WESTERN RATTLESNAKE (*CROTALUS OREGANUS*) MIGRATION AND HABITAT USE IN BRITISH COLUMBIA, CANADA

by

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ABSTRACT

Studies on migratory behaviour and habitat use are central to understanding the ecology of migratory animals and provide important data to inform the conservation and management of these species. However, spatial ecology can vary substantially among conspecific individuals, and failing to understand differences within or between populations may be problematic. In British Columbia, Canada, where Western Rattlesnakes (*Crotalus oreganus*) reach their northern range limit, individuals undertake seasonal migrations between communal hibernacula and summer hunting grounds. Mature snakes also show annual fidelity to their migratory paths, providing a useful system to examine the development of migratory behaviour and variation within and between populations. Knowledge on the spatial ecology and habitat use by juvenile vertebrates in general is sorely lacking, and we address this gap by comparing spring outbound migratory movements of juveniles to those of adult Western Rattlesnakes at a site in southern British Columbia (BC), Canada, and describe habitat use by juvenile snakes along their active-season movement paths.

Juvenile movement data were collected in 2021, and adult data (2011-2016) were drawn from a long-term project database. We found that compared with adult rattlesnakes, juveniles displayed similar directional orientation, direction of vertical migration, and path sinuosity, but initiated spring migrations later and exhibited shorter movements in terms of distances and rates. To assess juvenile habitat use, we measured habitat at two spatial scales along the active-season movement paths of snakes. Resembling adult rattlesnake behaviour elsewhere in BC, juveniles selected habitat features that provided structurally stable cover (e.g., woody debris, shrub, and rock cover). Additionally, we tested for differences in features at sites used for short- and long-duration stopovers but identified little difference in the microhabitat features associated with these two categories of stopover locations.

Western Rattlesnakes are commonly associated with low-elevation grasslands and open Ponderosa pine (*Pinus ponderosa*) habitats; however, recent work has shown that some animals undertake longer-distance migrations into higher-elevation Douglas-fir (*Pseudotsuga menziesii*) forests. Here, to further investigate multi-phenotypic migratory tactics and habitat use, we compiled all available raw data from radio-telemetry studies conducted on adult males ($n = 139$) between 2005 and 2019 from nine study sites across the Canadian range of Western Rattlesnakes. On average, snakes migrated 1364 ±781 m (ranging from 105 m to 3832 m) from their overwintering dens. Migratory distance differed significantly between sites and was higher among individuals using forests as their migratory destination, yet there was immense variation in migratory distance among snakes using forests and open habitats, suggesting more of a continuum of phenotypes than a dichotomy. Next, we used a linear mixed-modelling approach to assess potential drivers of long-distance migration and found that migratory distance was best predicted by a combination of physiological factors, landscape terrain, and vegetation. Even the top-performing model, however, left much of the variation in migratory distance unexplained ($r_s = 0.65$ based on k-fold cross-validation where $k = 10$), suggesting other factors not measured here, such as genetics and prey quality, may also be driving long-distance movements.

Overall, my thesis provides critical knowledge on the ecology of a young age class of rattlesnake and sheds light on some of the drivers of multi-phenotypic migration among mature snakes. The findings have implications for the conservation and management of rattlesnakes in the far north where seasonal movements are commonplace and contribute to our growing understanding of the complexity of patterns and variation in the movement ecology of this far-ranging snake.

Keywords: migration, movement, habitat use, Western Rattlesnake, *Crotalus oreganus*, radio-telemetry, British Columbia, juvenile, migratory continuum

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NOTE: I have elected to use plural pronouns throughout the core chapters of this thesis (Chapters 2, 3, and 4) to match the style of journal publication and in acknowledgement of the intellectual contributions of my supervisors and the critical role of field assistants.

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CHAPTER 1.

INTRODUCTION

ANIMAL MIGRATION

Migration in animals refers to the seasonal movements of individuals made between distinct habitat regions (Russell et al. 2005; Dingle and Drake 2007). Taking place across a range of spatial scales and time periods, migration is central to the ecology and life history of many species, allowing individuals to respond to changes in resource availability and to exploit habitats favourable for critical processes such as breeding, grazing, hunting prey, and overwintering (Hoare 2009). Within a species or population, multiple migratory phenotypes may be present (Sawyer et al. 2019). This variation often can be linked to identifiable subsets of a population, such as age class, sex, or reproductive condition (i.e., male, gravid female, or nongravid female; Adriaensen and Dhondt 1990). For example, migratory timing in Humpback Whales (*Megaptera novaeangliae*) varies between females with and without a calf, and between adult and juvenile whales (Craig et al. 2003), while migratory timing and destinations of young Cory's shearwaters (*Calonectris borealis*) progressively change with age (Campioni et al. 2020).

Differing forms of migratory behaviour are, however, not always linked to such obvious demographic units. In the case of phenomena like partial migration (where only part of the population migrates) – well documented in fish (Chapman et al. 2012), ungulates (Cagnacci et al. 2011; Gaidet and Lecomte 2013; Hebblewhite et al. 2018; Berg et al. 2019), birds (Lundberg 1988; Adriaensen and Dhondt 1990; Hegemann et al. 2019), and even insects (Menz et al. 2019) – or a migration continuum (mixed migratory behaviours within a population), variation within individual demographic groups of a population can also occur (Chapman et al. 2012; Cagnacci et al. 2016). Various factors, including environmental conditions, risk of predation, competition for mates or resources, or intraspecific niche diversity, may act concurrently to create complex patterns of multi-phenotypic movement tactics within populations (Chapman et al. 2011).

While migration offers many advantages for animals that inhabit environments with seasonal variation in resource quality and/or quantity (Dingle and Drake 2007; Hoare 2009;

Milner-Gulland et al. 2011), the conservation of migratory animals can be especially challenging (Reynolds et al. 2017), and conservationists have known for well over 10 years that migratory populations globally are in decline (Wilcove and Wikelski 2008). A key challenge lies in understanding the rules by which migratory animals determine where to go, how long to stay, and when to leave (Bauer et al. 2008). Accordingly, a thorough understanding of patterns of migration and habitat use, both within and across populations, is critical for developing effective management and conservation strategies for at-risk migratory species (Allen and Singh 2016).

MIGRATION IN SNAKES

Barring turtles, snakes are the only reptilian taxa where migration has been extensively studied (Russell et al. 2005). For migratory snakes, and northern species in particular, seasonal migrations between overwintering hibernacula and summer breeding and foraging grounds allow snakes access to important food resources and mates (Martin et al. 2017). Migration between overwintering habitat (hibernacula) and summer foraging sites commonly is associated with cold climates, presumably necessitated by the lack of sufficient summer resources (i.e., prey availability) in the immediate proximity of hibernacula (Larsen 1987). Extensive migratory movements have been documented in numerous temperate zone snakes (Macartney et al. 1988), while snakes at more southern latitudes generally exhibit comparatively reduced migratory distances, as seen with Prairie Rattlesnakes (*Crotalus viridis*; Bauder et al. 2015) and Western Rattlesnakes (*Crotalus oreganus*; Ashton 2003).

WESTERN RATTLESNAKE ECOLOGY & MIGRATION

The Western Rattlesnake (*Crotalus oreganus*) is a viper (Family Viperidae) that reaches its northern range limit in British Columbia (BC), Canada (Macartney 1985). In BC, the range of Western Rattlesnakes is largely limited to two warm, dry, valleys in the interior region of the province, stretching east-west through the Thompson-Nicola region, and roughly north-south in the Okanagan-Similkameen regions (Southern Interior Reptile and Amphibian Working Group 2016). Western Rattlesnakes in BC are found within the Bunchgrass (BG), Ponderosa Pine (PP), and Interior Douglas-fir (IDF) biogeoclimatic zones of the province (BEC; Forest Analysis and Inventory Branch: B.C. Ministry of Forest 2021), and are strongly associated with grassland, shrub-steppe, open forest, and rocky habitats. Western Rattlesnakes' diet consists primarily of small mammals, but birds and other small reptiles also are occasionally consumed (Macartney 1989; COSEWIC 2015; McAllister et al. 2016).

Western Rattlesnakes in Canada face a plethora of threats such as habitat fragmentation and loss, road mortality, and direct persecution (Environment and Climate Change Canada 2019), and the species is Blue Listed in the province of BC (B.C. Conservation Data Centre 2013) and as 'Threatened' at the federal level (COSEWIC 2015). Living at their northern range limit also comes with several unique challenges, including long cold winters, that force individuals to seek shelter in communal hibernacula for roughly half of the year (from October to April; Macartney 1985). Communal overwintering hibernacula in BC generally sit at ~400-800 m elevation (Southern Interior Reptile and Amphibian Working Group 2016) on southwest to southeast facing aspects (COSEWIC 2015), and Western Rattlesnakes are known to show high fidelity to individual hibernacula (Macartney 1985). As a result of the shorter active season, relative to conspecifics further south, rattlesnakes in BC exhibit slower growth rates and delayed maturity, with females experiencing longer reproductive cycles and smaller litter sizes, all of which drastically affect recruitment rates (Macartney and Gregory 1988).

Western Rattlesnakes undertake annual migrations beginning in the spring (April-May) that take them away from their hibernacula and into their summer foraging habitat (Macartney and Gregory 1988; Gomez et al. 2015; Lomas et al. 2019; Maida et al. 2020). These migrations can take individuals up to 4km away from their hibernacula (Harvey and Larsen 2020), though rattlesnake movement patterns and habitat use can vary dramatically across populations and even among individuals from within a single hibernaculum (Gomez et al. 2015; Lomas et al. 2019; Harvey and Larsen 2020; Maida et al. 2020).

For Western Rattlesnakes, the sources of variation in migratory patterns are relatively well understood in some subsets of the population, and poorly understood in others. For example, there are known migratory differences between reproductive and non-reproductive females (Graves and Duvall 1993; Eye 2022) and between males and females in non-reproductive years (King and Duvall 1990). On the other hand, little is known about how migratory tactics may vary ontogenetically (i.e., as individuals age). Perhaps most interestingly, however, is the variation that can be seen within a single subset of the population: adult males. Recent work on adult male Western Rattlesnake migratory behaviour in BC has revealed an apparent dichotomy in migratory phenotypes, both within and between den populations, with respect both to habitats and to distances travelled during migration. Specifically, studies by Gomez et al. (2015) and Harvey and Larsen (2020) suggest that both migratory distance and habitat use are dichotomous and linked (i.e., long-distance migrants use forests, short-distance migrants use open habitats) and that these varying tactics are highly den- and site-specific. At the same time, other studies have documented significant variation in the directionality, habitat associations, and extent of migration among individuals from within a single den (e.g., Lomas et al. 2019; Maida et al. 2020). Harvey and Larsen (2020) showed that rattlesnake migrations are, unsurprisingly, dictated at least in part by the thermal environment; beyond this, however, the drivers of this variation are not well understood, necessitating a larger-scale study to understand the broader patterns and sources of this variation.

One critical aspect in disentangling the sources of variation seen in adult Western Rattlesnake migratory behaviour is having a solid understanding of migratory ontogeny in the species; namely, whether individuals adopt particular migratory patterns early on in their lives, or if these differing behaviours develop later in life. Ideally, to answer this question, individuals would be tracked continually over successive years as they age, though current radio-transmitter technology and battery life render this extremely difficult, if not impossible. An alternative to this approach is tracking juvenile Western Rattlesnakes from hibernacula where adults are known to exhibit multi-phenotypic migration. Such hibernacula provide an excellent testing ground to examine how migratory tactics develop in juvenile animals, particularly when there is minimal interaction between juveniles and adults. At the same time, juvenile rattlesnakes are sorely understudied; by studying the spatial ecology and habitat use of this younger age class we will shed light on their ecology and behaviour, which will facilitate improved conservation and management for the species across a greater age range.

THESIS OBJECTIVES & METHODS

The objectives that I address in this thesis fall under two themes: (1) juvenile Western Rattlesnake movement ecology and microhabitat use, and (2) variation in adult Western Rattlesnake migration tactics and habitat use across their Canadian range. The specific objectives within each of these themes are outlined thusly:

1. **Juvenile Western Rattlesnake movement ecology and microhabitat use:**
    - **a.** Quantify juvenile Western Rattlesnake spring migration and determine if the variation and patterns of movements seen in juveniles are a reflection of the patterns seen in adult movements at the same study site. **Chapter 2**
    - **b.** Assess the habitat selection of juvenile Western Rattlesnakes along their migratory routes and determine whether these younger animals select similar habitat features on the landscape as has been recorded for adults. **Chapter 3**
    - **c.** Determine whether juvenile snakes utilize anchor (long-duration) and transient (short-duration) stopover sites with distinct differences in habitat features – do juvenile rattlesnakes have a preference for specific habitat features for long-duration stopovers? **Chapter 3**
2. **Variation in adult Western Rattlesnake migration tactics and habitat use across their Canadian range:**
    - **a.** Examine multi-phenotypic migration in rattlesnakes by combining data across studies to reveal patterns and dissimilarities of migratory behaviour in the species, specifically by comparing and contrasting migration distance, timing, direction and extent of vertical migration, home range sizes, and destination habitats used across the sample of study populations. **Chapter 4**
    - **b.** Examine the role that physiological conditions (e.g., temperature, body condition) and landscape features within an individual’s home range (e.g., vegetation and terrain) play in driving migratory behaviour. **Chapter 4**

In the remainder of Chapter 1, I provide an overview of my primary study site that is used in Chapters 2, 3, and 4, and a brief overview of the additional eight study sites used in Chapter 4. In Chapter 2, I address *Objective 1a* by quantifying and contrasting juvenile and adult outbound spring migration on the Osoyoos Indian Reserve (OIR) study site using data collected through radio-telemetry. In Chapter 3, I investigate the habitat selection of juvenile Western Rattlesnakes along their movement paths (*Objectives 1b* and *1c*), using habitat data collected concomitantly with the movement data, and analyzed in a paired use-availability design. In Chapter 4, I address *Objectives 2a* and *2b* by compiling existing radio-telemetry data collected between 2005 and 2019 at nine unique study areas, in both the Okanagan-Similkameen and Thompson-Nicola regions, to address multi-phenotypic migration in adult male Western Rattlesnakes across their Canadian range, and use a linear mixed modelling approach to address drivers of differing migratory distances. Finally, in Chapter 5, I revisit my main thesis findings and their significance for the future conservation and management of the Western Rattlesnake in British Columbia.

STUDY SITES

I studied juvenile Western Rattlesnake movement and habitat use at a site located on the southeast corner of the Osoyoos Indian Reserve (OIR), on the lands surrounding the Nk'Mip Desert Cultural Centre in Osoyoos, B.C., Canada (49.05° N, 119.43° W; Figure 1.1). The OIR site is 450-ha in area and is a dry arid ecosystem (Figure 1.2) dominated by low-elevation shrub-steppe habitat composed of Bluebunch Wheatgrass (*Agropyron spicatum*), Antelopebrush (*Purshia tridentata*), and Big Sagebrush (*Artemisia tridentata*). Areas of the site also contain sections of open forest consisting of Ponderosa Pine (*Pinus ponderosa*), Douglas Fir (*Pseudotsuga menziezii*), and steep rocky talus slopes. The study site also contains drastic habitat quality contrasts: sections are heavily altered from tourism development, while other areas are in near-pristine condition with negligible human impact or habitat fragmentation. While some snakes use disturbed areas frequently, many snakes never encounter developed areas or they leave developed areas completely during the active season (Lomas et al. 2019; Maida et al. 2020). Communal rattlesnake hibernacula are scattered across rocky southwest-facing slopes and sit at approximately 450−800m elevation. In 2021, temperatures in Osoyoos were above historical 30-year climate means during the months of June and July (Figure 1.3), largely due to the record-setting 'heat dome' that blanketed much of southern BC starting in the final days of June 2021 (Philip et al. 2021). Further, in mid-July the Nk'Mip Creek Wildfire burnt approximately 19,500 ha of land, including a large portion of the study site (British Columbia Wildfire Service 2021).

Accordingly, we restricted our movement analysis (Chapter 2) to data collected up to June 30th to avoid confounding effects of these extreme weather events that occurred later in the summer.

I studied adult rattlesnake migratory tactics across British Columbia using radio-telemetry data collected at nine unique study sites (Figure 1.4). Five of the study sites were located within the Okanagan-Similkameen region: Osoyoos (as described above), White Lake, Oliver, Cawston, and Vernon. The remaining four sites were located in the Thompson-Nicola region: Spences Bridge, Ashcroft, Kamloops East, and Kamloops West. See Figure 1.5 for representative photos of the ecosystems at each of these sites, and Figure 1.6 for historical climate normals across the sites.

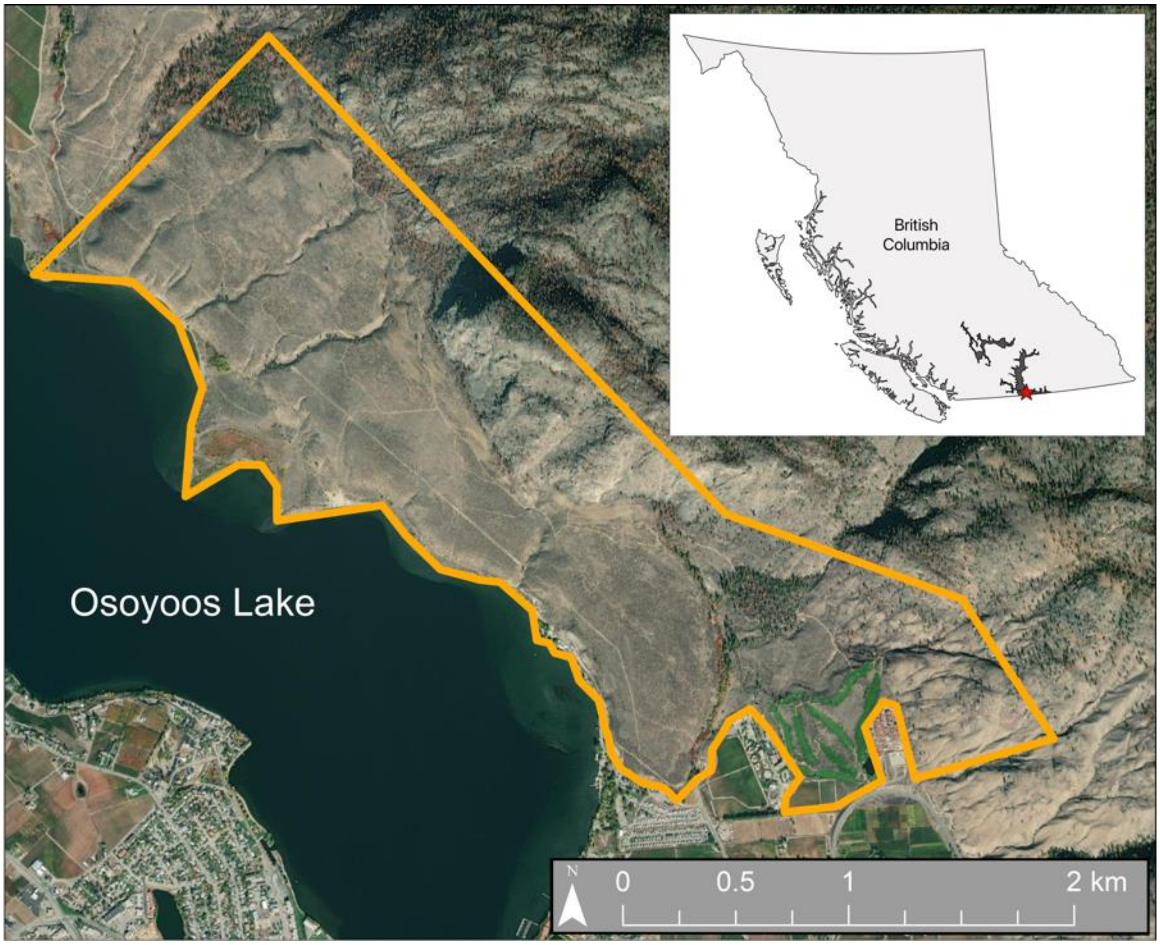

Figure 1.1. Map of Osoyoos Indian Reserve (OIR) study site (indicated in orange) near Osoyoos, B.C., Canada. Inset shows the northern extent of the Western Rattlesnake (*Crotalus oreganus*) range within British Columbia (dark gray), with the OIR study site indicated by a star. *Map projection: NAD 1983 UTM Zone 11N. Basemap imaging: Esri, Maxar, Earthstar Geographics, and GIS User Community. Shapefile for Western Rattlesnake range from NatureServe Canada (2020; https://www.natureserve.org/canada/ebar).*

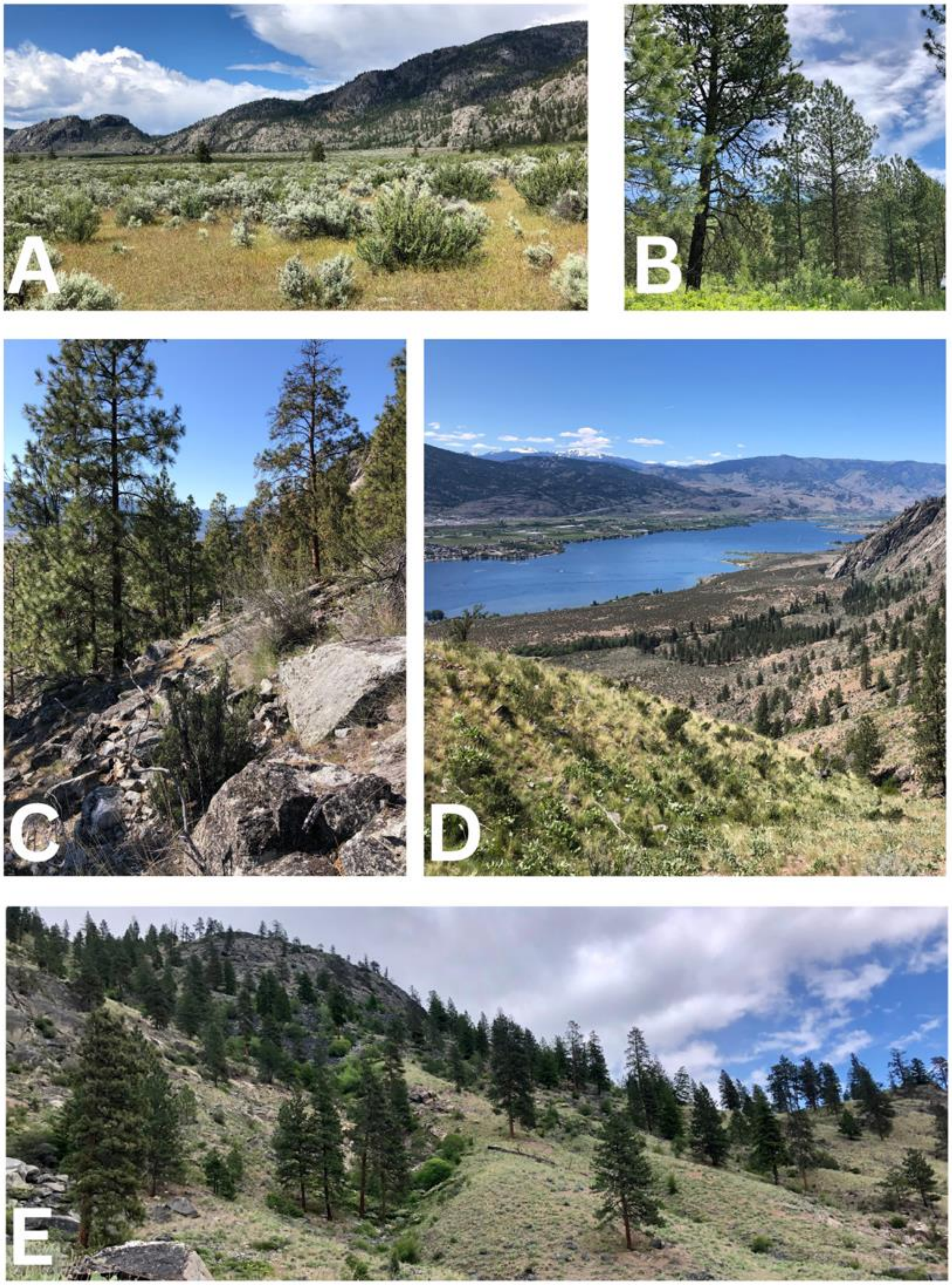

Figure 1.2. Examples of the dominant ecotypes on the Osoyoos Indian Reserve (OIR): (A) low-elevation grassland shrub-steppe habitat composed of Bluebunch Wheatgrass (*Agropyron spicatum*), Antelopebrush (*Purshia tridentata*), and Big Sagebrush (*Artemisia tridentata*); (B) open Ponderosa Pine (*Pinus ponderosa*) and Douglas-Fir (*Pseudotsuga menziezii*) forests; (C, D, & E) mid-elevation rocky slopes. Photos by the author.

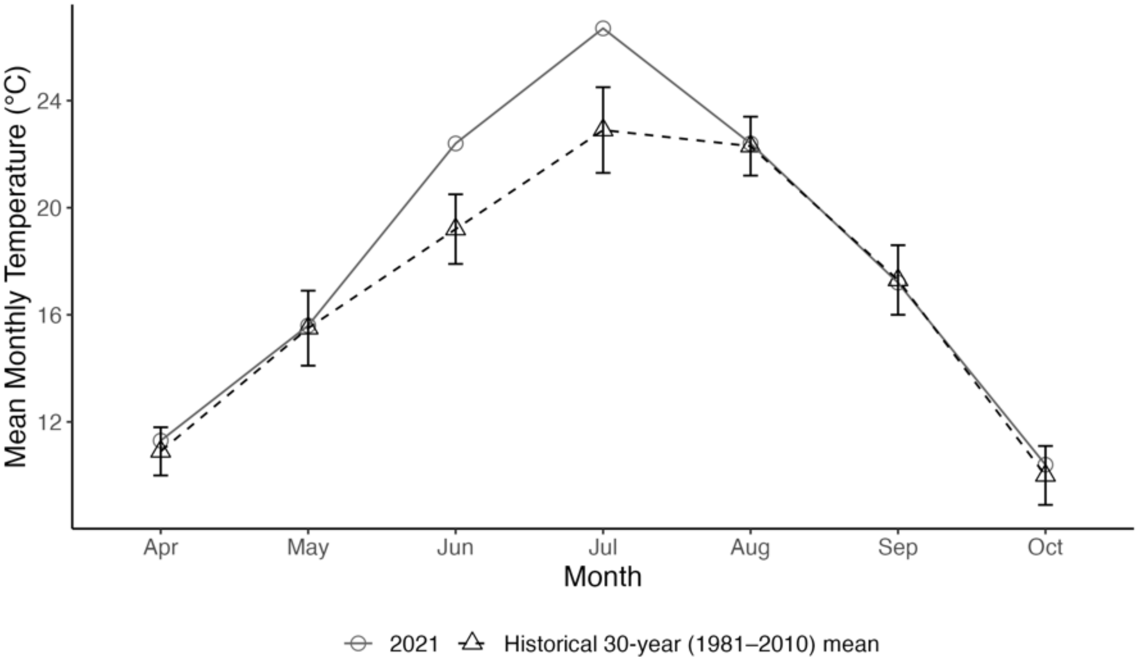

Figure 1.3. Mean monthly temperatures (°C) in Osoyoos, British Columbia, in 2021 (circles) compared to the historical 30-year mean (1981–2010; triangles) during the months of April through October (rattlesnake active season). Values measured at the Osoyoos weather station (49.03° N, 119.44° W). Data from Environment and Climate Change Canada (2023).

