TEMPORAL AND SPATIAL CHANGES IN A WESTERN RATTLESNAKE (*CROTALUS OREGANUS*) POPULATION IN BRITISH COLUMBIA

by

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ABSTRACT

Effective conservation strategies and management plans for wildlife species, especially species-at-risk, require demographic information on populations and an understanding of how local landscapes and management regimes impact them. Historic comparisons are especially important because gradual declines across large landscapes can go unnoticed as wildlife managers in each generation and region start with a lower initial population size estimation. This phenomenon is called the Shifting Baselines syndrome.

Replicating a historic study from 1981-1983, I conducted a mark-recapture study in 2018-2020 on Western Rattlesnakes in the North Okanagan region of British Columbia. The study area spanned two habitats with contrasting levels of human influence: Kalamalka Lake Provincial Park and Coldstream Ranch. The former receives an average of 32,500 visitors per month during the active season for snakes, while Coldstream Ranch allows cattle grazing but is off-limits to humans. In the 35 years since the original study, the Park population was estimated to have declined by 50% and the Ranch population by 31%, for an overall decline of 40%. A separate analysis using only adult snakes showed less severe declines, suggesting a lack of recruitment of snakes into the population may be contributing to this decline. Qualitative observations of behavioural differences between sites also prompted a standardized test of defensive behaviour in animals across the two contrasting habitats. Snakes in the area of high human visitation were 9.5× less likely to display defensive rattling behaviour, and allowed approaching investigators 2.5 m closer on average before initiating rattling behaviour, compared to snakes in habitats with negligible human presence.

This study highlights the pitfalls of using point estimates of populations to assess the status of a species over a broad geographic area. These results also suggest that protected areas may not necessarily serve as ‘anchors’ for conservation. Further research spanning multiple landscapes and management types is necessary to differentiate between natural and anthropogenic pressures on populations. Revealing the specific pressures that may be at play in varying locations should be addressed for continued conservation.

Keywords: *Crotalus oreganus*, population estimate, management, behaviour, rattling, shifting baselines, Western Rattlesnake, Northern Pacific Rattlesnake

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- To the adventure of a lifetime and becoming a 'snake guy'.

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CHAPTER 1

INTRODUCTION

Shifting Baselines

The effective management of wildlife requires a strong understanding of the long-term dynamics of ecosystems, communities, and populations (Lindenmayer et al., 2012). Ecological studies that monitor or revisit populations over many decades provide important information on complex processes, interactions, and trends that allow managers to produce tailored strategies as opposed to expert opinions or non-taxa-specific overarching management principles (Magnuson, 1990; Lindenmayer and Likens, 2010; Lindenmayer et al., 2012). Periodic assessments of wildlife populations are critical for quantifying ecological responses to natural and human disturbances (Likens, 1985; Carpenter et al., 1995). However, without historical reference data gradual declines over long time periods often go unnoticed; a phenomena termed the Shifting Baselines Syndrome (Pauly, 1995; Jackson, 1997; Bohnsack, 2003; Folk et al., 2004; Huitric, 2005; Papworth et al., 2009; Soga and Gaston, 2018). Shifting Baselines Syndrome is our collective tendency to not recognize gradual declines, shifting our perspective over time such that degraded ecosystems start to "look" normal and acceptable. 'Generational amnesia' (Papworth et al., 2009), whereby the experience and knowledge of past managers or knowledge holders is not passed onto future generations, allows newer perceptions of normality to develop that are ignorant of historical and healthier conditions (Pauly, 1995). The widespread acknowledgement of this phenomena is relatively new, and in recent decades many studies identifying shifting baselines have arisen that span taxa and disciplines (Baum and Meyers, 2004; Newsome et al., 2007; Pinnegar and Engelhard, 2008; Rittenhouse et al., 2010; Turvey et al., 2010; Vera, 2010; Whipple et al., 2011; Bender et al., 2013; Santini et al., 2017).

The establishment of shifting baselines is particularly worrisome given that species diversity is declining across the globe (Vors and Boyce, 2009; Potts et al., 2010; Barnosky et al., 2011; Ceballos et al., 2015; Ceballos et al., 2017; Saha et al., 2018) and that empirical data for many taxa are scarce or non-existent. According to the IUCN (2020), populations of mammals, birds, amphibians, reptiles, and fish have declined by an average of 68% since 1970. In the coming century, the proportion of threatened species is expected to substantially increase (Sala, 2000; Saha et al., 2018) due to human activities such as climate change, habitat destruction, resource exploitation, infectious diseases, and the invasion of exotic species (Cronin et al., 2014). When we consider the taxa that have been studied in a conservation context, there is greater cause for alarm. Cronin et al. (2014) assessed over 4,000 studies that mention “wildlife conservation” and identified a severe bias towards mammals (42.8% of studies) and birds (19.2% of studies). Alarmingly, less than 200 publications in this review investigated the conservation of reptiles (4.8%), fish (3.6%), or amphibians (2.1%). Underrepresentation of herpetofauna, despite a high proportion of species with conservation concern, and bias towards mammals and birds has been consistently identified (Clark and May, 2002; Lawler et al., 2006; Cronin et al., 2014) and there is little evidence to suggest an effort to increase parity of study taxa (Cronin et al., 2014).

Reptiles remain one of the least studied vertebrate groups and often are considered to be of less general interest than other taxa (Gibbons, 1988; Bonnet et al., 2002; Todd et al., 2010). In fact, the number of reptilian species that have been assessed globally remains dismal: just 6% as of 2010 (Baillie et al., 2004; Todd et al., 2010). Reptiles have declined >50% globally since 1970, although data on squamate species trends are severely limited (Saha et al., 2018). In Canada, only 46 of 102 (45%) reptile and amphibian species have usable data on populations (WWF, 2017; see also Seigel 1993; Bonnet et al., 2002; Lind et al., 2005). Demographic baselines and robust datasets on reptiles are sparse and difficult to obtain considering there are knowledge gaps on basic life history and ecology and many species display cryptic colouration and behaviour, patchy distribution, and that (Zug et al., 2001; Todd et al., 2010). These types of datasets are crucial for detecting population declines and for disentangling natural versus unnatural fluctuations and extinctions (Tinkle, 1979; Cody 1996; Gibbons et al., 2000). Furthermore, observations of reptile populations or behaviours can be used to identify changes or disturbances to the local environment (Beaupre and Douglas, 2009).

Rattlesnake Populations in British Columbia

Western Rattlesnakes inhabit dry valley bottoms in the south-central arid region of British Columbia (Fig. 1.1). Currently little is known about Western Rattlesnake population sizes in Canada, and estimates vary widely and may be exaggerated in many areas (COSEWIC, 2015; Environment and Climate Change Canada, 2017). At the time of writing, Western Rattlesnakes are federally listed as “Threatened”, and placed on the “Blue-List” (‘special concern’) in British Columbia. Projections of serious declines (30-70% over the next 3 generations) are based upon extrapolations of limited data from singular dens or small areas, habitat modelling, and surveys confounded by detection biases (COSEWIC, 2015; Environment and Climate Change Canada, 2017). The necessity for further monitoring of this snake is exacerbated by the fact that the Okanagan Valley, which contains the majority of Western Rattlesnake range in Canada, is experiencing one of the fastest rates of urban and agricultural growth in the country (Okanagan Valley Economic Development Society, 2013; Statistics Canada, 2014). Without periodic assessment or continued monitoring, the cause of decline may be impossible to identify (Gibbons et al., 2000). Since the 2015 COSEWIC assessment, baseline population estimates for two populations of Western Rattlesnakes in BC now exist (Maida et al., 2018; Winton et al., 2019), as well as a much better understanding of their genetic structure and basic ecology, including reproductive and migration habits, responses to disturbance, and the impact of roads (Lomas et al., 2015; Winton et al., 2018; Lomas et al., 2019; Maida et al., 2019; Winton et al., 2019; Harvey and Larsen, 2020; Schmidt et al., 2020). However, the relative state of current-day populations cannot be properly interpreted without long-term data or robust comparisons to historical baselines.

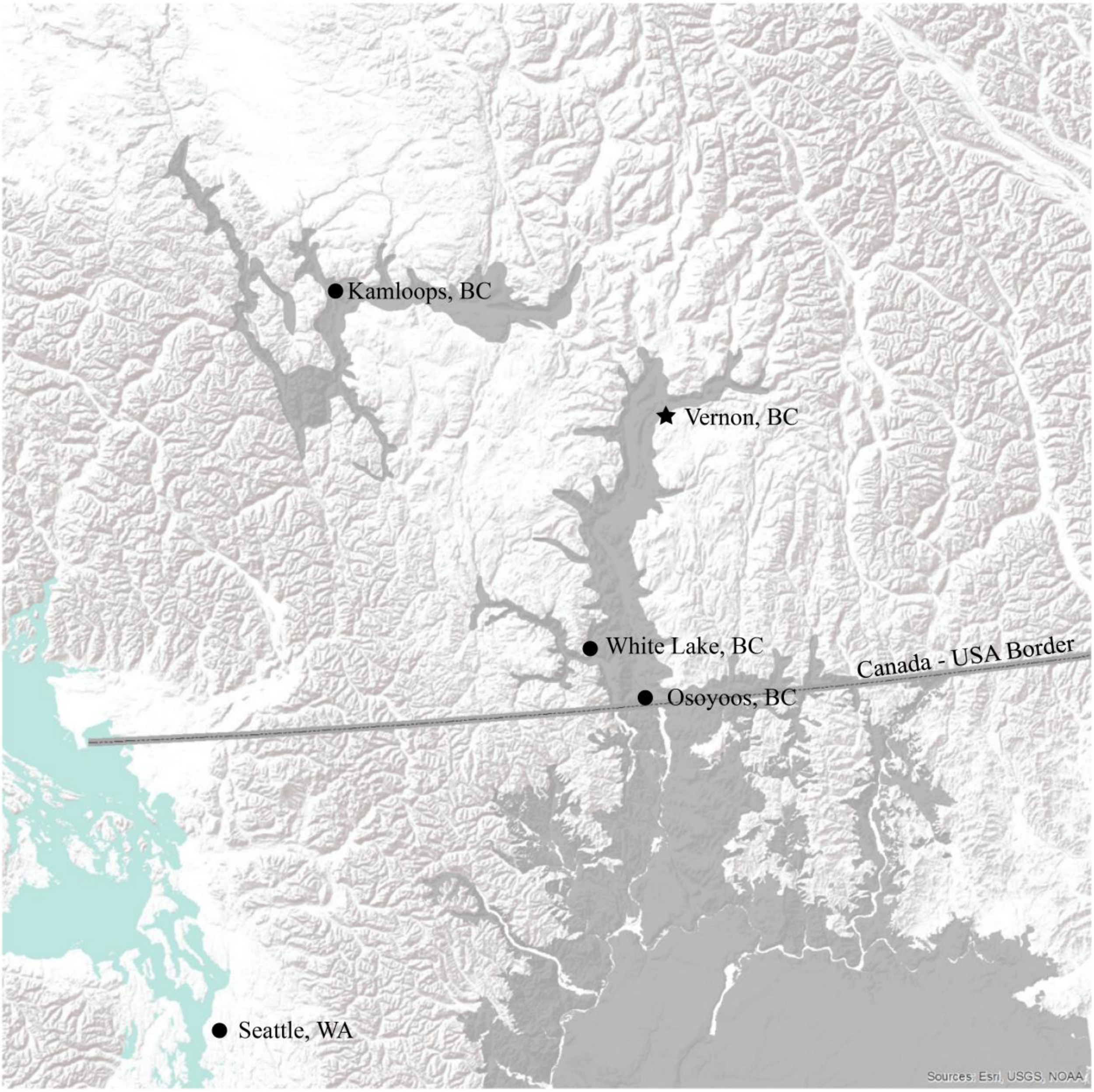

FIGURE 1.1. Western Rattlesnake (*Crotalus oreganus*) range in British Columbia, Canada. (Adapted from: R. Reudink, British Columbia Ministry of Forest, Lands, Natural Resource Operations and Rural Development).

In the early 1980’s a pioneering study by Macartney (1985) investigated the fundamental ecology of Western Rattlesnakes in the North Okanagan Valley of British Columbia (Macartney, 1985). Life-history parameters were documented through a three-year mark-recapture study at 24 communal dens from 1981 – 1983. The study focused on survival, growth, diet, and reproductive ecology. Radio-telemetry was also minimally employed in tracking several individual snakes to discern approximate home range size.

Macartney (1985) suggested that the populations surveyed at that time were rebounding from much lower levels in 1930s – 1950s. There is evidence to support that rattlesnakes were widely persecuted in the area in the early- to mid-20th century. For example, Cosens Bay was used as a WW2 training ground, and one soldier recalls his time in the area:

“One of the first things they taught us in Vernon was to catch rattlesnakes on the range at Rattlesnake Point. We had a big wooden barrel and in that barrel we usually kept five or six rattlesnakes.” - Walker MacNeil (Okanagan Historical Society Reports, 1983).

There are also historical records of over 4,000 rattlesnakes exterminated by Austin (Augustine) Mackie from the early 1920s into the 1960s (Okanagan Historical Society Reports, 1965) in a personal vendetta caused by the death of a childhood friend from a rattlesnake bite. The total number of rattlesnakes found by Macartney during his mark-recapture study (1985) were well below the numbers estimated to have been killed by Mackie over multiple decades. It is possible that rattlesnake populations in the area had begun to rebound from large-scale persecution by the time Macartney had conducted his study, further highlighting the need for periodic assessments to document long-term population trends.

Until recently, Macartney’s study represented the only empirical data on rattlesnake populations in British Columbia; it has been influential in informing conservation and management strategies at the provincial and federal level (COSEWIC, 2015). Now, over 35 years later, these data are important as a historical baseline for understanding how populations have changed over time.

Study Site

Kalamalka Lake Provincial Park (KLPP) and the adjacent Coldstream Ranch are located in the North Okanagan Valley, approximately 11 km south of the city of Vernon and bordering the District of Coldstream. The study area I surveyed encompassed approximately 1150 hectares divided between KLPP and Coldstream Ranch (Fig. 1.2). The study area within KLPP (3,218 hectares total) covers approximately 760 hectares bordered to the north by the district of Coldstream, to the east by Kalamalka Lake, to the west by the Coldstream Ranch boundary, and to the south by the forested edge of the lower grassland habitat (hereafter referred to as 'Park'). The Coldstream Ranch study area covered approximately 390 hectares and is bordered to the north by Coldstream Creek, to the east by KLPP, and to the east and south by the forested edge of lower grassland habitat (hereafter referred to as 'Ranch'). Figures 1.3 and 1.4 provide a comparison of the average monthly temperature and precipitation during my study and during the original Macartney study to a 30-year norm (1981 – 2010).

Ecologically, the study area is located within the North Okanagan Basin Ecosection and contains five biogeoclimatic subzone and variants as defined by the Province of BC (Meidinger and Pojar, 1991; British Columbia Parks, 2019)

- IDF dm1 (Interior Douglas-fir Dry Mild)
- IDF xh1 (Very Dry Hot)
- MS dm1 (Montane Spruce Dry Mild)
- ICH mk1 (Interior Cedar Hemlock Moist Cool)
- IDF mw1 (Interior Douglas-fir Moist Warm)

Due to the variety of available habitat, the area is home to a wide diversity of vertebrate and invertebrate species, including 19 ecological communities considered 'at-risk' in British Columbia (British Columbia Parks, 2019).

The Park site contains an unpaved access road for a lakeshore community (Cosens Bay Road; Fig. 1.5) that bisects the natural landscape near the delineation of Kalamalka Lake Provincial Park and Coldstream Ranch. Within Kalamalka Lake Provincial Park are >50 kilometers of popular, year-round hiking, horse-riding, and mountain biking trails. These trails are dispersed throughout the provincial park and lead to several day-use picnic areas, beaches, and pet-areas (Fig. 1.6). Data from traffic counters at three main parking areas within Kalamalka Lake Provincial Park suggest a conservative estimate of average monthly human use to be 32,600 visitors during the active season for rattlesnakes (April-October; Fig. 1.7). The rattlesnake population in this area is partitioned into two den complexes separated by Cosens Valley and Cosens Bay Road (Fig. 1.5): the Kal Lake Park Den Complex and Coldstream Ranch Den Complex. The entirety of the Kal Lake Park Den Complex lies within the boundaries of KLPP and contains dens of varied usage, one previously unidentified den site, and other important snake areas (*i.e.* solariums, basking sites, shedding sites, and rookeries). The majority of dens and important snake features within the Kal Lake Park complex are located in close proximity to trails and high-use park areas, some within a few meters of major trails. The majority of the Coldstream Ranch Den Complex is situated within Coldstream Ranch lands outside of the Park boundary, with one exception. Despite being within the Park boundary, the geographical position, barriers to dispersal, and observational evidence suggest this den is more contiguous with the Coldstream Ranch complex than the Kal Lake Park complex.

The situation at Macartney's study site in the North Okanagan lends itself perfectly to reassessment of rattlesnake populations. At roughly the time that Macartney's (1985) study concluded, the populations in the Kalamalka region were divided into two spatially segregated and contrasting management types: a Provincial Park accommodating recreational activities, and an active cattle ranch. Individual impacts from recognized threats would presumably have been negligible at first, however, over the last 35 years the landscape (and those who use it) has changed markedly. Most notably, the Park site now has substantial human presence across the landscape, and the effects of bordering an urban area are more noticeable when compared to the Ranch site. Recent investigation into the genetic relatedness of rattlesnake populations in British Columbia have suggested that rattlesnake denning populations between Kalamalka Lake Provincial Park and Coldstream Ranch are panmictic (Schmidt et al. 2020), despite obvious barriers to gene flow on the landscape. Thus, any differences detected in the demography and morphometry between the sites will likely be due to the effects of site-specific pressures, rather than variability within the gene pool.

FIGURE 1.2. Entire study area (~1075 ha) showing the area surveyed within Kalamalka Lake Provincial Park site (Park; ~710 ha; White) and the Coldstream Ranch site (Ranch; ~365 ha; Black).

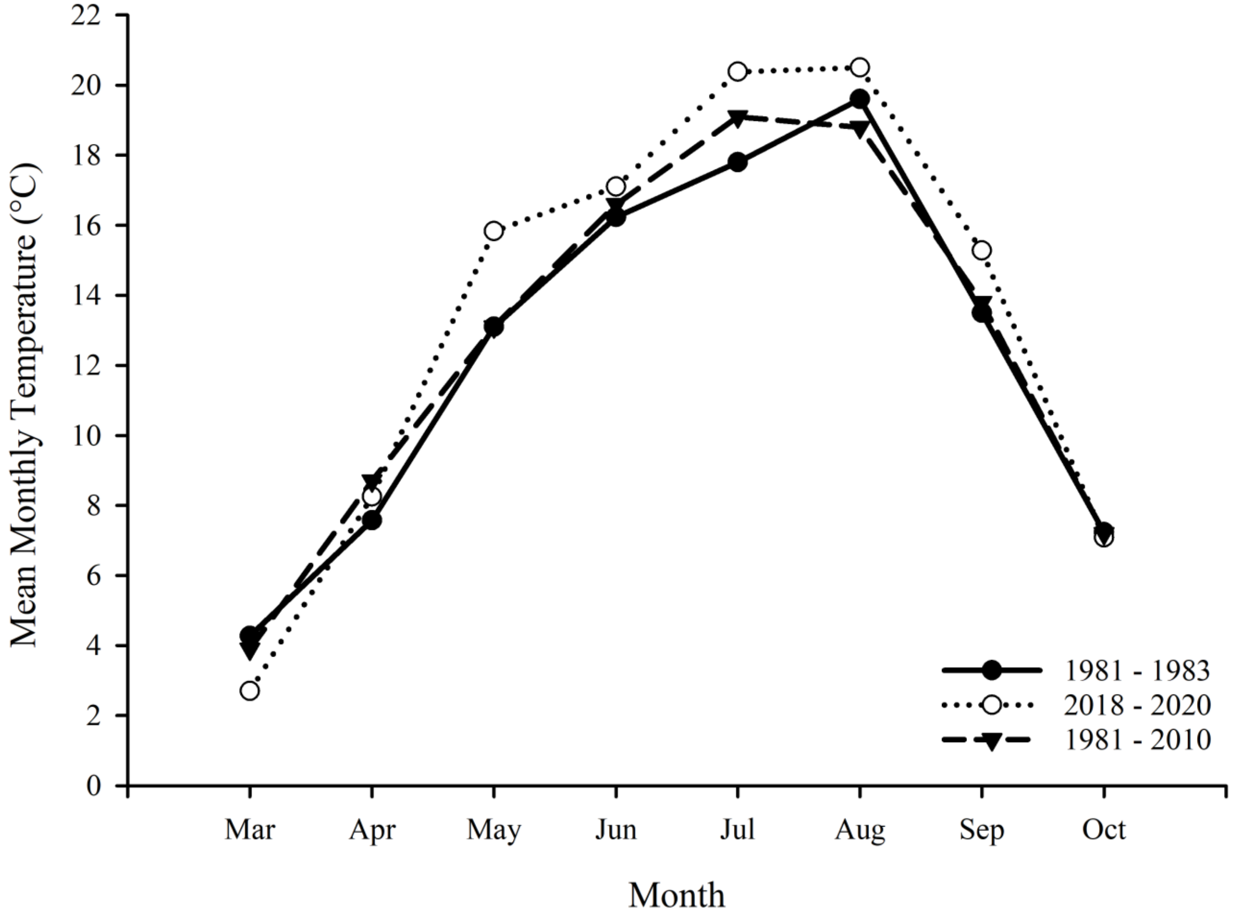

FIGURE 1.3. Mean monthly temperatures during the active season for Western Rattlesnakes (*Crotalus oreganus*) on Coldstream Ranch, B.C. during the previous study (1981 – 1983), and this study (2018 – 2020) compared to the historical 30-year mean (1981 – 2010). Data from Environment and Climate Change Canada.

