



The Biology of Rattlesnakes II

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An adult Tiger Rattlesnake (*Crotalus tigris*) set beautifully in its Sonoran desert habitat. Tiger Rattlesnakes occur from south-Central Arizona into southern Sonora, Mexico. The image titled, “Tiger Rattlesnake (*in situ*),” was painted by Tell Hicks and commissioned for the cover of *Biology of the Rattlesnakes II*. Limited edition prints of this painting are available at <http://telhicksprints.weebly.com/index.html>.

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

Javan M. Bauder^{1,2,3}, Holly Akenson⁴, and Charles R. Peterson¹

¹ Department of Biological Sciences, Idaho State University, Pocatello, Idaho, USA

⁴ Wallowa Resources, Enterprise, Oregon, USA

ABSTRACT.—Although Prairie Rattlesnakes (*Crotalus v. viridis*) are known to make lengthy migrations from communal hibernacula to summer foraging habitat, it is largely unknown how these patterns are influenced by mountainous topography. The objectives of this study were to determine how Prairie Rattlesnake movement patterns in a mountainous landscape were influenced by topography, habitat, and prey activity. We used radio telemetry to monitor the movements of 16 male and four nonpregnant female Prairie Rattlesnakes in the Frank Church Wilderness in central Idaho during the summer of 2008. We used GIS to test for selection for topographic features and habitats at multiple spatial scales and compared small mammal activity among habitats. Rattlesnakes moved across a wide range of topographic features including ridges, steep slopes, rivers, and creeks. Rattlesnakes appeared somewhat restricted by topography, particularly elevation, within three kilometers of their hibernacula while topography appeared to have little restrictive effect within their home ranges. Although rattlesnakes showed the greatest selection for riparian habitats at all spatial scales, we failed to detect a significant difference in small mammal activity among habitats. Our results indicate that topography does influence rattlesnake movement and that these effects vary by spatial scale. Although habitat and prey abundance likely influence rattlesnake movements in this system, topography may impose the greatest constraints on rattlesnake movements.

INTRODUCTION

Animal movements across the landscape may be thought of as a tradeoff between the need to acquire key resources and factors that restrict those movements (Bronmark et al., 2008). The distribution of important resources, such as food, potential mates, opportunities for thermoregulation, and overwintering refugia, often vary across space and time. Under such conditions, animal movements across the landscape are generally influenced by the spatio-temporal distribution of these resources (McIntyre and Wiens, 1999; Klaassen et al., 2006; Filipa-Loureiro et al., 2007; Noyce and Garshelis, 2011). In contrast, an animal's movements across the landscape may also be constrained by a variety of

factors including its size and mobility, ability to meet energetic requirements (Alerstam et al., 2003), predation risk (Fortin et al., 2005), abiotic conditions (Daltry et al., 1998; Bartelt et al., 2010), and habitat composition and configuration (Cushman et al., 2011). Anthropogenic disturbances, such as urbanization, intensive agriculture, and roads, may also restrict animal movements (Johnston and Frid, 2002; Coulon et al., 2008; Shepard et al., 2008). Tradeoffs between resource acquisition and constraints to movement may be particularly important for animals that are additionally constrained by the length of their activity seasons (e.g., ectotherms in temperate climates). Understanding these tradeoffs is not only important for understanding animal movement ecology but also from a management and conservation standpoint by allowing managers to evaluate the susceptibility of populations to anthropogenic disturbances. Species whose movements are strongly constrained by natural factors may be more susceptible to negative

² Correspondence e-mail: javanvonherp@gmail.com

³ Present address: Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts, USA

effects of anthropogenic disturbance. For example, if seasonal movements occur across a small number of movement corridors, anthropogenic disturbances within those corridors could greatly reduce access to key resources and inter-population dispersal (Epps et al. 2007; Sawyer et al., 2009) and lead to a reduction of population viability.

Topographic features, such as mountain ranges, ridges, and valleys, have strong potential to constrain animal movements. These constraints may occur through increased energetic expenditures (Johnson et al., 2002), environmental conditions (e.g., cold temperatures at high elevations), opportunity costs from increased travel times (Alerstam et al., 2003), or reduced perception of the surrounding landscape (Alderman and Hinsley, 2007; Graf et al., 2007). Reduced movements due to topographical constraints can impede site colonization in metapopulation dynamics (Harrison, 1989; Roland et al., 2000) and lead to reduced genetic connectivity among subpopulations (Funk et al., 2005; Giordano et al., 2007). Studies have reported restrictive effects of topography on animal movement and dispersal in multiple taxa including large mammals (Johnson et al., 2002; Dickson et al., 2005; Kie et al., 2005; Bruggeman et al., 2007; Dickson and Beier, 2007), amphibians (Funk et al., 2005; Richards-Zawacki, 2009), and insects (Harrison, 1989; Roland et al., 2000). However, other studies have reported minimally restrictive effects of topography on animal movements (Anderson et al., 2005; Coulon et al., 2008), including studies on small-bodied reptiles and amphibians (Pilliod et al., 2002; Bartelt et al., 2004; Bowne and White, 2004; Westgate et al., 2012). Topographically complex landscapes may provide beneficial resources such as shelter, escape terrain, or a greater diversity of habitat conditions in close spatial proximity (Rachlow and Bowyer, 1998; Epps et al., 2007; Sawyer et al., 2007; Leblond et al., 2010). In such situations, the costs imposed by moving across topographically diverse landscapes may be less than the potential benefits of using such a landscape.

The Prairie and Western Rattlesnakes (*Crotalus v. viridis* and *C. oreganus*) of the Intermountain West provide an excellent system with which to study the interactions between resource acquisition and factors potentially constraining individual movements. These species are closely related and were formerly classified as a single species (*Crotalus viridis*, Pook et al., 2000; Ashton and de Queiroz, 2001; Douglas et al., 2002). In many populations, rattlesnakes undertake migrations between communal hibernacula and summer foraging habitat, which may exceed 20 km (Jorgensen et al., 2008). Rattlesnakes typically cease their migratory movements upon encountering an area of high prey abundance and engage in shorter foraging movements (Duvall et al., 1990; King and Duvall, 1990; Jenkins and Peterson, 2008). Males will make additional extensive movements in

late summer to locate receptive females for mating (King and Duvall, 1990; Duvall and Schuett, 1997). Migration and mate searching movements are highly linear in some populations (Cobb, 1994; Duvall and Schuett, 1997; Jorgensen et al., 2008) which presumably allows for increased search efficiency for a spatially unpredictable resource (e.g., prey or mates, Duvall and Schuett, 1997). Although rattlesnake seasonal movements are strongly influenced by the distribution of resources, particularly overwintering sites and prey, little is known about the influence of topography on rattlesnake movements. Previous studies of snake movement have often taken place in areas with little or moderate topographic relief which may offer little resistance to their movements (but see Reed and Douglas, 2002; Greenberg and McClintock, 2008).

