NATURAL AND ARTIFICIAL HIBERNACULA USE BY THREE SYMPATRIC SNAKE SPECIES

by

VERONICA MARTHA LOUISE MCKELVEY

BSc (Hons), University of Toronto, 2021

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE IN ENVIRONMENTAL SCIENCE

Thompson Rivers University
Kamloops, British Columbia
May 2024

Thesis examining committee:

Karl Larsen (PhD), Thesis Supervisor
Professor, Department of Natural Resource Sciences, Thompson Rivers University

Leigh Anne Isaac (PhD), Thesis Co-Supervisor
Small Mammal and Herpetofauna Specialist,
Ministry of Water, Land and Resource Stewardship

Darryl Carlyle-Moses (PhD), Committee Member
Associate Professor, Department of Geography & Environmental Studies,
Thompson Rivers University

Nicholas Cairns (PhD), External Examiner
Curator of Non-Avian Vertebrates, Royal Alberta Museum

ABSTRACT

Species that persist at higher latitudes require specialized adaptations to survive decreased temperatures, inclement weather, and reduced resource availability during winter. As ectotherms, the internal temperature of snakes is determined by their external environment. Thus, within temperate ranges, snakes rely on hibernacula that meet the structural, thermal, and humidity conditions needed to survive overwinter.

The apparent scarcity of snake hibernacula in cooler climes makes understanding the selection of this critical habitat feature significant for conservation. I used a community of three sympatric snake species to explore how habitat features relate to the number of each species at hibernacula and determine how these species vary in their selection of overwintering habitat. Little to no measured habitat metrics effectively explained the detected number of Great Basin Gophersnakes (*Pituophis catenifer deserticola*), Western Yellow-bellied Racers (*Coluber constrictor mormon*) and Western Rattlesnakes (*Crotalus oreganus oreganus*) at hibernacula. Further, I reveal that although these species share the same landscape and, in some cases, hibernacula, they are not selecting habitat in the same way. This variation in habitat selection aligned with differences in detected egress behaviour.

Given the apparent scarcity of denning sites, one can theorize the tremendous impact on snake populations when they are destroyed. Constructing artificial hibernacula is one proposed conservation or mitigation measure to combat this loss. In this study, I used the creation of two artificial hibernacula following a disturbance event to (i) collect the internal temperature and humidity of the hibernacula and the internal temperatures of snakes and (ii) monitor the adoption of the main artificial hibernacula by the original cohort of displaced snakes. Both artificial hibernacula provided a range of thermal and humidity conditions, with temperature generally increasing with depth and distance to the hibernacula mouth. Internal hibernacula readings buffered against and were largely independent of external temperature fluctuations (including during a low of -30.4°C). Temperatures of overwintering Great Basin Gophersnakes within the main artificial hibernacula were comparable to those in natural hibernacula. In particular, the artificial hibernacula provided thermal microsites conducive to the survival of gophersnakes at depths ranging from 2.6 to 3.1m. Despite relocation efforts and six translocated snakes overwintering the first year, no translocated snake naturally adopted or returned to the main hibernacula two years post-disturbance. However, two newly identified snakes overwintered in the main hibernacula in the second winter.

Overall, my thesis highlights distinct interspecific variations in behaviour and hibernacula selection. Such variation indicates that conservation efforts and impact assessments that use hibernacula ‘models’ from well-studied species (e.g., Western Rattlesnakes) to extrapolate to other species may be ineffective. I recommend larger protection at the landscape level to avoid future disturbance of these hard-to-identify critical habitat features. In cases of disturbances, I show that artificial hibernacula can be built to be conducive to survival. However, we caution against using these structures as mitigation measures due to the low uptake of focal individuals, at least in the short term. Future research is needed to understand the use of these artificial structures over a longer period of time.

Keywords: Hibernacula, Artificial Hibernacula, Habitat Use, Microclimate, Critical Habitat, Communal Denning, Great Basin Gophersnake, Western Yellow-bellied Racer, Western Rattlesnake

ACKNOWLEDGEMENTS

I would like to acknowledge that my research took place on Tk'emlúps te Secwépemc territory, situated within the unceded ancestral lands of the Secwépemc Nation. As a settler from Ontario, I am so grateful to have experienced the raw beauty of the Lac du Bois Grasslands Protected Area. As I tracked snakes, I traversed this undulating landscape through the pulse of spring growth and ticks, through the smoke and heat of the summer, following them into the yellow hues of fall, and trudging through fresh blankets of snow. Each season was just as gruelling and magical as the last. I can attest that enduring a never-ending line of ticks crawling up my neck, wildfires, the 2021 heat dome, and a -30°C cold snap made me a stronger person. A special nod to the prickly pear cactus for always 'sticking' around, usually in the most undesirable of places (i.e., legs, hands, and... yes, even my butt).

To my supervisors, Dr. Karl Larsen and Dr. Leigh Anne Isaac, your guidance, wisdom, and constructive feedback shaped the trajectory of this thesis and my future. I am grateful for the mentorship and inspiration to continue my academic pursuit as I start a PhD. A special thanks to Karl for making edits just a little bit easier with all the curated character comments. Leigh Anne, I always looked forward to having you in the field and hope one day to have as good a field lunch as you do. Thank you to my committee member, Dr. Darryl Carlyle-Moses, for providing time and valuable insight from outside the snake bubble. I would also like to acknowledge my external examiner, Dr. Nicholas Cairns; thank you for all your feedback and interesting questions.

None of this work would have been possible without the hard work, dedication and immense flexibility of Dr. James Sudhoff, Dr. Fergus Alexander, Tracy Reynolds, and Paige McKnight. Thank you for always having the time for a snake surgery!

To my snake-wrangling partner in crime, Lily Ragsdale, I could not have done this without you. I am so grateful that we shared a snake farm and the rollercoaster ride in our Ford Expeditions that came with it. No one will understand how we name snakes except us, and I love that. Together, we supervised many amazing field assistants crazy enough to spend their summers catching snakes with us. I am forever grateful for the dedication, hard work, and love of snakes that Maria Collins, Hailey Wynnyk, Jade Spruyt, and Jake Veenman gave to this project.

When I started this Master's degree, I could have never imagined how many amazing people would come into my life and whom I would like to thank. To all my fellow grad students (and amazing friends), Jade Spruyt, Chloe Howarth, Calen Wong, Lindsay Whitehead, Kara Atkinson, Larisa Murdoch, Shannon Werden, and Mae Frank, thank you all for listening to me freakout out about my thesis, and for our weekly (sometimes daily) updates and tea-dropping sessions. It is not easy to chat through cubicles, but we made it work.

To my family, even though we are provinces apart, thank you for always being just a phone away… and for still picking up, even when my rants about this thesis became a broken record.

A very special thank you and immense gratitude goes to my personal chef (my partner), Jacob Tecca. Thank you for always encouraging me, loving snakes almost as much as I do, providing beautiful art (see in Dedication section below), and having a warm meal to come home to every night.

As I write this it is starting to feel like the Oscars' music is coming on. Thanks to everyone who played a role, both big and small. It takes a village… or something like that.

This work was supported by Trans Mountain, MITACS and the Natural Sciences and Engineering Research Council of Canada (NSERC). All snake handling, transportation, and surgical protocols were reviewed and approved by the Thompson Rivers University Animal Care Committee (File No: 102730). Data were collected under BC Wildlife Permit KA21-620041.

NOTE: In Chapters 2 and 3 of this thesis, plural pronouns have been chosen to align with journal publication conventions and to recognize the contributions of my supervisors and the significant role played by Lily Ragsdale.

DEDICATION

I would like to dedicate this thesis to **“*The Big Three*”**

To all the Great Basin Gophersnakes, Western Yellow-bellied Racers, and Western Rattlesnakes that were observed, handled, or tracked. Each snake played a significant role in making this research possible. I hope it can now be used for their conservation.

Illustration of (left to right) a Western Yellow-bellied Racer, Western Rattlesnakes, and a Great Basin Gophersnake at hibernacula. Illustration by Jacob Tecca.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION TO THE THESIS

OVERWINTER SURVIVAL

Species shift in their response to external seasonal changes, leading to differing behaviours, morphology, and physiology depending on the time of year (Nelson et al. 1990; Lisovski et al. 2017). Such shifts are pronounced more for species in highly seasonal environments, that increase in winter intensity towards the poles (Lisovski et al. 2017). These latitudes are characterized by long winters and short summers (Ultsch 1989). Here, summers provide access to increased light, temperature, and resource availability, resulting in heightened animal activity (Williams et al. 2017). Conversely, winters are characterized by shorter days, colder temperatures, and inclement weather, that limit the availability and access of resources and ultimately reduce animal activity (Williams et al. 2017).

Winters are arguably one of the most stressful times for organisms, with conditions constraining the northern range and resulting in the direct mortality of many individuals (C.M. Williams et al. 2015). For example, White et al. (2011) found that mountain goat (*Oreamnos americanus*) survival in coastal Alaska was influenced by snow conditions, particularly in years with snow higher than the long-term median. In contrast, Shine and Mason (2004) found that winters with lighter snow cover in central Manitoba led to major freezing events of Red-sided Garter Snakes (*Thamnophis sirtalis parietalis*). Further, Baccante and Woods (2010) revealed that higher mule deer (*Odocoileus hemionus*) fawn survival was linked to years with milder winters within the Peace Region of British Columbia. These strong selective forces, which in some regions persist for over half a year or longer, necessitate animals to possess specialized adaptations to survive winter (C.M. Williams et al. 2015).

OVERWINTERING IN REPTILES

As ectotherms, the body temperature of reptiles is determined largely by their external environment (Voituron et al. 2002). Thus, their persistence at higher latitudes requires specialized responses to survive through or avoid exposure to sub-zero temperatures during winter (Ultsch 1989; Voituron et al. 2002). As winter temperatures generally are below the normal thermal activity thresholds for reptiles, this leads to a period of dormancy called brumation (Holden et al. 2021). This period is controlled by temperature exposure and is a metabolic adaptation characterized by lower energy demands, metabolism, and heart rate, with periods of activity (Hoekstra et al. 2020; Holden et al. 2021). Depending on exposure, some reptiles may utilize further physiological adaptations to reduce their exposure to lethal temperatures (i.e. freeze tolerance or freeze avoidance) (White and Lasiewski 1971; Ultsch 1989; Costanzo et al. 1995; Moss and MacLeod 2022). With these adaptations, 'freeze tolerators' can endure some of their body being frozen, while 'freeze avoiders' can supercool by depressing their freezing point (Zachariassen 1985; Storey and Storey 1988, 1996; Voituron et al. 2002). For example, hatchling painted turtles that overwinter in shallow subterranean nests (5-10cm) can survive to -4°C as a 'freeze tolerator' or to -15°C as a 'freeze avoider' (Costanzo and Lee 2013). These strategies vary across species and ranges and largely depend on the risk of thermal exposure (Tsuji 1988; Moss and MacLeod 2022). Many reptiles, however, behaviourally avoid lethal temperatures by utilizing a shelter, also known as a den or hibernaculum (White and Lasiewski 1971; Ultsch 1989; Costanzo et al. 1995; Michels-Boyce and Zani 2015; Moss and MacLeod 2022).

SNAKE HIBERNACULA

Snakes inhabiting temperate zones must find adequate overwintering habitat to circumvent reduced food availability and extreme and variable temperatures over winter (Hein and Guyer 2009). Rather than creating new features, most snakes rely on subterranean habitats that superficially appear as crevices in a rockface, holes in the ground, or piles of rocks (Costanzo 1986; Prior and Weatherhead 1996; Gienger and Beck 2011; K.E. Williams et al. 2015). Previous studies have showcased that snakes select distinct habitat features for hibernacula compared to the broader landscape (Prior and Weatherhead 1996; Gienger and Beck 2011). For example, Western Rattlesnake (*Crotalus oreganus oreganus*) hibernacula in Washington State were found along low-grade south-facing talus slopes with intermediate-sized rocks compared to random sites (Gienger and Beck 2011). Further, Black Rat Snake *(Pantherophis obsoletus)* hibernacula within eastern Ontario were found on rocky south-facing slopes, with snakes preferring large, partially dead or hollow trees for basking during emergence (Prior and Weatherhead 1996).

Hibernacula must provide suitable conditions to ensure survival for upwards of half the year at northern range limits (Brown et al. 1974; Prior and Weatherhead 1996; Gienger and Beck 2011). These sites must be structurally stable to ensure snakes can safely hibernate without disturbances (Markle et al. 2020). Hibernacula vulnerable to collapse, flooding, or landslides can have catastrophic impacts on populations (Shine and Mason 2004; Gardiner and Sonmor 2011; Maida et al. 2017). Further, such sites are especially needed within northern latitudes to insulate against extreme and variable temperatures (Gregory 1982; Hein and Guyer 2009). Intuitively, the temperature within hibernacula must be within a tolerable range to ensure snakes do not freeze and are not expending energy reserves (Gregory 1982; Costanzo 1989a; K.E. Williams et al. 2015; Markle et al. 2020) while also providing sufficient humidity to prevent desiccation (Costanzo 1986). Hibernacula that meet these requirements may be a limiting resource in some environments, forcing some individuals to travel kilometres in order to return to the same denning location, presenting strong yearly fidelity to those sites (Prior et al. 2001; Gienger and Beck 2011). In fact, some Western Rattlesnake hibernacula may be used for hundreds of years (COSEWIC 2015a; Dyer et al. 2016b; Macartney 1985). The potential limitation of these sites is reinforced by increased instances of communal denning at higher latitudes, as numerous snakes must use a single hibernaculum (Gregory 1984, 2009).

COMMUNAL DENNING

Communal denning in snakes, pronounced in higher latitudes and altitudes of the northern hemisphere, is a phenomenon where seemingly solitary individuals congregate to overwinter (Gregory 1974, 1984, 2009). The epitome of this behaviour is the aggregations of thousands of Red-sided Garter Snakes at hibernacula in the Interlake region of Manitoba (Gregory 1973, 1977, 1984). This phenomenon, albeit not to the same degree, is also observed in other snakes: Western Rattlesnakes (Gienger and Beck 2011), Western Yellow-bellied Racers (*Coluber constrictor mormon*), Great Basin Gophersnakes (*Pituophis catenifer deserticola*) (Parker and Brown 1973), Black Rat Snakes (Prior and Weatherhead 1996), etc. Communal hibernacula also may support multispecies assemblages (COSEWIC 2013; K.E. Williams et al. 2015).

Although widely observed, the question of why snakes hibernate communally is largely unanswered. There are many potential explanations for why communal denning exists. A leading theory is that the scarcity of adequate hibernacula results in increased instances of communal denning (Bruckerhoff et al. 2021; Gregory 1984, 2009). Within northern latitudes, harsh winter weather may exacerbate this phenomenon by reducing sites that meet the requirements for survival (Gregory 1984). This phenomenon is quoted as being "undoubtedly the main cause of communal overwintering" (Gregory 1984) and although many studies reference this theory (Prior and Weatherhead 1996; Harvey and Weatherhead 2006; Gardiner and Sonmor 2011; Gardiner et al. 2013; Bruckerhoff et al. 2021), few have tried to assess the availability of hibernacula (Prior and Weatherhead 1996; Harvey and Weatherhead 2006; Williams et al. 2014; K.E. Williams et al. 2015).

ARTIFICIAL HIBERNACULA

Given the apparent scarcity of natural denning sites, their destruction likely has a tremendous impact on snake populations. Such loss of viable denning sites can result from anthropogenic and natural factors (Gardiner & Sonmor 2011; Maida et al. 2017). For instance, a rockslide at a talus slope hibernaculum in Osoyoos, British Columbia, was reported to have killed at least ten Western Rattlesnakes (Maida et al. 2017). Further, the slumping of an earthen hibernaculum in Grasslands National Park was suspected of killing at least 50% of the Eastern Yellow-bellied Racers (*Colubar constrictor flaviventris*) that overwintered at this site (Gardiner and Sonmor 2011; Dyer et al. 2016b). Besides natural disasters, habitat loss can result from anthropogenic development (Zappalorti et al. 2014; COSEWIC 2015a; Golder Associates Ltd 2022). One proposed conservation or mitigation measure to combat this loss is the construction of artificial hibernacula (Zappalorti and Reinert 1994; Zappalorti et al. 2014).

Artificial hibernacula are anthropogenic features intentionally or incidentally created (i.e. human-created slopes, construction debris, abandoned mine features, etc.) (Costanzo 1986; Ravesi et al. 2015; K.E. Williams et al. 2015; Bruckerhoff et al. 2021; Choquette et al. 2024). The former generally are used for research, conservation, or mitigation (Gillingham and Carpenter 1978; Zappalorti and Reinert 1994; Todd et al. 2009; Whiting and Booth 2012; Bryan 2015; Choquette et al. 2024). Previous research on artificial hibernacula suggests this approach has merit. For example, Zappalorti and Reinert (1994) found that 68% of overwintering refugia installed along sewer and electric line right-of-ways in New Jersey were used by nine snake species at the end of their 3-year study. Another study found that the occupancy rate of artificial hibernacula was similar to natural counterparts, however, natural hibernacula were mainly selected by pine snakes (*Pituophis m. melanoleucus*) in the New Jersey Pine Barrens (Zappalorti et al. 2014). More detailed research on incidental and experimental artificial hibernacula indicates the potential of these sites to provide optimal microclimatic conditions overwinter (Costanzo 1986; Choquette et al. 2024). However, little published research has examined artificial hibernacula built as a mitigation response to human-caused disturbance, an area of study that will only become more pertinent as habitat loss continues (Bruckerhoff et al. 2021). With the extreme winters of northern latitudes, this importance increases further due to the potentially limited availability of thermally-secure hibernacula.

STUDY ANIMALS

My three study species were the Great Basin Gophersnake, Western Yellow-bellied Racer, and Western Rattlesnake (Figure 1.1). As of 2024, each species is nationally listed under the Species at Risk Act as threatened (COSEWIC 2013, 2015a, b) and provincially blue-listed within British Columbia (BCCDC 2008, 2010, 2013). Threats to these species include road mortality, direct or indirect persecution, agriculture, and habitat loss (COSEWIC 2013, 2015a, b).

The largest snake in British Columbia, the Great Basin Gophersnake (Family Colubridae), is an oviparous constrictor that preys upon small mammals and birds (Shewchuk 1996; White 2008). The Western Yellow-bellied Racer (also Family Colubridae), is a medium-sized oviparous snake with a long yet slender body, aptly named “racer” for its fast movements (COSEWIC 2015b). This snake preys upon invertebrates and small animals and is suspected of feeding primarily on grasshoppers (Sarell 2004a; Hall and Cavitt 2011). Compared to the aforementioned two species, the northern populations of Western Rattlesnake (Family Viperidae) have arguably garnered the most research (Macartney et al. 1987; Gomez et al. 2007; Lomas et al. 2015; Harvey and Larsen 2020; Schmidt et al. 2020;

Howarth et al. 2023, etc.). This snake is viviparous and generally preys upon rodent species (COSEWIC 2015a).

All three species meet their northern extent in the southern interior of British Columbia (COSEWIC 2013, 2015a,b) and occur coincidently over most of this range (Matsuda et al. 2006). Within this range, these species can be found within shrub-steppe, grassland, and rocky areas, utilizing microhabitats such as shrubs, rocks, rodent burrows, talus slopes, and rocky outcrops (Shewchuk 1996; Bertram et al. 2001; Sarell 2004a; White 2008; COSEWIC 2015a,b). These species are active on this landscape from March to October, following their emergence from hibernacula (egress, March to May) (pers. observ.). During the active season, gophersnakes and racers mate in May after leaving hibernacula (Shewchuk 1996; Sarell 2004a; White 2008; COSEWIC 2013), whereas rattlesnakes mate in late summer (Sarell 2004b). Following the active season, these snakes return to hibernacula (ingress) from August to October and overwinter from roughly October to March (pers. observ.).

Western Rattlesnake hibernacula are well documented within British Columbia, with over 380 known hibernacula (COSEWIC 2015a). They are known to communally den within rocky outcrops and talus slopes (Macartney 1985; Macartney and Gregory 1988; Bertram et al. 2001; Gienger and Beck 2011), while gophersnakes and racers overwinter in deep talus, animal burrows and rock outcrops both communally or solitary (Haney and Sarell 2005; COSEWIC 2015b). All three species also have been known to share hibernacula (COSEWIC 2013; K.E. Williams et al. 2015). Rattlesnakes and racers display fidelity to their overwintering sites (Brown and Parker 1976; Macartney 1985; COSEWIC 2015b), however, previous studies on gophersnakes have shown variation across regions for site fidelity within the Okanagan (K.E. Williams et al. 2015). Through “Wildlife Habitat Areas” (WHAs), the communal hibernacula of all three of these species can be protected in British Columbia (COSEWIC 2015b; Dyer et al. 2016a,b). Typically, WHAs are small, protected areas around sensitive habitats for species at-risk: for communal snake hibernacula, WHAs extend 200-300 ha around hibernacula (MWLAP 2004; Williams et al. 2012).

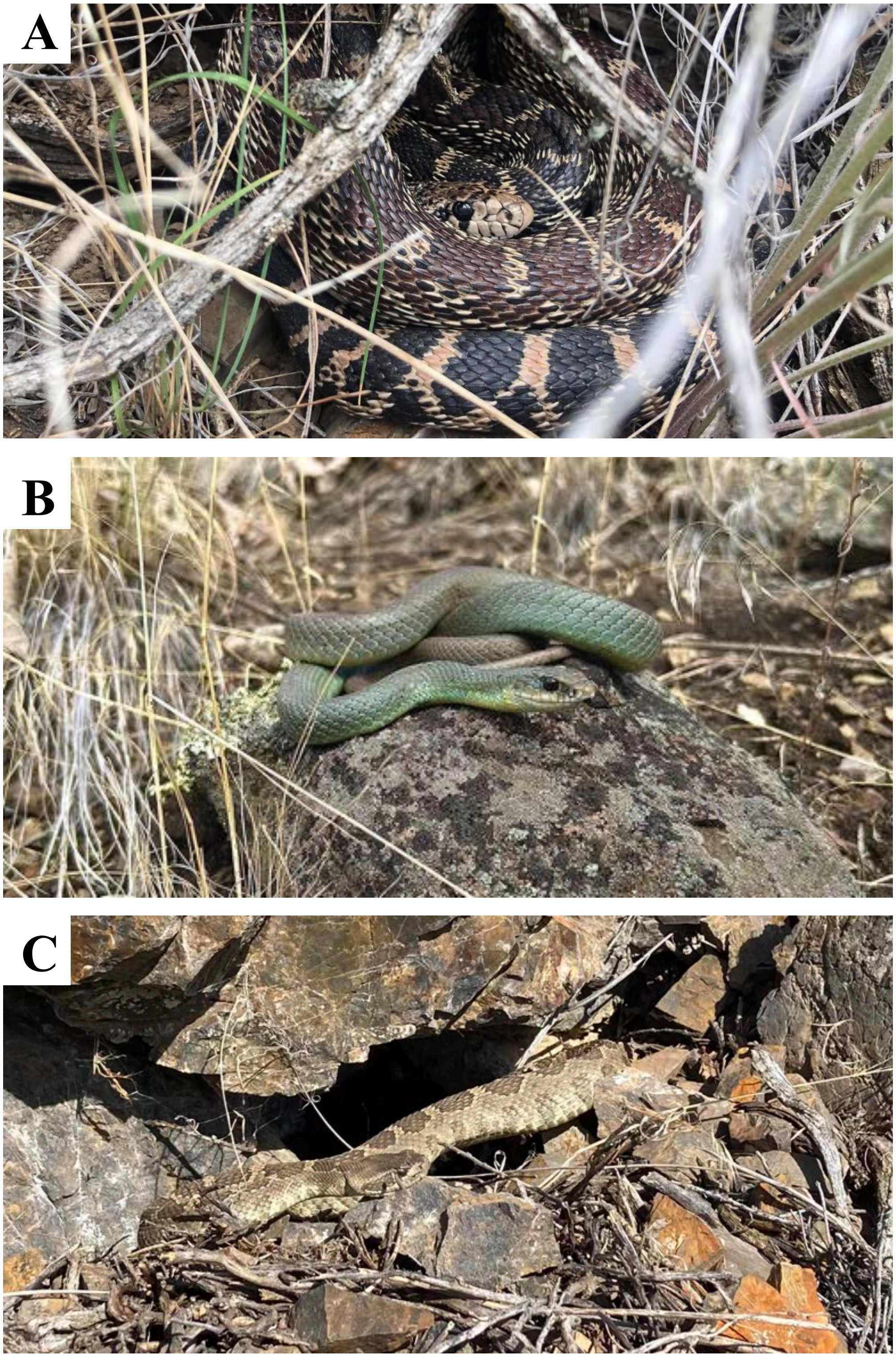


Figure 1.1: The three study species: A) Great Basin Gophersnake (*Pituophis catenifer deserticola*), B) Western Yellow-bellied Racer (*Coluber constrictor mormon)*, and C) Western Rattlesnake (*Crotalus oreganus oreganus*). Photos by author.

STUDY SITE

My primary study area lied within the Lac du Bois Grasslands Protected Area (51° N, 120.4° W) on the north-western side of the city of Kamloops, British Columbia, Canada (Figure 1.2) (GCC 2009; BC Parks 2017). This extensive grassland encompasses approximately 15,712 ha within the Thompson-Okanagan Ecoregion, supporting a variety of resident and migratory species, including at least 17 considered at risk, three of which are my study animals (BC Parks 2017). This ecoregion is known for having some of the hottest and driest climates within British Columbia (BC Parks 2017). See Figures 1.3 and 1.4 for representative average monthly temperature and precipitation during our study compared to a 30-year average (1991-2020). During my study period's winters, mean monthly temperatures during December 2021 and 2022 dropped to as low as -30°C, lower than the 30-year norm (Figure 1.3) (ECCC 2023).

Although the second largest protected grassland in British Columbia, Lac du Bois is isolated from further grassland habitats to the south and east (BC Parks 2017). This isolation is, in part, the result of residential and commercial development that borders the park (Figure 1.5). Due to the proximity, Lac du Bois offers easily accessible recreational activities to the over 98,000 residents of Kamloops in the form of biking, hiking, camping, hunting, fishing, off-roading, and horseback riding (BC Parks 2017). This site also is used for cow grazing, divided into two primary pastures that undergo grazing in a rotating three-year schedule (GCC 2009). In addition to these activities, this site is heavily fragmented by trails, off-roading tracks, barbed wire fencing, access roads, and, more recently, a pipeline right of way.

The study site is roughly 1100ha at the southeastern corner of the park (Figure 1.2) (BC Parks 2017), primarily comprised of lower and middle grassland dominated by Big Sagebrush (*Artemisia tridentata*), Bluebunch Wheatgrass (*Pseudoroegneria spicata*), and spring-blooming plants (GCC 2009; BC Parks 2017). Other habitats include upper grasslands, dry forests, rocky outcrops, talus slopes, ponds, wetlands, and lakes (BC Parks, 2017). This landscape affords the snakes environmental features important to their life histories (i.e., hibernacula, basking sites, refuges, egg-laying sites, shedding sites, and rookeries) (Figure 1.6).

Prior to my study, research on snakes within Lac du Bois had been restricted to only a few studies. Bertram et al. (2001) conducted a radiotracking study on gophersnakes and rattlesnakes, while Gomez (2007) focused on tracking rattlesnakes exclusively, both aiming to characterize habitat utilization and movement patterns within the area. Further, Hobbs (2007) studied the overwintering thermal conditions of rattlesnakes. From this past work, in addition to the present study, a total of 28 hibernacula have been identified in the study site within a variety of habitats (i.e., rocky outcrops, rodent burrows, holes under rocks, and blast rocks on the side of roads).

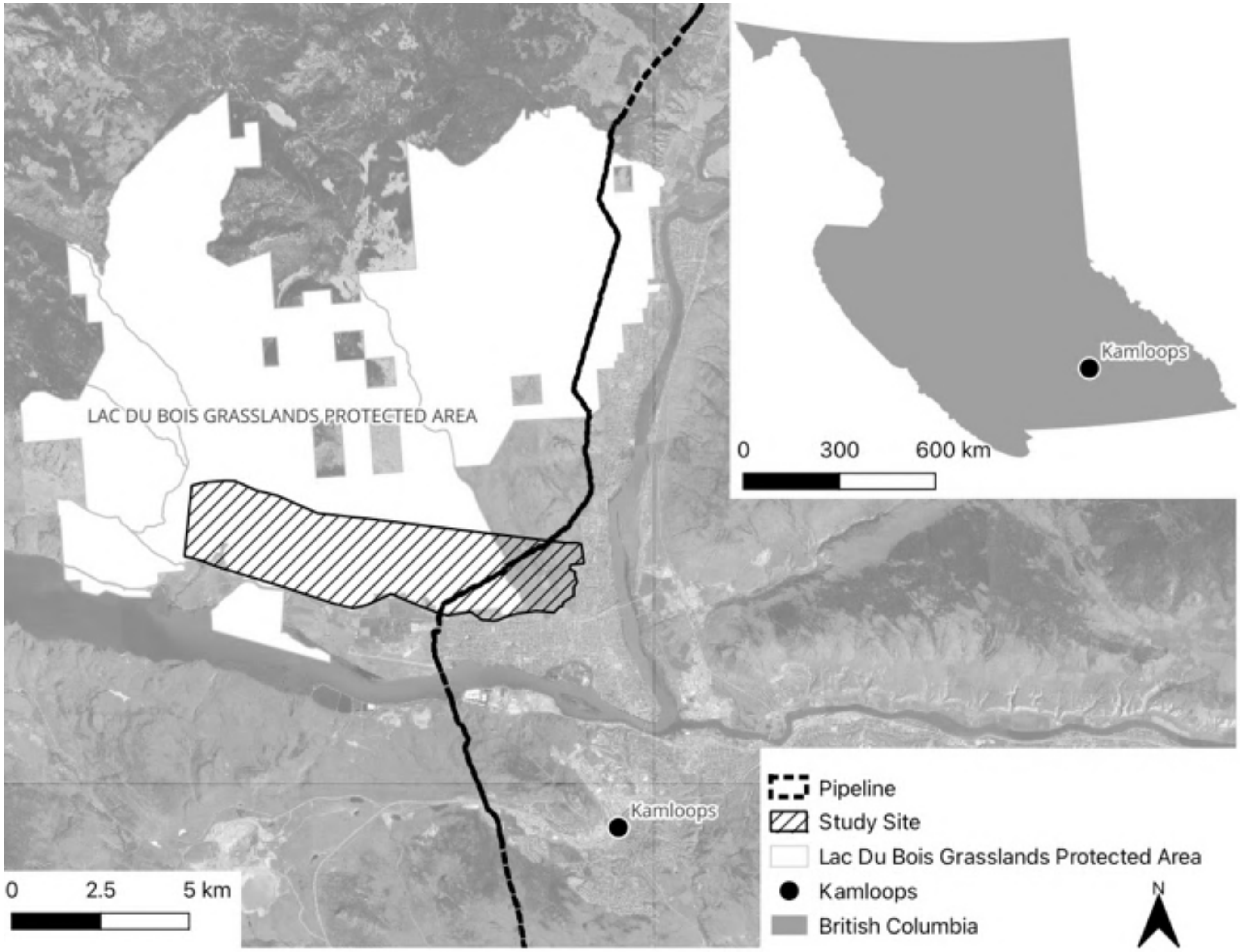


Figure 1.2: Location of the study site in the Lac du Bois Grasslands Protected Area, ~10 km from the City of Kamloops, BC (Google Earth 2023; GBC 2023). Also shown is the Trans Mountain Expansion Project (Pipeline).