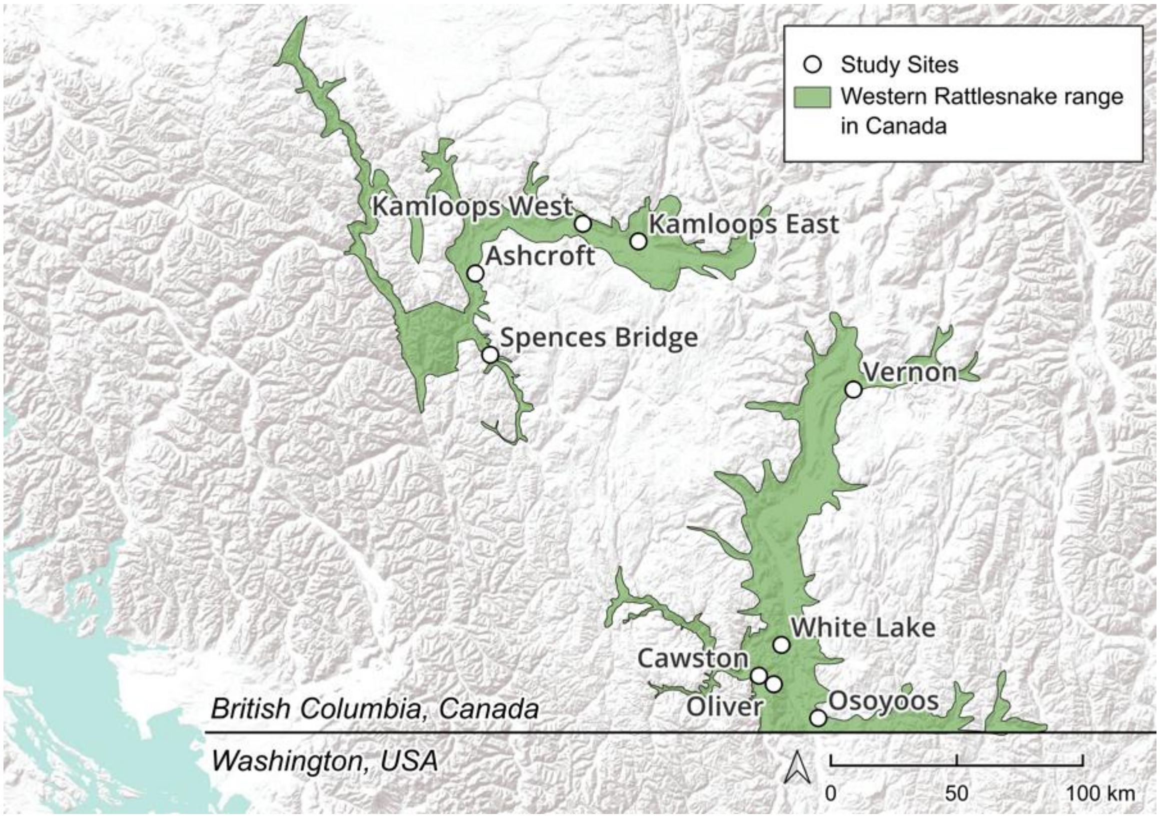

Figure 1.4. Map of study sites (*n* = 9) in British Columbia (BC), Canada, where telemetry has been conducted on the Western Rattlesnake (*Crotalus oreganus*). The green shaded map area indicates the range of Western Rattlesnakes in the Pacific Northwest region of North America. *Map imaging: Esri; BC Conservation Data Centre (2020). Projection: EPSG3857.*

The White Lake study site (49.31° N, 119.64 °W) is situated in the White Lake Basin, near Kaleden, BC. This site is characterized as open shrub-steppe grassland habitat containing Bluebunch Wheatgrass and Big Sagebrush, surrounded by steeper forested hills containing predominantly Ponderosa Pine, with higher elevation areas of Douglas Fir. This site was bisected by a paved two-lane road that sees an average of 350 vehicles/day between April and October. See Winton et al. (2020) for a detailed site description.

The Oliver site (49.17° N, 119.67° W) is situated to the west of Oliver, BC, and the nearby Cawston site (49.20° N, 119.75° W) is situated near Cawston, BC. Both sites are composed of Bluebunch Wheatgrass and Big Sagebrush grasslands at low elevations, transitioning to Ponderosa Pine and Douglas Fir forests at higher elevations.

The Vernon study site (50.20° N, 119.24° W) is situated near Vernon, BC, and straddles Kalamalka Lake Provincial Park and the adjacent Coldstream Ranch. This was the site used by Macartney (1985) and more recently Atkins (2021; 2022). The Vernon site is composed of forest habitats comprising Ponderosa Pine, Douglas Fir, and Western Redcedar (*Thuja plicata*), and lower-elevation grasslands containing Bluebunch Wheatgrass and several native shrub species. Kalamalka Provincial Park is a provincially protected area that averages roughly 32,600 monthly visitors between April and October, and sees year-round use for recreational activities including hiking, mountain biking, and horseback riding. The Coldstream Ranch portion of the study site is used for free-ranging cattle and has limited public access. See Atkins et al. (2022) for a detailed site description.

Spences Bridge site (50.32° N, 121.20° W) sits 15km southeast of Spences Bridge, BC, to the east of the Nicola River. The Ashcroft site (50.60° N, 121.28° W) sits 15km south of Ashcroft, BC, to the east of the Thompson River. Both the Ashcroft and Spences Bridge sites are composed of Bluebunch Wheatgrass and Big Sagebrush grasslands at low elevations, transitioning to Ponderosa Pine and Douglas Fir forests at higher elevations.

The Kamloops East site (50.71° N, 120.40° W) is located to the northwest of the city of Kamloops, BC, and is composed of open, rolling grasslands of Bluebunch Wheatgrass and Big Sagebrush with limited tree cover. This site encompasses an area of housing developments and a designated ATV-use area. There is a primary paved road that transects the site and sees relatively heavy use by the general public and forestry industry, and secondary gravel roads that cross the site typically experience relatively low levels of traffic. See Gomez (2007) for a detailed site description.

The Kamloops West site (50.77° N, 120.70° W) sits northwest of the city of Kamloops, to the west of the Kamloops East site. The site is composed of a mix of Bluebunch Wheatgrass and Big Sagebrush grassland, Ponderosa Pine forests, and Douglas Fir forests. The topography is rugged with abundant bedrock outcrops on steep, south-facing slopes. Forested areas are grazed by cattle during the summer months. See Gomez (2007) for a detailed site description.

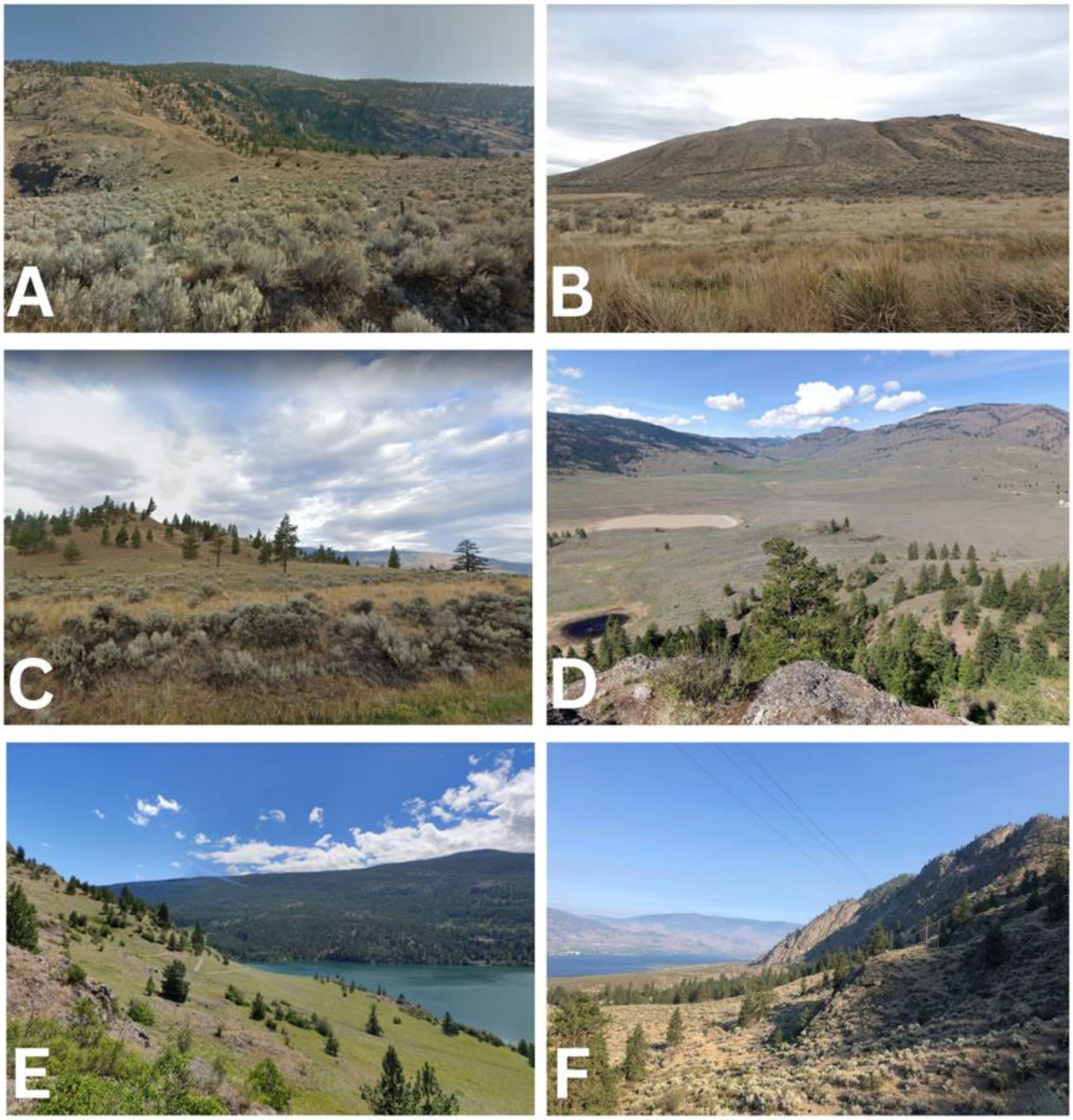

Figure 1.5. Representative photos of the study sites used in the BC-wide adult Western Rattlesnake migration and habitat use analysis. (A) Cawston / Oliver; (B) Kamloops East / Kamloops West; (C) Ashcroft / Spences Bridge; (D) White Lake; (E) Vernon; (F) Osoyoos. Photos A-E sourced from Google Streetview, photo F by the author.

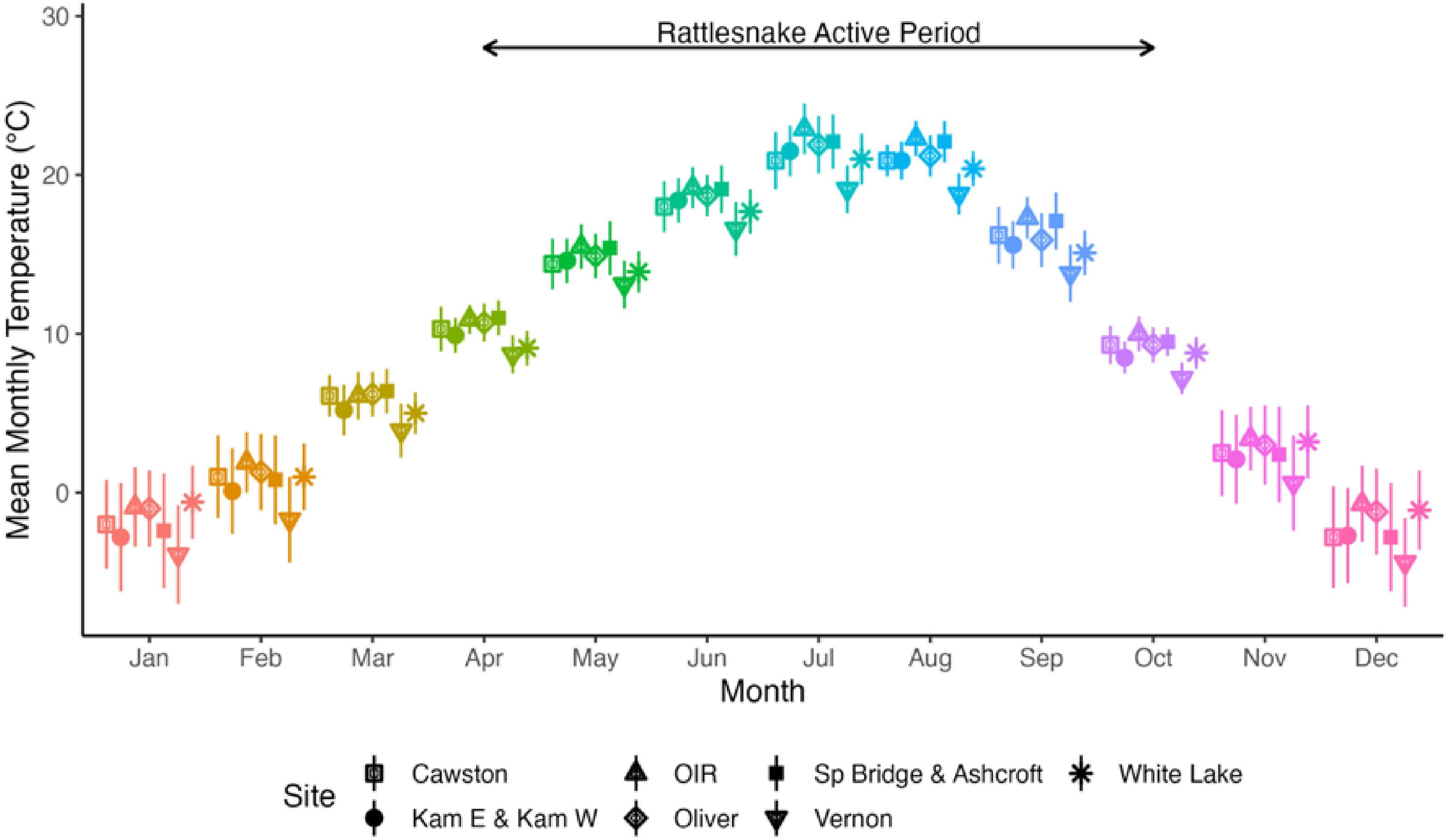

Figure 1.6. Historical 30-year (1981–2010) mean monthly temperatures (Environmental and Climate Change Canada 2023) across each of the nine study sites, using the closest available weather station (note that the same weather station was used for Kam E and Kam W, and for Spences Bridge and Ashcroft). Error bars represent ±1 standard deviation. Data from Environment and Climate Change Canada (2023). *Site abbreviations*: OIR = Osoyoos Indian Reserve; Kam E = Kam East; Kam W = Kam West; Sp Bridge = Spences Bridge. *Actual weather station names*: Cawston = Keremeos 2; Kam E & Kam W = Kamloops A; OIR = Osoyoos CS; Oliver = Oliver; Sp Bridge & Ashcroft = Spences Bridge Nicola; Vernon = Vernon Coldstream Ranch; White Lake = Penticton A.

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CHAPTER 2.

WESTERN RATTLESNAKE (*CROTALUS OREGANUS*) SPRING MIGRATION IN BRITISH COLUMBIA: A COMPARATIVE STUDY OF JUVENILES AND ADULTS

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INTRODUCTION

Migration is a phenomenon central to the ecology and life history of many species, occurring across multiple spatial scales and periods. Migration allows individuals to exploit changes in resource availability and habitats favourable for critical processes such as breeding, foraging, and overwintering (Dingle and Drake 2007; Hoare 2009). The spatial scale on which migration occurs can range from a few metres to thousands of kilometres, but generally consists of annual-cycle or life-cycle bidirectional movements on greater scales than the animal’s normal daily movements (Dingle and Drake 2007). Migration also may be influenced by age class, given that the ecology of early age classes differs considerably from adults in many species, especially those whose body mass increases by orders of magnitude over the lifespan. This ontogenetic change may lead to shifts in diet, susceptibility to predation, and habitat use, which in turn may influence migration (Stamps 1983; Werner and Gilliam 1984; Jellen and Kowalski 2007). Such shifts in migratory strategies have been documented for several taxa, including sea turtles (Scott et al. 2014), birds (Campioni et al. 2020; Rousseau et al. 2020; Verhoeven et al. 2022), crustaceans (Hines et al. 1995), and sharks (Andrews et al. 2010; Hoyos-Padilla et al. 2014).

The process through which migratory behaviour develops during an individual’s lifetime varies and may be driven by innate processes (insects, some birds), both in terms of decisions to migrate and direction of migration, while in other groups migratory behaviour develops through social learning (many mammals and birds) or may even be directed by environmental factors (e.g., sea currents, as with marine turtles) (Scott et al. 2014). Yet, in the absence of social learning or obvious environmental pressures, particularly when intraspecific variation in adult migratory tactics is present, the processes through which individuals adopt particular migratory behaviours as they age and/or grow are much less clear.

Shifts in diet and habitat use are widely documented across age classes in snakes (e.g., Lind and Welsh 1994; Eskew et al. 2009), but much less so for migratory behaviour. For temperate snake species, seasonal migrations between overwintering habitat (hibernacula) and summer ranges allow snakes access to food resources and mates (Gomez et al. 2015; Martin et al. 2017). These migrations typically are associated with colder climates, possibly driven by the spatial arrangement of resources (e.g., prey availability being scarce in the immediate proximity of hibernacula), with conspecifics at more southern latitudes generally exhibiting comparatively reduced migratory distances, as seen with Prairie Rattlesnakes (*Crotalus viridis*; Bauder et al. 2015) and Western Rattlesnakes (*Crotalus oreganus*; Ashton 2003). Radio-telemetry has been instrumental in understanding the movements, habitat use, and behaviour of adult snakes, but smaller individuals largely have been excluded from these studies due to the constraints on transmitter size and design; external attachment methods and technological advances in battery size, however, are opening the doors for the study of animals with smaller body sizes (Cobb et al. 2005; Jellen and Kowalski 2007). However, studies on movement behaviour across age classes in snakes are still sparse, although juvenile Black Ratsnakes (*Elaphe obsoleta*) exhibit decreased movement rates, travel shorter total paths and overall distances from their hibernacula, and possess smaller home ranges than adults (Blouin-Demers et al. 2007).

The North American rattlesnake clade reaches its extreme northern limits in southern Canada. In British Columbia (BC), the Western Rattlesnake (*Crotalus oreganus*) reaches its northern limits, occupying communal hibernacula between October and April (Macartney et al. 1988; Maida et al. 2020) to which they show strong fidelity (Brown et al. 2009; Gomez et al. 2015). These temperate snakes generally exhibit three distinct periods of movement and behaviour throughout an active season: a spring migration after egress away from hibernacula (outbound); a period of mid-summer movements within established hunting and mating grounds; and, a fall migration back to hibernacula, prior to ingress (inbound – Maida et al. 2020). In B.C., these periods occur in roughly April-June, July-August, and September-

October, respectively (Macartney 1985). The snakes are known to migrate up to 4 km from their hibernacula during the active season (Harvey and Larsen 2020), in some cases moving upwards in elevation (Gomez et al. 2015). This provides a rare if not unique example of altitudinal migration in a reptile (Hsiung et al. 2018). Moreover, recent work has revealed significant variation in migratory tactics employed by adult snakes both between and within den populations, ranging from individuals who undertake long-distance migrations into upland forested habitat, to individuals that exhibit limited, non-directional migrations, often remaining in low-elevation grassland habitat (Gomez et al. 2015; Lomas et al. 2019; Harvey and Larsen 2020; Maida et al. 2020). Regardless of their precise destinations, individual rattlesnakes in BC follow the same migratory paths year after year as adults (Gomez et al. 2015), suggesting stable migratory phenotypes in mature snakes.

Currently, scant information exists regarding the ontogeny of rattlesnake migration behaviour, save for a few studies focusing on neonatal dispersal and scent trailing in other *Crotalus* species in the United States (Cobb et al. 2005; Figueroa et al. 2008; Howze et al. 2012). All told, rattlesnake migration and the scale at which it occurs provides an excellent testing ground to examine how migratory tactics develop in juvenile animals, especially when minimal direct interaction exists between experienced and inexperienced migrants. Our objective in this study was to determine if the variation and patterns of movements seen in juveniles would be a reflection of the patterns seen in adult movements. Mark-recapture data at our long-term study site in southern British Columbia, Canada, suggests that juvenile rattlesnakes do move away from hibernacula during the active season; however, we hypothesized that the relatively smaller body size of juvenile snakes (and the associated differences in energetic requirements for long-distance movements) would cause the extent of their movements to occur on a smaller scale than that of adults.

MATERIALS AND METHODS

Study site

This study took place in the southeast corner of the Osoyoos Indian Reserve (OIR) near Osoyoos, British Columbia, Canada (49.05° N, 119.43° W). This 450-ha study site is a dry arid ecosystem dominated by low-elevation shrub-steppe habitat composed of Bluebunch

Wheatgrass (*Agropyron spicatum*), Antelopebrush (*Purshia tridentata*), and Big Sagebrush (*Artemisia tridentata*). The study site contained drastic habitat quality contrasts: sections are heavily altered from tourism development, while other areas are in near-pristine condition with negligible human impact or habitat fragmentation. While some snakes frequent disturbed areas regularly, many snakes never encounter developed areas or leave developed areas completely during their active season (Lomas et al. 2019; Maida et al. 2020). We had two focal hibernacula on the OIR site at which juveniles were targeted for capture; we hereafter refer to these as Den A and Den B (Indigenous designations in Nsyilxcən are *iʔ x̌aʔx̌aʔulaʔxʷ iʔ q̓ʷc̓iʔs* and *iʔ x̌aʔx̌aʔulaʔxʷ iʔ snʔilitns ʔasl̓ʔupnkst ɬ sisp̓lk*, respectively). Both dens are among the most populous on the OIR site and were selected in part to maximize the capture potential of suitable individuals during egress. Further, these dens were deliberately selected to minimize the likelihood of snakes venturing into developed areas (Lomas et al. 2019).

Radio-telemetry

Juvenile rattlesnakes were defined as individuals in their second and third year of growth, which corresponds roughly to snakes with a snout-vent length (SVL) ranging from 35cm to 45cm, thus excluding all sexually mature individuals (Macartney et al. 1990). Transmitter size in relation to snake size was a major constraint in this study; hence we were unable to include individuals in their first year of growth (<35cm SVL) as this would have required smaller transmitters with exceptionally short battery life spans.

Juvenile snakes were captured by hand (using snake tongs or hooks) during egress (April-May) at or near hibernacula, with the exception of four individuals captured opportunistically later in the season in their summer range. Individuals were brought back to a laboratory space and outfitted with radio-transmitters (BD-2, 1.0g; Holohil Systems Ltd., Carp, Ontario) following the subdermal stitch attachment method first described by Riley et al. (2017) (modified from Ciofi and Chelazzi 1991) and since used in other studies (Hudson 2019; Murphy et al. 2021). The subdermal stitch method (Figure 2.1) involves running a subdermal catheter and thread under the subcaudal scales and tying the transmitter to the dorsal surface of the snake. While initially invasive (although likely less so than surgical implantation), the sub-dermal stitch method allows for non-invasive transmitter replacements as needed over the course of the study. The transmitters and associated attachment materials (catheter, suture) weighed no more than 5% of the total body mass of each snake. Immediately after transmitter attachment, the snakes were administered Baytril and Metacam, following Brown et al. (2009), and monitored for 48 hours prior to release.

Telemetered snakes were located every 2-3 days over the course of the study until the point of transmitter removal, transmitter failure, accidental transmitter detachment, natural mortality, or the inability to follow the animals (see Results). A radio-telemetry receiver (TRX-3000; Wildlife Materials Inc., Murphysboro, Illinois) and a 3-element yagi antenna were used to track individuals and the latitude/longitude coordinates of each relocation were recorded using an SXBlue II+GPS device (Geneq Inc., Montreal, Quebec). Radio-transmitter battery life was approximately 5 weeks; thus, snake recapture and transmitter replacement was planned to occur on multiple occasions per individual over the course of the study. Additionally, approximately every 2-3 weeks (coinciding with transmitter replacement, when possible), snakes were momentarily captured and inspected to monitor health; during these check-ups, the transmitter attachment and catheter protrusion sites were checked, and snakes were weighed (g) to ensure that no significant decrease in body mass had occurred. Significant decrease in body mass was defined as >20%; this threshold was chosen as active-season relative loss of mass greater than 15% has been documented in this region for adults (Lomas et al. 2015), and fluctuating body mass up to 20% has been observed due to desiccation (Macartney 1985). If a body mass decrease >20% was detected, the transmitter was removed.

Ideally, we would have simultaneously tracked a subset of adult snakes from the same hibernacula, but logistics rendered this unfeasible given the exceptional distances and rate at which these animals can move. Instead, we compiled for comparison a dataset of adult male rattlesnakes tracked between 2011 and 2016 at the same study site. Though this makes our comparisons subject to temporal biases, this risk was minimized by the compilation of adult data across a six-year period. Adults in these previous studies all received surgically implanted transmitters (SB-2; Holohil Systems Ltd., Carp, Ontario) with surgical procedures following Reinert and Cundall (1982) and pharmaceutical procedures after Brown et al. (2009). Location data also were collected in analogous fashion to that used in this study. See Maida et al. (2020) for details on surgical and field methods used for adult snakes.

Figure 2.1. (A) A telemetered juvenile Western Rattlesnake (*Crotalus oreganus*) on the Osoyoos Indian Reserve (OIR) study site in July, 2021; (B) Radio-transmitter attachment on a juvenile rattlesnake using the sub-dermal stitch method. Photos by the author.

Spring migration and home range parameters

For all movement analyses, we included only juvenile rattlesnakes that were tracked starting at egress, originating at their hibernaculum, through to the end of June. Further, any snakes that made fewer than five movements of 5 m or greater were excluded, as required by some test statistics [e.g., Rao’s spacing test; Bergin (1991)]. Movements drawn from the historical data set for adult rattlesnakes had to meet these same criteria.

We calculated 10 metrics to quantify and compare juvenile and adult rattlesnake spring migration on the OIR study site. Six of these metrics were classified as ‘distance’ metrics, all dealing with the spatial scale of migration. Three metrics dealt with the type of movement path (e.g., direction, shape) that an individual traveled, and were classified as ‘path’ metrics. The final metric dealt with migratory ‘timing’. Table 2.1 lists the metrics belonging to each of these classifications, and summarizes each of the movement metrics outlined below.

Spring maximum net displacement (MND) was determined as the maximum straight-line distance (m) between the hibernaculum and the most distal point reached during outbound migration. This metric was calculated from each snake’s trajectory for each relocation using the package ‘adehabitatLT’ (Calenge 2006) in RStudio (RStudio 2021). In addition, we calculated MND for the entire season for those juvenile snakes tracked past outbound migration and into the inbound migration period (not used in any comparisons between juvenile and adult snakes). Spring migration path length (MPL) was the total sum distance (m) of each consecutive movement event. Mean movement rate (MMR) was the mean distance (m) moved per day; we measured the distance travelled between two consecutive locations, divided by the number of days between, measured across all sequential pairs of tracking events to create an average for each individual (Diffendorfer et al. 2005; Lomas et al. 2019). Vertical migration distance (VMD) was quantified by calculating the change in elevation (m, absolute value) during outbound migration (i.e., the difference in elevation between hibernaculum and the highest or lowest point reached). We further grouped snakes into vertical migration categories (VMC); those classified as not having undertaken a vertical migration (‘no vertical’) displayed an elevational change in habitat use less than or equal to 30 m; snakes that moved uphill more than 30 m in elevation were classified as ‘up’; and, snakes that moved downhill from their hibernaculum more than 30 m were classified as ‘down’. The 30 m designation was determined by visualizing data as a histogram and selecting a natural cut-off point (gap) in the data. We classified migration as having begun (START) when a snake reached a net displacement (total maximum straight-line distance) of ≥30 m from their hibernaculum (Parent and Weatherhead 2000; Lomas 2013).

We classified spring migration path orientation (MPO) by determining if a snake directed their migratory movements towards a fixed bearing (‘directed’) or had a random distribution of migratory movements (‘random’). To determine this, we used direction of travel between all consecutive pairs of locations for migratory movements greater than 5 m (Gomez 2007). The distribution of these bearing datasets for each snake was tested for von Mises distribution (equivalent to a normal distribution for circular data) using a Watson’s Test in the package ‘circular’ (Lund et al. 2017) in RStudio (RStudio 2021). As not all data fit a von Mises distribution, we used Rao’s spacing test to test for uniformity against a hypothesis of modality on each snake’s distribution of bearings (Bergin 1991; Landler et al. 2018). We used $\alpha = 0.05$ to categorize snakes as exhibiting either a ‘directed’ or ‘random’ movement path.

To quantify spring migration path sinuosity (MPS; rad/m$^{-0.5}$), we used the ‘equation 8’ calculation for sinuosity as defined by Benhamou (2004); this is a corrected version of the sinuosity index *S* (Bovet and Benhamou 1988) that can be applied to a wide range of turning angle distributions and does not require a constant step length. This calculation was done using the package ‘trajr’ (McLean and Volponi 2018) in RStudio (RStudio 2021).

We estimated rattlesnake seasonal spring home ranges using two methods: the 100% minimum convex polygon (MCP) and 95% weighted autocorrelated kernel density estimation (AKDE). The MCP method takes the outermost set of data points representing an animal’s locations and connects them to form a polygon with no concave sides (Mohr 1947). Admittedly, MCP has been widely criticized for overestimating home range size and for its general simplicity and lack of sensitivity to factors such as the number of estimates, duration of tracking, and serial autocorrelation (see Laver and Kelly 2008). Others, however, have suggested that MCP best reflects herpetofauna home range size compared to other estimation methods (Row and Blouin-Demers 2006; Shipley et al. 2013; MacGowan et al. 2017). This leads into the long-standing controversy on whether snakes truly maintain home ranges (Tiebout and Cary 1987), yet the inclusion of home range estimates – especially using MCP – is widespread in snake literature, including many studies on Western Rattlesnakes in British Columbia (Brown et al. 2009; Lomas et al. 2019; Maida et al. 2020), leading to our choice to include MCP in this study. We used the ‘adehabitatHR’ package (Calenge 2006) in RStudio (RStudio 2021) for estimation of 100% MCP home range.

