

**REPRODUCTIVE ECOLOGY OF FEMALE WESTERN RATTLESNAKES
(*CROTALUS OREGANUS*) IN CANADA**

By

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ABSTRACT

Female reproduction plays an important role in wildlife populations, especially those that face pressure from threats such as habitat loss, road mortality and stochastic events. Determining what factors cause the variation in reproductive success and life history traits in populations, particularly those that exist at northern peripheries, provides insight into their vulnerability to extinction. Reproductive female Western Rattlesnakes have been largely understudied in Canada, causing a considerable knowledge gap on female ecology, specifically, life history traits, spatial ecology, and most importantly the selection and use of habitat for parturition also known as rookery sites.

From 2017–2019 I conducted a detailed study on reproductive female Western Rattlesnakes at three sites in the Okanagan region of British Columbia, Canada. At the most southern and xeric site (Osoyoos) female rattlesnakes gave birth significantly earlier, had rookery sites significantly further away from hibernacula, exhibited larger home range sizes, and moved further distances (daily and postpartum) than rattlesnakes at two more northerly sites. Over 55% of telemetered females (majority belonging to Osoyoos) moved away from their hibernacula following parturition. Several rookery sites were identified across the three sites with a high degree of intraspecies communalism (~80%), and female rattlesnakes exhibited site fidelity to rookery sites with subsequent reproductive events. Habitat selection models from our main study site (Osoyoos) revealed that rock cover, shrub cover, and temperature attributes all were positively associated with rookery selection. Multi-site models revealed that rock cover was a strong predictor of rookery selection at all three scales across the sites.

The observed differences in postpartum movements across sites prompted a non-invasive *in situ* supplementation study. Gravid female rattlesnakes consumed supplemented food until late parturition (August–September) and had significantly higher postpartum body condition than controls. Contrary to my expectations, increased access to food and water by supplementation did not significantly halt, or alter, postpartum movements away from hibernacula. This suggests females in these populations may maximize their food (and possibly water) intake during reproductive years, regardless of their body condition.

This study highlights the variability in female rattlesnake life histories, movement, and behaviour in northern populations, and reveals the habitat and temperature variables required for rookery selection. Together, these results suggest that further study and mitigative measures may be required to effectively protect this species.

Keywords: Viperidae, Reptile, Movement Ecology, Habitat Use, Reproduction, Female Ecology, Conservation, Radiotelemetry, Food Supplementation, Rookery Sites



Photo Credit: Frank Luca

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DEDICATION

*This thesis is dedicated to the snake mothers and pups that endured
my poking and prodding over the years.*

*I will remember every female I studied and the sacrifices they made.
Thank you for your resilience.*



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CHAPTER 1

FEMALE REPRODUCTION, VIVIPARITY, AND ECOLOGY

The Role of Female Reproduction in Animals

Female reproduction plays an essential and critical role in most wildlife populations. Populations that contain relatively few reproductive females are at risk of low recruitment and prone to extirpation, especially when under pressure from other threats such as habitat loss, road mortality and stochastic events. Determining the factors that cause variation of female reproductive success, especially in populations that are threatened will provide insight into vulnerability to extinction.

Lifetime reproductive success is determined by a female's reproductive life span, annual fecundity over their life span, and offspring survival (Brown 2016; Murray 1992). Female reproductive success also can be influenced by behavioural, physiological, morphological, ecological, and social factors (Brough et al. 2016). For example, female size and parturition timing are correlated with reproductive success in Bottlenose Dolphins (Brough et al. 2016), whereas physiological processes such as the rate of water uptake by a female's eggs and maternal nest-site choice are important for offspring survival in Keelback snakes (*Tropidonophis mairii*- Brown and Shine 2005).

Approaches to maximizing reproductive success typically fall into one of the two categories: (1) capital breeders or (2) income breeders (Brown 2016). Capital breeders use energy that is acquired previously and stored for future reproductive events, whereas income breeders utilize resources gained during a reproductive event (Brown 2016). However, these categories can be fluid, as the reliance a species has on capital versus income can vary from year to year in a population (Bonnet et al. 2001).

There are also two main modes of female reproduction, oviparity (egg laying) and viviparity (live bearing) (Blackburn 1999). Oviparity is a common reproductive mode; however, viviparity has evolved over 160 times and can be found in invertebrates, squamate reptiles, mammals, amphibians, and cartilaginous fishes (Blackburn 1999). Viviparity also is not always associated with sexual reproduction - some viviparous species reproduce asexually through parthenogenesis, such as the Southern Death Adder (*Acanthophis antarcticus*-Allen et al. 2018), the Green Anaconda (*Eunectes murinus*-Shibata et al. 2017),

and the Blacktip Shark (*Carcharhinus limbatus*- Chapman et al. 2008). Both these reproductive modes have their advantages and disadvantages (Blackburn 1999). Birds, being exclusively oviparous, have evolved incredibly diverse methods of protecting their eggs, such as high parental care, camouflaged eggs, and nest placement within inaccessible environments (Blackburn 1999). On the other hand, viviparity has proven to be an important reproductive mode in reptiles, particularly those that live in unfavourable environments (Shine 2005).

Viviparity in Reptiles

While a high proportion of reptiles are oviparous (Tinkle and Gibbons 1977), viviparity has evolved as many as 100 separate times in lizards and snakes, but never in turtles or crocodylians (Shine 2005). The evolution of viviparity in reptiles has been a topic of contention over the years (Shine 1995; Qualls and Andrews 1999; Murphy and Thompson 2011; Shine 2014). One hypothesis that garnered considerable support, and continues to be supported today, is the “Cold-Climate Hypothesis” developed by Rudolf Mell, Hazel Claire Weekes, and Alexei M. Sergeev (Shine 2014). Independently, Mell and Weekes simultaneously proposed that viviparity in reptiles evolved in cold climates as a method to protect eggs from low nightly soil temperatures, while Sergeev suggested viviparity evolved in cold climates where retention of eggs allows for accelerated development of eggs and earlier hatch time before cooler fall temperatures arrive (Shine 2014). According to the Cold-Climate Hypothesis, reproductive mode could limit the distribution of a species, making oviparous species relatively less abundant in colder climates (Shine 1985). This notion was further supported when experimentation revealed that cold temperatures were detrimental to oviparous species, by delaying the development of eggs, reducing hatching success, and producing poorer quality offspring (Qualls and Andrews 1999).

Following the cold climate hypothesis, Shine (1995) formulated the Maternal Manipulation Hypothesis (MMH), suggesting that viviparity allows a mother to manipulate phenotypic traits in her offspring to ultimately increase survival and fitness. According to the MMH, viviparity can occur in any kind of environment, even a relatively hot one, when uterine retention allows the mother to provide optimal conditions for her developing young. Thus, viviparity may be an advantageous reproductive strategy, particularly in harsh

environments where egg laying is less favourable (Shine 2015). However, viviparity does impose costs on mothers, including long embryonic development, periods with high metabolic demand, and reduced mobility causing reduced feeding opportunities and increased risk of predation (Macartney and Gregory 1988; Shine 2003).

Viviparity in Snakes

Viviparity has evolved from oviparity in approximately 30 different lineages of snakes, typically in colder climates, as predicted by the Cold Climate Hypothesis (Shine 2003). There have been a few cases where taxa have transitioned from viviparity back to oviparity (Surget-Groba et al. 2006; Lynch and Wagner 2010), but this seems to be a rare occurrence. Viviparity also is a common reproductive mode in many snake species in the tropics, where mothers can maintain more stable temperatures than what is present in nests, thus ensuring enhanced fitness of her offspring (Webb et al. 2006).

All told, female snakes have incredibly diverse reproductive tactics that adjust according to local food availability and predator densities (Shine 2003). Some of these tactics include frequency of reproduction, timing of reproduction, amount of energy allocated for reproduction, and offspring quality (Shine 2003). Furthermore, female snakes that select sites for parturition may exhibit behavioural thermoregulation that provides optimal temperatures and protection from predators (Macartney and Gregory 1988; Graves and Duvall 1993; Brown 2016). These parturition sites have been referred to as “rookery sites” and have been recorded in several viviparous species, such as the Timber Rattlesnake (*Crotalus horridus* - Martin 2002; Brown 2016) and the Western Rattlesnake (*Crotalus oreganus* - Macartney and Gregory 1988; Graves and Duvall 1993).

While considerable efforts have been made to study reproductive effort and success in viviparous snakes (Bonnet et al. 2001; Lourdais et al. 2002; Gignac and Gregory 2005; Brown 2016), there is a general lack of understanding of habitat use and the behavioural ecology of reproductive female viviparids, particularly in colder climates.

Western Rattlesnake Ecology

The Western Rattlesnake (*Crotalus oreganus*) is a viviparous snake that occupies the northern limit of its range in British Columbia (B.C.), Canada (Macartney 1985; Maida et al.

2018; Winton et al. 2020 – see Figure 1.1). Western Rattlesnakes currently are listed as “threatened” in Canada and “special concern” in B.C., with their primary threats being fragmentation, habitat loss, road mortality and direct persecution (ECCC 2019). Being at a northern latitude, rattlesnake populations in B.C. face more environmental challenges than their southern counterparts, such as a shorter active season due to the cold climate that forces individuals to seek shelter in hibernacula for six months of the year (Macartney 1985). Consequently, female rattlesnakes in B.C. demonstrate slower growth rates, delayed maturity, longer reproductive cycles, and smaller litter sizes, all drastically affecting recruitment rates (Macartney and Gregory 1988). Additionally, individual Western Rattlesnakes exhibit high fidelity to specific hibernacula that may contain large assemblages of snakes, including multiple species (Gienger and Beck 2011); destruction of these hibernacula by human disturbance or stochastic events likely is detrimental to snake populations (ECCC 2019).

In Canada, extensive research has been conducted over the years on the Western Rattlesnake, including studies on the effects of disturbance on body condition, movement ecology, hibernacula use and fidelity, effect of road mortality on populations, and much more (Lomas et al. 2015; Maida et al. 2018; Harvey and Larsen 2020; Maida et al. 2020; Winton et al. 2020). Although these studies have certainly been instrumental in furthering our knowledge of this species, they have primarily focused on male rattlesnakes. Males have been predominately used in this research due to their larger body sizes that facilitate surgical transmitter implants while avoiding any unforeseen impacts on female reproduction. This bias has produced a conspicuous knowledge gap on female rattlesnake reproductive ecology and biology at the northern edge of its range.

Most of our “current” knowledge of reproductive female rattlesnakes in B.C. stems from a detailed population study conducted on Western Rattlesnakes 40 years ago in Vernon, B.C (Macartney 1985). From that study, through mark/recapture of adult females, Macartney (1985) detected infrequent reproductive cycles (biennial or triennial), low growth rates, late maturity, small litter sizes, and parturition dates that occurred between September and October. Notably, Macartney (1985) reported that gravid females had relatively small home range sizes (less than 0.22 ha in size) and gestation or “rookery” sites were no further than 50 m from hibernacula.

Several studies elsewhere have examined gravid female rattlesnake habitat use and ecology (Taylor and DeNardo 2005; Cardwell 2007; Schuett et al. 2011; Schuett et al. 2013; Brown 2016 Wastell and Mackessy 2016; Petersen et al. 2019), including the importance of rookeries (Macartney and Gregory 1988; Graves and Duvall 1993). Despite these efforts, there continues to be a lack of in-depth (and up to date) studies on female reproductive rattlesnakes, particularly species in northern latitudes like the Western Rattlesnake, where females (and populations) likely are subject to environmental constraints. Furthering our knowledge in this area will improve our understanding of the evolutionary ecology of rattlesnakes and how they may cope with future threats. Specifically, we need a better understanding of female behaviour and movement before, during, and after parturition, the timing of parturition in northern latitudes, and the factors used to determine rookery selection. These aspects are particularly relevant for the conservation and management of Western Rattlesnakes.

For this thesis, I examined the life history traits, movement ecology, and habitat selection for pre- and postpartum female Western Rattlesnakes (*Crotalus oreganus*) in southern B.C., through mark-recapture, extensive radiotelemetry, habitat surveys, and a supplementation experiment.

The research objectives of my thesis were:

1. Improve our understanding of the basic ecology of female rattlesnakes before, during, and after parturition (**Chapter 2**);
2. Compare reproductive female home ranges and movement between populations in B.C. (**Chapter 2**);
3. Determine habitat features selected at rookery sites and describe their structure, location, and use (**Chapter 2**); and
4. Examine the effect of food and water supplementation on postpartum movement and postpartum body condition (**Chapter 3**).

In the last remaining portion of Chapter 1, I provide a detailed overview of my main study site and a brief description of two secondary sites. In Chapter 2, I address Objectives 1–3 by quantifying and comparing rookery selection dates, parturition dates, movement, and use of rookeries across my three study sites. In Chapter 3, I investigate the drivers of

postpartum movement through an *in situ* food and water supplementation experiment (Objective 4). Finally, in Chapter 4, I revisit my main thesis findings and their meaning for the future conservation of the Western Rattlesnake.

Study Sites

I studied reproductive female Western Rattlesnakes at three separate locations within the Okanagan Valley of British Columbia, Canada (Figure 1.1). The Osoyoos study site sits just north of the Canada–USA border, while the White Lake and Vernon study sites are approximately 37 km and 175 km north of the Osoyoos study site respectively. Reproductive female Western Rattlesnakes (*Crotalus oreganus*) were studied at the Osoyoos study site for three consecutive years (2017–2019) and for one year (2019) at the Vernon and White Lake study sites (Figure 1.1).

The primary study site in my research was located on the southeast corner of the Osoyoos Indian Reserve (OIR), specifically the lands surrounding the Nk'Mip Desert Cultural Centre in Osoyoos, B.C., Canada (119.4° W, 49.28° N; Elevation: 283 m). For brevity, hereafter this site will be referred to as ‘Osoyoos’. This site was approximately 450 ha (Maida et al. 2020) in area and contained a dry arid ecosystem generally considered to be Canada’s lone representation of a “true desert”. This site was dominated by shrub-steppe habitat containing Bluebunch Wheatgrass (*Agropyron spicatum*), Antelope Brush (*Purshia tridentata*), Big Sagebrush (*Artemisia tridentata*), and Little Prickly Pear Cactus (*Opuntia fragilis*) (Figure 1.2). This site also contained extents of open forest consisting of Ponderosa Pine (*Pinus ponderosa*), Douglas Fir (*Pseudotsuga menziesii*), and steep rocky talus slopes (Figure 1.2). Rattlesnake communal hibernacula were scattered across rocky southwest facing slopes approximately 450–800m in elevation. The southern portion of the study site was more heavily disturbed and included a golf course, RV campground, horse stables, resort, vineyard, and many associated roads and parking lots. The northern portion was relatively untouched by urban development (Eye et al. 2018; Maida et al. 2020 for further details) (Figure 1.3).

The second study site was approximately 3,960 ha in area and situated in the White Lake Basin (49.29°N, 119.6°W; Elevation: 478 m) near Kaleden, BC. This site was characterized as open shrub-steppe grassland habitat containing Bluebunch Wheatgrass

(*Agropyron spicatum*) and Big Sagebrush (*Artemisia tridentata*), in addition to steep forested hills containing predominantly Ponderosa Pine (*Pinus ponderosa*) (Figure 1.4). This site was bisected by a paved two-lane road that sees an average of 350 vehicles/day from April–October (see Winton et al. 2020 for detailed site description).

My third study site was situated near the City of Vernon. Approximately 1,150 ha in size, it straddled Kalamalka Lake Provincial Park and the adjacent Coldstream Ranch (50.20°N, 119.3°W; Elevation: 482 m). This was the site used by Macartney (1985) and more recently Atkins (2021). This site was characterized by Ponderosa Pine (*Pinus ponderosa*), Douglas Fir (*Pseudotsuga menziesii*), and Western Redcedar (*Thuja plicata*) forests, and lower-elevation grasslands containing Bluebunch Wheatgrass (*Agropyron spicatum*) and several native shrub species (Figure 1.4). Kalamalka Provincial Park is a provincially protected area that averages 32,600 visitors per month from April–October and contains year-round recreational activities including hiking and mountain biking and horseback riding. The Coldstream ranch portion of the study site contained free-range cattle and limited public access (see Atkins et al. 2022 for detailed site description).

During the three years of study in Osoyoos, mean monthly temperatures were higher than historical norms, with slightly warmer temperatures in 2017 (Figure 1.5). Additionally, during these years, mean precipitation was lower in February and in the summer-months compared to historical norms (Figure 1.5).

During 2019, Osoyoos had consistently higher mean monthly temperatures and lower monthly precipitation (excluding July–late September) compared to Vernon and White Lake. White Lake had considerably higher precipitation in the spring (March–June) than Osoyoos or Vernon (Figure 1.6). Annual total precipitation in Osoyoos (148.8 mm) was less than half that compared to Vernon (386.0 mm) and White Lake (391.3 mm).

