THERMAL INFLUENCES ON SUMMER HABITAT USE BY WESTERN RATTLESNAKES (*CROTALUS OREGANUS*) IN BRITISH COLUMBIA

by

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ABSTRACT

The importance of thermal features to habitat selection by terrestrial ectotherms such as reptiles has been well documented, but rarely has it been considered in larger-scale analyses of habitat use and selection, such as those routinely conducted using more-standard habitat features such as vegetation types and physical structure. Selection of habitat based on thermal attributes may be of particular importance for ectothermic species, especially in colder climates. In British Columbia, Canada, Western Rattlesnakes (*Crotalus oreganus*) reach their northern limits. While commonly associated with low-elevation grasslands and open Ponderosa pine habitats, recent work indicates that some populations of these animals may use higher-elevation Douglas-fir forests. The reasons and implications for this striking contrast of habitat use patterns by these animals was the subject of this thesis. I investigated the reason(s) for this phenomenon by monitoring the migratory movements of 35 snakes away from 10 different den sites, and comparing it to thermal landscape GIS maps generated for different periods of the active season. My work confirmed that dichotomous habitat use by denning populations of these snakes occurs throughout much of their range, and rattlesnakes in this region can no longer be strictly associated with grassland habitat. I found that snakes utilizing the higher-elevation forests not only moved relatively further during the course of their annual migrations, but were also more likely to use warmer areas of the landscape during their annual migration. In addition to thermal benefits, prey availability and/or outbreeding may be at least partially responsible for these patterns, but at this time there is limited data to test these alternative hypotheses. Regardless, snakes utilizing the higher-elevation forests had better body condition, indicating a definite advantage to this strategy. On a smaller scale, thermoregulatory behaviours appear to be less constrained by thermal factors in forest habitats, potentially allowing forest snakes increased time for hunting and travelling. Insight into these and other behavioural differences between neighbouring rattlesnake populations will allow managers to tailor management strategies to specific dens. Finally, the local and landscape scale patterns I detected have obvious repercussions for snakes in the event climate change produces shifting ecosystem boundaries and thermal regimes.

Keywords: migration, thermoregulation, Western Rattlesnake, habitat use

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CHAPTER 1. GENERAL INTRODUCTION AND BACKGROUND INFORMATION

Understanding habitat and resource use on multiple scales is fundamental to the conservation and management of any wildlife species. Habitat and resource selection can be defined as a hierarchical process through which an animal "decides" by innate and/or learned behaviours what resources and components of a habitat to utilize (Johnson 1980, Hall et al. 1997). Habitat itself has been defined by Hall et al. (1997) as the resources and conditions in an area that enable the survival and reproduction of an organism. This includes vegetation attributes, geographic features, and a host of other factors. Within the past decade, the measurement of habitat and resource selection by animals has grown increasingly complex (Rhodes et al. 2005, Frye et al. 2013, Byrne et al. 2014), with particular focus being directed towards different scales of selection. These scales include (but are not limited to) geographic range, home range and habitat use within a "home range" (Johnson 1980).

Temperature or thermal attributes on a variety of scales may be important in the selection of resources by ectotherms (such as reptiles), just as vegetation may be key to habitat selection by herbivores. However, the availability of heat is less-easily recognized, mapped, or quantified. The thermal landscape is a result of the complex relationship between incoming solar radiation, terrain and ground cover (Huang et al. 2014). Many studies have considered various aspects of behavioural thermoregulation in reptiles (Huey 1974, Diaz 1997), and there is consensus that habitat features influence thermoregulation are important factors in habitat selection by these animals (Diaz 1997, Blouin-Demers and Weatherhead 2001a). The relationship between the thermal environment and resource selection in reptiles has been investigated primarily on very fine scales. Thermal resource selection on a landscape scale, however, has rarely been considered. It is possible that ectothermic animals, such as reptiles, evaluate the thermal 'quality' of habitat, essentially viewing thermal regime as an environmental resource (Huey 1991) and a component of habitat selection.

Selection for thermal resources may be particularly important for reptiles in northern temperate zones, where they experience a broad suite of climatic conditions, both seasonally and on shorter time scales. Cooler temperatures and a shorter active season present challenges (Gregory 2009, Macartney et al. 1989). Thermal conditions also vary spatially as a result of environmental factors, such as vegetation cover and terrain (*e.g.,* slope and aspect). As many physiological processes in reptiles are temperature dependent, there exists an optimal range of internal temperatures that may be maintained by physiological, morphological and/or behavioural adaptations. Above and below this range, an animal's performance is suboptimal (Huey and Stevenson 1979). Operating within this optimal range will result in higher efficiency while foraging or avoiding predation, in turn leading to increased reproductive success and, eventually, increased fitness (Huey and Berrigan 2001). The benefit of an ectothermic strategy is that animals are able to convert a larger portion of assimilated energy into growth and reproduction (Gans and Pough 1982) and can therefore survive in less productive ecosystems. The cost, however, is that time devoted to thermoregulation is time not spent feeding or mating, both of which directly influence fitness (Blouin-Demers and Weatherhead 2001a), and that animals forced to expose themselves more during thermoregulatory activities (e.g., basking) may experience increased predation risk (Blouin-Demers and Weatherhead 2002b).

Reptiles have evolved life history strategies and tactics to deal with fluctuations in temperature. For some species, cold winter temperatures require hibernation (Aleksiuk 1976, Gienger and Beck 2011, Harvey and Weatherhead 2006, Leuth 1941), either in individual retreats (*e.g*., gopher snakes, Bertram et al. 2001) or in communal hibernacula (e.g., rattlesnakes and garter snakes, Bertram et al. 2001, Macartney et al. 1989). During the active season, snakes may undergo annual migrations on a variety of scales in search of resources, potentially including thermal conditions that would allow the snake to remain within tolerance limits for temperature. For instance, in rattlesnakes, the acknowledged optimal range of temperatures is 26.5ºC to 32ºC (Klauber 1982), although these snakes are able to withstand temperatures near the freezing mark (Hobbs 2007) and as high as 37ºC (voluntary maximum) (Klauber 1997). As reptiles have limited internal thermoregulatory mechanisms, they generally regulate body temperature through behaviour. Thermoregulation may include both small scale (local) movements (*e.g*. from open areas to cover objects) as well as large scale (migration) movements. Thermal selection at landscape scales may be particularly important to terrestrial reptiles that routinely undergo energetically expensive annual migrations, notably snakes in northern regions (Macartney and Gregory 1988, Macartney et al. 1988, Larsen et al. 1993, DeGregorio et al. 2011).

The conservation of snakes living in temperate zones is of increasing concern, to a large extent due to the thermal constraints placed on these animals by living in cooler regions. Understanding the thermal ecology of these species, and the relationship between thermal ecology and resource selection, is important in successful conservation of snake and lizard species at northern latitudes. As temperatures affect physiological processes including reproduction and growth, thermal ecology can be directly linked to population dynamics (Peterson et al. 1993). Cooler environments contribute to limitations on population growth, by way of biennial (or longer) reproductive cycles and costly migrations, and therefore, can impact overall success of a species. These natural population constraints are then coupled with anthropogenic stressors, making these populations more susceptible to impacts. As most ectothermic species in Canada occur at their northern most range limit, and at low density (Lesica and Allendorf 1995), increasing our knowledge of thermal ecology and effectiveness of protection and management strategies is imperative for conservation. Now, more than ever, we need to understand how animals are responding to their environment in terms of resource use and selection, including thermal relationships.

The Western Rattlesnake: status and ecology

The Western Rattlesnake (*Crotalus oreganus*; Figure 1.1) is the northernmost viper (Family Viperidae) in the Western Hemisphere. The species' range extends from northern California, USA, to the southern interior of British Columbia, Canada. Within British Columbia, the animals have a disjunct range: The northern part of their range stretches east from the town of Lytton, south to Merritt, and north to the city of Kamloops, approximately 190 km north of the USA border. In southern BC, they are found throughout the Okanagan valley as far north as the city of Vernon, approximately 140 km from the USA border. Two small populations occur in the Boundary regions of Grand Forks and Christina Lake, close to the border with the USA (Figure 1.2). Due to the limited range of the animal in Canada, and the high degree of human pressure in this part of British Columbia, the Western Rattlesnake currently is considered of 'Special Concern' within the province of British Columbia (BC Conservation Data Centre 2015), while being designated as 'Threatened' at the federal level (Committee on the Status of Endangered Wildlife in Canada 2015).

Western rattlesnakes are one of three venomous snakes in Canada (Matsuda et al. 2006), and one of the larger snake species in British Columbia, with adult snout-to-vent lengths (SVL) reaching 1.2 m (Ashton 2001, Macartney et al. 1990). Western rattlesnakes prey upon a variety of animals across their range. Small mammals make up the bulk of their diet and can include squirrels, marmots, chipmunks, voles, shrews, deer mice, and rabbits (Macartney 1989, Wallace and Diller 1990). In British Columbia, birds, amphibians, and other snakes are occasionally consumed as well (Macartney 1989).

Western rattlesnakes are viviparous snakes, with females giving birth to live young on a triennial or longer cycle (Macartney and Gregory 1988). Mating occurs in June though to August; however, fertilization is delayed until emergence from hibernation the following spring (Macartney 1989). Following a gestation period of 3-4 months during which gravid females generally remain in the vicinity of the den and abstain from feeding (Macartney 1989), young are born in August or September, and enter hibernation shortly thereafter. The physical condition and survival of post-parturient mothers is reduced compared to non-reproductive and gravid females (Macartney 1985). This is related to high rates of energy loss during gestation and reduced energy intake in the reproductive year (Amarello et al. 2011). Delayed physical recovery from reproduction is associated with the relatively lengthy reproductive interval (Macartney 1985). Males and non-gravid females generally migrate away from the hibernacula into habitats used for foraging and mating (Macartney 1985). In British Columbia, rattlesnakes are generally associated with dry, semi-arid grassland ecosystems and open Ponderosa pine forests (Matsuda et al. 2006). Hibernacula are typically found on south-facing slopes, between 500-625 m of elevation and associated with rocky outcrops, fissures and talus slopes (Macartney and Gregory 1988, Bertram et al. 2001).

Rattlesnakes in British Columbia occupy hibernacula from approximately October to April (Macartney 1985, Macartney and Gregory 1988). The distribution of rattlesnakes during the active season, from May to September, is considerably less clear. Recent work by Gomez et al. (2015) has led us to question the stereotypic association between rattlesnakes and grassland habitats. Both large and small movements in grassland and open forested habitats have been documented (Charland et al. 1993, Gomez et al. 2015, Brown et al. 2009, Lomas et al. 2015). Movements and habitat associations appear to vary considerably

Figure 1.1. An adult Western Rattlesnake (*Crotalus oreganus*) in coarse woody debris north of Kamloops, British Columbia (photo by author).

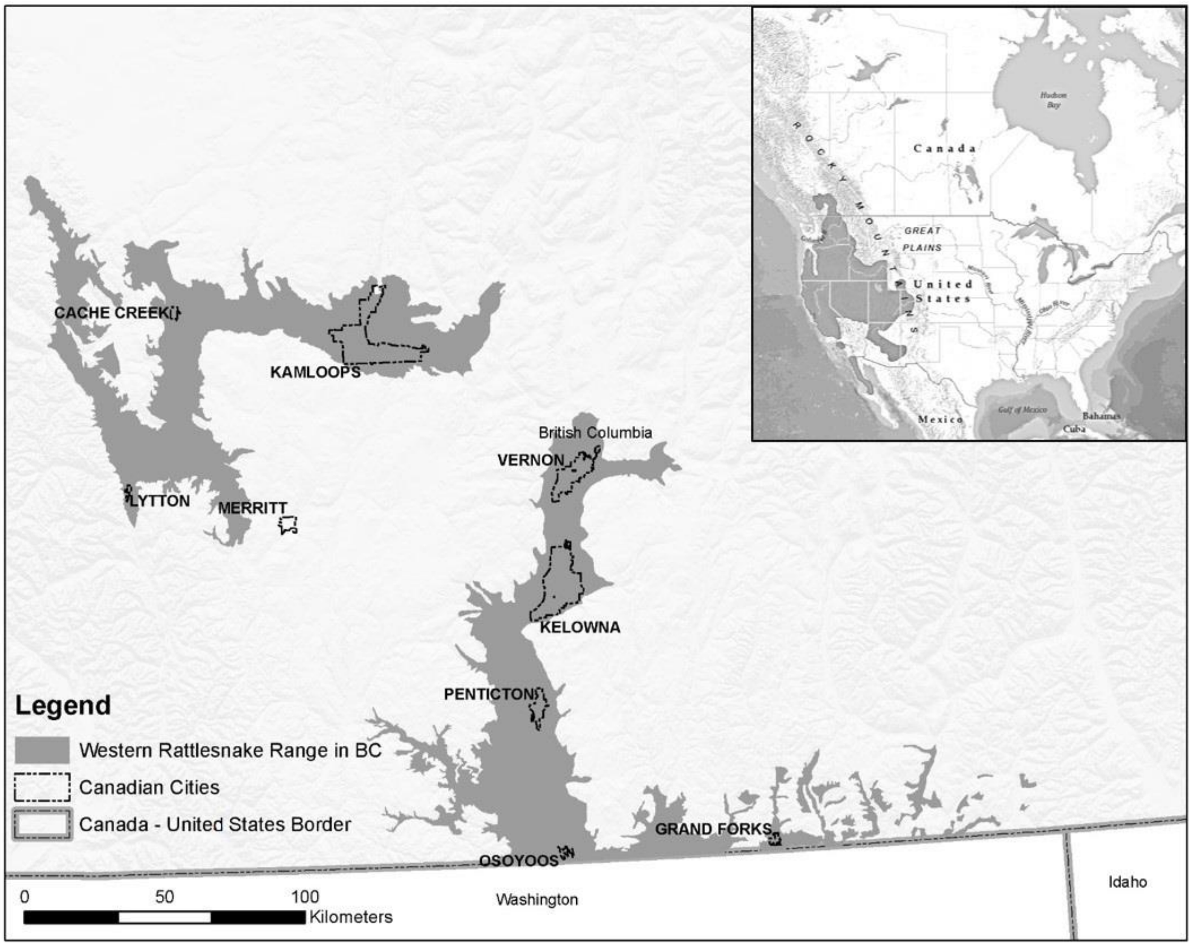


Figure 1.2. The range of the Western Rattlesnake (*Crotalus oreganus*) in the Southern Interior of British Columbia (adapted from BC Conservation Data Centre 2015). Inset (International Union for Conservation of Nature 2015) depicts the location of the species' range relative to North America.

between populations, and snakes in at least one population have been documented travelling to and using higher elevation Douglas-fir forests as summer habitat, rather than staying in the 'traditional' lower-elevation grasslands habitat and mid-elevation Ponderosa pine open-forest (Gomez et al. 2015). This observation supports anecdotal reports of rattlesnakes using forested habitats (Charland et al. 1993). While the use of forest habitat by rattlesnakes has been documented in other parts of North America (Reinert and Zappalorti 1988, Harvey and Weatherhead 2006, Waldron 2006), this phenomenon has yet to be thoroughly examined in British Columbia. The motivation for using these atypical habitats is unclear, although thermal habitat selection at various levels may explain significant departures from traditional habitat associations.

In this thesis, I explore the relationship between active season movements of Western Rattlesnakes and the thermal properties of the landscape. Radio-telemetry and GIS modelling were used to study the seasonal movement patterns of rattlesnakes originating from a number of dens within the range of the animal in British Columbia. For each denning population, I predicted the snakes' migratory behaviour according to the thermal properties of the surrounding landscape.

More specifically, my thesis addresses the following questions:

1. Do thermal patterns on the landscape dictate the migratory movements of rattlesnakes in British Columbia?
2. Do thermal attributes of landscapes influence the snakes' habitat selection on a fine scale?
3. Are there costs and benefits associated with using habitats that differ in thermal properties?

In the remaining portion of this chapter, I will provide a more detailed overview of my study sites within the range of rattlesnakes in the Thompson-Nicola and Okanagan-Similkameen valleys of British Columbia. In Chapter 2, I combine radio-telemetry locations of rattlesnakes with a Geographic Information System (GIS) model to investigate and characterize the thermal properties of open and forested habitats used by the animals. In Chapter 3, I examine the thermoregulatory consequences to the snakes of occupying different habitats over the summer months. Lastly, in Chapter 4, I summarize my findings and discuss the implications that my results have on management and conservation of the Western Rattlesnake in British Columbia.

Study site description

Over two field seasons in 2010 and 2011, I studied Western Rattlesnakes at 6 sites in the Thompson-Nicola region (50.8°N, 120.6°W) and 4 sites in the Okanagan-Similkameen region (49.3°N, 119.6°W), two of the largest areas in the rattlesnakes' range in the Southern Interior of British Columbia (Figure 1.3).

The Thompson-Nicola and Okanagan-Similkameen valleys consist of mostly semi-arid grassland and dry-forest habitats (Grassland Conservation Council 2004) (Figure 1.4). At lower elevations, bunchgrass grasslands dominate, with dominant species being Bluebunch Wheatgrass *(Agropyron spicatum)* and Big Sagebrush *(Artemisia tridentata*). Under the province's biogeoclimatic classification system (Meidinger and Pojar 1991), this vegetation community is denoted as the Bunchgrass zone. In most areas, the Bunchgrass zone transitions into the Ponderosa zone, which is characterized by dry forest of primarily Ponderosa Pine (*Pinus ponderosa)* with a bunchgrass understory. In some locations; however, the Bunchgrass zone transitions directly into the Interior Douglas-fir zone. With increasing elevation, and/or a shift to north-facing slopes, Douglas-fir (*Pseudotsuga menziesii*) becomes the more prominent tree species with a low understory of shrubs and grasses. Open habitats were characterized as having less than 10% canopy cover and generally occurred at elevations of 300 to 800 m in the Bunchgrass and Ponderosa Pine biogeoclimatic zones. Forested habitats, those with greater than 10% canopy cover, generally occur at elevations of 500 to 1200 m, and in the Interior Douglas-fir biogeoclimatic zone.

The climate in these valleys is characterized by hot, dry summers and cold (below zero) winters with little precipitation. The average temperatures in the Thompson-Okanagan during this study (2010 and 2011) were similar to the temperatures seen over the last 40 years (Figures 1.5 and 1.6). Precipitation during the study varied, although not significantly, from the 30-year historical average, with increased rain in the late springs and drier conditions in late summers (Figure 1.7; Environment Canada 2013).

