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Movement Patterns of Prairie Rattlesnakes (*Crotalus v. viridis*) across a Mountainous Landscape in a Designated Wilderness Area

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ABSTRACT.—Many snake species make lengthy linear migrations between overwintering sites and summer foraging or mating habitats. Although mountainous topography may restrict migratory movements, most previous studies on migratory snake populations have occurred in areas with low to moderate topographic relief. The objectives of this study were to describe the movement patterns of Prairie Rattlesnakes (*Crotalus v. viridis*) in a mountainous landscape, compare those patterns to those of migratory snake populations from areas with lower topographic relief, and test for variation in movement patterns between sexes and among years. We used radiotelemetry to monitor the movements of 21 male and 6 nonpregnant female Prairie Rattlesnakes in the Frank Church Wilderness in central Idaho during the summers of 2006–2008. Mean total distance moved during the entire activity season in 2008 was 4.46 km (range 1.38–7.67); mean maximum distance moved from the hibernaculum was 1.46 km (range 0.69–2.71). Although the movement distances reported here are intermediate to those reported for other migratory snake populations, they are similar to some distances reported from areas with low to moderate topographic relief. This suggests that rattlesnakes are capable of making considerable movements in a mountainous landscape, although factors such as prey availability could also contribute to differences in reported movement distances. Rattlesnakes displayed moderate fidelity to summer activity areas but had similar mean bearings during outbound migration across multiple years. We hypothesize that linear migrations reported from rattlesnakes in many populations actually represent the most-direct movement to annual foraging areas rather than true searching movements.

Landscape features exhibit a multitude of influences on animal movements. For example, the availability of key resources such as food, water, mates, and refugia may vary spatially across the landscape and their spatial arrangement may influence animal movement patterns (McIntyre and Weins, 1999; Klaassen et al., 2006; Filipa-Loureiro et al., 2007). Landscape features may also impose costs on animal movements, thereby confronting individuals with tradeoffs between the benefit of acquiring key resources and the costs associated with movements (Werner and Anholt, 1993). Costs imposed by landscape features may include risks of predation (Fortin et al. 2005), physiological stress (Daltry et al., 1998; Bartelt et al., 2010), and increased energy expenditures (Johnson et al., 2006). Such costs may be particularly important for migrating species as a result of extended movements between spatially separate habitats. Species whose migrations are restricted to fixed migration routes may also be more susceptible to natural and anthropogenic disturbances along those routes (Berger, 2004). Understanding the movement patterns of migratory species and the factors which may restrict those movements can help better understand how those movement patterns may be affected by both natural and anthropogenic disturbances.

Many populations of snakes from multiple taxa undertake seasonal migrations between overwintering sites and summer activity areas, particularly at northern latitudes (Gregory et al., 1987; Larsen, 1987; Jorgensen et al., 2008; Smith et al., 2009; Williams et al., 2012; Gardiner et al., 2013). In contrast, conspecifics or closely related species at more-southerly latitudes often show reduced movement distances or nonmigratory movement patterns (Reed and Douglas, 2002; Rodriguez-Robles, 2003; Brown et al., 2008; Dugan et al., 2008; Klug et al., 2011). Migrations in snakes may be caused by limited numbers of suitable hibernacula, spatial separation between hibernacula and foraging habitats, and attempts to minimize

conspecific competition near communal hibernacula (Hirth et al., 1969; Gregory, 1984; Larsen, 1987; Jorgenson et al., 2008). Migrations are often lengthy (e.g., over several kilometers) and very linear (King and Duvall, 1990; Jorgenson et al. 2008; Wastell and Mackessy, 2011; Martino et al. 2012). The high directionality of these movements is hypothesized to be an efficient search pattern in response to spatially unpredictable prey or mates (King and Duvall, 1990; Duvall and Schuett, 1997). Although resource availability is known to influence movement patterns in migratory snake species, relatively little attention has been focused on the role of landscape characteristics, such as habitat types, in influencing those movements. In particular, the effects of topography have received relatively little attention, perhaps because many studies on migratory snake populations occurred in areas with low to moderate topographic relief or did not comment on the effects of topography (e.g., Brown et al., 2009; Gardiner et al., 2013).

Where resource availability in a given area is relatively stable across time, it is often advantageous for an individual to exhibit fidelity to those areas if the benefits of reusing that resource exceed the costs of searching for new resources (Switzer, 1993). Site fidelity has been demonstrated in diverse taxa at a range of spatial and temporal scales spanning temporary refugia (Webb and Shine, 1997; Beck and Jennings, 2003) to seasonal and annual home ranges (Andersen, 1991; Janmaat et al., 2009; Scouler et al., 2011; Trierweiler et al., 2013). Snakes in cold-temperate climates should show strong fidelity to hibernacula because most hibernacula are persistent over time, and the consequences to fitness of surviving the winter are high. Many studies of snakes in such environments do show strong fidelity to specific hibernaculum (e.g., Blouin-Demers et al., 2007; Parker and Anderson, 2007; Clark et al., 2008; Smith et al., 2009). However, less attention has focused on fidelity to migration routes and summer activity areas. If resources such as prey and mates are fairly stable in space and time, we would expect individuals to return to the same summer activity areas over multiple years. In contrast, varying resource availability or predictability (or both) may cause individuals to show low fidelity to activity areas over time (Edwards et al., 2009). Most