While traditional kernel density estimators (KDEs) of home range have been criticized for their sensitivity to the choice of smoothing parameter(s) and their need for independent data (Fieberg 2007), autocorrelated kernel density estimation (AKDE - Fleming et al. 2015; Silva et al. 2022) accounts for these issues and is appropriate for reptile home range estimation (Crane et al. 2021). AKDE is a home range estimator that assumes the data represent a sample from a non-stationary, autocorrelated continuous movement process by incorporating the movement of animals through an autocorrelation function derived from movement models fit to the data (Silva et al. 2022). Further, the optimal weighting method can correct for irregular sampling schedules (Fleming et al. 2018). We estimated optimally weighted 95% AKDE home ranges for each snake using the R package ‘ctmm’ (Calabrese et al. 2016).

Statistical analysis

All data were analyzed using RStudio (RStudio Version 2021.09.0 "Ghost Orchid"; RStudio 2021). We log-transformed MPS values and square-root-transformed MCP, AKDE, and mass values prior to statistical analysis to meet the assumption of normality (confirmed using Shapiro-Wilk tests). We used two-way ANOVA to compare eight of the 10 movement metrics (Table 2.1) between juvenile and adult rattlesnakes, and between snakes originating from our two main focal dens. We included an interaction term between age class and den in each of these models. The VMC and MPO movement metrics were analysed differently (Table 2.3): for VMC we used Fisher’s exact test to compare the proportion of snakes that moved ‘up’ versus those that moved ‘down’ and to compare the proportion of snakes that undertook a vertical migration in one direction or the other (i.e., ‘up’ and ‘down’) to ‘no vertical' snakes between the juvenile and adult datasets, and between the two hibernacula. We also used Fisher's exact test to compare the proportion of 'directed' snakes to 'random' snakes (MPO) between the juvenile and adult datasets and between the two hibernacula. Additionally, we used linear regression to investigate the relationship between the mass of telemetered juvenile and adult rattlesnakes and spring MCP area (using square-root-transformed data); this relationship is commonly examined in studies of home range allometry (Tamburello et al. 2015).

Variation around means is reported as ±1 SE. To reduce the chances of obtaining false-positive results (type I errors) when multiple pair-wise tests are performed on a single set of data (the multiple comparisons problem), we applied the Bonferroni correction (Holm 1979); the level of significance for all tests was set to $\alpha = 0.05$, which was then divided by the total number of comparisons made ($n = 11$ comparisons; two comparisons for VMC, one for each of the other nine metrics), yielding an adjusted level of significance of $\alpha = (0.05 / 11) = 0.0045$.

RESULTS

Between mid-April and mid-October of the 2021 active season, 21 juvenile rattlesnakes were radio-tracked for durations ranging from 19 to 140 days ($\bar{x} = 72 \pm 30$ days). This considerable range was due largely to the Nk'Mip Creek Wildfire that burnt approximately 19,500 ha of land in July, including a large portion of the study site (British Columbia Wildfire Service 2021). The fire resulted in the confirmed mortality of several juvenile snakes and prevented access to several more such that their fate could not be ascertained. Further, there were two predation mortalities, three individuals' transmitters detached early during the tracking period, and one individual was excluded due to insufficient relocations (fewer than five movements of 5 m or greater). The tracking period also fell within the record-setting 'heat dome' that blanketed much of southern BC starting in the final days June of 2021 (Philip et al. 2021). On a few occasions, transmitter batteries died before snakes could be recaptured, especially during this 'heat dome' period when snakes were seeking refuge from the heat. Two transmitters were removed in mid-July due to a decrease in body mass >20%, likely caused by desiccation following the 'heat dome'.

Although several snakes in our initial sample were tracked for relatively long periods of time, we restricted our analysis to data collected up to June 30th to avoid confounding effects of tracking duration and of the extreme weather events that occurred later in the summer (heat dome and wildfire), and we further excluded the four individuals caught opportunistically during the active season away from dens. Our dataset thus was restricted to nine juveniles (7 Den A + 2 Den B; mean SVL: 35.5 ±1.6 cm; mean mass: 35.9 ±7.1 g) that were tracked an average of 72 ±5 days, encompassing an average number of 27 ±4 tracking events per snake. The adult dataset was comprised of 16 individuals (11 Den A + 5 Den B). The mean SVL of these animals was 68.2 ±4.7 cm, and mean mass was 222.8 ±37.0 g. All adult snakes were tracked from egress through to June 30th in their respective years of study, with an average tracking duration of 69 ±4 days and an average of 22 ±7 tracking events per snake. Juvenile and adult rattlesnake movement paths are shown in Figure 2.2.

Spring migration and home range parameters

Despite the smaller sample sizes, our analyses indicated that the juvenile animals were displaying similar movement patterns to adults but on a smaller scale, in line with our predictions. Significant differences (all Ps ≤ 0.001) were detected between juveniles and adults in the one ‘timing’ metric and in all of the ‘distance’ metrics, save for ADKE which was near significant ($P = 0.0047$**)** using the Bonferroni corrected level of significance ($\alpha = 0.0045$). Meanwhile, significant differences were not detected in any of the ‘path’ metrics. No significant differences were detected in the metrics between snakes from the two dens (A and B), and no interactions between age class and den of origin were detected. See Table 2.2 for all two-way ANOVA results, and Table 2.3 for Fisher’s exact test results. Of the 21 tracked individuals, three animals travelled over 800 m (MND) from their hibernacula, with an extreme of 885 m. Linear regression on the relationship between snake mass and MCP was insignificant ($F_{1,14} = 0.18$, $P = 0.68$, $R^2 = 0.01$). The same regression was borderline insignificant for the juveniles ($F_{1,7} = 4.89$, $P = 0.06$, $R^2 = 0.41$), although oddly the relationship tended towards an inverse one (

Figure 2.3).

Table 2.1. Spring migration and home range parameter descriptions for each metric within the three categories (distance, path, and timing) used to compare juvenile and adult Western Rattlesnake (*Crotalus oreganus*) movement on the Osoyoos Indian Reserve (OIR) near Osoyoos, BC.

	METRIC	***ABBR.***	***DESCRIPTION***
Distance metrics	Spring maximum net displacement (m)	MND	Maximum straight-line distance between hibernaculum and most distal point
	Spring migration path length (m)	MPL	Total sum distance of consecutive movement event
	Mean movement rate (m/day)	MMR	Mean distance moved per day
	Vertical migration distance (m)	VMD	Absolute change in elevation during outbound migration
	Spring home range minimum convex polygon (ha)	MCP	Home range polygon using 100% of outermost telemetry locations throughout the spring tracking period
	Spring home range autocorrelated kernel density estimate (ha)	ADKE	Home range polygon (95% estimate) calculated using optimally weighted autocorrelated kernel density estimation
Path metrics	Vertical migration category	VMC	Direction of vertical migration, categorized as 'no vertical' ($VMD \leq 30$m), 'uphill' ($VMD \geq 30$m uphill from hibernaculum), or 'downhill' ($VMD \geq 30$m downhill from hibernaculum)
	Spring migration path orientation	MPO	Orientation of movement as determined by Rao's spacing test, categorized as either 'directed' (migratory movements oriented towards a fixed bearing) or 'random' (random distribution of movements)
	Spring migration path sinuosity ($rad/m^{-0.5}$)	MPS	Sinuosity of movement trajectory; higher values = more crooked paths, lower values = straighter paths
Timing	Beginning of migration (Julian date)	START	Date that a snake began migrating, indicated by a snake reaching a total maximum straight-line displacement ≥ 30m from hibernaculum

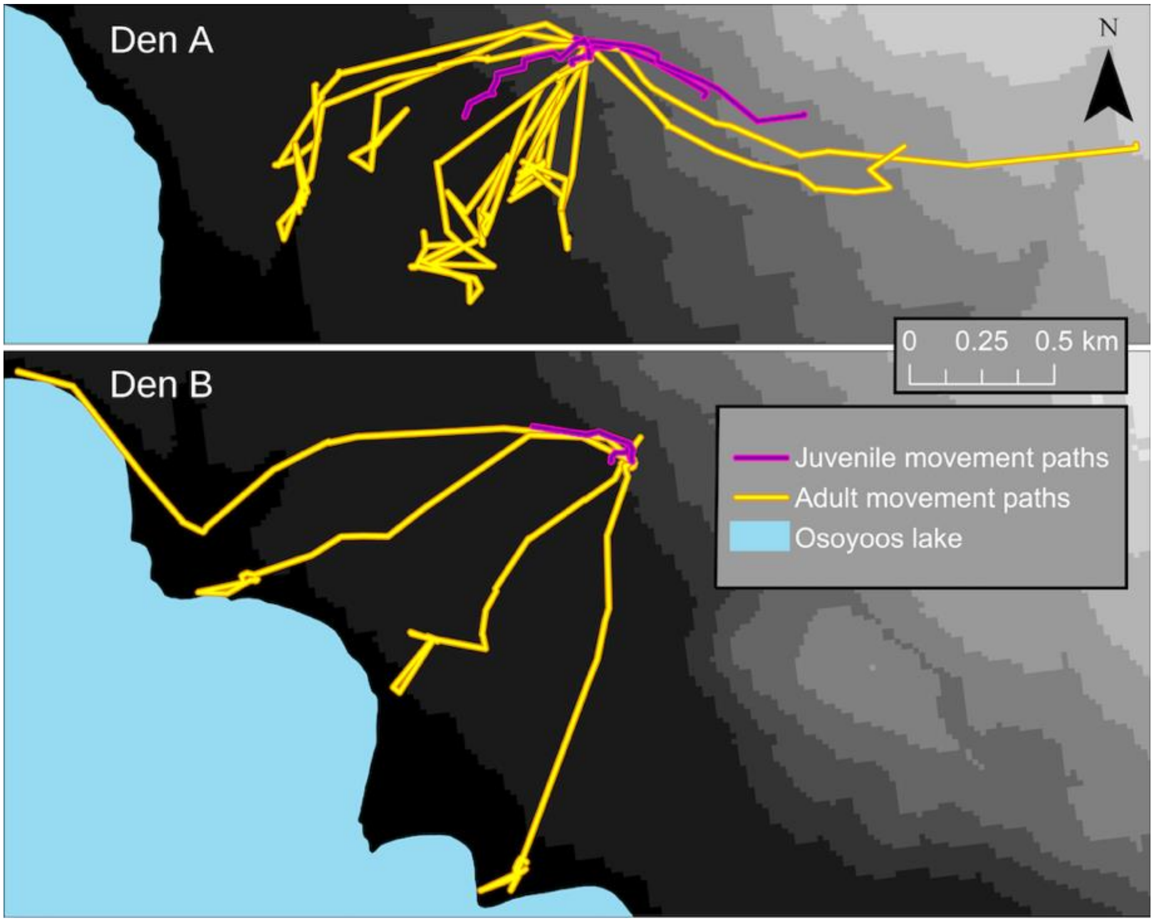

Figure 2.2. Movement paths of juvenile (*n* = 9; purple) and adult (*n* = 16; yellow) Western Rattlesnakes (*Crotalus oreganus*) on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada from Den A (top) and Den B (bottom) in the years 2011-2016 (adult) and 2021 (juvenile). Osoyoos lake (blue) sits at 280m elevation; shaded contours represent increases of 100m in elevation. Plotted paths assume straight-line movement between telemetry locations. *Map imaging: Government of British Columbia*, *Natural Resources Canada.*

Table 2.2. Results of two-way ANOVA tests comparing seven of the 10 outbound spring migration metrics between juvenile (n=9) and adult (n=16) Western Rattlesnakes (*Crotalus oreganus)* on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C. Included are results for comparison between age classes (juvenile mean ±SE, adult mean ±SE, test statistic, and *P*-value), between Den A and Den B, and for the interaction term between age class and den. Bolded *P*-values are significant at $\alpha = 0.0045$ (adjusted from $\alpha = 0.05$ using the Bonferroni correction). See Table 2.1 for a detailed description of each metric, and see Table 2.3 for results of Fisher's exact tests.

	METRIC	***AGE CLASS***				***DEN***		***INTERACTION***	
		Juvenile $\bar{x}$ *n = 9*	***Adult*** $\bar{x}$ *n = 16*	***Test Statistic***	***P***	***Test Statistic***	***P***	***Test Statistic***	***P***
Distance	**MND** (m)	262 ±90	1069 ±134	$F_{1,21} = 17.2$	**<0.001**	$F_{1,21} = 0.88$	0.36	$F_{1,21} = 0.66$	0.43
	MPL (m)	319 ±95	1670 ±156	$F_{1,21} = 34.3$	**<0.001**	$F_{1,21} = 0.03$	0.87	$F_{1,21} = 0.05$	0.82
	MMR (m/day)	4.96 ±1.5	26.72 ±2.4	$F_{1,21} = 39.1$	**<0.001**	$F_{1,21} = 0.24$	0.63	$F_{1,21} = 0.02$	0.89
	VMD (m)	83 ±25	203 ±22	$F_{1,21} = 14.5$	**0.001**	$F_{1,21} = 7.35$	0.01	$F_{1,21} = 1.01$	0.34
	MCP (ha)	1.2 ±0.5	15.8 ±3.5	$F_{1,21} = 17.2$	**<0.001**	$F_{1,21} = 0.30$	0.59	$F_{1,21} = 0.14$	0.71
	AKDE (ha)	19.1 ±10.4	168.6 ±39.3	$F_{1,21} = 10.0$	0.0047	$F_{1,21} = 0.32$	0.57	$F_{1,21} = 0.49$	0.49
Path	**MPS** (rad/m$^{-0.5}$)	0.26 ±0.06	0.15 ±0.05	$F_{1,21} = 3.5$	0.074	$F_{1,21} = 0.11$	0.75	$F_{1,21} = 0.64$	0.43
Timing	**START** (days)	May 26 ±5	May 5 ±3 *	$F_{1,20} = 17.2$	**<0.001**	$F_{1,20} = 0.41$	0.53	$F_{1,20} = 0.05$	0.88

* Adult sample size for START: *n* = 15

Table 2.3. Results of Fisher's exact tests comparing two of the 10 outbound spring migration metrics between juvenile and adult Western Rattlesnakes (*Crotalus oreganus)* on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C. Sample size (*n*) of each categorical variable is listed for each age class. Results listed for comparison between age classes and between Den A and Den B include the variables used in each Fisher's Exact Test and the associated *P*-value. Bolded *P*-values are significant at $\alpha = 0.0045$ (adjusted from $\alpha = 0.05$ using the Bonferroni correction). 'Vertical' refers to an 'uphill' or 'downhill' vertical migration. See Table 2.1 for a detailed description of each metric, and see Table 2.2 for results of ANOVA tests.

	METRIC	***AGE CLASS***				***DENS***	
		Juvenile (n)	***Adult (n)***	***Fisher's: Variables***	***P***	***Fisher's: Variables***	***P***
Path	**VMC**	$n_{\text{uphill}} = 2$ $n_{\text{downhill}} = 4$ $n_{\text{no vertical}} = 3$	$n_{\text{uphill}} = 2$ $n_{\text{downhill}} = 13$ $n_{\text{no vertical}} = 1$	Age Class & Vertical vs. no vertical	0.120	Den & Vertical vs. no vertical	0.280
				Age Class & Uphill vs. downhill	0.540	Den & Uphill vs. downhill	1
	MPO	$n_{\text{directed}} = 4$ $n_{\text{random}} = 5$	$n_{\text{directed}} = 7$ $n_{\text{random}} = 9$	Age Class & Directed vs. random	1	Den & Directed vs. random	0.66

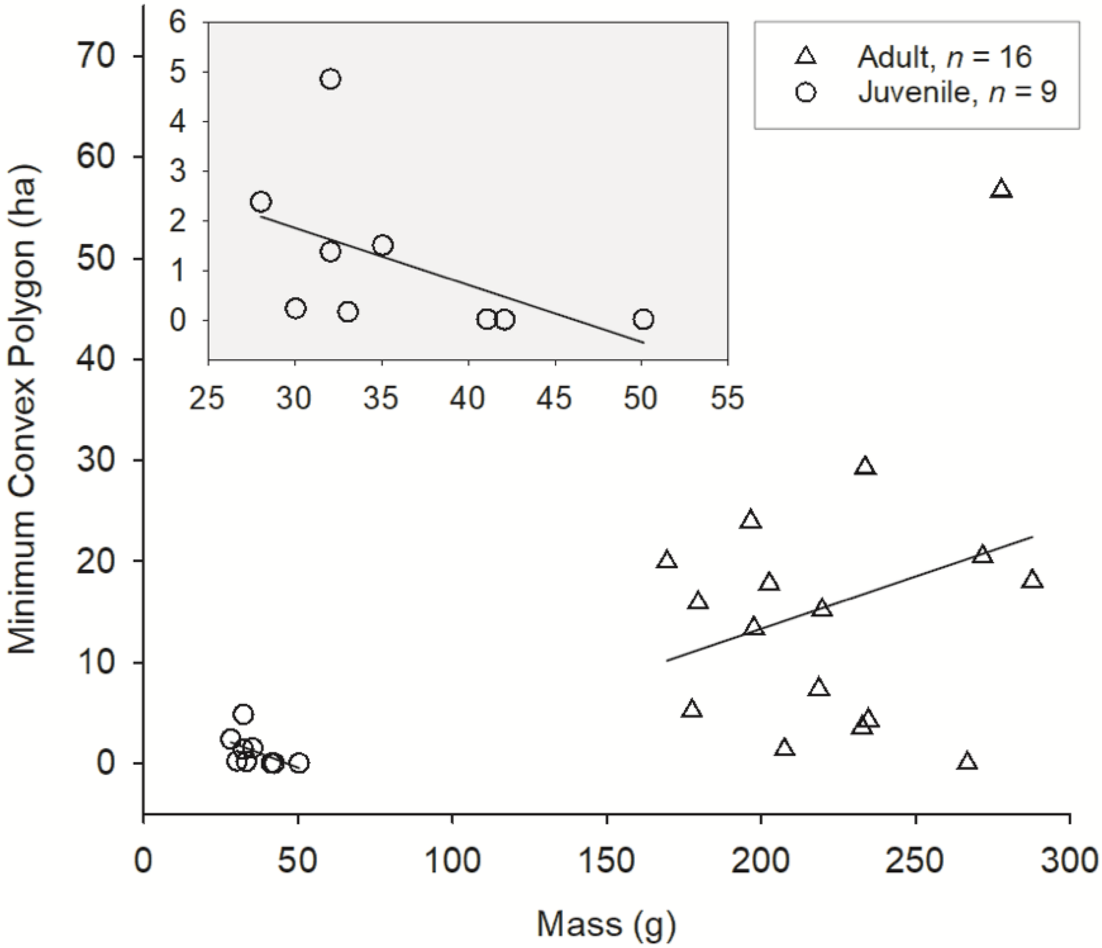

Figure 2.3. Relationship between mass (g) of telemetered juvenile (n = 9; circles) and adult (n = 16; triangles) Western Rattlesnakes (*Crotalus oreganus*) and minimum convex polygon (MCP; ha) on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada from 2011-2016 (adult) and 2021 (juvenile). The upper-left inset shows an enlarged view of the juvenile regression. The regressions for both the juvenile and adult age classes were statistically insignificant (*P*s = 0.06 and 0.68, and R^2 = 0.41 and 0.01, respectively).

DISCUSSION

This is one of the first studies to examine how the movements of juvenile terrestrial reptiles compare to larger-scale migratory movements conducted by adults. As such, it contributes to our understanding of the development of movement behaviour in a migratory population, specifically one where juveniles or neo-migrants do not migrate alongside experienced conspecifics or where there is no evidence of direct social learning; this phenomenon has been documented in some birds (Berthold and Helbig 1992) and insects (Mouritsen et al. 2013), but, to our knowledge, is largely absent for reptiles. We found that juvenile rattlesnakes exhibited smaller-scale movements as compared to adults at the same site but displayed similar tactics in terms of their movement paths. This suggests the variation in migratory behaviour seen in adult snakes may be developing at a young age, albeit on a reduced scale.

The magnitude of the movement distances calculated for adult male snakes in this study was consistent with similar measurements observed in previous studies at the same site (Lomas et al. 2019; Maida et al. 2020). Even movements made by gravid females (normally more sedentary), also at the same study site, appear greater than those we recorded for juveniles (Eye 2022). The shorter distances travelled by the small snakes was expected and intuitive given the size discrepancy between adult and juvenile rattlesnakes (Macartney et al. 1988), though it remains unclear whether juveniles and adults move similar differences relative to their size. While studies on allometric scaling of home range size are abundant, particularly for mammals and birds (Tamburello et al. 2015), the relationship between body size and home range or movement is largely understudied in snakes, and to our knowledge there is no well-established scaling methodology. A handful of studies have investigated the relationship within a single species of snake (e.g., Whitaker and Shine 2003; Roth 2005; Blouin-Demers et al. 2007; Hyslop et al. 2014), but the value of these studies for comparison to ours is limited due to the immense variation in the scale and strength of reported relationships. This variation is unsurprising; scaling relationships can differ significantly within and between taxa, and it can be exceptionally challenging to control for the influence of ecological variability (Nilsen and Linnell 2006; Tamburello et al. 2015). Nevertheless, the lack of significant relationship between body size and home range within both the juvenile and adult age classes in our study adds to our growing understanding of how challenging and complex it can be to predict migration distances for populations of these snakes, even when environmental factors are considered (Harvey and Larsen 2020). Although insignificant, the inverse relationship between juvenile body size and home range is intriguing, but at this time it is impossible to tell if this is an artifact of the small sample size or a reflection of an actual trend.

Clearly, juvenile snakes are not yet attempting to maximize reproduction, yet the cohort moved away from dens despite their reproductive immaturity. Even for adult Western Rattlesnakes, it is not clear if the relatively long seasonal movements in fact are driven by reproductive success, including outbreeding, and/or other factor(s). Recent genetic work by Schmidt et al. (2020) in our study region suggested that snakes from discrete dens were mating with individuals from nearby dens within the same complex, suggesting other factors such as foraging success may be relatively more involved in dictating adult movements. By virtue of their smaller body and gape (Rodríguez-Robles et al. 1999), juvenile snakes often have a narrower diet niche than adults. Further south in their range, juvenile Western Rattlesnakes (and other species in the clade) rely primarily on small ectothermic prey (e.g., lizards, amphibians - Mackessy 1988); in our study region, lizards are very rare in the grasslands, making neonatal and juvenile rattlesnakes largely reliant on mammalian prey (Macartney 1989). Indeed, Macartney 1989 found that over 90% of juvenile rattlesnake stomach contents consisted of shrews and juvenile mice and voles. At our study site, only two species of muroid rodents (*Perognathus parvus* and *Peromyscus maniculatus*) have been detected in the grasslands, and in relatively low densities (Maida et al. 2020). If juvenile rattlesnakes are relying largely on immature small mammals in the low-elevation arid grasslands (including shrews, also very rare), the benefits of moving further to access more productive ecosystems may not be fully realized until the snakes reach a larger size; for example, snakes that travel into forested habitat likely have a wider and more profitable suite of prey species (e.g., red squirrels, *Tamiasciurus hudsonicus*). It is impossible at this point, however, to conclude whether the movements we detected in the small snakes represents development of route familiarity that could provide dividends later in life.

Elevational differences in migration is another aspect of rattlesnake movement in the far north that has linkages to habitat selection. As per our other movement metrics, juveniles in our study did not travel up or down in elevation to the same extent as adults. Beyond this, we observed high variation across all age classes in the direction (i.e., VMC) and degree of vertical migration. This variability is consistent with Gomez et al. (2015) and Harvey and Larsen (2020), wherein study populations of rattlesnakes elsewhere in BC demonstrated striking variation in migratory tactics, with some individuals moving uphill into forested habitat and others remaining in lower-elevation grasslands. Certainly, the extent and drivers of this variation deserve further study for Western Rattlesnakes across their range and across age classes. Our study, though, highlights the importance of not linking summer habitat use by these animals to the stereotypic perspective on rattlesnake habitat selection as low elevation, arid grasslands.

The lack of age class differences in the 'path' metrics suggest that an individual's approach to how they occupy space on the landscape may be established from a young age, although as discussed, juveniles move at a spatial scale that is significantly reduced compared to adult snakes. This leaves questions concerning the drivers of differing migratory behaviour: specifically, whether young snakes' migratory tactics are innate, adopted at random, or are driven by environmental factor(s) or experience. Studies on neonate movement in other *Crotalus* species suggest that newborn snakes use scent trailing to locate communal hibernacula (Cobb et al. 2005; Figueroa et al. 2008; Brown and Maclean 2010; Howze et al. 2012); this implies that it is possible scent-trailing factors in the establishment or modification of movement behaviour in juvenile snakes during the outbound portion of their migration. Ideally, questions concerning migratory drivers would be addressed through manipulative experiments designed to test the influence of adult movements on those of juveniles, although this would be difficult to conduct. And, at the same time, multi-year radio-telemetry studies of the same individuals to determine if and how migratory behaviour changes over time, but this would be difficult given current limitations on the lifespan for transmitters.

Juvenile snakes appear to initiate their outbound migration from the dens later than adults. While the differing timing could be attributed to varying environmental conditions year-to-year, similar patterns have been observed for the species further south in their range (Fitch 1949) and elsewhere in BC (Macartney 1985), with juveniles emerging from hibernacula at a similar time but dispersing later. Discrete migratory timing has been observed in many other taxa, and Campioni et al. (2020) attribute delayed juvenile migration to an adaptive strategy to reduce competition between experienced adults and inexperienced juveniles. Potentially, this may apply to our study species; waiting for adults to disperse could limit competition for resources in the areas that juveniles will eventually occupy throughout their active season, closer to hibernacula. Further, because of differences in body size, juvenile snakes heat and cool more quickly than adults (Stevenson 1985; Blouin-Demers et al. 2007), which could result in a delayed migratory schedule while waiting for temperatures to rise sufficiently.

Although this study has yielded critical insight into the movement behaviour of juvenile rattlesnakes, the small sample sizes make future complementary work a necessity. Notably, a diversity of movement patterns was detected even within our small sample, which may reflect variation in migratory tactics employed by juvenile snakes at this site, or other locations. There is, also, the possibility that not all juvenile rattlesnakes use communal hibernacula, similar to that seen in garter snakes (Larsen and Hare 1992; Pisani 2009) and black ratsnakes (B. Charland personal communication 2023) and suggested by research on Western Rattlesnakes in this and other areas of their range (Macartney 1985; Bruckerhoff et al. 2021). Thus, there could be a subset of the juvenile population not captured in this study (literally and figuratively), and migratory behaviour among these cohorts may vary quite substantially. Tracking juveniles encountered away from hibernacula may reveal an ‘underworld’ of juvenile snakes that do not use the communal dens for the early part of their life , akin to the bird underworld postulated by Smith (1978). The underworld phenomenon, wherein some individuals leave their natal group (often termed ‘floaters’), is well documented in birds (e.g., Penteriani and del Mar Delgado 2012) and mammals (e.g., Huck and Fernandez-Duque 2017), and the behaviour of underworld floaters is often poorly understood (Huck and Fernandez-Duque 2017).

Finally, though we attempted to minimize temporal biases in our adult sample by compiling data across multiple years, our conclusions are based on a single year of juvenile data and some inter-year variability is to be expected. While our inferences would be strengthened by obtaining data in additional year(s), significant landscape alterations inflicted by the Nk’Mip Creek Wildfire in the latter part of our study year would make it impossible to disentangle changes in migratory tactics caused by year effects, aging, or the altered landscape.

Rattlesnake migration at the northern extent of their range provides a particularly interesting backdrop against which to study the migratory behaviour of young snakes, with mature snakes in this region undertaking annual migrations and showing fidelity to migratory paths. Understanding the movement patterns of animals and the sources of variation in migratory behaviour is critical for making effective wildlife and habitat management decisions, particularly when considering threatened or endangered species such as the Western Rattlesnake (COSEWIC 2015; Allen and Singh 2016). This study represents a starting point in documenting the earlier movements of juvenile rattlesnakes as precursors to adult forms of migratory behaviour, thus contributing to our increasing knowledge of the complexity of patterns and variation in this species, as well as to our growing understanding of age-based behavioural and migratory variation more broadly.

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CHAPTER 3.