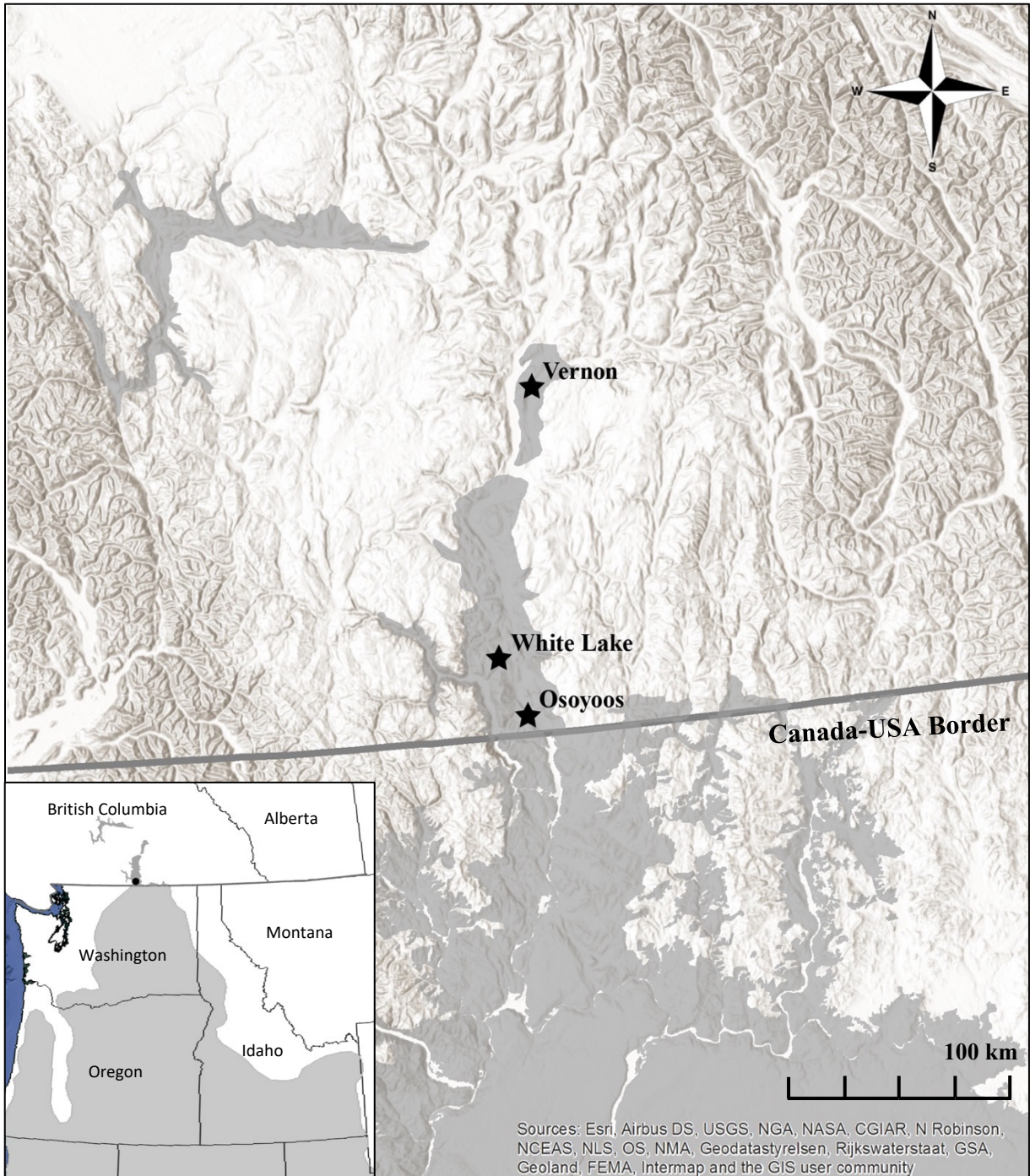


Figure 1.1. Location of study sites within the Western Rattlesnake (*Crotalus oregonus*) range (grey areas) in North America. (Adapted from: R. Reudink, British Columbia Ministry of Forest, Lands, Natural Resource Operations and Rural Development). Inset shows location of Osoyoos study site within the range of *C.oregonus* in Canada and USA.



Figure 1.2. Representative habitats for the Western Rattlesnake in Osoyoos, British Columbia, Canada, including: A) Rocky talus slopes, B) Shrub-steppe, and C) Open Forest. (Photo A by author, photos B & C by Frank Luca).



Figure 1.3. (A) Southern portion of study site in Osoyoos, British Columbia, containing fragmented landscape and development and (B) Northern portion containing unfragmented habitat. Photos by author.



Figure 1.4. A) Vernon study site - photo by Marcus Atkins, and (B) White Lake study site - photo by Jade Spruyt.

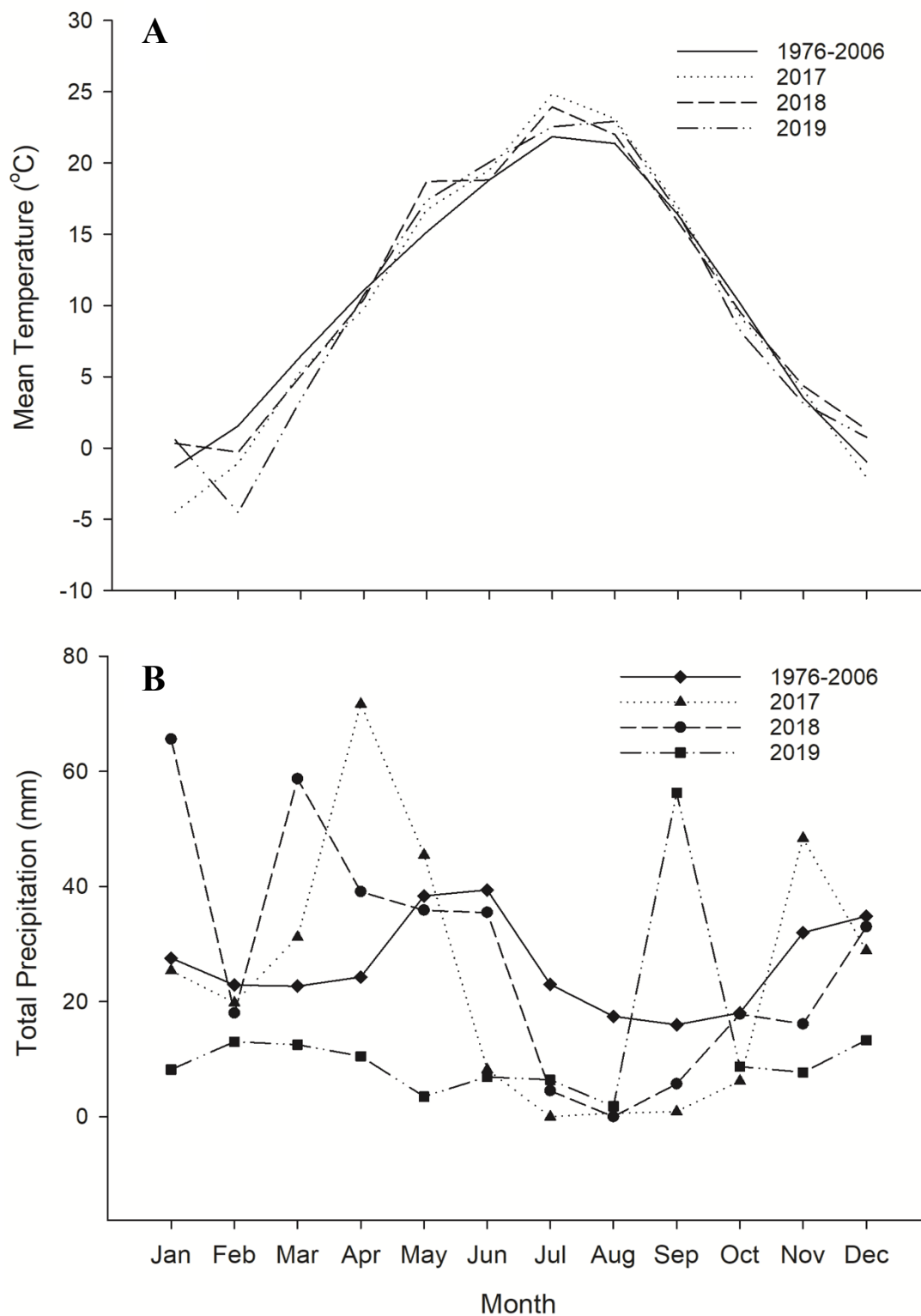


Figure 1.5. A) Mean monthly temperatures (°C) and B) total monthly precipitation (mm) in Osoyoos, British Columbia from 2017–2019, compared to the historical 30-year mean (1976–2006). Values measured at the Osoyoos weather station (49° N, 119°W) (Environment and Climate Change Canada 2021).

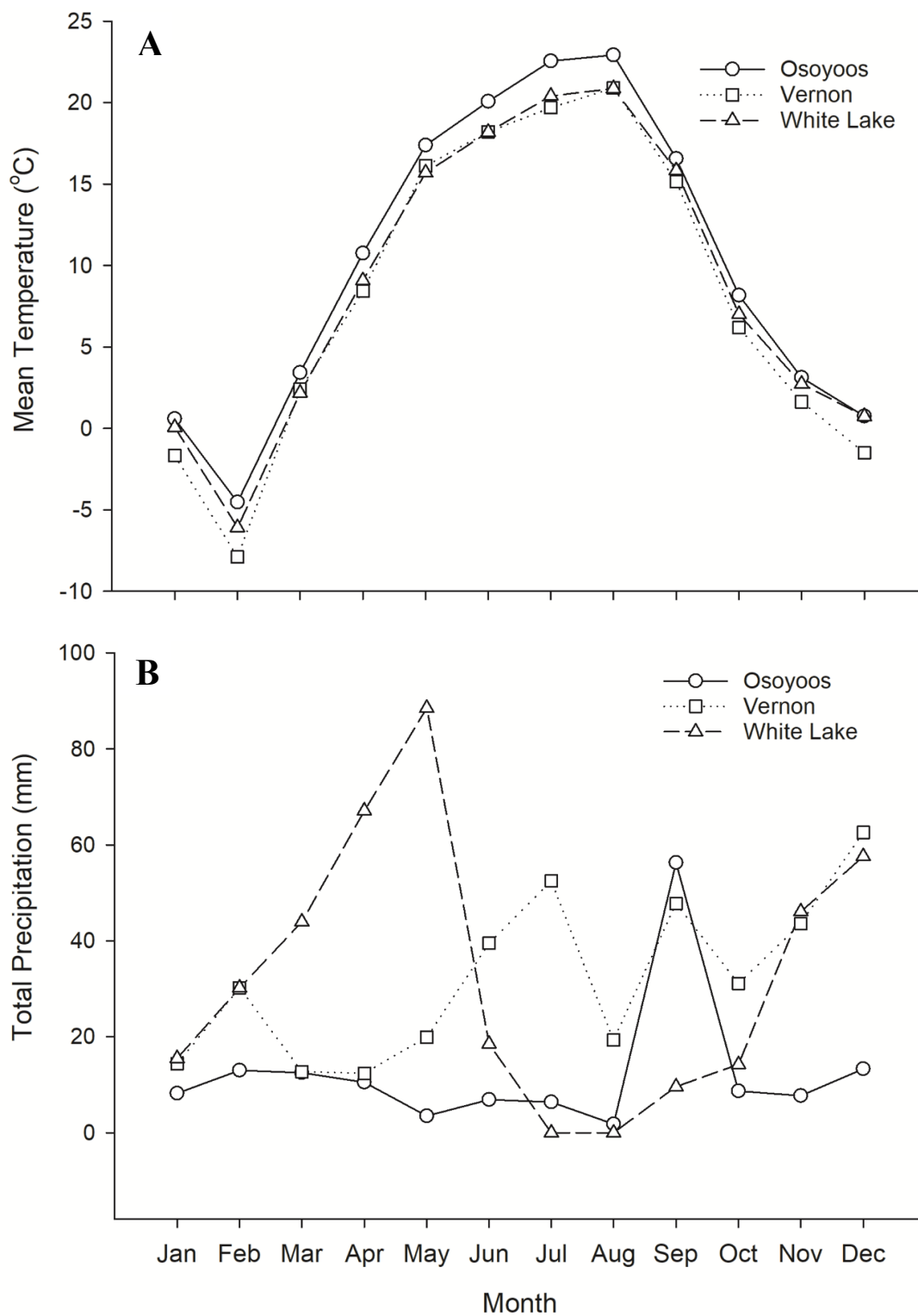


Figure 1.6 A) Mean monthly temperatures (°C) and B) total monthly precipitation (mm) in Osoyoos, Vernon and White Lake, British Columbia in 2019. Values measured at the Osoyoos weather station, Coldstream weather station, and Penticton Regional Airport respectively (Environment and Climate Change Canada 2021).

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CHAPTER 2
REPRODUCTIVE LIFE HISTORY, MOVEMENT, AND MICROHABITAT SELECTION
FOR PARTURITION OF FEMALE WESTERN RATTLESNAKES
(*CROTALUS OREGANUS*)

INTRODUCTION

Conservation strategies for threatened species typically involve protection of habitat considered essential for key life-history stages. Specifically, identifying these ‘critical habitats’ has become a major focus for protecting species-at-risk (SAR) (Camaclang et al. 2015; Palm et al. 2020). However, determining the habitat attributes essential for species persistence can be challenging, especially when scientific data are lacking; the societal will to protect critical habitat can also be controversial, particularly if it resides in resource-rich areas or those deemed valuable for development and recreation (Martin et al. 2017).

For temperate zone species that hibernate, the management of ‘critical habitat’ often focuses on locating and protecting overwintering sites (hibernacula). This is because suitable hibernacula often are coincidentally scarce and essential for overwinter survival. For example, Black Bears (*Ursus americanus*) in British Columbia rely on hibernacula to survive inclement weather and avoid predation, and they may reuse these sites if they are limited on the landscape (Davis et al. 2012); several species of *Myotis* bats rely heavily on underground hibernacula, such as caves and mines, that provide stable temperatures to survive winter in North America, and these habitats can be limited on the landscape and may require migration to access them (Johnson et al. 2017).

Communal hibernacula are key features considered ‘critical habitat’ for temperate zone snakes. The importance of these sites is implied due to a heavy reliance on hibernacula for overwinter survival by multiple animals, high fidelity to individual hibernacula, and for some species, the use of hibernacula for reproduction (Macartney and Gregory 1988; Gregory 2009; Gienger and Beck 2011). Communal snake hibernacula also receive attention when mass aggregations of snakes at these structures aid conservation efforts by facilitating mark-recapture for population estimates (Macartney 1985; Larsen and Gregory 1989; Maida et al. 2018). However, while the protection of communal hibernacula is a key step in protecting snake populations, it only addresses a single resource (albeit an important one)

used by snakes to complete one stage of their life-history. Summer habitats essential for foraging, mating, shedding and parturition (or oviposition) remain relatively unquantified among snake species in B.C. (ECCC 2019).

Being viviparous, female rattlesnakes appear to be capital breeders, relying on previously stored energy to successfully reproduce successfully (Macartney and Gregory 1988). This constraint, in addition to shorter active seasons due to inclement weather, leads to infrequent female reproduction (biennial and triennial), slower growth rates, delayed maturity, and smaller litter sizes, all drastically affecting recruitment rates in northern rattlesnake populations (Macartney and Gregory 1988). Furthermore, all viviparous female snakes demonstrate reduced mobility, and must actively thermoregulate to develop their young; these costs may lead to an increased chance of predation and high metabolic demands respectively (Shine 2003). These reproductive constraints and challenges reveal the potential fragility of northern rattlesnake populations, especially when faced with threats such as road mortality and habitat loss. Identifying critical habitat linked to the summer ecology of female rattlesnakes in B.C. has been largely ignored. In particular, the specific resources required by gestating (viviparous) females has received little attention.

The use of radiotelemetry to collect information on habitat use and ecology by gravid female rattlesnakes has become increasingly common outside of B.C. (Taylor and DeNardo 2005; Cardwell 2007; Schuett et al. 2011; Schuett et al. 2013; Wastell and Mackessy 2016; Maag 2017; Petersen et al. 2019); some of this work has revealed that much like traditional hibernacula, reproductive females may show fidelity to traditional gestation or ‘rookery’ sites (Graves and Duvall 1993; Martin 2002; Brown 2016). Repeated use of rookery sites over a female’s lifetime may enhance fitness by ensuring gestation and parturition occur at a site that previously proved successful, analogous to the repeated use of traditional hibernacula (Gregory 2009; Gienger and Beck 2011). By selecting rookeries with suitable microclimates, gravid rattlesnakes also may benefit by shortening the development time of their young, thus allowing for a shorter pregnancy and reducing the cost of less mobility (Lorioux et al. 2013). Additionally, rookery sites may minimize predation risk by providing accessible refuge, and in some cases, an assemblage of females may increase predator deterrence (Graves and Duvall 1993). However, these studies fail to examine rookery selection, and structure in

detail, particularly, across the range of a species to provide a broader understanding of the importance of these features.

In this study, I conducted a focused investigation on the movement, behaviour, and habitat use by reproducing female Western Rattlesnakes near the northern limit of their range. My objectives were to determine the degree of reliance on specific habitat features, notably rookeries. I also examined the movements of individuals pre and postpartum and relate this to the location of rookeries in relation to hibernacula.

METHODOLOGY

Western Rattlesnake Ecology in Northern Latitudes

The Western Rattlesnake (*Crotalus oreganus*) is a viviparous snake that resides at the northern extent of its range in British Columbia (B.C.), Canada (Macartney 1985; Lomas et al. 2015; Maida et al. 2018, Figure 1.1). Here, Western Rattlesnakes are considered at-risk both provincially and federally. Western Rattlesnakes in this region overwinter in communal hibernacula from October–April, and during spring and fall, male and non-gravid female rattlesnakes make migratory movements between hibernacula and summer foraging habitats (Macartney and Gregory 1988; Winton et al. 2018; Maida et al. 2020). The age at maturity for female Western Rattlesnakes has been estimated to range between 5–7 years (Macartney and Gregory 1988) and more recently between 4.9–8.5 years (Maida et al. 2018). Mating for this species has been reported during late summer, with ovulation occurring in May–June, and parturition between September and October (Macartney and Gregory 1988).