The objectives of this study were to evaluate the effects of topography, habitat, and prey abundance on Prairie Rattlesnake movements in a mountainous landscape. We expected that topography would show a restrictive effect on rattlesnake movements and therefore predicted that rattlesnakes would select topographic features that minimized their movements over broad topographic gradients at multiple spatial scales, such as low elevations, gentler slopes, and valley bottoms. We also expected that rattlesnakes would preferentially use areas with greater abundances of small mammal prey. However, we were unable to measure small mammal abundance directly due to logistical constraints and instead used a measure of small mammal surface activity. Foraging rattlesnakes may selectively forage in areas with greater small mammal surface activity because of increased chemosensory signals (Duvall et al., 1990; Theodoratus and Chiszar, 2000; Clark, 2004), higher prey encounter rates, and a potentially higher probability of successfully foraging, which may be important for ambush predators such as rattlesnakes (Glaudas and Rodriguez-Robles, 2011). We therefore predicted that rattlesnakes would select habitats with greater small mammal surface activity.

MATERIALS AND METHODS

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 study area was centered on the University of Idaho's Taylor Wilderness Research Station (TWRS). This area is dominated by a rugged mountainous landscape (1100–2780 m elevation). Vegetation communities varied strongly by aspect with southerly aspects supporting a mixed bunchgrass community (primarily Idaho Fescue, *Festuca idahoensis*, and Bluebunch Wheatgrass, *Pseudoroegneria spicata*) and northerly aspects supporting Douglas Fir (*Pseudotsuga menziesii*) forests. Riparian habitats were dominated by a mixed hardwood and shrub

community. Exposed rocky outcrops and bare talus slopes were widespread along the valley sides. Large fires burned much of the study area in 2000 and 2006.

Rattlesnake radiotelemetry.—The rattlesnakes used in this study were collected from three hibernacula within 1.5 km of each other on either side of Big Creek, except for one individual that overwintered solitarily approximately 0.60 km from the nearest of the three complexes. All hibernacula complexes were between 1235 and 1420 m elevation. For additional descriptions of the study area and hibernacula, see Bauder (2010). We surgically implanted radio transmitters into 16 male and six nonpregnant female rattlesnakes. Rattlesnakes were captured near the hibernacula during the spring and brought back to the TWRS. 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 11 and 13.5 g SI-2 and SI-2T

and 5 g SB-2 and SB-2T transmitters (Holohil 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 snakes were alert and responsive before release. Telemetered rattlesnakes were monitored 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 two to four days and recorded its Universal Transverse Mercator (UTM) coordinates using a handheld GPS unit (Garmin GPSmap 76CS, Garmin International Inc., Olathe, Kansas, USA). Reported accuracy ranged from 2–13 m (mean approximately 5 m). We were unable to locate telemetered rattlesnakes between 28 June and 11 July 2008 due to an injury to JMB.

Topography analysis.—We visually assessed the effects of topography on rattlesnake movements by overlaying each rattlesnake's movement pathway on a three dimensional image of our study area created using 2004 digital orthoimages (NAIP, Inside Idaho, <http://inside.uidaho.edu/geodata/NAIP2006/index.htm>) and a 10 m digital elevation model (DEM) in ArcScene 9.3 (ESRI, Inc., Redlands, California, USA). To better determine if topography had a restrictive effect on rattlesnake movements, we conducted a resource selection analysis for topographic features. We excluded two snakes whose transmitters malfunctioned during the summer so as to only include individuals that were monitored for the entire activity season ($N = 20$). We recorded the elevation, slope, aspect, and convexity for each telemetry observation using a 10 m DEM in ArcGIS 9.2. To convert aspect from a circular variable to a continuous variable, we calculated the absolute degree departure from north and east for each observation. Each of these variables could range from 0° to 180° with smaller values being closer to north or east and larger values being closer to south or west. We calculated convexity as a measure of topographic position (Kvamme, 1988; Ager et al., 2003; Kie et al., 2005). Convexity was calculated as the difference in elevation between each pixel and the mean elevation of a neighborhood of surrounding pixels. Negative values indicated valley bottom topography while positive values indicated ridge top topography. We calculated convexity using 30×30 m and 90×90 m window sizes to test if rattlesnakes responded to fine or coarse scale variation in topographic position. We also measured the Euclidean distance from each telemetry observation to the nearest water source.

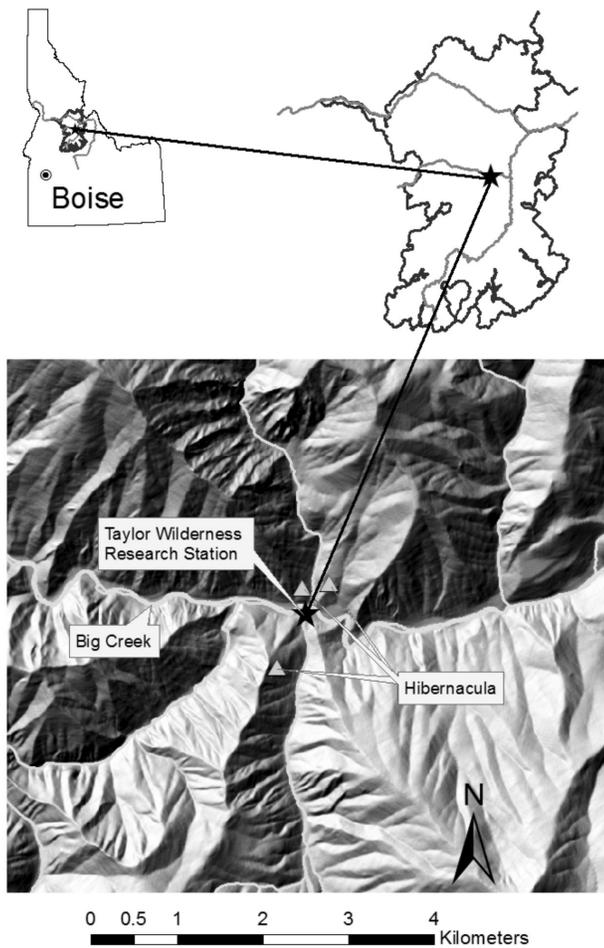


Figure 1. Map of the study area showing the Frank Church River-of-No-Return Wilderness, the Taylor Wilderness Research Station, and the three Prairie Rattlesnake (*Crotalus v. viridis*) hibernacula used in this study.

