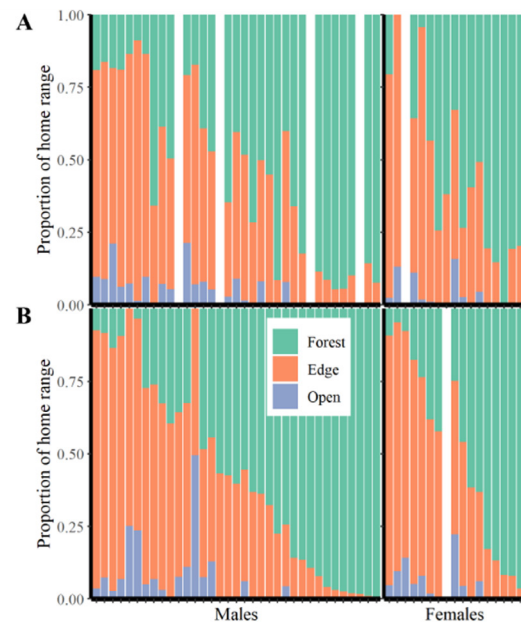


FIGURE 4. Home range composition by volume of 53 individual male and female Western Ratsnakes (*Pantherophis obsoletus*) during (A) the early (April-June) and (B) the late (July-September) time periods in central Missouri, USA, 2010–2013. Home range estimation is based on the 95% Utilization Distribution (UD) contour. Bars in the early and late time periods are aligned to correspond to the same individual snakes.

behavior has previously been linked to both climate change and habitat fragmentation. Habitat and space use varied seasonally between sexes and among individuals, but snakes used forest and forest-field edges more than open habitats.

Whereas ratsnake annual home range areas were similar between sexes, males had larger home ranges than females from April to June. Likewise, twice as many males were captured, and males were twice as likely as females to be visually observed when radio-tracked early in the season. Ratsnakes in Missouri and other regions also show seasonal differences between sexes, with males more active, more likely

TABLE 2. Estimated coefficients for the best supported models of the effects of time period, sex, and snout-vent length (SVL) on home range size and distance moved per day for Western Ratsnakes (*Pantherophis obsoletus*) in central Missouri, USA, 2010–2013.

Response	Parameter	Coefficient	SE	Lower 95% CI	Upper 95% CI
Home range	Intercept	5.39	1.63	2.20	8.59
	Late period	1.54	1.70	-1.78	4.87
	Male	6.79	2.15	2.57	11.0
	Late period \times male	-6.63	2.22	-11.0	-2.29
Distance moved	Intercept	2.55	0.41	1.74	3.37
	Late period	0.45	0.50	-0.53	1.43
	Male	1.27	0.51	0.26	2.28
	Late period \times male	-1.70	0.62	-2.91	-0.49

TABLE 3. Estimates of unstandardized Resource Utilization Function (RUF) coefficients for 53 male and female Western Ratsnakes (*Pantherophis obsoletus*) during the early (April–June) and late (July–September) time periods in central Missouri, USA, 2010–2013.

Time period	Sex	n	Parameter	Coefficient	SE	Lower 95% CI	Upper 95% CI
Early	Male	31	Canopy density	0.04	0.12	-0.19	0.26
			Edge distance	-0.44	0.13	-0.70	-0.17
			Understory	-0.25	0.12	-0.48	-0.01
	Female	16	Canopy density	0.19	0.35	-0.50	0.88
			Edge distance	-0.84	0.30	-1.43	-0.25
			Understory density	-0.48	0.27	-1.01	0.06
Late	Male	35	Canopy density	-0.03	0.13	-0.28	0.23
			Edge distance	-0.31	0.17	-0.64	0.03
			Understory density	-0.13	0.23	-0.59	0.32
	Female	16	Canopy density	-0.01	0.16	-0.32	0.31
			Edge distance	-0.83	0.29	-1.40	-0.27
			Understory density	-0.24	0.29	-0.81	0.33
Combined		98	Canopy density	0.03	0.09	-0.14	0.20
			Edge distance	-0.52	0.10	-0.72	-0.32
			Understory density	-0.24	0.11	-0.46	-0.02

to be observed, or using larger home ranges than females (Durner and Gates 1993; Blouin-Demers and Weatherhead 2001a; Carfagno and Weatherhead 2008; George et al. 2015). Increased activity and space use by males is consistent with mate searching behavior; male snakes become active earlier in the spring and move more frequently than females because males gain a direct fitness advantage by mating with as many females as possible (Gibbons and Semlitsch 1987).