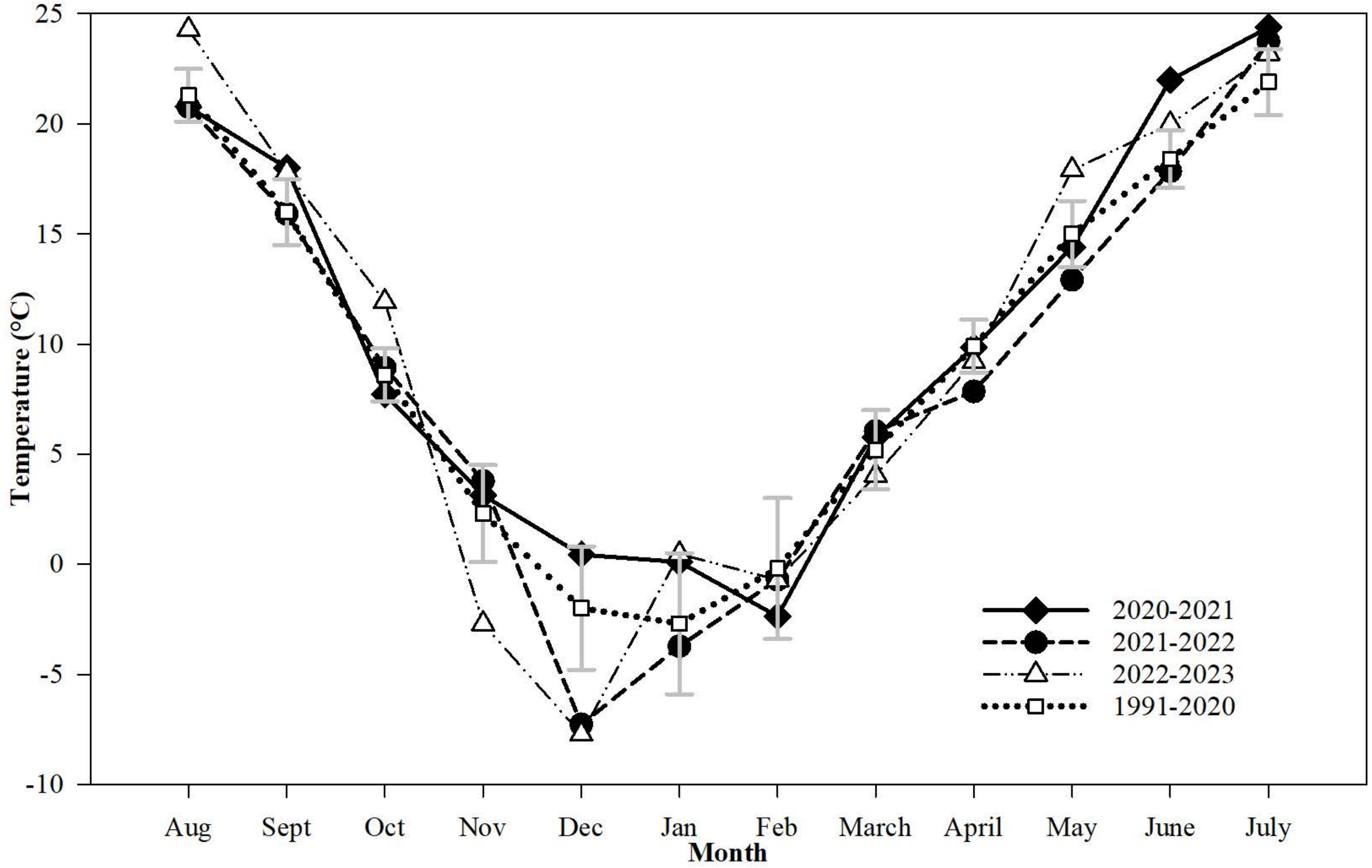


Figure 1.3: Mean monthly temperatures (°C) in Kamloops, British Columbia, from 2020-2023, compared to the historical 30-year mean (1991-2020). Data presented in order of ingress (August to October), the overwintering period (October-March), and egress (March-May). Values measured at the Kamloops A (50 ° N, 120 ° W) weather station (49° N, 119°W) (ECCC 2023). Standard error bars are present on the historical 30-year mean (1991-2020).

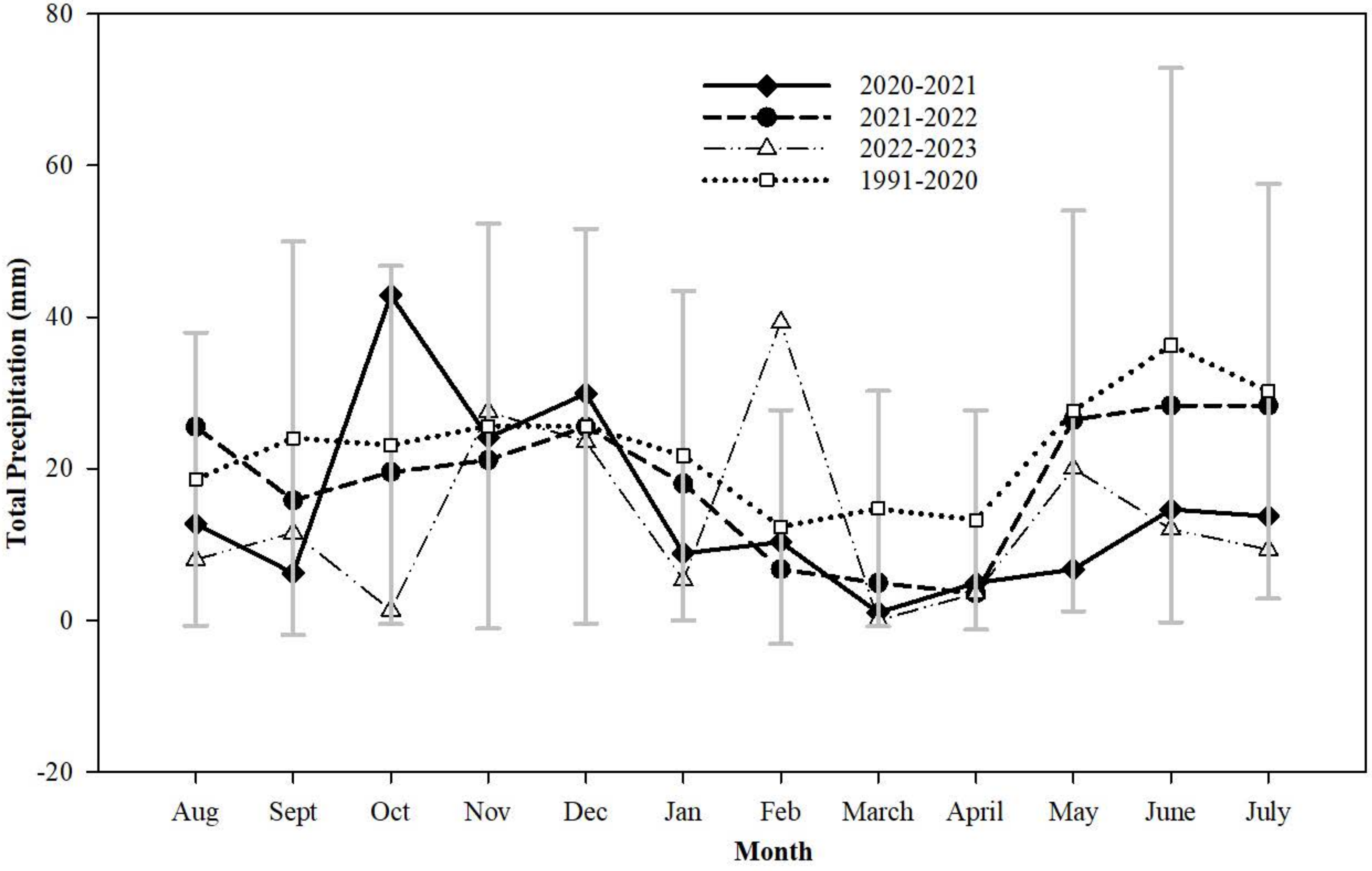


Figure 1.4: Total precipitation (mm) in Kamloops, British Columbia, during the study years (2020-2023) compared to the historical 30-year mean (1991-2020). Data presented in order of ingress (August to October), the overwintering period (October-March), and egress (March-May). Values measured at the Kamloops A (50 ° N, 120 ° W) weather station (49° N, 119°W) (ECCC 2023). Standard error bars are present on the historical 30-year mean (1991-2020).

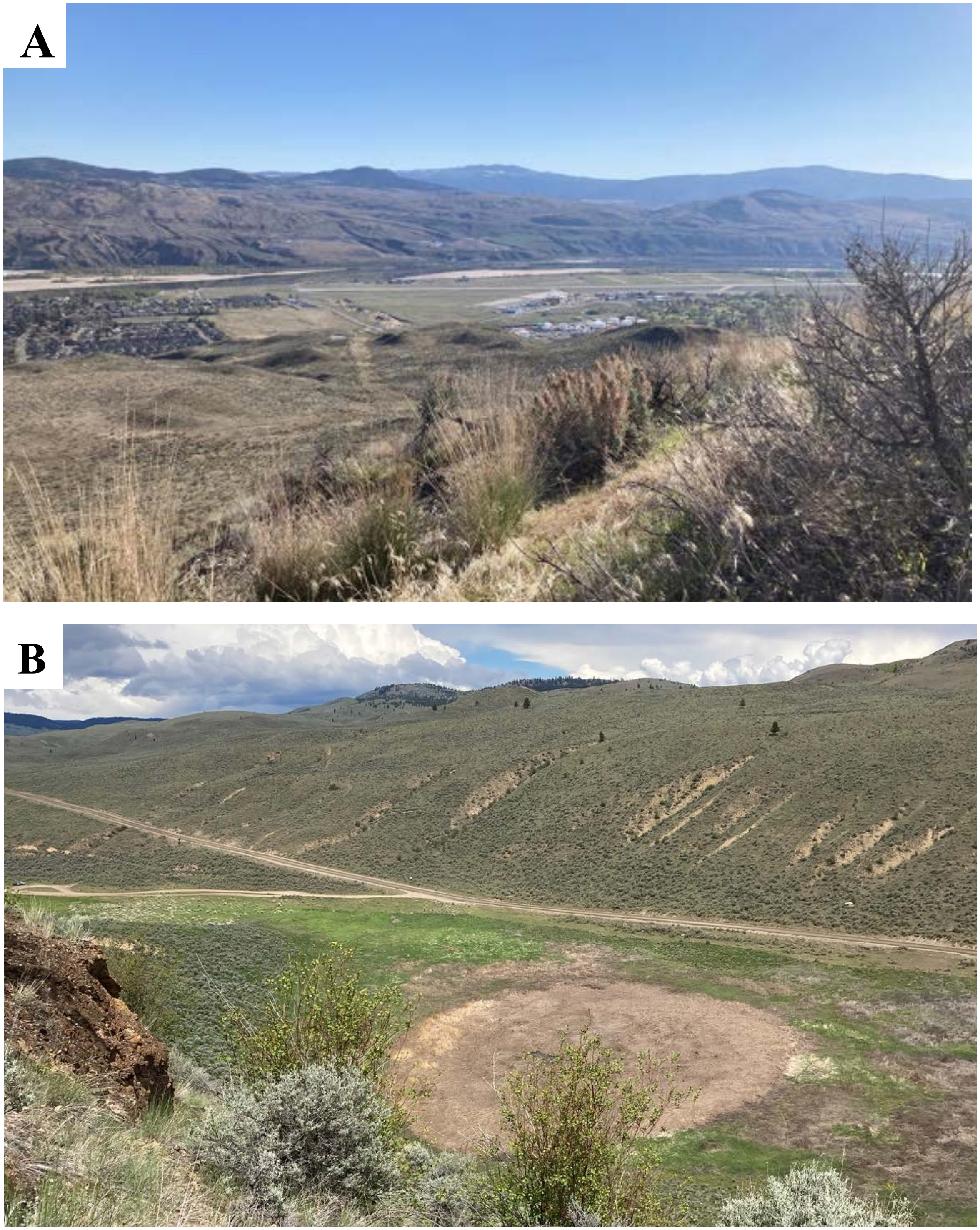


Figure 1.5: Representative photos of the study site in the Lac du Bois Grasslands Protected Area: A) Displays the south-western view of the site towards the development in Kamloops. B) Shows the north-eastern view of the site towards further park. Photos by author.

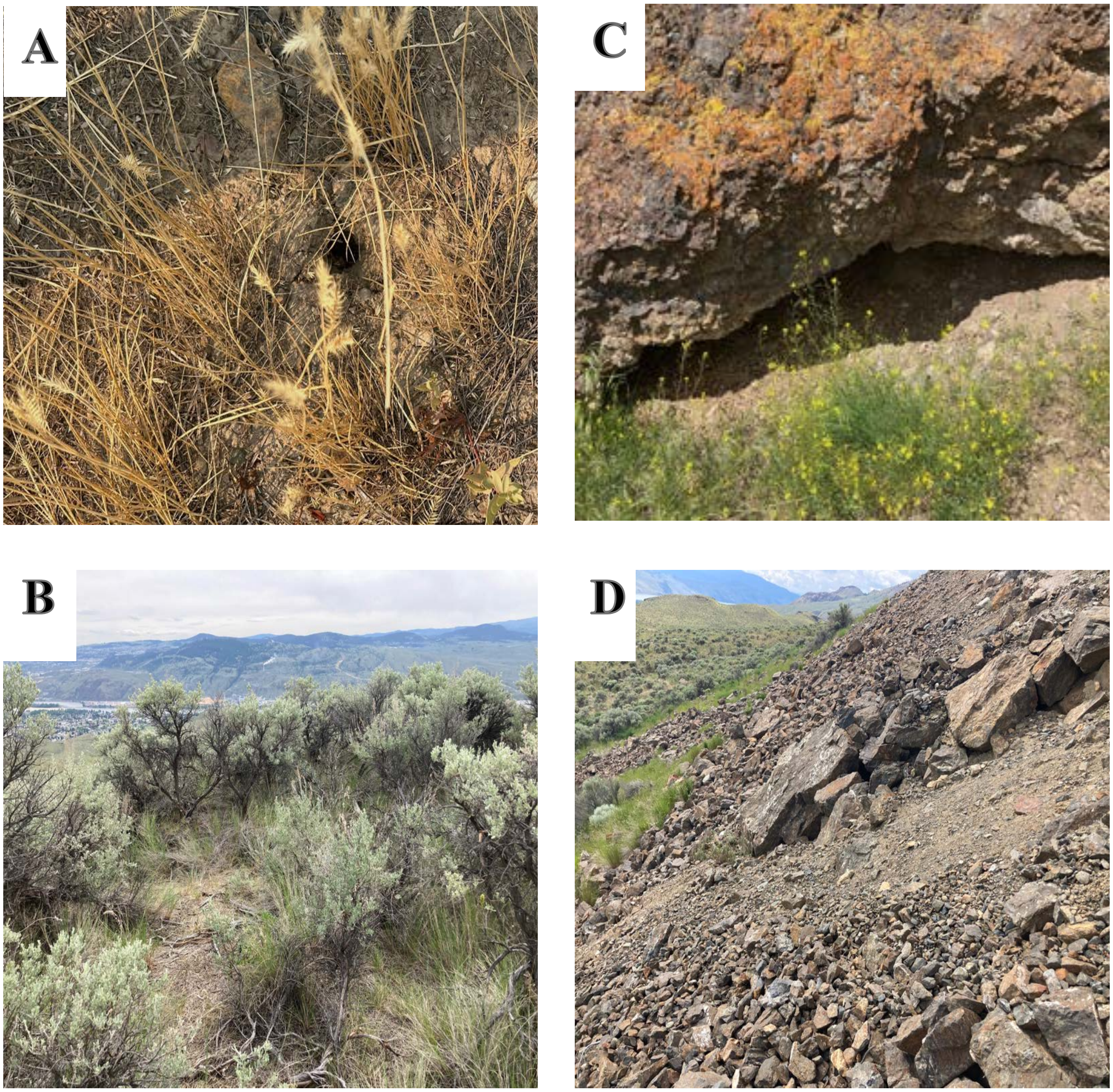


Figure 1.6: Representative microhabitats for the Great Basin Gophersnake, Western Rattlesnake, and Western Yellow-bellied Racer in Kamloops, British Columbia, Canada, including: A) Rodent burrows, B) Lower grassland, C) Rocky outcrops and D) Talus slopes. Photos by author.

DISTURBANCE EVENT

The Trans Mountain Expansion Project (TMEP) was initiated to increase the transportation of crude oil by twinning an existing pipeline built in 1951, running from Edmonton, Alberta, to Burnaby, British Columbia (GC 2022; Trans Mountain 2023a,b). This project commenced construction within Kamloops in June 2020 (Trans Mountain 2021c). Within Lac du Bois, the TMEP pipeline right-of-way disturbance stretched 9.2 km and was, on average, 30 m wide during construction (Figure 1.2, 1.7) (Trans Mountain Pipeline ULC 2017).

Before construction, TMEP was obligated by the Ministry of Forests, Lands, and Natural Resource Operations to obtain required provincial permits and conduct a snake inventory on the site (Heinrich 2020). From September 21, 2020, to October 16, 2020, habitat assessments, reptile sweeps, and snake salvages were performed (Heinrich 2020). During this timeframe, three communal snake hibernacula were excavated during construction along the pipeline right of way within a 1.6 km straight-line distance (Heinrich 2020). The snakes salvaged from this disturbance included 51 gophersnakes, 71 racers, and 10 rattlesnakes (Table 1.1) (Heinrich 2020). Snakes retrieved before October 15 (10 rattlesnakes, 12 gophersnakes, and 13 racers) were moved to three natural hibernacula in the area and were not marked for future identification as it is not a regulatory requirement (Table 1.1) (Heinrich 2020), a situation that later on complicated my work. Snakes recovered after October 15 (including 37 gophersnakes and 56 racers) were transferred to the BC Wildlife Park for artificial overwintering and were implanted with Passive Integrated Transponders (PIT tags) to permit individual identification (Table 1.1) (Heinrich 2020).

Two artificial hibernacula were constructed between April and May 2021 to replace the lost natural sites. The first artificial snake hibernacula (ASH1) was completed in late April 2021, and all snakes artificially overwintered were released here between April 31 and May 3, 2021 regardless of their point of origin. This release strategy was necessary as the second artificial snake hibernacula (ASH2) remained incomplete until after the natural emergence period for snakes in the region.

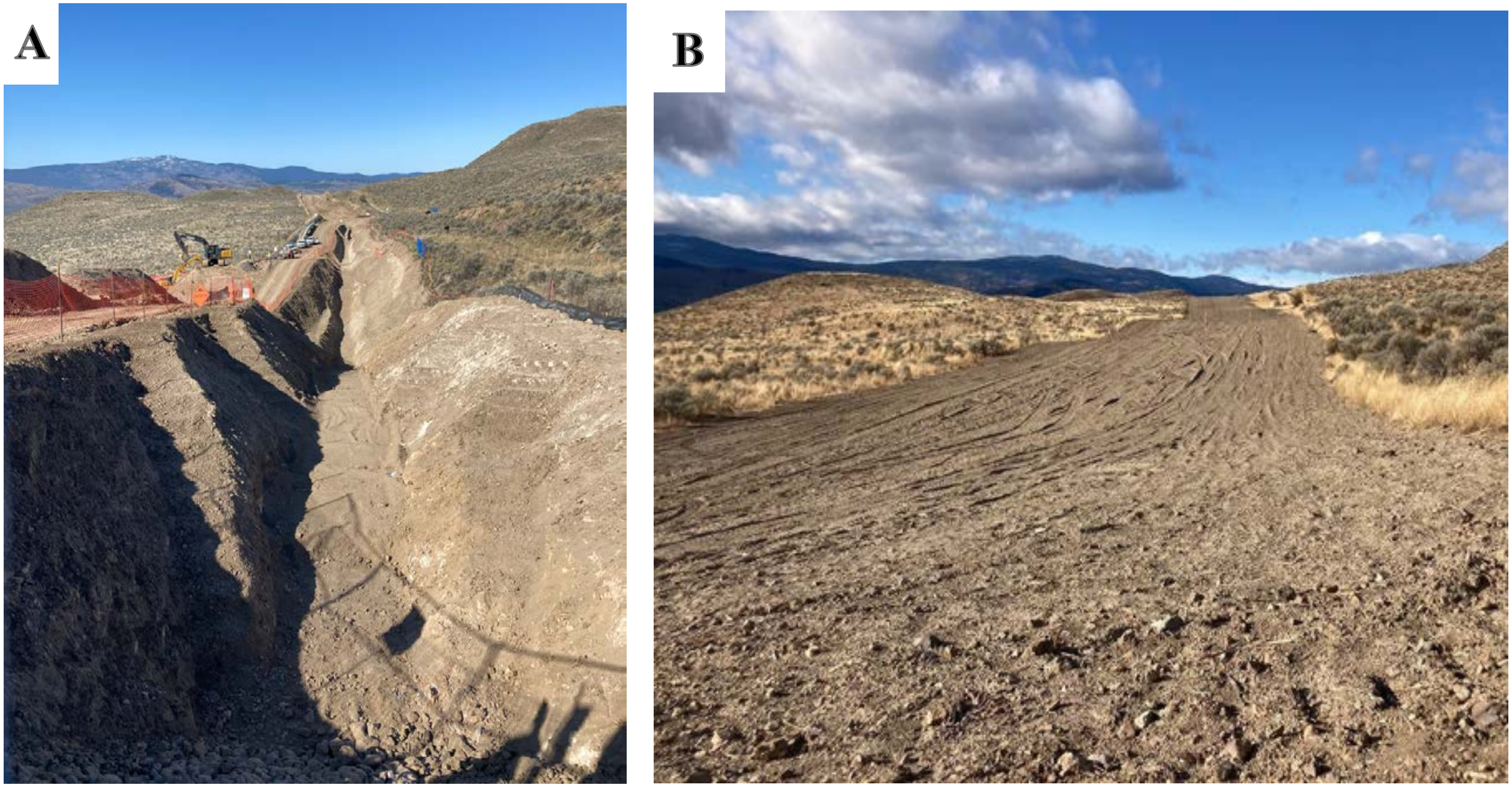


Figure 1.7: Pipeline construction within the Lac du Bois Grasslands Protected Area, Kamloops, British Columbia. A) Displays active excavation for pipeline placement. B) Displays the landscape just after construction and seeding. Photos by author.

Table 1.1: The salvage summary for snakes retrieved from three excavated hibernacula between September 21, 2020, to October 16, 2020 (Heinrich 2020). Snakes were either released at natural hibernacula, moved to the BC Wildlife Park for artificial overwintering, or died.

Hibernaculum	Species	Released	BC Wildlife Park	Died
1	Western Rattlesnake	10	0	0
	Great Basin Gophersnake	10	20	0
	Western Yellow-bellied Racer	13	44	2
2	Western Rattlesnake	0	0	0
	Great Basin Gophersnake	1	5	1
	Western Yellow-bellied Racer	0	1	0
3	Western Rattlesnake	0	0	0
	Great Basin Gophersnake	1	12	1
	Western Yellow-bellied Racer	0	11	0

THESIS OBJECTIVES

Given the significance of snake hibernacula and their apparent scarcity, it is crucial to properly protect and avoid disturbance of these critical habitat features. Understanding the habitat selection of a species or multiple species utilizing hibernacula in a given community may help elucidate where to protect these sites. If disturbance cannot be avoided, ensuring the efficacy of artificial hibernacula used as mitigation is crucial. In this thesis, I use the community of three sympatric snake species, Great Basin Gophersnake, Western Yellow-bellied Racer, and Western Rattlesnake, following the outlined disturbance event to pursue the following objectives:

In Chapter 2, I explore the variation in hibernacula habitat use between the three snake species by collecting habitat features at documented hibernacula and analyzing data using a match case-control design. My objectives in this chapter were to:

a. Document hibernacula and their species assemblages on our study site.
b. Investigate how the habitat features relate to the degree of communal occupation present at hibernacula.
c. Explore how these three species vary in their selection of overwintering habitat.

In Chapter 3, I studied the efficacy of the newly built artificial hibernacula following the disturbance event. To do so, I collected the internal temperature and humidity of two artificial hibernacula and the internal temperatures of snakes via remote data loggers. My objectives in this chapter were to:

d. Highlight the available microclimate within each hibernaculum and assess how well they buffer against external environmental conditions.
e. Determine whether the internal thermal conditions of the artificial hibernacula are comparable to those naturally experienced by snakes.
f. Monitor the adoption of the main artificial hibernaculum by the original cohort of displaced snakes.

In the final Chapter (Ch. 4), I revisit the key findings of the previous chapters and contextualize them within the realm of conservation, biology, management and the need for future research.

LITERATURE CITED

Baccante D, Woods R. 2010. Relationship between winter severity and survival of mule deer fawns in the Peace Region of British Columbia. BC JEM. 10(3):145-153.

[BCCDC] B.C. Conservation Data Centre. 2008. Species summary: *Pituophis catenifer deserticola*. BC Ministry of Environment; [accessed 2024 Feb 2]. https://a100.gov.bc.ca/pub/eswp/

[BCCDC] B.C. Conservation Data Centre. 2010. Species summary: *Coluber constrictor*. BC Ministry of Environment; [accessed 2024 Feb 2]. https://a100.gov.bc.ca/pub/eswp/.

[BCCDC] B.C. Conservation Data Centre. 2013. Species summary: *Crotalus oreganus*. BC Ministry of Environment; [accessed 2024 Feb 2]. https://a100.gov.bc.ca/pub/eswp/.

BC Parks. 2017. Lac du Bois Grasslands Protected Area management plan. Kamloops.

Bertram N, Larsen KW, Surgenor J. 2001. Identification of critical habitats and conservation issues for the Western Rattlesnake and Great Basin Gopher Snake within the Thompson-Nicola region of British Columbia. Kamloops.

Brown WS, Parker WS, Elder JA. 1974. Thermal and spatial relationships of two species of Colubrid snakes during hibernation. Herpetol. 30(1):32–38.

Brown WS, Parker WS. 1976. Movement Ecology of *Coluber constrictor* near communal hibernacula. Copeia. 225-42.

Bruckerhoff LA, Kamees LK, Holycross AT, Painter CW. 2021. Patterns of survival of a communally overwintering rattlesnake using an artificial hibernaculum. Ichthyol Herpetol. 109(1):64–74.

Bryan DL. 2015.Survival and natural history of the Timber Rattlesnake (*Crotalus Horridus*) at Center Hill Lake in Dekalb County, Tennessee [thesis]. [Cookville (TN)]: Tennessee Technolgical University.

Choquette JD, Mokdad AI, Pitcher TE, Litzgus JD. 2024. Selection and validation of release sites for conservation translocations of temperate-zone snakes. MethodsX. 12:1-11

COSEWIC. 2013. COSEWIC assessment and status report on the Great Basin Gopersnake *Pituophis catenifer deserticola in* Canada. Ottawa.

COSEWIC. 2015a. COSEWIC assessment and status report on the Western Rattlesnake *Crotalus oreganus* in Canada. Ottawa.

COSEWIC. 2015b. COSEWIC assessment and status report on the Eastern Yellow-bellied Racer *Coluber constrictor flaviventris* and the Western Yellow-bellied Racer *Coluber constrictor mormon* in Canada. Ottawa.

Costanzo JP. 1986. Influences of hibernaculum microenvironment on the winter life history of the garter snake (*Thamnophis sirtalis*). OJS. 86(5):199–204.

Costanzo JP. 1989. Effects of humidity, temperature, and submergence behavior on survivorship and energy use in hibernating garter snakes, *Thamnophis sirtalis*. Can J Zool. 67:2486–2492.

Costanzo JP, Lee RE, Dcvries AL, Wang T, Layne JR. 1995. Survival mechanisms of vertebrate ectotherms at subfreezing temperatures: applications in cryomedicine. FASEB J. 9(5):295–459.

Costanzo JP, Lee RE. 2013. Avoidance and tolerance of freezing in ectothermic vertebrates. J Exp Biol. 216(11):1961–1967.

Dyer O, Bishop C, Govindarajulu P, Anderson L, Cunnington D, Hobbs J, Huntley M, Larsen K, Reudink R, Sadler K, Sarell M, Steciw J, et al. 2016a. British Columbia recovery strategy series recovery plan for the Gopher Snake, deserticola subspecies (*Pituophis catenifer deserticola*) in British Columbia.

Dyer O, Bishop C, Govindarajulu P, Anderson L, Cunnington D, Hobbs J, Huntley M, Larsen K, Reudink R, Sadler K, Sarell M, Tedesco L, et al. 2016b. British Columbia recovery strategy series recovery plan for the Western Rattlesnake (*Crotalus oreganus*) in British Columbia.

[ECCC] Environment and Climate Change Canada. 2023. Historical climate data; [accessed 2023 Jul 18]. http://climate.weather.gc.ca/.

Gardiner LE, Sonmor KW. 2011. Reptiles major slump event at grasslands national park snake pit in southwestern Saskatchewan. Blue Jay. 69(3):120–124.

[GCC] The Grasslands Conservation Council of British Columbia. 2009. Working together for the conservation of BC’s grasslands. Kamloops.

Gienger CM, Beck DD. 2011. Northern Pacific Rattlesnakes (*Crotalus oreganus*) use thermal and structural cues to choose overwintering hibernacula. Can J Zool. 89(11):1084–1090.

Gillingham JC, Carpenter CC. 1978. Snake hibernation: construction of and observations on a man-made hibernaculum (Reptilia, Serpentes). J Herpetol. 12(4):495–498.

Golder Associates Ltd. 2022. Site C Wildlife Mitigation Structures Snake Hibernacula Monitoring 2021. Nanaimo.

Gomez LM. Habitat use and movement patterns of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) in British Columbia [thesis]. [Victoria (BC)]: University of Victoria.

Google Earth. 2023. Google Earth; [accessed 2024 Mar 2]. https://www.google.com/earth/index.html.

[GBC] Government of British Columbia. 2023. B.C. Conservation data centre; [accessed 2023 Jul 19]. https://www2.gov.bc.ca/gov/content/environment/plants-animals-ecosystems/conservation-data-centre.

[GC] Government of Canada. 2022. What is the Trans Mountain Expansion Project?; [accessed 2023 Nov 9]. https://www.canada.ca/en/campaign/trans-mountain/what-is-tmx.html.

