Spatial Ecology of Eastern Yellow-Bellied Racer (*Coluber constrictor flaviventris*) and Great Plains Rat Snake (*Pantherophis emoryi*) in a Contiguous Tallgrass-Prairie Landscape

SPATIAL ECOLOGY OF EASTERN YELLOW-BELLIED RACER (*COLUBER CONSTRICTOR FLAVIVENTRIS*) AND GREAT PLAINS RAT SNAKE (*PANTHEROPHIS EMORYI*) IN A CONTIGUOUS TALLGRASS-PRAIRIE LANDSCAPE

PAGE E. KLUG[1,3,4], JENNIFER FILL[2], AND KIMBERLY A. WITH[1]

[1]*Laboratory for Landscape and Conservation Ecology, Division of Biology, 116 Ackert Hall, Kansas State University, Manhattan, KS 66506, USA*
[2]*Department of Biological Sciences, 401 Coker Life Sciences, University of South Carolina at Columbia, Columbia, SC 29208, USA*

ABSTRACT: The Flint Hills region of Kansas and Oklahoma encompasses the largest, contiguous tallgrass prairie in North America and is an important conservation area for many tallgrass-prairie species. We conducted a radiotelemetry study with the use of temperature-sensitive transmitters to characterize the spatial ecology of two species of snakes within a portion of this contiguous grassland. We monitored Eastern Yellow-Bellied Racers (*Coluber constrictor flaviventris*) from 2006 to 2008 and Great Plains Rat Snakes (*Pantherophis emoryi*) from 2007 to 2008 at the Konza Prairie Biological Station in the northern Flint Hills. Although racers (mean = 67.3 ± 10.6 m, *n* = 12) and rat snakes (mean = 41.3 ± 4.7 m, *n* = 12) differed in the distance moved per day, they did not differ significantly in home-range size. The minimum convex polygon (MCP) home range averaged 11.45 ha (SE = 3.06, *n* = 12) for racers and 15.06 ha (SE = 2.48, *n* = 12) for rat snakes. By analyzing the autocorrelation of locations (Mantel correlograms), we found that racers exhibited irregular movements, whereas rat snakes exhibited long periods of inactivity between directed movements. The body temperatures of racers were significantly greater in woody (30.7 ± 0.4°C) than in grassy habitats (29.8 ± 0.3°C). The body temperatures of rat snakes were significantly greater aboveground (26.9 ± 0.3°C) than underground (26.1 ± 0.2°C). Our study benefits the conservation of native snakes by elucidating space requirements and providing a baseline for comparisons between contiguous and fragmented landscapes.

Key words: Autocorrelation; Body temperature; *Coluber constrictor*; Flint Hills; Home range; Movement; *Pantherophis emoryi*; Radiotelemetry; Snake; Space use

GIVEN that snakes are difficult to monitor, species that appear common may nevertheless be experiencing declines that are currently undetected (Brown et al., 2008; Gibbons et al., 2000). Snakes dependent on grassland habitat are of particular concern given that the estimated loss of grassland ecosystems in North America has exceeded 80%, with less than 4% of the historical tallgrass prairie remaining (Samson and Knopf, 1994). The loss and fragmentation of tallgrass prairie by human development and agriculture has resulted in declining snake populations in many regions (e.g., Cagle, 2008). In the Flint Hills of Kansas, where native grasslands are relatively intact, much of the region is under private landownership and managed for beef cattle production (e.g., With et al., 2008). A decline in grassland snakes is therefore hypothesized to occur on private lands within this region, because of intensive cattle grazing and fire management practices that denude and homogenize vegetation (Beever and Brussard, 2004; Cavitt, 2000). Conversely, suppression of grazing and fire around urban areas is facilitating the woody invasion of grasslands in parts of the region, potentially reducing habitat for grassland snakes (Fitch, 2006). In contrast to private lands, publicly owned conservation areas within the Flint Hills, such as the Fort Riley Military Reservation, which uses less-intensive fire and graze management than grazed rangelands in this region, have not witnessed major changes in herpetological assemblages over the past 100 yr (Busby and Parmelee, 1996). Because the population status of snakes varies both within and among regions, and the overall trend for many species is unknown, more effort should be invested in understanding the

[3] PRESENT ADDRESS: University of Notre Dame Environmental Research Center, Department of Biological Sciences, 089 Galvin Life Sciences, University of Notre Dame, Notre Dame, IN 46556, USA
[4] CORRESPONDENCE: e-mail, pklug@nd.edu

ecology of snakes that are relatively common, in addition to those in need of conservation. Through an understanding of the spatial ecology of snakes that are locally abundant within a landscape of contiguous habitat, such studies may provide a baseline for comparison to regions where snakes are declining because of habitat loss, fragmentation, and degradation.

The distribution and abundance of resources such as food, mates, and shelter affect space use in snakes (Brown and Weatherhead, 1999; Gregory et al., 1987; Roe et al., 2004). For example, increased habitat heterogeneity may afford increased prey abundance (Anderson et al., 2003), thermoregulation sites (King and Duvall, 1990) and refugia from predators (Wilgers and Horne, 2007). Home-range size, distance of movement, and frequency of movement in individual snakes can also be influenced by sex and reproductive condition (Fitzgerald et al., 2002; Whitaker and Shine, 2002), which is dependent on time of season (Waldron et al., 2006). In addition, maintenance of an optimal body temperature has a profound influence on snake behavior (Huey, 1991). Body temperature in snakes is directly linked to environmental temperature, and therefore is an indicator of how habitat may influence daily and seasonal movement, foraging success and overall fitness (Blouin-Demers et al., 2003; Whitaker and Shine, 2002).