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MATERIALS AND METHODS

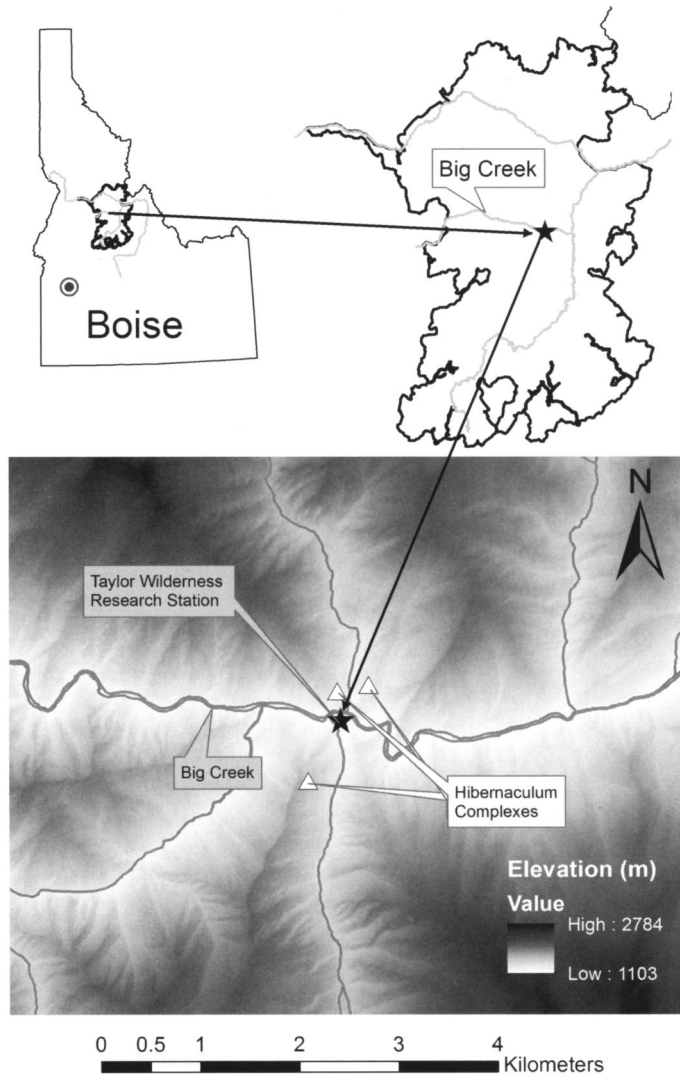


FIG. 1. Map of the study area showing the Frank Church—River of No Return Wilderness, the Taylor Wilderness Research Station, and the three Prairie Rattlesnake (*Crotalus v. viridis*) hibernaculum complexes used in this study.

studies monitoring snake movements over multiple activity seasons have found that snakes do indeed use the same general summer activity areas (Kapfer et al., 2008; Pattishall and Cundall, 2008; Smith et al., 2009). However, few, if any, studies have examined fidelity to migration routes over time in snakes.

An accurate description of ecological patterns and processes is first necessary to understand the factors influencing those patterns and processes. Therefore, the objective of this study was to describe the movements of Prairie Rattlesnakes (*Crotalus v. viridis*) in a mountainous landscape. To address this objective, we asked three specific questions: 1) How do the movement patterns of Prairie Rattlesnakes in a mountainous landscape compare to those of populations from areas with lower topographic relief; 2) do males and nonpregnant females display differences in movement patterns that may be caused by male mate-searching; and 3) do rattlesnakes display high fidelity to summer activity areas? Additionally, we tested for an effect of body size on several movement statistics because movement patterns have varied with body size in multiple snake taxa (Blouin-Demers et al., 2007; Jorgensen et al., 2008; Hyslop et al., 2014).

Study Area.—We conducted this study in the lower Big Creek drainage of the Frank Church—River of No Return Wilderness in central Idaho, USA (45°05'N, 114°51'W, Fig. 1). Our field work was based out of the University of Idaho's Taylor Wilderness Research Station (TWRS, 1,200 m). The topography of the lower Big Creek drainage is characterized by steep valleys and high ridges (1,100–2,780 m in about 4.8 km). Southerly aspects support several species of xeric shrubs and grasses including mountain mahogany (*Cercocarpus ledifolius*), big sagebrush (*Artemisia tridentata*), Idaho fescue (*Festuca idahoensis*), and bluebunch wheatgrass (*Pseudoroegneria spicata*). Cooler, northerly aspects support Douglas fir (*Pseudotsuga menziesii*) and mallow ninebark (*Physocarpus malvaceus*). Riparian vegetation includes black cottonwood (*Populus trichocarpa*), Rocky Mountain maple (*Acer glabrum*), hawthorn (*Crataegus douglasii*), serviceberry (*Amelanchier alnifolia*), alder (*Alnus* spp.), chokecherry (*Prunus virginiana*), raspberry (*Rubus idaeus*), thimbleberry (*Rubus parviflorus*), rose (*Rosa* spp.), and other shrub species. Exotic cheatgrass (*Bromus tectorum*) is also present throughout lower Big Creek. Exposed rocky outcrops and bare talus slopes are widespread along the valley sides. Large fires burned much of the Big Creek drainage in August 2000, including most of the forested habitat near the TWRS, and the effects of the fire are still clearly seen. A second fire burned a wide area north of the TWRS during July 2006.

The overwintering locations of the vast majority of rattlesnakes observed during this study occurred in three clusters (0.05–1.96 ha) within 1.5 km of each other and within 800 m of the TWRS. We refer to these clusters as hibernaculum complexes. Within a complex, the number of rattlesnakes captured at a given crevice or opening during spring egress ranged from one to three and the distances between neighboring crevices or openings within a cluster was approximately 5–75 m. All complexes observed during this study were along the side of the Big Creek Valley or its tributary valleys. Two complexes were north of Big Creek and the third was south of Big Creek. The southern complex, approximately 1.96 ha, consisted of scattered rock outcrops and small talus patches at 1,302–1,468 m elevation with a mean aspect of 214°. The first northern complex consisted of two disjunct talus patches; a 0.58-ha subcomplex at 1,245–1,311 m with a mean aspect of 96° and a 0.04-ha subcomplex at 1,317–1,321 m with a mean aspect of 141°. The second northern complex consisted of several small rock outcrops and was approximately 0.05 ha at 1,248–1,262 m with a mean aspect of 103°. One rattlesnake overwintered solitarily north of Big Creek in the south-facing junction of a rock outcrop complex and talus slide at 1,264 m and was approximately 1.2 km from the nearest hibernaculum complex.

Rattlesnake Radiotelemetry.—We surgically implanted radio transmitters into 29 male and nonpregnant female rattlesnakes during this 3-yr study. Rattlesnakes were captured near the hibernacula 28 April–1 May 2006, 2 May and 8–10 May 2007, and 16 April–23 May 2008 and brought back to the TWRS. In 2007, we were unable to capture a sufficient number of rattlesnakes around the hibernacula in the spring, so we implanted transmitters into five rattlesnakes that were opportunistically encountered around the TWRS between 17 May and 18 June. Rattlesnakes were anesthetized using Sevoflurane as an inhalant following the procedures described in Reinert (1992). Transmitters were implanted using the technique described in Reinert and Cundall (1982). We used 3.8-g PD-2, 9-, 11-, and 13.5-g SI-2T, and 5-g SB-2T transmitters (Holohill Systems Ltd., Carp, Ontario,

Canada). Transmitters were $\leq 5\%$ of the rattlesnake's body mass at time of surgery. Each rattlesnake was held for 8–36 h before being released at their respective capture sites and all rattlesnakes were alert and responsive before release. Telemetered rattlesnakes were monitored 11 May–6 August 2006, 17 May–11 August 2007, and 16 April–28 September 2008. We located each rattlesnake using a three-element Yagi antenna (Wildlife Materials International Inc., Murphysboro, Illinois, USA) and a Telonics TR-2 receiver (Telonics Inc., Mesa, Arizona, USA) approximately once every 2–4 d and recorded its position (Universal Transverse Mercator, UTM) using a handheld GPS unit (Garmin GPSmap 76CS, Garmin International Inc., Olathe, Kansas, USA). GPS accuracy ranged from 2–13 m (mean approximately 5 m). We attempted to capture each rattlesnake to determine its mass at the end of the 2006 field season and once per month in 2007 and 2008.

