EFFECTS OF DISTURBANCE ON THE NORTHERN PACIFIC RATTLESNAKE (*CROTALUS OREGANUS OREGANUS*) IN BRITISH COLUMBIA

by

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ABSTRACT

The indirect effects of anthropogenic disturbances on wildlife are relatively difficult to detect, much less study, yet understanding these more subtle influences are particularly critical for the conservation of species-at-risk. In this study, I used radio-telemetry and mark-recapture methods to investigate the indirect effects of human disturbance and habitat development on the body characteristics, behaviour, and spatial ecology of a population of rattlesnakes (a threatened species) in Osoyoos, British Columbia. I collected data in 2010 and 2011 to augment a data set spanning 2002 to 2012. Individuals in highly disturbed landscapes had lower body condition than snakes in other areas, and lost body weight over the foraging season. Strong trends in spatial ecology parameters across disturbance gradients were not apparent, although snakes in disturbed sites tended to have smaller core areas, shorter range lengths, and took a greater number of days to travel a given distance than snakes in less-disturbed habitat. No major differences were observed in snake behaviour, exposure risk, or other spatial ecology parameters among habitats under different disturbance pressures. Wildlife managers can apply the results of this study to put recovery goals into action for the Northern Pacific Rattlesnake. The findings also contribute to our understanding of how wildlife may be impacted in discrete ways within disturbed habitat, and highlight the importance of using multiple indicators to assess stability of animal populations.

Keywords: Northern Pacific Rattlesnake, *Crotalus oreganus oreganus*, British Columbia, disturbance, habitat fragmentation, body condition, spatial ecology, radio-telemetry

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CHAPTER 1: INTRODUCTION

The loss of biodiversity associated with increasing human population is widely acknowledged (Aitken 1998, Pimm and Raven 2000, Czech et al. 2000, McKinney 2002, Mullin and Seigel 2009, MacDougall et al. 2013). Specifically, habitat loss, alteration, and degradation associated with anthropogenic changes are the greatest threats to wildlife around the globe (Wilcove et al. 1998, Gibbons et al. 2000, Hanski 2005). The direct effects of habitat loss on animal populations are apparent, with extinction and local extirpation of a species from an area occurring as either an immediate or eventual consequence (Fahrig 1997, Hanski 2005). Obvious examples include roads in altered and fragmented habitats that serve as proximate sources of mortality for many species (Case 1978, Mader 1984, Rosen and Lowe 1994, Andrews and Gibbons 2005). Indirect effects of habitat alteration, however, are less readily understood.

Habitat alteration can indirectly affect wildlife in a multitude of ways. Degraded habitat can leave insufficient resources for animal populations to exist in the long-term (Hanski 2005), or affect the composition of species in remaining patches due to changes in native vegetation (Mills et al. 1989). Habitat fragmentation can interrupt movement, mating and gene flow, causing genetic isolation (Prior et al. 1997, Ujvari et al. 2006, Clark et al. 2010). In order to create mitigation options for the recovery and preservation of animal populations, a detailed understanding of the direct and indirect effects of habitat alteration is needed. However, indirect effects are complicated, cumulative, and despite their importance, poorly documented (Theobald et al. 1997).

Habitat loss and alteration are unfortunately not the only obstacles animals face near urban areas: the physical presence of humans and human activities also act as disturbances in altered landscapes. In addition to the inevitable contact of people and animals in urban sites, outdoor recreation and human-use of natural landscapes is on the rise (Boyle and Samson 1985, Gray et al. 2003). Although some human activity in wilderness areas, such as hiking, may be considered benign, any disturbance that causes shifts in the normal behaviour of animals may result in nontrivial consequences for their populations (Boyle and Samson 1985, Theobald et al. 1997, Taylor and Knight 2003). Changes to activity and feeding patterns (Theobald et al. 1997), increased energetic costs or reduced use of high quality habitats from avoidance or flushing (e.g. Papouchis et al. 2001), increased metabolic rates or stress (Gabrielsen and Smith 1995), and direct persecution are among the potential consequences of human-animal contact. Any or all of the above may cause serious effects at the population level, including population decline (e.g. Garber and Burger 1995).

Habitat loss can occur along a gradient, with the interface between human development and so-called ‘natural habitat’ representing a transitional area where the impact on animals is not clear. The periphery of metropolitan areas is one such example, where animals may be present at intermediate densities. The maintenance of these populations is a common conservation goal, yet assessing the effects of both habitat alteration and human disturbance on the health and longevity of these ‘fringe’ populations is difficult and relatively uncommon. Conducting studies of this type may face logistical hurdles, requiring participation from landowners, community members and researchers, and often long-term data collection. These difficulties have produced a knowledge gap on whether populations of species considered ‘at risk’ that remain near urban centres are sustainable or not in the long-term.