Additionally, this species is known to reproduce infrequently (biennially and triennially) and have a mean litter size of 4.6–5.5 (Diller and Wallace 1984; Macartney and Gregory 1988). Currently little is known about the behavioural ecology of female reproductive *C.oreganus*, particularly in the northern extent of its range. Past studies in B.C. reported that rookery sites were located at hibernacula or within a 50m radius, and based on mark-recapture data, female *C.oreganus* appeared to have significantly smaller home range sizes than adult male or non-gravid rattlesnakes (Macartney 1985; Macartney and Gregory 1988).

Study Sites

I studied reproductive female Western Rattlesnakes at three separate locations within the Okanagan Valley of British Columbia, Canada (Figure 1.1). My primary study site was located on the Osoyoos Indian Reserve (OIR), near the town of Osoyoos, B.C. (119.4° W, 49.3° N). The Osoyoos site has been the subject of continuous study of rattlesnakes since 2002 (Brown et al. 2009; Lomas et al. 2015; Eye et al. 2018; Maida et al. 2018; Harvey and Larsen 2020; Maida et al. 2020). A second study site was located within the White Lake Basin (49.29°N, 119.6°W) near Kaleden, B.C., and a third study site was situated between the Kalamalka Provincial Park and adjacent Coldstream Ranch (50.20°N, 119.3°W) near Vernon, B.C. Female rattlesnakes were studied in Osoyoos for three consecutive years (2017–2019) and for one year (2019) in White Lake and Vernon. See Chapter 1 of this thesis, Macartney (1989), Winton et al. (2018), Maida et al (2020), and Atkins et al. (2022) for detailed study site descriptions.

The entire Okanagan Valley consists of a dry, semi-arid ecosystem dominated by grasslands, shrubs, notably Big Sagebrush (*Artemisia tridentata*), and Ponderosa Pine (*Pinus ponderosa*) forests. Within this range, there is a north-south gradient in average temperatures, wherein White Lake and Vernon have cooler mean temperatures in the summer (June–August) than Osoyoos (Table 2.1). Additionally, White Lake and Vernon had higher annual precipitation than Osoyoos in 2019 (Table 2.1).

The active season for snakes, or the time between hibernation periods, typically is from April to October at these northern study sites; snakes in Osoyoos generally emerge earlier in the spring (late March) and return to hibernacula later in the fall than snakes in White Lake or Vernon (Larsen, pers. comm).

Table 2.1. Comparison of the geography and weather metrics of three study sites, Osoyoos, Vernon, and White Lake B.C., Canada. Mean summer temperatures are based on 01 June to 31 August, expressed as year: mean (+/- SE). Values measured at the Osoyoos weather station, Penticton Regional Airport, and Coldstream weather station (Environment and Climate Change Canada 2021).

Study Site	Lat/Long	Elevation (m)	Mean (SE) Historical Summer Temperature (°C)	Mean (SE) Summer Temperature (°C) During Study	Annual (2019) Total Precipitation (mm)
Osoyoos	49.3° N, 119.4° W	283	20.7 (0.9)	2017: 22.4 (1.6) 2018: 21.6 (1.5) 2019: 21.8 (0.9)	148.8
Vernon	50.20°N, 119.3°W	482	18.2 (0.8)	2019: 19.6 (0.8)	386.0
White Lake	49.29°N, 119.6°W	478	19.7 (1.0)	2019: 19.8 (1.0)	391.3

Radiotelemetry and Mark-Recapture

Rattlesnakes were captured during focal mark/recapture work at hibernacula during egress and ingress, and opportunistically throughout the active season (April–October). Upon capture, all snakes were measured (mass and Snout-Vent-Length or SVL) and marked in the field using Passive Integrated Transponder (PIT) tags implanted subcutaneously (Biomark).

Adult females captured during egress had their reproductive status determined through gentle palpation (Macartney and Gregory 1988). Gravid individuals that appeared healthy were surgically implanted with radio-transmitters (SB-2T, 3.8g: Holohil Systems Inc., Ontario, Canada) by qualified veterinarians at nearby clinics, following procedures outlined elsewhere (Reinert and Cundall 1982; Reinert 1992; Bryant et al. 2010). Transmitters were implanted along the left side of the coelomic cavity. Female Western Rattlesnakes in Canada are relatively small (in this study, max 873 mm SVL); this constraint, and the need to ensure the implanted transmitter did not affect gestation or parturition, meant relatively small transmitters (SB-2T, 3.8g: Holohil Systems Inc., Ontario, Canada) with a life span of 5–6 months were used. As a result, I was not able to track some individuals for the entirety of their active season (April–October). In these cases, I assumed that these individuals would return to the hibernacula that they were captured at during egress, or in some cases I could confirm their return to the den through mark/recapture work. Any individuals where this method was not possible, were not included in analysis. Removal of transmitters occurred in the Fall (September–October), or in the case of battery failure, the following spring upon egress.

Released snakes were located every 3–4 days starting in April–May, continuing through to the end of their active season (September–October). The UTM coordinates (Garmin GPSMAP 64, ± 5 m) at the location of the snakes were recorded. A snake was considered to have moved if it was greater than five meters from its previous location, and a new UTM location was recorded. I collected location data within 1 m of the location of the snake and then moved 10 m away to ensure low disturbance and to avoid change in behaviour.

I recaptured telemetered females 1–2 times each season to briefly monitor health (visual inspection and body mass using a hand-held Pesola spring scale) and reproductive

status. I considered snakes to be gravid if they contained enlarged follicles or discernable embryos, and postpartum if they showed longitudinal folds on their bodies, an empty or collapsed abdomen, and a significant decrease in body mass (Macartney and Gregory 1988, Figure 2.1). These physical inspections typically took five minutes with the snake released immediately thereafter.

Home Range and Movement Parameters

I considered a gravid female to have adopted a rookery when movements remained centred at a precise location (± 3 meter) for ~ 10 consecutive days. These sites were deemed communal when more than one individual gravid female was detected for long periods of time (i.e., June–August). I defined parturition date as the date when females first were confirmed to be postpartum (collapsed abdomen and longitudinal folds on their bodies—sometimes discernable from a distance, or if necessary, through capture), and/or I observed neonates and/or neonatal shed skins. Postpartum females were captured, weighed, and immediately released.

I estimated home ranges and the movements of gravid and postpartum rattlesnakes via location data obtained from radiotelemetry. Home range methodology often is contested in wildlife research (Row and Blouin-Demers 2006; Wauters et al. 2007; Boyle et al 2008): The use of minimum convex polygons (MCP) is argued to overestimate home range size with unpredictable bias (Powell 2000; Nilsen et al. 2007). Kernel Density Estimates (KDE) can be a potential solution to this problem; however, an accurate estimate of home range requires at least 30–50 locations per animal (Seaman et al. 1999). I opted to use the MCP method to calculate home range, due to the low number of relocations I obtained during my study from the sedentary behaviour of gravid females during parturition. Although these home range estimates may be overestimates, they are suitable for snakes (Row and Blouin-Demers 2006) and provide a baseline for future conservation efforts. For these calculations I used the `adehabitatHR` package and `MCP` function (Calenge, 2006) in Rstudio (Version 4.0.4, The R Foundation for Statistical Computing 2021).

To quantify and compare movements by reproductive females at each study site, I calculated distance per day (DPD), distance moved postpartum (DPP) and distance from each female's rookery to her hibernaculum (ROOKDIST). The DPD metric was based on the total

path length (summation of Euclidean straight-line distances from successive points) divided by the number of days elapsed between observations. For DPP I identified the parturition date for each individual and combined the straight-line distances between successive points from this date to the last recorded data point before hibernation. I used the `as.ltraj` function in the `adehabitatLT` package (Calenge, 2006) from RStudio to estimate the DPD and DPP metrics. I estimated ROOKDIST by measuring the straight-line distance between each individual's known hibernaculum and rookery site using the measure tool in Google Earth Pro (Version 7.3.3).

Finally, I quantified the tactics that postpartum females took after leaving their rookery. To do this, I first calculated the straight-line direction that would have taken each female from her rookery directly to her hibernaculum; I then determined the furthest actual point (Euclidean distance) the postpartum female travelled and calculated the direction of this point from the rookery. The difference in degrees between these two vectors produced an 'angular departure' metric. If for example the bearing of a hibernaculum was 2 degrees and the bearing to the furthest point was 358 degrees, the resulting angular departure was 4 degrees. Individuals with high angular departures ($>50^\circ$) and high DPP (greater than the distance to their hibernaculum) were considered to have moved away from their hibernaculum. Females that simultaneously displayed a low angular departure ($< 50^\circ$) but a high DPP (greater than distance to hibernaculum) had moved towards but beyond their hibernaculum, again reflecting movement surpassing that needed to simply reach the hibernaculum. Conversely, individuals with low angular departure ($< 50^\circ$) and DPP = distance to hibernaculum were considered to have returned more-or-less directly to their den following parturition. I confirmed the effectiveness of this approach through a visual examination of snake movement trajectories in Google Earth.

Microhabitat Selection

At all three study locations I collected habitat data on natural (i.e., anthropomorphic rookeries were excluded) rookery sites and corresponding, paired random plots at three different scales: small (1m radius), medium (3m radius) and large (10m radius), using a matched case-control study design (Harvey and Weatherhead, 2006). I established random circular sites 40 meters away from the center of each rookery site, to avoid overlap of plots,

in a random direction using a direction generator. I measured habitat features (Table 2.2) at all three scales including percent cover of rock, shrub, grass, tree, and woody debris. I considered shrubs to be vegetation < 2 m tall and trees to be > 2 m in height. Additionally, I measured percent slope, aspect, elevation and UTM coordinates (Garmin GPSMAP 64, +/- 3 m) at each site (Table 2.2). I assessed cover data through ocular estimation using a canopy cover technique whereby each layer of vegetation or substrate was determined by its vertical projection (Jennings et al. 1999; Korhonen et al. 2006). Although ocular estimation is subjective and can change seasonally (Korhonen et al. 2006), I ensured habitat data at all sites were collected by myself within a 3-week timeframe for consistent assessment of cover at all three study sites. Percent slope was measured with a clinometer and a downslope target of equal height, and aspect, or the direction of the downslope, was measured with a compass at the centre of each site.

At the Osoyoos site, surface temperatures were recorded at rookery sites and the corresponding random plots during late parturition (month of August) in 2018. I chose this month to record temperature as it was the time when females were in the sedentary phase of their parturition, and I could confirm the exact location of their rookery. To record temperature, I placed temperature data loggers (iButtonsTM, model DS1922, accuracy +/-0.5 °C) at each site, three iButtons per scale (sm, med, lg), spaced evenly in random locations, that recorded surface temperature every 15 minutes for approximately 3–4 weeks (iButtons recorded for this period due to logistical constraints). I placed the iButtons in a waterproof container to ensure consistent temperature recordings and secured them to the ground with stakes or taped them to a rock. All iButtons were positioned out of direct sun exposure to avoid direct solar radiation. Analogous temperature data were not measured at the other two study sites due to logistical constraints.



Figure 2.1. Postpartum female Western Rattlesnake with longitudinal folds in Osoyoos, BC, 2017. Coloured segments were used to identify the telemetry snake (3 dark blue segments) and the year of study (1 green segment). Photo by author.

Table 2.2. Description of habitat and temperature variables measured for microhabitat analysis at three different plot scales (sm, med, lg). Conditional logistic regressions were run for the Osoyoos site (including temperature and habitat variables) and for all sites (excluding temperature variables). See text for detailed description of specific assay methods.

Variable	Definition	Location Sampled
MaxDay	Maximum Daytime Surface Temperature (°C)	Osoyoos only ↓
MinDay	Minimum Daytime Surface Temperature (°C)	
AvgDay	Average Daytime Surface Temperature (°C)	
MinNight	Minimum Overnight Surface Temperature (°C)	
AvgNight	Average Overnight Surface Temperature (°C)	
%Rock	Percent Rock Cover	All sites ↓
%Shrub	Percent Shrub Cover	
%Grass	Percent Grass Cover	
%Tree	Percent Tree Cover	
%WoodyDebris (%WD)	Percent Woody Debris Cover (includes logs, branches, stumps, dead material, medium–large sized debris, anything usable by a rattlesnake for cover)	
Slope	% Slope	
Aspect	Slope Aspect (0–360)	

Statistical Analysis

Statistical analyses were conducted in RStudio (v. 4.0.4) and Minitab19. All means are reported with ± 1 standard error (SE).

I estimated body condition scores using the residuals from a regression of mass on snout-vent-length (SVL) (Brown et al. 2009; Lomas et al. 2015). I used a univariate one-way ANOVA to compare body size (Snout-Vent-Length (SVL), Mass), body condition, and movement parameters of the female snakes between the three study sites, with Tukey's Honest significant difference for *post hoc* comparisons. I used a similar approach to compare rookery selection dates, parturition dates, elevation, and aspect between the three sites. All dates were converted into Julian date. I also ran a Pearson's correlation test (r_p) to determine if body condition was correlated with rookery selection date, and if female body size (Mass & SVL) and body condition were correlated with parturition date. Furthermore, ran the same test to determine if ROOKDIST was correlated with rookery selection date and parturition date. Linear regression and r_p were used to investigate the effect body size (SVL) on home range size and the relationship between the number relocations and home range size. I ran an independent T-Test to compare body condition between postpartum females that moved immediately to their dens following parturition and those that did not. I checked all data for normality using histograms and residual plots and made transformations (logarithmic) when normality assumptions were not met.

I ran conditional logistic regression models at three scales comparing my metrics from the rookery and random sites. I did this separately for the Osoyoos dataset that contained temperature data, as well as the multi-site dataset that included all three study sites (but excluding temperature data). I used the clogit function in the Survival Package of RStudio (v. 4.0.4) (Therneau 2020). Aspect values were converted to radians and cosine-transformed, and once transformed, an aspect value of +1 represented due North and -1 represented due South (Mardia and Jupp 2000). I tested for autocorrelation (Spearman Correlation: r_s) between all habitat values before selecting the candidate variables for entry into Conditional logistic regression models (Appendix A). At all three scales, top models were selected via Akaike Information Criterion (AIC) backward stepwise selection (Mazerolle 2006).

RESULTS

Radio Telemetry: Rookeries, Timing of Selection, and Parturition

A total of 31 female Western Rattlesnakes (*Crotalus oreganus*) (Osoyoos: $n=19$, Vernon: $n=3$, White Lake: $n=9$) were radio-tracked during the active season (April–October), resulting in a total of 974 relocations. At the beginning of the study, these animals had an average weight of 246.3 g (± 10.7 g, range 134–357 g) and an average SVL of 633.0 mm (± 10.0 mm, range 542–783 mm). The snakes at the Osoyoos site were on average significantly smaller (SVL: $F_{2,28} = 10.85$, $P < 0.001$) and weighed less (Mass: $F_{2,28} = 6.40$, $P < 0.005$) than telemetry snakes in Vernon and White Lake, however, body condition did not significantly differ between sites ($F_{2,28} = 2.38$, $P = 0.11$).

From the telemetry animals I identified a total of 24 unique rookery sites (Osoyoos: $n=15$, Vernon: $n=3$, White Lake: $n=6$, Table 2.3). Nearly 80% ($n=19/24$) of these sites showed communal use (Table 2.3). One rookery site in Osoyoos showed communal use for three consecutive years, involving as many as 8 gravid female rattlesnakes at a time. Rookery sites were located on south/south-west facing slopes ($\bar{x} = 182.9 \pm 6.21^\circ$) at an average elevation of 510.6 m (± 19.8 m) with 27.3 % (± 1.54 %) slope incline (Table 2.3). The aspect of rookeries did not significantly differ between sites ($F_{2,25} = 2.62$, $P = 0.09$), however, rookeries in Osoyoos were found at significantly lower elevation than the other two sites ($F_{2,25} = 21.70$, $P < 0.001$); Table 2.3).

Rookery selection dates ranged from May 5th–July 29th (2017–2019) with high individual variation and no significant difference between the three study sites ($F_{2,26} = 1.13$, $P = 0.34$, Table 2.3). Additionally, body condition was not correlated with rookery selection date ($r_P = 0.006$, $P = 0.97$). Telemetry snakes in Osoyoos had the earliest parturition dates (August 9th), compared to snakes in Vernon and White Lake that gave birth significantly later (September 16th and 19th) ($F_{2,26} = 20.83$, $P < 0.001$, Table 2.3). Additionally, non-telemetry females were detected giving birth as late as October 5th (Vernon). Female body size (Mass and SVL) and body condition were not correlated with parturition date (Mass: $r_P = 0.359$, $P = 0.36$; SVL: $r_P = 0.102$, $P = 0.10$; Body Condition: $r_P = -0.172$, $P = 0.36$).

Table 2.3. Number of rookeries detected by radio-tracking gravid Western Rattlesnakes (*Crotalus oreganus*) in Osoyoos (2017–2019), Vernon (2019) and White Lake (2019), B.C. The number of tracked snakes appear in the column headings. Also shown are the range of rookery selection and parturition dates, and the mean aspect and elevation of rookeries. Mean values are accompanied by SE (parenthetical) and range (*italicized*). Those with differing superscript letters represent significant difference at $\alpha = 0.05$.

