MOVEMENTS AND HABITAT SELECTION OF PRAIRIE RATTLESNAKES (CROTALUS V. VIRIDIS) ACROSS A MOUNTAINOUS LANDSCAPE IN A DESIGNATED WILDERNESS AREA

JAVAN M. BAUDER

To the staff, researchers,
Students, and visitors of
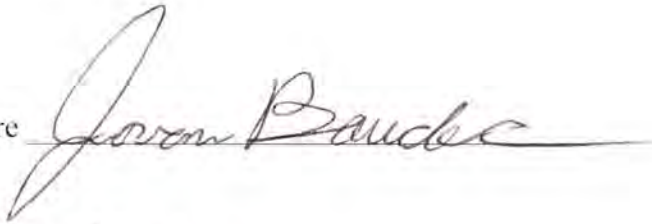the Taylor Wilderness Research
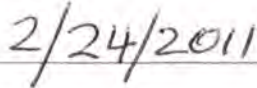Station.
Thanks for all the memories.

Javona Bowden

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MOVEMENTS AND HABITAT SELECTION OF PRAIRIE RATTLESNAKES

(*CROTALUS V. VIRIDIS*) ACROSS A MOUNTAINOUS LANDSCAPE IN A

DESIGNATED WILDERNESS AREA

By

Javan M. Bauder

A thesis

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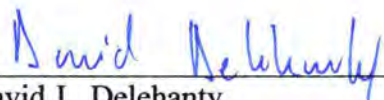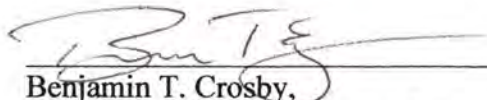
To the Graduate Faculty:

The members of the committee appointed to examine the thesis of JAVAN M. BAUDER find it satisfactory and recommend that it be accepted.

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Christ for without his strength and grace the completion of this project would not have

been possible. To God be the glory.

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Movements and Habitat Selection of Prairie Rattlesnakes (*Crotalus v. viridis*) across a Mountainous Landscape in a Designated Wilderness Area

Thesis Abstract – Idaho State University (2010)

Although prairie rattlesnakes (*Crotalus v. viridis*) are known to make lengthy movements 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 characterize rattlesnake movement patterns in a mountainous landscape and describe the factors influencing those movements. I used radio telemetry to monitor the movements of 21 male and six nonpregnant female prairie rattlesnakes in central Idaho in 2006-2008. Mean total distance moved during the entire activity season in 2008 was 4.46 kilometers; mean maximum distance moved from the hibernaculum was 1.46 kilometers. Topography, vegetation cover type, and the density of conspecifics all appeared to influence rattlesnake movement patterns, while prey abundance probably had little effect on the patterns I observed. High densities of conspecifics at communal hibernacula may play an important role in directing rattlesnake movements away from the hibernaculum.

Chapter 1

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

ABSTRACT

Prairie rattlesnakes (*Crotalus v. viridis*) are known to make lengthy and linear migratory movements between over-wintering habitat and summer foraging habitat. However, it is largely unknown if rattlesnakes in mountainous landscapes make similar extensive movements. The objectives of this study were to describe the movement patterns of prairie rattlesnakes in a mountainous landscape in central Idaho with the objective of determine if those movement patterns fit the current model of rattlesnake migration (i.e., migration followed by foraging and male mate-searching movements). I used radio telemetry to monitor the movements of 21 male and six nonpregnant female prairie rattlesnakes in the Frank Church Wilderness in central Idaho during the summers of 2006-2008. I used time series segmentation to identify different categories of individual movement segments. Mean total distance moved during the entire activity season in 2008 was 4.46 kilometers (range 1.38-7.67); mean maximum distance moved from the hibernaculum was 1.46 kilometers (range 0.69-2.71). Significantly more time was spent in core areas relative to outbound migration, mate searching, and inbound migration and core area movements were significantly shorter and slower. Migration movements were more linear than both core area and mate searching movements. Rattlesnakes displayed

moderate to high fidelity to summer activity areas. Although the movement distances reported here are intermediate to those reported for prairie and western (*C. oreganus*) rattlesnakes, they are comparable to some distances reported from areas with low to moderate topographic relief. Prairie rattlesnake movements in a mountainous landscape appear to fit the current model of rattlesnake movement. This suggests that that rattlesnakes are still capable making considerable movements in a mountainous landscape and any restrictive effects of topography are relatively weak compared to factors known to drive the current model of rattlesnake movement (i.e., the spatial distribution of over-wintering sites and small mammal prey).

INTRODUCTION

Animal movements across the landscape may be thought of in a cost/benefit framework where animals face tradeoffs between the benefits and costs of those movements (Werner and Anholt 1993). The acquisition of key resources, such as food, water, mates, and shelter from the abiotic environment, is one such benefit (Andrewartha and Birch 1954, 1984). The spatial arrangement of these resources across the landscape can play an important role in influencing movement distances and patterns (McIntyre and Weins 1999, Klassen et al. 2006, Filipa-Loureiro et al. 2007). Movement among resource patches may also reduce the effects of competition (Hamilton et al. 1967). Some costs associated with such movements may include increased energetic expenditures associated with travelling greater distances and increased exposure to predations (Werner and

Anholt 1993). Therefore, we may expect animals to move across the landscape when the benefits of doing so outweigh the costs associated with those movements.

Prairie and western rattlesnakes (*Crotalus v. viridis* and *C. oreganus*) are known to make lengthy movements across the landscape (Jorgensen et al. 2008). Formerly classified as a single species (*C. viridis*), the *C. viridis* complex has been split into eastern (*viridis*) and western (*oreganus*) clades (Pook et al. 2000, Ashton and de Queiroz 2001, Douglas et al. 2002). Many studies have described the movement patterns of the *C. viridis* complex (Jorgensen et al. 2008) and from these studies a general model of rattlesnake movement patterns has emerged. Upon emergence in the spring, males and nonpregnant females will undertake lengthy migratory movements (up to 20 km, Jorgensen et al. 2008) to summer foraging habitat. In contrast, pregnant females remain relatively close to their hibernaculum and spend most of the summer thermoregulating to aid embryo development (Graves and Duvall 1993, Cobb 1994). When migrating individuals encounter an area with a high abundance of small mammal prey, they often cease their migratory movements and often engage in shorter foraging movements (Duvall et al. 1990, King and Duvall 1990). Nonpregnant females will forage throughout the summer while males will make additional extensive movements during July and August to locate receptive females (King and Duvall 1990, Duvall et al. 1992, Jenkins and Peterson 2005). Fidelity to migration routes and foraging areas across years has also been observed (Jenkins 2007, Parker and Anderson 2007). Individual snakes typically return to the same hibernaculum in the fall (Parker and Anderson 2007). However, rattlesnakes in some areas may not undertake highly migratory movements during their activity season (Reed and Douglas 2002, Dugan et al. 2008).

Previous studies of rattlesnake movement have indicated that the spatial and temporal availability of overwintering sites, small mammal prey, and receptive females are important factors driving rattlesnake movement. Rattlesnakes often over-winter communally in groups ranging from a few to over several hundred individuals (Hirth et al. 1969, Klauber 1972, Gannon and Secoy 1985, Diller and Wallace 2002), particularly at the northern portions of their range. Suitable hibernacula may be limited in cold climates and lead to communal over-wintering (Gregory 1984). In contrast, populations in milder climates may over-winter singly or communally (Fitch 1949, Klauber 1972, Reed and Douglas 2002, Dugan et al. 2008). Long-distance migratory movements may occur, in part, because of a spatial separation between these hibernacula and summer foraging habitat (Larsen 1987). The linear migration movements seen in many populations are also thought to represent an efficient search pattern for widely scattered and spatially unpredictable prey resources and mates (King and Duvall 1990, Duvall and Scheutt 1997). Rattlesnakes in areas with an abundance of over-wintering sites and prey that overlap spatially may exhibit shorter and less directional movements (Reed and Douglas 2002). Intraspecific competition also has a strong potential to influence rattlesnake movements, particularly in communally overwintering populations where the density of conspecifics is highest near the hibernaculum. Moving away from the hibernaculum may therefore result in a lower density of conspecifics and less competition for foraging spaces, prey, or mates (Hamilton et al. 1967). However, few researchers have considered the effects of the presence of conspecifics on rattlesnake movements (Hirth et al. 1969, Jorgensen et al. 2008).

Little is known about the influence of mountainous landscapes on rattlesnake movements. The majority of rattlesnake movement studies have occurred in areas with low to moderate topographic relief which may offer little resistance to their movements (but see Reed and Douglas 2002, Greenberg and McClintock 2008). Topography may increase movement costs through the energetic costs associated with travelling up and downhill and may impose environmental constraints, such as low temperatures and short growing seasons at high elevations. Topography may also impose opportunity costs if animals spend more time travelling over or around topographic features. These costs may be particularly important for animals that already face environmentally constrained activity seasons, which include ectotherms at high elevations or altitudes. Studies of animal movement in mountainous landscapes may therefore provide excellent systems to help better understand the tradeoffs that animals face between the benefits and costs of movement, which can lead to a better understanding of the factors influencing those movements and the relative importance of those factors.

However, before we can understand the factors influencing ecological patterns and processes, an accurate description of those patterns and processes is needed. Therefore, the objective of this study was to describe the movements of prairie rattlesnakes in a mountainous landscape. To address this objective, I asked three specific questions regarding prairie rattlesnakes in a mountainous landscape: 1) Do their movements fit the general model of rattlesnake movements consisting of lengthy and linear migrations between over-wintering sites and summer foraging habitat, foraging within one or more relatively restricted areas, male mate-searching in the late summer, and high den fidelity?, 2) How do those patterns compare to those in areas with lower

topographic relief?, and 3) Do rattlesnakes display high fidelity to summer foraging areas? Additionally, I tested for an effect of sex and body size because both factors have the potential to influence movement patterns and therefore must be considered when characterizing rattlesnake movement patterns (Jorgensen et al. 2008).

Given that rattlesnake movements in other systems are strongly influenced by the distribution and availability of key resources, I hypothesized that these factors would have a greater influence on rattlesnake movement than the potentially restrictive effects of topography. I therefore expected that rattlesnake movements in a mountainous landscape would fit the general model of rattlesnake movement despite the presence of potentially restrictive topographic features. I also expected that rattlesnakes would move distances that were comparable to those reported in areas of lower topographic relief. However, because topography probably imposes some additional costs on movement, I did not expect to observe the extreme long distance movements that have been reported in other populations. Finally, I expected to observe fidelity to movement routes and summer foraging areas over multiple years.

STUDY AREA

I conducted this study in the lower Big Creek drainage of the Frank Church-River of No Return Wilderness in central Idaho (Figure 1.1). My field work was based out of the University of Idaho's Taylor Wilderness Research Station (TWRS, 1200 m). Big Creek flows east and four tributaries join Big Creek at roughly perpendicular angles within three kilometers of the TWRS (Figure 1.1). The topography of the lower Big

Creek drainage is characterized by steep valleys and high ridges (1100-2780 m in about 4.8 km). This complex landscape results in a diversity of vegetation communities. 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 tricocarpa*), 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.

Most rattlesnakes used in this study overwintered in three hibernacula complexes within 1.5 km of each other and within 800 m of the TWRS. These complexes consist of clusters of over-wintering snakes within scattered talus patches or rock outcrops on bunchgrass slopes. All snakes over-wintered 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 occurred on an east aspect (mean aspect = 101°) between 1327 and 1420 m elevation. The first northern complex included two disjunct talus patches, one on a southwestern aspect (mean aspect = 226°) between 1271 and 1305 m

and the second on a south-southeast aspect (mean aspect = 156°) between 1304 and 1321 m. The second northern complex was located on a southeast aspect (mean aspect = 149°) between 1235 and 1269 m. One rattlesnake over-wintered solitarily north of Big Creek in the south facing junction of a rock outcrop complex and talus slide at 1264 m.

METHODS

I surgically implanted radio transmitters into 29 male and nonpregnant female rattlesnakes during this three year study. Rattlesnakes were captured near the hibernacula 28 April-1 May 2006, 2 May & 8-10 May 2007, and 16 April-23 May 2008 and brought back to the TWRS. In 2007, I was unable to capture a sufficient number of rattlesnakes around the hibernacula in the spring so I 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). I used 3.8 g PD-2, 9, 11, & 13.5 g SI-2 and SI-2T, and 5 g SB-2 and SB-2T transmitters (Holohill Systems Ltd., Carp, Ontario, Canada). Transmitters were ≤5% of the rattlesnake's body mass at time of surgery. Each rattlesnake was held for 8-36 hours before being released at their respective capture sites and all snakes were alert and responsive before release.

Telemetered rattlesnakes were monitored between 11 May-6 August 2006, 16 May-11 August 2007, and 16 April-28 September 2008. Battery failures prevented me from monitoring some rattlesnakes for an entire field season. I located each rattlesnake

using a three element Yagi antenna (Wildlife Materials International Inc., Murphysboro, IL) and a Telonics TR-2 receiver (Telonics Inc., Mesa, AZ) approximately once every two to four days and recorded its UTM coordinates using a handheld GPS unit (Garmin GPSmap 76CS, Garmin International Inc., Olathe, KS). GPS accuracy ranged from 2-13 meters (mean approximately 5 meters). I attempted to capture each telemetered rattlesnake to weigh it at the end of the 2006 field season and once per month in 2007 and 2008. I was unable to locate snakes between 20 and 25 July 2006 due to the wildfire north of the TWRS and between 28 June and 11 July 2008 due to an injury.

STATISTICAL ANALYSIS

Movement Patterns

To describe individual rattlesnake movement patterns, I entered the UTM coordinates for all telemetry locations that were separated by at least one day, including the over-wintering location, into ArcGIS 9.2 (ESRI, Redlands, CA). I then calculated several movement statistics that would allow me to describe these patterns. I 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, Redlands, CA). I 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 (ESRI, Redlands, CA). Topographic distances were used in all subsequent analyses. I 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. Movement rate was calculated for each movement segment as

meters moved per 24 hours. Short movements made immediately before the snakes

started consistently moving away from the hibernacula in the spring and movements

between consecutive radio telemetry observations that were separated by >7 days were

excluded for rate and absolute turning angle calculations to ensure that the most accurate

data were used for these calculations. Movements <5 m were excluded to facilitate

comparisons with previous studies (Jorgensen et al. 2008). I also calculated an inverse

meandering ratio (Wlliamson and Gray 1975) for each rattlesnake 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. 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. One snake that was apparently

washed >3 km down Big Creek in 2007 was also excluded.

I calculated home ranges using 95% fixed kernels (FK) in Home Range Tools

(Rodgers et al. 2005) and ArcGIS 9.2. To determine the appropriate smoothing

parameter, I decreased the reference bandwidth (h_{ref}) incrementally by 0.1 until I had

found the smallest contiguous polygon with no lacuna that included all telemetry

observations (Berger and Gese 2007). I also calculated a 50% FK for each snake to

represent an area of concentrated activity. The UTM coordinates of multiple identical

telemetry locations were altered by 1-2 m to avoid computational problems. The over-

wintering point was also included. Because of the extensive topographic relief in my study area, planimetric home ranges will underestimate the size of the home range (Greenberg and McClintock 2008). I therefore converted my home range polygons into three-dimensional TIN (triangular integrated network) using a 10 m DEM and calculated the topographic area (Greenberg and McClintock 2008). I buffered each home range polygon by 5 m to allow the TIN to cover the full extent of the polygon. 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, $r_s = 0.8776$, $p = < 0.0001$). For this reason, I did not use home range size in analyses testing for differences in movement patterns between over-wintering locations, sex, and among years. Unless otherwise noted, all statistical analyses were conducted in SAS 9.1 (SAS Institute, Carey, NC, U.S.A.). All means are reported ± one standard error.

To assess the degree of fidelity to summer activity areas, I calculated the percentage of 95% and 50% FK overlap between years for snakes 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 snake's core activity area during year 1 was 100 m^2, during year 2 was 200 m^2, and the area of overlap was 50 m^2, the index of overlap would be calculated as Overlap = 50/[(200-50)+100]. To test for differences in fidelity among years, I compared the percentage of

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95% and 50% FK overlap among all three year combinations (2006/2007, 2007/2008, and 2006/2008) using a repeated measures analysis of variance (ANOVA).

I then conducted a series of analyses to test for an effect of over-wintering 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). I used an un-equal variance t-test to test for differences between rattlesnakes overwintering on either side of Big Creek for each year separately. I used mixed effects linear models (PROC MIXED), followed by a Tukey's pairwise test, to test for an effect of sex, initial body mass, and year on each movement statistics. Data from all three years were pooled and the number of telemetry observations for each individual for each year was included to correct for differences in sampling intensity among years. Individual was included as a repeated measure. A series of analyses of covariance (ANCOVA) were used to test for an association between the percent change in body mass and each movement statistic in 2008 while controlling for sex. The meandering ratio did not meet the assumptions of these parametric tests despite transformations. I therefore I 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. I 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.