MICROHABITAT AND STOPOVER SITE SELECTION BY JUVENILE WESTERN RATTLESNAKES (*CROTALUS OREGANUS*)

INTRODUCTION

Wildlife habitat selection studies are central to our understanding of animal ecology and provide important knowledge for the conservation and management of species. Individuals presumably preferentially select habitats and microhabitats that will improve their ecological performance and evolutionary fitness (Huey 1991; Hecnar and Hecnar 2011). Selection also may occur at multiple spatial scales that can be viewed as a hierarchical process, with animals choosing habitats at a broader landscape scale and selecting microhabitats sites within that habitat (Harvey and Weatherhead 2006). Habitats selected at the largest scale intuitively contain all resources needed by an animal to survive and reproduce, while sites selected at the other extreme (microhabitats) contain key resources used by animals to address specific requirements (Orians and Wittenberger 1991). In many species, patterns of movement and habitat use shift as animals age, possibly reflecting changes in resource needs, predator avoidance, life history strategies, or intraspecific competition (Werner and Gilliam 1984; Blouin-Demers et al. 2007).

Unfortunately, studies quantifying the ecology (including habitat use) of early age classes are sorely lacking in general across vertebrate taxa (e.g., aves - Cox et al. 2014; Dunn et al. 2017; marine megafauna - Hays et al. 2016; reptiles - Delaney and Warner 2016; Vesy et al. 2021), and filling these gaps should be of paramount conservation concern (Roznik et al. 2009; Cox et al. 2014). For example, there is mounting concern that a reduction in juvenile songbird survival may be the cause of species declines, though knowledge gaps remain prominent hinder effective conservation initiatives (Cox et al. 2014; Boynton et al. 2020). Understanding variation in the ecology and habitat use of animals across age classes is a necessity for effective planning and management of critical habitat for species at risk, and decisions ideally should not be made based solely on knowledge of adult habitat selection (Roznik et al. 2009).

The North American rattlesnake clade reaches its extreme northern limits in southern Canada. In British Columbia (BC), the federally and provincially threatened Western Rattlesnake (*Crotalus oreganus;* BC CDC 2013; COSEWIC 2015) reaches its northern limits, occupying communal hibernacula between April and October (Macartney et al. 1988; Maida et al. 2020) to which they show strong site fidelity (Brown et al. 2009; Gomez et al. 2015). Western Rattlesnakes typically are associated with grassland and open forested habitats, though they are also known to utilize closed-canopy forests during their annual migrations (Gomez et al. 2015; Harvey and Larsen 2020). Within these landscapes, rattlesnake microhabitat selection can largely be described by proximity to cover (Macartney 1985; Bertram et al. 2001; Gomez 2007), with snakes showing a particular preference for structurally stable cover objects (i.e., shrubs and rocks), as compared to less-stable herbaceous plant or grass cover (Gomez 2007). This is unsurprising, as the importance of cover objects for many snakes is well documented (Huey et al. 1989; Row and Blouin-Demers 2006). Features beyond proximity to cover, such as prey availability and thermal environment, also may influence Western Rattlesnake microhabitat selection. Indeed, these structurally stable features for which adult male Western Rattlesnakes show a preference can provide refuge from predators but may also provide superior thermoregulatory opportunities (Reinert et al. 1984; Huey et al. 1989) and high-quality ambush sites for small-mammalian prey that also select for this attribute on the landscape (Blair 1940; Reinert et al. 1984). These features may be important for juvenile rattlesnakes as well, as smaller-bodied snakes are at an even higher risk of predation than larger individuals (Gregory and Tuttle 2016).

In studies of Western Rattlesnakes, like many species, locations of telemetered individuals have typically served as points to conduct habitat assessments, often in comparison to random or unused sites (Thomas and Taylor 2006). However, this approach has several drawbacks, not the least of which is that specific locations may see repeated use by the animals, while the length of stay at a particular location is seldom considered (Bastille-Rousseau et al. 2010). The duration of stay at specific location(s) may vary greatly depending on the ‘intention of the stop’, and longer stays may reflect sites of higher habitat suitability or importance (Bastille-Rousseau et al. 2010). For instance, gravid Western Rattlesnakes preferentially select rookery (i.e., gestation and birthing) sites with higher rock cover at multiple spatial scales than control sites, where they may remain sedentary for multiple months (Eye 2022). On a larger scale, the concept of stopover or staging sites is well established in avian studies, generally being defined as sites where birds stop to rest and feed during migration (Kaiser 1999; Warnock 2010). The term ‘anchor point’ has been used to describe locations used by animals for periods of relatively sedentary behaviour (Douglas et al. 2012). Here, we differentiate stopover sites used by juvenile Western Rattlesnakes into two categories: we use ‘anchor point’ to describe long-duration stopover sites (potentially with high habitat suitability) and ‘transient points’ for shorter-duration stopover locations.

Snakes are cryptic organisms, and for them, radio-telemetry has been instrumental in understanding the movements, habitat use, and behaviour of larger adults, but smaller individuals generally have been excluded from these studies due to constraints on transmitter size and design. With advances in external attachment methods and battery technology, however, the study of smaller-bodied animals is expanding (Cobb et al. 2005; Jellen and Kowalski 2007). Ontogenetic shifts in habitat use have been documented in colubrid snakes [e.g., Black Rat Snakes (*Pantherophis obsoletus*) - Blouin-Demers et al. 2007] as well as vipers such as *Gloydius shedaoensis* (Shine et al. 2002) and *Agkistrodon piscivorus* (Eskew et al. 2009), highlighting the value of understanding habitat use across all demographic groups. Yet, studies documenting juvenile ecology and habitat use in snakes still are extremely rare; to our knowledge, there are no studies documenting habitat selection in immature snakes within the North American rattlesnake clade, save for a study on neonatal *Crotalus oreganus helleri* in California that documented habitat use but did not incorporate habitat availability \ into the analyses (Figueroa et al. 2008).

In Chapter 2 of this thesis, we reported on the movement paths taken by telemetered juvenile rattlesnakes. In this chapter, we assess the habitat selection of these younger animals. Our two competing hypotheses on juvenile habitat selection were as follows: *(1)* if juvenile rattlesnakes select similar habitat features on the landscape as adults, we would expect to see positive selection for structurally stable cover objects, such as rocks and shrubs; *(2)* since the use of larger structurally stable cover objects could lead to competition (for food, space, etc.) with adult snakes, and since small-bodied individuals should be able to make use of a relatively wider variety of cover (Gregory 2009) such as small and isolated cover objects (including those not suitable for adult snakes), we would expect little or no measurable difference between stopover sites and paired random locations if juvenile snakes are choosing to avoid shared cover with adults (i.e., spatial niche partitioning). We also sought to determine whether juvenile snakes utilized anchor and transient sites with distinct differences in habitat features. Given that the smaller juveniles should be able to make use of a relatively wide variety of cover objects (Gregory 2009), we hypothesized that *(3)* there would be relatively little measurable difference in habitat attributes between the two categories of stopover sites.

MATERIALS AND METHODS

Study site

This study took place in the southeast corner of the Osoyoos Indian Reserve (OIR) near Osoyoos, British Columbia, Canada (49.05° N, 119.43° W). See Chapters 1 and 2 of this thesis for a detailed description of the study site. We had two focal hibernacula on the OIR site that we targeted for capture of juvenile snakes; we hereafter refer to these as Den A and Den B (Indigenous designations in Nsyilxcən are *iʔ x̌aʔx̌aʔulaʔxʷ iʔ q̓ʷc̓iʔs* and *iʔ x̌aʔx̌aʔulaʔxʷ iʔ snʔilitns ʔasl̓ʔupnkst ɬ sisp̓lk*, respectively). Both dens are among the most populous on the OIR site (Howarth unpubl.) and were selected in part to maximize the capture potential of suitable individuals during egress. Further, these dens were deliberately selected to minimize the likelihood of snakes venturing into developed areas, as observed by Lomas et al. (2019).

Radio-telemetry

Juvenile snakes are relatively more difficult to encounter, particularly once the animals depart from communal hibernacula. Thus, most of our study animals were found by intensively searching the areas around Den A and Den B during egress (April-May). Individual snakes used in this study were involved in a larger concurrent study of juvenile Western Rattlesnake migratory movements (Chapter 2 / Howarth et al. 2023). We defined juvenile rattlesnakes as individuals in their second and third year of growth, which corresponds roughly to snakes with a snout-vent length (SVL) ranging from 35 to 45 cm, thus excluding all sexually mature individuals (Macartney et al. 1990; Petersen et al. submitted). Transmitter size in relation to snake size was a major constraint in this study;

hence we did not include individuals in their first year of growth (<35 cm SVL) as the appropriate transmitters would have had exceptionally short battery life spans (~two weeks).

Individuals were transported a short distance to a laboratory space and outfitted with radio-transmitters (BD-2, 1.0g; Holohil Systems Ltd., Carp, Ontario). We followed the subdermal stitch attachment method described by Riley et al. (2017) (modified from Ciofi and Chelazzi 1991) and since used in other studies (Hudson 2019; Murphy et al. 2021). The subdermal stitch method involves running a subdermal catheter and thread under the subcaudal scales and tying the transmitter to the dorsal surface of the snake. Likely less invasive than surgical implantation, the sub-dermal stitch method also allows for rapid transmitter replacements as required by the lifespan of the batteries. The transmitters and associated attachment materials (catheter, suture) weighed no more than 5% of the total body mass of each snake. Immediately after initial transmitter attachment, the snakes were administered Baytril and Metacam (Brown et al. 2009), and monitored for 48 hours prior to release.

A handheld radio-telemetry receiver (TRX-3000; Wildlife Materials Inc., Murphysboro, Illinois) and a 3-element yagi antenna were used to track individuals, and the latitude/longitude coordinates of each snake were recorded using an SXBlue II+GPS device (Geneq Inc., Montreal, Quebec) that generally was accurate to ± 0.5 m. Radio-transmitter battery life was approximately five weeks; thus, snake recapture and transmitter replacement occurred on multiple occasions per individual over the course of the study. Telemetered snakes were located every two to three days over the course of the study until the point of transmitter removal, transmitter failure, accidental transmitter detachment, or natural mortality. Additionally, approximately every two to three weeks (coinciding with transmitter replacement, when possible), snakes were opportunistically re-captured and quickly inspected to monitor health; during these check-ups, the transmitter attachment and catheter protrusion sites were checked, and snakes were weighed (g) to ensure that no significant weight loss (>20% body mass) had occurred. If this was detected, the transmitter was removed.

Habitat data collection

Any shift in locations >5 m by a snake [half the distance used in Gomez's (2007) study of adult habitat use, conservatively adjusted for juveniles] was considered a new stopover site and habitat data were collected. These data were not re-measured if a snake returned to a previously used stopover site or moved less than 5 m from their previous location. We also did not collect habitat data at locations that were within 10 m of the snake's hibernaculum. Habitat data were collected using a paired use-availability design (Thomas and Taylor 2006). At each rattlesnake stopover site, we set up one habitat plot and one paired plot at a randomly selected reference location. The paired plot was constrained within 30m from the habitat plot and was placed in a random direction at a random distance, selected using a number generator app (The Random Number Generator, Nicholas Dean, 2013). Following Gomez (2007), at each plot we directly measured three types of habitat features: (1) microhabitat (1 m^2 plot); (2) mesohabitat (10 m^2 plot), and (3) minimum distance to specific habitat features within the surrounding 30 m of plot centre (see

Table 3.1).

Microhabitat and mesohabitat features measured included the percentage cover of substrate, shrub, herbaceous plant, and rocks. For the microhabitat plot, percentage cover was visually estimated within a 1 m^2 plot using the snake's location, or the randomly selected reference location, as plot centre (Gardiner et al. 2015). For the mesohabitat plot, percentage cover was estimated within 10 m^2 plot using the same method. Percentage cover estimates were performed by two observers (consistent throughout study) and were averaged in the case of inter-observer estimate discrepancy. The minimum distance to habitat features (e.g., tree, rock, shrub, anthropogenic features) within 30m of plot centre were measured to the nearest 1 m using a rangefinder (Bushnell Prime 1700, Bushnell Outdoor Products, Concord, Ontario); features were recorded as absent if not present within 30 m of plot centre.

Statistical analysis

All data were analyzed using RStudio (RStudio Version 2021.09.0 - RStudio 2021) with $\alpha = 0.05$ unless otherwise noted. We considered all habitat data as a single sample and did not consider the effect of season in our analysis. We used a series of univariate analyses to compare habitat features between snake location plots and paired plots. Normality was assessed using Shapiro-Wilk tests. We used arcsine- and log-transformations when variables were non-normal (for percentage cover and distance variables, respectively). If the resulting underlying distributions remained non-normal, we used untransformed values and non-parametric tests for all further analyses.

Following Hosmer and Lemeshow (2000), we established a list of putative explanatory variables: we used Wilcoxon signed-rank tests (paired sample) or paired t-tests and retained variables whose Wilcoxon signed-rank test or paired t-test had a *P*-value of <0.25 for use in subsequent analyses. We tested for autocorrelation between all retained habitat variables using Spearman rank correlation tests. When variables were highly correlated ($\rho > 0.7$), we retained only the variable that accounted for the most variation as indicated by the Wilcoxon signed-rank test or paired t-test (Mason and Perreault 1991). We included all variables that were retained at this stage in the global multivariable conditional logistic regression models.

Habitat variables were modelled in two separate groups; microhabitat was modelled alone, while mesohabitat and minimum distance to habitat features were modelled together. We used conditional logistic regression with paired plots as strata, using the ‘clogit’ function in the ‘survival’ package (Therneau and Grambsch 2000) in RStudio (RStudio 2021). Top models were determined via Akaike Information Criterion (AIC) stepwise selection (Mazerolle 2006) using the ‘stepAIC’ function in the ‘MASS’ package (Venables and Ripley 2002) in RStudio (RStudio 2021). Models with differences in AIC values of <2 were considered equally well-supported (Burnham and Anderson 2002).

We performed more specific analysis on snake stopover locations that received relatively greater use by the snakes. We defined these migration ‘anchor points’ as locations where a snake remained within a 5 m radius for five or more days (confirmed through multiple tracking events), to ‘transient points’, defined as locations where a snake was found for fewer than five days. The five-day cutoff point was determined by visualizing data as a histogram and selecting a natural cut-off point (gap) in the data, while ensuring that there were sufficient locations falling into each of the two categories (see Appendix A). All analysis was conducted in the same manner as described above; however, general logistic regression was used in place of conditional logistic regression as anchor and transient point plots were not paired.

RESULTS

Twenty-one juvenile animals were captured for telemetry during this study, all at the target den sites, save for four animals captured opportunistically in June (*n* = 3) and July (*n* = 1). Five of 17 denning-site animals remained <10 m from their hibernacula throughout their respective tracking periods (largely attributable to very short tracking periods as a result of transmitter removal) and thus were excluded from the habitat analysis. Among the remaining 16 animals, snakes were tracked for an average of 83 days (SD = 25; range = 45 to 140 days). Habitat data were collected between May 17 and September 29, 2021, though exact dates of tracking varied among individuals. The mean number of times that we tracked each snake to a new stopover location warranting a habitat plot was 8.6 (SD = 7.8; *n* = 137; range = 1 to 24 relocations). Of 137 snake locations, we identified 32 as anchor points.

The underlying distributions of all habitat variables were non-normal even after transformations, so Wilcoxon signed-rank tests were used to establish the preliminary list of putative habitat variables. This resulted in retaining five microhabitat and seven mesohabitat variables (including two minimum distance features) for the habitat analysis (see

Table 3.1). No pairs of retained variables showed autocorrelation. The preliminary multivariable conditional logistic regression models (hereafter, ‘global models’) for the microhabitat and microhabitat (including minimum distance to habitat features) were significant, as were the highest-ranked models at both scales (Table 3.2). Reduced models received stronger support at both microhabitat and mesohabitat scales. See Appendix B for individual regression coefficients and *P*-values for the global models.

At the microhabitat scale (1 m^2) the top models suggested that the presence (positive association) of shrub, woody debris, and rock, and the absence (negative association) of grass predicted juvenile microhabitat selection (Figure 3.1 and Figure 3.2). At the mesohabitat scale (10 m^2), the top models suggested that the presence (positive association) of shrub, woody debris, and rock, and smaller minimum distances to the nearest cover object and nearest shrub, together best predicted juvenile mesohabitat selection (Figure 3.3 and Figure 3.4). The preliminary list of putative explanatory variables for comparison of movement anchor points and transient points, using Wilcoxon-signed rank tests (retaining variables with a *P*-value of <0.25), resulted in only one variable ('leaf litter') being retained at the microhabitat scale, and at the mesohabitat level only two variables ('leaf litter' and 'soil') were entered into the analysis (see

Table 3.1). No pairs of retained variables showed autocorrelation.

The global multivariable conditional logistic regression models for comparison of anchor points and transient points (at both scales) are shown in Table 3.3 along with results of the stepwise AIC analysis. See Appendix B for individual regression coefficients and *P*-values for the global models. At the microhabitat scale, the top model suggested that juvenile anchor point selection was negatively associated with the presence of leaf litter (Figure 3.5). At the mesohabitat scale, top models suggested that the absence (negative association) of leaf litter and soil predicted anchor point selection (Figure 3.5). However, the mesohabitat model containing both variables (global model) did not yield a statistically significant regression, while the model containing only the variable 'leaf litter' was statistically significant.

Table 3.1. Features measured in habitat plots centered at stopover sites used by juvenile Western rattlesnakes moving away from their hibernacula. Variables retained in the preliminary list of putative variables for both the habitat analysis and anchor point analysis are indicated by subscript symbols.

DESCRIPTION	***MICROHABITAT*** *(1 m^2 plot)*	***MESOHABITAT*** *(10 m^2 plot)*
% cover bare soil	SOIL1 *	SOIL10 *†
% cover grass	GRASS1 *	GRASS10 *
% cover shrub	SHRUB1 *	SHRUB10 *
% cover tree	TREE1	TREE10
% cover woody debris	WD1 *	WD10 *
% cover leaf litter	LL1 †	LL10 †
% cover rock	ROCK1 *	ROCK10 *
% cover herbaceous plants	HERB1	HERB10
	MINIMUM DISTANCE	
Distance to nearest tree	MD_TREE	
Distance to nearest rock	MD_ROCK	
Distance to nearest cover object	MD_COVER *	
Distance to nearest shrub	MD_SHRUB *	
Distance to nearest anthropogenic feature	MD_ANTH	

* variables retained in the preliminary list of putative variables for the habitat analysis

† variables retained in the preliminary list of putative variables for the anchor point analysis

Table 3.2. Results of habitat assessments for locations used by juvenile Western rattlesnakes. Global models at two scales (1 m^2 microhabitat and 10 m^2 mesohabitat) included all putative variables for discriminating between used and random habitat plots. Listed for each model is the AIC, ΔAIC (difference between the model's AIC and the minimum AIC) support for the model (weight, *w*), Wald χ^2, and associated *P*-value for the Wald test. The top three models at each scale and the global model (denoted by *G*) are included (global model included in top three models at microhabitat scale). See

Table 3.1 for key to habitat variable abbreviations.

	Microhabitat					
#	***MODEL***	***AIC***	***ΔAIC***	***w***	***WALD*** χ^2	***P***
1	SHRUB1 + WD1 + ROCK1	140.8	0	0.52	31.72	<0.001 *
2	GRASS1 + SHRUB1 + WD1 + ROCK1	142.4	1.6	0.22	31.75	<0.001 *
G	SOIL1 + GRASS1 + SHRUB1 + WD1 + ROCK1	144.4	3.6	0.07	31.73	<0.001 *
	Mesohabitat and minimum distance to habitat features					
#	***MODEL***	***AIC***	***ΔAIC***	***w***	***WALD*** χ^2	***P***
1	WD10 + ROCK10 + DIST_COVER + DIST_SHRUB	153.5	0	0.13	25.09	<0.001 *
2	SHRUB10 + WD10 + ROCK10 + DIST_COVER + DIST_SHRUB	154.1	0.6	0.09	25.23	<0.001 *
3	SOIL10 + SHRUB10 + WD10 + ROCK10 + MD_COVER + MD_SHRUB	155.9	2.3	0.03	25.61	<0.001 *
G	SOIL10 + GRASS10 + SHRUB10 + WD10 + ROCK10 + MD_COVER + MD_SHRUB	157.4	3.9	0.01	26.01	<0.001 *

* Indicates the model is significant ($\alpha = 0.05$), per model evaluation tests (Wald)

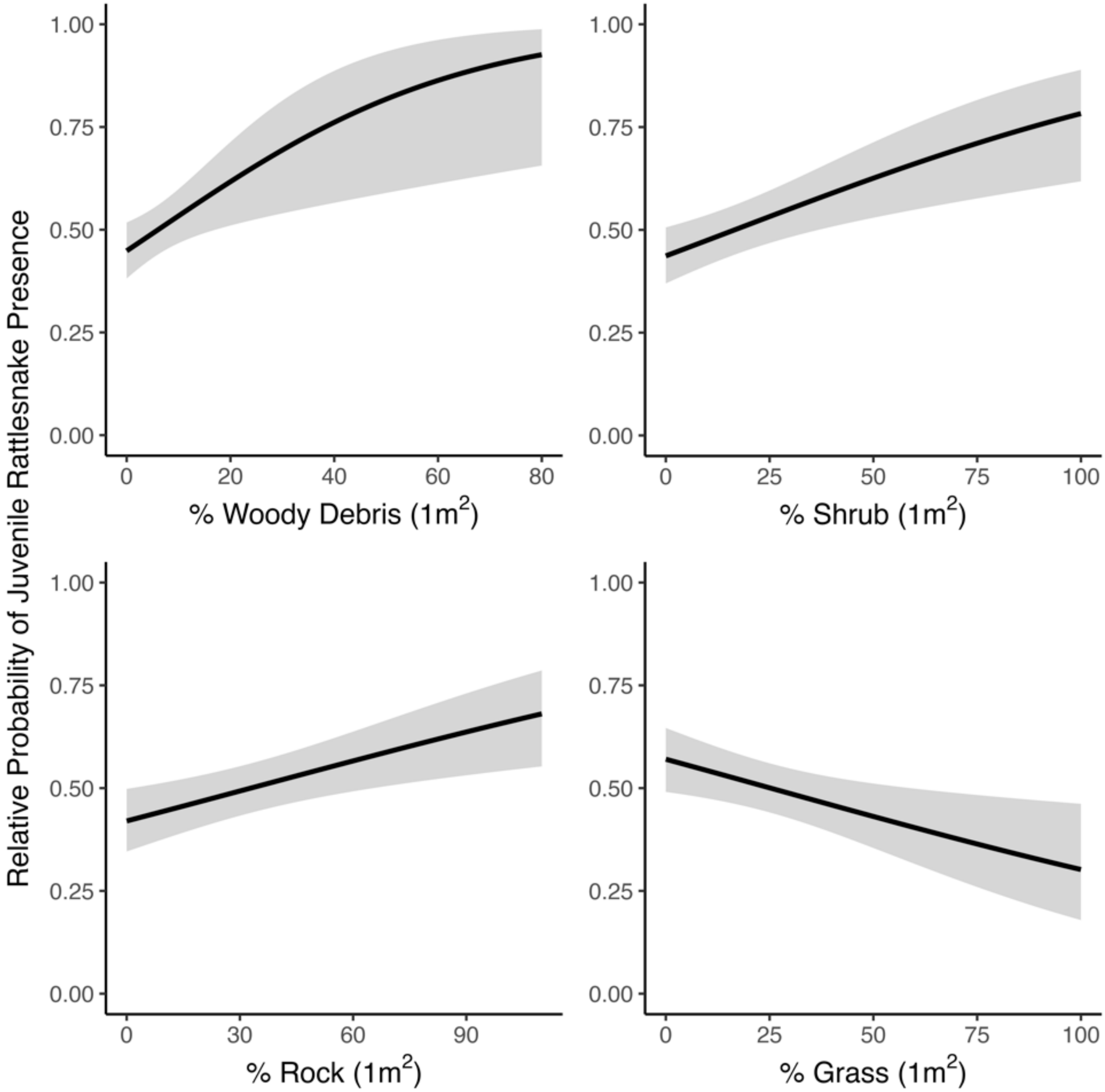

Figure 3.1. Relationships between juvenile rattlesnake habitat use and top-ranked habitat variables determined by selection models at the microhabitat (1 m^2) scale, near Osoyoos, BC, Canada. Greater cover of woody debris, shrub, and rock cover were positively linked to the probability of use by juvenile rattlesnakes, and grass cover was negatively associated. Gray areas around regression lines represent 95% confidence intervals.

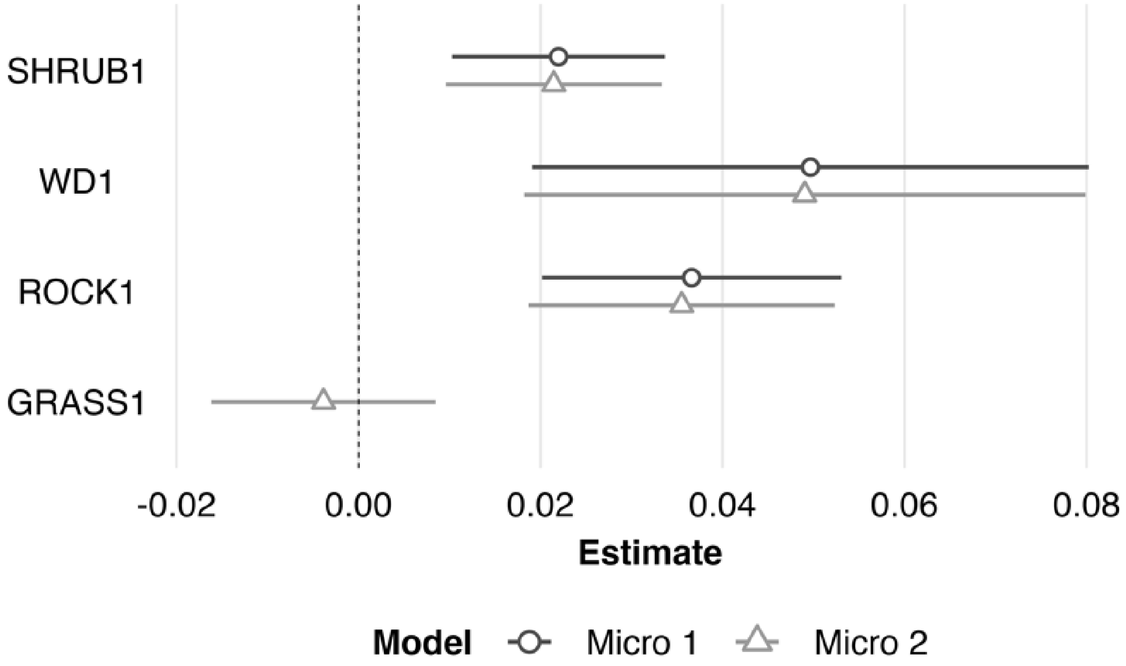

Figure 3.2. Scaled model coefficient estimates (logit scale with adjusted 95% CI) for the predicted microhabitat (1 m^2) use by juvenile Western Rattlesnakes at the Osoyoos Indian Reserve (OIR) study site near Osoyoos, BC, Canada in 2021. Shown are the coefficient estimates for the top two models (Micro #1 and Micro #2, as indicated in Table 3.2). Positive coefficient estimates show active selection for habitat features, whereas negative estimates show avoidance. Scaled confidence intervals that do not overlap with the dashed line (i.e., 0) show significance. See

Table 3.1 for key to habitat variable abbreviations.