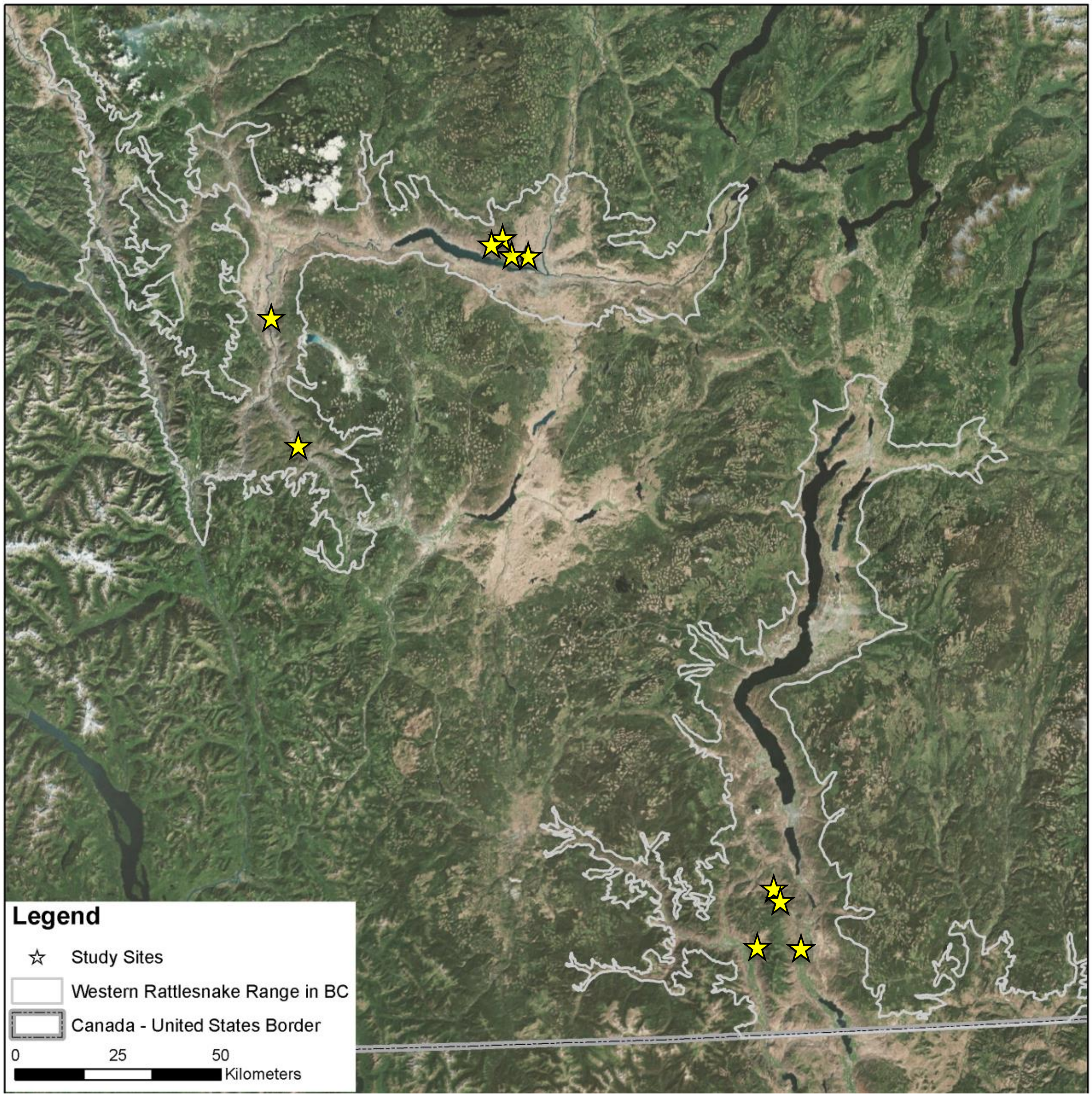


Figure 1.3. Location of study sites within the range of the Western Rattlesnake in British Columbia, Canada.

Figure 1.4. Typical and atypical habitat associations for the Western Rattlesnake in British Columbia. Open grassland habitats generally occur at elevations of 300 to 800 m in the Bunchgrass and Ponderosa Pine biogeoclimatic zones. Forested habitats generally occur at elevations of 500 to 1200 m in the Interior Douglas-fir biogeoclimatic zone (Meidinger and Pojar 1991). Hibernacula typically occur at elevations of 500 to 625 m on south-facing, rocky slopes (photos by author).

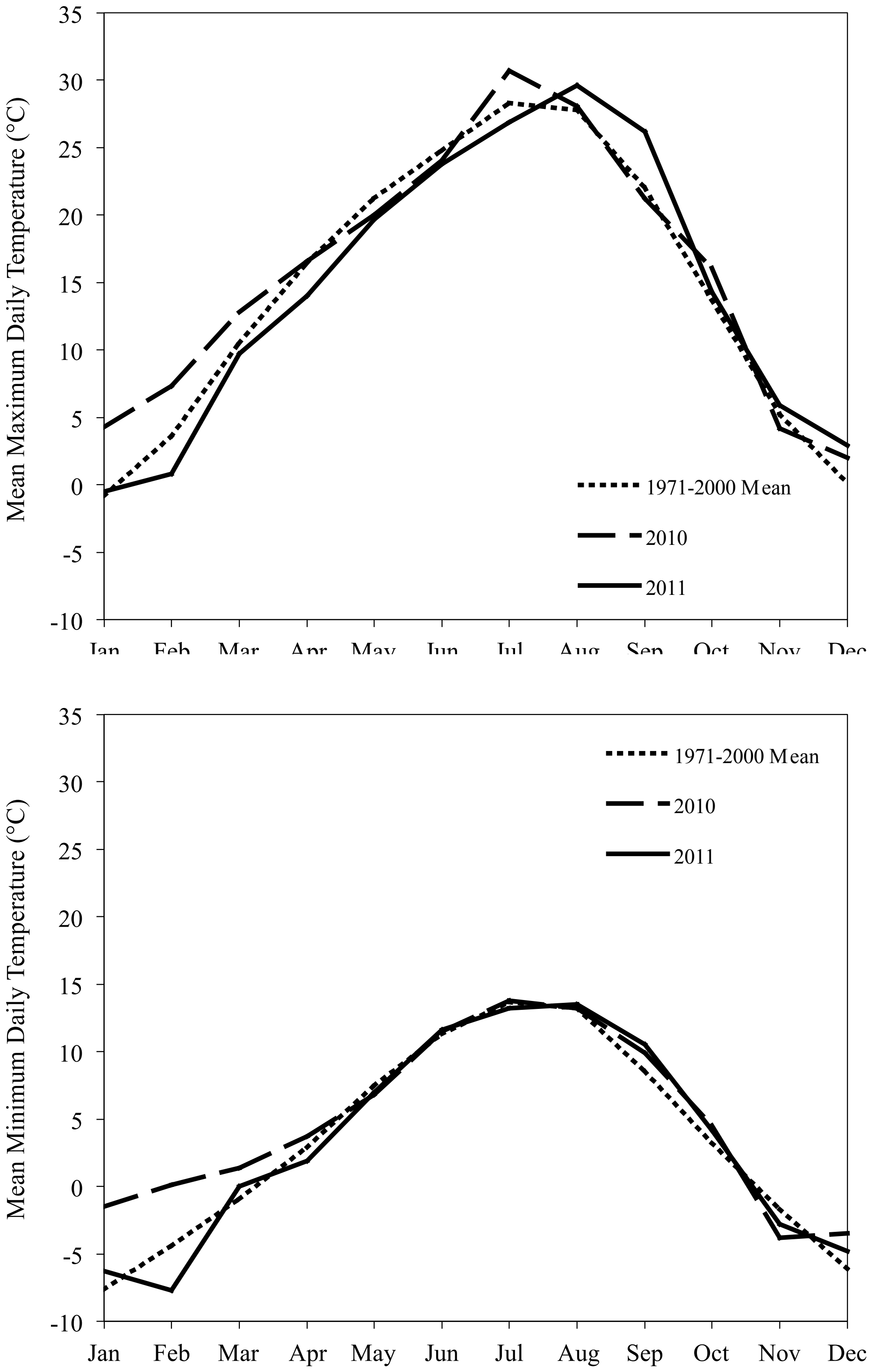


Figure 1.5. The mean maximum and minimum daily temperatures in the Thompson-Nicola region during the year of this study (2010 and 2011) as compared to the historical 30-year average daily maximum and minimum temperatures (Environment Canada 2013). Temperatures measured at the Kamloops Airport.

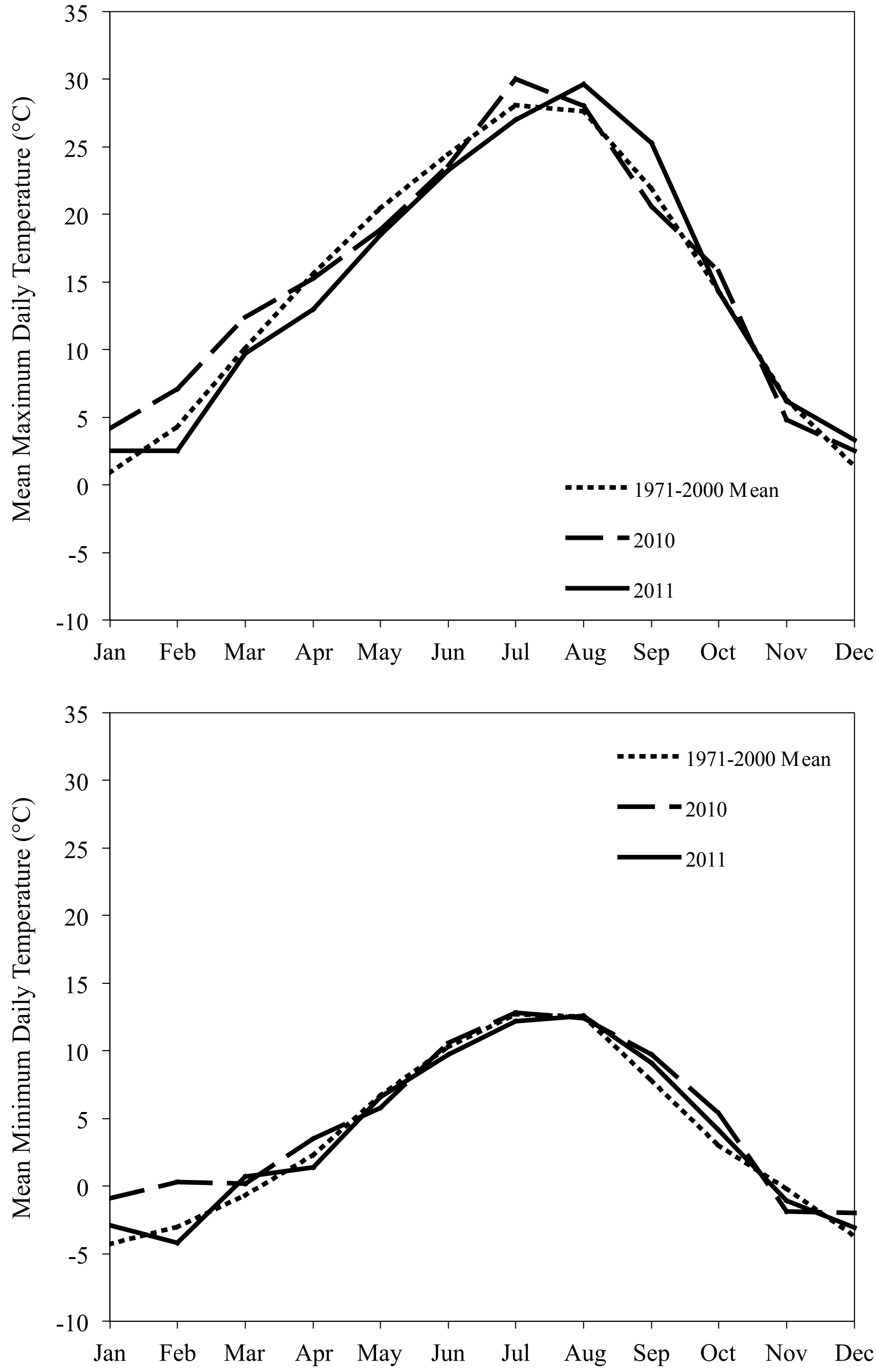
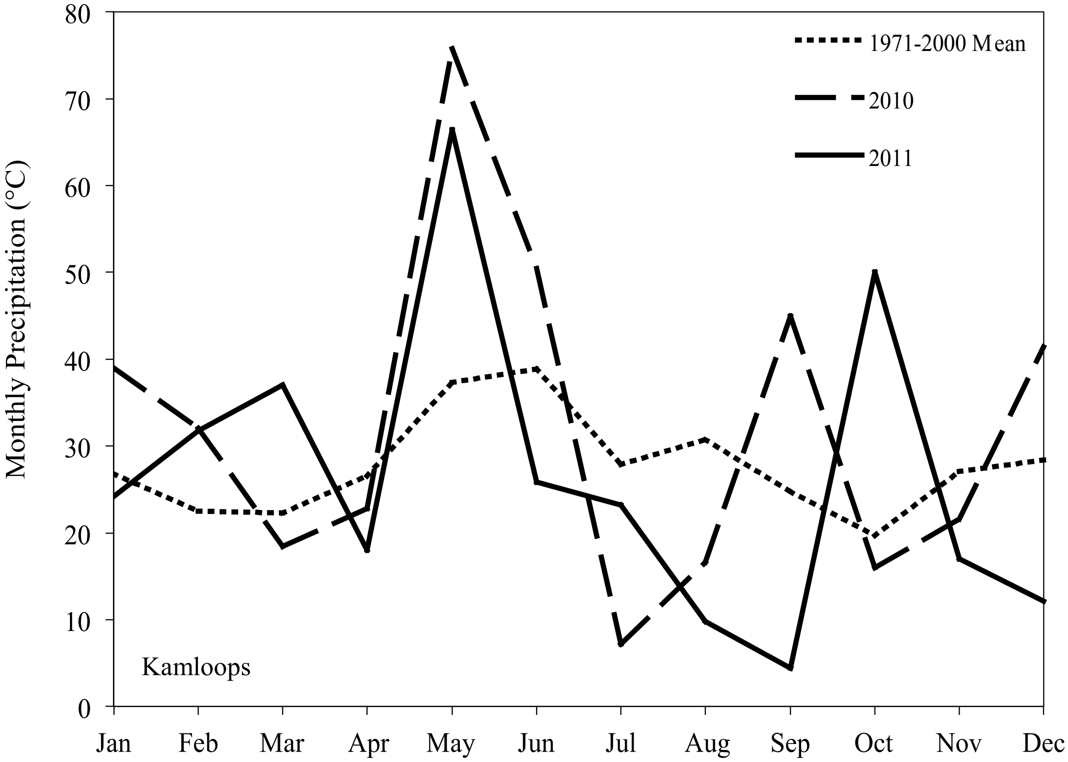


Figure 1.6. The mean maximum and minimum daily temperatures in the Okanagan-Similkameen region in 2010 and 2011 as compared to the historical 30-year average daily maximum and minimum temperatures (Environment Canada 2013). Temperatures measured at the Penticton Airport.



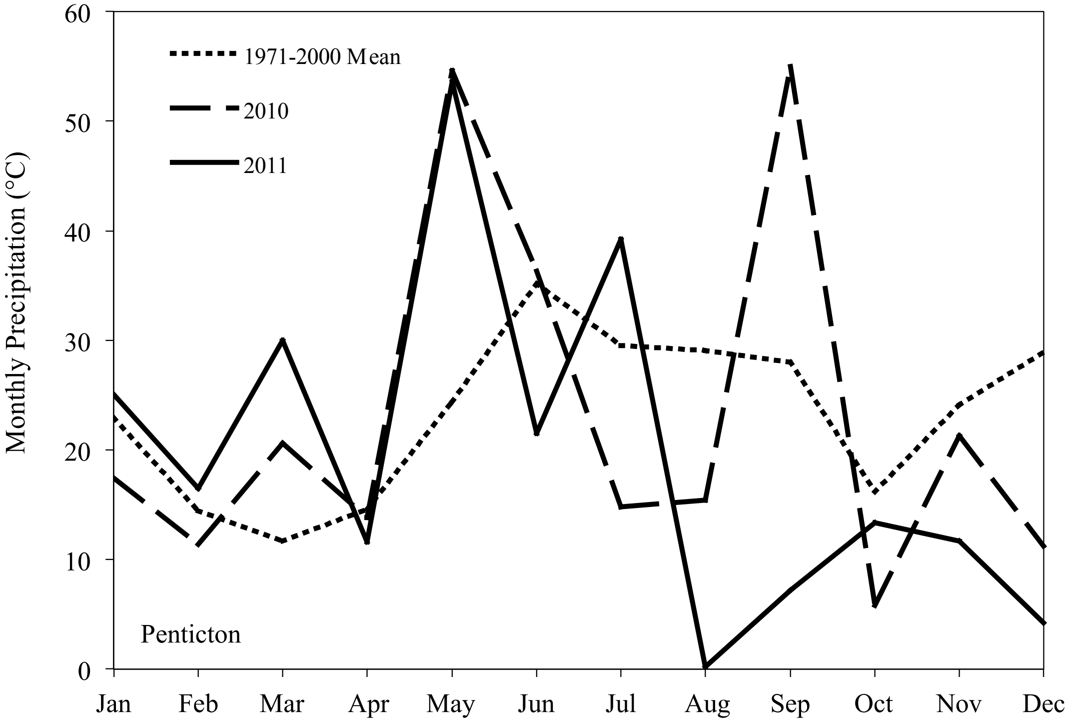


Figure 1.7. Monthly precipitation in the Thompson-Nicola (above) and Okanagan-Similkameen (below) regions in 2010 and 2011 as compared to the historical 30-year average (Environment Canada 2013). Precipitation measured at the Kamloops and Penticton Airports.

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CHAPTER 2. MODELLING USE OF FOREST HABITATS BY WESTERN RATTLESNAKES: DO THERMAL PATTERNS ON THE LANDSCAPE DICTATE SNAKE MOVEMENT PATTERNS?

INTRODUCTION

Migrations occur when animals move explicitly to take advantage of resources that are distributed through the environment (Duvall et al. 1990, Dingle and Drake 2007, Ramenofsky and Wingfield 2007, Dingle 2014, Hopcraft et al. 2014). Generally, these resources will be food, water or mates (Ashton 2003), although refuge from environmental conditions may also come into play (Dingle 2014). For animals inhabiting cooler regions, heat is a resource that potentially drives migration. Both endotherms and ectotherms may need to respond to the availability of heat that is distributed unequally across habitats, both spatially and temporally [e.g. reptiles (Huey 1991), birds (Barnagaud et al. 2013), mammals (Wiemers et al. 2014), gastropods (Bates et al. 2005)]. Ectotherms occupying relatively harsh or variable environments may need to be particularly responsive to the thermal properties of landscapes in order to complete basic life histories. Thus, there is consensus that a prominent factor in habitat selection by ectotherms is temperature (Huey 1991, Diaz 1997, Blouin-Demers and Weatherhead 2001), although this relationship has been primarily studied on a fine-scale (Brown et al. 1982, Diaz 1997, Harvey and Weatherhead 2006, Row and Blouin-Demers 2006). The role of large-scale thermal properties of landscapes on seasonal migration patterns remains largely unexplored.

In temperate regions, reptiles at their northern range extents may experience challenging thermal conditions, allowing large-scale thermoregulatory behaviours to evolve. Reptiles that occur in areas with cooler climates may be dependent on specific hibernation sites, and during the short active season may have limited time to fulfill basic life history requirements. The scales at which reptiles respond to these challenges are unknown. While thermal microclimate selection may enable reptiles to use any habitat(s) encountered, large scale thermal habitat properties may play a role.