Movement Classifications

Although statistics such as total distance moved and meandering ratio convey important information, they may mask variation in movement patterns that are a result of different behaviors within a single activity season. I therefore wanted to describe rattlesnake movement patterns using a more detailed and biologically based approach. To accomplish this, I used time series segmentation (Dettki and Ericsson 2008) to identify and classify individual movement segments with similar characteristics (e.g., distance from hibernacula, rate, and directionality) and that reflected similar and biologically meaningful patterns and processes (e.g., migration, foraging, and mate searching). I created time series graphs for each snake by plotting the topographic displacement (i.e., distance from hibernaculum) against time (Figure 1.2). I calculated the difference in net displacement between two points using $dx = x_{i+1} - x_i$ and then normalized these values using $dx_n = dx / dx_{max}$ following Dettki and Ericsson (2008). Large values indicate an abrupt change in the distance from the hibernaculum and are often indicative of changes in movement patterns or rapid movements away from the hibernaculum (e.g., migration). However, normalized displacement values may not capture large displacements that occur at equal distances from the hibernaculum. For this reason, I also used normalized rates ($Rx_n = Rx / Rx_{max}$) to identify sharp changes in movement rates. I then developed a rules based classification system to classify each individual movement segment into one of four movement categories: outbound migration, core area, mate searching, and inbound migration (Table 1.1).

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Outbound Migration

Outbound migration movements were defined as relatively rapid and consistent movements away from hibernaculum and between core areas in the spring and summer, often showing an abrupt increase in movement rate and/or directionality. Short, single movements that occurred prior to consistently moving away from the hibernacula were not included. Outbound migrations were often interrupted by one or more core areas throughout the activity season. Outbound migration typically ceased at the furthest core area from the hibernaculum, although movements between two core areas that brought the rattlesnake closer to the hibernaculum were still classified as outbound migration if the rattlesnake resumed movement away from the hibernaculum at a later date.

Core Area Movements

Core area movements were defined as movements occurring at a relatively stable distance from the hibernaculum and within a small area relative to the entire home range for ≥ 8 days, often with low directionality and/or low movement rates relative to the other movement categories. Core area movements occurred throughout the activity season. Core areas began at the first point where a rattlesnake showed a sharp and consistent decrease in movement rate, including ceasing movement altogether, and/or a consistent decrease in movement directionality. The core area ended at the first point at which the rattlesnake showed a sharp increase in movement rate or resumes travel along a relatively fixed bearing. Core areas were usually indicative of behaviors such as foraging, digesting, or shedding. Single long, rapid movements within the bounds of the core area were classified as core movements. Visual assessments of the data revealed that

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normalized values ≤0.20 for both displacement and rate tended to represent the relatively short movements within core areas.

Mate searching

Mate searching movements were defined as relatively lengthy and rapid movements by male rattlesnakes in July and August, which is when mate searching is known to occur in most rattlesnakes and when I observed all mating behavior. These movements covered a large area relative to the male's entire home range and were distinguished from migration movements by their low directionality. Mate searching movements typically connected two core areas.

Inbound Migration

Inbound migration movements were defined as relatively long and rapid movements consistently moving towards the overwintering area in the late summer or fall. Inbound migrations may include short (<9 day) periods of slow movement or may be interrupted by a core area.

I tried to ensure my classifications were meaningful representations of the animal's biology rather than rigidly adhere to a mathematically based classification scheme. Classifications using normalized displacement and rates occasionally conflicted with classifications from visual assessments of the raw data. Situations also arose when a movement segment could be classified in two different categories. In these cases, I used the context of a particular movement segment by examining several previous and subsequent segments, rather than trying to classify each segment in isolation. For example, if a series of segments in the spring were directed away from the hibernaculum but the rate of those segments were similar to the rates of other core segments, I classified

those segments as core segments. Or, if a segment had a higher rate than the previous

core segment but less than subsequent rapid migration segments, I would classify that

segment as a migration segment. Field observations of rattlesnakes feeding, shedding,

mating and changes in body weight were also very important in the classification process.

I estimated topographic area of each core area by using the core area telemetry

observation to construct a 95% FK using the same procedures described above.

After completing this classification process, I calculated a series of movement

statistics and compared these statistics among the four categories. I included data from all

telemetered rattlesnakes, even if they were not tracked for an entire season, so long as I

was able to identify at least one movement category (e.g., a complete outbound migration

or complete core area). I calculated the number of days spent in each category. These

data did not meet the assumptions of parametric statistics despite transformations so I

compared the mean number of days spent in each category separately for each year using

three Friedman's tests, followed by a series of Bonferroni-corrected pairwise Wilcoxon

sign-rank tests for each year. I used a chi-square test of homogeneity to test whether the

mean proportion of time spent in each category was significantly different among years.

I calculated the mean movement length, rate (m/24 hrs), and turn angle ($0°$ to

$180°$) for each movement category. Movements <5 m were again excluded for

consistency with earlier studies (Jorgensen et al. 2008). Mean movement length was

calculated as the number of ≥ 5 m movements divided by the total distance moved

following King and Duvall (1990). Results using this measurement were identical to

those using the true mean movement length. I also calculated the mean angle of

movement (φ) and the length of the mean vector (r) for each rattlesnake's movement

category (Batschelet 1981, Zar 1996). The length of the mean vector is a measure of angular concentration and indicates how straight a series of movements are (Batschelet 1981). Angular statistics were calculated using Oriana 2.0 (Kovach Computing Service, Pentraeth, Wales, U.K.). Movements that occurred >7 days without intervening locations were excluded from all calculations except total distance moved and number of movements. These results are biased towards lower total distances and fewer movements because multiple movements were certainly made during this period. These movements were still classified into one of the four movement categories using the criteria described above. The total distance for inbound migration was only included for snakes that were monitored for the entire inbound migration period in 2008.

I tested for differences in mean movement length, total movement distance, rate, turn angle, and length of the mean vector among the four movement classes in 2008 using mixed effects linear models (PROC MIXED) followed by a Tukey's pairwise test. I also tested for an effect of sex and year. The number of telemetry observations was included to correct for differences in sampling intensities and individual was included as a repeated measure. All variables were $\log_{10}$ transformed, except turn angle which was square root transformed, to meet the test assumptions. I also tested for differences in total distance, maximum distance, mean rate, mean turn angle, meandering ratio, and number of days spent in core areas between males that exhibited mate searching movements and those that did not. I pooled data from all three years and used a mixed effects linear model including year and number of observations with individual as a repeated measure. Maximum distance was $\log_{10}$ transformed and meandering ratio was transformed by taking the square root of the arcsin.

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Fidelity to Summer Activity Areas

I tested whether rattlesnakes followed the same bearing during outbound and inbound migration in 2008 using a non-parametric Moore's test for circular uniformity of paired data (Zar 1996). The null hypothesis under this test was that snakes followed the same mean bearing during outbound and inbound migration. Because outbound and inbound migrations typically occurred in opposite directions, I added 180° to the mean inbound migration bearing to calculate the angular difference between inbound and outbound migration. I 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. I only used snakes for which I had complete outbound migration data (n = 12). Because this test can only be conducted between two samples, I ran the test for each pairwise year combination using Bonferroni corrections.

RESULTS

Movement Patterns

I monitored the movements of twelve male rattlesnakes in 2006, twelve male and three nonpregnant females in 2007, and sixteen males and six nonpregnant females during 2008 for a total of 29 rattlesnakes (Table 1.2). Five rattlesnakes were telemetered during all three years of this study, one in 2006 and 2007, six in 2007 and 2008, and two

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. A total of 27 rattlesnakes provided data for 44 snake years that met the criteria for inclusion in some or all of the analyses (21 males and six nonpregnant females). 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.

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 1.3). However, these overall means are likely biased because not all individuals were monitored throughout the activity season or the study. Additionally, the spring hibernacula searches in 2007 probably occurred after peak emergence, further biasing the results of that year to snakes that remained closer to the hibernacula. Since 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 moved a mean total distance of 4.46 km (± 0.37 km) and a mean maximum distance of 1.46 km (± 0.15 km, Table 1.3). During 2008, mean rate was 42.76 m/24 hrs (± 3.82 m/24 hrs), mean turn angle was 70.92° (± 2.84°), 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.

There were no differences in movement patterns between rattlesnakes overwintering on the south and north sides of Big Creek. There was no significant

difference in total distance moved (t = -0.56, df = 18.1, p = 0.5815), maximum distance

moved (t = -0.17, df = 20, p = 0.8649), mean rate (t = -1.12, df = 18.2, p = 0.2776),

percent change in body mass (t = 0.02, df = 17.9, p = 0.9834), mean turn angle (t = 0.90,

df = 19.9, p = 0.3805), and meandering ratio (Z = 0.13, p = 0.8947) between north side

and south side snakes during 2008. There were no differences in these variables between

north and south side rattlesnakes in 2006 and 2007.

There were few differences in movement patterns between males and nonpregnant

females. There was no significant effect of sex on total distance moved ($F_{1,24}$ = 0.03, p =

0.8682), $\log_{10}$ maximum distance moved ($F_{1,24}$ = 1.74, p = 0.1991), log10 mean

movement rate ($F_{1,24}$ = 0.01, p = 0.9430). There was a marginal effect of sex on mean

turning angle ($F_{1,24}$ = 3.83, p = 0.0621) with males having a higher mean turning angle

(81.01° ± 2.52°) than females (65.63° ± 5.79°). There was a significant difference in

meandering ratio between males and non-pregnant females in 2008 (0.71 ± 0.02 versus

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 ($F_{1,14}$ = 6.15, p

= 0.0265, Figure 1.3) and $\log_{10}$ mean movement rate ($F_{1,14}$ = 6.05, p = 0.0275, Figure

1.4). There was no effect of initial body mass on maximum distance moved ($F_{1,14}$ = 1.10,

p = 0.3128) or mean turning angle ($F_{1,14}$ = 0.19, p = 0.6678). There was no correlation

between meandering ratio and percent change in body mass in 2008 (r_s = -0.1528, p =

0.5201). 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 effect of total distance moved ($F_{1,17} = 0.08$, $p = 0.7749$), maximum distance moved ($F_{1,17} = 0.00$, $p = 0.9553$), mean movement rate ($F_{1,17} = 0.26$, $p = 0.6193$), mean turn angle ($F_{1,17} = 0.36$, $p = 0.5586$), and meandering ratio ($F_{1,17} = 0.12$, $p = 0.7363$) on the percent change in body mass in 2008.

Movement Classification

Classifying individual movement segments as outbound migration, core area, mate searching, and inbound migration proved highly informative. In 2008, outbound migration began as early as 6 May and continued into mid August. Core areas were observed during the entire activity season from late April to late September. Mate searching movements occurred between 12 July and 16 August. The first inbound migration was observed on 9 August, although one snake began moving back towards its hibernaculum in early July, and the last observed inbound migration began 18 September. These patterns are consistent with the 2006 and 2007 data, although males began mate searching in late June 2006.

Rattlesnakes varied the amount of time spent in each category, spending a mean of 67 days (50.75%) in core areas, 22 days (16.54%) in outbound migration, 25 days (18.87%) mate searching, and 18 days (13.83%) in inbound migration. Time spent in each category differed significantly during 2008 (Friedman's $X^2 = 25.93$, df = 3, p < 0.0001) with significantly more time spent in core areas than in outbound or inbound

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migration (p < 0.0006). There were no significant differences in time spent among other categories (p ≥0.1400). These same trends were evident in 2007 and 2006 (Friedman's $X^2 = 20.80$, df = 3, p < 0.0001 for 2007 and Friedman's $X^2 = 7.33$, df = 3, p = 0.0621 for 2006). However, the comparisons were non-significant after Bonferroni correction, although this is likely due to small sample sizes and monitoring for only part of the activity season (May-August) during these years. The mean proportions of time spent in each movement category were not significantly different among years ($X^2 = 10.64$, df = 6, p = 0.1001). Because the 2008 data set covers the entire activity season, I will present the results from that data set.

Rattlesnakes in all three years often displayed multiple core areas. In 2008, rattlesnakes had a mean of 2.85 core areas (range 1-5). Most snakes had one core area at or near the hibernaculum until late May to mid June, a second core area in late June to late July, and a third core area in August (Figure 1.2). I recognized two types of core areas. Staging core areas were defined as a core area beginning before the end of May and ending before mid June where the rattlesnake remained for <40 days. Staging core areas were identified in 13 rattlesnakes (65%) in 2008 (Figure 1.2). Foraging probably did not occur in most staging core areas although four snakes appeared to feed in staging cores. Staging core areas were also observed in the fall as rattlesnakes neared their hibernacula the end of inbound migration. Rattlesnakes stayed in fall staging cores significantly less than in spring staging cores (11 days versus 30 days, t = -5.04, df = 13.7, p = 0.0002).

Each rattlesnake had one to three foraging/shedding core areas in 2008 (Figure 1.5) and most had two. Foraging/shedding core areas typically occurred from mid June to

mid September disjunct from the hibernacula. However, three individuals had foraging/shedding core areas that included their hibernacula, where they stayed into late June and mid July (Figure 1.5B). Prey consumption and/or shedding was directly observed or inferred (through increases in body mass or the addition of a new basal rattle segment) in 29 of 39 (74%) foraging/shedding core areas. Feeding occurred from May into September and shedding occurred in late June through early September, with the greatest intensity of shedding occurring late June to early July. The size of foraging/shedding core areas (95% FK) was variable and ranged from 0.01 to 63.61 ha (mean = 5.22 ha ± 1.75). The core area of one male rattlesnake in 2008 appeared to represent concentrated mate searching movements as he circled within a 0.44 ha core area for nine days before being found copulating with a telemetered female that had been shedding in that same area.

Mate searching movements were observed in 19 out of 35 (54%) male snake years during this study (Figure 1.5C). Eleven of 12 males (92%) that were monitored for multiple years were observed mate searching in at least one year. Males that did so spent a mean of 25 days (± 2.04 days) mate searching. The two copulation events observed were observed on 26 July 2007 and 2008. There was no significant difference in total distance moved ($F_{1,5}$ = 3.46, p = 0.1221), log10 maximum distance ($F_{1,5}$ = 0.51, p = 0.5055), mean rate ($F_{1,5}$ = 2.30, p = 0.1899), mean turn angle ($F_{1,5}$ = 0.23, p = 0.6506), initial body mass ($F_{1,5}$ = 1.92, p = 0.2249), percent change in body mass (2008 only, t = 0.86, df = 12.7, p = 0.4047), or number of days spent in core areas ($F_{1,5}$ = 4.22, 0.0951) between males that engaged in mate searching and males that did not. However, males that exhibited mate searching had a mean weight gain of 1.7% (± 4.3%) compared to

6.9% (± 4.2%) for males that did not and spent 60 days in core areas compared to 81 days

for males that did not. Males that made mate searching movements did meander

significantly more than males that did not (arcsine-square root transformation, $F_{1,5} = 6.94$,

$p = 0.0463$).

The characteristics of the individual movement segments within each movement

category differed greatly (Table 1.4). There was a significant difference in the log10

mean movement length ($F_{3,55} = 17.70$, $p = <0.0001$), log10 total distance moved ($F_{3,55} =$

27.55, $p = <0.0001$), log10 mean movement rate ($F_{3,56} = 22.22$, $p < 0.0001$), square root

mean turning angle ($F_{3,56} = 11.74$, $p < 0.0001$), and the length of the mean movement

vector ($F_{3,56} = 31.78$, $p < 0.0001$) among the four movement classes. Core movements

were significantly shorter than outbound migration, mate searching, and inbound

migration movements ($t = -5.24 - -7.23$, df = 55, $p < 0.0001$). Total distance moved was

significantly greater during migration and mate searching than in core areas ($t = -5.56 - -$

9.06, df = 55, $p < 0.0001$). Total distance moved was also greater while mate searching

than during outbound migration ($t = 3.91$, df =55, $p = 0.0014$) and marginally greater than

during inbound migration ($t = -2.55$, df = 55, $p = 0.0629$). There was no significant

difference in the total distance moved during inbound and outbound migration ($p =$

0.8910). The mean rate of core area movements was significantly less than the mean rate

of the outbound migration, mate searching, and inbound migration movements ($t = -6.15$

$- -7.96$, df = 55, $p < 0.0001$). Mean turning angle was significantly higher in core areas

and during mate searching than during outbound migration ($t = 4.10 - 5.50$, df = 56, $p \leq$

0.0008). Mean turn angle was also significantly lower during inbound migration than

during mate searching ($t = -2.96$, df = 56, $p = 0.0226$) but was not significantly different

from mean turn angle in core areas (t = 2.25, df =56, p = 0.1219). Migration movements were significantly more directional than both core area movements and mate searching movements (t = -9.47 - 6.68, df = 56, p ≤ 0.0022). The mean bearing during outbound and inbound migration was not significantly different (R' = 0.37, p > 0.60).