Movement Patterns.—To describe individual rattlesnake movement patterns, we entered the UTM coordinates for all telemetry locations that were separated by at least 1 d, including the overwintering location, into ArcGIS 9.2 (ESRI, Inc., Redlands, California, USA). We then calculated several movement statistics that would allow us to describe these patterns. We measured the straight line distance between each location for each rattlesnake using the Animal Movement Extension (Hooge and Eichenlaub, 1997) in ArcView GIS 3.2 (ESRI, Inc.). We measured the maximum straight line distance (i.e., displacement) a rattlesnake moved from its spring capture point. These distances were converted into topographic distances using 10-m digital elevation models (DEM) in ArcGIS 9.2. Topographic distances were used in all subsequent analyses. We measured the bearing of each movement segment using Hawth's Analysis Tools (Beyer, 2004) in ArcGIS 9.2. These were converted to a turn angle (0° to 180°) representing the departure from the previous bearing, which served as a measure of directionality. We also calculated an inverse meandering ratio (Williamson and Gray, 1975) for each rattlesnake as a second measure of directionality by dividing the maximum distance moved from the hibernaculum by the total distance moved and subtracting that value from one so that high values represent high meandering. Movement rate was calculated for each movement segment as meters moved per 24 h. Movements between consecutive radiotelemetry observations that were separated by more than 7 d were excluded for rate and absolute turning angle calculations to ensure that the most-accurate data were used for these calculations. Movements less than 5 m in length were excluded to facilitate comparisons with previous studies (Jorgensen et al., 2008). Only snakes captured at their hibernacula and monitored for an entire field season were included in subsequent analyses to avoid biasing the results towards snakes that had already begun moving away from their hibernaculum.

Estimating Summer Activity Areas.—We estimated summer activity areas (i.e., active season home ranges) using two approaches. We calculated 100% minimum convex polygons (MCP) and 95% fixed kernels (FK) for each rattlesnake in Home Range Tools (Rodgers et al., 2005) and ArcGIS 9.2. To determine the appropriate smoothing parameter (h), we decreased the reference bandwidth (h_{ref}) incrementally by 0.1 until we found the smallest contiguous polygon with no lacuna that included all telemetry observations (Berger and Gese, 2007). We also calculated a 50% FK for each snake to represent areas of concentrated activity. For each rattlesnake, many UTM coordinates were identical, which reflected multiple telemetry observations of that rattlesnake at identical locations. Because these

duplicate UTM coordinates caused computational problems with our kernel estimation, we altered these duplicate coordinates by 1–2 m to generate useful kernel estimates while retaining the information provided by observing our telemetered rattlesnakes in the same location on multiple occasions. Because of the extensive topographic relief in our study area, planimetric activity areas underestimated the size of the activity area (Greenberg and McClintock, 2008). We therefore converted our activity area polygons (MCP and 95% FK) and 50% FK into three-dimensional TIN (triangular integrated networks) using a 10-m DEM and calculated the topographic area of each TIN (Greenberg and McClintock, 2008). We buffered each summer activity area polygon by 5 m to allow the TIN to cover the full extent of the polygon. Unless otherwise noted, all statistical analyses were conducted in SAS 9.1 (SAS Institute, Cary, North Carolina, USA). All means are reported \pm one standard error.

Statistical Analysis.—We then conducted a series of analyses to test for an effect of overwintering site, sex, initial body mass, change in body mass, and year on several movement statistics (i.e., total distance, maximum distance, mean rate, mean turning angle). We used an unequal variance *t*-test to test for differences between rattlesnakes overwintering on either side of Big Creek for each year separately. We use linear mixed-effects models with the lme function (Pinheiro et al., 2014) in R 3.0.2 (R Core Team, 2013) to test for an effect of sex, initial body mass, and year on total distance moved, maximum distance moved, rate, turn angle, and meandering ratio. We initially included a sex by mass interaction, but if this proved statistically nonsignificant ($P < 0.05$), we removed the interaction term from the model and made inferences using only main effects. Maximum distance moved and mean rate were \log_{10} transformed to meet assumptions of normality. Data from all 3 yr were included and the number of telemetry locations (e.g., telemetry fixes) for each individual in each year was included to correct for differences in sampling intensity among years. Individual was included as a random effect to control for repeated measures from the same individual. We also used linear mixed-effects models with the lme function to test for an association between the percent change in body mass, sex, and each movement statistic using the 2008 data, testing for interactive effects as described earlier. The meandering ratio did not meet the assumptions of these parametric tests despite transformations. We therefore tested for differences in meandering ratio between males and nonpregnant females and between rattlesnakes overwintering north and south of Big Creek using a Mann-Whitney *U*-test. We used a Spearman's Rank Correlation to test for an association between initial body mass and percent change in body mass to determine if larger rattlesnakes lost more weight and an unequal variance *t*-test to test if percent change in body mass differed between males and females.

Fidelity to Summer Activity Areas.—To assess the degree of fidelity to summer activity areas, we calculated the percentage of 95% and 50% FK overlap between years for rattlesnakes that were captured at their hibernacula and monitored over an entire field season for multiple years ($N = 12$). Percent overlap was calculated following Jenkins (2007) by dividing the area of overlap (i.e., the area used in both years, only overlapping) by the total cumulative use area (i.e., the total area used in both years, overlapping and nonoverlapping). In calculating the total cumulative use area, the area of overlap was not counted twice. For example, if a rattlesnake's home range during year 1 was 100 ha, during year 2 was 200 ha, and the area of overlap was 50 ha, the index of overlap would be calculated as $\text{Overlap} = 50 / [(200 - 50) + 100]$. To test for differences in fidelity among years,

TABLE 1. Size and radiotelemetry tracking dates of 27 Prairie Rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage of central Idaho 2006–2008. Means and ranges are presented for mass, SVL, number of days monitored with radiotelemetry, and number of radiotelemetry locations (i.e., telemetry fixes per individual).

