

**DIRECT AND INDIRECT EFFECTS OF ROADS ON A COMMUNITY OF THREATENED  
SNAKE SPECIES**

*by*

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## ABSTRACT

Expanding road networks pose a significant threat to wildlife, both through direct mortality and habitat fragmentation. These effects especially are pronounced in reptiles, that globally are among the most road-vulnerable vertebrates. In particular, snakes are increasingly at risk due to their movement patterns and small body size that make them ill-suited to coping with fragmented landscapes and the risk of road mortality. Many snake species exhibit high site fidelity, undergo seasonal migrations between overwintering and foraging habitats, and rely on environmental thermal gradients to regulate key physiological functions. At northern latitudes, these pressures are further amplified by shorter active seasons, and life history characteristics such as delayed sexual maturity, infrequent reproduction, and high adult survival, that together reduce capacity for demographic recovery following anthropogenic disturbance.

This thesis evaluates the mitigative effect of ecopassage installation on snake mortality and population persistence within a multi-species community of threatened snakes along two roads in the White Lake Basin, British Columbia, Canada; an otherwise minimally disturbed grassland ecosystem. Using a 10-year mark-recapture dataset of Western Rattlesnakes (*Crotalus oreganus*), paired with road surveys and traffic monitoring, I modelled population trends and estimated road mortality rates before and after mitigation. I recorded a significant reduction in road mortality rates post-installation ( $0.029 \pm 0.012$  SD deaths/km/day; 2018-2024), relative to pre-installation rates ( $0.052 \pm 0.012$  SD deaths/km/day; 2015-2017). Despite this reduction, I observed no evidence of population recovery across the study period which I suggest is a result of the adverse indirect effects of roads, and/or the ongoing habituation to the ecopassages on the landscape.

In addition, to better understand the behavioural mechanisms underlying road interactions, from 2023-2024 I conducted a radiotelemetry study on three snake species inhabiting the same community: the Western Rattlesnake, Great Basin Gopher Snake (*Pituophis catenifer deserticola*), and Western Yellow-bellied Racer (*Coluber constrictor mormon*). Seasonal movement patterns were compared to null model simulations to assess road avoidance behaviour. All three species exhibited significantly fewer road crossings than expected under null models, indicating an avoidance of roads. These patterns suggest that roads do function as partial barriers to movement, reducing access to critical resources, and limiting available habitat.

This study highlights that even minimal disturbance to a landscape can greatly alter the movement patterns of snake species, and that while ecopassages may work to reduce direct mortality, road effects are more complex and should prompt a broader approach to mitigation. This work contributes rare long-term data on northern snake populations and calls for an integrative approach to road ecology that addresses both the direct and indirect impacts of roads on movement and survival, to best protect the future persistence of this snake community.

**Keywords:** Western Rattlesnake, Great Basin Gopher snake, Western Yellow-bellied Racer, road ecology, road mortality, movement ecology, mitigation, conservation

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**NOTE:** In Chapters 2 and 3 of this thesis, I have chosen to use plural pronouns to align with journal publication conventions and to recognize the contributions of all those listed above who contributed to this project.

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## Chapter 1

### INTRODUCTION

#### HUMAN – WILDLIFE CONFLICT

As the world experiences an increasing human population, and development fragmenting much of the intact natural habitat, negative interactions (i.e., conflict) between humans and wildlife are becoming increasingly concerning. While some species have shown the ability to live alongside humans (i.e., synanthropic species), those unable to adapt (i.e., exoanthropic species) face continuous threats from urbanization (Guetté et al. 2017). Regardless of adaptability, human expansion has led to numerous negative environmental changes that profoundly impact both the population persistence and/or individual behaviours of wildlife species (Soulsbury and White 2015). Beyond simply reducing the area where species can live, human-driven stressors such as climate change, habitat fragmentation, food depletion, disturbance, and pollution have additional adverse effects throughout the natural world (Grimm et al. 2008). The impacts of these stressors have been shown to cause direct mortality (Hill et al. 2019), shift migration patterns (Maida et al. 2020, Cooke et al. 2024), inhibit reproductive successes (Vandersteen et al. 2020), and decrease genetic diversity (Epps et al. 2005, Schmidt et al. 2020a) for wildlife species worldwide.

In Canada, federal legislation aims to protect species and limit human-wildlife conflict, particularly for at-risk species (*Species at Risk Act* 2002). Similarly, conservation efforts increasingly are focused on strategies to minimize conflict and promote coexistence using tools such as wildlife corridors, urban green spaces and community-based conservation programs (Soulsbury and White 2015). Despite these initiatives, the human ecological footprint continues to expand into previously undisturbed habitats, presenting wildlife species with novel stressors and increasing threats to biodiversity.

One of the most widespread drivers of human-wildlife conflict is the expansion of the global road network that exerts substantial pressure on surrounding ecosystems (Forman and Alexander 1998, Shepard et al. 2008). While road networks play an important part of socio-economic development by improving access to resources and enhancing global connectivity, they also have direct and non-direct impacts on intact natural habitats (Amador-Jimenez and Willis 2012). New road projects fragment previously undisturbed habitat, and the upgrading of roads to

accommodate more vehicles further reduces the rate of successful wildlife crossings (Andrews and Gibbons 2005, Robson and Blouin-Demers 2013, Gonçalves et al. 2018, Loraamm et al. 2021). Roads not only restructure landscapes but also increase the risk of wildlife mortality and alter animal movement patterns, creating significant challenges for conservation.

### **EFFECTS OF ROADS ON WILDLIFE**

Broadly, roads can negatively affect wildlife in several ways: (1) through direct mortality, (2) through indirect mechanisms such as habitat fragmentation (that prevents movement), and (3) animal avoidance of nearby habitat due to lack of available cover, or increased anthropogenic presence (Forman & Alexander, 1998). The latter two categories functionally act in a similar manner, generally being referred to as the ‘barrier effect’, where animals movement and usage of habitat is diminished by features on the landscape (Bennett 2017). While most species are susceptible to some level of barrier effect, the severity varies depending on species-specific behavioural responses and road characteristics such as width, traffic volume, and vehicle speed (Forman and Alexander 1998, Tipton et al. 2023). Even when roads are not fully impermeable, they can selectively filter movement based on demographic traits, thereby changing population structure, reducing genetic diversity (Clark et al. 2010) and amplifying long-term adverse impacts (Andrews and Gibbons 2005, Tipton et al. 2023).

The direct impacts of road mortality are easier to study as carcasses present a quantifiable way to measure effect (Row et al. 2007, Winton et al. 2020, Anđelković and Bogdanović 2022). In contrast, the indirect effects of roads (those related to habitat fragmentation and behavioural changes) are more difficult to quantify but may pose an equally serious threat to species persistence. For example, Eastern Hognose snakes (*Heterodon platirhinos*) avoid crossing paved but not unpaved roads, limiting resource access and available habitat (Robson and Blouin-Demers 2013). North American Elk (*Cervus elaphus canadensis*) alter the timing of their natural movements, crossing roads less frequently during periods of high traffic (Loraamm et al. 2021). In freshwater turtles, nesting adult females are disproportionately found near roads, thus increasing mortality risk and creating a sex-biased population (Aresco 2005). Furthermore, simulated traffic noise alone reduces abundance in bird communities, with some species exhibiting complete avoidance (McClure et al. 2013).

## MITIGATION

Solutions to reduce direct mortality from vehicle strikes and to mitigate the barrier effects of roads are increasingly being incorporated into the planning of new and existing transportation systems. Mitigation of this nature can be split into two categories: strategies that attempt to modify human behaviour (warning signs, lower speed limits) and strategies that attempt to modify animal behaviour (fencing, crossing structures; Forman et al. 2003). Among these, wildlife crossing structures paired with directional fencing are perhaps the most effective and widely recognized solution (Rytwinski et al. 2016). Designed to strategically guide animals across roads without the risk of a vehicle strike, these structures connect previously fragmented habitat by providing a path over or under roads. Globally, transportation agencies are increasingly receptive to incorporating wildlife crossing structures to address safety and ecological needs, as strong evidence of structure use for a variety of taxa has been documented (Berthinussen and Altringham 2012, Soanes et al. 2013, Sawaya et al. 2014, Colley et al. 2017, Boyle et al. 2021). One of the most notable Canadian success stories is found in Banff National Park (Canada), where a complex of six overpasses, 38 underpasses (hereafter referred to as ‘ecopassages’), and 82 km of directional fencing has reduced wildlife-vehicle collisions by more than 80% while maintaining landscape connectivity (Clevenger et al. 2001). However, despite some successes, and numerous recommendations for the use of crossing structures, published literature largely is failing to demonstrate the effectiveness of such tools for maintaining landscape connectivity.

A global review by Soanes et al. (2024) assessing crossing structures and their ability to mitigate road barrier effects found that most studies were qualitative or narrative in nature. Of 313 studies that collected quantitative data, only 7.6% ( $n = 24$ ) evaluated the effects of crossing structures on movement relative to an unmitigated road (Soane et al. 2024). Most commonly, studies only assessed whether crossing structures facilitated the movement of wildlife with no comparison to pre-structure crossing rates, overall population trends or mortality. In addition to this, most studies monitored for two or fewer years post-installation, during which habituation to structures likely was occurring (Gagnon et al. 2011, Soanes et al. 2013, Spruyt 2024). All told, there is need for long-term, standardized monitoring that includes appropriate benchmarks to fully understand the effectiveness of this mitigation measure over time and across diverse ecological contexts (Rytwinski et al. 2016, Soanes et al. 2024).

In addition to a lack of monitoring, road-crossing research often is biased toward large-bodied animals, due in some extent to the increased risk posed to human safety. Far fewer studies have examined the effectiveness of mitigation on smaller taxa where the risk to human safety is lessened (Soanes et al. 2024). Slow-moving species show the greatest risk of collision, often compounded by these taxa having antipredator adaptations that further reduce the probability of a successful crossing (Andrews and Gibbons 2005, Jacobson et al. 2016). Species that migrate seasonally or maintain large home ranges have an increased likelihood experiencing barrier effects (Seidler et al. 2015), while small bodied or crepuscular species experience higher mortality rates from vehicles due to reduced visibility and low light movement times (Teixeira et al. 2013, Bliss-Ketchum et al. 2016). These patterns of susceptibility are especially pronounced in reptiles, and snakes in particular, where body size, movement behaviours (Andrews and Gibbons 2005), physiological traits (Mccardle and Fontenot 2016), and poor public perception leading to intentional killings (Soulsbury and White 2015) amplify the vulnerability to road impacts.

## **SNAKES AND ROADS**

Snake populations are declining globally, due in part to the adverse effects of roads (Reading et al. 2010, Böhm et al. 2013). In northern latitudes, where yearly temperatures fluctuate more, snake populations may be particularly vulnerable to these structures because of a shortened active season, that restricts available time for foraging, mating, and finding suitable overwintering sites (Macartney 1985). Furthermore, the life history strategies of many northern snakes include delayed sexual maturity, high adult survival, and infrequent reproduction (Macartney et al. 1990, Maida et al. 2018), that limit the ability to adapt rapidly to selection pressures imposed by habitat fragmentation (Waldron et al. 2013).

In Canada, snakes exhibit strong site fidelity to specific habitats throughout their annual cycle (Eye 2015, Gomez et al. 2015, Howarth et al. 2023). Fidelity to summer foraging sites likely allows for consistent year-to-year resource availability (Waldron et al. 2013), while fidelity to overwintering sites may result from a scarcity of habitat that provides the thermal requirements for survival (Gregory 1984). The mechanisms behind fidelity in snakes has been attributed to cognitive memory and/or the use of chemosensory trails to properly spatially orient themselves across the landscape (Ford 1986, Holtzman et al. 1999, Gomez et al. 2015). But when

anthropogenic disturbances create novel barriers, movement patterns may be altered substantially, and population viability may be compromised if it cannot respond appropriately (Waldron et al. 2013, Maida et al. 2020).

As one of the major threats to snake populations, the direct and indirect effects of roads have been well documented (Böhm et al. 2013). Road mortality has been shown to have population-level consequences for multiple species (Row et al. 2007, Winton et al. 2020, Anđelković and Bogdanović 2022), while behavioural avoidance of roads can have energetic, physiological and genetic implications on species (Robson and Blouin-Demers 2013, Siers et al. 2014, Paterson et al. 2019). Attempts to mitigate road effects on snake populations have had mixed results, with only one study finding significant decreases in snake mortality attributed to ecopassages and directional fencing (Colley et al. 2017). Conversely, others have shown limited success or even an increase in mortality because of improper design and installation (Baxter-Gilbert et al. 2015, Markle et al. 2017). There are many accounts documenting the widespread occurrence of snake road mortality, most all of which suggest ecopassages as a mitigation strategy (Shepard et al. 2008a, Choquette and Valliant 2016, Gonçalves et al. 2018, Anđelković and Bogdanović 2022). However, with so few studies properly monitoring the effectiveness of this mitigation measure, and even fewer showing positive results, there is a profound knowledge gap as to whether ecopassages are an effective tool

## **HISTORY OF THE THESIS STUDY SITE**

In October 2024, the White Lake Snake Research Program completed a decade of research focused primarily on road mortality mitigation of Western Rattlesnakes (*Crotalus oreganus*) in south-central British Columbia, Canada. This 10-year project has been accomplished through the work of various graduate students and research technicians, including the author of this thesis. In 2015, the White Lake Basin was identified as a spatial ‘hotspot’ for snake road mortality, and an initial population and roadkill assessment was conducted by Winton et al. (2020). More specifically, their study quantified rattlesnake road mortality in conjunction with a population estimate and assessed the long-term persistence probability of the population under the additive threat imposed by direct road mortality. They estimated a yearly population mortality rate of ~6.6%. A subsequent population viability analysis (PVA) revealed that under that rate, the population would decrease by ~97% within 100 years and any increase in mortality, would likely

hasten population extirpation (Winton et al. 2020). This pre-mitigative work resulted in the installation of eight wildlife ecopassages within the basin during a scheduled re-paving of both roads. Four ecopassages were newly installed at identified mortality hotspots (Winton 2017), while modifications were made to four pre-existing drainage culverts making them suitable for wildlife. In 2019, to investigate the preliminary use of the ecopassages, Spruyt (2024) installed wildlife cameras at both entrances of each ecopassage in addition to the continuation of the long-term population and road mortality study. That same year, drift fencing was added haphazardly to some entrances of the ecopassages to increase the likelihood of snake usage, resulting in a total of 0.4 km of fencing of the 23 km available (combining both lengths from both directions of traffic flow).

In Chapter 2 of this thesis, I complete this long-term project by adding the data I personally collected (2022-2024) to the long-term database established by Winton (2015-2016) and maintained by Spruyt (2019-2020). Standardized mark-recapture surveys were conducted regularly during the egress and ingress periods of each year, paired with consistent road surveys throughout the entire season. Figure 1.1 provides a visual timeline of historical works and the primary researchers throughout the study. As part of my thesis, the scope of the project was increased in 2023 to include both the Great Basin Gopher snake (*Pituophis catenifer deserticola*) and the Western Yellow-bellied Racer (*Coluber constrictor mormon*), two other threatened species living in the same community as the Western Rattlesnake (see below). During the 2023 and 2024 active seasons, individuals of all three species were equipped with radio transmitters to monitor their seasonal movement patterns with a specific focus on movement near roads.

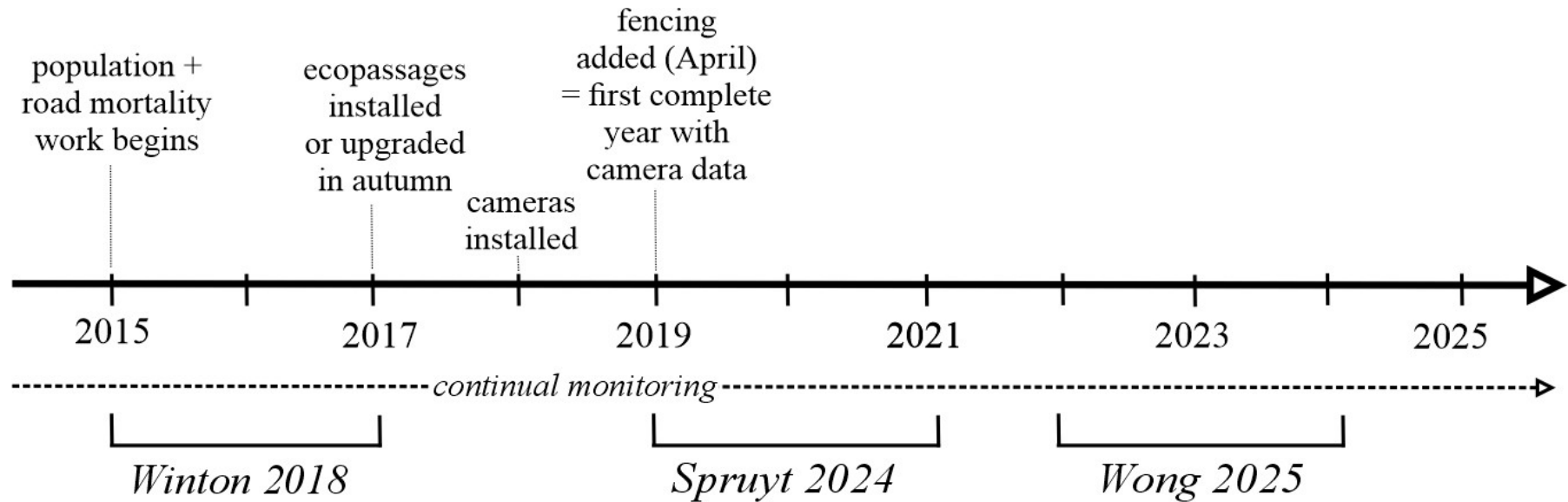


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## STUDY SPECIES

The subjects of my studies were the Western Rattlesnake, the Great Basin Gopher snake, and the Western Yellow-bellied Racer (Figure 1.2). Currently, all three species are listed federally as ‘Threatened’ under the Species at Risk Act (COSEWIC 2013, 2015a, 2015b) as well as provincially ‘Blue-listed’ in British Columbia (B.C. Conservation Data Centre 2018a, 2018b, 2018c). Listing of these species is due in part to their small area of occurrence at their coincidental northern ranges (Figure 1.3) but primarily because of threats to the extant populations. The major threats to all three species are similar, including road mortality, habitat fragmentation, habitat loss due to land conversion, and direct/indirect persecution (COSEWIC 2013, 2015a, 2015b). With much of these species’ populations residing near Canada’s southern border (Statistics Canada 2020), and the increased urbanization in the same area (Statistics Canada 2023), all three species have seen population declines across their ranges within British Columbia (COSEWIC 2013, 2015a, 2015b).

Within my study area, I have observed that these species are active on this landscape from approximately mid-April to October following spring emergence (‘egress’) from hibernacula. Gopher snakes and racers are known to hibernate communally in rocky outcrops, and solitarily in deep talus or animal burrows (COSEWIC 2015b, Williams et al. 2015), while rattlesnakes exclusively hibernate in communal rocky outcrop dens (Gienger and Beck 2011). During the active seasons, all three species travel various distances to their summer habitats, where much of the time presumably is spent foraging and searching for mates. Rattlesnake and gopher snakes’ diet consists primarily of small mammals and birds (Reinert et al. 1984, White 2008), while racers are near exclusive insectivores, (Fitch 1963, Shewchuk and Austin 2001). Following the active season, I have observed individuals of all three species return to hibernacula (‘ingress’) from late August to October and overwinter until March of the following year.