To measure the range of topographic features available for selection, we generated random points and measured elevation, slope, aspect, convexity, and distance to water at each point. Random points were generated at two spatial scales to test for hierarchical differences in selection due

to scale (Johnson, 1980). The first scale (landscape scale) represented the area available to all rattlesnakes from the hibernacula used in this study and was defined as a unique 3 km radius buffer (28.27 km²) around each telemetered rattlesnake's spring capture point. Three kilometers includes the maximum distance moved from a hibernaculum by a rattlesnake in this study (2.93 km in 2006). The number of random points per buffer was eight times the number of telemetry observations ($N = 272-352$) to ensure the distribution of available values was adequately represented. We used each rattlesnake's home range to define availability at the second scale. We felt that spacing our telemetry observations by 2-4 days was sufficient to reduce spatial autocorrelation while still providing an accurate representation of each individual's space use (Fieberg, 2007; Kie et al., 2010). We calculated home ranges as 95% fixed kernel utilization distributions (UD) in Home Range Tools (Rodgers et al., 2005) and ArcGIS 9.2. Although the minimum convex polygon (MCP) is often recommended as a home range size estimator for reptiles (Row and Blouin-Demers, 2006), the MCP suffers from many shortcomings including a greater sensitivity to sample size and outliers and its potential to include large areas not used by an individual (Powell, 2000; Kernohan et al., 2001; Borger et al., 2006). Although kernel UD are sensitive to the kernel bandwidth (h , Worton, 1995; Seaman and Powell, 1996), we used an approach to calculate h which avoids issues of over- or under-smoothing prevalent in other approaches (e.g., the reference bandwidth or least-squares cross-validation, respectively, Hemson et al., 2005; Kie et al., 2010). We decreased the reference bandwidth incrementally by 0.1 until we had found the smallest contiguous polygon that included all telemetry observations (Berger and Gese, 2007). This approach resulted in a more appropriately shaped home range estimate for our data given our analysis goals. To avoid computational problems caused by duplicate telemetry observations, we altered these duplicate coordinates by 1-2 meters in order to retain the spatial information provided by an individual's repeated use of specific locations. Because the home ranges were much smaller than the 3 km buffers, the number of random points for each home range was three times the number of telemetry observations ($N = 102-132$). These two scales were analogous to Johnson's second and third orders of habitat selection (Johnson, 1980).

We used conditional logistic regression with $m:n$ matching (PROC LOGISTIC, SAS Institute, Carey, North Carolina, USA) to test for selection for topographic variables. Under this design, m telemetry points were matched with n random points that were unique to that same individual. This procedure allows for the stratification of individuals while still using all telemetry locations (Compton et al., 2002; Boyce et al., 2003). Because this analysis treats the individual as the sampling unit, our sample size was the number of telemetered rattlesnakes. We used a Spearman's

rank correlation to identify variable colinearity ($r_s \geq 0.60$). Distance to water was highly correlated with elevation ($r_s \geq 0.60$) at both scales and was eliminated from the analysis. The two measures of convexity were also highly correlated ($r_s \geq 0.77$) while colinearity was lower for the other variables ($r_s \leq 0.47$, Table 1).

We created a series of conditional logistic regression models by combining all uncorrelated topographic variables ($N = 23$ models and $K = 6$ parameters). A null model (intercept only) was also included. The two measures of convexity were included in separate models. Models were evaluated using Akaike's Information Criteria adjusted for small sample sizes (AIC_c, Burnham and Anderson, 2002). Model weights were calculated to evaluate the probability that a given model was the best out of the entire set of models. Models with $\Delta AIC_c < 2$ were considered to have equal support and model averaging was used to calculate parameter estimates and 95% confidence intervals (Burnham and Anderson, 2002). We calculated parameter weights, a measure of the importance of each variable, by summing the model weights across all models that included a given variable (Burnham and Anderson, 2002). Although parameter weights are not recommended if the model set is unbalanced (i.e., each parameter is not included in an equal number of candidate models), the variables used in our analysis were included in an equal number of models, making parameter weights an appropriate tool to assess variable importance (Burnham and Anderson, 2002).

Habitat selection.—To test if rattlesnakes selected or avoided certain habitats, we created a habitat map in ArcGIS 9.2 using 2004 digital orthoimages and 2002 multispectral ADAR imagery (Airborne Data Acquisition and Registration 5500 System, Positive Systems, Whitefish, Montana, USA, 10 m pixels). We manually digitized polygons representing seven habitat classes: bunchgrass, burned conifer, unburned conifer, rocky outcrop, bare talus, riparian, and water/sandbar (Table 2). Burned and unburned conifer were distinguished as having approximately >50% and ≤50% burned trees within a patch, respectively, based on observations in the field. Field photographs and notes were used as references whenever possible and ground-truthing during field work showed that our classifications were sufficiently accurate for our needs. We never located a telemetered rattlesnake in the water/sandbar habitat so we excluded it from subsequent analyses.

We tested for habitat selection at both the landscape and home range scale using our 2008 data. The proportion of each rattlesnake's telemetry observations within each habitat represented the use of that habitat. The proportion of each habitat within each rattlesnake's 3 km buffer or home range represented the availability at each scale. We conducted a third analysis to test if rattlesnakes selected

Table 1. Spearman's rank correlation coefficient matrix for topography variables used in the topography analysis for Prairie Rattlesnakes (*Crotalus. v. viridis*) in central Idaho.

	Parameters	Water	CON99	CON33	DEGE	DEGN	Slope
Landscape scale	ELEV	0.7747	0.1719	0.1089	-0.0166	-0.0878	0.0723
	SLOPE	0.0805	0.0473	0.0301	-0.0255	0.0369	
	DEGN	-0.0999	0.0109	0.0034	-0.0062		
	DEGE	0.0840	-0.0052	-0.0141			
	CON33	0.1018	0.7828				
	CON99	0.1627					
Home range scale	ELEV	0.5992	0.3140	0.1734	-0.1108	0.1069	0.4725
	SLOPE	0.3315	0.1822	0.0973	-0.0581	-0.0347	
	DEGN	-0.1809	0.1109	0.0459	-0.0135		
	DEGE	-0.0130	-0.0259	-0.0222			
	CON33	0.1459	0.7715				
	CON99	0.2398					

Table 2. Description of habitats in the lower Big Creek drainage used in the habitat selection analysis for Prairie Rattlesnakes (*Crotalus. v. viridis*) in central Idaho.