Year	N	Mass (g)	SVL (cm)	Number of days monitored	Number of locations	Start date of telemetry	End date of telemetry
2006	11 ♂	314 (210–436)	81.6 (72.5–92.2)	85 (83–87)	27 (26–30)	11 MAY	6 AUG
2007	9 ♂ and 2 ♀	287 (185–421)	78.2 (68.3–86.0)	85 (83–87)	30 (29–31)	17 MAY	11 AUG
2008	16 ♂ and 6 ♀	303 (138–487)	81.8 (71.8–93.8)	144 (110–164)	39 (28–44)	16 APR	28 SEP
Mean	NA	302	80.7	115	34	NA	NA

we compared the percentage of 95% and 50% FK overlap among all three combinations of years (2006/2007, 2007/2008, and 2006/2008) using a repeated measures analysis of variance (ANOVA). We tested whether rattlesnakes followed the same bearing during outbound and inbound migration in 2008. Migratory movements were identified using the procedures described in Bauder (2010) but generally consisted of lengthy, rapid, and linear movements away from or towards the hibernaculum during the spring and fall, respectively, in contrast to the shorter, less-directional movements associated with foraging. We used a nonparametric Moore's test for circular uniformity of paired data to test if the mean bearing of inbound and outbound migrations were different (Zar, 1996). The null hypothesis under this test was that rattlesnakes followed the same mean bearing during outbound and inbound migration. Because outbound and inbound migrations typically occurred in opposite directions, we added 180° to the mean inbound migration bearing to calculate the angular difference between mean bearing for inbound and outbound migration. We used Moore's test for circular uniformity of paired data to test whether rattlesnakes followed the same mean bearing during outbound migration during different years. We only used snakes for which we had complete outbound migration data ($N = 12$). Because this test can only be conducted between two samples, we ran the test for each pair-wise year combination using Bonferroni corrections.

RESULTS

Rattlesnake Radiotelemetry.—We monitored the movements of 12 male rattlesnakes in 2006, 12 male and 3 nonpregnant females in 2007, and 16 males and 6 nonpregnant females during 2008 for a total of 29 rattlesnakes (Table 1). Five rattlesnakes were telemetered during all 3 yr, one in 2006 and 2007, 6 in 2007 and 2008, and 2 in 2006 and 2008 for a total of 49 snake-years. Seven of these snake-years were partial data sets due to battery failure or late capture dates. Twenty-seven (21 males and 6 nonpregnant females) rattlesnakes provided data from 44 snake-years that met the criteria for inclusion in some or all of the analyses. Mean body mass of these 27 individuals at the time of transmitter implantation was 323 g (± 14.5 g, range 172–487 g) for males and 207 g (± 13.97 g, range 138–255 g) for females. Mean

snout–vent length was 75.7 cm (± 1.57 cm, range 68.3–93.8 cm) for males and 76.3 cm (± 1.90 cm, range 70.3–81.7 cm) for females.

Movement Patterns and Home Range Size.—Rattlesnakes moved a mean total distance of 4.04 km (± 0.24 km) and a mean maximum distance of 1.32 km (± 0.11 km; Table 2). The maximum distance moved from a hibernaculum was 2.93 km by a male in 2006. However, these overall means are likely biased because not all individuals were monitored throughout the activity season or the entire study. Additionally, the spring hibernacula searches in 2007 probably occurred after peak emergence, further biasing the results of that year to rattlesnakes that emerged later in the spring. Because the 2008 data were collected during the entire activity season, and snakes were captured throughout their spring emergence, these results are probably the most-accurate representation of rattlesnake movements in this landscape. During 2008, telemetered rattlesnakes ($N = 22$) moved a mean total distance of 4.46 km (± 0.37 km) and a mean maximum distance of 1.46 km (± 0.15 km). During 2008, mean rate was 42.76 m/24 h (± 3.82 m/24 h), mean turn angle was 70.92° ($\pm 2.84^\circ$), and mean meandering ratio was 0.66 (± 0.03). Mean 95% and 50% FK size was 109.21 ha (± 22.60 ha) and 23.98 ha (± 4.58 ha), respectively, while mean MCP was 48.34 ha (± 7.00 ha). Estimates for 95% FK and MCP that incorporated topographic relief were a mean of 16% (range 6–28%) and 16% (range 8–23%), respectively, larger than those that did not. Total distance moved was strongly correlated with the size of the 95% FK ($r_s = 0.7502$, $P < 0.0001$) and 50% FK ($r_s = 0.7594$, $P < 0.0001$), as was maximum distance moved (95% FK, $r_s = 0.8961$, $P < 0.0001$; 50% FK, $r_s = 0.8776$, $P < 0.0001$). Total distance moved and maximum distance moved were also highly correlated with MCP ($r_s = 0.7864$, $P < 0.0001$ and $r_s = 0.9060$, $P < 0.0001$, respectively). For this reason, we did not use home range size in analyses testing for differences in movement patterns between overwintering locations, sex, and among years. We found no differences in any movement statistics in each year between rattlesnakes overwintering on the north and south side of Big Creek.

There were few differences in movement patterns between males and nonpregnant females, and the interactive effect between sex and body mass (either initial body mass or change in body mass) was not significant in any analyses ($P \geq 0.2661$). There was no significant effect of sex on total distance moved (t

TABLE 2. Mean annual movement statistics from 27 Prairie Rattlesnakes (*C. v. viridis*) monitored with radiotelemetry in the lower Big Creek drainage of central Idaho 2006–2008. FK = fixed kernel and MCP = 100% minimum convex polygon.

	Total distance (km)	Max. distance (km)	Rate (m/24 h)	Meandering ratio	Turn angle (°)	95% FK (ha)	50% FK (ha)	MCP (ha)
2006	4.20	1.42	59.98	0.66	87.79	113.50	24.42	53.37
2007	3.03	0.95	42.66	0.68	82.98	54.45	12.44	29.43
2008	4.46	1.46	42.76	0.66	70.92	109.21	23.98	48.34
Mean	4.04	1.32	47.04	0.67	78.22	96.30	21.14	44.79