In British Columbia, extensive annual movements (*e.g.,* up to several kilometres) away from the overwinter hibernacula have been documented for Western Rattlesnakes, *Crotalus oreganus* (Macartney 1985, Charland et al. 1993, Bertram et al. 2001, Hobbs 2007, Brown et al. 2009, Gomez et al. 2015). The driving mechanisms for these summer migrations remain unclear. Access to food and/or avoidance of conspecifics during the foraging period may be responsible, as may be access to mates later in the summer [mating takes place away from the hibernaculum, unlike that in northern denning populations of garter snakes (Gregory 2009)]. Thermal resource selection may be at least partially dictating these seasonal movements, both for thermoregulatory advantage and because mountainous terrain and a relatively cool climate create a matrix of thermal patches within which the snakes must operate.

Thermal selection at the landscape level may help explain departures from traditional habitat associations recently detected for these rattlesnakes. In British Columbia, this animal has been generally associated with grassland ecosystems and open Ponderosa pine forests (Matsuda et al. 2006), but recent work by Gomez et al. (2015) has documented at least one departure from the stereotypic association between rattlesnakes and grassland habitats in this region. In that study, rattlesnakes from one population were documented travelling to higher-elevation forests (Douglas-fir) as opposed to staying in 'traditional' lower-elevation grasslands habitat and mid-elevation Ponderosa pine open-forest.

Differences in movements and habitat use between denning populations may be caused in part by temperature selection at the landscape level. Thermal characteristics on the ground will be influenced by the incident solar radiation (Iqbal 1983) that, in turn, is influenced by the substrate ruggedness, day length, topographical shadows, and solar azimuth at the given latitude. On an annual time scale, seasonal and daily variation in these dynamics likely do not cause major changes in vegetation communities used by ecologists to delineate 'habitats'; however, they may provide significantly different resources, from a snake's point of view, at different points in the season and across a heterogeneous landscape. Over the course of the active season, the average thermal properties of the landscape may influence migratory and large-scale movement patterns. If snake movements could be linked to the thermal attributes of the landscapes, it would provide powerful new insight into how the migration ecology of these animals may be influenced. Being able to predict such movements also would be an important conservation tool.

Geographic Information Systems (GIS) allows habitat use and animal movements to be examined on increasingly larger scales (Erickson et al. 1998). Use of pre-existing digital maps, such as those containing ecological zones, combined with the use of algorithms, like a solar radiation calculator, enables one to extrapolate the result of empirical research over a much larger and potentially heterogeneous spatial scale, such as the range of a species. Solar insolation has been used to predict hibernacula locations (Hamilton and Nowak 2009), but to date it has not been applied to investigate snake summer habitat use.

The goal of this chapter is two-fold. First, I use telemetry to monitor the seasonal migration of snakes from a larger sample of hibernacula than in the Gomez et al. (2015) study. From the resulting data, I demonstrate the dichotomy of habitat use more clearly. This allows me to use GIS to examine the role that thermal attributes of the landscape may play in large-scale habitat selection by these animals. My working hypothesis is that snakes select warmer areas within the available habitat (‘landscape’) to gain thermoregulatory benefits over the course of the northern summer. Thus, I examine whether thermal properties, like other long-term resource distributions, are correlated with habitat use by animals.

METHODS

Study animal and site selection

This study was conducted in 2010 and 2011 in the Thompson-Nicola (50.8°N, 120.6°W) and Okanagan-Similkameen (49.3°N, 119.6°W) regions of British Columbia, Canada. This area encompassed nearly the entire range of the Western Rattlesnake in the province. Study hibernacula were selected to ensure a diversity of thermal conditions was present across the landscape surrounding the hibernacula. This was done using preliminary thermal maps of the area created with GIS (see Mapping and Analysis for details). Considerations also were made for logistics, land ownership and access. Hibernacula only were considered for the study if the estimated population was more than 12 rattlesnakes (BC Conservation Data Centre 2009). This was to reduce the likelihood that the study would impact the viability of the population. In total, ten hibernacula were chosen for study – six in the Thompson-Nicola region (6 in 2010, and 1 in 2011) and 4 in the Okanagan-Similkameen region (in 2011) (see Chapter 1, Figure 1.3).

Seventeen snakes from 6 hibernacula were selected for inclusion in the study in 2010, and 18 snakes from 5 hibernacula were selected in 2011. I targeted at least three snakes from each hibernaculum in order to provide replication. However, at 2 sites only 1 and 2 snakes were found to be suitable for inclusion in the study. At the remaining 9 sites, either 3 or 4 snakes were selected as study animals.

Animal capture, processing, selection and surgery

I visited each targeted hibernacula repeatedly (*i.e*., at least twice) during the spring emergence period (April 15 – May 7). During this time, any rattlesnakes encountered were captured using snake tongs and placed temporarily in a collapsible mesh laundry basket. Snakes were weighed individually in a canvas bag. Snakes within the target weight range for telemetry (*i.e*., heavier than 400g) then were ushered individually into a plexiglass tube for sex determination via hemipenal probing (Schaefer 1934). I selected only male snakes for radio-telemetry as female rattlesnakes are known to adjust their migratory behaviour according to the timing of their individual reproductive cycle (Macartney and Gregory 1988). While in the plexiglass tube, snakes were injected with sterile Passive Integrative Transponder (PIT) tags for permanent identification. The tag was inserted subcutaneously in the posterior 1/3 of the animals' body using a plastic syringe-style implanter. The use of PIT tags has been successful in snake mark-recapture studies and has been reported to have minimal negative effects on the animals (Jemison et al. 1995). To enable quick identification of individual snakes in the field, including those not involved in the telemetry study, I also marked the snakes with a unique colour pattern on sides of their rattle using commercial nail polish. Animals selected for telemetry were transported by vehicle to a veterinary clinic in a towel-lined, aerated rubber container.

Radio-telemetry

Each study animal was surgically implanted with an SB-2 radio-transmitter (Holohil Systems Inc., Ontario, Canada), weighing 3.8 - 5.2 grams. No implant package exceeded 2.7% of the snake's weight and transmitter lifespans ranged from 5-10 months. Surgeries were carried out by veterinarians following the protocols described by Reinert and Cundall (1982) with modifications by Reinert (1992). The implanted snakes were held for approximately 24-48 hours post-operation to permit recovery from sedation and allow adequate rehydration. Each animal was then released at its exact point of capture. Transmitters were removed from re-captured snakes either when they returned to their hibernacula in autumn of the same year, or as they emerged from hibernation the following spring.

I tracked and located telemetered snakes every 3 to 7 days between emergence (April/May) and egress (September/October) using an R-1000 telemetry receiver and RA-159 handheld Yagi directional antenna. When each snake was located, I recorded date, time, UTM coordinates using a handheld GPS unit (Garmin, GPS 76Cx), canopy closure using a spherical crown densitometer (Forestry Suppliers, Convex model A), and habitat type (see below).

Mapping and analysis

Snake location data were filtered to include only those that constituted independent movements, defined as more than 10 m from the previous location (Gomez et al. 2015). Each location was assigned to one of two habitat types to enable comparison: those with <10% canopy closure (bunchgrass and open-canopy Ponderosa Pine) were designated as "Open" habitats, while locations with >10% canopy closure (Interior Douglas-fir forests) were classified as "Forest" habitat. Additionally, each snake was later assigned a category based on the type of habitat reached at the end point of the snakes' migration, the 'Destination habitat'. This classification of habitats allowed comparison between snakes using typical (open grassland) habitats and atypical (forested) habitats.

Annual migration paths were created for each individual snake by connecting locations. The maximum straight-line distance travelled by each snake was calculated using the furthest detected location from each animal's hibernaculum. Outgoing migration was defined as the snakes' movements up to the most distant point (i.e. the snake's 'turn-around' point); homeward migration constituted those movements that brought the animal back to its hibernaculum. Home ranges were measured using mean minimum convex polygons (MCP), which has been suggested to be suitable for home range estimation in herptofauna (DeGregorio et al. 2011, Row and Blouin-Demers 2006).

I created a thermal model of the landscape surrounding each hibernaculum, using solar insolation as a proxy for temperature. Thus, these maps did not show the actual temperatures a snake would experience in any given year, but the general topographic patterns in temperature expected across the landscape. Incident solar radiation simulations were run using the Area Solar Radiation tool in the Spatial Analyst extension in ArcGIS 9.3 (Environmental Systems Research Institute 2009). The simulation was based on a 25 m digital elevation model (DEM). The algorithm used by the tool uses slope, aspect, elevation, day length, latitude and solar azimuth to calculate the expected incident solar radiation at a given point on the landscape. The parameters used in the simulation included a sky size of 512 and a 14-day interval. The resulting landscape simulation was composed of raster images built on the predicted incident solar radiation for a cell size (pixel) of 25 m^2, with the thermal values being expressed in average daily Watt-hours per square meter (Wh/m^2).

After the landscape models had been constructed, I compared the thermal properties of the snakes' migratory movements to those theoretically available on the landscape. To start, the migration of each snake was divided into two major stages. The Outgoing migration captured the movements of the snake from the hibernaculum to its furthest point of displacement from the hibernaculum, and the Homeward migration or the return trip from the turn-around location to the hibernaculum. As snakes tend to use similar return paths back to the hibernaculum during the Homeward migration, the analyses were limited to the Outgoing migration. The Outgoing migration was further divided into an Initial stage and a Late stage, summarizing the movements of each snake in May/June and July/August respectively. I created three thermal metrics representing different aspects of the outgoing annual movements of the animals. The thermal metrics were calculated by averaging the incident solar radiation values for all pixels of the thermal landscape crossed by the migration path.

To create a set of random walk pathways to simulate the ‘available’ outgoing migration paths for each snake, I used Hawth’s tools (Beyer 2004) to generate 100 random walks originating at the hibernaculum. The actual movements of each snake were used to parameterize the random walks generated for that particular snake and landscape. Random walks were restricted in length to the maximum distance measured from the hibernaculum during the study, using an average turn angle equal to that measured in the field. For each of the 100 simulated random walks, I then calculated the three thermal metrics using the same procedure as described above for the outgoing migration pathway.

I compared the empirical thermal metrics for the telemetered snakes against the simulation distributions in three ways. Firstly, I determined what proportion of the empirical measurements fell within the top 50% of the 100 simulations (respective to each snake). I tested gross differences in these frequencies between snakes using forest destination habitat and snakes using open habitats, using χ^2 analysis (H_o: 50% of empirical observations will fall into the top half of the 100 simulations). Secondly, I determined the actual percentile value of each empirical thermal metric in relation to the 100 simulated values. I then compared these percentiles between the two categories of snakes using *t*-tests. Finally, I used Z-tests (Zar 1999) to determine the probability of selecting each empirical thermal measurement from the simulated distributions, respectively; I present the $\overline{x}$ and SD values for these metrics for each of the two categories of snakes, and once again use *t*-tests to test for the significance of the differences. These three analyses were repeated for each of the three stages of snake migration (Outgoing, Initial, and Late). Normality of the data were confirmed in all cases prior to analyses.

To coarsely depict the landscape surrounding each hibernaculum, I calculated a ruggedness index. A ruggedness value was calculated for each pixel (25 x 25 m) on the landscape using Relative Topographic position and the raster calculator tool in ArcGIS 9.3 (Environmental Systems Research Institute 2009). The topographic position of each pixel was identified with respect to its surrounding pixels (Jenness 2004, Riley et al. 1999). The average value of these pixels for each of the snakes’ outgoing migration paths was then determined. In addition, the average value of these pixels for an area with a radius of 4000 m surrounding each hibernaculum (determined based the maximum distance travelled by the snakes in this study) was then calculated, resulting in an average ruggedness value for each study hibernacula.

To determine the relationship between habitat ruggedness, thermal landscape characteristics, and habitat use, I examined the data in two ways. First, I examined the relationship between Destination habitat type and ruggedness index using a t-test, in a similar manner to the comparison between thermal migration path percentiles and the two categories of snakes. Next, I used a linear regression to examine the relationship between ruggedness index and percentile (as the dependent variable) in all three categories of migration.

Statistical considerations

All statistical analyses were performed in the program R version 2.12.1 (R Development Core Team 2011). Data were tested for normality by examination of histograms and using the Shapiro-Wilk test or the Kolmogorov-Smirnov test (Zar 1999). Homogeneity of variances between groups was tested using the Fligner-Killeen test (Conover et al. 1981, Crawley 2007). Percentage data were transformed using an arcsine transformation for analysis. A significance value of $\alpha=0.05$ was used to guide the interpretation of the results. Means are reported ± 1 standard deviation, unless otherwise stated.

RESULTS

In total, I used 35 snakes for radio-telemetry study. Morphology data of the telemetered animals, including length and weight, are detailed in Appendix A.

Twenty-nine of 35 telemetered snakes were tracked through their entire annual migration. Six snakes did not have their entire migration route completely documented. One snake could not be located between June and August, and only partial data and no turn-around point were obtained, so the snake was excluded from the migration analysis. Five snakes were predated upon in May and June, prior to reaching their migratory turn-around point. The transmitters of three of these snakes (all from the same hibernaculum) were recovered from an active red-tailed hawk (*Buteo jamaicensis)* nest. The transmitters from the other two snake mortalities also were recovered, but the deaths could not be linked to a specific predator. These snakes were not considered in the analysis due to incomplete data sets. One snake was predated upon in August, approximately 300 m from its hibernaculum during the return migration. As the snake had clearly reached its turn-around point, the data from this animal were included in the analysis as if the entire migration had been completed. In total, the migration data from 30 snakes were included in the analysis.

As expected, the snakes travelled away from the hibernaculum to summer habitats (Outgoing migration), reaching their most distant point from the hibernaculum on an average date of August 8 (with a range from June 23 to September 21). Snakes then returned to the hibernaculum (Homeward migration); most utilized the same approximate path back to the hibernaculum.

The mean maximum straight-line distance measured from the hibernaculum to the 'turn-around' point for the telemetered snakes was 1847.8 m ± 930.0 m (n=30, range=373.0 m to 3985.7 m). The mean MCP home range size observed for the tracked snakes was 52 ha ± 47.9 ha (n=30, range=1.5 ha to 194.7 ha). The mean migration metrics are presented in Table 2.1. No relationship between migration distance and home range size was observed (Figure 2.1). There were no significant differences observed between straight-line migration distances or home range sizes between the Thompson-Nicola and Okanagan-Similkameen regions [migration (t_{26}=1.42, P=0.170); home range (t_{24}=-0.36, P=0.720)].

All study hibernacula (and thus the starting points of all monitored migrations) were located in open habitats. From these sites, the mean distance to forest habitat was 656 m (± 958 m). Fifteen of the 30 snakes, henceforth termed 'Forest snakes', travelled to and used forests as a Destination habitat (*i.e.,* in the latter part of their outgoing migrations during July and August), while the use of open habitats through the entire migration was observed in the other 15 study snakes (henceforth termed 'Open-Habitat snakes' - see Table 2.1). Maximum straight-line distances reached from the hibernaculum were significantly longer for Forest

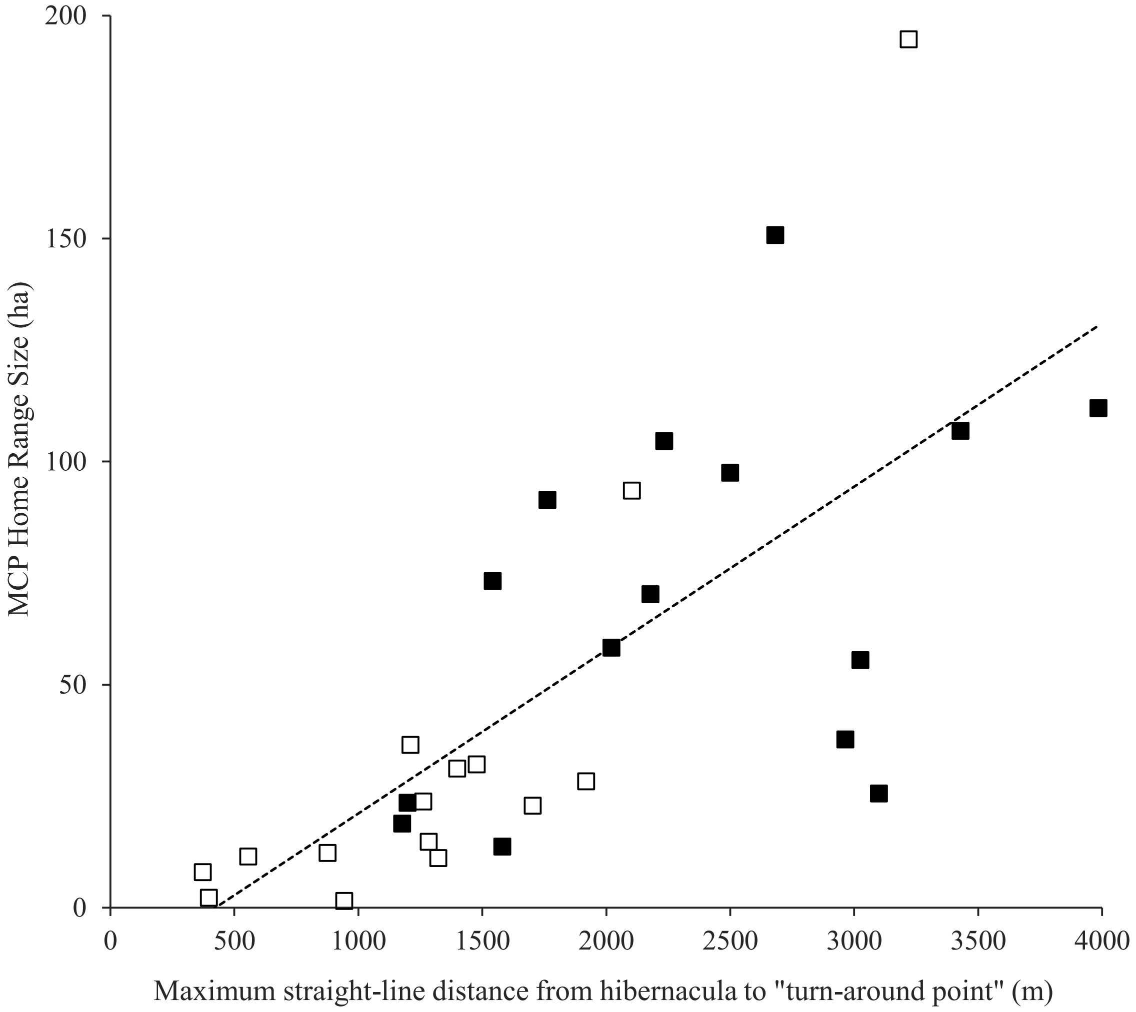
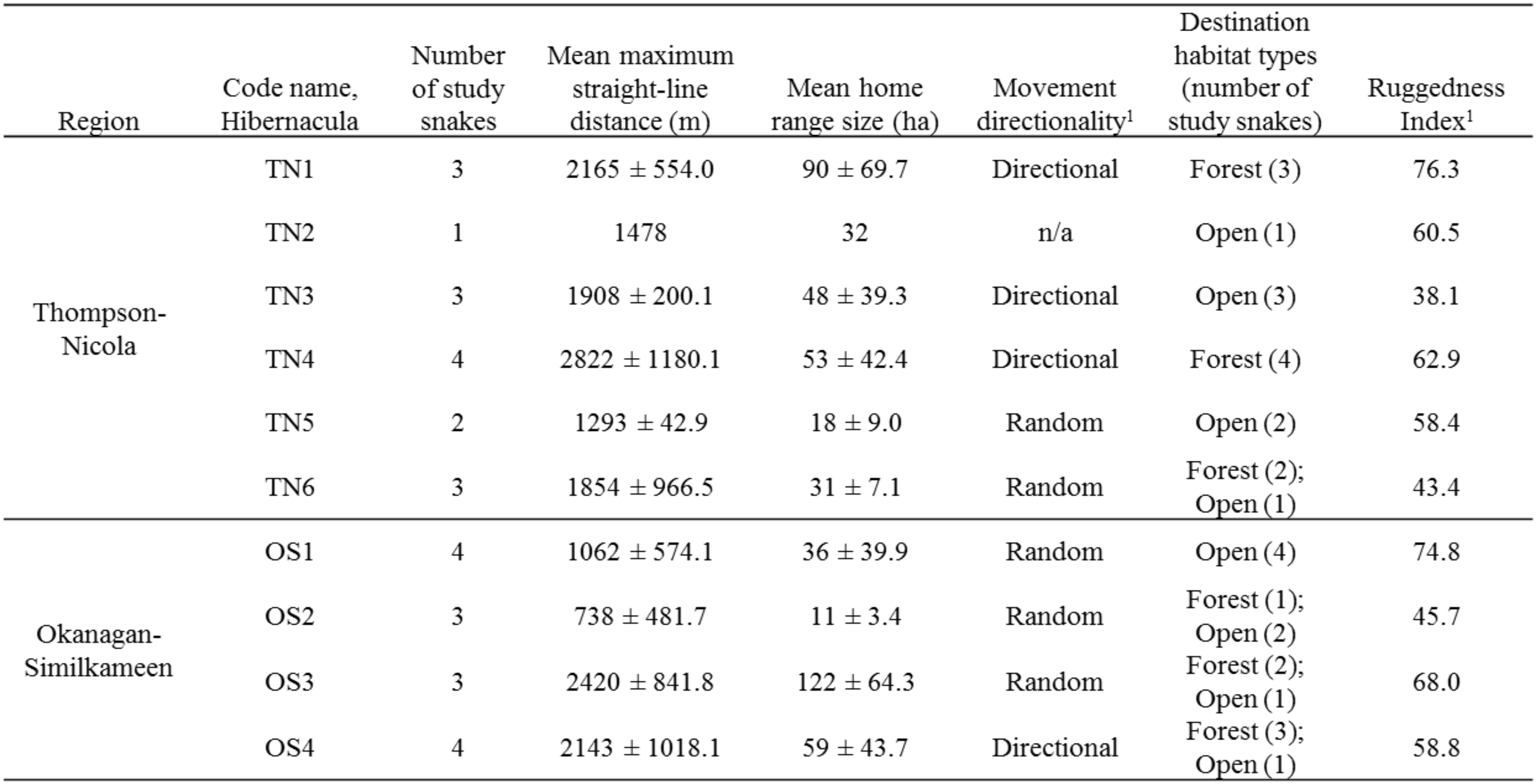


