

**Habitat use and movement patterns of the  
Northern Pacific Rattlesnake  
(*Crotalus o. oregonus*)  
in British Columbia**

by

Liumila Michelle Gomez  
Bachelor of Natural Resource Science,  
Thompson Rivers University, 2002

A Thesis Submitted in Partial Fulfillment of the  
Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

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**Abstract**

The selective use of habitat is a fundamental aspect of ecology, and differential patterns of habitat use reflect the underlying cues that guide selection. I assessed the habitat use and movement patterns of Northern Pacific Rattlesnakes (*Crotalus o. oregonus*) during the summers of 2005 and 2006 near Kamloops British Columbia, Canada. Contrary to my expectations, rattlesnakes used upper - elevation forested habitat when available and traveled farther from the den than previously reported for this species. Though the distance and orientation of travel differed among individuals, there was an apparent trend for snakes from one site to travel farther from the den than snakes from a second site. Snakes often were associated with structurally stable cover objects and small mammal sign in microhabitats with less canopy cover than otherwise available. Results from this study have implications for management and conservation of the Northern Pacific Rattlesnake.

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## **CHAPTER ONE: GENERAL INTRODUCTION AND BACKGROUND**

An understanding of where animals are found, and why, is central to the study of wildlife ecology. The habitat or environment that an animal occupies and with which it interacts shapes the animal's ecology and has evolutionary consequences. Habitat, as defined by Hall et al. (1997), includes the resources and conditions present in an area. Studies of habitat use measure both used and available habitats to obtain a quantitative estimate of the probability that an animal will select a specific habitat relative to another available habitat (Manly et al. 2002).

Ultimately, the goal of many habitat studies is to predict animal occurrence given specific habitat features. An ideal predictive tool can distinguish habitat from non-habitat using relatively few, easily measured features (Burnham and Anderson 2002). For comparison between studies, the features that are used to predict the probability of habitat use should be selected from four spatial scales (Hall et al. 1997; Johnson 1980).

It is challenging to identify and describe the habitats used by animals in rapidly changing environments. Worldwide, species are being extirpated as a direct result of human activities. Thus, results from habitat selection studies are increasingly important for managers for making informed decisions that might mitigate the impact of human activities on wildlife and its habitat.

The aim of my research was to identify and describe the habitat use and movement patterns exhibited by mature male rattlesnakes during the summer active season (Figure 1). The Northern Pacific Rattlesnake (*Crotalus o. oregonus*) typically is associated with dry habitats (Matsuda et al. 2006). Shelter from winter weather extremes is important for the survival of Northern Pacific Rattlesnakes at northern latitudes and hibernation occurs between October and March (Macartney 1985). Foraging on voles and mice occurs primarily during the spring and summer, and mating occurs in late summer (Macartney 1989; Macartney et al. 1990). Reproductive condition affects the habitats used by Northern Pacific Rattlesnakes (Charland and Gregory 1989; Macartney 1985). Adult male and non-gravid female rattlesnakes venture several kilometers from the den during the summer, but gravid females remain close to the den during the summer

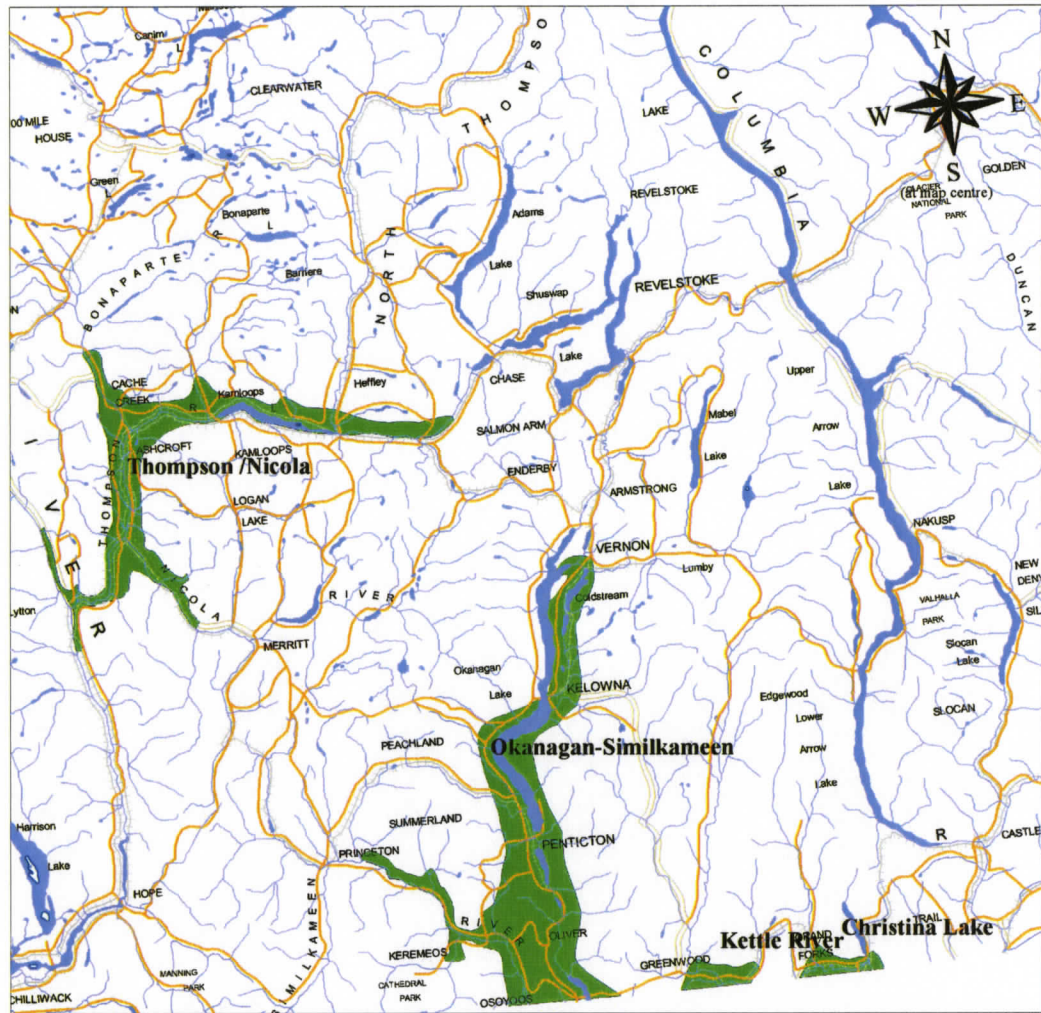
months (Macartney 1985). Since females follow a multi-year reproductive cycle, the patterns of movement and habitat use of individual females will fluctuate between years.

Habitat use varies between populations within the same species (Reinert 1984a; Reinert 1984b). Thus, it is important that the patterns of habitat use exhibited by multiple individuals from multiple populations be examined. The range of the Northern Pacific Rattlesnake extends from California to the southern interior of British Columbia (Ashton and de Queiroz 2001). In Canada, the Northern Pacific Rattlesnake occurs in two geographically isolated regions: 1) the Thompson- Nicola, 2) Okanagan-Similkameen, Kettle, and Granby regions (Matsuda et al. 2006, Figure 2). I studied populations in the Thompson-Nicola region. I selected two study sites in close proximity to Kamloops, British Columbia (Figure 3). The distance between these sites was approximately 25 kilometers, well beyond the maximum distance known to be moved by Northern Pacific Rattlesnakes from their hibernation sites in summer (Bertram et al. 2001; Macartney 1985).



**Figure 1. Northern Pacific Rattlesnake, *Crotalus o. oreganus*. Photo provided by A. Burianyk**



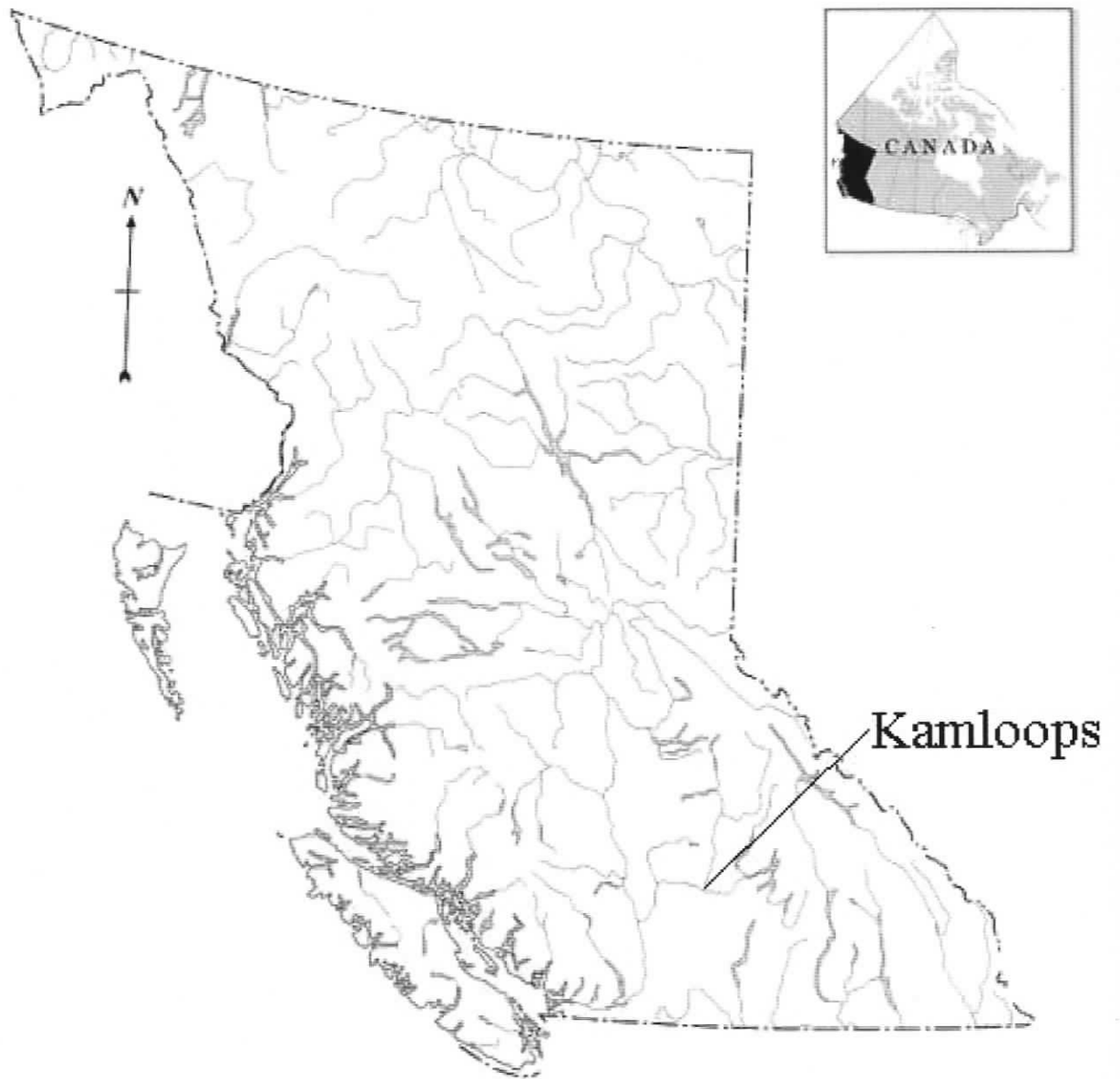


1:2,000,000

20 0 20 Kilometers

Western Rattlesnake Range in BC

**Figure 2. Distribution (solid green) of the Northern Pacific Rattlesnake (*Crotalus oregonus*) in British Columbia (Hobbs 2003).**