The issues surrounding the measurement of indirect effects of habitat alteration and human disturbance on wildlife are further complicated when dealing with cryptic species, such as snakes. In addition to their cryptic nature, snakes are ectotherms: they have physiological constraints which tie them closely to specific habitat features and activity periods (Huey 1983, Reinert 1993, Parent and Weatherhead 2000). Further, in regions such as Canada, these animals are generally at the northern extent of their range. Effective conservation strategies for these animals must recognize that snakes experience relatively short activity periods than conspecifics in more southern portions of their range, have specific seasonal habitat requirements, and have restrictive movement capabilities. Adding to the problem is that snakes experience limited sympathy from the public relative to more conventionally charismatic animals, despite their contribution to the diversity of Canadian fauna.

Conservation of the Northern Pacific Rattlesnake

The Northern Pacific Rattlesnake (*Crotalus oreganus oreganus*) occurs at the northern extent of its range within the province of British Columbia, Canada. It is found in the province's dry south-central interior valleys within Bunchgrass, Ponderosa pine, and Interior Douglas-fir biogeoclimatic zones (Matsuda et al. 2006, Southern Interior Reptile and Amphibian Recovery Team 2008). The snake is associated with a variety of habitats, including shrub-steppe, open forest, riparian areas, rock outcrops, and talus slopes (Southern Interior Reptile and Amphibian Recovery Team 2008). These diverse habitats, however, are undergoing drastic landscape changes to meet the needs of expanding towns, and the agriculture and tourism industries.

The Northern Pacific Rattlesnake is greatly affected by urban development and habitat alteration (Didiuk et al. 2004). The species is listed federally as 'threatened' and is on the Blue List ('special concern') in B.C. (COSEWIC 2004, Southern Interior Reptile and Amphibian Recovery Team 2008). Habitat loss, degradation, fragmentation and road mortality are the main identified threats to these animals (Southern Interior Reptile and Amphibian Recovery Team 2008). Recovery from the impacts of habitat loss is presumably made even more difficult for these rattlesnakes in the north due to slower juvenile growth rates, delayed sexual maturity (7 to 8 years in females; 3 to 7 years in males) and infrequent (triennial or longer) parturition (Macartney 1985).

After spending the winter in communal hibernacula from approximately October to March, Northern Pacific Rattlesnakes embark on annual migrations to and from summer foraging habitat (Macartney and Gregory 1988). Like many venomous snakes, these animals are persecuted out of fear by the public, and they also face increasing difficulties navigating travel routes from hibernacula to their summer ranges due to altered land use and roads (Bertram et al. 2001, Didiuk et al. 2004). Snakes occurring near urban landscapes may also experience changes to their foraging areas through habitat fragmentation, degradation and development. The fidelity that these animals show towards their hibernacula, summer foraging grounds and movement corridors (Sealy 2002, Travsky and Beauvais 2004, Jenkins and Peterson 2005, Brown 2006, Gomez 2007, this study) further reveals the gravity of the situation confronting rattlesnakes in B.C.. In order to persist, one of two 'strategies' must unfold: snakes must either change their movement patterns and find undeveloped habitat (unlikely, given their high range fidelity), or cope with the disturbed landscape and the stressors it may introduce to the animal's life history.

A handful of studies have examined rattlesnake ecology in British Columbia (e.g. (Macartney 1985, Charland 1989, Gomez 2007, Hobbs 2007), but few have focused on conservation issues for the species (e.g. Bertram et al. 2001), and none have assessed the potential impacts of human disturbance on rattlesnake populations, much less focused on indirect effects of development on these animals. Current work suggests that rattlesnakes living in or near disturbed areas may not experience low survival (Bishop et al. 2012, unpubl. data), but the indirect effects on the individuals remain unknown. As an increasing number of populations become peripheral to urban landscapes, it is important to understand the impacts of development and disturbance on these animals, if we are to accurately assess whether their populations will continue to persist in the long-term.

The overarching goal of my research was to improve our knowledge of how anthropogenic activities may influence wildlife species living in marginal habitats. I investigated indirect effects of disturbances on a population of Northern Pacific Rattlesnakes occupying a human-altered landscape within British Columbia. In doing so, I also sought to contribute much needed information for the future management and recovery of the species. I used mark-recapture and radio-telemetry along with a long-term data-set to compare groups of rattlesnakes across a spectrum of human-disturbed and undisturbed sites. In the following chapter, I examine the body characteristics and behaviour of rattlesnakes in these two types of habitats. Then, in Chapter 3, I compare the spatial ecology of the snakes between the same areas. Finally, in Chapter 4, I briefly summarize my main findings and discuss the management implications of this research for the species. I conclude with recommendations for recovery efforts and identify areas of future research priorities for Northern Pacific Rattlesnakes in British Columbia.

