IMPACTS OF FENCING AND DEVELOPMENT ON WESTERN RATTLESNAKE (*CROTALUS OREGANUS*) SPRING MOVEMENTS IN BRITISH COLUMBIA

by

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ABSTRACT

Due to increasing anthropogenic pressures, the process of natural animal migration is undergoing alterations across many different taxa. To investigate these impacts is difficult on large-scale migrations, yet small-scale migrants will provide useful and tractable systems to understand the effects of disturbance and landscape barriers on natural movement patterns and migrations. The Western Rattlesnake (*Crotalus oreganus*) in British Columbia is a small, migratory predator that undertakes annual spring movements from communal hibernaculum to summer hunting grounds. In this thesis, I examined changes to these migration movements in male rattlesnakes that encountered both snake exclusion fencing barriers and disturbed habitats from 2011-2016. My thesis field work included 2015 and 2016, and data from 2011-2014 was drawn from a long-term project database. Individuals moving through disturbed habitats or intercepted by snake exclusion fencing demonstrated shorter migration distances and reduce spring path sinuosity (more crooked routes) compared to individuals migrating in undisturbed habitats. Specifically, individuals encountering a snake fence during spring movements had shorter total spring migration path lengths and smaller home ranges. Regardless, migration distance was strongly associated with the distance individuals travelled until they first encountered human disturbance. Despite this difference, duration of the migration did not differ between rattlesnakes that encountered a snake exclusion fence, experienced other forms of disturbance, or migrated through undisturbed habitats. Overall, my work reveals the importance of looking closely at seasonal movement patterns, including migration, of smaller-scale migrants in response to abrupt and long-term landscape changes and barriers. Small-scale migrants can be used as an important indicator of landscape and community connectivity and can be used as an important reference for managing ecosystem function and health on a changing, anthropocentric landscape.

Keywords: British Columbia, Conservation, *Crotalus oreganus,* Migration, Radio-telemetry, Species-at-Risk

Table of Contents

LIST OF FIGURES

LIST OF TABLES

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CHAPTER ONE: ANIMALS, BEHAVIOUR AND DISTURBANCE

DISTURBANCE AND WILDLIFE

With the human population continuing to increase, habitat loss, fragmentation and alteration have emerged as the dominant threats to global biodiversity and wildlife species persistence (Wilcove et al. 1998; Gibbons et al. 2000; Saha et al. 2018). Habitat loss and fragmentation due to anthropogenic activities are responsible for the majority of the rapidly increasing extinction events globally, and remain a primary cause for the displacement and elimination of local wildlife species (Czech et al. 2000; Kjoss and Litvaitis 2001; Marzluff 2001; Mckinney 2002). In Canada, federal legislations exist to protect species, specifically those at risk, from human disturbance. However, urban sprawl, resource extraction, tourism and outdoor recreation continue to present novel stressors and selection pressures on wildlife populations. Individuals or species unable to cope with these novel pressures may suffer both short and long-term consequences including direct mortality and/or indirect consequences (Nattrass and Lusseau 2016).

The direct effects (mortality) of disturbance and habitat loss often are readily apparent, and at times, simple to quantify. Road mortality (Souza et al. 2015), illegal and/or over-harvesting (Wittemyer et al. 2014) and human persecution (Venter et al. 2006) are among the obvious sources of mortality for wildlife populations globally, and such impacts may result in the immediate extirpation of a species. Conversely, indirect effects of disturbance on wildlife often are challenging to quantify and understand, but may represent severe, long-term consequences on individual health and species persistence (Ohashi et al. 2013). For example, Cougars (*Puma concolor*) avoid roadways and trails during high traffic seasons, likely altering resource selection (Morrison et al. 2014). Bird population densities decrease along busy roadways, and males in these areas may have difficulties attracting mates (Reijnen et al. 1997; Kociolek et al. 2011). In the presence of ecotourism activity, Woodland Caribou (*Rangider tarandus caribou*) are more vigilant at the expense of time spent resting and foraging (Duchesne et al. 2000; Fortin et al. 2016). Repeated alterations in normal behaviour due to disturbance, such as presented here, may have negative impacts on individuals - especially when the individuals affected have difficulties compensating for potential lost opportunities (Nattrass and Lusseau 2016).

Behavioural alterations in response to disturbance or human presence can result in long-term biologically-significant impacts on individuals, and therefore populations (Gill et al. 2001; Christiansen and Lusseau 2015). These impacts may include elevated stress levels (e.g., Brown Bears, *Ursus arctus* - Støen et al. 2015), increased nestling mortality (e.g., European Storm Petrels, *Hydrobates pelagicus* - Watson et al. 2014), reduced juvenile growth and body mass (e.g., Hoatzins, *Opisthocomus hoazin* - Müllner et al. 2004), and negative effects of genetic drift through a reduction in dispersal (e.g., Spanish Imperial Eagle, *Aquila adalberti* - Martínez-Cruz et al. 2004). Therefore, the persistence *per se* of animals on disturbed landscapes may not always be indicative of long-term population health and stability (Lomas et al. 2015).

Despite recent research, there are very few clear patterns in the behavioural (and physiological) responses animals demonstrate to disturbed habitats and direct human interactions (Tablado and Jenni 2017). This lack of clarity may presumably reflect each species' specific evolutionary adaptations and furthermore, not all species appear to be negatively impacted by disturbance (Devictor et al. 2008). How animals respond and behave on disturbed landscapes is predicated by disturbance type, species-specific tolerance and life history, as well as the local conditions (Madsen 1988; Béchet et al. 2004; Marini et al. 2017). Specifically, niche breadth has been hypothesized as the main contributor in an animal's ability to respond to disturbed and changing landscapes (Kitahara and Fujii 1994; Vásquez and Simberloff 2001).

Species that follow generalist strategies are typically better suited to adapt to novel environments created by disturbance due to their broad habitat preferences, behavioural flexibility, and/or malleable life history strategies (Kark et al. 2007; Lowry et al. 2013; Šálek et al. 2014). Conversely, specialists rely on a narrow range of habitat requirements and resources (Rousseau et al. 2012; Matthews et al. 2014), and/or dispersal and migration to locate specific resources and avoid genetic isolation (Martin and Fahrig 2018). These specialists typically are more prone to negative consequences when facing novel environments and anthropogenic pressures. The persistence (and at times influx) of species may mask the decline of specialists in fragmented and disturbed areas (Matthews et al. 2014), providing more evidence that species persistence should not be a sole indicator of population or community health. Rather, tracking behavioural responses of individuals as an index of disturbance is extremely important for wildlife managers. However, assessing behavioural responses alone may have a number of potential limitations and may not identify the underlying issues (Beale and Monaghan 2004). Overall, understanding the adaptive limits and behavioural niches of a species is incredibly important to consider in wildlife conservation and management.

DISTURBANCE AND SNAKES

Snakes are relatively small-bodied, meso-predators that typically specialize in annual site fidelity to specific habitats throughout the course of a year, or over the course of their lifetime (Waldron et al. 2013; Bauder et al. 2015; Gomez et al. 2015). It is likely advantageous for individuals to exhibit fidelity to areas where resource availability and habitats are stable through time (Waldron et al. 2013), especially if the benefits of reusing these areas exceed the cost of searching for resources in other areas (Switzer 1993). Further, snakes as ectotherms rely directly on the thermal properties of their environment to ensure natural physiological processes (i.e., hibernation, digestion, and reproduction; Putmann and Clark 2017). To re-locate and use areas of value (i.e., hibernacula, migration corridor, summer foraging habitat), snakes have well-developed orientation abilities (Landreth 1973; Larsen 1987; Lawson 1991), and their movement patterns may change substantially if re-orientation is needed after natural movement patterns are blocked and/or individuals are displaced (Butler et al. 2005; Brown et al. 2009).

Species that exhibit high spatial fidelity are associated with stable habitats and are likely not suited to effectively respond to abrupt changes on the landscape. For example, adult snakes have typically demonstrated the inability to re-orientate themselves on the landscape in response to habitat removal and/or barriers limiting movement and access to desired areas (Waldron et al. 2013). Northern snakes likely are particularly vulnerable to these abrupt anthropogenic-influenced changes on the landscape due to the restricted and shortened active season (Gregory 2007). Snake migrations and seasonal movements appear associated with accessing and/or searching for prey (King and Duvall 1990; Bauder et al.

2015). Therefore, abrupt changes in the environment may have serious repercussions: short active seasons likely do not leave enough time for individuals to adjust to abrupt landscape changes and still successfully find prey (and mates, and effective hibernacula) compared to their southern counterparts. Furthermore, most northern snake species exhibit life history attributes that include delayed maturation, high adult survival, and infrequent parturition (Macartney and Gregory 1988; Gregory 2007; Maida et al. 2018); novel and abrupt changes in anthropogenic-influenced landscapes can abruptly change selection pressures, and these animals cannot rapidly respond to sudden, dynamic changes (Waldron et al. 2013).

In northern regions, snakes den communally and undertake seasonal migrations primarily due to the long, cold winters they face (for example: Western Rattlesnakes in British Columbia, see below). Communal denning and migration between overwintering habitat (hibernacula) and summer foraging sites are closely linked behaviours associated with cold climates and scarce suitable hibernacula habitat (Gregory 2007; Bauder et al. 2015). In contrast, snakes at more southern latitudes typically show reduced movement distances and more flexible overwintering behaviours (Bauder et al. 2015). Within these northern regions, the lack of sufficient summer resources (i.e., prey availability) in the proximity of hibernacula obligates individuals to undertake seasonal migrations between overwintering sites and summer activity areas. Therefore, novel barriers on the landscape, or habitat loss, that interferes with these important movements may impact the survival (much less fitness) of animals.

The impacts of human disturbance on snake populations are most apparent through road mortality (Hartmann et al. 2011; Garrah et al. 2015; Marsh and Jaeger 2015; Meek 2015) and accidental or intentional killing from humans (Bonnet et al. 1999; Gomez et al. 2004; Pitts et al. 2017). However, disturbance may have other indirect behavioural and physiological implications for snakes. For example, snake behavioural patterns change in the presence of roads and golf course fairways (Shine et al. 2004; Robson and Blouin-Demers 2013; Goode 2010). Further, rattlesnake home range sizes and migration path straightness tend to become altered in fragmented landscapes (Breininger et al. 2011; Martin et al. 2017). Roads limit dispersal and genetic diversity (Clark et al. 2010) and may cause alterations to physiological stress responses (Owen et al. 2014). Increased human interactions and outdoor recreation activities can increase concealment behaviour by snakes (Beale et al. 2016) and reduce movement frequencies (Parent and Weatherhead 2000). Urban snakes also are less likely to have prey present in their stomachs and are relatively lighter and smaller than non-urban snakes (Wolfe et al. 2017). Lastly, landscape disturbances result in reduced growth rates, fecundity and lower offspring body conditions in rattlesnakes (Jenkins et al. 2009).

Snakes are an important component of the natural communities they reside in and have strong effects on community dynamics (Lind et al. 2005), yet they are often viewed as a nuisance animal in urban and other human-dominated environments (Pitts et al. 2017); not surprisingly, persecution has been identified as a leading threat to a number of at-risk snake species. In Canada, and the rest of North America, human social issues play a large role in the conservation of snakes (Gregory 2007). Fear and misconceptions for snakes compounds the challenges of conservation initiatives for these animals as they typically receive limited sympathy and support compared to more charismatic animals (Gomez et al. 2004; Ballouard et al. 2012). Monitoring snake populations is hampered by their small size, cryptic and nocturnal behaviour, and often low-population densities (Durso et al. 2011; Ward et al. 2017). Despite this, snakes on the landscape are critically important for ecosystem health and biodiversity. Specifically, as meso-predators, snakes are a crucial component of energy flow in the complex food web, and can be used as an important indicator species to monitor ecosystem health and function (Lind et al. 2005; Beaupre and Douglas 2009).

SNAKES AND FENCING

Historically, wildlife fencing has predominantly been used to reduce large mammal-vehicle collisions on major highways (Sawyer et al. 2012; Huijser et al. 2016). These types of fencing structures are typically very large (e.g. 2.4 m high for large ungulates), but do not inhibit the passage of small animals like snakes, and can be used over a large scale (Evans and Wood 1980). However, more recently, the use of snake exclusion fencing has been used to mitigate negative interactions between humans and snakes and other reptiles (Baxter-Gilbert et al. 2015; Jackson et al. 2015; Colley et al. 2017; Markle et al 2017), and have often proved to be effective at reducing mortality rates.

For small-bodied animals such as snakes that are highly susceptible to mortality on roads and other human-influenced areas, fencing is valuable for the persistence and viability of local populations. Yet these structures still pose an abrupt, physical barrier for individuals. Encountering abrupt barriers such as snake exclusion fences likely has a large impact on snake behaviour, especially in areas where individuals must annually migrate between overwintering hibernacula and summer foraging areas, as these structures will effectively exclude animals from accessing areas they previously utilized. For example, the Mojave Desert Tortoise (*Gopherus agassizzii*), who have similar annual site fidelity traits as many snake species, demonstrate a decrease in home range size and an alteration of normal behaviours in response to impenetrable roadside fencing (Peaden et al. 2017). Based on adaptive traits and behaviour, snakes likely are unable to avoid barrier structures, and therefore impermeable snake exclusion fences likely exert negative influences on individual behaviour and home range attributes.

There are currently two main management approaches to reducing negative human-snake interactions on the landscape: relocating animals and erecting exclusion/barrier fencing. Efforts to manage and limit snake-human interactions historically have included the relocation of individuals (Brown et al. 2009; Holding et al. 2014). However this strategy often is only a short-term solution (Brown et al. 2009), and comes with potential negative consequences on translocated snakes such as longer movements, increased home range sizes, and a reduction in survival (Nowak et al. 2002; Brown et al. 2009; Wolfe et al. 2018). Fencing structures are intended to redirect movement of animals away from certain areas and/or eliminate access to specific areas (i.e., roads, urban areas), and can be useful for research and inventory purposes (Willson and Gibbons 2010; Hanson and McElroy 2015; Markle et al. 2017). However, although fencing can be very effective at limiting negative impacts, particularly road mortality (Colley et al. 2017), it may come with unintended consequences for individual snakes (Eye et al. 2018) and other herpetofauna species (Ferronato et al. 2014).

Globally, and for a suite of different target species, fencing is becoming a very common conservation tool. Yet considering the prevalence of these structures, there has been an obvious lack of research-based initiatives focusing on the effects of these structures on individuals and populations (Jakes et al. 2018). In order to better understand the long-term implications (both positive and negative) of wildlife fences, efforts need to also be directed at understanding the potential shift in the ecology of individuals and populations after fences have been installed.