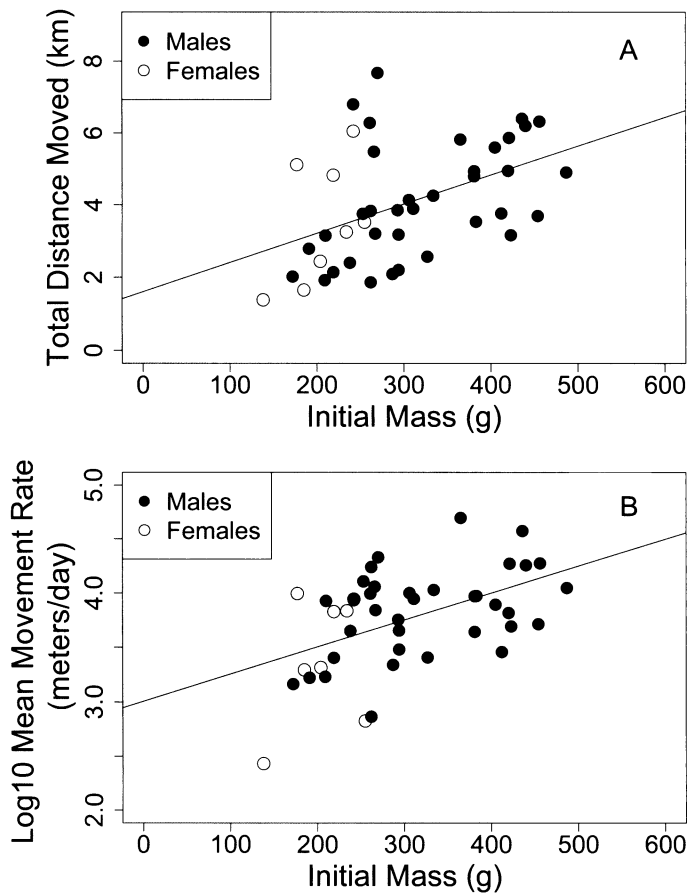


FIG. 2. (A) Relationship between initial body mass (g) and total distance moved (km), and (B) \log_{10} mean movement rate (m/day) for male ($N = 21$) and female ($N = 5$) Prairie Rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage of central Idaho 2006–2008. Some individuals were monitored for multiple years, so each point on the graph represents one snake-year ($N = 41$).

$= -0.21$, $df = 25$, $P = 0.8324$), \log_{10} maximum distance moved ($t = -1.16$, $df = 25$, $P = 0.2569$), or \log_{10} mean movement rate ($t = 0.07$, $df = 25$, $P = 0.9472$). There was a marginal effect of sex on mean turning angle ($t = 1.86$, $df = 25$, $P = 0.0751$), with males having a higher mean turning angle ($81.01^\circ \pm 2.52^\circ$) than females ($65.63^\circ \pm 5.79^\circ$). There was a significant difference in meandering ratio between males and nonpregnant females in 2008 (0.71 ± 0.02 vs. 0.54 ± 0.05 , $Z = -2.66$, $P = 0.0077$), indicating that males meandered more than nonpregnant females. There was no difference in percent change in body mass between males and females in 2008 ($t = 0.98$, $df = 4.34$, $P = 0.3769$).

Initial body mass had some effect on rattlesnake movement patterns. There was a significant positive effect of initial body mass on the total distance moved ($t = 2.59$, $df = 13$, $P = 0.0223$; Fig. 2A) and the \log_{10} mean movement rate ($t = 2.51$, $df = 13$, $P = 0.0259$; Fig. 2B). There was no effect of initial body mass on maximum distance moved ($t = 1.07$, $df = 13$, $P = 0.3032$) or mean turning angle ($t = 0.57$, $df = 13$, $P = 0.5813$). Initial body mass was correlated with meandering ratio, but only in 2008 ($r_s = 0.4348$, $P = 0.0431$), and the strength of this association was low. There was no correlation between initial body mass and percent change in body mass in 2008 ($r_s = -0.3385$, $P = 0.1444$). There was no correlation between meandering ratio and percent change in body mass in 2008 ($r_s = -0.1528$, $P = 0.5201$). None of

the movement statistics we measured had an effect on change in body mass in 2008.

Fidelity to Summer Activity Areas.—There were few differences in rattlesnake movement statistics among years. After correcting for the number of telemetry observations, there was no significant difference in total distance moved, maximum distance moved, or mean turning angle among years ($P \geq 0.1446$). There was a marginal effect of year on \log_{10} mean movement rate ($F_{2,13} = 3.66$, $P = 0.0547$) with higher movement rates in 2006 compared to 2007 and 2008 (Table 2). There were no significant differences in the mean bearings of outbound migration for rattlesnakes monitored during multiple years ($R' = 0.37$ – 0.68 , $P > 0.60$). The mean difference in outbound migration bearings between years ranged from $29.61^\circ (\pm 5.45^\circ)$ between 2007 and 2008 to $70.03^\circ (\pm 43.22^\circ)$ between 2006 and 2007. Mean percentage overlap in 95% FK home ranges was $35\% (\pm 3.83\%)$ and $18\% (\pm 2.73\%)$ for 50% FK home ranges (Fig. 3). The percentage of 95% FK overlap was not significantly different among the three pairwise year combinations ($F_{2,8} = 0.10$, $P = 0.9094$) nor was the percentage overlap of 50% FK ($F_{2,8} = 0.97$, $P = 0.4204$).

DISCUSSION

Seasonally migrating snake populations in north-temperate climates may show wide variation in movement distances both within and among taxa (Table 3). For example, Prairie Rattlesnakes from three separate populations in southern Canada exhibited more than a 6-fold difference in mean maximum distance moved (Didiuk, 1999; Jorgensen et al., 2008; Gardiner et al., 2013) and all moved greater distances than the Prairie Rattlesnakes in this study (Table 3). Similarly, Martino et al. (2012) and Gardiner et al. (2013) found significant differences in home range size and daily movement rate, but not maximum distance moved, among three species of snakes within the same study area. The movement distances observed in our study were intermediate to those reported for other seasonally migrating snake populations from multiple taxa in areas with low to moderate topographic relief (Table 3).

Most studies of snake movements do not discuss how snakes moved in relation to topographic features, although Williams et al. (2012) found that Great Basin Gophersnakes (*Pituophis catenifer deserticola*) at one study population (elevation 435–635 m) moved primarily away from hibernacula on hills into the adjacent valley. Rattlesnakes in our study area did not restrict their movements to valley bottoms and often moved over and along ridges (Fig. 4). We also observed multiple crossings of Big Creek and its smaller tributaries. Our observed movement distances were also similar to or greater than those reported for rattlesnakes from areas with less topographic relief (Jenkins, 2007; Parker and Anderson, 2007; Shipley et al., 2013). This suggests that topography may not be wholly responsible for the intermediate movement distances observed in our study compared to those of other seasonally migrating snake populations. Variation in movement distances among populations may be caused by variability in resource availability, particularly suitable hibernacula, prey, and mates, which may force individuals to travel further to locate sufficient resources (Duvall et al., 1990; Pearson et al., 2005; Beaupre, 2008; Gardiner et al., 2013). Additionally, variation in population sizes of communal denning species could lead to higher population densities in foraging habitats and may force individuals to move greater distances to locate sufficient resources (Jorgensen et al., 2008). Low topographic relief may provide snakes with