Figure 2.1. Relationship (R^2=0.51) between maximum straight-line distance travelled from the den to the furthest point of the migration and minimum convex polygon (MCP) home range size of Western Rattlesnakes in British Columbia. Forest snakes are represented by solid markers, Open-Habitat snakes are represented by open markers.

Table 2.1 Distances and trends of movements by Western Rattlesnakes departing from ten hibernacula. The snakes were radio-tracked throughout their summer migration in British Colombia in 2010 and 2011. The movements of snakes originating at the same den were considered Directional if all snakes tracked from the hibernaculum travelled trajectories a 40º range of each other and Random if snakes' trajectories ranged over more the 40º. The ruggedness index for each hibernaculum was calculated for an area surrounding the hibernaculum using Relative Topographic position.



Region	Code name, Hibernacula	Number of study snakes	Mean maximum straight-line distance (m)	Mean home range size (ha)	Movement directionality[1]	Destination habitat types (number of study snakes)	Ruggedness Index[1]
Thompson-Nicola	TN1	3	2165 ± 554.0	90 ± 69.7	Directional	Forest (3)	76.3
	TN2	1	1478	32	n/a	Open (1)	60.5
	TN3	3	1908 ± 200.1	48 ± 39.3	Directional	Open (3)	38.1
	TN4	4	2822 ± 1180.1	53 ± 42.4	Directional	Forest (4)	62.9
	TN5	2	1293 ± 42.9	18 ± 9.0	Random	Open (2)	58.4
	TN6	3	1854 ± 966.5	31 ± 7.1	Random	Forest (2); Open (1)	43.4
Okanagan-Similkameen	OS1	4	1062 ± 574.1	36 ± 39.9	Random	Open (4)	74.8
	OS2	3	738 ± 481.7	11 ± 3.4	Random	Forest (1); Open (2)	45.7
	OS3	3	2420 ± 841.8	122 ± 64.3	Random	Forest (2); Open (1)	68.0
	OS4	4	2143 ± 1018.1	59 ± 43.7	Directional	Forest (3); Open (1)	58.8

[1] See text for additional details on the determination of movement directionality and ruggedness index values.

snakes (2359 m ± 837.0 m; t_{27}=3.57, P=0.001), than Open-Habitat snakes for the entire season (1337 m ± 729.0 m). Additionally, MCP home range sizes for the entire season were larger for Forest snakes (69.3 ha ± 40.9 ha; t_{27}=2.07, P=0.047), than Open-Habitat snakes (35.0 ha ± 49.4 ha).

Due to my sample size of snakes at each study site (<4 from the majority of the study hibernacula), statistical analysis of migration directionality by the snakes from each hibernaculum was not possible. I therefore used a less-rigorous approach by classifying migrations from a particular hibernaculum as directional when the telemetered snakes leaving that hibernaculum displayed mean migration bearings within 40º of one another (Table 2.1). Within-hibernaculum groups of snakes whose migration bearings were more than 40º from one another were considered to have a random distribution. This distinction was made based on a natural break in the data and qualitative judgement of snakes' travel directions.

The snakes' movement paths over the simulated thermal landscape are shown in Figure 2.2 and 2.3. The empirical thermal metrics of the Forest snakes tended to occur in the upper half of the distribution of simulated migration paths significantly more often than Open-Habitat snakes, in all three categories of the migration (Outgoing, Initial and Late stages; see Figure 2.4, Table 2.2 A).

In all three categories of the migration (Outgoing, Initial, Late) the empirical thermal values derived from the migratory pathways of the Forest snakes were significantly higher than the same values for the Open-Habitat snakes, as compared to their respective simulated movements (Table 2.2 B). These differences were most noticeable during the Late stage of migration, when the thermal values of the empirical (observed) pathways for Forest snakes averaged near the 80th percentile, compared to a 50th percentile average for the snakes that remained in open habitats. In fact, the thermal values for the Open-Habitat snake migrations averaged close to 50th percentile scores in all three of the migration categories (Table 2.2 B, Figure 2.4.).

The average probability values (from z-test scores) as determined for the Outgoing portion of the migration were significantly lower for Forest snakes than Open-Habitat snake (Table 2.2 C). Very similar comparisons were seen for the Initial and Late stages of the migration (Table 2.2 C).

The ruggedness index values for migration paths were significantly higher for Forest snakes ($\bar{x}=77.7 \pm 23.0$; $t_{22}=3.09$, $P=0.005$) than for Open-Habitat snakes ($\bar{x}=56.6 \pm 13.2$). A significant effect of ruggedness was found for the percentile score of the empirical migration-path values for the Late migration category ($F_{1,28}=4.31$, $P=0.047$; $R^2=0.13$), but not for either the Outgoing migration ($F_{1,28}=4.05$, $P=0.054$; $R^2=0.13$) or Initial migration stages ($F_{1,28}=2.97$, $P=0.095$; $R^2=0.09$; Figure 2.5). Rattlesnake hibernacula with higher average ruggedness values were more likely produce snakes that migrated to forest habitat ($t_{25}=3.99$, $P=<0.001$).

DISCUSSION

Overall, the results of my study indicate that the annual migrations of these northern snakes are dictated, at least in part, by thermal attributes of landscapes at a relatively large scale. For ectotherms occurring at a high latitude, this in itself is intuitive, but what is more interesting is the fact the animals appear to travel relatively longer distances to access this habitat, and their movements take them out of the lower arid grassland valleys that might have been predicted to afford better summer habitat. This pattern was also not universal: exactly half of the animals I followed undertook the longer migrations into the higher-elevation forests, and slightly greater than half of the animals travelled into relatively warmer areas on the landscape. Thus, the thermal parameters I examined in this study do not fully explain the dichotomy of movements exhibited by snakes in this and previous study (Gomez et al. 2015), but they do shed light on the factors influencing migration patterns in northern herpetofauna.

Use of forest habitat by rattlesnakes is well-documented, but in locations considerably further south than my study location (Parker and Anderson 2007, Waldron et al. 2006,

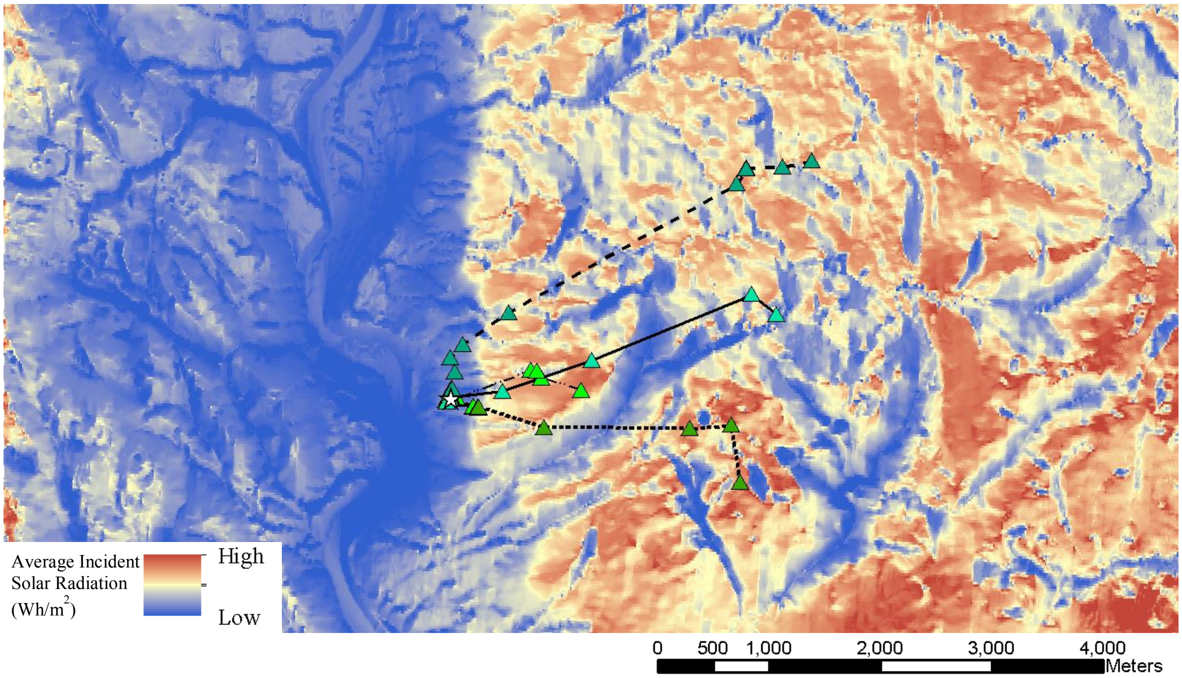


Figure 2.2. Examples of Western Rattlesnake migrations from the hibernaculum to destination habitat. Study hibernaculum is represented by ☆, and different snake movements are represented by different coloured symbols and connecting lines. In this example, all telemetered snakes utilized forest habitat. The thermal landscape is represented using modelled average incident solar radiation as a proxy for temperature. Telemetered snakes in this examples used warmer areas of the thermal landscape.

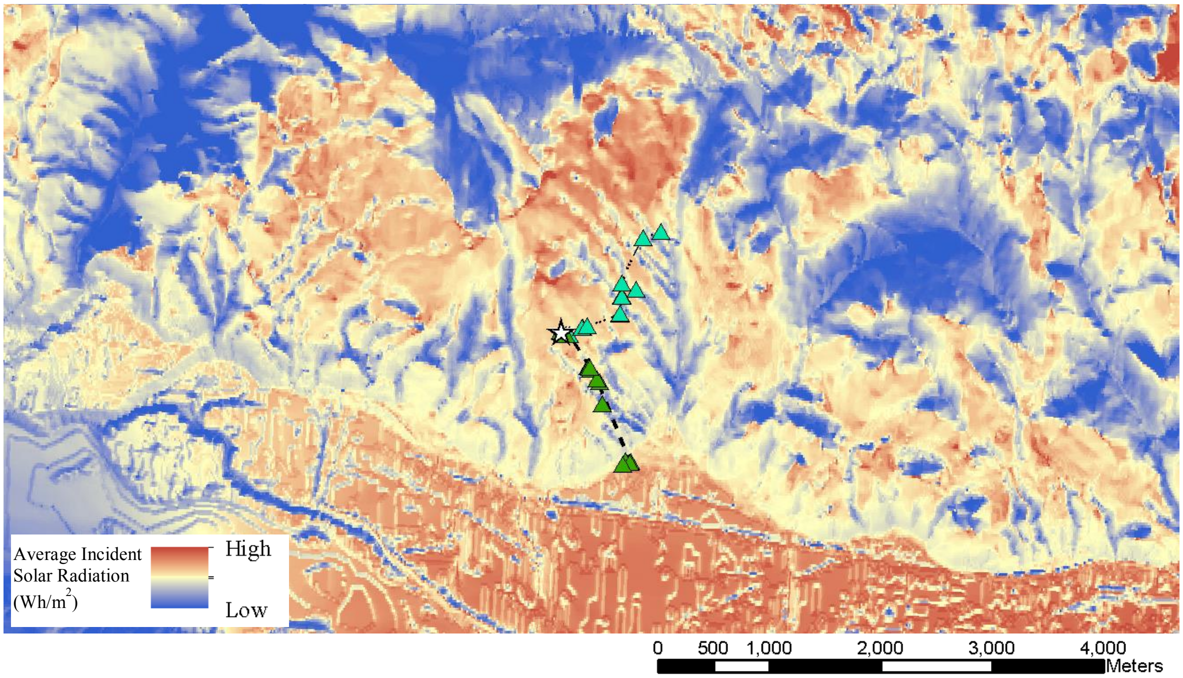


Figure 2.3. Examples of Western Rattlesnake migrations from the hibernaculum to destination habitat. Study hibernaculum is represented by ☆, and different snake movements are represented by different coloured symbols and connecting lines. In this example, all telemetered snakes utilized open habitat. The thermal landscape is represented using modelled average incident solar radiation as a proxy for temperature. Telemetered snakes in this examples used neutral areas of the thermal landscape.

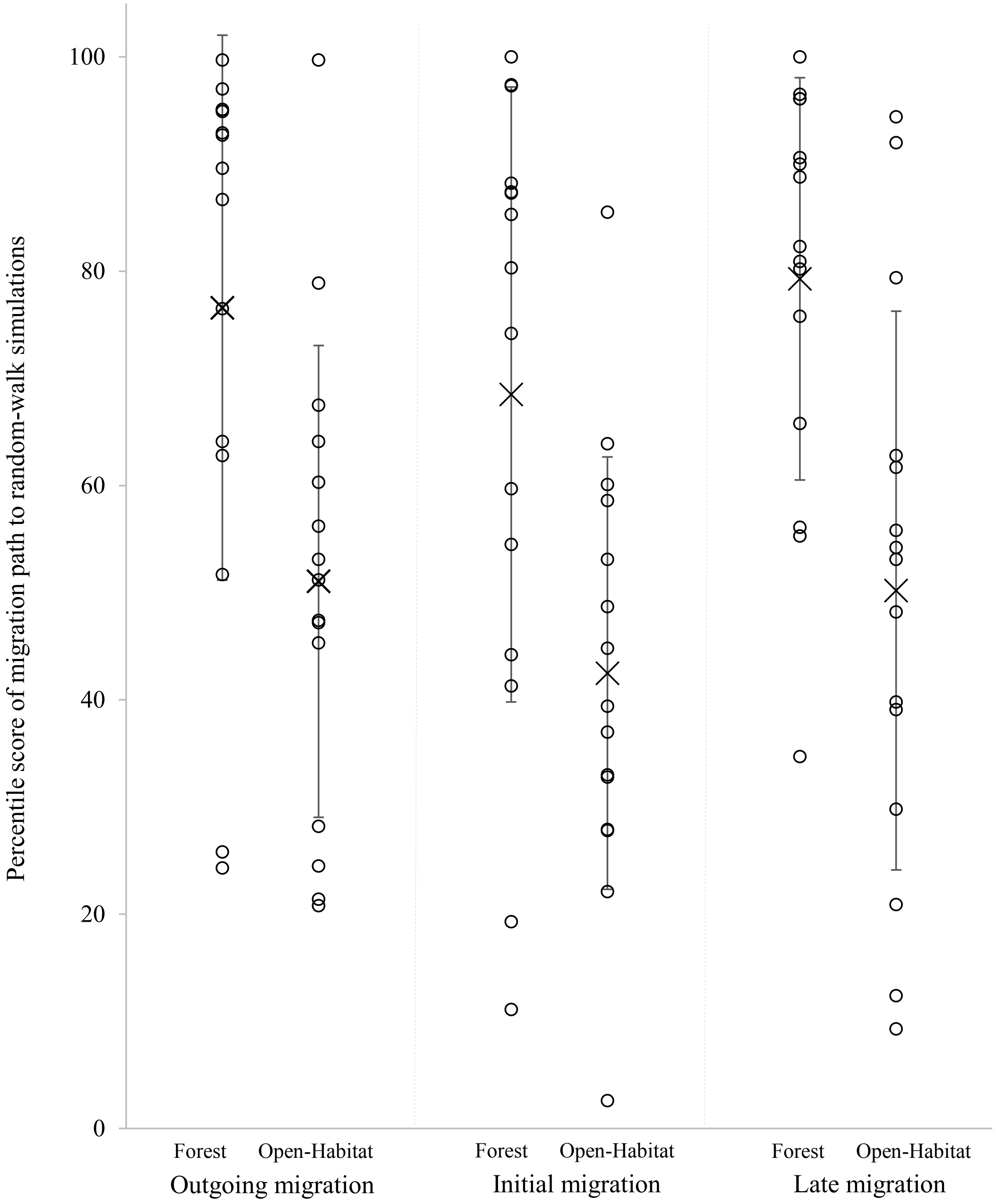


Figure 2.4. Comparison of the thermal metrics of snakes’ migration paths to simulated migration paths for snakes reaching either forest or open destination habitats. The ○ symbols represents the percentile of individual snakes within each group; the × symbols represents the mean percentile for the group ± 1 standard deviation.