Habitat	Description
Bunchgrass	Open slopes of grasses, primarily composed of Bluebunch Wheatgrass (<i>Pseudoroegneria spicata</i>), Idaho Fescue (<i>Festuca idahoensis</i>), and smaller amounts of Cheatgrass (<i>Bromus tectorum</i>). May contain scattered patches of talus or small rock outcrops
Burned conifer	Primarily Douglas Fir (<i>Pseudotsuga menziesii</i>) forests with > 50% burned timber. Burned in summer 2000 and/or 2006. Now consists of standing burned timber, patches of live Douglas Fir, Mallow Ninebark (<i>Physocarpus malvaceus</i>), Pinegrass (<i>Calamagrostis rubescens</i>), and Cheatgrass. May contain scattered patches of talus or small rock outcrops
Unburned conifer	Primarily Douglas Fir and Ponderosa Pine (<i>Pinus ponderosa</i>) forests with ≤ 50% burned timber. Mallow Ninebark and Pinegrass present on cooler, northerly aspects while various native grasses are present on drier, southerly aspects.
Riparian	Vegetation adjacent to perennial streams. Consists of a variety of trees and shrubs including Black Cottonwood (<i>Populus richocarpa</i>), Rocky Mountain Maple (<i>Acer glabrum</i>), alder (<i>Alnus</i>), Chokecherry (<i>Prunus virginiana</i>), Serviceberry (<i>Amelanchier alnifolia</i>), Thimbleberry (<i>Rubus parviflorus</i>), rose (<i>Rosa</i>), other shrubs and forbs.
Rock outcrops	Large outcrops of rock often containing Mountain Mahogany (<i>Cercocarpus ledifolius</i>) or scattered Douglas Fir and interspersed with small talus, grass, and shrub patches
Talus	Exposed surfaces of loose rock with little or no vegetation
Water/sandbar	Open water of Big Creek and Rush Creek and associated bare sandbars

habitats while foraging relative to what was available within their home range. We identified all telemetry observations that occurred in foraging/shedding core areas (Bauder, 2010) where feeding took place and calculated the proportion of each rattlesnake's core area observations within each habitat as habitat use. Feeding events were identified based on changes in rattlesnake body mass from monthly measurements of body mass and/or the presence of prey bolus. Although compositional analysis is a common technique for evaluating habitat selection (Aebischer et al., 1993), compositional analysis can produce strong misclassification errors depending on the substitution values (e.g., 0.001) used to replace zeros for unused habitats (Bingham and Brennan, 2004; Bingham et al., 2007). Since some habitats were unavailable (i.e., not within their home range) and/or were not used by some rattlesnakes, we used resource selection ratios to evaluate habitat selection. We

calculated ratios by dividing the proportion of use by the proportion of availability for a given habitat class. A ratio greater than one indicates selection while a ratio less than one indicates avoidance. A ratio of one indicates that habitat is used in proportion to its availability. We generated 10,000 bootstrap estimates for each habitat class and calculated the mean and the 2.5% and 97.5% quantiles of the distribution to obtain 95% confidence intervals using R 2.15.2 (The R Foundation for Statistical Computing, Vienna, Austria). Selection or avoidance was considered significant if the bootstrapped 95% confidence interval did not overlap one. When a rattlesnake's home range did not include a particular habitat class, we excluded that rattlesnake from the calculations for that habitat class.

Prey activity.—To test our expectation that rattlesnakes were selecting the most prey abundant habitats, we sought to

compare small mammal abundance in 2008 among habitat types. However, logistical constraints and the rugged terrain prevented us from using live-trapping to estimate small mammal abundance so we used tracking tubes to provide a measure of small mammal surface activity. Tracking tubes have been used previously to sample small mammal abundance in lieu of live-trapping (Mabee, 1998; Glennon et al., 2002; Rytwinski and Fahrig, 2007) and have been shown to provide a reliable index of abundance (Drennan et al., 1998; Glennon et al., 2002; Wiewel et al., 2007; Wilkinson et al., 2012). However, tracking tubes do not distinguish between multiple individuals and it is possible that high track counts could reflect high surface activity by one or a few individuals rather than high abundance. We therefore consider our results to reflect small mammal surface activity rather than abundance. Because of logistical constraints, we could not consider our 3 km buffer as our potential small mammal sampling area. We therefore constrained our sampling area by creating a 98% adaptive kernel UD using our telemetry locations from 2006 and 2007. We used the reference bandwidth (Worton, 1989) and 98% of the UD volume because this combination created a sampling area that included all previous telemetry observations and yet was small enough to allow us to access the entire sampling area. We used a stratified random sampling design to select small mammal sampling points, stratifying our sampling by habitat and using three to four replicate points per habitat.

We measured prey activity using tracking tubes between June and September 2008. Tracking tubes were made from 30.5 cm sections of plastic rain gutter downspout. A strip

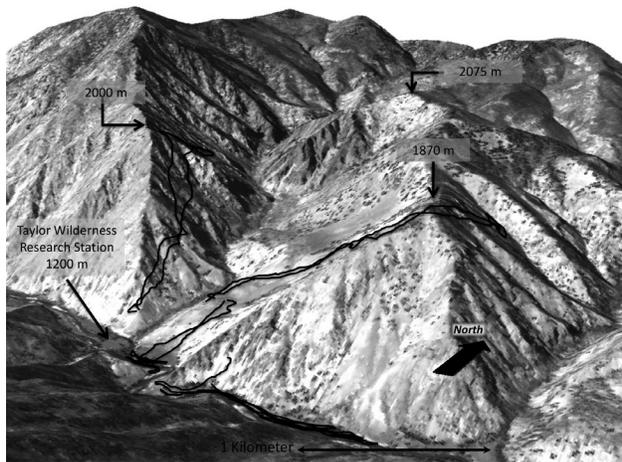


Figure 2. The movements of 2 male (southernmost movements) and 2 nonpregnant female (northernmost movements) Prairie Rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage of central Idaho from April-September 2008 display the range of topographic features traversed. The metrics on this figure refer to elevation.