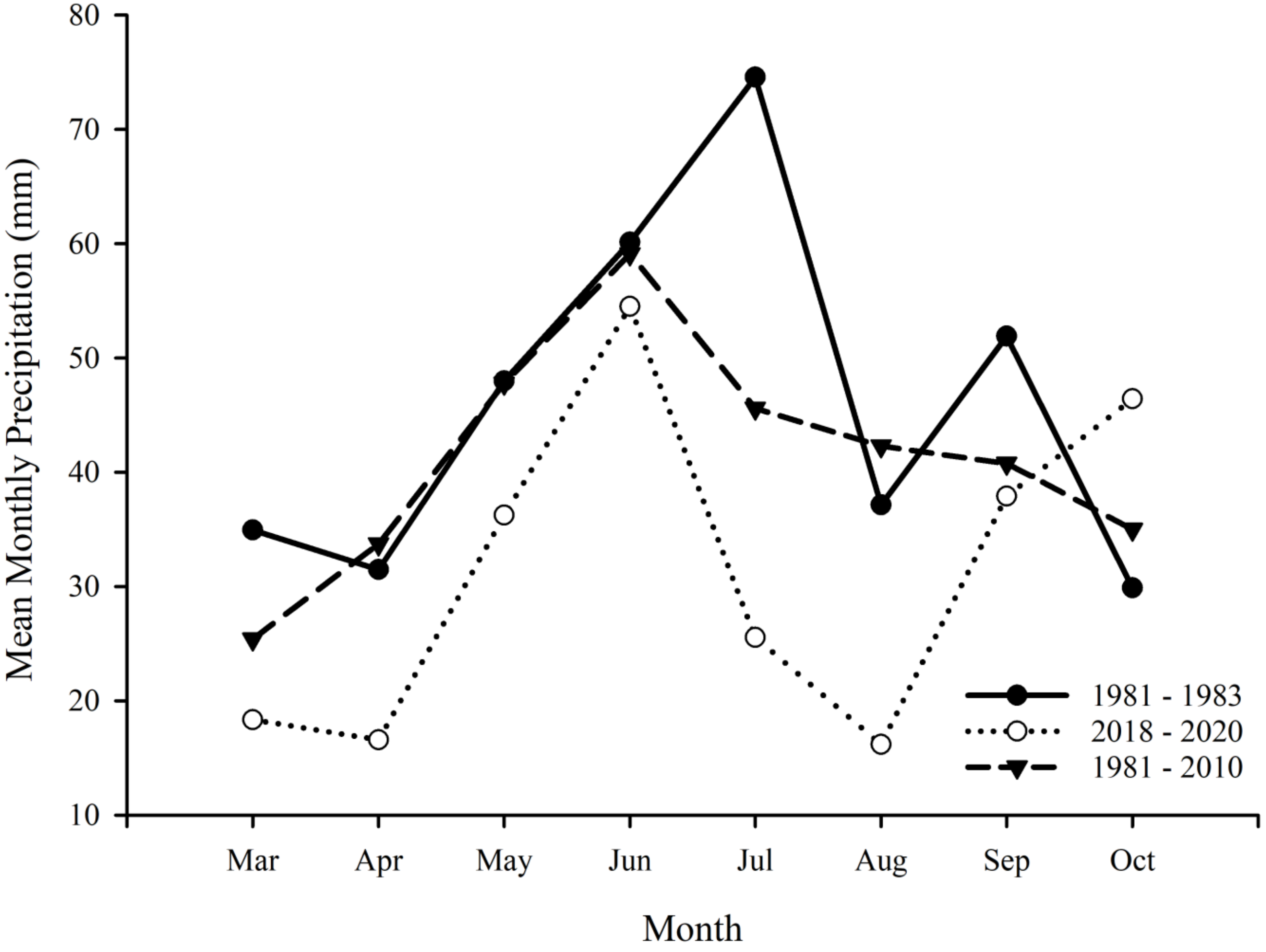

FIGURE 1.4. Mean monthly precipitation on Coldstream Ranch, B.C. during the previous study (1981 – 1983), and this study (2018 – 2020) compared to the historical 30-year mean (1981 – 2010) during the active season for Western Rattlesnakes (*Crotalus oreganus*). Data from Environment and Climate Change Canada.

FIGURE 1.5. Aerial photo of Cosens Valley in Kalamalka Lake Provincial Park, British Columbia, Canada taken looking north-east from within Kalamalka Lake Provincial Park. Cosen’s Bay Road (centre) is an unpaved access road for a lakeshore community (photo: M.C.P. Atkins).

FIGURE 1.6. Aerial photo of ‘Rattlesnake Point’ in Kalamalka Lake Provincial Park, British Columbia, Canada showing one of the recreational trails within the park (photo: M.C.P. Atkins).

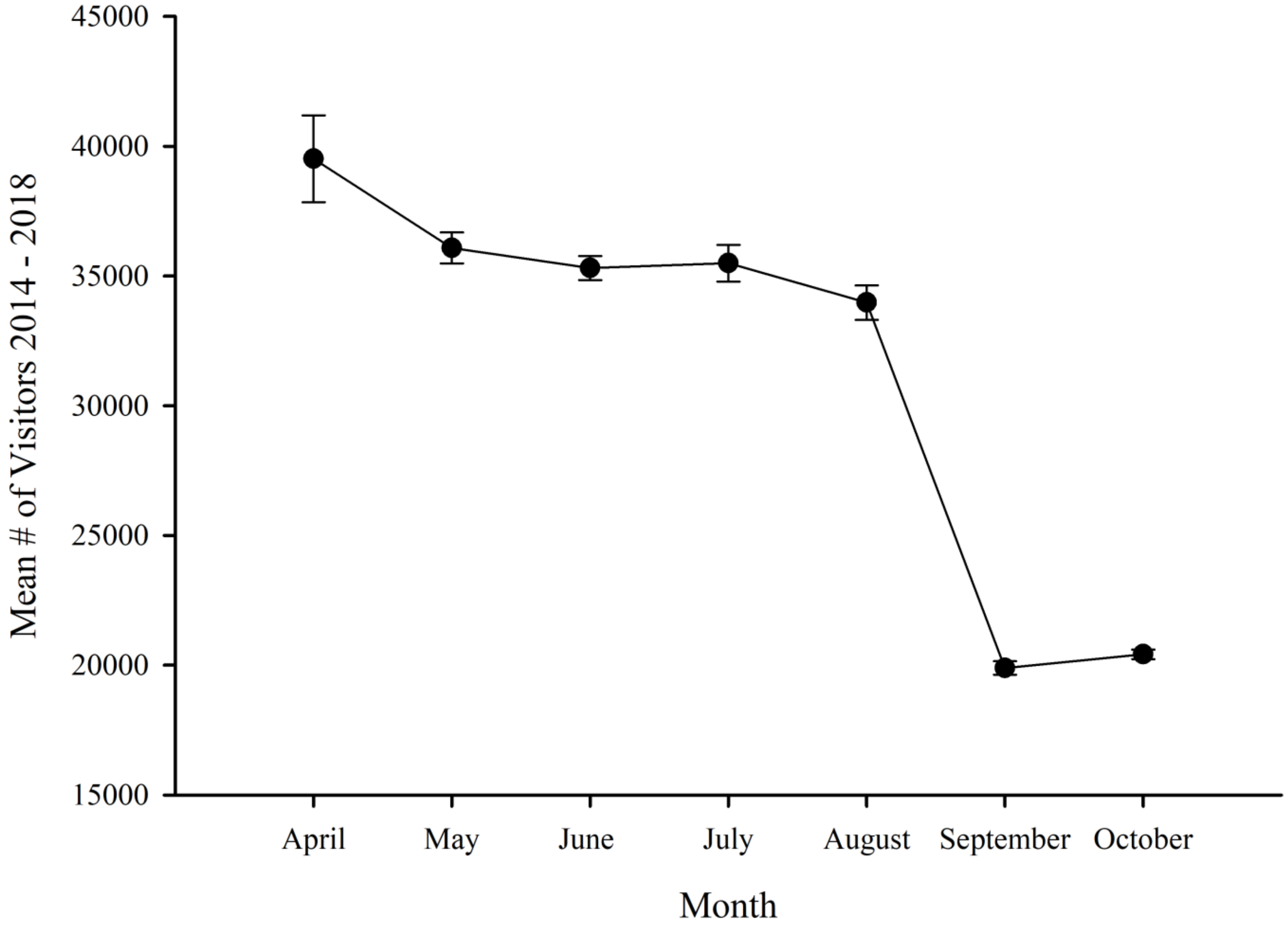

FIGURE 1.7. Mean monthly number of visitors to Kalamalka Lake Provincial Park during the active season for Western Rattlesnakes (*Crotalus oreganus*) using data from traffic counters from 2014 – 2018 at three main parking areas (British Columbia Parks, unpublished data). Each vehicle was assumed to contain two people. These data largely underrepresent actual visitorship as they exclude people who arrive by means other than motor vehicle and do not include another popular parking area.

A concurrent inventory of small mammal communities across the north Okanagan valley (Gamble and Larsen, unpublished data) provided cursory data on the relative abundance of prey. Two traplines were established within Kalamalka Lake Provincial Park and one trapline within Coldstream Ranch (Fig. 1.8). Transects of Longworth-style live traps 15 m apart were laid across each landscape, with pre-baiting of traps conducted for three consecutive nights, followed by three nights of trapping (Aug 6-8, 2019). All trapped animals were marked using Monel no. 1 eartags and released at their point of capture.

The highest relative abundance of small mammals was recorded on trapline 2 (Fig. 1.8) within the Park site, and the lowest relative abundance was recorded on trapline 3 (Fig. 1.8) on the Ranch site. A total of 94 Deer Mice (*Peromyscus maniculatus*), 19 Great Basin Pocket Mice (*Perognathus parvus*) and 2 Meadow Voles (*Microtus pennsylvanicus*) were recorded in the area (Table 1.1). To appropriately discern relative prey abundance for rattlesnakes, additional relative abundance data connected to specific high-use habitat areas for rattlesnakes is necessary.

TABLE 1.1. Small mammal relative abundance data (Gamble and Larsen, unpublished data) collected August 6 – 8, 2019 on two traplines within Kalamalka Lake Provincial Park (Trapline 1 & 2) and one trapline in Coldstream Ranch (Trapline 3). Data on relative abundance and mean weight (wt) ± standard deviation (SD) shown for Deer Mice (PIMA; *Peromyscus maniculatus*), Great Basin Pocket Mice (PEPA; *Perognathus parvus*), and Meadow Voles (MIPE; *Microtus pennsylvanicus*).

Trapline	**PIMA/trap**	**Mean PIMA wt ± SD**	**PEPA/trap**	**Mean PEPA wt ± SD**	**MIPE/trap**	**Mean MIPE wt ± SD**
Trapline 1	0.6	17.6g ± 2.6	0.27	17.7g ± 2.8	-	-
Trapline 2	1.37	18.4g ± 2.6	-	-	0.067	n/a
Trapline 3	0.37	17.4g ± 2.6	-	-	-	-

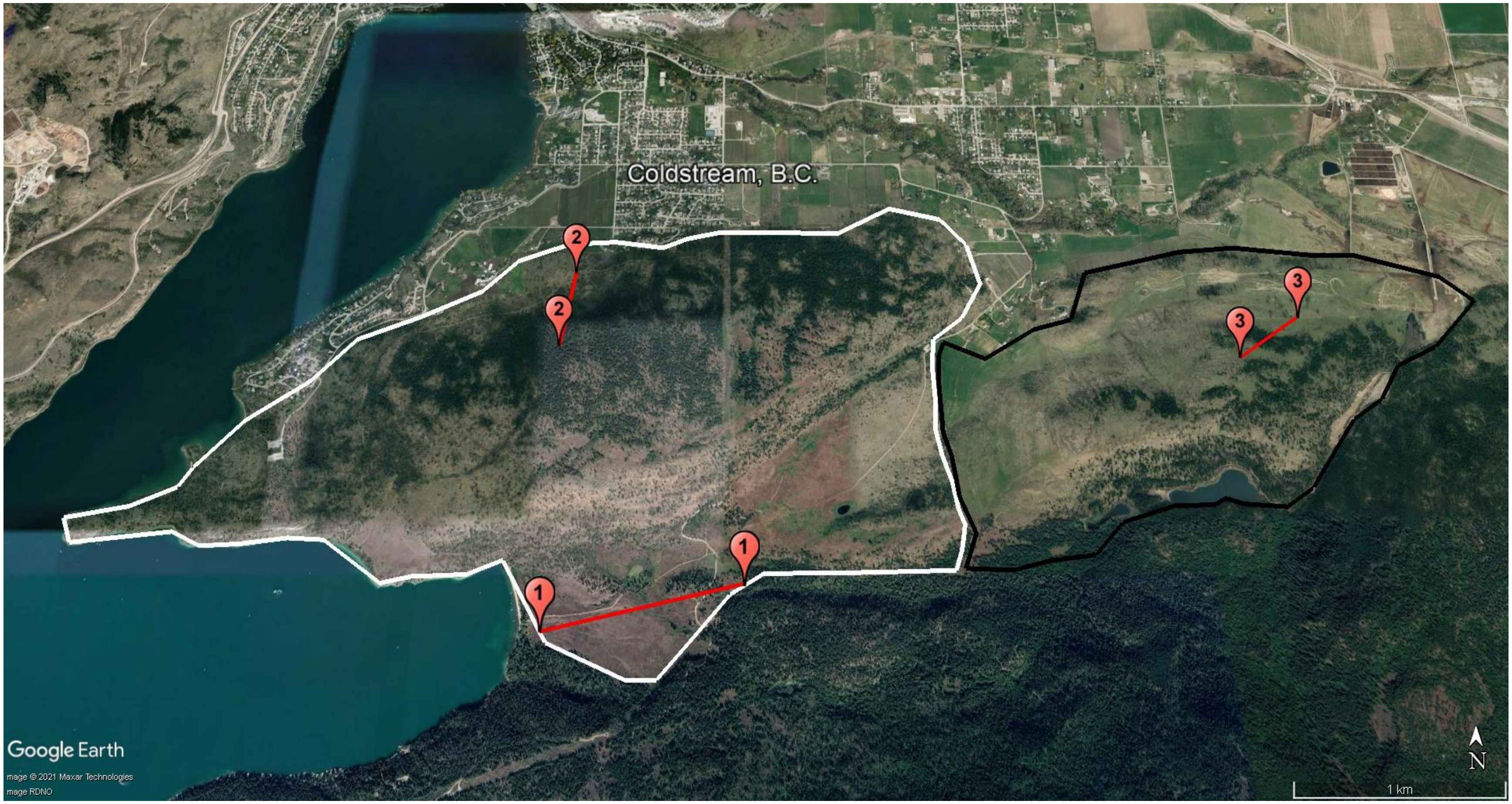

Figure 1.8. Trapline locations for a concurrent small mammal relative abundance assessment (Gamble and Larsen, unpublished data) in Kalamalka Lake Provincial Park (White; 1 & 2) and Coldstream Ranch (Black; 3). Data was collected from Aug 6 – 8, 2019.

Research Questions and Methods

To quantify population changes of Western Rattlesnakes in British Columbia over the last 35+ years, I conducted a mark-recapture based population assessment in the North Okanagan within Kalamalka Lake Provincial Park and the adjacent Coldstream Ranch for comparison with data from the previous study (Macartney, 1985). I sampled rattlesnakes at overwintering dens during Spring 2018, Autumn 2018, Spring 2019, Autumn 2019, and Spring 2020 (5 sampling periods) to collect demographic and morphometric data on the population that closely followed the methodology within Macartney (1985). Based on observations during our first field season, I also conducted a behavioural study of animals from both sites to determine whether changes on the landscape were associated with behavioural shifts. This work provides contemporary empirical data on the population size and structure for the rattlesnake population previously surveyed by Macartney (1985) and allows for temporal and spatial comparisons within this population over time.

The specific questions I address in this thesis are:

1. *How have rattlesnake population sizes and size-class distributions in the North Okanagan changed over the last 35+ years?* ***Chapter 2***
2. *Are the changes in population sizes and size-class distributions different depending on landscape type (Provincial Park versus Cattle Ranch)?* ***Chapter 2***
3. *Is a high-level of human visitation associated with changes in rattlesnake defensive behaviour?* ***Chapter 3***

The main tools I used in collecting demographic data for this study were the same mark/recapture techniques used by Macartney, with some modifications (see Chapter 2). In addition to recording recaptures of individually-tagged snakes, I also collected data on length, body mass, and gender. I assessed the differences in defensive behaviour of the snakes using their propensity to rattle as a metric in field experimental enclosures (see Chapter 3).

I also conducted telemetry on 21 animals, to investigate habitat use both within and outside the immediate study area (Atkins, unpublished data). These data contributed to delineating the effective population area (Chapter 2). Telemetry data from gravid female snakes also provided data on rookery use for a coincidental study (Eye, MSc. Thesis, in prep.)

LITERATURE CITED

Baillie, J. E., M., Hilton-Taylor, C. Stuart, S. N., eds. 2004. 2004 IUCN red list of threatened species: a Global Species Assessment. Cambridge (UK): IUCN Publications Services.

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L.,… and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction already arrived? Nature. 471(7336): 51–57.

Baum, J. K., & Myers, R. A. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecology Letters. 7(2): 135–145.

Beaupre, S. J., and L. E. Douglas. 2009. Snakes as indicators and monitors of ecosystem properties. *In* Snakes: ecology and conservation. Pp. 244-261.

Bender, M. G., S. R. Floeter, and N. Hanazaki, 2013. Do traditional fishers recognize reef fish species declines? Shifting environmental baselines in Eastern Brazil. Fisheries Management and Ecology, 20(1): 58–67.

British Columbia Parks. 2019. Kalamalka Lake park management plan. Ministry of Environment and Climate Change Strategy, Victoria, British Columbia. Pp. 59.

Bohnsack, J. A. 2015. Shifting baselines, marine reserves, and Leopold's biotic ethic. Gulf and Caribbean Research. 14(2): 1–7.

Bonnet, X., R. Shine, and O. Lourdais. 2002. Taxonomic chauvinism. Trends in Ecology & Evolution. 17(1): 23–46.

Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. Ecosystem experiments. Science. 269(5222): 324–327.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. Garcia, R. M. Pringle, and T. M. Palmer. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Science Advances. 1(5): e1400253–e1400253.

Ceballos, G., P. R. Ehrlich, and R. Dirzo. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences. 114(30): E6089–E6096.

Clark, J. A. and R. M. May. 2002. Taxonomic bias in conservation research. Science. 297(5579): 191-192.