Fidelity to overwintering sites is a trait thought to be common to all three species (Brown and Parker 1976, Parker and Brown 1980, Macartney 1985), though gopher snake populations across regions within the British Columbia have shown some variation (Williams et al. 2012). After leaving their hibernacula, rattlesnakes will undertake annual migrations of up to 3 km towards and into their summer foraging habitat (Gomez et al. 2015, Lomas et al. 2019, Maida et al. 2020). Males (1 – 4 km) move significantly farther from overwinter sites than both juveniles (0.2

– 0.3 km; Gomez et al. 2015, Howarth et al. 2023) and gravid females (Eye 2015), though movement patterns can vary across populations and even among individuals from within a hibernaculum (Gomez et al. 2015, Lomas et al. 2019, Harvey and Larsen 2020). Comparatively, little is known about the movement patterns of gopher snakes and racers at their northern extents. Northern adult populations of gopher snakes have shown some evidence of spring directional movements, though the scale at which varies (Bertram et al. 2001, White 2008). Movement of adult racers in a population from Utah have shown extreme variation in dispersal distance (0 – 1.6 km), and while year-to-year fidelity to forage sites and directional movements were shown for some individuals, population level trends were not discernible (Brown and Parker 1976). Within British Columbia, a study investigating the movement ecology of both species is currently nearing completion and is expected to provide further insights into these patterns (Ragsdale 2025).

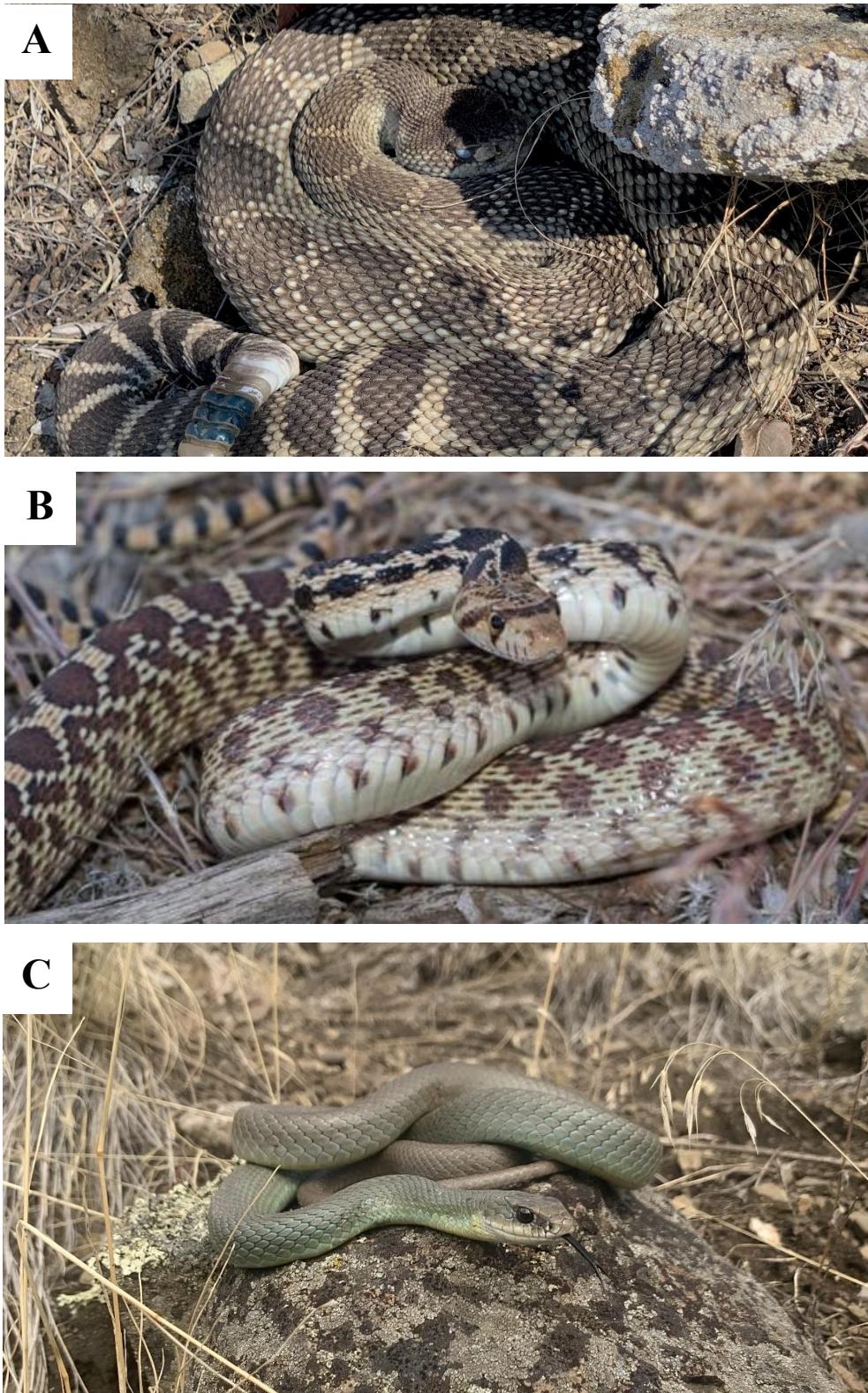
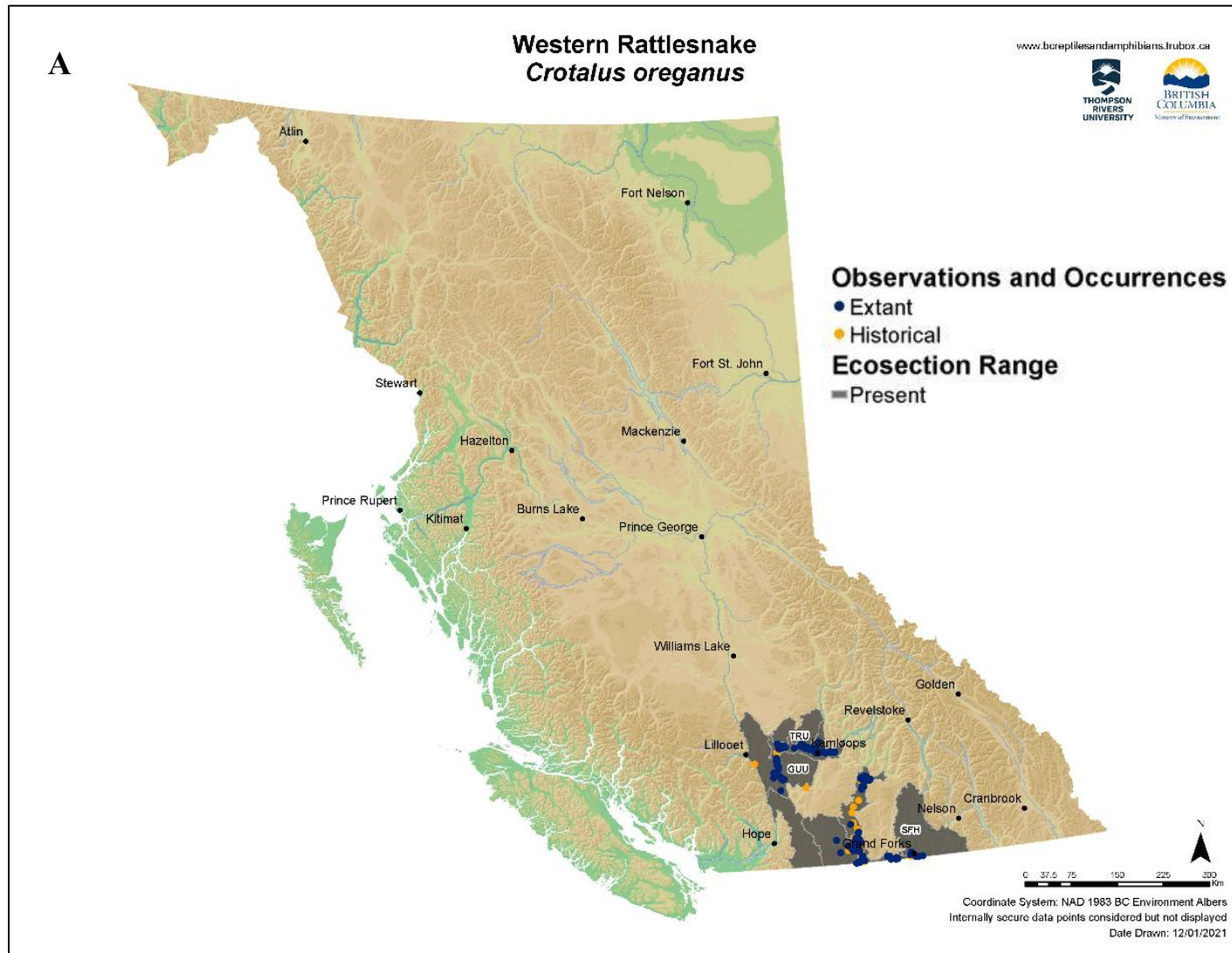
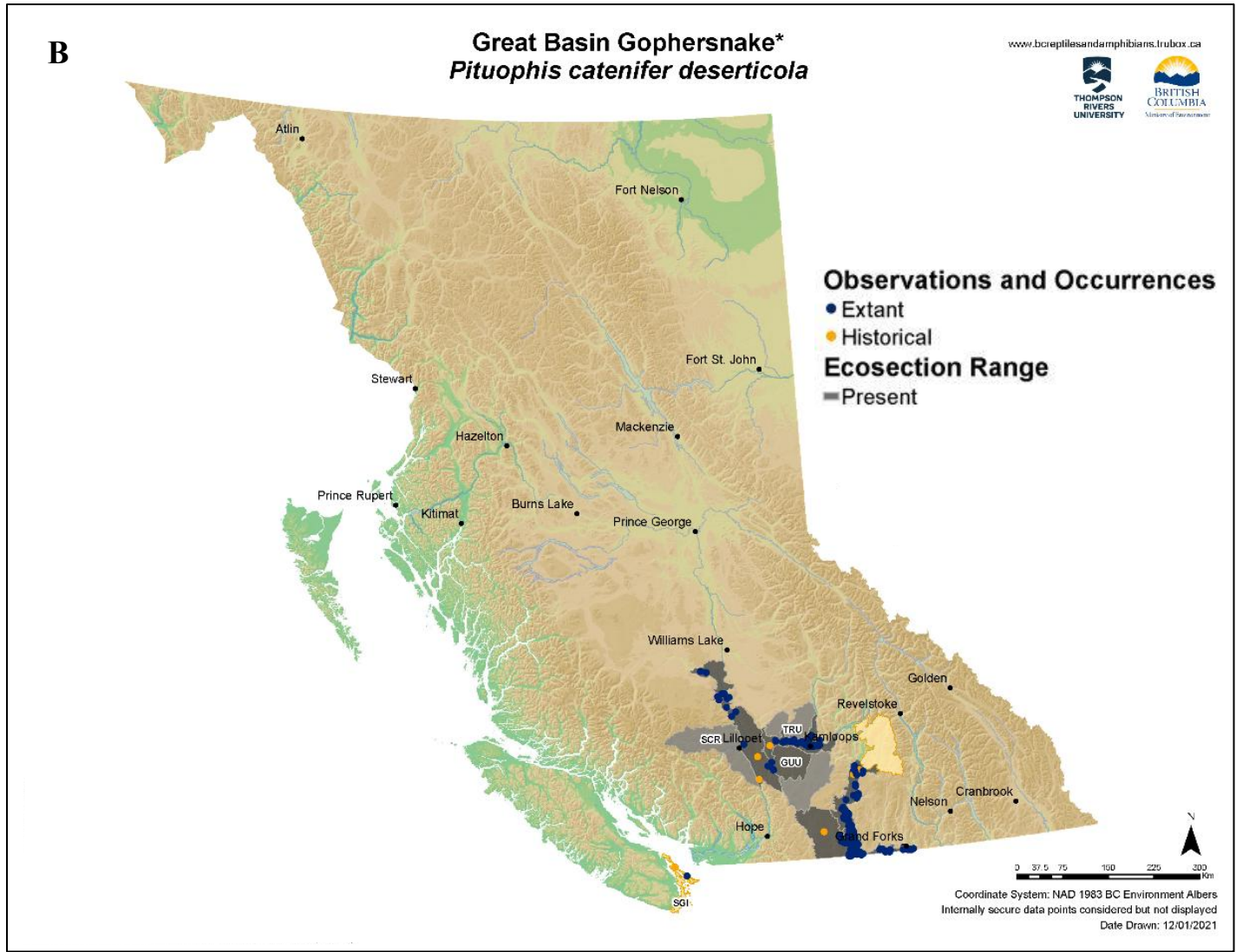


Figure 1.2. The three study species: A) Western Rattlesnake (*Crotalus oreganus*), B) Great Basin Gophersnake (*Pituophis catenifer deserticola*), and C) Western Yellow-bellied Racer (*Coluber constrictor mormon*). Photos by author.





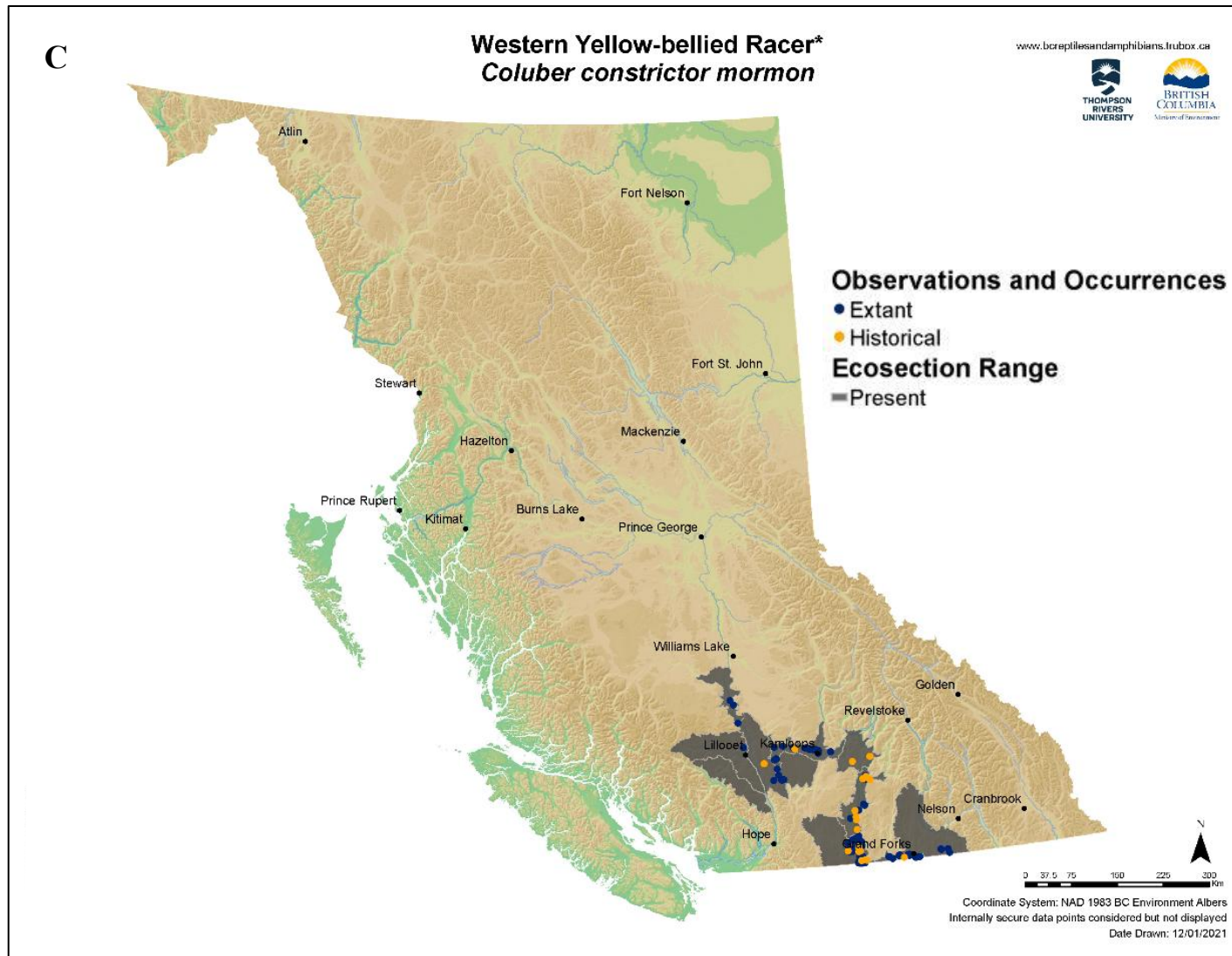


Figure 1.3. Extent of occurrence within British Columbia for A) Western Rattlesnake, B) Great Basin Gopher snake, and C) Western Yellow-Bellied Racer. Maps used with permission from the BC Reptiles & Amphibians website (<https://bcreptilesandamphibians.ca/>); accessed on June 23, 2025.

## STUDY SITE

The primary study site where work was conducted is in the White Lake Basin (latitude 49.318° N, longitude 119.638° W) in the South Okanagan region of British Columbia (Figure 1.4). The site lies on the traditional unceded territory of the Syilx Okanagan peoples, but under federal law, is owned and tenured by both the provincial and federal governments. Most of the area lies on National Research Council property, for use by the Dominion Radio Astrophysical Observatory (DRAO). To minimize radio signal interference, DRAO is surrounded by over 5,000 acres of undeveloped grassland (National Research Council Canada 2023). This area is subsequently leased and jointly managed in an innovative fashion by the Nature Trust of British Columbia and the Clifton ranch whereby cattle are rotated throughout the area to sustain the grassland and ranching industry while protecting over 30 species-at-risk and another 57 species of special concern (The Nature Trust of British Columbia 2021). A smaller provincial portion of the basin lies within the White Lake Grasslands Protected Area, a 9,301-acre conservation area, used primarily by residents and tourists for recreational activities (e.g. Hiking, cycling, horseback riding; B.C. Parks 2024). The ecosystem within the basin is characterized by agricultural ranch lands, rolling hills and steep bluffs. While BC's biogeoclimatic classification system has the area categorized as a Ponderosa Pine (*Pinus ponderosa*) ecosystem (Meidinger and Pojar 1991), it is a predominantly open shrub-steppe grassland. The dominant vegetation in the grassland area includes Bluebunch Wheatgrass (*Agropyron spicatum*), Big Sagebrush (*Artemisia tridentata*), and the non-native Cheatgrass (*Bromus tectorum*), while the elevated forested area is dominated by Ponderosa Pine and Douglas Fir (*Pseudotsuga menziesii*; Meidinger and Pojar 1991)

Running through the valley bottom of the White Lake Basin are two paved, undivided, two-lane roads that bisect the valley floor (Figure 1.5). White Lake Road primarily runs East-West, while Willowbrook Road primarily runs North-South, meeting at a "T" intersection in the middle of the basin. There is an unposted speed limit of 80 km/h on each of the roads, although, I have observed that local residents are known to drive notably faster than 80 km/h. Traffic through the White Lake Basin is typically at its highest during the summer months with tourism and recreation adding to the traffic volumes of local residential vehicles using the roads.