	Osoyoos (n=19)	Vernon(n=3)	White Lake (n=9)
Number of Rookeries	15	3	6
Communal Rookeries	12	2	5
Rookery Selection Date Range	May 5–July 29 ^a	May 14–July 24 ^a	May 10–July 28 ^a
Parturition Date Range	August 9–August 30 ^a	August 19–September 16 ^b	August 22–September 19 ^b
Aspect (°)	190.7 (7.57) ^a <i>128–239</i>	179.5 (16.3) ^a <i>140–213</i>	159.16 (8.12) ^a <i>130–185</i>
Elevation (m)	445.4 (15.3) ^a <i>370–558</i>	566.8 (50.5) ^b <i>420–650</i>	642.6 (12.0) ^b <i>608–674</i>
Slope (%)	26.12 (1.77) ^a <i>17–45</i>	39.50 (1.66) ^b <i>35–42</i>	22.67 (1.17) ^a <i>18–25</i>

Opportunistically, at the Osoyoos study site, I observed that neonates stayed with their mother at the rookery site for approximately 5–7 days (based on $n=19$ litters). Following this period, I found shed skins of neonates and an adult, presumably the postpartum mother, at 60% of vacated rookery sites. It is possible that shed skins were present at every rookery site, but rock structures and other microhabitat features rendered this impossible to verify.

Mark-recapture data at Osoyoos revealed 5 cases of telemetry females and 7 cases of other females demonstrating fidelity to a specific rookery over multiple reproductive bouts. These females exhibited apparent biennial reproduction, and successfully gave birth at the same rookery site in 2017 and 2019. More recent observations (pers. comm. Chloe Howarth, July 2021) confirmed one of these females continued to use the same rookery for three consecutive reproductive events (i.e., 2017, 2019, 2021). I did not detect any instance where females did not show fidelity to their rookery site (i.e., using different sites for different breeding attempts).

Home Range and Movement Parameters

Mean home range size for reproductive female snakes was 2.95 ha (± 1.70 ha). Snakes in Osoyoos had significantly larger home range sizes compared to snakes in White Lake, but not compared to Vernon snakes ($F_{2,28}=7.92$, $P<0.002$, Table 2.4). Individual home range size was not explained by female snout-vent-length (SVL) (\log_{10} MCP [ha] = $9.47 - 5.35 \log_{10}$ SVL [mm], $r^2=.28$, $F_{1,29}=1.08$, $P=0.30$), or the number of telemetry relocations ($r_p=0.099$, $P=0.59$). During the length of the study, females moved an average of 5.47 m (± 1.43 m) per day (DPD). DPD differed significantly between Osoyoos and White Lake snakes ($F_{2,28}=7.01$, $P<0.003$; Table 2.4).

On average, rookery sites were approximately 210 m (± 22.32 m) away from hibernacula. Over half (53%) of the females in Osoyoos had rookery sites greater than 100m away from hibernacula and one individual in Osoyoos adopted a rookery 1 km away from their hibernaculum. On average, rookery sites in Osoyoos were further away from hibernacula than those in Vernon and White Lake, however this difference was not statistically significant (ROOKDIST: $F_{2,28}=1.49$, $P=0.24$ - Table 2.4). Additionally,

ROOKDIST was not correlated with rookery selection date ($r_P = 0.22$, $P = 0.27$) or parturition date ($r_P = -0.13$, $P = 0.53$).

A total of 13 (Osoyoos: $n = 4$, Vernon: $n = 1$, White Lake: $n = 8$) out of 29 snakes moved immediately back to their dens following parturition ($< 50^\circ$ angular departure and DPP = straight-line distance to their den), while 16 snakes (Osoyoos: $n = 14$, Vernon: $n = 1$, White Lake: $n = 1$) made movements away from their den following parturition (angular departure $> 50^\circ$ (or $< 50^\circ$) and DPP $>$ straight-line distance to their den) (Figure 2.2). Postpartum females that moved directly towards their hibernaculum travelled significantly shorter distances ($r^2 = 0.36$, $y = 135.65 + 3.85x$, $F_{1,27} = 15.3$, $P < 0.001$; Figure 2.2). I was unable to determine the postpartum movements of two females due to early transmitter expiration. Postpartum snakes that moved away from their hibernaculum did not have significantly lower body condition than those who moved immediately back to their hibernaculum ($t(18) = -1.16$, $P = 0.26$). Additionally, postpartum snakes moved significantly greater mean distances (DPP) in Osoyoos compared to Vernon and White Lake snakes ($F_{2,26} = 10.95$, $P < 0.001$; Table 2.4). See Appendix B. for individual home range maps and approximate rookery locations.

Table 2.4. Summary of movement parameters for gravid female Western Rattlesnakes (*Crotalus oreganus*) in Osoyoos (2017–2019), Vernon (2019), and White Lake (2019), B.C. The number of tracked snakes appear in the column headings. Mean values are accompanied by SE (parenthetical) and range (*italicized*). Those with differing superscript letters represent significant difference at $\alpha=0.05$.

	Osoyoos, n=19	Vernon, n=3	White Lake (n=9)
100% MCP (ha)	4.8 (1.73) ^a <i>0.51–22.53</i>	3.1 (3.04) ^{ab} <i>0.03–9.18</i>	.95 (0.35) ^b <i>0.001–3.59</i>
DPD (m)	9.46(1.35) ^a <i>1.86–23.2</i>	4.64(2.24) ^{ab} <i>0.27–13.0</i>	2.32(0.70) ^b <i>0.19–7.61</i>
DPP (m)	605.5(93.8) ^a <i>20.1–1251.0</i>	82.1(82.2) ^b <i>82.1–246.5</i>	19.9(13.4) ^b <i>0.01–150.0</i>
ROOKDIST (m)	135.30 (43.71) ^a <i>7.6–987.7</i>	17.93 (5.20) ^a <i>11.4–110.3</i>	56.78 (18.07) ^a <i>2.0–165.7</i>

*DPD represents Euclidean distance travelled per day, DPP is the Euclidean distance travelled postpartum, and ROOKDIST is the Euclidean distance between an individual's rookery and their hibernaculum.

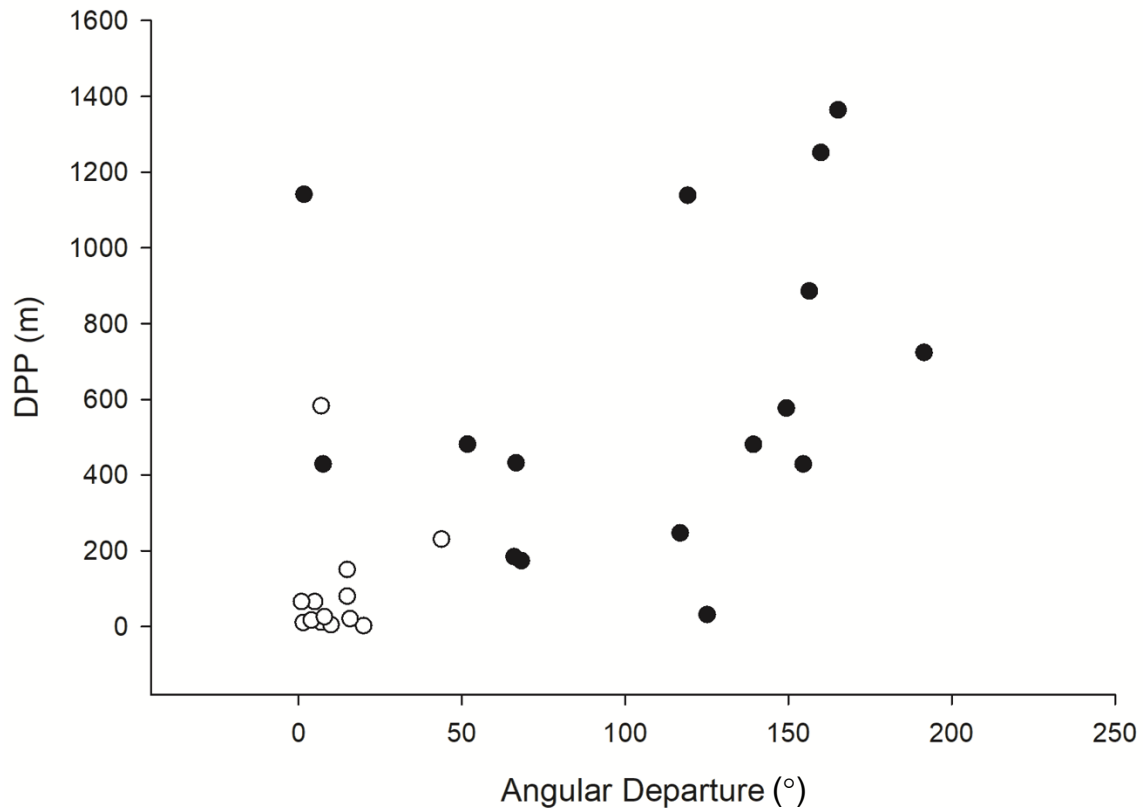


Figure 2.2. Range of movements shown by female rattlesnakes following parturition at rookery sites. DPP (ordinate) = total distance females travelled between parturition and arriving at their hibernaculum. Angular Departure (abscissa) represents the difference (degrees) between a straight-line vector from rookery to hibernaculum, and a second vector drawn from the rookery to the postpartum snake's furthest location point from hibernacula. Angular departure values approaching zero indicate females that came relatively closer to following the shortest and most direct route to hibernaculum. Data points are coded according to whether individual females initially moved further away (●) or returned immediately (○) to the hibernaculum. Postpartum females that moved directly towards their hibernaculum clearly tended to travel relatively shorter distances ($r^2=0.36$, $y= 135.65 + 3.85x$, $F_{1,27}= 15.3$, $P=0.001$).

Habitat Selection for Parturition

Telemetry snakes gave birth under medium to large sized boulders, flat table rocks, rock piles, or in their hibernaculum (Figure 2.3). Two snakes in White Lake gave birth under cement barriers <1 m from a paved road (350 vehicles/day average-Winton et al. 2018), and a female nearby gave birth in a slope <3 m from the same road. These three individuals were excluded from further habitat selection analysis, because only natural rookery sites were included in the selection models.

In the Osoyoos models I characterized the habitat of 14 rookeries and 14 paired random locations at three scales. Due to high autocorrelation between variables, only 6 of the 12 variables metrics were used in these models. The top models (Table 2.5) suggested maximum daytime surface temperatures (MaxDay) and rock cover predicted rookery selection at the small scale, rock and shrub cover at the medium scale, and minimum nightly surface temperature (MinNight) was positively associated with rookery selection at the large scale.

In the multi-site models (excluding temperature), I characterized the habitat of 24 rookery sites (Osoyoos: $n=14$; Vernon: $n=4$; White Lake: $n=4$) and 24 paired random sites at three scales. Due to high intercorrelation between variables, 4 variables were used in the multi-site models. Based on the variables that significantly attributed to the top models, rock cover was a strong positive predictor of rookery selection at all three scales (Table 2.6, Figure 2.4).



Figure 2.3. Examples of identified rookery sites of the Western Rattlesnake in Osoyoos, White Lake and Vernon, B.C. (2017–2019). Top photos are examples of rookeries at hibernacula, middle photos are rookeries in rock piles and bottom photos resemble boulder (left) and flat table rock (right) rookeries. Photos by author.

Table 2.5. Paired conditional logistic regression models for habitat selection at three different scales in Osoyoos, B.C ($n=24$). AIC was used to determine top models. See Table 2.2 for description of the habitat metrics. The * symbol indicates an interaction term.

Small Scale	AIC	ΔAIC
MaxDay+%Rock	11.20	0.00
MaxDay+%Rock+MinNight	11.71	0.51
%Rock	12.08	0.88
MaxDay+%Rock+MinNight+Slope	12.61	1.41
MaxDay+%Rock+MinNight+Slope+%Shrub	14.49	3.29
%Rock*Aspect	18.84	7.64
MaxDay	21.34	10.14
Medium Scale		
%Rock+%Shrub	13.02	0.00
%Rock	13.98	0.96
%Rock+%Shrub+%WD	14.74	1.72
MaxDay+%Rock+%Shrub+%WD	16.74	3.72
MaxDay+MinNight+%Rock+%WD	18.73	5.71
MaxDay+MinNight+%WD+%Shrub	23.32	10.30
Large Scale		
MinNight	11.75	0.00
MinNight+%Rock	12.01	0.26
MinNight+%Rock+%Shrub	13.10	1.35
MaxDay+MinNight+%Rock+%Shrub	14.48	2.73
MaxDay+MinNight+%Rock+%Shrub+%WD	16.45	4.70
MaxDay+%Rock+%Shrub+%WD	20.35	8.60

Table 2.6. Paired conditional logistic regression for habitat selection at three scales from three study sites in B.C., Canada. ($n=48$). AIC was used to determine top models. See Table 2.2 for description of the habitat metrics. The * symbol indicates an interaction.

Small Scale	AIC	ΔAIC
%Rock	12.90	0.00
%Rock+%Shrub	13.88	0.98
%Rock+%WD +%Shrub	15.02	2.12
%Rock + %WD	16.23	3.33
%Rock*%Grass	29.52	16.62
%Rock*%Shrub	31.50	18.60
Medium Scale		
%Rock	16.64	0.00
%Rock+%Shrub	16.68	0.04
%Rock+%Shrub+%WD	18.38	1.74
%Shrub+%WD	33.23	16.59
Large Scale		
%Rock	19.35	0.00
%Rock+%Grass	20.41	1.06
%Rock+%Grass+%WD	22.15	2.80
%Rock+%Grass+%WD+%Shrub	24.03	4.68
%Grass+%WD+%Shrub	32.06	12.71

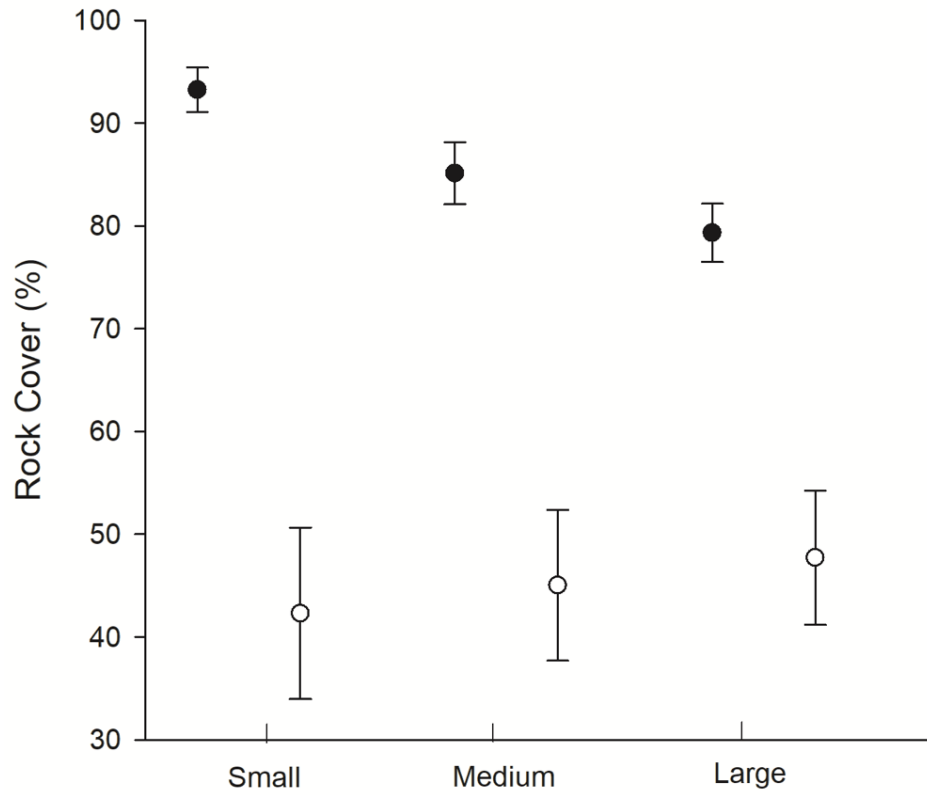


Figure 2.4. Mean \pm SE percent rock cover was higher at Western Rattlesnake (*Crotalus oreganus*) rookery sites (solid symbols, n=24) than random sites (open symbols, n=24) at three habitat plot scales (Small, Medium, Large).

DISCUSSION

Of 24 rookeries identified from the telemetered females (n=31) in this study, 19 (~80%) were communal. This finding is not entirely surprising; aggregations of gravid females at rookery sites have been detected in other viviparous species including Timber Rattlesnakes (*Crotalus horridus* - Martin 1993), Prairie Rattlesnakes (*Crotalus v. viridis* - Graves and Duvall 1993), and more recently in the oviparous Bullsnake (*Pituophis catenifer sayi* - Johnson et al. 2020). Earlier, Macartney (1985) reported aggregations of gravid *C. oreganus* at the Vernon study site.

Rookery selection dates were highly variable and did not significantly differ between sites, indicating that not all females move quickly to their rookery sites upon leaving their hibernacula. Similar behaviour has been reported for gravid Prairie Rattlesnakes (*C. viridis*) in Wyoming (Graves and Duvall 1993). Presumably this behaviour is driven by opportunities to forage and/or obtain water prior to adopting more sessile behaviour at the rookery, although in this study rookery selection dates were not correlated with body condition, suggesting that at some point females must select a rookery site, regardless of their body condition, because the summer is relatively short for these individuals. Furthermore, it is also possible the individual variability observed was due to the difference in “life experience” each female has had. For example, perhaps females that have had successful reproduction at a particular rookery are able to relocate that site for reuse, whereas other females may not have this knowledge or familiarity, and hence take longer to select a site. This hypothesis requires further investigation, because I was not able to accurately determine the number of pregnancies each female had had over their lifetime.

