IMPACTS OF ROAD MORTALITY ON THE WESTERN RATTLESNAKE (*CROTALUS OREGANUS*) IN BRITISH COLUMBIA

by

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ABSTRACT

Direct mortality due to wildlife-vehicle collisions has emerged as a major and worldwide conservation threat to wildlife. This source of mortality may be particularly adverse for populations persisting at the periphery of their range, where existing natural constraints already limit population growth and vigour. As a result, conservation assessment and planning for many peripheral species-at-risk will benefit from a fundamental understanding of the impacts of road mortality, yet these can be difficult to isolate due to the interaction of a number of factors. Using population viability analysis (PVA) I evaluated the persistence of a Western Rattlesnake (*Crotalus oreganus*) population threatened by road mortality in the dry interior of British Columbia, Canada. From 2015-2016 I quantified road mortality through methodical road surveys and coincidental assessments of scavenging rates and observer detection probability using planted snake carcasses. Additionally, I conducted intensive mark-recapture and radio-telemetry to estimate population density, size, and the range of the study population. After accounting for sources of error, my modelling showed that the estimated number of rattlesnake deaths was 2.7× the number of carcasses detected through unadjusted surveys and incidental observations. Overall, an estimated 6.6% of the population was killed on the road annually under traffic conditions that amounted to a maximum of only 350 vehicles per day. The PVA indicated that the population still was likely to persist for the next 100 years, but with a continual decline under the current, observed road mortality rate. With the loss of 6.6% of the population/year, the projected probability of extinction was <0.01 in 100 years and 0.0 in 50 years. At simulated road mortality rates of ≤6% there was zero probability of extinction for this population of rattlesnakes within the next 100 years. However, at the extinction threshold of road mortality of 6%, the stochastic growth rate was -0.032, and the mean population size was estimated to decrease by 96% in 100 years. Simulations with road mortality rates >6% consistently put the population at risk of extinction over 100 years. In comparison, the growth rate in the absence of road mortality was 0.0047 and the population was projected to increase (60% increase over 100 years). My results also suggest that in theory, improving adult female survival as well as overall longevity of rattlesnakes would significantly increase the population growth rate. My method

of estimating population size for the area impacted by road deaths likely presents an overestimate, suggesting that the actual risk to this population is greater than what the models have implied. The detailed PVA using refined road mortality estimates provides strong evidence that road mortality is and will be a significant contributor to population decline, and adds to the growing body of evidence that large populations of long-lived species will face extirpation under low levels of road mortality, even in the absence of other sources of disturbance. Conservation priorities should focus on reducing road mortality and improving habitat availability away from roads.

Keywords: *Crotalus oreganus*, observer detection, population estimate, population viability analysis, road mortality, scavenging, Western Rattlesnake.

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DEDICATION

For the Greek gods and mythical creatures that allowed me into their world

Every individual matters. Every individual has a role to play. Every individual makes a difference.

– Jane Goodall

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CHAPTER 1

INTRODUCTION

Wildlife Road Mortality

The fragmentation of ecosystems by roads inevitably results in movements of animals across roads to reach habitats or other resources. Some animals may even be attracted to the roads themselves (e.g. nesting habitat - Aresco 2005; scavenging - Schwartz et al. 2018). Much the same as other human developments, there is a high density of roads located in productive areas (Ibisch et al. 2016) where there is also high biodiversity (Luck 2007), exacerbating the rate of wildlife-vehicle encounters. More often than not these confrontations with roads have negative results for animals (Trombulak and Frissell 2000; Fahrig and Rytwinski 2009). The most visible effect of roads on wildlife is direct mortality from traffic collisions, an event that likely has repercussions on populations beyond just the death of an individual. Direct road mortality also may be closely tied to the barrier effect, when animals are prevented from crossing a road through either severe mortality or road avoidance. This in turn effectively fragments populations and leads to genetic isolation (Andrews et al. 2008; Shepard et al. 2008). Other indirect effects of roads include easier access for predators and human hunters (e.g. DeMars and Boutin 2018), the spread of invasive species and disease, and alteration, degradation, pollution, and loss of habitat (see Coffin 2007). The compounding of all these effects in turn may culminate in even greater impacts at the population or community levels.

The burgeoning field of road ecology primarily seeks to identify, address and mitigate issues related to roads, yet to date entirely effective solutions still are lacking, possibly due to an incomplete understanding of road mortality impacts on populations (Andrews et al. 2008). Although a considerable amount of research has focused on assessing roadkill patterns, fewer studies have looked at the impact on a larger scale (Forman et al. 2003; van der Ree et al. 2011). This likely is due to the difficulty in quantifying road effects: to understand fully the effects of road mortality on populations, studies must be intensive, long-term, and accompany assessments of the surrounding wildlife populations rather than just collect evidence on the road itself. Without this information, it is difficult to tease out effects of road mortality from other threats a population may be facing.

Part of understanding the fundamental and ecological effects of roads is revealing how factors influence population growth singularly or in combination. For example, does road mortality simply limit populations, or does it play a regulating role (e.g. Hels and Buchwald 2001)? Factors that constrain population growth and density either by affecting birth or death rates are considered limiting, while factors that stabilize populations around an equilibrium through increases and decreases are regulating (Fryxell et al. 2014). Multiple factors likely exert both types of effects on populations (catastrophes, weather, competition for food or mates, predation, disease, etc.). In rare cases, roadkill may act as a regulating factor on a population based on the ecology of the affected animals (e.g. territorial species); however, in these cases roadkill is simply a proximate but not ultimate cause of regulation (Elfström et al. 2012). How a population responds after roadkill has been reduced or eliminated is a valuable indicator of how that specific source of mortality is affecting the population. In many cases, populations have rebounded once the limiting effect of road mortality has been removed. For example Jones (2000) observed a 50% recovery of an Eastern Quoll (*Dasyurus viverrinus*) population in two years after roadkill was reduced through mitigation efforts. Similar recoveries have been detected in snake populations after the cessation of illegal harvest events that are comparable to roadkill (Webb et al. 2002). Ramp and Ben-Ami (2006) showed that simulated reductions in roadkill, but not inter-specific competition or wildfire effects, resulted in increases in a Swamp Wallaby (*Wallabia bicolor*) population, suggesting that road mortality was exerting a limiting effect.

Multiple factors exerting effects on populations may work in additive, compensatory, or synergistic fashion (Breitburg et al. 1998; Vinebrooke et al. 2004). Situations where healthy, reproductively-important individuals are removed from populations via road mortality provide strong evidence of non-compensatory (i.e. additive or synergistic) effects. An example of this was shown by Bujoczek et al. (2011) for three bird species, where individuals killed on roads had better body condition compared to those taken by predators. Declines in populations that are impacted by roadkill further support the argument that road mortality is exerting an effect beyond that expected through a compensatory mechanism (Fryxell et al. 2014): for example, an increase of 2-3% in *additional* mortality due to roadkill was shown to result in negative population growth rates in turtle populations (Brooks et al. 1991; Gibbs and Shriver 2002). However, Ramp and Ben-Ami (2006) showed that a 20% reduction in roadkill of Swamp Wallabies allowed the population to reach carrying capacity, suggesting that road mortality may be compensatory to a certain point. All told, there is uncertainty around how road mortality interacts with natural mortality and it is probable that populations of concern respond differently (Fahrig and Rytwinski 2009).

The effect of roadkill and other parameters on the long-term persistence of wildlife can be explored through Population Viability Analysis (PVA). This tool uses simulation models to estimate population projections, particularly under threats to survival (Boyce 1992; Lacy 1993). If used cautiously (see Beissinger and Westphal 1998 for recommendations) predictions of how populations respond to road mortality and/or mitigation efforts can be highly accurate (Brook et al. 200) and valuable for conservation practitioners, especially when limited empirical information is available. The flexibility and breadth of PVAs allows for assessment of direct and indirect effects; for example, if genetic analysis is incorporated into a model it can strengthen the assessment and further illuminate the degree of isolation of populations (Frankham et al. 2014). Effects of road mortality may be assessed separately or in combination with other threats (e.g. fire - Miller 2006), presenting a more realistic scenario for some species-at-risk and addressing integrated management questions.

Despite the growing interest in using PVA to explore road effects, efforts to quantify mortality rates are hampered by several sources of error (Smallwood 2007; Boves and Belthoff 2012; Bishop and Brogan 2013). Vehicle-struck animals dying off of roads (crippling effects) and areas along roads obscured by vegetation or topography (habitat bias) are two such issues. Particularly problematic is the removal of carcasses by scavengers (scavenging effects) and the failure of observers to detect carcasses (observer error; Kline and Swann 1998; Slater 2002; Santos et al. 2011; Teixeira et al. 2013; Loss et al. 2014; Santos et al. 2016). Addressing these sources of error is critical for accurate assessments of road mortality rates, that in turn are imperative for robust PVAs that ensure rates and consequently extinction probabilities are not underestimated.

Conservation of Northern Reptile Species

Specific groups of animals can be especially susceptible to both direct road mortality and subsequent population declines. Reptiles, a group of global conservation concern (Saha et al. 2018), can be highly sensitive to road mortality effects (Kushlan 1988; Gibbs and Shriver 2002; Roe et al. 2006; Andrews et al. 2015). In a risk assessment of Californian reptiles and amphibians, Brehme et al. (2018) found over 50% of all reptiles evaluated were at high risk from road mortality. They also identified snakes, including all rattlesnake species (Family Viperidae), to be at the highest risk to road effects at the population level.

Rattlesnakes at northern ranges are liable to encounter roads during annual migrations (Fortney et al. 2012; Gardiner et al. 2013), a situation potentially exacerbated by strong fidelity in movement patterns (Gomez et al. 2015). While some road avoidance has been documented specifically in timber rattlesnakes (*Crotalus horridus*; Sealy 2002; Andrews and Gibbons 2005) it is generally accepted that large snakes show minimal road avoidance (Fahrig and Rytwinski 2009) and it is even suggested that snakes may be attracted to roads for thermoregulation (Sullivan 1981; Mccardle and Fontenot 2016). As large-bodied, venomous predators, rattlesnakes travel across roads slowly, freeze at oncoming traffic, and are difficult to distinguish on the road making them easily killed by vehicles (Andrews and Gibbons 2005). Additionally drivers may purposefully run-over rattlesnakes (Crawford and Andrews 2016).

The Western Rattlesnake (*C. oreganus*) near the northern limits of the species range (British Columbia, Canada) is a good subject for studying the population-level effects of road mortality. The cold climate requires these snakes to hibernate in traditional communal dens for six months each year (October – April; Macartney 1985), enhancing overwinter survival but also limiting the time available to the snakes for growth and reproduction (Macartney et al. 1990). Consequently, female Western Rattlesnakes exhibit delayed maturity, small litter size, and long reproductive cycles resulting in reduced reproductive rates (Macartney 1985; Macartney and Gregory 1988). These snakes are further constrained by the availability of adequate overwinter habitat leading to natal philopatry and likely low immigration rates between hibernacula (den sites) as seen in other *Crotalus* species (Clark et al. 2008). As a long-lived reptile species with low reproductive output and high philopatry, Western

Rattlesnake populations are unlikely to be able to compensate for losses through roadkill (Parker and Plummer 1987; Andrews et al. 2015; Brehme et al. 2018) and therefore their vulnerability to road mortality likely threatens northern populations.

In this thesis, I quantified direct road mortality and its effect on the persistence of a Western Rattlesnake (*C. oreganus*) population in British Columbia, Canada. I conducted methodical road surveys and assessments of scavenging rates and observer detection probability using planted snake carcasses. Additionally, I conducted intensive mark-recapture and radio-telemetry of the rattlesnake population to estimate population density, size, and home range.

The research objectives of my thesis were to:

1. Quantify rattlesnake road mortality accurately by accounting for associated sources of error (scavenging and observer detection);
2. Characterize the rattlesnake population affected by road mortality; and
3. Assess the long-term persistence of the population under the threat of roadkill and sensitivity to changes in mortality rates.

In the remaining portion of this chapter, I provide an overview of my study site and what is known of the ecology of Western Rattlesnakes in British Columbia, Canada. In Chapter 2, I investigate the relationship between roadkill and scavenging rates to determine the annual road mortality rate. In Chapter 3, I use PVA to incorporate these results with demographic and life history traits of the rattlesnake to assess extinction probability for the study population. Finally, in Chapter 4, I briefly summarize the key findings of my research and discuss the significance of these results for management of the species. I conclude with suggestions for further research and recovery strategies for conservation of the Western Rattlesnake in British Columbia.

Study Site

My research was conducted within the White Lake Basin (latitude 49°N, longitude 119°W) in the South Okanagan region of British Columbia, Canada (Figure 1.1). This arid basin ecosystem consists of open Ponderosa Pine (*Pinus ponderosa*) forests, rolling hills, and

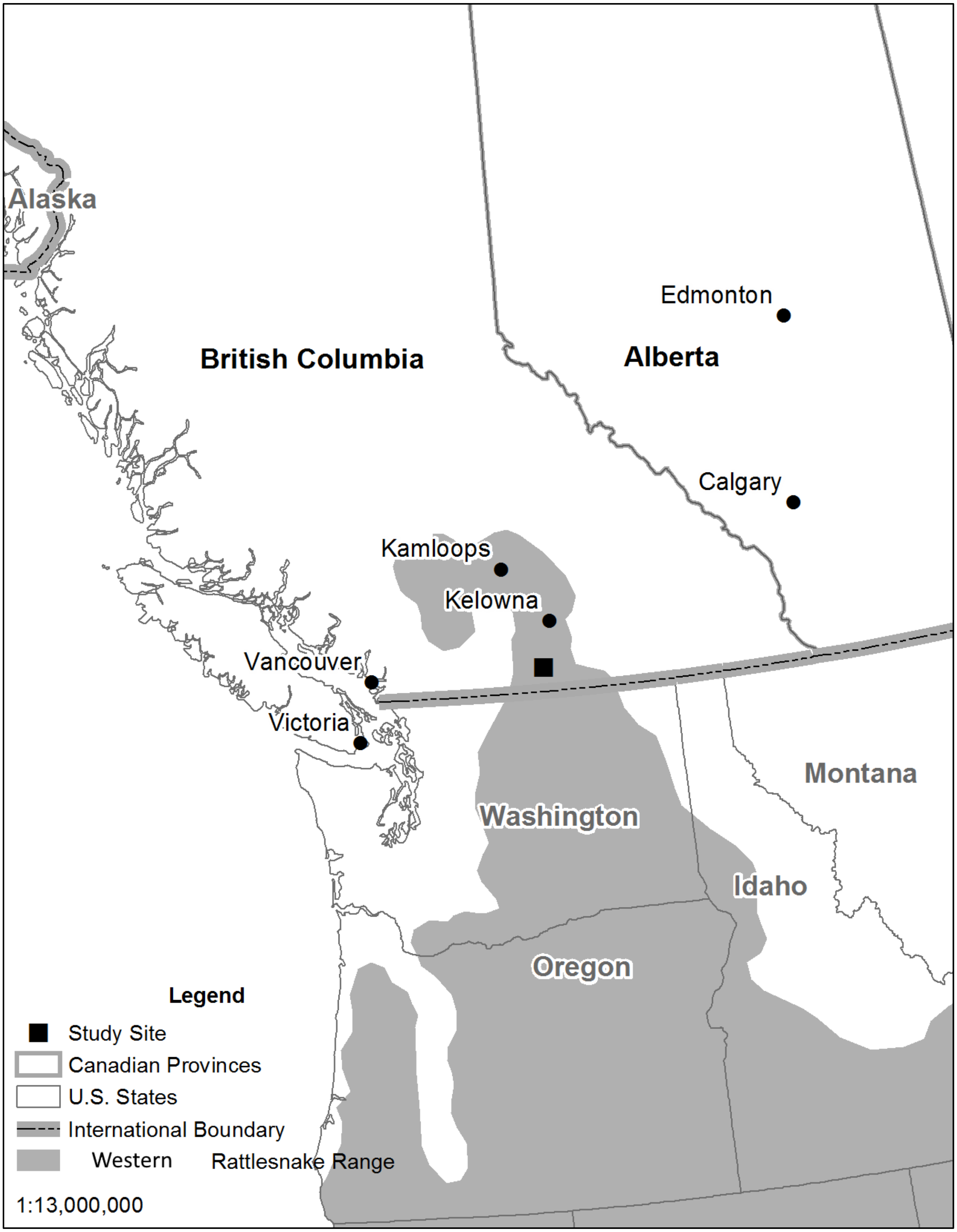
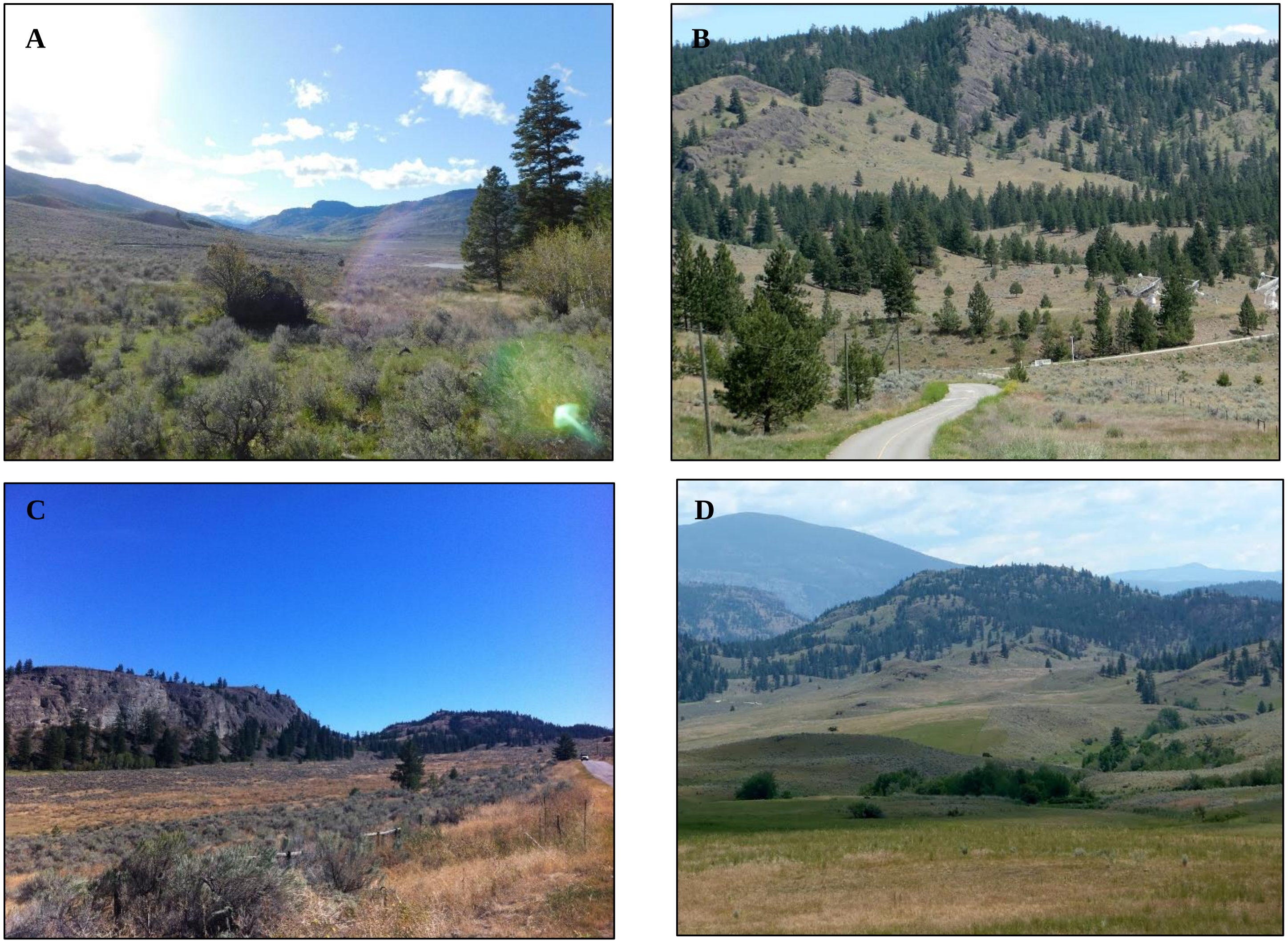