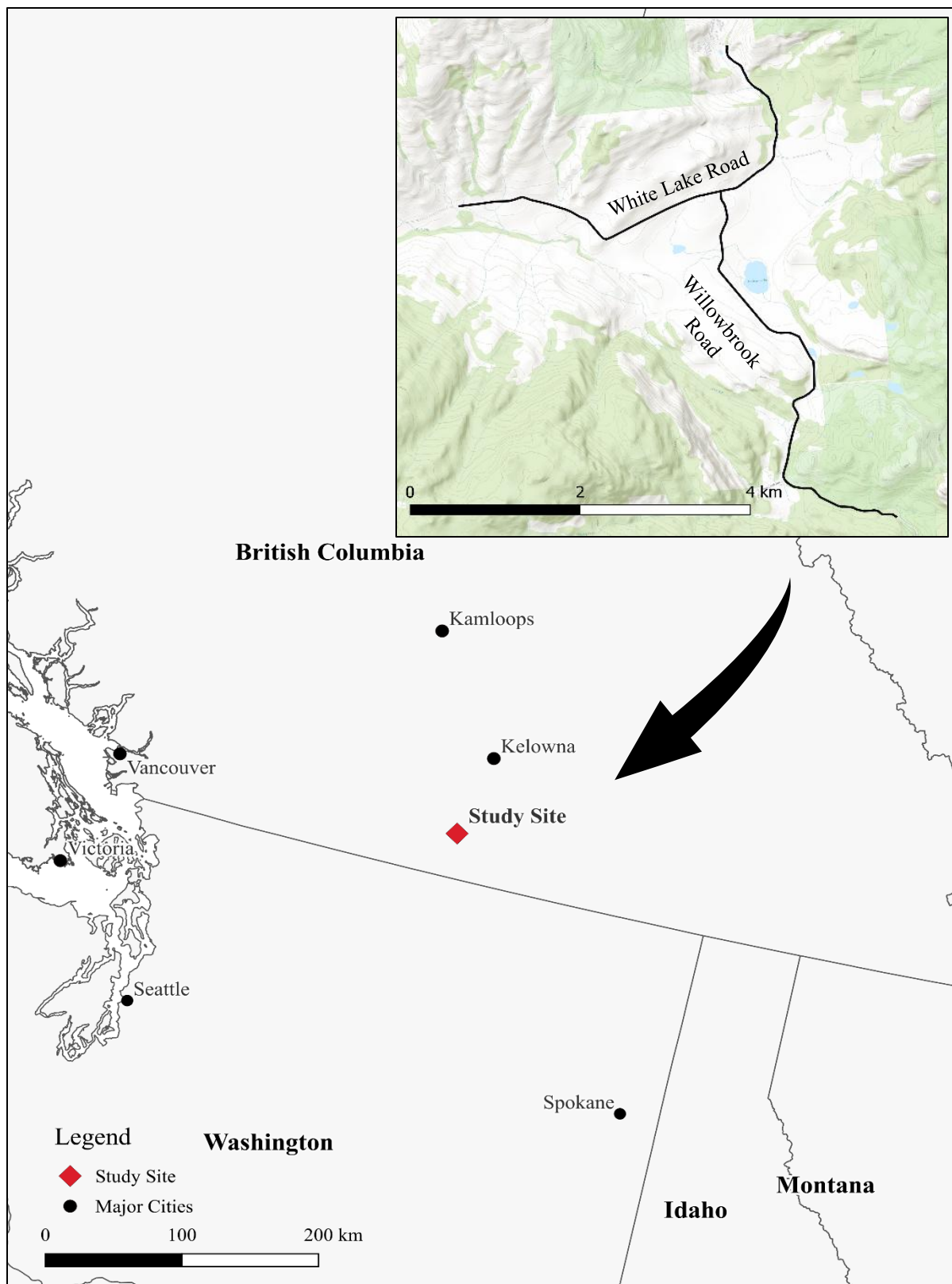


Figure 1.4. Study site location within the South Okanagan region of British Columbia, Canada. Black lines within the inset map denote the surveyed sections of both roads.

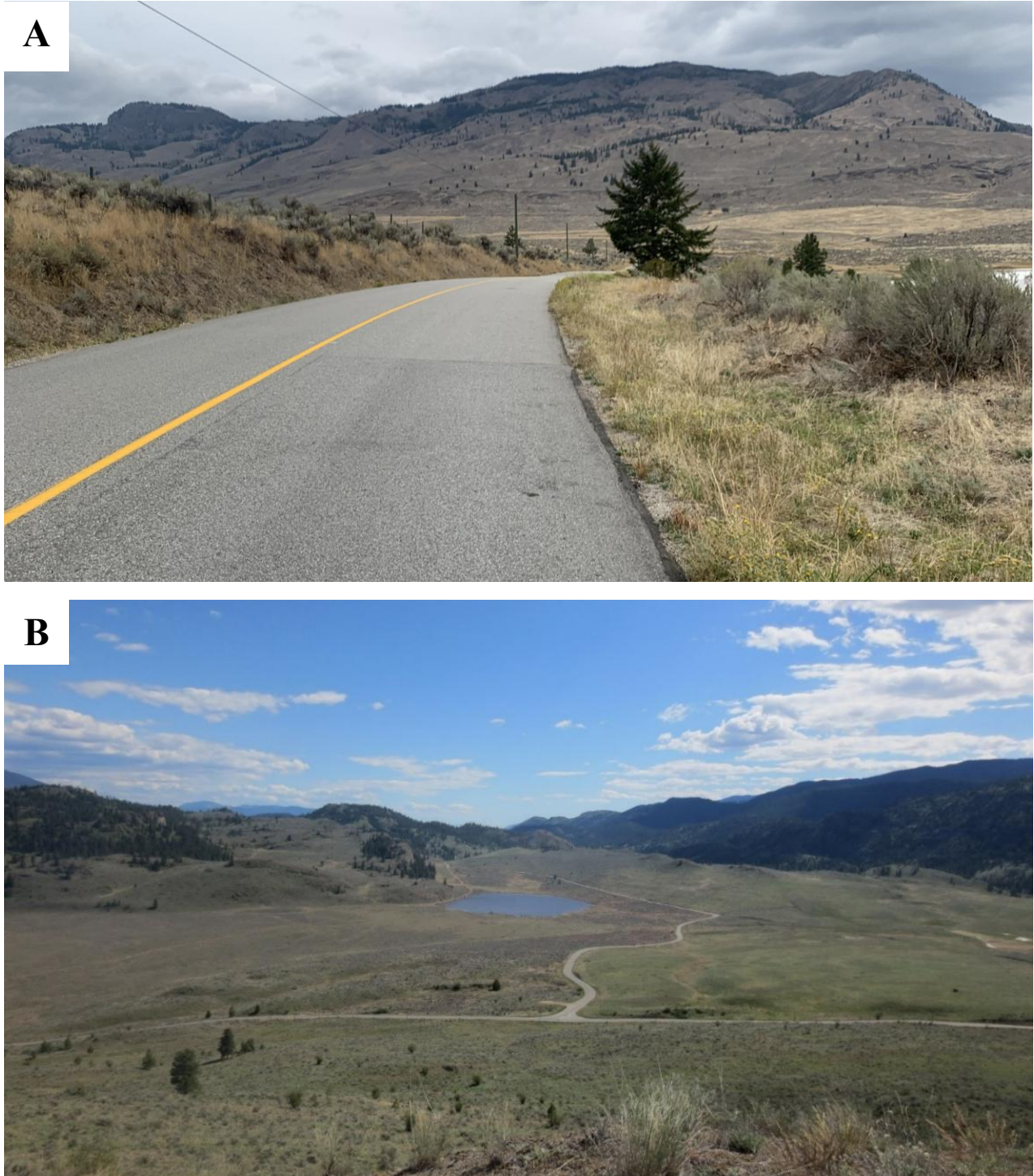


Figure 1.5. A) A representative section of the paved, two-lane road that traverses the White Lake Basin in south-central BC, and (B) the configuration of the two roads within the Basin (facing south). White Lake Road runs horizontally across this photo, while Willowbrook Road runs vertically. Photos by author.

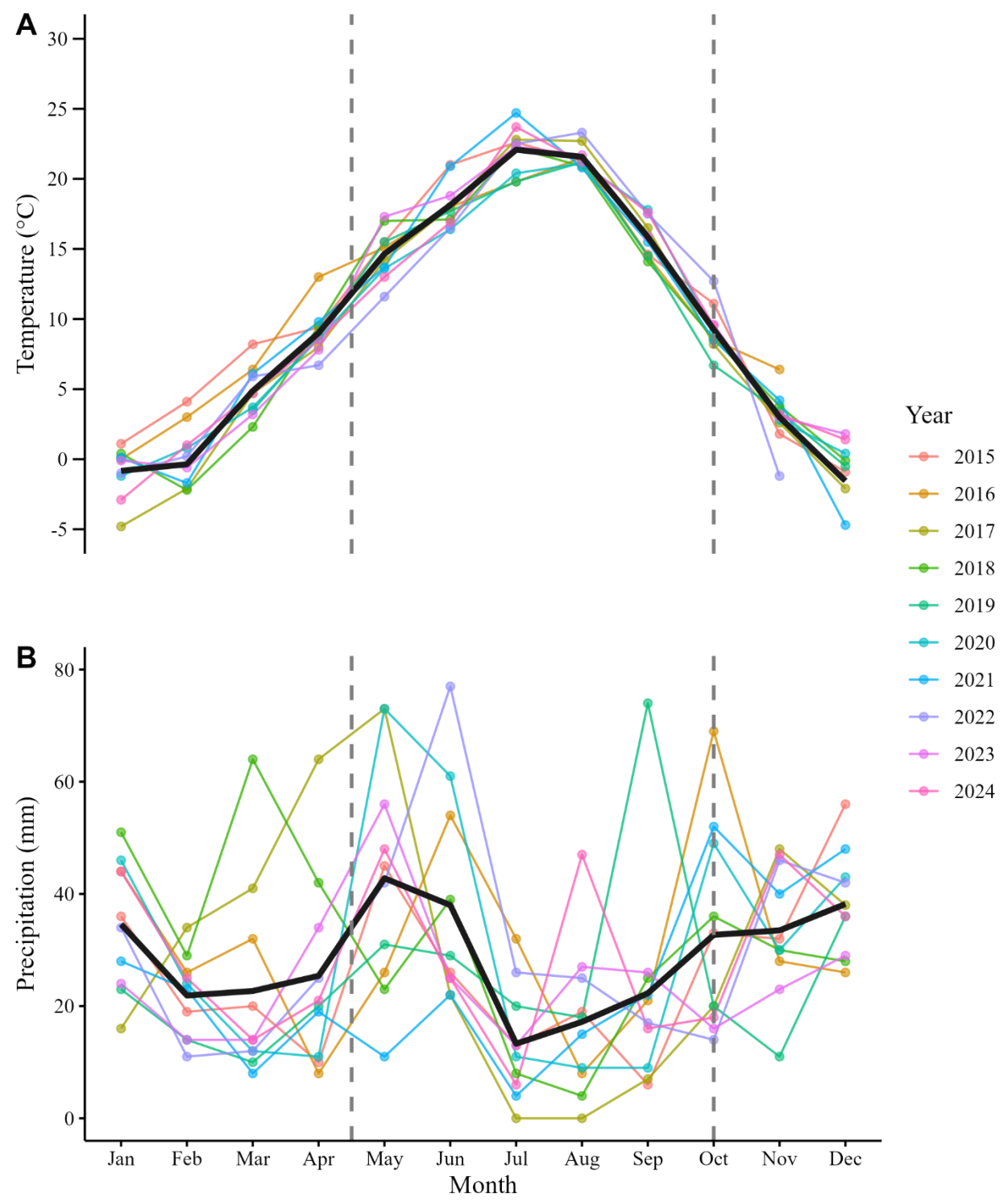


Figure 1.6. A) Mean monthly temperature (°C) and B) total monthly precipitation (mm) in the White Lake Basin (49.316°N, 119.640°W) during the study years (2015 – 2023). Black lines denote mean values across all years. Data retrieved from Climate BC.

## THESIS OBJECTIVES

The overarching goals of my thesis were to (1) document the response of the White Lake rattlesnake population to the creation of under-road ecopassages as an effective tool in reducing road mortality, and (2) compare the interspecies implications of roads on seasonal movement patterns.

My specific goals were as follows:

In Chapter 2, I use the recently completed, long-term database to:

- a. Quantify change in Western Rattlesnake road mortality since 2015 and determine if the 2017 installation of ecopassages have been noticeably effective in reducing road mortality.
- b. Pair road mortality observations with population abundance estimates to determine the role of ecopassages on population recovery.
- c. Provide a comprehensive assessment of the impacts of direct road mortality on snakes to date.

In Chapter 3, I present a rare, coincidental movement study of the three at-risk snake species. While comparative movement studies between species are not uncommon, few exist where movements are tracked in the same location at the same time. This removes extraneous spatial and temporal variables, allowing for a more precise and accurate measure of movement and road avoidance. To that end the specific objectives in this chapter were to:

- d. Quantify differences in seasonal movement patterns between the three species.
- e. Assess the barrier effect of roads on movement patterns, i.e. do roads act as a barrier to movement?
- f. Ask whether the effect size is equal across the three species?

Lastly, in Chapter 4, I summarize my findings, identify knowledge gaps, and make management recommendations relevant to snake mitigation and research within the context of conservation biology.

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## Chapter 2

### **A 10-YEAR EVALUATION OF ROAD ECOPASSAGES AS AN EFFECTIVE MITIGATION TOOL FOR A POPULATION OF WESTERN RATTLESNAKES (*CROTALUS OREGANUS*)**

#### **INTRODUCTION**

Roads pose a significant threat to the persistence of many vertebrate populations (Choquette & Valliant, 2016; Winton et al., 2020), with adverse impacts far extending the physical space occupied by the roads themselves (Laurance and Balmford 2013, Ibisch et al. 2016). While transportation infrastructure enhances connectivity between humans, the inverse often is true for natural habitats and wildlife populations (Roedenbeck et al., 2007).

As an identified mitigation measure, wildlife-crossing structures (herein referred to as ecopassages) are becoming an increasingly common tool to improve landscape connectivity and mitigate road mortality (Dillon et al. 2020, Boyle et al. 2021). Particularly effective is mitigation that combines directional fencing (to prevent animals from accessing the roads and guide them towards crossing structures) and ecopassages (to facilitate movement; Rytwinski et al. 2016). Wildlife ecopassages have been shown to effectively mitigate mortality for a diverse array of taxa including ungulates (Clevenger et al. 1973), bears (Sawaya et al. 2014), bats (Berthinussen and Altringham 2012), snakes (Colley et al. 2017), and amphibians (Boyle et al. 2021).

Road mortality is a particularly pervasive threat to many reptile populations, adding to the conservation crisis faced by one of the world's most threatened taxa (Böhm et al. 2013, Cox et al. 2022). Within Reptilia, snakes are among the groups most likely to be impacted by roads, and direct mortality from roads perhaps is second only to habitat loss as a threat to population persistence (Wright 2007, Soanes et al. 2024). The defensive adaptations of many snake species provide little protection against vehicles, and relative to other vertebrate taxa, snakes generally have smaller body sizes, are slower moving and have potentially less awareness to the dangers imposed by roads (Ashley and Robinson 1996, Wright 2007).

Despite this increased threat level, studies on the effectiveness of road mortality mitigation for snakes are exceptionally scarce worldwide (Soanes et al. 2024). At northern latitudes, these threats may be additionally heightened given the naturally smaller populations, greater environmental stressors and larger seasonal migrations (Gregory et al. 1987). Within Canada,

reptile populations fare on average worse than global assessments of the taxa (Cox et al. 2022), with 82% of the country's assessed species falling under the category of 'risk' (Endangered, Threatened, or Special Concern) and 20 out of 25 of those having road mortality listed explicitly as a threat (COSEWIC 2023).

Studying the effects of road mortality at a population level ideally requires the simultaneous monitoring of road mortality rates, and population demographics. For cryptic species (many snakes), the collection of demographic data is hindered by an inability to locate and capture individuals. For some snake populations, this can be overcome by the phenomenon known as communal denning. More pronounced in higher latitudes, communal denning occurs when individuals gather to use the same site to overwinter, often with multiple species present at one den (Gregory 1982, 1984). This behaviour allows for efficient sampling at high density sites while year-to-year site fidelity permits accurate population estimates over time.

In this study we focus on the road ecology of the Western Rattlesnake (*Crotalus oreganus*) in British Columbia, Canada. Here, the snake is considered a species-at-risk, being listed federally as Threatened, due in large part to its occurrence at the northern extent of its range (see Chapter 1, Figure 1.3; Andrusiak and Sarrell 2015). The active season for this population spans approximately mid-April to mid-October, when maximum daytime air temperatures typically exceed 10°C (Macartney 1985, COSEWIC 2015a). In the spring, males make seasonal migrations of up to 4 km away from communal hibernacula to forage and search for mates (Harvey and Larsen 2020). Gravid females and juveniles make movements away from den sites but at a significantly smaller scale (Eye 2015, Howarth et al. 2023). These seasonal migrations often take the animals into low elevation grasslands and forests, and in Canada, areas frequently bisected by roads.

Road mortality is a major identified threats to this population with environmental and phylogenetic constraints making the animal highly susceptible to large scale population declines (COSEWIC 2015a). Relevant behavioural characteristics of this species include communal denning (Gienger and Beck 2011), seasonal adult migrations (Harvey and Larsen 2020) and a 'freeze' response when encountering vehicles on roads (Andrews and Gibbons 2005, Jacobson et al. 2016). Demographic characteristics include low survivorship, long generation times, low fecundity, and infrequent reproduction (Macartney and Gregory 1988, Macartney et al. 1990,

Maida et al. 2018). All told, these traits make the Western Rattlesnake particularly vulnerable to road impacts, as their freeze response increases the likelihood of vehicle collisions, and adult mortalities during migration having disproportionate effects on the population, as low reproductive rates and long generation times limit population recovery.

The results of this study are based on a 10-year period of monitoring a Western Rattlesnake population experiencing both road mortality and mitigation efforts. This work involved a decade of mark-recapture demographic data that provides robust population estimates before and after the establishment of eight ecopassages. Road mortality surveys occurring over the same period subsequently allowed us to monitor the magnitude of mortality on the overall rattlesnake population within our study site. With studies on wildlife crossing structures overwhelmingly evaluating movement and mortality only post-mitigation (Soanes et al. 2024), we provide a robust design with mortality rates before and after mitigation paired with simultaneous population estimates.

## **METHODS**

### **STUDY SITE**

Our study was conducted in the White Lake Basin (latitude 49.318° N, longitude 119.638° W) in the South Okanagan region of British Columbia, Canada (See Chapter 1, Figure 1.4). The area is used by the Dominion Radio Astrophysical Observatory (DRAO) and is surrounded by over 20 km<sup>2</sup> of undeveloped land to minimize radio signal interference (National Research Council Canada 2023). A smaller portion of the study site lies within the White Lake Grasslands Protected Area, a 37.6 km<sup>2</sup> conservation area (B.C. Parks 2024). The ecosystem within the basin is primarily semi-arid grassland characterized by agricultural ranch lands, rolling hills, steep bluffs, and Ponderosa Pine (*Pinus ponderosa*) forests in the upper elevations.