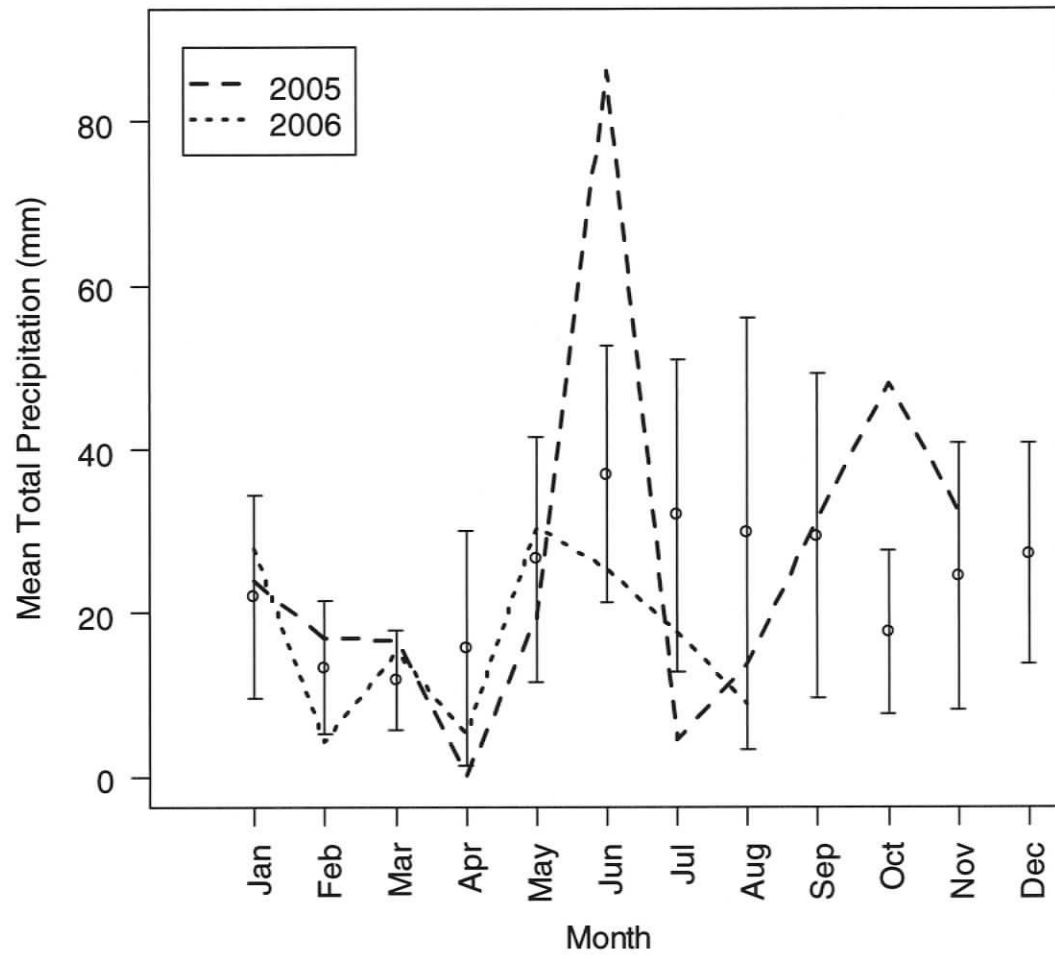


**Figure 3. Study sites were located within 25km of Kamloops, British Columbia**

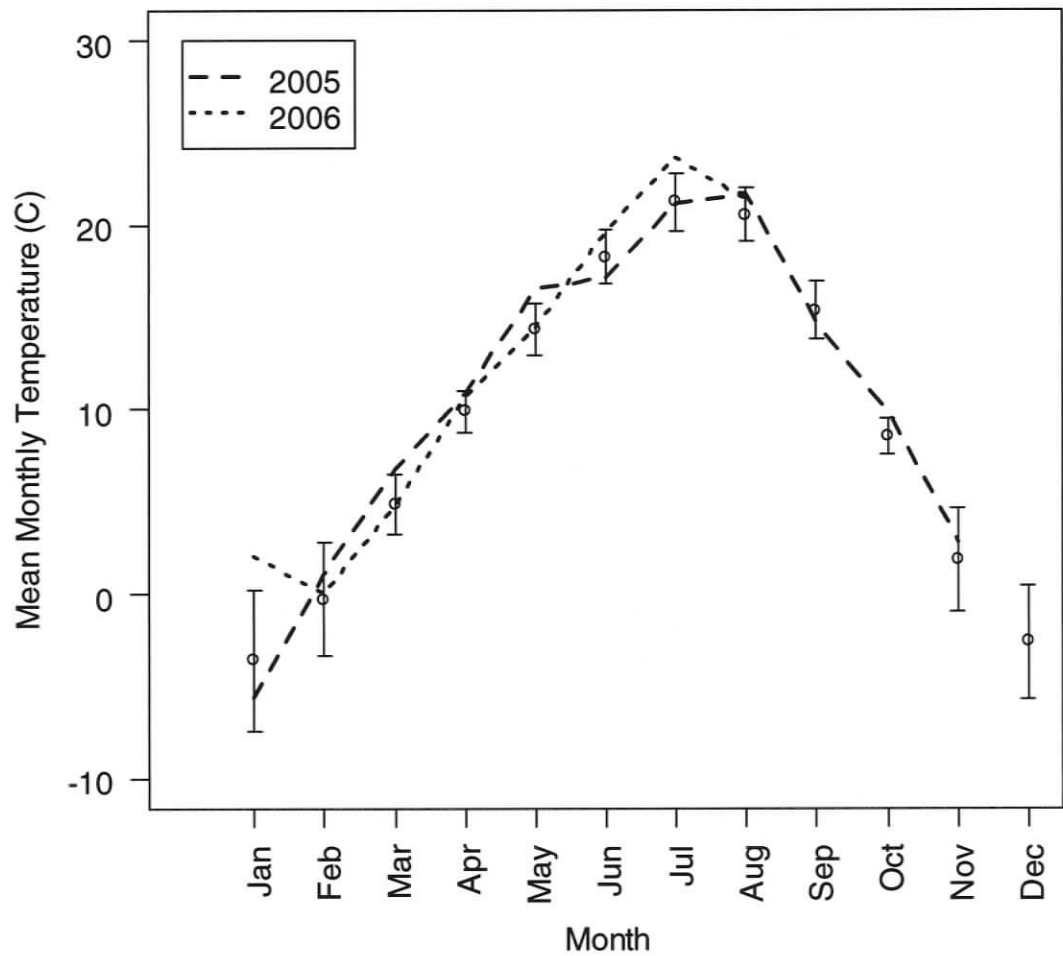
Site 1 was composed of 27% Bunchgrass, 35% Ponderosa pine and 38% Interior Douglas-fir biogeoclimatic zones (Meidinger and Pojar 1991). The topography at site 1 generally was rugged with abundant bedrock outcrops on steep, south-facing slopes. Elevation at site 1 ranged from 350m to 1350m. There was a well-developed shrub and grass layer in the lower elevations of site 1, and the higher elevations were composed of grass, shrub and tree layers. A portion of this site was designated as a wildlife management area and proposed wildlife habitat areas encompass the rattlesnake hibernacula at this site. Timber harvest has been conducted in the higher-elevation forested areas and, most recently, there has been widespread salvage of beetle-killed timber. Secondary gravel roads provided access to, but did not transect this site. Forested areas were grazed by cattle during the summer.

Site 2 was located entirely in the Bunchgrass biogeoclimatic zone (Meidinger and Pojar 1991). It was composed of open, rolling grasslands at approximately 550m elevation with well-developed grass and shrub layers and limited tree cover. Site 2 was owned by the Crown, private landowners and the municipality of Kamloops. This site encompassed an area of housing developments and a designated area for ATV use. The primary paved road that transected this site was heavily used by the general public, as well as the forest industry. Secondary gravel roads that crossed this site typically experienced relatively low levels of traffic.

The Bunchgrass, Ponderosa Pine and Interior Douglas-fir zones occur at low elevations and receive some of the highest temperatures in British Columbia (Meidinger and Pojar, 1991). The weather (temperature and precipitation) during my two-year study generally was similar to that of the previous 30-year period, but mean monthly total precipitation was higher in June and October 2005 and 2006 (Figure 4) and January 2006 was warmer than average for the Kamloops area (Figure 5).



**Figure 4.** Mean monthly total precipitation (open circles  $\pm$  SD) from the previous 30 years in the Kamloops area (Environment Canada 2006). Differences between precipitation levels during the study and the previous 30 years are evident during June, July and October, 2005.



**Figure 5 . Mean monthly temperature (open circles  $\pm$  SD) from the previous 30 years in the Kamloops area (Environment Canada 2006). January 2005 was warmer and other monthly temperatures were similar to temperatures from the previous 30 years.**

I address my research questions in three chapters. In **Chapter Two** I describe the general patterns of habitat use and movements exhibited by mature male rattlesnakes. I use vegetation type as defined by biogeoclimatic zone to describe habitat use during the active season and present the patterns of movement exhibited by rattlesnakes in relation to those vegetation types. For individuals tracked in both years of the study, I compare their movement patterns between years. In **Chapter Three** I describe the microhabitats used by mature male rattlesnakes. Descriptions of microhabitats include fine-scale features of habitat within a 0.5m-radius circular plot and minimum distances to habitat features within a 30m-radius circular plot. In **Chapter Four** I summarize my results and highlight potential contributions to management of the Northern Pacific Rattlesnake in British Columbia.

**CHAPTER TWO: PATTERNS OF SEASONAL MOVEMENT AND HABITAT  
USE OF THE NORTHERN PACIFIC RATTLESNAKE**

**INTRODUCTION**

The environment can be viewed as an assemblage of habitats and these habitats will be perceived differently by the animals that use them, as well as by human observers. Thus, the study of habitat use by animals is inherently challenging (Lidicker 1999). Furthermore, the complexity of determining habitat use extends to the scale at which observations are made. Johnson (1980) delineated four scales of habitat selection based on the spatial extent at which an animal is able to perceive its environment. First order selection refers to the geographical range of a species, second order determines the home range, third order refers to habitat components within the home range and fourth order pertains to use of items within the components of the third order (Johnson 1980). An animal's habitat requirements and patterns of movement will vary depending on the spatial scale of inquiry and the use of habitat at one scale is dependent upon "decisions" made at other, larger scales (Johnson 1980; Levin 1992). Knowledge of an animal's habitat requirements at large spatial scales determines the scope of further investigation of habitat use at smaller scales (Johnson 1980) and different mechanisms guide selection at each scale (Levin 1992).

Environmental heterogeneity and limited resources are precursors for habitat selection, a process by which individuals preferentially use or occupy a non-random set of habitats (Morris 2003). Thus, the way that an animal interacts with its environment reflects the heterogeneity of habitats and likely the resources they contain. Many studies use movement patterns exhibited by the individual to describe how animals use their surroundings and to identify the habitats used during a predetermined time (Charland and Gregory 1995; Diffendorfer et al. 2006; Marshall et al. 2006). Such observational studies allow the researcher to formulate hypotheses about the causes that underlie patterns of movement through habitats (Garton et al. 2001).

The study of movement patterns provides a description of patterns of habitat use by animals (Gregory et al. 1987). Seasonal movement patterns of many animals take the form of round-trip migrations (Ricklefs 1979). Though migrations are widespread in nature, much of our understanding of the theory of migration has been acquired from studies of birds. According to these studies, migration likely has evolved as a strategy to maximize fitness in a seasonal environment (Alerstam et al. 2003). Migratory behaviour will presumably be exhibited when the benefits of movement outweigh its potentially significant costs. Costs of migration include increased risk of mortality and reduced time and energy available for activities such as reproduction and foraging. Ultimate benefits of migration include increased reproductive output (Alerstam et al. 2003).

Individuals from populations of the same species often exhibit very different types of movement. For example, in birds, some individuals may be nearly sedentary and others migrant (Berthold 1999). The proportion of individuals within a population that migrate or remain sedentary presumably will be influenced by both genetics and by extrinsic factors such as population density and resource availability (Berthold 1999). Parameters used to describe migration, such as maximum displacement, vary along a continuum and differences in these parameters among individuals, populations and species may reflect variable resources (Gregory et al. 1987).

We can apply knowledge of migration gained from studies of birds to other animals. Snakes from northern populations exhibit migratory behaviour (Gregory and Stewart 1975; King and Duvall 1990; Larsen 1987). Migratory behaviour has been noted in several genera of snakes (Duvall et al. 1990; Gregory and Stewart 1975; Madsen and Shine 1996). Within the genus *Crotalus*, much of our knowledge about migration comes from studies of the Prairie Rattlesnake (Duvall et al. 1990; Duvall and Schuett 1997; King and Duvall 1990). Thus, the extent and prevalence of migratory behaviour in northern populations of Northern Pacific Rattlesnakes is largely unknown.

Knowledge of movement patterns and habitat use may be used to mitigate conflict between the habitat requirements of the Northern Pacific Rattlesnake and human populations in the Interior of British Columbia. The Northern Pacific Rattlesnake occupies a restricted range in British Columbia and critical denning habitats occur almost exclusively in the lower elevation grasslands. Grasslands are readily converted for



agriculture and urban development and pressure to convert native grassland habitat continues to increase. To mitigate this potential conflict, managers need to identify the habitats that are used by rattlesnakes so that their preservation may be incorporated into development planning scenarios. Ideally, managers should be able to calculate the probability that a specific habitat will be used by a rattlesnake. To date, three studies have described the habitats occupied by rattlesnakes in British Columbia (Bertram et al. 2001; Brown 2006; Macartney 1985), but none have compared used with available habitat.

I address this knowledge gap with an examination of habitat use and patterns of movement in Northern Pacific Rattlesnakes at two sites near Kamloops, BC. I use Johnson's (1980) second-order of selection to sample vegetation type in areas used and available to rattlesnakes. This comparison of used with available habitat allows me to test whether snakes use habitats randomly. I compare individual patterns of movement by site and, for individuals tracked in both years of the study, I compare movement patterns between years.

For ectotherms such as snakes, factors such as sex and reproductive status often determine the resources that are important to an individual and influence its pattern of movement (Gregory et al. 1987; Madsen 1984; Waldron et al. 2006). Male Canebrake Rattlesnakes (*Crotalus horridus*) in search of mates moved farther between successive locations and moved more frequently than females during the breeding season (Waldron et al. 2006). Movement rates of female garter snakes (*Thamnophis* spp.) differed with reproductive status (Charland and Gregory 1995). Movement rates of gravid females were lower than those of nongravid females. Following parturition, these rates were the same.

I studied only mature, male rattlesnakes, which (a) minimized variability due to sexual differences, and (b) focused my attention on those snakes that were most likely to be consistent, long-distance migrants over a variety of habitats.

## **METHODS**

### **Telemetry**

I used radio-telemetry to study the movement patterns and habitat use of the twelve individual rattlesnakes over time. I captured twelve adult male rattlesnakes at hibernacula in sites 1 and 2. Eight individuals were from site 1 and 4 were from site 2. Some of the animals died ( $n = 3$ ) and others were added ( $n = 2$ ) during the course of my study; therefore, the total number of study animals varied. The radio-transmitters (Holohil Systems Incorporated, Ontario) weighed between 3.2 g and 5.2 g and comprised less than 5% of the snake's body mass. All surgical procedures were carried out by the Animal Health Department at Thompson Rivers University and were approved by the University of Victoria Animal Care Committee.

The veterinarian followed surgical methods outlined by Reinert and Cundall (1982). Prior to implantation, radio-transmitters were disinfected in a solution of Betadine®. Snakes were anaesthetized with 3 to 4% Isoflurane® and the transmitter was implanted in the body cavity through a lateral incision made approximately mid-length of the snake's body. After the incision was sutured, the veterinarian administered lactated Ringer's solution to combat dehydration. Muscle tone and respiratory rate were monitored throughout the procedure until the snakes had fully recovered from the effects of the anesthetic (Manfield 2007). I supplied the snakes with fresh water, and released them at their exact point of capture several days after surgery. At the end of the study, the transmitters were removed using a similar procedure.

### **Sampling procedures**

Fieldwork for this project occurred between April and October, 2005 and April and July, 2006. I used radio-telemetry receivers (AVM instrument Co, LA 12-Q; Communications Specialists Inc., R-1000) to locate each study animal as often as possible, typically one or two times per week. I recorded the locations (Universal Transverse Mercators – UTM) of radio-tagged rattlesnakes with a hand-held GPS (Garmin Ltd.) and used the locations to assess habitat use, aggregative behaviour and to describe patterns of movement. Analyses were conducted in R Version 2.4.1 (Ihaka and Gentleman 1996) and in SAS (SAS 2002).

## **Movement**

To quantify an individual's movement pattern I used net displacement and distribution of bearings. Net displacement refers to the total distance (maximum straight line distance) between the beginning and end of a path (Turchin 1998). I calculated net displacement for each individual using ArcGIS 9.0, Multiple Minimum Distance Extension Tool. For each snake, I combined the directions of travel between all pairs of locations for an individual's distribution of bearings. I considered the migratory movements of each individual as a single path. I defined migratory movements as those moves that occurred once the individual had moved from the den entrance until it attained the maximum displacement from the den. I used regression to test the relationship between month and distance from den for snakes from each site. I also present figures detailing movement paths from snakes tracked in both years of the study ( $n = 5$ ). I used a paired t-test to compare the maximum distance attained from the den between years for individuals.

## **Orientation of Movements**

To identify the individuals that oriented their migratory movements (i.e. non-random distribution of movements – 'directed' snakes), I applied Rao's spacing test to each snake's distribution of bearings, in each year, in order to test the hypothesis of uniformity against a hypothesis of modality. I used this test because the data did not follow a Von-Mises distribution (circular equivalent to a normal distribution). I used an alpha of 0.05 and included only those snakes that moved more than five times, as required by the test statistic (Bergin 1991). When distributions appeared to be bimodal, I tested whether snakes oriented along a single axis using a Rao's spacing test applied to transformed data (Zar 1999). To transform the data, angles were doubled and then reduced *modulo*  $360^{\circ}$ . To test whether 'directed' snakes from a den migrated towards a common bearing, I applied a Rao's spacing test to the distributions.

## Habitat

I classified the habitats available to rattlesnakes during the summer season using the Biogeoclimatic system (Meidinger and Pojar 1991). I chose this system because digital data were available from the Province of British Columbia and because this system often is used for management. I used ArcGIS 9 and ArcView GIS 3.3 and several program extensions to capture habitat data (Environmental Systems Research Institute 1999; Hooge and Eichenlaub 1997). The three habitat types at site 1 were Bunchgrass, Ponderosa pine, and Interior Douglas-fir (Figure 6). Site 2 was composed entirely of Bunchgrass habitat; thus comparisons of second-order habitat use at site 2 were not possible.

To define used habitat at site 1, I systematically sampled the habitat types at 100m intervals along the migration paths of radio-tagged snakes. To define available habitat at site 1, I used the maximum distance attained from the den by a radio-tagged snake to define the area available to snakes during the summer. I then used ArcGIS 9 to sample this area 1000 times in 2005 and 2006.



Bunchgrass Zone

Ponderosa pine Zone

Interior Douglas-fir Zone

**Figure 6. Habitat types**

**Comparison of Used and Available Habitat**

To compare the used and available habitat data, I first pooled all data among individuals for each year. I analyzed these data with a Chi-squared test. I used the estimated coefficients from a logistic regression model of use to indicate the direction of association with each habitat. I used the c statistic as a measure of the model's ability to correctly classify use or non-use.

I treated used and available habitats as the binary dependent variable (1 = used and 0 = available) and habitat type as the independent categorical variable (Bunchgrass, Ponderosa pine, and Interior Douglas-fir). I first converted habitat type to dummy variables and used Ponderosa pine as the reference category (Zar 1999).