Cody, M. L. 1996. Introduction to long-term community ecological studies. *In* Long-term Studies of Vertebrate Communities. Cody, M. L., Smallwood, J. A. (eds). Academic Press, San Diego, California, USA.

Committee on the Status of Endangered Wildlife in Canada (COSEWIC). (2015). COSEWIC Assessment and Status Report on the Western Rattlesnake Crotalus oreganus in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 44 p.

Cronin, D.T., J. R. Owens, H. Choi. S. Hromada, R. Malhotra, F. Roser, and R. A. Bergl. 2014. Where has all our research gone? A 20-year assessment of the peer-reviewed wildlife conservation literature. International Journal of Comparative Psychology. 27(1): 101–116.

Environment and Climate Change Canada. 2017. Recovery Strategy for the Western Rattlesnake (Crotalus oreganus), the Great Basin Gophersnake (Pituophis catenifer deserticola) and the Desert Nightsnake (Hypsiglena chlorophaea) in Canada. Species at Risk Act Recovery Strategy Series, 1: 28–37.

Environment and Climate Change Canada. 2020. Historical Climate Data. [Accessed 2020 November, 23]. Available from: https://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=1068&dispBack=0&month1=0&month2=12

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Ann. Rev. Ecol. Evol. Syst. 2004(35): 557 – 581.

Gibbons, J. W. (1988). The management of amphibians, reptiles and small mammals in North America : the need for an environmental attitude. Ecology: 6–10.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberviller, B. S. Metts, J. L. Greene,…, and C. T. Winne. 2000. The global decline of reptiles, dèjá vu amphibians. BioScience. 50(8): 653 – 666.

Harvey, J. and K. W. Larsen. 2020. Rattlesnake migrations and the implications of thermal landscapes. Movement Ecology. 8:21.

Huitric, M. (2005). Lobster and Conch fisheries of Belize: A history of sequential exploitation. Ecology and Society. 10(1).

International Union for Conservation of Nature (IUCN) Standards and Petitions Committee. 2019. Guidelines for using the IUCN Red List Categories and Criteria Version 11. Standards and Petitions Subcommittee. http://www.iucnredlist.org.

Jackson, J. B. C. 1997. Reefs since Columbus. Coral Reefs. 16: S23–S32.

Lawler, J. J., J. E. Aukema, J. B. Grant, B. S. Halpern, P. Kareiva, C. R. Nelson, K. Ohleth,… and P. Zaradic. 2006. Conservation science : a 20-year report card in a nutshell. Frontiers in Ecology and the Environment. 4(9): 473–480.

Likens, G. E. 1985. Experimental approach for the study of ecosystems. Journal of Ecology. 73: 381-396.

Lind, A. J., H. H. Welsh, and D. A. Tallmon. 2005. Garter snake population dynamics from a 16-Year Study: considerations for ecological monitoring. Ecological Applications. 15(1): 294–303.

Lindenmayer, D. B. and G. E. Likens. 2010. The science and application of ecological monitoring. Biological Conservation. 143(6): 1317–1328.

Lindenmayer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C. R. Dickman…, and G. M. Wardle. 2012. Value of long-term ecological studies. Austral Ecology. 2012(37): 745 – 757.

Lomas, E., K. W. Larsen, and C. A. Bishop. 2015. Persistence of Northern Pacific Rattlesnakes masks the impact of human disturbance on weight and body condition. Animal Conservation. 18(2015): 548 – 556.

Lomas, E., J. R. Maida, C. A. Bishop, and K. W. Larsen. 2019. Movement ecology of Northern Pacific Rattlesnakes (Crotalus o. oreganus) in response to disturbance. Herpetologica. 75(2): 153 – 161.

Macartney, J.M. 1985. The ecology of the Northern Pacific Rattlesnake, Crotalus viridis oreganus, in British Columbia. M.Sc. Thesis, University of Victoria, Victoria, British Columbia, Canada. 289pp.

Maida, J. 2018. Impacts of fencing and development on Western Rattlesnake (Crotalus oreganus) spring movements in British Columbia. MSc. Thesis, Thompson Rivers University. Kamloops, BC. 89pp

Maida, J. R., D. A. Kirk, O. McKibbin, J. R. Row, K. W. Larsen, C. Stringham, and C. A. Bishop. 2018. Population estimate, survivorship, and generation time of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) at its northern-most range limits. Herpetological Conservation and Biology. 13(3): 662 – 672.

Maida, J., C. A. Bishop, and K. W. Larsen. 2019. Migration and disturbance: Impact of fencing and development on rattlesnake spring movements in British Columbia. Canadian Journal of Zoology. 98(1): 1 – 12.

Magnuson, J. J. 1990. Long-term ecological research and the invisible present. BioScience. 40(7): 495–501.

Meidinger, D. V. and J. Pojar. 1991. Ecosystems of British Columbia. Special Report Series 6, Victoria, BC. B.C. Ministry of Forests and Range Research Branch.

Newsome, S. D., M. A. Etnier, D. Gifford-Gonzalez, D. L. Phillips, M. van Tuinen, E. A. Hadly, D. P. Costa…, and P. L. Koch. The shifting baseline of northern fur seal ecology in the northeast Pacific Ocean. PNAS. 104(23): 9709 – 9714.

Okanagan Historical Society, 1965. Okanagan Historical Society Reports, 1965. https://okanaganhistoricalsociety.org

Okanagan Historical Society, 1983. Okanagan Historical Society Reports, 1983. https://okanaganhistoricalsociety.org

Okanagan Valley Economic Development Society. 2013. 2013 Economic profile of the Okanagan Valley. Okanagan Valley Economic Development Society, Kelowna, British Columbia, Canada. 126 p.

Papworth, S. K., J. Rist, L. Coad, and E. J. Milner-Gulland. 2009. Evidence for shifting baseline syndrome in conservation. Conservation Letters. 2(2009): 93 – 100.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. 1995. Trends in Ecology and Evolution. 10(10): 430.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology and Evolution. 25(6): 345–353.

Pinnegar, J. K. and G. H. Engelhard. 2008. The ‘shifting baseline’ phenomenon: a global perspective. Reviews in Fish Biology and Fisheries. 2008(18): 1 – 16.

Rittenhouse, C. D., A. M. Pidgeon, T. P. Albright, P. D. Culbert, M. K. Clayton, C. H. Flather, and V. C. Radeloff. 2010. Conservation of forest birds: Evidence of a shifting baseline in community structure. PLoS ONE. 5(8): 1–9.

Saha, A., L. McRae, C. K. Dodd, H. Gadsden, K. M. Hare, V. Lukoschek, and M. Böhm. 2018. Tracking global population trends: population time-series data and a living planet index for reptiles. Journal of Herpetology. 52(3): 259–268.

Sala, O. E., F. S. Chapin III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, O. Huber-Sanwald,… and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science, 287(5459), 1770–1774.

Santini, L. M. González-Suárez, C. Rondinini, and M. Di Marco. 2017. Shifting baseline in macroecology? Unravelling the influence of human impact on mammalian body mass. Diversity and Distributions. 2017(23): 640 – 649.

Schmidt, D., P. Govindarajulu, K. W. Larsen, and M. A. Russello. 2020. Genotyping-in-thousands by sequencing reveals marked population structure in Western Rattlesnakes to inform conservation status. Ecology and Evolution. 2020(00) 1 – 16.

Seigel, R. A. 1993. Summary: future research on snakes, or how to combat "lizard envy". Snakes, ecology and behavior: 395-402.

Soga, M. and K. J. Gaston. 2018. Shifting baseline syndrome: causes, consequences, and implications. Frontier in Ecology and the Environment. 16(4): 222 – 230.

Tinkle, D. W. 1979. Long-term field studies. BioScience. 29(12): 717

Todd, B. D., J. D. Wilson, and J. W. Gibbons. 2010. The global status of reptiles and causes of their decline. *In* Ecotoxicology of Amphibians and Reptiles, Second Edition. Sparling, D. W., C. A. Bishop, and S. Krest (Eds). CRC Press, Pensacola, FL, USA. Pp. 47 – 67.

Turvey, S. T., L. A. Barrett, H. Yujiang, Z. Lei, Z. Xinqiao, W. Xianyan, H. Yadong, Z. Kaiya…, and W. Ding. 2010. Rapidly shifting baselines in Yangtze fishing communities and local memory of extinct species. Conservation Biology. 2(3): 778 – 787.

Vera, F. 2010. The shifting baseline syndrome in restoration ecology. *In* Restorarion and history: The search for a usable environmental past. Routledge Publishing. Pp. 98 – 110.

Vors, L. S. and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology. 15(11): 2626–2633.

Whipple, A. A., R. M. Grossinger, and F. W. Davis. 2011. Shifting baselines in a California Oak Savanna: nineteenth century data to inform restoration scenarios. Restoration Ecology. 19(101): 88 – 101.

Winton, S. A., R. Taylor, C. A. Bishop, and K. W. Larsen. 2018. Estimating actual versus detected road mortality rates for a northern viper. Global Ecology and Conservation. 16(2018): e00476.

Winton, S. A., C. A. Bishop, and K. W. Larsen. 2019. When protected areas are not enough: low-traffic roads projected to cause a decline in a northern viper population. Endangered Species Research. 2020(41): 131 – 139.

World Wildlife Fund Canada. 2017. Living planet report Canada: A national look at wildlife loss. World Wildlife Fund Canada, Toronto, Ontario, Canada. 57 p.

Zug, G. R., L. J. Vitt, and J. P. Caldwell. 2001. Herpetology, Second Edition. Academic Press, San Diego.

CHAPTER 2

THIRTY-FIVE YEARS ON THE NORTHERN RANGE: CHANGES IN SUBPOPULATIONS OF WESTERN RATTLESNAKES (*CROTALUS OREGANUS*) IN BRITISH COLUMBIA

INTRODUCTION

Crafting effective conservation plans requires a strong understanding of the dynamics of populations (Lindenmeyer et al., 2012), along with a way to associate those with different landscape-level effects. Such information is especially important for quantifying species' responses to ecological, natural, and anthropogenic disturbance (Coulso et al., 2001; Jones et al., 2017). Unfortunately, the majority of ecological studies represent snapshots, or short-term glimpses of populations, and long-term continuous monitoring is rare despite being argued as necessary (White, 2019). Given this, opportunities to repeat historic studies, or periodically re-assess populations, are particularly valuable and help avoid the shifting baselines syndrome (SBS) (Liken, 1985; Pauly, 1995; Jackson, 1997; Bohnsack, 2003; Folk et al., 2004; Huitric, 2005; Papworth et al., 2009; Soga and Gaston, 2018).

The SBS involves accepting contemporary data as a standard for populations, without considering historic baselines. This can lead to 'generational amnesia' (Papworth et al., 2009) whereby the experience and knowledge of past mangers or knowledge holders is not passed onto future generations, thus re-setting perceptions of normality while forgetting past conditions (Pauly, 1995). The widespread acknowledgment of this phenomenon is rooted in fisheries and marine ecosystems, though in recent decades many studies identifying shifting baselines have arisen that span taxa, disciplines, and ecosystems (Baum and Meyers, 2004; Newsome et al., 2007; Pinnegar and Engelhard, 2008; Rittenhouse et al., 2010; Turvey et al., 2010; Vera, 2010; Whipple et al., 2011; Bender et al., 2013; Santini et al., 2017).

Identifying shifting baselines in marine systems has been aided by commercial harvest records, but similar robust datasets are sparse for herpetofauna where relatively fewer species are harvested commercially; further, herpetofauna may demonstrate patchy distributions, cryptic colouration and behaviours, and knowledge gaps on basic life history and ecology still exist (Zug et al., 2001; Todd et al., 2010). Thus, gathering data on reptile populations over time is essential for detecting population declines and disentangling natural versus human-caused fluctuations in the future (Cody, 1996; Gibbones et al., 2000).

Very little is known about how populations of Western Rattlesnakes (*Crotalus oreganus*) change over time and space, and individual populations are reported to be likely overestimated in many areas (COSEWIC, 2015). Western Rattlesnakes in Canada represent the northern periphery for the species, and a northern extreme for rattlesnakes in general (Fig. 1.1). The first and (until recently) only detailed Canadian population study of the species was conducted by Macartney from 1981 – 1983 in the Okanagan Valley, over 35 years ago (Macartney, 1985; Macartney, 1989; Macartney and Gregory, 1988; Macartney and Gregory, 1990). More recently, other studies have provided demographic data on other populations in British Columbia (Maida et al., 2018; Winton et al., 2019), as well as insight into other aspects of the species' ecology and conservation (Lomas et al., 2015; Eye et al., 2017; Winton et al., 2018; Lomas et al., 2019; Winton et al., 2019; Schmidt et al., 2020; Harvey and Larsen, 2020). However, data from the Macartney study provides the only benchmark to examine temporal changes in rattlesnake populations in the north. This is of particular importance given the species is considered threatened in Canada, and the region where the majority of Western Rattlesnakes occur is subject to one of the fastest rates of urban and agricultural growth in the country (Okanagan Valley Economic Development Society, 2013; Statistics Canada, 2014, Maida et al., 2018).

To assess historical changes in Western Rattlesnakes, we replicated the Macartney (1985) study at the same locations and overwintering dens, closely following his methodology and sampling effort. Macartney conducted his work in an area that included both a fledgling provincial park and an adjacent private cattle ranch, although leading up to his study the entire land area was managed jointly for cattle. Within a year of the cessation of Macartney's field work, management of the park shifted to exclude cattle, while becoming a popular destination for recreationists, whereas the cattle ranch has remained largely unchanged and void of people. This situation thus has created a unique natural experiment to assess population changes over time and space. Herein we examine how the population of rattlesnakes has changed at the Macartney site over the past 35 years, and whether differences exist correlated with the two landscapes. We also compare our recent estimates of rattlesnake density to those obtained from other sites in the region.

MATERIALS AND METHODS

Study Sites

Our field work took place near the municipality of Vernon (50.2670° N, 119.2720° W), within the northern extent of the Okanagan Valley in British Columbia. Rattlesnakes in this area den communally in rocky crevices, usually on south-facing slopes. This life-history trait enables a relatively large numbers of animals to be sampled in each local populations. Emergence from dens (egress) occurs in late March through April, the animals disperse throughout the landscape to feed and reproduce, and return to the dens (ingress) in late September-early October. See Chapter 1 for additional details on the climate and biogeography of the study area.

We conducted mark-recapture work between April 2018 and May 2020 within the two neighbouring sites, namely Kalamalka Lake Provincial Park (50.2043° N, 119.2800° W – 'Park') and the adjacent Coldstream Ranch ('Ranch') (Fig. 1.2). Both sites are characterized by a mosaic of grassland and forest patches dominated by blue-bunch wheatgrass (*Psuedoregneria spicatum*), various fescue species (*Festuca* spp.), Ponderosa pine (*Pinus ponderosa*), Western Redcedar (*Thuja plicata*), and Douglas-Fir (*Psuedotsuga menziesii*) surrounded by rolling hills and steep bluffs. Barbed wire fencing excludes cattle from the Park but poses no obstacle to the snakes, although there exists an unpaved road bisecting the sites that may act as a partial barrier as snakes may avoid the road or may be killed when crossing. Mark-recapture (this study) and radio-telemetry data (Atkins, unpublished data) suggest inter-site movements by snakes are infrequent, although Schmidt et al. (2020) found no significant genetic differences between animals drawn from two dens, one within the park and one within the cattle ranch.

Kalamalka Lake Provincial Park is a provincially-designated protected recreational area that receives an average 32,600 visitors per month during the active season (April-October) for rattlesnakes (Fig. 1.7; BC Parks, unpublished data) and contains >50 kilometers of popular, year-round hiking, horseback riding, and mountain biking trails. The Ranch site is located on Coldstream Ranch, an active cattle grazing operation that prohibits access by the public. A robust assessment of grazing intensity within the Ranch landscape and vegetation cover differences between the sites was beyond the scope of this study. Cattle from the Ranch are ‘free-ranging’ for 4 weeks in May and 6 weeks in October/November, or approximately 3.75 AUM per hectare (1 AUM = animal unit/month, equivalent to the forage removed by one 454 kg cow or cow-calf pair in one month - T. Osborn, Coldstream Ranch (2002) ltd., personal communication). For the remainder of the year, cattle are restricted to feed-lots and pastures outside of the study area.

Sampling Procedure

We collected data between April and October in 2018 and 2019, and from April 3 to May 5 in 2020. The active season was divided into two periods for analysis, spring (April 1 – June 15) and fall (June 15 – October 15), for a total of five sampling periods. All snakes were captured, processed, and released in the field at their capture location. In each spring and fall sampling period, we visited all dens described by Macartney (1985) within our study sites. In total, Macartney surveyed 16 independent dens, 6 of which we excluded early on due to negligible snake counts (< 5 individuals), safety concerns, and/or accessibility. Thus, our study was able to directly compare data from 10 dens (Park = 5, Ranch = 5) surveyed by Macartney; we also included a previously undescribed and well-populated den on the Park site, for a total of 11 dens (Table 2.1; Park = 6, Ranch = 5). Data from the previous study included neonatal animals that were born and processed in captivity. To avoid issues with inflated proportions of juvenile animals in the historical dataset, we removed data from animals born in captivity from the dataset.

TABLE 2.1. A comparison of Western Rattlesnake dens surveyed by Macartney (1985) and the present study in Canada. Multiple dens are listed together as a den complex if in close proximity to each other and deemed to be contiguous. Dens marked with a '✓' were included in analysis. Dens marked with '*' were deemed largely abandoned or extirpated.

Site	**Den**	**Macartney (1985)**	**Atkins (2020)**
Park	East Den/Den 21/Den 22	✓	✓
	Den 14	✓	✓
	Den 2/4/23/24	✓	✓
	Den 5/6/6a/6b	✓	✓
	Den 7	✓	✓
	Den 3	✓	*
	Restoration	✓	*
	Beach House		✓
Ranch	Den 8/13a	✓	✓
	Den 9/10/11	✓	✓
	Den 17	✓	✓
	Den 16	✓	✓
	Eyrie Den	✓	*
	Den 15	✓	✓
Off-Site	Den 27	✓	
	Den 28	✓	
	Beacon Den	✓	

Captured rattlesnakes were implanted with sterile passive integrated transponder (PIT) tags (Biomark Model TX1411SSL; Biomark, Boise, Idaho, USA) for individual recognition. We measured snout-vent length (SVL) using the tube-restraint method (Murphy, 1971), which is now considered safer for both animals and handlers than the noose-stretch method (Gregory, 1989); our field tests showed no appreciable differences in measurements obtained using the two different techniques (Appendix A; Atkins and Larsen, 2020). We also recorded weight (g) and sex for each individual (see Macartney and Gregory, 1988). All individuals were processed on site and released immediately afterwards.

Following Macartney (1985) we intensively collected snakes at den sites during spring egress and fall ingress. Den sites were visited at least twice per week, and this rate was increased to every second day during peak periods of egress/ingress. In general, egress tapered substantially by early-mid May, and afterwards the majority of snakes were encountered away from dens, with only a rare sighting of a snake occurring at the dens into June of each year. The arrival of snakes back at the dens during ingress was not substantial until early- to mid-September. All told, we are comfortable that our field methods closely paralleled those used by Macartney (1985), given the senior author on this paper served as a field assistant on the original project. Further corroboration was provided through a site visit by Macartney in 2019.

Statistical Analyses

We estimated population size for five capture periods for both the previous study (1981 – 1983; Macartney, 1985) and this study. Raw data from the Macartney study were digitized from original field records and analyzed in the same manner as data from this study to allow for direct comparisons. Analyses were conducted using the Rcapture package (Baillargeon and Rivest, 2007) in R (R Development Core Team, 2020). We ran an open-population mark-recapture model based on a Jolly-Seber log-linear approach (Cormack, 1985; 1989) for the total population (both sites combined), as well as the Park and Ranch sites independently. We assessed model fit via χ^2 goodness of fit tests and visual inspection of the Pearson residuals and capture frequency. In instances of poorly-fitted data we limited frequencies of capture within the analyses and/or removed data with high residual values (see Baillargeon and Rivest, 2007; Maida et al., 2018). We produced population estimates and assessed morphometric data for the entire population (all age classes) and for adults only (≥ 540 mm SVL; Maida et al., 2018) to allow direct comparisons with other recent population estimates in the region (Maida et al., 2018; Winton et al., 2019). We assessed morphometric data for adult males and females separately as rattlesnake reproductive ecology greatly affects the behaviour, growth, and feeding ecology of female rattlesnakes (Macartney and Gregory et al., 1988; Graves and Duvall, 1993).