Gregory PT. 1973. Life history parameters of a population of Red-Sided Garter Snakes *(Thamnophis sirtalis parietalis)* adapted to a rigorous and fluctuating environment [thesis]. [Winnipeg (MB)]: University of Manitoba.

Gregory PT. 1974. Patterns of spring emergence of the Red-sided Garter Snake (*Thamnophis sirtalis parietalis*) in the Interlake region of Manitoba. Can J Zool. 52:1063–1069.

Gregory PT. 1977. Life-history parameters of the Red-sided Garter Snake (*Thamnophis Sirtalis Parietalis*) in an extreme environment, the Interlake Region of Manitoba. Ottawa (ON): National Museums of Canada.

Gregory P. 1982. Reptillian hibernation. In: Gans C, Pough FH, editors. Biology of the Reptillia. Vol. 13. New York (USA): Academic Press. p. 53–154.

Gregory PT. 1984. Communal denning in snakes. In: Seigel R, Hunt L, Knight J, Malaret L, Zuschlag N, editors. Vertebrate Ecology and Systematic A Tribute to Henry S. Fitch. Lawrence: University of Kansas Publications. p. 57-76.

Gregory PT. 2009. Northern lights and seasonal sex: the reproductive ecology of cool-climate snakes. Herpetol. 65(1):1–13.

Hall LK, Cavitt J. 2011. *Coluber constrictor mormon* (Western Yellow-bellied Racer) and *Pituophis catenifer deserticola* (Great Basin Gopher Snake). Herpetol Rev. 42(2).

Haney A, Sarell M. 2005. Conservation analysis for the Great Basin Gophersnake (*Pituophis catenifer deserticola*) in British Columbia.

Harvey JA, Larsen KW. 2020. Rattlesnake migrations and the implications of thermal landscapes. Mov Ecol. 8(1).

Hein AM, Guyer C. 2009. Body temperature of overwintering Cottonmouth snakes: hibernaculum use and inter-individual variation. J Ala Acad Sci. 80(1): 35-44.

Heinrich R. 2020. Technical memorandum. Kamloops (BC): Triton Environmental Consultants.

Hobbs J. 2007. Thermal factors in relation to the denning ecology of northern Pacific rattlesnakes in British Columbia [thesis]. [Victoria (BC)]: Royal Roads University.

Hoekstra LA, Schwartz TS, Sparkman AM, Miller DAW, Bronikowski AM. 2020. The untapped potential of reptile biodiversity for understanding how and why animals age. Funct Ecol. 34(1):38–54.

Holden KG, Gangloff EJ, Gomez-Mancillas E, Hagerty K, Bronikowski AM. 2021. Surviving winter: physiological regulation of energy balance in a temperate ectotherm entering and exiting brumation. Gen Comp Endocrinol. 307: 1-10.

Howarth, Bishop CA, Larsen KW. 2023. Western Rattlesnake (*Crotalus oreganus*) spring migration in British Columbia: a comparative study of juveniles and adults. Can J Zool. 101(7): 530-540.

Lisovski S, Ramenofsky M, Wingfield JC. 2017. Defining the degree of seasonality and its significance for future research. Integr Comp Biol. 57(5):934–942.

Lomas E, Larsen KW, Bishop CA. 2015. Persistence of Northern Pacific Rattlesnakes masks the impact of human disturbance on weight and body condition. Anim Conserv. 18(6):548–556.

Macartney J. 1985. The ecology of the Northern Pacific Rattlesnake, *Crotalus viridis oreganus*, in British Columbia [thesis]. [Victoria (BC)]: University of Victoria.

Macartney JM, Larsen KW, Gregory PT. 1987. Body temperatures and movements of hibernating snakes (*Crotalus* and *Thamnophis*) and thermal gradients of natural hibernacula. Can J Zool. 67:108–114.

Macartney JM, Gregory PT. 1988. Reproductive biology of female rattlesnakes (Crotalus viridis) in British Columbia. Copeia. 5(1):47–57.

Maida J, Larsen K, Hooper C, Bishop C. 2017. *Crotalus oreganus* (Western Rattlesnake) Mortality. Herpetol Rev. 48(2):447.

Markle CE, Moore PA, Waddington JM. 2020. Temporal variability of overwintering conditions for a species-at-risk snake: Implications for climate change and habitat management. Glob Ecol Conserv. 22: 1-9.

Matsuda BM, Green DM, Gregory PT. 2006. Amphibians and reptiles of British Columbia. Victoria: Royal BC Museum.

Michels-Boyce M, Zani PA. 2015. Lack of supercooling evolution related to winter severity in a lizard. J Therm Biol. 53:72–79.

[MWLAP] Ministry of Water Land and Air Protection. 2004. Identified wildlife management strategy accounts and measures for managing identified wildlife southern interior forest region.

Moss JB, MacLeod KJ. 2022. A quantitative synthesis of and predictive framework for studying winter warming effects in reptiles. Oecologia. 200(1–2):259–271.

Nelson RJ, Badura LL, Goldman BD. 1990. Mechanisms of seasonal cycles of behavior. Annu Rev Psychol. 41(1):81–108.

Parker WS, Brown WS. 1973. Species composition and population changes in two complexes of snake hibernacula in northern Utah. Herpetol. 29(4):319–326.

Prior KA, Blouin-Demers G, Weatherhead PJ. 2001. Sampling biases in demographic analyses of Black Rat Snakes (*Elaphe obsoleta*). Herpetol. 57(4):460–469.

Prior KA, Weatherhead PJ. 1996. Habitat features of Black Rat Snake hibernacula in Ontario. J Herpetol. 30(2):211–218.

Ravesi M, Tetzlaff SJ, Kingsbury B. 2015. *Sistrurus catenatus* (Massasauga) overwintering Site. Herpet Rev. 46(3):454.

Sarell M. 2004a. Racer. Victoria: Ministry of Water, Land and Air Protection; [accessed 2024 Mar 2]. https://www.env.gov.bc.ca/wld/frpa/iwms/accounts.html

Sarell M. 2004b. Western Rattlesnake. Victoria: Ministry of Water, Land and Air Protection; [accessed 2024 Mar 2]. https://www.env.gov.bc.ca/wld/frpa/iwms/accounts.html

Schmidt DA, Govindarajulu P, Larsen KW, Russello MA. 2020. Genotyping-in-thousands by sequencing reveals marked population structure in Western Rattlesnakes to inform conservation status. Ecol Evol. 10(14):7157–7172.

Shewchuk CH. 1996. The natural history of reproduction and movement patterns in the Gopher Snake (*Pituophis melanoleucus*) in southern British Columbia [thesis]. [Victoria (BC)]: University of Victoria.

Shine R, Mason RT. 2004. Patterns of mortality in a cold-climate population of garter snakes (*Thamnophis sirtalis parietalis*). Biol Conserv. 120(2):201–210.

Storey KB, Storey JM. 1988. Freeze tolerance in animals. Physiol Rev. 68(1):27–84.

Storey KB, Storey JM. 1996. Natural freezing survival in animals. Annu Rev Ecol Syst. 27:365–386.

Todd J, Amiel J, Wassersug R. 2009. Factors influencing the emergence of a northern population of Eastern Ribbon Snakes (*Thamnophis sauritus*) from artificial hibernacula. Can J Zool.

Trans Mountain. 2021. Time flies: one year of construction in the Kamloops urban area; [accessed 2024 Feb 3]. https://www.transmountain.com/news/2021/time-flies-one-year-of-construction-in-the-kamloops-urban-area#:~:text=What%20a%20year%20it%20has,the%20Trans%20Mountain%20Expansion%20Project.

Trans Mountain. 2023a. Expansion project. [accessed 2024 Mar 24]. https://www.transmountain.com/project-overview.

Trans Mountain. 2023b. Our history. [accessed 2024 Mar 24]. https://www.transmountain.com/history.

Trans Mountain Pipeline ULC. 2017. Lac du Bois Grasslands Protected Area reclamation plan for the Trans Mountain pipeline ULC Trans Mountain Expansion Project. Calgary (AB): Kinder Morgan Canada Inc.

Tsuji JS. 1988. Thermal acclimation of metabolism in sceloporus lizards from different latitudes. Physiol Zool. 3:241–253.

Ultsch GR. 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. Biol Rev. 64:435–516.

Voituron Y, Mouquet N, De Mazancourt C, Clobert J. 2002. To freeze or not to freeze? An evolutionary perspective on the cold-hardiness strategies of overwintering ectotherms. Am Nat. 160(2): 255-270.

White FN, Lasiewski RC. 1971. Rattlesnake denning: theoretical considerations on winter temperatures. J Theor Biol. 30:553–557.

White KE. 2008. Spatial ecology and life history of the Great Basin Gophersnakes (*Pituophis catenifer deserticola*) in British Columbia’s Okanagan Valley [thesis]. [Kelowna (BC)]: University of British Columbia.

White KS, Pendleton GW, Crowley D, Griese HJ, Hundertmark KJ, McDonough T, Nichols L, Robus M, Smith CA, Schoen JW. 2011. Mountain goat survival in coastal Alaska: Effects of age, sex, and climate. J Wildl Manag. 75(8):1731–1744.

Whiting C, Booth HJ. 2012. *Adder Vipera berus* hibernacula construction as part of a mitigation scheme for flood defence works, Horsey Corner, Norfolk, England. Conser Evid. 9: 9-16.

Williams CM, Henry HAL, Sinclair BJ. 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. Biol Rev. 90(1):214–235.

Williams KE, Hodges KE, Bishop CA. 2012. Small reserves around hibernation sites may not adequately protect mobile snakes: the example of great basin gophersnakes (*Pituophis catenifer deserticola*) in British Columbia. Can J Zool. 90(3):304-312.

Williams KE, Hodges KE, Bishop CA. 2015. Hibernation and oviposition sites of Great Basin Gophersnakes (*Pituophis catenifer deserticola*) near their northern range Limit. J Herpetol. 49(2):207-216.

Williams CM, Ragland GJ, Betini G, Buckley LB, Cheviron ZA, Donohue K, Hereford J, Humphries MM, Lisovski S, Marshall KE, et al. 2017. Understanding evolutionary impacts of seasonality: an introduction to the symposium. Integr Comp Biol. 57(5):921–933.

Zachariassen KE. 1985. Physiological reviews physiology of cold tolerance in insects. APS. 65(4):799-832.

Zappalorti RT, Reinert H. 1994. Artificial refugia as a habitat improvement strategy for snake conservation. Contributions to Herpetology. 11:369–375.

Zappalorti RT, Burger J, Burkett DW, Schneider DW, McCort MP, Golden DM. 2014. Fidelity of northern pine snakes (*Pituophis m. melanoleucus*) to natural and artificial hibernation sites in the New Jersey Pine Barrens. J. Toxicol. Environ. Health - A: Curr. Issues. 77(21):1285–1291.

CHAPTER 2

AN INTRA- AND INTERSPECIFIC APPROACH TO IDENTIFYING AND PROTECTING CRITICAL OVERWINTERING HABITAT FOR SNAKES

INTRODUCTION

By definition, designated critical habitat represents those features on the landscape essential for the survival, recovery, persistence, and conservation of species-at-risk (Murphy and Noon 1991; Hall et al. 1997; Camaclang et al. 2015; GC 2023). In turn, determining where and why critical habitat features exist allows for a deeper understanding of the habitat requirements of these species (Mayor et al. 2009; Boyce et al. 2016; Northrup et al. 2022). These habitats may be broadly distributed over space and time or tied to specific spatial features or temporal periods (Mayor et al. 2009), such as migration, dispersal, reproduction, or overwintering (Krausman 1999; Goldberg et al. 2020).

Critical habitat for northern wildlife may include distinct features that enable survival through winter (Burger et al. 1988; Prior and Weatherhead 1996; Gienger and Beck 2011; Goldberg et al. 2020). This period of time is particularly stressful for animals as it reduces the availability of resources and potentially exposes them to thermal extremes, thus placing emphasis on the selection of habitat (Huey 1991; Krausman 1999; Mayor et al. 2009; Dubiner et al. 2023). Species may respond to winter with migration (Winger et al. 2019), morphological or physiological changes (Zimova et al. 2018), hibernation (Prior and Weatherhead 1996; Gienger and Beck 2011; Goldberg et al. 2020), or a combination thereof (Goldberg et al. 2020; Howarth et al. 2023). In particular, animals hibernating may require distinct habitats to meet their differing requirements over winter, such as a specific structure, temperature, or humidity (Brown et al. 1974; Prior and Weatherhead 1996; Hein and Guyer 2009; Goldberg et al. 2020). Due to the use of spatially and temporally distinct critical habitats, such sites warrant the need for identification to conserve species in colder climates outside their active season.

The use of hibernacula as a habitat feature that enables overwinter survival in northern snakes has received considerable attention, in part because they warrant designation as ‘critical habitat’ but also because large communal hibernacula provide valuable research opportunities to study behaviour, demography, and habitat selection (Shine et al. 2001; Shine and Mason 2004; Gienger and Beck 2011). As a result, several well-studied systems [ex. Red-sided garter snake (*Thamnophis sirtalis parietalis* - Gregory 1974; Shine et al. 2001; Shine and Mason 2004; Gregory 2011), Western Rattlesnake (*Crotalus oreganus oreganus* - Lomas et al. 2015; Maida et al. 2018; Howarth et al. 2023)] have become iconic and almost synonymous with the phenomenon of 'communal denning' in snakes, even serving as tourist destinations (Manitoba 2024). However, not all northern snakes are associated with large communal hibernacula; they instead may be found denning alone or in low numbers (Parker and Brown 1973; Williams et al. 2015). Due to this variation, it is important to consider how species shift in their habitat selection when the degree of communal occupation changes. For our study, we define communal denning as an aggregation of individuals of the same species, where the degree of communal occupation would refer to how many individuals of a given species use a site. By way of example, Williams et al. (2014; 2015) assessed eight communal and 25 solitary hibernacula for the Great Basin Gophersnake (*Pituophis catenifer deserticola*) in western Canada, finding that rocky areas were used within the southern part of the study, where one-third of snakes were denning communally; in the north, the snakes tended to hibernate in grassy hillsides, with only one-fifth denning communally (Williams et al. 2015). No research, save for the aforementioned study, has provided a comparison of habitat as it relates to communal occupation of snakes at hibernacula. Communal denning makes populations vulnerable to mass mortality events through persecution, natural disasters, and habitat loss (Shine and Mason 2004; Gardiner and Sonmor 2011; COSEWIC 2015a; Maida et al. 2017). Therefore, understanding the factors influencing the occurrence of species-specific communal denning is essential for the conservation of these critical habitats.

No studies have explored both the common selection and species-specific preferences of denning habitats for sympatric snake species that, in some cases, share the same overwintering sites. Many studies have looked at hibernacula habitat characteristics for single snake species (Prior and Weatherhead 1996; Harvey and Weatherhead 2006), such as the Great Basin Gophersnake (Williams et al. 2015) and Western Rattlesnake (Gienger and Beck 2011). However, some sites have interspecific importance, with multiple species known to share hibernacula (Parker and Brown 1973; Prior and Weatherhead 1996; COSEWIC 2013; Williams et al. 2015). This provides opportune conditions for studying how and why hibernacula selection varies between sympatric species, particularly within an environment where natural selection should be relatively strong for the use of effective hibernacula. Variation between species will highlight unique qualities for species-specific management (including monitoring and inventory) and protection of hibernacula. Finally, through comparison, this approach has the potential to provide further context for habitat selection of little-known and hard-to-study species.

In British Columbia, Canada, three threatened species of snakes occur coincidentally over much of their respective northern range extremes. The Great Basin Gophersnake and the Western Yellow-bellied Racer (*Coluber constrictor mormon*) each hibernate communally or solitarily in rocky outcrops, deep talus, or animal burrows (Haney and Sarell 2005; COSEWIC 2015b; Williams et al. 2015), while the Western Rattlesnake largely dens communally within rocky outcrops and talus slopes (Gienger and Beck 2011; COSEWIC 2015a). Within southern British Columbia, these species routinely are found denning with each other (COSEWIC, 2013; Williams et al., 2015). In this study, we use a community of these three snake species occurring at coincidental northern limits to compare hibernacula selection and communal denning. We (i) document the hibernacula and their species assemblages on our study site; from these sites, we (ii) investigate how the habitat features relate to the degree of communal occupation present at hibernacula and (iii) explore how these three species vary in their selection of overwintering habitat.

METHODOLOGY

Study Site

This study was conducted within and around the Lac du Bois Grasslands Protected Area (51° N, 120.4° W) on the northern edge of the City of Kamloops, in south-central British Columbia, Canada (Figure 1.2). The area is dominated by lower and middle grasslands and, to a lesser extent, upper grassland, rocky outcrops, talus slopes, and wetlands (BC Parks 2017). The major plants of this study site consist of Big Sagebrush (*Artemisia tridentata*), Bluebunch Wheatgrass (*Pseudoroegneria spicata*), and a variety of spring-blooming plants (BC Parks 2017). Although protected, this area is not immune to anthropogenic practices such as recreational use, livestock grazing, bordering residential development, and pipeline construction (GCC 2009; BC Parks 2017; Trans Mountain 2021a).

Refer to Chapter 1 for further details on the climatic and biogeographic conditions of the study area.

Our site lies within the coincidental northern limits of the Great Basin Gophersnake, Western Yellow-bellied Racer, and Western Rattlesnake (Matsuda et al. 2006). The study area has critical habitat features supporting basking, oviposition, gestation, birthing, and overwintering of our study species. The overwintering period commences when snakes return to their hibernaculum (ingress) between August and October and is completed when snakes leave their hibernaculum (egress) between March and May (pers. observ.). Snakes are active on the study site from when they emerge until returning to their hibernacula (April to September) (pers. observ.). Data collection in this study was centered around the emergence and return of snakes to hibernacula.

This project was established as part of the mitigation efforts following the unearthing of several snake hibernacula during construction of the Trans Mountain Expansion Project (Heinrich 2020). Three hibernacula, containing variable numbers of the three aforementioned species, were displaced late in Autumn 2020 through active pipeline construction (Heinrich 2020; Trans Mountain 2021b – Figure 1.2). A total of 10 rattlesnakes, 49 gophersnakes, and 69 racers were salvaged from the excavation (Heinrich 2020). Prior to the involvement of the authors and this research project, a portion of these snakes (10 rattlesnakes, 12 gophersnakes, and 13 racers) were relocated to natural hibernacula in the immediate area (Heinrich 2020). These snakes were not marked for future identification as it is not a regulatory requirement. The remaining 37 gophersnakes and 56 racers were overwintered in captivity at the BC Wildlife Park, providing an opportunity to study the response of the animals to the attempted mitigation. In the spring of 2021, the artificially-overwintered snakes were released at an artificial hibernaculum built to compensate for lost habitat (Heinrich 2020). All released individuals were implanted with a passive integrated transponder (PIT tags) (Biomark Inc., Boise, ID, United States) to allow for future identification and a subset of these snakes were tracked to newly identified hibernacula (see Locating Hibernacula below). Refer to Chapter 1 for further details on the disturbance event.

Locating Hibernacula

We located existing hibernacula using historical records, hibernacula surveys, and radiotelemetry. Historical records of hibernacula were obtained through the Province of British Columbia's Conservation Data Centre (Bertram et al. 2001; GBC 2023).

We conducted routine surveys of known hibernacula to ensure sites were still active and to obtain count data (see Count of Snakes at Hibernacula below). Surveys were conducted at a subset of identified hibernacula during periods when snakes emerged or returned to hibernacula. When additional hibernacula were identified, they were added to the surveys. Between April 6 to May 6, 2022, 17 hibernacula were surveyed each at least 10 times; from August 25 to October 17, 2022, 19 hibernacula were surveyed each at least 19 times; and between April 1 to May 10, 2023, 24 hibernacula were surveyed each at least 16 times. Surveys began well in advance of the first observed snakes and continued until snakes were no longer observed or the same individuals were recaught over more than one visit across multiple sites. To survey hibernacula, we would initially survey the hibernacula entrance, followed by thoroughly searching for snakes within a ~5m radius around the entrances. Special attention was given to checking the underneath of cover objects in the vicinity (i.e., shrubs, rocks, etc.). These searches would, at times, be limited to a smaller area depending on the topography of hibernacula (i.e. increased slopes/cliffs). New hibernacula were discovered opportunistically when a snake or snakes were found using a particular habitat during these windows and subsequent surveys.

In addition to the subset of translocated gophersnakes and racers (see Study Site above), we also tracked a sample of undisturbed, free-ranging snakes to collect comparative data on movement behaviour (Ragsdale, MSc. Thesis, in prep.). Racers tracked in the study were generally too small to carry transmitters large enough to enable tracking throughout the active season to hibernacula. Rattlesnakes were not tracked as (i) described above, rattlesnakes from the disturbed hibernacula were relocated to natural hibernacula without permanent marking, and (ii) considerable telemetry on that species has been conducted in BC (Bertram et al. 2001; Gomez et al. 2007; COSEWIC 2015a; Lomas et al. 2015; Harvey and Larsen 2020; Schmidt et al. 2020; Atkins 2021; Eye 2022; Howarth et al. 2023, etc.), including in the Lac du Bois area (Bertram et al. 2001; Gomez 2007; Hobbs 2007), such that communal denning is known to be virtually ubiquitous in this region, and (iii) as a result, a number of rattlesnake hibernacula in the study area already were known.

We selected gophersnakes for intracoelomic radio transmitter implantation when the transmitters (SB-2T 5.2g or SB-2T and ibutton modification 9.5g with 12-month battery, or SB-2T 3.8g with six month battery; Holohil Systems Ltd., Carp, ON, Canada) did not exceed 4% of snake body mass (Bryant et al. 2010). Surgeries were performed at nearby veterinary clinics and followed similar methodologies to Reinert and Cundall (1982) with minor modifications; the transmitter implants occurred on the left side of the body at ~55% of the SVL as measured caudally from the snout. The antennae were fed caudally under the skin rather than cranially. Animals were tracked every 2-3 days throughout the two active seasons until each hibernaculum location was determined. Hibernaculum location was confirmed when a telemetered snake remained in a location through the fall and into winter. The hibernaculum mouth was identified as the closest opening to the point of strongest signal from radiotelemetry (Harvey and Weatherhead 2006). Radio transmitters were surgically removed at the end of the battery life following the same procedure.

Precise locations of the hibernacula identified and monitored in this study cannot be revealed, given restrictions on the publication of sensitive/secured data. None of the displaced snakes naturally adopted the newly-created hibernaculum in the subsequent fall (see Study Site above and Chapter 3). Instead, many found and used other hibernacula (all used with other snakes) that would have been extremely difficult to locate otherwise. We do not use the newly created artificial hibernacula in our sampling of denning sites.

Counts of Snakes at Hibernacula

Following the previously described survey methodology (see Locating Hibernacula above), 2023 egress hibernaculum surveys (April 3, 2023, to May 10, 2023) were used to gauge the number of snakes occurring at the hibernacula. If no snakes were found at a known site during the 2023 egress hibernacula survey period, the highest number from the 2022 egress (April 6, 2022, to May 6, 2022) or ingress hibernacula survey period (August 25, 2022, to October 17, 2022) was used. The overall data from these previous survey periods were not used in combination with 2023 egress data, as not all hibernacula had been identified until the end of the 2022 ingress period. During surveys, individual snakes were caught and implanted with a PIT tag (Biomark Inc., Boise, ID, United States) to permit identification in subsequent surveys. The displaced snakes were included in this count of snakes. Because snakes were transplanted directly into new hibernacula by contractors (see Study Site above), we could not unequivocally eliminate them from our samples. Snakes seen but not caught were only included in the count if we could confirm they were unique individuals (i.e., caught and tagged two gophersnakes, but four were seen). The count of snakes at a given hibernacula was the total number of unique individuals found over the entire survey period. Hibernacula were only included in this inventory if they could be surveyed with effort similar to the other sites. Two hibernacula were omitted due to distance from other sites as they could not be evenly surveyed with the other hibernacula. An additional two hibernacula were omitted as they were not evenly surveyed along with the other hibernacula during this period. Overall, 24 hibernacula out of 28 known hibernacula were surveyed to estimate the number of snakes occupying them.

Habitat Measurements

Habitat data were collected at each recorded hibernaculum and a paired random site, using a matched case-control design (Harvey and Weatherhead 2006; Thomas and Taylor 2006; Eye 2022). From the hibernaculum entrance, a random direction and distance (40 - 300 m) were chosen to identify the random site (Prior and Weatherhead 1996; Harvey and Weatherhead 2006; Gienger and Beck 2011; Eye 2022). The range of distances used to find the random sites was selected based on previous studies to ensure hibernacula and the random site did not overlap and to represent the greater environment available to snakes (Harvey and Weatherhead 2006; Eye 2022). The entrance of each hibernaculum was used as the epicenter for data collection. If a site had multiple entrances, the entrance with the largest area was used for measurements. Following Prior & Weatherhead (1996), measurements at the random site were taken around the closest feature within 5 m of the site found from the random distance and direction, representing an underground opening (i.e., rodent burrow, hole under rock, crack in a rockface, etc.). At each known hibernaculum and random site, three types of habitat features were measured: microscale features (1m radius), macroscale features (10m radius), and objects within 30m of the site (Table 2.1) (Howarth 2023). Habitat features were selected based on similar studies (Prior and Weatherhead 1996; Harvey and Weatherhead 2006; Gienger and Beck 2011; Williams et al. 2015; Eye 2022; Howarth et al.

2023) (Table 2.1). The percent cover of shrub, grass, dirt, and rock were visually estimated in 1m and 10m radius plots. At the microscale, slope, aspect, elevation, number of openings, and the average area of those openings were measured. The distance to the nearest shrub and rock over 20cm in length was recorded (if found within 30m) (Williams et al. 2015). The height of the nearest shrub and the volume of the nearest rock over 20cm in length were measured (if found within 30m). Distances and size metrics were obtained using a tape measure.

Table 2.1: Habitat features measured around the entrances to hibernacula and random sites. Habitat features were measured at the microscale (1m radius), macroscale (10m radius), and within 30m of the site.

Abbreviation	Description	Scale
OPEN	Number of openings or mouths	micro
AREA	Area (cm^2) of largest opening	micro
SLOPE	Average of three slope (%) measures	micro
ELE	Elevation (m)	micro
ASP	Aspect (°) converted to radians	micro
S1	%Shrub cover at 1m	micro
G1	%Grass cover at 1m	micro
R1	%Rock cover at 1m	micro
D1	%Exposed dirt at 1m	micro
AVGRV	Average volume of 10 randomly selected surface rocks volumes (cm^3)	micro
S10	%Shrub cover at 10m	macro
G10	%Grass cover at 10m	macro
R10	%Rock cover at 10m	macro
D10	%Exposed dirt at 10m	macro
RD	Distance (cm) of nearest rock >20cm in length within 30m	30m
RV	Volume of nearest rock (cm^3) >20cm in length within 30m	30m
SD	Distance to nearest shrub (cm) within 30m	30m
SH	Height of nearest shrub (cm) within 30m	30m

Statistical analysis

All statistical analysis was performed using RStudio (Posit Software 2023). The effects of season were not accounted for in this analysis (Howarth 2023). For analysis, habitat variables were modelled in two separate groups: microscale was modelled alone, while macroscale features and objects measured within 30m were modelled together (Howarth 2023). Rarely, habitat plots on neighbouring hibernacula overlapped at the macroscale. When this occurred, the two plots were analyzed as one at that scale by taking the average value of the habitat metrics across both plots; also, in these situations, the number of snakes at those sites was pooled, and a single random site was chosen randomly. Aspect was converted from degrees into radians (Mardia and Jupp 2000; Eye 2022).

Number of Snakes at Hibernacula

The relationship of hibernacula features on the count of snakes was assessed separately for gophersnakes, racers, and rattlesnakes, at both the micro and macroscale (Figure 2.1). Data within these groups were assessed for correlation using Spearman rank correlation tests (Hauke & Kossowski, 2011). When a correlation coefficient between a pair of metrics was ≥0.7, only one of the variables was retained if deemed more biologically relevant than the other from the habitat selection analysis (see Habitat Selection below). Using the ‘glm’ function in base R (Posit Software 2023) and ‘glm.nb’ function from the ‘MASS’ package (Ripley et al. 2023) in RStudio (Posit Software 2023), Poisson and negative binomial regressions were fit for each species at both scales. The negative binomial model preferentially was selected when overdispersion of the data was significant, and AICc values were lower than the Poisson regression model (Ismail and Jemain 2007). Top models were determined using the difference in AICc values obtained from the ‘dredge’ function in the ‘MuMIn’ package (Bartoń 2023) in RStudio (Posit Software 2023). Models with △AICc value <2.0 were considered equally supported (Burnham and Anderson 2002).

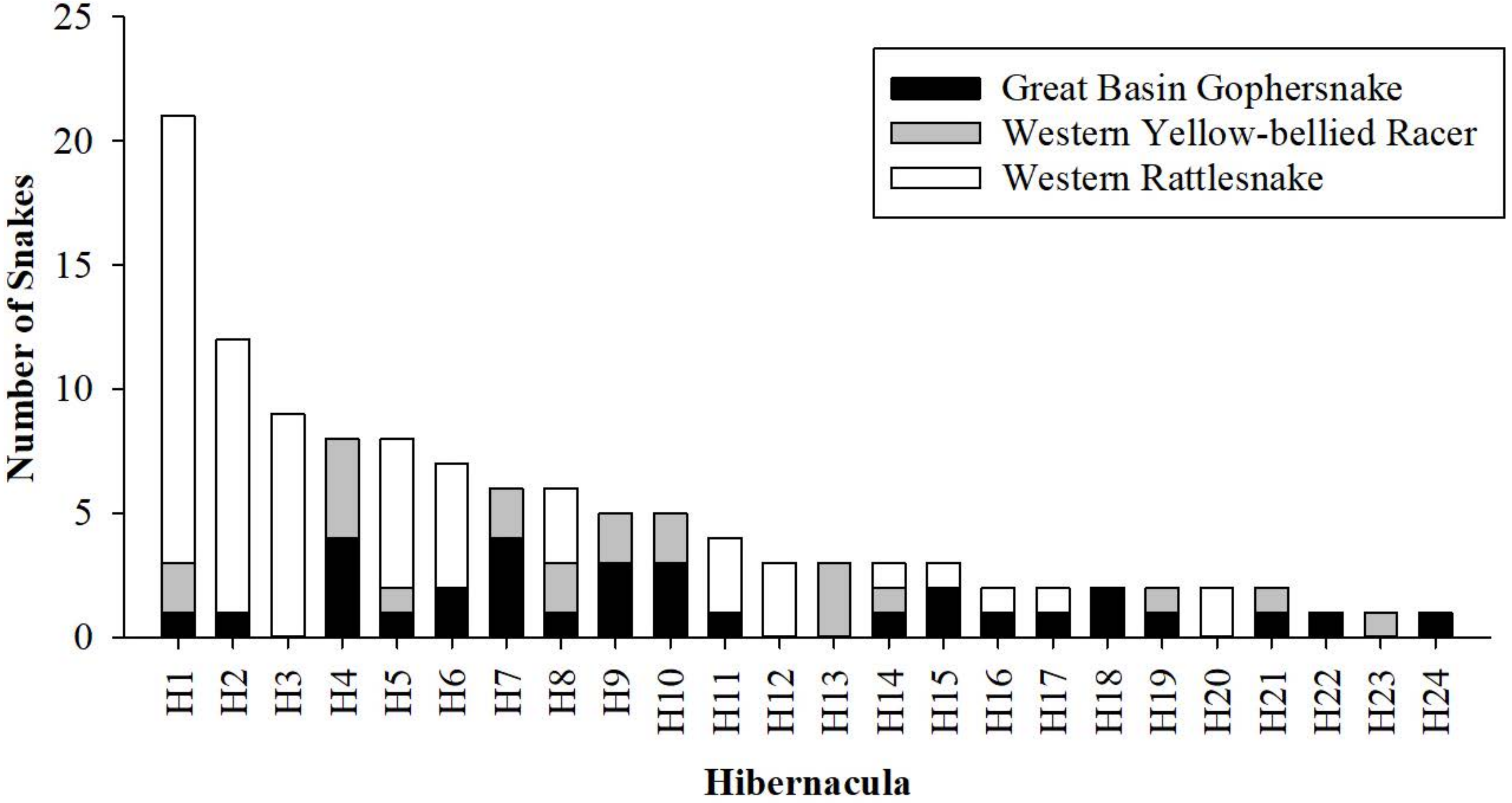


Figure 2.1: Numbers of snakes and species composition at 24 hibernacula distributed across the study landscape. Snakes were surveyed during the 2023 emergence period. If no snakes were found at a hibernaculum during this survey period, the next highest survey period from 2022, ingress or egress, was used to estimate the number of snakes at that hibernaculum. Bars are subdivided according to the number of snakes of each species.