THE WESTERN RATTLESNAKE IN BRITISH COLUMBIA –DEALING WITH DISTURBANCE

In British Columbia (B.C.), **t**he Western Rattlesnake (*Crotalus oreganus*) inhabits areas undergoing particularly rapid development and widespread habitat disturbance. Coincidentally, the rattlesnakes in this province represent the northernmost extent of the clade that extends from northern California through Oregon, Washington and central Idaho. In B.C., suitable rattlesnake habitat is represented by the dry, arid valley bottoms of the province's southern interior, occurring in the Fraser, Thompson, Nicola, Okanagan, Similkameen and Kettle watersheds within four distinct areas (Southern Interior Reptile and Amphibian Working Group 2016; Figure 1.1). Rattlesnakes are found in the Bunchgrass (BG), Ponderosa Pine (PP), and Interior Douglas-fir (IDF) biogeoclimatic zones of the province (BEC; Biogeoclimatic Zones of British Columbia 2018), and are strongly associated with shrub-steppe, open forest, riparian and rocky ecotypes.

Overwintering occurs in communal hibernacula between October–April with known hibernacula ranging between ~400–800m elevation within B.C. (Southern Interior Reptile and Amphibian Working Group 2016). During the early spring and into the summer (April–May), rattlesnakes embark on annual migrations moving away from their hibernacula to their summer foraging habitat (Macartney and Gregory 1988; Gomez et al. 2015; Lomas et al. 2015), with maximum distances from hibernacula recorded up to 4.0 km (Harvey 2015). At the same time, rattlesnake home range attributes, sizes, and movement patterns can vary dramatically across populations, individuals within a hibernacula and available habitat (Lomas 2013; Gomez et al. 2015; Harvey 2015).

Rattlesnakes in B.C. show life-history attributes that likely render them particularly susceptible to the impacts of disturbance. The Okanagan Valley represents a large part of the rattlesnake range in B.C., and contains one of the fastest rates of human population growth and development in Canada (Statistics Canada 2014). In some areas of the Okanagan Valley, up to 90 percent of natural vegetation communities have been lost (Lea 2008). Specifically, rapid increases in urbanization, outdoor recreation activities and agriculture (primarily vineyards) are placing increased pressures on these animals. As fallout from the transformation of natural landscapes, recent population estimates suggest a dramatic decrease in rattlesnake densities within the south Okanagan Valley over the last 30 years (Maida et al. 2018). Consequently, Western Rattlesnakes have become federally listed as ‘threatened’ (Species At Risk Public Registry 2018) and provincially the species is considered of ‘special concern’ (Southern Interior Reptile and Amphibian Working Group 2016). Various life history strategies and constraints of this species limits potential recovery from habitat loss and renders them vulnerable to declines including delayed sexual maturity of females (5–8 years; Maida et al. 2018), infrequent parturition (typically every 3 years or longer for females; Macartney and Gregory 1988), and reduced juvenile growth and survival (Charland 1989). Although rattlesnake life histories often include high adult survival rates, novel threats and the dynamics of anthropogenic landscapes (i.e. road mortality or persecution) can quickly change the selection process, potentially resulting in normal strategies becoming dysfunctional and negatively influencing the viability of populations. The high annual fidelity these animals show towards their hibernacula, movement corridors and summer foraging grounds likely further compounds the potential impacts disturbance may have on these rattlesnakes (similar to Eastern Diamondback Rattlesnakes, see: Waldron et al. 2013).

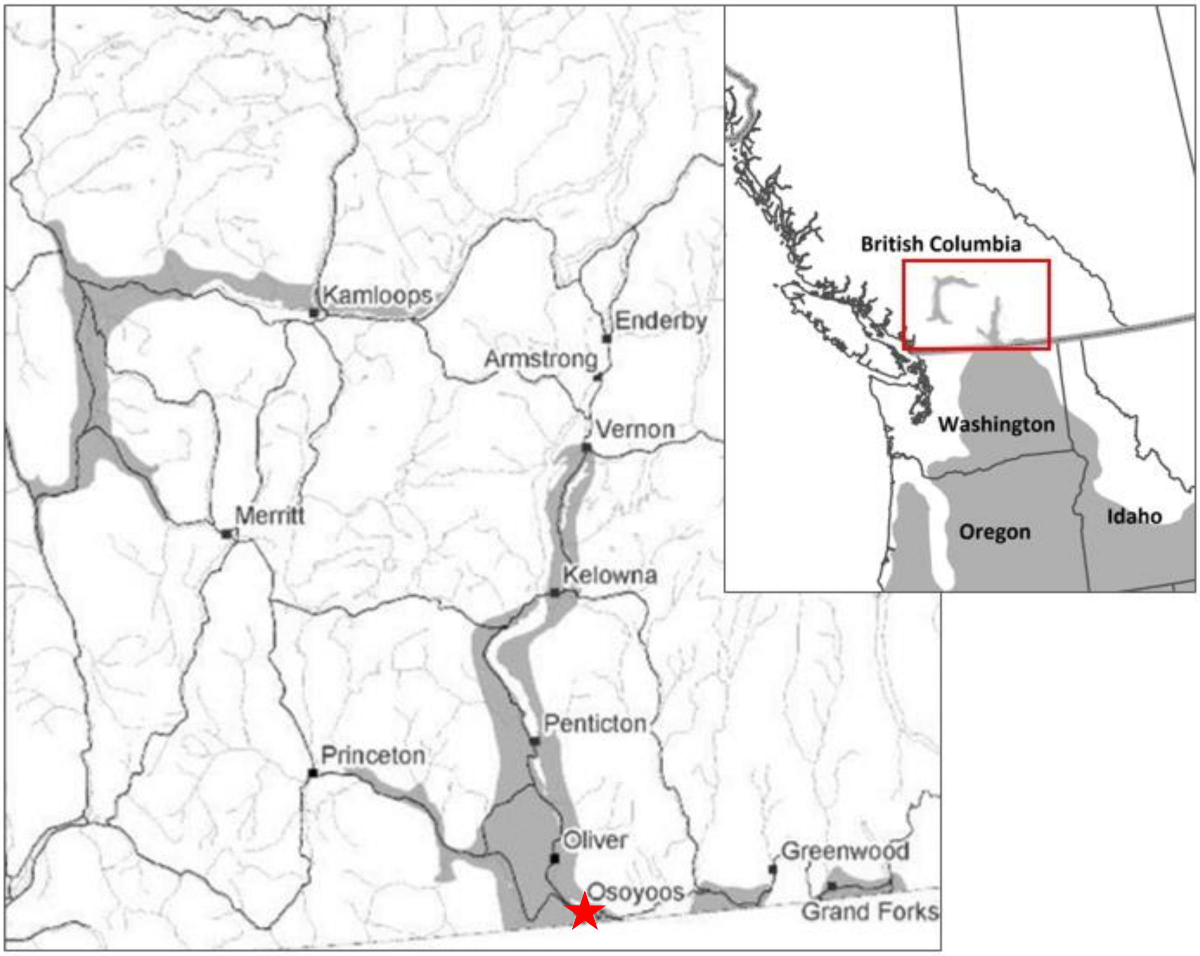

Figure 1.1. Western Rattlesnake (*Crotalus oreganus*) range in the southern interior of British Columbia (B.C.) with inset showing the species' northern range limits in North America (Produced by Robyn Reudink). Osoyoos, B.C. (indicated by red star) was the location of my study site (see below). B.C. map produced by Rene McKibbin.

OSOYOOS INDIAN RESERVE (OIR) AND THE NK'MIP SNAKE PROGRAM

The Osoyoos Indian Reserve (OIR) is located in the south Okanagan Valley near Osoyoos, B.C. approximately 4.5 km north of the Canada-USA border (Figure 1.1). Like most of the Okanagan Valley, these lands have been exposed to drastic changes to the natural vegetation communities and landscape (see Figure 1.2). The site encompasses the extreme southern portion of rattlesnake range in B.C (Figure 1.3), and the habitat is primarily comprised of low elevation (300–400 m) arid shrub-steppe habitat characterized by Big Sagebrush (*Artemesia tridentata*), Antelope Brush (*Prushia tridentata*) and native grasses. The area is bordered by Osoyoos Lake to the west and by open Ponderosa Pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziezii*) forests and rocky mountain slopes to the east, which contained rattlesnake communal hibernacula for the study area (~450–600m hibernaculum elevation; Maida et al. 2017; Figure 1.4). To the south, the OIR is bordered by a major highway (Highway 3), extensive agriculture, primarily orchards and vineyards, and housing.

At the time of this study, the OIR contained drastic habitat quality contrasts, from heavily developed and fragmented portions, to those in near-pristine condition with minimal human involvement or habitat fragmentation (Figure 1.5). Intensive human activity and development has been primarily situated in the southern areas of the OIR, targeting tourism by including a golf course, winery and vineyard, cultural centre, walking trails, a large campground and condominium resort with associated parking lots and roads. A ~ 4 km snake exclusion fence surrounded most of the resort, parking lots and roadways, as well as the campground in efforts to reduce negative human-snake conflict. The north and eastern portions of the study area had limited human influence and lacked any landscape alterations or disturbance. Mean daily temperatures during this study were similar to historical means over the previous 30 years (1981–2010; Figure 1.6).

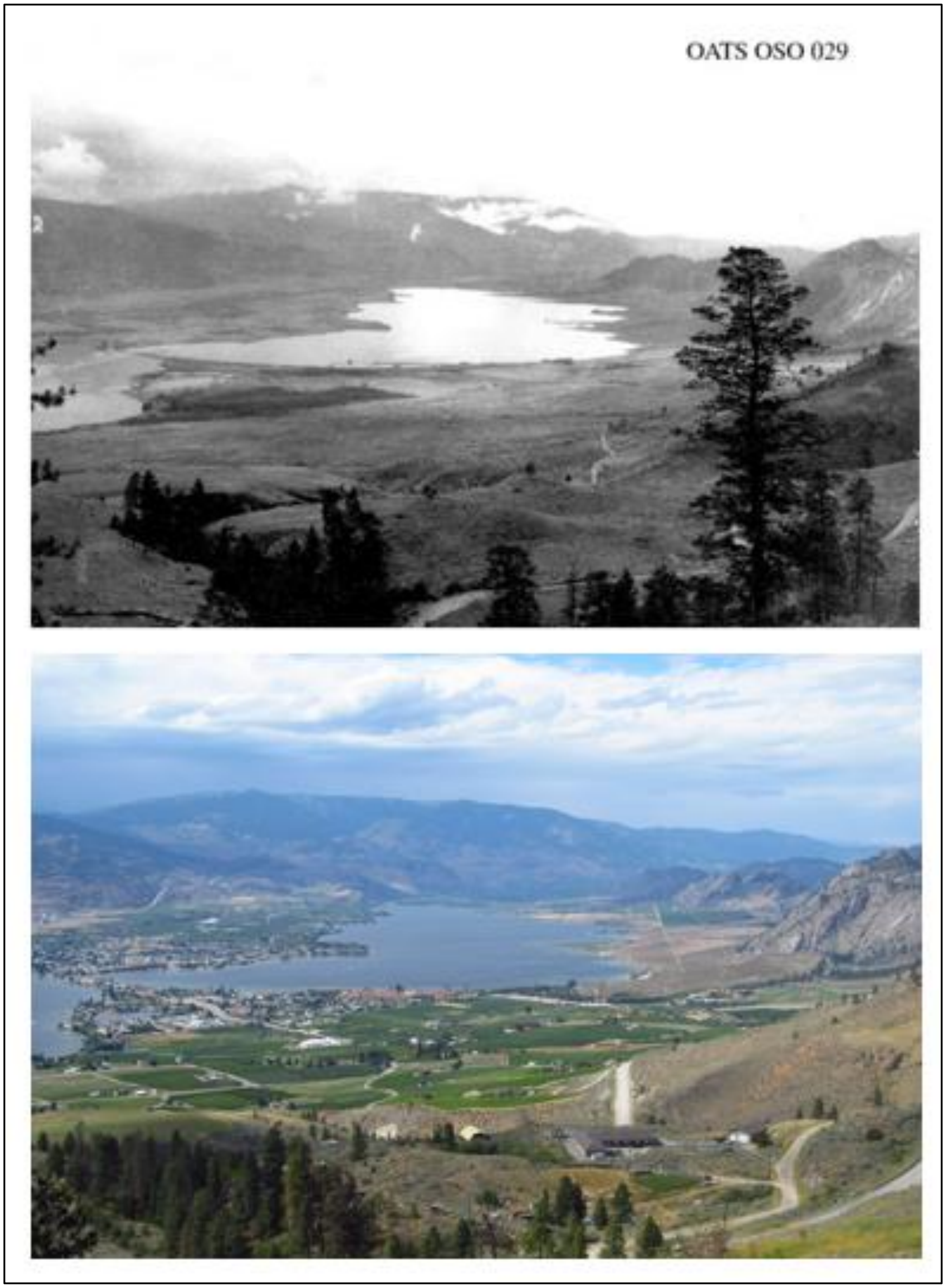

Figure 1.2. Above: Photograph of the Osoyoos Valley looking north over Osoyoos Lake in 1935 (photograph from the Okanagan Archive Society; www.oldphotos.ca); Below: same area in 2012 (photograph from Emily Lomas)