Concurrent to this study we (Atkins and Larsen, unpublished) used radio-telemetry to track the locations of 21 rattlesnakes over the active season in 2019. Using the aggregated movements from telemetry data in Garmin BaseCamp (version 4.6.2, 2016) and summer captures of non-telemetered (but marked) snakes, we created minimum-convex polygons (MCPs) to calculate the population home range area for rattlesnakes on the Park and Ranch sites (Row et al., 2006; Winton, 2019). We used these estimates with our population estimates to determine density for both the Park and the Ranch combined and each site separately. We applied our current estimate of population home ranges to our analysis of the Macartney (1985) data as the previous study did not record capture locations and contained minimal telemetry data.

RESULTS

We made 1264 captures of 702 individual Western Rattlesnakes over the course of this study. This included 972 captures of 511 adults (Table 2.2). Macartney’s study produced 2704 captures of 1387 individual rattlesnakes, with 1797 captures of 845 adults (Table 2.2). In both studies, later sampling periods contained relatively high proportions of recaptured individuals (Table 2.2).

TABLE 2.2. Tabulated capture data for Western Rattlesnakes (*Crotalus oreganus*) captured during the Macartney (1985) study (1981-1983) and the current study (2018-2020). New individuals represent first time captures of previously unmarked individuals. Total Number of Captures includes all individuals capture in the sampling session, including recaptures. Proportion New in Sample is the number of New Individuals divided by the Total Number of Captures.

	Total Population			**Adult Population**		
Period	**New Individuals**	**Total Number of Captures**	**Proportion New in Sample**	**New Individuals**	**Total Number of Captures**	**Proportion New in Sample**
Spring 1981	246	251	0.98	147	149	0.99
Fall 1981	351	549	0.64	170	294	0.58
Spring 1982	257	457	0.56	186	315	0.59
Fall 1982	313	749	0.42	185	527	0.35
Spring 1983	220	698	0.32	157	512	0.31
Total Study	1387	2704	0.51	845	1797	0.47
Spring 2018	169	207	0.82	126	153	0.82
Fall 2018	157	281	0.56	115	224	0.51
Spring 2019	186	354	0.53	116	260	0.45
Fall 2019	94	214	0.44	65	157	0.41
Spring 2020	97	208	0.47	89	178	0.50
Total Study	702	1264	0.56	511	972	0.53

Population and Density Estimates

Table 2.3 shows our population estimates, along with those calculated using the raw data drawn from Macartney (1985). We estimated a mean decline of 40% (29-50%) for the combined population over both sites; the population within the Park site declined by 50% (35-63%), and the populations within the Ranch site declined by 31% (19-42%) (Fig. 2.1a). Using only data on adult snakes, we estimated a decline of 22% (10-33%); the adult population within the Park site declined by 28% (7-47%), and the corresponding decline in the Ranch site was 23% (10-34%) (Fig. 2.1b). We assessed population density (Table 2.3) using an estimated population home range of 7.6 km^2 for the Park site, and 3.9 km^2 for the Ranch site, for a combined home range estimate of 11.5 km^2

Population Structure

Size-class distributions from the present study (♂♂ $n = 292$, $\bar{x} = 64.6$ cm, SD = 18.2; ♀♀ $n = 312$, $\bar{x} = 57.2$ cm, SD = 15.3) were significantly different for both sexes than those from the Macartney study (♂♂ $n = 689$, $\bar{x} = 61.1$ cm, SD = 22.8; ♀♀ $n = 668$, $\bar{x} = 56.2$, SD = 19.0) according to Kolmogorov-Smirnov tests (♂♂ $D = 0.15$, $P < 0.001$; ♀♀ $D = 0.13$, $P = 0.002$; Fig. 2.2). Compared to the Macartney study, the proportion of juveniles in the population decreased by 33% and 14% for males and females, respectively.

TABLE 2.3. Summary and comparison of open-population mark-recapture models using historical (Macartney, 1985 – data collected during 1981 - 1983) and current data (2018 – 2020) for subpopulations of Western Rattlesnakes (*Crotalus oreagnus*) within Kalamalka Lake Provincial Park (Park), Coldstream Ranch (Ranch), and both sites combined (Both) near Vernon, British Columbia. Separate estimates are provided for all snakes encountered and only those considered adults (≥ 540 mm SVL). Shown are N_{tot} (total population estimate), standard error (StE), 95% confidence intervals (95% CI) and model fit (χ^2) results. We calculated the range of decline using absolute minimum and absolute maximum estimates from 95% confidence intervals.

Population Subset	**Site & Time Period**	**Ntot**	**StE**	**95% CI**	**χ^2**	**Density (snakes/km^2)**	**Range of Decline**
Total Population	Park 1983	937.96	37.17	72.85	0.42	123	
	Park 2020	470.18	47.73	93.55	0.34	62	35 – 63%
	Ranch 1983	856.38	26.22	51.38	0.23	220	
	Ranch 2020	591.64	31.65	62.03	0.23	152	19 – 42%
	Both 1983	1776.62	44.28	86.79	0.27	154	
	Both 2020	1066.27	66.56	130.45	0.10	93	29 – 50%
Adult Population	Park 1983	445.31	15.23	29.84	0.22	59	
	Park 2020	320.28	34.24	67.11	0.13	42	7 – 47%
	Ranch 1983	506.46	13.15	25.77	0.12	129	
	Ranch 2020	391.37	19.86	38.95	0.19	100	10 – 34%
	Both 1983	963.96	17.23	33.77	0.27	84	
	Both 2020	750.99	43.79	85.83	0.09	65	10 – 33%

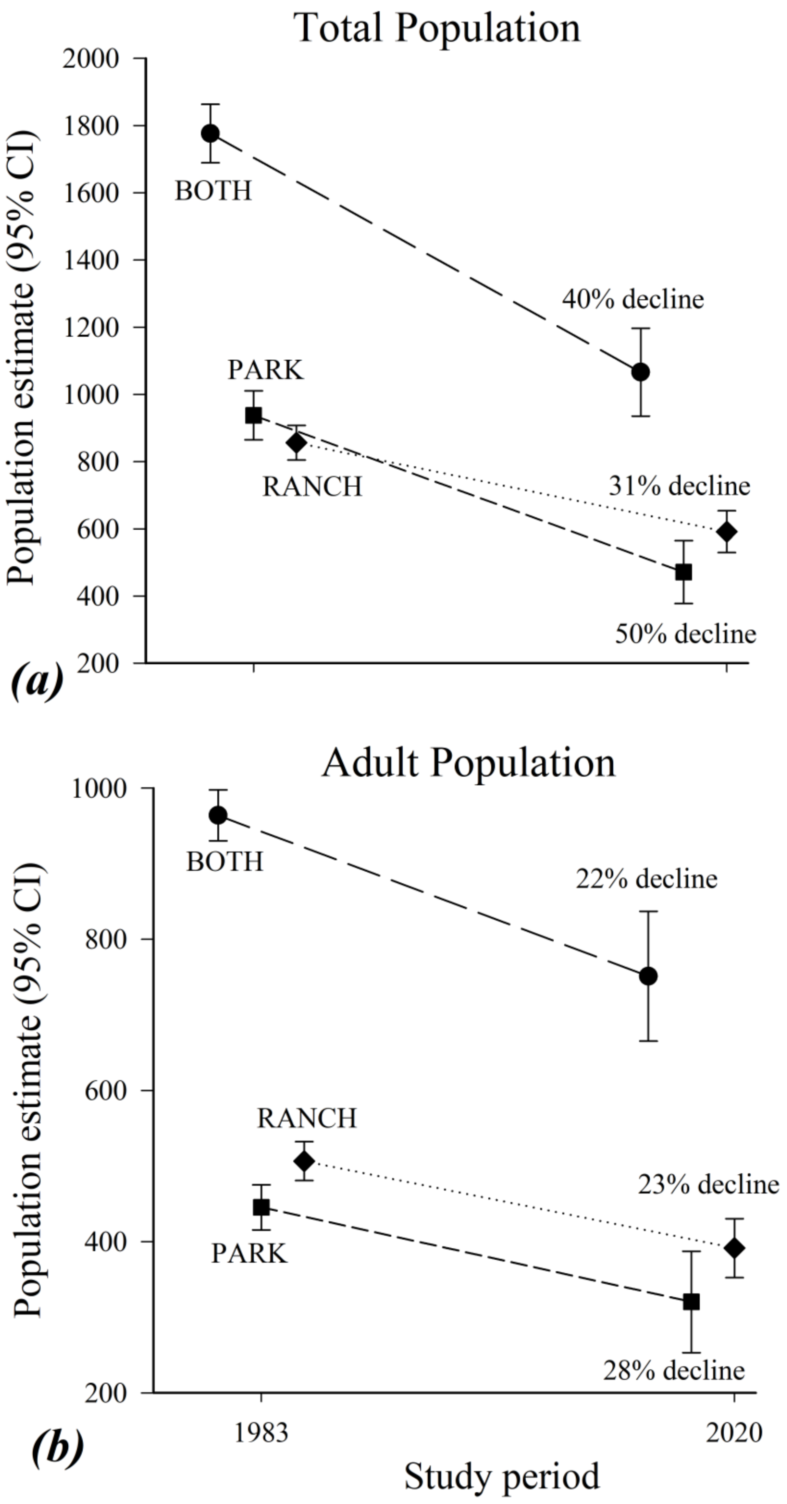

FIGURE 2.1. Temporal and spatial comparisons of Western Rattlesnake (*Crotalus oreganus*) population estimates ± 95% CI from this study and historical data (Macartney, 1985) for the entire population ***(a)*** and the adult (≥ 540 mm SVL) population ***(b)*** within Kalamalka Lake Provincial Park (Park), Coldstream Ranch (Ranch), and for both sites combined (Both).

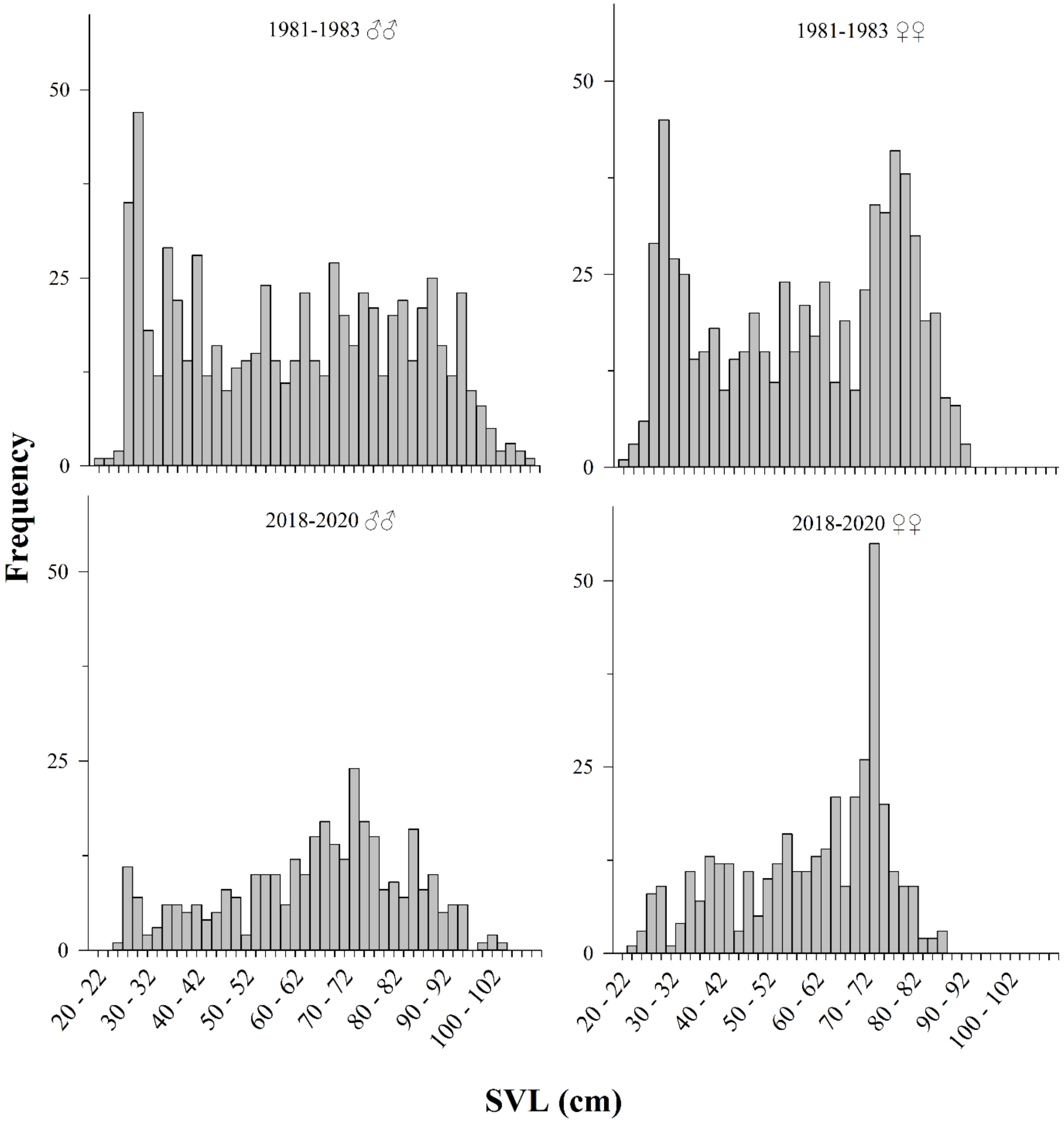

FIGURE 2.2. Size-class capture frequency histograms of male and female Western Rattlesnakes (*Crotalus oreganus*) captured in this study (bottom) and by Macartney (1985) (top). Size-classes (Snout-vent length) binned at 2 cm intervals.

Table 2.4 summarizes changes in mean length, weight, and body condition of adult male and female rattlesnakes by site between the two studies. On average, rattlesnakes encountered on the Park site in the present study were significantly heavier than those found by Macartney (♂♂ *t* = -5.3, df = 183, P < 0.0001; ♀♀ *t* = -5.3, df = 203, P < 0.0001; Fig. 2.3a, b), while only females displayed lower average SVL (♂♂ *t* = -0.2, df = 269, P = 0.81; ♀♀ *t* = 2.4, df = 268, P = 0.017; Fig. 2.3c, d) both sexes displayed a substantial increase in body condition over time (♂♂ *t* = -7.2, df = 184, P < 0.0001; ♀♀ *t* = -7.3, df = 203, P < 0.0001; Fig. 2.3e, f). On the Ranch site, snakes encountered in the present study showed no difference in average weight compared to the Macartney study (♂♂ *t* = -0.97, df = 241, P = 0.33; ♀♀ *t* = -1.50, df = 265, P = 0.14; Fig. 2.3a, b), but both sexes were significantly shorter (♂♂ *t* = 4.9, df = 375, P < 0.0001; ♀♀ *t* = 3.13, df = 348, P = 0.002; Fig. 2.3c, d) and showed a significant increase in body condition (♂♂ *t* = -2.8, df = 241, P = 0.005; ♀♀ *t* = -3.20, df = 265, P = 0.002; Fig. 2.3e, f).

TABLE 2.4. Comparison of mean snout-vent length (SVL), weight, and body condition for adult Western Rattlesnakes (*Crotalus oreganus*) captured in Kalamalka Lake Provincial Park (Park) and Coldstream Ranch (Ranch) using data from this study (2018-2020) and a historical study (Macartney, 1985; data collected 1981-1983). Statistically significant changes marked with ‘*’.

Site	Gender, Year	Mean SVL (cm) ± SD	Mean Weight (g) ± SD	Mean Body Condition (g/cm) ± SD
Park	♂♂ 1983	72.9 ± 12.6	208.4 ± 125.8	2.7 ± 1.2
	♂♂ 2020	73.3 ± 10.7	320.7 ± 158.7	4.2 ± 1.6
	%△	↑1%	↑35%*	↑36%*
	♀♀ 1983	70.2 ± 8.6	192.0 ± 91.7	2.7 ± 1.0
	♀♀ 2020	67.7 ± 7.2	264.3 ± 101.2	3.8 ± 1.3
	%△	↓4%*	↑27%*	↑29%*
Ranch	♂♂ 1983	80.4 ± 12.8	324.3 ± 167.0	3.9 ± 1.5
	♂♂ 2020	74.0 ± 11.6	346.5 ± 177.5	4.5 ± 1.7
	%△	↓8%*	↑6%	↑13%*
	♀♀ 1983	71.9 ± 8.5	249.4 ± 103.4	3.3 ± 1.1
	♀♀ 2020	69.2 ± 7.13	268.5 ± 103.1	3.8 ± 1.2
	%△	↓4%*	↑7%	↑13%*

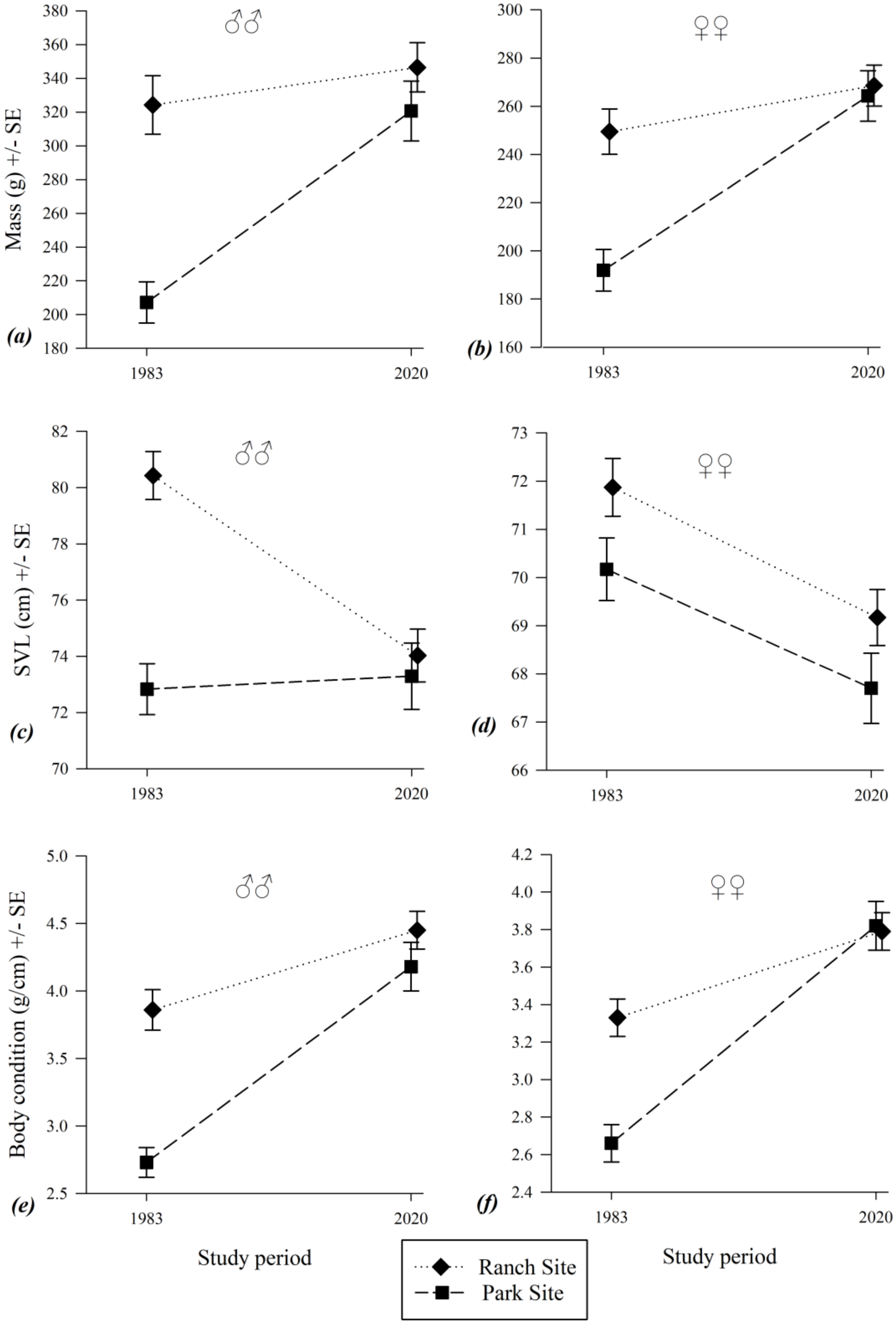

FIGURE 2.3. Temporal comparisons of mean male and female mass (a, b), length (SVL; c, d), and body condition (e, f) for Western Rattlesnakes (*Crotalus oreganus*) captured during this study and during a historical study (Macartney, 1985) within Kalamalka Lake Provincial Park (Park) and Coldstream Ranch (Ranch).