Traversing the valley bottom are two paved, undivided, two-lane roads that meet at a “T” intersection in the middle of the basin (See Chapter 1, Figure 1.5), with an unposted speed limit of 80 km/h on each road. Vehicle flow through the White Lake Basin typically is at its highest during the summer tourism months, adding to regular residential traffic. See Chapter 1 for additional details on the study site.

## **HISTORY OF MITIGATION EFFORTS**

From 2015 – 2017, Winton et al. (2018, 2020) conducted baseline research on the White Lake rattlesnake population. The results of their population viability analysis (PVA) predicted in the next 100 years a 97% decrease in mean population size (from 2131 to 72) under current estimated road mortality rate (6.6% of population yr<sup>-1</sup>). This study prompted the creation of eight under-road ecopassages in September 2017, during scheduled re-paving of the two roads. Four new ecopassages were installed at identified snake mortality hotspots, and four previously installed drainage culverts were altered for wildlife (Figure 2.1). Using these ecopassages as the basis for mitigation, we evaluated post-mitigation road mortality rates from 2018-2024. In April 2019, funding for the installation of directional fencing at the ecopassage entrances was obtained, but bedrock severely constrained where fencing could be erected. As a result, fencing (model AMX-SP40, Animex Wildlife Fencing Solutions) was haphazardly added to 7 of the 16 ecopassage entrances (see further details in Spruyt 2024). From 2018 – 2023, cameras were positioned at each of the 16 ecopassage entrances to monitor preliminary use (Spruyt 2024). Ecopassage and fence physical dimensions as well as camera monitoring methods are provided in Appendix A.

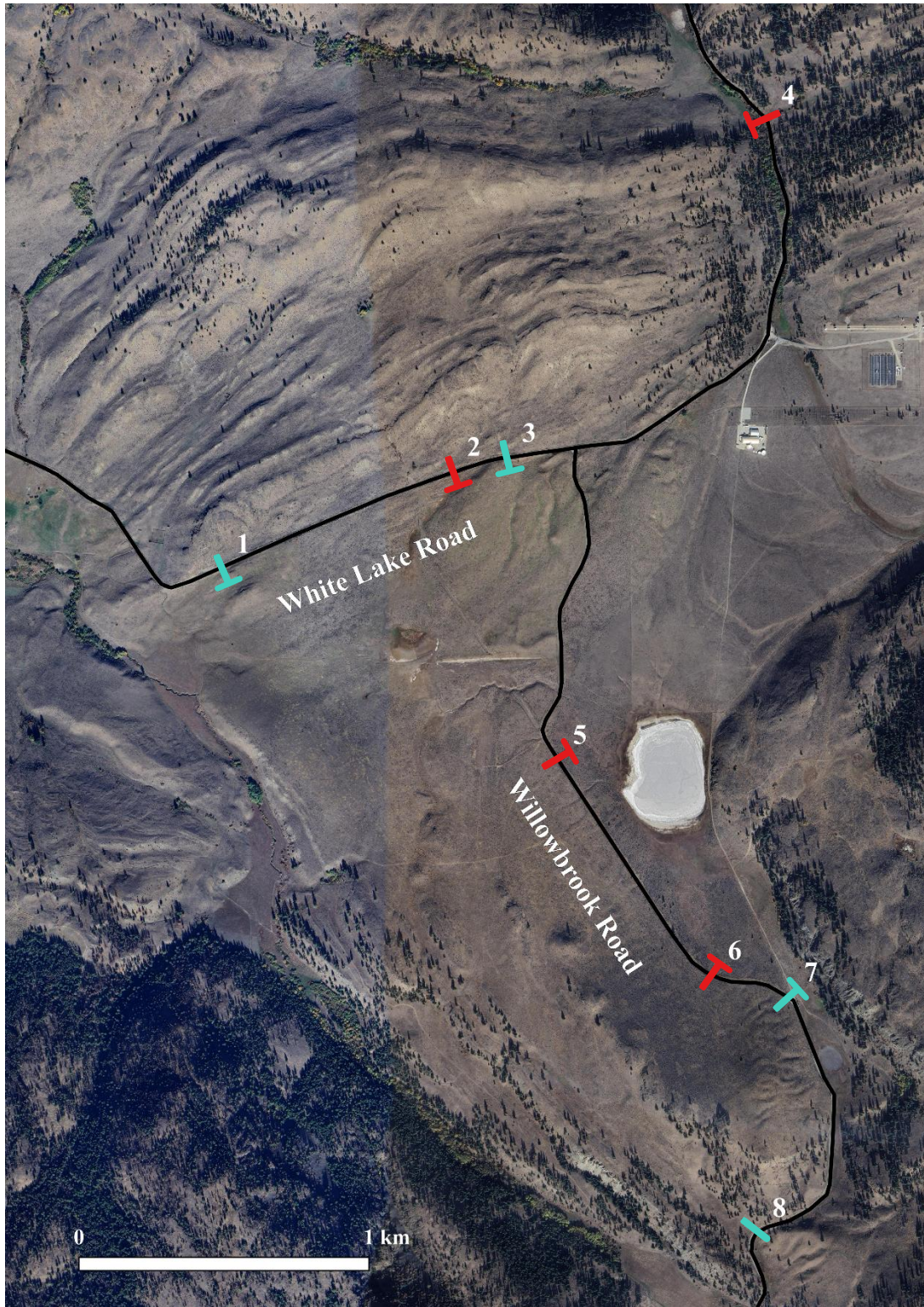


Figure 2.1. Map of ecopassage locations in the White Lake Basin in British Columbia, Canada. Locations in red were modified pre-existing culverts, while locations in blue were newly installed eco-passages at snake roadkill hotspots. Lines denote the side of the ecopassage where directional fencing is installed.

## MARK-RECAPTURE

Following methods outlined in Winton et al. (2018) and reiterated in Spruyt (2024), we conducted mark-recapture surveys to estimate population size for rattlesnakes in the White Lake Basin. Most of the mark-recapture work occurred during spring egress and fall ingress at known hibernacula from Spring 2015 to Fall 2024 inclusive. We surveyed six hibernacula in proximity of the two roads, which to our knowledge support most of the snake population in the basin. Surveys were supplemented with opportunistic field captures throughout the active season (May – September). Upon capture, all snakes were weighed (g), measured (cm, snout-vent length (SVL), and sexed (cloacal probing). Marking of snakes was done *in situ* by subcutaneous implantation of an 8 mm passive integrated transponder (PIT) tag (Mini HPT8 PIT Tag, Biomark, Inc.). To illustrate the distribution of sizes, I binned the snakes into age classes based on SVL, with adults having an SVL greater than 55.0 cm (Macartney and Gregory 1988, Petersen et al. 2024).

## POPULATION ESTIMATES

A 10-year binary mark-recapture dataset was constructed for all adult snakes throughout the lifespan of the project (2015-2024). We truncated the data to include only adults, thereby satisfying the assumption of our model's homogeneous mortality rate (Jolly 1965). From these capture histories, we estimated yearly population sizes and survival rates using a modified Jolly-Seber model (Jolly 1965, Seber 1965). This involved restricted dynamic occupancy parameterization, augmented with 500 unobserved individuals that were assumed to be present but not marked (English, pers. comm., Royle and Dorazio 2008). To account for expected correlation within demographic parameters and heterogenous recapture effort through time, we included terms for environmental (sampled from a bivariate normal distribution) and temporal stochasticity (sampled from a univariate normal distribution). From these estimates, we derived annual population growth rates ( $\lambda$ ) as  $N_{t+1}/N_t$ , where  $N_t$  is the population size at time  $t$  and where values  $>1$  and  $<1$  indicate population growth and declines, respectively. We implemented this fully time-dependent model in version 1.1.0 of the Nimble statistical model compiler (de Valpine et al. 2017) in RStudio. We interpreted successful model convergence when statistics for all monitored parameters from four Markov chain Monte Carlo (MCMC) algorithms were below 1.01 (Vehtarh et al. 2021).

## ROAD MORTALITY RATES

Over the duration of this study, we quantified rattlesnake mortality using the methods originally outlined by Winton et al. (2018) and Spruyt (2024) for conducting road surveys. To count vehicle use, a traffic logger (TRAFx G4) was buried on the shoulder of the road along each transect to record the number of vehicles using the roads each day. Road surveys were conducted on foot and by vehicle along each road within the basin. A total of 11.5 km were surveyed, consisting of two transects 5.7 and 5.8 km long, respectively. Surveys on foot typically were performed in the mornings with two observers walking on opposite sides of the road scanning both the road as well as approximately 1.8 m into the vegetated controlled zone of the road shoulder. Walking surveys were supplemented with occasional driving surveys to account for mortalities that occurred in between walking surveys. Driving surveys were performed primarily in the afternoon, with a driver and an additional observer travelling no faster than 20km/h. Both directions were driven on each transect to ensure both lanes were observed equally. During the surveys, mortalities of all vertebrate species were recorded, and any live snakes encountered were captured, processed and added to our mark-recapture dataset.

Observer-detection bias experiments were conducted yearly to determine the effectiveness of the observers. During scheduled walking surveys, a third researcher left previously collected road killed snakes in random locations along the survey route, and the proportion of snakes detected was used to determine observer detection bias ( $p$ ) and ensure consistent replication of methods. With the exception of 2022, observer detection experiments were conducted each year new personnel were collecting data.

### *Estimating Road Mortality Rates*

To estimate the magnitude of mortality attributable to vehicle collisions, we used the mathematical model previously developed by Winton et al. (2018):

$$\lambda = \frac{N(t)/xp}{P_0 t + \frac{1}{a}(1 - P_0)(1 - e^{-at})} \quad (1)$$

This model assumed a constant rate of mortality, with  $\lambda$  as the estimated rate of rattlesnake deaths per kilometer per day, and  $N(t)$  is the number of carcasses found on the road by observers. The rate of carcass removal by scavenger or otherwise is defined as  $a$ , while  $P_0$  is the proportion of carcasses that remained on the roads after 14 days and presumably had no remaining value for scavengers. As calculated by observer detection experiments, the probability of detection ( $p$ ), is the proportion of carcasses on the road that are observed by surveyors.  $t$  is the time between surveys in days, and  $x$  is the number of kilometers surveyed (Winton et al. 2018). Because the probability of detection is inherently different according to the method of survey (walking, driving), we calculated mortality rates based on a subset of surveys that only included walking surveys but included observations of incidental mortalities found during driving surveys, or otherwise. The number of yearly surveys throughout the project varied substantially based on the ratio of walking to driving surveys conducted.

Using a two-sample t-test, we compared the rates of mortality before and after ecopassage installation. To model the overall trend in mortality across all years of study, we used an exponential decay function with weighted least squares to account for the heteroscedasticity within our mortality estimates (Ruppert and Wand 1994).

## RESULTS

Using our mark recapture dataset comprised of 1192 observations and 646 individuals, we derived annual population estimates of *C. oreganus* within the White Lake Basin that ranged from 192 – 350 animals ( $\bar{x} = 290 \pm 57$  SD; Figure 2.2 A). When paired with estimates of road mortality, our long-term data reflected a population impacted by road mortality. Over the entire study we collected 292 rattlesnake road mortalities, with adult snakes making up 49% of observed rattlesnake mortalities. This occurred despite traffic volume being relatively low compared to neighbouring highways. Minimum yearly traffic volume occurred in 2015 while 2022 saw volume at its maximum with an average of 266 and 534 vehicles per day, respectively (Figure 2.3). Pre-mitigation years had a mean of  $314 \pm 34$  SD vehicles per day while post mitigation years had a mean of  $487 \pm 44$  SD vehicles per day. Across all years, we registered a 74% increase in traffic through the summer months (yearly averages; Figure 2.3). Unfortunately, the 2018 traffic data were lost when counters were removed prematurely by highway workers.

With multiple personnel conducting road surveys throughout the study, we accounted for yearly variation around the detection rates. We report no large deviation in observer detection rate ranging from  $p = 0.71 - 0.79$  ( $\bar{x} = 0.74 \pm 0.03$ ). There was no bias towards the detection of larger snakes ( $\chi^2 = 0.0$ ,  $df = 1$ ,  $P = 0.988$ ) nor was there bias in detection by transect ( $\chi^2 = 3.7$ ,  $df = 1$ ,  $P = 0.052$ ) in any year. The number of road surveys averaged  $101.4 \pm 20.4$  surveys/year (range 80-148). While roadkill rates varied over the 10 years, the most recent year of our study (2024) showed mortality rates to be at their lowest (0.015 rattlesnake deaths/km/day; Figure 2.3).

### POPULATION ESTIMATES

Our Jolly-Seber model showed population fluctuations over time, but overall, the population appeared to remain in decline even after the installation of the ecopassages and the subsequent addition of partial fencing. Across all our estimated parameters, large confidence intervals inhibit the ability to draw firm conclusions on the status and future trends of the population. Total captures (new individuals and recaptures) throughout the study ranged from 55 (2022) to 176 (2020) individuals per year ( $\bar{x} = 119 \pm 42$  SD). Estimates of population size varied substantially between 2015 and 2024, with a population high in 2019 at 350 (95% CI = 314 to 393) individuals (Figure 2.2 A) and a population low of 192 (95% CI = 151 - 235) individuals in the most recent year of study (2024). Annual rates of survival ranged from 0.65 to 0.83 with a mean of  $0.74 \pm 0.06$  SD (Figure 2.2 B). Annual population growth rate ranged from 0.80 to 1.08 with a mean of  $0.95 \pm 0.09$  SD. Since the beginning of this project, mean estimates for the population have declined by 42.1%, though wide confidence intervals again hamper the ability to definitively draw conclusions (Figure 2.2 C).

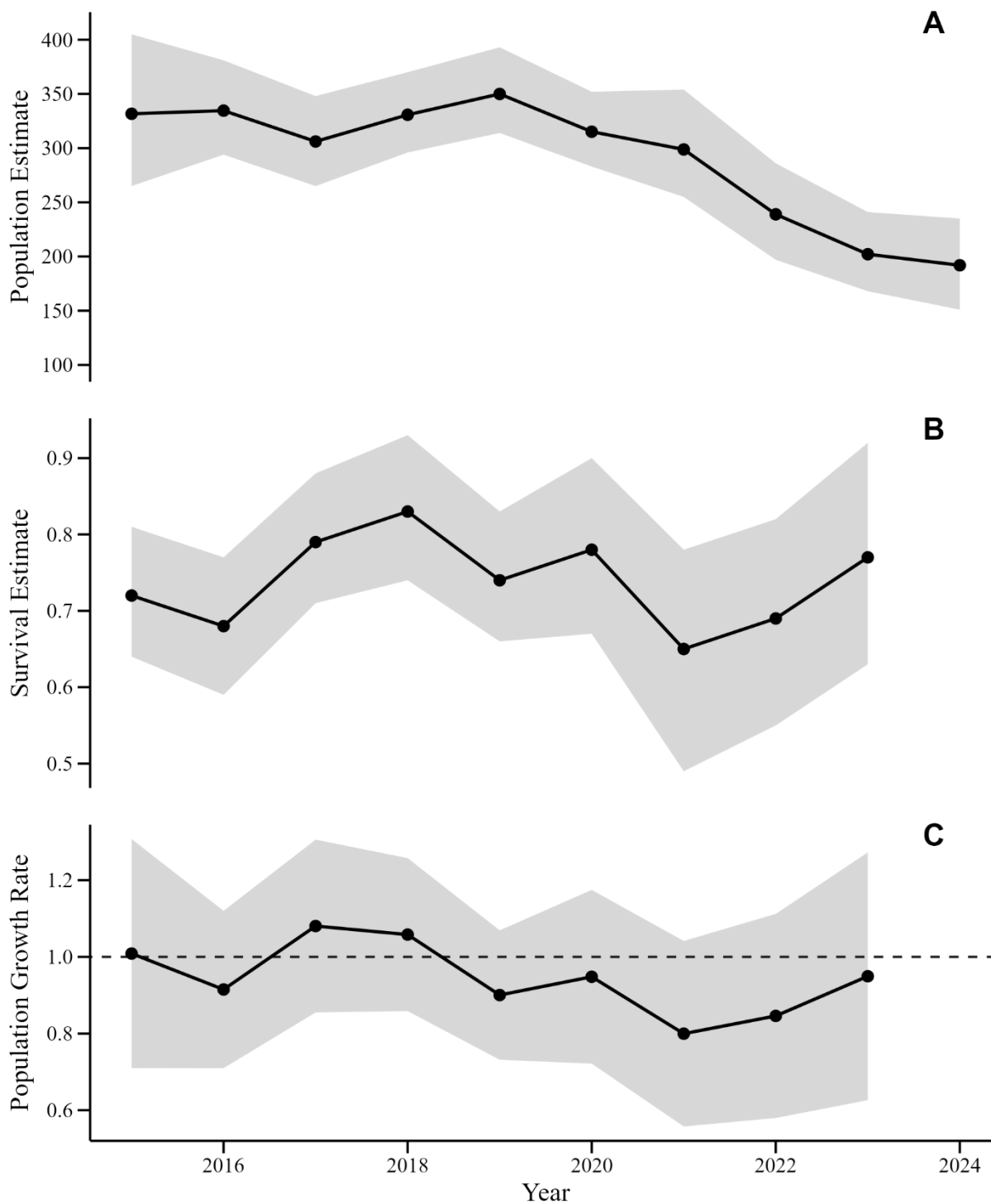


Figure 2.2. Jolly-Seber parameter estimates of A) population size, B) apparent annual survival and C) annual population growth rate. Rates above 1 (dashed line) reflect increases in overall population size, while rates below 1 reflect population declines. Shaded regions correspond to 95% confidence intervals in A and B, and 5% - 95% quantiles in C around parameter means (black lines). Dashed line (1) represents no change in population growth rate; values above indicate population increases, while values below indicate population declines.

## ROAD MORTALITY

Across the entire study, there was an average of  $3.0 \pm 0.6$  SD days between any survey (range 1.8 to 3.5) and an average of  $3.8 \pm 0.7$  SD days between walking surveys (range 2.9 to 4.9). Yearly rattlesnake mortalities ranged from 14 to 56 observed snakes ( $\bar{x} = 29.2 \pm 11.9$  SD). Estimated mortality rate on the roads over the study years averaged 0.04 rattlesnake deaths/km/day ( $\pm 0.016$  SD, range 0.015 - 0.07; Figure 2.3), with a significant difference in rates of mortality between pre-mitigation rates ( $\bar{x} = 0.052 \pm 0.012$  SD) and post-mitigation rates ( $\bar{x} = 0.029 \pm 0.012$  SD;  $t(8) = 2.43$ ,  $p = 0.02$ ). Weighted nonlinear regression showed an annual mortality decay rate of 9.7% with near significant declines throughout the 10-year period ( $t(8) = 2.21$ ,  $p = 0.058$ ). Despite the decreasing trend observed in road mortality and increases in vehicle volume, road mortality was not significantly correlated with population size ( $F_{1,8} = 3.90$ ,  $p = 0.084$ ) or traffic volume ( $F_{1,7} = 2.22$ ,  $p = 0.18$ ).

## DISCUSSION

Despite our strong 10-year dataset, considerable variation in the confidence limits associated with annual population growth rates and survival prevents us from making definitive conclusions on the direction and significance of changes (if occurring at all) in the population size. Similarly, it becomes impossible to draw a firm conclusion on the overall efficacy of the ecopassages as there is no evidence of a prominent recovery in the target population. However, a significant reduction in road mortality rates post mitigation (despite an increase in traffic volume) suggests that the mitigation efforts may be effective at an individual level. All told, our data suggest a multitude of additional factors, such as shifts in animal road-crossing behaviour, seasonal movement patterns, and indirect adverse effects from roads, may have a more pronounced impact on this population and mortality rates than initially anticipated (Chapter 3). Ultimately, this study underscores the complexity of this system and highlights multiple challenges inherent in assessing road impacts.