Figure 1.1. Study site location within the Western Rattlesnake (*Crotalus oreganus*) range in western North America.

rocky bluffs surrounding open shrub-steppe and grassland habitat, predominantly characterized by Bluebunch Wheatgrass (*Agropyron spicatum*), and Big Sagebrush (*Artemisia tridentata*) and containing numerous riparian areas and wetlands (Meidinger and Pojar, 1991; Figure 1.2). The area provides critical habitat for Western Rattlesnakes (COSEWIC 2015), including overwinter hibernacula, seasonal migratory corridors, and summer foraging habitat. At least 26 rattlesnake dens have been identified throughout this area. Elevation within the basin ranges from 500 – 1100 m.

Species and habitat within my study site are protected by both federal and provincial designation. The larger portion of the area lays predominantly on National Research Council property surrounding the Dominion Radio Astrophysical Observatory, which is in turn leased and managed by The Nature Trust of British Columbia as the White Lake Basin Biodiversity Ranch. Ranching is permitted to continue in this area in an integrated manner with habitat conservation (TNTBC 2018). A smaller portion of the study site is located within the provincial White Lake Grasslands Protected Area. A variety of recreational activities occur in the area including hiking, bicycling, horseback riding, and bird watching (BC Parks 2003). A small number of private farms also are located in the area and there are residential communities located to the north, south, and west of the study site.

A paved, undivided two-lane road (BC Class 5 highway) with an unposted speed limit of 80 km/h traverses the White Lake Basin bottom (Figure 1.3). Traffic counters placed by the BC Ministry of Transportation and Infrastructure show this road experiences relatively low average traffic volume (maximum of 350 vehicles/day) during April-October. The north-south portion of the road consistently receives higher volumes of traffic (310-350 vehicles/day) compared to the east-west portion (170-240 vehicles/day) although both roads see increases in traffic volumes during the summer months (Figure 1.4). The east-west portion had a substantial increase in traffic volume from 2015 to 2016. Vegetation along the road shoulder was maintained in each year of the study by annual mowing to a height of less than 0.5 m for a distance of 1.8 m from the road edge. A barbed wire fence was located approximately 5 m from the road edge. The road bisects rattlesnake habitat within the basin and separates rattlesnake hibernacula, which are located between 5 m - 1.4 km from the road. Records show that roadkill has been affecting the population of rattlesnakes in the White Lake Basin for the past 30 years at least (Pickard 2009).



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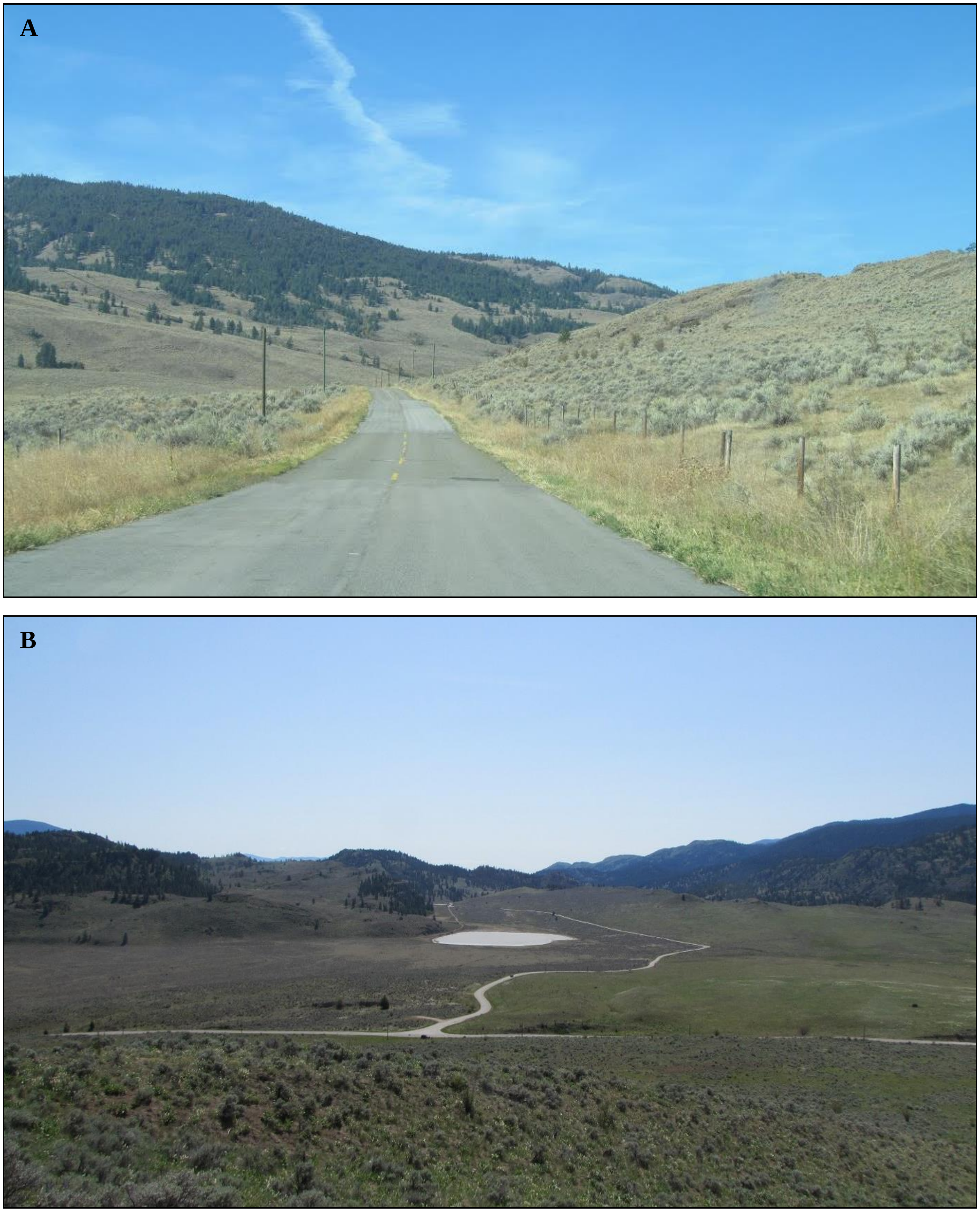

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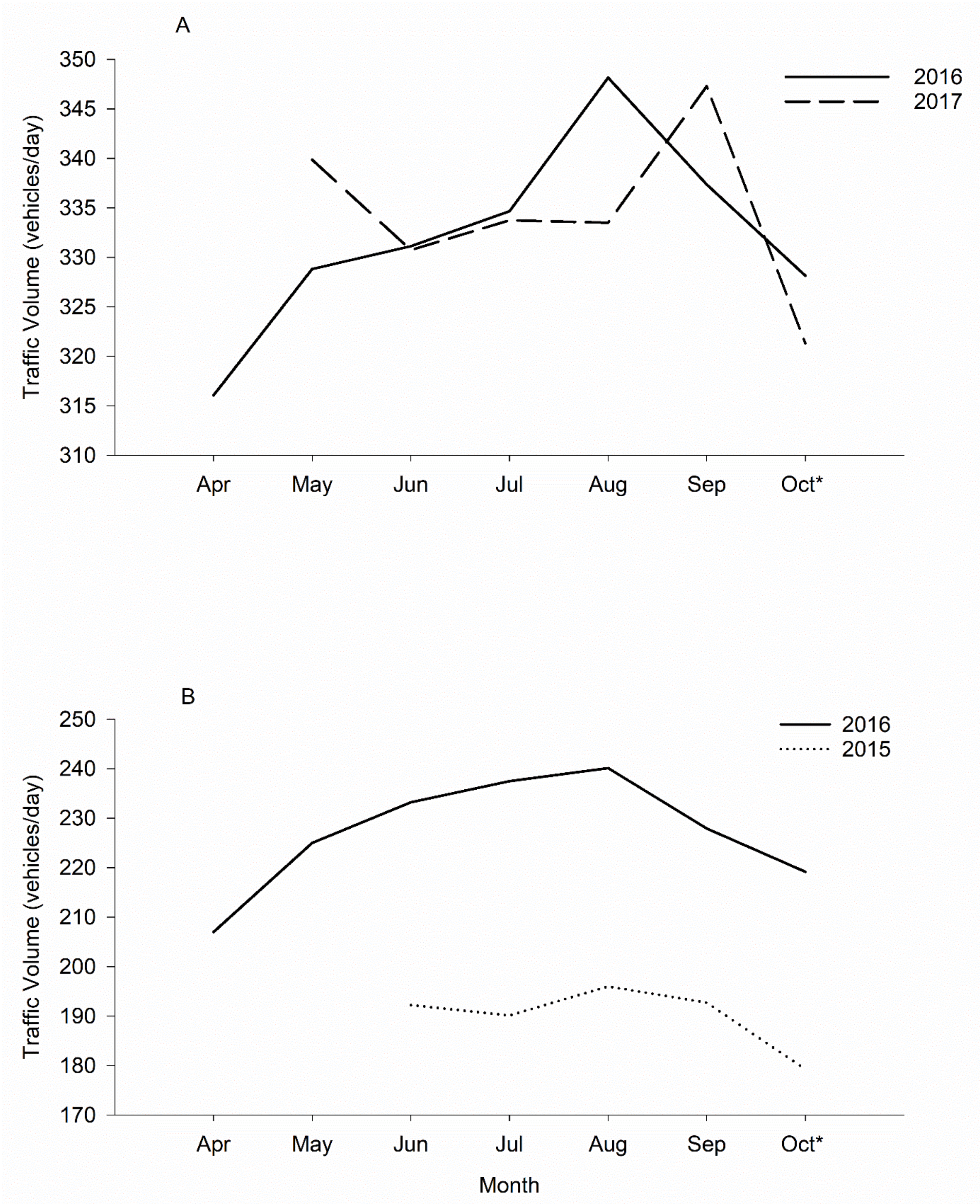

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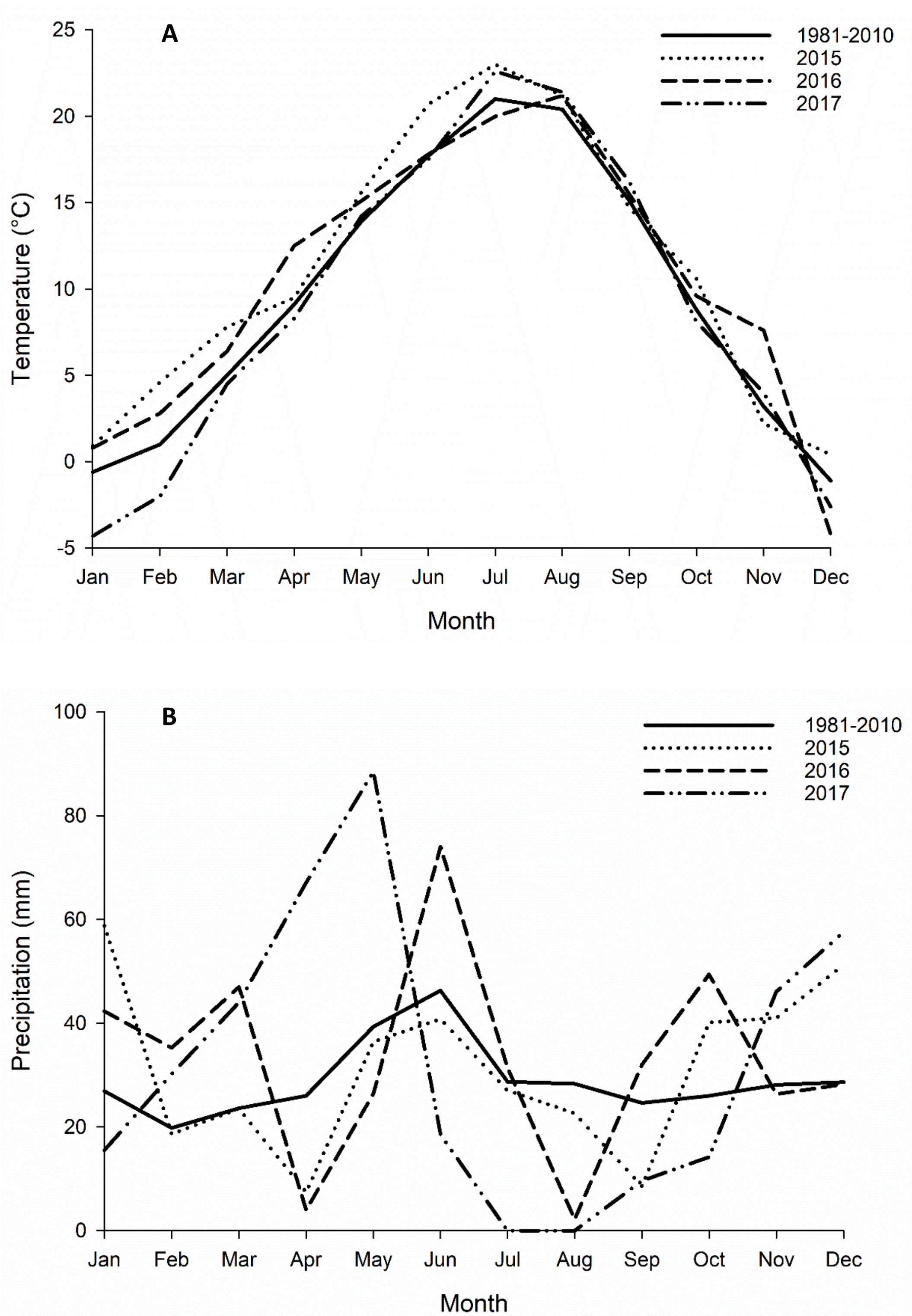
The White Lake Basin, within the South Okanagan valley, is characterized by hot, dry summers and long, cold winters with temperatures reaching below freezing (Meidinger and Pojar 1991; Figure 1.5). In 2015, it was slightly warmer than average from May to July, and it was colder than average from December 2016 to February 2017; however, the mean monthly temperatures over the three years did not differ appreciably from the 30-year mean. Total monthly precipitation also followed a similar trend to the 30-year mean with greater variation and with the exception of 2017, which had high amounts of precipitation in May and none in July or August.