DISCUSSION

This study provides insight into temporal and spatial differences in population numbers, size-class distributions, size, and body condition of rattlesnakes at the northern extent of their range. Population declines were more drastic when considering the entire population versus solely the adult population. Furthermore, the population within the Park site declined considerably more than the population within the Ranch site and three dens appear to have been abandoned or extirpated since the Macartney study. Further study is necessary to discern whether the cause of these population declines is rooted in natural fluctuations or anthropogenic pressures, and to better understand natural cycles of rattlesnake demographic trends.

The apparent overall decrease of rattlesnakes detected over the last 35 years is disconcerting, given the study area is composed of two sites, namely a protected area and a landbase largely off limits to human activity save for limited cattle grazing. In Canada, Western Rattlesnakes have been listed as ‘threatened’ (COSEWIC, 2015) due to suspected declines of 30% or greater over three generations (~45 years; Maida et al., 2018). At least at our study site, this level of decline has been observed and possibly surpassed.

Changes to population structure and morphometrics since the Macartney study may provide some insight into the population decline. The size-class distribution of both males and females in our sample was significantly different from that of Macartney, with a lower proportion of juveniles found during our study. The higher proportion of juveniles in Macartney’s data may be due, at least in part, to more directed sampling for neonatal animals focusing on reproductive ecology when compared to this study. Alternatively, a lower proportion of juveniles in the population also may suggest decreases in adult reproductive output and/or juvenile survivorship that may be reflected in the more drastic declines observed when juveniles were included in the overall population estimate.

Mean snake mass and body condition appeared to increase substantially in the Park site where population estimates declined relatively more. This is at odds with data presented by Lomas (et al., 2015) for the south Okanagan valley, where Western Rattlesnakes in human-disturbed habitats showed lower body condition and reduced weight gain over the active season when compared to snakes occupying areas largely devoid of humans (Lomas et al., 2015). Given that the population has apparently declined since the previous study, intraspecific competition for resources may be lower among snakes reaching larger sizes, enabling the animals to acquire more mass. This also may explain why we observed more marginal increases in body condition and mass for snakes on the Ranch site where declines were less severe. A decrease in mean SVL for females, but not for males, remains puzzling. Females may be reproducing at smaller lengths, thereby allocating more energy to the accumulation of fat reserves for gestation as opposed to linear growth compared to females from the Macartney era. Preliminary data suggests relative prey abundance is marginally different across the landscape (see Chapter 1), however, further investigation into growth rates, reproduction, and prey availability may help enlighten the above phenomena.

Is it likely that the differences detected between the two sites in this study are directly attributable to land management? A reoccurring problem with so-called ‘natural experiments’ is that sample sizes often can be reduced to only one ‘experiment’ and one ‘control’. In this study, we only have one site in each of our two categories of land management (Park versus Ranch). It would be presumptuous to conclude that the two management regimes are directly responsible for the differences in rattlesnake populations that we observed herein. More information is clearly needed on how juxtaposed rattlesnake populations vary demographically. However, the close proximity of the two areas in this study, and the fact that historic baseline data exists does suggest the differences are attributable to site-specific conditions that may or may not be directly related to the overarching land use over the past 35 years. While the Ranch landscape has remained largely unchanged since the Macartney study, the exclusion of cattle within the Park area is coupled with an increase in human visitation. In addition to differences in population declines, rattlesnakes also display significant differences in defensive behaviour between the two sites that may be attributable to the relative abundance of humans or cattle (Chapter 3). Along with more human foot-traffic, this increased visitorship also has resulted in the widespread establishment of invasive plants, to the extent that many areas in the Park are completely devoid of most native species (BC Parks, 2019). How this may affect the prey base of the snakes is unclear. Additionally, vehicle traffic along Cosens Bay Road (Fig. 1.5) may contribute to mortality within the Park, both directly and indirectly, as even small roads have been shown to impact dispersal and gene flow in snakes (Clark et al., 2010); although more data on the level of road mortality in the Park is needed to affirm this assumption. However, road mortality from a low-traffic backroad further south in the region to be removing 6.6% of the Western Rattlesnake population per year, leading to a projected 97% decrease in mean population size over 100 years (Winton et al., 2019). Regardless, our data argue there may be risk in assuming protected areas inherently provide ‘anchors’ in the protection of species, especially if other uses of the landscape are intertwined with a conservation interest.

Despite the declines suggested in this study, the estimated density of adult rattlesnakes across our study sites still is substantially higher than that reported at sites a short distance away in the same region of the province. Our estimate of ≈84 animals/km^2 is over 30% higher than that reported in a more xeric site (~225 km due S, 58/km^2; Maida et al., 2018), and 60% greater than recent estimates at another location marginally closer to our site (~140 km due S, 35/km^2; S. Winton, unpublished data). Because these studies used near-identical methods to those used by us, they suggest substantial variation in densities may exist in the northern portion of this snake’s distribution. These differences could be attributed to a variety of independent and synergistic factors including, climatic differences, prey availability, predator density, human development, road mortality, direct persecution, or more severe population declines in these other areas. Unfortunately, without historical baselines for these other populations, we cannot compare the relative rate of decline over time across the species’ range to disentangle these effects. All told, these results clearly highlight the pitfalls of using single point-source estimates of densities for status assessments or management.

Was the rattlesnake population during the Macartney study closer to a historic carrying capacity? Or, are we perhaps succumbing to the Shifting Baseline Syndrome by using the Macartney data as a base by which to draw comparisons with our more contemporary data? Without historical baselines antecedent to Macartney, we may never know. There is evidence to suggest that targeted persecution of rattlesnakes was commonplace from at least 1920-1970 (see Chapter 1). Perhaps the population already was degraded when Macartney began his study, and the population numbers we see today are a continuation of that. In any case, the data presented in this study draws attention to the ongoing declines in species, both those at-risk and those still considered common, and calls for additional investigation to understand local pressures to wildlife populations to develop conservation measures that increase capacity for wildlife populations in our natural areas.

LITERATURE CITED

Atkins, M. C. P. and K. W. Larsen. 2020. Measuring snakes across the decades. Are tube-restraint measurements compatible with an earlier method? Herpetological Conservation and Biology. 15(2): 350 – 353.

Baillargeon, S. and L. P. Rivest. 2007. Rcapture: loglinear models for capture-recapture in R. Journal of Statistical Software. 19:1 – 31.

Baum, J. K. and R. A. Myers. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecology Letters. 2004(7): 135 – 145.

Clark, R. W., W. S. Brown, R. Stechert, and K. R. Zamudio. 2010. Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. Conservation Biology. 24(4): 1059 – 1069.

Cody, M. L. 1996. Introduction to long-term community ecological studies. *In* Long-term studies of vertebrate communities. Cody, M. L., and J. A. Smallwood (Eds). Academic Press, San Diego, CA, USA. Pp. 1 – 15.

Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2015. COSEWIC Assessment and status report on the Western Rattlesnake *Crotalus oreganus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 44 p.

Cormack, R. M. 1985. Example of the use of GLIM to analyze capture-recapture studies. Pp. 242—274 *In* Statistics in Ornithology. Lecture Notes in Statistics. Volume 29. Morgan, B. J. T. and P. M. North (Eds.). Springer, New York, New York, USA.

Cormack, R. M. 1989. Loglinear models for capture-recapture. Biometrics. 45: 395 – 419.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Ann. Rev. Ecol. Evol. Syst. 2004(35): 557 – 581.

Graves, B. M. and D. Duvall. 1993. Reproduction, rookery use, and thermoregulation in free-ranging, pregnant *Crotalus v. viridis*. Journal of Herpetology. 27(1): 33 – 41.

Gregory, P.T., G.J. Davies, and M.J. Macartney. 1989. A portable device for restraining rattlesnakes in the field. Herpetological Review 20:43–44.

Harvey, J. and K. W. Larsen. 2020. Rattlesnake migrations and the implications of thermal landscapes. Movement Ecology. 8:21.

Huitric, M. 2005. Lobster and Conch fisheries of Belize: a history of sequential exploitation. Ecology and Society. 10(1): 21.

Lindenmeyer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C. R. Dickman…, and G. M. Wardle. 2012. Value of long-term ecological studies. Austral Ecology. 2012(37): 745 – 757.

Jackson, J. B. C. 1997. Reefs since Columbus. Coral Reefs. 1997(16): S23 – S32.

Jones, P. C., R. B. King, R. L. Bailey, N. D. Bieser, K. Bissell, H. Campa III, T. Crabill,… and M. J. Dreslik. 2017. Range-wide analysis of Eastern Massasauga survivorship. Journal of Wildlife Management. 76: 1576 – 1586.

Lomas, E., K. W. Larsen, and C. A. Bishop. 2015. Persistence of Northern Pacific Rattlesnakes masks the impact of human disturbance on weight and body condition. Animal Conservation. 18(2015): 548 – 556.

Lomas, E., J. R. Maida, C. A. Bishop, and K. W. Larsen. 2019. Movement ecology of Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) in response to disturbance. Herpetologica. 75(2): 153 – 161.

Macartney, J. M. 1985. The ecology of the Northern Pacific Rattlesnake, *Crotalus viridis oreganus*, in British Columbia. MSc Thesis, Thompson Rivers University, Victoria, British Columbia. 289 pp.

Macartney, J. M. 1989. Diet of the Northern Pacific Rattlesnake, *Crotalus viridis oreganus*, in British Columbia. Herpetologica. 45(3): 299 – 304.

Macartney, J. M. and P. T. Gregory. 1988. Reproductive biology of female rattlesnakes (*Crotalus viridis*) in British Columbia. Copeia 1988: 47–57.

Macartney, J. M., P. T. Gregory, and M. B. Charland. 1990. Growth and sexual maturity of the Western Rattlesnake, *Crotalus viridis*, in British Columbia. Copeia 1990: 528–542.

Maida, J. R., D. A. Kirk, O. McKibbin, J. R. Row, K. W. Larsen, C. Stringham, and C. A. Bishop. 2018. Population estimate, survivorship, and generation time of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) at its northern-most range limits. Herpetological Conservation and Biology. 13(3): 662 – 672.

Murphy, J. B. 1971. A method for immobilizing venomous snakes at Dallas Zoo. International Zoo Yearbook. 11:23.

Newsome, S. D., M. A. Etnier, D. Gifford-Gonzalez, D. L. Phillips, M. van Tuinen, E. A. Hadly, D. P. Costa…, and P. L. Koch. The shifting baseline of northern fur seal ecology in the northeast Pacific Ocean. PNAS. 104(23): 9709 – 9714.

Okanagan Valley Economic Development Society. 2013. 2013 Economic profile of the Okanagan Valley. Okanagan Valley Economic Development Society, Kelowna, British Columbia, Canada. 126 p.

Papworth, S. K., J. Rist, L. Coad, and E. J. Milner-Gulland. 2009. Evidence for shifting baseline syndrome in conservation. Conservation Letters. 2(2009): 93 – 100.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. 1995. Trends in Ecology and Evolution. 10(10): 430.

Pinnegar, J. K. and G. H. Engelhard. 2008. The 'shifting baseline' phenomenon: a global perspective. Reviews in Fish Biology and Fisheries. 2008(18): 1 – 16.

Row, J. R., G. Blouin-Demers, and S. F. Fox. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia*. 2006(4): 797 – 802.

Santini, L. M. González-Suárez, C. Rondinini, and M. Di Marco. 2017. Shifting baseline in macroecology? Unravelling the influence of human impact on mammalian body mass. Diversity and Distributions. 2017(23): 640 – 649.

Schmidt, D., P. Govindarajulu, K. W. Larsen, and M. A. Russello. 2020. Genotyping-in-thousands by sequencing reveals marked population structure in Western Rattlesnakes to inform conservation status. Ecology and Evolution. 2020(00) 1 – 16.

Soga, M. and K. J. Gaston. 2018. Shifting baseline syndrome: causes, consequences, and implications. Frontier in Ecology and the Environment. 16(4): 222 – 230.

Statistics Canada. 2020. Canada's population estimates: subprovincial areas, July 1, 2020. Minister of Industry, Ottawa, Ontario, Canada.

Todd, B. D., J. D. Wilson, and J. W. Gibbons. 2010. The global status of reptiles and causes of their decline. *In* Ecotoxicology of Amphibians and Reptiles, Second Edition. Sparling, D. W., C. A. Bishop, and S. Krest (Eds). CRC Press, Pensacola, FL, USA. Pp. 47 – 67.

Turvey, S. T., L. A. Barrett, H. Yujiang, Z. Lei, Z. Xinqiao, W. Xianyan, H. Yadong, Z. Kaiya…, and W. Ding. 2010. Rapidly shifting baselines in Yangtze fishing communities and local memory of extinct species. Conservation Biology. 2(3): 778 – 787.

Vera, F. 2010. The shifting baseline syndrome in restoration ecology. *In* Restorarion and history: The search for a usable environmental past. Routledge Publishing. Pp. 98 – 110.

Whipple, A. A., R. M. Grossinger, and F. W. Davis. 2011. Shifting baselines in a California oak savanna: nineteenth century data to inform restoration scenarios. Restoration Ecology. 19(101): 88 – 101.

White, E. R. 2019. Minimum time required to detect population trends: the need for long-term monitoring programs. BioScience. 69(1): 40 – 46.

Winton, S. A., R. Taylor, C. A. Bishop, and K. W. Larsen. 2018. Estimating actual versus detected road mortality rates for a northern viper. Global Ecology and Conservation. 16(2018): e00476.

Winton, S. A., C. A. Bishop, and K. W. Larsen. 2019. When protected areas are not enough: low-traffic roads projected to cause a decline in a northern viper population. Endagered Species Research. 2020(41): 131 – 139.

Zug, G. R., L. J. Vitt, and J. P. Caldwell. 2001. Herpetology, Second Edition. Academic Press, San Diego.

CHAPTER 3

EVIDENCE OF INTRAPOPULATION SHIFTS IN RATTLESNAKE DEFENSIVE BEHAVIOUR ACROSS NEIGHBOURING HABITATS

INTRODUCTION

Protected areas are a key tool for sustaining wildlife and biodiversity. However, protected areas often have conflicts between conservation, human visitation, and recreation, and their effects on behaviour, distribution, and migratory pathways of many species (Sarmento and Berger, 2017). Even non-consumptive recreational activities may have profound effects on wildlife through both direct and indirect disturbance (McGowan et al., 2014). Single and multi-purpose landscapes represent natural experiments for assessing how the behaviour of species shifts in response to the levels of human visitation resulting from different landscape use.

The manner in which species perceive and respond to human presence varies tremendously with the level of human activity (Laundré et al., 2010). The importance of understanding these responses is clear in situations where direct contact between humans and animals can occur – particularly when those encounters pose a threat to one or both parties (e.g. large predators). Frequent human encounters can influence risk assessment and subsequent fight-or-flight decisions amongst wildlife if humans are perceived as a threat (Frid and Dill, 2002; Ohashi et al., 2013; McGowan et al., 2014). In time, repetition of relatively benign stimuli, such as a passing hiker, can lead to habituation; i.e. a decreased responsiveness by animals as a means to avoid costly responses that produce no benefit (Rankin et al., 2009; Blumstein, 2016). Habituation is of concern to wildlife managers and conservation biologists as such behaviour can lead to increased tolerance and closer contact with humans, or potential predators, without overt reaction (Herrero et al., 2005; Samia et al., 2015; Blumstein, 2016).

Variation in levels of tolerance demonstrated by habituated animals may be driven by other processes such as phenotypic sorting, behavioural plasticity, and natural selection (Lowry et al., 2013; Møller et al., 2015; Williams et al., 2020). Phenotypic sorting occurs when individuals settle in different habitats (or micro-habitats) based on each animal’s tolerance to the local environments (Edelaar et al., 2008). For example, a higher abundance of bold versus shy birds may occur in urban environments (Clergeau et al., 2006; Croci et al., 2008). Under natural conditions, behavioural plasticity allows an animal to adjust its behaviour to best suit the conditions of its environment and potentially increase its fitness (Lowry et al., 2013). However, animals that habituate to interactions with harmless humans are at higher risk to injury or death from hunters, poachers, resentful humans, or natural predators (Geffroy et al., 2015); this may be especially concerning for species-at-risk or those occupying areas with high levels of illegal harvest (Blumstein, 2016). Understanding how animal behaviour varies based on local landscape conditions, such as levels of human activity, is critical for developing effective conservation plans (Sarmento and Berger, 2017).

The rattlesnake rattle is a novel trait, emerging only once in the evolutionary history of rattlesnakes (Klauber, 1956), and is absent in all of the >3,000 other snake taxa (Allf et al., 2016), though other species display non-auditory tail vibration. The rattle produces an audible buzz between 2 – 20 khz (Fenton and Licht, 1990) and has been shown to be an effective warning signal to predators (Klauber, 1956; Greene, 1988; Prior and Weatherhead, 1994; Allf et al., 2016). Tail vibration creating a buzzing rattle is a distinctive defensive adaptation that epitomizes rattlesnakes (Family Viperidae), even though the primary antipredator tactic of rattlesnakes is crypsis (Duvall et al., 1985). Tail vibration (and resultant rattling) in snakes is only expressed when threatened (Greene, 1988); thus rattling is an environmentally-induced trait and represents behavioural (or phenotypic) plasticity (Allf et al., 2016). When disturbed, rattlesnakes typically remain motionless or cease movement relying on camouflage to avoid detection (Duvall et al., 1985). At a certain level of disturbance, rattlesnakes will abandon crypsis and begin to rattle, move away, assume a strike position, and eventually bite (Kissner et al., 1997).

There has been a longstanding assumption by biologists that rattlesnakes in disturbed areas are less likely to rattle than snakes in relatively pristine habitats, presumably caused by humans' selective elimination of snakes that choose to rattle (Fitch, 1949; Klauber, 1956). Field studies have attempted to correlate rattling behaviour with snake sex, reproductive status, body size, body temperature, and exposure to handling (Kissner et al., 1997; Holding et al., 2014). Other studies have investigated the habituation potential of this behaviour in the laboratory (Place and Abramson, 2008). To our knowledge, a population-level shift in rattling behaviour by rattlesnakes has never been quantified in the field, much less within context of human activity.

In this study we examined the defensive behaviour (rattling) of Western Rattlesnakes (*Crotalus oreganus*) in British Columbia, Canada in two neighbouring subpopulations/areas subject to different levels of human presence. Prompted by *ad hoc* observations, we predicted that snakes within the area subject to high levels of human visitation would rattle less often and initiate rattling at shorter distances from an approaching human than snakes occupying a neighbouring site with negligible human activity. The close proximity (<1 km) of these two subpopulations allows comparison of the behaviours among individual rattlesnakes at a fine spatial scale, while controlling for other elements of population history (e.g. shared ancestry over time).