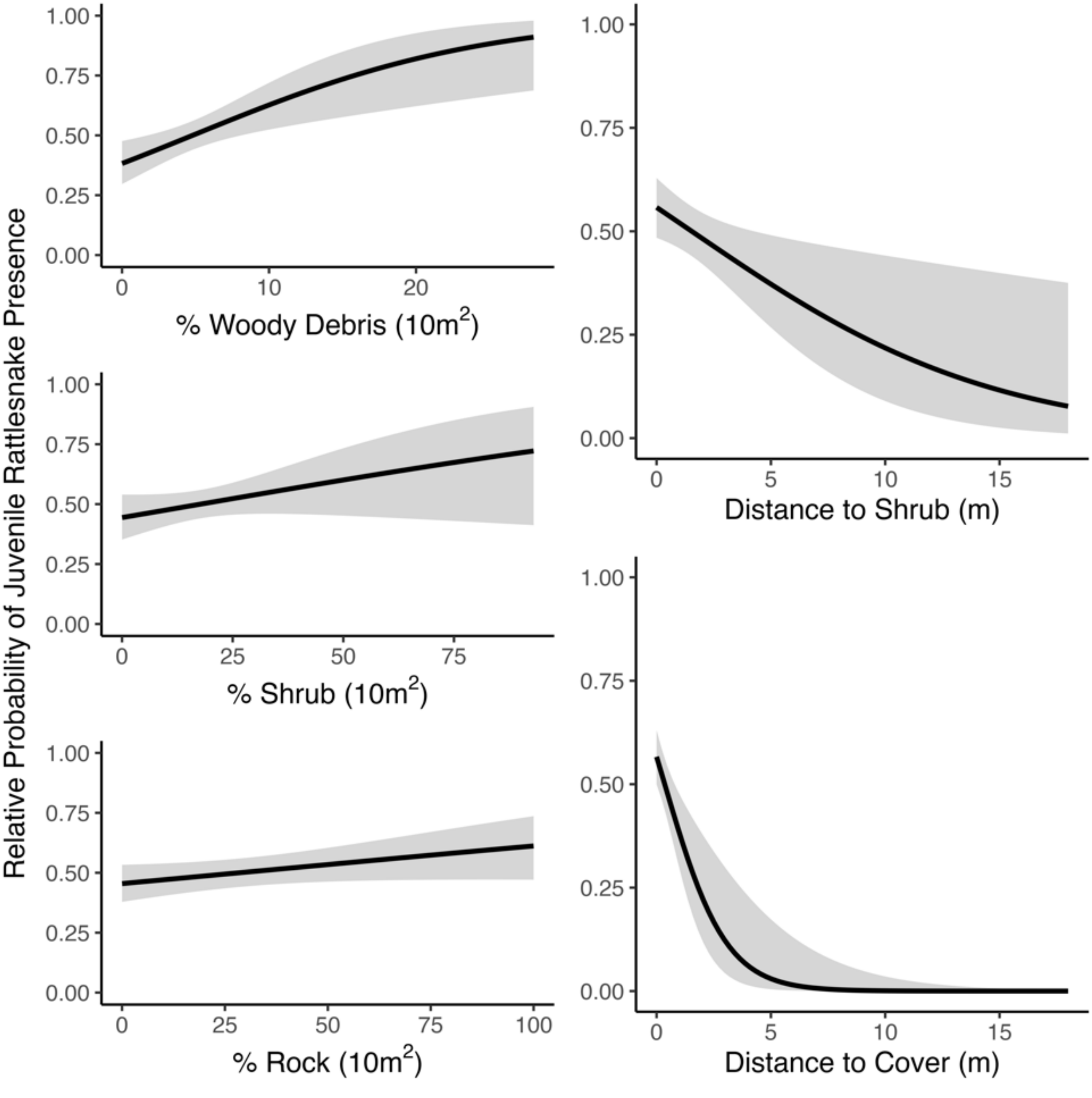

Figure 3.3. Relationships between juvenile rattlesnake habitat use and top-ranked habitat variables determined by selection models at the mesohabitat (10 m^2) scale including minimum distance variables, near Osoyoos, BC, Canada. Greater cover of woody debris, shrub, and rock cover were positively linked to the probability of use by juvenile rattlesnakes, juvenile use was associated with smaller minimum distances to the nearest

cover object and nearest shrub. Gray areas around regression lines represent 95% confidence intervals.

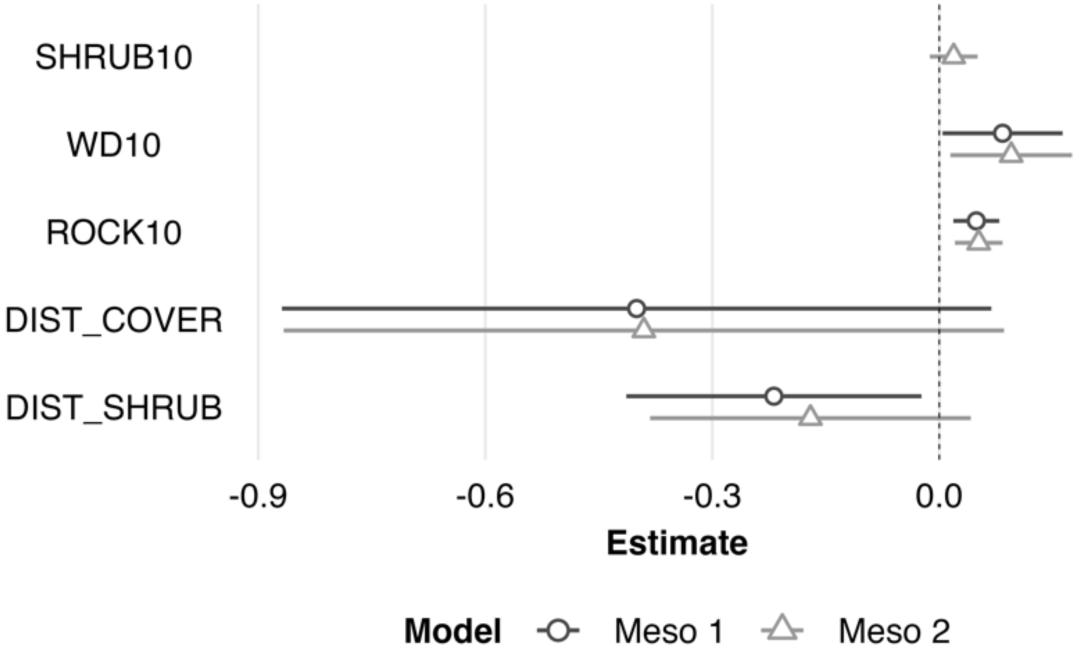

Figure 3.4. Scaled model coefficient estimates (logit scale with adjusted 95% CI) for the predicted mesohabitat (10 m^2) use by juvenile Western Rattlesnakes at the Osoyoos Indian Reserve (OIR) study site near Osoyoos, BC, Canada in 2021. Shown are the coefficient estimates for the top two models (Meso #1 and Meso #2, as indicated in Table 3.2). Positive coefficient estimates show active selection for habitat features, whereas negative estimates show avoidance. Scaled confidence intervals that do not overlap with the dashed line (i.e., 0) show significance. See

Table 3.1 for key to habitat variable abbreviations.

Table 3.3. Comparisons using logistic regression of habitat features at anchor points and transient points used by juvenile rattlesnakes over the active summer. Global models at two scales (1 m^2 microhabitat and 10 m^2 mesohabitat) included all putative variables for discriminating between used and random habitat plots. Listed for each model is the AIC, ΔAIC (difference between the model's AIC and the minimum AIC), support for the model (weight, *w*), Wald χ^2, and associated *P*-value for the Wald test. The top three models at each scale, including or in addition to the global model (denoted by *G*) and the null model (denoted by *N*), are included. See

Table 3.1 for key to habitat variable abbreviations.

	Microhabitat					
#	***MODEL***	***AIC***	***ΔAIC***	***w***	***WALD χ^2***	***P***
G	LL1	136.44	0	1.00	10.8	<0.01 *
N	null	151.47	15.0	0.00	-	-

	Mesohabitat					
#	***MODEL***	***AIC***	***ΔAIC***	***w***	***WALD χ^2***	***P***
1	LL10	143.31	0	0.51	6.1	0.013 *
G	SOIL10 + LL10	143.40	0.1	0.47	1.7	0.190
N	null	151.47	8.2	0.01	-	-

* Indicates the model is significant (α = 0.05), per model evaluation tests (Wald)

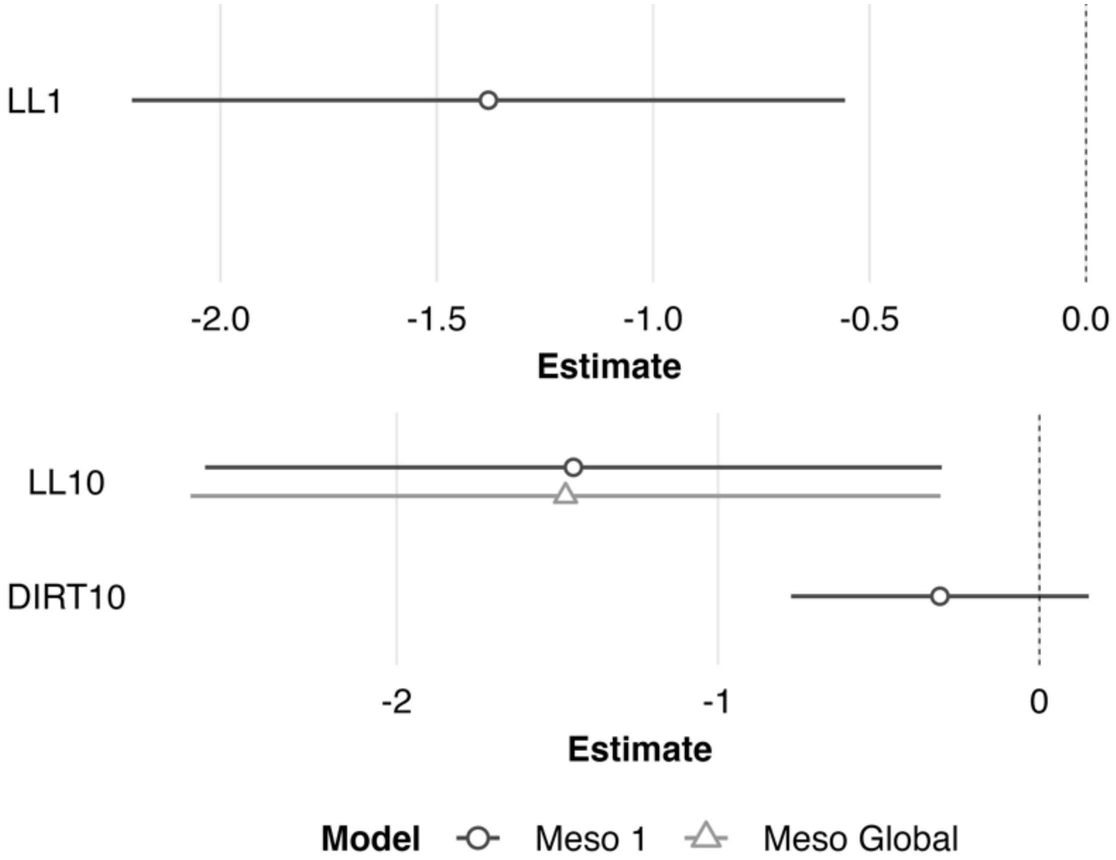

Figure 3.5. Scaled model coefficient estimates (logit scale with adjusted 95% CI) for the predicted microhabitat (1 m^2; top) and mesohabitat (10 m^2; bottom) use by juvenile Western Rattlesnakes at the Osoyoos Indian Reserve (OIR) study site near Osoyoos, BC, Canada in 2021. Shown are the coefficient estimates for the top microhabitat model, and the top two mesohabitat models (Meso #1 and Meso Global, as indicated in Table 3.2). Positive coefficient estimates show active selection for habitat features, whereas negative estimates show avoidance. Scaled confidence intervals that do not overlap with the dashed line (i.e., 0) show significance.

DISCUSSION

The results of our study suggest juvenile Western Rattlsnakes in this species select for similar habitat features as shown in adults, despite their smaller size and smaller movement scale. Specifically, juvenile snakes selected sites non-randomly at both spatial scales (micro- and mesohabitat) for greater cover on the landscape (in the form of rock, shrub, and woody debris) and avoided grass cover at the microhabitat scale. Supporting our first hypothesis, this suggests a preference for cover objects that are structurally stable, consistent with the preferred habitat of adult conspecifics elsewhere in British Columbia (Gomez 2007).

Contrary to our second hypothesis, despite the substantial difference in body size between juvenile and adult Western Rattlesnakes, we observed juvenile animals selecting for similar habitat features as adult conspecifics, suggesting that spatial niche partitioning may not be occurring between age classes. Habitat use was positively associated with the presence of cover at both scales, indicating that rather than finding a single isolated microhabitat site that fulfils their immediate needs (which in theory could be a very small cover object for these small-bodied individuals), juveniles may seek more heterogeneous patches of habitat that provide multiple opportunities for their ongoing hunting, crypsis, and thermoregulatory needs.

It is possible that the association of small snakes to cover objects is closely linked to the microhabitat selection (and therefore, availability) of prey on the landscape. For adult snakes, the selection of ambush sites is related to the presence of chemical cues left by prey (Theodoratus and Chiszar 2000). With a paucity of small reptilian prey in the grasslands (e.g., lizards – a common feature in the prey base of the species further south; Mackessy 1988), the diet of Western Rattlesnakes in British Columbia consists primarily of small mammals such as mice, voles, and shrews (McAllister et al. 2016), with young and smaller-bodied rattlesnakes largely limited to the smallest of these mammals, presumably consuming neonatal and juvenile prey (Macartney 1989). Thus, for these smaller snakes, it is likely important to base oneself in locations near small mammal nesting sites, though this remains untested. Moreover, the lack of spatial niche partitioning that we may have observed here between adult and juvenile could be attributed to this partitioning of diet between age classes, with juveniles preferentially (and necessarily) selecting the smallest of available prey, while larger adult rattlesnakes select for larger, higher-reward, prey items (e.g., adult rodents, lagomorphs, etc.), thereby allowing these age classes to concurrently occupy similar habitats without being in competition. Even so, some level of spatial partitioning may be occurring between age classes at a scale that we did not detect and/or did not measure here.

In support of our third hypothesis, there was little difference in habitat features between sites used as anchor and transient stopover sites. We found that compared to transient points, juvenile snakes were using anchor points locations with lower leaf litter cover at both scales, and with less bare soil cover at the mesohabitat scale, though neither the presence nor absence of these substrates provide any form of cover or opportunity for thermoregulation. As previously mentioned, the lack of association between anchor points and any of the measured habitat features may be explained by the ability of smaller snakes to make use of a wider variety of cover objects (Gregory 2009) including small mammal tunnels, making suitable stopover sites more prevalent on the landscape for them. Despite utilizing similar habitat types as adult rattlesnakes as suggested by the broader habitat use analysis, juvenile snakes may be able to find suitable locations in which to remain for extended periods of time more readily than adults, however, the specific habitat features used as anchor points by adults remains to be tested.

Although we obtained habitat data for 16 juvenile rattlesnakes, representing data over 137 stopover sites, we were still forced to pool data across individuals with variable tracking durations; this is a common issue in habitat selection studies that use animal relocations as experimental units (Marzluff et al. 2004; Thomas and Taylor 2006). We attempted to average habitat features per snake and to then use the snakes as strata, but due to the variation and generally low number of locations for each individual, we were not able to fit individual models to each snake (Row and Blouin-Demers 2006). As such, some caution should be taken in interpreting our results as they are based on the behaviour of a limited sample of snakes, and it is known that habitat use can differ markedly among individuals (Shine 1987). Further, we did not consider the effect of season in our analysis, and it is possible that habitat preferences may not be consistent throughout the active season. We also did not incorporate cover object size into our analysis, the inclusion of which could reveal a more detailed understanding of juvenile rattlesnake habitat preferences; a finer-scale study of this nature across all age classes could expose ontogenetic shifts in cover object preferences, should they exist. Regardless, this initial step in understanding the habitat preferences of immature snakes adds to our overall understanding of snake ecology.

It is likely that our findings here for juveniles are of broad relevance. Namely, selection for cover objects such as rocks and shrubs (or burrows, in prairie landscapes) appear relatively consistent for adults across North American rattlesnake species (e.g., *Sistrurus catenatu*s – Harvey and Weatherhead 2006; *Crotalus mitchellii* – Glaudas and Rodríguez-Robles 2011; *Crotalus viridis* – Gardiner et al. 2015). As such, it is conceivable that the trends we observed for juvenile rattlesnakes in this study may also be consistent, or similar, for juveniles across snake taxa.

Wildlife habitat selection studies provide knowledge that is critical for species conservation and management. While knowledge of habitat preferences at multiple scales allows wildlife conservationists and managers to assess the distribution and abundance of critical habitat, understanding these habitat preferences across all demographic groups within populations is vital for effective management (Roznik et al. 2009). However, studies quantifying the ecology of early age classes generally are lacking across vertebrate taxa. Here, we address this considerable knowledge gap for an at-risk northern viper and contribute to a growing understanding of the complexity of habitat requirements for the species. Ultimately, our study underscores the crucial role of habitat selection research, considering the unique needs of early age classes, in informing conservation practices for the long-term survival of wildlife populations.

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CHAPTER 4.

LANDSCAPES, HABITAT, AND MIGRATORY BEHAVIOUR: WHAT DRIVES THE SUMMER MOVEMENTS OF A NORTHERN VIPER?

INTRODUCTION

Migration in animals occurs across multiple spatial and temporal scales, allowing individuals to exploit changes in resource availability and habitats favourable for critical processes such as overwintering, foraging or hunting, and breeding (Dingle and Drake 2007; Hoare 2009). The spatial scale at which migration occurs can range from a few metres to thousands of kilometres, but typically consists of annual-cycle or life-cycle bidirectional movements at a greater scale than the animal's normal daily movements (Dingle and Drake 2007). Despite the advantages that migration confers on animals that inhabit environments with seasonal variation in resource quality and/or quantity (Dingle and Drake 2007; Hoare 2009; Milner-Gulland et al. 2011), the conservation of migratory animals can be challenging, despite the fact migratory populations were shown over 10 years ago to be in decline globally (Wilcove and Wikelski 2008). At a basic level, an understanding of patterns of migration and habitat use, both within and across populations, is critical for developing effective management and conservation strategies for at-risk species (Allen and Singh 2016).

Complicating the study of migration is the fact that the behaviour is not always ubiquitous, even among 'typical' migratory species (Sawyer et al. 2019): multiple migratory phenotypes may be present within a species or population. This phenomenon is particularly well-documented when divergent movement patterns are linked to identifiable subsets of a population, such as age class, sex, or reproductive condition (Adriaensen and Dhondt 1990), though cases of partial migration (only part of the population migrates) or a migration continuum (mixed migratory behaviours) within individual demographic groups of a population also occur (Chapman et al. 2012; Cagnacci et al. 2016; Berg et al. 2019; Hegemann et al. 2019). In such cases, various elements (e.g., competition for resources or mates, predation risk, intraspecific niche diversity) may act in conjunction to create complex patterns of multi-phenotypic movement tactics within populations (Chapman et al. 2011).

Migration and habitat use are closely related processes, with movement patterns largely occurring as a result of interactions between animals and their environments (Johnson et al. 1992; Schick et al. 2008; Avgar et al. 2013). Migratory behaviour and concomitant habitat selection may be driven by the distribution of food, water, refuges, or mates on the landscape (Ashton 2003), where movement rates decrease in resource-rich areas (Avgar et al. 2011), as well by the physical structure of the environment when movement is physically impeded by substrate or topography (Morales et al. 2002; Avgar et al. 2013). Migration also may be impacted by physiological processes: for example, migration generally incurs fewer costs for individuals with high body condition (Chapman et al. 2011; Goossens et al. 2020), and the thermal environment – particularly in the case of ectotherms – may also influence migratory behaviour (Huey 1991; Harvey and Larsen 2020).

In general, migratory behaviour is particularly well-studied in mammals, birds, insects (e.g., Monarch butterflies), and some marine organisms such as sea turtles. However, the phenomenon also is well-documented in snakes, including temperate-zone colubrids and viperids. One extreme northern species, the Western Rattlesnake (*Crotalus oreganus*), has a large North American range that extends north into the southern portion of British Columbia (BC), Canada. This limited range coupled with anthropogenic threats has resulted in the Canadian population being listed as ‘Threatened’ (COSEWIC 2015). In their peripheral northern region, individuals demonstrate high fidelity (Brown et al. 2009; Gomez et al. 2015) to communal hibernacula (dens) between October and April (Macartney et al. 1988; Maida et al. 2020). After emerging from hibernacula in the spring, the snakes undertake annual migrations ranging up to 4 km from their dens over the summer active season (Harvey and Larsen 2020), and in some cases moving upwards in elevation, thus providing a rare if not unique example of altitudinal migration in a reptile (Gomez et al. 2015; Hsiung et al. 2018). These migrations are associated with the relatively colder climates experienced by northern populations, possibly driven by the spatial arrangement of resources (e.g., prey availability being scarce in the immediate proximity of hibernacula), with conspecifics at more southern latitudes exhibiting comparatively reduced migratory distances (Ashton 2003).

Recent work in BC has revealed significant variation in migratory tactics employed by Western Rattlesnake, both between and within den populations. Individual rattlesnakes follow the same migratory paths year after year as adults (Gomez et al. 2015) with individual tactics ranging from limited, non-directional migrations (often remaining in stereotypic low-elevation grassland habitats) to long-distance, linear migrations into upland forested habitat (Gomez et al. 2015; Lomas et al. 2019; Harvey and Larsen 2020; Maida et al. 2020). Specifically, the studies by Gomez et al. (2015) and Harvey and Larsen (2020) suggest that both migratory distance and habitat use are dichotomous and linked (i.e., long-distance migrants use forests, short-distance migrants use open habitats) and that these varying tactics are highly den- and site-specific, which may suggest either high plasticity or trait canalization in these peripheral populations (Lesica and Allendorf 1995; Debat and David 2001). At the same time, other studies in the same region have documented significant variation in the directionality, habitat associations, and extent of migration among individuals from within a single den (e.g., Lomas et al. 2019; Maida et al. 2020). All of the aforementioned studies, however, are based on data collected from a limited number of individual snakes drawn from a few sites. Combining data across these and additional studies will provide an improved understanding of broad-scale patterns and drivers of multi-phenotypic migration and habitat use across regional populations of the same species.

Our first objective was to combine historical data sets to quantify variation in migration distance, timing, direction and extent of vertical migration, home range sizes, and destination habitats used across the sample of study populations. We then compared individual migratory distances between sites, between snakes using contrasting destination habitats (building on the suggestion of a dichotomy – Gomez et al. 2015, Harvey and Larsen 2020), and across varying body conditions. Our second objective was to examine the role that physiological conditions (e.g., temperature, body condition) and landscape features within an individual's home range (e.g., vegetation and terrain) play in driving migratory behaviour, using a linear mixed modelling approach.

MATERIALS AND METHODS

Compiling the dataset

Raw data from all known telemetry studies on the Western Rattlesnake in British Columbia since the early 2000s were compiled from nine unique study areas (Table 4.1). Telemetered snakes had to meet several criteria to be included in the final dataset. The snake’s hibernaculum (den) of origin had to be known, and the snake had to be tracked from egress (originating at a den in the spring) through to mid-July, or starting no later than mid-July and tracked through to ingress (back to a den). If tracking began mid-season, the location of the individual’s known den (determined by either prior capture history or the eventual return of the snake to that den) was assumed and used for calculations of migration distance from the den. If a snake was not tracked for the full season, we confirmed that their first location (if tracking began mid-season) or last location (if tracking ended mid-season) also was not the apogee point (Harvey and Larsen 2020), i.e., we confirmed that our data encompassed at least a portion of both outbound and inbound migration, with an identifiable turnaround point (apogee). All individuals had a minimum of eight location (i.e., unique) data points.

Only adult males were included in the dataset: overwhelming, these were the only data available for this species with exception of one recent telemetry study focused on gravid female rattlesnakes (Eye 2022) and another that included three non-gravid females (Atkins 2021). These female data were further excluded to avoid the confounding effect of known migratory differences in reproductive females (Graves and Duvall 1993; Eye 2022) and between males and females in non-reproductive years (King and Duvall 1990). Male Western Rattlesnakes in these previous telemetry studies all received surgically implanted transmitters (SB-2; Holohil Systems Ltd., Carp, Ontario) with procedures following Reinert and Cundall (1982) and pharmaceutical procedures after Brown et al. (2009). Maida et al. (2020) provides additional details on surgical and field methods used for adult snakes. A radio-telemetry receiver (various models) and a 3-element Yagi antenna were used to track individuals, and the UTM coordinates of each relocation were recorded using a GPS device.

Table 4.1. Summary of sites used in this study across British Columbia, Canada, at the northern extent of Western Rattlesnakes' (*Crotalus oreganus*) range. Associated studies refer to the use of the same datasets.

Site Name	**Abbreviation**	**Coordinates**	**Dens (*n*)**	**Snakes (*n*)**	**Years of study**	**Associated studies**
Ashcroft	Ashcroft	50.60° N, 121.28° W	1	4	2010	Harvey and Larsen 2020
Cawston	Cawston	49.20° N, 119.75° W	1	1	2011	Harvey and Larsen 2020
Kamloops East	Kam E	50.71° N, 120.40° W	5	14	2005, 2006, 2010	Gomez et al. 2015; Harvey and Larsen 2020
Kamloops West	Kam W	50.77° N, 120.70° W	2	7	2005, 2006	Gomez et al. 2015; Harvey and Larsen 2020
Osoyoos	Osoyoos	49.05° N, 119.43° W	16	72	2006–2012 & 2014–2016	Lomas et al. 2019; Maida et al. 2020
Oliver	Oliver	49.17° N, 119.67° W	1	3	2011	Harvey and Larsen 2020
Spences Bridge	Sp Bridge	50.32° N, 121.20° W	1	3	2010	Harvey and Larsen 2020
Vernon	Vern	50.20° N, 119.24° W	3	5	2019	Atkins 2021
White Lake	WL	49.31° N, 119.64 °W	6	30	2011, 2015, 2016	Harvey and Larsen 2020; Winton et al. 2020

Migration metrics

Migration distance (MD) was determined as the maximum straight-line distance (m) between an individual's hibernaculum and its apogee point. The MD metric was calculated from each snake's trajectory of relocations using the R package 'adehabitatLT' (Calenge 2006). As a preliminary method of assessing the relationship between migration distance and habitat use, we assigned each snake to a 'destination habitat' category ('Open' or 'Forest') based on the type of habitat reached at the apogee point, following Harvey and Larsen (2020). Locations with < 10% canopy closure [bunchgrass and lower-elevation open-canopy stands of Ponderosa Pine (*Pinus contorta*)] were designated as 'Open' habitats, while locations with > 10% canopy closure [Interior Douglas-fir (*Psuedotsuga menziesii)* forests] were classified as 'Forest' habitat. We deemed this categorization appropriate in the interior BC region given the arid nature and the typical canopy closure in the low-elevation Ponderosa Pine stands, and for continuity with the categories used in Harvey and Larsen (2020). The locations within the Bunchgrass (BG), Ponderosa Pine (PP), and Interior Douglas-fir (IDF) ecosystems were determined using the BC Biogeoclimatic Ecosystem Classification (BEC) system and mapped using ArcGIS 10.8. For additional details on habitat and climate across the region see Chapter 1 of this thesis. Fisher's exact test was used to determine if there was a significant association between site and destination habitat category.

We estimated rattlesnake home ranges using two methods: the 100% minimum convex polygon (MCP) and 95% weighted autocorrelated kernel density estimation (AKDE). The former takes the outermost set of data points representing an animal's locations and connects them to form a polygon with no concave sides (Mohr 1947). Admittedly, the MCP approach has been criticized for its oversimplicity and lack of sensitivity to the number of estimates, duration of tracking, and serial autocorrelation (see Laver and Kelly 2008), yet others have suggested that MCP best reflects herpetofauna home range size (Row and Blouin-Demers 2006; Shipley et al. 2013; MacGowan et al. 2017). Further still, there is long-standing controversy on whether snakes truly maintain home ranges (Tiebout and Cary 1987). Still, the inclusion of home range estimates – especially MCP – is common in the literature on snakes, including numerous studies on Western Rattlesnakes in British Columbia (Brown et al. 2009; Lomas et al. 2019; Maida et al. 2020), leading to our choice to include MCP in this study. We estimated 100% MCP home ranges for each snake using the R package ‘adehabitatHR’ (Calenge 2006).

While traditional kernel density estimators (KDEs) of home range have been criticized for their sensitivity to the choice of smoothing parameter(s) and their need for independent data (Fieberg 2007), autocorrelated kernel density estimation (AKDE – Fleming et al., 2015; Silva et al., 2022) accounts for these issues and is appropriate for quantifying herptile home ranges (Crane et al. 2021). AKDE assumes the data represent a sample from a non-stationary, autocorrelated continuous movement process by incorporating the movement of animals through an autocorrelation function derived from movement models fit to the data (Silva et al. 2022). Furthermore, AKDE reduces to a conventional kernel density estimator when locations are truly independent, and the optimal weighting method can correct for irregular sampling schedules (Fleming et al. 2018). Specifically, we estimated optimally weighted 95% AKDE home ranges and 50% AKDE core areas of use for each snake using the R package ‘ctmm’ (Calabrese et al. 2016).

To quantify the patterns and extent of vertical migration in Western Rattlesnakes, snakes were classified based on the direction of vertical migration (‘uphill’ or ‘downhill’) during their outbound migration, and for each snake we calculated elevational distance (m) using the difference in the elevation of the individual’s den and the highest (uphill) or lowest (downhill) elevation reached during its travels. A χ^2 test of independence was used to examine the relationship between the direction of vertical migration and destination habitat category, and a t-test was used to compare MD between snakes that travelled uphill and downhill.

Finally, we assessed the body condition of each snake. Following Parent and Weatherhead (2000), Brown et al. (2009), and Lomas et al. (2015), we used the residuals from a regression between snake mass and SVL as an index of body condition. We used ANOVA and t-tests to compare body condition between snakes using different destination habitat zones (i.e., BG, PP, and IDF) and categories (i.e., Open, Forest) and used Tukey tests for post-hoc comparisons.