There was no effect of sex on log10 mean movement length ($F_{1,25}$ = 0.04, p = 0.8430 and $F_{2,15}$ = 1.20, p = 0.3294), log10 total distance moved ($F_{1,25}$ = 0.01, p = 0.9380 and $F_{2,15}$ = 1.76, p = 0.2056) or log10 mean rate ($F_{1,25}$ = 0.15, p = 0.6972 and $F_{2,15}$ = 2.46, p = 0.1188) for the four movement categories. Males tended to have higher turn angles than females (77.47 ± 2.90 versus 57.76 ± 6.73, $F_{1,25}$ = 3.54, p = 0.0717) and greater mean vector lengths (0.62 ± 0.07 versus 0.46 ± 0.03, $F_{1,25}$ = 4.02, p = 0.0560).

Fidelity to Summer Activity Areas

Rattlesnakes telemetered for multiple years were typically consistent in travelling along the same migration routes and returning to the same general foraging areas in subsequent years. After correcting for the number of telemetry observations, there was no significant difference in total distance moved ($F_{2,12}$ = 2.30, p = 0.1431), maximum distance moved ($F_{2,12}$ = 2.32, p = 0.1407), log10 mean movement rate ($F_{2,12}$ = 2.28, p = 0.1452), or mean turning angle ($F_{2,12}$ = 0.22, p = 0.8073) among years. After controlling for movement category and number of observations, year had no significant effect on log10 mean movement length ($F_{2,15}$ = 1.20, p = 0.3294), log10 total distance moved ($F_{2,15}$ = 1.76, p = 0.2056), or log10 mean rate ($F_{2,15}$ = 2.46, p = 0.1188). However, snakes did have lower turn angles in 2008 than in 2007 (64.15 ± 3.44 versus 83.39 ± 4.99, $F_{2,15}$ =

3.97, p = 0.0414). The length of the mean vector also differed slightly among years ($F_{2,15}$ = 2.72, p = 0.0984) with snakes again moving slightly straighter in 2008 than in 2007 (0.55 ± 0.04 versus 0.39 ± 0.04).

There was no significant difference in the mean bearing of outbound migration for snakes 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° (± 5.45°) between 2007 and 2008 to 70.03° (± 43.22°) between 2006 and 2007. Mean percentage overlap in 95% FK home ranges was 35% (± 3.83%) and 18% (± 2.73%) for 50% FK home ranges. 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

The movement patterns of prairie rattlesnakes in lower Big Creek appear to fit the general model of rattlesnake movement. Following spring emergence, rattlesnakes often remained at or near the hibernacula before undertaking lengthy, rapid, and directional migratory movements up to 2.93 km away from their hibernacula. These movements ceased when the rattlesnakes reached a summer core area, typically corresponding to foraging or shedding, in which the rattlesnakes made significantly shorter and less directional movements. Many snakes resumed migratory movements and travelled to another core area before returning to their hibernaculum. Male rattlesnakes would often leave their core areas during July and August and make lengthy, meandering movements

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to locate females. In the fall, the rattlesnakes returned to their hibernacula along approximately the same migration route. All telemetered rattlesnakes showed high den fidelity. Only one of 96 individually marked rattlesnakes during this study switched hibernacula (J. Bauder, unpublished data).

Rattlesnakes typically remained near the hibernacula for some length of time in the spring, resulting in the recognition of the staging core area. Staging core areas were so named because rattlesnakes may have used this period to acclimate to warmer temperatures and prepare for a summer of movement. Although a few snakes stayed near the hibernacula through mid June, and most snakes that did were shedding or foraging, most snakes had begun outbound migration between mid May and mid June. Some snakes did eat within their staging core area, indicating that feeding is not restricted to only foraging/shedding core areas. Rattlesnakes in other populations are also known to remain near the hibernacula following spring emergence (Fitch 1939, Hirth et al. 1969, Wallace and Diller 2001) while some populations may exhibit both behaviors (Cobb 1994). The slow and infrequent movement in staging core areas was likely due, in part, to several days of cold wet weather in May and early June. However, it is possible that some staging core areas were artifacts of the transmitter surgeries while the snakes allowed their incisions to heal. Hirth et al. (1969) also suggested that emerging rattlesnakes use this time to reset their biological clocks. It is quite likely that the staging core area serves as a transition period between the previous seven months spent underground and the subsequent activity season.

Male and nonpregnant female rattlesnakes showed no differences in movement distances, either total distance or maximum distance moved, or movement rate. Males

tended to have higher turn angles and meandering ratios as a result of male mate searching movements, which were long, rapid, and had low directionality. Other studies have reported differences in movement patterns between male and nonpregnant female rattlesnakes ascribed to male mate searching (King and Duvall 1990, Jenkins and Peterson 2005, Jorgensen et al. 2008), although other studies have found no differences in movement between the sexes (Parker and Anderson 2007). About half of the males in my study exhibited distinct mate searching movements during July and August. The mate searching movements observed in my 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 these results and my results suggests that females within the lower Big Creek drainage were more spatially predictable, thereby allowing males to forgo linear mate searching movements.

The opportunity costs of mate searching in relation to foraging appeared to be relatively low in my study. There were no significant differences in the amount of time spent in core areas or percent change in body mass by males that exhibited mate searching movements and those that did not. However, males that did not mate search spent a mean of three weeks more in core areas and most mate searching males lost weight while mate searching. These results suggest that mate searching may impose some costs in terms of reduced foraging time or success. Jenkins and Peterson (2005) suggested that some large male Great Basin rattlesnakes (*C. o. lutosus*) in their study did not feed

for an entire year in order to focus on mate searching. These males had high body conditions in the spring, moved further, and covered greater distances but did not appear to feed during the summer. Although all of my males appeared to feed at least once each year, I did find that total distance moved was correlated with initial body mass. Larger males may be more likely to search a greater area for females if they are better able to withstand weight loss while mate searching.

During a complete activity season in 2008, prairie rattlesnakes in the lower Big Creek drainage moved a mean total distance of 4.46 km and a mean maximum distance of 1.46 km. These distances are intermediate compared to those reported from other prairie and western rattlesnake populations with lower topographic relief. Prairie rattlesnakes in southern Alberta moved a mean total distance of 8.17 km and a mean maximum distance of 2.76 km (Jorgensen et al. 2008) while Didiuk (1999) reported a mean total distance moved of 43.8 km and a mean maximum distance of 20.0 km for four prairie rattlesnakes in southern Alberta. Non-pregnant female Great Basin rattlesnakes in southeast Idaho moved a mean total distance of 10 km and mean maximum distance of 4.8 km (Cobb 1994). However, other studies in areas with low to moderate topographic relief have reported movement distances that are comparable to those observed in this study. King and Duvall (1990) reported mean total distances moved of 3.51 and 2.76 km (males and non-pregnant females, respectively) for prairie rattlesnakes from southern Wyoming, although maximum distance moved was likely greater in their study (see below). Midget faded rattlesnakes (*C. o. concolor*) in southwest Wyoming moved a mean total distance of 2.12 and 1.96 km and a mean maximum distance of 0.78 and 0.61 (males and females, respectively, Parker and Anderson 2007), all of which were lower than

observed in my study. Jenkins (2007) reported mean total and maximum distances of 1.47 and 5.08, respectively, in Great Basin rattlesnakes in southern Idaho.

The majority of studies on rattlesnake movement provide information that summarize individual movements over the entire year, making comparisons of distinct movement types (e.g., migration, foraging) difficult. Prairie rattlesnakes in southern Wyoming made vernal migrations of 2.57 and 2.03 km (males and females, respectively, King and Duvall 1990), which were greater than the mean outbound migration distances of my study (1.38 in 2008). Despite the mountainous landscape in my study area, the migration movements I observed were often very directional (mean r = 0.794 and 0.698 for outbound and inbound migration, respectively). These values were comparable to the highly directional migration movements in Wyoming (r = 0.61-0.87, King and Duvall 1990) and southeastern Idaho (r = 0.907-0.928, Cobb 1994). The movement rates during migration and mate searching from my study were similar to movement rates for prairie rattlesnakes in southern Wyoming and Canada (Duvall et al. 1985, King and Duvall 1990, Jorgensen et al. 2008) while the movement rates in core areas in my study were similar to those reported for Grand Canyon rattlesnakes (*C. o. abyssus*, Reed and Douglas 2002) and midget faded rattlesnakes (Ashton 2003).

Rattlesnakes monitored for multiple years generally made similar movement patterns among years. Telemetered rattlesnakes tended to follow the same bearing during their outbound migrations over multiple years and there was a fairly strong tendency to return to the same foraging area. I also failed to detect a difference in movement distances, rate, or directionality among years. Summer fidelity has been observed in rattlesnake populations where the same individuals were monitored for multiple years

(Jenkins 2007, Parker and Anderson 2007). Jenkins (2007) found that Great Basin rattlesnakes returned to the same general areas in subsequent years even in years of low prey abundance. However, movements during these years were more directional, suggesting that rattlesnakes adjusted their foraging movements to increase their searching efficiency in response to perceived prey availability (King and Duvall 1990, Duvall and Schuett 1997).

The pattern of summer fidelity observed in multiple rattlesnake studies may have some implications for the hypothesis that linear migration movements represent efficient search patterns for widely distributed or spatially unpredictable prey resources. If rattlesnakes do travel to a familiar 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 previously known foraging area. I hypothesize that migratory movements are relatively fixed and independent of perceived prey availability compared to movements within a core area. When a snake reaches a core area, it may then adjust its movements in response to perceived prey availability, perhaps continuing to make linear movements if prey availability is low. This could explain the linear movements of prairie rattlesnakes in southern Wyoming (King and Duvall 1990) and Great Basin rattlesnakes in low prey years (Jenkins 2007). However, further research is needed to evaluate the degree of summer fidelity, particularly during fluctuations of prey abundance, and to test the hypothesis that rattlesnakes modify core area movements, not migration routes, in response to prey availability.

The results of this study strongly indicate that the general model of rattlesnake movement observed in areas with low to moderate topographic relief is robust to the effects of topography within lower Big Creek. Despite the rugged mountainous topography, prairie rattlesnakes in this landscape undertook lengthy, rapid, and directional migrations from communal hibernacula. Rattlesnakes often moved upslope and crossed ridge lines during migration. These results also suggest that the effects of topography on rattlesnake movement are of less importance than other factors known to influence the general model of rattlesnake movement, such as the spatial distribution of over-wintering sites, prey, and mates.

Time series segmentation provided a useful and informative approach for classifying rattlesnake movements in a biologically meaningful manner and allowed for meaningful comparisons with other studies. Dettki and Ericsson (2008) used this technique to classify the movement patterns of individual moose as migratory, dispersal, or nomadic. Jenkins (2007) first applied this technique to snake movement data to identify the core activity areas of Great Basin rattlesnakes. Using my six criteria, I was able to classify 92% of all movement segments, most of the time using only distance from hibernaculum, rate, and directionality. There were a small number of cases where it was unclear where a segment should be classified. In these cases, I used the context of the segment and my experience with the system to make a classification. Other snake researchers have used 50% fixed kernel (FK) home range as a measure of core area (Marshall et al. 2006, Roth and Greene 2006, Parker and Anderson 2007, Jenkins and Peterson 2008). Although the 50% FK generally corresponded to core areas in my study, the locations included in kernel may or may not be associated with behaviors that would

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occur in core areas, such as foraging or shedding. For example, in my study, the 50% FK often contained large portions of the migration route. Additionally, the kernel analysis does not incorporate information about the timing of different behaviors.

Time series segmentation may provide a powerful approach to understanding snake movements and I wish to offer some considerations for future applications of this technique. First, data should be collected at regular and frequent intervals to provide a fine enough temporal resolution. Secondly, the exact criteria used for classification should be modified depending on the biology of the study organism. Dettki and Ericsson (2008) suggested using a normalized displacement value of 0.5 to identify changes in movement type, yet for this study I found that a normalized displacement value of 0.2 was rather successful at distinguishing between core and migration/mate searching movements. Third, the biology of the organism should be kept at the forefront of the analysis rather than a rigid set of rules. Finally, there may be limits to this approach in terms of its ability to distinguish some movement types. For example, some snakes may appear to exhibit only a single movement type, such as migration or core area movements for their entire activity season (e.g., King and Duvall 1990, Reed and Douglas 2002, Parker and Anderson 2007). More applications of time series segmentation are needed to test the robustness of this method across multiple populations, taxa, and habitats.

Table 1.1. Rules for classifying prairie rattlesnake (*Crotalus v. viridis*) movement

patterns in the lower Big Creek drainage in central Idaho.

	Outbound Migration	Core Area	Mate Searching	Inbound Migratic
Distance From Hibernaculum	Increasing	Stable	Variable	Decreasing
Rate	Medium to High	Low to Medium	Medium to High	Medium to High
Directionality	Medium to High	Low to Medium	Medium to High	High
Time of Year	May to August	May to September	July to August	August to Septem
Normalized Displacement or Rate	>0.20	<0.20	>0.20	>0.20
Length (Time)	≥3 days	≥12 days	≥3 days	≥3 days
Behavioral Context	Leaving the hibernaculum area	Foraging, digesting, shedding, mating, refuge from weather	Males searching for receptive females	Returning to the hibernaculum are

Table 1.2. Size and monitoring dates of 27 radio telemetered prairie rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage of central Idaho 2006-2008. Mean values are presented for the first five variables.

Year	N	Mass	SVL	Number of days monitored	Number of observations	Start date of monitoring	End date of monitoring
2006	11 ♂	314	81.6	85	27	11-May	6-Aug
2007	9 ♂ & 2 ♀	287	78.2	85	30	17-May	11-Aug
2008	16 ♂ & 6 ♀	303	81.8	144	39	16-Apr	28-Sep
Mean	NA	302	80.7	115	34	NA	NA

Table 1.3. Mean annual movement statistics from 27 prairie rattlesnakes (*Crotalus v. viridis*) monitored with radio telemetry in the lower Big Creek drainage of central Idaho 2006-2008.

	Total Distance (km)	Max. Displacement (km)	Rate (m/24 hrs)	Meandering Ratio	Turn Angle (°)	95% FK (ha)	50% FK (ha)
2006	4.20	1.42	59.98	0.66	87.79	113.50	24.42
2007	3.03	0.95	42.66	0.68	82.98	54.45	12.44
2008	4.46	1.46	42.76	0.66	70.92	109.21	23.98
Mean	4.04	1.32	47.04	0.67	78.22	96.30	21.14

Table 1.4. Movement category summary statistics from 27 prairie rattlesnakes (*Crotalus v. viridis*) monitored with radio telemetry in the lower Big Creek drainage of central Idaho 2006-2008. Values with the same letter within a column are not significantly different (p > 0.05).