Habitat Selection

We compared the habitat features at random sites to hibernacula used by gophersnakes, racers, and rattlesnakes at both micro- and macro-scales. Univariate analysis was performed to reduce the number of variables imputed into the final models (Hosmer and Lemeshow 2000; Howarth 2023). This was done by conducting a Wilcoxon signed-rank test (paired sample) or paired t-test, depending on normality, for each habitat variable between hibernacula and random sites. Habitat variables were retained for modelling when $P<0.25$ (Hosmer and Lemeshow 2000; Howarth 2023). The selected habitat variables were then assessed for correlation using Spearman rank correlation tests (Hauke and Kossowski 2011). When a correlation coefficient was ≥0.7, the variable with the least variation, as determined from the univariate analysis, was removed from further analysis (Dormann et al. 2013). Following univariate analysis and checking for correlation, we compared the habitat at hibernacula to paired random plots using conditional logistic regression. These models were created at the two scales for each of the three snake species. We used the 'clogit' function in the 'survival' package (Therneau et al. 2023) in RStudio (Posit Software 2023) to fit these models. Top models were determined as described in Number of Snakes at Hibernacula. If a global model did not converge, the variable with the next lowest variation, as determined from the univariate analysis, was removed. Following this, if the model still did not converge, interpretations were carried out using the initial univariate analysis following the removal of correlated variables (Ballantyne and Nol 2011).

RESULTS

We identified 28 hibernacula within the study site: Of these, 7 were known historically, 6 were identified through our hibernacula surveys, and 15 were located through telemetry on 44 gophersnakes (19 from the displaced population and 25 reference). Among the 15 hibernacula discovered through radiotelemetry, 5 were found from displaced snakes, and 10 were found from reference individuals. Of the 28 hibernacula, gophersnakes were detected at 21, with racers and rattlesnakes occurring in 15 hibernacula each (Figure 2.2). All told, 5 hibernacula (18%) supported all three species (Figure 2.2). Habitat data were collected at each hibernaculum and 28 paired random sites; 46 sites were surveyed following egress in 2022, and the remaining 10 were collected during ingress in 2022. Hibernacula were located in rodent burrows (18%, n=5), at the base of rocky outcrops (61%, n=17), within anthropogenically-placed boulders on the side of roads (blast rock) (11%, n=3), and in holes found under rocks (11%, n=3) (Figure 2.3). Racers and gophersnakes were found in hibernacula across all of these four categories, while rattlesnakes overwintered exclusively in rocky outcrops and blast rock.

Number of Snakes at Hibernacula

A total of 24 hibernacula (19, 13, and 12 for gophersnakes, racers, and rattlesnakes, respectively) were used to examine the effect of habitat on the number of snakes detected at each location for each species. Overall, the top model suggested that no habitat features explained the number of racers and gophersnakes at hibernacula at the microscale, with the top models for these species being the null models (i.e. the models without any habitat features) (Table 2.2; Appendix A). However, for gophersnakes, models with $\triangle$AICc <2.0 suggested the number of those snakes detected at hibernacula was negatively associated with the number of openings and shrub cover, and racers were positively associated with rock cover (Burnham and Anderson 2002) (Table 2.2; Appendix A). The number of rattlesnakes detected at a hibernaculum was negatively associated with average rock volume and dirt cover, and positively associated with the number of openings and aspect at this scale (Table 2.2.; Appendix A).

The top model suggests that no habitat features using macroscale measurements explained the number of detected racers and gophersnakes, with the top models for these species being the null models (Table 2.2; Appendix A). However, models with a $\triangle$AICc value <2.0 suggest gophersnakes are negatively associated with rock cover and volume of the nearest rock (Table 2.2; Appendix A). At this scale, dirt cover and volume of the nearest rock were negatively associated with the number of rattlesnakes present, while shrub cover was positively associated (Table 2.2; Appendix A).

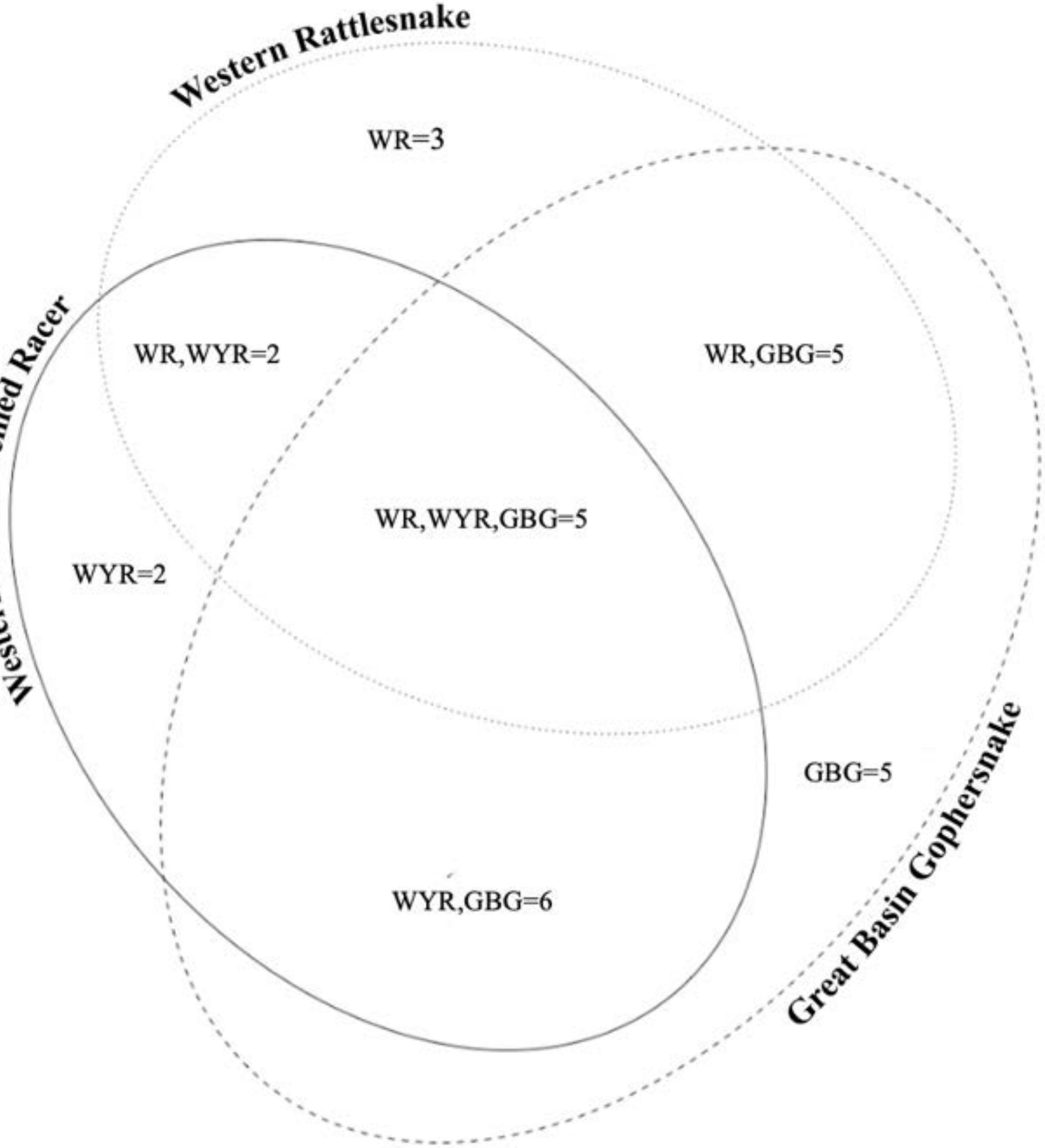


Figure 2.2: The number of hibernacula used and shared by the Western Yellow-bellied Racer "WYR", Western Rattlesnake "WR", and Great Basin Gophersnake "GBG" in Lac du Bois Grasslands Protected Area.

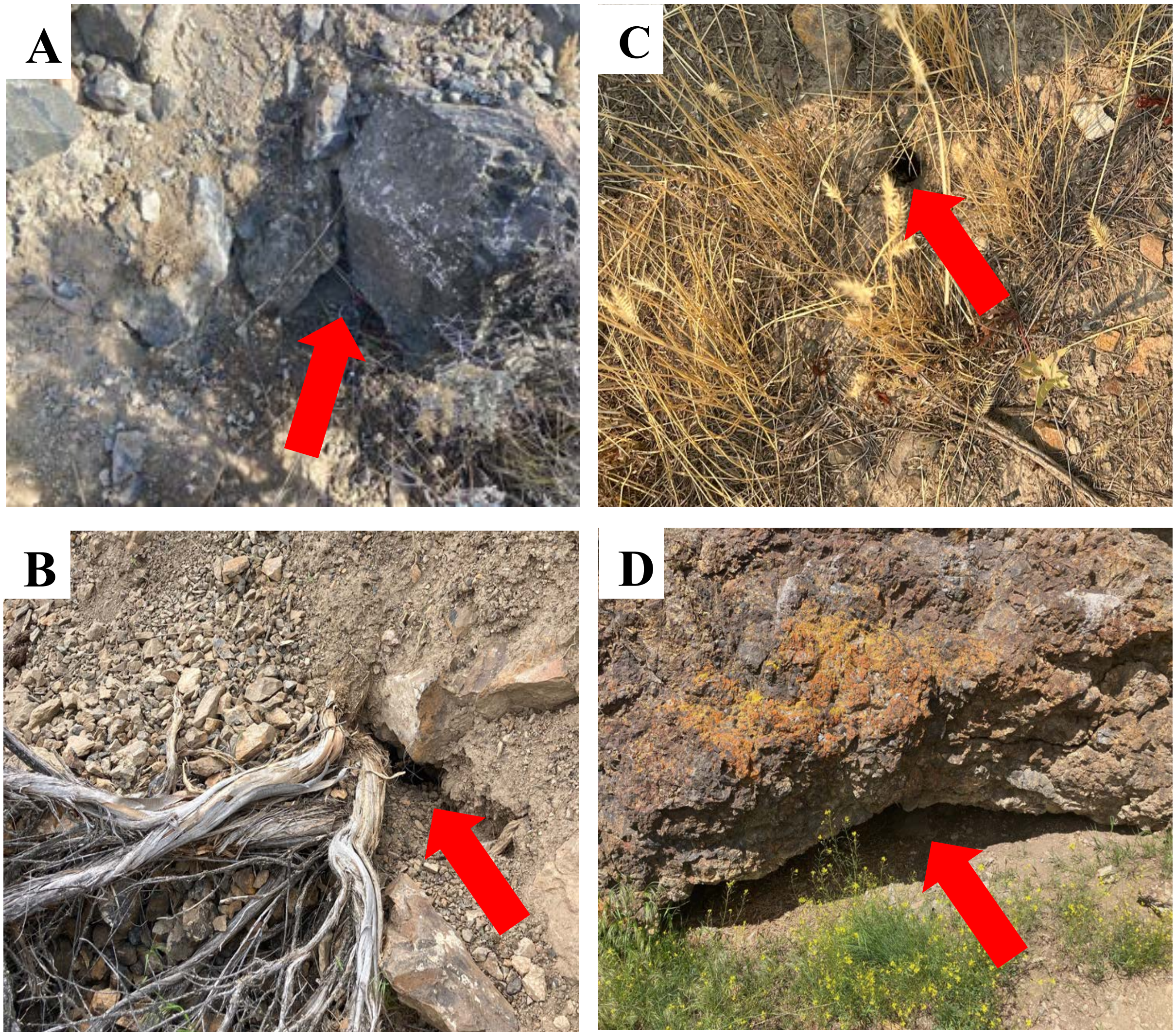


Figure 2.3: Examples of snake hibernacula within Lac du Bois Grassland Protected Area (2021-2023). A) Found in the blast rock off the side of the road. B) Found under a rock. C) Found in an animal burrow. D) Found in a rocky outcrop. Red arrows identify the location of the hibernaculum entrance. Photos by author.

Table 2.2: Candidate models investigating the effect of habitat on the numbers of snakes detected at hibernacula at a micro- and macroscale. Models for the Great Basin Gophersnake, Western Rattlesnake, and Western Yellow-bellied Racer were ranked based on the Akaike Information Criterion small sample equivalent (AICc) and ΔAICc (difference of AICc of the best model (minimum AICc) to the model being compared). This table also includes the models' weight (w_i). The top models with ΔAICc value <2.0 (Burnham and Anderson 2002*)* are shown, along with the global model (G) that contained all of the selected habitat variables. The relationship of habitat variables in the top models is indicated with a superscript, + describes habitat features associated with increased snakes, and - describes variables not associated with them (Appendix A). Full names and detailed descriptions of explanatory variables are found in Table 2.1.

Scale	Group	#	Model	AICc	ΔAICc	w_i
Micro	Gophersnake	1	Null Model	56.9	0	0.12
		2	OPEN$^-$	58.5	1.6	0.05
		3	S1$^-$	58.8	1.9	0.05
		G	ASP+ELE+AREA+R1+D1+OPEN+S1+G1	89.5	32.6	0.00
	Racer	1	Null Model	39	0	0.15
		2	R1$^+$	40.6	1.6	0.07
		G	ASP+ELE+OPEN+AREA+R1+D1+AVGRV+S1+G1	161.9	122.9	0.00
	Rattlesnake	1	AVGRV$^-$+D1$^-$+OPEN$^+$	59.8	0	0.40
		2	ASP$^+$+AVGRV$^-$+D1$^-$+OPEN$^+$	60.9	1.1	0.24
		G	ASP+OPEN+AREA+R1+D1+AVGRV+S1+G1	145.8	86	0.00
Macro	Gophersnake	1	Null Model	55.7	0	0.21
		2	R10$^-$	57.6	1.9	0.08
		3	RV$^-$	57.6	1.9	0.08
		G	RV+R10+D10+SD+SH+S10	76.7	21.0	0.00
	Racer	1	Null model	40.4	0	0.21
		G	RD+RV+R10+G10+SD+SH+S10	87.0	46.6	0.00
	Rattlesnake	1	D10$^-$	63.3	0	0.35
		2	D10$^-$+RV$^-$	65.1	1.8	0.14
		3	D10$^-$+S10$^+$	65.1	1.8	0.14
		G	RD+RV+R10+D10+S10+G10	96.2	32.9	0.00

Habitat Selection

Habitat information was collected at each of the 28 hibernacula and a paired random site. At the microscale, gophersnake hibernacula were associated with an increased area of the main hibernaculum mouth, number of openings, shrub cover, and slope (Tables 2.3; Appendix B). At this scale, the racer model did not initially converge; following the removal of the variable with the next lowest variation as determined from the univariate analysis, ASP, convergence was achieved (Appendix C). Racers selected for steeper slopes, an increased area of the main hibernaculum mouth, and rock and shrub cover (Tables 2.3; Appendix B). At this scale, the rattlesnake model did not converge regardless of variable removal; thus, univariate analysis following correlation testing was used to compare known hibernacula to random sites. Known rattlesnake hibernacula had significantly larger openings (Wilcoxon signed-rank tests**,** *P*=0.0001), were found on steeper slopes (Paired t-test=3.72, *P*=0.0023), and had less grass cover than random sites (Wilcoxon signed-rank tests, *P*=0.0007) (Appendix C).

At the macroscale, gophersnakes selected for rock cover, and increased height of the nearest shrub (Tables 2.3; Appendix B). At this scale, racers and rattlesnakes selected against grass cover (Tables 2.3; Appendix B). All three species selected larger distances to the nearest shrub and smaller distances to the nearest rock (Tables 2.3; Appendix B).

DISCUSSION

This study provides the first direct comparison of surface habitat at hibernacula used by multiple snake species within the same community. At these hibernacula, we observed variation in the extent of communal occupation for all three species. However, our habitat metrics around these sites failed to effectively explain the numbers of gophersnakes, racers, and rattlesnakes at the hibernacula. Further, we reveal that although these three species share the same landscape and, in some cases, hibernacula, they do not appear to be selecting habitat in the same fashion. Overall, this research provides compelling evidence to reconsider our approach in identifying and protecting these critical habitats.

Table 2.3: Candidate models comparing habitat features of hibernacula and paired random sites at the micro and macroscale. Models for the Great Basin Gophersnake, Western Rattlesnake, and Western Yellow-bellied Racers were ranked based on Akaike Information criterion (AIC) small sample equivalent (AICc) and ΔAICc (difference of AICc of the best model (minimum AICc) to the model being compared). This table also includes the models' weight (w_i). The top models with △AICc value <2.0 (Burnham and Anderson 2002) are shown, along with the global model (G) that contained all of the selected habitat variables. The relationship of habitat variables in the top models is indicated with a superscript, where + describes habitat features selected for, and - describes variables selected against (Appendix B). Full names and detailed descriptions of explanatory variables are found in Table 2.1. The Western Rattlesnake model at the microscale did not converge.

Scale	Group	#	Model	AICc	ΔAICc	w_i
Micro	Gophersnake	1	SLOPE^{+}+AREA^{+}	21.5	0	0.18
		2	SLOPE^{+}+AREA^{+}+S1^{+}+OPEN^{+}	21.9	0.4	0.15
		3	SLOPE^{+}+AREA^{+}+S1^{+}	21.9	0.4	0.15
		4	SLOPE^{+}+OPEN^{+}	22.4	0.9	0.12
		G	SLOPE+AREA+S1+OPEN+G1	25.3	3.8	0.03
	Racer	1	R1^{+}	13.6	0	0.14
		2	R1^{+}+SLOPE^{+}	14.4	0.8	0.10
		3	SLOPE^{+}+AREA^{+}	14.8	1.2	0.08
		4	R1^{+}+S1^{+}	15.4	1.8	0.06
		5	R1^{+}+SLOPE^{+}+S1^{+}	15.4	1.8	0.06
		G	SLOPE+AREA+S1+OPEN+AVGRV +R1	27.5	13.9	0.00
Macro	Gophersnake	1	SH^{+}+R10^{+}	13.4	0	0.43
		2	SH^{+}+SD^{+} +R10^{+}	14.2	0.8	0.29
		3	SH^{+} +RD^{-}+R10^{+}	15	1.6	0.19
		G	RD+SD+SH+R10	17.3	3.9	0.06
	Racer	1	G10^{-}	25.8	0	0.30
		2	G10^{-}+SD^{+}	26.4	0.6	0.23
		3	G10^{-}+RD^{-}	26.7	0.9	0.19
		G	G10+RD+SD	28.5	2.7	0.11
	Rattlesnake	1	G10^{-}+RD^{-}	13	0	0.45
		2	G10^{-}+SD^{+}+RD^{-}	14.9	1.9	0.18
		G	G10+SD+RD+S10	19.1	6.1	0.02

We now know that Western Yellow-bellied Racers and Great Basin Gophersnakes appear to be more generalist in their selection of habitat, overwintering in rodent burrows, holes under rocks, rocky outcrops, and blast rock features in comparison to rattlesnakes present at rocky outcrops and blast rock on this study site. Gophersnakes, racers, and Western Rattlesnakes all are known to overwinter together (COSEWIC 2013,2015a,b). While we observed this phenomenon, there were cases where animals overwintered individually or in alternate groupings of the species. Coincidental occupation of hibernacula occurred the most between gophersnakes and racers at six sites. The generalist nature of these species may provide more opportunities for racers and gophersnakes to overlap. Overall, the variation between assemblages and the difference in the counts of snakes at hibernacula suggests that these species are selecting differently and may coincidentally overlap at select hibernacula.

Rattlesnakes were found increasingly at hibernacula with more entrances on southwestern and southern aspects. Rattlesnakes typically congregate during ingress or egress in the immediate entrance area to hibernacula (Brown and Parker 1982; Gienger and Beck 2011); presumably, more entranceways would allow increased snakes to bask and provide adequate refuge should individuals need to evade. As with this study, previous research has shown Western Rattlesnake hibernacula occur on south-facing slopes in Washington State (Gienger and Beck 2011), receiving increased solar radiation in comparison to north-facing slopes (Gates 1980; Bonon 2002; Geiger et al. 2003; Gienger and Beck 2011). Presumably, heightened solar radiation increases opportunities for thermoregulation in the form of basking.

Gophersnakes and racers demonstrate a broad range of habitat preferences for hibernation sites. This variability might help to explain why none of the habitat features (of those measured) effectively explain their count at hibernacula, as the null models were the top models at the micro and macroscale. Further, the potential underrepresentation of racers and gophersnakes due to detection bias may contribute to these results (Kéry 2002; Biro and Dingemanse 2009; Johnstone et al. 2021). For example, Parker and Brown (1973) found that the number of detected racers increased from 5 to 149 when their hibernaculum was fenced. This generalist behaviour and low detectability at hibernacula compared to rattlesnakes may contribute to the absence of habitat features that differentiate their count.

Regardless, gophersnakes and racers are not using hibernacula like rattlesnakes on our study site. Western Rattlesnakes conspicuously congregate at hibernacula (Brown and Parker 1982; Gienger and Beck 2011), whereas racers and gophersnakes are more cryptic and generally found away from the hibernaculum entrance (Parker and Brown 1973; Brown and Parker 1982; Kéry 2002). This behavioural heterogeneity may contribute to the lack of effect habitat has on their numbers (Williams et al. 2015).

Certain features were commonly selected among the species. Our study demonstrated that gophersnake, racer, and rattlesnake hibernacula were situated on steeper slopes with relatively larger openings of the main hibernaculum entrance compared to random sites. Previous research on Western Rattlesnake hibernacula in Washington States, USA, found 56+/-12° slopes compared to random sites 62+/-7° (Gienger and Beck 2011). Stability and access decrease as slopes increase due to potential rockfall, landslides, and near-vertical climbs (Giani 1992; Gienger and Beck 2011). In contrast, as slope increases, solar exposure increases, providing increased soil temperature and basking opportunities (Barry and Chorley 1976; Brady and Weil 2002; Hamilton and Nowak 2009). Presumably, these midrange slopes would provide the optimal balance between stability, access, and solar radiation. One of the most vulnerable times for snakes is during egress when they are cold, less responsive to potential risk, and thus seeking to bask (Angilletta et al. 2002; Harvey and Weatherhead 2006; Gienger and Beck 2011). Larger entrances would help to provide adequate refuge to evade predation and room to bask.

The variation in the selection of cover and open habitat features at the micro and macroscale aligns with observed behavioural differences between these species (pers. observ). During egress, racers and gophersnakes are more cryptic and generally found away from hibernacula entrances (Parker and Brown 1973; Brown and Parker 1982). In contrast, Western Rattlesnakes conspicuously bask at the hibernacula (Brown and Parker 1982; Gienger and Beck 2011). We found that rattlesnake hibernacula were associated with open habitat, with those sites having significantly less grass cover than random sites at both the micro and macroscale. Such habitat could provide more basking opportunities with increased solar exposure and better visibility to potential predators. Open habitat surrounding hibernacula is crucial for various snake species, including the Timber Rattlesnake (*Crotalus horridus*) (Brown 1993), where the lifespan of hibernacula may be constrained by the shading caused by nearby trees (Brown 1993). This limitation is also speculated to affect Western Rattlesnakes in forested regions (COSEWIC 2015b). Although our study site is an open grassland, and trees are not a dominant feature this example showcases the potential dependence of some snakes to open habitat at their hibernacula. In contrast, we found that gophersnakes and racers were associated with further cover features at the microscale, with gophersnakes selecting for more openings and shrub cover and racers selecting for increased rock and shrub cover. Gophersnakes are thought to rely on cover objects for thermoregulation and security around their hibernacula (Parker and Brown 1980; COSEWIC 2013)**.** Their selection of further cover features (i.e. increased rock cover) at the macroscale would support this behaviour. However, such behavioural differences may not capture the whole story, as racers selected against grass cover, and all three snakes selected for larger distances to the nearest shrubs and smaller distances to the nearest rock at the macroscale. Such habitat would provide open conditions conducive to basking and cover rocks in the greater vicinity.

Why do rattlesnakes exclusively overwinter in rocky outcrops and blast rock features on our study site, whereas the other two species appear much more catholic in hibernacula site selection? One obvious factor distinguishing racers and gophersnakes from rattlesnakes is the reproductive mode. Racers and gophersnakes are oviparous, retaining eggs until oviposition occurs (COSEWIC 2013; COSEWIC 2015b), whereas rattlesnakes are viviparous (COSEWIC 2015a). Rookeries, distinct sites where parturition occurs, are generally found far closer to hibernacula than active season foraging sites (as reviewed in Graves and Duvall 1995). For example, Western Rattlesnakes within the Okanagan were found to utilize hibernacula or the general area (on average less than <140m from hibernacula) outside of winter as rookeries (Macartney and Gregory 1988; Eye 2022). Sites physically closer to hibernacula benefit gravid females by reducing the distance needed to migrate while gravid (Duvall et al. 1985; Graves and Duvall 1995). Additionally, proximity to hibernacula would aid neonates by making it easier to locate these sites and reducing the potential energy expenditure associated with searching for a suitable site (Graves and Duvall 1995). Thus, the selection of rocky outcrops and blast rock features as hibernacula for rattlesnakes may facilitate or be influenced by the selection of habitat for these reproductive behaviours. In the

Okanagan, gravid Western Rattlesnakes selected for rock cover at their rookeries across multiple scales and sites (Eye 2022).

We did not track rattlesnakes or racers for this study, and we acknowledge that this may bias results by not providing the full breadth of sites selected. However, rattlesnakes are one of the most heavily studied reptiles within the province of British Columbia, with over 380 known hibernacula and multiple research studies (Bertram et al. 2001; Gomez et al. 2007; COSEWIC 2015a; Lomas et al. 2015; Harvey and Larsen 2020; Schmidt et al. 2020; Atkins 2021; Eye 2022; Howarth et al. 2023, etc.). Further, rattlesnakes were previously tracked within the study site (Bertram et al. 2001; Gomez 2007; Hobbs 2007). Given this, we believed that additional tracking of rattlesnakes would not have revealed anything outside the scope of our results. Racers, however, are understudied, and any data regarding their overwintering behaviour is valuable. Although we may not have represented the full scope of their potential selection, their presence at all habitat types (i.e., rodent burrows, rocky outcrops, holes under rocks, and blast rock) is similar to gophersnakes in this study.

Our work has implications for future research studies, impact assessments, and protection of these critical habitat features. We have identified key habitat characteristics related to the number of snakes at hibernacula and distinguished these sites from the broader environment. In practice, the ability to readily distinguish a hibernaculum, communal or not, with these features is not likely (Prior and Weatherhead 1996). Instead, these features only provide a general guide to personnel conducting surveys. Unfortunately, these features may not encompass all of the attributes and environmental cues these species are selecting for (Gienger & Beck, 2011), instead portraying only “average hibernacula” features. These features also are restricted to surface habitat, arguably pertaining more to shoulder season use. Due to the limited access, underground hibernacula habitat has largely been unexplored. We also showcase variation of habitat selection between these unique species that, in some cases, share these habitats. Thus, we caution against using hibernacula ‘models’ from certain iconic, tractable species (e.g., Western Rattlesnakes) to extrapolate to other species with less-well known denning habits, even within the same ecosystem.

Within British Columbia, protection mechanisms currently apply to 200-300 ha around communal hibernacula (MWLAP 2004; Williams et al. 2012; COSEWIC 2015a; Dyer et al. 2016a,b). However, protection only is effective if this habitat can be identified.

Prior to our study, only seven out of 28 hibernacula were known on this landscape, six of which were rocky outcrop hibernacula with a strong presence of rattlesnakes. To ensure the protection of cryptic hibernacula, especially for racers and gophersnakes, protection must be extended to the broader landscape where these hibernacula occur. As per Prior and Weatherhead (1996), radiotelemetry may be the most effective way to identify hibernacula in a new area, being responsible for the location of 15 of 28 hibernacula (54%) in this study. Such results support our findings that these sites are not easily visually identified through surveys (Prior and Weatherhead 1996), a point worth considering during future research and impact assessments. Overall, this study offers argument that we need to rethink how we identify and protect critical habitats for even species that share habitat within a community of snakes.

LITERATURE CITED

Angilletta MJ, Niewiarowski PH, Navas CA. 2002. The evolution of thermal physiology in ectotherms. J Therm Biol. 27:249–268.

Atkins MCP. 2021. Temporal and spatial changes in a Western Rattlesnake (*Crotalus oreganus*) population in British Columbia [thesis]. [Kamloops (BC)]: Thompson Rivers University.

Ballantyne K, Nol E. 2011. Nesting habitat selection and hatching success of whimbrels near Churchill, Manitoba, Canada. Waterbirds. 34(2):151–159.

Barry RG, Chorley RJ. 1976. Atmosphere, weather, and climate. 3rd ed. London: Methuen.

Bartoń K. 2023. MuMIn: Multi-model inference; [accessed 2023 Apr 13]. https://cran.r-project.org/web/packages/MuMIn/index.html.

BC Parks. 2017. Lac du Bois Grasslands Protected Area management plan. Kamloops.

Bertram N, Larsen KW, Surgenor J. 2001. Identification of critical habitats and conservation issues for the Western Rattlesnake and Great Basin Gopher Snake within the Thompson-Nicola region of British Columbia. Kamloops.

Biro PA, Dingemanse NJ. 2009. Sampling bias resulting from animal personality. Trends Ecol Evol. 24(2):66–67.

Bonon GB. 2002. Ecological climatology concepts and applications. Cambridge: Cambridge University Press.