of white paper was placed on the bottom of the tube and a felt pad containing an ink made of mineral oil and printer toner (1:2 ratio) was stapled on either end of the paper strip. Clear plastic wrap was placed between the felt pad and the paper to prevent the ink from seeping onto the paper. Tubes were baited with oats and left out for two nights to record small mammal tracks. At each sampling point, we placed a grid or transect of 6–15 tracking tubes, depending on the size and shape of habitat polygon. We used the proportion of tubes with tracks in each grid as an index of total small mammal activity (p_T). We also calculated indices using tracking tubes with small tracks (p_S , Deer Mice [*Peromyscus maniculatus*] and voles [*Microtus*]) and large tracks (p_{Li} , ground squirrels [*Spermophilus*], chipmunks [*Tamias*], and woodrats [*Neotoma*]). We used an analysis of covariance (ANCOVA) to compare p_T and p_S among habitat, using elevation as a covariate. Since p_L failed to meet the assumptions of the ANCOVA despite data transformation we compared p_L among habitat using a non-parametric Kruskal-Wallis test, followed by Bonferroni-corrected pairwise Wilcoxon Sign-Rank tests. All analyses of prey activity were conducted in R.2.15.2. We then compared the results of these analyses to the habitat selection analyses to see if rattlesnakes selected habitats with high prey activity.

RESULTS

Topography analysis.—We obtained 798 telemetry locations from 20 telemetered rattlesnakes (16 males and two nonpregnant females). Telemetered rattlesnakes were located between 1148 and 1898 m (mean = 1388 m). Elevation at random points ranged from 1128 to 2400 m (mean = 1578 m) at the landscape scale and from 1143 to 1971 m (mean = 1405 m) at the home range scale. The slope at random points at the landscape scale ranged from 0% to 63% (mean = 32.54%) while rattlesnakes were observed on 0% to 54% slopes (mean = 27.92%). This difference was less for random points at the home range scale (mean = 29.40%, 0–56%). Aspect of telemetry observations showed a strong bimodal distribution around east and west aspects.

A visual inspection of rattlesnake movements across this mountainous landscape was very informative. Telemetered rattlesnakes moved across all of the major topographic features of the landscape, including valley bottoms, ridge sides, and ridge tops (Fig. 2). Nine of the twelve rattlesnakes that moved ≥ 1.74 km from the hibernacula travelled parallel to tributary valleys. However, these movements most frequently occurred along the sides of the valleys, rather than along the valley bottoms, as well as along ridge tops and valley bottoms, despite the fact that the sides of the valleys in this landscape are heavily dissected by smaller ridges and valleys. We recorded 17 river/creek crossings by six telemetered rattlesnakes during this study.

The global model containing all variables was the highest ranked landscape model (Table 3). CON99 (convexity with a 90×90 m window) was included in the top model.

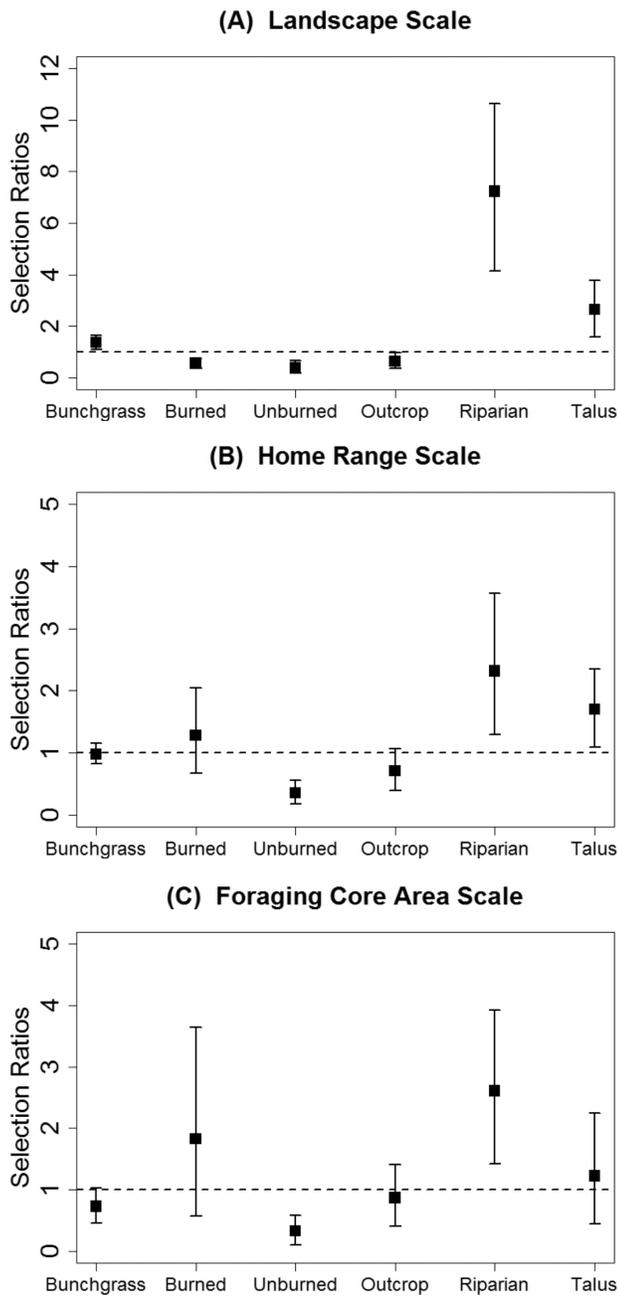


Figure 3. Mean selection ratios and bootstrapped 95% confidence intervals at the landscape (A), home range (B) and foraging core area (C) scales. The dashed horizontal lines represent one. Selection ratios less than one and whose confidence intervals do not overlap one indicate avoidance of that habitat while selection ratios greater than one and whose confidence intervals do not overlap one indicate selection for that habitat. Confidence intervals that overlap one indicate use proportional to availability.

Among models that included convexity, models containing CON99 were always ranked higher than the corresponding models containing CON33 (convexity with a 30×30 m window) indicating greater support for convexity measured at a coarse spatial scale. The landscape global model had very strong support ($w_i = 0.9700$). Rattlesnakes appeared to strongly select low elevations, less steep slopes, and southerly aspects at this scale (Table 4). There was also strong selection for higher convexity (i.e., ridge top topography). Elevation and slope had parameter weights of 1.000 and occurred in all of the top six models (cumulative $w_i = 1.000$). Aspect and convexity also had high parameter weights (0.9993 and 0.9707, respectively).