Migration distance analysis

We used square-root transformed migration distance (MD) values in all analyses to meet assumptions of normality (Osborne 2002). We used univariate one-way ANOVA to compare migration distance between study sites and between destination habitat categories and zones, and used Tukey tests for post-hoc comparisons.

We used linear mixed models to assess the relationship between various predictor variables and snake migration distance (MD). We calculated the mean value of various raster-based landscape variables within individual home ranges (95% AKDE), including elevation, slope, aspect (north/south), vector ruggedness measure (VRM), normalized difference vegetation index (NDVI), canopy cover, and mean maximum temperature. Note that using the mean habitat value within an individual’s home range is commonplace in the literature when computing individual responses to landscape variables (Gillies et al. 2006; Hebblewhite and Merrill 2008; Aarts et al. 2013). We chose this approach over the random walk approach used by Harvey and Larsen (2020), whereby they extracted habitat values from points at predefined intervals along individuals’ movement paths. In that study, infrequent telemetry-checks over a large range required the assumption of straight-line movement paths between each consecutive relocation; in our study, this approach was considered suboptimal as it would bias accuracy towards individuals with high numbers of relocations and/or individuals who make frequent short-distance movements over those individuals who make fewer or rapid long-distance movements (i.e., there is a greater portion of the path that is assumed for these rapid long-distance movements). Further, we determined the minimum distance from each individual’s hibernaculum to the nearest closed-canopy forest habitat. We also included body condition as a predictor variable in these mixed models. Variable details are provided in Table 4.2, and see Appendix C for a detailed overview of each predictor variable, including explanations, sources/derivations, and justification for use.

Linear mixed models were fit using the R package ‘lme4’ (Bates et al. 2015). All predictor variables were centred and scaled to have mean 0 and SD 1 to facilitate model convergence (McNit et al. 2020; Muff et al. 2020) and were included as fixed effects in the models. We generated four candidate models (Physiology; Vegetation; Terrain; Combined) based on various hypotheses and included in each model random intercept terms for den and site to account for expected variation within these groups (Table 4.3). We were unable to include a random intercept term for ‘year’ as this generated 0 variance estimates and impeded convergence. We tested for multicollinearity and excluded collinear variables with $\rho > 0.7$.

Candidate models were ranked using an information-theoretic approach based on Akaike Information Criteria scores corrected for small sample size (AICc), where the lowest AICc score reflects the most parsimonious model with the most explained deviance (Akaike 1998; Burnham and Anderson 2002). We used k-fold cross-validation to validate each candidate model [seed set to (1234) in R], whereby data were split into k = 10 folds, and each subset was evaluated using models trained with k – 9 alternative subsets; Spearman-rank correlation (r_s) between actual and predicted MD values are reported (Boyce et al. 2002; Wiens et al. 2008).

Statistical considerations

All statistical analyses were performed in the program R version 4.2.2 (R Core Team 2021). Where appropriate, data were tested for normality by examination of histograms and using the Shapiro-Wilk test and/or the Kolmogorov-Smirnov test. A significance value of $\alpha = 0.05$ was used to guide the interpretation of results. Means are reported ±1 standard deviation (SD) unless otherwise stated.

Table 4.2. Predictor variables used in Western Rattlesnake (*Crotalus oreganus*) migration distance linear mixed models.

Variable	**Description**	**Type; resolution**	**Source/Derivation**
Elevation	Digital Elevation Model (DEM)	Raster; 30m	Natural Resources Canada 2015
Slope	Slope (gradient or steepness) in degrees	Raster; 30m	Derived from DEM using the slope tool in the Spatial Analyst extension in ArcGIS 10.8
Aspect	Aspect as a measure of *Northness*, where 1 is North, -1 is South, and 0 is flat (East or West)	Raster; 30m	Derived from DEM using ‘raster’ package (Hijmans 2015) in R; Aspect (degrees) cosine transformed
VRM	Vector ruggedness measure (VRM) of terrain as defined by (Sappington et al. 2007). Values can range between 0 (flat) and 1 (most rugged), though values on natural terrains very rarely exceed 0.2.	Raster; 30m	Derived from DEM using ‘spatialEco’ package (Evans et al. 2021) in R.
NDVI	Mean weekly best-quality maximum NDVI for calendar week 28 (mid-July) between the years 2000 and 2020	Raster; 30m	Agriculture and Agri-Food Canada 2021
Canopy Cover	% Forest canopy cover over 2m in height	Raster; 30m	Matasci et al. 2018
Mean Max Temp	Monthly mean-maximum climate 79ormal for the month of July between 1981 and 2010	Raster; 1000m	Pacific Climate Impacts Consortium, University of Victoria, and PRISM Climate Group 2014
Distance to Forest	Minimum distance from hibernacula to forest (forest defined as Interior Douglas-fir, Interior Cedar-Hemlock, and Montane Spruce BEC Zones)	Straight-line distance; m	Forest Analysis and Inventory Branch BC 2021
Body Condition Index	Index of body condition, following Parent and Weatherhead (2000), Brown et al. (2009), and Lomas et al. (2015)	-	Derived using residuals from a regression between snake weight and SVL

Table 4.3. Candidate models for explaining Western Rattlesnake (*Crotalus oreganus*) migratory distance in Canada and their corresponding hypotheses. All candidate models included random intercept terms for 'site' and 'den'.

Model name	**Model variables**	**Hypotheses: *Rattlesnake migratory distance is best predicted by***
Physiology	Body Condition, Mean Max Temp	Physiological processes, including body condition and thermoregulation
Vegetation	Distance to forest, NDVI, Canopy Cover	Vegetation structure, including productivity and canopy cover
Terrain	Elevation, Slope, Aspect, VRM	Physical terrain attributes
Combined (global model)	Mean Max Temp, Body Condition, Distance to forest, NDVI, Canopy Cover, Elevation, Slope, Aspect, VRM	The combined effects of physiology, vegetation, and terrain

RESULTS

Migration metrics

The final dataset comprised telemetry data from the years 2005-2012, 2014-2016, and 2019, and included a total of 139 snakes from 36 individual dens across nine unique study sites. See Table 4.1 for a breakdown of the number of individual dens and snakes per site and Appendix D. for details on each individual snake. The complete dataset comprised 4691 telemetry locations across the 139 snakes, with an average of 34 ±17 ($\bar{x}$ ±SD) tracking events per individual (range = 8 to 74 tracking events).

All snakes (*n* = 139) travelled away from hibernacula to summer habitats, reaching their apogee on an average date of July 16 ±30 days, which is approximately the midpoint of the active season in this region. The earliest apogee occurred on May 14 and the latest on September 12. The mean MD measured for outbound migration (from hibernaculum to apogee) of the telemetered snakes was 1364 ±781 m (range = 105 m to 3832 m). The mean 100% MCP was 34.8 ±33.5 ha (range = 0.8 ha to 199.6 ha). Mean 95% AKDE home range was 108.4 ±114.4 ha (range = 0.9 ha to 773.8 ha), and mean 50% AKDE core area of use was 26.5 ±28.7 ha (range = 0.2 ha to 191.0 ha). There were 50 individuals (36%) who migrated uphill, with uphill elevational distances travelled ranging from 40 m to 912 m ($\bar{x}$ = 369 ±280 m). The other 89 individuals (64%) migrated downhill, with downhill elevational distances ranging from 28 m to 295 m ($\bar{x}$ = 145 ±63 m). Using absolute values for all snakes (uphill and downhill), the mean elevational migration distance was 226 ±205 m (n = 139, range = 28 m to 912 m). Snakes that moved uphill migrated further (MD; $\bar{x}$ = 1862 ±925 m) than those who moved downhill ($\bar{x}$ = 1084 ±509 m; t_{137} = 6.41, P <0.0001).

All study hibernacula were in open habitats except for three dens at the Vernon site that lay within the Interior Douglas-fir zone. Among the dens located in open habitat (n = 33), the mean distance to forest habitat was 1228 ±849 m (range = 116 m to 4095 m). Of the 139 snakes, 28 individuals (20%) used forests as their destination habitat (including all five individuals from the Vernon site), while the remaining 111 individuals (80%) used open habitats as their destination. Figure 4.1 shows the frequency distribution of the MD values colour-coded by destination habitat category, and by site. There was a significant relationship between site and destination habitat category (P <0.0001; Figure 4.2). The actual habitat zones used as destinations were Bunchgrass (BG; 53%), Ponderosa Pine (PP; 27%), and Interior Douglas-Fir (IDF; 20%). There was a significant relationship between an individual's direction of vertical migration and destination habitat category (χ^2_1 = 17.26, P <0.0001), with snakes travelling uphill more likely to use forests as their destination.

Body condition index values ranged from -0.47 to 0.39 ($\bar{x}$ = 0.0 ±0.16). Body condition did not differ significantly between snakes using forests as destination habitat ($\bar{x}$ = 0.05 ±0.16) and snakes that occupied open habitats ($\bar{x}$ = -0.01 ±0.16; t_{137} = -1.79, P = 0.08). Body condition was marginally different between destination habitat zones ($F_{2,136}$ = 3.07, P = 0.05), with near significant differences in body condition specifically detected between IDF ($\bar{x}$ =0.05 ±0.16) and BG ($\bar{x}$ = -0.03 ±0.17; P = 0.07), but not between IDF and PP ($\bar{x}$ = -0.02 ±0.12; P = 0.80) or between BG and PP (P = 0.21).

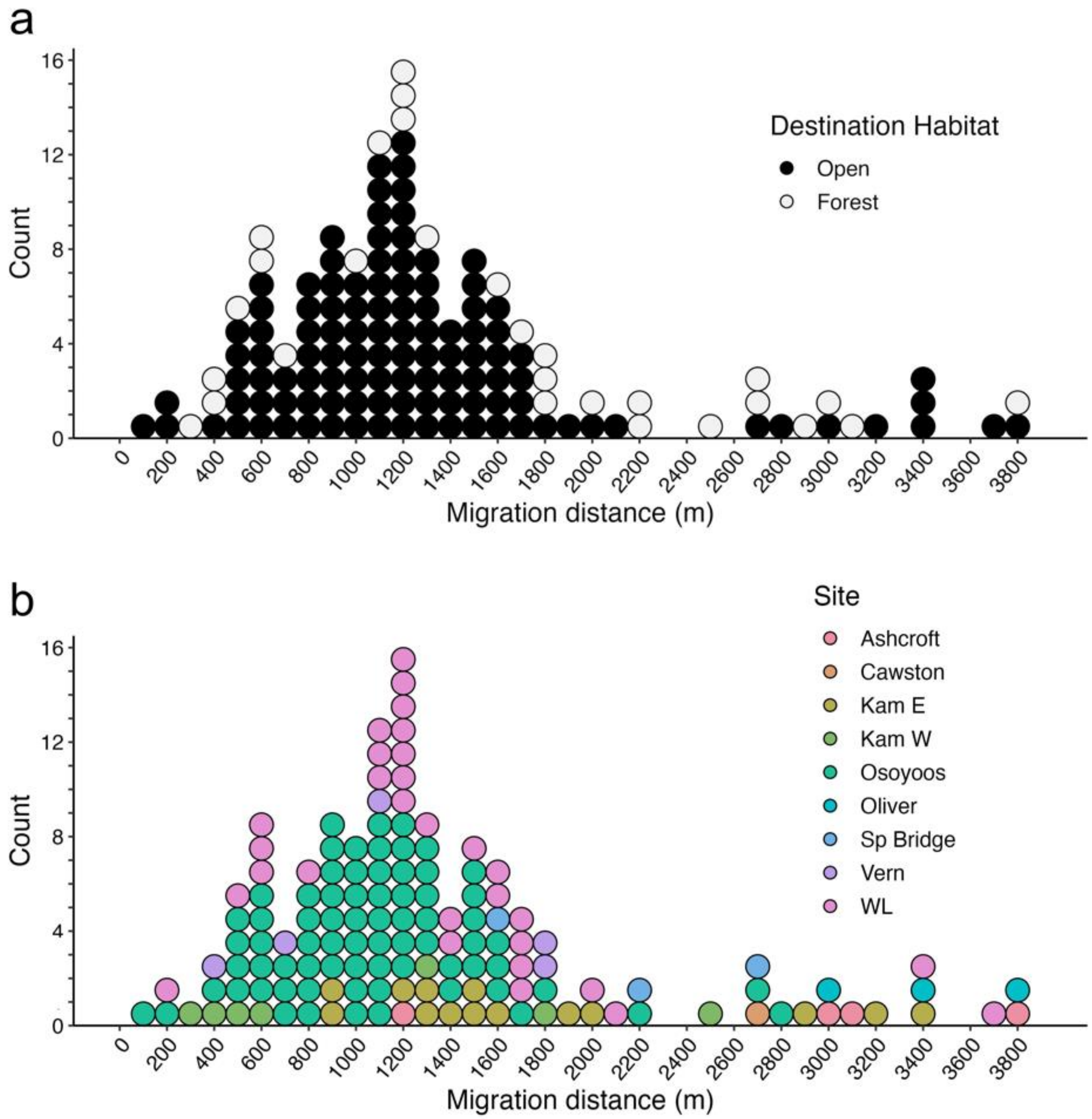

Figure 4.1. Dot plot showing the frequency distribution of migration distance (MD; m) of individual radio-tracked Western Rattlesnakes (*Crotalus oreganus; n* = 139) in Canada, colour-coded by (**a**) the individual's destination habitat and (**b**) the study site from which the individual originates. Each circle represents one individual.

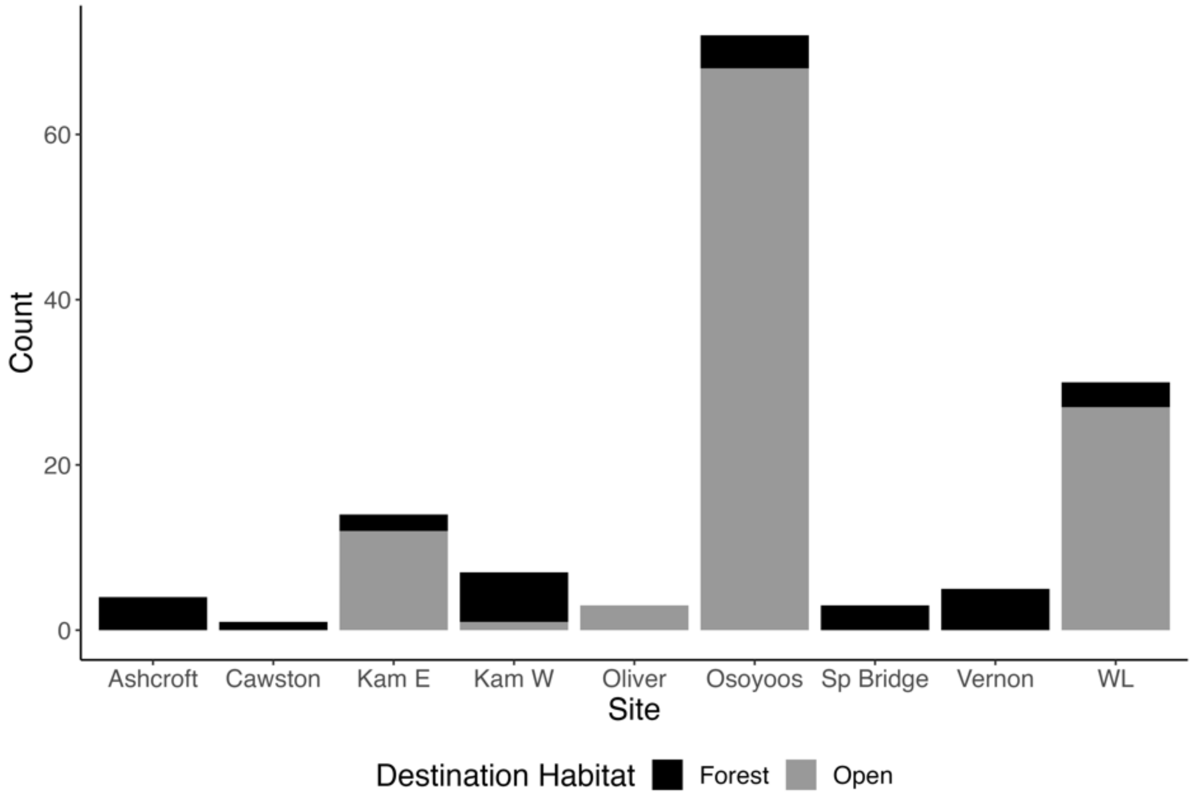

Figure 4.2. Proportion of Western Rattlesnakes (*Crotalus oreganus*) from the nine study sites in Canada that used each category of destination habitat (Black = Forest; Gray = Open).

Migration distance analysis

Migration distance (square root transformed) was significantly different between sites ($F_{8,130} = 11.59$, $P < 0.001$; Figure 4.3), between destination habitat zones ($F_{2,136} = 29.08$, $P < 0.001$; Figure 4.4a), and between destination habitat categories ($t_{137} = -7.49$, $P < 0.001$; Figure 4.4b). See Figure 4.5 for a visual representation of movement paths, distances, and destination habitats.

Among the four candidate linear mixed models, there was strong support for the combined effects (global) model (

Table 4.4): Migratory distance was best predicted by a combination of physiological effects (body condition, mean maximum temperature), vegetation (distance to forest, NDVI, canopy cover), and terrain (elevation, slope, aspect, VRM). Second-best was the terrain model, and the vegetation model outperformed the physiology model. Since we knew there was a possibility that the true 'best model' contained some subset of variables from the combined model that we did not investigate, we used the *dredge* function in the R package 'MuMIn' (Barton 2015) to compare all possible combinations of covariates; the combined effects model was within the top 2 ΔAICc of all possible variable subsets, further establishing it as being the best model for explaining Western Rattlesnake migratory distance.

Model estimates from the combined effects model are shown in

Table 4.5 and Figure 4.6. There was a significant positive relationship between migration distance and mean elevation within an individual's home range ($\beta_{elevation} = 7.30$, CI = 3.09 to 11.51, $P < 0.01$), and a significant negative relationship between migration distance and mean slope within an individual's home range ($\beta_{slope} = -4.32$, CI = -7.04 to -1.60, $P < 0.01$). There was a marginally significant positive relationship between migration distance and mean percentage canopy cover within an individual's home range ($\beta_{canopy} = 2.10$, CI = -0.25 to 4.45, $P = 0.08$).

No other variables showed significance. See Figure 4.7 for predicted effects curves of significant and marginally significant predictor variables.

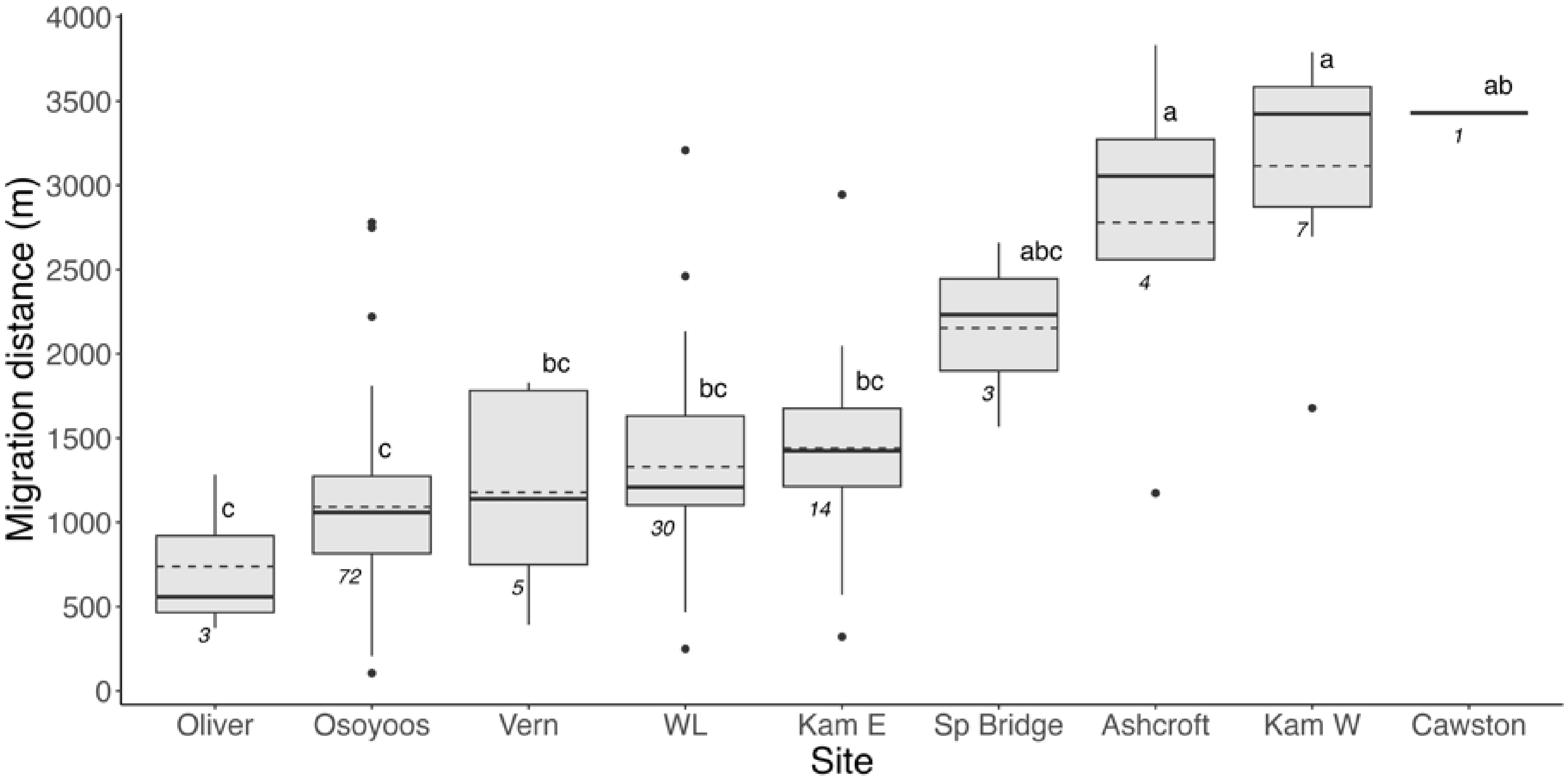

Figure 4.3. Boxplot showing migration distances (m) travelled by male Western Rattlesnakes (*Crotalus oreganus; n* = 139) for each of nine sites in Canada. The median is represented by the solid line, and mean is represented by the dashed line. Means not sharing any letter are significantly different by the Tukey test, using square-root transformed migratory distance (MD) values, at the $\alpha = 0.05$ level of significance. Sample size (*n*) at each site is indicated below boxes. See Table 4.1 for a guide to site abbreviations.

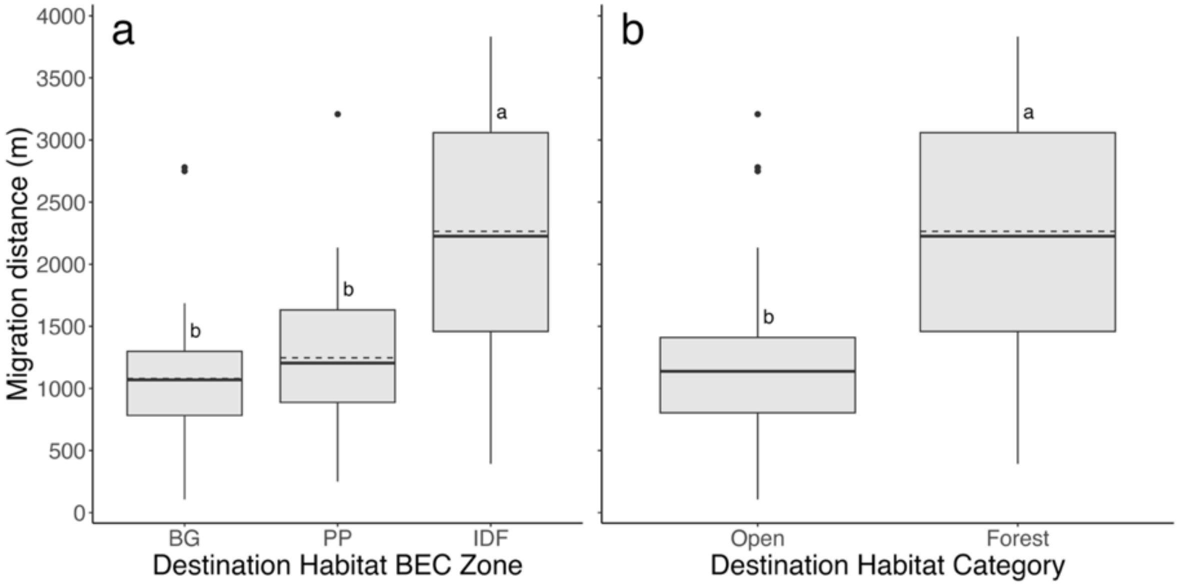

Figure 4.4. Boxplot showing migration distances (m) travelled by male Western Rattlesnakes (*Crotalus oreganus; n* = 139) in Canada by destination habitat: (**a**) destination habitat by zone (BEC); (**b**) destination habitat by category. The median is represented by the solid line, and mean is represented by the dashed line. Means not sharing any letter are significantly different by the Tukey test, using square-root transformed migratory distance values, at the $\alpha = 0.05$ level of significance. *Destination Habitat Zones*: BG = Bunchgrass; PP = Ponderosa Pine; IDF = Interior Douglas Fir.

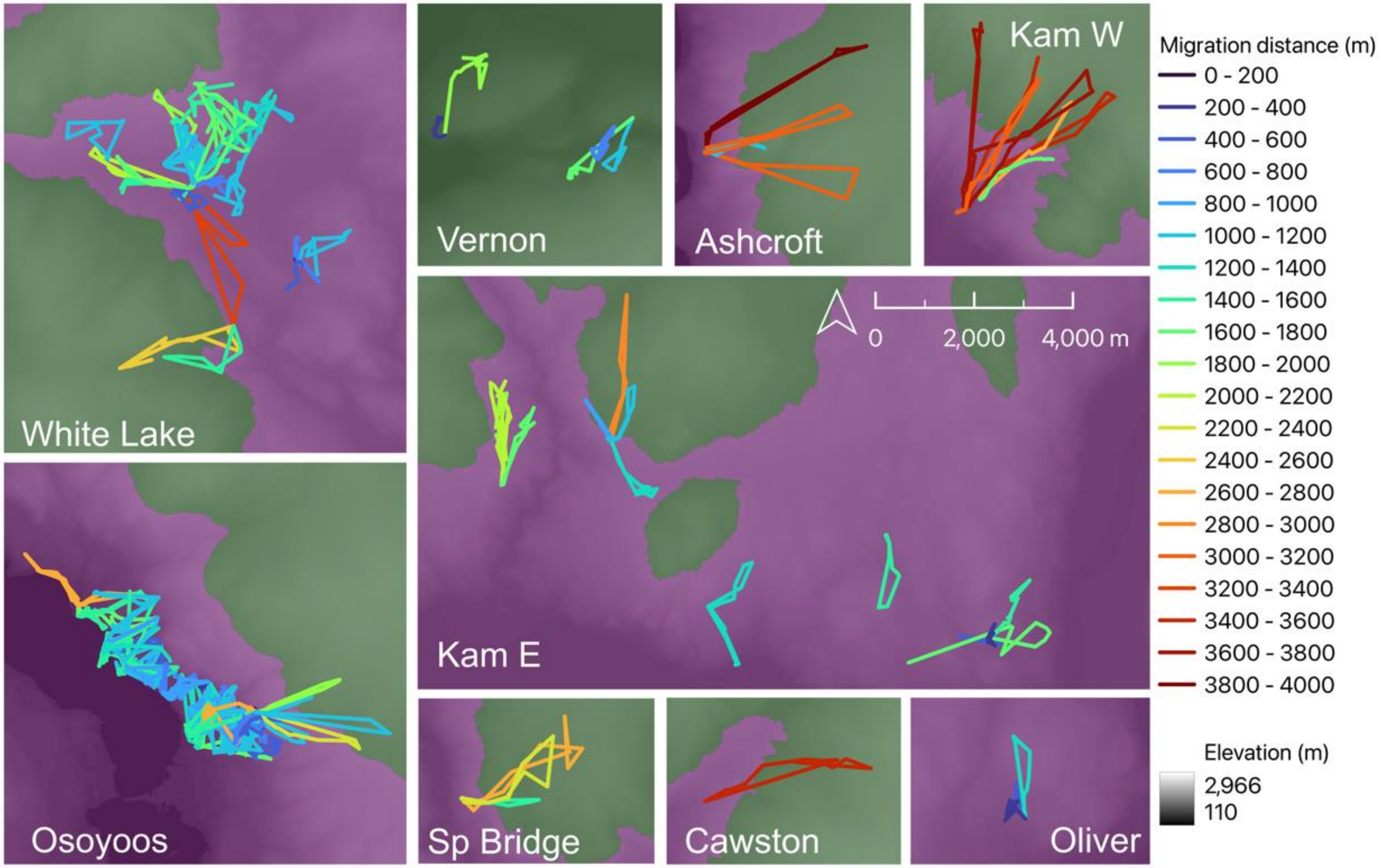

Figure 4.5. Movement paths of Western Rattlesnakes (*Crotalus oreganus; n* = 139) in Canada across nine unique study areas (panels). Movement paths are colour-coded by migration distance (MD; m). Paths assume straight line movements between consecutive tracking locations. Map background represents habitat categories (open = purple; forest = green), and shading represents elevation. See Table 4.1 for a guide to site abbreviations. *Map imaging: Natural Resources Canada (2015), Forest Analysis and Inventory Branch BC (2021). Projection: EPSG32611.*

Table 4.4. Comparison of candidate linear mixed models for predicting Western Rattlesnake (*Crotalus oreganus;* $n = 139$) migration distance in Canada and Akaike Information Criteria correction (AICc) results, including change in AICc, corresponding AICc weight, log-likelihood for each model, and Spearman-rank correlation (r_s) based on k-fold cross validation where $k = 10$. All models include random intercept terms for 'Site' and 'Den'. See Table 4.3 for corresponding model hypotheses.