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CHAPTER 2

ESTIMATING ACTUAL VERSUS DETECTED ROAD MORTALITY RATES FOR A NORTHERN VIPER

INTRODUCTION

Estimates of road mortality are essential for informing conservation efforts on many wildlife species, yet accurately quantifying these rates is not straightforward. Overall, experimental evaluations of road mortality survey errors involving terrestrial vertebrates show that actual mortality rates are at least two times higher than rates determined without adjustment for sources of error (Kline and Swann 1998; Slater 2002; Teixeira et al. 2013; Santos et al. 2016). Four main sources of error potentially bias conventional road-mortality surveys (Smallwood 2007; Boves and Belthoff 2012; Bishop and Brogan 2013): scavenger-removal, observer detection error, crippling bias (when injured animals leave the roadside before dying) and habitat bias all may cause researchers to underestimate the actual number of animals killed on the road, as the numbers of dead animals detected rarely represents an accurate death toll. The highest amount of uncertainty in road mortality rates comes from scavenger-removal and observer detection error (Loss et al. 2014).

In particular, road mortality rates for rare and cryptic species, such as snakes, are difficult to evaluate with accuracy and often are underreported. Santos et al. (2011) suggested that road surveys for snakes should be conducted on a daily basis to avoid missing significant numbers of carcasses before they are removed by scavengers. Degregario et al. (2011) determined that 50% of snake carcasses were removed by scavengers after only eight hours on the road, a pattern further supported by Enge and Wood (2002) who determined 70% of snake carcasses were removed within one day. Rapid removal is particularly evident on paved roads (Hubbard and Chalfoun 2012) where snakes are easily detected by scavengers (Antworth et al. 2005). However, human observer detection rates during reptile roadkill surveys, including those for snakes, generally are low: Gerow et al. (2010) and Santos et al. (2016) found detection rates of only four and six percent, respectively. Small-sized carcasses most commonly are overlooked (Santos et al. 2016); leading to data biases for species, sexes, and age classes (Hartmann et al. 2011).

The common method for evaluating mortality rates through road surveys provides snapshots of the density of dead animals on the road. At any given time, this density is determined by the mortality rate (which adds dead animals to the road) and the rate at which carcasses are removed by scavengers. Because these rates will reach an equilibrium over time (Teixeira et al. 2013), an indirect way to calculate the road mortality rate is by measuring the removal rate and the observed density. However, sources of error in road mortality estimates are not consistent across geographic locations or habitats (Slater 2002; DeGregorio et al. 2011), nor clades of species (Santos et al. 2011; Teixeira et al. 2013; Santos et al. 2016), and therefore must be assessed within a given region. Since road mortality affects a wide variety of animals, numerous scavenging and detectability studies often simultaneously monitor for a broad range of species and then group animals by class. Given the distinct morphological traits snakes possess compared to other reptiles, this is likely an inadequate approach for this taxon. Unfortunately, studies specific to snakes often independently consider either scavenger-removal or observer error but not both.

I assessed road mortality rates and associated sources of error for a population of Western Rattlesnakes (*Crotalus oreganus*) in an arid grassland ecosystem in British Columbia, Canada. Dead rattlesnake detections on a two-lane road were quantified along with scavenger-removal and observer detection rates. I predicted that, after accounting for these factors, the actual number of rattlesnake deaths would be at least two times higher than the number of rattlesnake carcasses detected.

METHODS

Study Site

The study was conducted in 2015 and 2016 within the White Lake Basin (latitude 49°N, longitude 119°W) in the South Okanagan region of British Columbia, Canada (Figure 2.1) during April-October. This basin consists of forested, rolling hills and steep bluffs surrounding open shrub-steppe and grassland habitat, predominantly characterized by Bluebunch Wheatgrass (*Agropyron spicatum*), Big Sagebrush (*Artemisia tridentata*) and Ponderosa Pine (*Pinus ponderosa*) (Meidinger and Pojar 1991). The Nature Trust of British

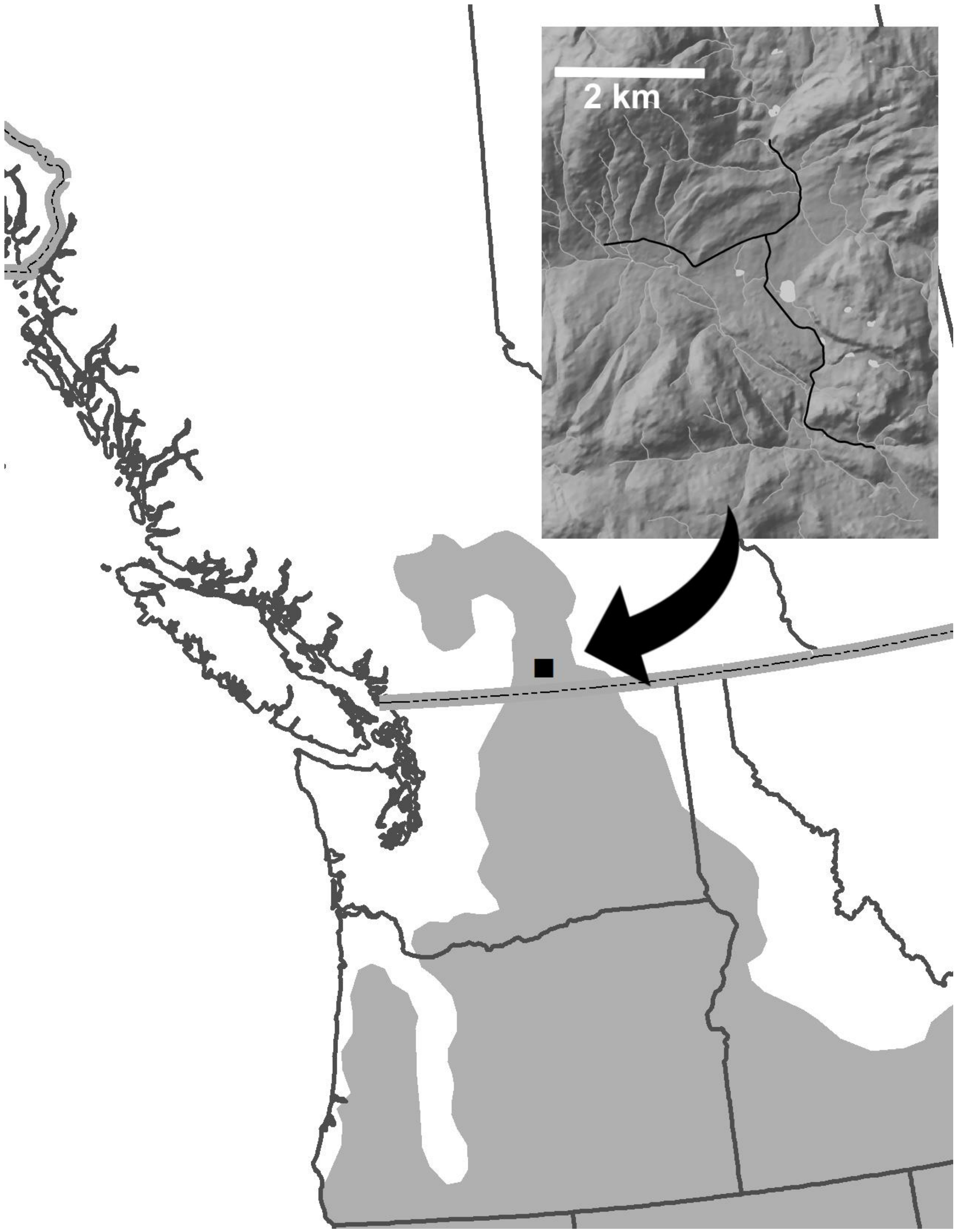

Figure 2.1. Location of the study site within the range of Western Rattlesnakes (*Crotalus oreganus*) in western North America and an inset of the survey route in the White Lake Basin, BC, Canada.

Columbia (TNTBC) manages the area with the objective to "integrate livestock management with conservation of habitat for species at risk" (TNTBC 2018).

A paved, undivided two-lane road (BC Class 5 highway) with an unposted speed limit of 80 km/h traverses the basin bottom (elevation 500 m). Through April-October of my study years, the average daily maximum traffic volume passing through the 11.7 km study area of the road (Figure 2.1) was 350 vehicles as measured by traffic counters provided by BC Ministry of Transportation and Infrastructure. During this time [hereafter referred to as 'the active season'] the rattlesnakes in the basin migrated to and from overwinter hibernacula (den sites) while foraging and reproducing. Within this area at least 26 rattlesnake hibernacula have been detected within 1.4 km of the road, with some as close as 5 m (Winton *in progress*). Vegetation along the road shoulder was maintained in each year of the study by annual mowing to a height of less than 0.5 m for a distance of 1.8 m from the road edge. A barbed wire fence was located approximately 5 m from the road edge along the entire survey route.

Road Surveys

Three different types of survey methods were conducted along the same 11.7 km route: walking, driving, and cycling (Table 2.1). For walking surveys, two observers scanned for dead and alive rattlesnakes in both road lanes as well as the 1.8 m vegetation control zone of the road shoulder as they walked along opposite edges of the road. Driving surveys were conducted by vehicle, travelling at 20 km/h or less, again with two observers, the driver and the passenger, scanning the road and the shoulder. For driving surveys conducted after sunset, high-beam headlights were used as well as a high-powered spotlight that was used in a back and forth scanning pattern across the road and shoulder. Bicycle surveys were conducted wherein only one observer cycled along the edge of the road while scanning the road and shoulders. Walking and cycling surveys were only conducted during daylight hours due to safety concerns. The road survey area was driven and cycled in both directions to ensure the two lanes were surveyed completely. The results of these two directional surveys were combined but individual roadkills were counted only once. The starting point and

Table 2.1. Timeframe and survey effort per road survey method in the White Lake Basin, BC, Canada, 2015 and 2016.

Survey method	Time of day	Survey start time range		Dates		Number of surveys		Total km surveyed	
		2015	2016	2015	2016	2015	2016	2015	2016
Walk	Day	6:00-11:55	6:41-10:32	May 12 - Aug 27	April 29 - Aug 28	23	28	116.2	253.5
Drive	Day	6:00-14:30	8:50-13:25	May 5 - Oct 2	April 11 - Sept 18	6	5	62.4	51.6
Drive	Night	20:30-23:38	18:17-22:30	May 16 - Sept 3	April 12 - Sept 29	25	22	233.3	257.4
Bike	Day	8:00-13:40	7:10-12:00	Aug 8 - Oct 3	April 15 - Sept 28	9	16	53.1	129.9
Incidental (Drive)	Day and night	-	-	April 9 - Oct 3	April 5 - Oct 11	-	-	1633.8	2382.4

direction of travel were varied between surveys, the start and end times for each survey were recorded, and the exact length of the transect on each occasion was measured with GPS.

All detections of dead or alive rattlesnakes on the survey route were noted whether during surveys or at other times. Detection points for rattlesnakes were recorded ±5m with a handheld GPS (Garmin 72H). Live rattlesnakes were captured, measured, and tagged with Passive Integrated Transponder (PIT) tags as part of an overarching mark-recapture study on the rattlesnake population (Winton *in progress*). After, captures were released at the fence line in the direction that the snake had been travelling, or if that was not obvious, the side of the road closest to the capture location. Carcasses were identified to species and scanned for the presence of PIT tags. The carcass was removed and, when possible, measured and weighed.

Incidental detections of roadkill (i.e. detections made when road surveys were not being conducted) were a common occurrence when working within the survey route. Observers were not actively surveying at these times, however, any carcasses I observed were documented in the same manner as detections made during surveys. Although the kilometers driven outside of survey times were not recorded, I was able to approximate the minimum amount based on my records. While the focus of this study was Western Rattlesnakes, detections of all vertebrates on the road including other snake species were recorded (Appendix A; Table A.1). Any detections of rattlesnakes made along the road in the greater study area of the White Lake Basin but outside of the survey route were also recorded (Appendix A; Table A.2).

Scavenging and Observer Error Experiments

To date habitat and crippling biases have not been quantified in this region for snakes. However, I assumed these biases were likely negligible due to the homogeneity of roadside habitat maintenance. I therefore chose to evaluate scavenger-removal and observer detection error as the probable main sources of bias in estimating snake road mortality in this area.

Experiments were conducted to examine the rate of carcass removal from the road due to scavengers and the detection probability of snake carcasses on the road by observers. The experiments involved using snake carcasses that had been previously collected off-site and were then thawed from storage. Because the supply of rattlesnake carcasses alone was insufficient, carcasses of all six species of snake native to the area were used (Western Rattlesnake, Great Basin Gophersnake (*Pituophis catenifer*), Western Yellow-bellied Racer (*Coluber constrictor*), Rubber Boa (*Charina bottae*), Western Terrestrial Garter Snake (*Thamnophis elegans*), and Common Garter Snake (*T. sirtalis*)). In addition to recording species, I also categorized carcasses by size (small, medium, large). Results were compared across size classes using the N-1 χ^2 statistic for observer detection probabilities, and using Kruskal-Wallis One Way ANOVA for scavenger-removal times. Statistical analyses were performed in SigmaPlot version 13.0 and $\alpha = 0.05$ was used to interpret significance.

Eleven scavenger-removal trials were conducted during May-September, 2016. Each carcass was placed at a previously recorded snake roadkill location (10-15 carcasses/trial) and monitored on a daily basis until it was no longer present or up to 14 days after placement. At least 200 m separated each carcass to reduce scavenger overlap. Motion-activated wildlife cameras were placed by 26 of the snake carcasses to observe scavenger species.

Three trials measuring observer detection probability were run by an independent person placing snake carcasses at locations unknown to the two observers in the study. The naïve observers then proceeded with a walking road survey following the previously outlined procedure; after this, all placement sites were revisited immediately following the survey (within approx. 30 min) to confirm whether each carcass had been detected or missed during the survey. Observer detection probability (p) was calculated as the mean of the three trials.

Road Mortality Rate Model

Calculation of rattlesnake road mortality rates was modified from Teixeira et al. (2013). The density of dead rattlesnakes on the road, $D(t)$ (dead rattlesnakes/km), was estimated from the number of dead rattlesnakes detected (N) per km surveyed (x) in walking surveys and corrected for observer detection error based on the mean probability of detection (p) determined from the experimental trials:

$$D(t) = \frac{N/x}{p} \tag{1}$$

The proportion (P) of carcasses remaining on the road over time from scavenger-removal trials was fit to the following model:

$$P(t) = P_0 + (1 - P_0)e^{-at} \tag{2}$$

where P_0 accounts for the proportion of carcasses that remained on the road for longer than 14 days and were not scavenged. The density of these non-scavenged carcasses, $D_n(t)$, differed from the density of the scavenged carcasses, $D_s(t)$. Non-scavenged carcasses were added to the road at a rate $P_0\lambda$, and scavenged carcasses were added at a rate $(1 - P_0)\lambda$. Non-scavenged carcasses were not removed from the road, while the scavenged carcasses were removed at a rate of $aD_s(t)$. Since all detected carcasses were removed by observers during surveys, the density of carcasses on the road was effectively set to zero after each survey. This provided the following estimates for the two densities:

$$\frac{D_s}{dt} = (1 - P_0)\lambda - aD_s, \;\; D_s(0) = 0 \qquad \frac{D_n}{dt} = P_0\lambda, \;\; D_n(0) = 0 \tag{3}$$

$$D_s(t) = (1 - P_0)\frac{\lambda}{a}(1 - e^{-at}) \qquad D_n(t) = P_0$$

Observers measured both densities during each survey, therefore $D(t_s) = D_s(t_s) + D_n(t_s)$ at the time t_s (days since the last survey). The road mortality rate, λ (deaths/km/day), however cannot be determined from density alone. As stated, two processes determine the density of carcasses on the road: dead snakes are added at a constant mortality rate, λ, and removed from the road by scavengers at a rate $aD(t)$. The amount of time $(1/a)$ required to reach equilibrium between the mortality rate and the scavenger-removal rate was determined by fitting an exponential model to the number of carcasses remaining on the road over time, up to 14 days (Eq. 2). $D(t_s)$ and subsequently λ can be calculated as follows where *x* is the number of km sampled in one walking survey and *N* is the number of dead snakes detected within that survey:

$$D(t_s) = D_s(t_s) + D_n(t_s)$$

$$D(t_s) = (1 - P_0)\frac{\lambda}{a}(1 - e^{-at_s}) + P_0\lambda t_s$$

Solving for λ:

$$\lambda = \frac{D(t_s)}{\frac{1}{a}(1-P_0)(1-e^{-at_s})+P_0 t_s}$$

$$\lambda = \frac{N/xp}{\frac{1}{a}(1-P_0)(1-e^{-at_s})+P_0 t_s} \tag{4}$$

Mean road mortality rates for rattlesnakes calculated from walking survey results were compared between years using a Mann-Whitney U Test. The mortality rates were scaled up to calculate the number of rattlesnake deaths within the study area during the active season for each year. The length of each active season for rattlesnakes was determined based on when rattlesnakes commenced egress from their overwinter den (first observations at den sites in the spring) and when return ingress was completed (last day of rattlesnake observations at the dens in the fall or found on the roads). Correction (adjustment) factors for the number of rattlesnake deaths were determined and applied to the detected dead rattlesnake densities to produce adjusted densities that reflect the calculated mortality rate. A paired t-test was used to compare the unadjusted and adjusted densities.