Female snakes in this study relocated and reused rookeries in subsequent reproductive events, indicating fidelity to these features. While I cannot conclude that all females in this study exhibited this behaviour, I did not observe any cases of females switching sites in the years they reproduced, implying that fidelity to rookery sites appears quite high in this part of the geographic range for this species. Repeated use of specific rookery sites was not unexpected: Western Rattlesnakes show high fidelity to other habitat, including summer ranges and hibernacula (Brown et al. 2009; Gomez et al. 2015). Additionally, Timber Rattlesnakes (*C. horridus*) have been found to exhibit fidelity to rookeries (Martin 2002; Brown 2016). It is

possible familiarity may play a factor in fidelity to sites, for example it may improve the species ability to avoid predation; A study on Wapiti (*Cervus elaphus*) in Alberta found that spatial familiarity was important for small scale habitat selection and foraging, where Wapiti would revisit sites of higher quality containing low predation, high forage, and moderate terrain (Wolf et al. 2009). Fidelity to rookery sites may change over time, with concurrent changes in microclimates caused by, say, vegetation growth: Martin (2002) detected changes in use by Timber Rattlesnakes (*C.horridus*) at a communal rookery due to shading from canopy trees. However, the choice to move to a more suitable rookery may not always be an option for some female rattlesnakes, particularly those living in more suboptimal habitats with limited habitat features such rock and shrub cover, making optimal rookery sites that much more important to females.

Parturition dates were significantly earlier at my most southern study site (Osoyoos) compared to those farther north, and these differences were not correlated with female body size or body condition. It is possible that varying weather may have been a factor: Lourdais et al. (2004) found that high summer temperatures sped up embryonic development in viviparous Aspik Vipers (*Vipera aspsis*), resulting in earlier parturition dates, whereas cool weather near the end of gestation (August for *V.aspsis*) caused high embryonic mortality. In this study, Vernon had cooler temperatures and high precipitation during parturition (June–August), which may have delayed parturition time, whereas Osoyoos had warmer temperatures and lower precipitation in these months (See Chapter 1). Interestingly, the timing of parturition in Vernon in this study was similar to observations made by Macartney (1985) over 35 years earlier. Although, at this time, it is unknown how exactly factors such as average egress dates, weather, and possibly foraging opportunities influenced the variation in rookery selection and parturition dates observed in this study.

Larger home ranges and greater distances (daily and postpartum) travelled by Osoyoos snakes may reflect longer and warmer active seasons or may be caused by the spatial distribution and availability of resources. Reported home range sizes and movements for female *C.oreganus* are limited. Macartney (1985) tracked two gravid snakes in Vernon that moved no more than 75m of their dens during the summer, resulting in small home range sizes (less than 0.22 ha). Conversely in this study, a female in Vernon had a home range of ~4 ha and moved distances

greater than 400 m from her hibernaculum, and a female in Osoyoos had a home range as large as 22 ha, larger than home ranges reported for male rattlesnakes at the same site (Lomas et al. 2015). I could not detect any apparent cost to larger movements such as those demonstrated by Osoyoos snakes. In addition, I observed that over 55% of telemetered females (majority belonging to Osoyoos) moved away from their hibernacula following parturition. This finding is surprising, as previous studies have reported postpartum females promptly returning to hibernacula (Macartney and Gregory 1988; Graves and Duvall 1993). Furthermore, the need to return to hibernacula is far greater for rattlesnake populations in northern latitudes, where there is pressure to seek refuge prior to the onset of colder temperatures (Macartney 1985). One plausible reason for this observed behaviour could be that these females are seeking food or water prior to hibernation, perhaps due to lack of availability of prey, or due to the extreme need to replenish reserves as postpartum rattlesnakes are reported to be emaciated, losing an average of 40% of their mass (Diller and Wallace 2002). I investigate the potential drivers of these movements further in Chapter 3.

Overall, it appears that differences in home range size and pre- and postpartum movements exist within the northern range of this species.

In this study, females occupied rookeries at a range of distances (max 1 km) from their respective hibernacula, suggesting that, at least in this region, protecting significantly large areas around hibernacula may capture rookeries as well. However, how this spatial pattern varies between species, ecosystems, and sites requires clarification. Over the years, few studies have examined rookery use or selection directly. At the northernmost study site (Vernon), a general mark/recapture study by Macartney (1985) reported gravid female rattlesnakes typically gave birth <50 m from their respective hibernacula. This matches the observations at this same study site and at White Lake, but at the third site (Osoyoos, the most xeric) more than 50% of rookeries were >100 m from the hibernacula (including one almost 1 km away). Females with rookery sites further away from hibernacula did not appear to have any disadvantages (i.e., later rookery selection or later parturition times) compared to those who chose sites close to hibernacula. It is possible the Osoyoos site, being the most southerly site, had more available suitable habitat for reproduction, such as sites with preferred microclimates for thermoregulation, compared to the other study sites where rookery sites were more likely to occur at or near hibernacula.

Habitat selection models from the main study site (Osoyoos) revealed that rock cover, shrub cover and temperature attributes were all associated with rookeries. At the same time, my multi-site models revealed that rock cover was a strong predictor of rookery selection at all three scales across the sites. These findings seem quite intuitive, given that accessible refuge (rock and shrub cover) likely will provide protection to pregnant snakes from nearby predators (Graves and Duvall 1993), and suitable microclimates may allow for shortened gestation period, thus reducing the associated costs of pregnancy (i.e., low mobility - (Lorion et al. 2013). Similarly, garter snakes (*Thamnophis sirtalis* and *T. elegans*) and Timber Rattlesnakes (*C. horridus*) utilize rocky clearings during gestation (Charland and Gregory 1995; Martin 2002). Although surface temperature was not quantified at the two secondary study sites, optimal rookery microhabitats may be limited at more northern sites, thus placing more of a premium on sites that are optimal for embryo development and parturition. Additionally, habitat (rock and shrub cover) and temperature could change over time at rookery sites; for example, the Osoyoos study site experienced a wildfire in the summer of 2021 that devastated a large portion of critical habitat. Stochastic events such as this could reduce the canopy cover (i.e., shrub cover) of rookery sites which could alter the efficiency of these sites (predator avoidance and/or temperature) and may discourage females from reusing these sites in the future, potentially impacting reproductive success and recruitment rates in these populations. Alternatively, events such as this could also make other sites more attractive to females by reducing shade from nearby tree canopy and thereby increasing their thermal qualities. Although, this is purely speculation and requires further study.

Three females in this study used artificial structures for rookeries less than 1 m from a nearby road, indicating that female rattlesnakes are willing to use anthropogenic structures. Clearly though, intentional, or inadvertent construction of rookery sites near roads or high human foot traffic will be counterproductive to potential survival (Winton et al. 2020).

Overall, this study reveals that much like hibernacula, a network of rookery sites is selected and used repeatedly in northern populations of rattlesnakes. These rookeries are occupied, often by multiple females, for long periods during reproductive bouts, and females will use the same sites across years. Therefore, protection of these sites seems important for the persistence of these populations.

Current protections for the Western Rattlesnake habitat fall under both provincial and federal policies and can be complex in nature. In the province of B.C., Wildlife Habitat Areas (WHAs) are a conservation tool used by managers that consist of small, protected areas (~200-300 ha) that surround identified rattlesnake hibernacula (Williams et al. 2012). While WHAs are an important step in the conservation of rattlesnakes in B.C., rookeries are often cryptic. Although this study identified some key features of rookeries, it would be necessary to survey WHAs to pinpoint rookeries that exist. For example, for Great Basin Gophersnakes in B.C., oviposition sites (Williams et al. 2015) and dispersal habitat (Williams et al. 2012) fell outside of WHAs and are also cryptic. Thus, WHAs, once established, require surveys to identify elements such as rookeries within the site or even nearby.

At the federal level, Western Rattlesnake hibernacula (and surrounding 2.8 km area) are protected through critical habitat designation, however these protections do not apply when hibernacula (or rookeries) are found on private lands (ECCC 2019). Thus, a large portion of critical habitat for rattlesnakes remains unprotected in this part of their range. With these limitations at both provincial and federal levels, it appears that further focused study on locating rookeries and monitoring is warranted. Even within critical habitat and protected areas, projects such road development, or capital projects such as pipeline access, for example, will require detailed surveys to identify rookery locations. A reasonable approach for this could be to conduct surveys during a specific “time window” such as during peak parturition time (Late July–September) that will increase the likelihood that females have selected their rookery site and neonates/neonatal shed skins may be found that may indicate a parturition site. Surveyors could utilize the information from the habitat analysis in this study that describes the structure, appearance, and requirements for rookery sites, to help them better identify potential rookery sites on the landscape. In addition to these methods, it would be beneficial to conduct radiotelemetry on gravid females where possible, as it would greatly increase the chance of locating rookery sites and would further our understanding of female rattlesnake ecology.

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CHAPTER 3

EFFECT OF RESOURCE SUPPLEMENTATION ON FEMALE WESTERN RATTLESNAKE POSTPARTUM MOVEMENT

INTRODUCTION

Viviparity (live-bearing) has evolved from oviparity (egg-laying) numerous times, including within squamate reptiles, mammals, amphibians, fishes, and invertebrates (Blackburn 1999). The costs and benefits of viviparity can differ between taxa; for example, viviparity was found to negatively impact the sprint speeds of the Common Striped Scorpion (*Centruroides vittatus*- Shaffer and Formanowicz 1996) but did not appear to affect movement in the lizard *Lerista bougainvillii* (Qualls and Shine 1998).

Compared to other taxa, viviparity has been studied in great lengths in squamate reptiles, likely because it has evolved over 100 separate times in lizards and snakes (Blackburn 2015). Viviparity has proven to be an important reproductive mode to reptiles with benefits that may be related to both protection and thermoregulation of developing young (Shine 2005). The latter advantage has been considered repeatedly as a mechanism for increasing reproductive success in extreme environments (Shine 2005; Shine 2014). In cold climates, behavioural thermoregulation (i.e., selecting gestation or 'rookery' sites for reproduction) allows female reptiles to maintain their developing offspring at warmer and more stable temperatures than those affecting a deposited clutch of eggs (Shine 2014). However, viviparity comes with many associated costs, including reduced mobility in females that may reduce feeding opportunities and increase predation risk, and a large investment of time and energy that may not be easily recouped over short, relatively cool summers (Macartney and Gregory 1988; Gregory 2009).

The costs and benefits of viviparity have been considered extensively in snakes, in part because the taxa contains numerous examples of closely-related species that have adapted different reproductive strategies, including viviparity and oviparity. Northern species of snakes are particularly good subjects for investigating the costs of viviparity to females. Several of these costs have been demonstrated, including delayed maturation, non-annual reproduction, and a severe depletion of female energetic reserves before re-entering hibernation (Macartney and Gregory 1988; Shine 2003; Gregory 2009).

As many as 80% of species in the Family Viperidae are viviparous (Fenwick et al. 2012). The clade reaches its northern limits in Canada where three extant species occur, namely the Western Rattlesnake (*Crotalus oreganus*), Prairie Rattlesnake (*Crotalus v. viridis*), and the Eastern Massasauga Rattlesnake (*Sistrurus catenatus*). The costs of viviparity in determining the northern limits of these animals have been previously examined: In northern populations of Western Rattlesnakes, females may demonstrate low growth rates, late maturity, small litter sizes, and biennial or triennial reproductive cycles (Macartney 1985; Macartney and Gregory 1988). Similarly, Eastern Massasauga Rattlesnakes at the northern tip of their range in Ontario, Canada, mature later than snakes in more southerly regions, and experience less-than-annual reproduction (Hileman et al. 2017). Non-annual reproduction has been associated with the inability of northern female rattlesnakes to replenish lost energy reserves before re-entering hibernation, necessitating one or more years before the next reproductive bout (Macartney and Gregory 1988; Graves and Duval 1993; Martin 2002; Maida et al. 2018). Indeed, it has been suggested that during and after parturition, female Western Rattlesnakes normally abstain from (or reduce) feeding before re-entering hibernation (Macartney 1985; Macartney and Gregory 1988; Wallace and Diller 1990). Thus, female Western Rattlesnakes, and many other rattlesnake species, have been deemed as ‘capital breeders’, meaning that they rely on previously acquired and stored energy for reproduction, compared to ‘income breeders’ that utilize resources gained during a reproductive event (Jenkins et al. 2009). However there have been some instances where reproductive female rattlesnakes have reported to feed before and after parturition (*Crotalus oreganus* - Wallace and Diller 1990; *Crotalus atrox* - Schuett et al. 2013), suggesting they may utilize both capital and income for reproduction.

The reliance of communal overwintering sites (hibernacula) in northern climes may exacerbate the energetic cost of viviparity, by requiring snakes to undertake lengthy annual migrations (Harvey and Larsen 2020) between summer and winter habitat. In Chapter 2, I explored another life history component of northern rattlesnakes, namely the use of traditional rookery sites by *C. oreganus* near the species’ northern limits in western Canada. As discussed, the brevity of the active season in this region has been thought to require postpartum females to return directly to their hibernacula following parturition (Macartney and Gregory 1988; Macartney 1985), despite the substantial loss (~40% of their body mass) of body condition due to parturition (Diller and Wallace 2002). However, I showed that just over half of telemetry

females did not display this behaviour, instead travelling further away from their hibernacula before returning to those sites for autumn ingress. I suggested this behaviour reflects a tactic by energy-depleted postpartum females to seek out food and/or water before entering hibernation. The putative advantages of this would be replenishment of fat reserves and rehydration prior to the long hibernation period; the potential costs of doing so include greater travel time, potentially further energy expenditure (especially if hunting is unsuccessful) and heightened risk of being subject to an early onset of cold weather.

To examine more closely the postpartum movement of Western Rattlesnakes, I conducted a non-invasive *in situ* supplementation experiment to test whether female vipers that maintain robust body conditions throughout parturition are more likely to return directly to the hibernaculum following parturition, rather than undertaking additional movements at the end of summer. Rattlesnakes, particularly those inhabiting xeric environments make excellent candidates for supplementation studies due to their low metabolic rates, sessile hunting behaviour, and lower energy demands (Taylor et al. 2005; Glaudas and Alexander 2017). Thus, small increases in resources through supplementation can have a large effect on these animals. To date, supplementation studies have focused heavily on female reproductive output (i.e., litter sizes, reproductive success, and frequency) (Lourdais 2002; Lourdais et al. 2003; Taylor et al. 2005; Capehart et al. 2016; Dezetter et al. 2021). The few supplementation studies that have focused on female spatial ecology found that, whether it be food or water, had virtually no effect on movement (Taylor et al. 2005; Capehart et al. 2016), although modest sample sizes (n=15 and n=7 respectively) are a common element of these studies.

I predicted that if postpartum movements were driven by the need to gain resources, then supplementing female rattlesnakes during parturition would halt, or alter, their need to forage prior to hibernation. Additionally, I predicted that this response would be strongest if females were provided with both food and water *ad libitum*, because these snakes would have a greatly reduced need to improve their body condition prior to hibernation.

Understanding how individual behaviour and life-history tactics of female rattlesnakes are affected by the availability of resources has important implications for the conservation of northern populations. Indeed, all three of Canada's rattlesnake species are federally listed as species-at-risk, with human development having an additive impact on populations already

experiencing climatic constraints. Furthermore, rattlesnakes typically inhabit xeric ecosystems (e.g., arid grasslands), where resources can be limited or inaccessible. Thus, a simultaneous test for the independent and interactive effects of food and water is particularly valuable, given that recent findings suggest desert-dwelling rattlesnakes may heavily rely on free-standing water for sufficient hydration (Murphy and DeNardo 2019).

METHODOLOGY

Study Sites

This study was conducted during the active season (April–October 2019) for the Western Rattlesnake, at three sites within the Okanagan Valley in British Columbia (B.C.), Canada (Figure 1.1). This valley represents one of the two narrow extents of this species' range in Canada. My primary study site was located on the Osoyoos Indian Reserve (OIR) in Osoyoos, B.C. (49.28°N, 119.4°W); additional work was conducted 37 km north of Osoyoos in the White Lake Basin near Kaleden, B.C. (49.29°N, 119.6°W), and outside the City of Vernon (50.20°N, 119.3°W), 175 km north of Osoyoos. All three sites occur within a xeric grassland ecosystem bordered by higher-elevation forests, although the Osoyoos site is relatively more arid, being considered Canada's only true desert ecosystem (Scudder 1999, See Figure 1.6, and Table 2.1, for comparison of site geography and weather metrics). Chapter 1, Winton (2018), and Atkins (2022), provide detailed study site descriptions.