## **RESULTS**

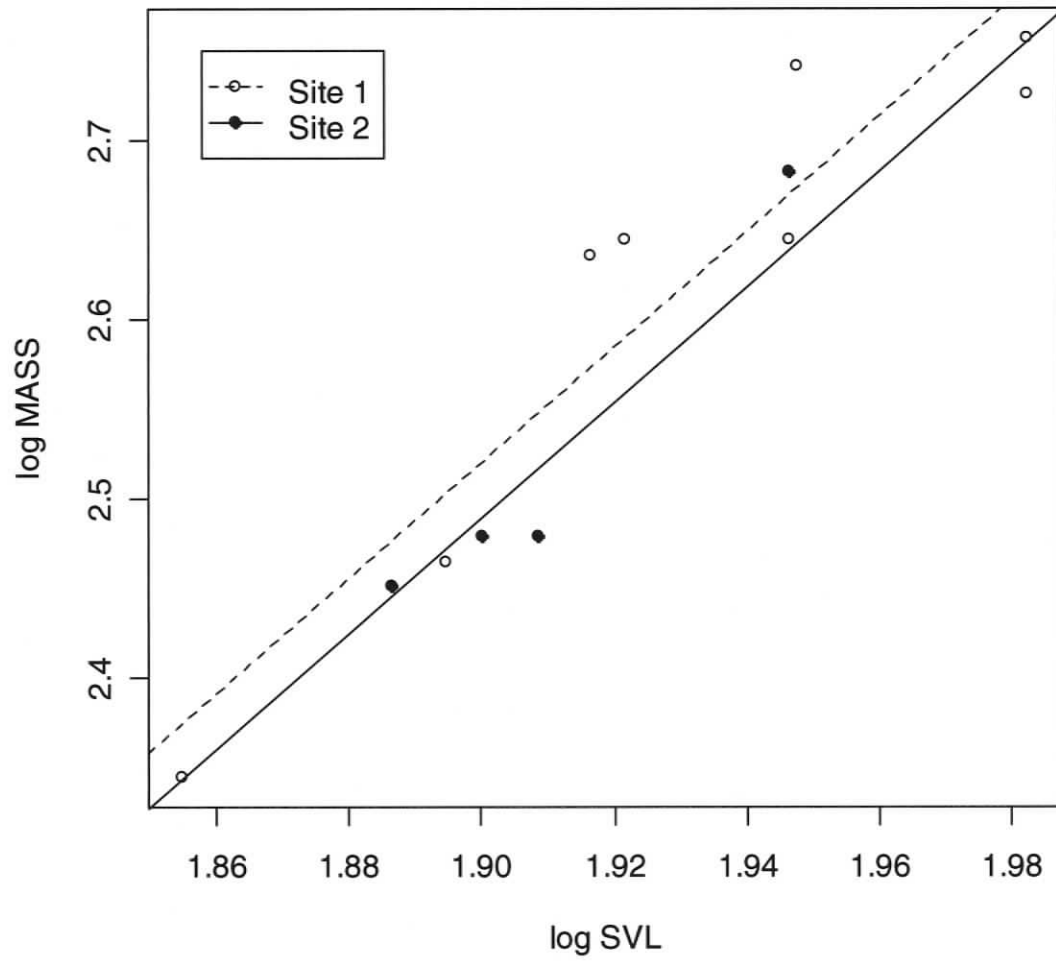
### **Study animals**

The twelve study animals were similar in mass and length (Table 1). Also, study animals from both sites had similar relative mass, or body condition (Figure 7). The interaction between site and log-transformed SVL was not significant ( $t_{11} = 0.58$ ,  $p = 0.47$ ) and neither was the effect of site ( $t_{11} = -0.98$ ,  $p = 0.35$ ). The regression model with log SVL as the predictor of log mass was significant ( $F_{1,10} = 72.48$ ,  $p < 0.0001$ ).

**Table 1. Summary of morphometric data from radio-tagged rattlesnakes at emergence in 2005 and 2006.**

	<i>TOTAL</i>	<i>SITE 1</i>	<i>SITE 2</i>
<i>Study animals (n)</i>	12	8	4
<i>Mean mass (g)</i>	402.73	433.93	340.35
<i>SD (g)</i>	119.61	124.08	93.51
<i>Range (g)</i>	220 - 570	220 - 570	281.4 - 480
<i>Mean SVL* (cm)</i>	83.25	84.64	80.47
<i>SD (cm)</i>	7.46	8.40	4.9
<i>Range (cm)</i>	70.61 - 95.00	70.61 - 95	76 - 87.38
<i>Mean tail length (cm)</i>	62.58	61.75	64.25
<i>SD (cm)</i>	4.66	5.51	1.73
<i>Range (cm)</i>	55.5 - 70	55.5 -- 70	62.20 - 66

\* SVL: Snout-vent length



**Figure 7.** The condition (mass at a given snout-vent length) of study animals at emergence from hibernation was the same between sites. Condition measures for each snake were recorded once during the study (n = 12 snakes).



### **Aggregations**

All aggregations of snakes away from hibernacula were observed between June and October. At site 1, the aggregations occurred primarily in the upper-elevation Douglas-fir forests. Between August 2 and 27<sup>th</sup> 2005, two aggregations were observed in the upper-elevation Douglas-fir forests. One aggregation involved one radio-tagged snake and at least 3 other rattlesnakes. The other aggregation involved two radio-tagged snakes and at least seven other rattlesnakes. Another radio-tagged snake was found within 75m of this aggregation. In July 2006, two aggregations involved separate radio-tagged snakes. Both occurred in lower-elevation Douglas-fir forests. At site 2, all aggregations occurred in Bunchgrass habitat.

### **Mortality**

All three mortalities occurred at site 1. Rattlesnakes are prey to hawks, badgers and coyotes (Macartney 1985). I found the remains of two study animals within several days of their predation. The radio-transmitters had been neatly removed and there were puncture holes in the snakes. The remains of the third study animal were not found until seven days after predation and by this time, they were scattered and contained mammal hair. In the days before death, the rate of movement by one snake appeared atypical. The distance moved per fix appeared to decrease prior to death; however, the rate of movement was not significantly different from the other study animals (Kruskal –Wallis  $X_7^2 = 4.88$ ,  $p = 0.67$ ).

### **Movement**

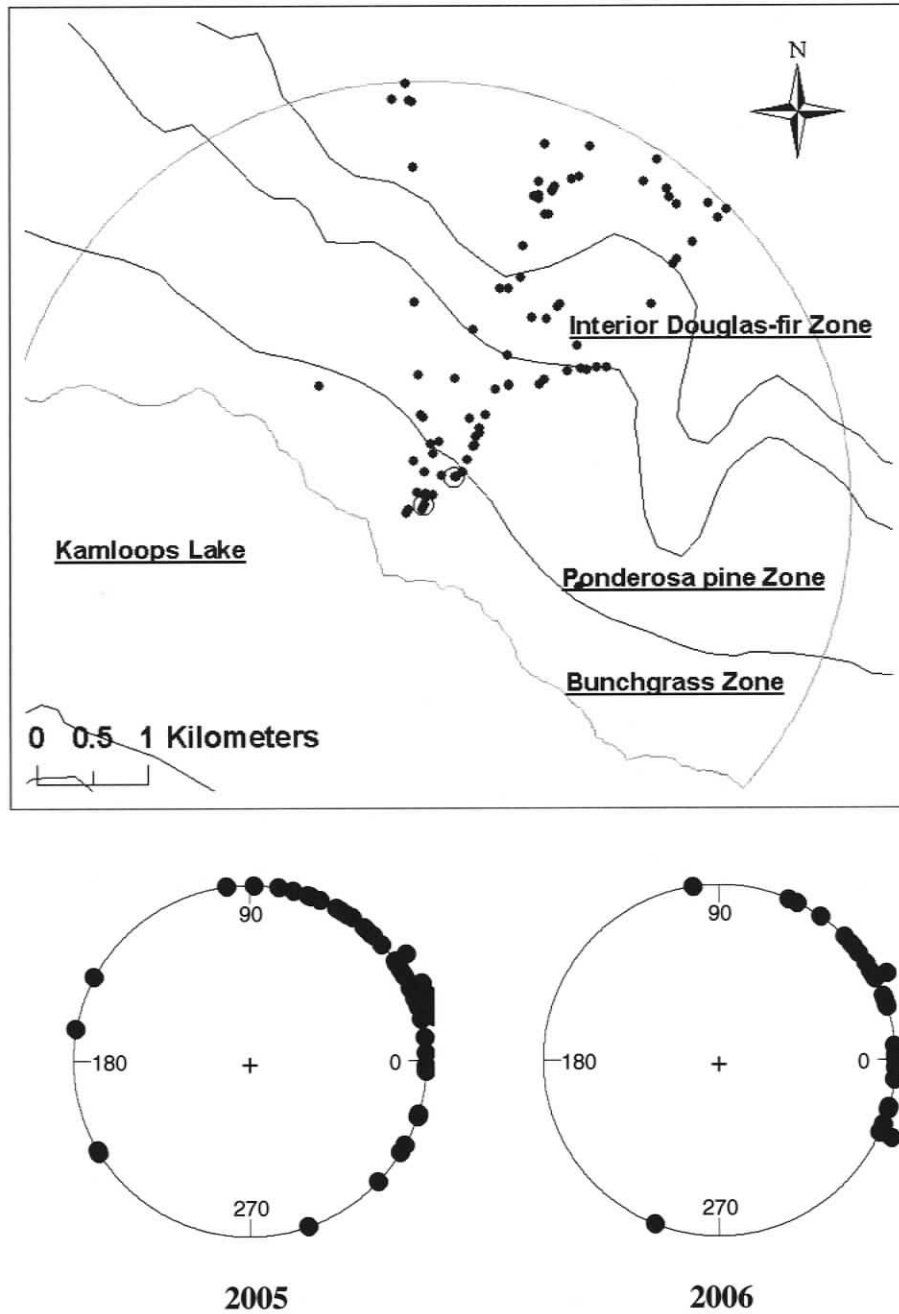
#### **Orientation**

I pooled the snakes between years and treated individuals tracked in both years as independent units in each year. I detected snakes to have moved between 7 and 17 times during migration in 2005 and 2006 (mean 11). I considered a movement to be any change in location greater than 10m. Eight individuals 'directed' their migratory movements towards a fixed bearing and nine snakes did not (Rao's spacing test,  $P < 0.05$ , Table 2). The two snakes from site 1 that did not direct their movements were not axially bimodal (Rao's spacing test,  $p > 0.05$ ).

Directed snakes did not migrate towards random bearings from the den in 2005 or in 2006 (2005, Rao's spacing test,  $p < 0.001$ ; 2006, Rao's spacing test,  $p < 0.001$ ). Instead, migrations were concentrated between 0 and 90 degrees (Figure 8).

**Table 2. Patterns of movement were either directed towards a fixed bearing or not directed (random). A Rao's spacing test was not applied to data from individuals that made fewer than 5 migratory movements (Bergin 1991).**

<i>YEAR</i>	<i>SITE</i>	<i># SNAKES</i>	<i>RANDOM</i>	<i>DIRECTED</i>
2005	1	6	1	5
2006	1	4	1	3
2005	2	3	3	0
2006	2	4	4	0



**Figure 8.** Orientation of movements from directed snakes at site 1 in 2005 ( $n = 5$ ) and 2006 ( $n = 3$ ). Overall, the snakes appear to have migrated in a common direction from the den in both years of the study. Map indicates the locations ( . ) of radio-tagged rattlesnakes in 2005 and 2006 at site 1 in relation to habitat types and the dens ( o ).

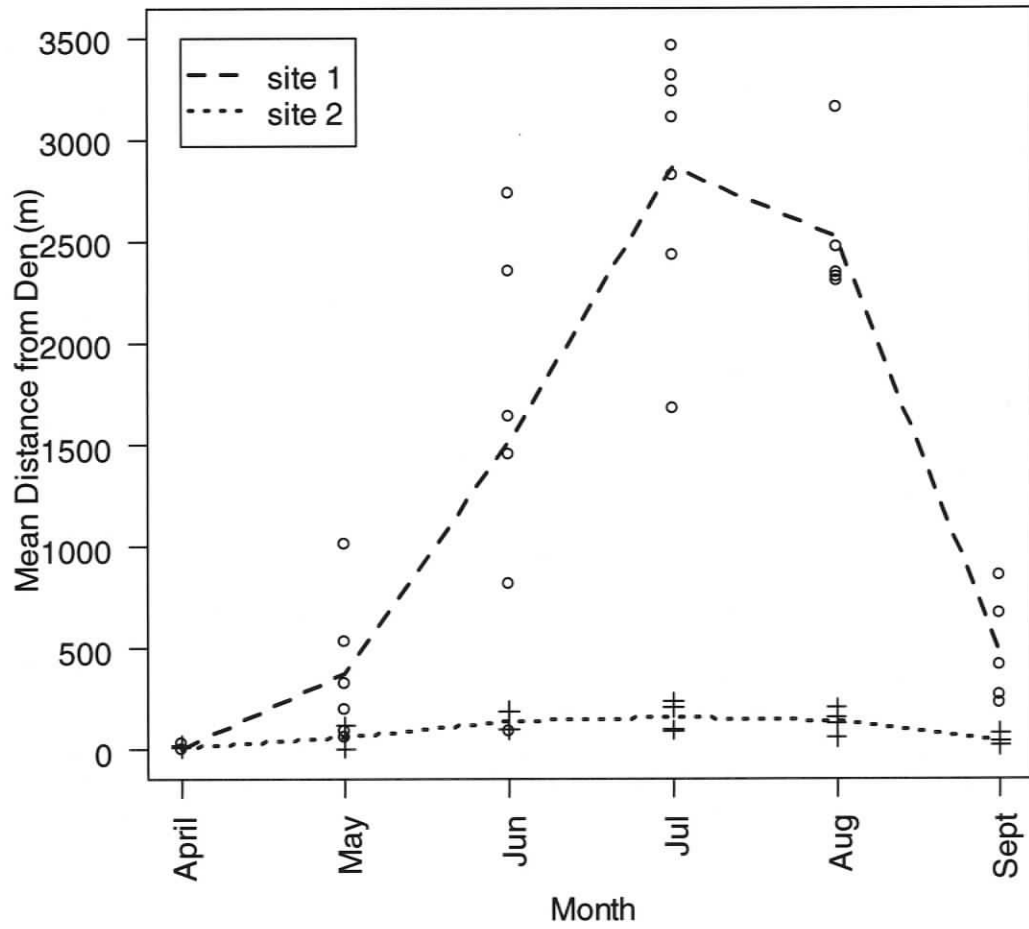
### **Net displacement and Orientation**

I used regression to analyze the interaction between month and distance from den during migration in 2005 and 2006. I pooled data from radio-tagged snakes at each site in 2005 and 2006. I used month as the independent predictor for mean distance from den. Since the month of April included time spent at the den, locations from this month were omitted. All snakes from site 1 consistently moved farther from the den during migration in both years of the study (2005,  $F_{1,18} = 38.6$ ,  $p < 0.0001$ ; 2006,  $F_{1,11} = 31.74$ ,  $p < 0.0001$ ). There was no relationship between distance from den and month for snakes from site 2 (2005,  $F_{1,9} = 2.49$ ,  $p = 0.15$ ; 2006,  $F_{1,10} = 4.47$ ,  $p = 0.06$ ).

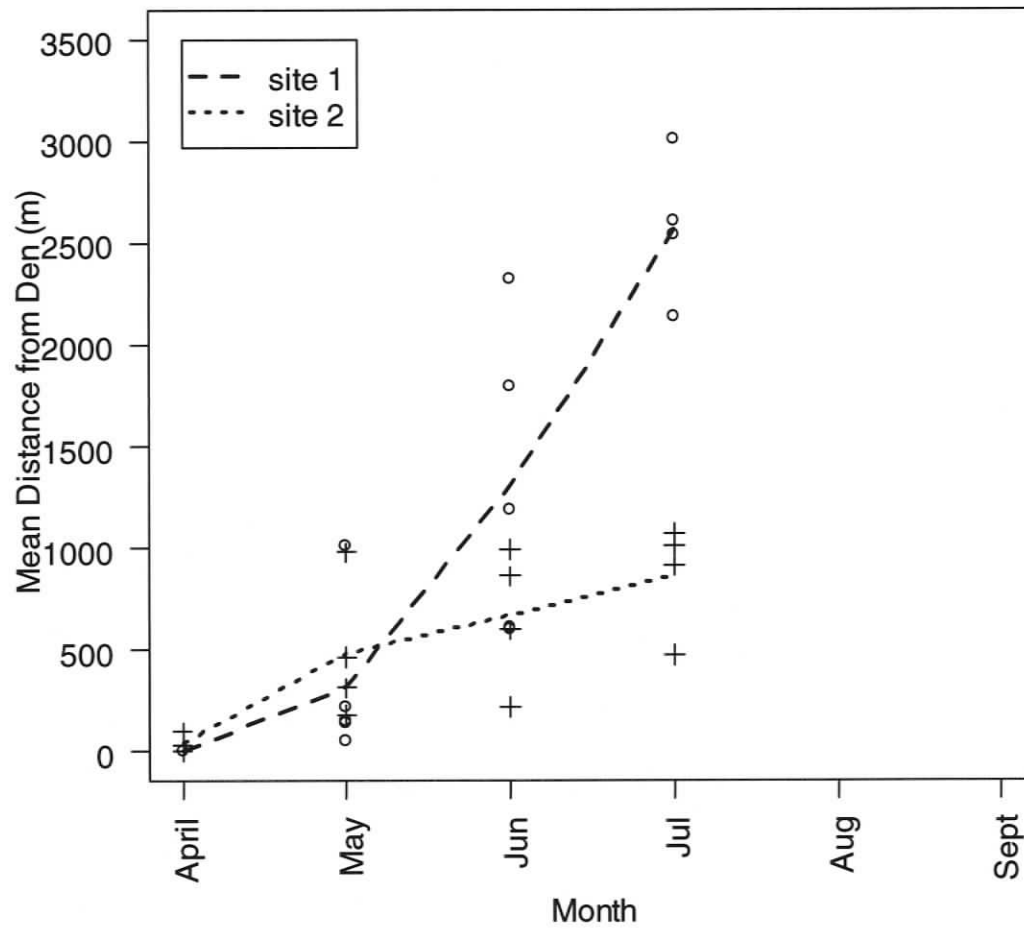
For the most part, snakes that directed their migratory movements towards a fixed bearing moved farther from the den than snakes that were not directed. The mean net displacement from the den of directed snakes was approximately twice that of non-directed snakes (Random,  $n = 9$ :  $1278.22\text{m} \pm 944.37\text{m}$ ; Directed,  $n = 8$ :  $2974.73 \pm 636.73\text{m}$ ).