Ratsnakes regularly used trees throughout the active season, and hollow trees were the most frequently used substrate for both sexes during the early period in our study and others (Durner and Gates 1993; Mullin et al. 2000). Ratsnakes might use trees for shelter as they digest meals or as places to hunt rodents or birds, their primary prey items (Weatherhead et al. 2003). We regularly observed multiple individuals simultaneously using the same trees during April and May, and directly observed reproductive behaviors on a few occasions, indicating that ratsnakes also used trees as mating sites. In 2011 and 2012 we occasionally observed snakes submerged in pools of water inside hollow trees for several days at a time. This behavior may aid in ecdysis or water regulation during periods when ratsnakes are limited by dry conditions (George et al. 2015; DeGregorio et al. 2021). The decline in tree use as the season progressed may indicate that trees did not provide adequate shelter from high temperatures during late summer (Bryant et al. 2012).

Forest-field edges were a central component of most ratsnake home ranges and probability of use was greatest near edges for males and females during both time periods. Ratsnake use of forest-field edges has

previously been suggested as a mechanism underlying fragmentation effects in eastern North America. Ratsnakes preferentially select forest-edge habitat because edges offer opportunities to thermoregulate (Blouin-Demers and Weatherhead 2001b; George et al. 2017). Edges may also provide access to rodents and nesting birds in adjacent habitats (Thompson and Burhans 2003). Thus, forest fragmentation may benefit ratsnake populations by increasing their preferred habitat. In contrast, two studies in Illinois reported avoidance of open habitats in favor of forests, prompting researchers to suggest that forest fragmentation could be detrimental to ratsnakes in the central part of their geographic range (Keller and Heske 2000; Carfagno and Weatherhead 2006). These studies, however, measured habitat use based on potentially arbitrary classifications of individual locations as either used or unused. Our use of RUFs permitted us to consider ratsnake habitat use as a continuous process that varied in intensity across the entire home range (i.e., the UD) instead of a limited number of discrete locations. We could therefore quantify the relative importance of vegetation structure such as forest-field edges based on its spatial arrangement within the home range. Old fields can seasonally provide fine-scale habitat structure and prey for foraging ratsnakes (Thompson and Burhans 2003; George et al. 2017). Our results suggest that use of old fields and other open habitats may be mediated by distance to woody cover, i.e., ratsnakes may readily use these habitats if they are in close proximity to forests.

High bird nest predation rates are often associated with habitat fragmentation, and ratsnakes have been

identified as the most frequent nest predators in fragmented landscapes in eastern North America (Robinson et al. 1995; Thompson 2007). For example, ratsnakes were responsible for 72% and 33% of predation events in old fields and forests, respectively, and were among the most frequent nest predators in fragmented landscapes, including on our specific study sites (Thompson and Burhans 2003; Cox et al. 2012). Two hypotheses, which are not mutually exclusive, have been suggested to explain why snakes might depredate more nests in forest fragments (Chalfoun et al. 2002; Weatherhead and Blouin-Demers 2004). First, snakes might be more abundant in fragmented areas, reflecting greater abundance or diversity of prey species or other resources (e.g., Fink et al. 2006). Alternatively, snakes might preferentially select edge habitats more often when they are available, and thereby encounter more nests of edge-nesting birds in fragmented regions (George et al. 2017). The first (i.e., numerical) hypothesis has not been directly tested, in part because a reliable method for measuring ratsnake abundance has not been developed. The results of our study provide support for the second (i.e., functional) hypothesis, albeit indirectly, by showing that ratsnake space use increases with proximity to edge.

Habitat loss and fragmentation are among the greatest threats to global biodiversity, including in eastern North America (Faaborg et al. 1995; Haddad et al. 2015). Future research that addresses the two aforementioned hypotheses (i.e., numerical vs. functional), especially among different populations or species, will better elucidate how snakes and their prey respond to habitat fragmentation. For example, snake radiotelemetry studies could compare seasonal behavior patterns between fragmented and contiguous landscapes in different geographic regions. Nevertheless, the spatial ecology of snakes and other secretive ectotherms remains understudied (Mullin and Seigel 2009). Effective snake conservation will continue to benefit from basic information on movement patterns and habitat use.