Two models received strong ($\Delta AIC_c < 2$) support at the home range scale and had a cumulative $w = 0.7029$ (Table 5). The highest ranked model had moderate support ($w_i = 0.4955$). CON33 was included in the best home range scale model and models with CON33 were consistently ranked higher than models with CON99. Rattlesnakes also appeared to select low elevations at this scale (Table 4). The estimates for both aspect variables indicated that rattlesnakes selected southwest aspects. At the home range scale, rattlesnakes showed the opposite pattern with regard to convexity, appearing to select lower convexities (i.e., valley bottom topography). Slope was not present in the highest ranked model and also had the lowest parameter weight (0.5115).

Habitat selection.—Selection ratios indicated significant selection for riparian, talus, and bunchgrass at the landscape scale (Fig. 3A). Burned and unburned conifer and rock outcrop were significantly avoided. At the home range scale, rattlesnakes selected riparian and talus and avoided unburned conifer (Fig. 3B). Bunchgrass, burned conifer, and rock outcrop were used in proportion to their availability. Rattlesnakes selectively foraged in riparian, avoided foraging in unburned conifer, and used all other habitats for foraging in proportion to their availability (Fig. 3C).

Prey activity.—Small mammal activity appeared to be similar among habitats. There was no significant effect of elevation ($P > 0.30$) so we removed it from subsequent analyses. There was no significant difference in total small mammal activity (ANOVA, $F_{5,15} = 0.68$, $P = 0.6445$) or the activity of small species (ANOVA, $F_{5,15} = 0.57$, $P = 0.7214$) among the six habitats (Fig. 4). The differences in large species activity were not significant after applying pair-wise Bonferroni corrections ($P \geq 0.45$).

DISCUSSION

This study shows that topography does influence the movement patterns of Prairie Rattlesnakes in a mountainous

landscape and that this influence varies by spatial scale. The effect of topography appeared strongest and most restrictive at the landscape scale. This is probably due in part to elevational limits for rattlesnakes in the Pacific

Northwest, which are generally reported as below ca. 2280 m (Nussbaum et al., 1983; Storm and Leonard, 1995; St. John, 2002). Most studies of rattlesnake movement in the Intermountain West have occurred near or below this

Table 3. Model selection results for the effects of topography on Prairie Rattlesnake (*Crotalus v. viridis*) radiotelemetry locations at the landscape (3 km buffer) scale. Abbreviations in the model terms are: ELEV = elevation, SLOPE = slope, DEGN = degrees from north (0°), DEGE = degrees from east (90°), CON33 = convexity measured at 30 × 30 m, CON99 = convexity measured at 90 × 90 m. The number of parameters in each model is given by *K*.

Model	<i>K</i>	-2Log(L)	AIC	AIC _c	ΔAIC _c	<i>w</i>
ELEV + SLOPE + DEGN + DEGE + CON99	5	4368.92	4378.92	4383.20	0.00	0.9700
ELEV + SLOPE + DEGN + DEGE	4	4379.93	4387.93	4390.59	7.39	0.0241
ELEV + SLOPE + DEGN + DEGE + CON33	5	4379.34	4389.34	4393.63	10.43	0.0053
ELEV + SLOPE + CON99	3	4390.34	4396.34	4397.84	14.64	0.0006
ELEV + SLOPE	2	4402.47	4406.47	4407.17	23.97	0.0000
ELEV + SLOPE + CON33	3	4401.73	4407.73	4409.23	26.03	0.0000
ELEV + DEGN + DEGE + CON99	4	4436.82	4444.82	4447.48	64.28	0.0000
ELEV + DEGN + DEGE	3	4442.32	4448.32	4449.82	66.62	0.0000
ELEV + DEGN + DEGE + CON33	4	4442.20	4450.20	4452.87	69.67	0.0000
ELEV + CON99	2	4456.85	4460.85	4461.55	78.35	0.0000
ELEV	1	4463.06	4465.06	4465.28	82.08	0.0000
ELEV + CON33	2	4462.89	4466.89	4467.59	84.39	0.0000
SLOPE + DEGN + DEGE	3	4707.43	4713.43	4714.93	331.73	0.0000
SLOPE + DEGN + DEGE + CON33	4	4705.20	4713.20	4715.87	332.67	0.0000
SLOPE + DEGN + DEGE + CON99	4	4707.42	4715.42	4718.08	334.88	0.0000
SLOPE	1	4751.45	4753.45	4753.67	370.47	0.0000
SLOPE + CON33	2	4749.40	4753.40	4754.11	370.91	0.0000
SLOPE + CON99	2	4751.45	4755.45	4756.15	372.95	0.0000
DEGN + DEGE + CON33	3	4861.92	4867.92	4869.42	486.22	0.0000
DEGN + DEGE	2	4865.53	4869.53	4870.23	487.03	0.0000
DEGN + DEGE + CON99	3	4864.02	4870.02	4871.52	488.32	0.0000
CON33	1	4900.85	4902.85	4903.07	519.87	0.0000
null	0	4904.32	4904.32	4904.32	521.12	0.0000
CON99	1	4903.06	4905.06	4905.28	522.08	0.0000

Table 4. Parameter estimates, standard errors, 95% confidence intervals, odds ratios, and parameter weights for the variables used in the topography analysis. Model averaging was used to calculate these values at the home range scale. Abbreviations in the parameter estimates are: ELEV = elevation, SLOPE = slope, DEGN = degrees from north (0°), DEGE = degrees from east (90°), CON33 = convexity measured at 30 × 30 m, CON99 = convexity measured at 90 × 90 m.

	Parameters	Estimate	SE	Lower bound	Upper bound	Odds ratio	Parameter weight
Landscape (3 km buffer) scale	ELEV	-0.0033	0.0002	-0.0036	-0.0029	0.9968	1.0000
	SLOPE	-0.0308	0.0037	-0.0381	-0.0235	0.9697	1.0000
	DEGN	0.0034	0.0007	0.0019	0.0048	1.0034	0.9993
	DEGE	-0.0005	0.0008	-0.0020	0.0010	0.9995	0.9993
	CON99	0.0346	0.0104	0.0142	0.0550	1.0352	0.9707
Home range scale	DEGN	0.0140	0.0009	0.0123	0.0157	1.0141	1.0000
	DEGE	0.0094	0.0016	0.0063	0.0124	1.0094	1.0000
	ELEV	-0.0039	0.0006	-0.0051	-0.0027	0.9961	1.0000
	CON33	-0.2842	0.1137	-0.5072	-0.0613	0.7526	0.7684
	SLOPE	-0.0097	0.0071	-0.0235	0.0041	0.9904	0.5115

Table 5. Model selection results for the effects of topography on Prairie Rattlesnake (*Crotalus v. viridis*) radiotelemetry locations at the home range scale. Abbreviations in the model terms are: ELEV = elevation, SLOPE = slope, DEGN = degrees from north (0°), DEGE = degrees from east (90°), CON33 = convexity measured at 30 × 30 m, CON99 = convexity measured at 90 × 90 m. The number of parameters in each model is given by *K*.