## POPULATION TRENDS

As with most wildlife, snake populations show natural fluctuations over time (Lind et al. 2005, Ferguson et al. 2019). Natural fluctuations in predator and prey abundance, environmental stochasticity, and density-dependent processes all may affect animal abundance, but to measure these parameters effectively was beyond the scope of this study

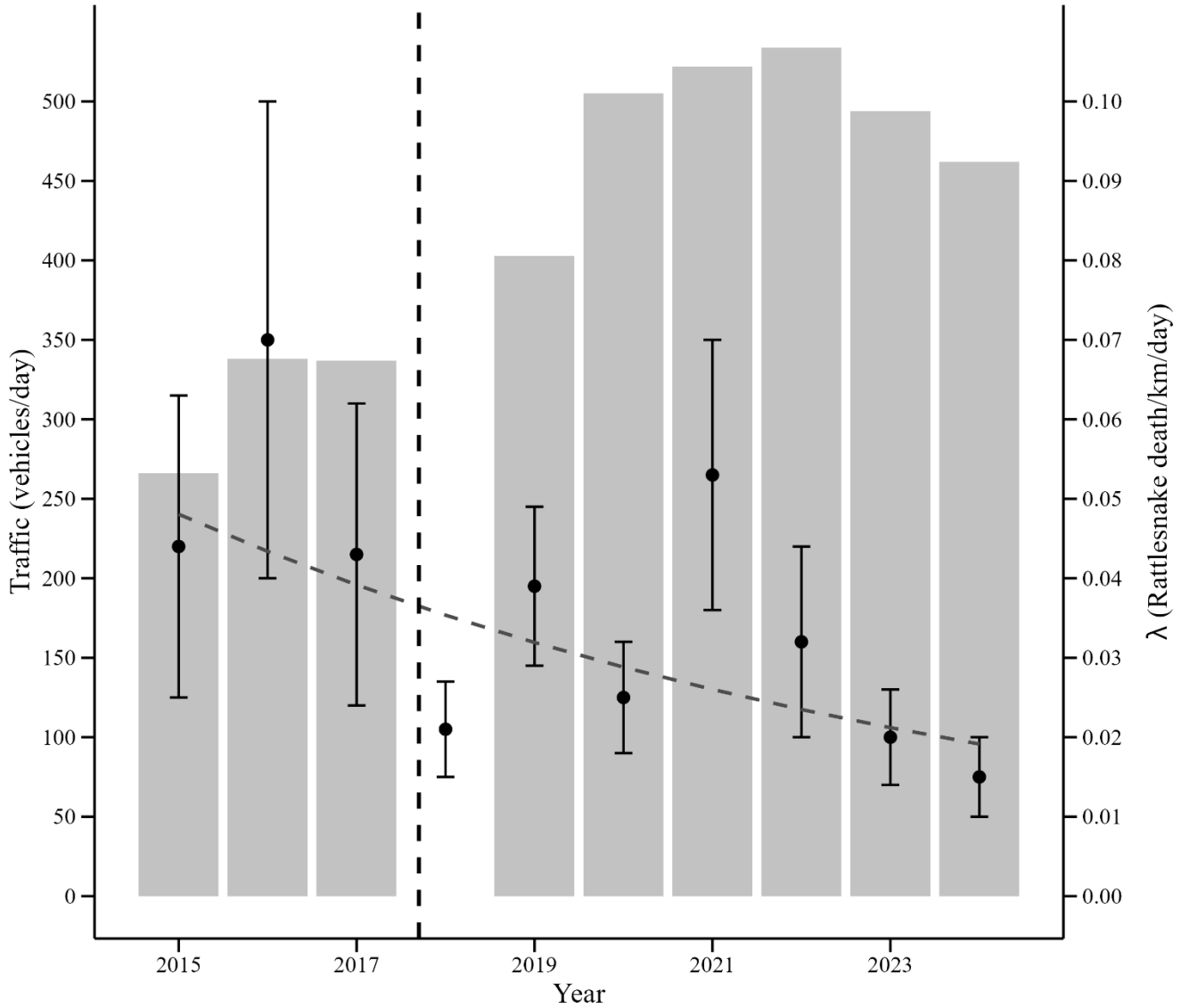


Figure 2.3. Estimated Western Rattlesnake yearly road mortality rates ( $\pm 1$  SE) (black points) expressed as rattlesnake death/km/day (right ordinate axis) from 2015 – 2024. Trend line represents the geometric trend  $y = 0.48 \times (1 - 0.097)^x$ . Black vertical dashed line marks the installation and modification of the 8 ecopassages. Grey bars reflect yearly traffic rates expressed as vehicles/day (left ordinate axis), with traffic data unavailable for 2018.

(Caughley 1994, Engen et al. 1998). In undisturbed habitats, these fluctuations typically are not cause for concern, however, in systems with additive sources of mortality, populations may not be able to recover from regular losses of breeding adults. While some studies have observed cyclical patterns in snake populations that fall within the bounds of our observations (Lind et al. 2005, Maida et al. 2018), snake populations globally are in widespread decline (Reading et al. 2010). The PVA conducted earlier by Winton et al. (2020) included various rates of simulated road mortality; they found negative population growth for all simulations, even at rates well below their measured value (6.6% annual population death). Declining populations can further be at risk of loss of genetic diversity, disease outbreaks and environmental catastrophes which can exacerbate the impacts of population declines (Fahrig 2003, Epps et al. 2005, Prentice et al. 2014).

Because the overarching goal of this study was to investigate the effects of ecopassages on the population, we chose to subset our data to include only focal hibernacula within 400m of a surveyed road, excluding all other known dens in the basin. With the majority of the impacted snakes overwintering at these sites, we considered this a more accurate reflection of the population being affected by roads. In rattlesnakes, demographic rates are known to vary with age class; estimates of year-to-year survival range from a minimum of 4% in neonates (Charland 1989) to a maximum of 94% in adults (Maida et al. 2018). Therefore, to satisfy the assumption of homogenous mortality rates in Jolly Seber models, we subset our data exclusively to adult snakes (Jolly 1965). Given that adults represented the largest proportion of observed road mortality in the study and the compensatory nature of any neonate or juvenile mortality found, our use of an ‘adults only’ dataset also better informs discussion around our estimates of road mortality.

In British Columbia, the current estimated generation time for this species is approximated at 13.7 years (Maida et al. 2018, Petersen et al. 2024), suggesting even our 10-year study (with 7 years post-mitigation) may not be long enough to show detectable results. Currently, there is insufficient evidence to argue that ecopassages are having a positive effect on the rattlesnake population in the White Lake Basin, 7 years post installation. Given their demographic and life history traits, northern rattlesnakes have been argued to have more “K- selected” populations relative to other vipers (Macartney and Gregory 1988, Brown 1991). If so, then changes in

populations should appear more robust to adverse impacts, requiring longer study periods to observe measurable effects. Despite the observed increase in estimated survival and annual growth rate in the final two years of our study (2023 – 2024), it is not certain at this time if this population will recover naturally, or if the PVA predictions estimated by Winton et al. (2020) still warrant concern. We suggest even longer-term work (uninterrupted or intermittent) may be needed to fully evaluate population trends.

### **ROAD MORTALITY RATE**

Perhaps one of the more striking trends in our data is the statistically significant decrease in the rate of road mortality despite the increase in vehicle counts, counter to intuitive expectations and published literature (Andrews and Gibbons 2005). In addition to being a popular summertime tourist destination, the South Okanagan region experienced an 8.6% increase in residents from 2016-2021, well above the national average growth of 5.2% (Statistics Canada, 2022). The White Lake Basin traffic count mirrored this trend, as 2024 saw an ~ 74% increase in traffic volume relative to 2015 rates. With the influx of year-round residents and tourism peaking in the summer months, expectations are for traffic in the basin to continue to increase during the active season for these snakes. Despite our current data showing that road mortality rate acts independently of traffic volume, a continued increase in vehicles certainly will not help in population recovery.

Data collected concurrently with this study through camera monitoring of the ecopassages also suggests familiarity (and possibly adoption) may be increasing in the rattlesnake population. Between 2019-2020, Spruyt (2024) reported an increase in the detection of snakes using ecopassages. Increasing adoption of crossing structures has been documented in ungulates (Reed et al. 1975, Gagnon et al. 2011), carnivores (Schmidt et al. 2021), and arboreal mammals (Soanes et al. 2013) but never in snakes. Following the natural-disturbance terminology of Warren et al. (1987), we postulate an increased adoption rate of the structures could occur subsequent to the initial ‘shock phase’ (Warren et al. 1987) caused by ecopassage installation and the accompanying changes in the shoulder areas of the roads. For example, conspecific scent trailing has been chiefly shown in neonatal rattlesnakes (Brown and Maclean 1983, Muellman et al. 2018). However, adult fidelity to overwintering sites, rookeries (Lafond, 2024) and a tendency for individuals to re-visit specific summer habitat features suggests some level of year-

to-year memory and/or the use of chemosensory trails (Ford 1986, Gomez et al. 2015). While the time it takes for full adoption of new structures by snakes remains to be revealed, the decline in observed road mortality in this study paired with the strategic placements of ecopassages suggests that this mitigation measure may help reduce road mortality but also warrants a precautionary approach as an effective tool for the conservation of populations.

With wildlife crossing structures expected to become more prevalent on the landscape, (possibly becoming a condition of approval for new/existing road projects) it should be stated that the addition of ecopassages to disturbed landscapes has yet to demonstrate no net loss and full restoration of movement in snake populations relative to undisturbed landscapes (Meijer et al. 2018, Soanes et al. 2024). Despite widespread agreement on the need for mitigation measures to reduce mortality and improve connectivity, population recovery through ecopassages is a long-term, multi-step process, that requires proper identification of goals, site selection informed by data (Polak et al. 2019) and a sufficient monitoring period to assess effectiveness (Rytwinski et al. 2016). For rattlesnake populations facing extirpation, the addition of ecopassages to abate road mortality should not be applied as the sole mitigation measure (see Chapter 4). The implementation of these ecopassages also requires long-term monitoring to show their true effects, as evidenced by this study. Ultimately, our work highlights that ecopassages are not a fix-all solution for the mitigation of rattlesnake road mortality but rather a tool that over time may reduce the magnitude of the impact.

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## Chapter 3

### MOVEMENT PATTERNS OF THREE SYMPATRIC SNAKE SPECIES SHOW DIVERSITY OF BEHAVIOURS BUT CONSISTENT ROAD AVOIDANCE

#### INTRODUCTION

With fragmentation across the global landscape projected to increase in the future (Meijer et al. 2018), the ability for animals to move through their environment continues to change. The degree to which individual species are affected by habitat loss and fragmentation will depend on both the biology of the species and the scale at which habitat is lost (Webb and Shine 1997). Movement ecology has been increasingly incorporated into biodiversity research linking the behaviour of individuals to larger populations and entire species (Jeltsch et al. 2013, Allen and Singh 2016). Conservation planners and wildlife biologists in turn may incorporate movement into mitigation efforts, particularly when designing and implementing strategies for imperiled species that are flexible in both time and space (Jenks et al. 2015, Allen and Singh 2016). Indeed, movement data have been used to make management suggestions for a variety of wildlife species including site closures for Boreal Woodland Caribou (*Rangifer tarandus caribou*) (Pinard et al. 2012, Walker et al. 2021), placement of highway crossing structures for King Cobras (*Ophiophagus hannah*; Jones et al. 2022), and the identification of critical habitat for Gray Bats (*Myotis grisescens*; Moore et al. 2017).

Road infrastructure is among the most significant anthropogenic threats to wildlife populations globally, with millions of vertebrate deaths estimated each year due to vehicle collisions (Rytwinski et al. 2016, Gonçalves et al. 2018, Boyle et al. 2021). While the direct impacts of wildlife-vehicle collisions are more visible and relatively easier to quantify (Chapter 2 of this thesis), indirect effects of roads such as vehicle disturbance and behavioural road avoidance may play a much larger role for species than previously thought; some consider these ecological effects to have a greater impact than direct road mortality (Forman and Alexander 1998). Indirect effects of roads can constrain population and species distributions (Robson and Blouin-Demers 2013), disrupt movement and gene flow (Epps et al. 2005), and prevent recolonization of suitable habitats through behavioural avoidance of roads and surrounding areas (Forman and Alexander 1998, Bennett 2017). As the global road network continues to expand, habitat loss and fragmentation (Laurance and Balmford 2013), both of which are recognized as

driving forces behind the global loss in biodiversity, are being increasingly linked to local population declines and extirpations (Fahrig 2003, Shepard et al. 2008b, Winton et al. 2020). Though direct effects attract more attention within published literature (Bennett 2017), the full ecological consequences of the road network may be more pervasive and difficult to detect, suggesting that the true impact on wildlife likely is underestimated.

In snakes, the impact of direct road mortality has been well documented (Row et al. 2007, Baxter-Gilbert et al. 2015, Choquette and Valliant 2016, Colley et al. 2017, Winton et al. 2020), but other important questions remain unanswered. While road avoidance may mitigate direct mortality, it also may restrict access to necessary habitats and resources, causing populations to become genetically isolated. *In-situ* snake road avoidance has been previously shown in Eastern Hognose snakes (*Heterodon platirhinos*; Robson and Blouin-Demers 2013), Eastern Massasagua Rattlesnakes (*Sistrurus catenatus*; Paterson et al. 2019), and Brown Treesnakes (*Boiga irregularis*; Siers et al. 2014). Additionally, Andrews and Gibbons (2005) found nine snake species avoided crossing roads when soft-released at road edges. When forced to make a crossing, all tested species moved perpendicular to the roads, suggesting that snakes were trying to minimize crossing distance (Andrews and Gibbons 2005). Differences in movement patterns and tolerance to roads between species occupying the same landscape should reveal the differing factors threatening species. Theoretically, this implies species with weaker road avoidance may be more threatened by direct mortality, while species with stronger road avoidance may be more susceptible to threats associated with fragmentation and barrier effects.

Under a conservation framework, species-specific behavioural responses to roads should directly inform mitigation strategies. Snake species showing relatively less road-avoidance behaviour may require a more acute management response to slow direct mortality, whereas snake species that show a strong road-avoidance response may benefit more from management strategies that protect available habitat. Either way, understanding how animals move through their environment is critical. In snakes, movement patterns are affected by both ectothermic physiology and present weather conditions (Seebacher and Franklin 2005). Despite this, previous studies comparing the movements of multiple populations/species often use data collected from multiple study sites where topography may differ or from different times when environmental and climatic variables vary. Few studies (Carfagno and Weatherhead 2008, Klug et al. 2011)

have directly compared snake movement patterns across species under shared spatial and temporal scales. By controlling for space and time, interspecific differences in movement can be better attributed to inherent behavioural traits such as seasonal site fidelity, foraging strategy, and dispersal tendency. These traits not only shape how snakes use the landscape but also influence their likelihood of encountering and crossing roads and their propensity to use mitigation features like ecopassages. Such comparisons are more powerful for determining differences in movement patterns and overall road effects, consequently leading to more effective species-specific mitigation strategies.

This study focused on the comparative movement ecology of three at-risk species of snakes occurring in the same community near coincidental northern range limits (See Chapter 1, Figure 1.3). The Western Rattlesnake (*Crotalus oreganus*; hereafter referred to as ‘CROR’), the Great Basin Gopher Snake (*Pituophis catenifer deserticola*; hereafter referred to as ‘PICA’) and the Western Yellow-Bellied Racer (*Coluber constrictor mormon*; hereafter referred to as ‘COCO’) all are considered threatened in Canada, with road mortality being viewed as a universal contributing factor (COSEWIC 2013, 2015a, 2015b). In southern Canada, considerable work has focused on the implications of direct mortality from roads to the Western Rattlesnake population (see Chapter 2 and references therein), while all three species are commonly captured by hand in the field, detected on ecopassage camera traps (Spruyt 2024) and found dead on roads within our study area suggesting that road mortality is a significant mortality factor across all species. Given the differences in species ecologies (see Study Species, below), multiple hypotheses predict that different movement patterns should be seen across our study species. Using two years of radiotelemetry data and 36 individual snakes, we first verified these differences in movement patterns through the simultaneous radio-tracking of each species. Following that, we evaluated whether the snakes were demonstrating road avoidance behaviour, and if so, whether it was more pronounced in one species over the others.

## **METHODS**

### **STUDY SITE**

This study took place during the 2023 and 2024 active seasons for snakes (April – October) within the White Lake Basin (latitude 49.318° N, longitude 119.638° W), in south-central British Columbia, Canada. During these months temperatures ranged from 8.6 – 28.7°C ( $\bar{x}$  = 18.7°C), and monthly precipitation ranged from 13.9 – 42.2 mm ( $\bar{x}$  = 27.8 mm) with no weather events drastic enough to have caused variation between years (see Chapter 1 for more details; also Wang et al. 2016). The site is a relatively intact grassland ecosystem, apart from two roads bisecting the valley bottom. One road runs East-West while the other runs North-South causing much of the low grassland habitat to be separated from higher elevation rocky outcrop sites with known snake hibernacula. Both roads see moderate traffic in the summer with a daily average of 478 cars in 2023 and 2024 (Chapter 2 of this thesis).

We selected individuals for telemetry from locations within our study site within proximity to roadways and a capture history of all three target species. Six sites were confirmed overwintering hibernacula while the remaining two were areas of high snake encounters. The eight locations have a mean distance of  $172 \pm 126$  m (range 4 - 389 m) from the nearest roadway (Appendix B). See Chapters 1 and 2 of this thesis for more detailed descriptions of the larger study site.

### **STUDY SPECIES**

Movement of Western Rattlesnakes (Viperidae) at northern latitudes is characterized by seasonal migrations between overwintering communal hibernacula to summer foraging grounds (Lomas et al. 2019, Harvey and Larsen 2020, Howarth et al. 2023). In this region, diet consists largely of small mammals (McAllister et al. 2016) with the snakes using a ‘sit and wait’ ambush foraging strategy (Reinert et al. 1984). At northern latitudes, rattlesnakes require more specific habitat characteristics for overwintering, occupying exclusively communal rocky outcrop dens. Adults demonstrate a high year-to-year fidelity to both summer and overwintering sites with a tendency to re-visit specific summer habitat features (Ford 1986, Gomez et al. 2015).

Compared to the extensive knowledge on rattlesnakes, relatively fewer studies have been conducted on Great Basin Gopher Snakes (Colubridae) (but see Shewchuk 1996, Bertram et al. 2001, White 2008) in Canada. These snakes spend much of the active season foraging in

grasslands and open coniferous forest ecosystems with a prey composition primarily of small mammals and birds (White 2008, McAllister et al. 2016). This species hunts actively but can remain underground or under cover for extended periods of time ranging from days to months (Parker and Brown 1980, Andrusiak and Sarell 2013, Wong, pers. observation). In Utah, gopher snakes appear to have high year-to-year site fidelity with respect to egg laying and foraging sites (Parker and Brown 1980). Overwintering site selection is more catholic, with the species being observed to hibernate under rocks, in animal burrows, and rocky outcrop dens (McKelvey, 2024). At its northern limits, directional movement patterns from overwintering sites to summer foraging habitat have been observed, though reports of scale vary substantially (453 m - 2365 m; Bertram et al. 2001, White 2008).