Radiotelemetry

At all three sites, gravid female Western Rattlesnakes (*Crotalus oreganus*) were captured during surveys at hibernacula and/or opportunistically between April 1 and May 30, 2019. Reproductive status was determined through gentle palpation (Macartney and Gregory 1988), and individuals randomly selected for telemetry were taken to nearby veterinary clinics for transmitter implantation (Reinert and Cundall 1982; Reinert 1992; Bryant et al. 2010). Female Western Rattlesnakes in Canada are relatively small (in this study, max 873 mm SVL); this constraint, and the need to ensure the implanted transmitter did not affect gestation or parturition, meant relatively small transmitters (SB-2T, 3.8g: Holohil Systems Inc., Ontario, Canada) with a life span of 5-6 months were used. As a result, some individuals were not tracked for the entirety of their active season, and those with too few relocations were omitted from analysis. Transmitters were positioned 25% of each snake's SVL from the cloaca, extending along the left

side of the coelomic cavity and weighing < 5% of the body mass of each individual snake. Removal of transmitters occurred in the Fall (September-October) or, if the snake eluded capture at this time, during egress in the following spring. Snakes were given 48 hours to recover (or longer if required) and were released at their exact capture location.

Snakes were given 7 days post-release to recover and re-acclimate to their release site, and thereafter were located every 3–4 days starting in April-May and continuing through to the end of their active season (September-October). Coordinates (Garmin GPSMAP 64, ± 5 m) were recorded upon locating the snakes. I considered snakes to have moved if their displacement from the previous location exceeded 5 m. I collected the location data within 1 m of the snake, trying to minimize disturbance to the animal, and then I promptly moved >10 m away.

In addition to the relocations of each snake, I recaptured telemetered snakes 1 to 2 times a season to briefly assess health (visual inspection and body mass using a hand-held Pesola spring scale) and reproductive status. I considered snakes to be gravid if they contained enlarged follicles or discernable embryos, and postpartum if they showed longitudinal folds on their bodies, an empty or collapsed abdomen, and a significant decrease in body mass (Macartney and Gregory 1988, Figure 2.1). These physical inspections typically took approximately five minutes with the snake released immediately thereafter.

I considered gravid females to have adopted their rookeries when their movements remained centred at a precise location (± 3 meter) for ~ 10 consecutive days). These sites were deemed ‘communal’ when more than one individual female was present for long periods of time (i.e., June–August). I defined parturition date as the date when females first were confirmed to be postpartum (collapsed abdomen and longitudinal folds on their bodies - sometimes discernable from a distance, or if necessary, through capture), and/or I observed neonates and/or neonatal shed skins. Postpartum females were captured, weighed, and immediately released.

Supplementation Experiment

Across my three sites I established three groups of snakes (Food (n= 3), Food+Water (n= 3), and Control (n= 3), for a total of 9 snakes per site. A complete two-factor crossed design was considered unrealistic, because creating a Water Only treatment would have required physically disturbing and repeatedly handling gravid females to administer water (see Capehart et al. 2016).

The telemetered snakes were randomly assigned into each of the three groups at each study site. Control snakes in this study also were simultaneously involved in a broader empirical study of rookery use by female snakes (Chapter 2).

To eliminate the possibility of contaminants, non-native parasites, or disease being introduced by commercial rodents, snakes receiving food were fed native Deer Mice (*Peromyscus maniculatus*), a common prey species (McAllister and Maida 2016) found at all three sites. The mice were snap-trapped in several locations within 300 km of the study sites under permit (Amendment #3-MRPE15-171661) and immediately frozen. To feed snakes, frozen mice were transported into the field, and when appropriate, warmed in a ziplock bag (~25-28°C) submerged in a Thermos® container filled with warm water. For the Food+Water treatment the warmed deer mice were injected with approximately 7-10ml of sterile, warm water immediately before feeding to the snakes.

Snakes that had adopted a rookery site (See Chapter 2) were presented with food using a 3 m long fishing pole equipped with ~2 m of fishing line and a quick-release spring-loaded clamp (Hayward 1965; Figure 3.1). This method enabled researchers to stay at least 5 m away from the snake to minimize disturbance. Mice were attached to the clamp by the tail or leg and were moved and agitated on the ground in front of the female snake; once a mouse was struck by a snake, it was released gently via the trigger line (see Figure 3.1 for more details). Observation of the snake continued for approximately for 10-30 minutes from a nearby location (~5 m away) to visually confirm consumption. Once consumption occurred, an additional mouse was offered to the snake and if taken, monitoring continued for another 10-30 minutes to confirm consumption. This process was repeated until each experimental snake would no longer feed. Non-consumed mice were collected prior to departure. Snakes in the Control group were exposed to a parallel treatment using the fishing pole and clamp, but without the provisioning of mice. Logistics demanded that this work was conducted by different personnel across the sites, but all individual workers involved in the project were given strict methodology descriptions while receiving standardized training by the lead author prior to beginning the study.

Data collected each time a snake was visited included the amount of food (g) and water (ml) consumed, percent body visible, and air and ground temperature near the location of the

snake. Feeding sessions were terminated between August 7–14, close to parturition when the female snakes became increasingly cryptic and less prone to feeding.

Statistical Analysis

A total of 16 gravid females were included in my analysis from two of the three locations (Table 3.1). In Vernon 8 gravid females were outfitted with transmitters in preparation for this study, but one individual died from predation mid-way through the experiment. Six gravid females were implanted with transmitters at the White Lake site but repeated attempts involving researchers from all three sites failed to elicit feeding in the Food and Food+Water snakes (~9 attempts per snake for a total of 58 feeding attempts).

I estimated body condition scores using the residuals from a regression of mass on snout-vent-length (Brown et al. 2009; Lomas et al. 2015). I compared initial mean body condition between sites and groups with a univariate one-way ANOVA and Tukey's Honest significant difference for *post hoc* comparisons. Next, I used a linear regression to test the relationship between the amount of food and water consumed with postpartum body condition. To compare snake size (Mass and SVL) and parturition date between groups I used a one-way ANOVA and Tukey's Honest significant difference for *post hoc* comparisons. I then used a two-sample t-test to compare parturition dates between study sites. To compare effort (telemetry relocations) between groups, I ran a Kruskal-Wallis Test.

I quantified several movement metrics and compared these among the three groups (Food, Food+Water, Control). I calculated distance moved postpartum (DPP) and quantified the tactics that postpartum females took after leaving their rookery. To estimate these metrics, I used the same methodology presented in Chapter 2 (see page 25). I then ran a *G*-test (likelihood ratio test – McDonald 2014) in Rstudio using the *RVAideMemoire* package (Hervé 2021) to compare postpartum movement frequencies between the groups (Food, Food+Water, Control). Following this test, I ran a *post-hoc* power analysis (Cohen 1988) on my *G*-tests using the *pwr* package (Champely 2020) in Rstudio. Statistical analyses were conducted in RStudio (v. 1.3.1093) and Minitab19. All means are reported with ± 1 standard error (SE). All data were checked for normality using histograms and residual plots.

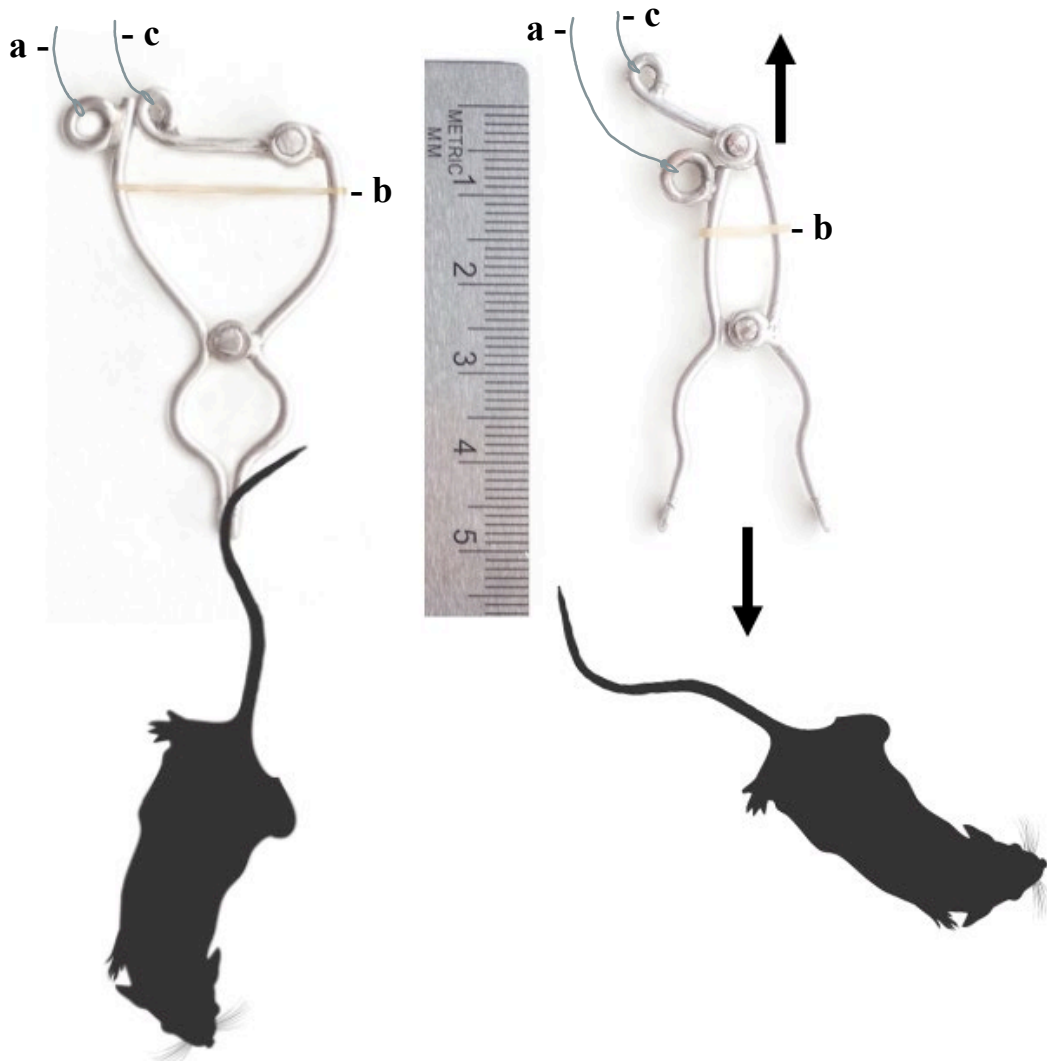


Figure 3.1. Feeding clip used in supplementation experiment to deliver dead deer mice to free-ranging gravid Western Rattlesnakes (2019). Two lines were attached to each clip and fed through a fishing pole for control by researchers. One fishing line (example in grey) was attached to the clip and used to lower and raise the entire apparatus (a); a small rubber band (b) was used to create tension and the release mechanism; the second line (c) when pulled released the trigger and caused the clip to spring open as shown in the diagram on the right. Apparatus adapted from Hayward (1965).



Figure 3.2. Example of author with a feeding clip and mouse attached to a fishing rod used to supplement female Western Rattlesnakes (2019). Photo by author.

RESULTS

Supplementation Overview and Body Condition

Each fed snake (including Food+Water snakes) over the course of the study consumed a mean of 149.0 ± 24 g of food which was an average of 8.5 mice (cumulative range: 56 g (3 mice consumed) – 322 g (19 mice consumed); Table 3.1). A maximum of 4 mice (with varying mass) were fed in one session. Snakes within the Food+Water treatment group had an intake of $\approx 49.6 \pm 9.6$ ml of water (range 26–77 ml; Table 3.2).

There were no significant differences in snake size (SVL and Mass) between the three groups at the beginning of the experiment (SVL: $F_{2,13}=0.08$, $P=0.93$; Mass: $F_{2,13}=0.14$, $P=0.88$), and initial body condition did not significantly differ between groups ($F_{2,13}=0.12$, $P=0.89$; see Figure 3.3) or between the three study sites ($F_{2,22}=1.01$, $P=0.38$). Interestingly, snakes at White Lake had the greatest body condition values ($\bar{x} = 0.016 \pm 0.008$) compared to snakes in Osoyoos ($\bar{x} = -0.0064 \pm 0.012$) and Vernon ($\bar{x} = -0.0126 \pm 0.025$), although these differences were not statistically significant.

Across the two study sites, the Control group had significantly lower postpartum body condition than the two treatment groups ($F_{2,8}=11.83$, $P < 0.004$, Figure 3.3). Snakes in the Food+Water group had the highest mean body condition scores ($\bar{x} = 0.18 \pm 0.03$) compared to the Food ($\bar{x} = 0.03 \pm 0.05$) and Control group ($\bar{x} = -0.16 \pm 0.05$), however there was no significant difference between the Food+Water group and the Food group (Figure 3.3). The amount of food consumed was positively associated with postpartum body condition ($y = -0.093 + 0.0013x$, $r^2=0.38$, $n=11$, $p=0.04$), as was the amount of water consumed ($y = -0.066 + 0.0038x$, $r^2=0.48$, $n=11$, $p=0.02$). Five individuals were excluded from this analysis due to failure to capture (hidden deep within hibernacula) and assess postpartum body condition.

Parturition Date

There were no significant differences in parturition dates between the three groups ($F_{2,10}=0.619$, $P=0.56$), yet snake size (Mass, SVL) was not correlated with parturition date (Mass: $r_p = 0.39$, $P < 0.202$; SVL: $r_p = 0.44$, $P=0.15$). Parturition date was significantly earlier in Osoyoos compared to Vernon ($t(4) = -4.24$, $P=0.01$). One individual gave birth as early as August 8th and one individual as late as September 16th (Table 3.3). I was not able to determine a precise

parturition date for four individuals due to a failure to conduct a visual assessment or capture before they departed from the rookery.

Postpartum Movements

A total of 16 reproductive female rattlesnakes (Osoyoos: $n=9$, Vernon: $n=7$) were radio-tracked every 2-3 days between April–October in 2019, resulting in a total of 464 relocations. The number of relocations did not significantly differ between groups (Kruskal-Wallis Test: $H_2 = 0.23$, $P=0.77$).

Distance moved postpartum (DPP) and angular departure did not significantly differ between groups (DPP: $F_{2,13}=1.49$, $P=0.27$; Angular Departure: $F_{2,13}=0.0637$, $P=0.94$, Table 3.3). A total of 8 snakes (Control: $n=3$; Food: $n=3$; Food+Water: $n=2$) moved immediately back to their dens following parturition ($<50^\circ$ angular departure and DPP= straight-line distance to their den), while 6 snakes (Control: $n=2$; Food: $n=2$; Food+Water: $n=2$) made movements away from their den following parturition ($>50^\circ$ (or $<50^\circ$) angular departure and DPP> straight-line distance to their den) (Figures 3.4 and 3.5).

The Control, Food, and Food+Water treatment groups did not display different postpartum movements away from their respective rookeries ($G=0.12$, $df=2$, $P=0.94$, Figure 3.3). Admittedly, the power of this test was low (Cramer's $V=0.091$ - Cohen 1988); High power ($>.80$) and a large effect size (Cramer's $V=0.35$ for this analysis would have required ≈ 78 individuals).

Table 3.1. Sample sizes of gravid female Western Rattlesnakes in food and water supplementation experiment Osoyoos and Vernon, B.C (2019).

Site	Food	Food+Water	Control
Osoyoos	3	3	3
Vernon	2	2	3

Table 3.2. Summary of feeding and hydration of female Western Rattlesnakes during supplementation experiment in Osoyoos and Vernon (2019) (n=10). Where F represents Food and FW represents Food+Water groups.

Site	ID	Number of Mice	Food Consumed (g)	Water Given (ml)
Osoyoos	F1	9	111.9	0
Osoyoos	F2	19	321.7	0
Osoyoos	F3	7	85.9	0
Vernon	F4	8	184.9	0
Vernon	F5	9	171.3	0
Osoyoos	FW1	3	56.4	26
Osoyoos	FW2	11	202.3	77
Osoyoos	FW3	3	55.5	30
Vernon	FW4	9	161.9	55
Vernon	FW5	7	137.8	45

Table 3.3. Summary of postpartum movement behaviour and parturition dates for gravid Western Rattlesnakes in Osoyoos and Vernon, B.C., Canada, in 2019. The number of tracked snakes appear in the column headings. Mean values are accompanied by SE (parentetical) and range (*italicized*). See methods for an explanation of how distance postpartum (DPP) and angular departure were determined.