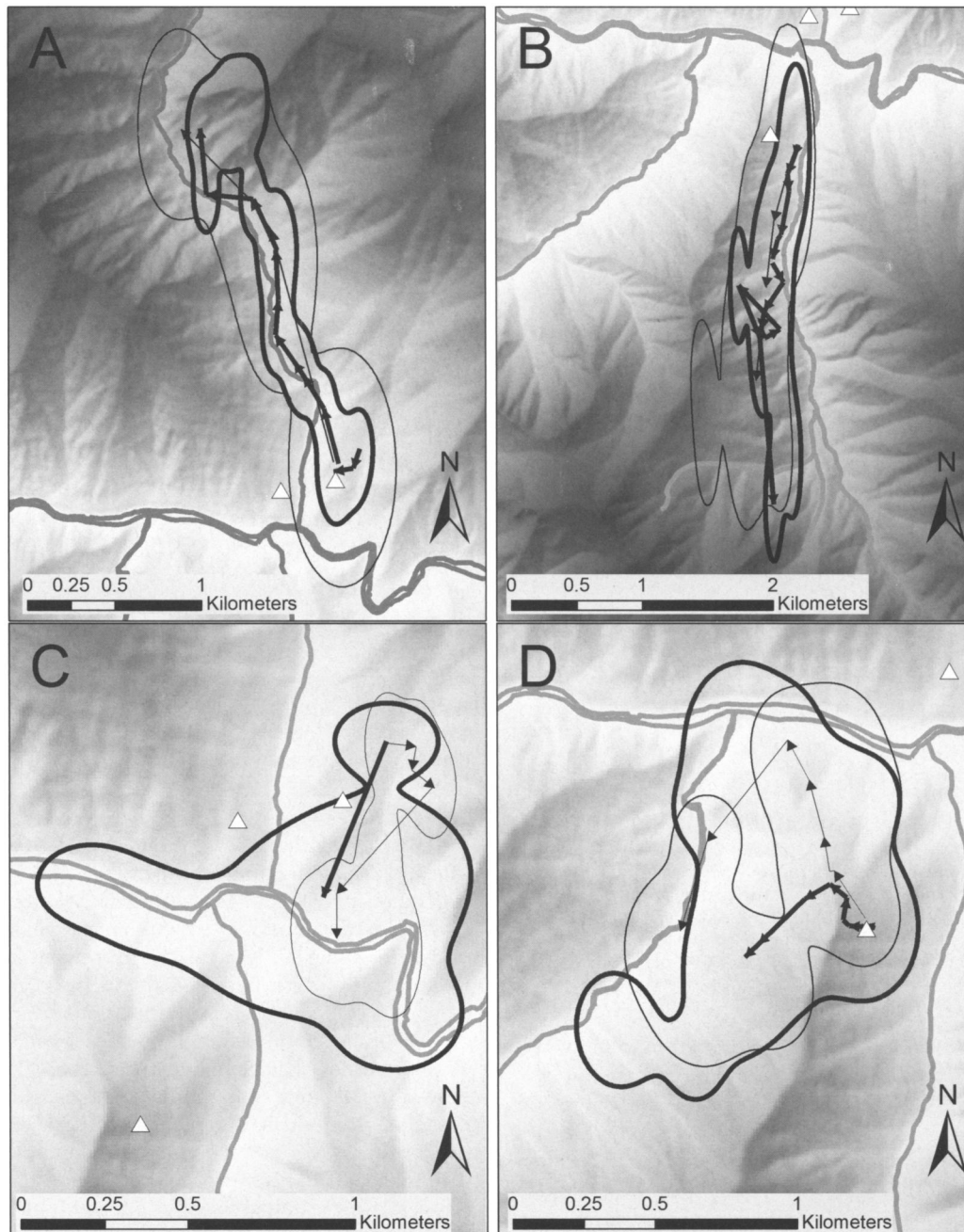


FIG. 3. Summer activity areas (95% fixed kernel utilization distribution [UD]) and outbound migration movements for one female (A) and three male (B–D) Prairie Rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage of central Idaho monitored for multiple years during 2006–2008. Each panel displays summer activity areas and outbound migration movements for 2 yr. Thick summer activity areas correspond with thick outbound migration movements. The three hibernaculum complexes are denoted by white triangles and rivers–creeks with dark gray lines as shown in Figure 1.

increased flexibility to travel further to locate summer foraging habitat. This may be particularly important for snakes in areas where hibernacula are limited, such as the northern edges of their ranges. Indeed, some of the longest movement distances reported for snakes occur near the northern edge of their range where cold winters may limit the availability of suitable hibernacula (Jorgensen et al., 2008; Martino et al., 2012). Although we did not conduct extensive hibernacula surveys during our study, we suspect that suitable overwintering sites are relatively abundant within our study area given the abundance of rocky, south-facing habitats and limited observations of solitary overwintering. However, topography may still have a restrictive effect on rattlesnake movements within our

study area. We never observed rattlesnakes >2,000-m elevation and observed strong selection for low elevations and gentle slopes within 3 km of the hibernacula (Bauder et al., In press). However, at the scale of the home range rattlesnakes showed much less selection for topographic features. Topography may therefore have an absolute restrictive effect on rattlesnake movements in lower Big Creek but primarily at broad spatial scales. Rattlesnakes could have moved up to 5 km from the hibernacula and still remain below 2,000 m by following drainages, yet the maximum distance moved from a hibernaculum was 2.93 km.

Overlap between overwintering sites and summer foraging habitat may lead to shorter or nonmigratory movements (Reed

TABLE 3. Mean movement distances, rates, and home range sizes (minimum convex polygon = MCP home range [HR]; 95% fixed kernel utilization distribution = UD HR) from studies of seasonally migrating snake populations from north temperate latitudes. Single elevation values were used when the study reported a single elevation value for the study site. Total distance and maximum distance are reported as kilometers, rate as meters moved per day, and home range estimates as hectares. Studies with two values represent the reported values for males and nonpregnant females, respectively. Values with NA were not directly reported in the original study.