We conducted a radiotelemetry study to gain a better understanding of the spatial ecology of the Eastern Yellow-bellied Racer (*Coluber constrictor flaviventris*) and Great Plains Rat Snake (*Pantherophis emoryi,* formerly *Elaphe emoryi*), hereafter referred to as racer and rat snake. Racers and rat snakes are among the most common snakes in Kansas (Fitch, 1993), and comprised 47% and 27% of the captures (*n* = 146), respectively, at the Konza Prairie Biological Station (KPBS) in the Northern Flint Hills (Klug et al., 2010). A landscape genetics analysis of populations in northeastern Kansas revealed that racers are an abundant and continuously distributed snake, which indicates this region may be well connected for racers (Klug et al., 2011).

The main objectives of this study were (1) to analyze the movement patterns and behavior of radiotagged snakes, (2) to analyze autocorrelation of movement trajectories to understand how locations of individual snakes are related over time, (3) to analyze the size and composition of home ranges for two species of snakes in the tallgrass prairie, and (4) to evaluate if body temperature varies with behavior or habitat. Such information on space use in a relatively intact grassland may indicate the vulnerability of snakes to future habitat alteration (Blouin-Demers and Weatherhead, 2001), their ability to colonize restored habitats, the effectiveness of relocation (Webb and Shine, 1997) and reserve design (Fitzgerald et al., 2002), or the impact of snakes on prey species of conservation concern (Klug et al., 2010). Based on their respective foraging strategies, we hypothesized that racers would move more frequently, display more erratic movements, and cover more area per day than rat snakes (Fitch, 1999).

Materials and Methods

Study Site

The study was conducted on the KPBS in the Flint Hills ecoregion of northeast Kansas (39°05′N and 96°35′W; datum = WGS84). The KPBS is a 3487-ha National Science Foundation long-term ecological research site owned by the Nature Conservancy and operated by the Division of Biology at Kansas State University. The site is topographically complex, with elevation ranging from 320 to 444 m. The KPBS contains tallgrass prairie managed with or without native Bison (*Bos bison*) and prescribed burns every 1–20 yr. In addition to grasslands, gallery forests occur in the lowlands. Shrubs (>1 m in diameter) occur within all watersheds along limestone outcrops, but are more prevalent in areas with 4–20-yr burn intervals. Shrub species include Rough-leaved Dogwood (*Cornus drummondii*), Sumac (*Rhus* spp.), Prickly Ash (*Zanthoxylum americanum*), and Eastern Red Cedar (*Juniperus virginiana*). The dominant grasses include Big Bluestem (*Andropogon gerardii*), Little Bluestem (*Schizachyrium scoparium*), Indian Grass (*Sorghastrum nutans*), and Switchgrass (*Panicum virgatum*).

Snake Capture and Radiotracking

Both racers and rat snakes are habitat and prey generalists with wide distributions. Eastern

Yellow-bellied Racers occur approximately from Montana to North Dakota and from Iowa to Texas. Great Plains Rat Snakes occur approximately from Illinois to Colorado and from New Mexico to northern Mexico (Fitch, 1999). We captured snakes by using cover boards (60 × 180 cm plywood), drift fences with funnel traps, and through opportunistic encounters (Cavitt, 2000; Parmelee and Fitch, 1995). In January 2006, we set out cover boards across the KPBS, which included treatments that mimic the historical pattern of disturbance in this system (i.e., combinations of burning and grazing). We constructed two drift fences in four focal watersheds that were not grazed by bison. Drift fences were 61-cm silt fences arranged in a Y shape with five funnel traps on each 15-m arm. We checked cover boards and drift fences daily prior to 1030 from April to June, and overturned rocks from April to May. In total, we tagged and monitored snakes within 16 watersheds representing five different treatment types. Unfortunately, the numbers and distributions of snakes captured among treatments were insufficient to analyze the effects of grazing and burning on snake movement.

We implanted temperature-sensitive radio-transmitters into the body cavities of snakes that weighed more than 100 g following accepted procedures (Hardy and Greene, 1999; Reinert and Cundall, 1982). We decided to begin tagging rat snakes as well as racers in 2007, after we saw how abundant rat snakes were in 2006. The fact that rat snakes can be nocturnal as well as diurnal, and have a different mode of hunting than racers, also made for an interesting comparison of space use between these two grassland snakes. The transmitters weighed 5 g and had a battery life of 6–12 mo at 20°C (model SI-2T, Holohil Systems Inc., Carp, Ontario, Canada). We released each snake at the location of capture within 48 h of surgery. The first location after release was not included in the analyses, given that snakes often remained under cover at the same location while habituating to the transmitter. After the snakes emerged from their initial retreat site, we tracked them every 24–48 h from 28 May to 1 August, and every 2 wk from 1 August until the snakes moved off site to their hibernacula. Given that the objective of this study was to relate activity patterns to habitat on summer home ranges, we did not analyze the transitional movements between hibernacula and summer home ranges. We recorded snake locations between 0400 and 2400 h with the use of a radiotelemetry receiver (Challenger 2100, Advanced Telemetry Systems, Isanti, MN), and we varied the time in which snakes were tracked to encompass all potential periods of activity.