Boyce MS, Johnson CJ, Merrill EH, Nielsen SE, Solberg EJ, van Moorter B. 2016. Can habitat selection predict abundance? Jour Anim Ecol. 85(1):11–20.

Brady NC, Weil RR. 2002. Elements of the nature of properties of soil. Upper Saddle River: Pearson Prentice Hall (NJ).

Brown WS, Parker WS, Elder JA. 1974. Thermal and spatial relationships of two species of Colubrid snakes during hibernation. Herpetol. 30(1):32–38.

Brown WS, Parker WS. 1976. Movement Ecology of Coluber constrictor near Communal Hibernacula. Copeia. 1976(2):225-242.

Brown WS, Parker WS. 1982. Niche dimensions and resource partitioning in a Great Basin Desert snake community. In: Scott, NJ. Herpetological Communities. A Symposium of the Society for the Study of Amphibians and Reptiles and the Herpotologist League; 1977 Aug; Washington (DC): United Stated Departments of the Interior Fish and Wildlife Service. p. 59–82.

Brown WS. 1993. Biology, status, and management of the Timber Rattlesnake (*Crotalus horridus*): A guide for conservation. Lawrence (KS): Society for the Study of Amphibians and Reptiles.

Bryant GL, Eden P, De Tores P, Warren K. 2010. Improved procedure for implanting radiotransmitters in the coelomic cavity of snakes. Aust Vet J. 88(11):443–448.

Burger J, Zappalorti RT, Gochfeld M, Boarman WI, Caffrey M, Doig V, Garber SD, Lauro B, Mikovsky M, Safina C, et al. 1988. Hibernacula and summer den sites of pine snakes (*Pituophis melanoleucus*) in the New Jersey Pine Barrens. J Herpetol. 22(4):425–433.

Burnham KP, Anderson D. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York (NY): Springer.

Camaclang AE, Maron M, Martin TG, Possingham HP. 2015. Current practices in the identification of critical habitat for threatened species. Conserv Biol. 29(2):482–492.

COSEWIC. 2013. COSEWIC Assessment and status report on the Great Basin Gopersnake *Pituophis catenifer deserticola* in Canada. Ottawa.

COSEWIC. 2015a. COSEWIC Assessment and status report on the Western Rattlesnake *Crotalus oreganus* in Canada. Ottawa.

COSEWIC. 2015b. COSEWIC Assessment and status report on the Eastern Yellow-bellied Racer *Coluber constrictor flaviventris* and the Western Yellow-bellied Racer *Coluber constrictor mormon* in Canada. Ottawa.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography. 36(1):27–46.

Dubiner S, Jamison S, Meiri S, Levin E. 2023. Squamate metabolic rates decrease in winter beyond the effect of temperature. J Anim Ecol.92(11): 2163-2174.

Duvall D, King MB, Gutzwiller KJ. 1985. Behavioral ecology and ethology of the prairie rattlesnake. Natl Geogr Res. 1:80–111.

Dyer O, Bishop C, Govindarajulu P, Anderson L, Cunnington D, Hobbs J, Huntley M, Larsen K, Reudink R, Sadler K, Sarell M, Steciw J, et al. 2016a. British Columbia recovery strategy series recovery plan for the Gopher Snake, deserticola subspecies (Pituophis catenifer deserticola) in British Columbia.

Dyer O, Bishop C, Govindarajulu P, Anderson L, Cunnington D, Hobbs J, Huntley M, Larsen K, Reudink R, Sadler K, Sarell M, Tedesco L, et al. 2016b. British Columbia recovery strategy series recovery plan for the Western Rattlesnake (Crotalus oreganus) in British Columbia.

Eye DM. 2022. Reproductive ecology of female Western Rattlesnakes (*Crotalus Oreganus*) in Canada [thesis]. [Kamloops (BC)]: Thompson Rivers University.

Gardiner LE, Sonmor KW. 2011. Reptiles major slump event at Grasslands National Park snake pit in southwestern Saskatchewan. Blue Jay. 69(3):120–124.

Gates DM. 1980. Biophysical ecology. New York(NY): Springer.

[GBC] Government of British Columbia. 2023. B.C. Conservation Data Centre; [accessed 2023 Jul 19]. https://www2.gov.bc.ca/gov/content/environment/plants-animals-ecosystems/conservation-data-centre.

[GC] Government of Canada. 2023. Critical habitat for species at risk national dataset – Canada; [accessed 2024 Mar 2]. https://data-donnees.az.ec.gc.ca/data/species/protectrestore/critical-habitat-species-at-risk-canada/

[GCC] The Grasslands Conservation Council of British Columbia. 2009. Working together for the conservation of BC’s grasslands. Kamloops.

Geiger R, Aron RH, Todhunter P. 2003. The climate near the ground. 6th ed. Oxford: Rowman and Littlefield Publishers.

Gienger CM, Beck DD. 2011. Northern pacific rattlesnakes (*Crotalus oreganus*) use thermal and structural cues to choose overwintering hibernacula. Can J Zool. 89(11):1084–1090.

Giani G. 1992. Rock slope stability analysis. Rotterdam: Balkema Publishers.

Goldberg AR, Conway CJ, Mack DE, Burak G. 2020. Winter versus summer habitat selection in a threatened ground squirrel. J Wildl Manag. 84(8):1548–1559.

Gomez LM. Habitat use and movement patterns of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) in British Columbia [thesis]. [Victoria (BC)]: University of Victoria.

Graves BM, Duvall D. 1995. Aggregation of Squamate reptiles associated with gestation, oviposition, and parturition. Herpetol Monogr. 9:102–119.

Gregory PT. 1974. Patterns of spring emergence of the red-sided garter snake (Thamnophis sirtalis parietalis) in the Interlake region of Manitoba. Can J Zool. 52:1063–1069.

Gregory PT. 2011. Temporal dynamics of relative-mass variation of red-sided garter snakes (thamnophis sirtalis parietalis) at a communal hibernaculum in manitoba. Écoscience. 18(1):1–8.

Hall LS, Krausman PR, Morrison ML. 1997. The habitat concept and a plea for standard terminology. Wildl Soc Bull. 25(1):173–182.

Hamilton BT, Nowak EM. 2009. Relationships between insolation and rattlesnake hibernacula. West N Am Nat. 69(3):319–328.

Haney A, Sarell M. 2005. Conservation analysis for the Great Basin Gophersnake (*Pituophis catenifer deserticola*) in British Columbia.

Harvey DS, Weatherhead PJ. 2006. Hibernation site selection by Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) near their northern range limit. J Herpetol.

Harvey JA, Larsen KW. 2020. Rattlesnake migrations and the implications of thermal landscapes. Mov Ecol. 8(1).

Hauke J, Kossowski T. 2011. Comparison of values of pearson's and spearman's correlation coefficients on the same sets of data. Quaest Geogr. 30(2):87–93.

Hein AM, Guyer C. 2009. Body temperature of overwintering Cottonmouth snakes: hibernaculum use and inter-individual variation. J Ala Acad Sci. 80(1): 35-44.

Hobbs J. 2007. Thermal factors in relation to the denning ecology of northern Pacific rattlesnakes in British Columbia [thesis]. [Victoria (BC)]: Royal Roads University.

Hosmer D, Lemeshow S. 2000. Applied logistic regression. 2nd ed. New York (NY): Wiley-Interscience.

Howarth CR., Bishop CA, Larsen KW. 2023. Western Rattlesnake (*Crotalus oreganus*) spring migration in British Columbia: a comparative study of juveniles and adults. Can J Zool. 101(7):530–540.

Howarth CR. 2023. Western Rattlesnake (*Crotalus oreganus*) migration and habitat use in British Columbia [thesis]. [Kamloops (BC)]: Thompson Rivers University.

Huey RB. 1991. Physiological consequences of habitat selection. Am Nat. 137:91–115.

Ismail N, Jemain AA. 2007. Handling overdispersion with negative binomial and generalized poisson regression models. In: Casualty Actuarial Society E Forum. p. 103–158.

Johnstone KC, McArthur C, Banks PB. 2021. Behavioural drivers of survey bias: interactive effects of personality, the perceived risk and device properties. Oecologia. 197(1):117–127.

Kéry M. 2002. Inferring the absence of a species: a case study of snakes. J Wildl Manag. 66(2):330-338.

Krausman PR. 1999. Some basic principles of habitat use. In: Launchbaugh KL, Sanders KD, Mosley JL, editors. Grazing Behaviour of Livestock and Wildlife. Moscow: University of Idaho. p. 85–90.

Lomas E, Larsen KW, Bishop CA. 2015. Persistence of northern Pacific Rattlesnakes masks the impact of human disturbance on weight and body condition. Anim Conserv. 18(6):548–556.

Maida J, Larsen K, Hooper C, Bishop C. 2017. *Crotalus oreganus* (Western Rattlesnake) Mortality. Herpetol Rev. 48(2):447.

Maida JR, Kirk DA, Mckibbin O, Row JR, Larsen KW, Stringam C, Bishop CA. 2018. Population estimate, survivorship, and generation time of the northern pacific rattlesnake (*Crotalus o. oreganus*) at its northern-most range limits. Herpetol Conserv Biol. 13(3):662–672.

Macartney JM, Gregory PT. 1988. Reproductive biology of Female Rattlesnakes (*Crotalus viridis*) in British Columbia. Copeia. 5(1):47–57.

Manitoba. 2024. Snakes of Narcisse; [accessed 2024 Feb 3]. https://www.gov.mb.ca/nrnd/fish-wildlife/snakes_narcisse/index.html.

Mardia K, Jupp P. 2000. Directional statistics. Barnett V, Cressie N, Fisher N, Johnstone I, Kadane J, Kendall D, Scott D, Silverman B, Smith A, Teugel J, editors. West Sussex: John Wiley and Sons Ltd.

Matsuda BM, Green DM, Gregory PT. 2006. Amphibians and reptiles of British Columbia. Victoria (BC): Royal BC Museum.

Mayor SJ, Schneider DC, Schaefer JA, Mahoney SP. 2009. Habitat selection at multiple scales. Écoscience. 16(2):238–247.

[MWLAP] Ministry of Water Land and Air Protection. 2004. Identified wildlife management strategy accounts and measures for managing identified wildlife southern interior forest region.

Murphy DD, Noon BR. 1991. Coping with uncertainty in wildlife biology. J Wildl Manag. 55(4):773–782.

Northrup JM, Vander Wal E, Bonar M, Fieberg J, Laforge MP, Leclerc M, Prokopenko CM, Gerber BD. 2022. Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. Ecol Appl. 32(1).

Parker WS, Brown WS. 1973. Species composition and population changes in two complexes of snake hibernacula in northern Utah. Herpetol. 29(4):319–326.

Parker WS, Brown WS. 1980. Comparative ecology of two Colubrid snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucus deserticola*, in northern Utah. Milwaukee (WI): Milwaukee Public Museum.

Posit Software. 2023. RStudio IDE; [accessed 2024 Feb 3]. https://posit.co/products/open-source/rstudio/.

Prior KA, Weatherhead PJ. 1996. Habitat features of Black Rat Snake hibernacula in Ontario. J Herpetol. 30(2):211–218.

Reinert HK, Cundall D. 1982. An improved surgical implantation method for radio-tracking snakes. Source: Copeia. 1982(3):702–705.

Ripley B, Venable B, Bates DM, Hornik K, Gebhardt A, Firth D. 2023. MASS: support functions and datasets for venables and Ripley's MASS; [accessed 2023 Apr 7]. https://cran.r-project.org/web/packages/MuMIn/index.html.

Schmidt DA, Govindarajulu P, Larsen KW, Russello MA. 2020. Genotyping-in-thousands by sequencing reveals marked population structure in Western Rattlesnakes to inform conservation status. Ecol Evol. 10(14):7157–7172.

Shine R, LeMaster MP, Moore IT, Olsson MM, Mason RT. 2001. Bumpus in the snake den: effects of sex, size, and body condition on mortality of red-sided garter snakes. Evol. 55(3):598–604.

Shine R, Mason RT. 2004. Patterns of mortality in a cold-climate population of garter snakes (*Thamnophis sirtalis parietalis*). Biol Conserv. 120(2):201–210.

Therneau TM, Lumley T, Elizabeth A, Cynthia C. 2023. survival: Survival analysis; [accessed 2024 Feb 3].https://cran.r-project.org/web/packages/survival/index.html

Thomas DL, Taylor EJ. 2006. Study designs and tests for comparing resource use and availability II. Source: J Wildl Manag. 70(2):324–336.

Trans Mountain. 2021a. Time flies: one year of construction in the Kamloops urban area; [accessed 2024 Feb 3]. https://www.transmountain.com/news/2021/time-flies-one-year-of-construction-in-the-kamloops-urban-area#:~:text=What%20a%20year%20it%20has,the%20Trans%20Mountain%20Expansion%20Project.

Trans Mountain. 2021b. Snakes on a plain – salvaging snakes in the BC Interior; [accessed 2024 Feb 3]. https://www.transmountain.com/news/2021/snakes-on-a-plain-salvaging-snakes-in-the-bc-interior.

Williams KE, Hodges KE, Bishop CA. 2012. Small reserves around hibernation sites may not adequately protect mobile snakes: the example of great basin gophersnakes (Pituophis catenifer deserticola) in British Columbia. Can J Zool. 90(3):304–312.

Williams KE, Hodges KE, Bishop CA. 2014. Phenology and demography of great basin gophersnakes (*Pituophis catenifer deserticola)* at the northern edge of their range. Herpetol Conserv Biol. 9(2):246–256.

Williams KE, Hodges KE, Bishop CA. 2015. Hibernation and oviposition sites of Great Basin Gophersnakes (*Pituophis catenifer deserticola*) near their northern range Limit. J Herpetol. 49(2):207–216.

Winger BM, Auteri GG, Pegan TM, Weeks BC. 2019. A long winter for the red queen: rethinking the evolution of seasonal migration. Biol Rev. 94(3):737–752.

Zappalorti RT, Burger J, Burkett DW, Schneider DW, McCort MP, Golden DM. 2014. Fidelity of northern pine snakes (*Pituophis m. melanoleucus)* to natural and artificial hibernation sites in the New Jersey Pine Barrens. J. Toxicol. Environ. Health - A: Curr. Issues. 77(21):1285–1291.

Zimova M, Hackländer K, Good JM, Melo-Ferreira J, Alves PC, Mills LS. 2018. Function and underlying mechanisms of seasonal colour moulting in mammals and birds: what keeps them changing in a warming world? Biol Rev. 93(3):1478–1498.

CHAPTER 3

ARTIFICIAL SNAKE HIBERNACULA PROVIDE SUITABLE MICROCLIMATIC CONDITIONS BUT ARE NOT READILY ADOPTED

INTRODUCTION

The irrevocable impact of habitat loss on global biodiversity demands innovative solutions to mitigate the effect (Hanski 2011; Banks-Leite et al. 2020; Gonçalves-Souza et al. 2020). To address this loss, artificial structures have gained popularity to compensate for lost habitat features (Rueegger 2016; Rueegger 2019; Fontaine et al. 2021; Tillman et al. 2021; McComb et al. 2022). These structures can include habitats such as nest boxes for birds (Fontaine et al. 2021; Sudyka et al. 2023), dens for mammals (McComb et al. 2022), ponds for amphibians (Cook et al. 2023), and refugia for reptiles (Arida and Bull 2008).

Habitat plays a crucial role in the thermoregulatory behaviour of organisms (Long et al. 2005; Scheffers et al. 2014; Milling et al. 2017). Ideally, the microclimatic conditions of artificial refugia should model natural habitat, enabling the target species to thermoregulate and, consequently, improving the overall success of the offset (Rueegger, 2019). However, studies have shown considerable variation in the quality of the microclimate of artificial structures compared to their natural counterparts (Griffiths et al. 2018; Fontaine et al. 2021; McComb et al. 2022; Sudyka et al. 2023). Such research underscores the need to understand the microclimate of artificial structures before their use or reliance as a conservation or mitigation measure.

As ectotherms, snakes are unable to metabolically regulate their internal temperature (Huey and Stevenson 1979; Hein and Guyer 2009). Thus, their behaviour, ecology, and physiology are largely dictated by available environmental temperatures (Huey and Stevenson 1979; Hein and Guyer 2009). In temperate regions overwinter, snakes either succumb to the elements or find a hibernaculum that meets the structural, thermal, and humidity conditions needed to survive (Brown et al. 1974; Prior and Weatherhead 1996; Hein and Guyer 2009). Such sites should sufficiently buffer against the external overwintering conditions to ensure snakes do not freeze and are not expending energy reserves (Gregory 1982; Costanzo 1989a; Williams et al. 2015; Markle et al. 2020) while also providing sufficient humidity to prevent desiccation (Costanzo 1986). For instance, the potential dependency on snow insulation has been shown at natural hibernacula for Red-sided Garter Snakes (*Thamnophis sirtalis parietalis*) in Manitoba (Shine and Mason 2004), where years with lighter snow cover result in major mortality events (Shine and Mason 2004). This dependency showcases the importance of understanding environmental factors and the specific seasonal requirements of the focal species when building artificial habitats.

The microclimate within artificial snake hibernacula has been investigated relatively little: research only has investigated the thermal requirements of snakes within incidental hibernacula created as a by-product of anthropogenic practices (i.e. human-created slopes, construction debris, abandoned mine features, etc.) or those intentionally created for research purposes, as opposed to those built for conservation or as mitigation measures (Gillingham and Carpenter 1978; Costanzo 1986; Bryan 2015; Choquette et al. 2024). For example, Costanzo (1986) monitored an incidental artificial snake hibernaculum within a buried cylindrical cistern that provided access to a stable thermal environment within water for Common Garter Snakes (*Thamnophis sirtalis*). More recently, unoccupied artificial hibernacula built out of plumbing hardware buffered against external environmental variation, while providing low mean temperatures, and high humidity (Choquette et al. 2024). These studies showcase the potential of artificial sites to provide optimal microclimatic conditions. However, due to differences in application, such results provide limited insight into the microclimate and its influence on the colonization and efficacy of artificial snake hibernacula built as mitigation measures.

The northern extremes for snake species (Matsuda et al. 2006) provide optimal locations to test the thermal suitability of artificial snake hibernacula. Within the Canadian province of British Columbia, artificial hibernacula are increasingly being turned to as a means to compensate for the loss (intentional or unintentional) of natural hibernacula for a number of snake species (MFLNRO 2016; TranBC n.d.). Given this trend, detailed work comparing the microhabitat afforded by natural and anthropogenic features is becoming increasingly important. This is imperative given the extreme winters of northern latitudes, where overwinter survival depends heavily on animals finding and using appropriate hibernacula. However, data of this nature remain scant.

The recent construction of artificial snake hibernacula following the excavation of hibernacula for three threatened snake species in British Columbia, Canada, provided a unique opportunity to monitor the thermodynamics of the structures. Our objectives were to (i) highlight the resulting microclimate within each hibernaculum and assess how well it buffered against external environmental conditions, (ii) determine whether the internal thermal conditions of the hibernacula were comparable to those naturally experienced by snakes, and (iii) monitor the adoption of the main artificial hibernaculum by the original cohort of displaced snakes.

METHODOLOGY

Study Site

This study was conducted near the city of Kamloops, British Columbia, Canada, in the Lac du Bois Grasslands Protected Area (51° N, 120.4° W) (BC Parks 2017) (Figure 1.2). This region experiences some of the driest and warmest conditions in the province, with short winters and hot summers (BC Parks 2017). The study area features a mosaic of Bluebunch Wheatgrass (*Pseudoroegneria spicata*), Big Sagebrush (*Artemisia tridentata*), and spring-blooming plants found primarily in lower and middle grasslands (BC Parks 2017). The park is impacted by anthropogenic activities, such as recreational use, bordering residential neighbourhoods, livestock grazing, and pipeline construction (GCC 2009; BC Parks 2017; Trans Mountain 2021a). Refer to Chapter 1 for further details on the climatic and biogeographic conditions of the study area.

Three threatened snake species, the Great Basin Gophersnake (*Pituophis catenifer deserticola*), Western Yellow-bellied Racer (*Coluber constrictor mormon*), and Western Rattlesnake (*Crotalus oreganus oreganus)*, all meet their northern range limit near our study site (Matsuda et al. 2006). Following spring emergence (egress, March-May) and an active season (April-September) spent foraging and reproducing, the snakes return to their hibernacula (ingress, August-October) (pers. observ.) to avoid inclement weather and sub-zero temperatures of winter (October-March) (Costanzo, 1986; Gienger & Beck, 2011; pers. observ.). Snakes in the study area overwinter in rocky outcrops, talus slopes, rodent burrows, and anthropogenic features (see Chapter 2).

Disturbance Event

Disturbance to natural snake hibernacula occurred during the Trans Mountain Expansion Project (TMEP), a venture to expand oil transportation in western Canada by constructing a twin pipeline parallel to the existing one built in 1951 (Trans Mountain 2023a,b). One portion of this project required a linear excavation ~9.2 km long (~30 m wide) within the boundaries of the Lac du Bois Grasslands Protected Area, starting in 2020 (Trans Mountain Pipeline ULC 2017; Trans Mountain 2021c).

Wildlife biologists contracted by TMEP conducted reptile sweeps, habitat assessments, and snake salvages from September 21 to October 16, 2020 (Heinrich 2020). During construction, three snake hibernacula were excavated within a 1.6km straight-line distance along the pipeline right-of-way (Heinrich 2020). Prior to October 15, salvaged snakes were relocated to neighbouring natural hibernacula; these animals included 10 rattlesnakes, 12 gophersnakes, and 13 racers (Heinrich 2020). Unfortunately, as it is not a regulatory requirement these snakes were not marked for future identification prior to release. Snakes recovered after October 15 were transferred to the BC Wildlife Park for artificial overwintering; this sample included 37 gophersnakes and 56 racers (Heinrich 2020). Snakes were overwintered in containers within fridges maintained at ∼4°C (ranging from 2°C to 8°C). The bottom of the container was filled with coconut fibre substrate, and each container was outfitted with a container of water to provide humidity.

Artificial Hibernacula

Mitigation efforts in the field began in late April to mid-May 2021, when TMEP designed and constructed two artificial hibernacula to compensate for the lost overwintering habitat (Figure 1) (Trans Mountain 2021a; Trans Mountain 2021b). Both artificial hibernacula were offset roughly 50 m south from the original hibernacula locations (Heinrich 2020; Trans Mountain 2021a,b). These locations were selected for their proximity to the original hibernacula and distance from future disturbance (i.e., pipeline maintenance and recreational trails) while ensuring a similar microhabitat, aspect, and slope (Heinrich 2020; Trans Mountain 2020).

Rock and soil salvaged during the excavation of the original hibernacula were strategically placed at the base of the artificial hibernacula to create interstitial spaces (Trans Mountain 2020, 2021). Small to medium-sized rocks (0.1-0.3m) were used towards the front of the hibernacula to reduce access to predators, with larger rocks being used towards the rear (0.3-0.75m) (Heinrich 2020; Trans Mountain 2021b). The rocks were installed at a 2.5% grade upwards from the front to promote drainage and reduce cold air (Heinrich 2020; Trans Mountain 2021a,b). A layer of geotextile cloth was placed over the rocks to prevent the 2.5-3.0m layer of soil placed on top from filling the interstitial spaces (Heinrich 2020; Trans Mountain 2021a,b). In total, the interior floor area of the first artificial snake hibernacula (ASH1) was ~ 262m^2, and the second (ASH2) was ~ 150m^2 (as estimated during construction). ASH1 was constructed at an elevation of ~520m, and ASH2 at ~480m.

During the construction of the artificial hibernacula, PVC standpipes were added to allow the monitoring of internal temperature and humidity data (Figure 3.1). Nine standpipes were added to ASH1, and eight to ASH2 (Figure 3.1). For each hibernaculum, temperature standpipes were arranged into three rows (Back, Middle, Front – see Figure 3.1). The back standpipes of ASH1 reach an average depth of 4.0m (ASH2 2.8m), the middle 3.6m (ASH2 3.0m), and the front 3.1m (ASH2 2.6m). HOBO U23 Pro v2 Temperature and Relative Humidity Data Loggers (ONSET, Bourne, MA, USA) were deployed into each standpipe to monitor the internal conditions every hour.

Snake Release

All snakes overwintering at the BC Wildlife Park were released at ASH1 between April 31 and May 3, 2021. No snakes were released at ASH2 as construction on that site was not completed until mid-May, after the natural egress of snakes in the region had been completed (McKelvey and Ragsdale, pers. obs.). All snakes released at ASH1 were implanted with passive integrated transponders (PIT tags) (Biomark Inc., Boise, ID, United States) to permit individual identification, and relatively larger animals were selected for radiotelemetry (see Radiotelemetry below). A 'soft release' approach was used to reintroduce snakes to the wild (Mitchell et al. 2011): To do this, a 1.8 m tall fence, created with overlapped chicken wire (outside) and window screen mesh (inside), was erected around the hibernacula mouth. To prevent escape, the foot of the fence was buried roughly 10 cm underground and the top was equipped with a 10 cm fold (90°) to hinder climbing.

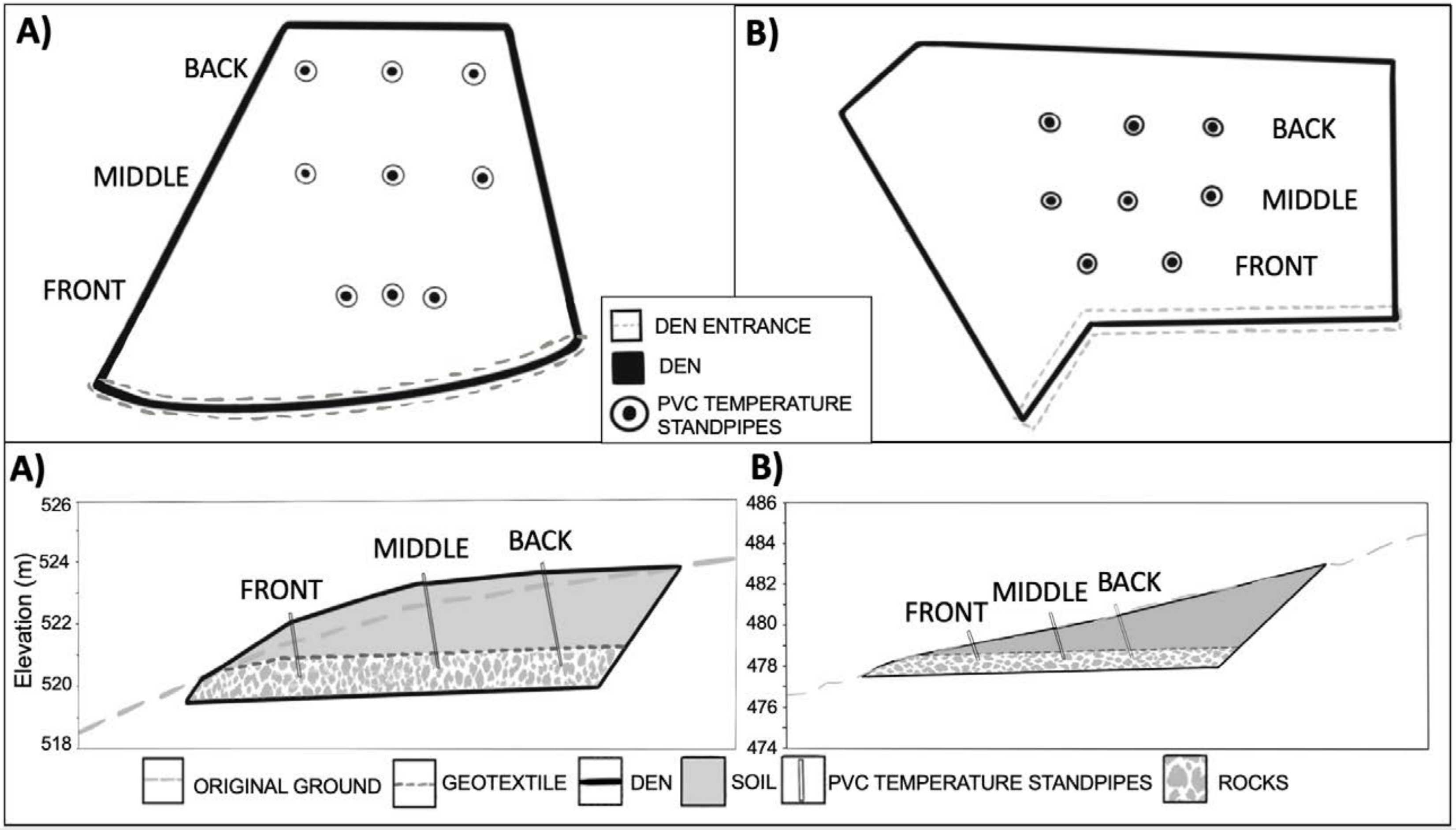


Figure 3.1: Schematic of (A) artificial hibernaculum 1 and (B) artificial hibernaculum 2. The figures in the top row provide an overhead view and shows the spatial relationship of the temperature standpipes in reference to each other and the hibernaculum mouth. The figures in the bottom row provide side profiles. ‘Back’ refers to temperature standpipes in the same row furthest from the hibernaculum entrance, with the front row being those closest to the hibernaculum mouth. All figures were adapted from Trans Mountain (2021b,c). Not drawn to scale.

Radiotelemetry

Radiotelemetry was employed to facilitate a concurrent study on the movement ecology of the translocated gophersnakes and racers (Ragsdale MSc *in prep*) but also helped this study record the overwintering temperatures of snakes. In 2021, telemetered snakes included a subset released at ASH1 plus 'reference snakes'. Reference snakes in 2021 and all telemetered snakes in 2022 were captured during hibernacula surveys or opportunistically during the active season. Snakes released at natural hibernacula and not marked following the disturbance event (see Disturbance Event above) could be included in our sample of reference snakes, as there was no way to differentiate these individuals reliably. Telemetered racers were excluded from this study. Due to their smaller size, racers often could not carry transmitters large enough to facilitate tracking to hibernacula. No rattlesnakes were tracked, as all displaced rattlesnakes were moved to natural hibernacula without prior identification.

Surgically-implanted transmitters did not weigh more than 4% of the body weight of the captured snakes (SB-2T 3.8g six-month battery, or SB-2T 5.2g 12-month battery; Holohil Systems Ltd., Carp, ON, Canada) (Bryant et al. 2010). Select gophersnakes in 2022 were implanted with SB-2T (12-month battery) transmitters with a temperature data logger (iButton DS1925L-F5 3g; Maxim Integrated Products Inc., San Jose, CA, United States) modification (9.5g, see Figure 3.2). After programming to record hourly temperature, the iButton was glued to the antenna-less end of the radio transmitter (Figure 3.2) (Hobbs 2007; Nordberg and Cobb 2017; Crowell 2019). Beeswax was added to streamline the connection, and the entire transmitter+iButton unit was coated twice in rubber Plasti Dip (Plasti Dip International, Inc, Blaine, MN, USA) to waterproof it (Figure 3.2) (Taylor et al. 2004; Hobbs 2007; Crowell 2019). Implantations were performed by licensed veterinarians following modified methodologies similar to Reinert and Cundall (1982). Implantations occurred just over midway between the distance from the cloacal vent to the snout of each animal. The antennae were fed caudally under the skin rather than cranially. Individuals were tracked every 2-3 days throughout the active season, from April to October. Monitoring continued until the animals selected hibernacula, which occurred when an individual persisted in a location from fall into winter. In winter 2021-2022, snakes with temperature-sensitive radio transmitters were tracked biweekly from ingress to egress to obtain temperature. Individuals were caught for transmitter removal in the ensuing egress.