Study ^a	Species	Location	Elevation range	Habitat	N	Total dist.	Max. dist.	Rate	MCP HR	UD HR
This study King and Duvall (1990)	<i>C. v. viridis</i>	Central Idaho	1148–1898	Bunchgrass/Douglas fir	22	4.46	1.46	43	48	109
	<i>C. v. viridis</i>	Southern Wyoming	2120	Sagebrush-steppe	16	3.51	2.57	196 ^b	NA	NA
Didiuk (1999) Jorgensen et al. (2008) Gardiner et al. (2013)	<i>C. v. viridis</i>	Southeast Alberta	600–>850	Prairie	5	2.76	2.03	133 ^d	NA	NA
	<i>C. v. viridis</i>	Southeast Alberta	NA	Prairie	19	40.00 ^c	17.08 ^c	NA	NA	NA
	<i>C. v. viridis</i>	Southwest Saskatchewan	760–950 ^d	Prairie	23	8.17	2.76	211 ^b	NA	NA
	<i>C. v. viridis</i>	East-central Colorado	1728–1783	Prairie	10	NA	2.81	92	109	14
Cobb (1994)	<i>C. v. viridis</i>	East-central Colorado	1728–1783	Prairie	10	3.71	0.57	116 ^b	18	NA
	<i>Crotalus oreganus lutosus</i>	Southeast Idaho	1470	Sagebrush-steppe	4	3.65	0.44	105 ^b	18	NA
Jenkins (2007) Parker and Anderson (2007)	<i>C. o. lutosus</i>	Southeast Idaho	1596–1697	Sagebrush-steppe	32	5.08	1.47	NA	NA	23
	<i>C. o. concolor</i>	Southwest Wyoming	1840–2125	Sagebrush-steppe	21	2.12	0.78	NA	118	301
Brown et al. (2009)	<i>C. o. oreganus</i>	Southern British Columbia	285–>700 ^d	Bunchgrass/ponderosa pine	14	1.96	0.68	142 ^b	64	196
	<i>Crotalus horridus</i>	Central Pennsylvania	200–550 ^d	Deciduous hardwood forest	10–12	5.84	1.08 ^e	37	25	NA
Reinert et al. (2011)	<i>Sistrurus catenatus edwardsii</i>	Southeast Colorado	1380–1470	Prairie/sandhill	12	5.53	2.11	37	89	NA
Wastell and Mackessy (2011) Smith et al. (2009)	<i>Agkistrodon contortrix</i>	Central Connecticut	80–220	Deciduous hardwood forest	10	4.53	1.89 ^e	32	42	104
	<i>Coluber constrictor flaviventris</i>	Southwest Saskatchewan	760–950 ^d	Prairie	23	4.32	0.77	NA	17	NA
Martino et al. (2011)	<i>Pituophis catenifer sayi</i>	Southwest Saskatchewan	760–950 ^d	Prairie	6	1.82	0.36	65	5	14
	<i>Pituophis catenifer deserticola</i>	Southern British Columbia	330–645 ^d	Bunchgrass/ponderosa pine	39	NA	1.71	52	87	NA
Williams et al. (2012)	<i>Pituophis catenifer deserticola</i>	Southern British Columbia	330–645 ^d	Bunchgrass/ponderosa pine	39	NA	0.52	NA	10.5	NA

^a Maximum distance reported by King and Duvall (1990) was calculated by summing the length of daily movement steps during outbound migration. Values from Brown et al. (2009) were for resident snakes only. Sample size range for Reinert et al. (2011) was sample size range over the 4-yr study and values were the mean annual values average across all 4 yr.

^b Represents distance per movement.

^c Values were calculated from raw data provided in the source document.

^d Elevation ranges (in meters) were estimated from Google Earth using the description of the study area provided in the original document.

^e Represents range length.

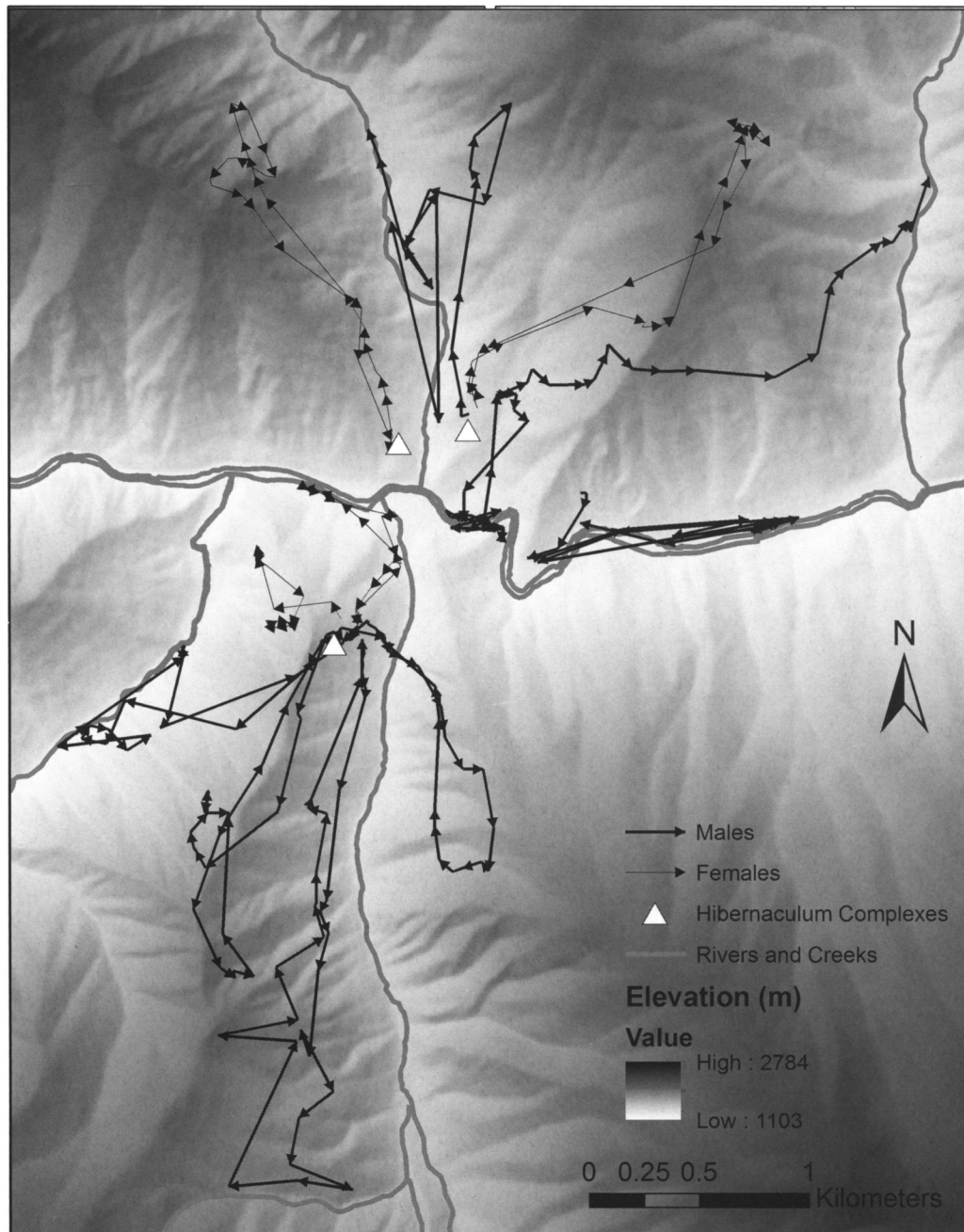


FIG. 4. Movement pathways for 11 selected Prairie Rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage of central Idaho monitored during 2006–2008. Pathways represent movements from a single activity season. Pathways not showing a return to a hibernaculum were collected in 2006 or 2007 when radio tracking ceased in August.

and Douglas, 2002; Dugan et al., 2008; Shipley et al., 2013). Bauder et al. (In press) found that small mammal surface activity (used as a proxy for prey availability) was similar across all habitats, that rattlesnakes foraged in most habitats in proportion to their availability, and that some rattlesnakes fed at their hibernaculum. These observations suggest that suitable overwintering sites and prey are sufficiently abundant within lower Big Creek to negate the need for more-extensive seasonal migrations. However, additional data on the distribution and availability of overwintering sites and prey and their interaction with population density are required to test this hypothesis.