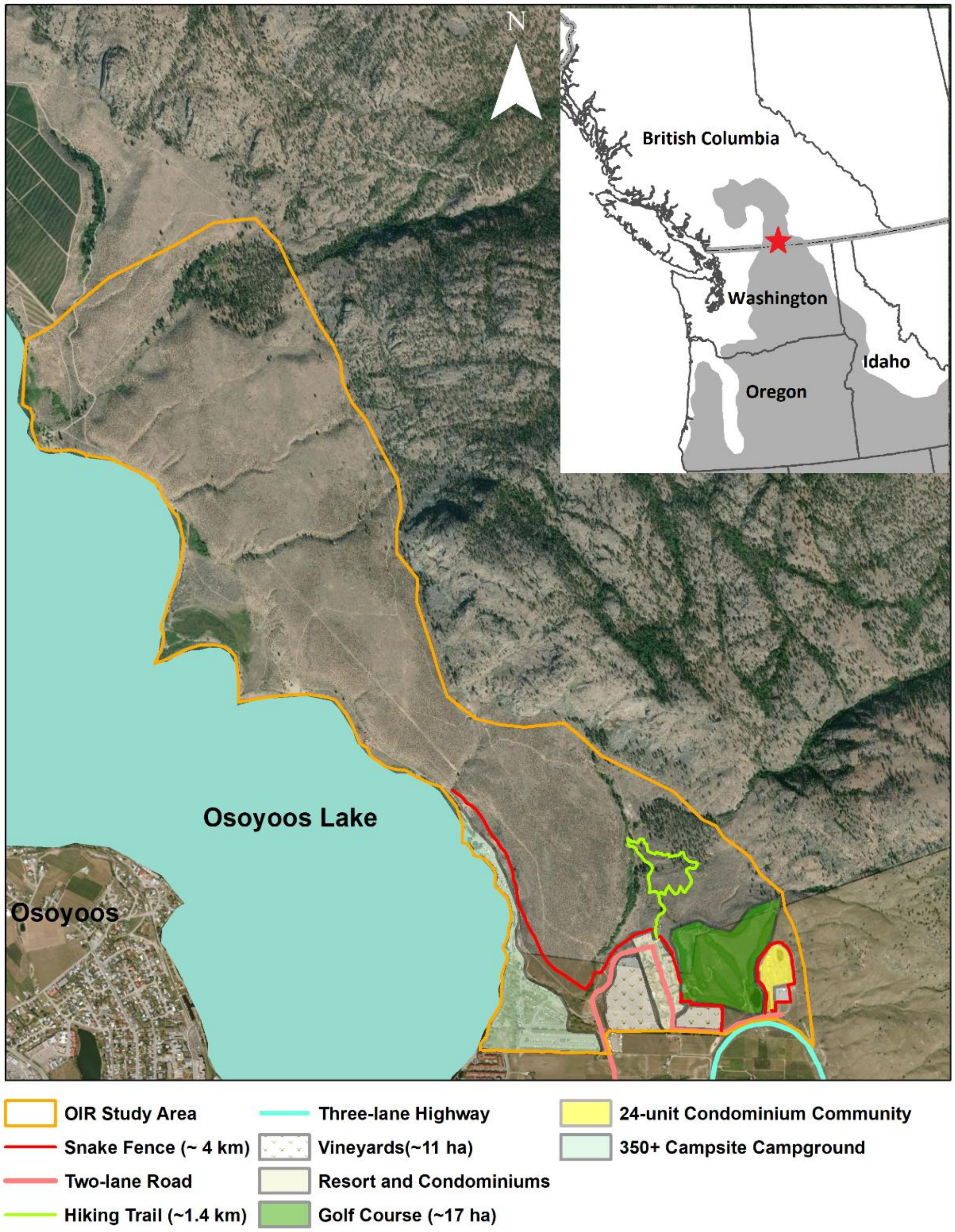

Figure 1.3. Map of the Osoyoos Indian Reserve (OIR) study site (indicated in orange) near Osoyoos, B.C., Canada. The northern and eastern portions remained undeveloped with developed areas concentrated to the southern and western portions of the study site. The condominium community and associated snake exclusion fence is located at the southeast corner of the study site. Inset shows the northern extent of the Western Rattlesnake (*Crotalus oreganus*) range with study site location (indicated by star).

Figure 1.4. Examples of the dominant ecotypes on the Osoyoos Indian Reserve (OIR): (A) open Ponderosa Pine (*Pinus ponderosa*) and Douglas-Fir (*Pseudotsuga menziezii*) forests, (B) Shrub-steppe habitat dominated by Big Sagebrush (*Artemesia tridentata*) and Antelope Brush (*Purshia tridentata*), (C) and mid-elevation rocky slopes.

Figure 1.5. Contrast in habitat quality and landscape disturbance between the southern developed (right) and northern undisturbed (left) portions of the Osoyoos Indian Reserve (OIR) study site. The northern portions containing no habitat barriers and limited human presence. Conversely, disturbance within the southern portions were geared towards tourism and the landscape fragmented by roads, condominiums, vineyards, snake exclusion fencing, golf course, hiking trials and a campground.

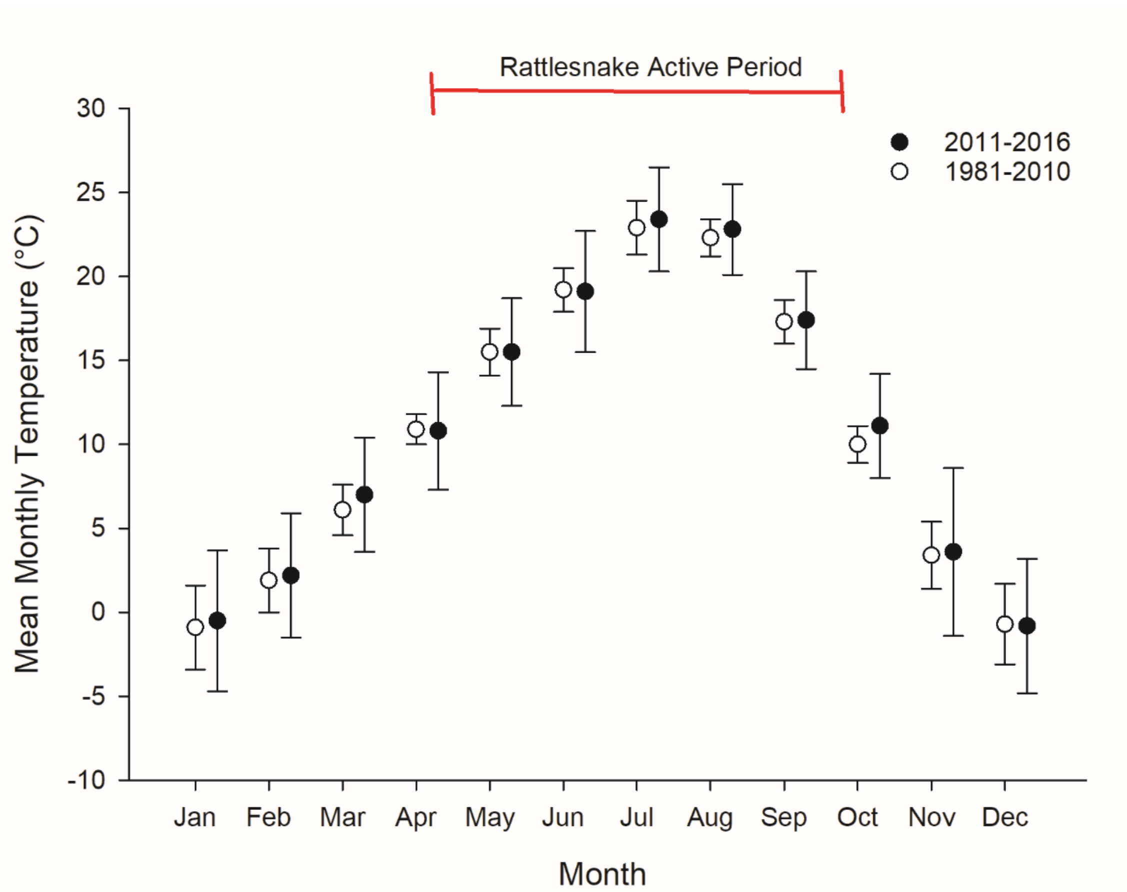

Figure 1.6. Mean monthly temperatures in Osoyoos, B.C. during the years of this study (2011– 2016) compared to the historical 30-year (1981–2010) mean monthly temperatures (Environmental and Climate Change Canada 2018). The Osoyoos Indian Reserve (OIR) study site was located approximately 2 km north-west of the location where the weather data was recorded.

The Nk'Mip Snake Program is a long-term rattlesnake population-monitoring program initiated in 2002 on the OIR, through a partnership with the Osoyoos Indian Band, Nk'Mip Desert Cultural Centre, Environment and Climate Change Canada, and later Thompson Rivers University. As such, the Nk'Mip Snake Program is one of the longest running mark-recapture (since 2002), radio-telemetry (since 2004), and public outreach and education snake programs in western Canada. The overarching objective of the program is to monitor the local snake community as development and human intrusions continue to increase, particularly in the southern areas of the OIR study site (Figure 1.7). The ongoing research has provided information on critical habitat (e.g., hibernaculum, shedding and gestation sites) within the OIR as well as long-term estimates of population size, density and survivorship (Maida et al. 2018). Research also identified that rattlesnakes frequenting the disturbed areas of the OIR demonstrate lower body conditions compared to individuals in the undisturbed portions of the study area (Lomas et al. 2015), and individuals residing in undisturbed habitats have larger home ranges and longer range lengths than animals in minimal to highly disturbed habitats (Lomas et al. in press). Furthermore, ongoing assessment of the effectiveness and implications of management strategies and techniques such as exclusion fencing (Eye et al. 2018) and short-distance translocation (Brown et al. 2009) continue to be explored. In addition to rattlesnakes, the Nk'Mip Snake program has provided inventory information for the conservation of other local snake species in B.C., including the Great Basin Gophersnake (*Pituophis catenifer desertocola*) and Western Yellow-bellied Racer (*Coluber constrictor mormon*), thus serving as a reference for recovery and management strategies (Southern Interior Reptile and Amphibian Working Group 2016). The analyses presented in this thesis includes data from my own field seasons on the OIR (2015–2016) as well as radio telemetry and capture data from 2011–2014.

Figure 1.7. Timeline showing progression of development and habitat loss in the southern section of the Osoyoos Indian Reserve (OIR) study site from 2004–2016. The campground, golf course and vineyards were established in 2004, and 2004–2016 saw the construction of the Spirit Ridge Resort, Nk'Mip Dersert Cultural Centre, hydro substation, expansion of roads, 4 km long snake fence, expansion of campground and construction of the condominium community.

Thesis Objectives

In 2012, construction began on a condominium community located between the east edge of the golf course and the rocky slopes bordering the study site to the east (labeled as "24-unit condominium community" in Figure 1.4; Figure 1.8). To minimize human-snake conflict, an associated permanent, wooden drift fence was built surrounding the ~4 ha community to limit snake access into the community and to re-direct snakes into neighbouring areas. This fence (~0.9 m tall) was approximately 800 m (~400 m circumference) in total length and was composed of galvanized mesh hardware cloth with 0.6 cm openings that was buried approximately 15 cm under the surface (see Eye et al. 2018 for more detail on the entire snake fence structure on the OIR study site), and wooden posts, and top and bottom rails supported the fence structure. Based on previous research and the location of the new development and fence (well within 400 m of some hibernacula), rattlesnakes embarking on spring migration into the valley bottom were expected to encounter the fence early in their annual spring migration. In the following chapter (Chapter 2), I investigate how these barriers and disturbances influenced the spring migration patterns of the snakes, with a specific focus on interactions with the snake fencing structure. I used radio-telemetry, spatial mapping and statistical analysis to quantify rattlesnake spring migration parameters, home range attributes and body characteristics.
More specifically, I address the following questions:

1. How does disturbance and varying degrees of land use impact Western Rattlesnake spring migration?
2. How does mitigative snake fencing spatially and behaviourally impact Western Rattlesnake spring migration?
3. How does spring migration influence home range attributes of the snakes during the course of the active season?
4. Is there a relationship between the initial spring migration experience and rattlesnake body characteristics at the end of the active season?

The novelty and conservation relevance of this thesis is two-fold. Firstly, spring migration is a notable and important life-history attribute of rattlesnakes in B.C. (see Chapter 2). However, spring migration specifically has never been investigated on this species intensively in B.C. Secondly, snake exclusion fencing is becoming an important and effective strategy to limit negative human-snake encounters, primarily road mortality (Colley et al. 2017; Markle et al. 2017). Although effective, these fencing barriers have recently been documented to have negative impacts on various herpetofauna species (Peaden et al. 2017; Wilson and Topham 2009; Eye et al. 2018). It thus has become of paramount importance to quantify the spatial and behavioural impacts these physical barriers have on individual snakes, and in doing so, assess the long-term consequences of this management technique. Quantifying behavioural shifts amongst individuals intercepted by fencing may lead to uncovering the potential trade-offs of reducing mortality rates while shifting and limiting animal behaviour.

In the last chapter (Chapter 3), I briefly summarize the key points of my study, identify important knowledge gaps and make recommendations for the OIR study site and northern snake management and research in general.

Figure 1.8. Condominium community and construction surrounded by a wooden, permanent snake exclusion fence.

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Chapter Two: Impacts of Fencing and Disturbance on Western Rattlesnake (*Crotalus oreganus*) Spring Movements

Introduction

How animals distribute themselves on the landscape is regulated by various factors including habitat quality and availability, access to food, predator avoidance, and mate acquisition (DeGregorio et al. 2011; Christiansen et al. 2017). One notable and high-profile example of this process is migration. Migratory behaviour is the seasonal movement by individuals within a population (Wilcove et al. 1998; Naidoo et al. 2016; Martin et al. 2017) and is categorized by having a distinguishable objective with a defined route. However, migration as a biological concept tends to be fluid and at times elusive, complicated by the variation seen in distances travelled, timing (annual to daily), and frequency within individual lifetimes (Hoare 2009).

Migration is critical for species survival (Hoare 2009), allowing individuals to respond to seasonal changes in resource availability and exploit habitats beneficial or critical for different life history processes such as breeding, overwintering and grazing or hunting prey (Alerstam et al. 2003). Therefore, interruptions to this phenomenon can restrict individuals from acquiring resources, in turn impacting fitness and ultimately population persistence (Gubili et al. 2016). Understanding the patterns and implications of migration within wildlife populations may be a critical component of maintaining functional and connected landscapes (Epps et al. 2011; Naidoo et al. 2016) crucial for both species conservation and community/landscape preservation.

Due to increasing anthropogenic pressures and continued land-use transformations globally, the process of animal migration has been undergoing alterations in many different taxa (Wilcove et al. 1998; Dobson et al. 2010; Naidoo et al. 2016). The specific drivers of these changes vary across species, locale and temporal scales, but the leading identifiable threats are the destruction of habitat, construction of physical barriers (e.g., dams and fences), animal exploitation and climate change (Harris et al. 2009). Disturbed and fragmented areas typically exhibit ecological traits that differ from natural habitat, specifically altering resource composition, abundance and access for animals (Shine et al. 2004). Furthermore, features and situations that present a barrier or restrict animal movement run the risk of fragmenting populations and presenting obstacles for individuals (Gubili et al. 2016). For example, weirs that fragment streams and tributaries prevent migratory trout (*Salmo trutta*) from reaching their spawning destinations (Gosset et al. 2006), and Reindeer (*Rangifer tarandus tarandus*) avoid crossing parallel power lines and roads, reducing migration area and access to grazing habitat (Vistnes et al. 2004). Geese (*Anser brachyrhynchus*) that stage their migration within disturbed, human-influenced farmland habitat display relatively lower growth rates and reduced reproductive success (Madsen 1995).