**Scale of migratory movement between years (Maximum distance from den)**

I described the patterns of migratory movement of mature male rattlesnakes during the summers of 2005 and 2006 using the maximum straight-line distance attained from the den and the directedness of the travel path. The maximum straight-line distances that individual rattlesnakes migrated from the den varied between individuals and between sites. Snakes from site 1 (n = 6 to 7) consistently increased their distance from the den from April until July and remained within 1.5 to 3.5 kilometers from the den during August (Figure 9). Snakes from site 2 (n = 2 to 4) remained closely associated with the den throughout the summer of 2005 and a similar trend occurred in 2006 (Figure 10).

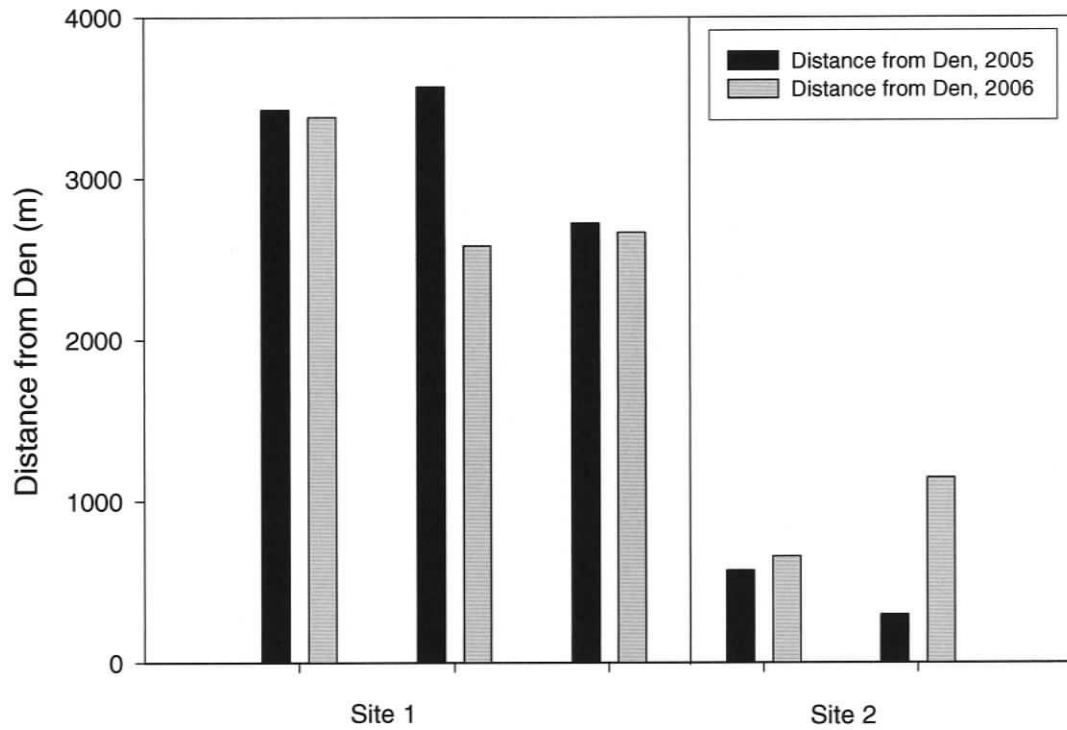


**Figure 9.** The mean straight-line distance from the den attained each month by radio-tagged snakes in 2005. Dashed lines show the trend of the grand mean distance from the den.



**Figure 10.** The mean straight-line distance from the den attained each month by each radio-tagged snake in 2006. Dashed lines show the trend of the grand mean distance from the den. No data were collected after July, 2006.

I used data from rattlesnakes ( $n = 5$ ) that were tracked in 2005 and 2006 to examine the scale of migratory movements between years. The maximum straight-line distance that these animals moved from their dens ranged from 297m to 3568m, and these animals attained the same maximum distance between years (Paired t test,  $t_4 = 0.10$ ,  $p = 0.92$ ; Figure 11). Rattlesnakes tracked in both years also showed overlapping paths (Figures 12 and 13).



**Figure 11. The maximum distance from the den of 5 radio-tagged Northern Pacific Rattlesnakes did not differ between years but appears to differ between sites.**



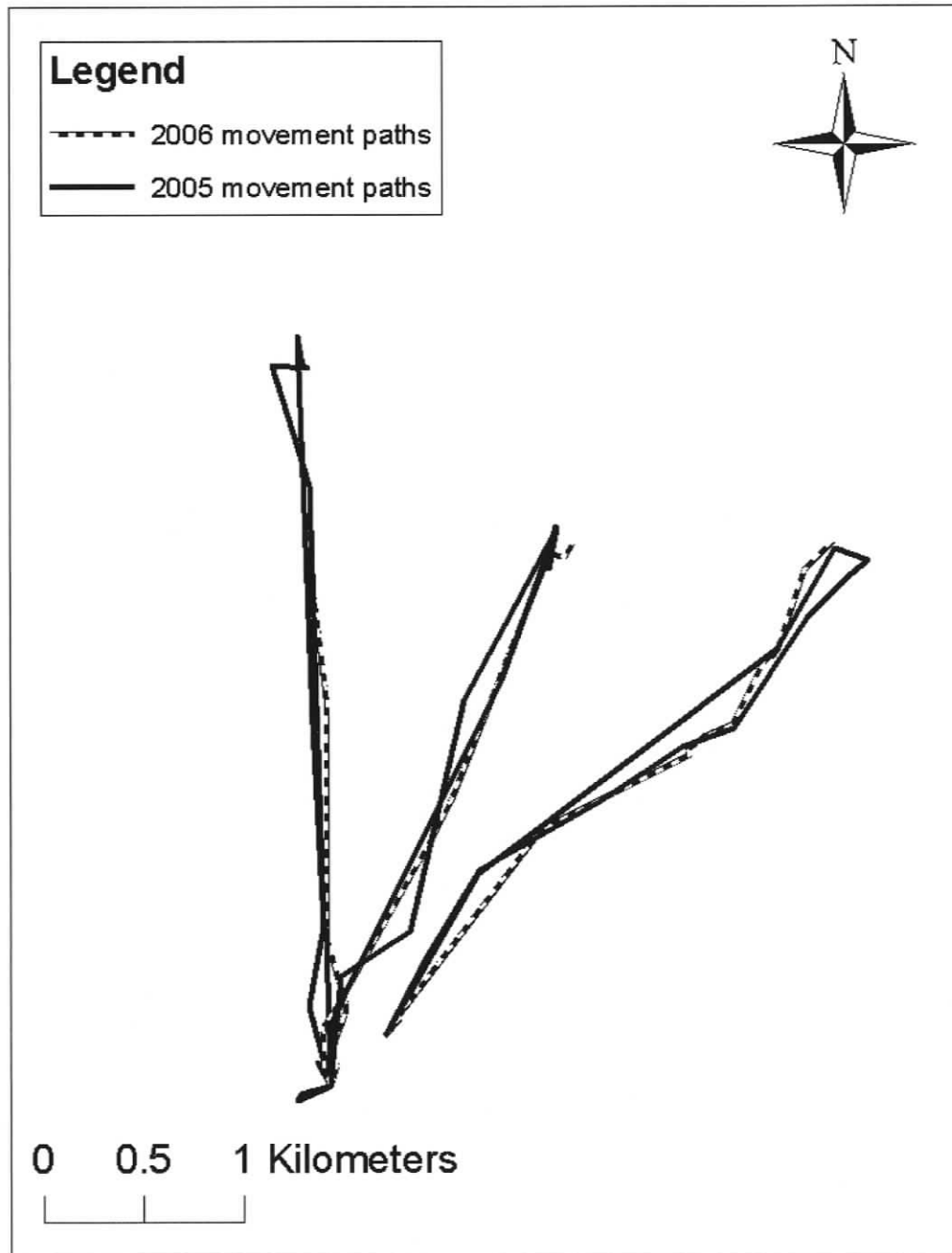
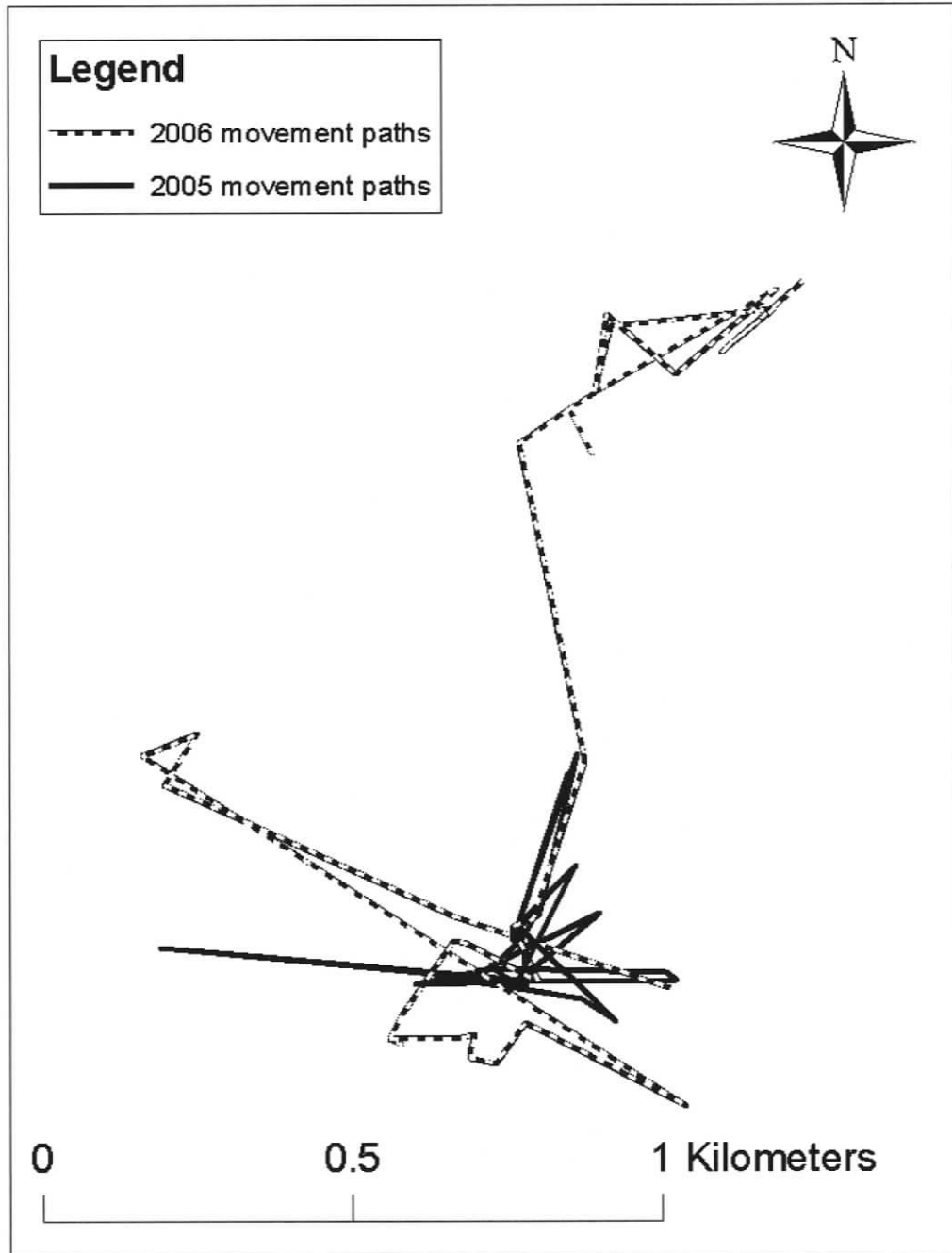


Figure 12. Movement paths exhibited by three radio-tagged snakes from site 1 in 2005 and 2006.



**Figure 13. Movement paths exhibited by two radio-tagged snakes from site 2 in 2005 and 2006.**

**Habitat**

I used habitat type to describe habitat use at site 1. The three habitat types considered were Bunchgrass, Ponderosa pine and Interior Douglas-fir. The habitat variable, 'Ponderosa pine' had values of 0 for each of the dummy variables 'Interior Douglas-fir' and 'Bunchgrass'. I sampled habitat type from 340 points along paths used by seven rattlesnakes and from 2000 points within the area available to snakes during the summer (Table 3).

**Table 3. Number of habitat samples that occurred within each habitat type in 2005 and 2006. Available data were a random sample from the area available to rattlesnakes during the summer. The radius of this area was the maximum distance attained by a radio-tagged snake. Used data were systematically drawn from the paths used by radio-tagged snakes during migration.**

	<i>BUNCHGRASS</i>	<i>PONDEROSA</i>	<i>INTERIOR</i>	<i>YEAR</i>
		<i>PINE</i>	<i>DOUGLAS-FIR</i>	
Available	252	344	404	2005
Used	33	76	104	2005
Available	273	362	365	2006
Used	16	50	61	2006

I used two techniques to analyze the habitat data. I first pooled data from all radio-tagged snakes from site 1 and compared the proportion of used with the proportion of available habitat samples. I compared these data with a Chi-Square test. The proportion of habitat types differed between used and available samples (2005,  $X_2^2 = 10.1$ ,  $p = 0.0064$ ; 2006,  $X_2^2 = 13.8$ ,  $p = 0.001$ ) and this suggests that individuals used habitats non-randomly. I then used logistic regression to examine the direction of the relationships with habitat types and to assess the utility of these data to discern used from available plots in each year. Habitat type significantly reduced the deviance of the null models in both years (2005: Likelihood ratio  $X_2^2 = 10.76$ ,  $p = 0.0046$ ; 2006: Likelihood ratio  $X_2^2 = 15.43$ ,  $p = 0.0004$ ). Compared with the Ponderosa pine and Bunchgrass zones, rattlesnakes were positively associated with the Interior Douglas-fir zone in 2005 and 2006 (Table 4). The c-statistic for the 2005 model was 0.56 and for the 2006 model was 0.59. Since a c-statistic of 0.5 indicates that the model is no better than randomly assigning observations into outcome categories, these models were only marginally useful at distinguishing used from available plots.