RESULTS

Road Surveys

Including results from all survey types and incidental observations, 92 dead rattlesnakes were detected on the road during the study (2015: 36, 2016: 56; Table 2.2) compared to 17 live rattlesnakes (2015: 13, 2016: 4). A high amount (39%) of roadkill detections were made incidentally, outside of road survey times (2015: 14, 2016: 22). Rattlesnakes were detected on the road from May 8 to October 1, 2015, and from April 20 to

Table 2.2. Detections of dead Western Rattlesnakes (*Crotalus oreganus*) and densities per km surveyed (unadjusted for observer error or scavenging rates) by road survey method in the White Lake Basin, BC, Canada, 2015 and 2016.

Survey method	**Time of day**	**Total km surveyed**		**Number of dead rattlesnakes detected**		**Unadjusted dead rattlesnake density (dead rattlesnakes/km)**	
		2015	**2016**	**2015**	**2016**	**2015**	**2016**
Walk	Day	116.2	253.5	6	13	0.052	0.051
Drive	Day	62.4	51.6	3	4	0.048	0.078
Drive	Night	233.3	292.5	12	9	0.051	0.031
Bike	Day	53.1	129.9	1	8	0.019	0.062
Surveys total		465	727.5	22	34	0.047	0.049
Incidental		1633.8	2382.4	14	22	0.009	0.009
Surveys + Incidental		2098.8	3109.9	36	56	0.017	0.018

October 11, 2016. We conducted 137 road surveys by walking, driving, or cycling and traveled 5210 km in total over the two years (Table 2.2).

Scavenger-Removal and Observer Detection Probability

The model of exponential carcass removal over time (Figure 2.2) revealed the amount of time required to reach equilibrium between the road mortality rate and the scavenger-removal rate to be 2.05 days (a = 0.49 day^{-1}), and that 52% of the carcasses were removed in this time. The proportion of carcasses remaining on the road after 14 days was $P_0 = 0.11$. Size class did not play a role in the length of time a carcass remained on the road (H=1.857, df=2, p=0.395). Camera-traps detected four scavenger species (*Canis latrans, Pica hudsonia, Cathartes aura*, and *Homo sapiens*; Appendix B), but missed recording more than half of the scavenging events. In five cases, the snake carcass disappeared from one photo to the next (time interval of 1-60 min) yet no scavengers were captured in the photos, possibly indicating aerial scavengers.

Observers detected 47 out of 61 total carcasses in the three trials for a mean detection probability (p) of 0.76 (±0.06 SE) for walking road surveys. Larger snakes were more readily detected (χ^2=5.7, df=2, p=0.057). Walking surveys were conducted on average 4.7 days since the last survey in 2015 and 3.1 days in 2016.

Mortality Rates

Road mortality rates calculated from walking surveys did not differ significantly between years (U-statistic = 313, p = 0.838); therefore, the mean road mortality rate on White Lake Road from 2015-2016 was 0.06 rattlesnake deaths/km/day or an average of 124 deaths per year (Table 2.3). From that mortality rate, which takes into account scavenger-removal and observer error, 2.7× as many rattlesnake deaths were estimated to have occurred compared to those actually detected (as dead animals) overall. Dead rattlesnakes detected during walking road surveys accounted for only 8% of the estimated number of deaths. There was a significant increase in the density of dead rattlesnakes between the unadjusted and adjusted values for all survey methods (t = -6.50, p < 0.001, Table 2.4).

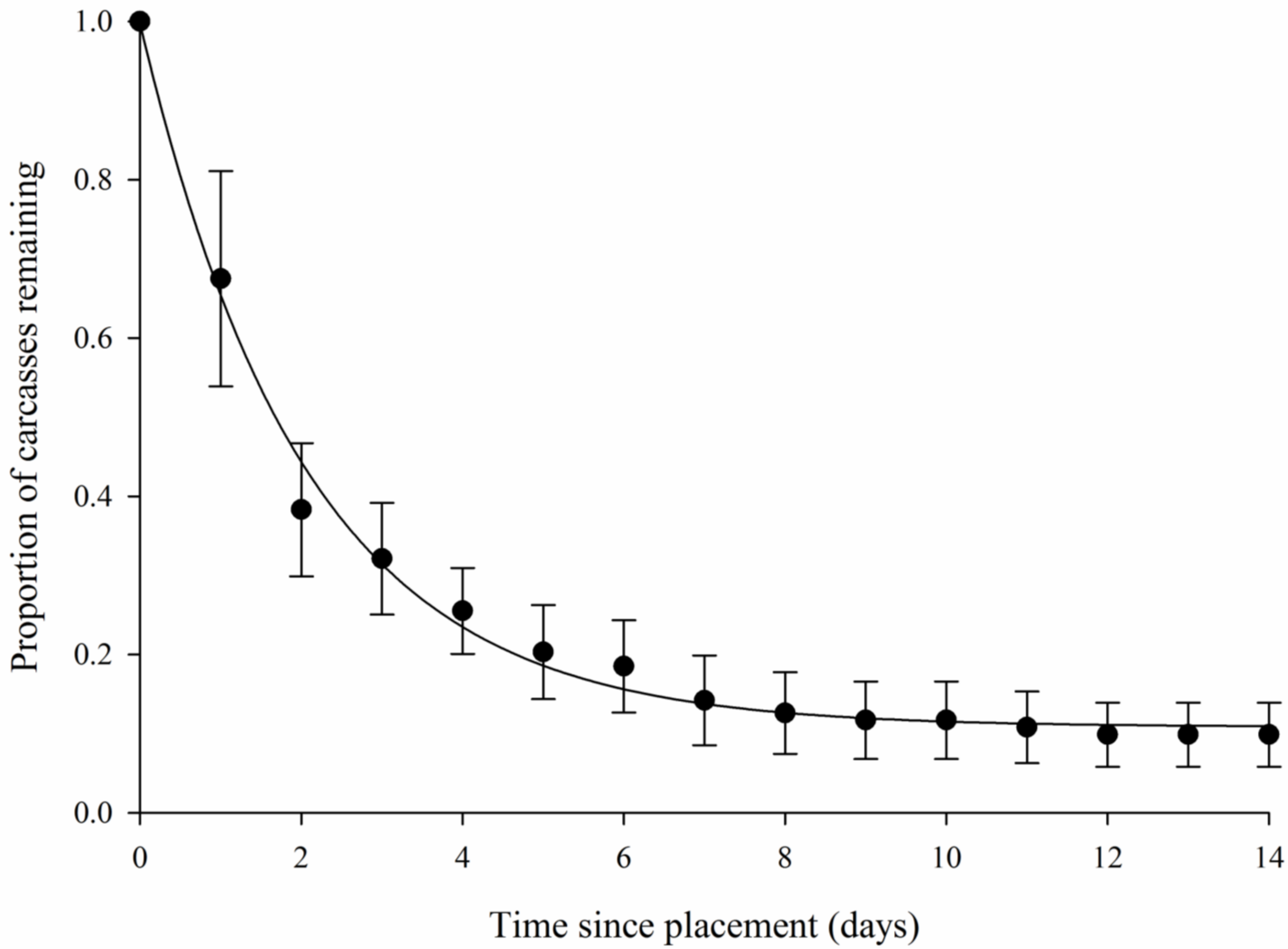

Figure 2.2. Mean proportion of snake carcasses remaining on a paved road over time in experimental scavenger-removal trials (n = 11; error bars = 95% confidence intervals; R^2 = 0.99) in the White Lake Basin, BC, Canada in 2016.

Table 2.3. Calculated road mortality rates (deaths/km/day) and number of Western Rattlesnake (*Crotalus oreganus*) deaths based on walking survey results and accounting for scavenger-removal and observer error during the active season (April-October) in the White Lake Basin, BC, Canada, 2015 and 2016.

	2015	**2016**	**Mean (2015-2016)**
Mean mortality rate (±SE) (rattlesnake deaths/km/day)	0.044 (0.019)	0.070 (0.030)	0.058 (0.018)
Active season length (days)	176	188	182
Calculated rattlesnake deaths per year	91	154	124
Correction factor	2.5	2.8	2.7

Table 2.4. Adjusted dead Western Rattlesnake (*Crotalus oreganus*) road densities (dead rattlesnakes/km), accounting for scavenger-removal and observer error, compared to unadjusted densities in the White Lake Basin, BC, Canada, 2015 and 2016.

Survey method	**Time of day**	**Unadjusted dead rattlesnake density (dead rattlesnakes/km)**		**Adjusted dead rattlesnake density (dead rattlesnakes/km)**	
		2015	**2016**	**2015**	**2016**
Walk	Day	0.052	0.051	0.130	0.143
Drive	Day	0.048	0.078	0.120	0.218
Drive	Night	0.051	0.031	0.128	0.087
Bike	Day	0.019	0.062	0.048	0.174
Surveys total		0.047	0.049	0.118	0.137
Incidental		0.009	0.009	0.023	0.025
Surveys + Incidental		0.017	0.018	0.043	0.050

Discussion

Overall, at White Lake in 2015-2016, the unadjusted rates of rattlesnakes found dead on the road by walking, driving, and cycling surveys, was consistent between years at 0.047/km in 2015 and 0.049/km in 2016. The adjusted rates (0.118/km in 2015 and 0.137/km in 2016), which take into account removal of carcasses by scavengers and observer error, were similar but much higher in total than the unadjusted ones. I also found that simply driving roads repeatedly and covering more than 1000 km incidentally detected the most dead rattlesnakes compared to walking, cycling, or driving less than 300 km while looking for snakes in any year. However, while the rates for incidental observation between years were also very consistent, the rates per km of incidental observations of dead rattlesnakes were at least two times less than careful and slow walking, driving, and cycling surveys whether they were adjusted or unadjusted rates (0.009/km or 0.024/km).

My prediction that the number of rattlesnake deaths calculated to occur on the road would double if detection and scavenging rates were considered was accurate. From April to October in 2015 and 2016, the estimated number of deaths was substantially greater (2.7×) than the actual number of dead rattlesnakes detected on the road during all surveys and incidental observations. Furthermore, road surveys conducted on foot detected only a small proportion of the estimated actual rattlesnake deaths (8%), although my observer detection probability rate was high (76%), emphasizing the impact of scavenging on road mortality estimates. My scavenger-removal trials revealed that 52% of snake carcasses were removed within 2.05 days and that 11% of the carcasses were never scavenged, elucidating multiple mechanisms that underlie scavenging of roadkilled snakes. Overall, my results emphasize the need to conduct standardized surveys and account for scavenger-removal and observer detection error when calculating road mortality rates.

The correction factor of 2.7× determined in this study is consistent with studies on other taxa and for reptiles where road mortality rates were corrected for scavenger-removal and observer error. Correction factors can be quite high (eg. 12-16× - Slater 2002) with broad ranges across various taxa, including amphibians, birds, mammals and reptiles (eg. 2-10× - Santos et al. 2016; 2-39× - Teixeira et al. 2013). However, studies examining reptiles show relatively lower correction factors than those for other taxa. Kline and Swann (1998) determined reptile mortality to be 5× that observed in Arizona, and Teixeira et al. (2013) estimated a correction factor of 2× in Brazil. Rosen and Lowe (1994) did not account for sources of error by experimental methods: however, they noted the limitations of their study and corrected their road mortality estimates for snakes in Arizona with a conservative value of 1.7×.

My calculated rattlesnake road mortality rate is not comparable to previous studies reporting snake road mortality, because the majority have not corrected for sources of error and therefore only report the density of dead snakes observed on the road (Tucker 1995; Enge and Wood 2002; Borczyk 2004; Shepard et al. 2008; DeGregorio et al. 2010; Hartmann et al. 2011; Jochimsen et al. 2014). Most report collective rates on more than one snake species (Enge and Wood 2002; Hartmann et al. 2011; Gonçalves et al. 2018) and some report combined encounter rates of dead and alive snakes (Mendelson and Jennings 1992; Sullivan 2000; McDonald 2012). With these differences in mind, I compare the density of dead snakes detected, without error corrections, to similar studies in comparable habitats: Jochimsen et al. (2014) found a density of 0.004 Western Rattlesnakes (*C. oreganus*) dead per km traveled in Idaho, which is less than the density reported in this study (0.018/km). Similarly, in Arizona and New Mexico, Mendelson and Jennings (1992) found densities for multiple rattlesnake species of 0.006/km and 0.008/km for two roadways. Road densities of *C. viridis* in California have been reported by Sullivan (2000) at a slightly higher level of 0.031/km (although less than the adjusted range of 0.043-0.050/km reported here). These results could potentially indicate site, range, or species differences for rattlesnakes in western North America; however, the values are not vastly different when compared to other areas with different snake species compositions. For example, in Florida and Illinois densities of roadkilled rattlesnakes were much lower at less than 0.001/km (Enge and Wood 2002; Shepard et al. 2008).

Based on the high number of incidental observations made in my study, travelling the route many times over a long period each year could therefore be a survey method that increases the total number of observations, but the rates detected per km will be very low. This is possibly because observer detection probability is low due the speed of the vehicle and observations are only incidental. Costa et al. (2015) indicated frequent surveys (once per week) during times of high activity for reptiles increases the efficacy of roadkill sampling but did not report a rate per km travelled.

Other factors that may influence rates of snake road mortality may be sex, age, and reproductive status of the individual as well as surrounding habitat, time of day, seasons, and weather conditions under which surveys occur. Alternative methods could be explored to improve the efficiency of road kill detection, e.g. drone surveys (Sykora-Bodie et al. 2017), or trained dogs (Arnett 2006). However, the total number of dead animals detected in my study (both during formal surveys and incidentally) was 2.7× less than the estimated number of deaths that actually occur within a year; it cannot be expected that all dead animals will be detected regardless of survey method, and error corrections must be factored into road mortality studies.

Observer detection probability (0.76) as calculated in my study was considerably higher than that reported elsewhere for reptiles (0.04 - Gerow et al. 2010; 0.06 - Santos et al. 2016) and snakes (0.23 - Gonçalves et al. 2018). This is likely due to differences in methodologies. Other studies determined analogous values by comparing detections made while driving to those made while walking with the assumption that the detection probability was 1.0 when surveying on foot (Gerow et al. 2010; Teixeira et al. 2013; Santos et al. 2016). However, in my study planted carcasses were used to assess detection probability while walking and the outcome strongly indicated an assumption of perfect detection did not hold. Thus, results obtained from walking surveys may produce the maximum number of roadkill detections but still fail to enumerate all carcasses on the road. Detection probability of driving surveys will invariably be less than walking surveys (Langen et al. 2007). Since I could only examine observer detection probability for walking surveys and not other survey methods (driving, cycling), my results represent a conservative estimate of observer detection error.

The scavenger-removal rate of snakes estimated for my study site was lower than rates reported in warmer regions and latitudes, such as Portugal and the southern United States (Enge and Wood 2002; Antworth et al. 2005; DeGregorio et al. 2011; Santos et al. 2011). This may be due to global patterns of biodiversity that increase the density of scavengers and the intensity of competition for carcasses (DeVault et al. 2003). However, another study conducted in the more northern, temperate climate of Wyoming, USA, reported a 75% removal rate within 60 hours (Hubbard and Chalfoun 2012) similar to my results of 52% removal within 49 hours. My scavenger-removal trials revealed a portion of carcasses (11%) that remained on the road for an extended period of 14 days. Either those particular carcasses were not removed by scavengers when they were fresh (then reaching a state of decomposition that was undesirable to scavengers), or the carcasses became so damaged (possibly by multiple vehicle collisions) that they were unrecognizable to scavengers. The un-scavenged carcasses remained on the road until they appeared to be mostly decomposed. Interestingly, most of the carcasses that persisted were initially placed on the road shoulder compared to carcasses placed on the road surface. The latter disappeared quickly or, if not, were gradually pushed to the road edge probably due to traffic (Winton, pers. observ.). This could be a relevant factor when habitat near to roads is dense and could obscure observation of these carcasses (i.e. habitat and crippling bias).

My results highlight the importance for methodical and rigorous assessments of roadkill in any situation where the true magnitude of roadkill impacts needs to be quantified in order to trigger management actions. A consistent trend, supported by my results, that road mortality rates are significantly higher than what is reported either through simple, opportunistic observations or even structured road surveys alone indicates that accuracy largely may depend on quantifying observer detection probability and scavenger-removal rates. Ideally, intensive surveying, similar to my methods, should be conducted; however, the equation used herein for road mortality rate can be applied to less frequent surveys, as long as survey effort, time between surveys, carcass persistence time, and observer detection probability all are taken into account. I recommend that researchers conducting road mortality studies, particularly on smaller species, evaluate scavenger-removal and observer error for each study, and that observer detection probability be determined using planted carcasses to accurately assess this source of error for a given survey method. Studies such as mine will assist conservation practitioners in accurately determining rates of road mortality, which will be of particular importance for populations of at-risk animals when the loss of only a few individuals has a significant effect (Row et al. 2007; Colley 2015).