Migrations involving long distances and the mass movement of animal aggregations tend to attract relatively more attention (e.g. Wildebeest- Hopcraft et al. 2014; Pacific salmon- Kovach et al. 2015) compared to smaller scale, individual migrations such as performed by many temperate amphibians and reptiles (Duvall et al. 1990; Chiszar et al. 2014; Yermokhin et al. 2015). However, human disturbance and landscape barriers may have a large and less visible impact on the seasonal movement of these animals despite smaller annual travel distances and the variation of spatial use on the landscape. Smaller migratory species with small-scale home ranges and movement patterns therefore may provide useful systems for investigating the implications of disturbance and barriers on natural migration behaviour.

Many temperate snakes, particularly those at northern latitudes, undertake seasonal migrations between overwintering hibernacula to summer foraging and mating grounds (Landreth 1973; Duvall et al. 1990; Jørgensen et al. 2008; Chiszar et al. 2014; Gomez et al. 2015). Such migrations are dangerous and energetically expensive but necessary in cold climates where dependable suitable hibernacula are scarce. These scarce winter shelters are often used by individuals from a wide area and the lack of sufficient summer resources near communal hibernacula obligates these animals to migrate seasonally. These snakes typically exhibit three types of movement and behavioural patterns throughout the course of an active season, namely (1) spring migration away from hibernaculum, (2) mid-summer movements within established hunting and mating grounds, and (3) fall migration back to hibernaculum for overwintering. A number of factors have been posited to drive snake movements away from hibernacula, namely the spatial separation between hibernacula and foraging/mating grounds, limited suitable habitat for hibernacula, reduced intra-competition within a communal hibernacula community (Larsen 1987; Bauder et al. 2015), and the unequal dispersion of appropriate thermal habitat across the landscape (Huey 1991; Shine et al. 2004; Harvey 2015).

Spring migration can result in snakes travelling considerable distances from their hibernaculum while typically demonstrating linear pathways (Martino et al. 2012; Chiszar et al. 2014). These long and straight movements likely optimize encounter rates with irregularly distributed resources on the landscape such as prey and mates (Duvall and Schuett 1997; Duvall et al. 1997). Individual Prairie Rattlesnakes (*Crotalus viridis viridis*) presented with food, during a food supplementation study, had reduced movement frequencies and distance during spring migration (Duvall et al. 1990), suggesting a primary function of spring migration for this species was to locate and successfully hunt prey. However, detailed assessments of spring migration patterns in temperate climate snakes are rare.

Migratory effects aside, the impacts of human disturbance, habitat loss and fragmentation on snake behaviour and movements are widely recognized (Parent and Weatherhead 2000; Shine et al. 2004; Breininger et al. 2011; Lomas et al. in press). For example, Eastern Indigo Snakes (*Drymarchon couperi*) have smaller home ranges in fragmented landscapes in Florida (Breininger et al. 2011), while Western Diamondback Rattlesnakes (*Crotalus atrox*) and Eastern Massasauga Rattlesnakes (*Sistrurus c. catenatus*) both move less frequently in disturbed, human-influenced habitats (Parent and Weatherhead 2000; Beale et al. 2016). Furthermore, garter snakes (*Thamnophis sirtalis parietalis*- Shine et al. 2004), and Eastern Hognose Snakes (*Heterodon platirhinos*; Robson and Blouin-Demers 2013) appear to exhibit roadway avoidance. Prairie Rattlesnakes (*Crotalus v. viridis*) show more tortuous (crooked) movements and reduced body conditions in human-dominated landscapes (Martin et al. 2017).

Fencing infrastructure on the landscape is a common cause of habitat fragmentation. But, it also is used to reduce direct impacts of disturbance to herpetofauna, including snakes (Colley et al. 2017; Markle et al. 2017). Fencing is used to restrict snake access or movement into a specific area (Gregory 2007), or it can be used to deflect snake movement away from certain areas and/or towards favourable habitat (Willson and Gibbons 2009). These mitigative barriers can be very effective at reducing human-snake encounters in residential areas or roadways (Colley et al. 2017). However, fencing still constitutes a physical barrier obstructing natural movement patterns and behaviour that may have consequences for individuals (i.e., mortality- Ferronato et al. 2014; Eye et al. 2018). The effects on spring migration patterns and movements of snakes by fencing or other anthropogenic barriers have not been adequately assessed.

The Western Rattlesnake (*Crotalus oreganus*) exists at the northern limits of its range in British Columbia (B.C.) (Gomez et al. 2015; Lomas et al. 2015; Maida et al. 2018). Listed as "threatened" in Canada (COSEWIC 2015), the primary threats to Western Rattlesnakes are habitat loss, fragmentation, road mortality and human persecution. Rattlesnakes in B.C. occupy hibernacula between October and April (Macartney and Gregory 1988; Brown et al. 2009; Maida et al. 2017) and can move up to 4 km away from their overwintering habitat during the active season (Harvey 2015). Within B.C., this snake resides in southern, semi-arid valley bottoms that are subjected to increasing human development and some of the fastest rates of human population growth in Canada (Statistics Canada 2014; Lomas et al. 2015). Due to strong fidelity to hibernacula, summer foraging grounds and migration corridors (Brown et al. 2009; Gomez et al. 2015) these animals appear to lack the behavioural plasticity to adjust movement patterns and spatial distributions to avoid new development or other land-use changes, similarly to that documented for Eastern Diamondback Rattlesnakes (*Crotalus adamanteus*- Waldron et al. 2013).

Lomas et al (2015; in press) found rattlesnakes frequenting disturbed habitats demonstrated reduced body conditions, smaller home ranges and shorter range lengths at the extreme southern portion of their range in Canada. At that same study site, I investigated how human disturbance and fragmented landscapes altered rattlesnake spring migration patterns. I was specifically interested in shifts of spring migration behaviour by those snakes encountering mitigative fencing. I predicted that migrating rattlesnakes encountering barriers (landscape and fencing) would have shorter spring migration distances, shorter migration duration, and more tortuous movements compared to individuals moving through undisturbed landscapes. Further, I also predicted that alterations to spring migration would impact rattlesnake home range parameters, and have a negative influence on individual body characteristics (growth and body condition) over the course of the active season.

METHODOLOGY

Study Site

This study took place on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada (119.4° W, 49.28° N). The 450 ha area mainly was comprised of low elevation (300–400 m) arid shrub-steppe habitat characterized by Big Sagebrush (*Artemesia tridentata*), Antelope Brush (*Purhsia trdentata*) and native grasses (see Brown et al. 2009; Lomas et al. 2015). The site was bordered by Osoyoos Lake to the west and by open Ponderosa Pine (*Pinus ponderosa*) forests and rocky slopes to the east that contained rattlesnake communal hibernacula at ~500–650 m elevation (Maida et al. 2017). Hibernacula on the OIR study site ranged between ~280–1880 m to human disturbance.

On the study site, rattlesnakes demonstrate two main spring movement patterns: (1) move west and downslope into the valley bottom or (2) move east into the higher elevation forest (Lomas 2013). In this study, I focused on the animals moving from their hibernaculum into the valley bottoms in both the southern and northern portions of the study site. See Chapter 1 for a more detailed study site description.

Radio Telemetry

From 2011–2016 only adult male rattlesnakes were radio-tracked due to the extreme variations in movement patterns exhibited by females of different reproductive status (Macartney and Gregory 1988). Snakes were captured each year during egress (April-May) at or near hibernacula for transmitter implantation. Animals were transported to a nearby veterinary clinic for surgical implantation of radio-transmitters (SB-2; Holohil Sytems Ltd., Carp, Ontario, Canada). Surgical procedures followed Reinert and Cundall (1982) and pharmaceutical procedures followed Brown et al. (2009). Transmitters weighing on average 2.5% of total body weight (range: 1.6–3.7%) were implanted into the coelomic cavity. Rattlesnakes were held in captivity 24–48 hours following surgery to allow recovery and rehydration before being released at their original capture location.

Each telemetered snake was located approximately every 2–3 days throughout the entire active season (April–October). In doing so, snakes were tracked from hibernacula in the spring, throughout the summer season and then back to hibernacula in the fall (ingress), unless mortality and/or transmitter failure occurred. A 3-element yagi antenna and a portable radio-telemetry receiver (TRX-1000S; Wildlife Materials Inc., Murphysboro, Illinois) was used to track individuals and the Universal Transvers Mercator (UTM) coordinates of each location using a MobileMapper 6 device (Magellan Professional Inc, Santa Clara, California, USA) was recorded. Each snake was briefly recaptured approximately once a month and inspected to monitor health and ensure the surgery incision was healing appropriately; during these 'check-ups' individual snakes were weighed (g) and measured by directing their heads inside plastic tubing to safely record snout-vent length (SVL - cm). Apart from that, care was taken to collect location data of animals from 2–5 m away in order to limit disruption and changes in snake behaviour.

Spring Migration Parameters

I calculated a series of parameters to quantify rattlesnake spring migration on the study site (Table 2.1). Outbound spring migration was identified as ending when movements away from hibernaculum became < 50 m between consecutive locations and/or four days spanned between movements (Lomas et al. in press). I assessed spring migration distance (MD) as the total straight-line distance between the start of migration (hibernaculum) to the end (start of summer foraging). Spring migration path length (MPL) was the total sum distance of each yearly movement event until the start of the summer foraging season (i.e., shorter, more infrequent movements), calculated from all locational fixes. I calculated spring migration path sinuosity (MPS) as MD/MPL, creating a ratio ranging between 0 and 1, with values approaching 1 indicating straighter movements and values approaching 0 equating to more crooked movements (Saumure et al. 2010; Martin et al. 2017). Distance to nearest source of disturbance (DTD) was the straight-line distance from each individual's starting point in the spring (hibernacula) to the first confirmed contact with human disturbance. Rattlesnakes from the same hibernacula used dissimilar migration routes and corridors and may have come into first contact with disturbance at different times. Therefore, snakes from the same hibernacula often had different DTD values. Spring migration duration (DAYS) was calculated from the first move away from hibernaculum in the spring until the beginning of summer foraging. I calculated MD, MPL, and DTD using the measuring tool in Garmin

Basecamp (version 4.6.2).

Home Range Parameters

For the entire active season, I estimated rattlesnake home ranges using the 100% minimum convex polygon (MCP). The MCP method creates a polygon around the outermost points plotted on a map, including 100% of the individual's telemetry locations. I chose the MCP method to maximize comparisons with existing literature on snake activity studies, including many studies at the northern extent of the Western Rattlesnake's range in B.C. (Brown et al. 2009; Holding et al. 2014; Harvey 2015; Zappalorti et al. 2015; Lomas et al. in press). This method also has been suggested to best reflect herpetofauna home range size (Row and Blouin-Demers 2006; Shipley et al. 2013; MacGowan et al. 2017), compared to kernel estimators which are more appropriate for investigating habitat use (Row and Blouin-Demers 2006; Mata-Silva et al. 2018). I calculated the core area of use within each snake's home range using 50% fixed-kernel (KD) isopeths (Tiebout and Cary 1987; Mata-Silva et al. 2018; Lomas et al. in press). For this calculation, I used an *ad hoc* method to select the appropriate smoothing factor (h_{adhoc}) to prevent over or under-smoothing (Berger and Gese 2007). I decreased the reference bandwidth (*href*) by 0.1 until I found the home range estimate that included all telemetry locations and represented the smallest continuous polygon with no lacuna (Berger and Gese 2007; Kie 2013; Bauder et al. 2015), and I then used the 50% isopeths outputs from those estimates. I calculated both 100% MCP and 50% fixed kernel isopeths using the HRT extension (Home Range Tools; Rodgers et al. 2007) in ArcGis 10.2.2.

Table 2.1. Spring migration and home range parameter descriptions and overview of methods used to calculate each parameter for Western Rattlesnakes from 2011–2016 on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C.

Parameter	**Abbr.**	**Description**
Spring Migration Parameters		
Spring Migration Distance (m)	MD	Straight line distance (m) between hibernacula and beginning of summer foraging behaviour.
Spring Migration Path Length (m)	MPL	Total sum distance of each movement between start of migration and beginning of summer foraging behaviour.
Spring Migration Path Sinuosity	MPS	(MD/MPL) Estimating straightness of path. Values closer to 1 indicated straighter paths, values closer to 0 indicate more crooked paths
Distance to Disturbance (m)	DTD	The total straight line distance from hibernacula to the first confirmed contact with human disturbance
Spring Migration Duration	DAYS	Duration of spring migration, calculated from the first move from hibernacula until start of summer foraging behaviour.
Home Range Parameters		
Home Range (100% Maximum Convex Polygon) (ha)	MCP	Home range created by a polygon around all the outermost points of all telemetry locations throughout summer active season
Core Area of Use (ha)	CA	Calculated using the 50% kernel isopeths of a rattlesnake's home range

Body Condition and Growth

I calculated body condition index scores for each telemetered rattlesnake by using the residuals from a log-transformed regression between weight and SVL (*cf*. Parent and Weatherhead 2000; Taylor et al. 2005; Shipley et al. 2013; Lomas et al. 2015). A positive residual value indicated the mass for an individual snake was higher than predicted by its SVL, and vice versa. I considered weight, SVL and body condition data collected near the end of each active season to reflect summer foraging success and health. To this end, I used August measurements because not all snakes were successfully captured later in the active season (September/October).

To determine individual growth, I used a modification of Brody's formula to standardize instantaneous growth over the active season for each telemetered rattlesnake (Brody 1945; Maida et al. 2018):

$$\Delta GR = (log_e SVL_2 - log_e SVL_1)/((t_2 - t_1)/167)$$

In this equation, log_e is the natural base of the logarithm, SVL_1 is the SVL at the beginning of the active season (April/May), SVL_2 is the SVL at the end of the active season (August), t_1 is the date of first capture and t_2 represents the date at second (last) capture. Based on previous radio telemetry studies at this study site, the estimated active season for rattlesnakes is approximately 1 April – 15 September (Brown et al. 2009; Lomas et al. in press). Therefore, the constant (167) in the equation represents in days the estimated length of the active season or 'growth season' (*cf*. Maida at el. in press). We assumed that no growth occurred during hibernation (King et al. 2016).

Quantifying Migration Groups

I assigned individual telemetered rattlesnakes into one of three distinct categories based on their spring migration experience: Individuals in the FENCE category encountered the condominium snake fence during their spring migration, while DSTB snakes encountered other forms of disturbance (i.e. a hiking trail, golf course fairway or road) during migration but did not contact the snake fence. Lastly, UN snakes were individuals in the northern portion of the OIR study site that did not encounter any type of disturbance during migration or throughout the entire active season. For these snakes, I simply used the straight-line distance from the individual hibernaculum to the nearest source of human disturbance to quantify DTD.