	Movement Length (m)	Total Distance Moved (km)	Rate (m/24/hrs)	Turn Angle	Length of Mean Vector (r)
Outbound Migration	295^A	1.30^B	74.14^A	54.99^A	0.740^A
Core Areas	74^B	1.04^C	22.82^B	87.15^{BC}	0.276^B
Mate Searching	344^A	2.13^A	100.56^A	95.78^C	0.261^B
Inbound Migration	307^A	1.52^{AB}	92.72^A	63.45^{AB}	0.708^A
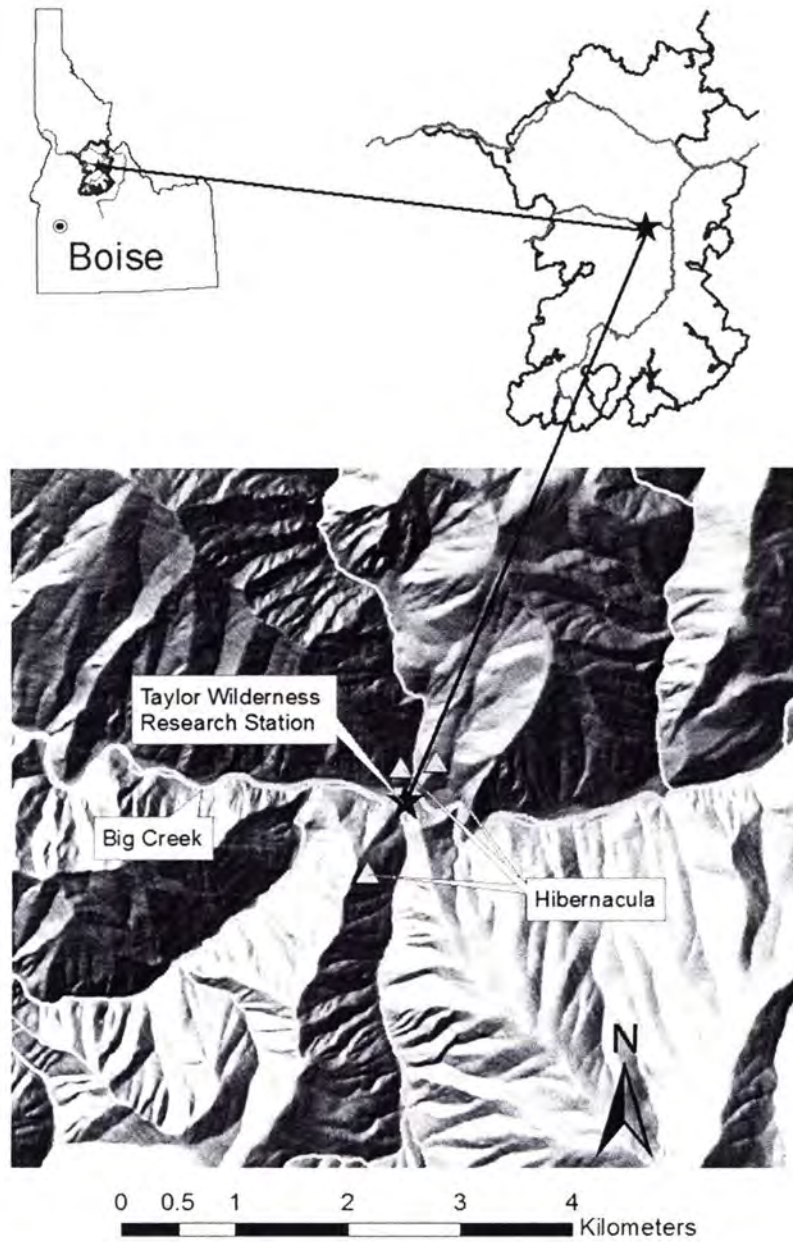
Figure 1.1. Map of the study area highlighting the Frank Church-River of No Return Wilderness, the Taylor Wilderness Research Station, and the three rattlesnake hibernacula complexes used in this study.
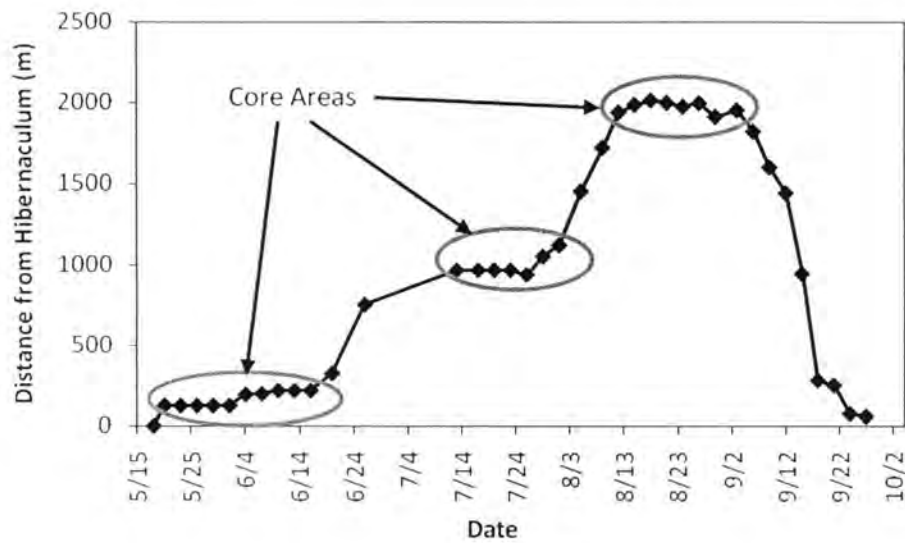
Figure 1.2. An example of a time series graph for a nonpregnant female prairie rattlesnake (*Crotalus v. viridis*) monitored with radio telemetry in the lower Big Creek drainage of central Idaho in 2008. Date is on the x-axis while topographic distance from the hibernaculum (m) is on the y-axis. The first core area is a staging core area while the second two are foraging/shedding core areas.
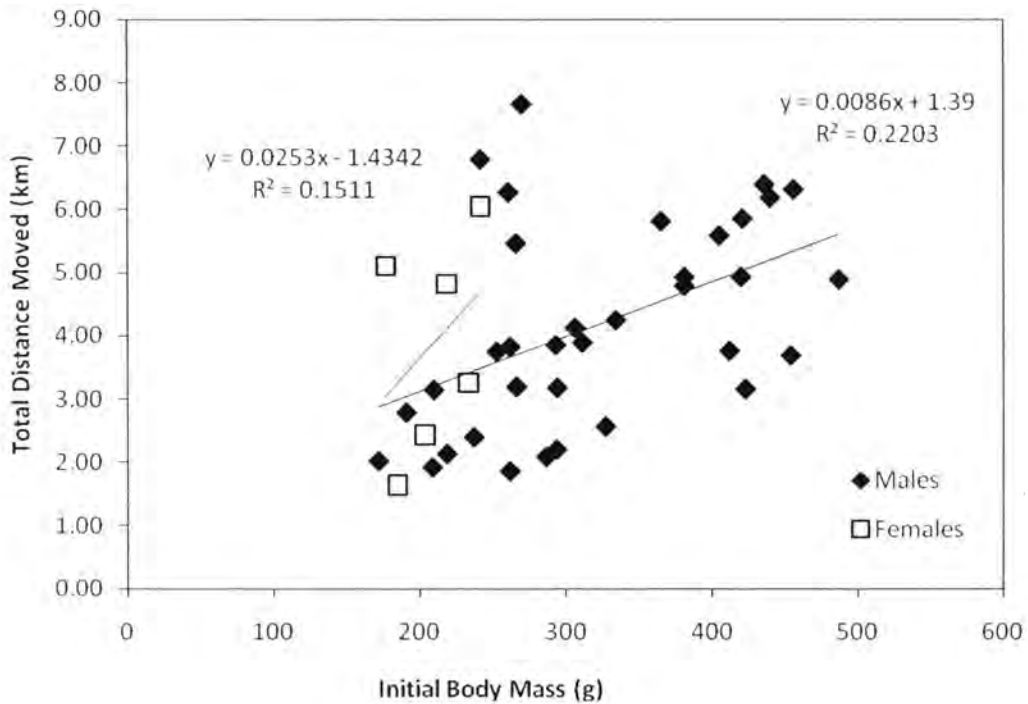
Figure 1.3. Relationship between initial body mass (g) and total distance moved (km) for male (n = 21) and female (n = 5) prairie rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage of central Idaho 2006-2008. The relationship between initial body mass is significant ($F_{1,14}$ =6.15, p = 0.0265). There is no significant effect of sex (p = 0.8682).
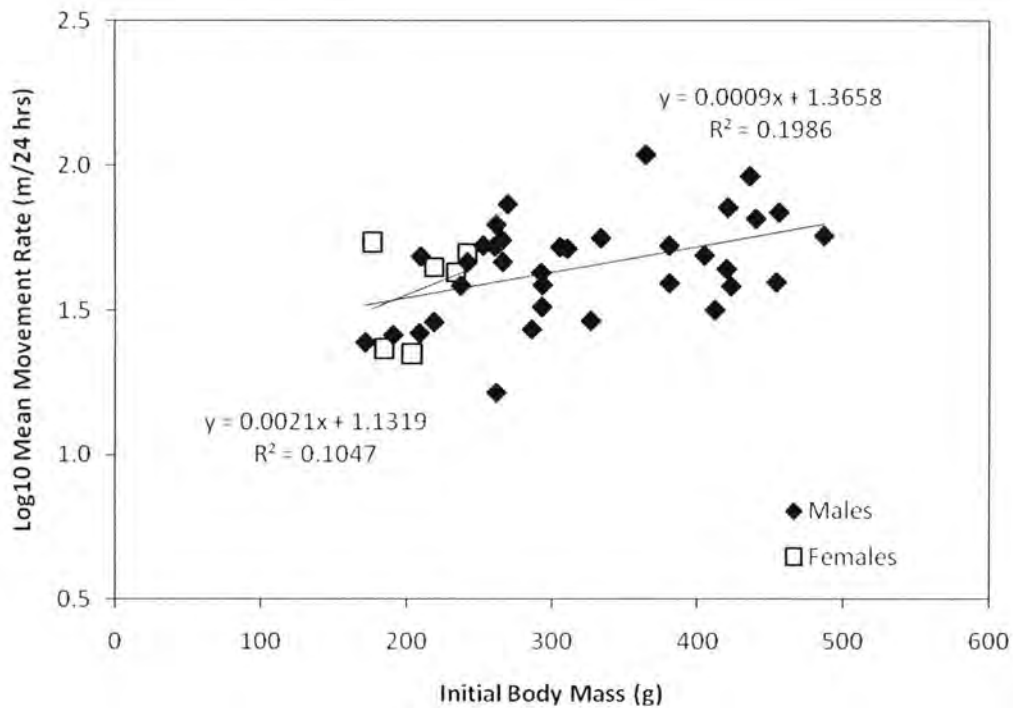
Figure 1.4. Relationship between initial body mass (g) and log10 mean movement rate (m/24 hrs) for male (n = 21) and female (n = 5) prairie rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage of central Idaho 2006-2008. The relationship between initial body mass is significant ($F_{1,14} = 6.05$, $p = 0.0275$). There is no significant effect of sex (p = 0.9430).
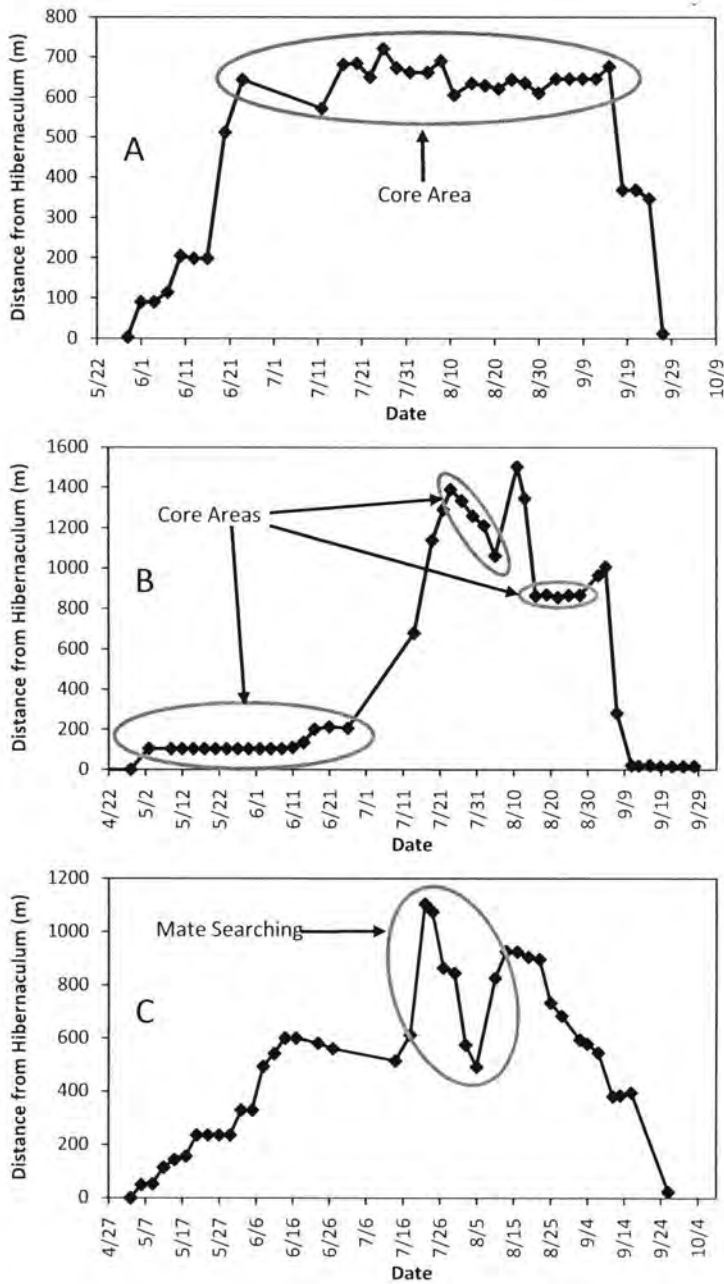
Figure 1.5. Time series graphs for three male prairie rattlesnakes (*Crotalus v. viridis*) monitored with radio telemetry in the lower Big Creek drainage of central Idaho April-September 2008. (A) shows a male with a single foraging/shedding core, (B) shows a male whose foraging/shedding core overlaps his hibernaculum, and (C) shows a male that exhibited mate searching movements.

Chapter 2

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

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, vegetation cover type, prey abundance, and conspecific density. I used radio telemetry to monitor the movements of 21 male and six nonpregnant female prairie rattlesnakes in the Frank Church Wilderness in central Idaho during the summers of 2006-2008. I used GIS to test for selection for topographic features and cover types at multiple spatial scales and compared small mammal abundance among cover types. Rattlesnakes moved across a wide range of topographic features including ridges, steep slopes, creeks, and rivers. Model selection analyses indicated that rattlesnakes were somewhat restricted by topography at the larger scale (three kilometer buffer) while this restriction was less evident at the smaller scale (home range). Although topography, particularly elevation, appears to restrict rattlesnake movements across broad spatial scales, it appears to have little restrictive effect within the home range. Rattlesnakes showed greatest selection for riparian cover types. However, I failed to detect a

significant difference in small mammal abundance among vegetation cover types. Because rattlesnakes can obtain prey throughout this landscape, the higher densities of conspecifics around communal hibernacula likely play an important role in directing rattlesnake movements away from the hibernacula. Differences in movement distances between this study and previous studies of rattlesnake movements may be better explained by variation in prey availability rather than differences in ruggedness of the study area.

INTRODUCTION

What factors influence animal movement patterns and distributions? This is a central question in animal ecology and its answer has important implications in understanding population ecology and species conservation. Animal movements across a landscape may be thought of in a benefit-cost framework (Werner and Anholt 1993). Some benefits of movement include the acquisition of important resources, such as food, water, mates, cover from predators, and shelter from the abiotic environment (Andrewartha and Birch 1954, 1984). The spatial and temporal distribution of these resources can have a strong influence on animal movement patterns (e.g., McIntyre and Weins 1999, Klassen et al. 2006, Filipa-Loureiro et al. 2007), particularly in landscapes where different resources occur in spatially separate habitats (Gregory 1984, Gregory et al. 1987). Movement among resource patches may also reduce the effects of competition (Hamilton et al. 1967). Animals must weigh the benefits of movements, realized through resource acquisition, against the costs of movement, which include predation risks and

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opportunity and energetic costs. The influence of both resource distribution and costs on animal movement can vary depending on the spatial scale (Wiens 1989, Johnson et al. 2002a, 2002b, Bowyer and Kie 2006). Animals often respond to habitat features at scales more extensive than their actual area of use (Kie et al. 2002, Anderson et al. 2005). For this reason, a multi-scale approach is important to better understand the benefits and costs to animal movements.

Landscape characteristics, such as topography, hydrology, and vegetation type and spatial arrangement, can enhance or mitigate the costs of animal movements (Forman 1995). Topographic features, such as mountain ranges, ridges, and valleys, are one group of landscape characteristics that has a strong potential to increase the costs of animal movements. These costs may occur through increased energetic costs (Johnson et al. 2006b) or environmental constraints, such as cold temperatures at high elevations. Topography is known to constrain the movements of large mammals by causing them to move along gentle slopes, valleys, or ridgelines and avoid travelling across steeper slopes (Johnson et al. 2002b, Dickson et al. 2005, Kie et al. 2005, Bruggman et al. 2007, Dickson and Beier 2007). Rugged topography may also restrict inter-patch movement (Harrison 1989, Roland et al. 2000) and lead to reduced genetic connectivity among subpopulations (Funk et al. 2005, Giordano et al. 2007). Topography may also impose opportunity costs if travel times are increased at the expense of foraging or mate searching. Alternatively, topography may prevent animals from obtaining knowledge about other resources across the landscape, thereby limiting them to their current area of use (Graf et al. 2007).

Even so, some studies report selection for rugged topography or high topographic relief (Rachlow and Bowyer 1998, Sawyer et al. 2007) or a minimal restrictive effect of topography on movements or habitat selection (Anderson et al. 2005, Coulon et al. 2008). Variable topography may provide shelter from the abiotic environment or escape terrain, although the effects of topography on individual movements are infrequently addressed in such cases. As a result, areas of greater topographic relief may actually facilitate animal movements (Epps et al. 2007). Some studies have observed animals, including small bodied reptiles and amphibians, traveling in a direct path across hills and ridges when moving between habitats, rather than following presumably less costly, but more roundabout pathways through lower elevation valleys (Pilliod et al. 2002, Bartelt et al. 2004, Bowne and White 2004). These studies indicate that topography does not always impose prohibitive costs to animal movements and may actually provide a beneficial resource, such as shelter or escape routes from predators.

A more accurate understanding of the effects of naturally occurring and potentially restrictive landscape characteristics, such as topography, on animal movements can help us better understand how animals balance the need for resource acquisition with the costs of moving across a restrictive landscape. These tradeoffs may be particularly important for animals with seasonally constrained activity seasons (e.g., ectotherms) that must move among separate habitats to acquire resources. This information can also lead to a better understanding of the factors influencing animal movements and the relative importance of those factors, which in turn can help us better explain patterns and processes in landscape and spatial ecology. It is also important from a management and conservation standpoint in allowing us to evaluate the susceptibility of

populations to anthropogenic disturbances. Species that are already restricted by natural barriers and have few corridors for movement may be more affected by anthropogenic disturbance if such disturbances occur within their movement corridors, thereby blocking access to key resources and inter-population dispersal (e.g., Epps et al. 2007).