Acknowledgments.—We thank Andy Mueller, Anna Zack, Andrew Cave, Sam Mayne, and Jon Wheeler who assisted with field work. Jenn Ballard and Susan Szczepanski helped with transmitter implantation. Ray Semlitsch, Jim Carrel, and Janet Zepernick provided constructive comments to an earlier draft of this manuscript. Funding for this project was provided by the USDA Forest Service Northern Research Station and the University of Missouri. All methods were approved by the Animal Care and Use Committee of the University of Missouri (#6605) and Missouri Department of Conservation (#14600).

LITERATURE CITED

- Blouin-Demers, G., and P.J. Weatherhead. 2001a. Habitat use by Black Rat Snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 82:2882–2896.
- Blouin-Demers, G., and P.J. Weatherhead. 2001b. Thermal ecology of Black Rat Snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology* 82:3025–3043.
- Blouin-Demers, G., P.J. Weatherhead, C.M. Shilton, C.E. Parent, and G.P. Brown. 2000. Use of inhalant anesthetics in three snake species. *Contemporary Herpetology* 2000. <https://journals.ku.edu/ch/article/view/11963>.
- Bowler, D.E., and T.G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80:205–225.
- Breining, D.M., M.R. Bolt, M.L. Legare, J.H. Drese, and E.D. Stolen. 2011. Factors influencing home-range sizes of Eastern Indigo Snakes in central Florida. *Journal of Herpetology* 45:484–490.
- Bryant, G.L., S.J. Dundas, and P.A. Fleming. 2012. Tree hollows are of conservation importance for a near-threatened python species. *Journal of Zoology* 286:81–92.
- Burbrink, F.T. 2001. Systematics of the Eastern Ratsnake complex (*Elaphe obsoleta*). *Herpetological Monographs* 15:1–53.
- Burnham, K.P., and D.R. Anderson. 2002. *Model Selection and Multimodel Inference*. 2nd Edition. Springer-Verlag, New York, New York, USA.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346–352.
- 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.
- Carfagno, G.L.F., and P.J. Weatherhead. 2006. Intraspecific and interspecific variation in use of forest-edge habitat by snakes. *Canadian Journal of Zoology* 84:1440–1452.
- Carfagno, G.L.F., and P.J. Weatherhead. 2008. Energetics and space use: intraspecific and interspecific comparisons of movements and home ranges of two Colubrid snakes. *Journal of Animal Ecology* 77:416–424.
- Chalfoun, A.D., F.R. Thompson, III, and M.J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* 16:306–318.
- Cox, W.A., F.R. Thompson, III, and J. Faaborg. 2012. Landscape forest cover and edge effects on songbird nest predation vary by nest predator. *Landscape*