Prey Population Monitoring

Small mammal live-trapping was performed on the study site to monitor the prey base population for rattlesnakes from 2012–2016. Sampling was performed once a year (end of June/early July) over four trapping grids. Fixed grid locations were used each year to encompass the main land use types on the landscape (Figure 2.1). To this end, a single grid was established in the golf course (in the shrub-steppe between fairways), a vineyard, undisturbed shrub-steppe, and the toe slope of the eastern mountains ('Hillside'- below hibernacula locations). Each grid was sampled using Longworth-style traps (Little Critter Live Traps, Rogers Manufacturing, West Kelowna, BC) set up in a 6 x 6 grid (36 traps in total) spaced 15 m apart, and each trap was covered with a board (~ 15 cm x 30 cm) to protect them from sun and rain (Larsen et al. 2007). Three baiting nights were followed by three trapping nights. Traps were baited with a piece of apple (source of water) along with rolled oats and sunflower seeds and were provided with synthetic bedding for warmth. During trapping nights, traps were baited and armed immediately prior to sunset and then checked the following morning starting at sunrise (~ 0500h). Captured small mammals were identified to species, sexed, ear-tagged (Monel #1; Kent Scientific Corporation, Torrington CT) and released immediately at the point of capture.

Due to low capture rates, mark-recapture models could not be fitted so I used counts (i.e. number of unique individuals captured within three days) to represent the small mammal population density within each grid (Torre et al. 2016). I assumed that the uncaptured proportion of the small mammal population is constant, and that individual counts within the grids would yield a representative density estimate (Slade and Blair 2000; Torre et al. 2016).

Figure 2.1. Map of the southern, developed portion of the Osoyoos Indian Reserve (OIR) study site near Osoyoos, B.C. Development included a golf course, vineyards, resort, cultural centre, hiking trails, campground, condominium community and construction, and associated roads and parking lots. Snake fencing represented in red. Small mammal trapping gird locations used from 2012–2016 are as follows: (1) golf course, (2) hillside, (3) vineyard, and (4) undisturbed shrub-steppe.

Statistical Analysis

I used R version 3.4.3 (R Development Team Core 2017) to perform all statistical analysis. I log-transformed migration distance (MD), 100% MCP and 50% KD to meet assumptions of normality. I used univariate one-way ANOVA to compare each migration and home range parameter as well as end-of-year body condition and instantaneous growth between the three migration categories. I used Tukey's honesty significant difference (HSD) test for *post hoc* comparisons. I also used linear regressions to investigate the relationship between migration and home range attributes and the distance to nearest source of disturbance. Data on telemetered snakes were used only if the animals were tracked for the entire spring migration (started at or within ~50 m of hibernacula), and for more than 75% of the active season, or they had provided at least 20 locations (Lomas et al. in press). However, due to mortality and/or transmitter failure, not all snakes were tracked for the entire active season. Given strong site fidelity to hibernacula (Maida et al. 2017), for animals not successfully tracked back to their hibernacula I used the location of their spring hibernacula as the predicted endpoint in home range calculations (note that every snake tracked during this study for an entire active season returned to the same hibernacula from which it originated). Considering GPS error was generally ± 5m, I assigned consecutive locations that were <10 m apart as identical, i.e. representing no movement. All statistical interpretation was guided by α=0.05 and all means reported include ± 1 standard error (SE).

RESULTS

A total of 78 adult male rattlesnakes were equipped with radio-transmitters from 2011–2016. Of those, 27 individual rattlesnakes (FENCE *n* = 7; DSTB *n* = 10; UN *n* = 10) were tracked for their entire spring migration (starting at or near hibernaculum) and for more than 75% of the active season, each furnishing more than 20 location points. No snakes from 2013 met this criteria and were thus excluded in my analysis (telemetry started in June that year). Four snakes tracked for their entire spring migration did not provide data through the entire active season due to road mortality (*n* = 1), predation (*n* = 1) and transmitter failure/unknown (*n* = 2). Both spring migration ($F_{2,24}$= 0.056, *P*= 0.95) and entire active season ($F_{2,24}$= 0.30, *P*= 0.74) monitoring effort (number of telemetry locations) did not differ across the three spring migration categories. During their spring migration, rattlesnakes within the DSTB or FENCE categories encountered either a snake exclusion fence, hiking trail or a golf course fairway. However, snakes in disturbed habitats also encountered roads, vineyards, fencing, fairways and hiking trails throughout the rest of the active summer period.

Migration Parameters

Monitoring effort (i.e., the number of times telemetry locations were recorded for each snake) did not influence spring migration distance (MD; $F_{1,25}$= 0.10, P= 0.75), spring migration path length (MPL; $F_{1,25}$= 2.53, P= 0.12), or spring migration path sinuosity (MPS; $F_{1,25}$= 2.96, P= 0.09) estimates. Mean MD was 892.6 m (± 92.1 m; FENCE: $\bar{x}$= 421m ±30.8 m; DSTB: $\bar{x}$= 780 m ±80.8 m; UN: $\bar{x}$= 1335 m ± 137.0 m), and there was a significant relationship with distance to disturbance (DTD; $F_{1,25}$= 58.7, P< 0.01). Log-transformed MD differed significantly between categories ($F_{2,24}$= 34.78, P< 0.01; Figure 2.2), with snakes in the UN category displaying significantly greater MD lengths than both FENCE and DSTB categories (FENCE: P< 0.01; DSTB: P< 0.01). In addition, snakes in the FENCE category had shorter MD than snakes in the DSTB category (P< 0.01).

The mean migration path length (MPL) for all snakes in my study was 1443.8 m (± 87.4 m), and there was a significant relationship between MPL and DTD ($F_{1,25}$= 14.1, P< 0.01). Rattlesnakes within the UN category ($\bar{x}$= 1714.1 m ±148.6 m) has significantly longer MPL than individuals in the FENCE category ($\bar{x}$= 1056 m ±142.9 m; P= 0.01).

The mean migration path sinuosity index (MPS) for all snakes in my study was 0.60 (± 0.04), and there was a significant correlation between this measurement and DTD ($F_{1,25}$= 23.1, P< 0.01; Figure 2.3). Furthermore, MPS differed significantly between the three migration categories ($F_{2,24}$= 13.62, P< 0.01) with the UN category ($\bar{x}$= 0.78 ±0.03) MPS being significantly straighter than both the FENCE and DSTB categories (FENCE: $\bar{x}$= 0.43 ±0.04; P< 0.01; DSTB: $\bar{x}$= 0.55 ±0.06; P< 0.01). Mean values indicate the FENCE category migration path was more tortuous than straight, whereas DSTB category sinuosity index indicated slightly more straight than crooked and UN snakes had almost completely straight migration movements. Furthermore, the lowest sinuosity index value for snakes in the UN category was 0.54 (range 0.54–0.89), compared to the highest sinuosity index values registered in the FENCE category (0.53, range 0.28 –0.53).

The mean spring migration duration (DAYS) across the study site was 41 days (± 2.4 days), and there was no relationship between DAYS and DTD ($F_{1,25}$= 0.1, P= 0.48). Moreover, there was no difference in DAYS between the three groups ($F_{2,24}$= 0.09, P= 0.91), nor was there a relationship in MD (the length of the individual's migration) and DAYS ($F_{1,25}$= 0.03, P= 0.87).

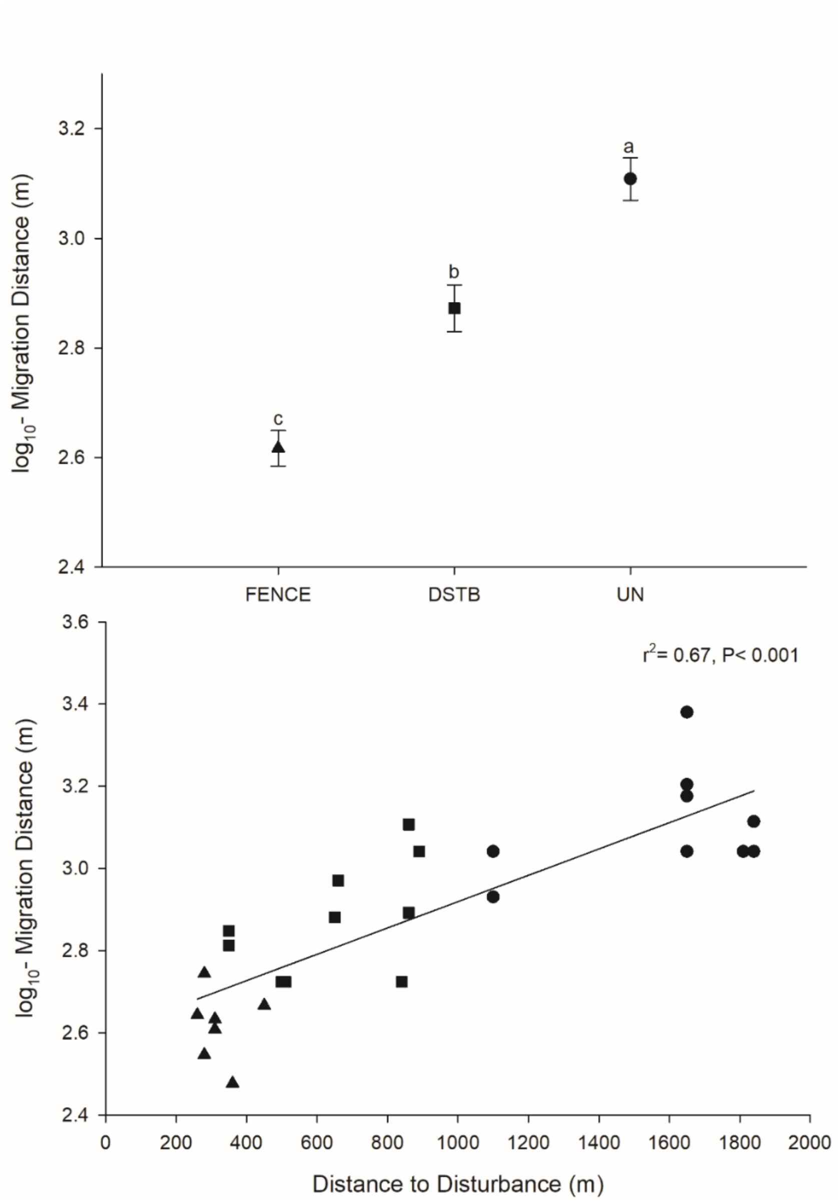

Figure 2.2. Mean ± SE of log-transformed migration distance (MD) of the three migration categories (top) and relationship between log-transformed migration distance and distance to disturbance (bottom) of male Western Rattlesnakes (*Crotalus oreganus*) on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada. Sample sizes for the categories are FENCE (*n*= 7), DSTB (*n*= 10), and UN (*n*= 10). Means with different letters indicate a significant difference at α= 0.05. Individuals in the FENCE category encountered the condominium snake fence during their spring migration, while DSTB snakes encountered other forms of disturbance. Thirdly, UN snakes were individuals in the northern portion of the study site that did not encounter any type of disturbance during spring migration or throughout entire active season.

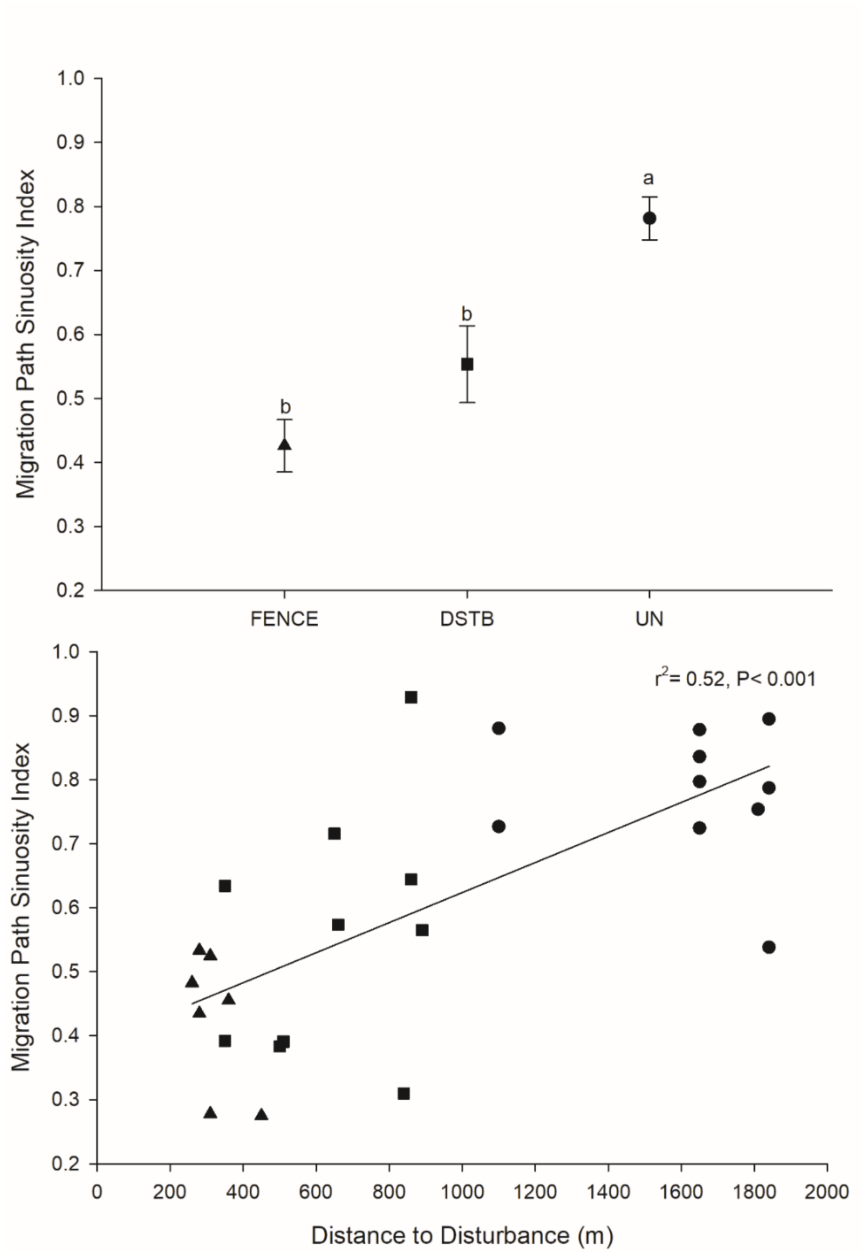

Figure 2.3. Mean ± SE of migration path sinuosity (MPS) of the three migration categories (top) and the relationship between migration sinuosity and distance to disturbance (bottom) of male Westner Rattlesnakes (*Crotalus oreganus*) on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada. Sample sizes for each group are FENCE (*n*= 7), DSTB (*n*=10), and UN (*n*=10). Means with different letters indicate a significant difference at α= 0.05. See Figure 2.2 caption for description of migration categories.