Model	<i>K</i>	-2Log(<i>L</i>)	AIC	AIC _c	ΔAIC _c	<i>w</i>
ELEV + DEGN + DEGE + CON33	4	1167.43	1175.43	1178.10	0.00	0.4955
ELEV + SLOPE + DEGN + DEGE + CON33	5	1165.55	1175.55	1179.84	1.74	0.2074
ELEV + DEGN + DEGE + CON99	4	1170.65	1178.65	1181.32	3.22	0.0991
ELEV + DEGN + DEGE	3	1173.92	1179.92	1181.42	3.33	0.0939
ELEV + SLOPE + DEGN + DEGE	4	1171.54	1179.54	1182.21	4.11	0.0634
ELEV + SLOPE + DEGN + DEGE + CON99	5	1168.81	1178.81	1183.10	5.00	0.0407
SLOPE + DEGN + DEGE + CON33	4	1206.22	1214.22	1216.89	38.79	0.0000
SLOPE + DEGN + DEGE + CON99	4	1207.92	1215.92	1218.58	40.49	0.0000
SLOPE + DEGN + DEGE	3	1214.11	1220.11	1221.61	43.52	0.0000
DEGN + DEGE + CON33	3	1220.71	1226.71	1228.21	50.11	0.0000
DEGN + DEGE + CON99	3	1221.04	1227.04	1228.54	50.44	0.0000
DEGN + DEGE	1	1230.23	1232.23	1232.45	54.35	0.0000
SLOPE	1	1695.89	1697.89	1698.12	520.02	0.0000
SLOPE + CON33	2	1694.21	1698.21	1698.92	520.82	0.0000
ELEV + SLOPE	2	1694.38	1698.38	1699.09	520.99	0.0000
ELEV + SLOPE + CON33	3	1692.99	1698.99	1700.49	522.39	0.0000
SLOPE + CON99	2	1695.87	1699.87	1700.57	522.48	0.0000
ELEV + SLOPE + CON99	3	1694.24	1700.24	1701.74	523.65	0.0000
ELEV	1	1699.61	1701.61	1701.83	523.74	0.0000
ELEV + CON33	2	1698.01	1702.01	1702.72	524.62	0.0000
CON33	1	1701.74	1703.74	1703.97	525.87	0.0000
ELEV + CON99	2	1699.57	1703.57	1704.28	526.18	0.0000
CON99	1	1703.90	1705.90	1706.13	528.03	0.0000

elevation (King and Duvall, 1990; Jenkins, 2007; Parker and Anderson, 2007; Jorgensen et al., 2008). The elevation at the highest random point at the landscape scale was 2400 m, about 414 m higher than the maximum elevation for a rattlesnake in this study (1986 m). Because much of the Big Creek drainage is above 2000 m, it is likely that elevation restricts rattlesnake movements across broad spatial scales and may even act as a barrier to long-distance movements. Our results at this scale may be somewhat biased in regards to elevation because the hibernacula in our study were already at relatively low elevations. This could enhance the appearance that individual movements are restricted to low elevations. It is possible that selection of low elevations by individual rattlesnakes may actually reflect elevational restrictions on potential overwintering habitat. Radio tracking rattlesnakes from hibernacula at a broader range of elevations could help determine if elevational limits are imposed upon suitable hibernacula sites, individual movements, or both. Although we did not conduct extensive hibernacula surveys, during three years of field work we found no evidence that hibernacula in our study area were present at higher elevations than those we observed (ca. 1235–1416 m).

Other factors may also contribute to a restrictive effect of topography at the landscape scale. Higher elevations

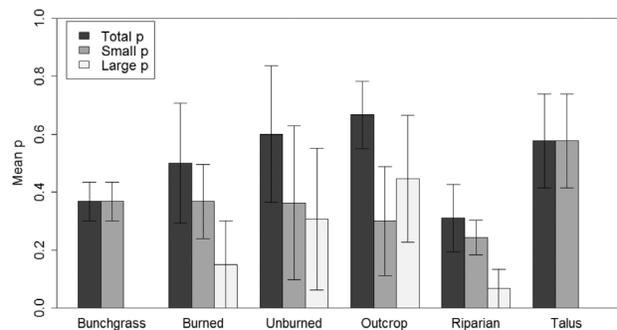


Figure 4. Variation in small mammal activity, measured using tracking tubes, among habitats in the lower Big Creek drainage June–September 2008. The y-axis denotes the mean proportion of tracking tubes visited (*p*, i.e., contained at least one track). “Total *p*” refers to the proportion of tracking tubes visited by all species while “Small *p*” and “Large *p*” refer to the proportion of tracking tubes visited by small and large species, respectively (see text for description of small and large species). Error bars represent ± 1 standard error.

may have poorer quality of thermal habitat due to shorter growing seasons or colder night temperatures. Changes in thermal conditions due to elevation can restrict the time available for surface activity which in turn may constrain potential foraging time (Beaupre, 1995). Avoidance of high elevations may also be a reflection of the differences in energetic costs of traveling a given distance uphill versus traveling that same distance on the level. Rattlesnakes did show a strong selection for lower slopes at the landscape scale which could suggest that they avoid moving across steep slopes. However, we are unaware of any data comparing the energetic costs of movement on an incline and the level for snakes and are therefore unable to evaluate the effects of energetics on our observed movement patterns. Selection for lower slopes may also reflect thermal habitat quality in a topographically complex landscape such as ours if steep slopes, particularly within narrow valleys, receive sunlight for a shorter amount of time compared to more exposed slopes. The selection for ridge tops we observed at the landscape scale is consistent with this hypothesis. Although selection for low elevations may appear contradictory to selection for ridge tops and low slopes, the topographic complexity of our landscape allows for a diversity of landforms across a range of elevations. Selection for southerly aspects at the landscape scale could reflect a selection for warmer aspects for thermoregulation, particularly in the spring, or the drier, open vegetation communities (e.g., bunchgrass and bare talus) that dominated southerly aspects. It is unlikely that this result is due to our hibernacula occurring on southerly aspects because the topographic complexity of our landscape provides a wide range of available aspects close to the hibernacula.