Table 2.2 Comparisons of empirical thermal metrics to the thermal metrics derived from 100 random-walk migration path simulations for Western Rattlesnakes in British Columbia. Using thermal landscape maps, both empirical thermal metrics and those of the simulated migrations were derived from the average incident solar radiation along the migration path for each migration category (Outgoing, Initial and Late stages). Forest snakes utilized forested habitats as the destination for their migration, while Open-Habitat snakes remained in sparsely-treed or open grasslands throughout the active season.

Comparison	Group	Outgoing Migration	Initial Stage	Late Stage
A. Proportion of snakes occurring in the upper half of the distribution of the simulated migration paths	Forest snakes	13/15	11/15	14/15
	Open–Habitat snakes	8/15	5/15	8/15
		χ^2=3.97, df=1, P=0.046	χ^2=4.82, df=1, P=0.028	χ^2=6.14, df=1, P=0.013
B. Average percentile scores of migration path values within values derived from the simulated migration paths	Forest snakes	76.6 ± 25.4	68.5 ± 28.7	79.3 ± 18.8
	Open–Habitat snakes	51.1 ± 22.0	43.7 ± 18.0	50.2 ± 26.1
		t_{27}=2.95, P=0.006	t_{21}=3.03, P=0.006	t_{28}=3.46, P=0.002
C. Average probabilities (as determined by z-test scores) of migration path values as tested against a distribution of values derived from the simulated migration paths	Forest snakes	0.24 ± 0.28	0.29 ± 0.26	0.25 ± 0.26
	Open–Habitat snakes	0.54 ± 0.30	0.68 ± 0.20	0.55 ± 0.27
		t_{28}=-2.66, P=0.013	t_{26}=-4.65, P<0.001	t_{28}=-3.17, P=0.004

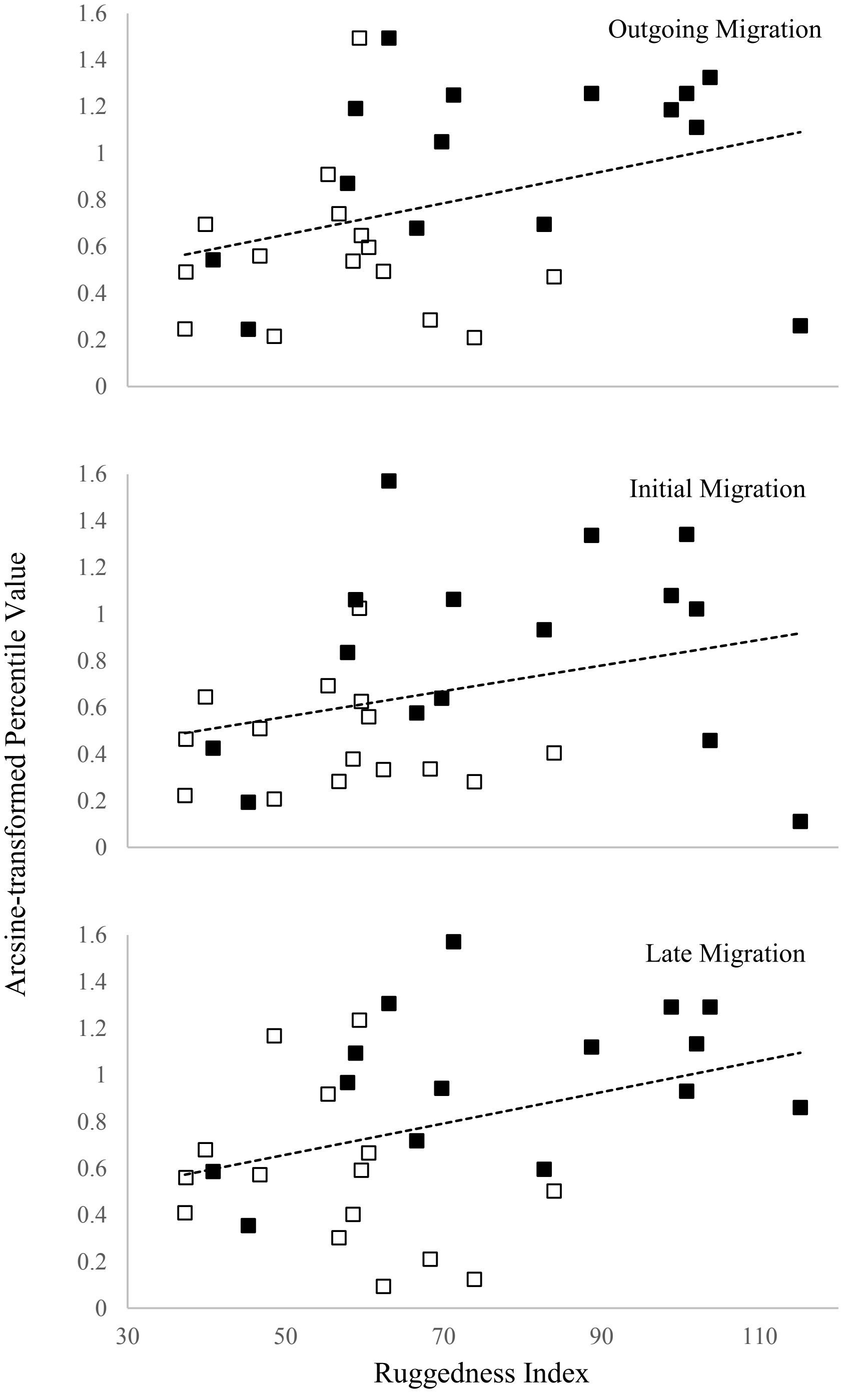


Figure 2.5 Average percentile scores of migration path values within values derived from 100 random-walk simulations, for each category of migration, compared to migration path ruggedness for telemetered Western Rattlesnakes in British Columbia. Trend lines (shown) were fit for the pooled group of snakes during the entire Outgoing migration ($R^2=0.13$), the Initial migration ($R^2=0.09$) and the Late stage of migration ($R^2=0.13$). Forest snakes are represented by solid markers, Open-Habitat snakes are represented by open markers.

Weatherhead and Prior 1992). Similarly, long-distance movements have also been reported elsewhere (Bauder et al. 2015, Duvall and Schuett 1997, Jorgensen 2009) and within the same region of my study (Gomez et al. 2015). Long-distance migratory movements for northern snakes in general have often been hypothesized to reflect widely-separated resources, such as hibernacula and summer foraging sites. In my study, the mean migration distances and home range sizes for this study were similar to those previously reported in this region; however, several of the maximum distances recorded in this study were longer than those previously reported (Bertram et al. 2001, Charland et al. 1993, Gomez et al. 2015, Macartney 1985). The prevalence of forest habitat use [first detected by Gomez et al. (2015) and now well-demonstrated by my study] is somewhat unexpected, given the presumption that the animals at their northern limits should be strongly tied to the arid, open grassland habitat of the valley bottoms.

My analysis explains some of the patterns of summer habitat use by these animals. The variable terrain of British Columbia coincides with the northern limit of the species, providing energetic and thermoregulatory challenges for the animals and raising the benefits of using habitat with optimal thermal attributes. In particular, the thermal landscape properties of the outgoing migration as a whole and the late stage of migration differed the most from the simulated random walks. During this time, most of the snakes travelled along warmer pathways, and snakes heading to or occupying forest habitats tended towards warmer pathways. Snakes appeared to move through less thermally-suitable conditions to reach destination habitats with ideal thermal properties, as evidenced by fewer snakes travelling warmer pathways during the initial migration stage. The consequences of using cooler paths are not known; however, it is likely that snakes perform microhabitat selection to compensate for temperature changes (Brown et al. 1982, Gannon and Secoy 1985, Wills and Beaupre 2000, Shoemaker and Gibbs 2010). This aspect of the ecology of snakes in the different habitats is discussed further in Chapter 3.

Rattlesnakes migrating through landscapes with higher ruggedness (more elevation variation in the terrain) were more likely to use forested habitats and had higher migration path percentiles during the late stage of migration. Although this relationship was significant, the amount of variation actually explained by ruggedness (R^2 value) was low. Nonetheless, ruggedness has been included as an important attribute in habitat selection for a variety of wildlife including caribou (Nellemann and Fry 1995), big horn sheep (Sappington et al. 2007), badger (Apps et al. 2002) and grouse (Carpenter et al. 2010), and my data support the assertion that this metric should be considered an important influence in snake habitat use (Fitzgerald et al. 2005, Greenberg and McClintock 2008), at least in northerly areas with noticeable variation in topography.

Thermal patterns of the landscape (as I measured them) appeared to be influencing the migrations observed in my study; however, there may be additional factors dictating migration routes that work in combination or separate from thermal attributes of the landscape. Animals may migrate in search of resources such as prey, mates or suitable habitat conditions, such as habitat type. Several studies have linked altered spatial behaviours to prey availability (Duvall et al. 1990, Wasko and Sasa 2012), whereas others have indicated limited support for this effect (Taylor et al. 2005, Nowak et al. 2015). In Wyoming, movement of male rattlesnakes has been attributed to mate-searching (Duvall and Schuett 1997). There is, however, insufficient knowledge to extrapolate these effects to other locations, such as in my northern study site. While my results indicate that there may be thermal influences on snake movements, investigation of other factors and the relationships between the putative driving factors is warranted.

As with all ecological models, thermal landscape simulations are simplistic representations of complex systems. The thermal models developed in this study provided insight into the role that thermal attributes of the landscape play in rattlesnake habitat use during the active season; however, they may be constrained by a spatial database resolution of only 25x25 m pixels. As the thermal landscape used in the analysis is based on this resolution, any variation occurring below this scale is not captured. A higher resolution digital elevation model, perhaps 3x3 m, in concert with a ground-cover mapping layer such as LIDAR, could be used to examine landscape dynamics through a finer lens. Small-scale thermal habitat features, including these small local variations, are discussed in Chapter 3.

The results of this study demonstrate that the relationship between hibernaculum location, migration distance and direction, and summer habitat utilization for these animals is far more complex than initially suspected. This is particularly important given that our understanding of northern rattlesnake ecology has been largely based on one study (Macartney 1985) where detailed information was collected on a population of snakes apparently restricted to open habitat. Clearly, widespread migratory differences exist between hibernating populations of these animals, and possibly other species. Realization of dichotomous habitat use, and revisiting the definition of "typical" habitats, is important in improving our understanding of the ecology and migration of animals (Diggins et al. 2015, Robson 2013).

Although the thermal attributes of the landscape appear to influence the migratory patterns of rattlesnakes in this study, this does not occur in an overwhelming manner that allows for precise predictions. Still, this work provides important clues as to the factors dictating snake movements from hibernacula. On a landscape scale, snakes use habitats that provide a thermal advantage through the short, northern summer. The role of thermal landscape attributes in colder environments, and how they affect migratory pathways of animals, warrants consideration along with other resource values in assessing habitat.

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CHAPTER 3. THERMOREGULATORY COSTS OF HABITAT USE: DO WESTERN RATTLESNAKES USING DIFFERENT HABITAT TYPES BEHAVE DIFFERENTLY?

INTRODUCTION

Organisms that thermoregulate have developed diverse strategies to maintain their body temperatures at optimal levels. These strategies include physiological mechanisms for temperature control and/or behavioural tactics, either of which may be employed to varying degrees. Behavioural thermoregulation has both ecological benefits and costs (Shoemaker and Gibbs 2010); for example, shifting positions to maintain optimal body temperatures (Gannon and Secoy 1985, Huey et al. 1989, Webb and Shine 1998) will be worthwhile for an animal only if the benefits outweigh the costs (Huey and Slatkin 1976). At the same time, thermoregulation may take time away from other tasks that contribute to fitness, such as mating success and feeding (Blouin-Demers and Weatherhead 2001, Dunham et al. 1989). Therefore, different thermoregulatory behaviours and relative degrees of active thermoregulation may impact fitness, underscoring the importance of different thermoregulatory tactics and their consequences on species of concern.

Thermoregulation may be considered a form of 'resource utilization' (Huey 1991) and the variable availability of heat as a resource across different habitats likely will have repercussions. In other words, varying thermal environments may impart costs and benefits to animals (van Beest et al. 2012). One example of this is the apparent contrasts in thermal resources between neighbouring forested and open habitats. A closed forest canopy should provide both insulation (heat retention at night) and shade (providing lower temperatures during the day) (Chen et al. 1999, Demarchi and Bunnell 1993, Ferrez et al. 2011). Subsequently, these sorts of habitat should demonstrate less temperature variation over 24 hours than adjacent habitats with little to no canopy cover. This relationship should be more pronounced in temperate systems, where general climatic patterns tend to relatively warmer days and cooler nights for much of the year. The dynamics between these and other contrasting habitats will be important in understanding habitat selection and its consequences, particularly so for ecthothermic species that are more reliant on external temperatures (Gotthard 2001).

Snakes in temperate regions appear to be a group of animals where the thermal consequences of habitat use are pronounced. In some cases, forests habitats have been considered lower thermal quality than open habitats (Blouin-Demers and Weatherhead 2001, Row and Blouin-Demers 2006, Harvey and Weatherhead 2011). Other studies have suggested that forest edges and openings may be of higher quality (Blouin-Demers and Weatherhead 2002). Intuitively, the ramifications of different habitat selection and thermal regimes should be best demonstrated in situations where conspecifics within the same regional population show marked differences in habitat selection. This occurs near the northern limits of rattlesnakes in North America, where Western Rattlesnakes, *Crotalus oreganus*, from neighbouring hibernacula show notable differences in summer habitat use. The stereotypic association of these snakes within the hot, dry grasslands has been shown to be inaccurate. Both Gomez (2015) and my data in Chapter 2 indicate that adult animals in some populations conduct summer migrations that place them in high-elevation forested habitat, whereas conspecifics emerging from other dens in the same region remain within the lower grasslands throughout the active season. Additionally, I showed in Chapter 2 that snakes, predominantly those using forested habitat, used warmer areas of the landscape during their annual migrations.

In this chapter, I investigate further the thermoregulatory implications of dichotomous migratory movements by Western Rattlesnakes. I explore the ramifications of the patterns in habitat selection observed in Chapter 2 by testing whether animals using forested habitat displayed higher body condition, similar to that reported by Lomas et al. (2015) for Western Rattlesnakes leaving areas of high human development. If such benefits are realized, it will partially explain the phenomenon of long distance migration into forest habitat described in Chapter 2. Additionally, I investigate whether snakes migrating into forest habitats display different thermoregulatory profiles and behaviours than those in open, grassland habitats. Given that forest habitat should provide less-extreme temperature dynamics, I hypothesized that snakes using these habitats would demonstrate different behavioural tactics relative to conspecifics in hotter, open habitats, while still allowing animals in forests to achieve optimal body temperatures over the course of 24 hour periods.

METHODS

Study animal and site selection

Rattlesnakes used in this study were involved in a larger study of the relationship between thermal landscape characteristics and migratory pathways (Chapter 2). Work took place in 2010 and 2011 on snakes emerging from 10 dens selected from known hibernating sites (see Chapter 1, Figure 1.3). The dens were selected based on logistics, the range of habitat (i.e., availability of forest habitat) within a 5 km radius, and an estimated population of at least 12 adult animals to minimize impacts on the population. Only adult male snakes were selected for telemetry to avoid negative effects on reproductive females. Seventeen snakes from 6 dens were selected for incusion in the study in 2010, and 18 snakes from 5 dens were selected in 2011. Three snakes from each den were targeted for telemetry in order to ensure adequate replication; however, at 2 sites only 1 and 2 captured snakes respectively were deemed large enough for telemetric study. At the remaining 9 sites, either 3 or 4 snakes were selected as study animals.

The study animals were surgically implanted with SB-2 radio-transmitters (Holohil Systems Inc., Ontario, Canada), weighing 3.8 - 5.2 grams, and a temperature data-logger (www.maxim-ic.com; DS1921G Thermocron iButton™), weighing approximately 3.3 g. The implanted iButtons™ were coated in Plastidip, an inert plastic that protects the instrument from moisture and the snakes from any harmful effects of corrosion. The iButtons™ were programmed to take internal body temperatures (T_b) every 2 hours for the length of the active season. The combined weights of the two implanted devices never exceeded 2.7% of snakes' body weight. Surgical protocols outlined by (Reinert and Cundall 1982) and Reinert (1992) were used. Following surgery and a 24-48 hr post-operative recovery period, the snakes were released precisely at their point of capture. Implants similarly were removed from re-captured snakes either when they returned to their hibernacula in autumn of the same year, or as they emerged from hibernation the following spring.

I tracked and located telemetered snakes every 3 to 7 days between emergence (April/May) and egress (September/October) using an R-1000 telemetry receiver and RA-159 handheld Yagi directional antenna. When each snake was located, I recorded date, time, UTM coordinates, weather, habitat description, canopy closure using a spherical crown densiometer (Forestry Suppliers, Convex model A), temperature measurements and snake behaviour.

Snake location data were filtered to include only those that constituted independent movements, defined as more than 10 m from the previous location (Gomez et al. 2015). Each location was assigned to one of two habitat types (‘Location habitat’) to enable comparison: those with <10% canopy closure (bunchgrass and open-canopy Ponderosa Pine zones) were designated as “Open” habitats, while locations with >10% canopy closure (Interior Douglas-fir forests) were classified as “Forest” habitat. Additionally, each snake was assigned post hoc to a category (“Open-Habitat snakes” or “Forest snakes”) based on the type of habitat reached at the end point of the snakes’ migration (‘Destination habitat’).

Body weight, length and condition

Weights of animals were collected at the point of capture (in spring during selection for telemetry, and in fall when animals were being recovered for transmitter removal). The lengths of each snake (SVL, snout-to-vent length) were measured while animals were under anesthesia to avoid error associated with measuring venomous snakes in the field (Bertram and Larsen 2004). These data allowed me to calculate body condition (weight:SVL ratio) and percent weight change over the active season. The weight:SVL ratios were arcsine-transformed and then compared between snakes using the two Destination habitat types using ANOVA with habitat and year as treatments. Using a similar methodology to that of Lomas et al. (2015), I used the residuals from the regression between weight and SVL as an index of body condition. Additionally, percentage weight change from spring to fall captures were arcsine-transformed and compared between Destination habitat types using t-tests.

Thermoregulatory behaviour

Upon the sighting of a telemetered snake, the behaviour of the animal was recorded immediately unless inadvertent disturbance to the animal occurred, in which case the observation was omitted from the dataset. Three categories of thermoregulatory behaviour were designated: basking (motionless, 25-100% of the snake's body exposed to the sky), active (including resting in the shade [>25% of the snake's body exposed, but in an area shaded by vegetation or a tree], mating, and travelling), and under cover [<25% of the snake's body exposed from the cover object (e.g., coarse woody debris) or retreat site (e.g., crevasse in rock)] (Figure 3.1). The mean relative frequency of each of the three behaviours was determined for each snake. Each snake was considered only once for each location habitat type (i.e., a forest snake was considered twice – once for its mean relative frequencies of behaviours in open habitats before reaching its Destination habitat, and once for its mean relative frequencies of behaviours in forest habitat when it had reached its Destination habitat type).