- Ecology 27:659–669.
- Cox, W.A., F.R. Thompson, III, and J.L. Reidy. 2013. The effects of temperature on nest predation by mammals, birds, and snakes. *Auk* 130:784–790.
- Cox, W.A., F.R. Thompson, III, J.L. Reidy, and J. Faaborg. 2013. Temperature can interact with landscape factors to affect songbird productivity. *Global Change Biology* 19:1064–1074.
- DeGregorio, B.A., J.H. Sperry, and P.J. Weatherhead. 2021. Factors influencing the use of water-filled tree cavities by Eastern Ratsnakes (*Pantherophis alleghaniensis*). *Herpetological Conservation and Biology* 16:173–182.
- DeGregorio, B.A., J.D. Westervelt, P.J. Weatherhead, and J.H. Sperry. 2015. Indirect effect of climate change: shifts in ratsnake behavior alter intensity and timing of avian nest predation. *Ecological Modelling* 312:239–246.
- Dorcas, M.E., and J.D. Willson. 2009. Innovative methods for studies of snake ecology and conservation. Pp. 5–37 *In* Snakes: Ecology and Conservation. Mullin, S.J. and R.A. Seigel (Eds.). Cornell University Press, Ithaca, New York, USA.
- Durner, G.M., and J.E. Gates. 1993. Spatial ecology of Black Rat Snakes on Remington Farms, Maryland. *Journal of Wildlife Management* 57:812–826.
- Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pp. 357–380 *In* Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues. Martin, T.E., and D.M. Finch (Eds.). Oxford University Press, New York, New York, USA.
- Fauvelle, C., R. Diepstraten, and T. Jessen. 2017. A meta-analysis of home range studies in the context of trophic levels: Implications for policy-based conservation. *PLoS ONE* 12(3):e0173361. <https://doi.org/10.1371/journal.pone.0173361>.
- Fink, A.D., F.R. Thompson, III, and A.A. Tudor. 2006. Songbird use of regenerating forest, glade, and edge habitat types. *Journal of Wildlife Management* 70:180–188.
- Fraser, K.C., K.T.A. Davies, C.M. Davy, A.T. Ford, D.T.T. Flockhart, and E.G. Martins. 2018. Tracking the conservation promise of movement ecology. *Frontiers in Ecology and Evolution* 6. <https://doi.org/10.3389/fevo.2018.00150/full>.
- George, A.D., G.M. Connette, F.R. Thompson, III, and J. Faaborg. 2017. Resource selection by an ectothermic predator in a dynamic thermal landscape. *Ecology and Evolution* 7:9557–9566.
- George, A.D., F.R. Thompson, III, and J. Faaborg. 2015. Isolating weather effects from seasonal activity patterns of a temperate North American Colubrid. *Oecologia* 178:1251–1259.
- Gibbons, J.W., and R.D. Semlitsch. 1987. Activity patterns. Pp. 396–421 *In* Snakes: Ecology and Evolutionary Biology. Seigel, R.A., J.T. Collins, and S.S. Novak (Eds.). Macmillan Publishing Company, New York, New York, USA.
- Gregory P.T., J.M. Macartney, and K.W. Larsen. 1987. Spatial patterns and movements. Pp. 366–395 *In* Snakes: Ecology and Evolutionary Biology. Seigel, R.A., J.T. Collins, and S.S. Novak (Eds.). Macmillan Publishing Company, New York, New York, USA.
- Haddad, N.M., L.A. Brudvig, J. Clobert, K.F. Davies, A. Gonzalez, R.D. Holt, T.E. Lovejoy, J.O. Sexton, M.P. Austin, C.D. Collins, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1:e1500052. <https://doi.org/full/10.1126/sciadv.1500052>.
- Howze, J.M., K.J. Sash, J.P. Carroll, and L.L. Smith. 2019. A regional scale assessment of habitat selection and home range of the Eastern Rat Snake in pine-dominated forests. *Forest Ecology and Management* 432:225–230.
- Kapfer, J.M., C.W. Pekar, D.M. Reineke, J.R. Coggins, and R. Hay. 2010. Modeling the relationship between habitat preferences and home-range size: a case study on a large mobile colubrid snake from North America. *Journal of Zoology* 282:13–20.
- Kays, R., M.C. Crofoot, W. Jetz, and M. Wikelski. 2015. Terrestrial animal tracking as an eye on life and planet. *Science* 348:aaa2478. <https://doi.org/abs/10.1126/science.aaa2478>.
- Keller, W.L., and E.J. Heske. 2000. Habitat use by three species of snakes at the Middle Fork Fish and Wildlife Area, Illinois. *Journal of Herpetology* 34:558–564.
- Kernohan, B.J., R.A. Gitzen, and J.J. Millspaugh. 2001. Analysis of animal space use and movements. Pp. 125–166 *In* Radio Tracking and Animal Populations. Millspaugh, J.J., and J.M. Marzluff (Eds.). Academic Press, San Diego, California, USA.
- Marzluff, J.M., J.J. Millspaugh, P. Hurvitz, and M.S. Hancock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85:1411–1427.
- Millspaugh, J.J., R.M. Nielson, L. McDonald, J.M. Marzluff, R.A. Gitzen, C.D. Rittenhouse, M.W. Hubbard, and S.L. Sheriff. 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70:384–395.
- Mullin, S.J., and R.A. Seigel (Eds.). 2009. Snakes: Ecology and Conservation. 1st Edition. Cornell University Press, Ithaca, New York, USA.
- Mullin, S.J., W.H.N. Gutzke, G.D. Zenitsky, and R.J. Cooper. 2000. Home ranges of rat snakes (Colubridae: *Elaphe*) in different habitats. *Herpetological Review* 31:20–22.
- Nakagawa, S., and H. Schielzeth. 2013. A general and