Study Area

All field work was conducted within Kalamalka Lake Provincial Park (50 °N, 119 °W) and the adjacent Coldstream Ranch in the North Okanagan region of British Columbia, Canada. The site is characterized by a mosaic of grassland and forest patches dominated by blue-bunch wheatgrass (*Agropyron spicatum*), various fescue species (*Festuca* spp.), Ponderosa pine (*Pinus ponderosa*), Western Redcedar (*Thuja plicata*), and Douglas-Fir (*Psuedotsuga menziesii*) surrounded by rolling hills and steep bluffs. The two sites differ considerably in the presence of people. Kalamalka Lake Provincial Park (Fig. 1.2) is a provincially protected recreational area that receives an average of 32,600 visitors per month throughout the season when rattlesnakes are active (April through October) (Fig. 1.7; British Columbia Parks, unpublished data). The site contains an access road for a lakeshore community (Fig.1.5) and >50 kilometers of popular, year-round hiking, horseback riding, and mountain biking trails (Fig.1.6). The Ranch site (Fig. 1.2) is located on Coldstream Ranch, an active cattle grazing operation that prohibits access to the public but allows cattle to range freely in the open dry forest/grassland complex for 10 weeks of the year (see Chapter 1). The Ranch and Park sites are separated by barbed wire fencing that excludes cattle from the Park site but presents no barrier to snakes. Mark-recapture and radio-telemetry work in the area (Atkins and Larsen, Thompson Rivers University, unpublished data) suggests inter-site movements are infrequent. However, Schmidt et al. (2020) found no evidence of significant genetic differences between snakes from two dens, one from each sample site; thus, some level of historic gene flow appears likely. In order to ensure fine-scale patterns were not masked by the broad scope of the analysis undertaken by Schmidt et al. (2020), we repeated the Bayesian clustering analysis of single nucleotide polymorphism (SNP) genotypic data using only the 41 individuals from Kalamalka Lake Provincial Park and Coldstream Ranch. We again found no evidence of genetic structure that distinguishes individuals between sites (Schmidt and Russello, University of British Columbia, unpublished data).

Although Kalamalka Lake Provincial Park was formally created in 1975, the two sites were managed jointly as grazing land under the regime of Coldstream Ranch until 1985 (T. Osborne, Coldstream Ranch 2002 Ltd., personal communication) when management of the Park site shifted to a multipurpose framework with cattle exclusion. Thus, the landscape provides a unique natural experiment whereby snakes on the Park site have been subject to a management regime focused on recreation with high levels of direct anthropogenic disturbance for nearly 35 years (or approximately 3 rattlesnake generations; Maida et al., 2018). Conversely, snakes on the Ranch site have had minimal interactions with humans for an even longer period of time, although interactions with cattle are probable and may confound this.

MATERIALS AND METHODS

During a concurrent demographic study of rattlesnakes (Chapter 2), we haphazardly selected 68 free-ranging rattlesnakes captured during the period May 27 – August 22, 2019 (34/site). We avoided neonatal animals because of difficulties assessing the precise initiation of rattling in very small individuals. Upon discovery, snakes were captured using reptile tongs and immediately placed under a transparent plexi-glass box (30 x 20 x 13 cm) with no bottom. The enclosure was situated on flat terrain, open side down, allowing the animal to contact the natural substrate. As much as possible, each trial was conducted in a location where the snake, in theory, had a 360° view unobstructed by tall grass, shrubs, or rocks. Once inside the enclosure the snake was left undisturbed for 5 minutes (following Kissner et al., 1997). During this time we did not approach within 10 m of animals. After the rest period, the snake was approached by the same observer starting at 10 m away along an unobstructed path. A metronome app on a cell phone (ProMetronome, EUMLab, Berlin, Germany) was used to standardize the walking pace 70 beats per minute. As the researcher approached the enclosure, stride lengths were estimated for distances between 5-10 m. When within 5 m of the snake, stride length was standardized by a flexible measuring tape with marks 70 cm apart. We set stride length and tempo standards to approximate walking patterns of the average recreational visitor. Upon the first detection of rattling behaviour (visual or auditory) the approaching researcher immediately halted and recorded the distance (to nearest 5 cm) from the toe of their forefoot to the front facing surface of the enclosure. Thus, our response variable was distance from the snake to an approaching observer upon first detection of rattling (rattle-distance), and could be comparable to Flight Initiation Distance (FID) in other behavioural studies (Ydenberg and Dill, 1986).

After each trial, we recorded Julian date (days elapsed since January 1; JDate), weather (percent cloud cover; Cloud), surface body temperature (°C; BodyT; Etekcity Lasergrip 1080, Etekcity, California, USA), snout-vent length (cm; SVL), body weight (g; Weight), body condition (g/cm; BodyCon), sex, and reproductive status (*see* Macartney and Gregory, 1988). We did not include gravid females in this study as their behaviour changes drastically during pregnancy (Macartney and Gregory, 1988; Graves and Duvall, 1993). After the trial, individuals were then implanted with a subcutaneous passive integrated transponder (PIT) tag (Biomark Model TX1411SSL; Biomark, Boise, Idaho, USA) to permit future individual recognition and avoid repeated use of the same individuals.

Data analysis was conducted using R (R Version 3.6.3, r-project.org, 2020) and the significance threshold for all analyses was set to $\alpha = 0.05$. We used *t*-statistic, F-statistic and classical linear regression for exploratory analyses. However, our rattle-distance measurements included a preponderance of zero-values. Log-transforming non-zero values provided a more symmetrical distribution, although the data remained zero-inflated as many animals did not initiate a rattle response. To address this issue, we developed a two-part model (Min and Agresti, 2002) to confirm results from the exploratory analyses.

Part 1 regressed the log of odds of the probability of no rattle occurring at either site using a logit model to assess the impact of each covariate.

$$logit[\pi_i] = \beta_0^* + \sum_{j=1}^{k} \beta_j^* x_{ij}$$

Conditional on non-zero values for rattle-distance, Part 2 assumed a log-normal regression model to assess the impact of each covariate.

$$\log(Y_i | Y_i > 0) = \beta_j^{**} x_{ij} + \epsilon_i^{**}$$

We used Akaike's Information Criterion (AIC) and the variable selection method to determine the appropriate final model. We excluded length and weight and kept only body condition in the model as these three variables were highly correlated with each other.

All field data collection was conducted under Thompson Rivers University Animal Use Protocol (#102039), British Columbia Wildlife Act Permit (MRPE15-171661), and British Columbia Park Use Permit (#108794).

RESULTS

Over the entire sample (N = 68) we recorded 14 zero-values (Fig. 3.1a; Park site = 12, Ranch site = 2) and 54 non-zero values (Fig. 3.1b; Park = 22, Ranch = 32) for rattle-distance. Mean rattle-distance was 1.15 m in the Park site, and 3.55 m in the Ranch site and was significantly different between the two sites (Fig. 3.1b; t = 4.86, df = 57.60, P < 0.001). Variation in rattle-distance was significantly greater among individuals on the ranch site (Fig. 3.1b; F = 2.24, df = (33, 33), P = 0.012). The final model identified site, body temperature, Julian date, and body condition as significant variables.

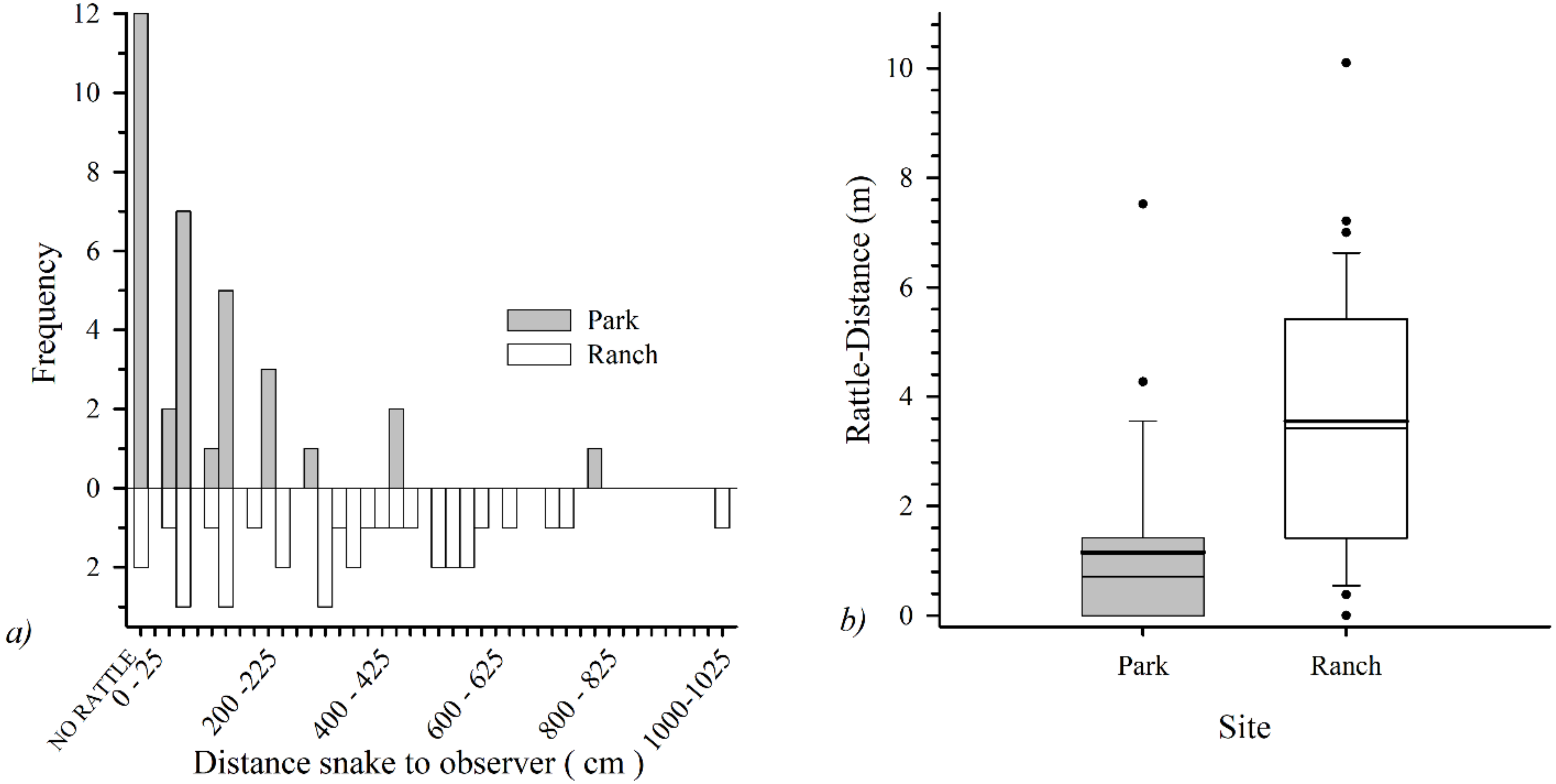

FIGURE 3.1. (a) Frequency distribution of the distance (m) from a Western Rattlesnake (*Crotalus oreganus*) at first observation of rattle behavior (rattle-distance) approached by an investigator simulating an approaching hiker. Grey bars = snakes at Park site, white bars = snakes at Ranch site. (b) Box plot of actual rattle distances for each site (n = 34/site), bold line = mean rattle-distance.

TABLE 3.1. The top three models explaining the rattle response of Western Rattlesnakes (*Crotalus oreganus*) as a function of the distance between the animal and an approaching investigator at first observation of rattling. Model variables included site, body temperature (BodyTemp), sex, weather, Julian date (JDate), and body condition (BodyCon). The model explanatory power was assessed by Akaike's Information Criterion (AIC). Combined AIC was the sum of AIC for both parts of each two-part model. Part 1 represents a logistic model for the log of odds of the probability of no rattle occurring, while Part 2 represents a log-normal regression model of non-zero values for estimating the distance at which the animal will exhibit the defensive behaviour.

Models	***Variables***	***AIC***	***Combined AIC***
Basic Model – Part 1	Site	62.02	
Basic Model – Part 2	Site	143.98	206
Full Model – Part 1	Site, BodyTemp, Sex, Weather, JDate, BodyCon	67.09	
Full Model – Part 2	Site, BodyTemp, Sex, Weather, JDate, BodyCon	140.28	207.37
Final Model – Part 1	Site, BodyTemp, JDate, BodyCon	63.28	
Final Model – Part 2	Site, BodyTemp, JDate, BodyCon	137.71	200.98

In Part 1 (occurrence of a rattle) of the final model, Site and BodyTemp emerged as significant variables (Table 3.2). The odds probability of a rattle occurring was 9.5× higher at the ranch than at the park, given all other variables were fixed. The odds probability of a rattle occurring increased by 0.44 times for every 5 °C increase in body temperature for the temperature range recorded (18.2 – 38.5 °C), given all other variables were fixed.

In Part 2 (distance when rattle present) of our final model, Site, Jdate, and BodyCon emerged as significant variables while the effect of BodyTemp was negligible (Table 3.2). The average rattle distance was 3.49 m closer in the Park site than at the Ranch site given all other variables were fixed. For every 30 days elapsed in the experimental period, the predicted rattle distance increased by 1.52 m during our observation period (Julian Days 147 – 234) given all other variables were fixed. For every 10% decrease in body condition, the expected rattle distance decreased by 1.30 m (i.e. snakes in poorer condition waited to rattle until a human was closer) given all other variables were fixed.

Table 3.2. Model parameters for the final model explaining the rattle response of Western Rattlesnakes (*Crotalus oreganus*) as a function of the distance between the animal and an approaching investigator at first observation of rattle behavior. Model variables included Site, body temperature (BodyTemp), Julian date (JDate), and body condition (BodyCon). Part 1 represents a logistic model for the log of odds of the probability of no rattle occurring, while Part 2 represents a log-normal regression model of non-zero values for estimating the distance at which the animal will exhibit the defensive behaviour.

Parts	**Variables**	**Estimates**	**Std. Errors**	**Test-Statistics**	**P-values**
Part 1	Intercept	-2.02	3.13	-0.64	0.52
	Site	2.25	0.87	2.54	0.01
	BodyTemp	-0.17	0.09	-1.86	0.06
	JDate	0.00	0.01	0.34	0.74
	BodyCon	0.02	0.02	0.88	0.38
Part 2	Intercept	0.44	0.88	0.50	0.62
	Site	-1.25	0.23	-5.43	<0.00
	BodyTemp	0.01	0.02	0.27	0.79
	JDate	0.01	0.00	3.34	<0.00
	BodyCon	-0.03	0.01	-2.61	0.01

DISCUSSION

Our experiment demonstrated a substantial difference in both the likelihood of rattling occurring and mean rattle-distance between areas of high and low human activity for this population of Western Rattlesnakes. Consistent with our *ad hoc* observations, snakes in the Park site were significantly less likely to engage in a stereotypic defense, allowing an approaching observer to come considerably closer before displaying defensive behaviour. Park snakes also displayed much less variation among individuals in rattle-distance compared to snakes on the Ranch site. These results are notable given our estimate of genetic relatedness among snakes between the two sites, the close proximity of the sites, and the relatively short time frame since their management divergence (approximately three Western Rattlesnake generations; Maida et al., 2018). Our results suggest that in the Park site the rattlesnakes rely more heavily on crypsis over costly warning signals. We believe that the low level of variation in responses from Park snakes, in addition to the magnitude of the observed difference, suggests possible population-level habituation to human-disturbance on the landscape. Determining the generality of this behavioural strategy in Western Rattlesnakes will require investigations at additional locations (Howarth, in prep).

Pseudoreplication often is difficult to counter in natural disturbance experiments (Guthery, 1987; Oksanen, 2001 Davies and Gray, 2015; Colegrave and Ruxton, 2018). Admittedly, this study lacks a completely randomized design, but given the backdrop and logistical constraints of the study this was impossible to achieve. Further, the lower density of rattlesnakes in their northern range makes it extremely difficult to obtain adequate samples of free-ranging snakes without a coincidental, intensive field study (as opposed to a shorter sampling period). Other factors than the presence of humans may be exerting confounding effects, but our analysis still is reasonable given we included several putative predictor variables in the model, ensuring their effects have been adjusted.

One long-standing theory for the evolution of the rattlesnake rattle suggests it evolved as a warning device to alert large grazing animals in the plains of North America (Hay, 1887; Garman, 1889; Barbour, 1922) but this hypothesis has been challenged by several authors (Schuett et al., 1984; Sisk and Jackson, 1997; Glaudas et al., 2005; Reiserer and Schuett, 2016). The interpretation of our results is confounded by the presence of cattle on the Ranch site, suggesting cattle presence may be influencing the difference in the snakes as much, or more than, human presence in the Park. Cattle are present in rattlesnake habitat on the Ranch site [approximately 3.75 AUM per hectare (1 AUM = animal unit/month, equivalent to the forage removed by one 454 kg cow or cow-calf pair in one month - T. Osborn, Coldstream Ranch (2002) ltd., personal communication).] for a short time period (~ 1/3rd of the snakes' active season). Thus, the potential for cattle-snake interactions is substantially lower compared to the potential for human-snake interactions on the Park site. Further, both the Park site and the Ranch site were managed jointly for cattle grazing until 1986 (T. Osborne, Coldstream Ranch (2002) Ltd., personal communication) at which point the former was opened to human visitation. Thus, we argue that snakes have been exposed to cattle presence for longer than they have been exposed to high levels of human traffic. Clearly further study on the effect of periodic exposure to grazing animals on rattlesnake defensive behaviour is warranted.

Differences in vegetation cover between our study sites due to the lack of cattle grazing in the Park could potentially confound the behavioural differences we detected. However, dichotomous habitat use (grassland versus upland forest) within multiple populations of Western Rattlesnakes in the same region, suggesting both open and closed habitats are important for rattlesnakes (Gomez et al., 2015; Harvey et al., 2020). Still, additional investigation into the correlation between microhabitat preference and rattling behavior across landscape gradients is needed in addition to how different levels of grazing intensity affects this relationship.

Although Site (reflecting high versus low human activity) was the strongest predictor of patterns of rattle behaviour in our study, other factors appeared to affect rattling. Body temperature and Julian date both were predictors of whether a snake would rattle or not. The majority of individuals in the study (85%) were within the thermal tolerance range for the species (16 - 31 °C; Putnam and Clark, 2017); it is reasonable to assume that the effect of body temperature on defensive behaviour would be more dramatic at temperatures outside of their thermal tolerance. Harvey and Weatherhead (2011) showed thermoregulatory behaviour of Massasauga rattlesnakes (*Sistrurus catenatus*) at their northern limits steadily decreased from June through August and rose sharply in September and October. This mid-summer decrease in thermoregulation generally coincides with the reproductive cycle of Western Rattlesnakes (Macartney and Gregory, 1988). Kissner et al. (1997) found a weak relationship between season and rattle-distance for Prairie Rattlesnakes (*Crotalus viridis*), with snakes allowing closer approaches in the spring, but no consistent relationship between body temperature and rattle-distance. It makes sense that early season priorities of thermoregulation and ambush hunting would increase the reliance on crypsis over costly anti-predator displays. The cost of such displays may be counter-balanced by the possibility of acquiring a mate during reproductive periods (August – October) which may explain the influence of body temperature and Julian date in our model.

Body condition also was a predictor of rattle-distance, but not for the presence/absence of rattling. This suggests that snakes in poorer condition tend to rely on crypsis over more costly displays for predator evasion. Lomas et al. (2015) demonstrated that Western Rattlesnakes in human-disturbed habitats had lower body condition and lost more weight over the season compared to snakes in undisturbed areas. We found no difference in mean body condition between the two sites in our study (Chapter 2). Rattlesnakes of poorer condition may become more reliant on less energy-intensive behaviours regardless of human-disturbance, and human-disturbance on the landscape may be additive to the pressures of poor condition. Massasauga rattlesnakes have been shown to reduce the length and frequency of their movements in a provincial park with high levels of human-disturbance despite no difference in body condition between disturbed and undisturbed sites (Parent and Weatherhead, 2000). Thus, it appears that body condition and human-disturbance on the landscape may promote an increased reliance on crypsis among rattlesnakes independently or synergistically.

Although it is extremely difficult to separate the effects of human disturbance from other confounding factors on the landscape, the results of our study follow other reports of animal defensive behaviour being linked to human disturbance. The general trend for bird, mammal, and reptile populations that are regularly exposed to human presence is increased tolerance of people, with habitat contrasts (i.e. populations under low versus high human disturbance) being one of the main drivers of habituation and tolerance to human disturbance (Samia et al., 2015; Levey et al., 2009; Engelhardt and Weladji, 2011; McGiffin et al., 2013;

Shen et al., 2020). If we accept that habituation occurs on the level of the individual (Blumstein, 2016; Williams et al., 2020) and that there exists a positive relationship between the frequency of human exposure and the degree of human tolerance (Samia et al., 2015), then it follows that the differences we detected between these two sites may be a reflection of population-level habituation to human visitors. However, more specific study is needed to quantify actual encounter rates between humans and snakes in habitats with different levels of human visitation.