The mean relative frequencies of the different thermoregulatory behaviours were arcsine transformed and compared between Location habitats using ANOVA, with individual snake as a treatment.

Snake body temperatures

Following retrieval and download of the surgically-implanted iButtons, I calculated the mean daily measured body temperatures for each snake. ANOVA, including an interaction term, was used to examine mean daily body temperatures were compared between snakes using Open and Forest habitats, by month, and by year.

Environmental temperatures

Each time a telemetered snake was located, I collected environmental temperatures at both the snake's location ('used') and at random points ('available'). Both ground-level air temperature and ground surface temperature, were measured using an infrared handheld thermometer (Testo 810). Due of the importance of collecting precise temperature data at the snake's exactly location, I often gently ushered the animal aside a short but safe distance.

Figure 3.1 Examples of snake daytime thermoregulatory behaviour, clockwise from top left: Basking - a snake is motionless and exposed to the sun; Active - the snake is not concealed and resting in the shade; Active - the snake is not concealed and engaged in feeding, mating or moving, or; Under cover- the snake is completely or partially under a cover object or in a retreat site (photos by author).

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Random temperatures were recorded at 8 points (4 at 1m radius and 4 at 5m radius, selected using randomly-chosen directions and a compass). Ground-level air temperature was measured horizontally at 10cm above ground, and ground surface temperature was measured by pointing the infrared thermometer directly at the surface immediately adjacent to the snakes' position. To further minimize error in measurements, the averages of 3 repeated measurements taken at each location and random location were used. Using the data set later retrieved from the implanted iButtons, I also determined the corresponding body temperature for each date and time of snake locations.

A multi-factorial, repeated measures ANOVA was used to compare the differences between snakes' body temperatures and the temperatures measured at the snakes' locations. Factors included Location habitat, year, month, and time of day (morning, afternoon, evening). Month was the repeated measure. Similar tests were also performed to compare the temperatures at the snakes' locations with those at random locations within the area surrounding the snake.

Statistical considerations

All analyses were performed in the statistical program R version 2.12.1 (R Development Core Team 2011). Data were tested for normality by examination of histograms and Shapiro-Wilk and/or Kolmogorov-Smirnov tests (Zar 1999). Homogeneity of variances between groups was tested using the Fligner-Killeen test (Conover et al. 1981, Crawley 2007). A significance value of $\alpha=0.05$ was used to guide the interpretation of the results. Means herein are reported ± 1 standard deviation, unless otherwise stated.

RESULTS

Telemetered snakes

Complete migratory data were collected on 30 of 35 telemetered snakes, with exactly half of those animals (n=15) reaching forested habitat. Overall, all snakes displayed typical directional movements, reaching their furthest point away from their respective dens in late summer (average August 8, range June 23 – Sep 21). Pathways used to return to the dens in late summer and early fall tended to retrace the outgoing movement pathways (see Gomez et al. 2015). All 30 snakes were monitored over the course of their entire migration, except for one animal that was predated on approx. 300 m from reaching its den in autumn. The data from this animal were included in the final data set. Partial data from the remaining five animals (all depredated) were used in some of the analyses for given stages of migration, but omitted from other analyses where more complete datasets were required.

Snake body conditions

I found a strong positive relationship between snake weight and length (Figure 3.2). This relationship was significant in both the spring ($R^2 = 0.78$, $F_{1,29} = 105.5$, $P < 0.001$) and in the fall ($R^2 = 0.59$, $F_{1,28} = 38.78$, $P < 0.001$). Forest snakes weighed relatively more for their length than their counterparts in open Destination habitats (Table 3.1) in both spring ($F_{1,28} = 4.72$, $P = 0.04$; year: $F_{1,28} = 4.06$, $P = 0.06$) and in fall ($F_{1,26} = 8.56$, $P = 0.007$; year: $F_{1,26} = 0.20$, $P = 0.66$). Analysis of the residuals shows that Forest snakes had significantly higher body condition indices than Open-Habitat snakes, in both spring ($F_{1,28} = 8.11$, $P = 0.008$; year: $F_{1,28} = 0.73$, $P = 0.40$) and in fall ($F_{1,26} = 18.2$, $P = 0.0002$; year: $F_{1,26} = 0.10$, $P = 0.75$). Of the telemetered animals, Forest snakes gained proportionally more weight over the active season than Open-Habitat snakes ($F_{1,26}=12.25$, $P=0.002$, Table 3.1). Post-hoc analysis indicated that the sample sizes provided acceptable levels of statistical power (power=>0.999; Cohen 2013).

Thermoregulatory behaviour

A total of 383 behaviour observations were recorded at snake telemetry locations: 305 observations were in open Location habitats, while 77 observations were in the forest Location habitat. The mean frequency observations of snakes being active (i.e., not basking or under cover) was significantly higher in forest Location habitat, while in open Location habitats, snakes were more frequently observed under cover in retreat sites or under cover objects (Table 3.2). The mean frequency of basking behaviour was not significantly different between snake locations within forest or open Location habitats. There were no differences detected within each Location habitat type (all Ps>0.05), meaning that Forest snakes behaved the same as Open-Habitat snakes while in open grassland and open Ponderosa pine habitats before they reached their Destination habitat.

Snake body temperatures

Implanted iButtons^{TM} were recovered from 29 snakes, being lost from all of the predated animals. Of these, 16 were downloaded successfully without data failure or corruption. Nine of these iButtons^{TM} were from Forest snakes and 7 were from Open-habitat snakes.

As the two groups of snakes, Forest and Open-Habitat, did not behave differently when in similar habitats, subsequent analyses focused on Location habitat type. ANOVA showed a significant effect on average daily body temperature by Location habitat category, month, year and the interaction (Location habitat: $F_{1,648}$=7.11, P=0.008; month: $F_{7,648}$=39.4, P=< 0.0001; year: $F_{1,648}$=3.88, P=0.049; all interactions: all Ps=>0.05). In 2010, snakes in forest and open Location habitats did not have different average daily body temperatures, nor was the interaction term significant. Expectedly, there was a significant effect on average daily body temperature by month ($F_{1,328}$=19.6, P=<0.0001). In 2011, there was a significant effect on average daily body temperature by Location habitat, month and the interaction term (Location habitat: $F_{1,328}$=26.5, P=<0.0001; month: $F_{6,328}$=38.9, P=< 0.0001; Location habitat X month: $F_{6,328}$=8.78, P=<0.0001). The significance of Location habitat and the interaction term were a result of the daily average body temperature being higher in Open-habitat snakes than Forest snakes in the month of July (t_{30}=10.7, P=<0.0001; see Figure 3.3).

Environmental temperatures

Overall, snakes' relationship to the temperature of their surroundings did not differ between Location habitat categories (all Ps≥0.05; Table 3.3). The ANOVA revealed that Location habitat category did not have an effect on the difference between snakes' body temperature and air or ground temperature at the snakes' location (all Ps≥0.05). The same result was found for the comparisons between snake location temperatures and available location temperatures at 1 m and 5 m scales, for both air and ground temperature measurements (all Ps≥0.05).

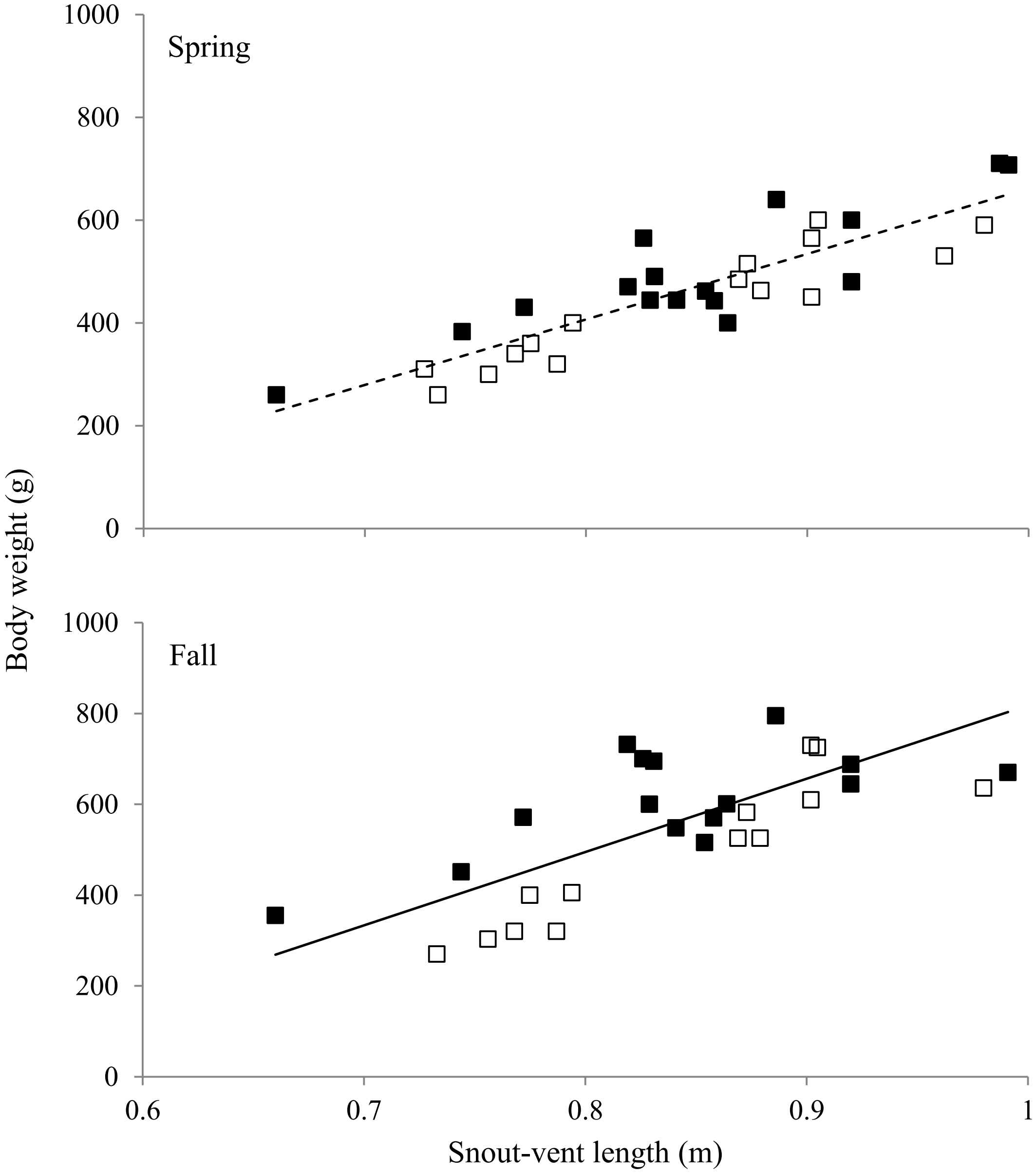

Figure 3.2 Relationship between body weight and length (snout-vent length: SVL) of Western Rattlesnakes in British Columbia that used open and forested habitats using linear regression. Spring weight:SVL ratios are shown in in the upper chart and fall weight:SVL ratios are shown in the lower chart. Trend lines (shown) were fit for the pooled group of snakes in spring (dashed; R^2=0.78) and in fall (solid; R^2=0.59). Forest snakes are represented by ■, Open-Habitat snakes are represented by □.

Table 3.1 Weight (g) to length (snout-to-vent; m) ratio for male Western Rattlesnakes radio-tracked in the Thompson-Nicola and Okanagan-Similkameen regions in British Columbia (2010 and 2011) grouped according the type of habitat the animals reached on their outgoing migrations. All values reported ± 1 standard deviation.

Group	**Spring Weight:SVL (g/m)**	**Fall Weight:SVL (g/m)**	**% weight change**
Pooled (n=30)	0.54 ± 0.10	0.66 ± 0.16	20.0 ± 16.5
Forest snakes (n=15)	0.58 ± 0.10	0.74 ± 0.13	29.2 ± 15.8
Open-Habitat snakes (n=15)	0.51 ± 0.10	0.57 ± 0.15	10.1 ± 11.9

Table 3.2 Mean frequency of thermoregulatory behaviours at snake locations (Basking - a snake is motionless and exposed to the sun; Active - the snake is not under cover and engaged in feeding, mating or moving, or resting in the shade; Under cover - the snake is under cover or partially under cover) of Western Rattlesnakes observed in open and forest habitats in southern British Columbia.

	Location Habitat type		
Behaviour	Forest	Open-Habitat	**ANOVA**
Basking	25% ± 23%	42% ± 24%	Habitat: $F_{1,12}=3.63$, P=0.081; Snake: $F_{31,12}=0.976$, P=0.549
Active	57% ± 27%	20% ± 17%	Habitat: $F_{1,12}=26.77$, P=0.002; Snake: $F_{31,12}=1.32$, P=0.311
Under cover	18% ± 20%	38% ± 22%	Habitat: $F_{1,12}=9.93$, P=0.008; Snake: $F_{31,12}=1.02$, P=0.512

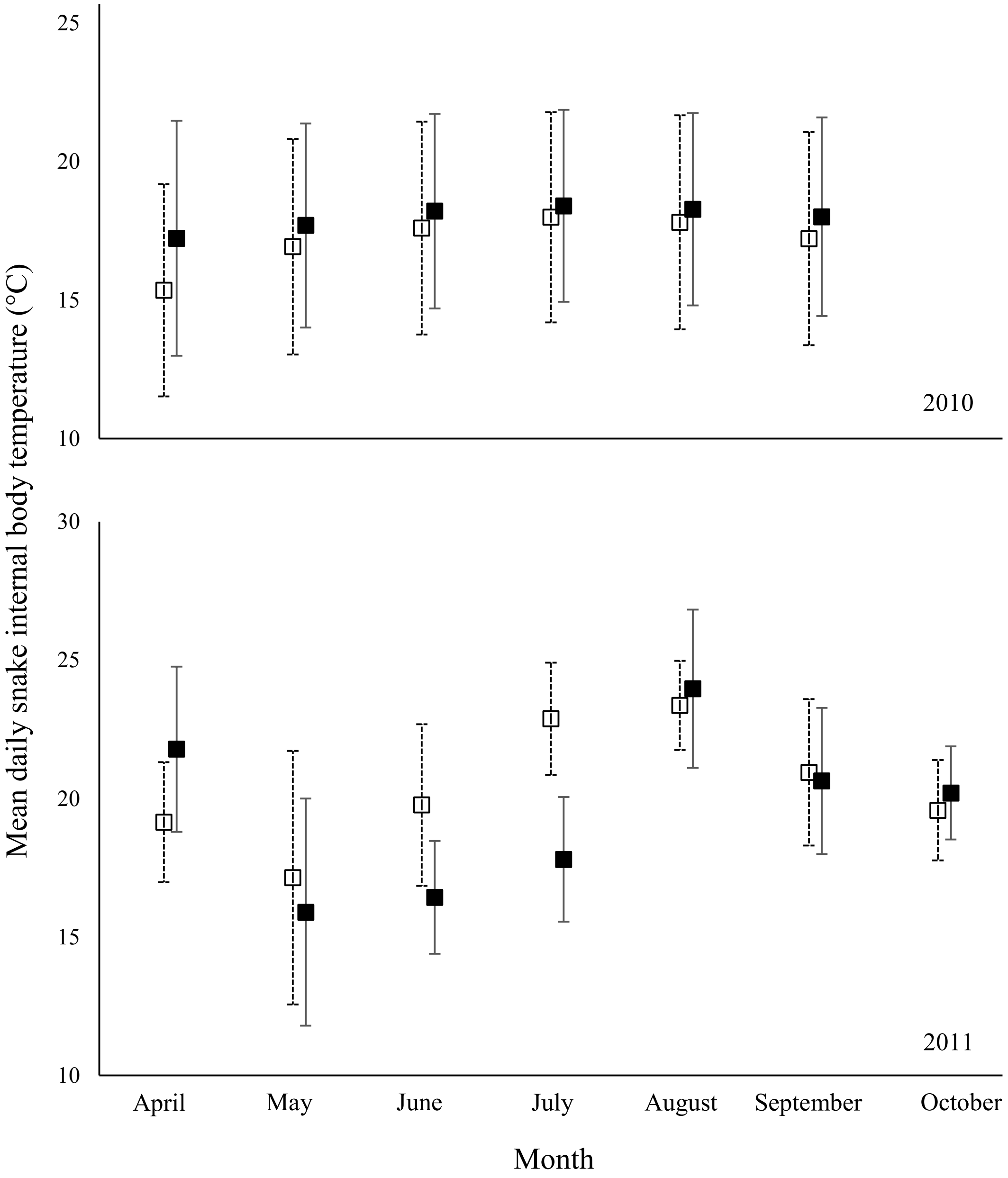

Figure 3.3 Mean daily body temperature for telemetered Forest snakes and Open-Habitat snakes by month during the active seasons of 2010 and 2011 in British Columbia. Forest snakes’ means are represented by ■, Open-Habitat snakes’ means are represented by □. Means are shown with 1 standard deviation, Forest snakes’ error bars are represented by solid lines, Open-Habitat snakes’ error bars are represented by dashed lines.

Table 3.3 Average differences between Western Rattlesnakes' body temperatures (°C) measured with implanted iButtons and environmental air and ground temperatures measured at the snake location and at random locations in the surrounding habitat within 5 metres in British Columbia. Air temperatures were measured at 10 cm above ground level.

Response		All locations	Locations in Forest habitat	Locations in Open habitat
Difference (°C) between snakes' body temperature and the air temperature measured at snakes' location		0.33 + 3.79	0.05+3.72	0.44+3.82
Difference (°C) between snakes' body temperature and the ground temperature measured at snakes' location		-4.06 + 6.20	-3.84+6.09	-4.15+6.27
Difference (°C) between the air temperature measured at snakes' location and the average measured at 4 random locations	1 m from snake location	0.64 + 4.39	0.47+4.76	0.69+4.28
	5 m from snake location	0.96+ 7.02	-0.33+5.03	1.37+7.51
Difference (°C) between the ground temperature measured at snakes' location and the average measured at 4 random locations	1 m from snake location	-0.64 + 7.51	-0.01+7.04	-0.84+7.66
	5 m from snake location	-0.42+8.32	-0.48+8.35	-0.40+8.33

DISCUSSION

Forest snakes had better body condition and proportionally more weight gain than Open-Habitat snakes. These observations suggest positive repercussions for the rattlesnakes that utilize forest habitat, similar to those observed by Lomas et al. (2015) in snakes that avoided disturbed areas of the landscape. In the forest, less variable environmental temperatures were expected to impose fewer thermal constraints on snakes' activities, and therefore, increased energy intake and subsequent weight gain (Huey and Berrigan 2001). Occurring year over year for snakes migrating to forest habitats, this effect would explain the observed better body condition observed in forest snakes. Increased energy intake (given increased time available for foraging), in combination with lower energy demands, may result in caloric excesses that would be allocated to growth, resulting in increased weight gain. It is unknown, however, whether the water balance between snakes in open and forest habitats might differ, as it is likely that increased exposure in open habitats may result in more rapid water loss and therefore, less weight gain.