Home Range Parameters

Rattlesnake MCP home range sizes varied from 4.4–103 ha (FENCE: $\bar{x}$= 10.1 ±1.4 ha; DSTB: $\bar{x}$= 21.1 ±2.9 ha; UN: $\bar{x}$= 36.8 ±8.2 ha) on the OIR study site, and there was a significant relationship between rattlesnake log-transformed (MCP) home range size and both DTD and MD (DTD: $F_{1,25}$= 23.3, P< 0.01; MD: $F_{1,25}$= 51.66, P< 0.01). Log-transformed home range size differed significantly between the three migration categories ($F_{2,24}$= 9.50, P< 0.01; Figure 2.4) with the FENCE category home range being significantly smaller than both DSTB and UN categories (DSTB: P= 0.02; UN: P< 0.01). Furthermore, rattlesnake home ranges in the FENCE category only extended an average of 106.9 m (±39.4 m; range 0–205 m) beyond the fencing structure (distance away from hibernacula). Mean core area of use was 8.9 ha (± 1.63 ha; FENCE: $\bar{x}$= 2.7 ±0.4 ha; DSTB: $\bar{x}$= 7.4 ±0.8 ha; UN: $\bar{x}$= 13.9 ±10.2 ha) and log-transformed core area was significantly related to DTD ($F_{1,25}$=23.9, P< 0.01). Log-transformed core area of use differed significantly between the three groups ($F_{2,24}$=18.3, P< 0.01), where the FENCE category core area was significantly lower than DSTB and UN categories (DSTB: P< 0.01; UN: P< 0.01). Lastly, snakes with larger home ranges (MCP) contained larger core areas ($F_{1,25}$=137.5, P< 0.01).

Body Characteristics

The mean initial spring body weight of telemetered snakes was 209.5 g (± 8.7 g), and mean SVL was 66.8 cm (± 1.3 cm); mass was strongly associated with SVL ($F_{1,25}$= 43.49, P< 0.01). The range of SVL in telemetered snakes was 54.5–78.5 cm, reflecting the bulk of the larger male rattlesnake sizes at the OIR study site (see Figure 2.5). From captures in 2011–2016 (n= 489), male rattlesnakes larger than 78.5 cm SVL represented 6.7% of total male captures. Furthermore, Maida et al (2018) estimated asymptotic SVL at this site as 73.4 cm SVL for the entire population. Undisturbed snakes (UN: $\bar{x}$= 71.7 ±1.5 cm) were longer than both FENCE ($\bar{x}$= 59.8 ±1.8 cm; P< 0.01) and DSTB snakes ($\bar{x}$= 65.6 ±1.9 cm; P= 0.04; Figure 2.6), and there was a positive, significant relationship between rattlesnake size (SVL) and DTD ($F_{1,25}$= 9.7, P< 0.01; i.e. smaller snakes travelled shorter distances to first encounter disturbance than bigger snakes). Due to snake mortality and transmitter failure, size and weight data were not recorded on two snakes within the sample in the month of August resulting in a body characteristics (body condition and growth) sample size of 25 individuals (FENCE n= 6; DSTB n= 10, UN n= 9).

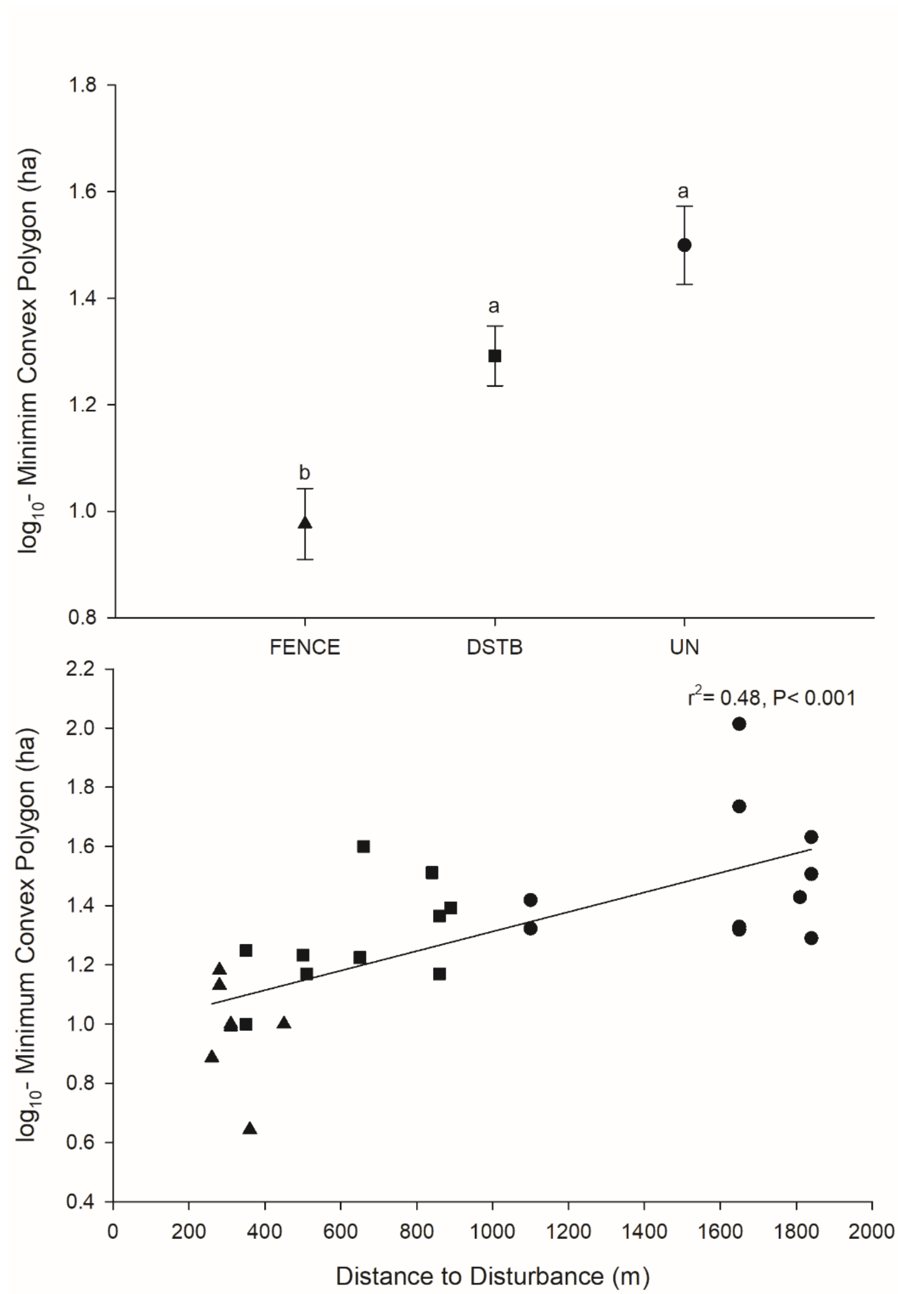

Figure 2.4. Mean ± SE of log-transformed minimum convex polygon (MCP) home range estimates of the three migratory categories (top) and the relationship between log-transformed MCP and distance to disturbance (bottom) of male Western Rattlesnakes (*Crotalus oreganus*) on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada. Sample sizes for the migration categories are FENCE (*n*= 7), DSTB (*n*= 10), and UN (*n*= 10). Means with different letters indicate a significant difference at α= 0.05. See Figure 2.2 caption for a description of migration categories.

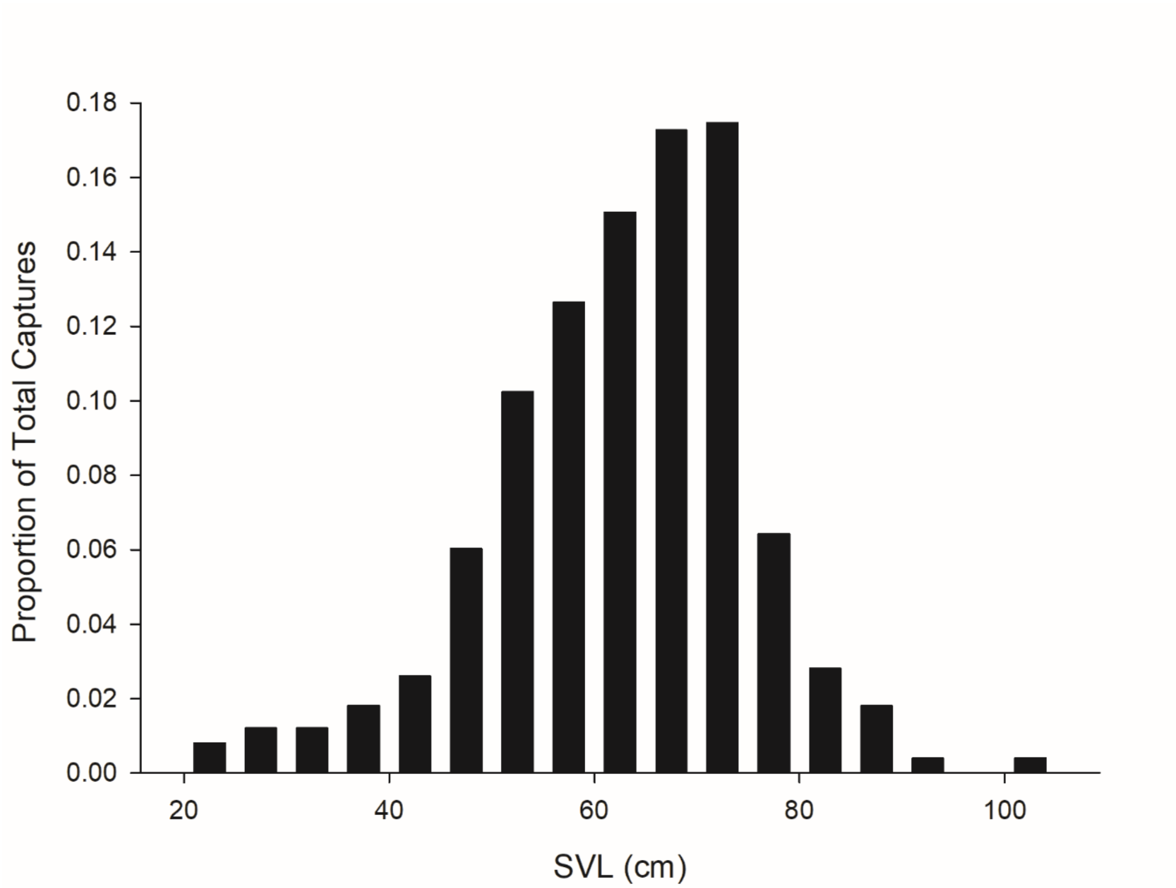

Figure 2.5. Size class distribution of male Western Rattlesnake (*Crotalus oreganus*) captures (*n*= 489) on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada from 2011–2016.

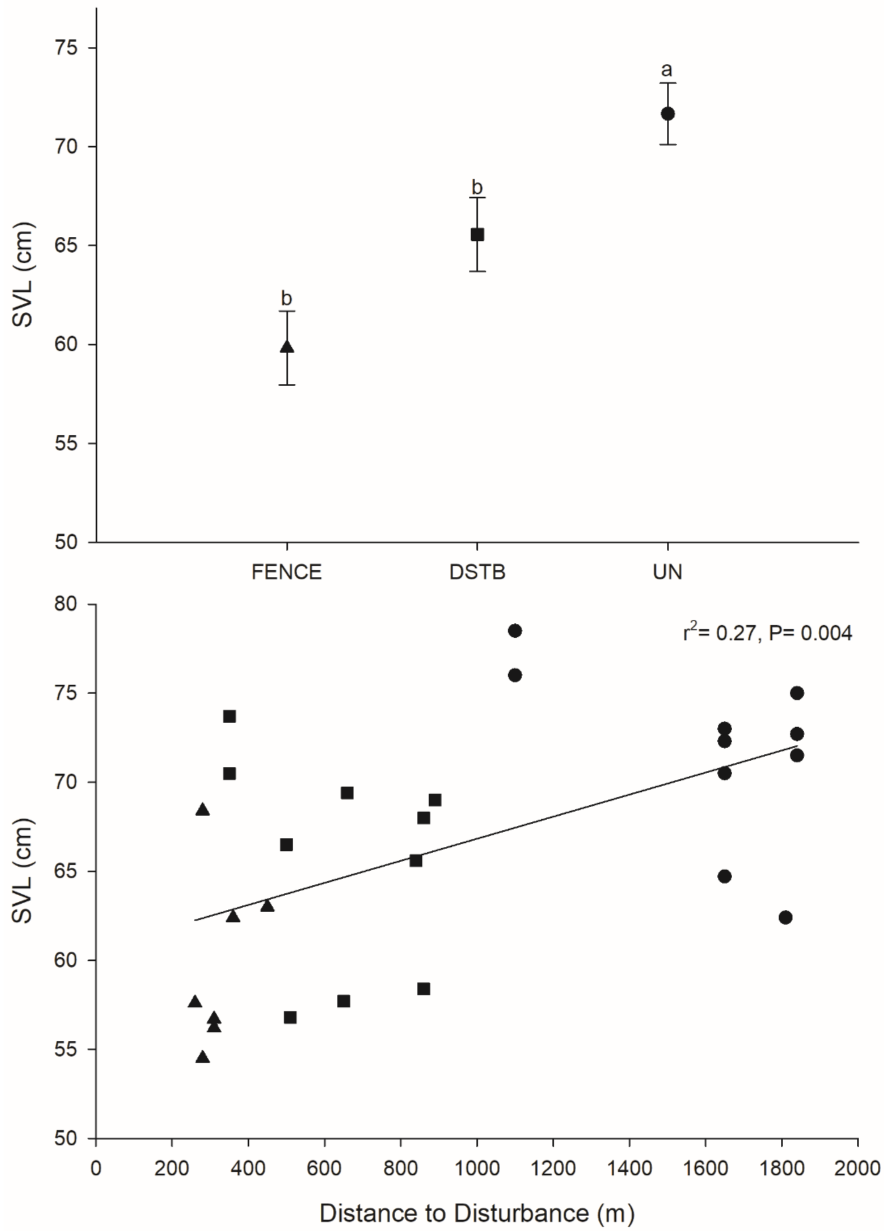

Figure 2.6. Mean ± SE of spring snout-vent-length (SVL) between the three migrations categories (top) and the relationship between spring SVL and distance to disturbance (bottom) of male Western Rattlesnakes (*Crotalus oreganus*) on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada. Samples sizes of each category are FENCE (*n*= 7), DSTB (*n*= 10), and UN (*n*= 10). Means with different letters indicate a significant difference at α= 0.05. See Figure 2.2 for a description of the migration categories.