Many studies on snake movements have found differences in total or seasonal movement distances between sexes and have

attributed such differences to male mate-searching, females searching for oviposition sites, or differing energetic requirements between sexes (Gregory et al., 1987; Blouin-Demers and Weatherhead, 2002; Pearson et al., 2005; Cottone and Bauer, 2013). Male and nonpregnant female rattlesnakes in our study showed no differences in movement distances, either total distance or maximum distance moved, or movement rate, although a relatively small female sample size may have prevented us from detecting differences. Males in many species of North American vipers show larger home range sizes compared to females (Roth, 2005; Waldron et al., 2006; Smith et al., 2009; Anderson, 2010; Glaudas and Rodriguez-Robles, 2011; Putnam et al., 2013), although differences in distance

moved or home range size may be absent or marginal in some populations (King and Duvall, 1990; Reed and Douglas, 2002; Parker and Anderson, 2007). Larger home range sizes are generally attributed to male mate-searching, which is a common mating system among North American vipers (Duvall et al., 1992). Although we did not observe sex-specific differences in distance moved we did observe differences in the pattern of movement. Several males undertook distinct mate-searching movements which were generally long, rapid movements made in July and August that tended to have low directionality (Bauder, 2010). This likely explains the higher turn angles and meandering ratios we observed in males.

The mate-searching movements observed in our study contrast with those observed in Prairie Rattlesnakes in southern Wyoming (King and Duvall, 1990; Duvall and Schuett, 1997). In those populations, females continued to forage during the late summer, but their spatial predictability was low because of the spatial unpredictability of prey. Straight line mate-searching movements allowed males to maximize their encounters with females (Duvall et al., 1992; Duvall and Schuett, 1997). The sharp contrast of our results and those of Duvall et al. suggests that females within lower Big Creek were more-spatially predictable, thereby allowing males to forgo linear mate-searching movements. Even so, only about half of the males in this study exhibited distinct mate-searching movements during July and August. The male depicted in Figure 3C undertook mate-searching movements in 2006 (indicated by the bold activity area outline) but did not in 2008 (indicated by the thin activity area outline). We are unsure why we did not observe mate-searching movements in all males, and we are unaware of how widespread this pattern is among other snake populations exhibiting male mate-searching. Although larger males may be more likely to exhibit courtship or mate-guarding behaviors (Clark et al., 2014), we found no difference in initial body mass between mate-searching and non-mate-searching males (Bauder, 2010). Males exhibiting mate-searching gained slightly less weight (1.7% vs. 6.9%) and spent less time foraging (60 days vs. 81 days), on average, than did males where mate-searching was unobserved, although these differences were not significant (Bauder, 2010). This suggests that there may be some opportunity cost to mate-searching which, given a restricted activity season, may cause some males to forgo searching for females at the expense of foraging. Alternatively, if receptive females are relatively accessible within our study area, males may have ample opportunities to encounter females while foraging and therefore negate the need for additional searching.

Consistent with several other studies from multiple snake taxa (Kapfer et al., 2008; Pattishall and Cundall, 2008; Smith et al., 2009), rattlesnakes in our study generally showed fidelity to summer activity areas although the degree of overlap in summer activity areas was relatively modest (range 0.06–0.65). In addition, telemetered rattlesnakes tended to follow the same mean bearing during their outbound migrations over multiple years. We observed comparatively less overlap in summer activity areas, particularly in areas used for foraging, among telemetered rattlesnakes within activity seasons (JMB, unpubl. data) although fully addressing interindividual space use overlap was beyond the scope of this study. Our rates of activity area overlap were lower than those reported by Jenkins (2007) for Great Basin Rattlesnakes (*Crotalus oreganus lutosus*) in southeast Idaho (mean = 0.63), although Jenkins (2007) considered overlap of summer foraging areas whereas our summer activity areas included inbound and outbound

migration. Additionally, portions of summer activity areas used one year but not another were often used during mate-searching (e.g., Fig. 3C). This results in less overlap in summer activity areas between years if males do not conduct extensive mate-searching movements every year, as suggested by our data. Differing methodologies used to calculate activity area fidelity in other studies also limits our ability to compare our results more broadly. The tendency for rattlesnakes to use similar migration bearings across time while showing modest activity area overlap may suggest greater fidelity to migration routes than to foraging areas. Fidelity to summer foraging areas should be expected if prey resources remain fairly stable in space and time. However, small mammal populations often fluctuate widely over time (Gillespie et al., 2008; Boonstra and Krebs, 2012), and Beaupre (2008) found that Timber Rattlesnakes (*Crotalus horridus*) foraged more and showed less reproductive activities during years of low prey abundance. One might therefore expect that snakes, such as rattlesnakes which prey on species with dynamic life histories, would adjust their foraging movements in response to shifts in prey abundance. However, Jenkins (2007) found that Great Basin Rattlesnakes returned to the same general foraging areas in subsequent years even in years of low prey abundance. Movements during these years were more directional, suggesting that rattlesnakes adjusted their foraging movements within their summer activity areas to increase their searching efficiency in response to perceived prey availability (King and Duvall, 1990; Duvall and Schuett, 1997).

The patterns of fidelity to migration routes and summer activity areas observed in this study may have some implications for the hypothesis that linear migration movements represent efficient search patterns for widely distributed or spatially unpredictable prey resources. If snakes do migrate to a familiar summer activity area year after year along a familiar route, then these movements are probably not true searching movements. Rather, linear migratory movements may represent the quickest and most direct route to a known foraging area. We hypothesize that migratory movements are relatively fixed and independent of perceived prey availability compared to foraging movements made during the summer. This may explain the linear migrations observed in many seasonally migrating snakes (Larsen, 1987; King and Duvall, 1990; Wastell and Mackessy, 2010). However, when a snake reaches its summer foraging area, it may then adjust its movements in response to perceived prey availability, perhaps continuing to make linear movements if prey availability is low. Jenkins (2007) found that Western Rattlesnakes in southeastern Idaho made more linear movements during low prey years. Rattlesnakes still returned to the same general foraging areas, suggesting that the more-linear movements were in response to more-spatially unpredictable prey resources. However, further research is needed to evaluate if summer fidelity is observed in other rattlesnake populations, particularly during fluctuations of prey abundance, and to test the hypothesis that rattlesnakes modify foraging movements, not migration routes, in response to prey availability.

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