Basking in the sun and retreating under cover to escape the heat of the day are thermoregulatory behaviours that snakes utilize to maintain their body temperatures within an optimal range (Huey and Stevenson 1979). Employing these behaviours at different frequencies represents unique use of thermoregulatory strategies to reflect differing thermal conditions encountered in open habitats and forest habitats. Snakes in forest habitats were observed being active (e.g., resting in the shade, moving, mating) at higher frequencies than snakes in open habitats, which were more frequently observed beneath cover objects or in retreat locations. Thus, snakes in forested habitats may be able to devote more time during the day to other aspects of life history, such as mating, as thermal insulation in the forest keeps daily temperatures lower than in open habitats. Blouin-Demers and Weatherhead (2001) suggest that snakes in the forest spent less time basking at sunrise to regain heat, allowing increased time spent foraging. In my study, however, the frequency of snakes basking was not different between the two habitats, suggesting that staying warm enough may not be a differentiating constraint between the two habitats and indicating that reaching the optimal body temperature range may not be more difficult in one habitat as opposed to the other. Rather, as the frequencies of being under cover and being active did differ, the results of my study suggest that avoidance of high temperatures may influence rattlesnake behaviour in open and forest habitats in British Columbia. In open habitat, snakes likely seek shelter from the heat of the day (Huey et al. 1989), while those in the forest were protected by the shade and thermal insulation provided by the canopy.

Snakes in this study maintained similar daily average body temperatures for most of the year, with the exception of July 2011 when snakes in open habitats had higher daily average body temperatures than those in forest habitats. Therefore, snakes in different habitats are likely adjusting their thermoregulatory behaviour to achieve similar body temperatures in environments with different temperatures. Moving between microsites (locations) in the local landscape is the basis of behavioural thermoregulation (Huey et al. 1989).

My study suggests that the thermal conditions in forest habitats may minimize behavioural thermoregulatory constraints; however, this result contrasts those by several other studies of snakes using closed-canopy habitats. The thermal homogeneity of dense forest in Australia was found to have constraining effects on snakes (Fitzgerald et al. 2003). Forest edges have been identified as being high quality thermal habitat, with environmental temperatures being closer to the optimal range of temperatures for snakes (Blouin-Demers and Weatherhead 2002), while open grasslands were lower quality and interior forest habitats were of intermediate value. In southern British Columbia; however, the Douglas-fir forests typically have semi-open canopies (Grasslands Conservation Council 2004, Meidinger and Pojar 1991), allowing for warm spots to occur within the forest while still providing thermal stability.

However, there may be trade-offs for animals using forest habitat. The forest canopy provides both thermal insulation and shade, but results in basking opportunities potentially being concentrated in openings that the sunlight can penetrate through. These openings also may be locations where aerial predators concentrate their attention on the forest floor (Blouin-Demers and Weatherhead 2002). This could increase the predation risk for rattlesnakes basking in forest habitats. This was not reflected in the comparative mortalities in my study, although my sample sizes were relatively small.

To compensate for the landscape-scale differences that exist both within and between hibernating populations of these animals that I showed in Chapter 2, snakes in different habitats perform microhabitat selection to compensate for temperature changes (Brown et al. 1982, Gannon and Secoy 1985, Wills and Beaupre 2000, Shoemaker and Gibbs 2010), as evident in my results. Additionally, animals using forested habitat displayed higher body condition, partly explaining the dichotomous migratory movements by Western Rattlesnakes.

For the Open-habitat snakes in my study, the thermoregulatory benefit of spending time under cover to escape the heat of the day has associated costs, such as lost time for movement or foraging, which in turn may explain the lower body condition in this group of snakes (Blouin-Demers and Weatherhead 2001, Dunham et al. 1989). Differential use of resources, habitats and behaviours, including thermoregulatory behaviours, have ecological costs and benefits (Shoemaker and Gibbs 2010). Animals performing movements and other behaviours must balance the costs with potential benefits (Fryxell et al. 2014, Sears and Angilletta 2015, Wishingrad et al. 2014). Small-scale movements and behaviours, such as shifting positions to maintain optimal body temperatures as discussed in this chapter, may be worthwhile for an animal if the benefits outweigh the costs (Huey and Slatkin 1976).

These results, in combination with existing knowledge of micro-habitat use by this species in British Columbia (Gomez et al. 2015), provide insight into aspects of animals' use of habitat attributes in varying habitat types. The results of the study presented in this chapter contribute to our understanding of microsite selection by Western Rattlesnakes throughout their range in British Columbia. Snakes that utilize forest habitats appear to spend more time being active, have fewer thermal constraints on their local habitat use and behaviour, and subsequently, have an advantage, evidenced by heavier bodied snakes. Animals in different habitats perform thermoregulatory behaviours to maintain physiologically optimal body conditions (Blouin-Demers and Weatherhead 2002, Manju and Sharma 2014, Row and Blouin-Demers 2006). The consideration of thermal attributes of habitat across a variety of scales, and contrasted between different habitats used by individuals in a population, may be particularly pertinent in temperate climates where thermal constraints can influence animals' activity and behaviour.

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CHAPTER 4. SUMMARY AND MANAGEMENT IMPLICATIONS

SUMMARY

This study strove to understand the role of thermal attributes of habitat in animals' habitat utilization and migratory movements on multiple scales. Radio-telemetry and GIS modelling were used to study the seasonal migration patterns, small-scale habitat use, and behaviour of rattlesnakes originating from a number of dens within the species range in British Columbia. Specifically, the objectives of this thesis were to investigate (a) whether forest habitat use by temperate snakes is unusual, (b) whether thermal patterns on the landscape dictate the movements of snakes in British Columbia on landscape and local scales and (c) whether there are costs or benefits associated with using habitats that differ in thermal properties.

Establishment of the prevalence of forest habitat use, observation of unique patterns of thermoregulatory behaviours between open and forest habitats, and identification of potential benefits of alternative habitat usage were among the notable results of this thesis research.

Expressly, key findings of this thesis are:

- Forest habitat use by arid-habitat snakes is common in British Columbia. The snake migrations documented in this thesis corroborate the findings of Gomez et al. 2015, and rattlesnakes in British Columbia can no longer be associated with only grassland habitats.
- Many snakes use warmer areas of the landscape during annual migrations and this result is significant in the late stage of the outgoing migration. Specifically, snakes that are associated with forested destination habitats use warmer areas of the landscape than those in open habitats.
- Snakes in the open habitats were more frequently observed under cover objects during the day, potentially to escape the heat, while snakes in the forest were more frequently observed active (*i.e.,* moving, mating). Snakes in both habitat types were observed basking at approximately equal frequencies.

- Snakes that used forest destination habitat appear to be in better condition than snakes that used open habitats throughout the active season. These snakes had better body condition indices (*i.e*., higher mass given their length) and gained more weight over the course of the active season.

The results of this research generally confirmed my predictions that snakes would be using both forest habitats and warmer areas of the landscape. On the local scale, microhabitat use and thermoregulatory behaviours appear to be less constrained by thermal factors in forest habitats, potentially contributing to a better body condition in snakes that use forest destination habitats. The results of this study contribute to our understanding of habitat use by reptiles in temperate regions and may have significant implications for the conservation of these animals.

MANAGEMENT AND CONSERVATION

Knowledge of habitat use patterns in migratory animals is imperative in designing effective management strategies. Migrating animals are particularly difficult to manage (Milner-Gulland et al. 2011), as migrations may be difficult to predict and may cause animals to leave protected areas.

The findings of my study have implications for the management and conservation of migratory snakes in British Columbia. Western rattlesnakes, Great Basin gopher snakes (*Pituophis catenifer*) and Western yellow-bellied racers (*Coluber constrictor*) are restricted to the grasslands and forests of the arid valleys of south-central British Columbia. Large expanses of these habitats have been lost to agriculture and urbanization in the Thompson-Nicola and Okanagan-Similkameen regions. Only a small portion (less than 15%) of the remaining arid land area is protected in provincial parks, protected areas, wildlife reserves, and ecological reserves [Grasslands Conservation Council (GCC) 2004]. Currently, management and conservation of snakes in these regions is largely focused on hibernating habitat, due to a lack of concrete information on large-scale habitat use during the active season. The results of my study, specifically increased knowledge of both local and landscape habitat use, will aid in the identification of high-value habitats, both within and outside of protected areas, and will enable more effective management of snakes during their active season. Increased knowledge will result in more effective designation of WHA protected areas, tailoring designs specifically to the hibernacula in question and the habitat available to the snakes (Appendix B).

Approximately 36% of arid habitats in Thompson-Nicola and Okanagan-Similkameen regions are subject to grazing leases (GCC 2004). Forestry activity in the Douglas-fir forests is also widespread. The thermal factors discussed in this thesis, in combination with existing knowledge of snakes' habitat use, can be used to identify potentially high-value areas of the landscape surrounding hibernacula. Forestry and ranching practices may be evaluated for their effect on snakes beyond the boundaries of grassland and open habitats. Practices may then be put in place that avoid areas identified as high-value habitat and that protect or work to maintain natural amounts of structural habitat features.

LIMITATIONS AND FUTURE RESEARCH PRIORITIES

The comprehensive design of this study provided a broad overview of the rattlesnake population across the species range in British Columbia. While the conclusions of this research are relevant across the species range, there may be individual snakes and populations that may behave differently. Natural variation in behaviours among individuals and populations of animals results in limitations in wildlife studies (Gillies et al. 2006). These limitations were minimized in this thesis but the accommodation of individual effects in the analysis.

Radio-telemetry studies are among the most labour-intensive and, therefore, expensive types of study to undertake. Experimental design must account for the trade-off between number of animals tracked and number of locations obtained per animal, as more study animals glean more accurate conclusions about the population as a whole; however, using fewer study animals allows researchers to collect more detailed information about individuals (Millspaugh and Marzluff 2001). Researchers must also be selective in what information is necessary to answer their research questions, as increased capacity of data loggers, life span of transmitter batteries, or range of transmitters, result in increased weight of transmitters and/or data loggers, which may affect animals' health or behaviour (Fedak et al. 2002). In my study, the goal of balance between number of study animals, number of study sites and avoidance of adverse effects on snake populations, led to the selection of three snakes per hibernacula, with ten hibernacula in total. This proved an effective method of gathering an adequate amount of information across a broad geographic range and a suite of dens in varying landscapes, allowing for more widely applicable conclusions.

It important to remember that this study, like many wildlife ecology investigations, was temporally limited and represents a 'snapshot in time', and should be interpreted as such. My study captured the movements of snakes from each hibernaculum for a single year. While there is evidence that snakes undertake migrations of similar lengths and directions in concurrent years (Gomez et al. 2015, Jorgensen 2009), it is unclear whether migrations evolve or change conspicuously over a snakes' lifespan. Long term monitoring of individuals within populations would provide insight into long-term migratory dynamics. Additionally, my study focused only on the day-time behaviour of rattlesnakes during the active season. Night-time behaviours could be considered in the future, as there is limited knowledge of the proportion of life history functions that occur during the night versus during the day and whether this changes over the course of the active season, or in response to changing temperatures.

The results of this research indicate that thermal attributes of habitat are important factors in the ecology of temperate snakes and should be included in developing both conservation and management strategies. A robust tool could be developed that may allow for better landscape planning and management strategies. This tool would allow wildlife and habitat managers to predict the potential use of the landscape. Results of this study could be incorporated, along with existing knowledge of rattlesnake habitat use on multiple scales, into a complex, comprehensive model of rattlesnake habitat use in British Columbia. This could be accomplished using a Resource Selection Function model, which may be verified using occurrence data from multiple studies, given similar data parameters. Monitoring of snake populations and model fit over the long term would be valuable, particularly with an eye to changes in temperature and vegetation due to climate change (see Appendix C).

A comprehensive habitat model for rattlesnakes would facilitate the evaluation of the efficacy of landscape management for temperate reptiles that is normally centred on hibernating habitats but does not take into account active-season habitat use. Combined with local knowledge and experience, this tool would allow much more effective designation of protected habitat areas. The model may be specifically applicable to other snake species in British Columbia such as gopher snakes and racers. The lessons learned could be extrapolated to other species and wildlife communities (short-eared owl, grassland birds).

The primary focus of this study was to determine whether thermal attributes of habitat act as a mechanism for active season migrations and small-scale habitat use; however, the roles of food supply, moisture limitations, and mate-searching in driving snake movements are unknown. These variables were beyond the scope of this project, but provide opportunity for further study.

CONCLUSION

Thermoregulation on multiple scales is crucial for reptiles in temperate regions, where animals have to deal with shorter active seasons and variable environmental conditions. Overall, the findings of this research indicate that long-distance migration to forest habitats may be driven, at least in part, by thermal requirements – a search for warmer habitats relative to the surrounding landscape. As expected, microhabitat selection in linked to thermoregulatory behaviours, especially for snakes in open habitats that are exposed to extreme day and night temperatures. This thesis also established that forest habitat use by arid-habitat snakes in temperate regions may be more common than previously thought and that there appear to be advantages to snakes using those habitats.

The knowledge of Western Rattlesnakes summer habitat use will further inform local and regional management of the species. Developing knowledge and tools that can aid in the prediction of behaviour and habitat use of Western Rattlesnakes, and perhaps other northern snake species, will greatly improve our ability to manage ecosystems that are fundamentally important to the economy of our province, where ranching and forestry coincide with high-value snake habitat. Not only that, these local and landscape scale patterns have obvious repercussions for snakes using forest habitats in the event of shifting ecosystem boundaries and thermal regimes under various climate change scenarios.

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APPENDIX A

MORPHOLOGY, CAPTURE AND SURGERY DATA FOR STUDY ANIMALS

In this Appendix, I provide the morphological measurements and details of snake capture, surgery, and telemetry for the animals from hibernacula in British Columbia that were included in this study.

Table A1. Morphology, capture and surgery data for Western Rattlesnakes radio-telemetered in 2010 in the Thompson-Nicola region of British Columbia.

Study Year	Snake ID	Den	Weight (g) - Spring	Weight (g) - Fall	SVL (mm)	VTL (mm)	iButton weight	Transmitter weight (g)	Hardware total % of body weight	Spring Capture Date	Spring Surgery Date	Spring Release Data	Fall Capture Date[1]	Fall Surgery Date	Fall Release Data	Surgery Notes – Adhesions [2]
2010	PI01	TN3	530	--	962	--	3.3	5.2	1.60	14-Apr	15-Apr	17-Apr	M-Jul	--	--	--
	PI02	TN3	360	400	775	--	3.3	3.6	1.92	14-Apr	15-Apr	17-Apr	20-Sep	21-Sep	24-Sep	None
	PI03	TN3	485	525	869	--	3.3	5.2	1.75	14-Apr	15-Apr	17-Apr	19-Sep	21-Sep	24-Sep	Minor
	SP01	TN6	565	730	902	66	3.3	5.2	1.50	14-Apr	15-Apr	17-Apr	19-Sep	21-Sep	24-Sep	Minor
	SP02	TN6	565	700	826	--	3.3	5.2	1.50	14-Apr	15-Apr	17-Apr	19-Sep	21-Sep	24-Sep	None
	SP04	TN6	430	571	772	57	3.3	5.2	1.98	14-Apr	15-Apr	17-Apr	19-Sep	21-Sep	24-Sep	Minor
	SP08	TN6	600	688	920	77	3.3	5.2	1.42	22-Jun	23-Jun	24-Jun	20-Sep	21-Sep	24-Sep	None
	RI01	TN5	463	525	879	70	3.3	3.6	1.49	16-Apr	20-Apr	22-Apr	22-Sep	23-Sep	25-Sep	None
	RI02	TN5	590	636	980	--	3.3	5.2	1.44	19-Apr	20-Apr	22-Apr	23-Sep	23-Sep	25-Sep	Major
	GM01	TN2	450	610	902	79	3.3	5.2	1.89	19-Apr	20-Apr	22-Apr	T-Sep	--	--	--
	FA01	TN1	640	795	886	70	3.3	5.2	1.33	18-Apr	20-Apr	23-Apr	22-Sep	23-Sep	25-Sep	Minor
	FA02	TN1	444	600	829	64	3.3	5.2	1.91	18-Apr	20-Apr	23-Apr	8-May*	9-May*	10-May*	Minor
	FA03	TN1	490	695	831	--	3.3	5.2	1.73	18-Apr	20-Apr	23-Apr	22-Sep	23-Sep	25-Sep	None
	PZ01	TN4	462	516	854	64	3.3	3.6	1.49	18-Apr	20-Apr	23-Apr	T-Sep	--	--	--
	PZ02	TN4	707	670	991	73	3.3	5.2	1.20	18-Apr	20-Apr	23-Apr	18-Sep	21-Sep	24-Sep	None
	PZ03	TN4	444	548	841	70	3.3	5.2	1.91	18-Apr	20-Apr	23-Apr	22-Sep	23-Sep	24-Sep	Minor
	PZ04	TN4	443	570	858	60	3.3	5.2	1.92	18-Apr	20-Apr	23-Apr	18-Sep	21-Sep	24-Sep	Minor

Notes: 1 M = snake mortality; T = transmitter failure; * = capture occurred the following spring

2 Adhesions = bands or casing of fibrous tissue that form around implanted hardware, classify Minor, Major, or None

Table A2. Morphology, capture and surgery data for Western Rattlesnakes radio-telemetered in 2011 in the Thompson-Nicola and Okanagan-Similkameen regions of British Columbia.

Study Year	Snake ID	Den	Weight (g) - Spring	Weight (g) - Fall	SVL (mm)	VTL (mm)	iButton weight	Transmitter weight (g)	Hardware total % of body weight	Spring Capture Date	Spring Surgery Date	Spring Release Data	Fall Capture Date[1]	Fall Surgery Date	Fall Release Data	Surgery Notes – Adhesions [2]
2011	G04	OS1	310	--	727	45	3.3	3.7	2.26	20-Apr	28-Apr	3-May	T-Jun	--	--	--
	G23	OS1	480	645	920	74	3.3	5.3	1.79	22-Apr	2-May	3-May	23-Sep	25-Sep	27-Sep	None
	G24	OS1	400	405	794	60	3.3	5.3	2.15	22-Apr	28-Apr	3-May	29-Sep	01-Oct	03-Oct	None
	GXY	OS1	515	582	873	--	3.3	5.3	1.67	22-Apr	28-Apr	3-May	23-Sep	25-Sep	27-Sep	None
	PS02	OS3	710	1003	987	76	3.3	5.3	1.21	23-Apr	26-Apr	3-May	23-Sep	25-Sep	27-Sep	None
	PS04	OS3	600	725	905	67	3.3	5.3	1.43	23-Apr	26-Apr	3-May	23-Sep	25-Sep	27-Sep	None
	PS05	OS3	400	601	864	60	3.3	5.3	2.15	23-Apr	26-Apr	3-May	23-Sep	25-Sep	27-Sep	None
	PS10	OS3	460	--	892	64	3.3	5.3	1.87	23-Apr	26-Apr	3-May	M-May	--	--	--
	J01	OS2	320	320	787	64	3.3	3.7	2.19	22-Apr	28-Apr	3-May	22-Sep	25-Sep	27-Sep	Minor
	J03	OS2	300	303	756	57	3.3	3.7	2.33	22-Apr	28-Apr	3-May	22-Sep	25-Sep	27-Sep	None
	J04	OS2	260	270	733	60	3.3	3.7	2.69	22-Apr	28-Apr	3-May	22-Sep	25-Sep	27-Sep	None
	V01	OS4	470	732	819	64	3.3	5.3	1.83	20-Apr	26-Apr	3-May	21-Sep	25-Sep	27-Sep	None
	V02	OS4	340	320	768	51	3.3	5.3	2.15	20-Apr	26-Apr	3-May	21-Sep	25-Sep	27-Sep	None
	V03	OS4	260	355	660	41	3.3	3.7	2.69	20-Apr	26-Apr	3-May	21-Sep	25-Sep	27-Sep	None
	VXY	OS4	383	451	744	--	3.3	3.7	1.83	20-Apr	26-Apr	3-May	21-Sep	25-Sep	27-Sep	None
	CH02	TN7	550	--	835	76	3.3	5.3	1.56	18-Apr	21-Apr	29-Apr	M-Jul	--	--	--
	CH03	TN7	550	--	822	57	3.3	5.3	1.56	19-Apr	21-Apr	29-Apr	M-Jun	--	--	--
	CH06	TN7	460	--	810	48	3.3	5.3	1.87	19-Apr	21-Apr	29-Apr	M-Jun	--	--	--

Notes:
1 M = snake mortality; T = transmitter failure
2 Adhesions = bands or casing of fibrous tissue that form around implanted hardware, classify Minor, Major, or None

APPENDIX B

EFFICACY OF EXISTING PROTECTED AREAS FOR WESTERN RATTLESNAKES IN BRITISH COLUMBIA

In this Appendix, I briefly examine the effectiveness of the existing protection mechanisms on rattlesnake hibernacula in British Columbia. Telemetry data from 10 hibernacula was used to investigate snakes' movements in relation to the boundaries protected areas surrounding the hibernacula.