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CHAPTER 3

PREDICTING POPULATION DECLINE OF A NORTH AMERICAN VIPER THREATENED BY ROAD MORTALITY

INTRODUCTION

One of the major adverse effects of roads on wildlife populations is direct mortality from wildlife-vehicle collisions (Fahrig and Rytwinski 2009). This removes individuals beyond natural causes, and thereby limits population size and growth (Kushlan 1988; Coffin 2007; Chambers and Bencini 2010). Populations living in proximity to roads often experience higher mortality rates than remote areas (Mumme et al. 2000) and roads are of particular concern in protected areas where they may constitute the only significant source of anthropogenic mortality (Andrews et al. 2008), yet any continual and additive source of mortality can have devastating consequences on local populations. Rapid and widespread declines in various animal populations caused by road mortality (Fahrig et al. 1995; Gibbs and Shriver 2002) also may have further consequences such as genetic isolation (Epps et al. 2005) and in extreme cases, extirpation (Jones 2000). Populations of at-risk species likely already suffer from depressed numbers, reduced genetic diversity, and combined threats (Mace et al. 2008), making them even more heavily affected by road mortality.

Population viability analyses (PVAs) are becoming an increasingly common tool for quantifying the effects of roads in species status assessments (Morris et al. 2002). The International Union for Conservation of Nature (IUCN) recognizes the validity of PVA as a mechanism to estimate the risk of extinction to endangered species (IUCN 2017). Similarly, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) also recognizes PVAs for assessing threat effects on populations and monitoring changes over time (e.g. Wood Turtle, *Glyptemys insculpta* - COSEWIC 2007; Fowler’s Toad, *Anaxyrus fowleri* - COSEWIC 2010). Additionally, PVAs can be used to recommend the most appropriate management practices for a population (Crouse et al. 1987; Lamberson et al. 1992; Lindenmayer and Possingham 1996; Diniz and Brito 2015), or specific characteristics of a population may be examined to determine factors that limit population growth (Vucetich and

Creel 1999). Extinction thresholds in relation to habitat loss (Fahrig 2002), a concept also applicable to road mortality, have been determined with PVA (Diniz and Brito 2015). However, to serve any of these purposes, particularly the assessment of threats from pervasive disturbances like roads, the construction of PVAs requires baseline research that generates defendable and accurate parameters for the analyses.

Road mortality of snakes has been well documented for decades (see Klauber 1939); however, as with many threatened taxa, little is known about the overall impact of roads at the population level (Andrews et al. 2008). In general, a significant threat to at-risk reptiles is the death on roads of long-lived, reproductively-mature individuals (Dalrymple and Reichenbach 1984; Rosen and Lowe 1994; Roe et al. 2006). Many vipers (F. Viperidae) are likely prone to this type of impact, particularly those living in temperate climates where they face extreme environmental conditions and rely on unique life history traits to survive (e.g. Aldridge and Duvall, 2002). Vipers also are relatively less fecund than many other snake taxa, producing fewer but larger young (Seigel and Fitch 1984; Parker and Plummer 1987). In northern populations, rattlesnakes (*Crotalus* and *Sistrurus*) may take a number of years to reach sexual maturity (Macartney et al. 1990; Jørgensen and Nicholson 2007), and following that, reproduction by females may be biennial or even more infrequent (Gannon and Secoy 1984; Macartney and Gregory 1988; Rouse et al. 2011). Further, northern rattlesnakes generally overwinter in traditional communal hibernacula (Gregory 1984), which may increase annual survival, but the required migration twice a year between these sites and summer habitats (Macartney 1985; Jørgensen et al. 2008; Gardiner et al. 2013) also limits productive active time (Gibbons and Semlitsch 1987). When hibernacula and/or migration pathways are located close to roads, the snakes face an increased risk of being killed by traffic (Fortney et al., 2012; Rouse et al., 2011; Rudolph et al., 1999; Seigel and Pilgrim, 2002; Chapter 2). The combination of these characteristics may make it difficult for rattlesnake populations to recover from continual sources of disturbance (Brooks et al. 1991; Andrews et al. 2015).

In this study, I used intense fieldwork and population viability analysis to assess the long-term viability of a northern population of Western Rattlesnakes (*C. oreganus*) experiencing road mortality. The goal of this study was to quantify the population trajectory and extinction risk due to road mortality, as well as model changes in the probability of extinction, population size, growth rate, and extinction threshold due to variable simulated road mortality rates. To estimate actual road mortality rates in the study population a thorough assessment of roadkill along with associated sources of bias was conducted in a related study (Chapter 2). I also used mark-recapture and radio-telemetry data to provide accurate estimates of several important parameters, namely population size, area of occupation, and annual percent mortality rate. Scenarios then were created that simulated increased or decreased rates of mortality stemming from possible traffic increases or successful mitigation measures, respectively. Models also were manipulated to assess the sensitivity of the population to variable adult female mortality, decreased life expectancy, and variable initial population sizes. This study provides a rare detailed analysis of unmitigated road impacts on a northern viper population.

METHODS

Study Site

My field research was conducted within the White Lake Basin (latitude 49°N, longitude 119°W) in the South Okanagan region of British Columbia, Canada (see Figure 1, Chapter 1). This arid ecosystem consists of forested, rolling hills and steep bluffs surrounding open shrub-steppe and grassland habitat, predominantly characterized by Bluebunch Wheatgrass (*Agropyron spicatum*), Big Sagebrush (*Artemisia tridentata*) and Ponderosa Pine (*Pinus ponderosa*) (Meidinger and Pojar 1991). The area provides critical habitat for Western Rattlesnakes (COSEWIC 2015), including overwinter hibernacula, seasonal migratory corridors, and summer foraging habitat. Twenty-six identified rattlesnake dens are located within 1.4 km of a road that traverses the basin bottom. The rattlesnakes and their habitat within my study site are protected by both federal and provincial designation, although the larger portion of the area lays predominantly in the White Lake Basin Biodiversity Ranch where ranching and farming are permitted; a smaller portion falls within the provincial White Lake Grasslands Protected Area. A variety of recreational activities occur in the area including hiking, bicycling, horseback riding, and bird watching (BC Parks 2003).

Population Viability Analysis

I modelled population and assessed persistence using VORTEX (version 10.2.7.0), a program suitable for long-lived reptiles with low reproductive rates and the application of road mortality data (Lacy 1993). Population models were simulated 500 times for a period of 100 years unless otherwise specified. The population was considered to be closed with no dispersal or inbreeding, and a quasi-extinction threshold of 10 individuals was used (hereafter extinction probability denotes the probability of reaching this quasi-extinction value). I classified input parameters for the population model into two categories: species-specific parameters and population-specific parameters. Species parameters were derived from research pertaining to life history and demographic traits of Western Rattlesnakes in the northern portion of their range, with particular emphasis on previous studies conducted on populations in British Columbia (Table 3.1). Population parameters, such as population size and road mortality rates, were based on data I collected via mark/recapture, telemetry, and roadkill surveys on the focal population (see Chapter 2 and *Population Estimate* and *Road Mortality Rates* below; Table 3.2). The PVA models were used to determine the probability of extinction, the extinction threshold (road mortality rate above which the probability of extinction was greater than zero), the stochastic population growth rate, and the mean size of extant populations.

Overall, species-specific parameters were chosen in order to create a best-case-scenario model of the population that would persist over time in the absence of roadkill (i.e. positive growth rate). Since road mortality inherently affects the White Lake population (see Chapter 2) and would be reflected in calculated mortality rates for this population (Bonnet et al. 1999), I used mortality rates from a historical study (Macartney 1985) and a long-term study (10 years - Maida et al. in press), both in the same region, but where road mortality is less of an immediate threat (Table 3.1). Additionally, long-term data were not available yet for the study population and therefore estimates of current mortality rates are preliminary and likely unreliable. The chosen mortality rates followed a Type III survivorship curve with low neonate and first year survival, and higher rates for older subadults and adults, typical of long-lived viperids (Parker and Plummer 1987) and similar to those used in other rattlesnake PVAs (e.g. Colley 2015). The lowest reported mortality rate for each age class was selected

Table 3.1. Species-specific parameters and sources used for population viability analysis of Western Rattlesnakes (*Crotalus oreganus*) in the White Lake Basin in British Columbia, Canada. All estimates were taken from other studies conducted on the species within the same region (Okanagan Valley, BC).

Parameter	Value	Range	Sources	Location
		Reproductive rates (polygynous system)		
Age at first litter (female)	7	6-9	Macartney 1985	Vernon, BC
			Macartney and Gregory 1988	
			Petersen et al. in prep	South Okanagan
			Maida et al. in press	Osoyoos, BC
Age at sexual maturity (male)	3	2-4	Macartney et al. 1990	Vernon, BC
Maximum age	21 - life table estimate		Macartney 1985	Vernon, BC
	11 - roadkill sample		Petersen et al., in prep.	South Okanagan
Mean neonates/litter	4.6±0.31	1-8	Macartney and Gregory 1988	Vernon, BC
1° sex ratio	0.5			
% breeding (female)	38			
% breeding (male)	100		Brown et al. 2009	Osoyoos, BC
		Mortality rates (%)		
Neonate (age 0-1)	54	54-94	Macartney 1985	Vernon, BC
Juvenile (age 1-2)	33	33-67		
Subadult (age ♀= 2-7, ♂= 2-4)	5	5-56		
Adult (age ♀= 7+, ♂= 4+)	19	15-49	Macartney 1985	Vernon, BC
			Maida et al., in press	Osoyoos, BC

and a standard deviation of 5% was applied to create the best-case model. Adult mortality rates differed between two other populations in the Okanagan valley. One range of rates (0.16-0.22) was calculated during 1980-1983 whereas another (0.15) was more recent (2002-2012). I therefore chose an average value that produced a conservative population growth rate overall. I chose a normal age distribution to avoid legacy effects of differential road mortality within the White Lake population or bias due to sampling methods.

I chose the highest estimate of longevity from life tables (21 years; Macartney 1985) given that recent estimates (Maida et al. in press; COSEWIC 2015) determined the average generation time (defined as “less than the age of the oldest breeding individual” - IUCN 2012) of Western Rattlesnakes to be between 12.4-15.6 years. Longevity also corresponded to the maximum age of reproduction since rattlesnakes do not show reproductive senescence (Macartney and Gregory 1988). I explored how variable longevity affected the population since recent research on ages of roadkilled rattlesnakes indicated they do not survive past 11 years when living in proximity to roads (Petersen et al., in prep.). Aside from longevity, which was possibly affected by roadkill, all other species parameters were considered intrinsic to the species and fixed in the models, as external influences would have very little sway over these factors. All of these parameter values reflect population characteristics presented by Parker and Plummer (1987) for viperid species with delayed maturity living at the northern extent of their range.

Population Estimate

I used the following procedure to calculate an estimate of the rattlesnake population impacted by mortality along the road traversing the White Lake Basin (Chapter 2). Firstly, a Jolly-Seber population estimate was calculated in the Rcapture package (Baillargeon and Rivest 2007) for R (version 3.4.2; R Core Team, 2017). I used mark/recapture data (following methodology in Lomas et al. 2015) collected at six hibernacula (den sites) within two separate areas of the study site (two separate “den complexes”). Dens were sampled in 2015, 2016, and 2017 during spring and fall migrations and captures ranged from 172-257 individuals per year. These six dens were sampled in all three years of study as they all lie within 400 m of the road. To determine the portion of the landscape that supported this population, I measured the extent of summer movements away from the focal dens by conducting telemetry on 23 rattlesnakes (min. 4/den complex); I also included data on four rattlesnakes tracked from the same den complexes by Harvey (2015; Appendix C). In addition, I incorporated all locations of rattlesnakes (n=25) marked at one of the six key dens and subsequently encountered over the summer months, either incidentally or during structured road surveys (Chapter 2). Based on the recommendation by Row and Blouin-Demers (2006) to calculate home range areas for snakes using minimum-convex polygons (MCPs), I then calculated a MCP area around each den complex using the aggregated movements and locations in Garmin BaseCamp (version 4.6.2, 2016). I calculated snake density using a Jolly-Seber estimate of the number of rattlesnakes from these dens within the combined area of the MCPs.

To determine the size of the overall rattlesnake population within the basin, I extrapolated the density estimate to the functional area used by the rattlesnakes (i.e. the population home range, PHR; see Macartney, 1985). To estimate PHR, I determined the maximum distance travelled by telemetered snakes from their respective hibernacula (n=32, including five snakes from two non-focal den sites; Appendix C). I then followed a process similar to Weir et al. (2011) to determine the area of occupation, by using the mean movement distance from hibernaculum (1.3 km) and applying buffers of this radius centred around all known hibernacula in the basin (n=26) using ArcGIS (version 10.2.2, 2014). In the event that an MCP area for a den site with tracked rattlesnakes exceeded the buffer area, the MCP was used. The resulting boundary of the den site buffers and MCPs established the PHR. With one exception, the PHR encompassed all locations of rattlesnake encounters (n=176) over the summer months, including road mortalities, and contained 13.3 km of the road. The previously calculated rattlesnake density then was applied to the entire PHR for an estimate of the total rattlesnake population size. If biased, this intuitive and simple method of estimating population size is likely to inflate the PHR area and therefore the population size, thus providing a relatively conservative assessment of the probability of extinction of the population under threat of road mortality.

Additionally I calculated an estimate of the minimum population size within the basin using all rattlesnake captures (i.e. combining captures at focal dens, non-focal dens, and captures away from dens) over the three years of the study. Each active season (April-

October) was considered a ‘capture session’ within the analysis for a total of three capture sessions which provided one Jolly-Seber estimate.

Road Mortality Rates

Road mortality was modelled within the PVA simulation as the annual removal of a constant percent of the population. Within the model, this removal factor was applied after breeding and mortality occurred but before aging, as road mortality constitutes an additive source of mortality to natural mortality. The mean road mortality rate for rattlesnakes (0.058/km/day) was determined from road surveys and adjustments to correct for bias due to scavenger-removal and observer error (see Chapter 2). The mean percentage of the population killed on the road annually was used to guide model development, analysis, and interpretation for variable rates of road mortality.

To determine the distribution of deaths across snake age and sex categories (Figure 3.1), detected dead rattlesnakes (Chapter 2) were classified by age class (young-of-year, subadult, adult) and sex (female, male, unknown). There was not enough evidence to suggest a significant difference between males and females within the young-of-year (YOY) and subadult age classes due to a high number of individuals of unknown sex (i.e. mutilation by vehicles preventing proper identification), so equal proportions were allocated between males and females in those categories. In the adult age class, there was a clear trend of higher road mortality for males than females. Variable adult female mortality rates were simulated as this has been identified as a limiting factor in other snake road mortality research (Row et al. 2007; Colley 2015). Based on the field samples, confirmed adult female roadkills comprised 0.08 of roadkilled rattlesnakes and potentially comprised a maximum of 0.17 of roadkilled rattlesnakes, if all samples of adults of unknown sex (i.e. sex could not be determined due to damage to carcass) were considered female. Population growth rates were compared for this range of differences in adult female road mortality using a one-tailed t-test. The proportion of confirmed adult females found dead on the road was 0.23 of roadkilled adults of known sex. Applying this proportion to the adults of unknown sex, 0.1 of roadkilled rattlesnakes were considered adult females. This value was used in all other models.

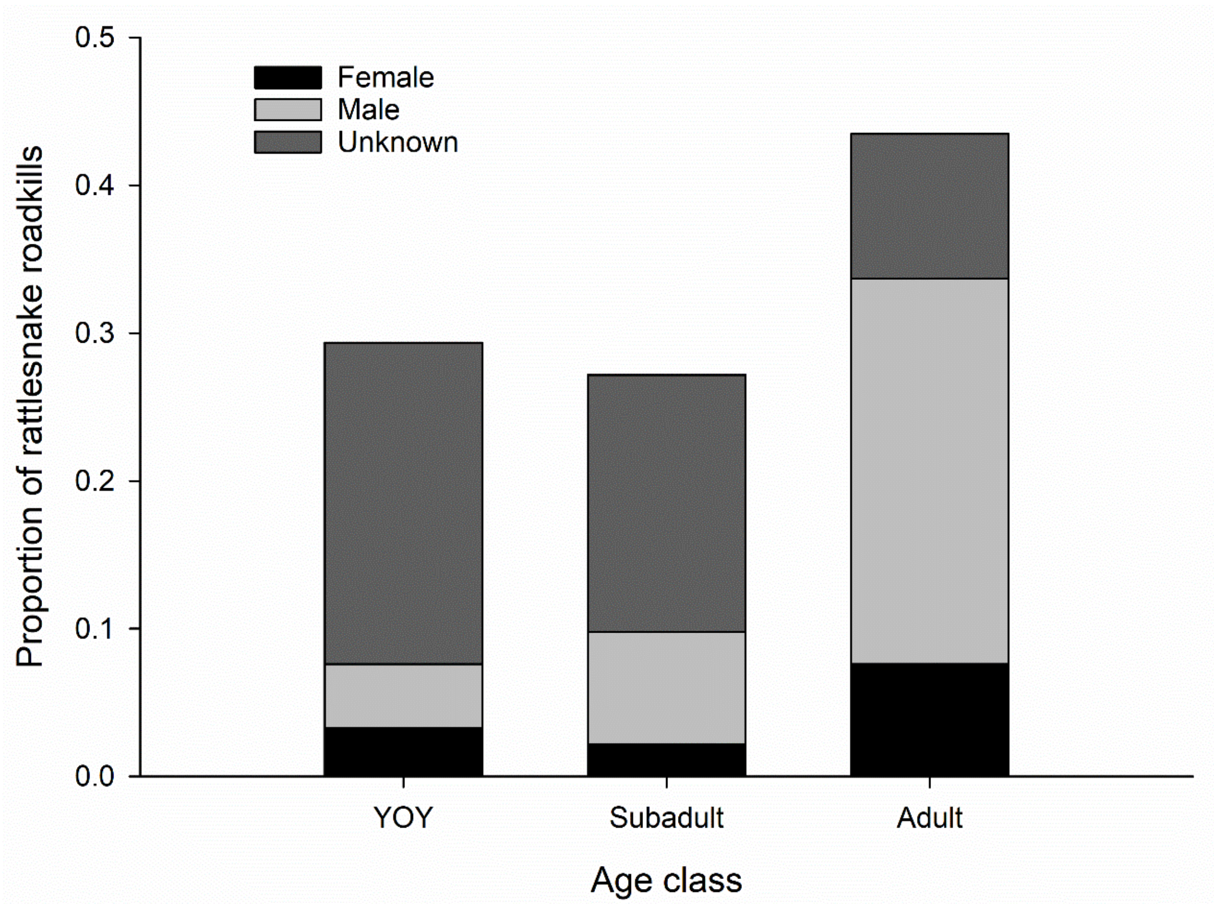

Figure 3.1. Proportion by sex (female, male, unknown) and age class (young-of-year, subadult, adult) of Western Rattlesnake (*Crotalus oreganus*) roadkill detected on White Lake Road, British Columbia, Canada in 2015-2016.