The prairie and western rattlesnakes (*Crotalus v. viridis* and *C. oreganus*) of the Intermountain West provide an excellent system with which to study the benefits and costs of movement, particularly the influence of topography. 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 exceeded 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 undertake 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 effects of topography on rattlesnake movements and whether or not it imposes substantial costs. 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, vegetation

cover type, small mammal abundance, and the density of conspecifics on prairie

rattlesnake movements in a mountainous landscape. I hypothesized that topography

would impose additional costs on rattlesnake movements. However, I was unable to

directly evaluate movement costs in this study. Instead, I asked the question does

mountainous topography have a restrictive effect on rattlesnake movements, specifically

do rattlesnakes still make extensive movements in a mountainous landscape, are their

movements restricted to valley bottoms, and do they select for topographic features like

low elevations, less steep slopes, and valley bottoms? I also hypothesized that the

abundance of small mammal prey would influence rattlesnake movements, as seen in

other studies. I therefore predicted that rattlesnakes would select vegetation cover types

with the highest abundance of small mammal prey. Finally, I hypothesized that high

densities of conspecifics near communal hibernacula would impose additional costs on

rattlesnakes through reduced availability of prey or increased intraspecific competition

for foraging areas. Although the effects of intra-specific competition have received much

less attention, this could also have an important influence on rattlesnake migrations,

particularly at communal hibernacula where the density of conspecifics is quite high

during the spring and early summer (Hamilton et al. 1967, Hirth et al. 1969, Jorgensen et

al. 2008). The density of conspecifics could have a similar effect in areas where multiple

hibernacula are located in close proximity. I therefore predicted that rattlesnake density

would be highest closest to the hibernacula, decrease with increasing distance from the

hibernacula, and that rattlesnakes would direct their movements away from the

hibernacula.

STUDY AREA

I conducted this study in the lower Big Creek drainage of the Frank Church-River

of No Return Wilderness in central Idaho (Figure 1.1). My field work was based out of

the University of Idaho's Taylor Wilderness Research Station (TWRS, 1200 m). Big

Creek flows east and four tributaries join Big Creek at roughly perpendicular angles

within three kilometers of the TWRS (Figure 1.1). The topography of the lower Big

Creek drainage is characterized by steep valleys and high ridges (1100-2780 m in about

4.8 km). This complex landscape results in a diversity of vegetation communities.

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

tricocarpa*), 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.

Most rattlesnakes used in this study overwintered in three hibernacula complexes within 1.5 km of each other and within 800 m of the TWRS. These complexes consist of clusters of overwintering snakes within scattered talus patches or rock outcrops on bunchgrass slopes. All snakes overwintered 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 occurred on an east aspect (mean aspect = 101°) between 1327 and 1420 m elevation. The first northern complex included two disjunct talus patches, one on a southwestern aspect (mean aspect = 226°) between 1271 and 1305 m and the second on a south-southeast aspect (mean aspect = 156°) between 1304 and 1321 m. The second northern complex was located on a southeast aspect (mean aspect = 149°) between 1235 and 1269 m. One rattlesnake overwintered solitarily north of Big Creek in the south facing junction of a rock outcrop complex and talus slide at 1264 m.

METHODS

Rattlesnake Movements

I surgically implanted radio transmitters into 29 male and nonpregnant female rattlesnakes during this three year study. Rattlesnakes were captured near the hibernacula 28 April-1 May 2006, 2 May & 8-10 May 2007, and 16 April-23 May 2008 and brought back to the TWRS. In 2007, I was unable to capture a sufficient number of rattlesnakes

around the hibernacula in the spring so I 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). I used 3.8 g PD-2, 9, 11, & 13.5 g SI-2 and SI-2T, and 5 g SB-2 and SB-2T transmitters (Holohill Systems Ltd., Carp, Ontario, Canada). Transmitters were ≤5% of the rattlesnake's body mass at time of surgery. Each rattlesnake was held for 8-36 hours before being released at their respective capture sites and all snakes were alert and responsive before release.

Telemetered rattlesnakes were monitored between 11 May-6 August 2006, 16 May-11 August 2007, and 16 April-28 September 2008. Battery failures prevented me from monitoring some rattlesnakes for an entire field season. I located each rattlesnake using a three element Yagi antenna (Wildlife Materials International Inc., Murphysboro, IL) and a Telonics TR-2 receiver (Telonics Inc., Mesa, AZ) approximately once every two to four days and recorded its UTM coordinates using a handheld GPS unit (Garmin GPSmap 76CS, Garmin International Inc., Olathe, KS). Reported accuracy ranged from 2-13 meters (mean approximately 5 meters). I attempted to capture each telemetered rattlesnake to weigh it at the end of the 2006 field season and once per month in 2007 and 2008. I was unable to locate snakes between 20 and 25 July 2006 due to the wildfire north of the TWRS and between 28 June and 11 July 2008 due to an injury.

I entered the UTM coordinates for all telemetry locations that were separated by at least one day into ArcGIS 9.2 (ESRI, Redlands, CA). For previously telemetered rattlesnakes in 2008, I included a single point for its overwintering location. I calculated

home ranges using 95% fixed kernels (FK) in Home Range Tools (Rodgers et al. 2005) and ArcGIS 9.2. To determine the appropriate smoothing parameter, I used the reference bandwidth (h_{ref}) and then decreased h_{ref} incrementally by 0.1 until I had found the smallest contiguous polygon that included all telemetry observations (Berger and Gese 2007). The UTM coordinates of multiple identical telemetry locations were altered by 1-2 meters to avoid computational problems. Unless otherwise mentioned, all analyses were conducted using SAS (SAS Institute, Carey, NC) and means are reported ±one standard error.

Topography Analysis

I visually assessed the effects of topography on rattlesnake movements by creating three dimensional animated graphics of each rattlesnake's movement segment in Microsoft PowerPoint. I generated a three dimensional (3D) image of my study area 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, Redlands, CA). I overlaid my telemetry observations for each snake on this imagery within ArcScene and exported the figure to PowerPoint where I created an animated movement path. This allowed me to examine both the spatial and temporal variation in movement in relation to topography.

To help determine if topography had a restrictive effect on rattlesnake movements, I conducted a resource selection analysis for topographic characteristics using the 2008 data. I restricted my analysis to this dataset because it was collected over the entire

activity season and contained the largest and most representative sample size. I excluded

two snakes whose transmitters died during the summer so as to include individuals that

were monitored for the entire activity season (n = 20). I recorded the elevation, slope,

aspect, and convexity for each telemetry observation using ArcGIS 9.2. These values

were derived from 10 m digital elevation models (DEM) using Spatial Analyst in ArcGIS

9.2. To convert aspect from a circular variable to a continuous variable, I 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. I calculated convexity as a measure of

topographic position (e.g., ridge top or valley bottom, Kvamme 1988, Ager et al. 2003).

Negative convexity values indicated valley bottom topography while positive values

indicated ridge top topography. Values close to zero indicated flat areas or slopes close to

45°. I calculated convexity using 3 x 3 (30 x 30 m) and 9 x 9 (90 x 90 m) pixel window

sizes to determine if rattlesnakes responded to fine or coarse scale variation in

topographic position. I also measured the Euclidean distance from each telemetry

observation to the nearest water source.

To measure the topographic features that were available for telemetered

rattlesnakes to select from, I 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 three kilometer

radius buffer (28.27 km^2) 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. The second scale (home range scale)

included each rattlesnake's 95% FK home range. Because the home ranges were much

smaller than the three kilometer buffer, 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).

I used conditional logistic regression with m:n matching (PROC LOGISTIC) to

test for selection for topographic variables. Under this design, m telemetry points are

matched with n random points that are 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, my sample size was the number of individual rattlesnakes. I used a

Spearman's Rank Correlation to identify highly correlated variables ($r_s \geq 0.60$). Distance

to water was always 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 colinearlity was lower for the other variables ($r_s \leq 0.47$, Table 2.1).

I created a series of conditional logistic regression models by combining all non-

correlated topographic variables (N = 23 models and k = 6 parameters). A null model (no

variables) was also included. The two measures of convexity were also included in

separate models. Models were evaluated using Akaike's Information Critera 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 $AIC_c < 2$ were considered to have equal support and model averaging was used to calculate parameter estimates and 95% confidence intervals (Burnham and Anderson 2002). I 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).

Cover Type Selection

To test if rattlesnakes selected or avoided certain vegetation cover types, I generated a vegetation cover map in ArcGIS 9.2 using 2004 digital orthoimages and 2002 multispectral ADAR imagery (Airborne Data Acquisition and Registration 5500 System, Positive Systems, Whitefish, MT). I manually digitized polygons representing nine habitat classes: bunchgrass, burned conifer, unburned conifer, rocky outcrop, bare talus, riparian, irrigated pasture, non-irrigated pasture, and water/sandbar (Table 2.2). Burned and unburned conifer were distinguished as having about > 50% and ≤50% burned trees within a patch, respectively. Irrigated and non-irrigated pasture was included to determine if rattlesnakes select habitats on and adjacent to the TWRS. Field photographs and notes were used as references whenever possible. Water/sandbar was never used and could be considered non-habitat so I excluded it from subsequent analyses.

I tested for cover type selection at both the landscape and home range scale as described in topography section. The proportion of each rattlesnake's telemetry observations within each cover type represented the use of that cover type. The

proportion of each cover type with each rattlesnake's three kilometer buffer or home range represented the availability of that cover type. I conducted a third analysis to test if rattlesnakes selected cover types while foraging relative to what was available within their home range. I identified all telemetry observations that occurred in foraging/shedding core areas (Chapter 1) where feeding took place and calculated the proportion of each rattlesnake's core area observations within each cover type as cover type use. Availability was calculated as the proportion of each cover type within the home range.

I used compositional analysis to test for disproportionate use of cover types at each scale (Aebischer et al., 1993). The irrigated and non-irrigated pasture habitats made up a very small proportion of the available cover types at the landscape scale ($\leq 0.19\%$) and $< 9\%$ of available cover types for all but three rattlesnakes at the home range scale. These small and variable values resulted in inconsistent results from the compositional analysis. I therefore combined irrigated pasture with riparian and nonirrigated pasture with bunchgrass for the compositional analyses. Compositional analysis correctly treats each animal as the sampling unit, rather than each telemetry observation, and provides a ranking of habitat use in proportion to that class's availability. However, compositional analysis does not indicate whether habitat classes are used disproportionately less (avoided) or more (selected). I therefore calculated resource selection ratios for each rattlesnake and cover type. Selection ratios are calculated by dividing the proportion of use by the proportion of availability for a given habitat class. A ratio > 1 indicates selection while a ratio < 1 indicates avoidance. A ratio of one indicates that habitat is used in proportion to its availability. I averaged the selection ratios of all rattlesnakes for

each cover type to calculate 95% confidence intervals and determine if that cover type was selected or avoided. These analyses were only performed using the 2008 data. Compositional analysis was conducted using Resource Selection for Windows (Leban 1999).

Prey Availability

To test my prediction that rattlesnakes were selecting the most prey abundant cover types, I sampled small mammal abundance in each cover type. My sampling area was defined as a 98% adaptive kernel based on telemetry locations from 2006 and 2007. I chose to define my sampling area using this approach rather than the three kilometer buffer used to define the landscape scale because of logistical constraints and the 98% adaptive kernel was the smallest adaptive kernel size that encompassed all the telemetry points. I used a stratified random sampling design to select small mammal sampling points, stratifying my sample by cover type and using three to four replicate points per cover type.

I measured prey abundance using tracking tubes between June and September 2008. Tracking tubes have been previously used to sample small mammal abundance in lieu of live trapping (Mabee 1998, Glennon et al. 2002) and are known to provide a reliable index of small mammal abundance (Drennon et al. 1998; Glennon et al. 2002). Live trapping was not feasible in this area because of the logistical difficulties of checking live traps every morning in very rugged terrain. Tracking tubes were made from a 30.5 cm section of plastic rain gutter downspout. A strip 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, I placed a grid or transect of 6-15 tracking tubes, depending on the size and shape of cover type polygon. I used the proportion of tubes with tracks in each grid as an index of total small mammal abundance (P_i). I also calculated indices using tracking tubes with small tracks ($Psmall_i$, deer mice [*Peromyscus maniculatus*] and voles [*Microtus*]) and large tracks ($Plarge_i$, ground squirrels [*Spermophilus*], chipmunks [*Tamius*], and woodrats [*Neotoma*]). I used an analysis of covariance (ANCOVA, PROC MIXED) to compare P and *Psmall* among cover types, using elevation as a covariate. *Plarge* failed to meet the assumptions of the ANCOVA despite data transformation so I compared *Plarge* among cover types using a non-parametric Kruskal-Wallis test, followed by Bonferroni-corrected pair-wise Wilcoxon Sign-Rank tests. I then compared the results of these analyses to the cover type selection analyses to see if rattlesnakes selected cover types with high prey abundance.

Conspecific Density

To evaluate the effects of conspecific density on rattlesnake movements, I created a histogram of the maximum distance moved from the hibernacula (Chapter 1) using the data from the 22 rattlesnakes monitored in 2008. I then used these data to create a histogram of expected rattlesnake density at 0.5 km intervals from the hibernacula. For

example, if five rattlesnake moved 1.0-1.5 km from the hibernacula, expected density was $5 / ((\Pi*1.5^2)-(\Pi*1.0^2))$. However, it is important to consider the primary direction of these movements because the hibernacula in this study were located on opposite sides of Big Creek and within 1.5 km of each other (Figure 1.1). Therefore, rattlesnakes travelling more than one kilometer towards the opposite hibernaculum will likely encounter conspecifics from that hibernaculum, as well as conspecifics from their own hibernaculum. I therefore split the 2008 data between snakes from the northern hibernacula complexes and the southern hibernacula complex. I then created a third histogram of expected density using the maximum distance moved and the primary direction of those movements (away or towards Big Creek). Expected density was calculated at 0.5 km intervals moving away from the northern and southern complexes following the same procedure described above except the area for each interval was halved to obtain the area of a half-circle ring. I estimated the area between each complex and Big Creek as a polygon extending 0.6 km north or south (depending on which side of Big Creek the complex was) to Big Creek and 2.0 km east-west. A 2.0 km width was chosen because all but one rattlesnake in this study that travelled towards Big Creek stayed within approximately one kilometer east or west of their hibernaculum. The individual that moved > 1 km east of its hibernaculum was a nonpregnant female that migrated 2.24 km east of its hibernaculum along Big Creek. I calculated a density estimate to correspond with this individual's migration as one divided by the area of a 0.8 km (maximum distance moved away from Big Creek) by 1.3 km (maximum distance moved from hibernaculum along Big Creek minus the one kilometer east of the hibernaculum covered by the 0.6 km x 2.0 km rectangle described above) rectangle.

I used the mean bearing of the outbound migration (Chapter 1) to test if rattlesnakes were primarily moving away from the opposite hibernacula, again using the data from the 22 rattlesnakes from 2008. I created circular histograms for north and south side rattlesnakes and calculated the mean angle (φ) of outbound migration (Batschelet 1981, Zar 1996). I tested if the migration bearings from each side were uniformly distributed using a Rao's spacing test (Batschelet 1981, Zar 1996). All angular statistics were calculated using Oriana 2.0 (Kovach Computing Service, Pentraeth, Wales, U.K.).

RESULTS

I monitored the movements of twelve male rattlesnakes in 2006, twelve male and three non-pregnant females in 2007, and sixteen males and six nonpregnant females during 2008 for a total of 29 rattlesnakes. Five rattlesnakes were telemetered during all three years of this study, one in 2006 and 2007, six in 2007 and 2008, and two 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. I obtained 798 telemetry locations from 20 rattlesnakes (16 males and four nonpregnant females) in 2008 that were used in the analyses.

Topography

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

percent 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 much 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 (Figure 2.1).

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 (Figure 2.2). Nine of the twelve rattlesnakes that made long distance (≥1.74 km

from the hibernacula) annual migrations travelled parallel to tributary valleys. However,

these long distance migrations most frequently occurred along the sides of the valleys, 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. I recorded 17

river/creek crossings by six telemetered rattlesnakes during this study.

The global model containing all variables was the highest ranked landscape model

in 2008 (Table 2.3). CON99 (convexity with a 90 x 90 m window) was included in the

top model. Models with CON99 were always ranked higher than models with CON33

(convexity with a 30 x 30 m window). 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 2.4). 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).

There were two equally well supported top models at the home range scale (ΔAIC_c < 2, Table 2.5). The highest ranked model had moderate support (w_i = 0.4955). All six variables were included in the final model after model averaging (Table 2.4). 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 2.4). The 95% confidence intervals 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 a lower parameter weight (0.5115). Elevation and aspect had parameter weights of 1.00 while the parameter weight for convexity was 0.7684.

Cover Type Selection

Rattlesnakes showed significant disproportionate use of vegetation cover types within their three kilometer buffers during 2008 (Wilk's Lamda = 0.1529, X^2 = 37.56, df = 5, p = < 0.0001). Bunchgrass had the highest ranking, followed by riparian and talus. Selection ratios indicated significant selection for these three cover types (Figure 2.3). Burned conifer was significantly avoided while unburned conifer and rock outcrop were used in proportion to their availability. The mean selection ratios for irrigated and non-irrigated pasture were positive, suggesting some selection for these cover types at a broad

scale. However, the upper and lower bounds of the 95% confidence intervals for both cover types varied by over an order of magnitude and overlapped one.