Research on the Western Yellow-Bellied Racer (Colubridae) is also relatively scant: This species is characterized by its alertness and speed (COSEWIC 2015b). Racers are found in similar ecosystems as the other two species, though riparian ecosystems and areas of increased moisture appear to be of particular importance for this species in the White Lake Basin (Wong, pers. observation). Elsewhere, this species have a diet composition consisting almost entirely of insects (>91%), and primarily grasshoppers (Fitch 1999, Shewchuk and Austin 2001), suggesting that they spend much of its season as an active forager. Racers are thought to have fidelity to forage sites (Shewchuk and Austin 2001), while overwintering site selection is similar to that of the gopher snake. Daily movements for this species have been shown to vary from tens of meters (Utah: ; Brown and Parker 1976) to more than a kilometer (Kansas: ; Fitch 1999), though no movement studies on the species have been conducted in Canada.

Intuitively, the degree and manner in which the three species respond to barriers (i.e. roads) would be expected to differ according to their differing movement ecologies, as covered above. Traits such as site fidelity, overwintering site selection, diet, and foraging strategy are key determinants of movement patterns and likely influence rates of road encounters and crossings (Allen and Singh 2016). Due in part to strong site fidelity to summer habitats and traditional hibernaculum, rattlesnakes may have less plasticity in road avoidance during seasonal migrations. In contrast, if roads are indeed partial barriers to movement, then a greater array of hibernating sites used by both racers and gopher snakes also may result in a stronger road avoidance behaviour if suitable overwintering sites can be found without crossing roads. Diet

and foraging strategy should then further differentiate the species' interactions with roads. Racers, being active, wide-ranging predators, should move frequently through the landscape to locate prey, following less directional pathways than rattlesnakes. Depending on where a specific individual's area of occupancy lies in relation to these roads, these constant, less-directional foraging movements governed by prey availability may predict a relatively higher or lower encounter rate with roads. Gopher snakes, although also active foragers, often show extended periods of inactivity, which may reduce road interactions. Rattlesnakes, being sit-and-wait predators, move less frequently but over larger distances when they do (Howarth et al. 2023), predicting greater road encounters during their outbound and inbound seasonal movements in the spring and fall and fewer encounters during the summer. Species with higher movement demands or broader ranging behaviour, such as racers and rattlesnakes, may be more likely to encounter and potentially cross roads, while those with more localized movements or prolonged inactivity may avoid them more readily.

#### **RADIOTELEMETRY**

We captured adult snakes of all three species through intensive searching during the Spring egress period (April-May) in 2023 and 2024, with the exception of two racers that were captured in July 2023. Individuals were chosen for telemetry based on snout-vent length (SVL; >550mm), weight (transmitter mass  $\leq 4\%$  of body mass), and sex (determined through cloacal probing), with an effort to select animals at varying locations throughout the site for homogenous representation. To remove potential sex-based movement bias, we ideally sought to track exclusively male snakes, but due to the size constraints posed by the transmitters, some non-gravid female racers (determined through abdominal palpations) were included in our sample, given previous work on racers has found no significant differences in movements between males and non-gravid females (Carfagno and Weatherhead 2008, Ragsdale 2025). We classified adults as those with an SVL greater than 550 mm (Fitch 1963, Macartney et al. 1990, Petersen et al. 2024) though telemetered individuals often were significantly larger and heavier than our minimum requirements (Appendix C). After being equipped with transmitters and released at their point of capture, snakes were tracked consistently until the point of transmitter removal (in October) or the loss of the individual (transmitter failure, natural predation, or road mortality). Snakes were relocated using a radio-telemetry receiver (TRX-3000; Wildlife Materials Inc., Murphysboro, Illinois) and a 3-element Yagi antenna.

### *Surgical Procedure*

Upon capture, individuals were transported to a field house where they were housed and monitored prior to surgery. The availability of veterinarians required us to house individual snakes up 7 days post-capture and prior to surgery. Radio transmitters were surgically implanted by trained veterinarians, following previously tested procedures (Reinert and Cundall 1982, Brown et al. 2009, Bryant et al. 2010). Owing to their larger body size, rattlesnakes and gopher snakes were implanted with Holohil SB-2T transmitters equipped with a 24 cm external antenna (5.0 g, 10-month battery life; Holohil Systems Ltd., Carp, Ontario), while racers were implanted with Holohil BD-2HX transmitters with an internally coiled antenna (1.9 g, 14-week battery life; Holohil Systems Ltd., Carp, Ontario). Rattlesnakes had transmitters implanted at approximately 25% SVL measured from the distal end and had the antenna run cranially, while gopher snakes had transmitters implanted at approximately 55% SVL and the antenna run caudally. In addition to the standard surgical technique, all snakes had transmitters anchored, using non-dissolvable sutures, to the snake's ribcage (Bryant et al. 2010). Immediately after surgery, all snakes were administered doses of Ceftazadime (antibiotic, DIN: 00886971) and Metacam (NSAID, DIN: 02237715) in accordance with Brown et al. (2009) and monitored for 24 hours before being released at the initial capture location.

### *Radiotelemetry Data Collection*

Throughout the active seasons, telemetered snakes were radio-tracked an average of twice weekly during daylight hours when ground temperatures would be sufficient for snakes to be active ( $>17^{\circ}\text{C}$ ; Lillywhite 1987). Upon relocation, we recorded the Universal Transverse Mercator (UTM) coordinates using various Garmin GPS units. Precise locations were taken as near the snake as possible, without triggering flight; after this, we moved approximately 5 m away from the snake to record additional data to limit undue stress and changes in behaviour. Throughout our study years, there were two instances in which telemetry was impeded. In 2023, to extend the period by which we could track them, four racers were removed from the field for 7 days for mid-season transmitter replacements and released back at the point of capture. Additionally, from August 18<sup>th</sup> – August 28<sup>th</sup>, 2023, data collection was interrupted because of a nearby wildfire outside of the study area that forced an evacuation.

## DATA ANALYSIS

### *Home Range and Movement Parameters*

To calculate metrics pertaining to home ranges and seasonal extents, we included only snakes that were tracked for the full season, starting at egress and running through to mid-September prior to ingress. Conversely, to increase our sample size, we included all tracked individuals when analyzing proportional metrics, road encounter and road crossing events.

We calculated eight metrics to quantify and compare the movement patterns for the three species of snakes within the White Lake Basin. Five of these metrics could be classified as ‘area metrics’, pertaining to the range and distance the snake moved throughout the season. Two additional metrics dealt with the proximity to roads, while one metric dealt with the overall shape of the movement. Table 3.1 describes the calculated metrics and whether the data sets excluded individuals lost or killed during the season.

Annual home ranges for each snake monitored through a full season were calculated using 90%, 95%, and 99% isopleths from Brownian Bridge utilization distributions models (BBDM), using the ‘*adehabitatHR*’ package (Calenge 2023) in RStudio. This method estimates expected movements based on the properties of a conditional random walk between successive locations, dependent on the time between relocations, the distance between relocations, and the Brownian motion variance related to the animal’s mobility (Horne et al. 2007). We chose not to report home range measurements as minimum convex polygons (MCP), and kernel density estimates (KDE) used in many previous snake studies often as a way to permit comparison with historic studies (Lomas et al. 2019, Maida et al. 2020, Howarth et al. 2023). The benefits of consistency notwithstanding, these metrics are sensitive to methodological differences, survey efforts and the use of varying smoothing factors, which combined introduce bias and misleading comparisons (Silva et al. 2020, Crane et al. 2021). Overall, a growing body of work suggests dynamic Brownian Bridge models are a more effective way to measure space-use and home range in reptiles (Mata-Silva et al. 2018, Jones et al. 2022, Eckert and Jesper 2024).

Four of our movement metrics were produced through simple calculations: Seasonal path length (SPL) was the total sum distance (m) of each consecutive movement event. Mean movement rate (MMR) was the mean distance (m) moved per day measured as the distance travelled between two consecutive locations, divided by the number of days between relocations,

Table 3.1. Movement and road encounter parameter descriptions for each metric used to compare Western Rattlesnake, Great Basin Gopher Snake and Western Yellow-bellied Racer movement patterns within the White Lake Basin

	<b>Metric</b>	<b>Abbreviation</b>	<b>Definition</b>	<b>Full Season Metric</b>
<b>Movement metrics</b>	Brownian Bridge home range estimation (ha)	BBDM	Home range polygon using 90%, 95%, and 99% isopleths	YES
	Seasonal path length (m)	SPL	Seasonal total distance moved	YES
	Mean Movement Rate	MMR	Mean distance moved per day	NO
	Movement frequency	MF	Proportion of relocations where location was different from previous location	NO
	Maximum net displacement	MND	Maximum straight-line distance between the point of origin and the most distal point	YES
	Path sinuosity	PS	Sinuosity of movement trajectory; high values = more crooked path, low values = straighter path	YES
<b>Road metrics</b>	Road encounter event	REE	Number of times relocated <3, 3<5, 5<10 meters from a road	NO
	Road crossing event	RCE	Number of times relocated on the other side of a road from previous location	NO

measured across all sequential pairs of tracking events to create an average for each individual (Lomas et al. 2019). Movement frequency (MF) was the proportion of times relocated that an individual had moved from the previous location. Maximum net displacement (MND) was the Euclidean distance between the release location and the most distal relocation.

To quantify path sinuosity (PS; rad/m-0.5), we used the ‘*trajr*’ package (McLean and Skowron Volponi 2018) in RStudio, a package appropriate for movement paths with unequal step-lengths (Benhamou 2004). This corrected index returns a sinuosity between 0 and 1, where values closer to zero indicate a straighter, more direct path and values closer to 1 represent a highly sinuous, more meandering path (McLean and Skowron Volponi 2018).

### *Road Avoidance*

Road encounter (REE) and crossing (RCE) events were determined using the ‘*sf*’ package (Pebesma 2018) in RStudio to create buffers that extended 3, 5, and 10 m from the edges of the roads. We then calculated the number of times that a snake was relocated within each buffer and classified that as an encounter. Data were binned and made independent such that an REE within three meters of a road would be excluded from the larger-scale (5 and 10 m) calculations. We manually inspected the telemetry data looking for discrete road crossing events. This was done instead of using pathway and intersection metrics as some straight-line distances between consecutive locations would erroneously record a crossing event due to the curvature of the road. Because road encounters and crossing events were metrics calculated for all individuals, and the total number of relocations between species differed, we standardized all species to a base of 360 relocations (Correction factor: rattlesnake: 1.0, racer: 1.33, gopher snake: 1.07).

To quantify road avoidance, we simulated animal paths as null models using the ‘*adehabitatLT*’ package with constrained correlated random walk models (Calenge 2019). To remain biologically relevant, these models simulate pathways based on individual movement parameters. We simulated 10 correlated random walk paths per individual using the same distribution of step length and turning angle as the individual’s observed path. Each simulated path began at the same starting point as one of our observed individuals but had step length, and turning angles randomized within the individuals’ observed distribution. We then counted the number of times that the simulated paths crossed the road to estimate the number of expected road crossings. If species avoided crossing roads, then the observed paths would cross less often

than simulated paths. To quantify the effect of road avoidance, we constructed a generalized mixed-effects model using the '*glmmTMB*' package (Brooks et al. 2017) for each species. Because our data were over dispersed and right skewed, we chose a zero-inflated negative binomial model, modelling the number of crossings as the response variable, and the category (observed vs. expected), the number of relocations, and distance from origin point of capture to the nearest road as fixed effects. The model also included a random intercept for 'individual' to account for variability across individuals. To compare road avoidance between species, we then constructed a pooled model under the same parameters but included species as an interaction term with category.

Finally, using data accumulated via all previous research at our site (see Chapter 2), we extracted the number of documented adult road mortalities for each of the three species from 2015 to 2024, filtered to only include adult snakes (SVL > 550 mm; See Chapter 2). Road mortality surveys were conducted using both walking and driving transects along a standardized road route within the study area (See Chapter 2 for more details). Surveys were conducted regularly throughout the active season, ensuring consistent coverage across years and equal sampling effort for all three species. These data provided us with a baseline for road mortality, and context for our results.

## RESULTS

Across two seasons (2023 – 2024), we tracked 36 snakes ( $n = 12$  per species) with full-season data being collected on 25 individuals (10 CROR, 8 PICA, 7 COCO). Partial data sets ( $n = 11$ ) were recorded on seven snakes that were known mortalities (predation: 6, road mortality: 1), two transmitter failures, and two mid-season captures. All told we recorded 360 rattlesnake locations ( $\bar{x} = 30 \pm 8.42$  SD,  $n = 12$ ), 270 racer locations ( $\bar{x} = 22.5 \pm 6.84$  SD,  $n = 12$ ), and 336 gopher snake locations ( $\bar{x} = 28 \pm 10.13$  SD,  $n = 12$ ). Full-season individuals were tracked between 99 and 132 days  $\bar{x} = 118 \pm 12.7$  and  $\bar{x} = 3.61 \pm 0.25$  days between relocations. Morphometric data and individual movement statistics for all individuals can be found in Appendix A.

## MOVEMENT METRICS

Despite our small sample size of snakes that recorded full season movement, one-way ANOVA tests found differences between species in seven of the eight metrics that we tested for. Using the Bonferroni corrected level of significance (Holm 1979), differences ( $P \leq 0.0063$ ) were found for 90%, 95% and 99% home range estimates, seasonal path length, maximum net displacement, mean movement rate, and path sinuosity (Table 3.3). Movement frequency was near significant but confounded by the high degree of similarity between rattlesnakes and gopher snakes. Tukey post-hoc tests were further run to test for significance between each pair of species (Table 3.3).

Overall, rattlesnakes had larger home ranges, dispersed further distances and moved more throughout the season than both gopher snakes and racers. Rattlesnakes also moved further per day and in a more direct path than gopher snakes and less frequently than racers. Post-hoc analysis detected no significant differences between the movement patterns of gopher snakes and racers, while rattlesnakes had six significant differences when compared to racers and seven when compared to gopher snakes (Table 3.3).

Table 3.2. Averages ( $\pm$  SE) for eight movement metrics collected from three species of snakes across two years (2023 – 2024) in the White Lake Basin. Sample sizes  $n = 12$  for all cells except those occurring in the ‘Full Season Individuals’ columns, where sample sizes are as follows: CROR = 10; COCO = 9; PICA = 8. Generally, Rattlesnakes showed larger home ranges, and more linear paths, while gopher snakes and racers showed similar results. See Appendix C for details of each metric and see Table 3.4 for comparative results.

Species	Mophometrics		Movement							
	All individuals		Full season individuals					All individuals		
	SVL (cm)	Mass (g)	90% BBDM (ha)	95% BBDM (ha)	99% BBDM (ha)	SPL (m)	MND (m)	MMR (m/day)	MF	PS (rad/m <sup>-0.5</sup> )
CROR	80.7 (2.5)	361 (32.0)	15.3 (3.3)	27.3 (4.6)	56.9 (6.4)	6900.5 (1056.4)	1468.0 (202.8)	158.5 (17.9)	0.67 (0.05)	0.10 (0.01)
COCO	59.5 (1.9)	85 (7.4)	6.0 (1.5)	9.7 (2.0)	17.8 (2.7)	3339.4 (497.5)	581.4 (43.7)	123.5 (13.8)	0.85 (0.04)	0.14 (0.01)
PICA	91.3 (2.1)	318 (24.9)	7.6 (1.6)	10.9 (2.9)	20.6 (4.3)	2665.8 (554.4)	473.0 (99.1)	79.0 (11.5)	0.68 (0.03)	0.17 (0.02)

Table 3.3. Results of one-way ANOVA tests comparing movement metrics between the Western Rattlesnake (CROR), the Great Basin Gopher Snake (PICA) and the Western-Yellow Bellied Racer (COCO) in the White Lake Basin. Included are the results of a Tukey post-hoc test for significance testing between pairs. Bolded  $P$ -values are significant at  $\alpha = 0.0063$  (adjusted from  $\alpha = 0.05$  using Bonferroni correction) for ANOVA results and at  $\alpha = 0.05$  for post-hoc tests.

Metric	One way ANOVA		Tukey post-hoc results		
	Test Statistic	$P$	CROR-COCO	PICA-COCO	PICA-CROR
90% BBDM (ha)	$F_{2,21} = 3.48$	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.560	<b>&lt;0.001</b>
95% BBDM (ha)	$F_{2,22} = 6.61$	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.449	<b>&lt;0.001</b>
99% BBDM (ha)	$F_{2,22} = 16.57$	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.459	<b>&lt;0.001</b>
SPL (m)	$F_{2,22} = 7.20$	<b>0.004</b>	<b>0.025</b>	0.867	<b>0.006</b>
MND (m)	$F_{2,22} = 14.97$	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.999	<b>&lt;0.001</b>
MMR	$F_{2,33} = 6.79$	<b>0.003</b>	0.115	0.052	<b>&lt;0.001</b>
MF	$F_{2,15} = 4.52$	0.029	<b>0.046</b>	0.053	0.997
PS (rad/m <sup>-0.5</sup> )	$F_{2,33} = 8.56$	<b>0.001</b>	0.105	0.119	<b>&lt;0.001</b>

## ROAD AVOIDANCE

Road crossings were uncommon, with all telemetered individuals confirmed to have crossed roads a minimum of 10 times (rattlesnake: 9, racer: 1, gopher snake: 0). Relative to crossing events, road encounter events were observed more frequently indicating that snakes were present near roads but did not cross them (Table 3.4). Under this comparison, rattlesnakes had the most road encounter events at all levels while racers had the least amount (Table 3.4). Two rattlesnakes were observed to have successfully crossed the road a minimum of three times, while one rattlesnake was killed during a crossing attempt (not recorded as a crossing in our data). From our larger road mortality dataset, we calculated a minimum of 136 ( $\bar{x} = 13.6$ , yearly range 2 – 24) rattlesnake deaths, 67 ( $\bar{x} = 6.7$ , yearly range 1 – 15) racer deaths, and 104 ( $\bar{x} = 10.4$ , yearly range 0 – 18) gopher snake deaths from 2015 – 2024.

Using our random walk models, simulated snakes crossed roads significantly more than our observed results (rattlesnakes:  $\bar{x} = 25.7$ , range 13 – 42; racers:  $\bar{x} = 22.1$ , range 13 – 32; gopher snakes:  $\bar{x} = 16.4$ , range 12 – 21). *In situ* rattlesnakes crossed  $0.75 \pm 0.35$  times per individual, while our simulations predicted  $2.1 \pm 0.29$  crossing events per individual. Racers crossed the road  $0.08 \pm 0.08$  times while simulations predicted  $1.84 \pm 0.38$  crossing events per individual. Similarly, we detected zero road crossings for gopher snakes, yet simulations predicted  $1.34 \pm 0.36$  crossing events per individual (Figure 3.1).