While differences in the level of human disturbance are recognized to affect the degree of tolerance displayed by populations across landscapes (Samia et al., 2015; Williams et al., 2020), decreased variation in tolerance among individuals may be driven by factors other than habituation such as phenotypic sorting and behavioural plasticity (Lowry et al., 2013; Møller et al., 2015; Williams et al., 2020). However, given the spatial heterogeneity of sampling (i.e. snakes both near and far from areas of high human traffic) and large sample size per site, phenotypic sorting is unlikely. Although our study population may be behaviorally plastic to low levels of human disturbance (as evidenced by the high level of variation in rattle-distance among individuals at the Ranch site), the relatively low level of variation in rattle-distance among individuals at the Park site suggests a more uniform, population-level response to human activity.

Selection pressure can also give rise to tolerance (Lowry et al., 2013; Cooper et al., 2015). If unnecessary defensive displays directed toward benign humans result in an increased energetic cost to rattlesnakes within the Park site, then increased tolerance of humans would represent an energetic advantage, and variance in tolerance would decrease over time. While it is possible that such selection processes may be operating on this population, phenotypic changes are unlikely to have permeated throughout the population in just three generations. However, vehicle traffic along Cosens Bay Road may be acting as a barrier to gene flow, as even small roads can have a large impact on the genetic diversity of snake populations (Clark et al., 2010). A genome-wide association study employing reduced representation (e.g. restriction-site associated DNA sequencing; Baird et al., 2008), or whole genome sequencing (e.g. Therkildsen & Palumhi, 2017) could be designed to explicitly test this. Regardless, if increased tolerance of humans conveys a significant advantage then it is possible microevolutionary processes driven by human activity may be at work within this population. Further study of the heritability of tolerance among rattlesnakes and other species is warranted, as human visitation is projected to continue to rise in many areas, and the long-term effects on wildlife may be more ecologically impactful than simply individual habituation to non-confrontational human stimuli.

In short, the exhibition of different behavioural strategies within a single population across landscape gradients is of interest for biologists and managers alike. We argue the strength of our results suggests this phenomenon may exist elsewhere. To confirm this relationship, similar work needs to be conducted in other populations of rattlesnakes spanning different land-use regimes with various level of direct human presence.

LITERATURE CITED

Allf, B. C., P. A. P. Durst, and D. W. Pfennig. 2016. Behavioral plasticity and the origins of novelty: the evolution of the rattlesnake rattle. American Naturalist. 188(4): 475 – 483.

Baird, N. A., P. D. Etter, T. S. Atwood, M. C. Currey, A. L. Shiver, Z. A. Lewis, E. U. Selker, W. A. Cresko, and E. A. Johnson. 2008. Rapid SNP discovery and genetic mapping using sequenced RAD markers. PLoS ONE. 3(10): e3376. doi:10.1371/journal.pone.0003376

Barbour, T. 1922. Rattlesnakes and spitting snakes. Copeia. 1922: 36 – 38.

Blumstein, D.T. 2016. Habituation and sensitization: new thoughts about old ideas. Animal Behaviour. 120: 255 – 262.

Clark, R. W., W. S. Brown, R. Stechert, and K. R. Zamudio. 2010. Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. Conservation Biology. 24(4): 1059 – 1069.

Clergeau, P., S. Croci, J. Jokimäki, M. Kaisanlahti-Jokimäki, and M. Dinetti. 2006. Avifauna homogenization by urbanization: analysis at different European latitudes. Biological Conservation. 127: 336 – 344.

Colegrave, N., and G. D. Ruxton. 2018. Using biological insight and pragmatism when thinking about pseudoreplication. Trends in Ecology and Evolution. 33(1): 28 – 35.

Cooke, S. J., D. T. Blumstein, R. Buchholz, T. Caro, E. Fernández-Juricic, C. E. Franklin, J. Metcalfe, C. M. O'Connor, C. C. St Clair, W. J. Sutherland, and M. Wikelski. 2014. Physiology, behavior, and conservation. Physiological and Biochemical Zoology. 87(1): 1 – 14.

Cooper, W. E. Jr., and D. T. Blumstein. 2015. Escape behavior: importance, scope, and variables In: Cooper W. E. Jr., and D. T. Blumstein, editors. Escaping from predators: an integrative view of escape decisions. Cambridge: Cambridge University Press. 18 – 37.

Croci, S., A. Butet, and P. Clergeau. 2008. Does urbanization filter birds on the basis of their biological traits? Condor. 110: 223 – 240.

Davies, G. M., and A. Gray. 2015. Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). Ecology and Evolution. 5(22): 5295 – 5304.

Duvall. D., M. B. King, and K. J. Gutzwiller. 1985. Behavioral ecology and ethology of the prairie rattlesnake. National Geographic Research. 1: 80 – 111.

Edelaar, P., A. M., Sipielski, and J. Clobert. 2008. Matching habitat choices causes directed gene flow: a neglected dimension in evolution and ecology. Evolution: International Journal of Organic Evolution. 62(10): 2562 – 2472.

Engelhardt, S. C., and R. B. Weladji. 2011. Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels. Canadian Journal of Zoology. 89: 823 – 830.

Fenton, M. B., and L. E. Licht. 1990. Why rattle snake? Journal of Herpetology. 24: 274 – 279.

Fitch, H. S. 1949. Study of snake populations in Central California. The American Midland Naturalist. 41(3): 513 – 579.

Frid. A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology. 6(1): 11.

Garman, S. 1889. On the evolution of the rattlesnake. Proceedings of the Boston Society of Natural History. 24: 170 – 182.

Geffroy, B., D. S. M. Samia, E. Bessa, and D. T. Blumstein. 2015. How nature based tourism might increase prey vulnerability to predators. Trends in Ecology and Evolution. 30(12): 755 – 765.

Glaudas, X., T. M. Farrell, and P. G. May. 2005. Defensive behavior of free-ranging Pygmy Rattlesnakes (*Sistrurus miliarius*). Copeia. 2005: 196 – 200.

Graves, B. M., and D. Duvall. Reproduction, rookery use, and thermoregulation in free-ranging, pregnant *Crotalus v. viridis.* Journal of Herpetology. 27(1): 33 – 41.

Greene, H. W. 1988. Antipredator mechanisms in reptiles. Pp. 1-152, In C. Gans and R.B. Huey (Eds.). Biology of the reptilia: defense and life history. Alan R. Liss, New York, NY. 672 pp.

Guthery, F. S. 1987. Guidelines for preparing and reviewing manuscripts based on field experiments with unreplicated treatments. Wildlife Society Bulletin. 15(2): 306

Harvey, D. S. and P. J. Weatherhead. 2011. Thermal ecology of Massasauga Rattlesnakes (Sistrurus catenatus) near their northern range limit. Canadian Journal of Zoology 89: 60 – 68.

Harvey, J. A., and K. W. Larsen. 2020. Rattlesnake migrations and the implications of thermal landscapes. Movement Ecology. 8: 21.

Hay, O. P. 1887. The Massasauga and its habits. American Naturalist. 21: 211 –218.

Herrero, S., T. Smith, T. D. DeBruyn, K. Gunther, and C. A. Matt. 2005. From the field: Brown Bear habituation to people – safety, risks, and benefits. Wildlife Society Bulletin. 33(1): 362 – 373.

Holding, M. L., J. A. Frazier, S. W. Dorr, S. N. Henningsen, I. T. Moore, and E. M. Taylor. 2014. Physiological and behavioral effects of repeated handling and short-distance translocations on free-ranging Northern Pacific Rattlesnakes (*Crotalus oreganus oreganus*). Journal of Herpetology. 48(2): 233 – 239.

Kissner, K. J., M. R. Forbes, and D. M. Secoy. 1997. Rattling behavior of prairie rattlesnakes (Crotalus viridis viridis, Viperidae) in relation to sex, reproductive status, body size, and temperature. Ethology. 103(12): 1042 – 1050.

Klauber, L. M. 1956. Rattlesnakes. Vol. 1. University of California Press, 1956.

Laundré, J. W., L. Heranández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. The Open Ecology Journal. 3: 1 – 7.

Levey, D. J., G. A. Londono, J. Ungvari-Martin, M. R. Hiersoux, J. E. Jankowski, J. R. Poulsen, C. M. Stracey, and S. K. Robinson. 2009. Urban mockingbirds quickly learn to identify individual humans. Proceedings of the National Academy of Sciences. 106: 8959 – 8962.

Lomas, E., K. W. Larsen, and C. A. Bishop. 2015. Persistence of Northern Pacific rattlesnakes masks the impact of human disturbance on weight and body condition. Animal Conservation. 18: 548 – 556.

Lowry, H., A. Lill, and B. B. M. Wong. 2013. Behavioral responses of wildlife to urban environments. Biological Reviews. 88: 537 – 549.

Macartney, J. M. 1985. The ecology of the Northern Pacific Rattlesnake, *Crotalus viridis oreganus*, in British Columbia. MSc Thesis, Thompson Rivers University, Victoria, British Columbia. 289 pp.

Macartney, J. M. and P. T. Gregory. 1988. Reproductive biology of female rattlesnakes (*Crotalus viridis*) in British Columbia. Copeia. 1988: 47 – 57.

Maida, J. R., D. A. Kirk, O. McKibbin, J. R. Row, K. W. Larsen, C. Stringam, and C. A. Bishop. 2018. Population estimate, survivorship, and generation time of the Northern Pacific rattlesnake (*Crotalus o. oreganus*) at its Northern-most range limits. Herpetological Conservation and Biology. 13(3): 662 – 672.

McGiffin, A., A. Lill, J. Beckman, and C. P. Johnstone. 2013. Tolerance of human approaches by Common Mynas along an urban-rural gradient. Emu. 113: 389 – 399.

McGowan, M. M., P. D. Patel, J. D. Stroh and D. T. Blumstein. 2014. The effect of human presence and human activity on risk assessment and flight initiation distance in skinks. Ethology. 120: 1081 – 1089.

Min, Y., and A. Agresti. Modeling nonnegative data with clumping at zero: a survey. JIRSS 1(1-2): 7 – 33.

Møller, A.P., P. Tryjanowski, M. Díaz, Z. Kwieciński, P. Indykiewicz, C. Mitrus, and M. Polakowski. 2015. Urban habitats and feeders both contribute to flight initiation distance reduction in birds. Behavioral Ecology. 26. 861-865.

Ohashi, H., M. Saito, R. Horie, H. Tsunoda, H. Noba, H. Ishii, T. Kuwabara, Y. Hiroshige, S. Koike, Y. Hoshino et al., 2013. Differences in activity pattern of the wild boar, *Sus scrofa*, related to human disturbance. European Journal of Wildlife Research. 59: 167 – 177.

Oksanen, L. 2001. Logic of experiments in ecology: Is pseudoreplication a pseudoissue? Oikos. 94(1): 27 – 38.

Parent, C., and P. J. Weatherhead. 2000. Behavioral and life history responses of Eastern Massasauga Rattlesnakes (Sistrurus catenatus catenatus) to human disturbance. Oecologia. 125(2): 170 – 178.

Place, A. J., and C. I. Abramson. 2008. Habituation of the rattle response in Western diamondback rattlesnakes, *Crotalus atrox*. Copeia. 4: 835 – 843.

Prior, K. A., and P. J. Weatherhead. 1994. Response of free-ranging Eastern Massasauga Rattlesnakes to human disturbance. Journal of Herpetology. 28(2): 255-257.

Putnam, B. J., and R. W. Clark. 2017. Behavioral thermal tolerances of free-ranging rattlesnakes (Crotalus oreganus) during the summer foraging season. Journal of Thermal Biology. 65: 8 – 15.

Rankin, C. H., T. Abrams, R. J. Barry, S. Bhatnagar, D. Clayton, J. Colombo, G. Coppola, M. A. Geyer, D. L. Glanzman, S. Marsland, et al., 2009. Habituation revisited: An updated and revised description of the behavioral characteristics of habituation. Neurobiology of learning and memory. 92(2): 135 – 138.

Reiserer, R. S. and G. W. Schuett. 2016. The origin and evolution of the rattlesnake rattle: misdirection, clarification, theory, and progress. *In* Rattlesnakes of Arizona (Volume 2). Eds. Schuett, G. W., M. J. Feldner, C. F. Smith, and R. S. Reiserer. ECO Publishing, Rodeo, New Mexico, USA.

Samia, D. S. M., S. Nakagawa, F. Nomura, F. Rangel, and D. T. Blumstein. 2015. Increased tolerance to humans among disturbed wildlife. Nature Communications. 6(1): 1 – 8.

Sarmento, W. M. and J. Berger. 2017. Human visitation limits the utility of protected areas as ecological baselines. Biological Conservation 212: 316 – 326.

Schmidt, D., P. Govindarajulu, K. W. Larsen, and M. A. Russello. 2020. Genotyping-in-thousands by sequencing reveals marked population structure in Western Rattlesnakes to inform conservation status. Ecology and Evolution. 2020(00) 1 – 16.

Schuett, G. W., Clark, D. L., and F. Kraus. 1984. Feeding mimicry in the rattlesnake *Sisrturus catenatus*, with comments on the evolution of the rattle. Animal Behaviour. 32: 625 – 626.

Shen, C., J. Yu, H. Lu, L. Wang, H. Wang, and W. Liang. 2020. Warblers perform less nest defense behavior and alarm calls to human intruders: A result of habituation. Global Ecology and Conservation. 2020: e01187.

Sisk, N. R., and J. F. Jackson. 1997. Tests of two hypotheses for the origin of the crotaline rattle. Copeia. 1977: 485 – 495.

Therkildsen, N. O. and S. R. Palumhi. 2017. Practical low-coverage genome wide sequencing of hundreds of individually barcoded samples for population and evolutionary genomics in non-model species. Molecular Ecology Resources. 17: 194 – 208 (2017).

Williams, D. M., P. Nguyen, K. Chan, M. Krohn, and D. T. Blumstein. 2020. High human disturbance decreases individual variability in skink escape behavior. Current Zoology. 66(1): 63 – 70.

Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advances in the Study of Behavior. 16: 229 – 249.

CHAPTER 4

CONCLUSION

Summary of Thesis

The overarching goal of my thesis was to understand how rattlesnake populations in British Columbia have changed over time and across contrasting space to inform evidence based conservation and management strategies. Specifically, I looked at how the population studied in the 1980s in the North Okanagan by Macartney (1985) has changed over time and in relation to changing landscapes. I investigated the changes in this population in three main ways: (a) how abundance has changed on the landscape, (b) how the population has changed morphometrically, and (c) whether defensive behaviour (i.e. rattling) differs depending on landscape use.

The principal findings from my thesis were:

- The total population of Western Rattlesnakes within our sample has declined by an average of 40% over the entire study area.
- This decline was more severe on average on the Park site (50%) when compared to the Ranch site (31%).
- The decline was more severe when juveniles were included in the estimates, suggesting that age/size classes may be differentially susceptible to decline.
- Adult snake density in the Kalamalka Lake Provincial Park and Coldstream Ranch population declined by 22% overall over time, but the density remained considerably higher than recently calculated in two other populations approximately 200 km further south in the same drainages.
- The average length of adult snakes declined or remained the same for both males and females in both sites, while mass and body condition increased substantially for both sexes, and across both sites, since the previous study.
- Snakes on the Ranch site were 9.5 times more likely to rattle at researchers when compared to snakes on the Park site. When snakes on the Park site did rattle, they initiated the behaviour at a distance 68% closer on average than snakes in the Ranch site.

- The strongest predictor of rattling was site (Park vs. Ranch). Encounter rates between rattlesnakes and people are expected to be higher in the Park, which could suggest rattlesnakes become more reliant on crypsis over defensive displays with increasing levels of human visitation.

Overall, these findings reflect that substantial population declines of Western Rattlesnakes have occurred over time, and that the magnitude of these declines differ across these two neighbouring landscapes. These results also support the notion that high levels of human visitation, as a result of management direction, may be impacting rattlesnake populations and may produce highly uniform, population-level behavioural changes. Our results suggest that protected areas, especially those managed in part for recreation, may not be acting as 'anchors' of conservation, and emphasizes the need for continued monitoring of this threatened species to understand the specific threats for continued conservation.

Implications of Thesis for the Management of Snakes in the Region

According to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), the main threats to Western Rattlesnakes are habitat loss and fragmentation from urban and agricultural developments, road mortality, and human persecution (COSEWIC, 2015). Rattlesnakes within Kalamalka Lake Provincial Park are arguably subject to all three of these pressures. Here I present suggestions stemming from thesis data but also from anecdotal observations collected over 2.5 years of work in Kalamalka Lake Provincial Park and Coldstream Ranch. Thus, further detailed investigation on some points is still warranted.

Habitat Loss

- Substantial rural development at the northern periphery of the Park, occurring progressively since before the Macartney study, is reducing the overall amount of summer habitat for snakes.
- Increased fragmentation within the Park from recreational interests. Additional mapping of recreational features in relation to snake dens and foraging habitat is necessary.

- Snakes from dens surveyed within the Park are highly likely to encounter footpaths, trails, or roads during their summer movements. Some trails are within a few meters of well-populated dens.
- The ideal mitigation strategy would remove or redirect all trails that intersect denning habitat or high-density summer use areas for rattlesnakes, though this is unlikely to occur given the multipurpose framework and variety of stakeholders within the Park.
- To mitigate further fragmentation or increased human-rattlesnake encounters, plans for new, or changes to existing, trails, parking areas, and day-use areas should consider the habitat quality for rattlesnakes, proximity to overwintering dens, and the intended use of the development.

Road Mortality

- Quantification of road mortality was not feasible in this study, though roadkill is typically underestimated in even the most robust studies (Winton, 2018).
- Even small backroads can pose barriers to dispersal and gene flow, causing reduced genetic diversity in snake populations (Clark et al., 2010).
- Given the development in the lakeshore community that the road services, and that there are calls to construct additional parking along Cosens Bay Road for park users, it is reasonable to assume that road traffic will continue to increase over time.
- Given the unknown level of road mortality in the Park, and considering the results of Winton et al. (2019) in combination with the declines suggested in this study and anecdotal evidence of road mortality, additional study into the extent of roadkill on Cosens Bay Road should be quantified before proceeding with infrastructure development.

Human Persecution

- Premeditated, largescale persecution of rattlesnakes in the Park and the Ranch no longer occurs.
- Human persecution of snake species within the Park may still occur on an opportunistic basis, both directly and indirectly, in three main formats:

1. Road mortality in the form of drivers purposefully swerving to harm snakes
2. Mortality from cyclists running over snakes
3. Indirect mortality from maintenance staff translocating rattlesnakes.

- The simplest and most inexpensive option for reducing the effects of (1) & (2) would be revitalization and increased presence of educational and interpretive signs within the Park. The current signs could be renewed to highlight the diversity within the Park, educate park users on the status of endangered species, and give instructions for safely navigating encounters with rattlesnakes and other species.
- Additional signage in areas where users are most likely to encounter rattlesnakes may help to promote awareness of the potential of encounters and prevent fear-based responses.
- To mitigate the effects of (3), additional mapping of ideal translocation drop-off points for common 'problem' areas should be undertaken.

Conclusion

Wildlife populations in general are declining globally, with many aspects of anthropogenic disturbance such as habitat loss and fragmentation, road-mortality, direct persecution, introduction of invasive species, pollution, and fire suppression claiming responsibility. These threats are magnified for reptilian species at their northern range limits that are already faced with physiological, ecological, and climatic limitations. I investigated how a northern rattlesnake population has changed over time and space by closely repeating a historical study. The difference in demographic and behavioural data we collected between these two landscapes suggests these sites are producing differential pressures on this population, despite other potential confounding factors. In light of these declines, and the established threats to this species in British Columbia, it appears likely declines could continue. However, given historical population estimates and the amount of suitable habitat within the Park, there is still hope to develop conservation strategies that will allow the population to increase. Maintaining connectivity between the Park and the Ranch should remain a priority.

The risk of succumbing to the SBS is at an all-time high. Without historical reference points of population levels, determining whether populations are dangerously declining or naturally fluctuating in the wake of rapidly changing environments becomes extremely difficult or impossible. The looming threat of mass extinctions, coupled with a widespread lack of historical data on population numbers for many species, make it increasingly difficult to pinpoint benchmarks of success for recovering populations and to develop effective conservation strategies going forward. Perhaps the best return on the investment of conservation dollars would be the revisitation of populations with historical data, rather than initiating new studies of previously undescribed populations. However, both sets of work are needed to combat SBS.