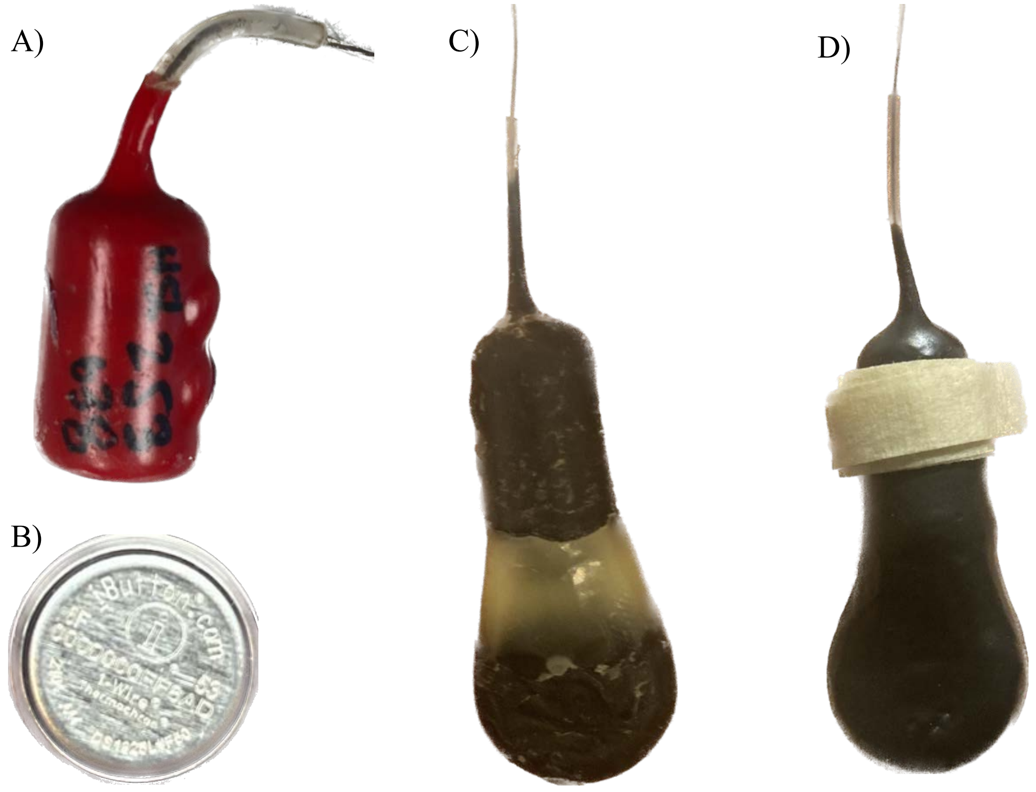


Figure 3.2: SB-2T radio transmitter (Holohil Systems Ltd., Carp, ON, Canada) and DS1925L-F5 iButton (Maxim Integrated Products Inc., San Jose, CA, United States) modification. A) The transmitter prior to modification. B) The iButton prior to modification. C) The iButton and transmitter after one coat of rubber Plasti Dip and beeswax. D) The final product with another layer of rubber Plasti Dip (note that the tape held a magnet on the battery and was removed before implantation). In all photos the antenna has been cropped (actual length was 22cm). Photos by author.

Hibernacula Monitoring

During egress and ingress, hibernacula surveys took place daily at ASH1. Natural hibernacula were coincidentally monitored during these periods to mark when snakes had started naturally returning or leaving. During these periods, the fence was erected and equipped with funnel traps (Figure 3.3). The direction of the funnels and the coupling of mesh holding boxes (traps) allowed us to intercept all snakes attempting to leave (egress) or enter (ingress) the hibernaculum. Funnels equipped with traps were monitored twice daily (in the morning when entering the field and late afternoon when leaving the field) and closed if (i) overnight temperatures dropped below 5°C or (ii) the monitoring schedule could not be adhered to. Cover boards provided the traps with shade from the elements, and a synthetic upholstery covered the exposed trap floors (Burgdorf et al. 2005). The fencing apparatus on ASH1 was erected well before the first observed snakes at natural hibernacula and kept in place until the emergence of snakes at natural hibernacula was complete (i.e. no snakes were detected and/or the same individuals were recaptured across multiple visits).

To establish the artificial hibernacula and ensure displaced snakes reached overwintering habitat, snakes found in this area previously impacted by the disturbance were actively moved into the ASH1 fence line during ingress 2021. Coincident to our own work, Trans Mountain had the responsibility to move any snakes (both displaced and reference) found in the pipeline construction footprint to the closest hibernacula (by default ASH1) during ingress 2021. The following ingress, we monitored for the natural return of snakes, and since construction was over, no snakes were forcefully moved to ASH1 in 2022. Any captured individuals not already tagged were subcutaneously implanted with a PIT tag.

External Conditions

In conjunction to monitoring the internal artificial hibernacula conditions, HOBO TidbiT v2 Water Temperature Data Loggers (ONSET, Bourne, MA, USA) were placed in the shade around the study site to monitor external air temperature. Wildlife cameras (Reconyx, Holmen, WI, United States) assessed snow depth on top of and in front of both artificial hibernacula mouths by taking pictures of mounted meter sticks every hour throughout winter.

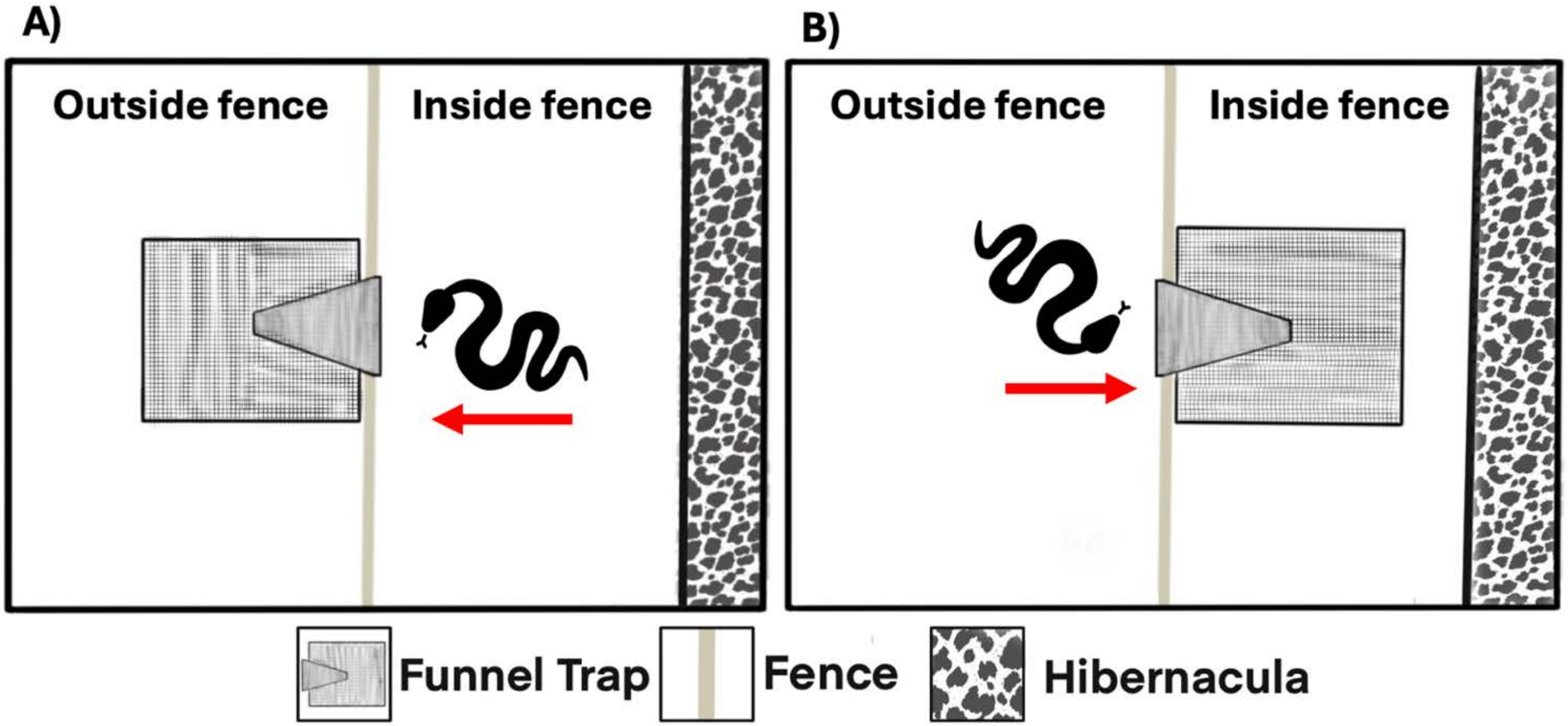


Figure 3.3: Funnels traps used to catch snakes at artificial snake hibernaculum 1 (A) Spring emergence (egress) orientation to catch snakes as they exit, (B) Fall return (ingress) orientation to catch snakes as they return. Arrows indicate the direction of snake movement. Not drawn to scale.

Statistical Analysis

Daily average temperature and humidity readings were used for all subsequent analyses as the mean of the 24 consecutive hourly data points recorded on a given calendar day (Amat-Valero et al. 2014). For each artificial hibernaculum, temperature and humidity recorded by loggers within the same row were averaged together (Back, Middle, Front – see Figure 3.1). Weekly or monthly oscillation was calculated as the difference between the maximum and the minimum value in that period (Amat-Valero et al. 2014). All statistical analyses were performed using RStudio (Posit Software 2023).

Environmental Variation

Data from November 1st, 2021, to March 31st, 2022, were used to determine the impact of external conditions on the internal microclimate. External air temperature profiles collected across the site were averaged together (Griffiths et al. 2018). Relative humidity of the broader environment was measured at the Kamloops A (50 ° N, 120 ° W) weather station (ECCC 2023). We assessed the temporal coherence of the average daily temperature and humidity between outside and inside conditions for both hibernacula using Spearman's coefficient (Hachem et al. 2012; Nordberg and Cobb 2017). To determine the importance of snow insulation on internal hibernacula conditions, we compared weekly temperature oscillation for each hibernaculum at every position for time with snow and without snow utilizing either an unpaired t-test or a Wilcoxon rank sum test depending on normality.

Temperature of Snakes

The temperatures of telemetered snakes that overwintered in ASH1 in 2021-2022 were compared to those of reference and displaced snakes that overwintered elsewhere in natural hibernacula. This comparison was conducted using either an ANOVA or a Kruskal-Wallis test, depending on normality.

To determine if and where the artificial hibernacula met the thermal requirements for overwintering snakes, the average daily temperature at the different positions within the artificial hibernacula was compared against the average, maximum, and minimum daily snake body temperature obtained through transmitter+iButton implantation from November 1st, 2022, to March 31st, 2023. All comparisons were made using a repeated measures ANOVA or non-parametric Friedman rank sum test depending on normality (Thierry et al.

2009; Roznik and Alford 2012). In all cases, temperature or humidity was the dependent variable, position (or snake) was the factor, and time between measures was the repeated measure (Roznik and Alford 2012). If significant, a pairwise t-test or exact p-values post hoc test was performed (Eisinga et al. 2017; Pohlert 2023). To determine what region of the artificial hibernacula best corresponded to the temperatures being experienced by snakes in natural hibernacula, we superimposed the snakes' temperature profiles with the temperature profiles of the artificial hibernacula over time (Forget-Klein and Green 2021).

RESULTS

Microclimate of Artificial Hibernacula

Data from November 1st, 2021 - March 31st, 2022 were used to compare the overwintering microclimate between and within the artificial hibernacula. All nine deployed loggers were recovered from ASH1, three in each position (Figure 3.1). At ASH2, a failure in the ropes used to retrieve the monitors enabled only six of the eight deployed loggers to be recovered, two in each position (Figure 3.1). Overall, the artificial hibernacula experienced average interior winter temperatures of 9.3°C (ASH1) and 7.9°C (ASH2), ranging from 3.3°C to 16.6°C (ASH1) and 2.5°C to 14.2 °C (ASH2) (Figure 3.4). The back of ASH1 was warmer on average (10.7±1.9°C) than the middle (9.6±2.5°C) or front (7.9±2.5°C), with lower average monthly oscillation (1.3±0.5°C) than the middle (1.7±0.7°C) or front (2.3±0.7°C). Similarly, the back of ASH2 (8.8±2.4°C) was warmer on average than the middle (8.1±2.2°C) and the front (6.9±2.2°C), with lower average monthly oscillation (2.0±1.1°C) than the middle (1.7±0.9) or front (2.4±0.7). The artificial hibernacula experienced average relative humidity of 99.5% (ASH1) and 97.4% (ASH2), ranging from 84.7% (ASH1) and 77.4% (ASH2) to 100% (Figure 3.5). No obvious trend was found in the average humidity between positions, with similar average humidity recordings in the back (ASH1 99.9±0.2%; ASH2 99.9±0.02%), middle (ASH1 100.0±0.0%; ASH2 93.7±4.9%) and front (ASH1 98.7±1.7%; ASH2 98.5±2.5%). However, the front of ASH1 had the most unstable humidity (3.9±3.6%) with higher average monthly oscillation than the middle (0.0±0.0%) or back (0.3±0.3%). While the middle (12.4±6.5%) of ASH2 had the most unstable monthly humidity compared to the back (1.4±3.2%) and front (7.5±6.1%).

Effect of Environmental Variation

From November 1, 2021, to March 31, 2022, six loggers recorded ambient air temperature across the study site, averaging -0.4°C and ranging from 27.4°C to -30.4 °C (Figure 3.4). During this time, relative humidity measured at the Kamloops A (50 ° N, 120 ° W) weather station (ECCC 2023) was, on average, 72.8%, ranging from 99.0% to 16.0% (Figure 3.5). All correlations between external ambient and internal hibernacula temperatures were found to be negative, weak correlations with Spearman's ρ ranging from -0.04 to -0.25 (ASH1 back and middle, ρ= -0.25, P=<0.01; ASH1 front, ρ= -0.22, P=<0.01; ASH2 Back, ρ= -0.21, P=<0.01; ASH2 middle, ρ= -0.16, P=0.06; ASH2 front, ρ= -0.04, P=0.65). Similarly, correlation between external ambient and internal hibernacula humidity were found to be weak correlations ranging from -0.05 to 0.29 (ASH1 back, ρ= 0.29, P=<0.01; ASH1 front, ρ= -0.26, P=<0.01; ASH2 back, ρ= 0.07, P=0.43; ASH1 middle, ρ= -0.1, P=0.24; ASH1 front ρ= -0.05, P=0.56). No Spearman correlation coefficient could be determined for the middle of ASH1 as it sat consistently at 100% relative humidity throughout this period. Although some of these correlations were significant, the relationships were still weak or negative, indicating low and sometimes inverse correlation with external conditions. The lack of temporal coherence was further supported during a cold snap between December 22, 2021, and January 3, 2022, as internal hibernacula conditions remained relatively stable (Figure 3.4). When the external temperature dropped to a minimum of -30.4°C on December 27, 2021, internal conditions ranged from 8.3°C to 11.7°C (ASH1) and 6.1°C to 9.4°C (ASH2) (Figure 3.4). External humidity reached a minimum of 16% on March 8, 2022, and internal conditions in ASH1 ranged from 98.4.0 to 100%, and ASH2 ranged from 94.5% to 100.0%.

Due to the failure of two cameras overwinter (top and bottom of ASH2), the average reading of snow depth was retrieved from the wildlife cameras positioned on the top and bottom of ASH1. No significant variance was seen in the fluctuation of weekly temperatures between periods with snow and without snow from November 1, 2021, to March 31, 2022, across the various datalogger positions and hibernacula (Appendix D).

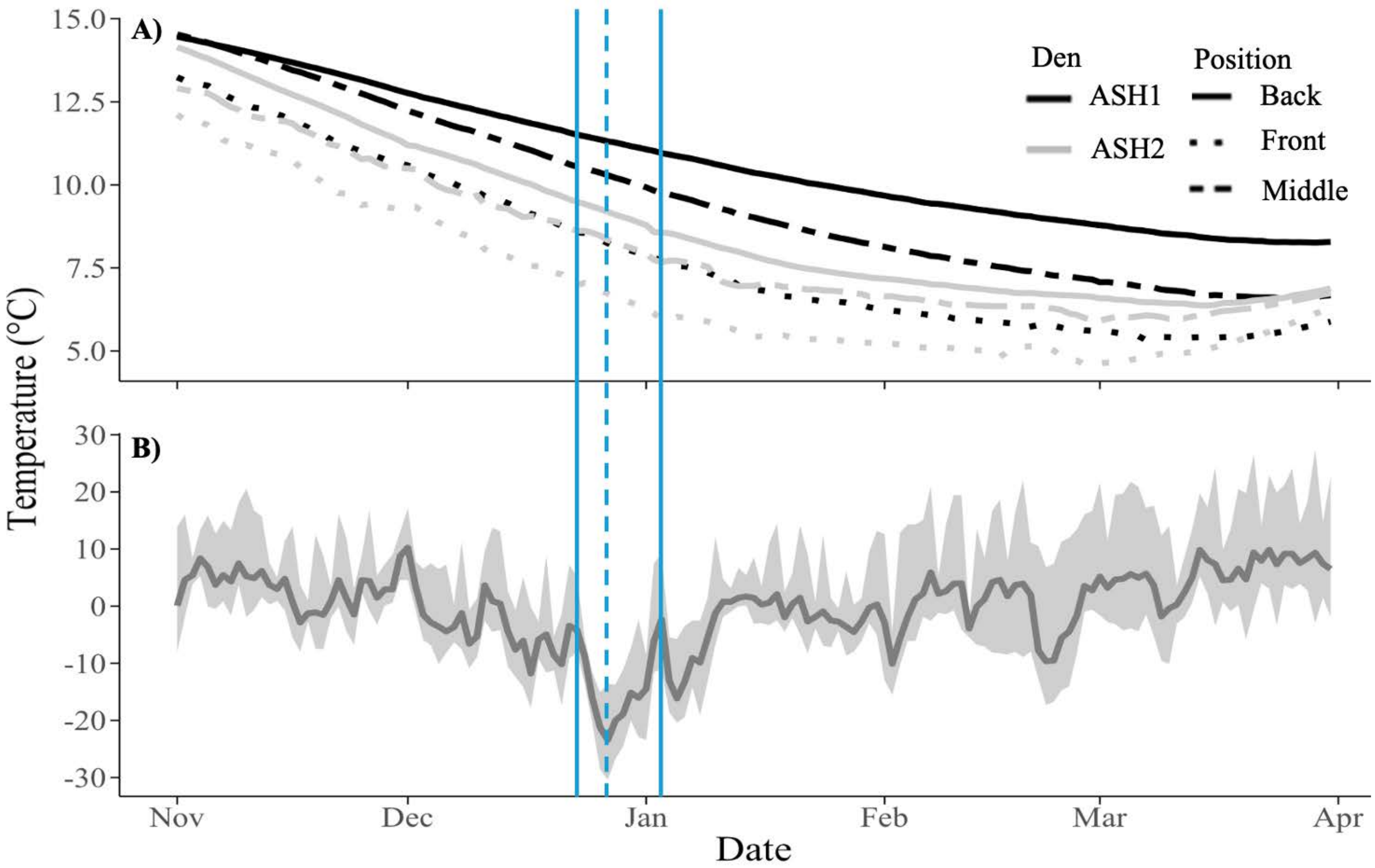


Figure 3.4: The average daily winter temperature from November 1, 2021, to March 31, 2022, for (A) each position within artificial snake hibernaculum 1 (ASH1) and artificial snake hibernaculum 2 (ASH2) and (B) the external ambient air. 'Position' refers to the distance of loggers to the hibernaculum mouth, where 'Back' is the furthest and 'Front' is the closest (Figure 3.1). Each line is the average of the loggers (n=3 for each position in ASH1, n=2 for each position in ASH2, and n=6 for external). The cloud around the ambient line represents the daily maximum and minimum. The solid vertical lines indicate a severe cold interval from December 22, 2021, to January 3, 2022, with the dashed vertical line showcasing the minimum external temperature (December 27, 2021).

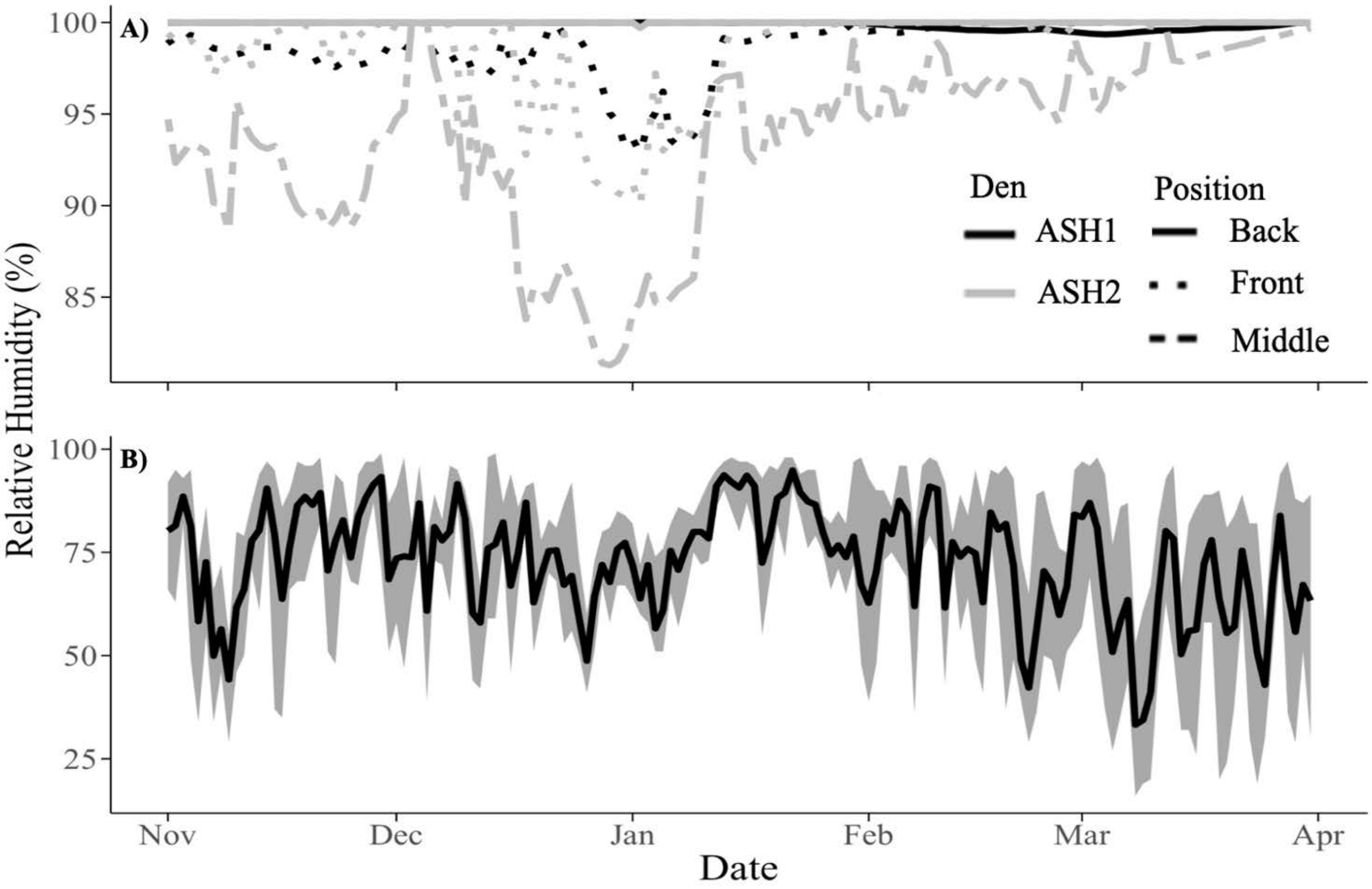


Figure 3.5: The average daily relative humidity from November 1, 2021, to March 31, 2022, for (A) each position within artificial snake hibernaculum 1 (ASH1) and artificial snake hibernaculum 2 (ASH2) and (B) the external ambient air. ‘Position’ refers to the distance of loggers to the hibernaculum mouth, where ‘Back’ is the furthest and ‘Front’ is the closest (Figure 3.1). Each line is the average of the loggers (n=3 for each position in ASH1, n=2 for each position in ASH2). Ambient relative humidity data was obtained from the Kamloops A (50 ° N, 120 ° W) weather station (ECCC 2023). The cloud around the ambient line represents the daily maximum and minimum.

Temperature of Snakes

Comparison of snakes in artificial and natural hibernacula

Overall, 13 telemetered gophersnakes had their body temperatures recorded remotely on five occasions from December 6, 2021, to February 1, 2022. One snake in a natural hibernaculum was omitted from the comparison due to missing values during this period. Temperatures taken after February 1, 2022, were omitted when many telemetry batteries had expired. During this period, the two snakes overwintering in ASH1, on average, 12.5°C, ranging from 9.6°C to 14.9°C. Snakes previously displaced and overwintering in natural hibernacula (n= 6) were, on average, 11.4°C, ranging from 7.1°C to 15.3°C. Reference snakes in natural hibernacula (n=4) were, on average, 13.0°C, ranging from 7.0°C to 18.9°C. Overall, gophersnakes overwintering in ASH1 did not experience significantly different overwintering temperature from snakes naturally overwintering on the same landscape (ANOVA, $F_{2,57=}2.90$, P=0.06).

Artificial hibernacula conditions versus naturally overwintering snakes

Four of 7 gophersnakes implanted with radio transmitters+iButtons were successfully retrieved following the 2022-2023 winter. All individuals overwintered in different natural hibernacula. The overwintering body temperatures of these snakes were, on average, 7.8 °C, ranging from 4.5°C to 17.0°C from November 1st, 2022, to March 31st, 2023 (Figure 3.6). At the same time, only five loggers were retrieved from each artificial hibernacula: two from the front of ASH2, three from the middle of ASH1, one from the middle of ASH2, and two from the front of each hibernacula. Internal temperatures were, on average, 9.2°C (ASH1) and 7.9°C (ASH2), ranging from 4.2°C to 16.3°C (ASH1) and 2.4°C to 16.1°C (ASH2) (Figure 3.6).

The overall difference between average daily temperature profiles at different positions within the artificial hibernacula and the maximum, minimum, and average temperature of snakes was significant (Friedman rank sum test, $\chi\,2$ = 950.35 (7), P< 2.2e-16) (Figure 3.6; Appendix E). All positions were significantly different from naturally overwintering snakes except the average daily temperature of snakes with the front of ASH1 (Post hoc exact test, P= 0.3674) and the middle of ASH2 (Post hoc exact test, P= 0.1107), the back of ASH2 and the maximum daily snake temperature (Post hoc exact test, P= 0.5414), and the front of ASH2 and the minimum daily snake temperature (Post hoc exact test, P= 1.0000) (Figure 3.6; Appendix E). This is reflected in a comparison of the thermal profile of the average, overall maximum and overall minimum of these gophersnakes with the thermal profiles of the artificial hibernacula (Figure 3.6). In particular, the average daily temperature of these snakes mirrored the temperature profile of the front of ASH1 and the middle of ASH2, found at depths of 3.1m and 3m, respectively. The maximum snake temperatures overwinter mirrored the temperature profile of the back of ASH2 found at a depth of 2.8m, and the minimum snake temperatures mirrored the front of ASH2 at a depth of 2.6m.

Snake Adoption of ASH1

Overall, 41 snakes (9 gophersnakes, 29 racers, and 3 rattlesnakes) were placed in ASH1 in the fall of 2021. Of these animals, 19 (4 gophersnakes, 15 racers) were from the original displaced population. All of these snakes were introduced by the research team or consultants, except for 3 individuals found trying to enter the fence or funnel traps on their own (1 gophersnake, 2 racers), with the gophersnake and one racer being from the original displaced population. Only 7 of these 41 snakes (3 gophersnakes, 4 racers), 6 being from the displaced population (3 gophersnakes, 3 racers), were confirmed to have overwintered when caught the following spring. We cannot comment on the overall survival of snakes, as during ingress (Fall) 2021, we observed at least 15 individuals, previously placed inside the fenced enclosure, outside of ASH1 (i.e. escaping the fence line, or finding an alternative exit). Although the snakes were placed back into the ASH1 enclosure if found, it is unclear how many left during this time. Three newly identified snakes naturally came to ASH1 in the fall of 2022 (2 rattlesnakes and 1 racer), and the two rattlesnakes were confirmed to have overwintered in the spring of 2023.