The population parameters derived from my fieldwork and incorporated into the PVA are listed in Table 3.2. Henceforth, for clarity, these parameters will be referred to as ‘actual values’, although it is recognized that these are by definition estimates based on empirical data. Other values used in the PVA for these parameters are simulated and represent possible scenarios that could occur but have not been confirmed through field work.

RESULTS

Population Parameter Estimates

The estimated Jolly-Seber population size of the six focal dens (combined) from 2015-2017 was 452 ± 59 (SE) rattlesnakes. These rattlesnakes occupied an estimated area of 8.35 km^2 around the den sites (Figure 3.2), yielding a density of 54.1 rattlesnakes/km^2. The larger PHR area occupied by rattlesnakes from all 26 known dens was 39.4 km^2 (Figure 3.2) and after extrapolation from the density estimate, this area was considered to support a population of 2131 ± 279 (SE) rattlesnakes. The mean annual road mortality rate (actual rate) along the portion of road encompassed by the PHR was 141 rattlesnake deaths per year equal to 6.6% of the population. The estimated minimum Jolly-Seber population size based on all captures was 532 ± 73 (SE) rattlesnakes.

Population Viability Analysis

At the actual road mortality rate of 6.6%, the probability of extinction was <0.01 in 100 years and 0.0 in 50 years. I modeled extinction probabilities at annual road mortality rates of 0-20% of the population (Figure 3.3). At simulated road mortality rates of ≤6% there was zero probability of extinction for this population of rattlesnakes within the next 100 years. Above the extinction threshold of 6%, the probability of extinction increased with road mortality up to a rate of 14% at which point the probability of extinction reached 1.0. For a period of 50 years, a simulated road mortality rate of 14% was the extinction threshold with a similar increasing trend in extinction probability observed for higher road mortality rates.

Table 3.2. Population-specific parameters derived from field data on Western Rattlesnakes (*Crotalus oreganus*) at the White Lake Basin in British Columbia, Canada, and used for population viability analysis.

Parameter	**Value**
Population size	2131 rattlesnakes (see Results)
Road mortality rate	141 rattlesnakes/year or 6.6% of the population (see Results)
Proportion of roadkill:	
Adult female	0.1 (range: 0.08-0.17)
Adult male	0.33 (range: 0.26-0.35)
Subadult	0.28
Young-of-year	0.29

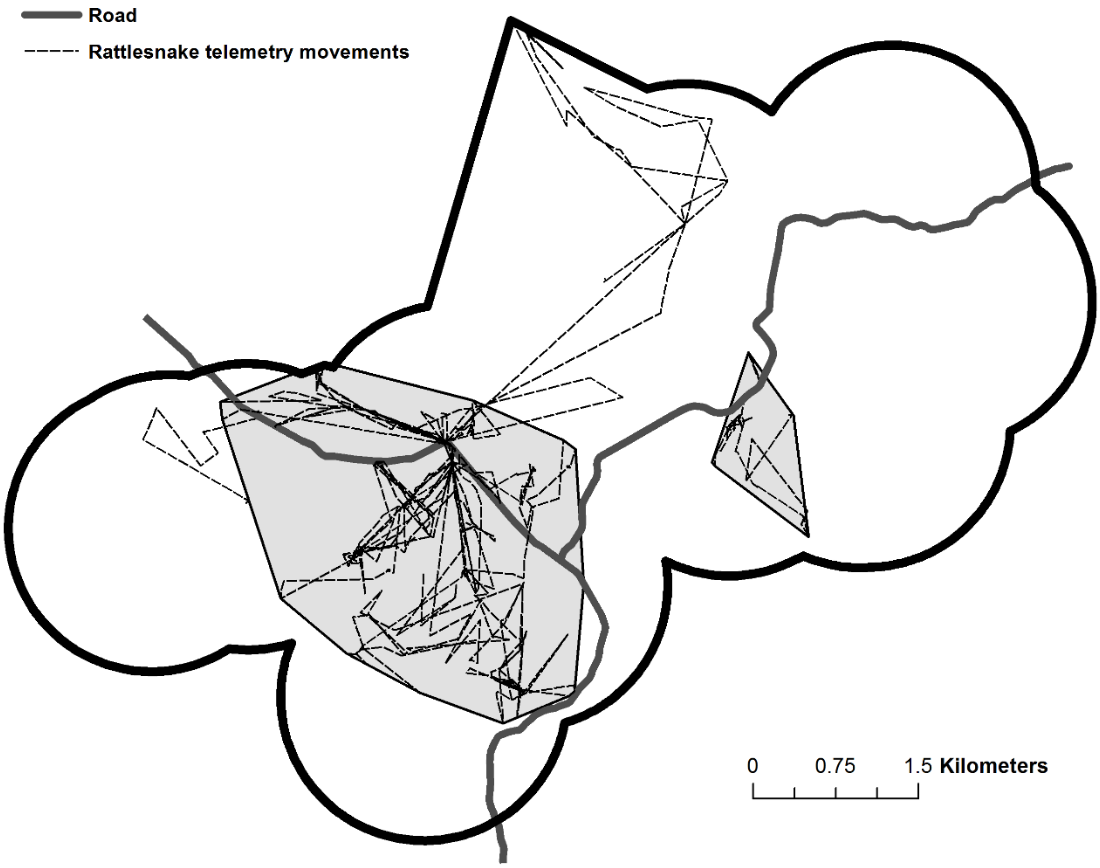

Figure 3.2. Population Home Range (PHR) of the Western Rattlesnake (*Crotalus oreganus*) population in the White Lake Basin, British Columbia, Canada. Minimum-convex polygons (MCP) of the two focal den complexes (grey) were used to determine the population density while 1.3 km buffers centred over den sites in combination with den MCPs were used to establish the PHR area. Supporting data used to calculate these areas include rattlesnake den site locations, encounter locations, and telemetry movements.

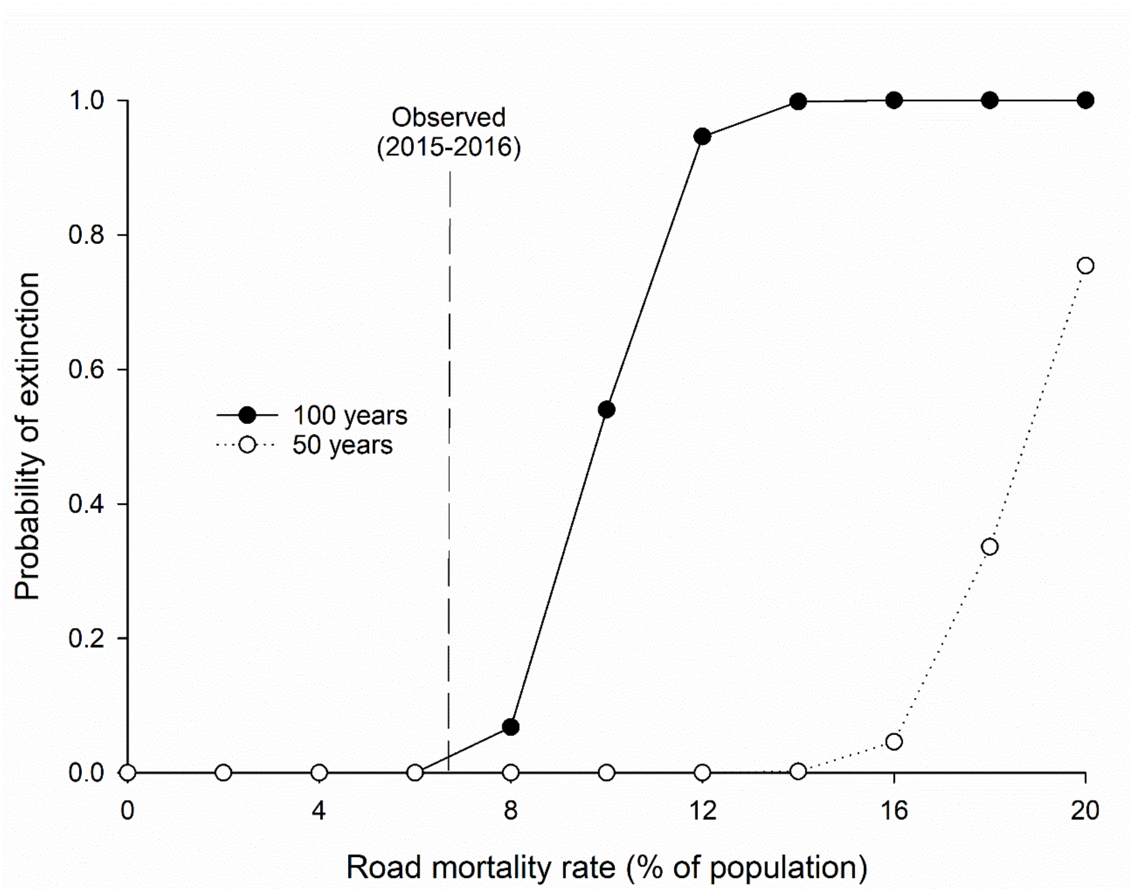

Figure 3.3. Probability of extinction within 100 and 50 years for a population of Western Rattlesnakes (*Crotalus oreganus*) in British Columbia, Canada under variable road mortality rates. Dashed line indicates the mean annual road mortality rate calculated from field data for the White Lake Basin population in 2015-2016 (6.6% of the population – see Chapter 2). Modelled using Vortex software (version 10.2.7.0).

Although the probability of extinction was low with the actual road mortality rate of 6.6%, the stochastic population growth rate (r) was consistently negative through the range of simulated road mortality rates, indicating that the population will decline over time (Table 3.3). Even though the population still was likely to persist for the next 100 years (99.6%), it would show a continual decrease. At the extinction threshold of 6%, the stochastic growth rate was -0.032, and the mean population size was estimated to decrease by 96% in 100 years. In comparison, the growth rate in the absence of road mortality was 0.005and the population was projected to increase (60% increase over 100 years).

Adult female mortality

Higher proportions of adult females dying on the road (with total adult mortality held constant) resulted in higher probabilities of extinction for simulated road mortality rates between 6-14% (Figure 3.4). When I used the actual rate of road mortality (6.6%), the modelled probability of extinction ranged from 0.0-0.1 over 100 years, depending on the proportion of adult females dying. There was a significant decrease in the population growth rate as the proportion of roadkilled adult females was shifted from the minimum (0.08) to the maximum (0.17) ($t = 3.169$, $P < 0.001$, $df = 998$). At the maximum, the extinction threshold was a reached at a simulated road mortality rate of 4% compared to 6% at the minimum proportion.

Longevity

The probability of population persistence increased when I adjusted rattlesnake longevity upwards (Figure 3.5). At a simulated level of low road mortality (4%), and with snakes reaching an age of 14 years, the population had a high probability (1.0) of persistence over 100 years; however, this probability dropped to 0.71 when the road mortality rate was moved upwards to 6%. At a road mortality rate of 8% the probability of persistence was only 0.93, even if snakes were simulated at a maximum age of 21 years (extremely high, and improbable). If the snakes were simulated to only live to 10 years of age, the probability of persistence for the population approached zero (<0.02) even under a simulated rate of low road mortality (4%) [well below the actual rate of 6.6%].

Table 3.3. Stochastic growth rate, mean population size, and mean time to extinction for the population of Western Rattlesnakes (*Crotalus oreganus*) in the White Lake Basin, British Columbia, Canada over 100 years at different rates of road mortality. Modelled using Vortex software (version 10.2.7.0).

Road mortality rate (% of population)	**Stochastic growth rate (r)**	**Mean population size (N)**	**Mean time to extinction (years)**
0	0.005	3414	>100
2	-0.008	988	>100
4	-0.014	527	>100
6	-0.032	95	>100
8	-0.043	35	94
10	-0.052	19	90.4
12	-0.062	16	80.7
14	-0.075	15	68.4
16	-0.086	0	59.5
18	-0.099	0	52.2
20	-0.111	0	46.8

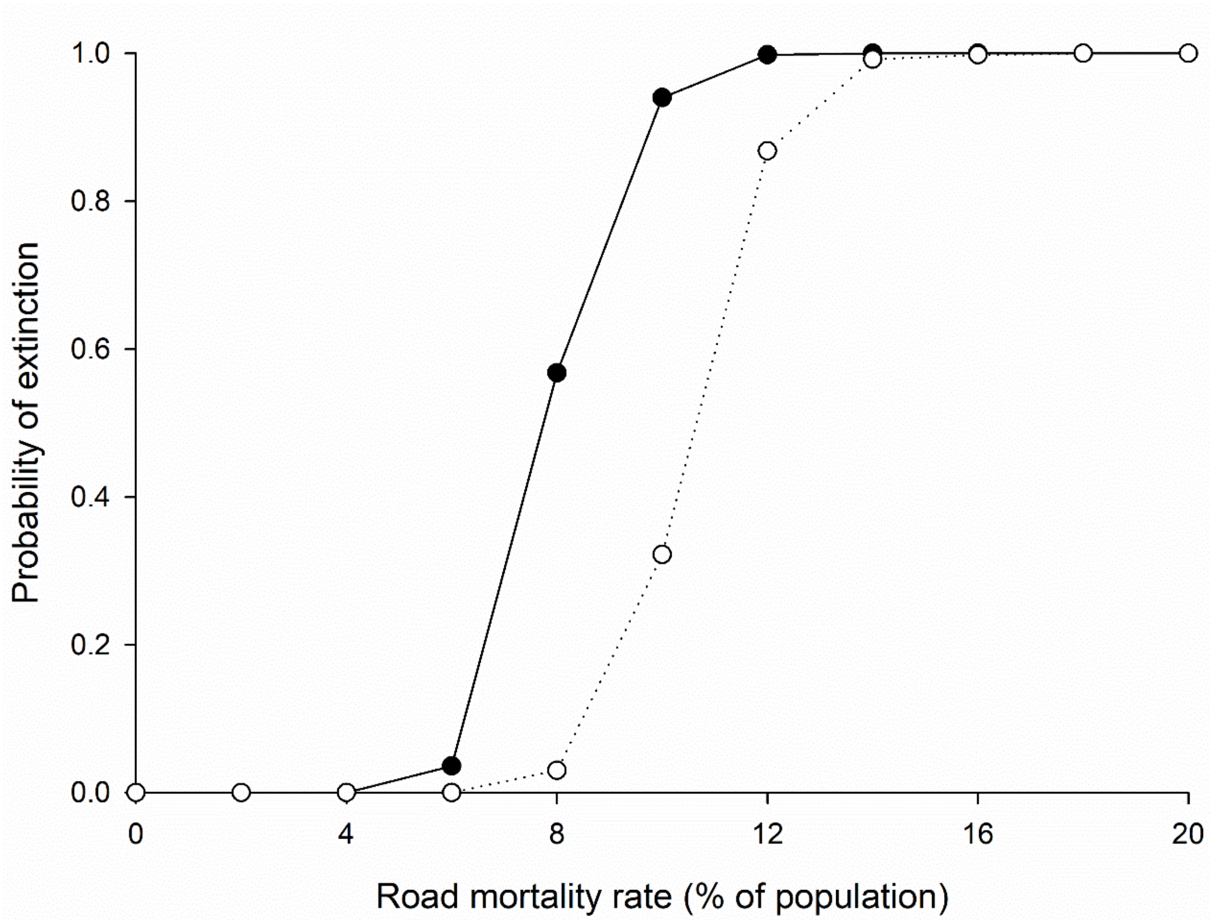

Figure 3.4. Probability of extinction within 100 years for a population of Western Rattlesnakes (*Crotalus oreganus*) as a function of overall road mortality rate with variable proportions of adult female roadkill. The minimum proportion of adult female roadkill (○) was 8% of roadkilled rattlesnakes and the maximum (●) was 17%. Overall proportion of roadkill for adult rattlesnakes was held constant. Modelled using Vortex software (version 10.2.7.0).