- simple method for obtaining R^2 from Generalized Linear Mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Nigh, T.A., and W.A. Schroeder. 2002. Atlas of Missouri Ecoregions. Missouri Department of Conservation, Jefferson City, Missouri, USA.
- Perry, G., and T. Garland. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. *Ecology* 83:1870–1885.
- Pe'er, G., M.A. Tsianou, K.W. Franz, Y.G. Matsinos, A.D. Mazaris, D. Storch, L. Kopsova, J. Verboom, M. Baguette, V.M. Stevens, and K. Henle. 2014. Toward better application of minimum area requirements in conservation planning. *Biological Conservation* 170:92–102.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team (2021). nlme: linear and nonlinear mixed effects models. R package version 3.1-153. <https://CRAN.R-project.org/package=nlme>.
- Pittman, S.E., M.S. Osbourn, and R.D. Semlitsch. 2014. Movement ecology of amphibians: a missing component for understanding population declines. *Biological Conservation* 169:44–53.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>.
- Reinert, H.K., and D. Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702–705.
- Robinson, S.K., F.R. Thompson, III, T.M. Donovan, D.R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- Rosenthal, M.F., M. Gertler, A.D. Hamilton, S. Prasad, and M.C.B. Andrade. 2017. Taxonomic bias in animal behaviour publications. *Animal Behaviour* 127:83–89.
- Row, J.R., and G. Blouin-Demers. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia* 2006:797–802.
- Sperry, J.H., G. Blouin-Demers, G.L.F. Carfagno, and P.J. Weatherhead. 2010. Latitudinal variation in seasonal activity and mortality in Ratsnakes (*Elaphe obsoleta*). *Ecology* 91:1860–1866.
- Stake, M.M., F.R. Thompson, III, J. Faaborg, and D.E. Burhans. 2005. Patterns of snake predation at songbird nests in Missouri and Texas. *Journal of Herpetology* 39:215–222.
- Tamburello, N., I.M. Côté, and N.K. Dulvy. 2015. Energy and the scaling of animal space use. *American Naturalist* 186:196–211.
- Thompson, F.R., III. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* 149:98–109.
- Thompson, F.R., III, and D.E. Burhans. 2003. Predation of songbird nests differs by predator and between field and forest habitats. *Journal of Wildlife Management* 67:408–416.
- Tilman, G.D., and P.M. Kareiva (Eds.). 1997. Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions. Princeton University Press, Princeton, New Jersey, USA.
- Todd, B.D., and A.J. Nowakowski. 2021. Ectothermy and the macroecology of home range scaling in snakes. *Global Ecology and Biogeography* 30:262–276.
- Weatherhead, P.J., and G. Blouin-Demers. 2004. Understanding avian nest predation: why ornithologists should study snakes. *Journal of Avian Biology* 35:185–190.
- Weatherhead, P.J., G. Blouin-Demers, and K.M. Cavey. 2003. Seasonal and prey-size dietary patterns of Black Ratsnakes (*Elaphe obsoleta obsoleta*). *American Midland Naturalist* 150:275–281.
- Weatherhead, P.J., J.H. Sperry, G.L.F. Carfagno, and G. Blouin-Demers. 2012. Latitudinal variation in thermal ecology of North American ratsnakes and its implications for the effect of climate warming on snakes. *Journal of Thermal Biology* 37:273–281.
- Winter, M., and J. Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. *Conservation Biology* 13:1424–1436.
- Young, M.E., W.A. Ryberg, L.A. Fitzgerald, and T.J. Hibbitts. 2018. Fragmentation alters home range and movements of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*). *Canadian Journal of Zoology* 96:905–912.



ANDREW D. GEORGE is Associate Professor of Biology at Pittsburg State University, Pittsburg, Kansas, USA, where his research focus is spatial ecology and habitat relationships in a variety of taxa. He holds a Ph.D. from the University of Missouri, Columbia, USA; an M.S. from Oklahoma State University, Stillwater, USA; and a B.S. from Arkansas Tech University, Russellville, USA. He is also a Research Associate with the Missouri Ozark Forest Ecosystem Project (MOFEP) and current President of the Kansas Herpetological Society. (Photographed by Andy Mueller).



FRANK R. THOMPSON is a Research Wildlife Biologist with the U.S. Forest Service Northern Research Station, Columbia, Missouri, USA. He received his Ph.D. from the University of Missouri, Columbia, USA, in Wildlife and Fisheries Science. His research primarily addresses the ecology and conservation of birds but has also included bats and herpetofauna and includes the development and application of population and landscape models to large spatial scales to understand the implications of land management and climate change on forests and wildlife. (Photographed by Frances Thompson).



JOHN FAABORG is Professor Emeritus in the Division of Biological Sciences, University of Missouri, Columbia, USA. His varied career has included studies on the ecology and conservation of Neotropical migrant songbirds during both breeding and wintering, long-term monitoring of Puerto Rican bird populations, and the evolution of polyandry in the Galapagos Hawk (*Buteo galapagoensis*). He holds a Ph.D. in Ecology and Evolution from Princeton University, Princeton, New Jersey, USA, and a B.S. in Fisheries and Wildlife Biology from Iowa State University, Ames, USA. (Photographed by Janice Faaborg).