Body Temperature

We recorded UTM coordinates, position (above or below ground), behavior (moving or stationary), and habitat (grassy or woody) at each snake location. Before approach, we would move around the snake and acquire multiple bearings (i.e., triangulate) to decipher if the snake was moving or stationary. We calculated body temperature from correlation curves of temperature against the pulse interval designed for each transmitter. We measured the pulse interval by recording the time (nearest ms) between 11 pulses and dividing by 10. We used an anemometer (model SM-18, Speedtech Instruments, Great Falls, VA) to record air temperature and wind speed at 1.5 m above the ground within 20 min of locating a snake. We used an infrared thermometer (model OS530LE, Omega Engineering Inc., Stamford, CT) to record surface temperatures of bare ground, litter, vegetation, and under rocks in the shade and within 50 m of the location.

Movement Patterns

We analyzed differences in movement behavior between racers and rat snakes. We measured total distance moved (sum of all movements over the season), average distance moved per day (total distance moved divided by the length of the entire monitoring period), and distance per move (distance moved between successive locations divided by the number of days between locations). Range length was the Euclidean distance between the two most divergent locations.

Autocorrelation is a useful ecological parameter that describes the scale-dependency of spatial patterns (Cushman et al., 2005; Legendre, 1993); therefore, we used autocorrelation to describe the structure of movement patterns in racers and rat snakes. The Mantel test can be

used to test the association between two distance matrices (Mantel, 1967) from which a multivariate correlogram can be built if one matrix is coded as a distance class (Oden and Sokal, 1986). The Mantel correlogram shows the strength of correlation between the two multivariate distance matrices across a range of lag values. Similar univariate correlograms (e.g., Moran's I or Geary's C; Legendre and Legendre, 1998) describe the correlation between one response variable and one lag variable across various lag distances. In this study, we used a Mantel correlogram to compare the distance between locations in multivariate geographical space (i.e., UTM X and UTM Y) with distance between locations in time for each snake (Cushman et al., 2005). Mantel correlograms were created in Program R 2.9.0 (R Development Core Team, 2005) with the use of modifications of the "ecodist" package (Goslee and Urban, 2007). We calculated Mantel correlograms with locations from 1 June to 1 August. We used lag times of 5 d for racers and 6 d for rat snakes. Patterns of movement can be inferred from Mantel correlograms by evaluating the type of correlogram structure (for examples, see Legendre and Fortin, 1989). If the same sampling interval is maintained, then autocorrelation can be used to compare patterns of behavior and range use among individuals. We compared patterns of autocorrelation within a species by computing pairwise Pearson correlations between the Mantel r at each lag distance. A high correlation coefficient would indicate that individual snakes have similar patterns of autocorrelation across all lag distances. We did not make interspecific comparisons between racers and rat snakes due to the different lag distances used.

Home-Range Size and Composition

We estimated summer home ranges (referred hereafter to as home ranges) based on 100% minimum convex polygon (MCP) and fixed kernel density estimates (KDE) within the Animal Movement Extension of ArcView 3.3 (Hooge et al., 1999). We attained the minimum number of locations needed for calculating the home range by plotting the number of locations against area of the MCP home range. We computed MCP home range starting with the first ten locations and increased the number of sequential locations

by 5 until the total number of locations was reached. The number of locations needed was estimated by evaluating the average asymptote of the curves.

The MCP method only gives an outline of locations, but does not indicate areas with a higher density of locations. We therefore used KDE to construct 95% probability contours and 50% probability contours to highlight core areas of use. KDE requires the selection of a smoothing factor (h), which is often obtained through arbitrary means such as least-squares cross validation (LSCV). Unfortunately, KDE-LSCV can result in a wide range of smoothing factor values because sample size and data structure influence the smoothing factor, and in turn, the size of the home range, thus contributing to inaccuracies in the estimates (Row and Blouin-Demers, 2006). Therefore, instead of KDE-LSCV, we used the MCP as the area of the home range and adjusted the smoothing factor until the area of the 95% probability contour equaled that of the MCP polygon (KDE-MCP; Row and Blouin-Demers, 2006). We used the KDE-MCP method when quantifying the proportion of woody habitat within home ranges, as it provided an objective smoothing factor while allowing us to identify areas of core use.

We classified habitat found on KPBS and in home ranges as grassy or woody (e.g., gallery forests and shrub islands) through a remotely sensed Quickbird image (Geoeye™) acquired on 13 August 2007. The Quickbird imagery had four multispectral bands at 4-m resolution and was pan-sharpened to an accuracy of 1 m. We used ENVI 4.3 to run a supervised classification based on maximum likelihood to classify each pixel as grassy or woody. We limited the number of habitat types to grassy and woody because they were the two dominant habitats on KPBS. We employed a KAPPA index to assess classification accuracy. Of the 245 pixels assessed, 97% were correctly classified with a KAPPA statistic of 0.81, which is sufficient for evaluation of land cover (Thomlinson et al., 1999). Woody cover was unlikely to change within the 3-yr time period of the study, and therefore classification of a single image was sufficient for capturing woody cover across all years.