Rattlesnakes also showed significant disproportionate use of vegetation cover types within their 95% FK home ranges during 2008 (Wilk's Lamda = 0.1765, X^2 = 34.69, df = 5, p = < 0.0001). Bunchgrass, riparian, and burned conifer were the highest ranked cover types. However, selection ratios indicated that rattlesnakes only selected for the riparian cover type at this scale, with some selection for talus as well (Figure 2.4). Bunchgrass, burned conifer, and rock outcrop were used in proportion to their availability while snakes avoided unburned conifer. Rattlesnakes also significantly avoid irrigated and nonirrigated pasture within their home ranges. When looking at where rattlesnakes foraged within their home ranges, they selectively foraged in the riparian cover type and avoided foraging in unburned conifer, nonirrigated pasture and, to some extent, bunchgrass (Figure 2.5). Rattlesnake foraging was neutral in regards to burned conifer, talus, or rock outcrop.

Prey Availability

Small mammal abundance appeared to be similar among cover types. There was no significant difference in total small mammal abundance ($F_{7,19}$ = 1.19, p = 0.3534) or the abundance of small species ($F_{7,19}$ = 0.86, p = 0.5567) among the eight cover types. Mean total small mammal abundance was greatest in rock outcrop, unburned conifer, and talus and lowest in riparian and irrigated pasture (Figure 2.6). Mean abundance of small species was greatest in talus and nonirrigated pasture. There was no significant effect of

elevation in theses analyses. There was a significant difference in the abundance of large species among cover types ($X^2 = 15.06$, df = 7, p = 0.0352). Large species abundance was significantly higher in rock outcrop than in bunchgrass or talus (Figure 2.6). However, these differences became nonsignificant after applying Bonferroni corrections.

Density of Conspecifics

A histogram of maximum movement distances showed that most rattlesnakes moved between 0.5 and 1.5 km (n = 12, 55%) from their hibernaculum in 2008 (Figure 2.7). A histogram of expected snake density at various distances from the hibernaculum using these data showed that expected density was highest between 0.5 and 1.0 km from the hibernacula and began to decrease beyond 1.0 km (Figure 2.7). After taking into account the primary direction of movement and location the hibernacula, density was highest in the bands along Big Creek between the northern and southern hibernacula (Figure 2.8a). This remained true after including only the 21 rattlesnakes from the three primary hibernacula complexes (Figure 2.8b). Density trailed off up to three kilometers away from either hibernaculum. The two distributions of expected density show some overlap. This is partly the result of including the one male that overwintered solitarily downstream from the three primary hibernacula complexes. It is also the result of one male from one of the northern hibernaculum whose core foraging area overlapped both sides of Big Creek. However, he never travelled more than 130 m from the north side of Big Creek. When this individual was placed with the other north side rattlesnakes, the histogram showed a much smaller amount of overlap between north and south side

density, with the highest density still occurring between the two complexes but on their respective sides of Big Creek. The nonpregnant female rattlesnake that moved 2.24 km from her hibernaculum downstream along Big Creek is represented by the solitary black square on the left side of Figure 2.8a. Although this individual crossed onto the south side of Big Creek, she after moving 1.90 km from her hibernaculum and did so in an area that no other telemetered rattlesnakes frequented during the three years of this study.

The mean migration bearing for rattlesnakes from the northern hibernacula was 41.40° and 212.85° for rattlesnakes from the southern hibernacula (Figure 2.9a). If only rattlesnakes from the two primary northern hibernacula complexes (excluding the nonpregnant female that moved 2.24 km downstream along Big Creek) are considered (n=10), the mean migration bearing becomes 23.92° (Figure 2.9b). When all migration bearings were pooled, the distribution was not significantly different from uniform (U = 140.48, 0.50 > p > 0.10). When north and south side bearings were analyzed separately, both southern migration bearings (U = 145.98, 0.50 > p > 0.10) and northern migration bearings were uniformly distributed (U = 151.43, 0.50 > p > 0.10). Circular-linear histograms displaying both mean migration bearing and maximum distance moved showed that all rattlesnakes that moved > 1.1 km from their hibernaculum directed their movements away from the opposite hibernacula. The one exception was the nonpregnant female that moved 2.34 km from her north side hibernaculum. However, her movements were directed downstream along Big Creek, away from both the northern and southern hibernacula.

DISCUSSION

In some respects, the results of this study strongly suggest that topography does not form a strong impediment to rattlesnake movement. A visual assessment of the data shows that topography did not strongly restrict the movements of some individuals and did not seem to act as an absolute barrier to their movements within their home ranges. Rattlesnakes used all of the major topographic features available to them and travelled up steep slopes and crossed ridge lines, as well as along valley bottoms. The results of the topographic selection analysis at the landscape scale indicate that rattlesnakes actually selected ridge tops within three kilometers of their hibernaculum. Although some snakes did restrict their movements to valley bottoms, these individuals were a minority compared to those that moved across more upland areas. Many rattlesnakes directed their movements away from Big Creek which entailed some uphill travel for most of the year. The movement distances and patterns observed in this study are also similar to those reported for prairie and western rattlesnakes in areas with low to moderate topographic relief (Chapter 1), further indicating that rattlesnakes are capable of making extensive and highly linear movements in a mountainous landscape.

However, the results of the topographic selection analysis suggest that topography has some restrictive effect on rattlesnake movements, particularly at broad spatial scales. Model support was greatest at the landscape scale, suggesting a stronger effect of topography at broad spatial scales. Rattlesnakes selected for low elevation and less steep slopes at the landscape scale and for valley bottoms at the home range scale. A restrictive effect of topography, particularly elevation, in the Big Creek drainage is expected at

broad spatial scales. Some of the elevation included within the three kilometer buffer around the hibernacula is higher than the maximum elevation used by a rattlesnake in this study. In the Pacific Northwest, rattlesnakes are typically found below about 2280 m (Nussbaum et al. 1983, Storm and Leonard 1995, St. John 2002) and most studies of rattlesnake movement in the Intermountain West have occurred near or below this 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 the maximum elevation used by rattlesnakes in this study, it is likely that elevation restricts rattlesnake movements across broad spatial scales and may even act as a barrier to long distance movements made perpendicular to Big Creek. The mechanisms for the avoidance of elevations over 2000 m could include the increased energetic costs of travelling long distances uphill, which may be suggested by the selection for low slopes at the landscape scale. Additionally, higher elevations may have poorer quality of thermal habitat due to shorter growing seasons or colder night temperatures. There may be some bias in these results because the hibernacula in this study were already at a relatively low elevation, thereby giving the appearance of selecting for low elevations. However, I found no evidence that hibernacula in the lower Big Creek drainage occurred at substantially higher elevations. Therefore, another mechanism for the selection for low elevation may be the restriction of hibernacula to habitats at 1235-1416 m elevation. Alternatively, if rattlesnakes did overwinter at higher elevations, the selection for low elevations at broad scales may become less apparent or may not even exist.

Other results of this study suggest that the energetic costs of moving across a mountainous landscape influence rattlesnake movements. Although rattlesnakes appeared to select ridge tops at the landscape scale, they appeared to select valley bottoms within their home ranges. This may reflect a selection for less energetically costly pathways, although this could also reflect selection for more sheltered or enclosed locations instead of open and exposed ridge tops or flat slopes. Most of the long distance movements observed in this study were parallel to tributary valleys, which may also provide a less energetically costly pathway relative to travelling up a steep slope. However, slope had low support at the home range scale. This may indicate that slope within the home range is already moderate, due to selecting a home range with lower slope relative to the three kilometer buffer, or that the shorter movements occurring within the home range are not of sufficient length to incur higher costs of travelling long distance up steep slopes. Rattlesnakes appeared to select for southerly aspects at both spatial scales. This 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.

Water was not a barrier to rattlesnake movement as several snakes crossed Big Creek and its tributaries. The ability to cross water probably allows for a high degree of genetic connectivity among the hibernacula in this study and with other hibernacula in the Big Creek drainage. Big Creek may also serve as a means of long distance dispersal. In May 2007, a male rattlesnake from the Pioneer Creek complex was captured on the TWRS and received a transmitter. One week later his signal went missing and I found him one week later over 3.5 km downstream along Big Creek. He spent the rest of the

summer in that same area and overwintered there. I suspect his downstream movement was made in only three days and that he tried to cross Big Creek or one of its tributaries and was swept downstream by high spring runoff.

Vegetation cover type seemed to have relatively little effect on rattlesnake movement as rattlesnakes moved through and utilized all eight cover types. 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 cover types while avoiding unburned conifer. Within their home ranges, rattlesnakes still selected the riparian cover type, avoided unburned conifer, and showed proportional use of other cover types. The riparian cover type was also selected and unburned conifer avoided at the core foraging area scale. 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 spent the entire summer at least a few hundred meters from water. Selection of talus at the landscape and home range scale may reflect its use as overwintering habitat, basking sites, or higher prey abundance (see below). Rattlesnakes probably select their home ranges in areas with access to open grassy and rocky habitats and riparian areas but then within their home range they show a more generalist pattern of habitat use. The tendency to avoid forested cover types is not surprising as prairie and western rattlesnakes are not a forest associated species (Nussbaum et al. 1983, Storm and Leonard 1995, c.f. St. John 2002). Conifer habitats,

particularly unburned conifer, may provide fewer basking sites and a lower quality of thermal habitat. Conifer habitats were also common at high elevations which may have contributed to or resulted from rattlesnake selection for low elevations.

Evaluating rattlesnake use of the TWRS habitats (irrigated and nonirrigated pasture) was more difficult because these habitats made up a small proportion of the available habitat and were used by only a few rattlesnakes that remained relatively close to their hibernacula. However, the selection ratio confidence intervals indicate that rattlesnakes either used these habitats in proportion to their availability or avoided them. Human use areas may attract rattlesnakes because of increased availability of water, prey, or shelter (Nowak et al. 2002). However, it does not appear that the TWRS is attracting a disproportionate number of rattlesnakes and the rattlesnakes that were observed on or near the TWRS would probably use that area if the TWRS was absent.

My results suggest that small mammal abundance, particularly the abundance of small species like deer mice, is relatively uniformly distributed across this landscape with regard to cover type. My results do appear to mirror the habitat associations of the most abundant small mammals in my study area. Deer mice are habitat generalists and one of the most abundant small mammals in the Big Creek drainage (Koehler and Hornocker 1989; Reid 2006). Golden-mantle ground squirrels (*Spermophilus lateralis*) and yellow-pine chipmunks (*Tamias amoenus*) are common in upland rocky habitats (Reid 2006) and were commonly observed in rock outcrop, talus, and conifer cover types. Koehler and Hornocker (1989) reported a higher abundance of deer mice in upland xeric habitats, consistent with the lower, but nonsignificantly different, abundance of deer mice I observed in riparian habitats, and comparable abundance of ground squirrel burrows

between mesic and xeric habitats. If small mammal abundance had shown strong
differences among cover types, I would have expected to see strong selection for those
cover types with higher prey abundances. Although prey abundance did not appear to
strongly differ among cover types, rattlesnakes did not selectively forage in the most prey
abundant cover types. This does not necessarily refute my hypothesis that rattlesnakes
were directing their movements to locate small mammal prey. Rather, my results suggest
that within lower Big Creek, rattlesnakes do not need to restrict their foraging by cover
type in order to maximize their access to prey. This does not necessarily mean that prey
availability is high but does suggest that prey availability is uniform with regard to cover
type. I did observe some rattlesnakes feeding at their hibernacula and most rattlesnakes
fed in multiple core areas throughout the year. This indicates that rattlesnakes can obtain
prey throughout this landscape and do not need to move to specific area or a specific
distance in order to acquire prey. These results also suggest that the patterns of cover type
selection or avoidance I observed are due to factors other than prey abundance, such as
access to water and shade or the quality of thermal habitat.

There are some limitations with my small mammal sampling design that call for
caution when interpreting my results. First, I had small number of replicates per cover
type and this may have failed to adequately capture the variation in small mammal
abundance within each cover type. The landscape in the lower Big Creek drainage is very
heterogeneous and there is a high variation in microhabitats within each cover type. The
spatial distribution of small mammal abundance may reflect this fine scale variation in
microhabitat rather than the broad scale differences in cover type. Second, the spatial
distribution of small mammals may be grouped into clusters that are distributed

independently of cover type. This type of spatial distribution would show little or no variation in small mammal abundance among cover types. However, rattlesnakes may still direct their movements towards these clusters. Finally, rattlesnakes may select certain small mammal species as prey that I did not distinguish in my track tube data.

The results of this study suggest that prairie rattlesnakes in lower Big Creek can obtain prey throughout the landscape, including at or near their hibernaculum. However, if this is true, why should these rattlesnakes migrate long distances from their hibernaculum and incur additional movement costs? The potentially competitive effects of high densities of conspecifics at communal hibernacula provide a potential answer. Hamilton et al. (1967) proposed a hypothesis relating to dispersion centers where the density of individuals decreases as one moves further from the dispersal center, such as a nest or colony. The results of this study indicate that rattlesnake density does decrease as the distance from the hibernaculum increases and suggest that rattlesnakes may migrate in order to forage in areas where the density of conspecifics is lower. Although rattlesnakes do not defend fixed territories like many birds or mammals, they may avoid foraging in areas where conspecifics are already present, as both intra- and interspecific competition for prey can occur in snakes (Himes 2003).

The presence of potentially competitive interactions may also explain why many rattlesnakes, including all those moving over 1.5 km from their hibernaculum, directed their movements away from Big Creek, or at least away from the opposite hibernacula. Because all the hibernacula in this study were located within 1.5 km of each other and on opposite sides of Big Creek, a rattlesnake moving downslope towards Big Creek may not only encounter conspecifics from its own hibernaculum but conspecifics from the other

hibernaculum. If rattlesnakes showed no regard to the presence of conspecifics, I would expect Figure 2.8 to show a high degree of overlap and shorter tails moving away from the hibernacula. Although some overlap was present, the tails were highly skewed. Furthermore, rattlesnakes never travelled past the opposite hibernacula and all long-distance movements were directed away from the opposite hibernacula, suggesting that rattlesnakes are directing their movements away from areas with high densities of conspecifics from other hibernacula.

Topography, vegetation cover type, and the density of conspecifics all appear to influence the movements of prairie rattlesnakes in a mountainous landscape. Topography appears to exhibit the most influence on rattlesnake movements at spatial scales > 3 km from the hibernacula. At these broad scales, high elevation appears to restrict rattlesnake movements, possibly through energetic or environmental constraints. However, within these apparent elevation limits rattlesnakes are capable of moving extensively across the landscape. Vegetation appears to have much less of an effect on rattlesnake movement and no strong restrictive effect. Although rattlesnakes certainly do direct their movements at locating small mammal prey, data from this study suggests that within lower Big Creek, prey is not a limiting resource in regards to movement. Instead, rattlesnakes may be directing their movements away from the hibernacula to avoid potentially competitive interactions with conspecifics.

Other studies have shown that prairie and western rattlesnakes are capable of moving extensive distances up to 20 km (Jorgensen et al. 2008). As such, the question remains of why prairie rattlesnakes in lower Big Creek do not move more than three kilometers from their hibernacula? The wide range of movement distances reported for

these species suggests that these differences are not due to inter- or intraspecific physiological differences but rather differences in the environmental conditions. Within lower Big Creek, rattlesnakes apparently are restricted to elevations below 2000 m in this landscape. Moving > 3 km from the hibernacula would exceed this elevation in many locations. However, by following the bottoms of tributary valleys, rattlesnakes could still move up to five kilometers from their hibernacula before exceeding 2000 m. The effects of topography within this three kilometer distance are probably less influential than the effects of prey availability and conspecific density. However, beyond three kilometers from the hibernacula or above 2000 m elevation, topography appears to become the most restrictive factor.

I hypothesize that rattlesnakes do not move further than three kilometers in lower Big Creek because overwintering sites and prey are located in close proximity and prey resources are readily available. Long distance snake migrations are believed to occur, at least in part, because of a spatial separation between suitable overwintering habitat and summer foraging habitat (Gregory 1984, Gregory et al. 1987). In contrast, an overlap of overwintering sites and summer foraging habitat can lead to shorter movements and smaller activity areas (Reed and Douglas 2002). Indeed, the movement rates of Grand Canyon rattlesnakes (*C. o. abyssus*) reported by Reed and Douglas (2002) were very similar to the core foraging area movement rates in this study (Chapter 1). Given the observations of feeding throughout the activity season at varying distances from the hibernacula, this study suggests that rattlesnakes in lower Big Creek simply do not need to move far in order to acquire prey resources. However, because of the potential for intraspecific competition near communal hibernacula, rattlesnakes may choose to move

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longer distances in order to have more exclusive access to foraging areas. Future

researchers should give greater attention to the effects of intraspecific competition in

snakes in order to evaluate its importance relative to prey availability and other resources

in influencing rattlesnake movement patterns.

Table 2.1. Spearman's rank correlation coefficient matrix for topographic variables used in the topographic resource selection analysis for prairie rattlesnakes (*Crotalus. v. viridis*) in lower Big Creek.