Our species-specific models suggested strong road avoidance for all three species. Rattlesnakes avoided crossing roads ( $z = -2.11$ ,  $P = 0.03$ ) with both number of relocations ( $z = 3.62$ ,  $P < 0.001$ ) and capture location ( $z = -2.18$ ,  $P = 0.03$ ) as significant predictors. Racers also showed significant road avoidance ( $z = -3.01$ ,  $P = 0.003$ ) with number of relocations ( $z = 2.52$ ,  $P = 0.01$ ) as a significant predictor. Lastly, Gopher snakes showed significant road avoidance ( $z = -2.749$ ,  $P = 0.006$ ) but neither capture location nor number of relocations were significant. Avoidance ratios derived from our pooled model showed that rattlesnakes crossed roads 2.6x less than expected ( $P = 0.02$ ), racers crossed roads 20.8x less than expected ( $P = 0.003$ ), and gopher snakes crossed roads 14.9x less than expected ( $P = 0.008$ ). Since each species' avoidance is statistically different, from expected crossings, this further supports the assertion that road avoidance varies significantly between species.

Table 3.4. Total road encounter events (REE) for each species using three magnitudes of road margins. Brackets represent inferred encounter values based on values standardized to 360 relocations.

Species	REE <3m	REE 3m - 5m	REE 5m -10m	Total REE
CROR	33	11	7	51
COCO	11 (14.7)	1 (1.3)	10 (13.3)	22 (29.3)
PICA	29 (31.1)	4 (4.3)	5 (5.6)	38 (40.7)

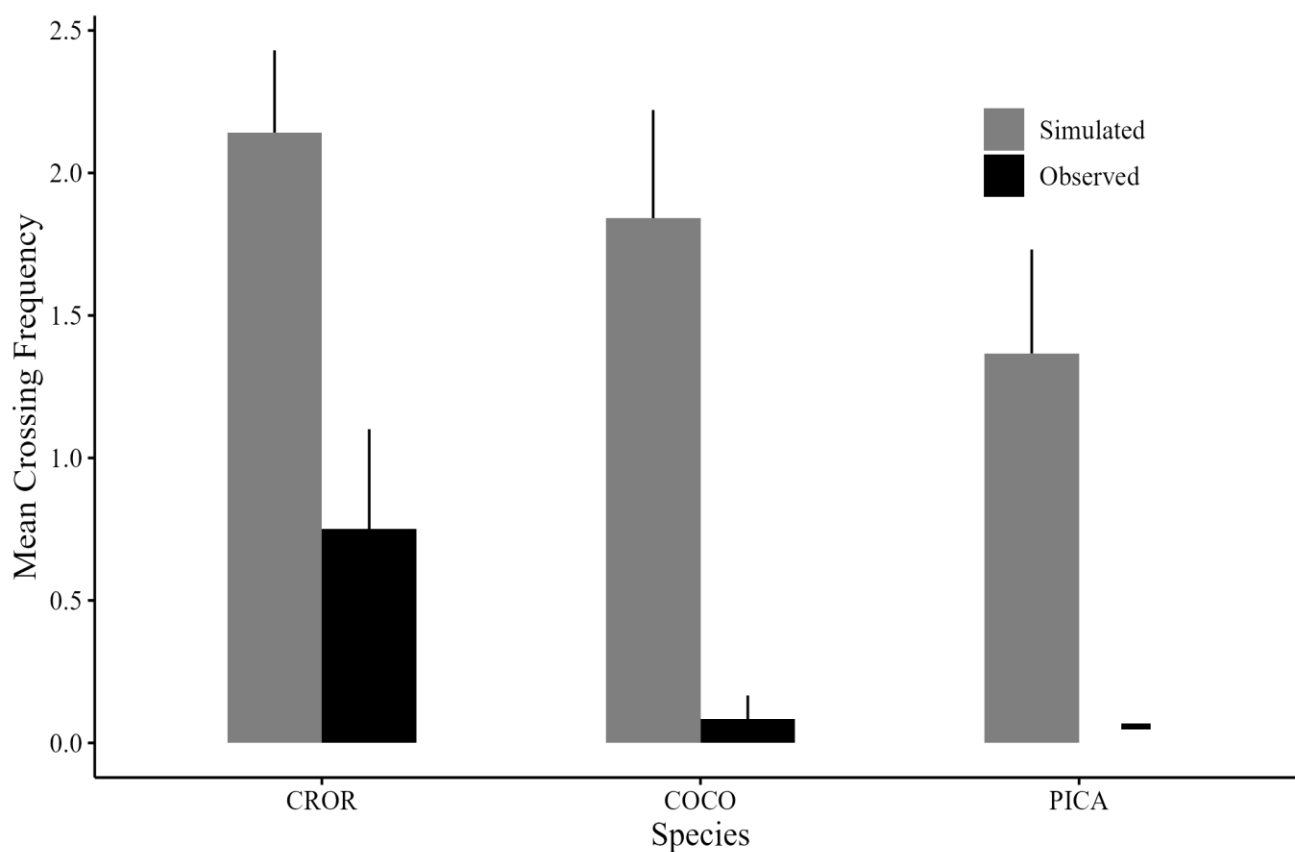


Figure 3.1. Mean ( $\pm$  SE) expected and observed road crossings by COCO ( $n = 12$ ), CROR ( $n = 12$ ), and PICA ( $n = 12$ ) across two seasons (2023 – 2024) in the White Lake Basin, BC, Canada. Simulated values represent the average of the total crossings in each simulation divided by the number of individuals. Dashed line reflects zero observed road crossings for gopher snakes.

## DISCUSSION

This study provides an in-depth look at the simultaneous movement patterns for three species of snakes. We detected significant differences in the movement patterns of Western Rattlesnakes, Great Basin Gopher snakes, and Western Yellow-bellied Racers within the White Lake Basin for seven of eight movement metrics tested. Further, when encountering and crossing roads, all three species strongly avoided crossing roads relative to predicted random walk/null models. The origin point of capture was found to significantly predict crossing events for rattlesnakes but not for racers or gopher snakes. Despite these avoidance behaviours, individuals of all three species still frequently appear within our road mortality dataset, indicating that avoidance is not ubiquitous across all members of the targeted populations.

## MOVEMENT METRICS

The three focal snake species differ markedly in their ecology, which we show to influence their movement patterns and, by extension, their interactions with roads. Consistent with previous research on other northern rattlesnake populations (Gomez et al. 2015, Maida et al. 2020, Howarth et al. 2023), our study animals exhibited nearly twice as large a home range than both sympatric colubrid species. Our telemetered rattlesnakes also moved longer distances, dispersed further from their dens, and exhibited more linear movement paths. Western Rattlesnakes are ambush predators that typically exhibit high site fidelity and undertake relatively long, linear seasonal migrations between hibernacula and summer foraging sites. These traits likely increase the probability of encountering roads, explaining the higher number of road crossings and lower rate of road avoidance observed relative to the other species.

In contrast, we detected no significant differences in movement metrics between our sample of Great Basin Gopher snakes and Western Yellow-bellied Racers. While this might suggest similar space use and movement patterns, we argue that these similarities are likely an artifact of temporal sampling limitations rather than true ecological equivalence. While gopher snakes and racers are both active foragers, they differ markedly in behaviour: gopher snakes tend to show longer periods of inactivity (Parker and Brown 1980) while racers generally are more mobile and require longer foraging bouts to meet dietary needs (Lillywhite 1987). While not significant, racers moved greater distances per day and more frequently throughout the season than gopher snakes, suggesting that we may be underestimating the total movements for racers. As

mentioned, a reliance on insects for prey suggests racers would be expected to move more frequently than gopher snakes. At the same time, extended periods of time at a single site have been previously established as a characteristic of gopher snakes which was further confirmed in our results (Parker and Brown 1980, COSEWIC 2013). The longest period of presumed inactivity we observed was 62 days, with multiple periods longer than two weeks. We observed no such prolonged stationary periods in racers, likely attributed to forage strategy. Given that all species were tracked using the same telemetry protocol, and the known behavioural distinctions between racers and gopher snakes, we suggest that higher-resolution tracking (i.e. more frequent locations) likely would reveal greater movement distances and potentially more frequent road encounters and crossings in racers.

### **ROAD AVOIDANCE**

Our results suggest that in this area all three species avoid crossing roads, but do not necessarily avoid habitats adjacent to roads. Despite infrequent detections of road-crossings in our study, the detection of individuals within 10 meters of a road was not uncommon. We considered 10 meters to represent a considerable distance at which a snake could detect the presence of a road, though in reality, noise and light pollution from vehicles may cause snakes to alter their movements from further away (McClure et al. 2013). It is important to note that although road avoidance appears present in our study community, our 10-year roadkill dataset in the same study area has provided consistent detections of adult road mortalities for all three species (rattlesnake:136, racer: 67, gopher snake: 104) over its entirety. Thus, we interpret road avoidance to be a functional barrier to movement for a portion of each adult population, though it clearly does not preclude animals from being killed by vehicles (Winton et al. 2020). With intraspecies movements associated with dispersal and foraging known to vary (Merrick and Koprowski 2017), the implication is that parts of the population may still see roads as adequate habitat for movement or will undertake the risk associated with roads to access better habitats.

Multiple hypotheses seek to explain the barrier effect of roads on snakes (and animals in general), but these predictions are not mutually exclusive. For example, if vehicles themselves are perceived as a threat, then a predatory response would cause individual snakes to flee, avoid, or pause (Lian et al. 2011, Jacobson et al. 2016). This behaviour has been previously shown in reptiles, with road avoidance becoming more pronounced in times of higher traffic (Szerlag and

McRoberts 2006). Roads generally lack ground cover, which for snakes can result in an increased perceived predation risk, again factoring into avoidance (Forman et al. 2003). While the above factors no doubt affect snake species to varying degrees, the seasonal movement patterns in our study community may further reveal the proximate causes in interspecies road avoidance.

The differences in the degree of road avoidance shown by the three species may be at least partially explained by our movement metrics. Racers had the highest avoidance, followed by gopher snakes, and then rattlesnakes. Rattlesnakes are known to make large scale directional movements towards summer foraging habitat in the spring, then largely reversing their steps in autumn back to their traditional hibernacula (Gomez et al. 2015, Lomas et al. 2019, Maida et al. 2020). Directionality in our study was found to significantly differ between rattlesnakes and the other two species, suggesting that rattlesnakes have more canalized and less plastic movement relative to the other species. This may occur due to the exclusive communal denning behaviour seen in this species, requiring them to disperse further to avoid competition, find mates and improve genetic outbreeding (Schmidt et al. 2020). Racers and gopher snakes, being more plastic in their overwintering habitat selection (Mckelvey 2024), may not need to cross roads to find adequate overwintering sites and may not need to disperse as far to forage and mate, accounting for the stronger estimated road avoidance. Studies on racers also indicates weak directional movements away from den sites (Brown and Parker 1976, Ragsdale 2025), suggesting that movement patterns are dictated increasingly by movements towards suitable forage habitats and away from areas high risk areas.

Previous work within our study site caused the establishment of eight ecopassages and subsequent exclusion fencing along the two roads, being placed at various snake mortality hotspots (Winton et al. 2020, Spruyt 2024; Chapter 2 of this thesis). Spruyt (2024) showed an increase in usage of these passageways in the years immediately following installation, and earlier in this thesis (Chapter 2) we detected a significant reduction in the mortality rate within the rattlesnake population over the same period. While these trends may be partially explained through the road avoidance behaviour seen in this study, road mortalities of all three species still occur. It is well documented that snakes have the capacity for positively reinforced spatial memory, finding suitable overwintering sites, forage areas and shelter year-after-year (Gregory

et al. 1987, Holtzman et al. 1999, Robson and Blouin-demers 2021). It stands to reason then, that an individual who narrowly avoids a collision on the road thereafter may show a tendency to avoid the area in the future. However, if road avoidance behaviour requires a ‘close call’, road deaths still will occur as seen throughout the years of road survey work at our site. With an estimated 3.0 – 4.7 million kilometers of new roads projected to be added worldwide by 2050 (Meijer et al. 2018), both direct and indirect road effects merit increased concern. Thus, to enable the persistence of all three species in this region, we recommend improvements to landscape connectivity paired with the protection of hibernacula and critical summer forage habitats is a crucial mitigative tool. With road barrier effects established across all studied species, future research on snake road ecology should shift focus towards the indirect effects of roads. While direct mortality remains a critical concern, understanding the mechanisms behind road avoidance is essential for informing a more effective species-specific response. A logical next step would be to investigate whether road avoidance is an innate behaviour, or a learned response developed through exposure to traffic. Additional research should seek to identify and quantify the driving mechanisms (i.e. vibrational/visual stimuli, absence of suitable cover) behind this avoidance behaviour.

The interspecies differences observed herein suggest that the specific avoidance response may be shaped by a combination of movement ecology, diet and hunting techniques, and other species-specific life-history traits. As such, both direct and indirect mitigation efforts aimed at reducing adverse effects from roads should account for interspecific differences, ensuring that conservation measures are tailored to the movement patterns and behavioural responses of each species. In this study, rattlesnakes displayed a lower rate of avoidance than both racers and gopher snakes while also demonstrating higher occurrences of adult road mortalities. This suggests that mitigation for this species should focus more on the direct effects of road mortality while racers and gopher snakes may be more at risk of the long-term effects associated with habitat fragmentation and thus should have mitigation measures focused landscape connectivity. Ergo, when designing mitigation strategies and identifying critical habitat, the knowledge of one species should not be applied to other species in an incautious way, even if the species share hibernacula and habitat. Ultimately, mitigation efforts that address both direct mortality and habitat connectivity will benefit all three species, ensuring a more comprehensive approach to conservation that accounts for both immediate threats and long-term landscape level impacts.

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## **Chapter 4**

### **CONCLUSION**

#### **SUMMARY OF THESIS**

The overall goal of my thesis was to broaden the understanding of the direct and indirect impacts of roads on snake populations. The management goal of my thesis was to better inform mitigation measures that will properly protect this specific community of snakes. Specifically, I used populations of the Western Rattlesnake, the Great Basin Gopher snake and the Western Yellow-bellied Racer in British Columbia as a case study to investigate (1) the effects of ecopassages on long-term mortality rates and population recovery, and (2) the implications of roads on seasonal movement patterns between species. Within those two goals, the central objectives were as follows:

#### **1. Effects of ecopassages on mortality and population trends – (Chapter 2)**

- a. Quantify change in Western Rattlesnake road mortality since 2015 and determine if the 2017 installation of ecopassages have been noticeably effective in reducing road mortality.
- b. Pair road mortality observations with population abundance estimates to determine the role of ecopassages on population recovery.
- c. Provide one of the most comprehensive assessments of the impacts of direct road mortality on snakes to date.

#### **2. Implications of roads on seasonal movement patterns – (Chapter 3)**

- d. Quantify differences in seasonal movement patterns between the three species.
- e. Assess the barrier effect of roads on movement patterns; do roads act as a barrier to movement?
- f. Is the effect size equal across the three species?

**From Chapter 2, the principal findings of my thesis were:**

- Post-mitigation mortality rates were significantly lower than pre-mitigation mortality rates.
- Across all years of study, there was near significant decline in the rate of road mortality despite a 74% increase in traffic volume throughout the study period.

- Road mortality was not significantly correlated with population size or traffic volume.
- Wide confidence intervals around survival and population growth rate prevents firm conclusions from being drawn, but overall population abundance has not recovered.
- There are likely additional unmeasured factors within this system influencing this population; this underscores the complexity of this issue and the difficulties in managing recovery.

**From Chapter 3, the principal findings of my thesis were:**

- Movement patterns between rattlesnakes and both other species differed significantly in seven of the eight calculated metrics. Rattlesnakes had larger home ranges at all three levels (90%, 95%, 99%), moved further away from their initial release location, and travelled greater distances than both species.
- Rattlesnakes moved less frequently than racers and in a straighter path than gopher snakes.
- Movement patterns between gopher snakes and racers did not differ for any of the calculated metrics.
- When compared to null models, all three species significantly avoided crossing roads.
- Road avoidance differed between species. Racers had the highest rate of road avoidance, followed gopher snakes, and then rattlesnakes.

**CONSERVATION AND MANAGEMENT IMPLICATIONS**

Direct road mortality is listed as the primary threat to all three species in this study according to British Columbia's threat assessment resulting in the threat classification being listed as 'high' (COSEWIC 2015b, Environment and Climate Change Canada 2019). In the White Lake Basin, we show that the addition of ecopassages as a mitigation measure is an effective way to decrease the road mortality of the Western Rattlesnake. However, there was no indication that the overarching conservation goal of population recovery was achieved. Additionally, all three of our study species significantly avoided crossing roads suggesting that road barrier effects pose as an additional unaccounted-for threat. Combining our long-term road mortality dataset with telemetry movements on the same landscape allows for one of the most complete studies on snake road effects. These results reinforce the need to consider both direct and indirect impacts

of roads in mitigation planning and highlight the importance of species-specific movement data to inform conservation outcomes.

The findings of my thesis directly relate to multiple key objectives outlined in the recovery strategy for both Western Rattlesnake and the Great Basin Gopher snake (Environment and Climate Change Canada 2019), in particular:

1. “Continue to clarify the impact of human disturbance on snakes (both direct and through habitat alteration) and develop effective mitigation approaches.”
2. “Identify and strategically reduce movement barriers in terrestrial habitat where loss of habitat and connectivity is seriously affecting population viability.
3. “Develop and implement long-term research projects at several sites within the species’ range to clarify road mortality issues, associated population impacts, and effective mitigation options for existing and future roads, in collaboration with the Ministry of Transportation and Infrastructure and academia.”

At the current time of writing, the federal recovery strategy for the Western Yellow-bellied Racer is in preparation. I suggest that the objectives listed above can be applied to that species as well. To that end, with respect to the continued mitigation of the adverse effects of roads on these species, my recommendations for the conservation of these populations are as follows:

*1. Continue long-term population monitoring and road mortality surveys in the White Lake Basin*

Long-term mark-recapture programs for snake populations in Canada are exceptionally rare, making the data collected in the White Lake Basin especially valuable for informing future conservation measures. With a comprehensive database of previous research to draw upon, and multiple at-risk snake populations, this site has laid the groundwork for future research and cost-effective continued monitoring. The site’s proximity to the Dominion Radio Astrological Observatory (DRAO), which limits local development, also provides a unique opportunity to study the impacts that even minimal human disturbance can have on both individual behaviour and population persistence. Further, with Western Rattlesnake generation times estimated at 13.7 years (Maida et al. 2018, Petersen et al. 2024), even our extensive 10-year study may not fully capture the population effects of ecopassages on the landscape. While maintaining the current

intensity of research may be unrealistic, even periodic monitoring every few years will still yield important insights into population trends and provide a platform for future research.

## *2. Evaluate effectiveness of mitigation structures in an appropriate manner*

As suggested by Lesbarrères and Fahrig (2012) improving studies on ecopassage effectiveness is best accomplished through the inclusion of road ecology research at the earliest possible stage. Thus, new road projects aspiring to mitigate snake road mortality should include road ecologists throughout the process to ensure that the design, placement, and monitoring of the ecopassages are effectively managed and adhere closely to species-specific guidelines. Existing roads that wish to add ecopassages should evaluate pre-mitigation benchmarks of mortality, crossing rates, and/or population trends, as these benchmarks are the only way to demonstrate the effect (if any) of mitigation (Christie et al. 2019, Soanes et al. 2024). Ideally, to best evaluate the effectiveness of crossing structures, studies should have multiple treatment areas where road mortality is monitored prior to- and post-installation as well as multiple controls, where no mitigation is planned enabling a before-after-control-impact (BACI) design. If the evaluation of barrier effects is central to the mitigation strategy, study designs should additionally include a ‘no road’ treatment to evaluate the movement of individuals under no additive threat. While this can be costly and time consuming, ultimately this pre-mitigative work will provide the best information for the specific road project as well as rigorous results that advance the overall understanding for future road mitigation.