We compared habitats (grassy and woody) contained within the home ranges of snakes to the availability of those habitats across the study area to complement data previously presented on the selection of woody and grassy habitats within home ranges (Klug et al., 2010). We defined the study area for each species by creating a MCP that included all snake locations (racers = 858 ha, rat snakes = 1239 ha). We calculated the expected use as the proportion of habitat types in the entire study area and observed use as the proportion of habitat types within home ranges. We used a compositional analysis to test the hypothesis that the proportion of grassy and woody habitat used by snakes was in proportion to the availability (Aebischer et al., 1993). We took the log-ratios of the proportion of habitat used (home range) and the log-ratios of the proportion of available habitat (study site) for both racers and rat snakes. We considered habitat use to be random if the log-ratios of available and used habitat were approximately equal.

Statistical Analyses

We used a mixed-model analysis of variance (ANOVA) with snake as a random factor to test for the effect of position (above ground vs. below ground), behavior (moving or at rest), and habitat (woody or grassy) on body temperature. To determine which substrate was best correlated with body temperature based on P values < 0.05, we conducted a multiple linear regression (Kapfer et al., 2008). To analyze interspecific differences in home range, habitat composition, and space use (i.e., total distance moved, distance moved per day, distance per move, maximum daily movement, and range length), we used the Mann-Whitney test. We pooled data between sexes when making interspecific comparisons due to limited sample sizes. We computed nonparametric statistics in Minitab 15 (Minitab Inc., State College, Pennsylvania, USA) and parametric statistics in SAS 9.1.3 (SAS Institute, Cary, North Carolina, USA).

Results

Snake Capture and Radiotracking

Over 3 yr, we captured 57 racers between 30 April and 26 June. Racers had snout-to-vent lengths (SVL) ranging from 22 to 81 cm (mean = 56.8 ± 1.8 cm) and masses ranging from 14 to 256 g (mean = 80.4 ± 7.2 g). Of the 57 racers, 13 (12 found alive) were of sufficient size (>100 g) to permit the implantation of a transmitter. We tagged 12 racers, including 8 females (SVL: mean = 71.7 ± 1.9 cm; mass: mean = 160.3 ± 15.8 g) and 4 males (SVL mean = 65.5 ± 0.5 cm; mass: mean = 113.0 ± 2.8 g; Table 1). All racers survived the surgery and were followed in five watersheds consisting of four treatments (Table 1).

We found 34 Great Plains Rat Snakes between 7 May and 9 June over 3 yr. Rat snakes had a SVL ranging from 32 to 105 cm (mean = 74.3 ± 3.7 cm) and mass from 12 to 431 g (mean = 174.3 ± 17.3 g). Of the 34 rat snakes, 25 met the size criterion (> 100 g) for a radio transmitter. We tagged a total of 16 rat snakes, including four females (SVL: mean = 90.7 ± 7.1 cm; mass: mean = 295.3 ± 73.0 g) and 12 males (SVL: mean = 89.3 ± 3.0 cm; mass: mean = 236.4 ± 19.5 g; Table 1). One female rat snake died during surgery, most likely because of an overdose of Isoflurane. Three male rat snakes were preyed upon (which we inferred after recovering a clean transmitter) before a sufficient number of locations could be acquired; the three were removed from the analyses. The remaining (n = 12) rat snakes (SVL: mean = 88.5 ± 2.9 cm; mass: mean = 256.7 ± 25.4 g) occurred in six watersheds representing four treatment types (Table 1).

Body Temperature

Summarizing across all telemetry observations (n = 328), body temperature in racers ranged from 16.5 to 40.2°C (mean = 29.81 ± 0.20°C). Air temperature and surface temperature of litter were significantly correlated with racer body temperature ($F_{5,322}$ = 133.1, $P < 0.0001$) and explained 67% of the variation (multiple R^2 = 0.67). The surface temperatures of live vegetation, bare ground, and under rocks were not significant predictors in the multiple regression. Although racers were underground in 18% of observations, their body temperatures did not differ with position (F = 2.38, P = 0.12; Fig. 1A). Racer body temperatures were significantly

TABLE 1.—Space-use statistics for Eastern Yellow-bellied Racers and Great Plains Rat Snakes on Konza Prairie Biological Station.