Landscape Scale	Water	CON99	CON33	Deg. E	Deg. N	Slope
Elevation	0.7747	0.1719	0.1089	-0.0166	-0.0878	0.0723
Slope	0.0805	0.0473	0.0301	-0.0255	0.0369	
Deg. N	-0.0999	0.0109	0.0034	-0.0062		
Deg. E	0.0840	-0.0052	-0.0141			
CON33	0.1018	0.7828				
CON99	0.1627					

Home Range Scale	Water	CON99	CON33	Deg. E	Deg. N	Slope
Elevation	0.5992	0.3140	0.1734	-0.1108	0.1069	0.4725
Slope	0.3315	0.1822	0.0973	-0.0581	-0.0347	
Deg. N	-0.1809	0.1109	0.0459	-0.0135		
Deg. E	-0.0130	-0.0259	-0.0222			
CON33	0.1459	0.7715				
CON99	0.2398					

Table 2.2. Description of vegetation cover types in lower Big Creek used in analyzing

prairie rattlesnake (*Crotalus v. viridis*) cover type selection.

Habitat Class	Description
Bunchgrass	Open slopes of grasses, primarily composed of bluebunch wheatgrass, Idaho fescue, and smaller amounts of cheatgrass. May contain scattered patches of talus or small rock outcrops
Burned conifer	Primarily Douglas fir 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, pinegrass, and cheatgrass. May contain scattered patches of talus or small rock outcrops
Unburned conifer	Primarily Douglas fir and ponderosa pine 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, Rocky Mountain maple, alder, chokecherry, raspberry, thimble berry, rose, other shrubs and forbs.
Rock outcrops	Large outcrops of rock often containing mountain mahogany or scattered Douglas fir and interspersed with small talus, grass, and shrub patches
Talus	Exposed rock slides with little or no vegetation
Irrigated pasture	Taylor Wilderness Research Station airstrip and pastures that are harvested for hay, most of which are irrigated and grazed by research station stock.
Non-irrigated pasture	An old pasture which no longer receives irrigation and is not grown for hay but is grazed by research station stock during the spring
Water/sandbar	Open water of Big Creek and Rush Creek and associated bare sandbars.

Table 2.3. Topographic selection models for 20 prairie rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage April-September 2008 at the landscape (three kilometer buffer) scale.

Model	K	-2ln(log-likelihood)	AIC	AIC_c	ΔAIC_c	AIC_c weight (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 2.4. The best supported topographic selection models at the landscape (three kilometer buffer) and home range scale for 20 prairie rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage April-September 2008. In the lower table, + indicates that the 95% confidence intervals for the model averaged parameter estimates exceed zero, - indicates they are less than zero, and NS indicates that they overlap zero.

Landscape (Three Kilometer Buffer) Model					
	Estimate	SE	p-value	Odds Ratio	Parameter Weights
ELEV	-0.0033	0.0002	<0.0001	1.00	1.0000
SLOPE	-0.0308	0.0037	<0.0001	0.97	1.0000
DEGN	0.0034	0.0007	<0.0001	1.00	0.9993
DEGE	-0.0005	0.0008	0.541	1.00	0.9993
CON99	0.0346	0.0104	0.0009	1.04	0.9707

Home Range Model (Model Averaged)					
	Estimate	SE	Confidence Interval	Odds Ratio	Parameter Weights
DEGN	0.0140	0.0009	+	1.01	1.0000
DEGE	0.0094	0.0016	+	1.01	1.0000
ELEV	-0.0039	0.0006	-	1.00	1.0000
CON33	-0.2842	0.1137	-	0.75	0.7684
SLOPE	-0.0097	0.0071	NS	0.99	0.5115

Table 2.5. Topographic selection models for 20 prairie rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage April-September 2008 at the home range scale.

model	K	-2ln(log-likelihood)	AIC	AIC_c	ΔAIC_c	AIC_c weight (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
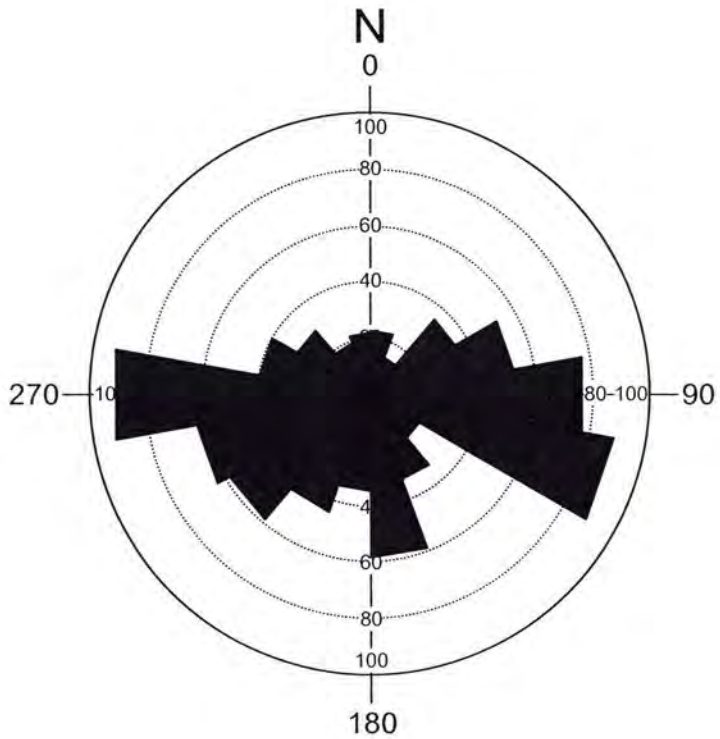
Figure 2.1. A circular frequency distribution showing the distribution of aspect at the telemetry observations of 20 prairie rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage from April-September 2008.
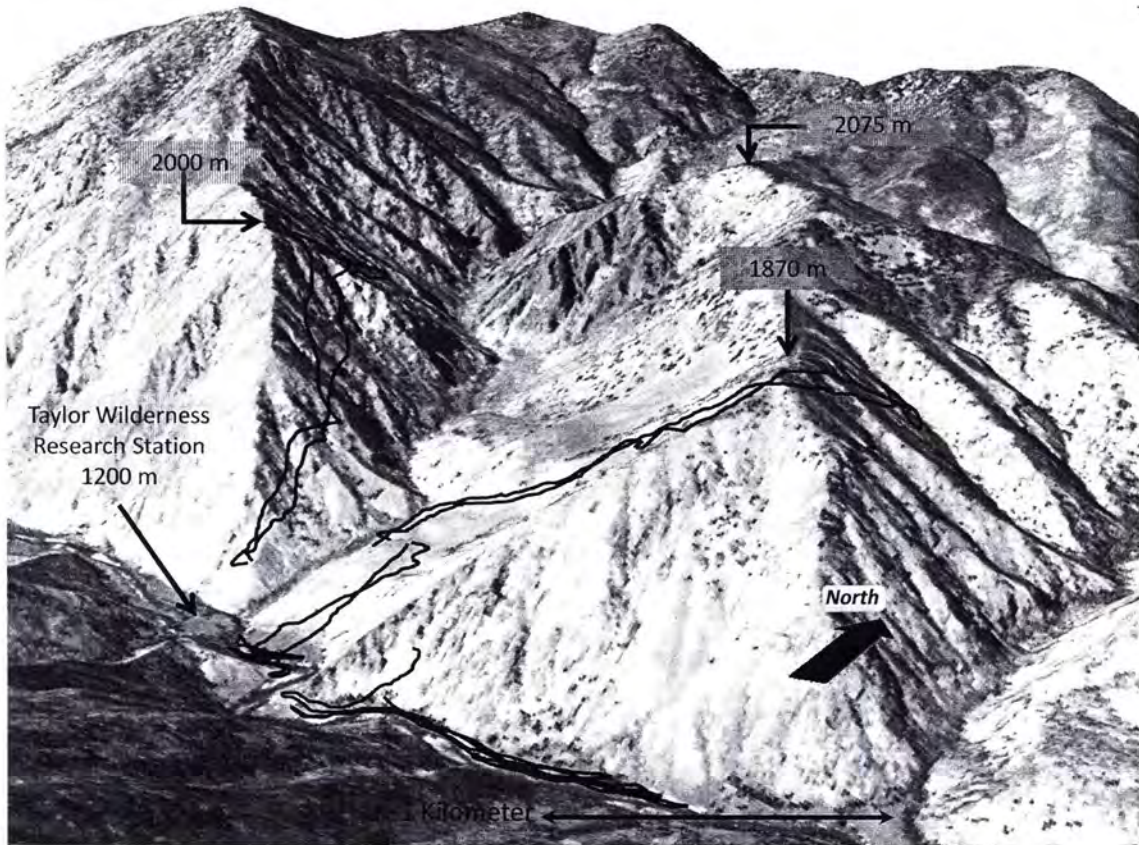
Figure 2.2. The movements of 2 male and 2 nonpregnant female prairie rattlesnakes

(*Crotalus v. viridis*) in the lower Big Creek drainage of central Idaho from April-

September 2008 display the range of topographic features traversed.
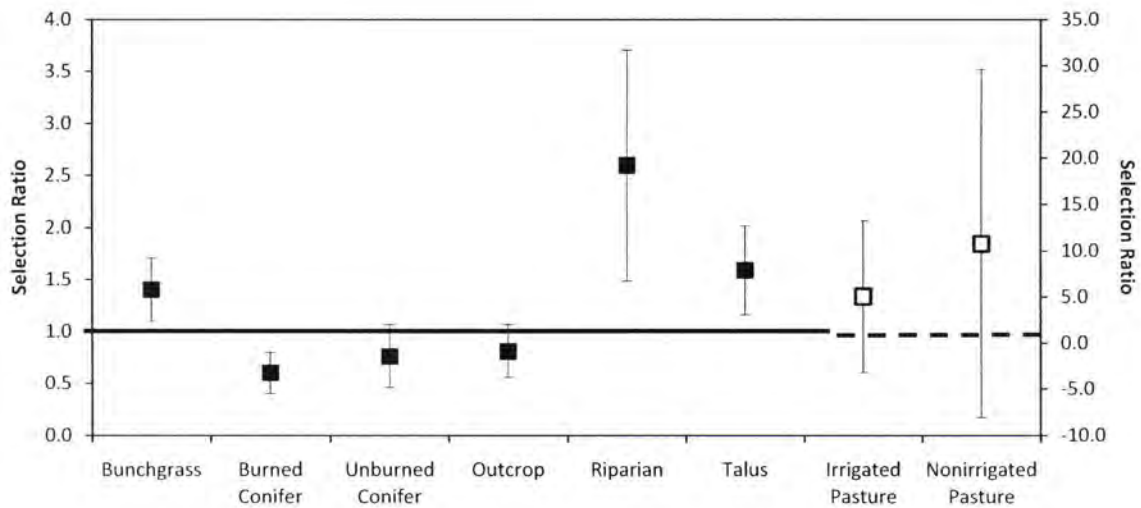
Figure 2.3. Mean landscape scale (i.e., three kilometer radius buffer) selection ratios and 95% confidence intervals for 20 prairie rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage April-September 2008. Selection ratios that are < 1 and whose confidence intervals do not overlap one indicate avoidance of that cover type while selection ratios that are > 1 and whose confidence intervals do not overlap one indicate selection for that cover type. Confidence intervals that overlap one indicate use proportional to availability. Solid squares are mean selection ratios for bunchgrass, burned conifer, unburned conifer, outcrop, riparian, and talus and correspond to the left y-axis while open squares are mean selection ratios for irrigated pasture and nonirrigated pasture and correspond to the right y-axis. The solid and dashed horizontal lines indicate one for the left and right y-axis, respectively.

Figure 2.4. Mean home range scale (95% FK) selection ratios and 95% confidence intervals for 20 prairie rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage April-September 2008. Selection ratios that are < 1 and whose confidence intervals do not overlap one indicate avoidance of that cover type while selection ratios that are > 1 and whose confidence intervals do not overlap one indicate selection for that cover type. Confidence intervals that overlap one indicate use proportional to availability. Solid squares are mean selection ratios for bunchgrass, burned conifer, unburned conifer, outcrop, riparian, and talus and correspond to the left y-axis while open squares are mean selection ratios for irrigated pasture and nonirrigated pasture and correspond to the right y-axis. The solid and dashed horizontal lines indicate one for the left and right y-axis respectively.

Figure 2.5. Mean foraging core area selection ratios and 95% confidence intervals for 20 prairie rattlesnakes (*Crotalus v. viridis*) in the lower Big Creek drainage April-September 2008. Selection ratios that are < 1 and whose confidence intervals do not overlap one indicate avoidance of that cover type while selection ratios that are > 1 and whose confidence intervals do not overlap one indicate selection for that cover type. Confidence intervals that overlap one indicate use proportional to availability.

Figure 2.6. Variation in small abundance, measured using tracking tubes, among vegetation cover types in the lower Big Creek drainage June-September 2008. Error bars represent ± 1 standard error.

Figure 2.7. Frequency distributions of maximum distances moved from the hibernacula

(open bars) and expected snake density (closed bars) for 22 prairie rattlesnakes (*Crotalus*

v. viridis) in the lower Big Creek drainage April-September 2008.

Figure 2.8. Frequency distribution of expected rattlesnake density using the maximum

distance moved from the hibernacula for prairie rattlesnakes (*Crotalus v. viridis*) in the

lower Big Creek drainage April-September 2008 while taking into account the mean

bearing of the outbound migration in relation to Big Creek and other hibernacula. The

open and dark triangles beneath the x-axis indicate the position of the southern and

northern hibernacula complexes, respectively. The point at which the lines intersect

represents Big Creek. Figure 2.8(A) includes all 22 rattlesnakes radio tracked in 2008

while Figure 2.8(B) excludes one individual that was not from the three primary

hibernacula complexes and an individual that moved 2.24 km from the hibernaculum

downstream along Big Creek. Those individuals are denoted by (*) and (**),

respectively.

Figure 2.9. Circular-linear histograms display the mean bearing of outbound migration

for prairie rattlesnakes (*Crotalus v. viridis*) from the northern and southern hibernacula

complexes in the lower Big Creek drainage, Idaho. Each arrow represents one rattlesnake

and the length of the arrow equals the maximum distance moved from the hibernaculum.

The solid black line is the mean migration bearing for the rattlesnakes from that

hibernaculum. Figure 2.9(A) and (B) includes all rattlesnakes radio tracked from the

northern and southern complexes in 2008 while Figure 2.9(C) excludes one individual

that was not from the three primary hibernacula complexes and an individual that moved

2.24 km from the hibernaculum downstream along Big Creek. Those individuals are

denoted by (*) and (**), respectively.

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Ecology of a Population of Prairie Rattlesnakes (*Crotalus v. viridis*) in the Frank
Church River of No Return Wilderness, Central Idaho

INTRODUCTION

The prairie and western rattlesnakes (*Crotalus viridis and C. oreganus*) have
some of the broadest distributions of North American pitvipers. These species were
formally classified as a single species (*Crotalus viridis*) but have since been split into an
eastern (*viridis*) and western (*oreganus*) clade (Pook et al. 2000, Ashton and de Quiroz
2001, Douglas et al. 2002), although the taxonomic status of many of the *oreganus*
subspecies remains unresolved (Douglas et al. 2002). Collectively, their distributions
extend from southern Canada to the American Southwest and the Pacific Ocean to the
Mississippi River (Stebbins 2003, Conant and Collins 1998). Such an extensive
distribution provides an excellent opportunity for comparing ecological traits among
populations. The morphology (Ashton 2001), movement patterns (Jorgenson et al. 2008),
reproductive ecology (Aldridge and Duvall 2002, Jenkins et al. 2009) have been
compared among multiple populations of prairie and western rattlesnakes. When
conducting hypothesis driven research, researchers may not record or report basic natural
history data for their study populations (e.g., population size, predation, reproductive
characteristics). Although such data may not be pertinent to the questions addressed in
some studies, not reporting basic population data may inhibit future attempts to better

understand the ecology of a wide ranging species through literature reviews or meta-analyses.

Although the prairie rattlesnake is primarily associated with the grasslands of the Great Plains, they may occur in a diversity of habitats, including sagebrush shrub-steppe, pinon-juniper woodlands, and montane woodlands (Campbell and Lamar 2004). Within Idaho, the prairie rattlesnake has a very restricted distribution, occurring in the upper Salmon River drainage in the central part of the state (Nussbaum et al. 1983). Much of its Idaho distribution encompasses very mountainous landscapes, including the Frank Church River of No Return Wilderness, the largest designated wilderness area in the lower 48 states. This environment provides a unique opportunity to study the ecology of the prairie rattlesnake in an environment that is atypical of most of its distribution. This area's status as a designated wilderness also provides a high measure of protection from human disturbance. The purpose of this appendix is to present basic population ecology data that was collected during the course of a three year study of prairie rattlesnake movement and habitat ecology and to compare these data to similar data collected for other populations of the *C. viridis* complex.