At finer spatial scales, our results suggest that topography is not a strong impediment to rattlesnake movement. A visual assessment of our data shows that topography did not strongly restrict the movements of some individuals and did not seem to act as an absolute barrier to movements within their home ranges. Rattlesnakes used all of the major topographic features available to them and travelled up steep slopes, crossed ridge lines, and moved along valley bottoms. Although we feel that the frequency of our telemetry locations was sufficient to capture the majority of our telemetered rattlesnakes' movements, we may have missed some movements that indicated additional use or avoidance of topographic features. Patterns of selection for elevation and aspect were similar at both the landscape and home range scales but the relationship with convexity was reversed at the home range scale. At the finer scale, rattlesnakes selected valley bottoms measured with the smallest window size suggesting that they responded to the shape of the landscape at a relatively fine scale. Selection for valley bottoms could occur if rattlesnakes selectively used valley bottoms as movement corridors during their migrations to summer foraging areas. Most of the long-distance migra-

tions (≥ 2 km moved from the hibernaculum) observed in this study were parallel to tributary valleys. However, these migrations would often occur along the valley sides or ridge tops rather than along the valley bottoms. This latter behavior is consistent with the selection for ridge tops we observed at the landscape scale and indicates that rattlesnake migrations in mountainous landscapes are not confined to the valley bottoms. Radio tracking rattlesnakes in portions of the lower Big Creek drainage where tributary drainages are lacking would allow us to test the hypothesis that tributary drainages facilitate rattlesnake migrations. Alternatively, rattlesnakes may select micro-topographic features within their home ranges that are more sheltered or enclosed.

Habitat seemed to have relatively little effect on rattlesnake movement as rattlesnakes moved through and utilized all six terrestrial habitat classes. There was some evidence for hierarchical selection as selection varied by spatial scale. Rattlesnakes selected home ranges with access to open (bunchgrass and talus) and riparian habitats while avoiding forested habitats. Rattlesnakes apparently became less selective in their habitat use with decreasing spatial scale, selectively using or avoiding fewer habitat classes. Riparian and unburned conifer were the only habitats selectively used or avoided, respectively, at all three spatial scales. Other studies on rattlesnake movements have also reported selection for riparian areas (Reed and Douglas, 2002). Riparian habitats may have higher prey abundance (but see below) and access to water, shade, and cooler temperatures. Water and shade may be increasingly important later in the summer and a few rattlesnakes did move closer to riparian areas in August and September. However, not all rattlesnakes used riparian habitats and a few rattlesnakes were never observed closer than a few hundred meters from water. Selection of talus at the landscape and home range scales may reflect its use as overwintering habitat, basking sites, or foraging habitat (see below). The tendency to avoid forested habitats is not surprising as Prairie and Western Rattlesnakes are not forest associated species (Nussbaum et al., 1983; Storm and Leonard, 1995; c.f. St. John, 2002). Forested habitats, particularly unburned conifer, may provide fewer basking sites and a lower quality of thermal habitat. Forested habitats were also common at high elevations that rattlesnakes strongly avoided at the landscape scale. Selection for low elevations may actually be a reflection of avoidance of forested habitats, particularly if forested habitats provide lower quality thermal habitat.

We did not detect a difference in small mammal surface activity among the habitats within our study area. This may suggest that rattlesnake use of the habitat classes we considered is not driven by prey activity. For example, the multi-scale selection we observed for riparian habitats may be due to thermal factors rather than perceived prey

availability. Koehler and Hornocker (1989) found that Deer Mice in the lower Big Creek drainage were less abundant in mesic habitats, which included riparian, than xeric habitats. Our results may also suggest that rattlesnakes do not need to restrict their foraging to particular habitats in order to maximize their access to prey. We did observe some rattlesnakes feeding at their hibernacula and rattlesnakes foraged in most habitats in proportion to their availability. There are some limitations with our small mammal sampling design that call for caution when interpreting our results. First, although many studies have shown that tracking tube data provides a suitable index to small mammal abundance (Fahrig and Merriam, 1985; Drennan et al., 1998; Glennon et al., 2002; Wiewel et al., 2007; Wilkinson et al., 2012), the suitability of this index may vary among species (Wiewel et al., 2007), season, or with true abundance (Wilkinson et al., 2012). Small mammal abundance can also vary across relatively fine spatio-temporal scales which could add additional variability to tracking tube data (Wilkinson et al., 2012). We are ultimately unsure of how well our tracking tube data reflects prey abundance. Second, we had small numbers of replicates per habitat and this may have failed to adequately capture the variation in small mammal abundance within each habitat, particularly in a landscape as heterogeneous as ours. Third, small mammal abundance may be spatially structured in a way that is independent of the habitat classifications we used. Finally, rattlesnakes may selectively prey upon certain small mammal species that were not present or identified in our tracking tube data. Although, we do not have prey data for the rattlesnakes in our study area, based on changes in body mass and size of prey boluses, rattlesnakes consumed both small-bodied (e.g., Deer Mice), and large-bodied prey species (e.g., chipmunks and ground squirrels). Both prey size classes were detected in our tracking tubes and are known prey for rattlesnakes in the Intermountain West (Jenkins, 2007; Glaudas et al., 2008).

Our study indicates that topography and habitat appear to influence the movements of Prairie Rattlesnakes in our mountainous study area at multiple spatial scales. Topography appears to exhibit the most influence on rattlesnake movements at broad spatial scales by restricting rattlesnakes to below a certain elevational limit. However, within observed elevational limits, the factors we examined in this study did not appear to strongly restrict rattlesnake movements and rattlesnakes used most of the available topographic features and habitats. We therefore encourage future researchers to examine the influence of factors other than those examined here on rattlesnake movements in this system. More labor-intensive and detailed small mammal sampling could further elucidate the spatial patterns in prey abundance and how they influence rattlesnake movements. Because small mammal populations may vary from year-to-year, it would be very informative to monitor changes in

small mammal abundance over time and determine if and how rattlesnakes respond to those changes. Future research should also examine the role of the thermal environment and the wide range of topographic conditions and habitat structures available within our relatively small study area may provide an excellent environment in which to address this topic.

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