Snake ID	Year	Treatment[a]	Mass (g)	SVL (cm)	Monitoring period[b] (d)	Number of locations[b]	Total distance moved (m)	Distance moved per day[c] (m)	Distance per move[d] (m)	Maximum distance per move (m)	Range length[e] (m)	MCP (ha)	50% KDE-MCP (ha)
Eastern Yellow-bellied Racer													
F-♂	2007	G01-Y	111	65	80 (47)	28 (23)	1,767	38	33	133	460	6.8	1.8
G-♂	2008	U01-Y	117	65	92 (59)	35 (29)	4,622	78	79	401	830	15.1	1.3
N-♂	2008	G04-N	118	67	85 (58)	34 (29)	7,983	138	135	390	1,020	31.1	1.3
T-♂	2008	G04-N	106	65	93 (58)	35 (30)	7,637	132	125	265	770	33.5	3.1
B-♀	2006	U01-Y	123	67	86 (52)	47 (43)	3,483	67	71	195	610	6.5	1.2
E-♀	2006	G01-Y	140	72	45 (32)	25 (24)	956	30	28	138	570	3.1	0.4
J-♀	2008	U01-Y	256	81	84 (59)	35 (30)	4,542	77	77	312	700	11.3	1.1
L-♀	2006	G04-N	154	67	57 (51)	40 (39)	1,908	37	42	142	165	1.2	0.2
M-♀	2006	G04-N	192	76	79 (46)	37 (35)	3,708	81	84	519	620	6.6	0.5
P-♀	2006	U01-Y	140	76	78 (45)	38 (35)	2,043	45	46	141	300	2.8	0.4
Z-♀	2008	U01-Y	122	66	81 (57)	35 (30)	1,666	29	28	80	355	6.2	0.7
U-♀	2008	G01-Y	155	69	50 (34)	24 (18)	1,918	56	62	409	1,790	13.2	2.2
Mean			144.5	69.7	75.8 (49.8)	34.4 (30.3)	3,519.4	67.3	67.5	260.4	682.5	11.45	1.2
SE			12.3	1.5	4.6 (2.7)	1.8 (2.0)	671.9	10.6	10.2	41.2	121.9	3.06	0.25
Great Plains Rat Snake													
A-♂	2007	G04-N	348	102	93 (63)	36 (32)	1,794	29	29	244	710	7.9	1.3
C-♂	2008	U04-Y	235	86	84 (58)	35 (30)	1,836	32	29	165	365	6.3	0.8
D-♂	2008	U01-Y	148	76	84 (57)	35 (30)	3,580	63	54	213	870	20.6	4.5
I-♂	2008	U01-Y	219	86	76 (59)	35 (31)	3,403	58	55	220	655	17.8	1.6
O-♂	2008	U04-Y	225	85	84 (58)	34 (29)	2,721	47	40	203	820	25.7	4.3
Q-♂	2007	G04-N	226	84	93 (61)	36 (31)	1,842	30	31	237	545	9.3	1.5
R-♂	2007	U01-Y	336	99	93 (61)	33 (30)	1,118	18	18	78	255	1.7	0.3
X-♂	2007	G20-N	320	99	92 (62)	36 (31)	3,715	60	55	650	1,900	29.9	5.0
Y-♂	2007	G20-N	137	74	56 (56)	28 (28)	2,246	40	36	136	1,145	18.0	1.6
H-♀	2007	U01-Y	431	104	78 (47)	27 (23)	2,977	63	49	424	1,190	21.9	3.8
S-♀	2008	G04-N	274	88	87 (58)	35 (30)	1,402	24	23	206	635	9.0	0.9
V-♀	2007	U01-Y	181	80	85 (61)	33 (31)	1,926	32	33	650	750	12.6	3.2
Mean			256.7	88.5	83.8 (58.4)	33.6 (29.7)	2,380.0	41.3	37.7	285.5	820.0	15.06	2.4
SE			25.4	2.9	3.0 (1.2)	0.87 (0.68)	252.9	4.7	3.7	54.5	125.9	2.48	0.48

[a] G = grazed, U = ungrazed, numbers indicate years between burns, Y = burned that year, N = not burned that year.
[b] Numbers in parentheses indicate data with regular interval sampling that were used in the movement statistics.
[c] Total distance moved divided by length of monitoring period.
[d] Distance moved divided by number of days between successive locations.
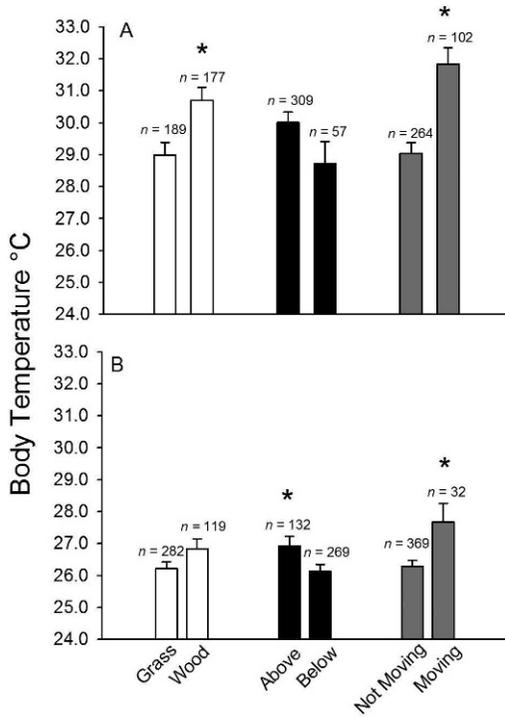[e] Euclidean distance between two most divergent locations.

FIG. 1.—Mean (±SE) body temperature of (A) Eastern Yellow-bellied Racers from 2006 to 2008 and (B) Great Plains Rat Snakes from 2007 to 2008 in different habitats (white bars), position above or below ground (black bars), and activity (gray bars). Sample sizes are the numbers of observed snake locations, including all tagged racers (n = 12) and rat snakes (n = 12) on the Konza Prairie Biological Station. Asterisks indicate statistically significant differences in body temperatures.
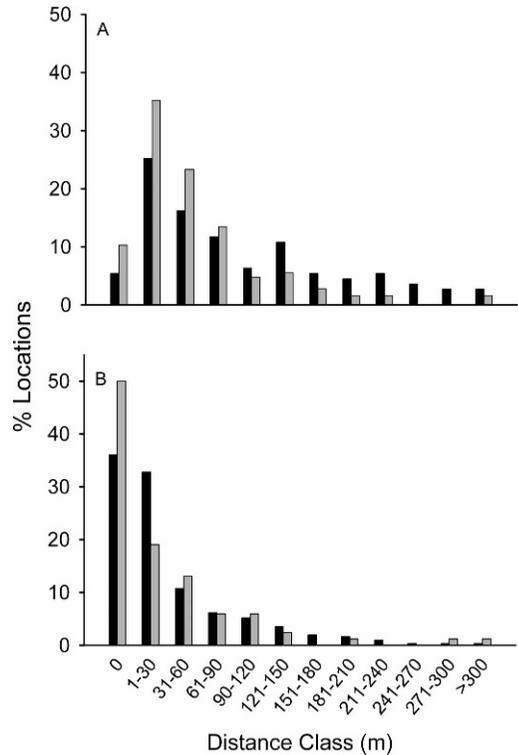