	Control (n=6)	Food (n=5)	Food+Water (n=5)
DPP (m)	258.0(112.7) <i>4.0–582.3</i>	331.3 (69.2) <i>211.4–530.1</i>	595.5(204.3) <i>30.1–1006.6</i>
Angular Departure (°)	39.9 (22.8) <i>0–116.6</i>	56.8 (31.9) <i>0–155.6</i>	46.1 (40.4) <i>0–166.7</i>
Parturition Date Range	Aug 16–Sep 16	Aug 14–Sep 13	Aug 8–Sep 13

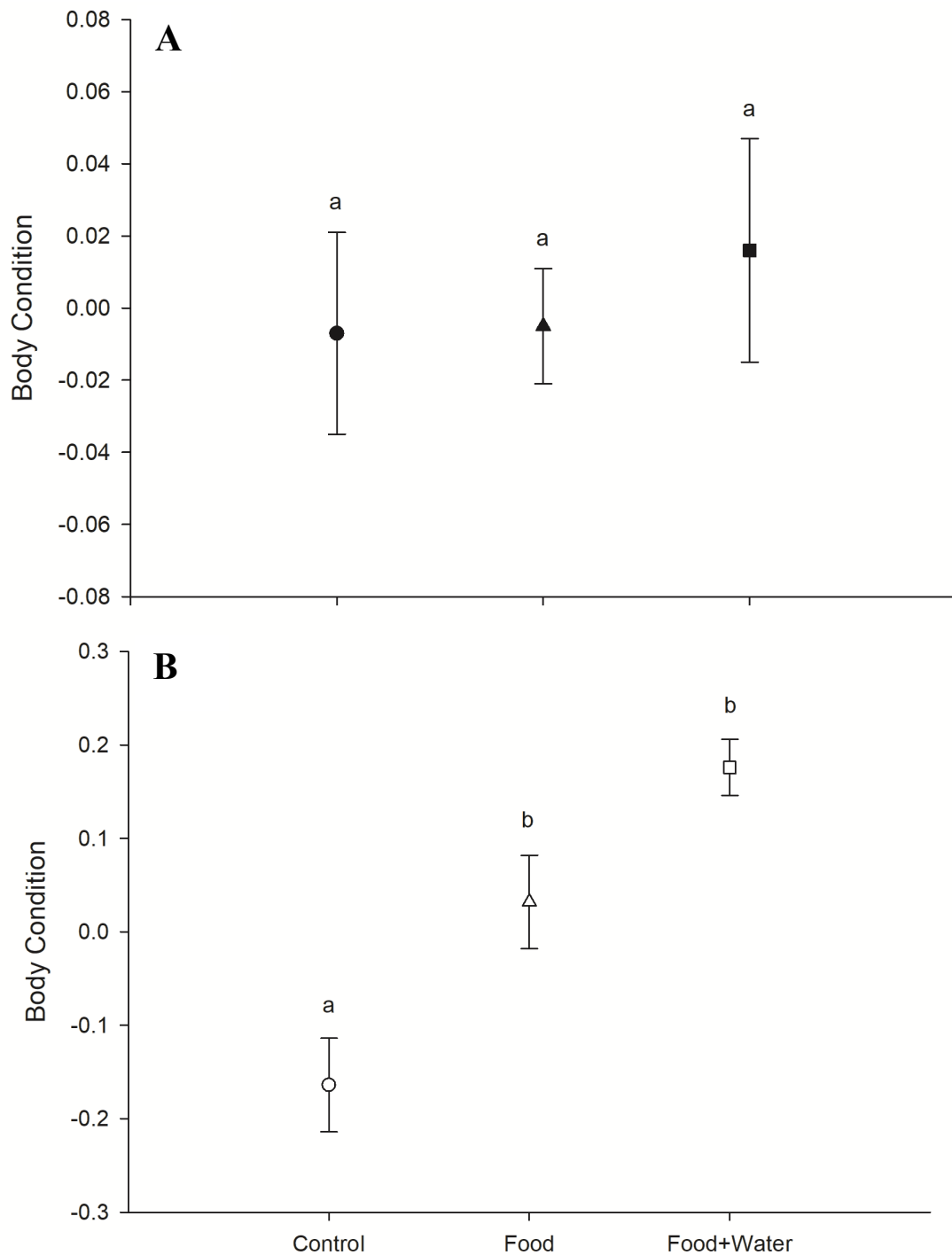


Figure 3.3. Comparison of mean body condition scores \pm SE between the three groups Control (n=4), Food (n=4), and Food and Water (n=3) of female Western Rattlesnakes in B.C., Canada. A) initial body condition prior to the experiment, B) postpartum body condition after the experiment. Different letters indicate significant difference (at $\alpha = 0.05$) in means between the treatment groups.

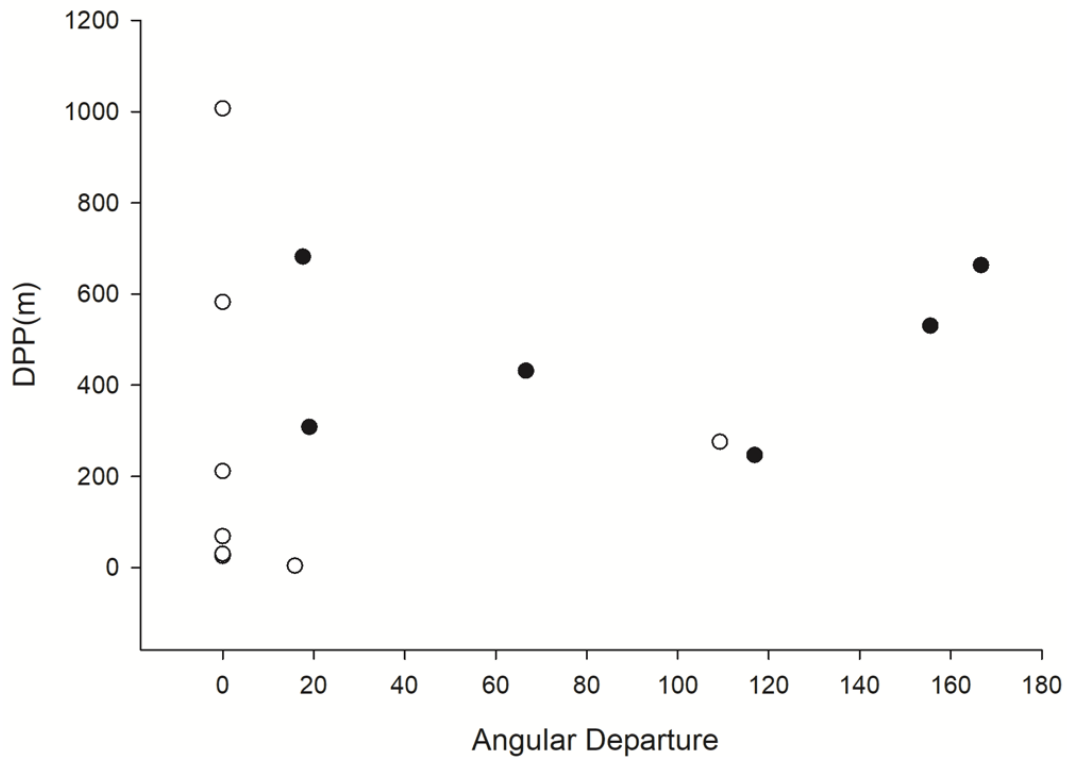


Figure 3.4. Range of movements shown by female rattlesnakes following parturition at rookery sites. DPP (ordinate) = total distance females travelled between parturition and arriving at their hibernaculum. Angular Departure (abscissa) represents the difference (degrees) between a straight-line vector from rookery to hibernaculum, and a second vector drawn from the rookery to the postpartum snake's furthest location point. Angular departure values approaching zero indicate females that came relatively closer to following the shortest and most direct route to their respective hibernaculum. Data points are coded according to whether individual females initially moved further away (●) or returned immediately (○) to the hibernaculum.

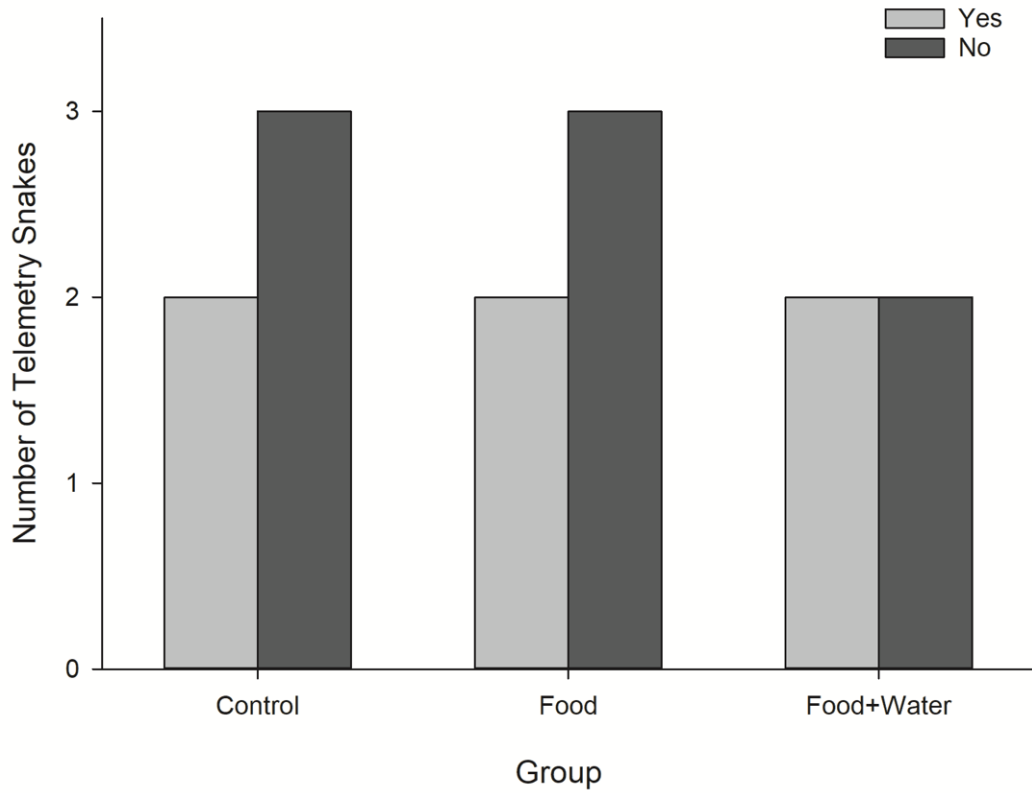


Figure 3.5. Comparison of postpartum movements of female Western Rattlesnakes (*Crotalus oreganus*) between three groups Control (n=5), Food (n=5), and Food and Water (n=4). Yes= Movement away from hibernacula and No= returned directly to hibernacula.

DISCUSSION

Snakes that received food (with or without water) had significantly higher postpartum body condition than control snakes, suggesting that supplemented snakes were provided with significantly more resources than they would have acquired naturally. This result is consistent with other supplementation studies on gravid female snakes (Gignac and Gregory 2005-*Thamnophis orinoides*; Gregory 2006-*Thamnophis sirtalis*; Taylor et al. 2005-*Crotalus atrox*; Capehart et al. 2016-*Crotalus oreganus*), and those on mammals, birds, and lizards (reviewed in Boutin 1990). Snakes in the Food+Water group did not have significantly higher postpartum body condition than snakes in the Food group, although the Food+Water snakes had the highest mean body condition scores. Parturition date was not affected by supplementation (i.e., supplemented snakes did not give birth earlier than controls), suggesting that this life history trait cannot be altered by changes in resource availability, at least not in the short term. Studies that have examined the relationship between supplementation and resource allocation in pregnant female snakes have found that supplemented energy was allocated to maternal body condition instead of the current reproductive bout (Taylor et al. 2005; Gignac and Gregory; Gregory 2006). Although I did not measure litter characteristics in this study, based on the results mentioned above, it is likely that supplemented resources were primarily allocated to mothers.

Contrary to my prediction, Food and Food+Water supplementation did not halt, or significantly alter, postpartum movements away from hibernacula into foraging grounds. These results suggest that female rattlesnakes, at least at this northern latitude, tend to maximize their energy intake (including hydration) despite the brevity of the active season. Although viviparity is advantageous for reproduction in northern climes (e.g., stable temperatures for embryos), it also imposes large costs on females, especially for those inhabiting colder xeric ecosystems where resource availability is highly variable or limited. To minimize these costs, at least some postpartum females, even those with good body condition, continue to seek out additional resources before returning to their hibernacula where survivorship is likely (Gienger and Beck 2011; Maida et al. 2018). Equally important to note is that not all postpartum females in this study exhibited this behaviour, suggesting that there is high variability in individual life histories and whether a female makes the 'choice' to increase their intake. Whether these movement behaviours remain consistent across reproductive years is uncertain, however, being that

rattlesnakes in these regions have been known to show high fidelity to migration routes (Gomez et al. 2015), it seems plausible.

It remains unclear as to why postpartum females with robust body conditions continue to assume the costs of moving away from hibernacula to feeding ranges prior to hibernation. One theory could be that these females may be attempting to increase their capacity to breed again in the near future, by increasing their food (and/or water) intake during a reproductive bout. For example reproductive female *C. oregonus* in northern Idaho were reported to feed before and after parturition which may explain how some females in this population were able to reproduce in two consecutive years (Wallace and Diller 1990). Feeding and hunting behaviours may be exaggerated in xeric environments, where the availability of resources can fluctuate considerably from year-year, causing females to maximize opportunities to feed when conditions are optimal (Schuett et al. 2013).

Similar to this study, Capehart et al. (2016) found that water supplementation did not affect spatial ecology (distance per day and home range) in gravid female *C. oregonus*. As with our research, logistical hurdles resulted in that study having relatively small sample sizes that impact the power of statistical comparisons. Also, rattlesnakes can drink rainwater (Repp and Schuett 2008; Mata-Silva et al. 2014), and researchers realistically cannot standardize natural variation in precipitation during study periods (see Figure 1.6). Still, the Food+Water females in our study showed the highest body condition scores suggesting hydration was relatively high in these animals, yet 50% of these animals still undertook extensive postpartum movements. Thus, my results imply that the need to immediately rehydrate after parturition alone is not a strong driver of the postpartum movements away from direction of the hibernacula. Further work isolating the effects of hydration versus food consumption would be advisable, but as mentioned earlier, forcing water consumption on free-ranging snakes is more difficult and likely more stressful. The threatened nature of the study populations and the reproductive status of our females together negated any thought of applying this type of manipulation.

The reluctance of snakes to feed via the lure at one of my study sites (White Lake) had a significant impact on my overall sample sizes, however it also prompts a perplexing question: why did gravid females at this site show little interest in feeding compared to the other two sites? Density and diversity of prey near rookery sites could have been higher in White Lake, providing

females more natural opportunities to feed. Prior to the experiment, White Lake snakes had some of the highest body condition scores compared to the snakes at the other two sites, indicating that White Lake snakes may have been in slightly better condition. During the year of this study, the Vernon and White Lake sites had very similar precipitation levels (386 and 391 mm, respectively- ECCO Historical Climate Data 2021; see Figure 1.6), yet snakes at the former readily fed, suggesting water availability alone did not explain the reluctance of White Lake snakes to consume the food offered to them. There is growing evidence that neighbouring populations of rattlesnakes can have considerable behavioural differences (Atkins et al. 2022), so the reluctance for snakes to feed at White Lake could be related to factors not obvious at the time of this study. Prey population monitoring and assessment of water availability at all three sites is required to understand this phenomenon further, something beyond the scope of this study.

Despite their inherent challenges, *in situ* food supplementation studies are particularly valuable in understanding resource allocation and plasticity of life histories in a wide range of animals (Reviewed in Boutin 1990; Taylor et al. 2005; Wasko and Sasa 2012; Schuett et al. 2013; Wellicome et al. 2013; Ruffino et al. 2014; Siitari et al. 2015). Vipers, being sit-and-wait predators are relatively good candidates for studies linking food consumption to life history strategies and behaviour tactics (Glaudias et al. 2020). Furthermore, vipers that exist in northern climes and semi-arid environments pose as excellent models for supplementation studies as they represent a group of reptiles that face limited access to resources within shorter and cooler active seasons. Analogous supplementation experiments within other clades would be ideal, such as far-northern populations of both viviparous and oviparous snakes (e.g., Family Colubridae - Common Gartersnake (*Thamnophis sirtalis*) versus Great Basin Gophersnake (*Pituophis catenifer*). But these species tend to be active hunters, making food delivery more difficult. Additionally, supplementing a population after a disturbance such as wildfire or extreme drought, may provide further insight on the ability of these animals to cope with abruptly altered resource availability.

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CHAPTER 4 CONCLUSIONS AND MANAGEMENT IMPLICATIONS

My thesis contributes to a broader understanding of how the behaviour of northern snakes appears tied at many life-history stages to resource use during relatively cooler and shorter summers. More specifically, it sheds light on reproductive female rattlesnake life history traits, habitat selection for parturition, movement, and feeding ecology. I used radiotelemetry and spatial analysis to estimate life history parameters, home range estimates, daily movements, and postpartum movements for female Western Rattlesnakes (*Crotalus oreganus*). Additionally, I created conditional logistic regression models to determine microhabitat selection of rookery sites for parturition at three spatial scales. Finally, I tested the effect food and water supplementation had on postpartum movement and body condition through a non-invasive field supplementation experiment. In my research I pursued the following general objectives:

1. Improve our understanding of the basic ecology of female rattlesnakes before, during, and after parturition,
2. Compare reproductive female home ranges and movement between populations in B.C.,
3. Determine the habitat features which are selected at rookery sites and describe their structure, location, and use,
4. Examine the effect of food and water supplementation on postpartum movement and postpartum body condition.

The major finding of my thesis was that much like hibernacula, female rattlesnakes in northern populations use a network of established rookery sites that they reuse in subsequent reproductive bouts. In addition to this overarching finding, I observed the following:

- Date of rookery selection was highly variable. Parturition dates of telemetry snakes ranged from August 9th to September 19th, a difference of 41 days within the relatively short summers of the study region. Snakes at the most southern study site (Osyoos) had significantly earlier parturition dates compared to the other study sites.

- Rookery site location varied greatly in relation to the female snake's hibernaculum, ranging from 2.0–987.68 m away. Rookery sites were further away from hibernacula at the most southern site (Osoyoos).
- Even within a change in latitude from 49.3° N to 50.20°N there was variation in female movements. Female snakes in the most southern site (Osoyoos) had larger home ranges, moved further distances per day, and moved further distances postpartum, compared to female snakes located at two sites 37 km and 175 km north of this site. Reproductive females had home range sizes as large as 23 ha, comparable to reported male rattlesnake home ranges. Over half (55%) of postpartum telemetry snakes moved away from their hibernaculum prior to hibernation.
- Habitat selection models from our main study site (Osoyoos) revealed that rock cover, shrub cover, and temperature attributes all were positively associated with rookery selection. Multi-site models revealed that rock cover was a strong predictor of rookery selection at all three scales.
- Rookery sites were located on S-SW facing slopes within 1 km of hibernacula or directly at a hibernaculum, contained aggregations of gravid females (80%), and over half (60%) contained snake sheds (adult and neonatal) 5-7 days after parturition. Together these features may help managers identify rookery sites on the landscape.
- Increased access to food and water by supplementation did not halt or alter postpartum movements. Females in these northern latitudes appear to rely on both capital and income for reproduction.