**Table 4. Results from logistic regression of habitat data at site 1. The habitat variable, 'Ponderosa pine' had values of 0 for each of the dummy variables 'Interior Douglas-fir' and 'Bunchgrass'. The sign of the coefficient estimate indicates a rattlesnake's relationship with the habitat. The Wald test statistic (p) indicates whether the variable is significantly associated with the probability of habitat use.**

<i>VARIABLE</i>	<i>DF</i>	<i>COEFFICIENT</i>	<i>SE</i>	<i>WALD X<sup>2</sup></i>	<i>p</i>	<i>YEAR</i>
Bunchgrass	1	-0.40	0.14	8.70	0.0032	2005
Interior Douglas-fir	1	0.28	0.10	6.88	0.0083	2005
Bunchgrass	1	-0.64	0.18	11.84	0.0006	2006
Interior Douglas-fir	1	0.41	0.14	9.27	0.0023	2006

## DISCUSSION

Contrary to my expectations, rattlesnakes from one site used upper-elevation forested habitat when available and traveled farther from the den than previously reported for this species. This study is the first to document that rattlesnakes that hibernate in the grasslands may use predominantly upper-elevation, forested habitat during the summer. It also is the first to document divergent trends of habitat use and movement patterns among denning populations. The directionality and maximum displacement of migratory movements varied between individuals; however, despite this variability, snakes from site 1 moved farther from the den than snakes from site 2. Also, individuals from both sites displayed fidelity to summer habitats between years.

The spatial availability of resources required during both the summer and winter should be used by managers to determine the habitats with which rattlesnakes are associated. The Northern Pacific Rattlesnake typically has been associated with dry grassland and open forested habitat (Bertram et al. 2001; Brown 2006; Macartney 1985; Matsuda et al. 2006). This association, at least in the northern part of the range, likely is caused by the availability of suitable overwinter retreats in these habitats (Gregory 1984).

Snakes from one site used upper-elevation Douglas-fir habitat during the summer when the habitat was available. In fact, use of this habitat was significantly greater than the use of the other available types. This suggests that the upper elevation forests were associated with resources required by snakes during the summer. What these resources are remains unknown. However resources sought by male rattlesnakes during the summer include prey and mates (King and Duvall 1990). In 2005, three radio-tagged snakes were observed in courting aggregations with non-telemetered snakes in upper elevation Douglas-fir habitat. In 2006, two radio-tagged snakes displayed aggregative behaviour in lower-elevation Douglas-fir forests. Prey abundance has been shown to influence habitat use by other snake species (Jenkins and Peterson 2005; Whitaker and Shine 2003). Radio-tagged snakes were observed in typical ambush postures in the Douglas-fir habitats. However, since no direct measures of prey were recorded, conclusions about the effects of prey abundance on habitat use by rattlesnakes are not possible.

The utility of cover types to predict habitat use by rattlesnakes cannot be determined from this study. To do so would require multiple study sites composed of different cover types. However, if use of habitat type is caused by underlying resource variability (Gregory et al. 1987), and if these resources are not associated with specific vegetation types, vegetation type will fail to accurately predict habitat use. Compton et al. (2002) reviewed a similar situation in studies of habitat selection by wood turtles (*Clemmys insculpta*). They concluded that, because use of cover types varied among populations, turtles likely were not selecting habitat based on cover types.

As generally found in other studies (Jenkins and Peterson 2005; Parker and Anderson 2007), rattlesnakes in this study displayed fidelity to habitats between years. Familiarity with an area may facilitate orientation if specific features are used for navigation (Able 1980). Fidelity to habitats also may reduce competition for resources among snakes by minimizing intraspecific interactions. In another study, individual rattlesnakes used the same summer habitats in two consecutive years, despite annual fluctuations of prey abundance (Jenkins and Peterson 2005). This suggests that factors other than foraging may contribute to habitat fidelity. Habitats used by radio-tagged snakes did not overlap during early summer. Fidelity to non-overlapping habitat supports the possibility of conspecific avoidance; however, a larger sample is needed for this to be tested.

These findings highlight the variable nature of movement patterns of snakes (Macartney et al. 1988; Shine 1987; Tiebout and Cary 1987). Dispersal distances (maximum displacement from the den) are variable within the genus *Crotalus* (Gregory 1984; Macartney et al. 1988; Parker and Anderson 2007) and within the species *oreganus* (Bertram et al. 2001; Brown 2006; Macartney 1985). The extent to which migratory movements are directed also varies within the genus *Crotalus* (Duvall et al. 1985; Duvall and Schuett 1997; King and Duvall 1990; Parker and Anderson 2007; Reinert and Zappalorti 1988).

On average, male rattlesnakes in this study moved farther from the hibernacula than male rattlesnakes from previous studies in British Columbia (Bertram et al. 2001; Brown 2006; Macartney 1985). Study animals reached straight-line distances of up to 3585 metres from the hibernacula. Bertram et al. (2001) recorded maximum straight-line



distances attained from the den ranging from 0.92 – 1.4 kilometers for adult male radio-tagged rattlesnakes and 0.29 – 3.0 kilometers for non-gravid female rattlesnakes (Bertram et al. 2001). Macartney (1985) used mark-recapture methods and found that most rattlesnakes remained within 1200 metres of the den during the summer. Brown (2006) recorded average maximum range length (maximum distance between any 2 radio locations after a full season) of  $1.08 \pm 0.32$  (mean, SD) kilometers from male rattlesnakes in the South Okanagan. However, these values were limited to snakes that remained closely associated with hibernacula during the summer.

The relatively long average migration distances in this study were primarily due to snakes at site 1. Snakes from site 2 moved similar distances from the hibernacula to those moved by snakes from previous studies (Bertram et al. 2001; Brown 2006). Similar to the study sites selected by Brown (2006) and Bertram et al. (2001), site 2 was located well within grassland habitat. The abundance of prey has been shown to influence habitat selection by snakes (King and Duvall 1990; Whitaker and Shine 2003) and it is likely that the availability of prey at site 2 was similar to that at Bertram's (2001) and Brown's (2006) study sites. Similarly, the long-distance migrations of snakes at site 1 may have been the result of low availability of prey near the hibernacula and/or greater availability of prey in the upper elevation Douglas-fir forests at Site 1. To test this, long-term inventory of prey abundance would need to be performed.

Migratory movements of snakes from this study were either directed or random. Directed and random migratory movements were recorded in a study of movement patterns of the Midget Faded Rattlesnake (*Crotalus oreganos concolor*, Parker and Anderson 2007) and in a study of the movement patterns of the Prairie Rattlesnake (Jorgensen unpublished). These patterns of movement may reflect the distribution of resources: directed movements occur in areas of low resource availability and multidirectional movements are the result of systematic searches in areas of high resource availability (Zollner and Lima 1999). Thus, since most snakes that directed their movements were from site 1, resource availability may have been lower at site 1 than at site 2. I can only speculate about what caused two snakes from site 1 to exhibit non-directed migratory movements. Overall, these snakes traveled far from the den (maximum distance from the den: 2722m and 2697m); however, each of their migrations

included several movements in a different direction. In 2005, one of the non-directed snakes from site 1 moved into a lower elevation field prior to migrating into upper elevation forests. In 2006, the other non-directed snake from site 1 altered his course in the Ponderosa pine forests prior to moving into the upper elevation Douglas-fir forests. Interactions with conspecifics, prey or other resources likely caused these patterns of movement. Directed snakes from site 1 migrated north from the den. Snakes that migrated in this direction would have had access to resources in Bunchgrass, Ponderosa pine and Douglas-fir habitats and would avoid the lake.

These findings have implications for movement patterns in general, and for movements of snakes in particular. Like many other animals, rattlesnakes in this study exhibited divergent patterns of movement (Alerstam et al. 2003); some rattlesnakes migrated large distances from the hibernacula, whereas others were relatively sedentary. This is the first time that divergent patterns have been recorded for the Northern Pacific Rattlesnake and lends support to Berthold's theory of migration (Berthold 1999). Berthold suggested that the widespread tendency for both migrant and sedentary individuals to co-occur in populations of birds could be rooted in genetic variation. Though genetic differences may have influenced the movement patterns exhibited by Northern Pacific Rattlesnakes, this hypothesis has not been tested. The possession of genes for a migratory as well as sedentary lifestyle could help explain the variability in movement patterns seen in studies of snake movement (Lawson 1994; Parker and Anderson 2007).

These results can be used to assist management of rattlesnake habitat in British Columbia. Snakes from my one site traveled farther than previously recorded; thus, the size of the areas that must be effectively managed to conserve rattlesnakes is larger than previously reported. Habitats such as upper-elevation forest should be regarded as potential rattlesnake habitat, and resource users, such as forest companies, may need to be involved with planning for management of rattlesnakes.

As with many studies of habitat use and movement patterns, my inferences are limited by several factors. Frequency of locations limited my ability to analyze movement patterns and make statistically rigorous comparisons between years. My interpretation of habitat use was derived from one study site (site 1); thus, it is not

possible to conclude that rattlesnakes selected the Douglas-fir forests (n = one study site with numerous habitat types). In fact, it is entirely possible that the differences between habitats, as defined by vegetation type, are not perceived by rattlesnakes. Simultaneous study of habitat use by rattlesnakes from numerous areas surrounded by similar habitat types would be needed to make such comparisons.

Regardless of these limitations, this study has made several key contributions to our understanding of the ecology of rattlesnakes in BC. Snakes travel farther from the den than previously recorded, and not all rattlesnakes undertake lengthy straight-line migrations. Rattlesnakes are capable of using diverse habitat types during the summer active season and mating aggregations may occur in upper-elevation Douglas-fir forests. However, the availability of critical resources was not included in my descriptions of habitat. Identifying the resources that cause habitat selection is the logical next step in furthering our understanding of how rattlesnakes use the landscape and why habitat use varies from place to place.

## CHAPTER 3: MICROHABITAT SELECTION BY THE NORTHERN PACIFIC RATTLESNAKE

### INTRODUCTION

Animals select habitat at multiple spatial and temporal scales (Johnson 1980) and different processes are part of selection at each scale (Wiens 1989). For example, factors that influence habitat selection patterns by Tundra Wolves (*Canis lupus*) at a large scale include availability of prey and den sites (McLoughlin et al. 2004). Availability of suitable nest trees influence habitat selection patterns by the Western Kingbird (*Tyrannus verticalis*) at the microhabitat scale (Bergin 1992). Habitats selected at the largest scale presumably contain all the resources needed by an animal to survive and reproduce. Conversely, habitats selected at the smallest scale (microhabitats) contain fewer resources that are used by animals to address specific requirements.

Habitat use is the end result of habitat selection (Jones 2001) which often is caused by conflicting processes (Morris 2003). For example, gravid garter snakes (*Thamnophis spp.*) must balance the need to thermoregulate with that of predator avoidance (Gregory et al. 1999), and elk (*Cervus canadensis*) must trade off foraging opportunities with predation risk (Frair et al. 2005). Because the details of these trade-offs are species-specific, it is important to incorporate an understanding of an animal's life history into studies of habitat use.

Underlying factors that influence microhabitat selection by snakes include reproductive condition (Charland and Gregory 1995), stage of ecdysis (Peterson et al. 1993), whether or not the animal is foraging, and digestive state (Reinert et al. 1984). Gravid female snakes select microhabitats that contain more rock cover than microhabitats selected by non-gravid snakes (Charland and Gregory 1995). Snakes that are in the final stages of ecdysis remain closely associated with cover objects, such as rocks (Peterson et al. 1993). Snakes that are foraging often select microhabitats that offer both cover (Reinert et al. 1984) and sign of prey activity (Theodoratus and Chiszar 2000). The majority of these underlying factors result in increased association with cover

objects. This association likely is the result of selection for the structural and thermal attributes provided by cover objects (Reinert 1993).

Features typically measured in studies of habitat use by snakes include cover objects such as rock, woody debris, canopy closure (Charland and Gregory 1995; Moore and Gillingham 2006; Reinert 1984a), as well as aspect (Harvey and Weatherhead 2006). Cover objects are particularly important for snakes (Gregory 2004) and other reptiles and play a key role in their selection of habitat (Heatwole 1977). Cover objects provide refuge from predators and act as ambush sites for predation (Reinert et al. 1984). They also provide thermal gradients that can be used for thermoregulation (Huey et al. 1989). Forest canopy will reduce the amount of solar radiation that reaches the ground. Wood turtles (*Clemmys insculpta*) were negatively associated with canopy cover (Compton et al. 2002) and Eastern Massasauga Rattlesnakes (*Sistrurus c. catenatus*) were associated with open canopy habitats (Moore and Gillingham 2006). The aspect of a microhabitat also will influence the amount of solar radiation that reaches the ground. The amount of solar radiation is greater on south-facing habitats than north-facing habitats. In thermally challenging environments, snakes select south-facing microhabitats as den sites and this presumably facilitates physiological processes (Huey 1991) and provides shelter from lethal temperatures.

Detailed descriptions of the habitats used by an animal can provide insight about the underlying causes of selection. Huey et al. (1989) found that garter snakes used rocks for thermoregulation. Although rocks may have afforded the snakes some protection from predators, the thermal gradient associated with rocks of specific thickness significantly affected their selection (Huey et al. 1989). Other cover objects, such as shrubs, also provide protection from predators yet may be less suited for thermoregulation (Heatwole 1976). Ideally, it is useful to be able to predict the probability with which a specific habitat will be used by a snake. Habitat features that are stable over time, such as perennial plants and rocks, can distinguish habitats used by different snake species (Reinert 1984a) and are ideal candidates for predictive models.

The Northern Pacific Rattlesnake (*Crotalus o. oregonus*) typically is associated with grassland and open forested habitats (Matsuda et al. 2006). Microhabitat selection within these areas can be described by proximity to cover (Bertram et al. 2001;

Macartney 1985). However, features other than proximity to cover may influence microhabitat use by the Northern Pacific Rattlesnake.

Availability of prey and exposure to solar radiation may also influence the microhabitats used by Northern Pacific Rattlesnakes. The diet of Northern Pacific Rattlesnakes consists primarily of voles (*Microtus spp*) and mice (*Peromyscus spp*) (Macartney 1989) and the selection of ambush sites is related to the presence of chemicals left by prey (Theodoratus and Chiszar 2000). Thus, while foraging, rattlesnakes may gauge the suitability of a microhabitat by the presence or absence of chemical cues associated with their prey. The effects of tree cover and aspect on habitat use by the Northern Pacific Rattlesnake are unknown. Because these features influence temperature, and temperature influences physiological processes, they may be important in the selection of microhabitat.

In Chapter 2, I found that the extent of habitats used by rattlesnakes spanned several kilometers surrounding the hibernacula. At this scale, movement patterns of snakes varied between individuals and between populations. Some snakes directed their movements towards a fixed bearing and thereby minimized the use of habitats close to the hibernacula. Others moved randomly and remained closely associated with the hibernacula throughout the summer. These divergent patterns of movement suggested that snakes were responding to differences in their surroundings. In this chapter, I describe the microhabitats used by adult male rattlesnakes and use descriptions of microhabitat to determine which habitat features are used or not used by rattlesnakes. I then test whether there is an interaction between movement patterns and habitat selection at the microhabitat scale.

## **METHODS**

### **Habitat**

I used radio-telemetry to study the habitats used by mature male rattlesnakes. I located each animal as often as possible, typically one or two times per week. Habitat data were collected as a paired use-availability design (Thomas and Taylor 2006). At each rattlesnake location I set up one (actual) habitat plot and one paired (random) plot at a randomly selected point. The random plot was constrained within a distance of 150 m – the mean distance moved per day by male rattlesnakes in previous studies (King and Duvall 1990). I directly measured two types of habitat features: 1) microhabitat and 2) minimum distance to habitat features within the surrounding 30m of plot centre. Microhabitat features measured included the percentage cover of substrate, shrub and rocks (Table 5). Percentage cover was estimated within one metre of plot centre using the line intercept method. Each of four 50-cm long transects originated at plot centre and radiated in a cardinal direction (i.e. N, S, E, W). The minimum distance to habitat features within 30 metres of plot centre was measured to the nearest centimetre. Specific features measured included minimum distance to tree and minimum distance to cover. When refugia were used, I recorded the type (e.g. rock, shrub) and took descriptive measures of structural features (e.g. height of rock). I recorded microhabitat features at each pair of plots once per year. For example, if a snake returned to a previously used plot, I did not re-measure the habitat (Thomas and Taylor 2006). For each snake, I measured microhabitat at plots separated by at least 10 metres as this was the arbitrary minimum distance that I defined as a movement.