This study has broadened the understanding of landscape changes on rattlesnake populations, though from a relatively coarse lens. Given the estimated declines, the long-term persistence of northern rattlesnake populations will require continued assessment of populations to avoid shifting baselines, further study of the suspected drivers of decline, and the continued commitment of managers to the conservation of these populations. These results highlight the need for conservation strategies tailored to specific populations and localized pressures, and emphasizes the pitfalls of point estimates for species-at-risk. This study provides unique snap shot comparison between two time intervals separated by over 3 decades in a population of Western Rattlesnakes in Canada, and provides a compelling case for continued monitoring of populations of cryptic species, especially those at risk.

LITERATURE CITED

Brown, W. S. 1993. Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. SSAR Herpetological Circular. 22: 1 – 78.

Butler, H., B. Malone, and N. Clemann. 2005*a*. Activity patterns and habitat preferences of translocated and resident tiger snakes (*Notechis scutatus*) in a suburban landscape. Wildlife Research. 32: 157 – 163.

Butler, H., B. Malone, and N. Clemann. 2005*b*. The effects of translocation in the spatial ecology of tiger snakes (*Notechis scutatus*) in a suburban landscape. Wildlife Research. 32: 165 – 171.

Clark, R. W., W. S. Brown, R. Stechert, and K. R. Zamudio. 2010. Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. Conservation Biology. 24(4): 1059 – 1069.

Colley M., S. C. Lougheed, K. Otterbein, J. D. Litzgus. 2017. Mitigation reduces road mortality of a threatened rattlesnake. Wildlife Research. 44:48–59.

Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2015. COSEWIC assessment and status report on the Western Rattlesnake *Crotalus oreganus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 44p.

Forman R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale L. Fahrig, R. L. France, K. Heanue, C. R. Goldman, et al. 2003. Road ecology: science and solutions. Washington, DC, USA: Island Press.

Gregory, P. T., J. M. Macartney, and K. W. Larsen. 1987. Spatial patterns and movements. Pp. 366 – 395 *in* R. A. Seigel, J. T. Collins, and S. S. Novak, eds. Snakes: ecology and evolutionary biology. Macmillan, New York, New York, USA.

Macartney, J. M. 1985. The ecology of the Northern Pacific Rattlesnake, *Crotalus viridis oreganus,* in British Columbia. MSc Thesis, Thompson Rivers University, Victoria, British Columbia. 289 pp.

Nowak, E. M., T. Hare, and J. McNally. 2002. Management of “nuisance” vipers: effects of translocation on western diamond-backed rattlesnakes (*Crotalus atrox*). Pp. 535 – 560 *in* J. A. Campbell and E. D. Brodie, eds. Biology of the vipers. Eagle Mountain, Eagle Mountain, Utah, USA.

Plummer, M. V. and N. E. Mills. 2000. Spatial ecology and survivorship of resident and translocated hognose snakes (*Heterodon platirhinos*). Journal of Herpetology. 34: 565 – 575.

Reinert, H. K., and R. R. Rupert. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. Journal of Herpetology. 33:45 – 61.

Rytwinski T., K. Soanes, J. A. G. Jaeger, L. Fahrig, C. S. Findlay, J. Houlahan, R. Der Van Ree, E. A. Van Der Grift. 2016. How effective is road mitigation at reducing road-kill? A meta-analysis. PLoS ONE. 11:e0166941.

Winton, S. A. 2018. Impacts of Road Mortality on the Western Rattlesnake (Crotalus oreganus) in British Columbia. MSc. Thesis. Thompson Rivers University, Kamloops, BC, Canada.

Winton, S. A., C. A. Bishop, and K. W. Larsen. 2019. When protected areas are not enough: low-traffic roads projected to cause a decline in a northern viper population. Endagered Species Research. 2020(41): 131 – 139.

APPENDIX A

MEASURING SNAKES ACROSS THE DECADES: ARE TUBE-RESTRAINT MEASUREMENTS COMPATIBLE WITH AN EARLIER METHOD?

Atkins and Larsen.—Comparison of length measurement methods for snakes.
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INTRODUCTION

A diversity of measurement techniques have been used through time to collect data on snake body length (snout-vent length or SVL; see Greenbaum 2003 and Tsai et al., 2018 and references within), offering flexibility to investigators, particularly those working on venomous animals. Tube-restraint has emerged as a favorable candidate for a universal length measurement technique for snakes as it is widely acknowledged as a consistently safe standard for the handling of venomous species (Murphy 1971; Murphy and Armstrong 1978; Lock 2008; Johnson 2011; Hogan 2015). This method requires readily available, inexpensive equipment, is practical for field studies, and drastically reduces the chance of injury to snakes and handlers. While tube-restraint for non-venomous snakes is not necessary to ensure handler safety, it offers protection to animals against potentially harmful manipulation of the sensitive head and cervical vertebrae, ensures measurement consistency across taxa, and is a practical handling method for veterinary services and taking caudal blood samples for genetic analyses. Tube-restraint requires several tubes of varying diameter; however, these are inexpensive and easily transportable.

While the historical shift in techniques reflects an increasing concern for accuracy and the ethical handling of animals, it creates the problem of comparing contemporary data with those taken in the past using a different technique. To ensure such comparisons are robust requires a statistical assessment of lengths using different measurement methods. There are several studies that have investigated the accuracy and precision of various body length measurement methods (Madsen and Shine 2001; Blouin-Demers 2003; Bertram and Larsen 2004; Setser 2007; Cundall et al., 2016), but with more attention put towards accuracy within the method, rather than making comparisons between methods.

In the process of studying a population of Western Rattlesnakes (*Crotalus oreganus*), we needed to compare contemporary data on snake lengths to those collected nearly 35 y prior at the same site. We used the tube-restraint method to measure snake lengths, while historical data were collected using noose-restraint poles (see Schmidt and Davis 1941; Conant 1958; Bellairs 1967; Fowler 1978; but specifically Gregory et al., 1989), hereafter referred to as the noose-stretch method. To our knowledge a specific comparison of tube-restraint and noose-stretch methods does not exist. Understanding the relationship between these two techniques would allow historical morphological data to be compared with measurements from current populations.

MATERIALS AND METHODS

We measured SVLs of Western Rattlesnakes in a population located in Vernon, British Columbia, Canada, in the fall of 2018. We first measured each snake using the tube-restraint method where, following Murphy (1971), we coaxed the snake to enter a clear acrylic tube until approximately one-third of the anterior end of the snake was inside. We carefully selected the appropriate tube size for the individual to ensure it could not turn its head around within the tube and to prevent contortion during handling. Once the snake was restrained, a handler guided the head of the snake into the distal end of the tube and secured the anterior section of the snake within the tube while another handler measured its length using a flexible measuring tape to trace along the dorsal surface along the vertebral ridge, starting from the snout and ending at the opening of the cloacal vent. We considered tube measurements precise when at least two recorded measurements were within 5 mm; thus, final tube measurements represent the mean of at least two tracings (see Blouin-Demers 2003).

After allowing each snake a 5-min rest period within holding baskets, we measured SVL on the same animal using the noose-stretch method. We approximated the methodology used in earlier studies on the same population of snakes (Macartney 1985, 1989; Macartney and Gregory 1988; Macartney et al., 1988, 1990) by using a noose-restraint pole following Gregory (1989). We placed the head of each snake in the noose, then slowly and carefully extended it along a meter stick to obtain a SVL measurement. We only conducted noose-stretch measurements once per individual to mitigate stress and injury potential. To avoid user bias and unnecessary additional measurements, the same investigator made all measurements.

To ensure unbiased comparisons, we ideally would have measured individual snakes using both techniques multiple times, with consecutive measurements being recorded by different investigators blind to prior measurements. Unfortunately, we were not able to hold our free-ranging study animals in captivity for extended periods (ethical considerations and permitting restrictions for species-at-risk), nor could we reliably recapture individual snakes for re-measurement except during sequential periods of den egress, between which times snake growth would have occurred. We thus could not completely eliminate the possibility that subconscious bias by the investigators would affect the repeatability of the two methods. Similar approaches have been taken to compare different measurement techniques, however (Madsen and Shine 2001; Measey et al., 2003; Bertram and Larsen 2004). Using a similar measurement technique, Rivas et al., (2008) suggest that measurements gathered independently by two experienced researchers are generally consistent. Finally, two field researchers worked side-by-side during the two types of measurement on each snake, acting as a double check on the length value being recorded.

We used R 3.6.1 (R Development Core Team 2019) for all statistical analyses. We compared tube-restraint and noose-stretch methods using several statistical tests. First, we used a paired *t*-test to estimate the mean difference in SVL between measurements of both methods on the same snake. Second, we used Linear Regression to assess the relationship between noose-stretch and tube-restraint measurements. We used the tube restraint measurement as the predictor variable and the noose-stretch measurement as the response. Both measurements were centered by subtracting the mean of each measurement method from measurements of individual snakes; this allowed us to estimate the difference between measurements for a snake of average size as the y-intercept. Lastly, we grouped measurements into ecologically relevant size classes of juvenile (250–550 mm SVL), subadult/adult (550–750 mm SVL), adult (700–800 mm SVL), and large adult (800–1,050 mm SVL) and we used a single factor ANOVA to assess measurement discrepancy between size classes. All tests met parametric assumptions, and for all tests, $\alpha = 0.05$.

RESULTS

We obtained paired measurements of SVL for 74 unique individuals. The mean measurement difference between methods was slight (3.2 mm ± 1.5 mm standard deviation, or 0.4% of mean body length in the tube sample). Paired measurements were not significantly different ($t = -1.84$, df = 73, $P = 0.071$; mean difference = -0.33; 95% confidence interval [CI] = -0.68, 0.028), with noose-stretch measurements generally being larger than tube-restraint. There was a strong relationship between measurement methods ($r^2 = 0.99$, $F_{1,73} = 6{,}502.3$, $P < 0.001$; Fig. A1) and there was no difference at the origin (95% CI of y-intercept, $-0.36 \leq \beta_0 \leq 0.36$) and no change in measurement difference between methods with changes in snake size (95% CI of slope, $0.97 \leq \beta_1 \leq 1.02$). Measurement discrepancy was not significantly different between size classes based on residual values from regression analysis ($F_{3,69} = 2.33$, $P = 0.082$). The most severe measurement discrepancies (top 5%; n = 4) were animals with SVLs of 927, 921, 885, and 635 mm (Fig. A1).

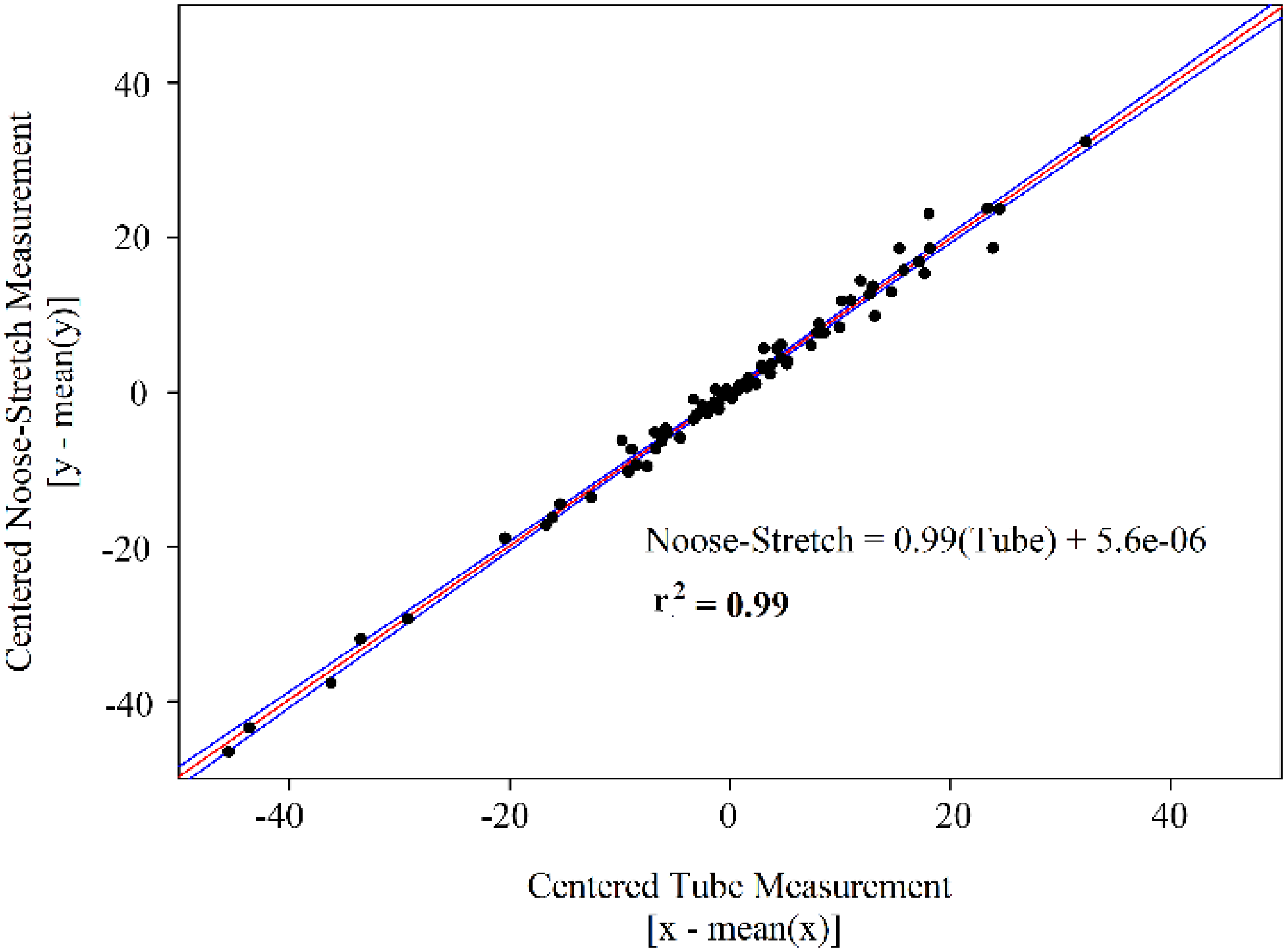

FIGURE. A1. Relationship of zero-centered measurements of Western Rattlesnake (*Crotalus oreganus*) snout-vent length (SVL) obtained via tube-restraint and noose-stretch methods (n = 74) in British Columbia, Canada. The red line represents the mean slope, and blue lines represent 95% confidence limits.

DISCUSSION

Our study indicates that tube-restraint SVL measurements were consistent with those obtained using the noose-stretch method. All differences in measurements were relatively small, although measurement difference tended to be greater for longer snakes, suggesting additional care should be taken when measuring particularly long animals. We attribute these greater discrepancies to variability in snake flexibility and cooperation during stretch measurements (Madsen and Shine 2001; Foster 2012; Astley et al., 2017) and measurement error during tube-restraint measurements for particularly long snakes. Our results did suggest that the measurement differences between methods were almost significant; however, we believe that for the purposes of comparing data collected using the different methodologies (i.e., to determine changes in population structure) this relationship is satisfactory. Furthermore, the differences in size obtained by different measurement methods are likely miniscule relative to ecologically relevant differences in size structure among populations or over time.

There has long been a call for a universal model of snake length measurement (Seigel and Ford 1988). We support this call for standardization and advocate for the adoption of tube-restraint as a universal standard for snake body length measurements. When appropriate, comparisons of data collected using this method versus those used historically should continue to be evaluated, particularly for species with varying body forms (i.e., Viperidae versus Colubridae, shorter snakes versus relatively longer ones, etc.).

LITERATURE CITED

Astley, H.C., V.E. Astley, D. Brothers, and J.R. Mendelson, III. 2017. Digital analysis of photographs for snake length measurement. Herpetological Review 48:39–43.

Bellairs, D.J. 1967. Reptiles. Pp. 830–852 *In* Zoo and Wild Animal Medicine. Fowler, M.E. (Ed.). W.B. Saunders Co., Philadelphia, Pennsylvania, USA.

Bertram, N., and K.W. Larsen. 2004. Putting the squeeze on venomous snakes: accuracy and precision of length measurements taken with the “squeeze box.” Herpetological Review 35:235–238.

Blouin-Demers, G. 2003. Precision and accuracy of body-size measurements in a constricting, large-bodied snake (*Elaphe obsoleta*). Herpetological Review 34:320–323.

Conant, R. 1958. A Field Guide to Reptiles and Amphibians of the United States and Canada East of the 100th Meridian. Houghton Mifflin Co., Boston, Massachusetts, USA.

Cundall, D., A. Deufel, G. Macgregor, A. Pattishall, and M. Richter. 2016. Effects of size, condition, measurer, and time on measurements of snakes. Herpetologica 72:227–234.

Foster, M.S. 2012. Dealing with live reptiles. Pp. 127–141 *In* Reptile Biodiversity. Standard Methods for Inventory and Monitoring. McDiarmid, R.W., M.S. Foster, C. Guyer, J.W. Gibbons, and N. Chernoff (Eds.). University of California Press, Berkeley, California, USA.

Fowler, M.E. 1978. Restraint and Handling of Wild and Domestic Animals. Iowa State University Press, Ames, Iowa, USA.

Greenbaum, E. 2003. A practical and safe method for the capture and restraint of venomous snakes in the field. Bulletin of the Chicago Herpetological Society 38:1–3.

Gregory, P.T., G.J. Davies, and M.J. Macartney. 1989. A portable device for restraining rattlesnakes in the field. Herpetological Review 20:43–44.

Hogan, M.P. 2015. Field venom extractions: saving fingers with tubes, forceps, and nerf bullets. Herpetological Review 46:339–342.

Johnson, R. 2011. Clinical technique: handling and treating venomous snakes. Journal of Exotic Pet Medicine 20:124–130.

Lock, B. 2008. Venomous snake restraint and handling. Journal of Exotic Pet Medicine 17:273–284.

Macartney, J.M. 1985. The ecology of the Northern Pacific Rattlesnake, *Crotalus viridis oreganus*. M.Sc. Thesis, University of Victoria, British Columbia, Canada. 289 p.

Macartney, J.M. 1989. Diet of the Northern Pacific Rattlesnake, *Crotalus viridis oreganus*, in British Columbia. Herpetologica 45:299–304.

Macartney, J.M., and P.T. Gregory. 1988. Reproductive biology of female rattlesnakes (*Crotalus viridis*) in British Columbia. Copeia 1988:47–57.

Macartney, J.M., P.T. Gregory, and K.W. Larsen. 1988. A tabular survey of data on movements and home ranges of snakes. Journal of Herpetology 22:61–73.

Macartney, J.M., P.T. Gregory, and M.B. Charland. 1990. Growth and sexual maturity of the Western Rattlesnake, *Crotalus viridis*, in British Columbia. Copeia 1990:528–542.

Madsen, T., and R. Shine. 2001. Do snakes shrink? Oikos 92:187–188.

Measey, G.J., J.B. Silva, and M. Bernardo. 2003. Testing for repeatability in measurement of length and mass in *Chthonerpeton indistinctum* (Amphibia: Gymnophiona), including a novel method of calculating total length of live caecilians. Herpetological Review 34:35.

Murphy, J.B. 1971. A method for immobilising venomous snakes at Dallas Zoo. International Zoo Yearbook 11:233.

Murphy, J.B., and B.L. Armstrong. 1978. Maintenance of rattlesnakes in captivity. University of Kansas Museum of Natural History Special Publication 3:1–40.

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https//www.r-project.org/.

Rivas, J.A., R.E. Ascanio, and M.D.C. Muñoz. 2008. What is the length of a snake? Contemporary Herpetology 2:1–3.

Schmidt, K.P., and D.D. Davis. 1941. Field Book of Snakes of the United States and Canada. G.P. Putnam’s Sons, New York, New York, USA.

Seigel, R.A., and N.B. Ford. 1988. A plea for standardization of body size measurements in studies of snake ecology. Herpetological Review 1988:9–10.

Setser, K. 2007. Use of anesthesia increases precision of snake length measurements. Herpetological Review 38:409–411.

Tsai, T., Z. Chen, C. Lin, and Y. Yeh. 2018. An improved technique for obtaining accurate and precise morphometric data on snakes. Zoological Science 35:233–242.