Model name	**Model variables**	**AICc**	**ΔAICc**	**AICc weight**	**Log-likelihood**	r_s
Physiology	Body Condition, Mean Max Temp	988.7	64.4	0.00	-488.0	0.37
Vegetation	Distance to forest, NDVI, Canopy Cover	977.1	52.8	0.00	-481.1	0.44
Terrain	Elevation, Slope, Aspect, VRM	933.8	9.5	0.01	-458.3	0.64
Combined effects (global model)	Mean Max Temp, Body Condition, Distance to forest, NDVI, Canopy Cover, Elevation, Slope, Aspect, VRM	924.3	0.00	0.99	-447.7	0.65

Table 4.5. Model estimates from the combined effects (global) model for variables affecting Western Rattlesnake (*Crotalus oreganus; n* = 139) migratory distances (MD) in Canada. Significant *P*-values are in bold ($\alpha = 0.05$).

Predictors					
Fixed Effects	**β**	**SE**	**t-value**	**df**	***P***
(Intercept)	38.0	3.4	11.1	7.1	**<0.001**
Body Condition	0.3	0.6	0.5	123.9	0.64
Mean Max Temp	3.2	3.2	1.0	93.3	0.31
Dist to Forest	-1.0	0.8	-1.2	49.7	0.25
NDVI	1.5	1.4	1.1	101.8	0.29
Canopy	2.1	1.2	1.8	71.0	0.08
Elevation	7.3	2.2	3.4	113.6	**<0.01**
Slope	-4.3	1.4	-3.1	108.0	**<0.01**
Aspect	-0.7	0.7	-1.1	117.8	0.28
VRM	-0.7	1.3	-0.6	87.4	0.56
Random Effects	**Variance**	**SD**			
Den (Intercept)	6.4	2.5			
Site (Intercept)	80.8	9.0			
σ^2	34.4	5.9			
N Observations	139				
N groups: Den	36				
N groups: Site	9				

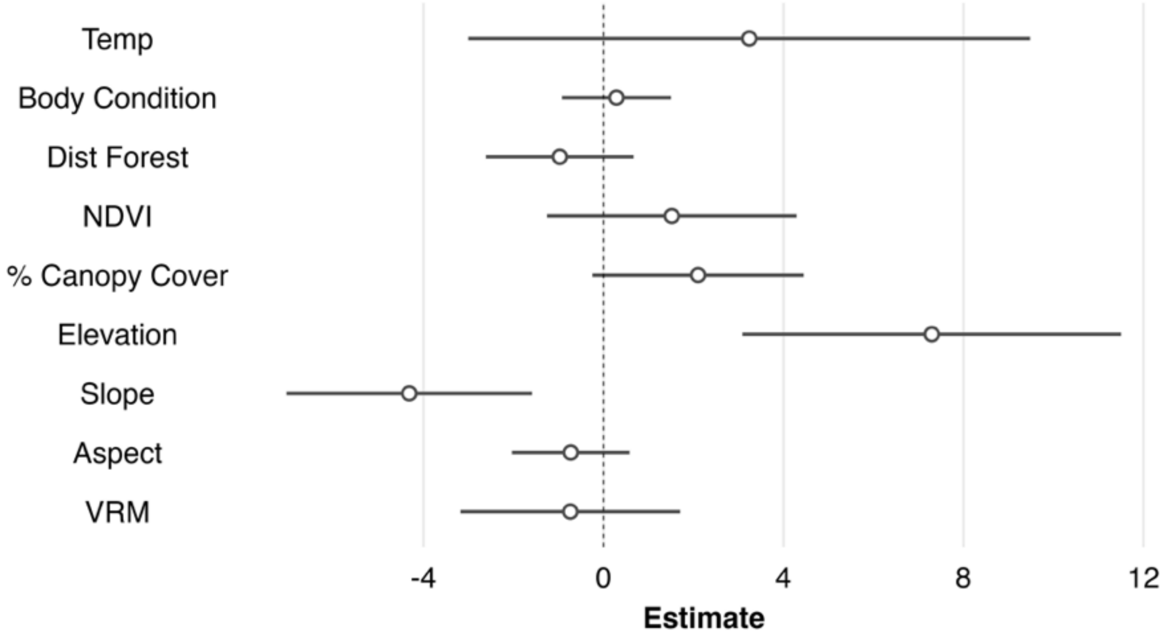

Figure 4.6. Scaled model estimates for fixed effects in the top linear mixed model (combined effects – see Table 4.3) assessing migratory distances undertaken by Western Rattlesnakes (*Crotalus oreganus; n* = 139) in Canada. Positive coefficient indicate a positive relationship between the model variable and migration distance, whereas negative estimates indicate a negative relationship. Lines represent 95% confidence intervals. Confidence intervals that do not overlap with the dashed line (i.e., 0) show significance.

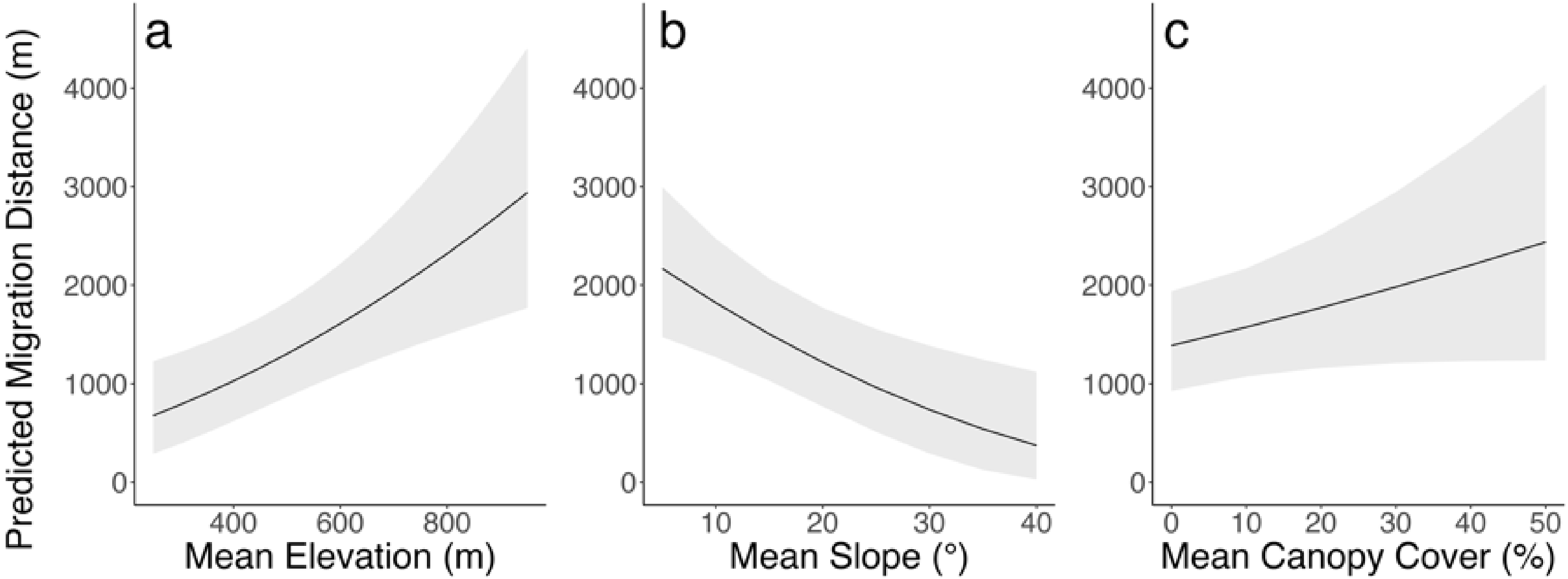

Figure 4.7. Predicted migration distance of Western Rattlesnakes (*Crotalus oreganus; n* = 139) in Canada as a function of the two significant predictor variables (**a** – elevation; **b** – slope) and one marginally significant variable (**c** – canopy cover), as predicted by the combined effects model (

Table 4.5).

DISCUSSION

The results of our study reveal the incredible diversity of movement tactics employed by Western Rattlesnakes across their range in Canada and the complication of predicting such patterns. Rattlesnakes exhibited a migratory continuum (Ball et al. 2001; Cagnacci et al. 2016), with substantial variation in migratory distances and use of destination habitats among individuals. While Western Rattlesnakes are typically linked to dry grassland steppes and open, sparsely treed habitat (Macartney 1985; Bertram et al. 2001; COSEWIC 2015; Gomez et al. 2015), here we observed that the use of cooler, wetter, Douglas-fir forests was also common (observed in 20% of individuals). Further, a combination of effects, including physiological effects, landscape vegetation, and terrain, best explained an individual's migratory distance, with elevation, slope, and canopy cover acting as the strongest drivers of longer migrations.

We observed migration distances ranging from just over a 100 m to nearly 4 km, in consistent with our knowledge of the base studies. The findings of Gomez et al. (2015) and Harvey and Larsen (2020) suggested a dichotomy in rattlesnake migratory tactics in which migratory distance and habitat use are linked and are highly site-specific, namely where long-distance (and often uphill) migration was observed to be closely tied to the use of forests as destination habitats. Here, our expanded data set also showed longer migration distances among snakes using forests as destination habitats, but the pattern was far from consistent; across the broad range of migratory distances observed, both categories of destination habitats were utilized. We also documented longer migration distances among snakes that migrated uphill and found that the use of forests as destination habitats was strongly associated with uphill migrations. So, while the pattern observed in these previous studies (Gomez et al. 2015; Harvey and Larsen 2020) does on average seem to hold true within our larger dataset, we would argue that migratory distance and destination habitat are not as clearly linked as previously thought. Migration distance itself, however, does appear to be moderately dichotomous (bimodal), with most individuals falling in a normal distribution of migrations below 2300m, and a handful of longer-distance migrants falling above this normal distribution.

Migration is affected by environmental factors including the distribution of resources and habitats on the landscape (Alerstam et al. 2003) and, in the case of ectotherms, the thermal environment (Harvey and Larsen 2020). Meanwhile, density-dependent factors including competition for resources or mates, or predation risk may lead to partial migration or a migratory continuum (Taylor and Norris 2007; Chapman et al. 2011). While partial migration has been long and widely studied across taxa such as birds (Lundberg 1988), fish (Chapman et al. 2012), insects (Menz et al. 2019), mammals (Ball et al. 2001; Berg et al. 2019), and even amphibians (Grayson and Wilbur 2009), literature on partial migration in reptiles is largely limited to sea turtles (e.g., Hatase et al. 2010; Shaw and Levin 2011). Here, we observed a continuum of migratory behaviour in which all individuals moved away from their overwintering habitat, though the spatial scale at which these movements occurred was vast; the furthest migration that we documented here was more than 35 times the distance of the shortest observed migration, and nearly three times the mean migratory distance of the full sample. At the same time, it is difficult to say to what extent density-dependent factors may be at play within the denning populations studied here.

We found that snakes' migratory distance was best predicted by our combined model, which included predictors in the physiology, vegetation, and terrain categories. Longer migrations were strongly associated with individuals whose home ranges have lower mean slopes, i.e., flatter terrain. Similarly, though contrary to the findings of Harvey and Larsen (2020), ruggedness was also negatively associated with migratory distance, albeit weakly. Given the energetic and mechanical difficulty of moving through steep and rugged terrain, it is not surprising that snakes in flatter areas undertook longer migrations, as has been documented in other taxa (Puyravaud et al. 2017; Reddy et al. 2019). Longer migrations were also strongly associated with individuals whose home ranges were at higher mean elevations. Again, this association is possibly linked to the presence of forests at higher elevations, in line with the higher mean migratory distances observed for snakes using forests as destination habitats.

Longer migrations were associated with individuals occupying home ranges with higher canopy cover. As has been suggested (Gomez et al. 2015; Harvey and Larsen 2020), it is possible that forested habitats may offer relatively greater prey availability (Kellner et al. 2013) and/or superior thermoregulatory opportunities. The thermal environment has links to migratory behaviour in ectotherms; individuals may seek habitats, from the microhabitat to landscape scale, that facilitate thermoregulation while still allowing them access to food resources and mates (Huey 1991; Díaz 1997; Blouin-Demers and Weatherhead 2001; Row and Blouin-Demers 2006; Harvey and Larsen 2020). Indeed, rattlesnakes using forested habitats use warmer areas of the landscape (Harvey and Larsen 2020), while also undertaking longer migrations than individuals remaining in more open habitats. In line with this, higher mean temperatures within individuals' home ranges were associated with longer migrations in our study, though our analysis of the thermal landscape occurred on a much coarser scale than in Harvey and Larsen (2020). Canopy cover also may have anti-predator benefits for snakes as they travel along their movement paths. Aerial predators – especially raptors – are a major predator of snakes (Greene 1988), and areas with high canopy cover may offer greater overhead protection (as seen for the broad-headed snake (*Hoplocephalus bungaroides* – Pringle et al. 2003) than open landscapes, which could facilitate longer movements. Individuals occupying more open habitats, conversely, would need to rely more heavily on cover objects such as rocks or shrubs (Bertram et al. 2001; Gomez 2007), and may consequently spend more time in stationary crypsis.

Though not significant, body condition was positively associated with longer migrations. Despite the added energy expenditure associated with travelling greater distances, long migrations seem to confer an energetic advantage, again possibly in the form of larger and more varied prey items associated with forests. While body condition was not significant in our model, it is conceivable that variability in conditions across years and sites (that we did not account for here) could be masking a stronger trend in body condition; average body condition within the Osoyoos site's population, for example, varies from year to year (Lomas et al. 2015). Some studies have linked varied spatial behaviours in snakes to the availability of prey (Duvall et al. 1990; Wastell and MacKessy 2011; Wasko and Sasa 2012), while others have suggested limited support for the role of prey to this effect (Taylor et al., 2005). Duvall and Schuett (1997) attribute the movements of male rattlesnakes to mate-searching, though in BC, genetic studies have shown that Western Rattlesnakes primarily mate with individuals from the same or nearby dens (Schmidt et al. 2020).

Higher body condition facilitates longer migrations – for example, in Aves, individuals with higher body condition often migrate further, facilitated by their higher energy stores (Lupi et al. 2016; Duijns et al. 2017; Anderson et al. 2019), allowing them to accrue energetic benefits via access to higher quality or more varied resources/prey (Gaidet and Lecomte 2013). Thus, it is possible that there is a feedback loop of sorts at play, wherein long-distance migrants gain access to better prey, affording them higher body condition, and consequently, these individuals have greater energy reserves to undertake a long distance, often uphill, migration again the following year; this, however, remains to be tested. Western Rattlesnakes consume a wide variety of prey (e.g., mice, voles, shrews, marmots, rabbits, squirrels, birds – Macartney 1989; McAllister et al. 2016); consistent with our findings here that these snakes are highly plastic in their movements and exploit a wide variety of habitats and elevations, similarly (or, perhaps due to the adaptability of the species) they are able to acquire a wide variety of prey. Admittedly, we do not know the true prey benefits of these habitats or differing migration distances, but presumably prey quality is an important driver about which we lack quantification between study sites and habitats. Targeted small mammal trapping and/or experimental food supplements (Taylor et al. 2005; Eye 2022) across varied habitat types used by Western Rattlesnakes and concurrent diet analysis could help to shed light on the role of prey quality in driving the range of migratory tactics observed here.

While the top model included all possible predictors of migratory distance, there was a high degree of variation within each of the predictors, and with a mediocre k-folds cross-validation score, even this top-performing model does not hold much predictive power. Using our larger dataset, we have shown that landscape features and factors influencing physiology/energetics do all a play role in determining how far an individual migrates, though these variables, even in combination, cannot fully explain why we see such variation in migratory tactics and distances, suggesting that other factors may be at play. On top of the unquantified prey base that may be playing a role, it is likely that there is a genetic basis to the continuum of migratory behaviour observed among Western Rattlesnakes in Canada, as seen in other taxa. In migratory birds for example, it has long been understood that the instinctual knowledge of migratory routes and destinations is inherited, while in populations of birds and ungulates exhibiting partial migration, the determination of whether an individual is a migrant or a non-migrant also has a genetic basis (Biebach 1983; Berthold 1991; Cavedon et al. 2019). More recently, it has been acknowledged that migration is controlled through many traits that are genetically correlated (Pulido 2007) and that the inheritance of migratory behaviour operates under a threshold that is environmentally mediated (Pulido 2011; Cobben and van Noordwijk 2016; Cavedon et al. 2019). In Western Rattlesnakes, where (presumably) little direct interaction exists between experienced and inexperienced migrants, and where landscape factors seem not to fully explain the observed variation, it is quite likely that the adoption of differing migratory tactics is to some extent inherited. Future studies should focus on combining genetic studies with classical radio-telemetry work and an analysis of habitat selection at multiple scales/orders of selection.

At the same time, it is conceivable that there is a somewhat ‘random’ nature to the adoption of these differing migratory tactics. Neonates in other *Crotalus* species use conspecific scent trailing to locate communal hibernacula (Cobb et al. 2005; Figueroa et al. 2008; Brown and Maclean 2010; Howze et al. 2012); thus, it is possible that scent-trailing may factor in the early establishment of migratory routes in young snakes. Individuals may choose a scent trail as the determinant of where they will migrate, which could lead to establishing a route that may then be used throughout that individual’s entire life. Nevertheless, scent trailing alone does not explain the variation in migratory distances observed here.

It is worth noting that, for northern species and peripheral species in particular, phenotypic diversity may be linked to the marginal habitat and resources in their environment, forcing animals to be more selective (Safriel et al. 1994). Given the short active season and limiting factors faced by this extreme northern viper, we might expect to see animals adopt migratory strategies that work best given their individual situation. Whether this represents trait plasticity or canalization (Debat and David 2001) within each population, though, is unclear. Further, peripheral populations can be expected to show founder effects (Safriel et al. 1994; Lesica and Allendorf 1995), including in behavioural traits, as seen in the songs of peripheral isolated populations of chaffinches (Baker and Jenkinst 1987). Similarly, peripheral populations of two European grassland butterfly species, *Coenonympha arcania* and *C. Hero* (Lepidoptera: Nymphalidae), differ consistently from their central-range counterparts in both their wing size and shape, attributed in part to the harsher conditions (e.g., wind) that they must endure during dispersal movements (Cassel-Lundhagen et al. 2009). In our analysis, however, we found that individuals from the same den do not always employ the same or even similar migratory tactics, suggesting that such effects may not be at play. Nevertheless, the interplay between genetic variation and extreme environmental conditions may be something to consider for all peripheral species undertaking notable movements.

Although combining data across multiple Western Rattlesnake telemetry studies has allowed us to perform analyses using a larger sample size and across a greater spatial scale, this approach is certainly not without limitations. Most notable of these limitations are the vastly uneven sample sizes between study sites: two study areas – Osoyoos and White Lake – are the sites of long-term research and monitoring programs, while some other sites received only a year of data collection, often on very few individuals. Second was our inability to adequately control for environmental variability from year to year. Admittedly, in our study, we have made the assumption that snakes follow identical migratory routes every year irrespective of annual conditions. We do know that Western Rattlesnakes in Canada show fidelity to their migratory routes (Gomez et al. 2015), though we do not know at how fine of a scale. Future studies in which the same individuals are tracked over multiple years could reveal to what extent route fidelity exists and could assess whether differences observed are attributable to environmental or climatic variation, or to differences in body condition between years. Further, tracking frequencies were variable among individuals, with some individuals receiving more than 9 times as many tracking events as others, thereby impacting the quality of the data between Individuals. And finally, as previously mentioned, our use of mean habitat values within an individual's home range comes with the underlying assumption that the average value sufficiently captures the availability of that particular landscape or resource (Jones et al. 2020), though in reality the mean value likely does not reflect the true encounter rate of an individual to that particular feature on the landscape.

In our study, we investigated the immense variation in migratory behaviour present in a migratory species occupying the northern periphery of their range, and sought to determine the role of habitat and landscape in driving the observed variation. Specifically, we addressed these objectives using a relatively large telemetry set of data on the movements of a northern viper collected over the past two decades. Our results here indicate that vegetation, terrain, and physiology all play a role in determining how far an individual migrates, although the explanatory power is not exceptionally strong. For at-risk species, being able to predict or at least understand the spatial ecology of populations across their range facilitates improved planning and management of critical habitat and movement corridors, but the strength our results indicate that such predictors are not straightforward to produce for this northern reptile, and that other factors not accounted for in this study are also at play. Overall, our study contributes to understanding of variation in migratory behaviour and of migratory continuums in a taxonomic group where this phenomenon has largely been unstudied.

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CHAPTER 5.

CONCLUSION

SUMMARY OF THESIS

The overarching goal of this thesis was to improve our understanding of the patterns and sources of variation in Western Rattlesnake migratory tactics and habitat use and selection at the northern extent of their range in British Columbia. Specifically, I looked at (1) juvenile Western Rattlesnake outbound spring migration and how it compares to movement patterns observed in adults, (2) the microhabitat and stopover site selection of juvenile snakes at two spatial scales, and (3) the patterns and drivers of multi-phenotypic migration and habitat use in adult male Western Rattlesnakes across their Canadian range.

The principal findings from my thesis were the following:

- Compared to adult rattlesnakes, juveniles displayed similar directional orientation, direction of vertical migration, and path sinuosity, but initiated spring migrations later and exhibited shorter movements in terms of distances and rates.
- Resembling adult rattlesnake behaviour elsewhere in BC, juvenile rattlesnakes selected habitat features on the landscape that provided cover (e.g., woody debris, shrub, and rock cover).
- In testing for differences in microhabitat features at sites used for short-duration (fewer than five days) and long-duration (five days or longer) stopovers, we detected negative selection for leaf litter at long-duration stopover sites, but otherwise identified no difference in the microhabitat features associated with these two categories of locations.
- Adult male Western Rattlesnake migration distance ranged from 105 to 3832 m, with a mean of 1364 ±781 m ($n = 139$). Further, 36% of individuals migrated uphill, and 20% of individuals utilized forests as their destination habitats.
- Migration distance was significantly different between some study sites, and snakes using forests as their destination habitats migrated significantly further on average than snakes using open habitats. Yet, the patterns of habitat use were not as closely linked to migratory distance (dichotomous) as previously documented by individual studies.

- We found that migratory distance was best predicted by a combination of physiology (temperature, body condition), vegetation (% canopy cover, NDVI, distance to forest), and terrain attributes (slope, elevation, aspect, ruggedness). However, there was a high degree of variation in migratory distance that was not fully explained by the model (r_s = 0.65 based on k-fold cross-validation where $k = 10$), indicating that other factors unaccounted for us in this study – including the role of genetics/inheritance and prey quality – are likely at play.

MANAGEMENT IMPLICATIONS

Understanding the movement patterns of animals and the sources of variation in their migratory behaviour is critical for making effective wildlife and habitat management decisions, particularly when considering threatened or endangered species such as the Western Rattlesnake (COSEWIC 2015; Allen and Singh 2016). In Canada, the range of the Western Rattlesnake is limited to the province of British Columbia (BC). In BC, the management of wildlife, especially at-risk species, is complex and multifaceted. The majority of terrestrial habitat in BC falls under the designation of provincial or 'crown' land, where various pieces of provincial legislation may be in effect. Parks, First Nations Reserves, and National Defense Lands fall under the jurisdiction of the federal government, where the Species At Risk Act (SARA) is in effect.

On provincial lands, the BC government mandates the protection of ~200-300 ha of habitat surrounding Western Rattlesnake hibernacula through the establishment of Wildlife Habitat Areas (WHAs), which ideally should contain all necessary travel corridors and foraging areas (B.C. Ministry of Water Land and Air Protection 2004; Williams et al. 2012). Currently, approximately 10,150 ha are protected in WHAs for Western Rattlesnakes across the province, with a mean WHA size of 241 ha (data from WHA database, last updated Oct 2022 – BC Ministry of Environment 2022). While WHAs appear to be an effective tool for the protection of overwintering habitat, they likely fail to protect migratory habitat for a large portion of Western Rattlesnakes in the province: an idealized circular 241 ha WHA surrounding a hibernaculum equates to roughly an 870 m radius buffer. While this buffer area would have adequately protected all migrating juveniles that we studied (Chapter 2) during their spring migrations, among the adult male rattlesnakes in our study (Chapter 4)

76% (106 of 139 individuals) would have travelled beyond the area that would be included within the average WHA, in some cases by several kilometres. Small or asymmetrical WHAs are likely to protect even fewer rattlesnakes during their active season migrations (Williams et al. 2012). As such, we recommend that WHAs be expanded to accommodate the migratory and highly mobile nature of Western Rattlesnakes; a WHA area of ~4500-5000 ha would adequately protect habitat for most individuals throughout the entire active season. Admittedly, this would encompass a very large area; alternatively, limited works that do not impact the intact habitat could take place within the 4500-5000 ha area in the non-active (hibernation) season only, while retaining full protection to the ~241 ha area year-round (with full protection expanded to 4500-5000 ha during the active season). This would, at the least, ensure that direct risks to the snakes are limited to the times when they are likely to be absent in those areas while ensuring that all migratory habitat receives year-round protection from more permanent disturbance.

Similarly, the recovery and protection of the Western Rattlesnake under federal legislation is based on the identification of critical habitat under the Species at Risk Act (SARA). This legislation applies only to federal lands (e.g., Parks Canada, National Defence Lands, First Nation Reserves, etc.), while SARA can be applied to provincial land only in dire conservation circumstances. Critical habitat for Western Rattlesnakes is based on documented rattlesnake hibernacula and includes a 2.8 km radius buffer area of essential terrestrial habitat surrounding hibernacula (ECCC 2019). The current designation of critical habitat means that roughly 8% of individuals (11 of 139 adult male rattlesnakes) in this study (Chapter 4) utilized destination habitats that would fall beyond the 2.8 km buffer area surrounding hibernacula. Further, connective habitat is not included under the designation of critical habitat due to a lack of knowledge on longer-distance dispersal in the species (ECCC 2019). Future studies should investigate these longer-distance dispersal events to better understand their prevalence and importance for the species and to inform improved legislation that takes connective habitat into account. Nevertheless, over 90% of individuals in this study remained within the currently definitely critical habitat area; if left unchanged, the current spatial designation may be sufficient to protect the majority of snakes during their active season movements.

In addition to the spatial considerations of how WHAs and critical habitat are defined, our findings (Chapter 4 specifically) highlight the importance of protecting not only grassland and open steppe habitat, but also cooler, higher-elevation forested habitats that typically have not been considered key Western Rattlesnake habitat. With one-fifth of individuals in our study migrating into these forests, it is important to ensure that forested habitat is included in the definition of 'essential terrestrial habitat' (i.e., critical habitat and residency habitat, representing the essential terrestrial areas required by the species for life history functions; ECCC 2019).

Arguably more problematic than the specifics of how WHAs or critical habitat are defined is the fact that these conservation tools do not apply when hibernacula are located on private lands (estimated at ~16% of known hibernacula; ECCC 2019), leaving a large portion of rattlesnake hibernacula and associated migratory and active season habitat unprotected from threats like habitat loss and fragmentation, development, and roads in BC. The findings of this thesis highlight the importance of continued and improved protection for the habitat surrounding Western Rattlesnake hibernacula across all land-management regimes, including private lands, to effectively conserve the species across all age classes during their entire annual cycle.

In summary, the principal management recommendations from my thesis are the following:

- *Provincial legislation via the establishment of Wildlife Habitat Areas (WHAs):* The current average WHA size is 241 ha; more than three-quarters of snakes in our study travelled beyond the area encompassed by the average WHA during their annual migration. As such, the size of WHAs should be expanded (to ~4500-5000 ha) to better capture both the overwintering and summer migratory habitat of Western Rattlesnakes.
- *Federal legislation via identification of critical habitat:* The current designation of critical habitat as a 2.8km radius buffer surrounding hibernacula is sufficient to capture the summer habitat of over 90% of snakes in this study.
- Continue to advocate for protection of habitat surrounding Western Rattlesnake hibernacula across all land-management regimes, including private lands, by working with landowners and managers to minimize threats like habitat loss and fragmentation, development, and roads.