**Table 5. Features measured at microhabitat plots.**

<i>HABITAT FEATURE</i>	<i>VARIABLE</i>	<i>PLOT RADIUS (m)</i>	<i>DESCRIPTION</i>
-	mslope	30	Mean slope
-	aspect	30	Aspect
Min. Distance	mdref	30	Minimum distance to a refuge
Min. Distance	mdbedrock	30	Distance to nearest bedrock
Min. Distance	mdgully bottom	30	Distance to nearest gully bottom
Min. Distance	mdroad	30	Distance to nearest road
Min. Distance	mdwater	30	Distance to nearest water
Min. Distance	mdtree	30	Distance to nearest tree
Microhabitat	rock	0.5	Percentage coverage of rocks
Microhabitat	soil	0.5	Percentage coverage of soil
Microhabitat	wood debris :wd	0.5	Percentage coverage of wood debris *
Microhabitat	litter	0.5	Percentage coverage of litter
Microhabitat	shrub	0.5	Percentage coverage of shrub
Microhabitat	grass	0.5	Percentage coverage of grass
Microhabitat	herb	0.5	Percentage coverage of herb
Microhabitat	talus	0.5	Percentage coverage of talus
Microhabitat	tree	0.5	Percentage coverage of tree
Microhabitat	water	0.5	Percentage coverage of water
Microhabitat	road	0.5	Percentage coverage of road
Microhabitat	hole	0.5	Percentage coverage of hole
Microhabitat	anth	0.5	Percentage coverage of anthropogenic feature
Microhabitat	ash	0.5	Percentage coverage of ash
Microhabitat	bedrock	0.5	Percentage coverage of bedrock
Microhabitat	moss	0.5	Percentage coverage of moss
Microhabitat	prey.runway	0.5	Pres / Absence of small mammal runway **
Microhabitat	prey.scat	0.5	Pres / Absence of small mammal scat **

\* Wood debris (wd) defined as any woody debris greater than 2 cm diameter.

\*\* The presence of prey sign was measured in 2006.



### **Selection of variables**

I compared microhabitat (i.e. percentage cover, minimum distance, slope and aspect) from used sites with features from available sites using a series of univariate analyses. I first arcsine-transformed all cover variables and log-transformed all distance variables. If the underlying distributions still were not normal, I used untransformed values in all subsequent non-parametric analyses. I applied parametric tests to transformed variables with normal distributions. I created dummy variables for aspect and slope. Aspect was divided into four categories of 90 degrees (North East  $0^{\circ} - 90^{\circ}$ , South East  $91^{\circ} - 180^{\circ}$ , South West  $181^{\circ} - 270^{\circ}$ , North West  $271^{\circ} - 359^{\circ}$ ). I used the inter-quartile break points to divide slope into four categories ( $Q_{25} = 23\%$ , median =  $35.50\%$ ,  $Q_{75} = 50\%$ ). North East aspect ( $0^{\circ} - 90^{\circ}$ ) and low-grade slopes (slope  $\leq 23\%$ ) were the reference categories.

To determine which features explained the greatest amount of variation between used and available plots, I used a Wilcoxon signed-rank test (paired sample), t-tests (paired), McNemar Chi-Square test, and univariable conditional logistic regression models. I retained variables whose Wilcoxon signed-rank test, t-test, or McNemar Chi Square (for categorical variables) had a p-value of  $< 0.25$  for use in the multivariable models (Hosmer and Lemeshow 1989). I used the Wald Test statistic from the univariable models to test the hypothesis that the slope coefficient was zero (Manly et al. 2002). As suggested by Hosmer and Lemeshow (1989), I retained variables that showed some association ( $p < 0.25$ ) with the outcome (used vs. available). When variables were highly correlated (Spearman's Rho  $> 0.7$ ), I retained the variable that accounted for the most deviance in its univariable model. I included all variables that were retained at this stage in a preliminary model. However, since the number of variables was restricted to 0.1 of the sample size (Peduzzi et al. 1996) I had to further reduce the preliminary model from 2006 (number of microhabitat plots in 2006 = 84, number of variables in the model could not exceed 8 including the stratification variable, 'plot'). To determine which variables to remove, I created separate models from the preliminary model, each reduced by one variable and used the Akaike's Information Criterion weights of the models to

determine which variables to discard. Variables eliminated from the models that received the most support were discarded.

### **Selection of models**

I used conditional logistic regression, in which used and available sites are paired for greater comparative power, to model microhabitat selection (Hosmer and Lemeshow 1989). This method uses conditional maximum likelihood to estimate coefficients in a linear model. The sign of a coefficient indicates the direction of association with the variable relative to what is available. I used Akaike's Information Criterion (AIC) to select the most parsimonious models from the preliminary model (Burnham and Anderson 2002). The AIC method incorporates the number of parameters as well as the deviance explained by the model into the assessment of model suitability (Burnham and Anderson 2002). I compared all combinations of variables from each preliminary model (separate preliminary model for 2005 and 2006). I used AICc (AIC corrected for small sample sizes) to rank these models and used model weight ( $\omega$ ) as a measure of support for the model. Support among models was calculated by dividing the model's weight by that of the global model. The models with the most support (AICc scores within 4 units of the "best" model) were retained as the final models (Burnham and Anderson 2002). I used the Wald test to assess the significance of the final set of supported models. I also was interested in whether the habitats selected by snakes were associated with their migratory patterns of movement and I tested this with logistic regression. All analyses were done in R Version 2.4.1 (Ihaka and Gentleman 1996).

### **Replication**

Habitat data were repeatedly measured from 12 mature male rattlesnakes, and pooled across individuals; thus my results are based on pseudoreplicated data (Hurlbert 1984). This is a common problem in studies that use telemetry to assess resource selection by animals (Gustine et al. 2006; Thomas and Taylor 2006). The correct way to analyze these data would be to include both site and snake as random effects in a mixed effects model (Gillies et al. 2006). However, low sample size precluded the separate analysis of

microhabitat use for each snake. Thus, to assess overall microhabitat selection by male rattlesnakes, I analyzed habitat data pooled among individuals separately for each year.

## **RESULTS**

I radio-tracked 11 snakes in 2005 and 10 snakes in 2006. Nine of these snakes were tracked for at least a portion of the summer in both 2005 and 2006. I located snakes in new locations 143 times in 2005 and 84 times in 2006. The number of times that I found each snake in a new location varied among individuals and between years (2005: min. 7, mean 13, max. 19; 2006: min. 2, mean. 8.4, max. 15).

### **Selection of variables**

I used p-values from the t- tests, Wilcoxon signed-rank tests and McNemar tests as criteria for retaining the variables in the regression analysis (Table 6). Due to infrequent occurrence (each variable occurred fewer than 8 times), I removed the variables 'anthropogenic', 'ash', 'water', 'road' and 'hole' from the 2005 and 2006 data sets and I removed the variables bedrock and water from the 2006 dataset. In addition to 'slope' and 'aspect', all variables retained from Table 6 were included in univariable conditional logistic regression models (Table 7). When any of the levels of categorical predictors were associated with the outcome (probability of use), all levels of the variable were retained for further analysis. For example, if only North West aspect was associated with use, the entire 'aspect' variable was retained.

**Table 6. Results of tests to determine regression coefficients. Variables that showed some association ( $\alpha \leq 0.25$ ) were retained for further analyses.**

<i>HABITAT FEATURE</i>	<i>STATISTICAL TEST</i>	<i>2005</i>	<i>2006</i>
		<i>p</i>	<i>p</i>
bedrock	Wilcoxon signed-rank	<0.0001	2.72E-01 *
wood debris	Wilcoxon signed-rank	2.61E-02	4.75E-02
grass	Wilcoxon signed-rank	<0.0001	2.30E-01
herb	Wilcoxon signed-rank	7.67E-01 *	5.21E-01 *
litt	Wilcoxon signed-rank	8.64E-01 *	5.34E-01 *
moss	Wilcoxon signed-rank	2.12E-01	8.89E-01 *
rock	Wilcoxon signed-rank	<0.0001	5.46E-04
shrub	Wilcoxon signed-rank	<0.0001	<0.0001
soil	Wilcoxon signed-rank	<0.0001	4.80E-03
talus	Wilcoxon signed-rank	5.81E-01 *	2.02E-01
tree	Wilcoxon signed-rank	5.05E-02	1.91E-01
prey.runway	McNemar Chi Squared	NA	1.40E-04
prey.scats	McNemar Chi Squared	NA	<0.0001
mdtree	t-test	4.27E-01 *	8.88E-02
mdwater	t-test	6.64E-01 *	NA
mdref	Wilcoxon signed-rank	<0.0001	<0.0001
mdbedrock	Wilcoxon signed-rank	6.23E-01 *	NA
mdgully bottom	Wilcoxon signed-rank	5.78E-01 *	4.22E-02
mdroad	Wilcoxon signed-rank	3.15E-01 *	1.56E-01

\* Indicates the variable was removed from further analyses ( $\alpha = 0.25$ )

**Table 7. Univariable conditional logistic regression models of habitat features. The sign of the estimate of the regression coefficient indicates the direction of rattlesnake relationships with the feature. Wald  $\chi^2$  indicates whether the variable was associated with use.**

<i>HABITAT FEATURE</i>	<i>YEAR</i>	<i>SAMPLE SIZE</i>	<i>REGRESSION COEFFICIENT</i>	<i>SE</i>	<i>WALD <math>\chi^2</math></i>	<i>p</i>
wood debris	2006	162	0.13	0.08	1.59	0.11
grass	2006	162	-0.01	0.01	-1.29	0.20
rock	2006	162	0.07	0.03	2.57	0.01
shrub	2006	162	0.03	0.01	3.42	6.0e-4
soil	2006	162	-0.01	0.01	-2.38	0.02
talus	2006	162	0.02	0.01	1.15	0.25
tree	2006	162	-0.01	0.01	-1.46	0.14
prey.runway	2006	128	0.56	0.44	1.26	0.21
prey.scats	2006	129	0.98	0.48	2.05	0.04
mdrefuge	2006	162	-0.48	0.15	-3.26	0.001
mdgully bottom	2006	49	-0.10	0.07	-1.48	0.14
mdroad	* 2006	29	0.09	0.08	1.08	0.28
mdtree	2006	68	1.79	1.11	1.61	0.11
aspect dummy SW	* 2006	163	0.06	0.36	0.18	0.86
aspect dummy NW			-0.22	0.67	-0.33	0.74
aspect dummy SE			-0.33	0.36	-0.89	0.37
slope dummy 2	* 2006	164	0.07	0.39	0.19	0.85
slope dummy 3	2006	164	-0.07	0.37	-0.19	0.85
slope dummy 4	2006	164	-0.20	0.45	-0.45	0.66
bedrock	2005	277	0.03	0.01	3.02	0.003
wood debris	2005	277	0.05	0.02	2.50	0.01
grass	2005	277	-0.02	0.01	-3.14	0.002
moss	* 2005	277	0.00	0.01	-0.47	0.64
rock	2005	277	0.08	0.02	3.51	4.0e-4
shrub	2005	277	0.03	0.01	4.69	<0.0001
soil	2005	277	-0.03	0.01	-4.86	<0.0001
tree	2005	277	-0.01	0.00	-1.84	0.07
mdefuge	2005	256	-0.43	0.12	-3.46	5.0e-4
aspect dummy NW	2005	258	1.03	1.32	0.77	0.44
aspect dummy SE	2005	258	0.54	1.25	0.43	0.66
aspect dummy SW	* 2005	258	0.72	1.27	0.57	0.57
slope dummy 2	2005	262	0.02	0.38	0.07	0.95
slope dummy 3	2005	262	0.62	0.41	1.51	0.13
slope dummy 4	2005	262	0.96	0.45	2.12	0.03

\* Variable is discarded from further analyses

I used Spearman's Rho to indicate correlation since exact p-values could not be calculated due to ties in the data. Only 'prey scat' and 'prey runway' were strongly correlated (Spearman's Rho = 0.73,  $p < 0.0001$ ). Since 'prey runway' accounted for less variability in the univariable model than did 'prey scat', it was discarded from further analysis ('Scat': Likelihood ratio  $X_1^2 = 4.72$ ,  $p = 0.03$ ,  $n = 129$ ; 'Runway': Likelihood ratio  $X_1^2 = 1.66$ ,  $p = 0.20$ ,  $n = 128$ ). Other variables that were moderately correlated were retained in further analyses (Spearman's Rho  $< 0.7$ ). 'Minimum distance to refuge' was moderately correlated with 'shrub' and 'rock' cover in 2005 (Spearman's Rho = - 0.43 and - 0.25 respectively). In 2006, 'minimum distance to refuge' and 'shrub cover' were moderately correlated (Spearman's Rho = - 0.54) and 'tree cover' and 'minimum distance to tree' were moderately correlated (Spearman's Rho = - 0.49).

I used the AICc weights to determine which variable to remove from the preliminary model so that it satisfied statistical requirements (Table 8). The variable excluded from the model with the greatest support was discarded from further analysis. Thus, 'refuge' was discarded from the preliminary model in 2006.

**Table 8. Results from comparing among nested subsets of the preliminary model in 2006. Each subset contained all but one of the variables from the preliminary model in 2006\*.**

<i>VARIABLE</i>	<i>SAMPLE (n)</i>	<i>AICc</i>	$\Delta AICc$	$\omega$
refuge **	127	41.72	0.00	3.03E-01
soil	124	41.80	0.08	2.92E-01
grass	124	42.25	0.53	2.32E-01
wd	124	43.18	1.46	1.46E-01
rock	124	46.96	5.24	2.21E-02
tree	124	50.39	8.67	3.98E-03
shrub	124	54.13	12.41	6.14E-04
prey scat	157	64.98	23.26	<0.0001

\* Preliminary model from 2006:

use = wd + grass + rock + shrub + soil + tree + prey.scat + mdrefuge

\*\* The variable that was excluded from the preliminary model

### **Preliminary models**

The preliminary multivariate models (Global models) of habitat use are shown in Table 9. There were few differences between the 2005 and 2006 preliminary models. The variables 'minimum distance to gully' and 'minimum distance to tree' had to be removed from further analyses because the maximum likelihood estimates of parameters could not converge. The 2005 preliminary model was significant (Wald's  $X_{11}^2 = 20.29$ ,  $p = 0.041$ ,  $n = 250$  and Likelihood ratio  $X_{11}^2 = 125$ ,  $p = 0$ ,  $n = 250$ ). The significance of the 2006 preliminary model depended on the statistical test. The likelihood ratio test indicated that the 2006 preliminary model was significant (Likelihood ratio  $X_7^2 = 43.4$ ,  $p < 0.0001$ ,  $n = 127$ ) and the Wald Chi Square test indicated that it was not significant (Wald's  $X_7^2 = 9.85$ ,  $p = 0.197$ ,  $n = 127$ ). Some literature suggests that the Likelihood ratio test may be more powerful than the Wald test (Chao-Ying Joanne Peng and So 2002). However, I hereafter took the more conservative approach and discuss my results in terms of Wald tests.



**Table 9. Results of fitting conditional logistic regression models to microhabitat data from 2005 and 2006. The sign of the estimate of the regression coefficient indicates the direction of rattlesnake relationships with the feature. The Wald test statistic and accompanying p-value indicate whether the variable is significantly associated with use.**

**Year 2005**

<i>HABITAT FEATURE</i>	<i>REGRESSION COEFFICIENT</i>	<i>SE</i>	<i>Wald X<sup>2</sup></i>	<i>p</i>
bedrock	0.08	0.03	2.28	2.30E-02
wood debris	0.22	0.09	2.60	9.50E-03
grass	0.01	0.01	0.57	5.70E-01
rock	0.23	0.08	2.79	5.30E-03
shrub	0.05	0.01	3.14	1.70E-03
soil	-0.03	0.01	-2.58	9.90E-03
tree	0.00	0.01	0.37	7.20E-01
mdrefuge	-0.12	0.17	-0.68	4.90E-01
slope dummy 2	0.74	0.77	0.97	3.30E-01
slope dummy 3	0.37	0.96	0.39	7.00E-01
slope dummy4	0.16	0.97	0.16	8.70E-01

**Year 2006**

<i>HABITAT FEATURE</i>	<i>REGRESSION COEFFICIENT</i>	<i>SE</i>	<i>Wald X<sup>2</sup></i>	<i>p</i>
wood debris	0.10	0.12	0.85	4.00E-01
grass	-0.02	0.02	-1.13	2.60E-01
rock	0.06	0.04	1.65	9.90E-02
shrub	0.08	0.03	2.20	2.80E-02
soil	0.01	0.01	0.77	4.40E-01
tree	-0.08	0.08	-0.89	3.70E-01
prey.scat	1.50	0.81	1.85	6.50E-02

### **Selection of models**

All of the models that received strong support in 2005 and two of the nine models in 2006 yielded statistically significant regressions (Wald's  $X^2$   $p < 0.05$ ; Table 10). In both years, support was stronger for reduced models. In 2005, a reduced model, which excluded the variables 'grass' and 'tree' had 35% support (i.e. model weight) among all models considered and was 7 times stronger than the global model. In 2006, the top model included all terms from the global model except 'grass' and 'soil' and had 2.5 times the amount of support of the global model. This model had 15% support among all models considered. Models from both years show that the percentage cover of 'rock' and 'shrub' had strong effects on the probability of habitat use. The effect of all other variables measured in both years differed between years (i.e. bedrock, wood debris, grass, soil, tree and slope). Since there was no clear 'best' model, I considered all models to be equally well supported (Burnham and Anderson 2002).