INTRODUCTION

Managed as a species-at-risk on both provincial and federal levels, there are several mechanisms in place for the protection of Western Rattlesnakes (*Crotalus oreganus*) and their habitat in British Columbia, Canada. The current protection of rattlesnakes varies depending on the land tenure and ownership.

The BC Wildlife Act (1982) affords protection to individuals of the species across all land types. Habitat is only protected under the BC Wildlife Act when designated as a wildlife management area, critical wildlife area or wildlife sanctuary. Under the Act, it is an offense to harass, harm, capture or kill an individual animal without a permit unless it poses a threat to a person or property. Since venomous snakes are perceived as threatening by their very nature, it is likely that the Act provides little real protection from persecution. On privately owned land, the BC Wildlife Act is the only protective legislation that applies.

On federal Crown Land (including Indian Reserves, Federal Parks, and Federal Wildlife management areas), the Species at Risk Act (*SARA*) protects both individual rattlesnakes and their habitats. The federal *Species at Risk Act* (*SARA*) prohibits killing, harming, or capturing an individual of a listed wildlife species. It is also prohibited to damage or destroy the residence of one or more individuals of a listed wildlife species, such as a hibernacula.

Rattlesnakes on provincial Crown Land are included in the Identified Wildlife Management Strategy (IWMS) under the Forest and Range Practices Act (FRPA). Habitat protection in the form of Wildlife Habitat Areas (WHAs) are intended to safeguard known denning sites and areas of known habitat including travel corridors and foraging areas (Committee on the Status of Endangered Wildlife in Canada 2004, Sarell 2004). The Provincial BMPs for Amphibians and Reptiles recommend that critical habitats for all life history stages are protected (Ovaska et al. 2004). WHAs for rattlesnakes are intended to maintain and link denning and foraging habitat, travel corridors, and egg-laying sites within and between adjacent populations, including habitats that are important for the conservation of this species (*e.g*., communal hibernacula, especially for multi-species hibernacula, and talus slopes, rock outcrops, or cliff habitats). Forty-two percent of hibernacula in British Columbia occur on provincial Crown Land where WHAs can be applied (Hobbs 2013). Due to limitations in knowledge of site-specific movement and migration patterns, and accommodation of existing land uses and tenure, generally, only habitat in the immediate vicinity of hibernacula is protected, while other critical habitats, including migration corridors, foraging and mating habitats, often are not within the boundaries. WHAs are generally approximately 200–300 ha in size, but size depends on site -specific factors such as suitable habitat, and adjacent land use and ownership. Within the WHA, range practices and recreation will be managed to limit disturbance (BC Ministry of Water, Land and Air Protection 2004).

Parks and protected areas are also established on provincial Crown Land to conserve biodiversity values and habitat for multiple species and ecological communities at once and may contain key habitats for multiple species. Certain types of development and disturbance are prevented or limited within their boundaries, but activities that may be detrimental to wildlife species (*i.e*., grazing, recreation) often are still allowed. Specific guidelines may be in place in parks to protect known resident species including rattlesnakes.

While there appears to be an abundance of protection options available for rattlesnakes in BC, scenarios exist where snakes remain unprotected. For example, limited protection applies where hibernacula and their habitat occur on privately owned land. Here, the BC Wildlife Act protects the snakes themselves, but habitat is not protected. Alternate avenues for management and protection of the species are education and stewardship of private landowners, ranchers and members of the community. In addition, the effectiveness of protection measures on provincial Crown Land may be limited by lack of site-specific information and existing land uses.

The objective of this appendix is to examine how effective the existing protection mechanisms are at capturing the full-life history of the animals they protect. The specific questions that I endeavor to answer in this appendix are as follows: (1) are snakes travelling outside of protected areas surrounding their hibernacula, (2) to what extent are snakes using habitat outside protected areas.

METHODS

As part of my thesis examining the thermal-spatial ecology of snakes, I radio-tracked rattlesnakes from a number of hibernacula throughout the Thompson-Nicola and Okanagan-Similkameen regions of British Columbia (see Chapter 1, Figure 1.3) during the summers of 2010 and 2011. Seven of the 10 hibernacula studied had established protected areas surrounding them (Table B1). Four of these hibernacula were located inside established or proposed parks (Lac du Bois Provincial Park [n=3] and Oliver Mountain [proposed; n=1]). Three hibernacula were located in established WHAs, and the remaining three hibernacula were unprotected, with no special designation designed to protect the animals.

I monitored the seasonal movements of snakes originating from these 10 hibernacula, discussed in Chapter 2 of this thesis. Where hibernacula occurred within protected areas, the distances travelled by the telemetered snakes were examined in relation to the park or WHA boundaries using ArcGIS 10.3. All statistics were performed in R (R Core Development Team 2011) and used a significance level of $\alpha=0.05$. Means were reported ± 1 standard deviation, unless otherwise stated.

RESULTS

Two of 11 telemetered snakes from hibernacula within parks moved outside the park boundaries, both from hibernaculum in Lac du Bois Provincial Park. The straight-line

Table B1. Existing habitat protection for Western Rattlesnakes at study hibernacula in the Thompson-Nicola and Okanagan-Similkameen regions of British Columbia.

Hibernaculum	Number of study snakes	Existing Habitat Protection	Size of Protected Area (ha)
TN3	3	Lac Du Bois Provincial Park	948.0
TN5	2	Lac Du Bois Provincial Park	
TN6	3	Lac Du Bois Provincial Park	
OS2	3	Oliver Mountain Provincial Park (proposed)	365.0
TN1	3	Wildlife Habitat Area 3-008	180.4
TN4	4	Wildlife Habitat Area 3-112	144.8
OS3	3	Wildlife Habitat Area 8-064	254.4
TN2	1	None	n/a
OS1	4	None	n/a
OS4	4	None	n/a

distance travelled beyond the park boundaries by these snakes, originating from different hibernacula, were 40 m and 425 m, respectively.

All telemetered snakes originating from hibernacula within WHAs travelled beyond the boundaries of their respective WHA (see Table B2; Figure B1). The average straight-line distance moved beyond the WHA boundaries was 1445.4 ± 926.8 m (n=10). The range of dates when animals were outside of the boundaries of their respective WHAs ranged from May 27 to September 29.

DISCUSSION

Based on the snakes and hibernacula I sampled, it appears those snakes originating within parks were afforded relatively effective protection over the course of their active season migrations, as only 2 of 11 snakes actually travelled beyond park boundaries. Overall, parks likely provide superior protection to species-at-risk such as snakes, due to more stringent restrictions of activities and land uses within their boundaries, but my work did not specifically address this issue.

All of the snakes emerging from hibernacula protected by WHA designations moved outside of the boundaries of the WHA for the bulk of the active season, using predominantly unprotected habitat. It is likely that this occurs at other hibernacula as well, and consequently, many of the male snakes and non-gravid female snakes (Macartney and Gregory 1988) performing long distance migrations from hibernacula protected by WHAs may be using unprotected habitat for much of the active season. A study of gopher snakes (*Pituophis catenifer deserticola*) by Williams et al. (2012) showed that establishment of typical, small WHAs around hibernation sites was inadequate to protect the animals. Idealized circular WHAs of 193 ha were superimposed on known hibernacula, based on the 200 – 300 ha size mandated by the government (Bertram 2004). Eighty-five percent of snakes in their study stayed within the hypothetical WHAs, while 15% of snakes moved beyond the boundaries (Williams et al. 2012). The actual WHAs in my study were also small, averaging 193 ha. In my study, 100% of the telemetered animals moved beyond the boundaries of the protected area, suggesting that these small protected areas may be even less effective for rattlesnakes than for gopher snakes.

Table B2. Distance (m) moved beyond Wildlife Habitat Area boundaries by Western Rattlesnakes in the Thompson-Nicola and Okanagan-Similkameen regions of British Columbia.

Wildlife Habitat Area (WHA)[1]	Study Snake	Distance from turn-around location to closest WHA boundary (m)	Mean distance outside WHA boundary (± 1 SD)
8-064	OS3-02	1309.25	1179.7 ± 657.2
	OS3-05	467.44	
	OS3-04	1762.45	
3-122	TN4-01	96.42	1867.9 ± 1295.7
	TN4-02	1791.57	
	TN4-03	2487.54	
	TN4-04	3096.16	
3-008	TN1-01	532.00	1147.7 ± 565.4
	TN1-02	1267.49	
	TN1-03	1643.66	

[1] Wildlife habitat areas are identified by numbers representing their planning region and individual identification numbers (BC Ministry of Environment, no date).

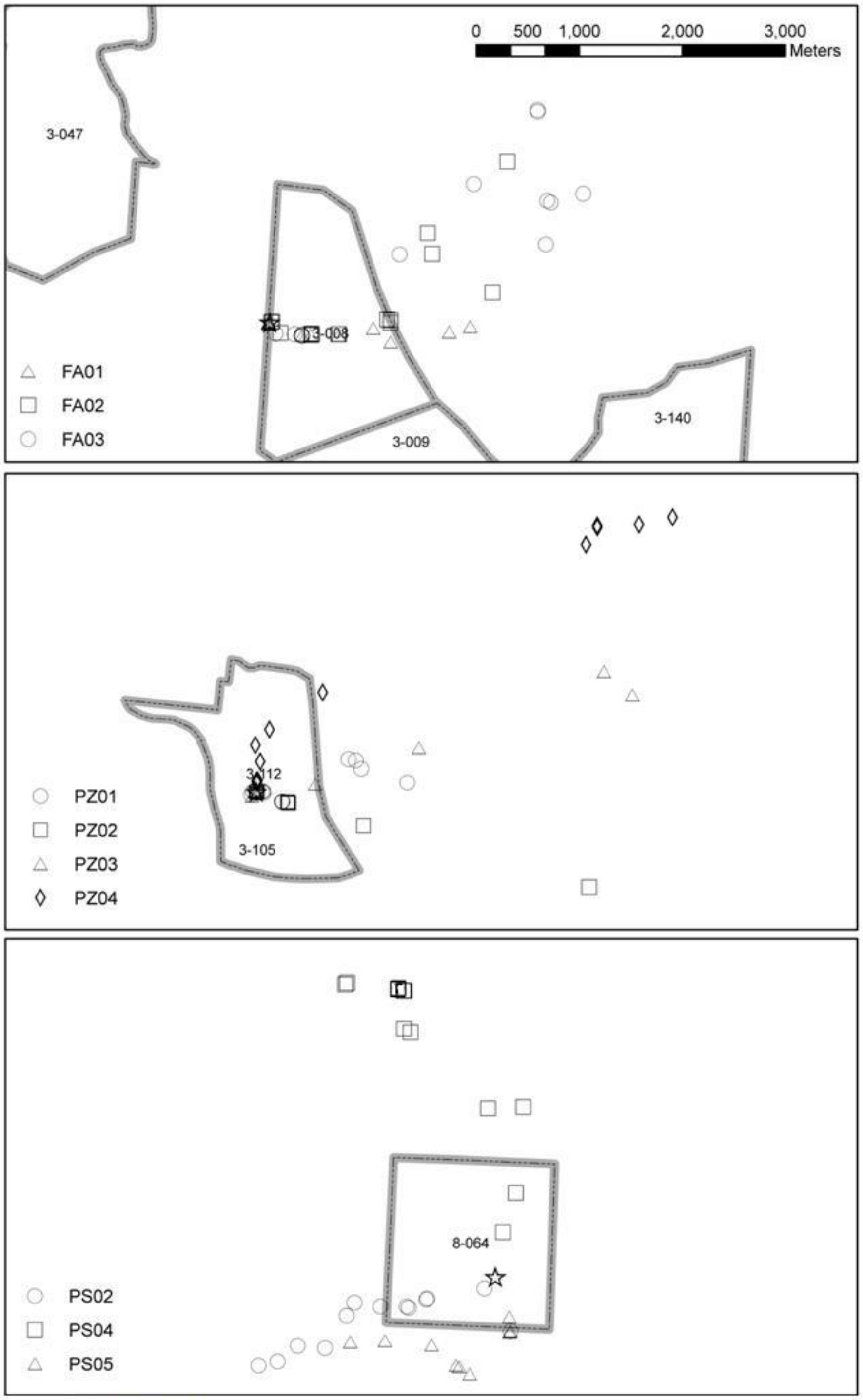

Figure B1. Snake movements relative to the boundaries of Wildlife Habitat Areas (WHAs) in the Thompson-Nicola and Okanagan-Similkameen regions of British Columbia, Canada. The locations of hibernacula are represented by star (☆) symbols, while the boundaries of the WHA are demarcated by the grey dashed lines. The snakes' locations over the course of their summer migration movements are represented by different symbols for each individual (☐,○, Δ).

The cursory analysis I present here demonstrates that existing habitat protection of WHAs may not be sufficient to fully protect rattlesnakes. To some degree, the results of my work presented in Chapters 2 and 3 of this thesis may allow for inferences to be better made by managers on summer habitats likely to be used by rattlesnakes using particular hibernacula. Knowledge of potential behavioural differences on large and small scales between rattlesnake populations will allow managers to increasingly adapt management strategies to specific hibernacula, including expanding the size of WHAs to the maximum extent possible, while managing the shape of protected areas to incorporate high quality snake habitat or areas known to be used by migrating snakes. As other populations of temperate snakes, including gopher snakes, racers (*Coluber constrictor*) and rubber boas (*Charina bottae*), likely exhibit similar habitat uses and face similar thermal and habitat constraints, these principles may be applied more broadly, potentially by creating multi-species protected areas.

While wildlife managers will aspire to improve the design of existing and future WHAs, and focus these areas on areas of high-value habitat, current land use and ownership will constrain these activities. Thus, the encouragement of stewardship and habitat protection by individual landowners and the public remains an important component in effective protection of species at risk.

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APPENDIX C

CLIMATE CHANGE AND THE EFFECTS OF CHANGING THERMAL REGIMES ON REPTILES IN BRITISH COLUMBIA: A QUALITATIVE NOTE

INTRODUCTION

In the last 100 years, the earth has warmed by 0.6°C, with most of that warming occurring in the latter part of the century (Walther et al. 2002). Worldwide, this has resulted in longer freeze-free periods, more variable precipitation regimes, and vegetation shifts, both over elevations and latitudes (Walther et al. 2002). While these shifts have affected many organisms, for instance, song-bird migration (Shamoun-Baranes et al. 2006), there may be particularly significant effects on ectothermic animals, as temperature is a key factor in most life processes. Thermal mapping of the landscape can also be used to assess changes in thermal characteristics under climate change scenarios. These changing thermal regimes potentially impact on ectotherm habitat selection.

Plasticity in phenotype and behavior may allow ectotherms to adapt to changing thermal regimes, but there are (presumably) limits to the speed at that animals can adapt (Fuller et al. 2010). Ectotherms in temperate regions may have broader thermal tolerance than those in tropical regions (Deutsch 2008), however, avoidance of extreme body temperatures remains key. Kearney et al. (2009) suggest that changing vegetation cover, due to climate change, may be the primary consideration for ectotherms under changed thermal regimes. Vegetation cover is one of two main types of feature used for small-scale behavioural thermoregulation, the other being structural features such as rocks and crevasses (Huey et al. 1989).

Climate change is a global phenomenon; however, some areas will remain within the current climate envelope, while others will experience a great deal of change (Penman et al. 2010). In British Columbia, significant change is expected, as the predicted average temperature increase is 0.5°C per decade (Hamann and Wang 2006). Effects of climate change are already being observed. In the southern part of the province, some reforestation efforts following natural or anthropogenic disturbance have failed due to drought and record high temperatures. The mountain pine beetle epidemic has been partly attributed to warmer than average winter temperatures (Hamann and Wang 2006). Under the majority of climate change scenarios, southern interior ecosystems are expected to get hotter and drier. This will likely result in vegetation shifts including: an increase in the area and elevation range of the bunchgrass zone, decreased regeneration of Ponderosa pine following fire, natural mortality and mountain pine beetle kill; and desertification of already dry areas (Hamann and Wang 2006).

EFFECTS ON REPTILES IN BRITISH COLUMBIA

Shifting ecosystem boundaries, such as encroachment of forests into grassland habitats, may have significant effects on the habitat use by reptiles (Jezkova et al. 2015, La Sorte and Jetz 2012). If there are thermoregulatory costs or benefits to using forested habitat, then this will potentially have far reaching impacts on reptile species that use these habitats in temperate regions (Dingle 1991).

The effects on snakes in the Thompson-Okanagan are likely to be two-fold. First, changes in the vegetation will modify the structure and heterogeneity of the landscape, requiring behavioral modifications to small- and large-scale thermoregulation. On a local scale, desertification in some areas will lessen the amount of vegetation (big sage brush, shrubs, grass) that can be used for shelter from the environment (hot or cold), limiting snakes to structural features that may be less available or more spread out. On a landscape scale, expansion of the bunchgrass zone would mean longer migrations to reach forested habitat and increased energy expenditure on travel, perhaps reducing overall fitness. Secondly, changing seasonal temperatures and precipitation regimes will affect the timing of the rattlesnake active season in these regions. Longer frost-free periods may incite earlier emergence from hibernation. Increased precipitation in the spring and fall, however, may decrease the effectiveness of the spring and fall basking periods, reducing any benefits incurred from a longer active season.

The information on thermal habitat use gleaned from this thesis, incorporated into a comprehensive habitat model could be applied to thermal regimes predicted under various climate change scenarios in order to predict local effects on snake habitat use. This was not feasible within the scope of this study, but provides promising future opportunities.

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