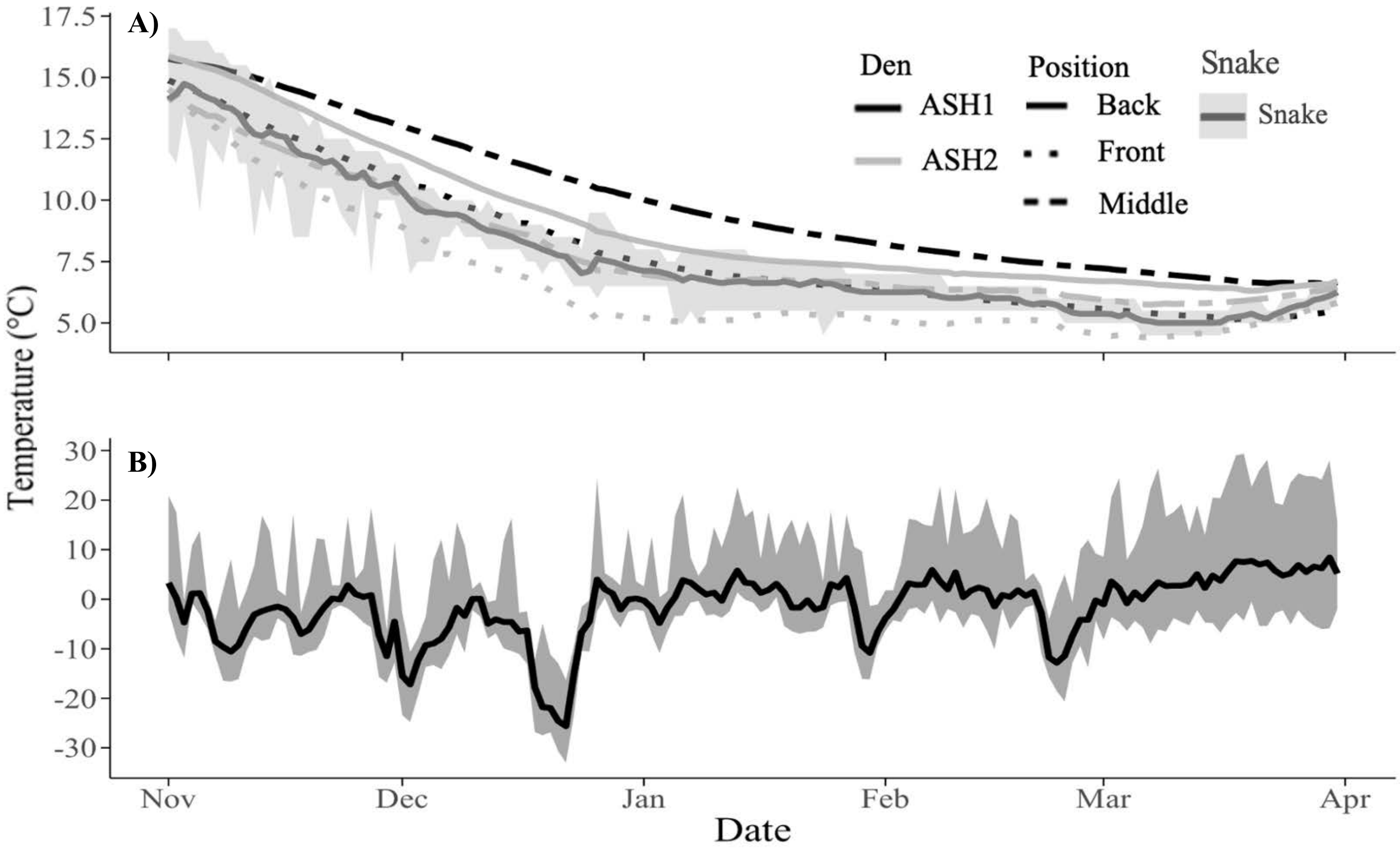


Figure 3.6: The average daily winter temperature from November 1, 2022, to March 31, 2023 of (A) Great Basin Gophersnakes hibernating in natural hibernacula superimposed on the temperature profiles of each position within artificial snake hibernaculum 1 (ASH1) and artificial snake hibernaculum 2 (ASH2) and (B) the external ambient air. 'Position' refers to the distance of loggers to the hibernaculum mouth, where 'Back' is the furthest and 'Front' is the closest (Figure 3.1). Each line is the average of the loggers (2 from the front of ASH2, 3 from the middle of ASH1, 1 from the middle of ASH2, 2 from the front of each hibernaculum, n=4 snakes, and 8 ambient temperature loggers). The grey clouds represent the daily maximum and minimum for snakes and ambient.

DISCUSSION

To the best of our knowledge, this study provides the first detailed analysis of the internal microclimate of artificial snake hibernacula purposely built as mitigation measures. Both hibernacula provided various thermal and humidity microenvironments, with temperatures generally increasing and becoming more stable with greater depth and distance from the hibernaculum mouth, while humidity did not appear to relate to depth. These microsites were not strongly impacted by external environmental fluctuation and sufficiently buffered against ambient thermal and humidity minima. Snow did not play a role in the insulation of the hibernacula, suggesting the sites would be thermally secure in winters with less snowfall. Temperatures of overwintering Great Basin Gophersnakes within ASH1 were comparable to those in natural hibernacula. In particular, the artificial hibernacula provided thermal microsites conducive to the survival of gophersnakes at depths ranging from 2.6 to 3.1m. Over the two study years, nine snakes were confirmed to have overwintered successfully within ASH1, providing additional evidence of favourable microenvironments for survival. Although conducive to survival, the initial adoption rate was poor, and will require additional research to understand the long-term use.

The artificial hibernacula offer a range of temperature that snakes could potentially exploit over winter. All measured positions within the artificial hibernacula remained well above freezing throughout winter, with the rear of each hibernacula providing the warmest and most thermally-stable conditions. In general, as the depth of each thermal datalogger increased, the temperature increased, and temperature oscillation decreased. Further, no position within either hibernaculum positively tracked external ambient temperature changes over time. A severe cold interval occurred from December 22, 2021, to January 3, 2022, with temperatures outside reaching values as low as -30.4°C, and during this event, temperatures within both hibernacula remained above a minimum reading of 6.1°C. Such results indicate the thermal security of these sites against the most extreme temperatures during these northern winters. Overall, thermal dynamics will be partially attributable to the lagged response of soil temperature at increased depths to external conditions (Al-Kaisi et al. 2017). Soil temperature lags with increasing depth due to a damping effect where heat is absorbed or released through the soil (Al-Kaisi et al. 2017). The distance away from the hibernacula entrances also may influence temperature. Drafts and airflow may be more apparent towards the front of the hibernacula and depend on the overall structure (Nordberg and Cobb 2017). Building these structures with a suite of depths and distances from the hibernaculum mouth may facilitate hibernation (Macartney et al. 1987; Lutterschmidt et al. 2006). As snakes enter the hibernaculum in the fall, they may shift to deeper depths as shallower depths cool and move with the reverse thermal gradient as they emerge to shallower and warmer depths in the spring (Sexton and Hunt 1980; Sexton and Marion 1981; Macartney et al. 1987; Lutterschmidt et al. 2006). Further, thermal variation may benefit snakes by providing a selection of potential microsites. This is an important consideration when building habitat, as individual snakes and species may vary in their selection and/or move between microsites during winter (Macartney et al. 1987; Lutterschmidt et al. 2006; Nordberg and Cobb 2017).

Although snow insulates soil (Shine and Mason 2004), it had no apparent impact on temperature oscillation within our artificial hibernacula. This may have resulted from sufficient insolation being provided by the soil at these depths, paired with the short and relatively mild Canadian winter experienced in this region (Environment Canada 2011; BC Parks 2017): the nearby city of Kamloops, British Columbia, is ranked thirteenth (out of 100 cities assessed) for the mildest winter in Canada (Environment Canada 2011). Elsewhere, years with lighter snow cover have resulted in major mortality events of Red-sided Garter Snakes in natural hibernacula in Manitoba, Canada (Shine and Mason 2004). In New York, decreased snow cover was suggested to potentially impact the overwintering temperature of Timber Rattlesnakes (*Crotalus horridus*) (Brown 1982). Although our hibernacula do not appear to be impacted by snow, future artificial snake hibernacula should factor this into the design in similar or colder climes. This is especially important given the ongoing and increasing impacts of climate change. For example, snow cover duration in Canada has been decreasing (GC 2019), and although the overall increasing temperature may compensate for this loss, less snow paired with variable and extreme cold events could be catastrophic (GC 2023).

Great Basin Gophersnakes overwintering in ASH1 in 2021-2022 experienced similar temperatures to those overwintering in natural hibernacula. This indicates that ASH1 provided conditions that were not only thermally conducive to survival (as these snakes emerged) but were within a range naturally experienced by snakes overwintering on the same landscape. Hibernacula need to afford conditions above some critical thermal minimum (to ensure snakes do not freeze) and maximum (not be too warm to minimize energy expenditures) (Gregory 1982; Costanzo 1989a; Williams et al. 2015; Markle et al. 2020; Huey et al. 2021). Although all positions within both hibernacula afforded temperatures well above freezing overwinter, only some appeared to be biologically relevant to the gophersnakes. The average daily temperature of naturally overwintering gophersnakes in 2022-2023 mirrored the temperature profiles in the artificial dens at depths from 2.6 to 3.1m. Overall, the overwintering body temperatures of these gophersnakes ranged from 4.5°C to 17.0°C and were, on average, 7.8 °C. However, temperatures that are potentially damaging appear to be subject to change with geography and the focal species. For example, Red-sided Garter Snakes (*Thamnophis sirtalis parietalis*) in Manitoba reached a thermal minimum of 1.1 ± 0.16°C overwinter (Lutterschmidt et al., 2006), while Macartney et al. (1987) found the average overwintering temperature of this species in the Northwest Territories to be 3.9°, hitting a minimum of 1.8°C. Further, the lowest Timber Rattlesnake (*Crotalus horridus*) temperature in Tennessee recorded by Nordberg & Cobb (2017) in one year was 5.9°C and the next 1.1°C. However, Hobbs (2007) found Western Rattlesnakes overwintered on average at 9.6 °C and ranged between 17.8 to 5.1°C on our study site. These results are very similar to those experienced by our gophersnakes, which in some cases share the same hibernacula as Western Rattlesnakes (COSEWIC 2013; Williams et al. 2015). Given this variation, when building artificial snake hibernacula the temperature requirements of the focal species in that location must be considered. Thus, having reference data from naturally hibernating snakes in a given area provides context and guidelines for the construction and assessment of artificial den performance.

The natural weight loss of snakes overwinter is believed to be mostly a result of water loss (Costanzo 1989a). Thus, humidity is another important factor to consider when constructing an artificial snake hibernaculum to ensure there is enough moisture to prevent the desiccation of snakes (Costanzo 1986; Costanzo 1989a). Humidity, as we recorded inside the artificial hibernacula, did not appear to relate to depth and for unknown reasons, the middle section of ASH2 was variable compared to other positions. Regardless of this variation, no position co-varied strongly in time with external relative humidity. Instead, the hibernacula buffered against external humidity changes: even when ambient, above-ground measurements reached a low of 16%, conditions inside the artificial hibernacula never dropped below 77%. The adverse effects of water loss due to the low humidity appears to be more of a concern than overly high humidity, given some snakes are known to overwinter submerged in water (Costanzo 1989a). Since the hibernacula stayed above 77.4%, with many regions remaining at or around 100%, the artificial hibernacula appeared conducive to overwinter survival by the snakes.

Despite affording apparent suitable hibernating conditions, the ASH1 failed to serve as replacement habitat for the 93 displaced snakes, as documented during the first- and second-year post-disturbance. This occurred even with our intervention and monitoring. For example, during ingress 2021, ASH1 was actively seeded by 19 displaced snakes. However, only six of these snakes were determined to have successfully overwintered. In year 2, only three snakes in total were detected at the hibernacula: two overwintered, none were displaced snakes, and none were returning from the first year. These results suggest that costly artificial dens will not necessarily achieve mitigation targets, at least in the short term. Without a concerted monitoring program (as conducted herein) this modicum of success will not be easily achieved or quantified. Unfortunately, it is unclear how long it takes for snakes to adopt a hibernaculum naturally, and other mechanisms beyond our knowledge and control may be at work (e.g., scent trails, visual cues, etc.) (Parker and Brown 1980; Costanzo 1986; Costanzo 1989b; Gienger and Beck 2011; Zappalorti et al. 2014). Thus, the value of artificial hibernacula and similar structures requires further research assessing their viability in the long term, perhaps decades.

LITERATURE CITED

Al-Kaisi MM, Lal R, Olson KR, Lowery B. 2017. Chapter 1 - fundamentals and functions of Soil Environment. In: Al-Kaisi MM, Lowery B, editors. Soil Health and Intensification of Agroecosytems. Massachusetts (USA): Academic Press. p. 1–23.

Amat-Valero M, Calero-Torralbo MA, Václav R, Valera F. 2014. Cavity types and microclimate: implications for ecological, evolutionary, and conservation studies. Int J Biometeorol. 58(9):1983–1994.

Arida EA, Bull MC. 2008. Optimising the design of artificial refuges for the Australian skink, *Egernia stokesii*. Appl Herpetol 5(2):161–172.

Banks-Leite C, Ewers RM, Folkard-Tapp H, Fraser A. 2020. Countering the effects of habitat loss, fragmentation, and degradation through habitat restoration. One Earth. 3(6):672–676.

BC Parks. 2017. Lac du Bois Grasslands Protected Area management plan. Kamloops.

Brown WS. 1982. Overwintering body temperatures of Timber Rattlesnakes (*Crotalus horridus*) in northeastern New York. Source: J Herpetol. 16(2):145–150.

Brown WS, Parker WS, Elder JA. 1974. Thermal and spatial relationships of two species of Colubrid snakes during hibernation. Herpetol. 30(1):32–38.

Bryan DL. 2015.Survival and natural history of the Timber Rattlesnake (*Crotalus Horridus*) at Center Hill Lake in Dekalb County, Tennessee [thesis]. [Cookville (TN)]: Tennessee Technolgical University.

Bryant GL, Eden P, De Tores P, Warren K. 2010. Improved procedure for implanting radiotransmitters in the coelomic cavity of snakes. Aust Vet J. 88(11):443–448.

Burgdorf S, Rudolph D, Conner R, Saenz D, Schaefer R. 2005. A successful trap design for capturing large terrestrial snakes. Herpetol Rev. 36(4):421–424.

Burger J, Zappalorti RT, Gochfeld M, Boarman WI, Caffrey M, Doig V, Garber SD, Lauro B, Mikovsky M, Safina C, et al. 1988. Hibernacula and summer den sites of Pine Snakes (*Pituophis melanoleucus*) in the New Jersey Pine Barrens. J Herpetol. 22(4):425–433.

Choquette JD, Mokdad AI, Pitcher TE, Litzgus JD. 2024. Selection and validation of release sites for conservation translocations of temperate-zone snakes. MethodsX. 12:1-11.

Cook DG, Stemle LR, Stokes DL, Messerman AF, Meisler JA, Searcy CA. 2023. Habitat value of constructed breeding pools for the endangered Sonoma population of California tiger salamander. J of Wildl Manag. 87(3): 1-18.

COSEWIC. 2013. COSEWIC Assessment and status report on the Great Basin Gopersnake *Pituophis catenifer deserticola* in Canada. Ottawa.

Costanzo JP. 1986. Influences of hibernaculum microenvironment on the winter life history of the garter snake (*Thamnophis sirtalis*). OJS. 86(5):199–204.

Costanzo JP. 1989a. Effects of humidity, temperature, and submergence behavior on survivorship and energy use in hibernating garter snakes, *Tharnnophis sirtdis*. Can J Zool. 67:2486–2492.

Costanzo JP. 1989b. Conspecific scent trailing by garter snakes (*Thamnophis sirtalis*) during autumn further evidence for use of pheromones in den location. J Chem Ecol. 15(11): 2531-2538.

Crowell HL. 2019. Comparative thermal ecology of coastal and inland Pacific Rattlesnakes (*Crotalus Oreganus*) [thesis]. [San Luis Obispo (CA)]: California Polytechnic State.

Dong H, Zhao J, Zhao W, Si M, Liu J. 2019. Study on the thermal characteristics of crude oil pipeline during its consecutive process from shutdown to restart. Case Stud Therm Eng. 14: 1-20

Edkins TL, Somers CM, Vanderwel MC, Sadar MJ, Poulin RG. 2018. Variable habitat selection and movement patterns among Bullsnake (*Pituophis catenifer sayi*) populations in Saskatchewan. Can Field-Nat. 132(2):126–139.

Eisinga R, Heskes T, Pelzer B, Te Grotenhuis M. 2017. Exact p-values for pairwise comparison of Friedman rank sums, with application to comparing classifiers. BMC Bioinform. 18(1): 1-18.

Environment Canada. 2011. Mildest winter. National Climate Data and Information Archive; [accessed 2024 Mar 22]. https://web.archive.org/web/20111125151335/http://climate.weatheroffice.gc.ca/winners/categorydata_e.html?SelectedCategory=4.

[ECCC] Environment and Climate Change Canada. 2023. Historical climate data; [accessed 2023 Jul 18]. http://climate.weather.gc.ca/.

Eye DM. 2022. Reproductive ecology of female Western Rattlesnakes (*Crotalus Oreganus*) in Canada [thesis]. [Kamloops (BC)]: Thompson Rivers University.

Fontaine A, Simard A, Dubois B, Dutel J, Elliott KH. 2021. Using mounting, orientation, and design to improve bat box thermodynamics in a northern temperate environment. Sci Rep. 11(1): 1-15.

Forget-Klein É, Green DM. 2021. Toads use the subsurface thermal gradient for temperature regulation underground. J Therm Biol. 99: 1-9.

Gonçalves-Souza D, Verburg PH, Dobrovolski R. 2020. Habitat loss, extinction predictability and conservation efforts in the terrestrial ecoregions. Biol Conserv. 246: 1-8.

[GC] Government of Canada. 2019. Changes in snow;[accessed 2024 Feb 6]. https://www.canada.ca/en/environment-climate-change/services/climate-change/canadian-centre-climate-services/basics/trends-projections/changes-snow.html.

[GC] Government of Canada. 2023. Climate change. Canadian Centre for Occupation Health and Safety; [accessed 2024 Mar 22]. https://www.ccohs.ca/oshanswers/safety_haz/climate/climate-change-extreme-weather-cold.html.

[GCC] The Grasslands Conservation Council of British Columbia. 2009. Working together for the conservation of BC's grasslands. Kamloops.

Gillingham JC, Carpenter CC. 1978. Snake Hibernation: Construction of and observations on a man-made hibernaculum (Reptilia, Serpentes). J Herpetol. 12(4):495–498.

Gienger CM, Beck DD. 2011. Northern pacific rattlesnakes (*Crotalus oreganus*) use thermal and structural cues to choose overwintering hibernacula. Can J Zool. 89(11):1084–1090.

Gregory P. 1982. Reptillian hibernation. In: Gans C, Pough FH, editors. Biology of the Reptillia. Vol. 13. New York (USA): Academic Press. p. 53–154.

Griffiths SR, Lentini PE, Semmens K, Watson SJ, Lumsden LF, Robert KA. 2018. Chainsaw-carved cavities better mimic the thermal properties of natural tree hollows than nest boxes and log hollows. Forests. 9(5): 1-27.

Hachem S, Duguay CR, Allard M. 2012. Comparison of MODIS-derived land surface temperatures with ground surface and air temperature measurements in continuous permafrost terrain. TC. 6(1):51–69.

Hanski I. 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio. 40(3):248–255.

Hein AM, Guyer C. 2009. Body temperature of overwintering Cottonmouth snakes: hibernaculum use and inter-individual variation. J Ala Acad Sci. 80(1): 35-44.

Heinrich R. 2020. Technical memorandum. Kamloops (BC): Triton Environmental Consultants.

Hobbs J. 2007. Thermal factors in relation to the denning ecology of northern Pacific rattlesnakes in British Columbia [thesis]. [Victoria (BC)]: Royal Roads University.

Huey RB, Stevenson RD. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am Zool. 19(1):357–366.

Huey RB, Ma L, Levy O, Kearney MR. 2021. Three questions about the eco-physiology of overwintering underground. Ecol Lett. 24(2):170–185.

Larsen KW. 1986. Ecology of the common garter snake, *Thamnophis sirtalis*, at the northern limit of its range. [Victoria]: University of Victoria.

Long RA, Martin TJ, Barnes BM. 2005. Body temperature and activity patterns in free-living arctic ground squirrels. J Mammal. 86(2):314–322.

Lutterschmidt DI, LeMaster MP, Mason RT. 2006. Minimal overwintering temperatures of red-sided garter snakes (*Thamnophis sirtalis parietalis*): A possible cue for emergence? Can J Zool. 84(5):771–777.

Macartney JM, Larsen KW, Gregory PT. 1987. Body temperatures and movements of hibernating snakes (*Crotalus and Thamnophis*) and thermal gradients of natural hibernacula. Can J Zool. 67:108–114.

Markle CE, Moore PA, Waddington JM. 2020. Temporal variability of overwintering conditions for a species-at-risk snake: Implications for climate change and habitat management. Glob Ecol Conserv. 22: 1-9.

Matsuda BM, Green DM, Gregory PT. 2006. Amphibians and reptiles of British Columbia. Victoria: Royal BC Museum.

McComb LB, Lentini PE, Harley DKP, Lumsden LF, Eyre AC, Briscoe NJ. 2022. Climate and behaviour influence thermal suitability of artificial hollows for a critically endangered mammal. Anim Conserv. 25(3):401–413.

Mitchell AM, Wellicome TI, Brodie D, Cheng KM. 2011. Captive-reared burrowing owls show higher site-affinity, survival, and reproductive performance when reintroduced using a soft-release. Biol Conserv. 144(5):1382–1391.

Milling CR, Rachlow JL, Johnson TR, Forbey JS, Shipley LA. 2017. Seasonal variation in behavioral thermoregulation and predator avoidance in a small mammal. Behav Ecol. 28(5):1236–1247.

[MFLNRO] Ministry of Forest Lands and Natural Resource Operations. 2016. Best management practice for amphibian and reptile salvages in British Columbia.

Naeth M, Chan Yk DA, McGILL W, Bailey A. 1993. Soil temperature regime in mixed prairie rangeland after pipeline construction and operation. Can Agric Eng. 35(2):89–95.

Nordberg EJ, Cobb VA. 2017. Body temperatures and winter activity in overwintering TimberRattlesnakes (*Crotalus horridus*) in Tennessee, USA. Herpetol Conserv Biol. 12(3): 606-615.

Parker WS, Brown WS. 1980. Comparative ecology of two Colubrid snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucus deserticola*, in northern Utah. Milwaukee (WI): Milwaukee Public Museum.

Pohlert T. 2023. Calculate pairwise multiple comparisons of mean rank sums extended; [accessed 2024 Feb 3]. https://CRAN.R-project.org/package=PMCMRplus.

Posit Software. 2023. RStudio IDE; [accessed 2024 Feb 3]. https://posit.co/products/open-source/rstudio/.

Prior KA, Weatherhead PJ. 1996. Habitat features of Black Rat Snake hibernacula in Ontario. J Herpetol. 30(2):211–218.

Reinert HK, Cundall D. 1982. An improved surgical implantation method for radio-tracking snakes. Source: Copeia. 1982(3):702–705.

Roznik EA, Alford RA. 2012. Does waterproofing thermochron iButton dataloggers influence temperature readings? J Therm Biol. 37(4):260–264.

Rueegger N. 2016. Bat boxes-a review of their use and application, past, present and future. Acta Chiropt. 18(1):279–299.

Rueegger N. 2019. Variation in summer and winter microclimate in multi-chambered bat boxes in Eastern Australia: Potential eco-physiological implications for bats. Environments. 6(2): 1-19.

Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA. 2014. Microhabitats reduce animal's exposure to climate extremes. 20(2):495–503.

Shine R, Mason RT. 2004. Patterns of mortality in a cold-climate population of garter snakes (*Thamnophis sirtalis parietalis*). Biol Conserv. 120(2):201–210.

Sexton OJ, Hunt SR. 1980. Temperature relationships and movements of snakes (*Elaphe obsoleta, Coluber constrictor*) in a cave hibernaculum. Herpetol. 36:20–26.

Sexton OJ, Marion KR. 1981. Experimental analysis of movements by Prairie Rattlesnakes, *Crotalus viridis*, During Hibernation. Oecologia. 51:37–41.

Sudyka J, Di Lecce I, Szulkin M. 2023. Microclimate shifts in nest-boxes and natural cavities throughout reproduction. J Avian Biol. 2023(1–2):1-17.

Taylor EN, DeNardo DF, Malawy MA. 2004. A comparison between point- and semi-continuous sampling for assessing body temperature in a free-ranging ectotherm. J Therm Biol. 29(2):91–96.

Thierry A, Lettink M, Besson AA, Cree A. 2009. Thermal properties of artificial refuges and their implications for retreat-site selection in lizards. Appl Herpetol. 6(4):307–326.

Tillman FE, Bakken GS, O'Keefe JM. 2021. Design modifications affect bat box temperatures and suitability as maternity habitat. Ecol Solut Evid. 2(4):1-12.

TranBC. Why we are making a bed for 200 snakes. [accessed 2024 Mar 24]. https://www.tranbc.ca/2018/02/07/why-we-are-making-a-bed-for-200-snakes/

Trans Mountain Pipeline ULC. 2017. Lac du Bois Grasslands protected area reclamation plan for the Trans Mountain Pipeline ULC Trans Mountain Expansion Project. Calgary (AB): Kinder Morgan Canada Inc.

Trans Mountain. 2020. Snake species of concern overwintering den reconstruction and monitoring plan.

Trans Mountain. 2021a. Time flies: one year of construction in the Kamloops urban area; [accessed 2024 Feb 3]. https://www.transmountain.com/news/2021/time-flies-one-year-of-construction-in-the-kamloops-urban-area#:~:text=What%20a%20year%20it%20has,the%20Trans%20Mountain%20Expansion%20Project.

Trans Mountain. 2021b. Trans Mountain Expansion Project artificial overwintering den #1 Kamloops Area-Lac du Bois.

Trans Mountain. 2021c. Trans Mountain Expansion Project artificial overwintering den #2 Kamloops Area-Lac du Bois.

Trans Mountain. 2023a. Expansion project. [accessed 2024 Mar 24]. https://www.transmountain.com/project-overview.

Trans Mountain. 2023b. Our history. [accessed 2024 Mar 24]. https://www.transmountain.com/history.

Walker ML, Kadlec ED, Miloshewski RD, Pisani GR. 2011. Associative behavior and affinity for anthropogenic habitats in two relocated Timber Rattlesnakes. Reptiles & Amphibians. 18(4): 235-237.

Williams KE, Hodges KE, Bishop CA. 2015. Hibernation and oviposition sites of Great Basin Gophersnakes (*Pituophis catenifer deserticola*) near their northern range limit. J Herpetol. 49(2):207–216.

Zappalorti RT, Burger J, Burkett DW, Schneider DW, McCort MP, Golden DM. 2014. Fidelity of northern pine snakes (*Pituophis m. melanoleucus*) to natural and artificial hibernation sites in the New Jersey Pine Barrens. J. Toxicol. Environ. Health - A: Curr. Issues. 77(21):1285–1291.

CHAPTER 4

CONCLUSION

SUMMARY OF THESIS

A central theme throughout this thesis is the potential scarcity of hibernacula in northern latitudes. Stemming from this, my overarching management goal was to inform how to better protect and properly compensate for disturbances to these critical habitat features. More specifically, I used a community of three sympatric snake species, the Great Basin Gophersnake, Western Yellow-bellied Racer, and Western Rattlesnake, to explore (1) variation in hibernacula habitat use and (2) artificial hibernacula efficacy. Below are the central objectives within each of these themes:

1. **Variation in hibernacula habitat use**

a. Document hibernacula and their species assemblages on our study site. (**Chapter 2)**

b. Investigate how the habitat features relate to the degree of communal occupation present at hibernacula. **(Chapter 2)**

c. Explore how these three species vary in their selection of overwintering habitat. **(Chapter 2)**

2. **Artificial hibernacula efficacy**

a. Highlight the available microclimate within each hibernaculum and assess how well they buffer against external environmental conditions. **(Chapter 3)**

b. Determine whether the internal thermal conditions of the artificial hibernacula are comparable to those naturally experienced by snakes. **(Chapter 3)**

c. Monitor the adoption of the main artificial hibernaculum by the original cohort of displaced snakes. **(Chapter 3)**

The principal findings of my thesis were:

- Racers and gophersnakes appear more generalist in their selection of hibernacula, overwintering in rodent burrows, rocky outcrops, holes under rocks and blast rock features compared to rattlesnakes found at rocky outcrops and blast rock features. **(Chapter 2)**

- Little to no measured habitat features explained the numbers of gophersnakes, racers, and rattlesnakes detected at individual hibernacula. **(Chapter 2)**
- Gophersnake, racer, and rattlesnake hibernacula were situated on steeper slopes with larger openings of the main hibernaculum entrance compared to random sites. **(Chapter 2)**
- I found variation in habitat selection between these species that, in some cases, share hibernacula. Rattlesnakes were associated with open habitat, with their hibernacula having significantly less grass cover than random sites at the micro and macroscale. In contrast, gophersnakes and racers were associated with further cover features at the microscale, with gophersnakes selecting for more openings and shrub cover and racers selecting for increased rock and shrub cover. This variation aligns with observed behavioural differences between these species (i.e. racers and gophersnakes found away from versus rattlesnakes conspicuously basking at the hibernacula entrance). **(Chapter 2)**
- Artificial hibernacula built as mitigation can provide overwintering habitat that meets the microclimatic conditions snakes need to survive. **(Chapter 3)**
- Temperatures of overwintering Great Basin Gophersnakes within the main artificial hibernaculum were comparable to those in natural hibernacula. In particular, the artificial hibernacula provided thermal microsites conducive to the survival of gophersnakes at depths ranging from 2.6 to 3.1m. **(Chapter 3)**
- Despite relocation and soft-release efforts, the main artificial hibernaculum failed to show adoption by displaced snakes two years after the disturbance. This indicates that although these sites afforded conditions conducive to survival, successful adoption may require more intensive monitoring and relocating of snakes to ensure the target population uses these artificial hibernacula. **(Chapter 3)**

MANAGEMENT IMPLICATIONS

Habitat loss is a predominant factor threatening biodiversity globally and is one of the primary drivers of species extinction (Hanski 2011; Banks-Leite et al. 2020; Gonçalves-Souza et al. 2020). Great Basin Gophersnakes, Western Yellow-bellied Racers, and Western Rattlesnakes are commonly threatened by habitat loss (COSEWIC, 2013, 2015a, b). The sensitivity of animals to habitat loss depends largely on their specialization and reliance on specific environmental features (Keinath et al. 2017); one such feature is snake hibernacula. Such sites warrant identification and protection as critical habitat features for the overall recovery and conservation of these species at risk (COSEWIC 2015b; ECCC 2019; GC 2023).

Identifying and protecting hibernacula

Within Canada, Great Basin Gophersnakes, Western Yellow-bellied Racers, and Western Rattlesnakes all exclusively occur within the province of British Columbia (COSEWIC, 2013, 2015a, b). Within this province, Wildlife Habitat Areas (WHA) can be used as a conservation tool to protect 200-300 ha around communal hibernacula (MWLAP 2004; Williams et al. 2012), assuming the hibernacula are identified. I acknowledge, however, that the characteristics I identified as separating hibernating sites from random sites will have limited value in pre-emptive planning, i.e. proactively guiding inventory personnel to rodent burrows used by gophersnakes and racers. Thus, "inventory" may not be straightforward. From our research, radiotelemetry is an effective approach to identifying hibernacula in a new area, helping us identify 15 of 28 hibernacula (54%) on our study landscape. However, this approach is relatively invasive and requires intensive monitoring. Thus, consideration should be given to expanding protection in areas where snakes occur rather than relying on the protection of hibernacula that are not readily identified.

Through WHAs, British Columbia has approximately 10114 ha (average size 241 ha) protected for rattlesnakes, 1909 ha for gophersnakes (average size 174 ha), and 100 ha for racers (data from WHA database, last updated Feb 2024 – Ministry of Environment 2024). From these data, it is apparent that rattlesnake hibernacula are protected to a greater extent than gophersnake and racer hibernacula (Ministry of Environment 2024). It should be noted, however, that only 22% of the 380 known rattlesnake hibernacula are protected (as of 2016), indicating that even though they are protected to a greater extent, they are still not sufficiently protected (ECCC 2019). The discrepancy between species does not come as a surprise, as Western Rattlesnakes have garnered considerable research attention within British Columbia (ex., Macartney et al. 1987; Lomas et al. 2015; Harvey and Larsen 2020; Howarth et al. 2023). Further, from our research, there is evidence to suggest that rattlesnake hibernacula are easier to identify: rattlesnakes have more specific den habitat requirements and the animals are much more conspicuous at hibernacula than gophersnakes and racers.