**Table 10. Results of comparing all possible combinations of covariates from the preliminary models (Global models). The models that received the most support ( $\Delta AIC < 4$  compared to the 'best' model) and the Global models are shown.**

<i>REMOVED</i>	<i>N</i>	<i>AICc</i>	$\Delta AICc$	$\omega$	<i>WALD X<sup>2</sup></i>	<i>DF</i>	<i>p</i>
<b>2005 Global model**:</b>							
<i>use = bedrock + wd + grass + mdrefuge + rock + shrub + slope + soil + tree</i>							
grass, tree	250	64.08	0.00	0.35	19.65	9	2.02E-02*
tree	250	66.00	1.92	0.13	20.2	10	2.75E-02*
grass, slope, tree	256	66.01	1.93	0.13	20.21	6	2.54E-03*
grass	250	66.20	2.12	0.12	19.66	10	3.26E-02*
grass, slope	256	68.00	3.92	0.05	19.93	7	5.72E-03*
Global	250	68.04	3.96	0.05	20.29	11	4.15E-02*
slope, tree	256	68.12	4.04	0.05	20.11	7	5.33E-03*
<b>2006</b>							
<b>Global model**:</b>							
<i>use = wd + grass + prey.scats + rock + shrub + soil + tree</i>							
grass, soil	127	39.91	0.00	0.15	9.02	5	1.08E-01
wd, soil	127	39.92	0.01	0.15	9.98	5	7.59E-02
soil	127	40.02	0.11	0.15	9.26	6	1.59E-01
wd, grass, soil	127	40.35	0.44	0.12	9.39	4	5.20E-02*
wd, grass	127	40.69	0.79	0.10	10.41	5	6.45E-02
grass	127	40.79	0.88	0.10	10.14	6	1.19E-01
wd	127	41.48	1.57	0.07	10.50	6	1.05E-01
Global	127	41.72	1.81	0.06	9.85	7	1.97E-01
wd, rock, soil	127	43.82	3.91	0.02	9.31	4	5.37E-02*

\*\*Global model: The Preliminary model that contains all the microhabitat variables that met criteria for inclusion in the conditional logistic regression analysis.

\* Results from model evaluation tests (Wald), an \* indicates the model is significant (alpha = 0.05)

-AICc: Akaike's Information Criterion, corrected for small sample size

- $\Delta AICc$ : difference between the model's AICc and the minimum AICc,

- $\omega$  : Support for the model (Weight) compared with all other models.

-N: Sample size

-REMOVED: Variables removed from Global model

**Movement patterns**

I described movement patterns as either 'directed' or 'random' in Chapter 2. To test whether this movement category had an effect on use, I added a categorical term to the preliminary model to indicate whether the snake exhibited directed or random movements. I removed data from snakes for which I could not define a movement pattern as 'directed' or 'random' (moved fewer than 5 times). I used general logistic regression instead of conditional logistic regression to test whether the inclusion of the movement variable to the preliminary general logistic model significantly reduced deviance. The effect of adding the movement variable was not significant in either year (2005: Likelihood Ratio  $X_1^2 = 0.078$ ,  $p = 0.78$ ; 2006: Likelihood Ratio  $X_1^2 = 0.024$ ,  $p = 0.88$ ). Thus, there was no association between movement pattern and microhabitat use.

## DISCUSSION

The main conclusions from this chapter are 1) microhabitats used by rattlesnakes can be distinguished from those available by structural features, topography (i.e. slope) and small mammal sign, 2) cover of shrub and rock are consistently associated with microhabitat use and, 3) a snake's movement pattern is not associated with its use of microhabitat.

Rattlesnakes in this study non-randomly used microhabitats characterized by various features. Non-random space use occurs when the distribution of critical resources is not homogeneous (Gregory et al. 1987). Since resources rarely are homogeneously distributed, non-random space use by animals at the smallest scale of selection is the norm. Wood turtles (*Clemmys insculpta*) select non-forested areas near water with low canopy cover (Compton et al. 2002), Western kingbirds (*Tyrannus verticalis*) nest in larger trees with more perch branches than available trees (Bergin 1992), non gravid female garter snakes (*Thamnophis* spp.) use microhabitats characterized by higher vegetation and canopy cover than available (Charland and Gregory 1995) and elk (*Cervus canadensis*) select diurnal bed sites with higher canopy closure and lower air temperature than available sites (Millsbaugh et al. 1998).

Alone, many microhabitat features could be used to predict the probability of microhabitat use by rattlesnakes (Table 7; Wald  $X^2 \leq 0.25$ ). In 2005, rattlesnakes were positively associated with wood debris, rock, shrub, distance to refuge and bedrock and negatively associated with grass, soil, and tree. The association of slope with probability of use also was significant in 2005. Snakes were positively associated with steep slopes (slope  $\geq 50$  %). In 2006, rattlesnakes were positively associated with gully bottoms, refugia, wood debris, rocks, shrub, talus, small mammal runways and scat. They were negatively associated with grass, soil, tree and distance to tree.

The association of rattlesnakes with cover objects facilitates many processes. Cover objects provide refuge from predators and promote crypsis (Stuart-Fox et al. 2004). They are associated with small mammal activity (Manning and Edge 2004) and used as ambush sites (Reinert et al. 1984). Cover objects create natural temperature

gradients that allow snakes to reach and maintain their body temperature within a preferred range (Huey et al. 1989). Thermoregulation is accomplished by shuttling between shaded and sunlit areas (Stevenson 1985). Body temperatures are then adjusted by altering body position and exposure (Huey 1991; Lillywhite 1987; Stevenson 1985). Rocks can store heat and thus are a common source of temperature gradients (Huey et al. 1989; Sabo 2003). Presumably, wood debris and shrubs would also provide temperature gradients; however this remains to be tested.

The importance of cover objects to snakes has been demonstrated by numerous studies (Gregory 2004; Huey et al. 1989; Reinert 1984a; Row and Blouin-Demers 2006). Thus, it is not surprising that rattlesnakes in this study were positively associated with cover objects. Though several types of microhabitat features potentially could provide cover, only those that were structurally stable were selected. Rattlesnakes were positively associated with wood debris, shrubs, rocks, bedrock and talus. They used herb in proportion to its availability and were negatively associated with grass. These results corroborate Heatwole's (1977) suggestion that the long-term stability of habitat features is associated with microhabitat use. Stable structural features could provide refuge from predators such as coyotes, hawks and badgers. Lack of selection for structurally unstable features such as herbs, and negative association with grass may indicate that these features provide insufficient thermoregulatory opportunities or protection from predators.

The interactions between cover and small mammal activity are complex and associations can differ between species (Jorgensen 2004; Kaufman et al. 1983; Manning and Edge 2004). Association with vegetation differed between species of voles (Douglass 1976). Survival of deer mice (*Peromyscus maniculatus*) was higher in areas with moderate ( $3.0 \text{ m}^3 / 0.01 \text{ ha}$ ) amounts of downed wood debris while survival of voles (*Microtus oregoni*) was higher in areas without downed wood debris (Manning and Edge 2004). *Peromyscus leucopus* were associated with well developed shrub layer and used rocks, shrubs and woody debris to avoid predation (Kaufman et al. 1983). Though interactions often are complex, there appears to be a general trend for small mammals to be associated with cover. Rattlesnakes from this study were positively associated with prey sign and with cover. Though prey sign and cover were not strongly correlated in this

study (Spearman's  $Rho < 0.7$ ), snakes that used cover objects may have had the additional benefit of proximity to prey.

Not surprisingly, several studies of habitat use by snakes have found correlations between prey availability and habitat use (Jenkins and Peterson 2005; King and Duvall 1990; Reed and Douglas 2002; Whitaker and Shine 2003). Correlations of habitat use with prey availability will be most apparent when the availability of prey varies across the landscape. Prairie rattlesnakes (*Crotalus viridis*) traveled from overwinter sites to areas with abundant small mammal prey (King and Duvall 1990). Male and female Brownsnakes (*Pseudonaja textilis*) moved from areas with low prey availability to areas with high prey availability (Whitaker and Shine 2003). However, Reed and Douglas (2002) found no relationship between prey availability and habitat use by Grand Canyon Rattlesnakes (*Crotalus v. abyssus*). They speculated that this was because prey availability was consistently high across the study area (Reed and Douglas 2002). Thus, in areas where the availability of prey varies, use of microhabitat may be correlated with prey. Similar to other studies, I found that snakes were positively associated with small mammal runways and scat (Pearson 1959; Reed and Douglas 2002). These findings suggest that rattlesnakes at my study sites may have used cues from their prey to select microhabitat. Further, it suggests that the availability of prey varied at the microhabitat scale.

Distance to gully and distance to tree also were associated with use; however, these associations were not evident in both years of the study. Sample size precluded the addition of 'minimum distance to gully' and 'minimum distance to tree' from preliminary models of use. Thus a larger sample size would be needed to confirm whether an association exists between these features and habitat use. Presumably, availability of cover is greater in the bottom of gullies and thereby provides migrating snakes with suitable stop-over sites. Greater distance from trees might suggest that microhabitat use may have been associated with open areas. This is supported by the negative association between use and percentage tree cover. Eastern Massasaugas (*Sistrurus catenatus catenatus*) and Eastern Milksnakes (*Lampropeltis t. triangulum*) used open microhabitats (Moore and Gillingham 2006; Row and Blouin-Demers 2006). Use of microhabitats with low canopy cover could facilitate thermoregulation. Though aspect has been found to

influence habitats used by rattlesnakes (Bertram et al. 2001), I did not find such a relationship at the microhabitat scale.

Microhabitats used by rattlesnakes could be described by many of the structural features measured in this study and combinations of these features were useful for predicting microhabitat use by mature, male rattlesnakes (Wald  $X^2 < 0.05$ ; Table 10). In 2005, microhabitat use was associated with percentage cover of bedrock, wood debris, grass, rock, shrub, soil, tree and distance to refuge. Removal of percentage cover of grass, tree and slope improved the fit of the model to the data ( $\Delta AIC < 4$ ; Burnham and Anderson 2002). Similarly in 2006, microhabitat use was associated with percentage cover of wood debris, grass, rock, shrub, soil, tree, distance to refuge, and presence of prey scat. Removal of wood debris, grass and soil improved the fit of the model to the data ( $\Delta AIC < 4$ ; Burnham and Anderson 2002). Thus, in both years of the study, percentage cover of rock and shrub were useful for predicting microhabitat use. Rock features helped predict microhabitat use by Eastern Milksnakes in Ontario (Row and Blouin-Demers 2006). Surface vegetation cover helped predict microhabitat use by Eastern Massasaugas (Moore and Gillingham 2006). Similarities between these studies highlight the potential utility of vegetation and rocks for predicting the probability of microhabitat use by snakes.

In this study, rattlesnakes that exhibited different patterns of movement presumably shared the same resource requirements (all study animals were mature, male rattlesnakes). To provide insight into the underlying factors that could cause different types of movement patterns I tested whether pattern of movement (i.e. directed and non-directed) helped predict use of microhabitat. For example, gravid and non-gravid snakes use different microhabitats, and this has been attributed to their different thermoregulatory requirements (Charland and Gregory 1995). The use of different microhabitats by directed and random snakes could suggest differences in resource availability. For example, the association of prey sign with microhabitats used by random snakes might suggest that directed snakes did not encounter prey and thus continued on a directed migration route (King and Duvall 1990). I found no association between microhabitat use and movement patterns. This suggests that factors other than structural



habitat features were responsible for the observed divergent patterns of migratory movements.

Unfortunately, these results are limited because all inference is drawn from a small sample of mature male rattlesnakes (2005,  $n = 12$  snakes; 2006,  $n = 10$  snakes) and the habitat use of each snake was sampled repeatedly. Thus, observations were not independent (Hurlbert 1984). Since the number of locations from each animal varied, and was generally quite low ( 2005; range = 7-19, median = 13, 2006; range = 2-15, median = 8.5 ) it was not possible to fit individual models to the data (Row and Blouin-Demers 2006). Therefore, I used location ( $n = 227$ ) rather than the individual, as the sample unit. Use of locations as sample units ignores the fact that the use of habitat often differs among individuals (Shine 1987). Clearly, some caution is required when interpreting results based on the behaviour of few individuals; however, the fact that I was able to detect selection of microhabitat that was consistent with the literature lends support to my findings.

These results contribute to our understanding of the microhabitat requirements of rattlesnakes in BC. Rattlesnakes were selective in their use of cover objects: they were positively associated with structurally stable objects such as rocks and shrubs, more so than with less stable objects such as herbs and grass. Rattlesnakes near site 2 are known to use microhabitats associated with human activity (Bertram et al. 2001). Fortunately, I found no associations between microhabitat use by snakes at site 2 and anthropogenic features such as road-side cement berms. Though much is now known about the associations of rattlesnakes with microhabitat, there still remains a lot of uncertainty in the models of microhabitat selection. Clearly, factors other than habitat features alone influence an individual's use of a particular microhabitat. The best models of microhabitat use still had much less than 90% support among all models considered. This highlights the need for future studies to address the causes of microhabitat use by rattlesnakes.

## **CHAPTER 4: SUMMARY AND MANAGEMENT IMPLICATIONS**

### **SUMMARY**

Patterns of movement and habitat use are fundamental and interconnected aspects of an animal's ecology. The habitats used by an animal contain resources essential for life processes. The patterns of movement exhibited by an animal determine the habitats that are available at any given time. The process of moving through and selectively using habitats allows an animal to obtain heterogeneously distributed resources. Thus, resources acquired from the habitats that individuals use will affect fitness. By identifying the patterns, which often vary geographically and temporally, testable hypotheses can be created to identify resources that direct an individual's patterns of movement and habitat use. Knowledge of the habitats used and resources required by wildlife contributes to their management.

At northern latitudes, the Northern Pacific Rattlesnake (*Crotalus o. oregonus*) overwinters in communal hibernacula and typically undertakes seasonal migrations between habitats within grasslands. The association of this snake with grasslands may be caused by the availability of suitable hibernacula, and habitat use during the summer likely is influenced by other resources.

My main objectives were to determine the habitat use and movement patterns of the Northern Pacific Rattlesnake. I used the patterns of habitat use and movement exhibited by rattlesnakes during the summer to identify potentially important resources. I documented habitat at sites used and available to rattlesnakes and used radio-telemetry to locate male rattlesnakes and document individual patterns of movement. I compared habitat type from migration paths to the habitats surrounding the den to assess second-order selection of habitat during migration. I compared descriptions of microhabitat from sites used by rattlesnakes with description of sites available to rattlesnakes to assess fourth-order selection of habitat. I used these descriptions to test whether rattlesnakes used habitat selectively at multiple scales and to determine the direction of association with specific features (e.g. negatively associated with tree cover). I used net

displacement and mean bearing to describe patterns of migratory and non-migratory movements by mature male snakes from two sites. These patterns allowed me to formulate hypotheses regarding the underlying cues that potentially caused these patterns of movement.