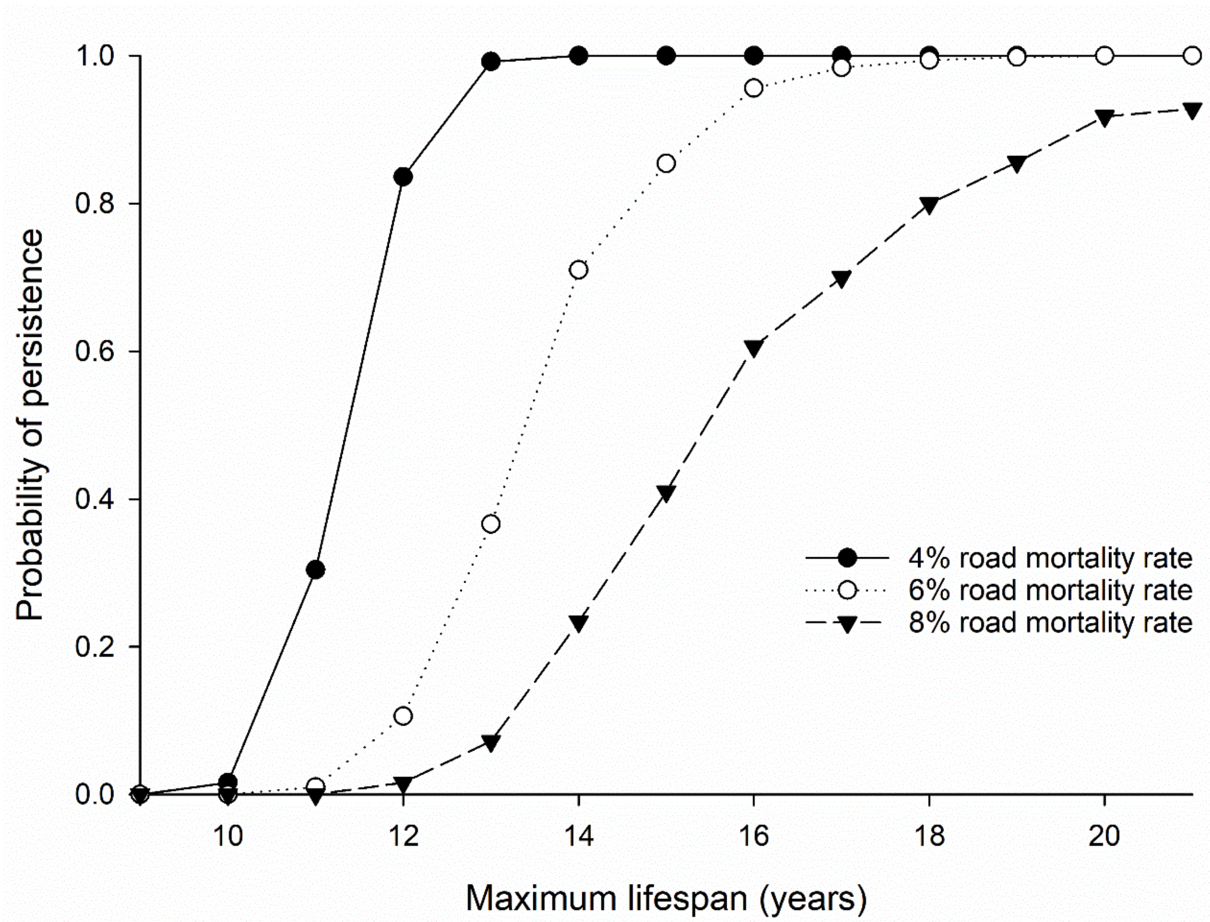

Figure 3.5. The influence of maximum lifespan on the probability of persistence over 100 years for a population of Western Rattlesnakes (*Crotalus oreganus*) in British Columbia, Canada with variable road mortality rates. Modelled using Vortex software (version 10.2.7.0).

Population size

Not surprisingly, a change in initial population size greatly influenced the extinction probability curves when the annual number of animals dying on the road was held constant (i.e. 141, my empirical estimate). For example, a total population of 532 rattlesnakes (estimated population size based on a Jolly-Seber analysis of all captures) with 141 deaths represented a road mortality rate of 26.5%, resulting in an extinction probability of 1.0 over 100 years. In comparison, the actual and much larger starting population (2131 rattlesnakes) resulted in a lower road mortality rate (6.6%, or 141/2131) and essentially no risk (<0.01) of extinction in 100 years. At a constant simulated road mortality rate of 6%, the probability of extinction was zero in 100 years for the actual population, while a population the quarter of the size had an extinction probability of 0.23 at the same road mortality rate (Figure 3.6). All simulated populations, irrespective of size, were liable to go extinct within 100 years if the road mortality rate reached or exceeded 14%. At a rate of 14% road mortality, the mean time to extinction was 19 years earlier for the smaller simulated population. The extinction threshold was less for a smaller population (road mortality rate of 4%) compared to the threshold for the actual population (6%).

DISCUSSION

My analysis here is built upon empirical population and movement data, along with adjusted road mortality rates drawn from intensive surveying and corrections for bias (Chapter 2). Thus, the foundation for the PVA is relatively robust, allowing for meaningful predictions. The PVA strongly supports the hypothesis that this population of snakes is declining principally due to road mortality; given my assessment of the current population size is likely an overestimate, the situation seems dire.

A simulated road mortality rate of 6% appeared to be the maximum that the population could tolerate without an appreciable risk of extinction in 100 years. Although this probability was not high for simulated road mortality rates ≤8%, the rate of population decline was severe. While it is possible that under current conditions (actual road mortality rate of 6.6%) the population will persist for the next 100 years, any increases in road mortality rates probably will result in extirpation. This also assumes that no other

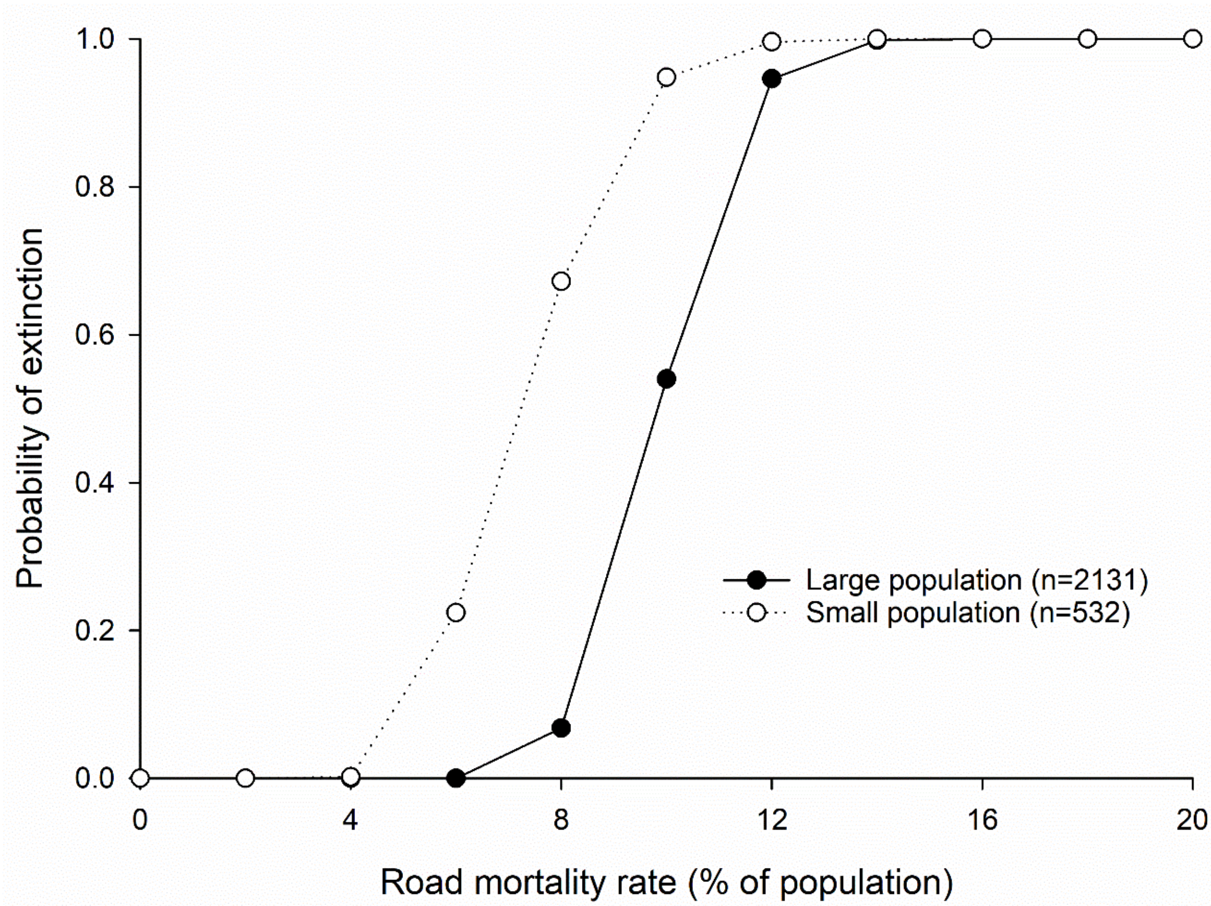

Figure 3.6. The influence of initial population size on the probability of extinction over 100 years for a population of Western Rattlesnakes (*Crotalus oreganus*) in British Columbia, Canada with variable road mortality rates. Modelled using Vortex software (version 10.2.7.0).

anthropogenic stressors or disease outbreaks that would further reduce population size are acting on the population. Similar results have been reported for other snake species threatened by roads. Colley (2015) found that without mitigation measures a road mortality rate of 5.3% would produce extinction of a Massasauga (*S. catenatus*) subpopulation in 100 years. The extinction probability over 500 years for a population of Black Ratsnakes (*Elaphe obsolete*) increased drastically from 0.07 with no roadkill to 0.99 with a very low estimated road mortality rate (0.36%; Row et al. 2007). These results highlight the difficulty of maintaining a viable population over time with any degree of persistent road mortality, and underscore the critical need to reduce this anthropogenic source of mortality, short of eliminating it altogether in some areas.

This study population is likely experiencing the full suite of natural, constraining factors (Gregory et al. 1987) associated with living at the northern periphery of the range of rattlesnakes in North America. Lengthy migrations required to access suitable winter hibernacula, short summers for feeding, growth, and reproduction, superannual reproduction, and perhaps a limited prey base (McAllister and Maida 2016) all will work in an additive or synergistic fashion to limit population growth. Anthropogenic factors then will place further restrictions on these northern populations. The effect of historical persecution by humans (COSEWIC 2015), a common situation for vipers, is another important factor that is very hard to quantify, particularly due to the 'shifting baseline' phenomenon (Pinnegar and Engelhard 2008). While habitat loss likely is not a current or future issue for this population given the protected land status, recent research in a neighbouring population (30 km away) has suggested that anthropogenic factors more discrete than direct habitat loss may be taking a toll (Lomas et al., 2015; Maida et al., in press; this study). The population density determined in my study and other recent estimates for rattlesnakes in British Columbia (Maida et al., in press) provide evidence for this, as these measurements are considerably lower than historical records in the region (Preston 1964; Macartney 1985). Although the White Lake population probably is relatively healthy due to minimal disturbance and development nearby, it is clear that the impact of roadkill on a road with only 350 cars per day at present and has the potential to increase with a rise in traffic, is considerable at the population level.

Predictions of population decline and extirpation in my PVA models showed high sensitivity to the proportion of adult females killed on the road, something expected given the importance of adult, breeding females to the persistence of wildlife populations (e.g. Hebblewhite et al. 2003; Ramp and Ben-Ami 2006). In particular, both Row *et al.* (2007) and Colley (2015) found this effect within other snake populations impacted by roads. It is unclear from my field data, whether differential female mortality (particularly on roads) occurs, but if it exists, could specific management recommendations address the issue? Although studies have started examining in detail the behaviour of female Western Rattlesnakes in this area (Eye et al. unpubl.), research elsewhere suggests that during years when female rattlesnakes are non-gravid their movement behaviour does not differ significantly from adult males (Reinert and Kodrich 1982; Gregory et al. 1987; Jørgensen et al. 2008). Gravid rattlesnakes in the region do not travel far from overwinter den sites compared to other non-gravid females or males (Macartney and Gregory 1988) or other species of northern snakes (Larsen 1987; Didiuk 1999). Still, recent work (Eye et al. unpubl.) shows gestation sites (rookeries) may be situated 400 m from hibernacula, and longer movements to foraging grounds may occur before or after the females become relatively sessile leading up to parturition. Any such exaggerated movements potentially put adult females at risk of encountering roads. The protection and enhancement of habitat a safe distance from roads, perhaps by establishing gestation or refugia sites in proximity to hibernacula, could improve adult female survival while enhancing reproductive success.

In my simulations, the probability of persistence for the population was always <1.0 with road mortality rates set at ≥8%, even if these simulations included snakes living to extreme ages. This strengthens my argument that road mortality rates > 6% pose a serious risk to the viability of this population by making it unlikely that individuals will survive to enter older age classes. It is not surprising that in my models lifespan had a strong effect on population persistence, considering that the longer an animal lives the more reproductive opportunities it will experience. In a recent skeletochronology assessment of 40 roadkilled rattlesnakes from near my site, Petersen et al. (in prep.) estimated the oldest snakes were eleven years, while the oldest female was only ten years. Earlier, Macartney and Gregory (1988) estimated female sexual maturity at a mean age of six, followed by reproduction on average every two years, and Maida et al. (in press) estimated average age at maturity to be

7.1 years. Heavier Western Rattlesnakes also were shown by Macartney and Gregory (1988) to reproduce more frequently and have larger litter sizes, suggesting that heavier (and likely older) snakes are clearly important to the population. Taken in tandem these observations are particularly problematic and exemplify the compounding effects that road mortality can have on a population through the continuous removal of reproductively-mature individuals, especially when natural limiting factors also are at play.

Any PVA comes with elements of uncertainty based on the input parameters (Beissinger and Westphal 1998). The PVA conducted in this study portrays a best-case scenario for this population to avoid inflation of extinction risk, as is the tendency with PVAs (Brook et al. 2000). Without the addition of road mortality to the model, the population was predicted to be growing at a rate of ~0.5%/y; a rate that is probably not unreasonable for a population near the northern periphery. Since my method of estimating population size for the area impacted by road deaths is likely an overestimate, making it probable that the actual risk to this population is greater than what my models estimate. The empirical road mortality rate calculated from my field data and all simulations using higher rates consistently predicted some risk of extinction within 100 years as well as negative population growth rates. Although variation in demographic traits have been found in separate populations of Western Rattlesnakes (Jenkins et al. 2009), I believe this is a representative PVA for Western Rattlesnakes in British Columbia and can be extrapolated with caution to other populations.

Future PVA models can build upon this one using longer-term population size estimates, survival rates, and road mortality rates (population parameters). Due to the intertwining of these factors, monitoring populations directly (i.e. through census work at communal dens) and tracking roadkill rates may be jointly required to observe sources of population declines, and the effects of mitigation work to reduce roadkill. Additional research into the meta-population dynamics of individual den sites and genetic assessments of den populations separated by the road will be beneficial in exploring further the effects of road mortality on the overall population.

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CHAPTER 4

CONCLUSION

The overarching goal of my thesis was to understand the effects road mortality has on wildlife populations. Specifically I chose to look at a population of long-lived snakes in the northern extreme of their range that face multiple conservation threats in addition to road mortality and exhibit pre-existing biological constraints to population growth. To this end, I pursued three main objectives: (a) measuring the amount of road mortality, (b) describing the population impacted, and (c) assessing the effect that road mortality had on population growth rate and probability of extinction.

The principal findings from my thesis were:

- Road mortality rates that account for scavenger-removal and observer detection error were 2.7× greater than unadjusted rates.
- Opportunistic/incidental observations of roadkill were the least accurate method of quantifying road mortality rates compared to methodical road surveys.
- Observer detection probability of carcasses was far less than 100% when conducting road surveys on foot, even for an experienced team of observers.
- The population was at risk of extinction within 100 years at all simulated annual road mortality rates > 6% of the population. Population growth rates were negative for all simulated road mortality rates.
- The population growth rate was -0.032 and the probability of extinction within 100 years was <0.01 at the actual calculated road mortality rate of 6.6%. Given that my method of estimating population size for the area of concern likely was biased towards an overestimate, the actual risk to this population likely was greater than this.
- Population growth rates and persistence probabilities were sensitive to adult female road mortality, initial population size, and longevity of rattlesnakes.