This discrepancy of protection paired with arguably harder-to-identify hibernacula (i.e. rodent burrows) indicates a need for further inventory of gophersnake and racer hibernacula in particular.

A multispecies approach has been recommended across management and recovery strategies (SIRART 2008; ECCC 2019). Some even emphasize this approach because gophersnakes and rattlesnakes use the same hibernacula (ECCC 2019). However, within this study, I showcase variation in habitat selection between these species that do not universally share hibernacula. Given this, I advised in Chapter 2 against using the selection of well-studied and inventoried species (e.g., Western Rattlesnakes) to extrapolate to other species with less well-known denning habits. Overall, a multispecies approach will only be practical if one first fully understands the unique variation between the species.

Building artificial hibernacula

As critical habitat features, the loss of hibernacula demands compensation. Within Chapter 3, I demonstrated that artificial hibernacula built as mitigation measures can provide microclimatic conditions conducive to the survival of snakes overwintering at a northern range limit. Managers wanting to construct such habitat should give particular attention to:

- Utilizing depth and distance to hibernacula entrance to provide a gradient of microclimatic conditions to facilitate hibernation.
- Ensuring the structure is sufficiently buffered from external conditions and is not dependent on snow insulation.
- Tailoring the construction approach to the needs of the focal species (i.e., temperature and humidity).

Currently, the “Best Management Practices for Amphibian and Reptile Salvages in British Columbia” offer artificial hibernacula as a potential site for the relocation of salvaged reptiles (MFLNRO 2016). Although, artificial hibernacula can be conducive to survival, I found that salvaged snakes did not readily adopt the main hibernacula even with soft-release and relocation efforts. Based on these results, I believe using artificial hibernacula to provide immediate overwintering habitat for salvaged snakes may be ineffective. However, there do not appear to be alternative mitigation options in times of disturbance. Thus, I want to emphasize the importance of adequately surveying and avoiding disturbance of critical habitat beforehand (Whiting and Booth 2012). Further research still is needed to understand the effectiveness of the use of artificial hibernacula as mitigation measures in the long term (see Adoption and long-term viability of artificial hibernacula below).

Incidental artificial hibernacula

Incidental artificial hibernacula may be a significant source of hibernacula at northern extremes where natural habitat might be limited (Costanzo 1986). Within our study site, there are numerous examples of 'accidentally' created artificial hibernacula (i.e. overtop of old pipeline construction, in blast rock on the sides of roads, or in other previously disturbed habitats). Excluding the newly installed artificial hibernacula in this study, 9 of the 28 (32%) known hibernacula on the landscape were found in anthropogenically disturbed habitats. Further, the three previously unknown hibernacula excavated by pipeline construction were found near the old pipeline installed in 1951. These observations of incidental anthropogenic hibernacula are not unique to this study; hibernacula have previously been found on human-created rocky slopes (Williams et al. 2015), in rockpiles beside buildings (Walker et al. 2011), and in other anthropogenic features (Brown et al. 1974; Costanzo 1986; Burger et al. 1988; Edkins et al. 2018). Although I could not find support in the literature, perhaps a preference for these sites comes from the interstitial spaces created by dumping rocks or garbage. Further, the preference for sites along the pipeline may be related to the presence of heat from the pipeline during the transportation of crude oil (Dong et al. 2019). For example, it has been found that natural gas pipelines can alter the thermal regime of soil due to the external heating of the pipeline (Naeth et al. 1993). During winter, these natural gas pipelines were found to affect the depth of the frost line in the adjacent soil (Naeth et al. 1993). Not only does this indicate the willing usage of anthropogenic structures (Eye 2022), but it also underscores the responsibility of managers to guarantee the absence of snakes at these sites prior to further disturbance.

Management of snakes in Lac du Bois

It is essential to consider direct management implications for this peripheral population of snakes as the Lac du Bois Grassland Protected Area lies within the coincidental northern limits of the Great Basin Gophersnake, Western Yellow-bellied Racer, and Western Rattlesnake (Matsuda et al. 2006). Through this research, I recommend the following:

- Providing protection through WHAs to all identified hibernacula found within this study.
- Continue monitoring the identified hibernacula to understand population dynamics in the long term.
- Expand inventory and protection of hibernacula within the park and periphery. It is crucial to consider the periphery landscape as some snakes may use the park during the active season and overwinter in critical habitat outside the park.
- Continue monitoring the artificial hibernacula to understand the uptake in the long term.
- Lac du Bois is impacted by many anthropogenetic activities (e.g., construction, hiking, biking, horseback riding, off-roading, cattle grazing, etc.) (BC Parks 2017). Thus, restricting activities around hibernacula (e.g., those near trails) may be beneficial to reduce potential human-wildlife conflict and the overall impact on snakes.
- Rodent burrow hibernacula have been found to collapse on our site. These events were suspected to be the result of cattle grazing. Similar occurrences of rodent burrow collapse by ungulates have been described elsewhere (Lovegrove and Painting 1987; Weihs and Shroder 2011). Although the overall impact of this event is unclear, future research should be conducted, and consideration should be given to the scope of future grazing.
- If development takes place within or around Lac du Bois, surveying efforts for hibernacula should occur around egress or ingress windows. Behavioural variation between the species should be considered during surveys (i.e. racers and gophersnakes found away from versus rattlesnakes conspicuously basking at the hibernacula entrance).

FUTURE RESEARCH CONSIDERATIONS

Continued identification of hibernacula

I have previously suggested that an increased inventory of hibernacula is needed, particularly for gophersnakes and racers, but that is relatively more difficult than for rattlesnakes. With increased inventory, I recommend collecting data on the habitat features at more overwintering sites. Future research could use this data to further elucidate the habitat selection of gophersnakes and racers at hibernacula. In doing so, I recommend focusing on certain types of hibernacula, such as earthen sites, to provide further context in their identification and subsequent protection.

Availability of hibernacula and communal denning

As previously mentioned, a central theme throughout the thesis is the limited availability of hibernacula at northern latitudes. One hypothesis in the literature theorizes that the limited availability of adequate overwintering sites results in increased instances of communal denning (Gregory 1984). This phenomenon is quoted as being "undoubtedly the main cause of communal overwintering" (Gregory 1984) and although many studies referenced this theory (Prior and Weatherhead 1996; Harvey and Weatherhead 2006; Gardiner and Sonmor 2011; Gardiner et al. 2013; Bruckerhoff et al. 2021), few have tried to assess the availability of hibernacula (Prior and Weatherhead 1996; Harvey and Weatherhead 2006; Williams et al. 2014; Williams et al. 2015). Prior and Weatherhead (1996) found the results were equivocal to whether communal hibernacula of Black Rat snakes in Ontario were limited after comparing their habitat features to the broader landscape. Increased rates of overwinter mortality for Massasauga Rattlesnak*es (Sistrurus catenatus catenatus*) in Ontario suggest a potential limitation in hibernacula that meet the requirements for survival (Harvey and Weatherhead 2006). William et al. (2014,2015) found that the solitary use of hibernacula, decreased fidelity, and high survival overwinter suggest that Great Basin Gophersnakes in the Okanagan have increased availability of hibernation sites. Further, within this study (and a concurrent study -Ragsdale MSc *in prep*), I observed snakes finding alternative hibernacula after they lost their original overwintering sites. Such plastic behaviour indicates a greater availability of hibernacula for gophersnakes and racers than first thought. To our knowledge, however, no research has concretely quantified the availability of hibernacula. Ideally, future research should assess the availability of hibernacula on a given landscape and then connect this to the occurrence of communal denning. Not only will this help to highlight the potential scarcity of these sites, but it will also help provide a theoretical understanding of the communal overwintering behaviour in northern snakes.

Adoption and long-term viability of artificial hibernacula

Following our research on the adoption of artificial hibernacula built as mitigation measures, many pertinent research questions have arisen. Although I indicate that the immediate adoption by salvaged snakes is poor, it remains unclear how long it takes for a hibernaculum (artificial or not) to be adopted by snakes. A long-term study on artificial hibernacula will elucidate this and possible mechanisms at work (i.e. scent trails, visual cues, conspecific attraction, etc.). Further, an experimental approach may be valuable to determine if seeding hibernacula with snakes is effective to aid in adoption. Additionally, despite the recent and increasing use of artificial hibernacula, it is unclear whether they have a lifetime or are at risk of environmental disturbances (i.e. flooding). Such research will shed light on the overall viability of such structures as a continued mitigation or conservation strategy.

CONCLUSION

Life in colder climates requires specialized adaptations to prevail during winter. Here, snakes must find an adequate hibernaculum to survive. Due to the biological importance and potential scarcity of hibernacula in northern climes, proper identification and protection are critical for conserving northern snakes. Based on this, I sought to understand how to identify and mitigate future disturbances of these critical habitat features. Using a community of three at-risk sympatric snake species at their northern range limits, I found that the patterns of hibernacula use in communities of snakes are more complex than initially understood. In particular, I discovered distinct interspecific variations in behaviour and hibernacula selection between three species that, in some instances, share the same hibernacula. Such results indicate the need to rethink how we identify and protect hibernacula for even closely related species, such as a community of snakes. Based on this variation, utilizing species-specific management approaches may be more effective than relying on the habitat selection and protection garnered by well-studied species. In cases where hibernacula are irrevocably destroyed, we showcase that artificial hibernacula can be built conducive to the survival of snakes but have a low immediate adoption from a displaced population. Thus, rather than just relying on artificial hibernacula, I recommend putting in every effort to avoid disturbances of these critical habitat features. Overall, I recommend larger protection at the landscape level to reduce the occurrence of hibernacula loss and compensate for the lack of protection around hard-to-identify hibernacula. If destruction is unavoidable, we need to use it as a transparent learning opportunity with ample discussion and attention paid to research design of artificial structures. Such an approach will help to answer the many questions that have arisen regarding the overwintering site selection of northern snakes and the long-term use of artificial hibernacula. Moving forward, the results of this study provide critical information to inform the management strategies of these at-risk species and will influence the identification, protection, and response to the disturbance of hibernacula.

LITERATURE CITED

Banks-Leite C, Ewers RM, Folkard-Tapp H, Fraser A. 2020. Countering the effects of habitat loss, fragmentation, and degradation through habitat restoration. One Earth. 3(6):672–676.

BC Parks. 2017. Lac du Bois Grasslands Protected Area Management Plan. Kamloops.

Brown WS, Parker WS, Elder JA. 1974. Thermal and spatial relationships of two species of Colubrid snakes during hibernation. Herpetol. 30(1):32–38.

Bruckerhoff LA, Kamees LK, Holycross AT, Painter CW. 2021. Patterns of survival of a communally overwintering Rattlesnake using an artificial hibernaculum. Ichthyol Herpetol. 109(1):64–74.

Burger J, Zappalorti RT, Gochfeld M, Boarman WI, Caffrey M, Doig V, Garber SD, Lauro B, Mikovsky M, Safina C, et al. 1988. Hibernacula and summer den sites of Pine Snakes (*Pituophis melanoleucus*) in the New Jersey Pine Barrens. J Herpetol. 22(4):425–433.

[ECCC] Environment and Climate Change Canada. 2019. Recovery strategy for the Western Rattlesnake (*Crotalus oreganus*), the Great Basin Gophersnake (*Pituophis catenifer deserticola*) and the Desert Nightsnake (Hypsiglena chlorophaea) in Canada.

COSEWIC. 2013. COSEWIC assessment and status report on the Great Basin Gopersnake Pituophis catenifer deserticola in Canada. Ottawa.

COSEWIC. 2015a. COSEWIC assessment and status report on the Western Rattlesnake Crotalus oreganus in Canada. Ottawa.

COSEWIC. 2015b. COSEWIC assessment and status report on the Eastern Yellow-bellied Racer Coluber constrictor flaviventris and the Western Yellow-bellied Racer Coluber constrictor mormon in Canada. Ottawa.

Costanzo JP. 1986. Influences of hibernaculum microenvironment on the winter life history of the garter snake (*Thamnophis sirtalis*). OJS. 86(5):199–204.

Dong H, Zhao J, Zhao W, Si M, Liu J. 2019. Study on the thermal characteristics of crude oil pipeline during its consecutive process from shutdown to restart. Case Stud Therm Eng. 14: 1-20.

Edkins TL, Somers CM, Vanderwel MC, Sadar MJ, Poulin RG. 2018. Variable habitat selection and movement patterns among Bullsnake (*Pituophis catenifer sayi*) populations in Saskatchewan. Can Field-Nat. 132(2):126–139.

Eye DM. 2022. Reproductive ecology of female Western Rattlesnakes (*Crotalus Oreganus*) in Canada [thesis]. [Kamloops (BC)]: Thompson Rivers University.

Gardiner LE, Somers CM, Martino JA, Parker DL, Poulin RG. 2013. Balancing the dumbbell: summer habitats need protection in addition to winter dens for northern snake communities. J Wildl Manag. 77(5):975–982.

Gardiner LE, Sonmor KW. 2011. Reptiles major slump event at Grasslands National Park Snake Pit in southwestern Saskatchewan. Blue Jay. 69(3):120–124.

Gonçalves-Souza D, Verburg PH, Dobrovolski R. 2020. Habitat loss, extinction predictability and conservation efforts in the terrestrial ecoregions. Biol Conserv. 246: 1-8.

[GC] Government of Canada. 2023. Critical habitat for species at risk national dataset – Canada; [accessed 2024 Mar 2]. https://data-donnees.az.ec.gc.ca/data/species/protectrestore/critical-habitat-species-at-risk-canada/

Gregory PT. 1984. Communal denning in snakes. In: Seigel R, Hunt L, Knight J, Malaret L, Zuschlag N, editors. Vertebrate Ecology and Systematic A Tribute to Henry S. Fitch. Lawrence: University of Kansas Publications. p. 57-76.

Hanski I. 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio. 40(3):248–255.

Harvey DS, Weatherhead PJ. 2006. Hibernation site selection by Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) near their northern range limit. J Herpetol. 40(1):66–73.

Harvey JA, Larsen KW. 2020. Rattlesnake migrations and the implications of thermal landscapes. Mov Ecol. 8(1).

Howarth, Bishop CA, Larsen KW. 2023. Western Rattlesnake (*Crotalus oreganus*) spring migration in British Columbia: a comparative study of juveniles and adults. Can J Zool. 101(7): 530-540.

Keinath DA, Doak DF, Hodges KE, Prugh LR, Fagan W, Sekercioglu CH, Buchart SHM, Kauffman M. 2017. A global analysis of traits predicting species sensitivity to habitat fragmentation. Global Ecology and Biogeography. 26(1):115–127.

Lomas E, Larsen KW, Bishop CA. 2015. Persistence of Northern Pacific Rattlesnakes masks the impact of human disturbance on weight and body condition. Anim Conserv. 18(6):548–556.

Lovegrove B, Painting S. 1987. Variations in the foraging behaviour and burrow structures of the Damara Molerat *Cryptomys damarensis* in the Kalahari Gemsbok National Park. KOEDOW. 30:149–163.

Macartney JM, Larsen KW, Gregory PT. 1987. Body temperatures and movements of hibernating snakes (*Crotalus and Thamnophis*) and thermal gradients of natural hibernacula. Can J Zool. 67:108–114.

Matsuda BM, Green DM, Gregory PT. 2006. Amphibians and Reptiles of British Columbia. Victoria: Royal BC Museum.

Ministry of Environment. 2024. Approved wildlife habitat areas. https://www.env.gov.bc.ca/wld/frpa/iwms/wha.html.

[MFLNRO] Ministry of Forest Lands and Natural Resource Operations. 2016. Best management practice for amphibian and reptile salvages in British Columbia.

[MWLAP] Ministry of Water Land and Air Protection. 2004. Identified wildlife management strategy accounts and measures for managing identified wildlife southern interior forest region.

Naeth M, Chan Yk DA, McGILL W, Bailey A. 1993. Soil temperature regime in mixed prairie rangeland after pipeline construction and operation. Can Agric Eng. 35(2):89–95.

Prior KA, Weatherhead PJ. 1996. Habitat features of black rat snake hibernacula in Ontario. J Herpetol. 30(2):211–218.

[SIRART] Southern Interior Reptile and Amphibian Recovery Team. Recovery strategy series rcovery strategy for the Gopher Snake, deserticola Subspecies (*Pituophis catenifer deserticola*) in British Columbia.

Walker ML, Kadlec ED, Miloshewski RD, Pisani GR. 2011. Associative behavior and affinity for anthropogenic habitats in two relocated Timber Rattlesnakes. Reptiles & Amphibians. 18(4): 235-237.

Weihs BJ, Shroder JF. 2011. Mega-terracettes and related ungulate activities in Loess Hills, Iowa, USA. ZfG. 55(1):45–61.

Whiting C, Booth HJ. 2012. *Adder Vipera berus* hibernacula construction as part of a mitigation scheme for flood defence works, Horsey Corner, Norfolk, England. Conser Evid. 9: 9-16.

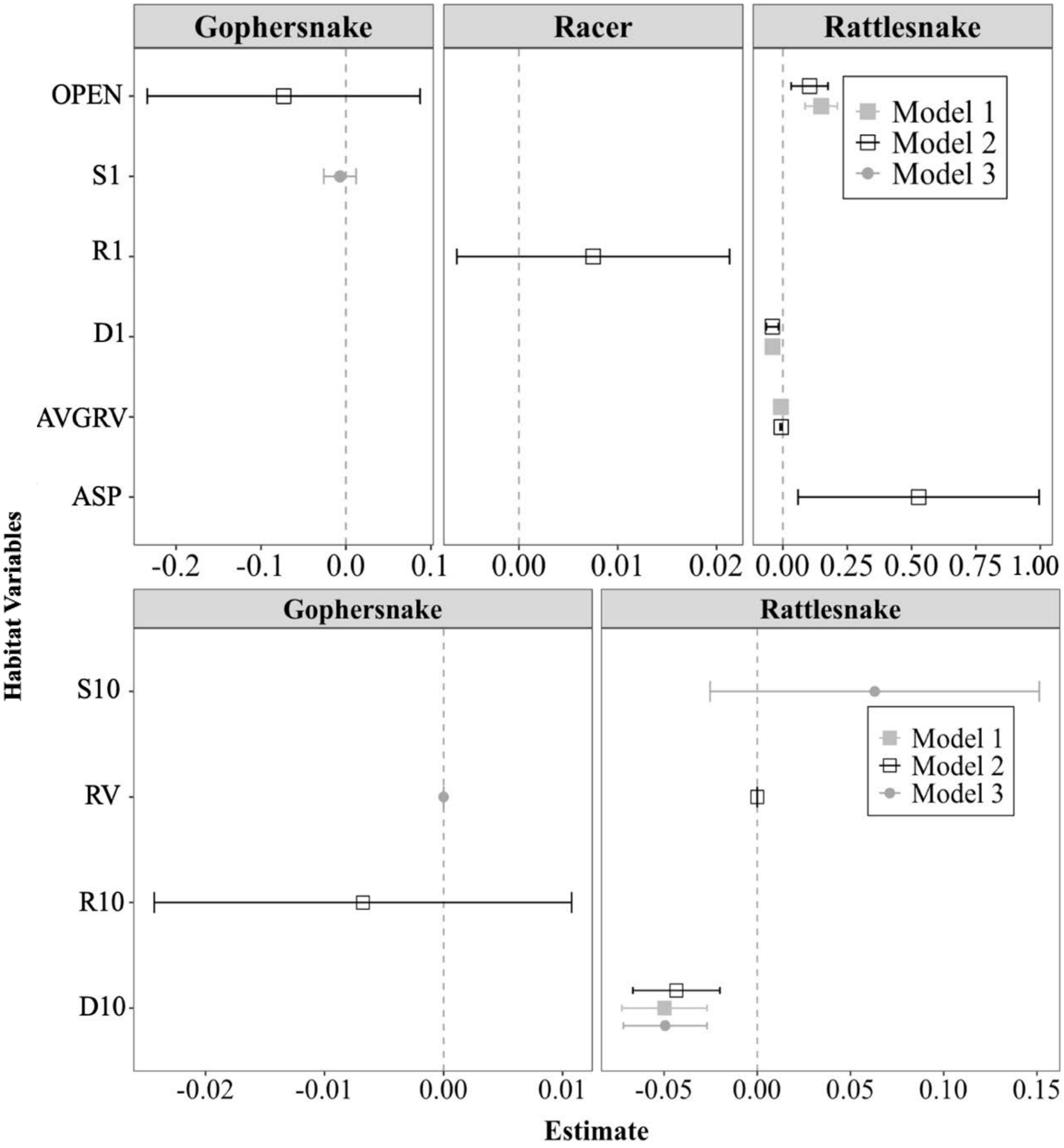
Williams KE, Hodges KE, Bishop CA. 2012. Small reserves around hibernation sites may not adequately protect mobile snakes: The example of great basin gophersnakes (*Pituophis catenifer deserticola*) in British Columbia. Can J Zool. 90(3):304-312.

Williams KE, Hodges KE, Bishop CA. 2014. Phenology and demography of great basin gophersnakes (*Pituophis catenifer deserticola*) at the Northern edge of their range. Herpetol Conserv Biol. 9(2):246–256.

Williams KE, Hodges KE, Bishop CA. 2015. Hibernation and oviposition sites of Great Basin Gophersnakes (*Pituophis catenifer deserticola*) near their northern range limit. J Herpetol. 49(2):207-216.

APPENDIX A

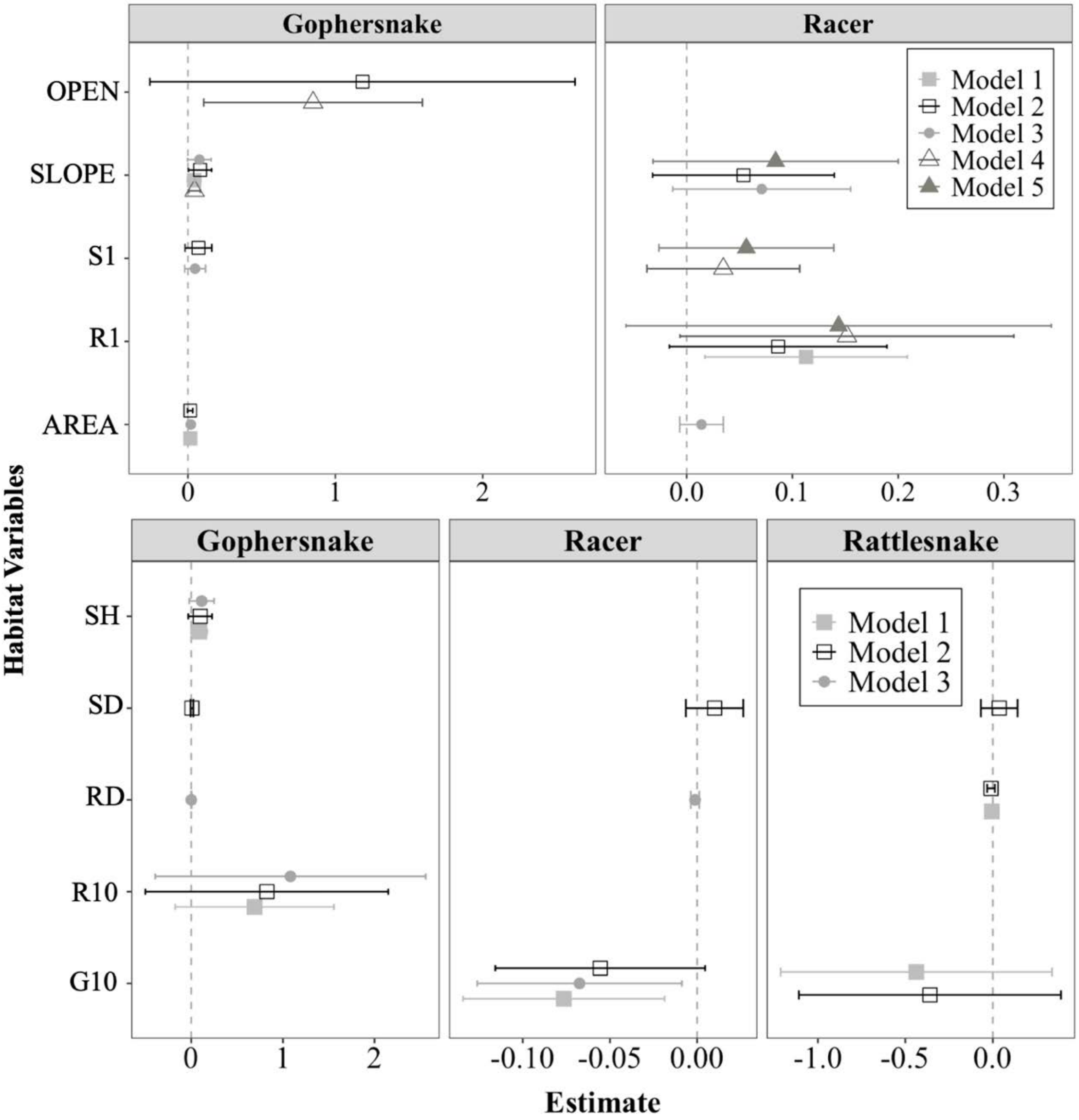
DIRECTION OF RELATIONSHIP OF HABITAT VARIABLES CORRESPONDING TO THE POISSON REGRESSION



Direction of relationship of habitat variables associated with top models with △AICc value <2.0 (Burnham and Anderson 2002) corresponding to the Poisson regression results for Great Basin Gophersnake, Western Yellow-bellied Racer, and Western Rattlesnake models at the microscale (top row) and macroscale (bottom row) (Table 2.2). Points correspond to the estimates of the coefficients (log scale with 95% confidence intervals (CI)) of the top models. Positive values describe habitat features associated with increased snakes, and negative values describe variables not associated with them. If the CI crosses the dashed line, the coefficient is not significant. Full names and detailed descriptions of explanatory variables are found in Table 2.1.

APPENDIX B

DIRECTION OF RELATIONSHIP OF HABITAT VARIABLES CORRESPONDING TO THE CONDITIONAL LOGISTIC REGRESSION



Direction of relationship of habitat variables associated with top models with △AICc value <2.0 (Burnham and Anderson 2002) corresponding to the conditional logistic regression results for Great Basin Gophersnake, Western Yellow-bellied Racer, and Western Rattlesnake models at the microscale (top row) and macroscale (bottom row) (Table 2.3). Points correspond to the estimates of the coefficients (log scale with 95% confidence intervals (CI)) of the top models. The rattlesnake model did not converge at the microscale. Positive values describe habitat features selected for, and negative values describe variables selected against. If the CI crosses the dashed line, the coefficient is not significant. Full names and detailed descriptions of explanatory variables are found in Table 2.1.

APPENDIX C

UNIVARIATE ANALYSIS RESULTS OF CANDIDATE VARIABLES FOR CONDITIONAL LOGISTIC REGRESSION

Univariate analysis results of candidate variables for conditional logistic regression analysis at the microscale for Great Basin Gophersnakes, Western Yellow-Bellied Racers, and Western Rattlesnakes. Candidate variables were selected following univariate analysis (Paired t-test or Wilcoxon signed-rank tests, depending on normality results, between used and random sites) with $P<0.25$ and Spearman rank correlation tests with correlation coefficients <0.7. When the correlation coefficient was greater than or equal to 0.7, the variable with the least variation, as determined from the univariate analysis, was dropped, and the other was selected for further analysis (Dormann et al. 2013). Significance of univariate analysis at $P<0.05$ is denoted by a *.

Group	**Variable**	**Test**	***P***
Gophersnake	AREA	Wilcoxon	<0.0001*
	SLOPE	Wilcoxon	0.0001*
	G1	Wilcoxon	0.0002*
	S1	Wilcoxon	0.0056*
	OPEN	Wilcoxon	0.0011*
Racer	AREA	Wilcoxon	0.0001*
	SLOPE	Paired t-test	0.0002*
	OPEN	Wilcoxon	0.0084*
	R1	Wilcoxon	0.0007*
	S1	Wilcoxon	0.0133*
	AVGRV	Wilcoxon	0.0376*
	ASP	Paired t-test	0.1602
Rattlesnake	AREA	Wilcoxon	0.0001*
	SLOPE	Paired t-test	0.0023*
	G1	Wilcoxon	0.0007*
	S1	Wilcoxon	0.0677
	D1	Wilcoxon	0.0603

APPENDIX D

COMPARISON OF WEEKLY TEMPERATURE OSCILLATION AT TIMES WITH SNOW AND WITHOUT SNOW

The comparison of weekly temperature oscillation at times with snow and without snow from November 1, 2021, to March 31, 2022. ASH1 refers to artificial snake hibernacula 1, and ASH2 refers to artificial snake hibernacula 2. Position refers to the distance of loggers to the hibernaculum mouth, where the back is the furthest and the front is the closest (Figure 3.1). Comparisons were run individually for each position. ∗Significant at $p < 0.05$. Average weekly temperature oscillations for periods with snow and without snow ± the standard deviations are displayed.

Hibernacula	**Position**	**With Snow (°C)**	**No Snow (°C)**	**Test**	***p***
ASH1	Back	1.0±0.10	0.9±0.2	t-test	0.1103
	Middle	1.3±0.2	1.1±0.2	t-test	0.0893
	Front	0.9±0.7	0.8±-0.3	Wilcox	0.6982
ASH2	Back	1.1±1.0	0.9±-0.2	Wilcox	0.341
	Middle	0.90±0.5	1.0±0.4	Wilcox	0.8046
	Front	1.7±0.6	1.7±00.8	t-test	0.9321

APPENDIX E

POST HOC EXACT TEST RESULTS FOR THE COMPARISON OF AVERAGE DAILY TEMPERATURE BETWEEN DIFFERENT POSITIONS IN ARTIFICIAL SNAKE HIBERNACULUM 1 AND 2 AND THE AVERAGE, MAXIMUM, AND MINIMUM SNAKE TEMPERATURE

The post hoc exact test results for the comparison of average daily temperature between different positions in artificial snake hibernaculum 1 and 2 and the average, maximum, and minimum snake temperature (n=4) between November 1, 2022, and March 31, 2023 (Figure 3.6). ASH1 refers to artificial snake hibernaculum 1, and ASH2 refers to artificial snake hibernaculum 2. Front, middle, and back refer to the distance of loggers to the hibernaculum mouth, where the back is the furthest and the front is the closest (Figure 3.1). The values correspond to the *p* values from the test results. ∗Significant at $p < 0.05$. Non significance is bolded. Average is the overall average daily temperature ± the standard deviation.

ID	Average (°C)	Average Snake	Maximum Snake	Minimum Snake
ASH1Front	8.020±2.833	**0.3674**	<0.0001*	<0.0001*
ASH1Middle	9.931±2.879	<0.0001*	<0.0001*	<0.0001*
ASH2Back	9.039±2.873	<0.0001*	**0.5414**	<0.0001*
ASH2Front	6.628±2.589	<0.0001*	<0.0001*	**1.0000**
ASH2Middle	7.945±2.406	<0.0001*	<0.0001*	<0.0001*
Average Snake	7.778±2.697	-	-	-
Maximum Snake	8.728±3.140	<0.0001*	-	-
Minimum Snake	6.758±2.192	<0.0001*	<0.0001*	-