FUTURE RESEARCH CONSIDERATIONS

1) Multi-year analysis of movement

In Chapter 2, we showed that juvenile Western Rattlesnakes migrate on a spatially reduced scale compared to adults, but that some of the variation in the path types that is present among adults already appears to be present in juvenile snakes. Nevertheless, it remains unclear exactly how young snakes adopt these different migratory tactics. Further, while there is some evidence that adults show fidelity to their migratory routes (Gomez et al. 2015), we do not know at how fine of a scale, and it is unclear whether migrations evolve or change throughout individuals' lifetimes on longer time scales, or dependent on annual conditions. Ideally, we should track individuals from birth through adulthood to determine how migratory tactics develop, how they change (or do not change) once snakes reach maturity, and whether these changes are related to annual environmental conditions. With present technology, this is not feasible but with the miniaturization of satellite technology, this could be possible.

2) Habitat selection modelling

In our study, we investigated the role of various landscape and habitat features in driving differing migratory tactics. The results of this analysis indicate that landscape features play an important role in the ecology of these temperate vipers, and while mean landscape factors may not be able to dependably predict how far a snake will travel, a more detailed analysis using a Resource Selection Function (RSF) approach, particularly where individual- and site-specific variation are considered, could further elucidate the relationship of these snakes to their environment. The results of such an analysis could further be used to develop more nuanced conservation and management tools for rattlesnakes both in British Columbia and elsewhere in their range.

3) Inheritance of migratory phenotypes

It is widely accepted that migratory behaviour can be inherited, and the expression of genes controlling migration generally is thought to be environmentally mediated (Pulido 2011; Cobben and van Noordwijk 2016; Cavedon et al. 2019). In our study, we have shown that landscape and site differences alone cannot fully explain the variation that exists in

Western Rattlesnake migratory tactics, suggesting that there may be other factors – including the inheritance of migratory phenotypes – at play. Thus, focused genetic studies paired with classical radio-telemetry work could help illuminate this missing piece. For example, at sites where there is a high degree of variation in migratory tactics, are individuals that employ similar migratory tactics more highly related than those with differing migratory phenotypes (as seen with caribou in partially migratory populations–- Cavedon et al. 2019)? Further, there could be epigenetic triggers that result in animals adopting different tactics, and that may or may not be linked to early life experiences. Radio-tracking family lineages could provide insight through observation of if and how parent-offspring migratory behaviour is consistent or differs, while also paired with manipulative studies where neonatal individuals are translocated to areas with suitable and varied habitats, but which lack conspecific scent trails, to observe how migratory routes are chosen at a young age. Such experiments may be difficult to implement on a species-at-risk, but ultimately, they may provide more valuable information than further empirical study.

4) Prey base monitoring across habitat types

It has previously been hypothesized that forests may harbour higher density and/or quality prey for Western Rattlesnakes (Gomez et al. 2015; Harvey and Larsen 2020), though this remains untested. Targeted small mammal trapping across varied habitat types used by Western Rattlesnakes and concurrent diet analysis of radio-telemetered individuals could help to shed light on the role of prey quality in driving the choice of destination habitat and migratory variation and could aid in understanding the role of different habitats in supporting Western Rattlesnake populations.

CONCLUSION

Migration is central to the life history and ecology of Western Rattlesnakes at the northern extent of their range, allowing them to access important habitats and resources during their short active seasons. Like many other migratory species, migratory behaviour can vary widely within and between populations of rattlesnakes in this area, though the causes of this variation are not well understood. My thesis has shed light on both ontogenetic variation and the ecology of a younger age class of rattlesnakes (an age class that has, to our knowledge, never been studied at this level of detail), while also digging deeper into the questions surrounding variation in habitat use and migration among adult snakes. We have documented the wide range of migratory tactics employed by rattlesnakes in British Columbia and shown that landscape and habitat features do play an important role in determining how far an individual may migrate. At the same time, the questions that remain from this work highlight important areas of future research that are needed to better understand multi-phenotypic migration in the species. Overall, the results, conclusions, and management recommendations outlined in my thesis contribute to more informed conservation and management strategies for Western Rattlesnakes living at the northern extent of their range in Canada, while also broadening our knowledge on multi-phenotypic migration and habitat use in animals.

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APPENDIX A.

DURATION OF STAY AT STOPOVER SITES BY JUVENILE WESTERN RATTLESNAKES

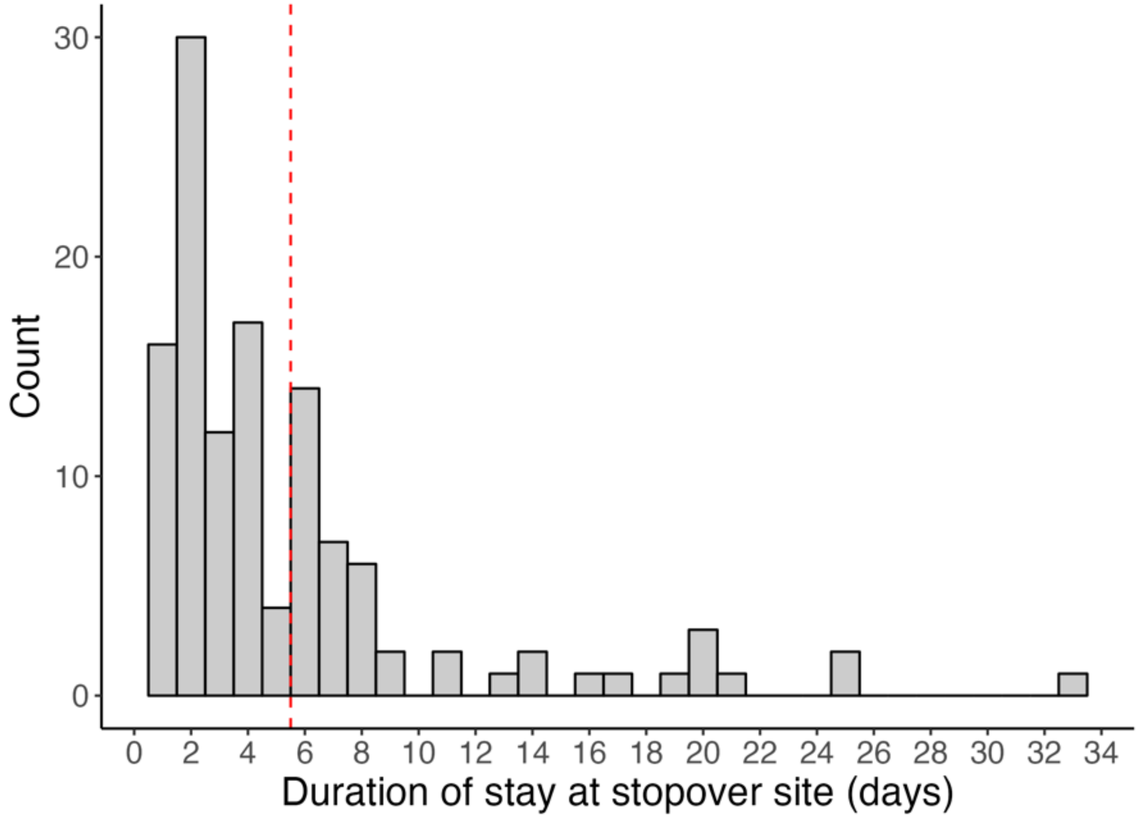

Figure A.1. Histogram showing the duration of stay in days at stopover sites by juvenile Western Rattlesnake (*Crotalus orgenaus*) on the Osoyoos Indian Reserve (OIR) study site near Osoyoos, British Columbia, Canada. Red dashed line shows the cut-off point for transient stopover sites (<5 days) and anchor stopover sites (≥5 days).

APPENDIX B.

INDIVIDUAL REGRESSION COEFFICIENTS AND *P*-VALUES FOR GLOBAL CONDITIONAL LOGISTIC REGRESSION HABITAT SELECTION MODELS

Table B.1. Results of fitting conditional logistic regression models to microhabitat data and to mesohabitat data with minimum distance to habitat features (global models) for comparison of stopover points used by juvenile Western Rattlesnake (*Crotalus orgenaus*) on the Osoyoos Indian Reserve (OIR) study site near Osoyoos, British Columbia, Canada, to paired random sites.

Microhabitat

VARIABLE	***REGRESSION COEFFICIENT ± SE***	***P***
SOIL1	-0.001 ±0.009	0.937
GRASS1	-0.004 ±0.008	0.601
SHRUB1	0.021 ±0.007	<0.01 *
WD1	0.049 ±0.016	<0.01 *
ROCK1	0.035 ±0.010	<0.001 *

Mesohabitat and minimum distance to habitat features

VARIABLE	***REGRESSION COEFFICIENT ± SE***	***P***
SOIL10	0.012 ±0.016	0.428
GRASS10	0.009 ±0.013	0.497
SHRUB10	0.023 ±0.017	0.178
WD10	0.102 ±0.042	0.015 *
ROCK10	0.059 ±0.019	<0.01 *
MD_COVER	-0.409 ±0.244	0.094
MD_SHRUB	-0.153 ±0.111	0.167

* Indicates statistical significance (α = 0.05)

Table B.2. Results of fitting logistic regression models to microhabitat data and to mesohabitat data (global models) for comparison of anchor points and transient points used by juvenile Western Rattlesnake (*Crotalus orgenaus*) on the Osoyoos Indian Reserve (OIR) study site near Osoyoos, British Columbia, Canada.

Microhabitat

VARIABLE	***REGRESSION COEFFICIENT ± SE***	***P***
LL1	-0.100 ±0.030	<0.01 *

Mesohabitat

VARIABLE	***REGRESSION COEFFICIENT ± SE***	***P***
SOIL10	-0.017 ±0.013	0.190
LL10	-0.115 ±0.046	0.013 *

* Indicates statistical significance (α = 0.05)

APPENDIX C.

DETAILED EXPLANATION OF MODEL COVARIATES: SOURCES, DERIVATIONS, AND JUSTIFICATIONS

Elevation: The elevation raster was sourced from Natural Resources Canada's 30m resolution Canadian Digital Elevation Model (DEM), 1945-2011 (NRCan 2015).

Slope: We created a slope raster from the 30m DEM (NRCan 2015) using the Slope tool in the Spatial Analyst extension in ArcGIS 10.8. Slope units are degrees, ranging from 0 (flat) to 90 (vertical).

Aspect: We created an aspect raster from the 30m DEM (NRCan 2015) using 'raster' package (Hijmans 2015) in RStudio (RStudio 2021). We then cosine transformed raster cell values to deal with the wrapped nature of aspect values (in degrees) to give a measure of Northness, where 1 is due North, -1 is due South, and 0 is flat (due East or due West) (Kupfer and Farris 2007; Hebblewhite and Merrill 2008).

Vector Ruggedness Measure (VRM): We quantified landscape ruggedness using the vector ruggedness measure (VRM) of terrain as defined by Sappington et al. (2007), which is based on a geomorphological method for measuring vector dispersion that is less correlated with slope than other ruggedness indices such as Terrain Ruggedness Index (TRI). VRM values can range between 0 (flat) and 1 (most rugged), though values on natural terrains very rarely exceed 0.2 (Sappington et al. 2007). We calculated VRM for 3x3 grids using the package 'spatialEco' (Evans et al. 2021) in RStudio (RStudio 2021) from the 30m digital elevation model (DEM) (NRCan 2015).

NDVI: To estimate environmental plant primary productivity (which could in turn affect prey densities; Stoner et al. 2018), we used the Normalized Difference Vegetation Index (NDVI). NDVI quantifies vegetation by measuring the difference between near-infrared (which is strongly reflected by vegetation) and red light (which vegetation absorbs). We sourced an NDVI raster from (Agriculture and Agri-Food Canada 2021), using the Mean Weekly Best-Quality Maximum-NDVI dataset for the years 2000-2020, for Calendar Week 28 (mid-July). Each raster cell value corresponds to the mean historical "Best-quality" Max-NDVI value for a given week, as calculated from the years 2000-2020. These data are also often referred to as "weekly baselines" or "weekly normals".

Canopy: To quantify canopy cover, we used a 30m resolution raster sourced from Matasci et al. (2018), where each raster cell represents the percentage area with canopy cover over 2m in height, derived from LiDAR point cloud data.

Mean Maximum Temperature: To roughly estimate the average active-season local temperature experienced by snakes at each hibernaculum, we used a monthly mean-maximum climate normal raster dataset (1000m resolution) for the month of July between 1981 and 2010 (Pacific Climate Impacts Consortium, University of Victoria, and PRISM Climate Group 2014).

Distance to Forest: We measured the minimum distance to forest as the shortest straight-line distance between the hibernaculum and nearest forest, with forest defined as Interior Douglas-fir, Interior Cedar-Hemlock, and Montane Spruce in the BC Biogeoclimatic Ecosystem Classification (BEC) system (Forest Analysis and Inventory Branch BC 2021). BEC zones were mapped and distance to forest was determined for each hibernaculum using the Proximity toolset in ArcGIS 10.8.

Body Condition Index: Following Parent and Weatherhead (2000), Brown et al. (2009), and Lomas et al. (2015), we used the residuals from a regression between snake weight and SVL as an index of body condition.

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APPENDIX D.

MORPHOLOGY, CAPTURE, AND CATEGORICAL DATA FOR STUDY ANIMALS USED IN CHAPTER 4

Table D.1. Records for the 139 male Western Rattlesnakes radio-tracked in this study, including all morphometric and categorical variables used. See end of table for study # citations (associated studies). *Abbreviations*: SVL = snout vent length; MD = migration distance; Dest Hab (BEC) = destination habitat biogeoclimatic zone; Dest Hab (Category) = destination habitat category; IDF = Interior Douglas Fir; BG = Bunchgrass; PP = Ponderosa Pine; Kam E = Kamloops East; Kam W = Kamloops West; OIR = Osoyoos Indian Reserve; Sp Bridge = Spences Bridge.

Site	**Den**	**Snake ID**	**Study #**	**Year**	**SVL (cm)**	**Mass (g)**	**Body Cond Index**	**MD (m)**	**Dest Hab (BEC)**	**Dest Hab (Category)**
Ashcroft	Chris	PZ01	1	2010	85.4	462	0.101	1173	IDF	Forest
Ashcroft	Chris	PZ02	1	2010	99.1	707	0.133	3088	IDF	Forest
Ashcroft	Chris	PZ03	1	2010	84.1	444	0.102	3022	IDF	Forest
Ashcroft	Chris	PZ04	1	2010	85.8	443	0.047	3832	IDF	Forest
Cawston	Vinces Den	V01	1	2011	81.9	470	0.229	3430	IDF	Forest
Kam E	Batchelor	Flathead	2	2005	78.5	300	-0.108	321	BG	Open
Kam E	Batchelor	Yeller	2	2005	80.0	300	-0.158	569	BG	Open
Kam E	Batchelor	Jack	2	2006	76.0	281	-0.086	1449	BG	Open
Kam E	Batchelor	Lucifer	2	2006	87.4	480	0.079	1686	BG	Open
Kam E	Gman	GM01	1	2010	90.2	450	-0.070	1476	BG	Open
Kam E	Pimple	Pi01	1	2010	96.2	530	-0.076	1899	PP	Open
Kam E	Pimple	Pi02	1	2010	77.5	360	0.108	1647	PP	Open
Kam E	Pimple	Pi03	1	2010	86.9	485	0.104	2048	PP	Open
Kam E	The Rib	RI01	1	2010	87.9	463	0.027	1262	BG	Open
Kam E	The Rib	RI02	1	2010	98.0	590	-0.018	1323	BG	Open
Kam E	Spen's Den	SP01	1	2010	90.2	565	0.158	1399	PP	Open
Kam E	Spen's Den	SP02	1	2010	82.6	565	0.390	2945	IDF	Forest
Kam E	Spen's Den	SP04	1	2010	80.6	430	0.182	924	PP	Open
Kam E	Spen's Den	SP08	1	2010	92.0	600	0.166	1197	IDF	Forest
Kam W	Waterfall	Gramps	2	2005	95.0	530	-0.043	1678	PP	Open
Kam W	Waterfall	Hulk	2	2005	95.0	570	0.030	3426	IDF	Forest

Kam W	Mitch's	Sexy	2	2005	87.4	440	-0.008	3744	IDF	Forest
Kam W	Waterfall	Spaz	2	2005	87.6	550	0.207	3791	IDF	Forest
Kam W	Mitch's	Tiny	2	2005	77.5	290	-0.107	3049	IDF	Forest
Kam W	Mitch's	Waldo	2	2005	70.6	220	-0.138	3423	IDF	Forest
Kam W	Waterfall	Luigi	2	2006	82.5	440	0.144	2696	IDF	Forest
Osoyoos	Den 25	Cleveland	3	2006	81.0	337	-0.075	887	BG	Open
Osoyoos	RC Den	Divola	3	2006	72.0	263	-0.011	1038	BG	Open
Osoyoos	Den 22	Homer	3	2006	68.5	273	0.158	632	BG	Open
Osoyoos	Den 5	Mr Eko	3	2006	73.5	270	-0.039	950	BG	Open
Osoyoos	Den 21	Ned	3	2006	77.5	289	-0.111	1025	BG	Open
Osoyoos	RC Den	Newman	3	2006	68.5	227	-0.027	1120	BG	Open
Osoyoos	Den 25	Stewie	3	2006	74.0	250	-0.134	904	BG	Open
Osoyoos	Den 21	Warrick	3	2006	65.5	211	0.019	1500	BG	Open
Osoyoos	Den 24	Wesley	3	2006	71.0	219	-0.157	1392	BG	Open
Osoyoos	Den 26	Wiggum	3	2006	76.5	285	-0.091	1307	BG	Open
Osoyoos	Den 22	Zaphod	3	2006	73.0	294	0.064	544	BG	Open
Osoyoos	Den 5	Kola	3	2007	71.0	293	0.134	206	BG	Open
Osoyoos	Den 6	Mr Wick	3	2007	73.0	297	0.074	1453	BG	Open
Osoyoos	Den 5	Noonan	3	2007	72.0	275	0.033	1111	BG	Open
Osoyoos	Den 7	Pembina	3	2007	71.0	261	0.018	1246	BG	Open
Osoyoos	RC Den	Yoho	3	2007	67.0	200	-0.095	963	BG	Open
Osoyoos	Den 6	Jasper	3	2008	71.5	301	0.142	1460	BG	Open
Osoyoos	Den 7	Kootenay	3	2008	72.3	298	0.103	650	BG	Open
Osoyoos	Den D	Nahanni	3	2008	90.2	381	-0.236	1671	BG	Open
Osoyoos	Rodney	Nashua	3	2008	68.5	253	0.082	682	BG	Open
Osoyoos	Den 5	MacKenzie	3	2009	59.0	190	0.190	674	BG	Open
Osoyoos	Den 5	Vuntut	3	2009	75.0	387	0.267	1297	BG	Open
Osoyoos	Den 5	Kazan	3	2010	69.0	239	0.006	826	BG	Open
Osoyoos	Den 6	Memphis	3	2010	68.5	213	-0.090	105	BG	Open
Osoyoos	RC Den	Missouri	3	2010	72.7	314	0.140	1023	BG	Open
Osoyoos	Den 6	Oka	3	2010	76.0	276	-0.106	1138	BG	Open
Osoyoos	Den 5	Phoenix	3	2010	69.0	224	-0.059	1267	BG	Open
Osoyoos	Den 22	Bajoran	3, 4	2011	73.5	250	-0.116	841	BG	Open
Osoyoos	Den 25	Carson	3, 4	2011	78.5	241	-0.327	1049	BG	Open

Osoyoos	Den D	Columbus	3, 4	2011	67.5	207	-0.080	1049	BG	Open
Osoyoos	Den 25	Data	3, 4	2011	76.0	234	-0.271	412	BG	Open
Osoyoos	Den 25	Gator	3, 4	2011	79.0	251	-0.303	1206	BG	Open
Osoyoos	Den 6	Kirk	3, 4	2011	67.5	212	-0.056	1069	BG	Open
Osoyoos	Den 26	McCoy	3, 4	2011	71.0	220	-0.153	828	BG	Open
Osoyoos	RC Den	Mowgli	3, 4	2011	71.0	203	-0.233	1266	BG	Open
Osoyoos	Den 25	Neelix	3, 4	2011	79.0	213	-0.467	1140	BG	Open
Osoyoos	Den 6	Picard	3, 4	2011	72.5	251	-0.076	1050	IDF	Forest
Osoyoos	Den 6	Riker	3, 4	2011	69.0	202	-0.163	2749	BG	Open
Osoyoos	Den 27	Scotty	3, 4	2011	72.5	266	-0.018	1148	BG	Open
Osoyoos	Den 20	Spock	3, 4	2011	72.0	212	-0.227	1221	BG	Open
Osoyoos	Den 26	Sulu	3, 4	2011	71.5	243	-0.072	1516	BG	Open
Osoyoos	Den 26	Tiberius	3, 4	2011	75.0	304	0.026	1534	BG	Open
Osoyoos	Den 6	Burrows	3, 4	2012	63.0	151	-0.213	1420	BG	Open
Osoyoos	Den 6	Geordi	3, 4	2012	73.7	218	-0.261	896	BG	Open
Osoyoos	Den 6	Greedo	3, 4	2012	63.5	266	0.332	1104	BG	Open
Osoyoos	Den 6	R2D2	3, 4	2012	68.0	197	-0.149	896	BG	Open
Osoyoos	Den 6	Seven	3, 4	2012	69.0	234	-0.016	761	BG	Open
Osoyoos	Den 6	Vader	3, 4	2012	65.2	243	0.172	782	BG	Open
Osoyoos	Den 6	Linden	4	2014	76.0	334	0.085	537	PP	Open
Osoyoos	Den 6	Lou	4	2014	63.2	270	0.360	782	BG	Open
Osoyoos	Den 10	Noah	4	2014	65.6	219	0.052	1008	BG	Open
Osoyoos	Den D	Suresh	4	2014	68.4	248	0.066	637	BG	Open
Osoyoos	Den 27	Bow	4	2015	73.0	277	0.004	2780	BG	Open
Osoyoos	Den 6	Congo	4	2015	56.7	177	0.224	582	BG	Open
Osoyoos	Den D	Fraser	4	2015	76.5	195	-0.471	539	BG	Open
Osoyoos	Den D	Hudson	4	2015	54.5	135	0.058	627	BG	Open
Osoyoos	Den D	Murray	4	2015	62.4	168	-0.081	472	BG	Open
Osoyoos	Den 6	Rhine	4	2015	60.2	179	0.077	732	BG	Open
Osoyoos	Den 26	Thompson	4	2015	72.7	245	-0.108	1627	BG	Open
Osoyoos	Den 6	Yukon	4	2015	69.4	271	0.116	1193	BG	Open
Osoyoos	Den 6	Bravo	4	2016	73.4	196	-0.356	1811	IDF	Forest
Osoyoos	Den 6	Charlie	4	2016	64.7	185	-0.081	1162	IDF	Forest
Osoyoos	Den 6	Echo	4	2016	70.1	233	-0.062	2220	IDF	Forest

Osoyoos	Den 6	Foxtrot	4	2016	69.0	196	-0.193	1240	BG	Open
Osoyoos	Den 6	Golf	4	2016	61.2	169	-0.024	1151	PP	Open
Osoyoos	Den 27	Hotel	4	2016	70.5	219	-0.139	1132	BG	Open
Osoyoos	Den 26	India	4	2016	62.4	160	-0.130	1138	BG	Open
Osoyoos	Den 27	Kilo	4	2016	64.7	179	-0.113	1573	BG	Open
Osoyoos	Den 27	Lima	4	2016	72.3	287	0.065	1558	BG	Open
Osoyoos	RC Den	Romeo	4	2016	56.8	178	0.225	910	BG	Open
Osoyoos	Den 8	Tango	4	2016	58.4	192	0.227	1298	BG	Open
Osoyoos	Zulu Den	Zulu	4	2016	57.7	202	0.310	906	BG	Open
OLIVER	Jordans Den	J01	1	2011	78.7	320	-0.050	1284	PP	Open
OLIVER	Jordans Den	J03	1	2011	75.6	300	-0.009	373	PP	Open
OLIVER	Jordans Den	J04	1	2011	73.3	260	-0.070	558	PP	Open
Sp Bridge	Falcon Nest	FA01	1	2010	88.6	640	0.330	1568	IDF	Forest
Sp Bridge	Falcon Nest	FA02	1	2010	82.9	444	0.140	2232	IDF	Forest
Sp Bridge	Falcon Nest	FA03	1	2010	83.1	490	0.232	2660	IDF	Forest
Vernon	Den 11	Anakin	5	2019	83.0	406	0.047	1139	IDF	Forest
Vernon	Den 11	Big Daddy	5	2019	107.0	680	-0.108	1782	IDF	Forest
Vernon	Den 14	Chewbacca	5	2019	88.5	430	-0.065	1830	IDF	Forest
Vernon	Den 8 (Vernon)	Darth Maul	5	2019	94.0	610	0.125	749	IDF	Forest
Vernon	Den 14	Obi-Wan	5	2019	74.0	260	-0.095	393	IDF	Forest
White Lk	Guernsey	G04	1	2011	72.7	310	0.128	875	PP	Open
White Lk	Guernsey	G23	1	2011	92.0	480	-0.057	1761	PP	Open
White Lk	Guernsey	G24	1	2011	79.4	400	0.150	529	PP	Open
White Lk	Paradigm Shift	PS02	1	2011	98.7	710	0.148	2461	IDF	Forest
White Lk	Paradigm Shift	PS04	1	2011	90.5	600	0.209	3208	PP	Open
White Lk	Paradigm Shift	PS05	1	2011	86.4	400	-0.074	1546	IDF	Forest
White Lk	Lil Rattle GG	Achilles	6	2015	74.0	315	0.097	593	PP	Open
White Lk	Guernsey	Apollo	6	2015	94.0	455	-0.168	1198	PP	Open
White Lk	White T	Ares	6	2015	75.0	295	-0.004	1585	PP	Open
White Lk	Guernsey	Dionysus	6	2015	81.0	385	0.059	1436	PP	Open
White Lk	Guernsey	Hades	6	2015	89.0	467	0.003	1647	PP	Open
White Lk	White T	Hephaestus	6	2015	80.0	340	-0.033	1207	PP	Open
White Lk	Guernsey C	Hercules	6	2015	90.5	678	0.331	2134	PP	Open
White Lk	Guernsey	Hermes	6	2015	81.0	380	0.046	1249	PP	Open

White Lk	Guernsey	Poseidon	6	2015	81.5	332	-0.106	1210	PP	Open
White Lk	Acropolis	Theseus	6	2015	91.0	598	0.191	1194	PP	Open
White Lk	Guernsey	Zeus	6	2015	90.0	460	-0.042	1188	PP	Open
White Lk	Guernsey	Aladar	6	2016	85.0	380	-0.082	1989	IDF	Forest
White Lk	White T	Drogon	6	2016	86.0	375	-0.126	1118	PP	Open
White Lk	White T	Falkor	6	2016	88.5	480	0.045	1733	PP	Open
White Lk	Guernsey C	Godzilla	6	2016	100.5	730	0.128	1493	PP	Open
White Lk	Guernsey C	Kaa	6	2016	90.5	420	-0.147	468	PP	Open
White Lk	Lil Rattle GG	Littlefoot	6	2016	81.0	365	0.005	1200	PP	Open
White Lk	Lil Rattle GG	Mushu	6	2016	71.0	210	-0.199	639	PP	Open
White Lk	Guernsey	Norbert	6	2016	83.5	360	-0.089	1653	PP	Open
White Lk	Lil Rattle GG	Ogopogo	6	2016	78.0	330	0.004	249	PP	Open
White Lk	Guernsey	Puff	6	2016	91.5	485	-0.033	777	PP	Open
White Lk	White T	Smaug	6	2016	81.5	420	0.129	1137	PP	Open
White Lk	Guernsey	Toothless	6	2016	80.5	360	0.008	1097	PP	Open
White Lk	White T	Toruk	6	2016	93.5	515	-0.030	1292	PP	Open

Study #: Associated study

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3: Lomas E, Maida JR, Bishop CA, Larsen KW. 2019. Movement ecology of northern pacific rattlesnakes (*Crotalus o. oreganus*) in response to disturbance. Herpetologica. 75(2):153–161.4: Maida 2020

4: Maida JR, Bishop CA, Larsen KW. 2020. Migration and disturbance: impact of fencing and development on western rattlesnake (*Crotalus oreganus*) spring movements in British Columbia. Canadian Journal of Zoology. 98(1):1–12.

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