Overall, these findings support my prediction that substantial and persistent road mortality has a detrimental effect on northern populations of long-lived snakes. Additionally the results support the prevailing findings that road mortality rates are underestimated if scavenging and observer error are not accounted for. My analysis provides an accurate and detailed understanding of population level effects of road mortality that could lead to quantifiable measures that can be used to assess the effects of mitigation to reduce or stop roadkill of snakes.

Management Implications

The greatest threat to Western Rattlesnakes in British Columbia is road mortality according to the provincial recovery plan (Southern Interior Reptile and Amphibian Working Group 2016a); however long-term monitoring is rarely undertaken (in part to unreliable long-term funding) and then generally only opportunistically. As has been shown in this thesis, opportunistic monitoring is ineffective for determining the magnitude of roadkill and likely biases the understanding of the issue. Therefore, methodical monitoring of roadkill should be expanded within the province to other areas of concern for Western Rattlesnakes. Ideally, intensive surveying, similar to the methods used in this thesis, should be conducted; however, less frequent surveys can still be used to calculate road mortality rates (see equation 4 in Chapter 2). The prudent application of the 2.7× correction factor found in my study would be reasonable to estimate a minimum road mortality rate for other snake species and/or areas of the Okanagan valley with similar traffic flow and insufficient resources for more stringent monitoring.

It is likely that the threat of road mortality to snake populations globally is greater than thought, given underestimates of roadkill. I recommend that researchers conducting road mortality studies in any area, particularly on smaller species, evaluate scavenger-removal and observer error for each study. Observer detection probability should be determined using planted carcasses to accurately assess this source of error for a given survey method and not rely on a comparison of walking survey results to other methods.

This is the first intensive snake road mortality monitoring project in BC that also considers population level impacts. Road mortality is listed as a main threat to three other at-risk snake species found at the northern extent of their range in British Columbia (Great Basin Gophersnake, *Pituophis catenifer deserticola* - Southern Interior Reptile and Amphibian Working Group 2016c; Western Yellow-bellied Racer, *Coluber constrictor* - Environment Canada 2015; and Desert Nightsnake, *Hypsiglena chlorophaea* - Southern Interior Reptile and Amphibian Working Group 2016b). As these species have different life history traits from rattlesnakes, similar studies assessing population persistence should be undertaken for each species to quantify the threat of road mortality (see Appendix A).

It appears that the protected status of much of the habitat in my study areas is not sufficient alone to prevent a continued decline in the rattlesnake population due to road mortality. This in turn suggests that efforts need to be taken to reduce the road mortality rate below the detected threshold value. Although a complete elimination of road mortalities would go the furthest in preventing a population decline and enabling the population to recover, such a target likely is not feasible without a major decrease in vehicle traffic. Numerous other mitigation measures are currently being studied and used to reduce mortality for various wildlife roadkill projects (Glista et al. 2009; Rytwinski et al. 2016). Possible solutions suitable for the White Lake Basin fall within three categories outlined by Forman et al. (2003): mitigation, compensation, and prevention.

Mitigation

Methods used to mitigate the impacts of existing roads on wildlife populations must be two-fold and reduce road mortality while at the same time maintaining habitat and genetic connectivity (Forman et al. 2003). Fences paired with underpasses have been shown to reduce roadkill and allow snakes to cross roads successfully (Rytwinski et al. 2016; Colley et al. 2017). In a separate analysis (Winton 2017) I recommended high priority locations for underpass culverts within the White Lake Basin that would protect rattlesnake movement corridors across roads and areas where high amounts of rattlesnake roadkill occurred (‘hot-spots’). Continued monitoring of road mortality and the rattlesnake population is imperative to determine any decrease in road mortality due to these mitigation measures.

Methods that modify human behaviour also may decrease the probability of road mortality. A reduced speed limit (as suggested by Farmer and Brooks 2012; Valero et al. 2015) along the roads in the basin is something that local communities would support (personal communication) and could be achieved through the use of dynamic signs (Hardy et al. 2006).

Compensation

Other practices may be used to compensate for road mortality, with or without mitigation methods that are not wholly effective at eliminating roadkill (e.g. Baxter-Gilbert et al. 2015). The results of my sensitivity analysis suggest that a relatively larger population is more resilient to the effects of road mortality; therefore augmentation of the population in theory would be a possible method of maintaining viability. This method has been successful in rescuing small inbred populations of snakes in Sweden (Madsen et al. 1999), although I am not aware of any attempts to captive-breed and reintroduce rattlesnakes. Combining the results of my sensitivity analysis with movement data from radio-telemetry and the current knowledge of rattlesnake ecology further suggests that protection/enhancement of connective and other critical habitat, particularly for reproductively mature females (e.g. rookery sites), away from roads would be beneficial.

Prevention

While few studies exist on the effectiveness of closing an existing road to traffic (but see Kline and Swann 1998), logically this would be an effective if not drastic method to prevent roadkill (Huijser et al. 2008; Bishop and Brogan 2013). Although this may not be an ideal solution for White Lake, it should be considered especially if mitigation methods are ineffective or if the situation worsens (i.e. road mortality rates increase). Seasonal closures during the snake active season, especially the spring and fall migratory periods (e.g. Palis 2016) or limiting the road to local traffic are potentially less stringent methods to explore. Further, I would strongly advise against the expansion of the existing road or any other activities that would encourage increased traffic in the area, as wider roads and increased traffic volumes have been associated with higher road mortality rates and increased barrier effects (Forman and Alexander 1998).

Finally, increasing awareness of both local residents and visitors to the area on the issue of road mortality may play a role in preventing roadkill. The information signs at the two areas of interest within the basin should include sections on roadkill impacts to wildlife populations and how drivers can reduce the risk of wildlife-vehicle collisions. Additional traffic signs could be installed at points of entry to the basin to supplement mitigation measures. Although simple and generally less costly, these methods admittedly are less studied, providing little support for their effectiveness (Rytwinski et al. 2016), and they should not be exclusively relied upon to reduce roadkill.

On a broader scale this study supports the argument for greater consideration of wildlife populations during road planning. Informed route selection may prevent mortality on new roads (Forman et al. 2003) and therefore studies should evaluate movement pathways, home ranges, habitat use, and general ecology of animals of concern prior to development. The management practices I have suggested are specific to rattlesnakes at this study site, however, differences among species affected by roadkill (Appendix A) and multi-species approaches to mitigation should be considered (Coelho et al. 2008). Regardless of the method(s) chosen, an experimental design should be applied to determine effectiveness (van der Grift et al. 2013; Rytwinski et al. 2015).

Limitations and Future Research

The intensive design of my study demonstrated that conventional road surveys without consideration of scavenging and observer error produce underestimates of road mortality rates for snakes. Since I did not assess observer error for survey methods other than those conducted on-foot, crippling effect (injured animals leaving the road before dying) or habitat bias, it is possible that a lack of understanding around these sources of error led to additional underestimates. Thus, the scenarios painted in this thesis overall should be considered conservative. Paired with the fact my population size calculations have likely provided an over-estimate, I am confident that the effects of road mortality on the population in this thesis have not been conflated; rather, they may be worse than indicated.

Short, even intense studies on road ecology are not without pitfalls. Given the duration of my study, the input parameters for the PVA model relied heavily on previous research and the assumption that population traits are consistent throughout the range of rattlesnakes in British Columbia. Although such work is currently underway (Atkins et al.

unpubl.), my study provides a strong framework and baseline data for future research, and continuing to sample the White Lake population in the long-term will provide accurate and specific reproductive and mortality rates that can be used to improve the PVA model. Changes in population size, age structure, sex distribution and road mortality rates over time can be tracked through continued mark-recapture work and road surveys. New data can then be used to test the predictions of the PVA and modify the model accordingly. Future questions for this site that build upon the existing PVA model might focus on a metapopulation study of individual den sites or complexes to determine which sites are at greater risk of extirpation and where to focus management efforts. A genetic assessment of the rattlesnake den populations with particular focus on areas separated by the road would further augment this research and could explore the influence of barrier effects and importance of road permeability.

Effective mitigation requires a fundamental understanding of why animals appear on roads in the first place. However, little research has been conducted to specifically identify the driving factors behind snake occurrences on roads. Are snakes simply moving between points on the landscape, or are they actively seeking some resource available on the road? Previous research (Fortney et al. 2012) has shown that Prairie Rattlesnakes (*C. viridis*) used paved roads at a higher rate than would be expected based on the availability of roads on the landscape, and rattlesnakes were found on roads more frequently than other snake species. This indicates that the rattlesnakes are attracted to and potentially prefer road habitat. Another study found that paved roads have higher temperatures in the evening compared to cooler surrounding areas (Shine et al. 2004). This occurs after the road has warmed up during the day and then after sunset the road surface retains the heat for a longer period. As ectotherms at the northern extent of their range, Western Rattlesnakes in BC exhibit behaviour that is highly influenced by the need to thermoregulate (Harvey 2015), and paved roads may offer preferential habitat at certain times of the day or season compared to the surrounding landscape. The hypothesis that rattlesnakes are actively using road surfaces for thermoregulation and thereby increasing probability of mortality requires testing. Research identifying predictors of rattlesnake behaviour as it relates to road thermodynamics, as well as the conditions associated with incidence of roadkill will be valuable in being able to predict when, where and for how long snakes are occupying roadside habitat. This information is needed to assess how effective certain mitigation methods (e.g. creating alternative basking or rookery habitat away from roads) may prove.

Conclusion

Populations constrained by physiological, ecological, and climatic limitations such as reptiles at their northern range limit are sensitive to anthropogenic disturbances. I assessed the impact of roadkill on a northern rattlesnake population, and in doing so I utilized a modified approach to quantifying road mortality rates and determining population size. I demonstrated that scavenger-removal, observer error, and survey methods have a high degree of impact when assessing roadkill on a small rural road. In pairing these results with a PVA, I provided a comprehensive evaluation of the population persistence. The actual road mortality rate detected during my study was above the extinction threshold, and all simulated road mortality rates (including very low ones) consistently produced negative population growth rates. It is apparent that mortality due to roads in addition to natural sources of mortality exceeds any counteractive influence of regulating factors (Fryxell et al. 2014) and ultimately will push populations to extinction. If mortality is reduced through management efforts, the population density may increase to a new carrying capacity provided other factors are not limiting the population. However, this has yet to be reported for reptile populations and underscores the need for long-term post-mitigation studies.

The understanding of population response to disturbance will aid conservation practitioners when assessing the threat of road mortality to wildlife populations and specifically assist in the maintenance of Western Rattlesnake populations. The results highlight the importance of methodical surveys and accounting for sources of error, and as such should guide method selection when planning road mortality studies. This work expands on the knowledge of a priority threat to a species-at-risk, and provides a framework to explore other threats to northern snake populations.

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APPENDIX A

ROAD MORTALITY IN THE WHITE LAKE BASIN

Table A.1. Frequency of roadkill detected for vertebrate species (not adjusted for observer error or scavenging rates) during surveys and incidentally along 11.7 km of road within the White Lake Basin, BC, Canada. Total survey effort approximately 5210 km from April 9 – October 3, 2015 and April 5 – October 11, 2016.

Common name	Scientific name	N
Amphibians		
Pacific Tree Frog	*Pseudacris regilla*	114
Great Basin Spadefoot[a]	*Spea intermontana*[a]	44
Long-toed Salamander	*Ambystoma macrodactylum*	23[b]
Western Tiger Salamander[a]	*Ambystoma mavortium*[a]	13
Reptiles		
Western Yellow-bellied Racer[a]	*Coluber constrictor*[a]	128
Western Rattlesnake[a]	*Crotalus oreganus*[a]	92
Great Basin Gophersnake[a]	*Pituophis catenifer*[a]	84
Common Garter Snake	*Thamnophis sirtalis*	20
Rubber Boa[a]	*Charina bottae*[a]	19
Western Terrestrial Garter Snake	*Thamnophis elegans*	9
Painted Turtle[a]	*Chrysemys picta*[a]	2
Unidentified Snake	-	21
Birds		
Vesper Sparrow	*Pooecetes gramineus*	23
California Quail	*Callipepla californica*	12
Brewer's Blackbird	*Euphagus cyanocephalus*	5
Eastern Kingbird	*Tyrannus tyrannus*	4
Western Bluebird	*Sialia mexicana*	4
Chipping Sparrow	*Spizella passerine*	3

Common Nighthawk	*Chordeiles minor*	2
Gray Catbird	*Dumetella carolinensis*	2
Western Meadowlark	*Sturnella neglecta*	2
American Goldfinch	*Spinus tristis*	1
American Robin	*Turdus migratorius*	1
Bullock’s Oriole	*Icterus bullockii*	1
Common Poorwill	*Phalaenoptilus nuttallii*	1
Dark-eyed Junco	*Junco hyemalis*	1
Grey Partridge	*Perdix perdix*	1
Lark Sparrow[a]	*Chondestes grammacus*[a]	1
Lazuli Bunting	*Passerina amoena*	1
Mallard	*Anas platyrhynchos*	1
Mountain Bluebird	*Sialia currucoides*	1
Northern Flicker	*Colaptes auratus*	1
Pine Siskin	*Spinus pinus*	1
Ruffed Grouse	*Bonasa umbellus*	1
Sage Thrasher[a]	*Oreoscoptes montanus*[a]	1
Song Sparrow	*Melospiza melodia*	1
Spotted Towhee	*Pipilo maculatus*	1
Tree Swallow	*Tachycineta bicolor*	1
Sparrow sp.	-	12
Galliform sp.	-	10
Hummingbird sp.	-	3
Wren sp.	-	1
Unidentified Bird	-	53
Mammals		
Great Basin Pocket Mouse[a]	*Perognathus parvus*[a]	43
North American Deer Mouse	*Peromyscus maniculatus*	7
Yellow-pine Chipmunk	*Tamias amoenus*	4
North American Red Squirrel	*Tamiasciurus hudsonicus*	2

Bushy-tailed Woodrat	*Neotoma cinerea*	2
North American Porcupine	*Erethizon dorsatum*	2
Yellow-bellied Marmot	*Marmota flaviventris*	2
Bobcat	*Lynx rufus*	1
Coyote	*Canis latrans*	1
Meadow Vole	*Microtus pennsylvanicus*	1
Mule Deer	*Odocoileus hemionus*	1
Northern Pocket Gopher	*Thomomys talpoides*	1
Mouse sp.	-	4
Bat sp.	-	3
Unidentified Small Mammal	-	14

[a]species-at-risk

[b]many more long-toed salamanders were likely killed; however, to prevent accidentally killing more individuals by driving or walking on them, surveys were stopped when high amounts of salamanders were encountered and thus counts are known to be underestimates.

Table A.2. Detections of dead and alive Western Rattlesnakes (*Crotalus oreganus*) on the road within and outside of the survey route in the White Lake Basin, BC, Canada, 2015 and 2016.

	Dead	**Alive**	**Total**
Survey route (11.7 km)	92	17	109
Outside survey route (3.3 km)	13	5	18
Total (15 km)	105	22	127

APPENDIX B

SCAVENGING EVENTS OF SNAKE CARCASSES MONITORED BY CAMERA-TRAPS

Figure B.1. Photographs of scavenging events from motion-activated wildlife cameras monitoring snake carcasses on White Lake Road, 2016. Scavenger species recorded by camera-traps were A) Coyote (*Canis latrans*), B) Human, C) Turkey Vulture (*Cathartes aura*), and D) Black-billed Magpie (*Pica hudsonia*).

APPENDIX C

RATTLESNAKE MOVEMENT DISTANCES IN THE WHITE LAKE BASIN

Table C.1. Maximum straight-line distance travelled from hibernacula by adult male Western Rattlesnakes (*Crotalus oreganus*; n=32) from eight den sites within the White Lake Basin, BC, Canada in 2011 (Harvey 2015), and 2015 & 2016 (this study).

	Rattlesnake	Den complex /site	Year	Maximum distance from hibernaculum (km)	Comments
Focal den complexes	1-1	1	2011	0.53	
	1-2	1	2011	0.88	transmitter failed
	1-3	1	2011	1.21	only one relocation
	1-4	1	2011	1.76	
	1-5	1	2015	1.19	
	1-6	1	2015	1.20	
	1-7	1	2015	1.21	
	1-8	1	2015	1.21	
	1-9	1	2015	1.25	
	1-10	1	2015	1.38	
	1-11	1	2015	1.44	
	1-12	1	2015	1.64	
	1-13	1	2015	2.13	lost (suspected DOR)
	1-14	1	2016	0.47	
	1-15	1	2016	0.78	
	1-16	1	2016	1.10	
	1-17	1	2016	1.10	
	1-18	1	2016	1.28	
	1-19	1	2016	1.31	lost (suspected DOR)
	1-20	1	2016	1.49	
	1-21	1	2016	1.65	lost

	1-22	1	2016	1.75	
	1-23	1	2016	1.99	
	2-1	2	2015	0.59	died (DOR)
	2-2	2	2016	0.25	
	2-3	2	2016	0.42	
	2-4	2	2016	1.20	
Other den sites	3-1	3	2011	0.91	died
	3-2	3	2011	1.54	
	3-3	3	2011	2.46	
	3-4	3	2011	3.21	
	4-1	4	2015	1.19	
Mean	-	-	-	1.30	