There was no significant relationship between DTD and end-of-year body condition ($F_{1,23}$= 0.58, P= 0.46), and body condition did not differ between the three migration categories ($F_{2,22}$= 0.19, P= 0.83). A *post hoc* analysis showed the observed power for this test was 11% (f= 0.18, Power (1-β)= 0.11). Given the variances in the samples, to achieve reasonable power (>0.80) in the analysis, the total sample size between the three migration groups would require ≈303 individuals. Rattlesnakes with higher end-of-year body condition had both larger home ranges and core areas of use (Home range: $F_{1,23}$= 7.5, P= 0.01; Core area: $F_{1,23}$= 5.0, P= 0.04).

Not surprisingly, smaller snakes grew at a faster rate than larger snakes ($F_{1,23}$= 5.5, P= 0.02) but instantaneous growth did not appear to differ between the three migration categories ($F_{2,22}$= 1.17, P= 0.33; Figure 2.7). *Post hoc* power for this analysis was 35% (f= 0.39, Power (1-β)= 0.35), and to obtain a power estimate > 0.80 would require ≈69 individuals in the analysis, compared to my own sample size of 25 individuals. Furthermore, there was no significant relationship between instantaneous growth and DTD ($F_{1,23}$=0.86, P= 0.36). Overall, a Pearson's correlation matrix showed no significant correlations between each spring migration parameter (MD, MPL, DTD, DAYS and MPS) with either rattlesnake end of year body condition or instantaneous growth (Table 2.2).

Prey Population Monitoring

Over the 2,160 trap nights conducted during 2012–2016 only two species of small mammals were captured: Great Basin Pocket Mice (*Perognathus parvus*) were the prominent species, with 179 animals caught (97.2% of total), compared to five individual Deer Mice (*Peromyscus maniculatus*). This equated to a mean annual population density of 16.4 animals/ha (range: 10.7–26.3 animals/ha; Table 2.3) across the study area. Furthermore, small mammal density appeared homogenous across the landscape (Table 2.3), with no significant differences in capture numbers occurring between the grids ($F_{3,16}$=1.03, P= 0.41).

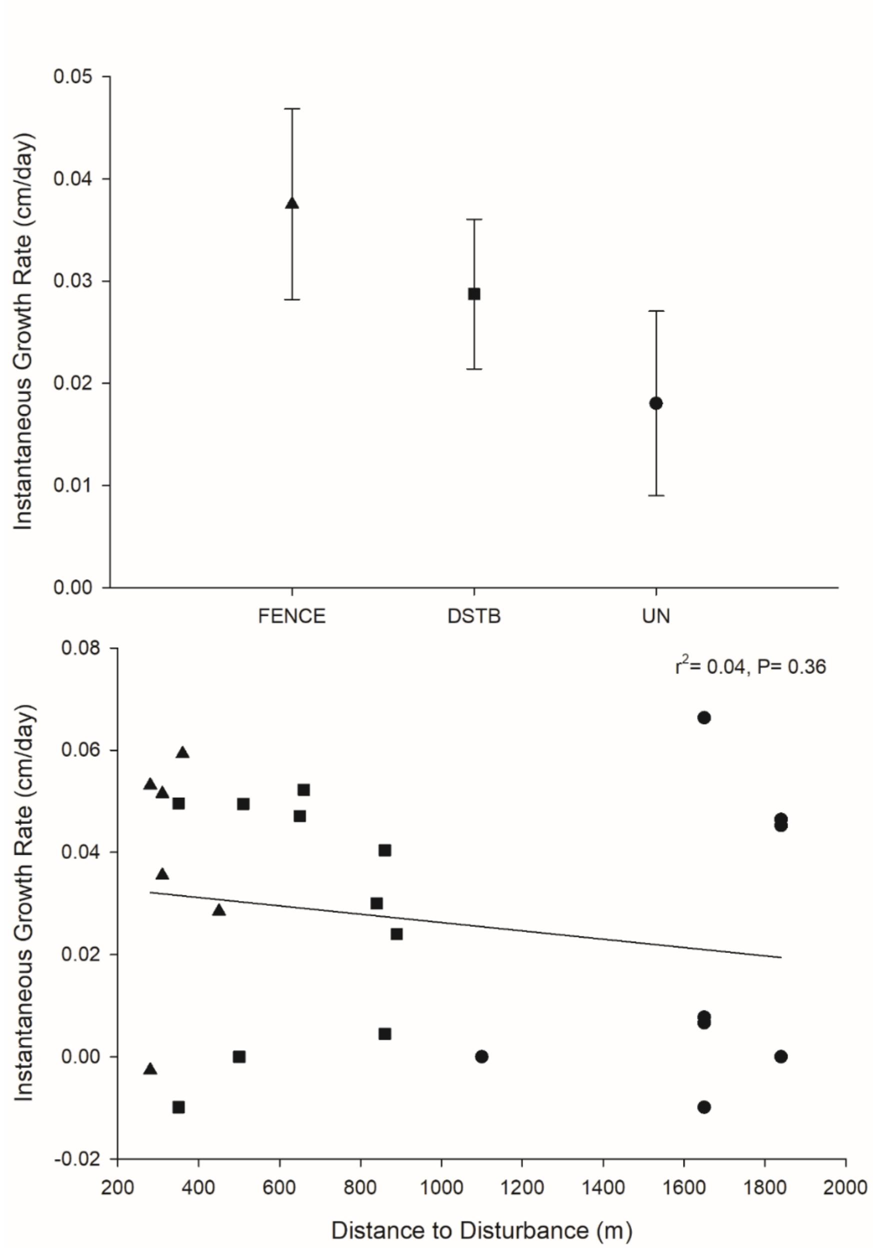

Figure 2.7. Mean ± SE instantaneous growth rate between the three migration categories (top) and the relationship between instantaneous growth rate and distance to disturbance (bottom) of male Western Rattlesnakes (*Crotalus oreganus*) on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada. Sample sizes for each category are FENCE (*n*= 6), DSTB (*n*=10), and UN (*n*=9). Means with different letters indicate a significant difference at α= 0.05. See Figure 2.2 for a description of the migration categories.

Table 2.2. P-values for Pearson's correlation tests between male Western Rattlesnake (*Crotalus oreganus*) end of year body condition and instantaneous growth and each migration parameter used (MD, MPL, DTD, DAYS, and MPS).

Migration Parameter	End of Year Body Condition	Instantaneous Growth
Spring Migration Distance (MD)	P= 0.20	P= 0.58
Total Spring Migration Path (MPL)	P= 0.14	P= 0.85
Distance to Disturbance (DTD)	P= 0.46	P= 0.77
Spring Migration Duration (DAYS)	P= 0.23	P= 0.59
Spring Migration Sinuosity (MPS)	P= 0.49	P= 0.44

Table 2.3. Small mammal population density estimates (animals/ha) of each trapping grid on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada from 2012–2016. Small mammals represented within the population were Great Basin Pocket Mice (*Perognathus parvus*) and Deer Mice (*Peromyscus maniculatus*).

Year	Hillside	Golf Course	Vineyard	Shrub-Steppe	Mean
2012	10.7	3.6	25.0	3.6	10.7
2013	28.6	0.0	5.4	8.9	10.7
2014	23.2	35.7	19.6	26.8	26.3
2015	30.4	8.9	21.4	12.5	18.3
2016	14.3	7.1	23.2	19.6	16.1
Mean	21.4	11.1	18.9	14.3	16.4

DISCUSSION

This is the first detailed study investigating rattlesnake spring migration in relation to human disturbance. More specifically, this is the first study addressing how fence barriers affect rattlesnake spring migratory behaviour and the consequences for summer home ranges and body characteristics. I observed a strong correlation between distance travelled to disturbance with all of the spring migration metrics calculated, home range estimates and animal body size (SVL). I also found that disturbed and fragmented habitats had a strong, consistent influence on rattlesnake spring migration distance and migration sinuosity compared to snakes migrating through undisturbed landscapes during the spring. Furthermore, encountering the fence structure during spring migration had a significantly negative influence on rattlesnake migration distance as well as home range and core area size, compared to snakes in disturbed areas that did not encounter the fencing structure. Physical construction was taking place on site during all/part of the study, and that may have had potential proximate impacts on snakes moving through adjacent habitat or along the fencing structure. Tremors created from the use of heavy machinery may have negative impacts on animals, such as snakes, that use vibrations as a source of communication and sensory input (Hartline 1971; Hill 2001; Lovich and Ennen 2017). However, I did not have the equipment to measure and quantify vibration intensity from the construction zone.

In contrast, variations in spring migration distance and path length did not correlate with migration durations within the three categories; in other words, individuals migrating shorter distances in disturbed areas took the same amount of time to complete their spring movements as individuals migrating further distances in undisturbed habitats. In addition, there did not appear to be a clear, consistent relationship between the animals' body characteristics and the spring migration metrics considered in this study.

On the study site, there were two general types of barriers on the landscape interrupting rattlesnake spring migration: physical (fence) and permeable 'landscape' barriers (golf course and hiking trails), and both appeared to influence rattlesnake spring migration compared to snakes travelling through undisturbed landscapes. Snakes and other reptiles have been previously observed avoiding or altering their behaviour along open areas including hiking trails and golf course fairways (Parent and Weatherhead 2000; Andrews and

Gibbons 2005; Goode 2010;). In Arizona, Gila Monsters (*Heloderma suspectum*) tend to avoid golf course fairways, while Tiger Rattlesnake (*Crotalus tigris*) home range sizes and shapes alter in golf course habitats (Goode 2010). Furthermore, Massassauga Rattlesnakes (*Sisturus c. catenatus*) and Western Diamondback Rattlesnakes (*Crotalus atrox*) exhibit a reduction in movement frequency within areas of high human use (Parent and Weatherhead 2002; Beale et al. 2016) including hiking trails. The scale of my analysis was insufficient to determine if rattlesnakes avoided golf course fairways and hiking trails on the OIR study site. However, reductions in spring migration distances, total migration path lengths and lower path sinuosity (more crooked movements) in these 'habitats' suggest the animals altered their spring migration behaviour compared to individuals in areas lacking human involvement and landscape disturbance. Shorter, more tortuous movements may be a behavioural response to perceived threats or predator avoidance caused by human influence and landscape alterations, and may help decrease the probability of encountering predators and/or humans (Martin et al. 2017).

Encountering the snake fence appeared to have a large influence on rattlesnake spring migration, specifically migration distance, migration path length and migration sinuosity compared to individuals migrating in undisturbed habitats. Furthermore, individuals encountering the fence had greatly reduced spring migration distances compared to all other snakes in our study (including both disturbed and undisturbed). Previous studies (see above) show avoidance of open areas associated with landscape disturbance; however, individuals still have the ability to cross these features. Animals encountering barriers such as a golf course fairway or hiking trail face trade-offs between the costs of crossing these impedances versus moving around them (Beyer et al. 2016). On the other hand, individuals encountering a fence do not have this option and must either halt movement or circumnavigate the barrier. Having alternative movement options when encountering an impediment (golf course and/or hiking trails) or a non-permeable barrier (fence) appears to strongly influence the total distance a rattlesnake travels during its spring migration on the OIR study site. Furthermore, rattlesnakes exhibit a high level of fidelity to various areas/habitats throughout their life history (hibernacula, corridors, summer foraging areas). Specifically, adult rattlesnakes seem to contain high spatial and site fidelity on the landscape and are not likely to redistribute themselves on the landscape (Waldron et al. 2013). A novel obstruction, such as a fencing structure, likely impedes access to areas used in previous years. Again, in response to this, individuals may or may not attempt to skirt the barrier (altering path sinuosity and likely distance travelled).

Overall, home range patterns and sizes I observed appear to be similar to that previously reported from rattlesnakes at the OIR study site and in other areas at the northern extent of the species' range (B.C.). Harvey (2015) found MCP home ranges in undisturbed habitats throughout B.C. ranged from 1.5–184.7 ha ($\bar{x}$= 52 ha). Furthermore, at the OIR study site, Brown et al. (2009) calculated average rattlesnake MCP to be 25.1 ha and Lomas et al. (in press) calculated mean MCP home ranges at 20.0 ha. Previously, Macartney (1985) determined that den population home ranges (estimated size of area used by individuals in a given den) averaged 26.0–122.3 ha in a study area approximately 140 km north of the OIR study site. Although home range estimates among previous studies, as well as results presented herein, are comparable, it is also indicative of the range of home range sizes across individuals and populations. This is likely determined by a variety of factors including habitat, level of disturbance on the landscape and potentially latitudinal position.

Using a disturbance rating (DR) system (Parent and Weatherhead 2002), Lomas et al. (in press) found that rattlesnakes in the undisturbed areas of the OIR study site had larger home ranges than animals within minimal to highly-disturbed areas. I found similar trends, however, interactions with the fencing structure during spring migration had a drastic influence on rattlesnake summer home range size and core areas of use compared to both undisturbed and disturbed snakes. Regardless of disturbance, my results further indicate that home range size was strongly associated with the length of an individual's spring migration distance, and with respect to disturbance, rattlesnake home range size decreased when in closer proximity to disturbance (shorter DTD = shorter MD). Similarly, Mojave Desert Tortoise (*Gopherus agassizii*) home ranges decrease with proximity to roads and mitigative road-side fencing (Peaden et al. 2017). The authors inferred this may be a result of road avoidance or increased resources along road sides (water run-off or forbs). Based on anecdotal observations of vegetation and resources adjacent to the construction site and snake fence, this does not appear to be the case on the OIR study site, and changes to home range size likely result from the interaction and behavioural shifts in migration of individuals in response to landscape disturbance and fencing.

Growth and body condition are the two most common metrics used to quantify rattlesnake physiology, health and individual/population success (Moore et al. 2000; Jenkins et al. 2009; Lomas et al. 2015; King et al. 2016). One of the primary functions of spring migration in communally-denning rattlesnakes appears to be finding habitats with food (Duvall et al. 1990). Prairie Rattlesnakes (*Crotalus v. viridis*) with straighter, longer range lengths had higher end of year body condition (Martin et al. 2017), while increased body condition in male Timber Rattlesnakes (*Crotalus horridus*) allowed individuals to allocate more time to finding mates than hunting (Lind and Beaupre 2015). Furthermore, in B.C., Harvey (2015) observed rattlesnakes in forested habitats moved farther distances and contained higher body conditions than rattlesnakes within the valley bottoms. In support of this, I found individuals with higher body conditions at the end of the active season had maintained larger home ranges and larger core areas. Being a sit-and-wait ambush predator, larger home ranges and core areas, regardless of habitat quality, likely reflect more time for rattlesnakes to search for mates during the summer months, rather than hunting. However, I did not notice any significant trends or differences in end-of-year body condition among the three migration categories. The lack of significant difference and the large sample size required (303 individuals) to achieve statistical power suggests body condition index scores may not be a feasible physiological metric for gauging the effects of different migratory tactics, at least at this specific study area.