FIG. 2.—Percent of locations in each distance class for (A) Eastern Yellow-bellied Racers from 2006 to 2008 and (B) Great Plains Rat Snakes from 2007 to 2008 on the Konza Prairie Biological Station. Male = black shading; females = gray shading. We calculated "distance" as the distance moved between successive locations divided by the number of days between relocations.

greater (F = 32.3, P < 0.0001) when moving (mean = 32.31 ± 0.70°C) than when at rest (mean = 28.73 ± 0.57°C; Fig. 1A) and greater (F = 6.42, P = 0.01) in woody (mean = 30.59 ± 0.46°C) than in grassy habitats (mean = 29.07 ± 0.44°C; Fig. 1A).

Summarizing across all telemetry observations (n = 381), body temperatures in rat snakes ranged from 16.5 to 37.5°C (mean = 26.40 ± 3.39°C). Air temperature and surface temperature under rocks were significantly correlated with rat snake body temperature ($F_{5,375}$ = 99.4, P < 0.0001) and explained 57% of the variation (multiple R^2 = 0.57). The surface temperatures of live vegetation, bare ground, and litter were not significant predictors in the multiple regression. Rat snakes were underground at 67% of the locations; their body temperatures were significantly

greater whenever the snakes were above-ground than when they were underground (F = 5.16, P = 0.02; Fig. 1B). Rat snake body temperatures were significantly greater (F = 4.30, P = 0.04) when the snakes were moving (mean = 27.60 ± 0.63°C) than when the snakes were stationary (mean = 26.32 ± 0.27°C; Fig. 1B). The body temperatures of rat snakes did not vary among habitats (F = 0.23, P = 0.63; Fig. 1B).

Movement Patterns

We monitored racers for 32–59 d (mean = 49.8 ± 2.7, n = 12) between 28 May and 1 August 2006–2008, with the number of locations per snake ranging from 18 to 43 (mean = 30.3 ± 2.0; Table 1). Distance per move was skewed to short-range distances, with 20% of relocations within 10 m of the previous location (Fig. 2A). We observed

racers moving in 28% of the telemetry observations. On average, racers moved 67.5 m per move, for a total of 3.5 km per season (Table 1). Average range length was 682.5 m, with a maximum move of 260.2 m between subsequent locations.

We monitored rat snakes for 47–63 d (mean = 58.4 ± 1.2, n = 12) between 28 May and 1 August in 2007 and 2008, and recorded 23 to 32 (mean = 29.7 ± 0.7) locations per snake (Table 1). The distance per move was skewed to short-range distances, with 50% of relocations within 10 m of the previous location (Fig. 2B). We observed rat snakes moving in 8% of the telemetry observations. On average, rat snakes moved 37.7 m per move, for a total of 2.4 km per season (Table 1). Average range length was 820.0 m, with a maximum move of 285.4 m between subsequent locations (Table 1).

Racers and rat snakes did not differ significantly in the total distance moved (U = 167, P = 0.34), range length (U = 131, P = 0.29), or maximum daily movement (U = 144, P = 0.75). The mean distance moved per day (U = 186, P = 0.04) was 1.7 times greater and the mean daily movement (U = 188, P = 0.03) was 1.8 times greater for racers than rat snakes. Racers were 3.5 times more active than rat snakes; we observed racers moving during 28% of the relocations compared to only 8% for rat snakes, which would explain the higher daily movement distance of racers than rat snakes.

Only 10 racers had a sufficient number of locations for inclusion in autocorrelation analyses (we removed E-female and U-female from the analysis). Racer locations were not spatially autocorrelated at an average lag time of 9.0 d (SE = 3.9; n = 10; see Fig. 3A, for example). Racers exhibited random movements within their home ranges, based on the shape of the Mantel correlograms, which showed irregular fluctuations around a Mantel r = 0 (see Fig. 3A, for example). Weak similarities between the Mantel correlograms (pairwise Pearson's correlation = 0.36) indicated that individual variation existed in the movement patterns, and individual racers did not exhibit the same behaviors over space and time.

Rat snake locations were not spatially autocorrelated at an average lag time of 14.5 d (SE = 4.8; n = 12; see Fig. 3B for example). Rat snakes appeared to have long periods of inactivity between directed movements, based on the shape of the Mantel correlograms, which showed a gradual decrease from positive to negative autocorrelation as lag time increased (see Fig. 3B, for example). Moderate to strong similarities between Mantel correlograms (pairwise Pearson's correlation = 0.62) indicated that individual rat snakes were similar in their movement patterns across time and space.