The main conclusions from this study were:

**1) Male Northern Pacific Rattlesnakes exhibit divergent patterns of movement.**

Populations that consist of migratory and non-migratory individuals exist in many other taxa; however, this is the first study to document the patterns of movement of migratory and non-migratory Northern Pacific Rattlesnakes. Some snakes exhibited directed, linear migratory movements and moved several kilometers to summer habitats. Other snakes did not migrate and thus remained closer to the den during the summer. Despite this variability, there was a trend for snakes at site 1 to move farther and in a more consistently directed pattern than snakes from site 2. Divergent patterns of movement suggested that the availability of resources differed between the study sites. The identification of other underlying cues which may influence patterns of movement holds promise for future research.

**2) All radio-tagged snakes that over-wintered in low-lying grasslands used higher-elevation forested habitats during the summer when those habitats were available.**

This finding was entirely unexpected and should form the basis of future efforts to isolate the underlying causes of habitat use. The Northern Pacific Rattlesnake consistently has been associated with grassland habitat and this may be a consequence of winter rather than summer requirements. Differences in the availability of resources and conditions important to rattlesnakes between grassland and forested habitat will highlight possible cues used by rattlesnakes during the process of habitat selection.

**3) Microhabitat features are useful predictors of habitat use.**

Rattlesnakes consistently used microhabitats characterized by greater shrub and rock cover than was generally available. These associations may be related to physiological processes such as thermoregulation (Stevenson 1985), foraging behaviour (Theodoratus and Chiszar 2000) and predator avoidance. Additional research is required to test these hypotheses.

To understand the reasons *why* patterns exist, the mechanisms that dictate habitat use and patterns of movement must be identified. Natural history studies such as mine improve understanding of an animal's ecology. This understanding can guide future efforts to identify resources used by animals. The distribution of these resources may then help predict patterns of habitat use and movement. My study highlights the variability of movements and habitat use exhibited by rattlesnakes between sites. This relationship must be acknowledged in plans to manage populations of the Northern Pacific Rattlesnake in British Columbia. My study also highlights the need to re-assess rattlesnake management in lower-elevation forests that border on known rattlesnake winter habitat.

#### **Current status and protection measures**

The Northern Pacific Rattlesnake is of conservation concern provincially (Nature Serve Conservation Status Ranks-S3, vulnerable) and federally ('Threatened' in Canada; COSEWIC 2004). It is threatened by habitat loss, persecution and the potential of genetic isolation (Didiuk et al. 2004). These threats are caused by the rapid expansion of human activities that typically occur on privately owned lands. Measures exist to protect critical habitat (hibernacula) in Provincial parks, ecological reserves and Wildlife Habitat Areas. However, legal measures still are needed to protect Northern Pacific Rattlesnakes that exist outside these areas.

### **THREATS AND MANAGEMENT**

#### **Habitat Loss**

Loss of habitat is a key reason why the Northern Pacific Rattlesnake is threatened in British Columbia (Didiuk et al. 2004). The southern interior grasslands of British Columbia are experiencing a high rate of fragmentation (Grassland Conservation Council of British Columbia 2005). Habitat loss and fragmentation affect rattlesnakes directly, by removing and altering habitat and resources, and indirectly, by increasing the frequency of interactions between snakes and the people. Many snakes are accidentally killed on

roads (Andrews and Gibbons 2005) or are discovered by the public in urban areas (Bonnet et al. 1999).

Habitat loss from urbanization at site 1 is unlikely to occur in the near future. Besides the general lack of infrastructure (e.g. roads, electrical power) at this site, the Crown maintains ownership of it and has designated it as a Wildlife Management Area (Anthea and MacNaughton 1998). Wildlife Management Areas (WMA's) are managed primarily to support wildlife and their habitats, but other uses are permitted. The WMA at site 1 originally was established for Bighorn Sheep (*Ovis canadensis*), but the area coincides with the habitats used by rattlesnakes at site 1.

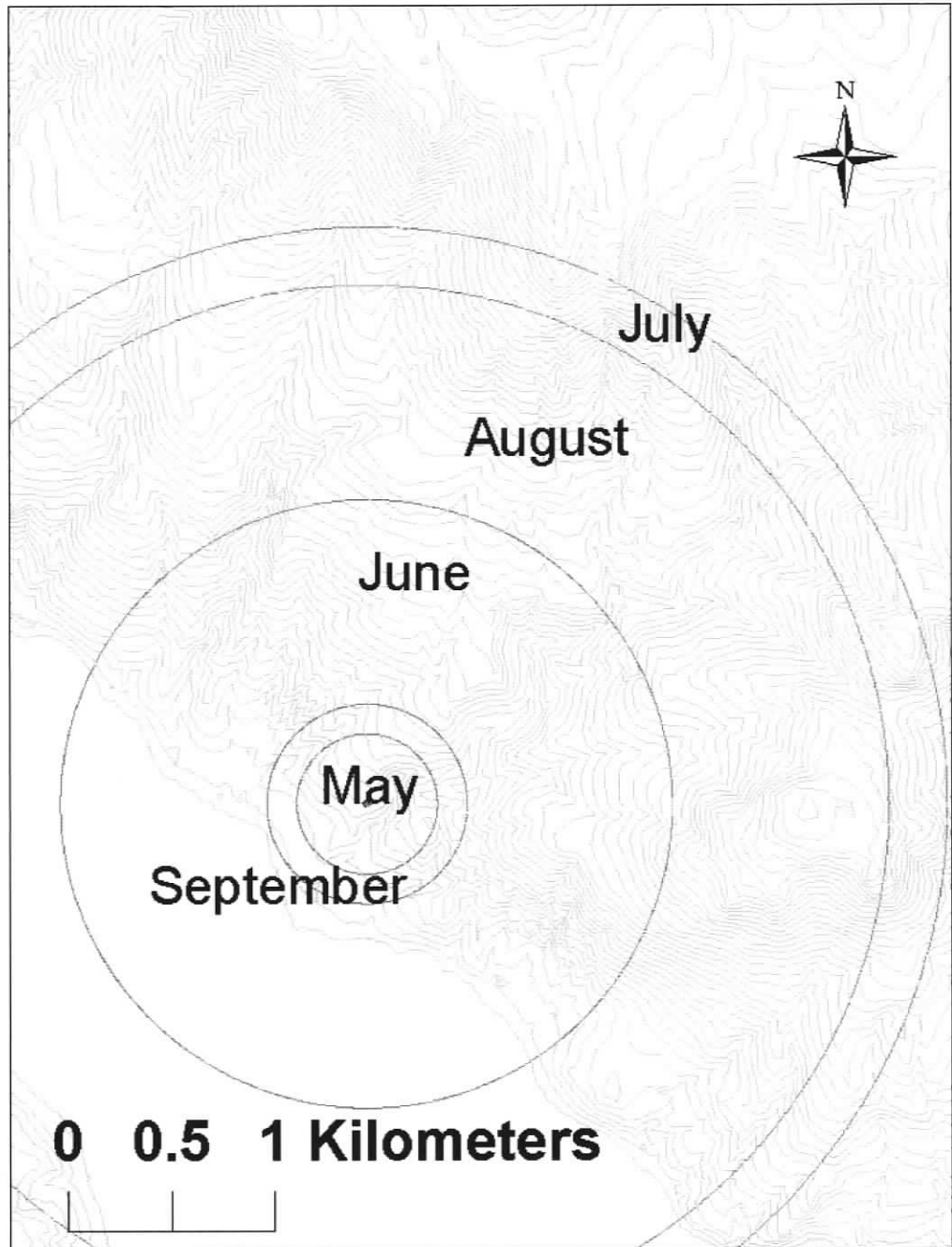
Development at site 2 already has reduced the amount of suitable rattlesnake habitat available to snakes and since there currently is no legislation to protect rattlesnake habitat on privately owned land, habitat loss may continue to occur at this site. The long-term effects on the population of removing summer habitat are unknown, but, if fewer resources are available now than in the past, population numbers can be expected to decline. Due to localized steep terrain, the area around the den at site 2 may not be developed in the near future (City of Kamloops 1997). Thus, as long as no further loss of habitat occurs at site 2, there may be sufficient winter and summer habitat available to support this population in the near future.

Knowledge of the distribution of a population at any given time is important for effective management (Thompson 2004). To mitigate the effects of habitat loss, it is essential that managers have a complete description of the habitats used by rattlesnakes and knowledge of when those habitats are used. This information can be difficult to acquire for migratory populations (Thirgood et al. 2004; Thompson 2004). Fortunately, data on individual movement parameters and timing of habitat use can be used to determine the spatial pattern of a population at any given time (Turchin 1998). Knowledge of these parameters can be used to delineate management boundaries and to direct the timing of resource users' activities.

Radio-tagged snakes at site 1 traveled several kilometers from the den during the summer. The distance of these snakes from the den varied over time (Figure 14) and the average maximum distance (attained in July) could be used to define the extent of the management area at site 1. To minimize direct effects on rattlesnakes, the activity of

resource users within this area (i.e. forest industry) could be concentrated during the winter and spring, when rattlesnakes are not in the upper elevation forests.

Land ownership limits the options available to manage wildlife. Radio-tagged snakes remained closely associated with the den during the summer at site 2. Theoretically, the delineation of a management boundary could include all areas used by these individuals. However, since much of site 2 is privately owned, legal protection of snakes and management options are limited. Stewardship initiatives and public awareness may be the best option for conserving snakes at this site.



**Figure 14.** Average distance of snakes from the den at site 1. The den is located at the centre of the buffer. Buffer radius was based on the mean monthly distance from the den of radio-tagged male rattlesnakes ( $n = 12$ ) in 2005.

**Persecution**

An indirect effect of habitat loss from urbanization is an increased potential for persecution. Fear of snakes is widespread and can be manifest in unwarranted killing of snakes. Lack of knowledge of rattlesnakes also can lead to their persecution. Limited access to site 1 restricts use by the public; thus, the threat of persecution at site 1 is very small. Because of the proximity of site 2 to urban areas, rattlesnakes at this site are at risk of persecution.

If snakes are detected by the public at their hibernacula, persecution could endanger the entire denning population. The aggregations of snakes that occur at the den in the spring and fall are conspicuous (Gregory 1984); thus the likelihood of detection is relatively high (Figure 15). Once a den is detected, the damage inflicted to a population can be quite high because, in the spring and fall, the ability of snakes to evade predators is reduced due to low temperatures (Klauber 1982). Because fidelity to dens is high (Macartney 1985), snakes that escape persecution at the den in a given year will continue to be at risk in the future.





**Figure 15. Aggregation of Northern Pacific Rattlesnakes at a communal hibernaculum.**

Interactions between snakes and the public that occur in the summer can be used to promote education and awareness. Persecution of rattlesnakes could be minimized by educating the public (Bertram et al. 2001). Encounters that couple education with live specimens are most effective at improving attitudes towards snakes (Morgan and Gramann 1989). Rattlesnake removal programs provide *in situ* advice and education coupled with the opportunity to observe a rattlesnake safely (Bertram et al. 2001). Removal programs target people most likely to encounter rattlesnakes on private property and thus would be a valuable addition to current management procedures. Since the positive effects of such a program may be short-lived, multiple visits may be required to improve the effectiveness of this type of program (Gomez et al. 2004). Rattlesnakes associated with recently altered habitats may be particularly susceptible to encounters with humans. Construction materials often are the only available cover in recently cleared areas and could attract snakes that have been displaced from natural microhabitats. Thus, construction workers involved in the conversion of natural habitat should be better informed about what to do in the event of an encounter with a rattlesnake. Though rattlesnakes were observed on four separate occasions in an active construction zone at site 2, workers were unaware of what to do in the event of an encounter with a rattlesnake.

## **RESEARCH PRIORITIES**

Knowledge of the spatial and temporal distribution of rattlesnakes throughout the year is essential for effective management of populations. During the fall and spring, aggregations at communal hibernacula facilitate detection of new populations and fidelity to hibernacula ensures that populations will persist at a given location in the near future. The patterns of movement and habitat use detected by this study have important management implications because they indicate where rattlesnakes may potentially be found during the summer. The extent of habitat accessible and type of habitat used by male rattlesnakes during the summer is larger and more diverse than previously thought. The existence of migratory and non-migratory individuals means that male rattlesnakes may be present near the hibernacula year-round as well as within a several-kilometer radius during the summer. In addition to grasslands, rattlesnakes use Interior Douglas-fir forests during the summer. Given this diversity, management plans would benefit from a way to predict the movement patterns and habitat use exhibited by rattlesnakes in other locations. Therefore, the following research priorities encompass initiatives that will enable the prediction of movement patterns or habitat use at other sites.

### **1) Develop a resource selection function that predicts the occurrence of Northern Pacific Rattlesnakes during the summer**

Prediction of macrohabitat selection (second order) is particularly important because management occurs primarily at this scale. In addition to foraging and mate-searching behavior (King and Duvall 1990), other processes must influence use of second order habitats by mature male rattlesnakes during the summer. Since the process of thermoregulation is an extremely important factor in the selection of habitat by snakes (Huey et al. 1989), knowledge of the different thermoregulatory opportunities at a site could be of value for predicting rattlesnake occurrence at this scale (Blouin-Demers and Weatherhead 2001).

## **2) Determine why Northern Pacific Rattlesnakes are migratory or non-migratory**

The ability to predict rattlesnake occurrence must be confined to the area accessible from the hibernacula during the summer. The extent of habitat accessible to rattlesnakes during the summer will be constrained by their patterns of movement. Thus, an understanding of *why* an individual is either migratory or non-migratory is required to link predictions of habitat use with rattlesnake behaviour.

## **3) Conduct manipulative experiments to gain a better understanding of the processes that guide selection of microhabitat by Northern Pacific Rattlesnakes.**

Though most management initiatives target large scale habitat types (Gustine et al. 2006), management of habitat at smaller scales can also contribute to a species' survival (Webb et al. 2005). Rattlesnakes used microhabitats associated with cover objects and sign of prey (Chapter 3). Use of habitat at this scale has been associated with availability of prey (Duvall et al. 1985), yet additional processes must influence selection at this scale. For example, snakes may avoid microhabitats because of the presence of conspecifics, or their selection of microhabitats may be based on previous experience and knowledge of an area.

## **4) Research the habitat use and movement patterns of juveniles and female Northern Pacific Rattlesnakes**

Little is known about the processes that influence habitat use by female and juvenile rattlesnakes at any of these scales. Since physiological requirements differ among age classes and between the sexes, one would expect patterns of habitat use to differ as well. For example, unlike adult snakes, neonates are able to use small crevices beneath shrubs as cover objects, and grass cover may provide adequate opportunities for crypsis and cover from predators (personal observation).

Future studies likely will use radio-telemetry to examine these relationships (Ujvari and Korsos 2000). Since migration is a physiologically challenging process (Luschi 2003), the effects of transmitters on rattlesnakes may be greater for snakes that

migrate large distances than snakes that remain near the den. All three mortalities of radio-tagged snakes occurred at site 1. Though these mortalities appeared to be caused by predation, the energetic costs of recovering from surgery and carrying a radio-transmitter may have impaired anti-predator behaviour in these snakes. Transmitters have been shown to affect growth and reproduction in black ratsnakes (Weatherhead and Blouin-Demers 2004) and the implantation of transmitters led to high levels of mortality in Prairie Rattlesnakes (Duvall et al. 1985). Because radio-transmitters may adversely affect rattlesnakes, future studies on long-distance migrants should use light-weight transmitters and minimize the period over which transmitters are carried.

## **CONCLUSION**

In the presence of ongoing conversion and loss of grasslands, conservation of rattlesnakes will depend on the attitudes and actions of landowners, stakeholders and the public. The rugged and inconspicuous nature of denning habitats should afford many populations some protection. However, the ability of some snakes to travel large distances from the den likely will increase interactions with resource users and the public. Translocation of snakes away from urban areas generally is not an effective management tool (Brown 2006; Ernst 2004; Ministry of Environment 2007; Reinert and Rupert 1999), and there currently are few (if any) effective ways to mitigate the impacts of habitat loss on rattlesnake populations. The emphasis of management strategies must be on the reduction of habitat loss. When habitat loss already has occurred, strategies than maintain cover objects and small mammal populations may provide suitable habitat for rattlesnakes.

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