While not directly drawn from the results of my thesis, I have provided additional recommendations that are drawn both from direct observations in the field as well as knowledge of the ecosystem that I have accumulated over the course of this project. They are as follows:

## *3. Adding and increasing lengths of directional fencing*

Unsurprisingly, as the length of directional fencing near ecopassages increases, wildlife-vehicle collision rates tend to decrease (Huijser et al. 2016). Although there are currently no snake-specific studies that provide recommendations on the ideal length of fencing, longer fences generally are assumed to increase the effective funneling area toward safe crossings. At our site, there is little evidence that fenced entrances have shown increased ecopassage use by snakes (Spruyt 2024). However, in the absence of scientific certainty, the Precautionary Principle

for preventative action is warranted (Cooney 2004). One concern sometimes raised about the use of directional fencing and crossing structures is their potential to concentrate animal movement and inadvertently create 'prey-traps'. While such risks merit consideration, no instances of snake predation were observed at ecopassage entrances in White Lake (Spruyt, *pers. comms.*), and a global review suggests that these events are rare and typically reflect opportunistic rather than systematic predator behaviour (Little et al. 2002). Finally, if fences are to be added or upgraded, they should be robust in design and capable of withstanding variable weather conditions and animal interactions, as gaps or poor design have been shown to significantly compromise the effectiveness of ecopassages (Baxter-Gilbert et al. 2015).

### *3. Erect signage along roads and increase educational awareness around snakes*

While mitigation strategies for road mortality have primarily focused on altering animal movements, addressing human perceptions and behaviour also play a role in shaping outcomes. Despite mixed results on the effectiveness of wildlife warning signs alone (Gunson and Schueler 2012, Bond and Jones 2013), they remain a simple and cost-effective tool to alert drivers to the potential presence of snakes. There is considerable variation throughout the active seasons. There is a concern that increasing awareness of snakes on the road will increase intentional killings by drivers, however, if signage can be integrated alongside efforts to dispel common fears and misconceptions about snakes, I believe that this could still be an effective way to further mitigate direct road mortality. Experiential education programs that emphasize the ecological value of snakes and teach safe coexistence strategies have proven effective in shifting public perception (Larson et al. 2024). During fieldwork in the White Lake Basin, frequent engagement with residents has helped educate and foster awareness toward local snake populations. While difficult to quantify, the presence of researchers may have positively influenced the driving behaviour of residents, potentially contributing to reduced road mortality. Without continued study and visibility in the area, however, this influence may fade over time. As such, investing in long-term educational programs and while continuing to alert drivers to snake presence on roads could help sustain these positive effects and support long-term conservation outcomes.

## **FUTURE RESEARCH CONSIDERATIONS**

### *1. Detection and use of ecopassages by individual snakes*

Using the White Lake ecopassages, Spruyt (2024) assessed preliminary use with camera monitoring at the entrances of each ecopassages. While effective in quantifying appearances, cameras fail to properly discern the number of unique individuals using ecopassages. This makes it difficult to determine if use is more indicative of individual activity or if population level effects can be inferred. For example, ten rattlesnakes using an ecopassage once implies something substantially different than one rattlesnake using an ecopassages ten times. While many studies have deployed automated PIT tag scanners to detect individual use (Colley et al. 2017, Testud et al. 2019, Boyle et al. 2021), we chose to deploy camera traps to capture a broader spectrum of species, most of which have few to no tagged individuals. Ideally If sufficient individuals in the targeted species are tagged – either through PIT tags, or visual markings – future research should attempt to quantifying unique individuals using ecopassages as a more effective and precise way of monitoring use.

### *2. Historical changes in road mortality for gopher snakes and racers*

While population estimates in the basin have not been conducted for gopher snakes and racers, mortalities of all vertebrates were recorded during road mortality surveys. In the final two years of our study (2023-2024), there was an increased effort devoted to the mark-recapture of both gopher snakes and racers, however finding and capturing individuals (particularly racers) remains a major obstacle in estimating the population structure and abundance of these animals. While rattlesnakes were the primary focus of our 10-year road mortality study, temporal changes in the rates of road mortality for gopher snakes and racers can be calculated with the same formula used in Chapter 2 of this thesis. This will allow managers to see if ecopassages are effective in decreasing mortality rates across a broader spectrum of species and will inform mitigation measures at locations where there are multiple targeted species.

### *3. Investigate the proximate causes of road avoidance in snakes*

My thesis demonstrated consistent alterations in movement patterns near roads, indicating that all three focal species are strongly affected by the barrier effect. Although road avoidance behaviour is well documented in snakes (Robson and Blouin-Demers 2013, Siers et al. 2014,

Paterson et al. 2019), the underlying mechanisms driving this behaviour have not been clearly identified. Future studies should seek to determine whether road avoidance is an innate or learned response and quantify potential driving mechanisms such as vehicle noise, lack of available cover, or the perception of vehicles as predatory threats.

## CONCLUSION

Both the direct and indirect effects of roads represent a serious source of mortality and threat to population persistence for the Western Rattlesnake, Great Basin Gopher snake and Western Yellow-Bellied Racer populations within the White Lake Basin. While the results from my thesis provide one of the most comprehensive snake studies on the effectiveness of ecopassages, it also underscores the complexity of road networks on natural systems and the profound impacts that even minimal disturbance to a landscape can have on snake species. While ecopassages can be an effective tool to mitigate road mortality for Western Rattlesnakes, the lack of population recovery suggests additional unaccounted for factors. One such factor may stem from the results of my movement study (Chapter 3) that uncovered behavioural road avoidance across all three species. For species with a slow life history (common in populations of northern snakes) the consequences of direct mortality are likely a more immediate cause for concern than the barrier effect. However, given that the overarching goal of conserving and promoting population persistence through a reduction in direct road mortality (using ecopassages) was not demonstrated in this study, addressing the indirect effects of roads may play a larger role in mitigating the impacts of roads in this and other ecosystems.

I have been incredibly fortunate to have had the opportunity to work with these imperiled species and have developed a great appreciation for ecosystem in which they reside. My overarching objective is that the results, conclusions and management recommendations outlined in my thesis will aid in the conservation and development of management strategies that protect these three at-risk snake species and their environment. Further, I hope this work contributes to a more holistic understanding of the response of wildlife species to the growing anthropogenic threats faced around the world.

“To love a place is not enough. We must also find ways to heal it.”

- Robin Wall Kimmerer

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## APPENDIX A

### ECOPASSAGE INSTALLATION AND MONITORING SPECIFICATIONS

In September 2017, four ecopassages were newly installed through the study area at identified snake roadkill hotspots, and modifications were made to an additional four existing drainage culverts. This produced eight ecopassages within a 6.5 km stretch of road, with the intended purpose of lowering Western Rattlesnake road mortality. All eight ecopassages were made from corrugated metal, although, the newly installed ecopassages were more oval-shaped than the older, rounder drainage culverts. The ecopassages had an average length of  $12 \pm 1$  SD m, height of  $45 \pm 8$  SD cm, and width of  $67 \pm 12$  SD cm, with an average openness (= height \* width / length) of  $2.5 \pm 0.5$  SD cm. A substrate of sand (~ 5 cm deep) lined the bottom of the culverts.

In April 2019, drift fencing was added to some of the entrances of the ecopassages, with a design specifically targeted towards directing snake movement (model AMX-SP40, Animex Wildlife Fencing Solutions) into the ecopassages. Construction of the fences was hampered by bedrock, drainage patterns, and cattle use, thus preventing a robust experimental design, such as altering fencing on upslope versus downslope entrances of the ecopassages. Still, drift fences (varying lengths, and ~ 75 cm in height) were established at one end of each of seven ecopassages, while one received no fencing. Fence lengths flanking the entrances of the ecopassages ranged from a total length of 43-63 m, with an average length of  $51.5 \pm 8.3$  SD m. A total of 0.4 km of the 23.4 km of road edge within the study area were fenced (Spruyt 2024).

Bushnell HD Natureview cameras (model numbers 119439, 119440, and 119740) equipped with 46 cm focal lenses were used to monitor snake use of the ecopassages. The cameras were located immediately inside the entrances of all eight ecopassages, resulting in a total of 16 deployed cameras. Cameras were set to high sensitivity and took 3 consecutive photos (each 1 second apart) when activated by movement, as well as timed captures each hour on the hour. The cameras were active from early April to early October each year from 2019 – 2023. Every two weeks the Secure Digital (SD) cards were switched out and the batteries replaced if necessary. Photos were manually processed to identify the presence of snakes. Data recorded for each animal captured on camera included date, time, species, culvert entrance ID, field scan/ motion sensor activation, and direction of travel [see Spruyt (2024) for further details].

Ecopassage and directional fencing dimensions for the eight installed structures in the White Lake Basin.

Ecopassage Code	Ecopassage Entrance	New/ Existing	Mouth width (cm)	Mouth height (cm)	Distance from ecopassage mouth to road (m)	Fence length from centre of ecopassage (m)	Fence direction from culvert
1	North	New	78	31	1.05	19.6	East
1	South	New	77	43	3.85	23.4	West
2	North	Existing	65	60	2.7	27.2	East
2	South	Existing	74	46	2.25	24	West
3	North	New	79	35	1.27	40	East
3	South	New	77	44	3.5	2.8	West
4	West	Existing	48	46	3.1	30.5	North
4	East	Existing	45	36	2.42	16.8	South
5	West	Existing	47	35	0.7	33	North
5	East	Existing	53	48	1.45	29.7	South
6	West	Existing	66	58	3.34	31.2	North
6	East	Existing	59	49	2.7	31.2	South
7	West	New	76	43	1	44.2	North
7	East	New	73	46	5.4	6.6	South
8	West	New	77	49	2.54	NA	NA
8	East	New	74	49	2.18	NA	NA

## APPENDIX B

### YEARLY TRAFFIC VALUES AND SURVEYED DENS

Maximum daily average traffic values along White Lake and Willowbrook roads from approximately April – October. Yearly values reflect the mean value from both roads. Data in 2018 was lost when traffic counters were removed from the field prematurely by highway workers.

Year	Maximum daily average traffic
2015	266
2016	338
2017	337
2018	-
2019	403
2020	505
2021	522
2022	534
2023	494
2024	462

Abbreviated names and distance to nearest road (m) for eight surveyed locations within the White Lake Basin. Six locations were surveyed for mark-recapture surveys while the remaining two locations (EWL, WLDF) were surveyed only for telemetry individuals. For location data, please refer to the BC Conservation Data Centre.

Den Code	Den name	Distance to nearest road (m)	Mark Recapture Location
BD	Bear's Den	140.5	Y
EWL	East White Lake	388.8	N
GG	Green Gate	154	Y
G	Guernsey	76.8	Y
GC	Guernsey Corner	4	Y
LR	Little Rattle	176.2	Y
WLDF	White Lake Drift Fence	85	N
WT	White T	353.6	Y

## APPENDIX C

### INDIVIDUAL MORPHOMETRIC, MOVEMENT AND ROAD METRICS

Column description key for summary statistics (below).

Column Code	Description	Units
Species	CROR = Western Rattlesnake PICA = Great Basin Gopher snake COCO = Western Yellow-Bellied Racer	-
ID	Individual identification code	-
90%, 95%, 99% BBDM	Home range derived from Brownian Bridge utilization distribution models	Hectares
SPL	Seasonal path length	Meters
MMR	Mean movement rate	Meters/Day
MF	Movement frequency	-
PS	Path sinuosity	Radians/meter <sup>-0.5</sup>
MND	Maximum net displacement	Meters
REE 3m, 5m, 10m	Road encounter events	-
RCE	Road crossing events	-
Origin location	Initial point of capture. Refer to Appendix B for longform names	-
Whole season	Y/N – Was the snake tracked for the full season	-
SVL	Snout-vent length	Centimeters
Mass	Weight	Grams
# fixes	Number of times relocated	-
Total days	Days from spring release until fall capture, or loss of individual	-
Days/fix	Days in between relocations	-

Summary statistics for 36 individual snakes (12 Western Rattlesnake (CROR), 12 Great Basin Gopher snake (PICA), 12 Western Yellow-Bellied Racer (COCO)) radio tracked in 2023 and 2024 in the White Lake Basin, in South-central British Columbia.

Species	ID	90% BBDM	95% BBDM	99% BBDM	TPL	MMR	MF	PS	MND	REE 3m	REE 5m	REE 10m	RCE
COCO	CO23-1	0.14	0.20	0.30	5218.6	174.1	1.00	0.13	823.24	1	1	1	0
COCO	CO23-2	0.03	0.05	0.16	1409.3	93.89	0.79	0.14	818.67	0	0	0	0
COCO	CO24-1	0.12	0.15	0.20	1609	201.17	-	0.13	534.84	0	0	1	1
COCO	CO23-3	0.01	0.03	0.09	2302.3	92.22	0.91	0.14	551.14	1	1	3	0
COCO	CO23-4	0.07	0.09	0.15	2807.8	108.03	0.91	0.15	390.52	2	2	2	0
COCO	CO24-2	0.01	0.02	0.06	1345.1	79.25	-	0.13	595.96	1	1	1	0
COCO	CO23-5	0.03	0.04	0.13	824.6	51.56	0.77	0.18	377.00	2	2	4	0
COCO	CO24-3	0.05	0.07	0.12	1883.7	104.28	-	0.14	462.39	1	1	1	0
COCO	CO24-4	0.05	0.10	0.22	2273.1	162.36	-	0.09	764.51	0	1	2	0
COCO	CO23-6	0.07	0.12	0.21	2596.2	83.86	0.74	0.14	569.25	1	1	3	0
COCO	CO24-5	0.06	0.12	0.25	5463.4	202.42	-	0.11	663.38	2	2	2	0
COCO	CO24-6	0.03	0.05	0.13	3103.5	129.38	-	0.17	426.35	0	0	2	0
CROR	CR24-1	0.30	0.46	0.81	7529.6	284.89	-	0.09	1895.44	5	5	5	0
CROR	CR23-1	0.16	0.25	0.46	6288.4	119.64	0.74	0.07	1386.36	0	0	0	0
CROR	CR24-2	0.00	0.03	0.07	138	27.6	-	0.21	113.95	0	1	1	0
CROR	CR24-3	0.19	0.32	0.62	4827.6	208.2	-	0.11	1785.99	8	9	9	3
CROR	CR23-2	0.07	0.14	0.58	11848	162.82	0.52	0.06	1763.44	3	9	9	0
CROR	CR23-3	0.12	0.16	0.29	6124.6	185.67	0.81	0.10	1903.02	0	0	3	0
CROR	CR23-4	0.13	0.26	0.51	7719.6	149.56	0.71	0.09	1562.44	2	2	2	0
CROR	CR24-4	0.06	0.15	0.40	4872.1	147.72	-	0.10	595.48	0	0	0	0
CROR	CR23-5	0.15	0.33	0.78	14028.9	221.36	0.74	0.05	2757.88	0	0	0	1
CROR	CR24-5	0.37	0.56	0.89	4819.4	160.62	-	0.09	2040.00	0	0	0	0
CROR	CR24-6	0.13	0.29	0.55	4035.3	130.17	-	0.10	1160.72	0	3	6	2
CROR	CR23-6	0.01	0.06	0.25	3199.8	103.21	0.52	0.12	651.16	15	15	16	3
PICA	PI23-1	0.02	0.04	0.10	2456.5	42.39	0.63	0.20	224.45	2	3	4	0
PICA	PI23-2	0.05	0.06	0.09	1986.5	34.89	0.61	0.21	154.99	0	0	2	0

PICA	PI23-3	0.16	0.29	0.49	6148.6	111.52	0.56	0.10	1211.13	3	3	3	0
PICA	PI24-1	0.05	0.07	0.16	4176.9	135.72	-	0.10	505.92	0	0	0	0
PICA	PI24-2	-	0.02	0.12	815.2	74.15	-	0.20	242.03	6	8	8	0
PICA	PI23-4	0.02	0.04	0.07	1664.7	110.9	0.71	0.17	285.56	0	0	0	0
PICA	PI23-5	-	-	0.00	406.4	63.58	0.64	0.20	150.28	8	9	11	0
PICA	PI24-3	0.12	0.18	0.28	2262.6	91.55	-	0.12	951.78	1	1	1	0
PICA	PI24-4	0.05	0.10	0.19	1389.3	50.3	-	0.19	328.94	9	0	9	0
PICA	PI23-6	-	0.01	0.13	1348.3	30.28	0.92	0.31	146.51	0	0	0	0
PICA	PI24-5	0.08	0.17	0.31	2608.8	155.5	-	0.14	826.32	0	0	0	0
PICA	PI24-6	0.08	0.12	0.22	1557.7	47.24	-	0.13	647.93	0	0	0	0

Species	ID	Initial den	Whole season	SVL	Mass	# fixes	Total days	Days/fix
COCO	CO23-1	GC	Y	72.1	137	31	132	4.26
COCO	CO23-2	GC	N	55.2	65	16	62	3.88
COCO	CO24-1	EWL	N	60	75	9	36	4
COCO	CO23-3	WLDF	Y	60.7	87	26	94	3.62
COCO	CO23-4	GC	Y	58.8	76	27	99	3.67
COCO	CO24-2	GC	N	64	102	19	60	3.16
COCO	CO23-5	WLDF	N	50.4	70	17	60	3.53
COCO	CO24-3	GC	Y	52	47	28	101	3.61
COCO	CO24-4	CUL7	N	71	132	15	50	3.33
COCO	CO23-6	WT	Y	55.4	66	32	121	3.78
COCO	CO24-5	GC	Y	57	78	25	91	3.64
COCO	CO24-6	EWL	Y	57	79	25	91	3.64
CROR	CR24-1	GG	Y	83	361	32	119	3.72
CROR	CR23-1	GC	N	85	382	21	72	3.43
CROR	CR24-2	G	N	89	538	5	14	2.8

CROR	CR24-3	G	Y	80	393	31	113	3.65
CROR	CR23-2	GC	Y	81.3	452	35	132	3.77
CROR	CR23-3	GG	Y	81.2	392	35	125	3.57
CROR	CR23-4	GC	Y	76.5	347	35	132	3.77
CROR	CR24-4	EWL	Y	89	494	34	119	3.5
CROR	CR23-5	WT	Y	88.2	392	36	126	3.5
CROR	CR24-5	G	Y	88	240	31	119	3.84
CROR	CR24-6	WT	Y	64	186	32	119	3.72
CROR	CR23-6	G	Y	63.1	157	33	119	3.61
PICA	PI23-1	GC	Y	95	309	33	120	3.64
PICA	PI23-2	LR	Y	104	485	38	132	3.47
PICA	PI23-3	GC	Y	92	308	36	132	3.67
PICA	PI24-1	EWL	Y	88	302	34	119	3.5
PICA	PI24-2	GC	N	78	200	12	39	3.25
PICA	PI23-4	BD	N	97.2	372	11	43	3.91
PICA	PI23-5	GC	N	88.8	284	11	41	3.73
PICA	PI24-3	GC	Y	81	196	35	119	3.4
PICA	PI24-4	GC	Y	99	460	34	119	3.5
PICA	PI23-6	BD	Y	85.4	254	34	132	3.88
PICA	PI24-5	LR	N	90	281	24	87	3.63
PICA	PI24-6	WT	Y	97	366	34	119	3.5

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