Home-Range Size and Composition

Racers for which we recorded more than 20 locations were included in the analyses, and had monitoring periods ranging from 45 to 93 d (mean = 75.8 ± 4.6, n = 12; Table 1). We estimated the MCP home-range sizes to be 1.2–33.5 ha (mean = 11.45 ± 3.06, n = 12; Table 1). The MCP home ranges for males (mean = 21.64 ± 6.41 ha, n = 4) were 3.5 times greater than female MCP home ranges (mean = 6.36 ± 1.46 ha, n = 8). Only one of the female racers was gravid upon initial palpation (U-female; Table 1).

All rat snakes had monitoring periods ranging from 56 to 93 d (mean = 83.7 ± 3.0, n = 12; Table 1), and we included all rat snakes with more than 20 observed locations in the analysis of home ranges. The estimated MCP home ranges were 1.7–29.9 ha (mean = 15.06 ± 2.48; Table 1). The MCP home ranges for males (mean = 15.24 ± 3.16, n = 9) were similar to those of females (mean = 14.52 ± 3.85, n = 3). Initial palpation did not indicate that any of the females were gravid.

The 50% core areas for racers (mean = 1.18 ± 0.25) were significantly different from those of rat snakes (mean = 2.40 ± 0.48) when estimated with the use of KDE-MCP (U = 116, P = 0.05; Table 1). Woody habitat comprised 1–39% of the 95% KDE-MCP and 1–54% of the 50% KDE-MCP home ranges for racers. The proportion of woody habitat in racer home ranges did not differ significantly from what was available (t = 0.70, P = 0.48). In further classifying locations, we observed that 33% of the locations were in shrub patches within grasslands, for a total of 87% of locations within grasslands (whether shrub or grass dominated); the remaining 13% in gallery forests (Fig. 4). For rat snakes,
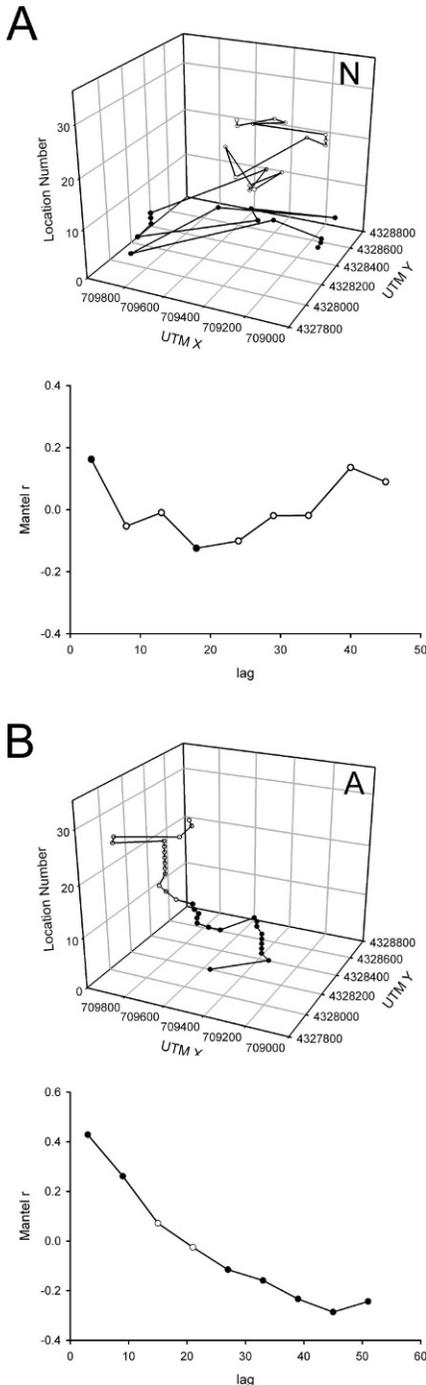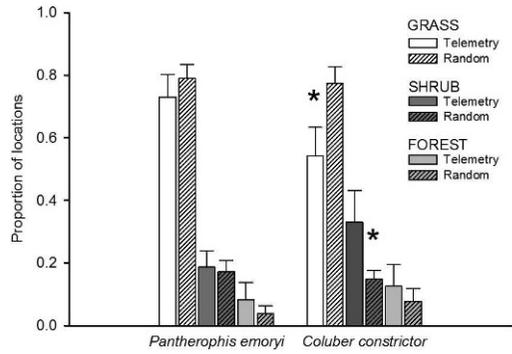
FIG. 4.—The proportion of recorded locations ($\pm$SE) for Eastern Yellow-bellied Racers from 2006 to 2008 and Great Plains Rat Snakes from 2007 to 2008 in grass, shrub, and gallery forest as compared to proportion of random locations in each habitat on Konza Prairie Biological Station (adapted from Klug et al., 2010). Asterisks indicate statistically significant differences.

woody habitat comprised 1–29% of the 95% KDE-MCP and 0–74% of the 50% KDE-MCP home range. Woody habitat within home ranges was not significantly different from what was available ($t = 1.31$, $P = 0.22$). The home ranges of racers and rat snakes had similar woody cover for both MCP (Mann-Whitney, $U = 128$, $P = 0.21$) and KDE-MCP ($U = 159$, $P = 0.64$).