My observations of rattlesnakes being smaller (SVL) when travelling shorter distances to disturbance mirrors previous observations by Lomas et al. (2015) at the OIR study site; similar trends also were noticed in a Western Rattlesnake population south of the OIR study site in Idaho (rattlesnakes living in disturbed areas were smaller: Jenkins et al. 2009). Furthermore, this trend has been observed in other snake species, such as urban-living Dugites (*Pseudonaja affinis*) being smaller than non-urban individuals in Australia (Wolfe et al. 2017). Typical snake growth rates involve a highly correlated, linear, negative relationship between size and growth (i.e. smaller snakes grow faster than larger snakes; *cf*. Macartney et al. 1990; King et al. 2016; Dreslik et al. 2017; Maida et al. 2018). With mean SVL of snakes in disturbed areas (both fence and disturbed categories) being significantly smaller than undisturbed snakes and previously estimated population asymptotic SVL (Maida et al. 2018), we would expect to find an increased rate of growth in snakes in the two disturbed migration categories compared to snakes in the undisturbed category, but this appeared not to be the case in this study. However, due to the lack of power in the analysis, further investigation the impacts on growth (and body condition) based on rattlesnake spring movements and behaviour may be required.

Previously, an analysis of road-killed rattlesnakes from the broader region of the south Okanagan showed a relatively large suite of mammalian prey species (McAllister et al. 2016). In contrast, the OIR study site appears to support only two microtine mammal species, Deer Mice and Great Basin Pocket Mice, and in relatively low densities. The homogenous array of low densities and a low species diversity of mammalian prey across the OIR study site suggests the ability for rattlesnakes to successfully find prey may be of particular significance. However, the similarity in prey density estimates between grids in natural landscapes and disturbed areas (i.e., golf course, vineyard) suggests that prey abundances does not appear to be a likely contributor to changes in home ranges and movements that I documented above.

Overall, spring migration and behaviour of these animals appear to be highly influenced by human disturbance including interactions with associated exclusion fencing. Similar to the effects of disturbance on rattlesnake body condition outlined by Lomas et al (2015), these effects are not readily apparent when rattlesnakes remain persistent on the landscape. Furthermore, this study does not measure the long-term implications of these impacts. Snake exclusion fencing is becoming a very important conservation tool to reduce the direct impacts of road mortality and other negative consequences of human interactions with snakes (and a variety of species and taxa). However, my findings show that fencing also needs to be considered as a disturbance in itself. Fencing can be effective at reducing direct impacts (i.e., road mortality) of human interactions on snakes. Yet, these structures also pose influences on animals that have been overlooked to date.

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CHAPTER THREE: CONCLUSION AND MANAGEMENT IMPLICATIONS

SUMMARY

My thesis contributes to the broad understanding of the impacts of disturbance, habitat loss and fragmentation on animal behaviour. Specifically, I used a small-bodied, migrant predator to investigate shifts in migration patterns due to disturbance and human-influenced changes on the landscape. Using radio-telemetry and GIS analysis I investigated alterations to spring migration patterns of Western Rattlesnakes in the southern interior of British Columbia, and the potential implications these movement alterations had on individual body characteristics and home ranges throughout the active season. To recap, the general objectives of my thesis were to:

(1) Attain baseline information of rattlesnake spring migration movements in shrub-steppe ecosystems in B.C.,

(2) Outline how disturbance and barrier fencing influence rattlesnake spring migration movements, and

(3) Describe the influence of alterations in spring migration has on rattlesnake body characteristics and home range attributes throughout the active season.

The major results of my thesis are:

- The distance individual rattlesnakes traveled until they first encountered a disturbance had a large influence on spring migration patterns and home range sizes.
- Encountering disturbance (both landscape and barrier fencing) reduced both the total distance moved in the spring, and path sinuosity of spring migration in rattlesnakes.
- Individuals who encountered the snake fence barrier had reduced spring migration distances, home range and core area sizes compared to all other snakes in the study.

- Rattlesnakes migrating shorter distances to first encounter disturbance were smaller than snakes moving further distances to first encounter disturbance in the spring. Contrary to my predictions, I did not observe a significant influence on end of year body condition for rattlesnakes based on their migration experience. My results also showed no significant difference in growth rates between rattlesnakes encountering a fence, other forms of disturbance or moving through undisturbed habitats during their spring movements. However, modest sample sizes indicated relatively low power (in both body condition and growth rate) in these analysis suggesting further work may be warranted.

CONSERVATION AND MANAGEMENT IMPLICATIONS

The province-wide threat assessment for Western Rattlesnakes in B.C. has been classified as high (Southern Interior Reptile and Amphibian Recovery Team 2016), with the primary threats identified include direct population loss from road mortality and human persecution. Furthermore, lower-ranked threats include habitat loss and fragmentation (specifically from agriculture, housing, and recreation). These threats are magnified by the south Okanagan Valley representing one of the fastest growing regions in Canada (Statistics Canada 2014) resulting in a considerable reduction of natural grassland and shrub steppe ecotypes associated with many species-at-risk, including rattlesnakes (Lea 2008). Moreover, less than 15% of the remaining land area within the rattlesnake's range in B.C. is represented by provincial parks, protected areas, and ecological reserves (Grassland Conservation Council of British Columbia 2004). Animals do not abide by jurisdictional boundaries, so within protected areas, animals with large home ranges and/or migration patterns, like rattlesnakes, may leave these protected areas (Thirgood et al. 2006; Harvey 2015; Allen and Singh 2016). This results in areas of reduced habitat quality (i.e., golf courses, urban areas, vineyard and orchards, etc.) becoming a common aspect of rattlesnake home ranges and habitats used throughout the active season and lifetime of individuals. Therefore, understanding shifts in rattlesnake ecology within disturbed landscapes will lead to more thoughtful and effective management strategies for these animals within less desirable habitat and high human influence.

My thesis work provides important baseline ecological information to help address several key objectives outlined for the recovery of this species, namely:

(1) “Continue to clarify the impact of human disturbance (both direct and through habitat alteration) on snakes and develop effective mitigative strategies”,

(2) “Address biological knowledge gaps regarding distribution, movements, population structure, metapopulation dynamics, prey relationships, genetic and landscape connectivity, and health impacts from threats”, and

(3) “Identify and strategically reduce movement barriers in terrestrial habitat where loss of habitat and connectivity is seriously affecting population viability”.

The objectives listed above are all identified as essential priorities for rattlesnake conservation in B.C. (Southern Interior Reptile and Amphibian Recovery Team 2016). Based on the results of my thesis, I make the following specific management recommendations:

1) Ensure habitat complexity along fencing structures

Barrier fencing has been proven to be effective at reducing direct negative snake-human conflict (Colley et al. 2017) as well as protecting other herpetofauna species primarily from road mortality (Aresco 2005; Baxter-Gilbert et al. 2015; Markle et al. 2017). However, undoubtedly these fences also likely prevent animals from accessing previously used areas prior to construction (Peaden et al. 2017). Fences can also have direct consequences to animals as previously observed along the exclusion fencing near the campground (on the OIR study site), where dead snakes were observed likely dying due to overheating while trying to navigate this feature (Eye et. al. 2018). Ensuring a complex habitat mosaic along these structures should be considered during the planning and construction phases of establishing new exclusion fencing. The addition of complex vegetation and rock cover provides an important mosaic of different thermal opportunities along these structures (Croak et al. 2010). Secondly, it ensures snakes would have access to important habitats for basking, shedding and mating. Lastly, the addition of cover habitat would increase habitat opportunities for small mammals and other species, increasing the hunting opportunities for snakes while navigating exclusion fencing.

2) Continue long-term population monitoring and research on OIR

The Nk'Mip Snake Program is one of the longest running research programs of its kind in western Canada. But, their relatively small sizes, cryptic nature, often irregular distribution and predominantly nocturnal behaviour makes studying snakes challenging and obtaining long-term population data difficult (Maida et al. in 2018). Long-term data accumulation and research is a crucial component to develop insightful conservation plans for long-lived species-at-risk (Blouin-Demers et al. 2002; Schneider et al. 2018). The OIR study site also contains a unique situation of a drastic landscape gradient from highly disturbed and fragmented with high human use to near-pristine with limited human influence on the landscape. Furthermore, the OIR study site provides the opportunity to monitor the rattlesnake population as development and human involvement (likely) continues to increase in many areas. Considering habitat loss and fragmentation accounts for one of the main threats to rattlesnakes in B.C., this makes the Nk'Mip program very valuable for rattlesnake conservation moving forward. Furthermore, the OIR study site contains two other at-risk snake species: the Great Basin Gopher Snake (*Pituophis catenifer deserticola*) and the Western Yellow-bellied Racer (*Coluber contrictor*) providing a great opportunity to determine important baseline demographic assessments for these species as well as species' niche partitioning and comparing influences of disturbance on these three meso-predator snakes.

KNOWLEDGE GAPS AND FUTURE RESEARCH CONSIDERATIONS

1) Fine-scale behavioural and physiological assessment of fencing

The scale of my data collection and analysis did not allow me to assess the fine-scale movements of rattlesnakes directly associated with responding to the fencing barriers. Therefore, an important next step is investigating how rattlesnakes respond and behave when they are directly trying to navigate a fencing barrier. Comparing and contrasting fine-scale behaviour as well as physiological impacts such as stress hormones and body temperatures on individuals navigating fencing will help lead to more effective implementations of these structures. Considering the results of my thesis, it is clear that fencing alters rattlesnake movement and behaviour.

2) Long term spatial and behavioural assessment of individuals along fencing

Adult rattlesnakes do not appear to have the behavioural plasticity to redistribute themselves on the landscape (Waldron et al. 2013). My results outline a short term behavioural response to encountering fencing during rattlesnake spring movements. Investigating the long term (annual) spatial and behavioural movements of individual snakes coming into contact with this fencing would be insightful. Understanding how migratory and spatial behaviour potentially changes (or remains static) over time in response to fencing and other influences or on the landscape would be beneficial to conservation and management techniques of this species.

3) Rattlesnake ecology in different land-use types

Urban development and agriculture are two primary land-use disturbances on the landscape in the Okanagan Valley. Specifically, wineries and vineyards account for approximately 4,000 ha of the valley bottoms of the Okanagan Valley (not including orchards), and there are approximately 30 golf courses between Osoyoos and Vernon (approximately 140 km). Vineyards, orchards and golf courses have become three common land-use types that rattlesnakes either move through or remain in throughout their entire active season, however previous information on this animal in these land use-types are lacking. Detailed and targeted ecological information on rattlesnakes in these areas will help promote improved conservation strategies for these snakes and will likely enhance both snake and human safety.

4) Hibernaculum proximity to disturbance

My results indicated that individual snakes travelling shorter distances to disturbance were smaller (SVL) than individual snakes that travel further to disturbance or didn’t encounter disturbance at all on the OIR. Previously, Lomas (2013) observed that snakes frequenting undisturbed areas appeared larger than rattlesnakes in various disturbance intensities on the same OIR study site. Both of these examples suggest that disturbance appears to consistently affect rattlesnake size, and the proximity of hibernacula in regards to disturbance may have a large impact on individuals within that community. Assessing the influence that proximity to disturbance has on individual hibernacula communities may assist with targeted management approaches and priorities.

5) Ecological drivers of movement/migration in rattlesnakes in B.C.

As described previously in this thesis, a number of factors have been hypothesized to drive rattlesnake movement in temperate regions (Bauder et al. 2015; Harvey 2015; Duvall et al. 1997). Previous studies suggest Prairie Rattlesnake (*Crotalus viridis viridis*) vernal (spring) movement is dedicated to finding food (Duvall et al. 1990) based on a food supplementation experiment. Whereas, water supplementation does not seem to influence Western Rattlesnake spatial ecology in the southern limits of the species' range (California - Capehart et al. 2016). Individuals in some hibernacula populations in B.C. show different migration and home range characteristics than individuals on the OIR study site. Within the valley bottoms, individuals in the OIR study site typically establish identifiable summer home ranges (Lomas et al. in press). Conversely, in other areas of B.C., rattlesnakes embark on a directional outward migration from their hibernaculum, reach an identifiable "turnaround" point, and then return back to the hibernaculum (Gomez et al. 2015; Harvey 2015). Identifying the motivations for rattlesnake movement in B.C. can lead to the discovery of this varying phenomena and improve managing for those potential ecological drivers on disturbed and fragmented landscapes.

6) "Mountain snakes"

Rattlesnakes are associated with both the dry, arid valley bottoms and also higher elevation forests throughout their range in southern B.C. (Lomas 2013; Gomez et al. 2015; Harvey 2015). Individuals moving from their hibernaculum into higher elevations typically move further distances on average than individuals moving into the valley bottoms (Lomas 2013; Gomez et al. 2015; Harvey 2015), and "mountain" snakes on the OIR study site grow larger and exhibit higher body conditions than valley individuals (Lomas 2013). However, intensive radio-telemetry and mark-recapture has been limited on these individuals mainly due to logistical and accessibility hurdles. Rattlesnake moving into the higher elevations appear to consist of a large portion of the OIR population (For example six of 15 telemetry rattlesnakes in 2015 moved into the mountains). Based on differences in landscape and vegetation structures, prey composition (Larsen personal communications) and thermal properties, these individuals likely have drastically different experiences throughout the summer active season than snakes in the arid valley bottoms. However, the "mountain" segment of the OIR rattlesnake population has not been investigated other than to define their migration direction in research-based initiatives.

CONCLUSION

Spring migration is an important aspect of snake ecology in temperate regions, and my results are the first to provide baseline information on spring migration patterns and behaviour of Western Rattlesnakes. However, like many other migratory species (large or small), landscape disturbance and barriers appear to be restricting natural spring migration behaviour in rattlesnakes on the OIR study site.

For a species with a slow life history, elevated adult survival is crucial for the viability of this species. Adult Western Rattlesnakes likely do not have the behavioural plasticity to respond to disturbance and anthropogenic threats by redistributing themselves on the landscape (Waldron et al. 2013). Therefore, barrier fencing is crucial for reducing adult mortality due to these anthropogenic threats (i.e., roads, urban communities, etc.). My thesis can act as an important point of reference for managers to consider when implementing mitigative barrier fencing for snakes or other reptile species moving forward, as it is clear that these fencing structures are not without impact to individuals. Moving forward, special attention must be given to understanding the trade-offs fencing has on individuals to ensure long-term efficacy of these important structures. Overall, the results, conclusion and recommendations moving forward outlined in this thesis can help contribute to more thoughtful and meaningful conservation and management strategies for this species and help promote a healthy coexistence between rattlesnakes and humans in B.C.

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