STUDY AREA

I conducted this study in the lower Big Creek drainage of the Frank Church-River of No Return Wilderness in central Idaho (Figure 1.1). My field work was based out of the University of Idaho's Taylor Wilderness Research Station (TWRS). The topography of the lower Big Creek drainage is characterized by steep valleys and high ridges (1100-

2780 m in about 4.8 km). Southerly aspects support xeric bunchgrass communities while northerly aspects support Douglas fir (*Pseudotsuga menziesii*) forests. Riparian vegetation is prevalent along Big Creek and its tributaries. Exotic cheatgrass (*Bromus tectorum*) is also present throughout lower Big Creek. Large fires burned much of the lower Big Creek drainage in August 2000 and July 2006 and the effects of the fire are still clearly seen. Additional details of the study area are provided in Chapters 1 and 2.

Most rattlesnakes used in this study overwintered in three hibernacula complexes within 1.5 km of each other and within 800 m of the TWRS. These complexes consist of clusters of overwintering snakes within scattered talus patches or rock outcrops on bunchgrass slopes. All snakes overwintered 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 occurred on an east aspect (mean aspect = 101°) between 1327 and 1420 m elevation. The first northern complex included two disjunct talus patches, one on a southwestern aspect (mean aspect = 226°) between 1271 and 1305 m and the second on a south-southeast aspect (mean aspect = 156°) between 1304 and 1321 m. The second northern complex was located on a southeast aspect (mean aspect = 149°) between 1235 and 1269 m. One rattlesnake overwintered solitarily north of Big Creek in the south facing junction of a rock outcrop complex and talus slide at 1264 m.

METHODS

Rattlesnakes were captured near the hibernacula 28 April-1 May 2006, 2 May & 8-10 May 2007, and 16 April-23 May 2008. Differences in these dates were due to

logistical issues and do not necessarily correspond to differences in emergence times. Each captured rattlesnake was brought back to the TWRS and was weighed, measured (snout-vent [SVL] and tail length [TL]), sexed by the presence of hemipenes, and marked with a Passive Integrated Transponder (PIT) tag (Biomark Inc., Boise, Idaho). The basal rattle segment was painted with an acrylic craft paint to identify marked snakes in the field and determine the frequency of shedding. Neonates were marked by painting their button a unique color combination. Pregnant females were identified by palpating for follicles. I estimated the number of follicles in each pregnant female. Rattlesnakes were continuously captured throughout the summer and unmarked rattlesnakes captured during the summer were processed as described above. All snakes were released at their original capture site unless they were captured on the TWRS. In these cases, rattlesnakes were moved off the TWRS (100-800 m from their original capture site) to minimize potentially negative encounters with field station personnel.

I conducted a series of analyses to describe the characteristics of this population and allow for comparisons with other studies. I compared SVL and TL between males and females and mass between males and nonpregnant females using a non-parametric Mann-Whitney U test. When multiple measurements were present for one individual, I used the first set of measurements in this analysis to minimize the effects of summer weight fluctuations. I compared mass, SVL, and TL between rattlesnakes over-wintering on the north side of Big Creek and those over-wintering on the south side of Big Creek. I used a Chi-square goodness of fit test to test for equal sex ratios between adult and juvenile males and females. Shedding rate for snakes captured during spring searches was calculated as the number of sheds per year. I calculated the percent change in body mass

for telemetered rattlesnakes in 2008 by dividing the change in initial body mass at the end of the activity season by their initial body mass. Because the hibernacula were monitored throughout the spring and fall in 2008, I was able to estimate spring emergence and fall retreat dates. I counted the spring emergence date as the capture date for non-telemetered snakes captured at the hibernacula or the first day after which a telemetered snake began consistent travel away from its hibernaculum. The date of fall retreat was counted as the first date a snake was captured at a hibernaculum in late September. I compared the mean emergence date among males, non-pregnant females, and pregnant females using an analysis of variance (ANOVA). All means are reported ± one standard error. Unless otherwise noted, all statistical analyses were conducted in SAS 9.1 (SAS Institute, Carey, NC).

RESULTS

I captured and marked 98 adult and juvenile rattlesnakes between August 2005 and September 2008. Only two neonates were captured during this study (15 and 30 July 2008). Thirty one snakes were recaptured at least once for forty five recaptures. Fifty three males and forty five females were captured and marked during this study. Thirty seven rattlesnakes were captured and marked from the southern hibernacula complex and 22 from primary northern complex during this study. Four were captured and marked from the secondary northern complex in 2008. The sex ratio of males to females was not significantly different from 50:50 (1:0.85, $X^2 = 0.50$, df = 1, p = 0.4795). Nine gravid females were captured and marked during this study, making up a mean of 16% of the

females captured each year. Six of these were captured in 2008, making up 26% of the females captured that year. The mean number of follicles was 5.7 (range 4-10).

Males were typically larger than females, having significantly higher body mass (264 g $\pm$ 19.3 vs. 199 g $\pm$ 14.4, $Z = -2.70$, $p = 0.0069$) and significantly longer tails (6.0 cm $\pm$ 0.19 vs. 4.01 cm $\pm$ 0.09, $Z = -6.86$, $p = <0.0001$). Males also tended to have longer SVL than females (74.4 cm $\pm$ 2.1 vs. 71.0 cm $\pm$ 1.4, $Z = -1.94$, $p = 0.0521$). There was no significant difference in mass ($Z = -0.5629$, $p = 0.5735$), SVL ($Z = -1.23$, $p = 0.2192$), or tail length ($Z = -0.3143$, $p = 0.7533$) between rattlesnakes overwintering on the north and south sides of Big Creek. Mean shedding rate was 1.3 sheds per year. Sixteen snakes (39%) shed twice in one year while one individual (a male in 2008) did not shed at all.

Emergence dates in 2008 ranged from 17 April-29 May with a mean date of 4 May $\pm$ 1.3 days ($n = 46$). Forty three percent of these rattlesnakes emerged between 3 May and 6 May. Pregnant females emerged significantly earlier than males (26 April $\pm$ 3 days versus 7 May $\pm$ 2 days, $F_{2,43} = 3.91$, $p = 0.0276$) but not non-pregnant females (3 May $\pm$ 1 day). Ingress ranged from 19 Sept-28 Sept although two of the 13 snakes with transmitters at the end of September had not yet reached their hibernacula. Mean ingress date was 25 September $\pm$ 0.7 days ($n = 21$). I was unable to record emergence dates in 2006 and 2007 because of short spring hibernacula searches.

DISCUSSION

This study is one of the first to report data on the population ecology of rattlesnakes in a designated wilderness area although other studies have been conducted

on rattlesnakes in large protected lands (Cobb 1994, Jenkins et al. 2009). The numbers of rattlesnakes captured in this study were less than those reported from some rattlesnake studies in the intermountain west (Hirth et al. 1969, Macartney and Gregory 1988, King and Duvall 1990, Diller and Wallace 2002, Jenkins et al. 2009). However, rattlesnakes in these populations overwinter communally in large numbers (i.e., hundreds of snakes). In lower Big Creek, I captured less than 40 rattlesnakes at each hibernaculum over a three year period. However, these numbers were comparable to those reported for communally denning midget faded rattlesnakes (*Crotalus o. concolor*) in southeast Wyoming (Parker and Anderson 2007). There was also some evidence of solitary overwintering in this study. Solitary denning, or denning in small groups, is often seen in rattlesnakes in relatively mild climates, such as the American southwest, where suitable hibernacula may be less limiting (Fitch 1949, Klauber 1972, Beck 1995, Reed and Douglas 2002, Dugan et al. 2008). Given the abundance of rocky, south facing habitat within the lower Big Creek drainage, suitable overwintering habitat is likely not limiting in this system. This probably contributed to the relatively low numbers of rattlesnakes captured at each hibernaculum and the single observation of solitary denning.

Although the sex ratio in this study was slightly male biased, this difference was not significant. Sex ratios in snakes are typically equal at birth (Klauber 1972, Shine and Bull 1977, Parker and Plummer 1991) but differential mortality later in life can result in skewed sex ratios. Female biased sex ratio were reported for midget faded rattlesnakes (Ashton and Patton 2001, Parker and Anderson 2007) while other studies on prairie and western rattlesnakes reported equal sex ratios (King and Duvall 1990, Diller and Wallace 2002) or both male and female biased ratios (Jenkins et al. 2009). Klauber (1972)

reported male biased sex ratios in assessing over 12,000 rattlesnakes. An equal sex ratio suggests that there are no strong differences in male or female mortality in my study population.

Of the 27 adult rattlesnakes that were monitored with radio telemetry for at least one field season, only three mortalities were recorded (11%). Potential predators of adults in this area include golden eagles (*Aquila chrysaetos*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*), although these species typically do not regularly prey on rattlesnakes (Klauber 1972). Red-tailed hawks are known to prey on rattlesnakes (Fitch 1949 but see Grothe 1992) but are very rare in lower Big Creek (personal observation). One telemetered male was probably killed by an avian predator in late April 2008 as the transmitter was found alone on the surface >280 m from the hibernaculum while all other telemetered rattlesnakes were still at the hibernacula. Another telemetered male died during the winter of 2007 and second was apparently killed in the fire of July 2006. Human mortality was fairly common in the past along Big Creek from hunters and outfitters but human mortality appears to have declined substantially in recent years (J. Akenson, personal communication).

The ratio of pregnant to non-pregnant females over multiple years can provide an indication of the interval length between litters although this value can be highly variable among years (Parker and Anderson 2007). Prairie and western rattlesnakes often reproduce every two to five years (Diller and Wallace 1984, Macartney and Gregory 1988, Cobb 1994, Graves and Duvall 1993, Jenkins et al. 2009). The frequency of reproduction is largely determined by the ability of the female to replenish her fat reserves (Seigel and Ford 1987, Duvall et al. 1992, Gregory 2006). In this study, only

16% of the females captured were pregnant which corresponds to roughly a six year reproductive cycle. However, most pregnant females were captured in the spring of 2008 when I was able to monitor emergence throughout the spring. Pregnant females emerged earlier than males and nonpregnant females and the short length of the spring hibernacula searches in 2006 and 2007 probably contributed to the low number of pregnant female captures. Although the data from 2008 suggests a four year reproductive cycle, caution should be used in interpreting these data because of the low numbers of pregnant females captured and the short duration of this study.

Sexual size dimorphism was observed in this study and is common among rattlesnakes (Duvall and Beaupre 1998). Males are typically larger in snake populations where male-male combat occurs (Shine 1994). Although I did not observe any male-male combat, this behavior has been reported in other rattlesnake populations (Beaupre and Duvall 1998, Aldridge and Duvall 2002), including Great Basin rattlesnakes (*C. o. lutosus*) in southeast Idaho (C. Peterson, personal communication). Alternatively, Taylor and DeNardo (2008) suggested that sexual size dimorphism in western diamondback rattlesnakes (*C. atrox*) is due to differences in energy intake between sexes. Large male size may simply be a result of greater allocation of energy to growth while females must devote more energy to reproduction.

The reproductive ecology of prairie rattlesnakes in lower Big Creek is very similar to that of Great Basin rattlesnakes at hibernacula with relatively low levels of habitat disturbance and higher prey availability (Jenkins 2007, Jenkins et al. 2009). In his study on the Idaho National Laboratory in the sagebrush-steppe of southeast Idaho, Jenkins found that rattlesnakes from hibernacula in areas of lower disturbance (i.e., fewer

wildfires or grazing) had higher body condition and greater reproductive output than rattlesnakes from hibernacula in more disturbed areas. Although my study size suffered from small sample sizes, the similarities between our studies should be expected given that both of our studies included populations in large protected lands with little habitat disturbance.

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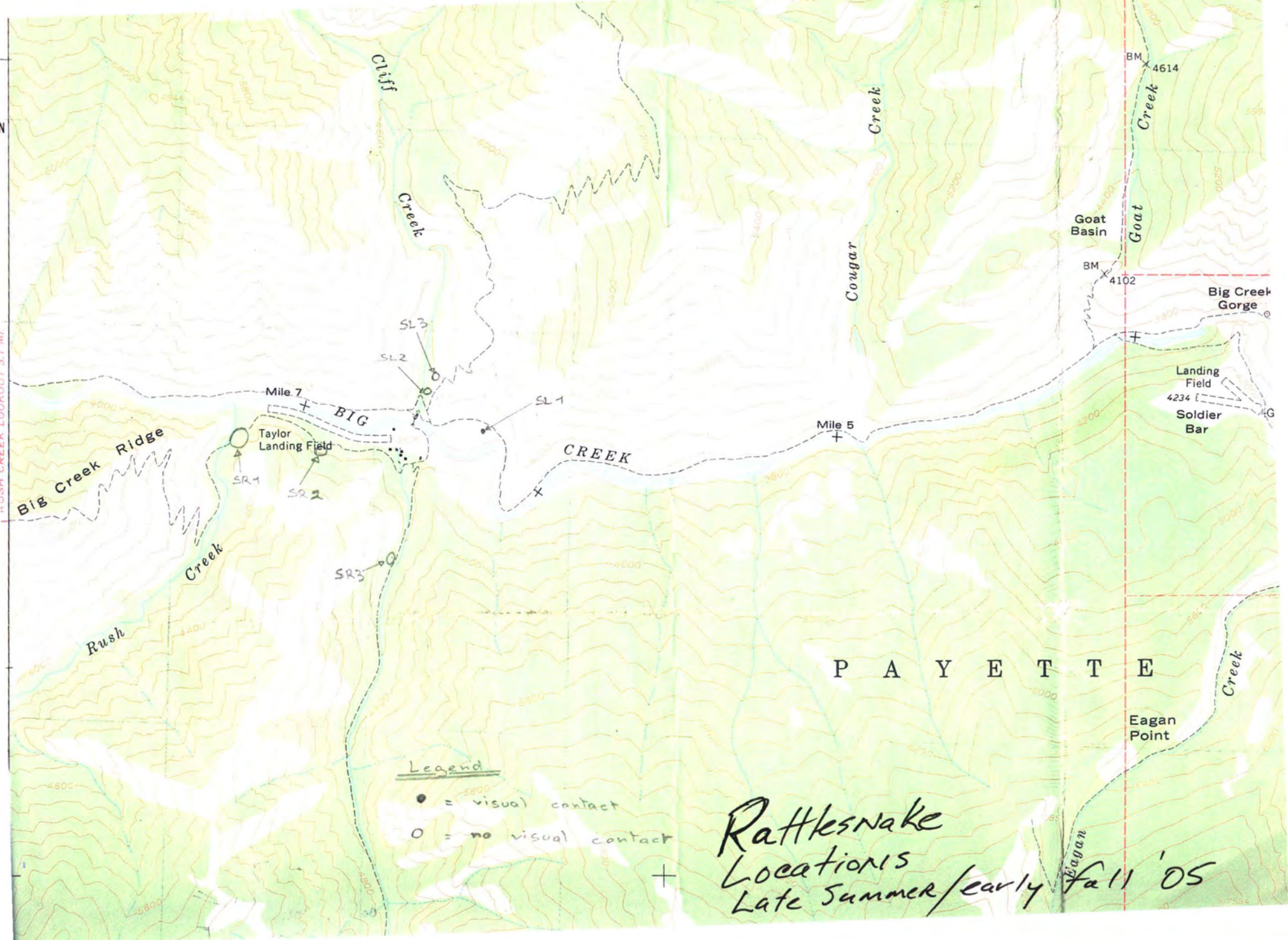Fitch, H. S. 1949. Study of snake populations in central California. American Midland Naturalist 41:513-579.

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Cliff

Creek

Creek

Cougar

Goat
Creek

BM ×4614

Goat
Basin

BM ×4102

Big Creek
Gorge

SL3

SL2

Mile 7

SL1

BIG

Taylor
Landing Field

SR1

SR2

SR3

CREEK

Mile 5

Landing
Field
4234

Soldier
Bar

G

Big Creek Ridge

Rush

Creek

Legend

● = visual contact

O = no visual contact

P A Y E T T E

Creek

Eagan
Point

Eagan

Rattlesnake
Locations
Late Summer/early Fall '05

Taylor Ranch

From: "Javan Bauder" <baud4576@uidaho.edu>
To: "Taylor Ranch" <tayranch@direcway.com>
Sent: Wednesday, September 28, 2005 2:32 PM
Subject: Re: data sheet?

If you would like to print out the data sheets and mail them to me, my dorm address is:
MSC 1853
1080 W 6th St
Moscow, ID
83843
Or you can fill them out electronically and email them back. If you don't have data for one of the fields (like habitat) don't worry about it. Date, time, and UTM coordinates are the important fields.
Thanks again
Javan

----- Original Message -----
From: Taylor Ranch <tayranch@direcway.com>
Date: Wednesday, September 28, 2005 8:01 am
Subject: data sheet?

> Javan,
>
> We still have not received a rattlesnake monitoring data form from
> you. If you want others to collect quality data for you, you must
> provide a data sheet to standardize data collection. Please email
> one to us as soon as possible, so Patrick can fill out forms for
> all the observations he has made to date. The Rush Creek snake
> has moved to Pioneer Creek and the Lower Pasture snake has moved
> to Cliff Creek.
>
> Holly
>
> Jim and Holly Akenson
> Managers/Scientists
> Taylor Ranch Field Station
> HC83 Box 8070
> Cascade, Idaho 83611
>