DISCUSSION

Our analysis of movement behavior and space use of Eastern Yellow-bellied Racers and Great Plains Rat Snakes has contributed to a more detailed understanding of their spatial ecologies, which is important for understanding snake populations in the largest contiguous tallgrass prairie in North America. The main differences in the movement behaviors of these two species were in the daily distances moved, average distances per move, and the sizes of 50% core areas when using KDE-MCP (Table 1). Racers moved farther per day, possibly because their active foraging strategy, in which a higher preferred

FIG. 3.—Examples of Mantel correlograms and movement trajectories for (A) Eastern Yellow-bellied Racer (cf. Table 1: N-male) and (B) Great Plains Rat Snake (cf. Table 1: A-male) on the Konza Prairie Biological Station. The closed circles represent Mantel *r*-values significantly different from zero. The correlograms for racers show a

drop in autocorrelation followed by a flat correlogram, indicating no relationship between space and time or random use of a temporary home range. The correlogram for rat snakes shows a gradual decrease from positive to negative autocorrelation as lag time increases, indicating directed movements between long periods of inactivity.

body temperature aids in the rapid pursuit of prey through increased muscle metabolism (Fitch, 1999). In contrast, rat snakes use a combination of sit-and-wait and active foraging, and therefore may often be found under rocks or other retreat sites (Fitch, 1999). For example, 39% of rat snake locations were at the same coordinates, whereas racers occurred at the same locations only 9% of the time (Fig. 2). Although racers move more often, when rat snakes do move they are capable of moving long distances, resulting in a significantly larger 50% core area for rat snakes than racers. These differences in foraging strategy were also reflected in the autocorrelations of locations, where racers appeared to move randomly throughout their home range, and with shorter, more frequent moves than exhibited by rat snakes (Fig. 3). Although small differences existed among individuals, the Mantel correlograms for all rat snakes were very similar. Therefore, we hypothesize that the spatial distribution of refuge sites (e.g., limestone outcrops present in all watersheds) shaped the movement patterns of rat snakes, and not vegetation or prey availability per se (Fig. 3B). This is in contrast to racers, whose movement trajectories showed individual variation that could potentially be due to a number of physiological, motivational, or environmental factors that we were unable to assess.

Our estimate of average MCP home range for racers on KPBS was 11.5 ha, which was similar to home ranges in South Carolina; mean = 12.2 ha (Plummer and Congdon, 1994), and Illinois; mean = 15.1 ha (Carfagno and Weatherhead, 2008), but more than 4.5 times greater than home ranges previously reported for racers in the Central Irregular Plains ecoregion of Kansas (2.5 ha; Fitch and Shirer, 1971). Although habitat differences exist between our study site in the Flint Hills and the Central Irregular Plains study site, the difference in reported home-range sizes could also be due to different study methods. The previous study force-fed transmitters to the snakes, which resulted in shorter monitoring periods and may have altered behavior by simulating a feeding event, thereby reducing snake movements and estimation of home range.

Our estimate of average MCP home range for rat snakes was 15.1 ha, which was slightly larger than the MCP home range of 10.2 ha reported for male rat snakes in Texas (Sperry and Taylor, 2008). Previous studies of rat snakes have also shown that they have a propensity for human-made structures, such as concrete gully plugs (Sperry and Taylor, 2008). We hypothesize that differences in the estimation of home-range sizes among these studies may have been due to differences in the availability of refuge sites or prey (e.g., small mammals) among study areas.

Although habitat composition of home ranges did not differ significantly from what was available across our study site, Klug et al. (2010) found that racers were located in woody habitat more than expected based on availability within their home ranges (Fig. 4). Data from a related study (Klug et al., 2010) has shown that racers were located in woody habitat more often (49%) than expected based on availability of woody habitat at random locations (25%; Fig. 4). Therefore, although racers may be selecting shrubby areas within their home ranges, they are still more likely to be found in grasslands than forests (Fig. 4), which is not surprising, given that they are considered grassland snakes in Kansas. The use of shrubby areas by racers within tallgrass prairie suggests that this habitat type may be an important consideration in evaluating their habitat requirements in this system. If so, then habitat management will obviously require a careful balance between providing woody cover and maintaining sufficient grassland habitat for this and other grassland species (Fitch, 2006; Wilgers and Horne, 2007). The woody invasion of tallgrass prairie in the Flint Hills is already a significant concern in some areas, and may represent an irreversible system state change (from open grassland to savanna; Briggs et al. 2005) that may favor opportunistic species such as the racer.

It is vital for the conservation of snake populations that are experiencing regional declines for us to understand the factors that influence snake movements and how these factors may ultimately scale up to influence population distributions. The loss of grassland habitat, along with its degradation and fragmentation, threaten the sustainability of snake

populations throughout historical tallgrass prairies of North America, as evidenced by documented declines in grassland snakes in Indiana, where habitat loss and fragmentation are pervasive (Cagle, 2008). The movement behaviors and home ranges of snakes can vary greatly, depending not only on the amount of preferred natural habitat, but also on the amount of unsuitable anthropogenic habitat that may be avoided (Kapfer et al., 2010). The largest remaining tallgrass prairie is located in the Flint Hills of Kansas (Knapp and Seastedt, 1998); therefore, our study on the KPBS provides a baseline of movement behaviors of snakes inhabiting a native prairie landscape for future comparisons between contiguous and more disturbed or fragmented landscapes elsewhere within the range of these species.

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