These findings support the argument that rookery sites play an important role in these populations, by providing habitat that is suitable for reproduction. Additionally, contrary to my expectations, increased food and water availability does not appear to alter postpartum movements, indicating that some of the females in these populations maximize their food (and water) intake during reproductive years, regardless of their body condition. Based on these findings I provide management recommendations below to help further protect this threatened species.

Management recommendations

The greatest threats to the Western Rattlesnake in Canada are road mortality, habitat loss and direct persecution (ECCC 2019; Kirk et al. 2021). In order to effectively recover this species, the provincial recovery plan has proposed three main objectives: (1) reduce mortality from roads and persecution to a level that is no longer affecting the viability of populations, (2) secure habitat (through stewardship with landowners, land tenures) that is crucial for the survival of the species such as den sites, gestation habitat, foraging and migration areas, and dispersal habitat throughout B.C., and (3) address any knowledge gaps that may exist such as distribution of the species and use of habitat, identify priority threats, measure the effectiveness of recovery efforts, habitat quality, population studies (ECCC 2019). Although these objectives are certainly important for the recovery of this species, my research suggests additional considerations should be made, which I now outline:

Identification of rookeries in WHAs and critical habitat definition to include rookeries

All of the Western Rattlesnake's range in Canada occurs within the province of B.C.; as per most provinces in Canada, conservation designations and legislation are complex. Provincial or 'crown' land represents the majority of terrestrial habitat in B.C., where various legislative acts within the province take hold. Federal lands (e.g., Parks Canada, National Defence Lands, First Nation Reserves, etc.) fall under the jurisdiction of the Species At Risk Act (SARA), which can be applied to provincial land only in dire conservation circumstances.

Currently in B.C., Wildlife Habitat Areas (WHAs) are a conservation tool used by provincial managers to protect rattlesnakes and consist of small reserves (~200-300 ha in size) that surround rattlesnake hibernacula (Williams et al. 2012). While protection of hibernacula is certainly an important step in conserving rattlesnakes, WHAs may fail to protect important habitat such as movement corridors, feeding ranges, or in some cases rookery sites. This has been demonstrated for the Great Basin Gophersnake in B.C., where oviposition sites (Williams et al. 2015) and dispersal habitat (Williams et al. 2012) fell outside of the protective boundary of WHAs. To determine where rookeries are located with WHAs, I recommend that managers conduct surveys to see where these sites are located within or outside these protected areas, to determine if an expansion of WHAs may be required.

At the federal level under SARA, the recovery of the Western Rattlesnake is based on identifying critical habitat, which is based on all documented rattlesnake hibernacula, including a surrounding 2.8 km area of essential terrestrial habitat (ECCC 2019). However, these areas do not include connective habitat for rattlesnakes, due to a current knowledge gap on longer distance dispersal (ECCC 2019). Furthermore, these protections do not apply when hibernacula are found on private and reserve lands, and it estimated that only 22% of known rattlesnake dens are protected on Crown and private conservation lands (ECCC, 2019). Thus, a large portion of rattlesnake hibernacula, and consequently rookeries, remain unprotected in B.C. I suggest that at the federal level we consider expanding the critical habitat definition to include rookeries. While we certainly have more to learn about rattlesnake rookeries and their importance to rattlesnakes, it may be necessary to protect these features now, to create a buffer against further habitat loss and potentially population decline. This will be particularly important for instances where development and destruction of rookeries may occur such as during road and housing development and pipeline construction.

Creation of human-made rookery sites

While my thesis revealed that rookery sites appear to be important to rattlesnakes, it remains unclear that if one of these structures were removed or destroyed if it would be a significant detriment to a population. To investigate this further, efforts should be made to determine if female rattlesnakes will use human-made rookery sites. My study already suggests this may be the case due to three snakes that were observed using anthropogenic features near a road. Human-made rookery sites could be adapted from the knowledge we have obtained from the creation of refugia structures for snakes such as those created in an ongoing project at the Osoyoos study site (Howarth *in press*), in addition to consultation with experienced individuals to ensure the sites are suitable for reproduction. Additionally, radiotelemetry would be beneficial in these efforts as it would allow researchers to determine if structures are being used by reproductive females and if they show fidelity to them.

Once a complex of human-made rookeries was created and reproductive females were actively using them, one could remove some of the rookeries and monitor how quickly females adjust to other rookeries that are still available. Other manipulations could be done such as removing or adding shrub cover to see how these changes would affect rookery use. I would

recommend only applying manipulations to human-made rookeries because we currently do not know how important rookery sites are to rattlesnakes and how these manipulations would affect them. This mitigative strategy would provide managers with a tool to further understand the relationship between rookeries and rattlesnakes and provide a potential solution for future habitat loss.

FUTURE RESEARCH CONSIDERATIONS

Continued identification and monitoring of rookery habitat

Given the immense variation in female ecology I detected just within the Okanagan valley, further research on female rattlesnakes is warranted at other locations. This would allow for a greater sample size of sub populations, altitudes, and habitat variability and would help us identify predictable patterns in life history traits, movement behaviour and selection of rookery sites. Specifically, it would be extremely beneficial to study female rattlesnakes at the most extreme northern limit of their range (e.g., Savona, B.C.), to make comparisons to southern populations.

Identifying rookery sites should be prioritized in B.C., particularly in locations that are experiencing immense habitat loss and alteration, such as the Okanagan Valley. While my research is certainly a good start in this effort, there remains many locations within the range of the Western Rattlesnake that still require surveys. This may be especially important for rattlesnake populations that have limited optimal habitat for reproduction and therefore rely heavily on what is available. I recommend putting forth focused efforts to identify rookeries in new regions throughout B.C., through intensive surveys and radiotelemetry, while maintaining less costly surveys that would involve site checks at known rookeries. Currently, most surveys in the province occur during egress and ingress at rattlesnake hibernacula and thus likely do not capture the necessary data to identify rookeries. I suggest that we also conduct surveys during a certain time window such as key parturition time (July-Late September) within 1-2 km of known rattlesnake hibernacula. This will increase the efficiency of these surveys and the likelihood of encountering gravid females at rookery sites. Information from these efforts will provide managers with a clearer picture of how scarce these structures are across the province and what we can do to protect them from future destruction.

Provision study following a stochastic event

Along with previous studies, my thesis work confirms that female rattlesnakes can be supplemented food and water successfully in the wild in a non-invasive manner. It would be interesting to apply this same methodology at a site that has experienced a stochastic event such as a wildfire. The Osoyoos study site, where I conducted part of my provisioning experiment in 2019, experienced a devastating wildfire in 2021, that swept through a large portion of the study site and likely heavily impacted feeding habitat and rookeries. This provides a perfect opportunity for a supplementation study due to the likely drastic changes in food (and water) availability and consequently reproductive success for snakes at this site. This type of study would give us an idea of how rattlesnakes cope under these pressures and whether mitigative measures, such as supplying resources, are required for reproductive success.

CONCLUSIONS

Female reproduction is critically important to most wildlife populations, especially those that face challenges and threats, such as snakes in northern climes. Snakes have evolved incredibly diverse reproductive tactics (viviparity, timing of reproduction, frequency of reproduction, low metabolic rates) to ensure reproductive success in harsh environments (Shine 2003). The factors that drive variation in these tactics can provide insight on how these populations may cope with future and current threats such as climate change, wildfire, invasive species, and much more. Thus, the effective recovery and conservation of the Western Rattlesnake hinges on our knowledge of female reproduction and ecology (ECCC 2019), and my thesis provides critical information for this purpose. Through detailed study on female rattlesnakes, I demonstrated noticeable variation in female life history and movements as they relate to rookery and resource use, and I have provided detailed descriptions of rookery habitat that can act as an aid for managers and future recovery strategies.

Moving forward I recommend that managers continue to locate and monitor rookery habitat across the province and ensure we maintain connectivity between rookeries, hibernating sites, and summer foraging/mating grounds through provincial and federal protections. Overall, my thesis can act as a source of critical information about female rattlesnake ecology in northern climates and can provide direction on how to help this threatened species persist for generations to come.

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APPENDIX A
Results of Spearman's Correlation Analysis for Habitat Selection Models

Spearman Correlations for Osoyoos model (n=24)

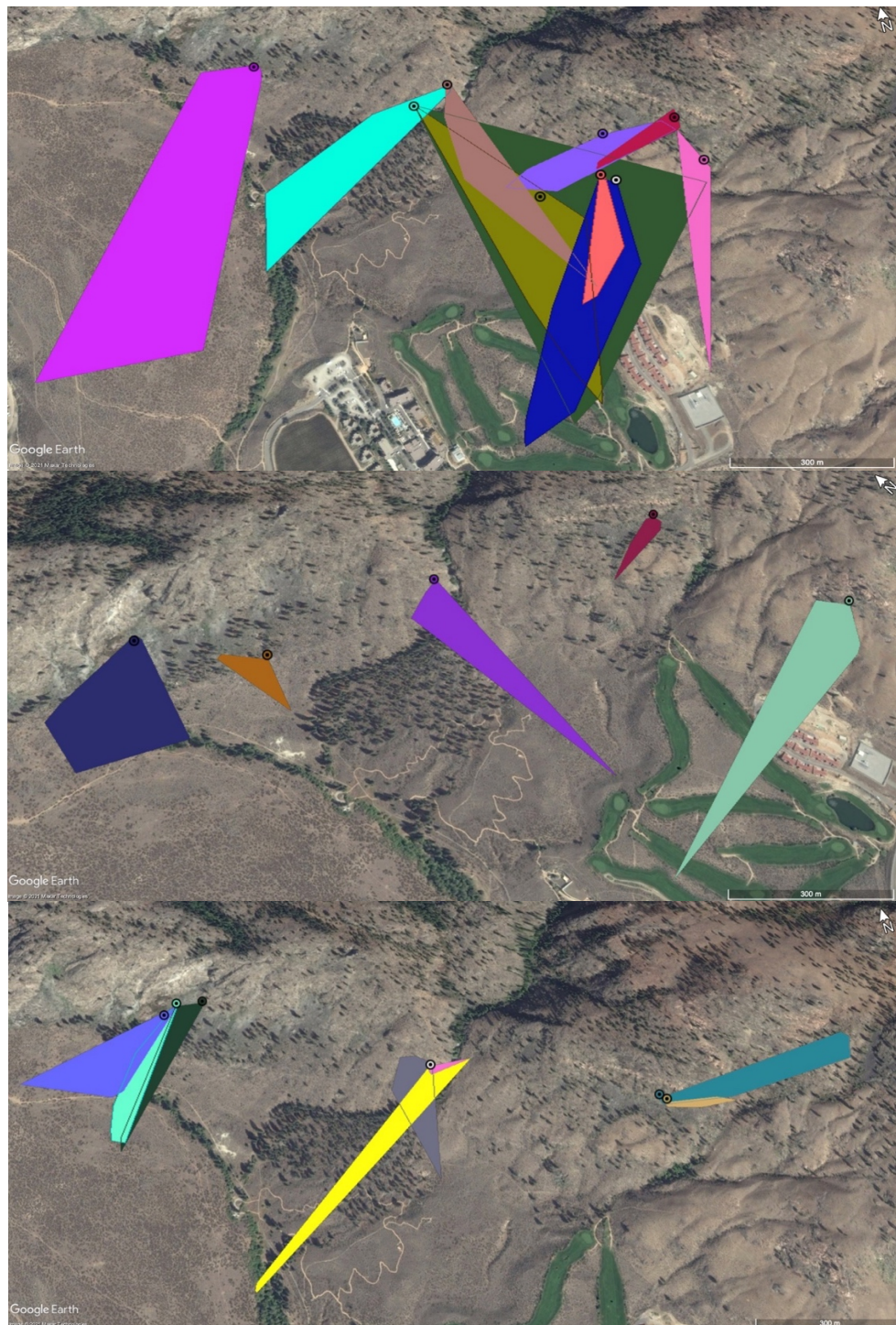
Scale	Variable 1	Variable 2	Correlation Coefficient	P-Value
1 m	MaxDay	AvgDay	0.981	0.000
	AvgNight	AvgDay	0.424	0.024
	AvgNight	MaxDay	0.380	0.046
	AvgNight	MinDay	0.853	0.000
	MinNight	MinDay	0.940	0.000
	MinNight	AvgNight	0.852	0.000
	%Grass	%Rock	-0.531	0.004
	Aspect	%Rock	0.406	0.032
	%WD	%Tree	0.539	0.003
3 m	MaxDay	AvgDay	0.845	0.000
	MinDay	AvgDay	0.381	0.046
	AvgNight	AvgDay	0.423	0.025
	AvgNight	MinDay	0.894	0.000
	MinNight	MinDay	0.961	0.000
	MinNight	AvgNight	0.932	0.000
	%Grass	%Rock	-0.625	0.000
	%Grass	%Shrub	0.640	0.014
	%WD	%Tree	0.539	0.003
10 m	MaxDay	AvgDay	0.746	0.000
	AvgNight	AvgDay	0.608	0.001
	MinDay	AvgDay	0.475	0.011
	AvgNight	MinDay	0.921	0.000
	MinNight	MinDay	0.973	0.000
	MinNight	AvgDay	0.487	0.009
	MinNight	AvgNight	0.941	0.000
	%Rock	AvgDay	-0.378	0.047
	%WD	%Tree	0.654	0.000
	%Grass	%Rock	-0.574	0.001

Spearman Correlations for multi-site model (n=48)

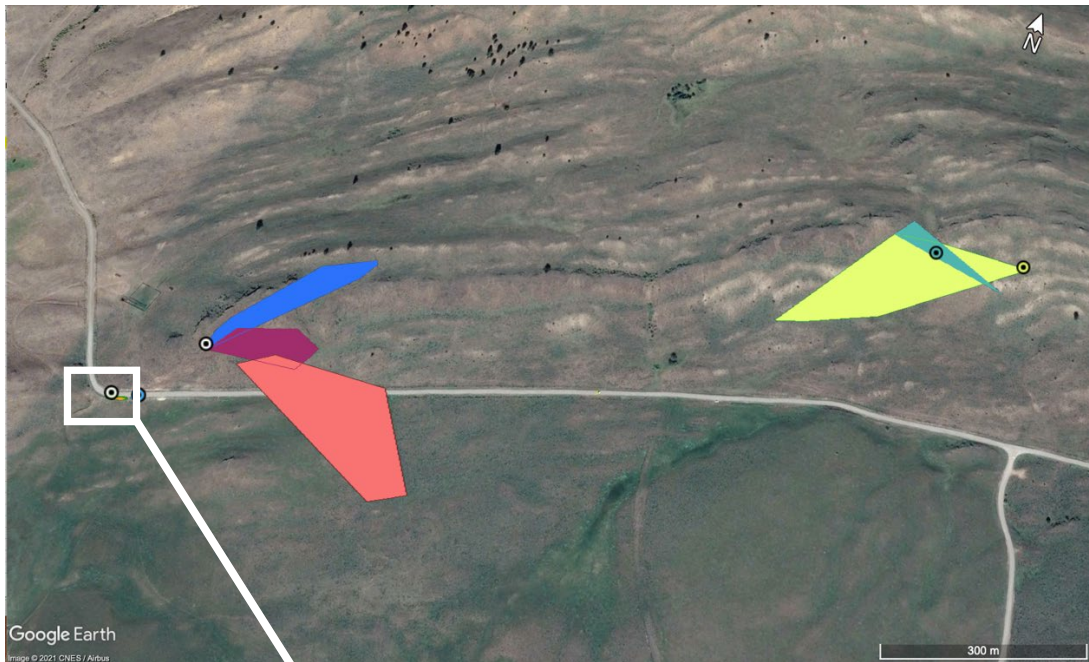
Scale	Variable 1	Variable 2	Correlation Coefficient	P-Value
1 m	%Grass	%Rock	-0.610	0.000
	%Rock	%Shrub	-0.285	0.050
3 m	%Grass	%Rock	-0.628	0.000
	%WD	%Tree	0.449	0.002
	%Grass	%Shrub	0.425	0.004
10 m	%Shrub	%Tree	-0.304	0.045
	%Shrub	%Rock	0.304	0.045

APPENDIX B

Home Range Maps and Approximate Rookery Site Locations



MCP (100%) home range maps for female Western Rattlesnakes (*Crotalus oreganus*) in Osoyoos, B.C. for 2017 (top), 2018 (middle) 2019 (bottom). Each colour represents a different individual and dots with corresponding colours represent that individual's rookery site. White dots represent a rookery site shared by multiple telemetry animals.



MCP (100%) home range maps for female Western Rattlesnakes (*Crotalus oreganus*) home range in White Lake, B.C. (2019). Each colour represents a different individual. Each colour represents a different individual and dots with corresponding colours represent that individual's rookery site. White dots represent a rookery site shared by multiple telemetry animals.



MCP (100%) home range maps for female Western Rattlesnakes (*Crotalus oreganus*) home range in Vernon, B.C. (2019). Each colour represents a different individual. Each colour represents a different individual and dots with corresponding colours represent that individual's rookery site. White dots represent a rookery site shared by multiple telemetry animals.