Study area

My study took place on the Osoyoos Indian Reserve (OIR) in the extreme southern Okanagan valley of British Columbia, Canada (119.4° W, 49.28° N), approximately 1 km north of the US-Canada border (Figure 1.1). The 900 ha area is bordered by the town of Osoyoos to the south and south-west, Osoyoos Lake to the west, Anarchist Mountain (elev. 1491 m) to the east, and the remaining OIR to the north (Figure 1.2). The site was comprised

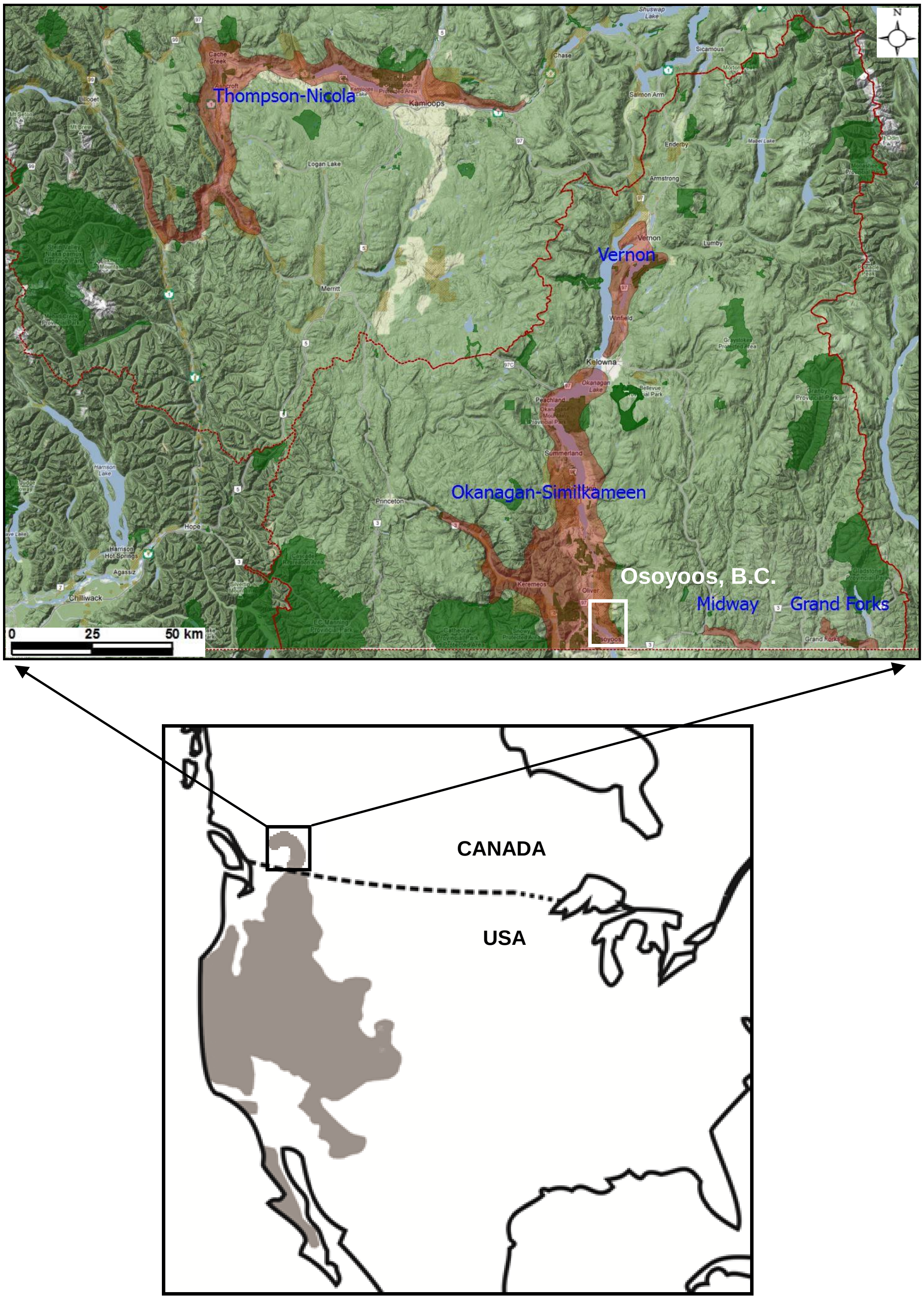

Figure 1.1. Combined range of all Western Rattlesnake (*Crotalus oreganus*) subspecies in North America and inset showing range (in red) of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) in British Columbia. The area of study (Osoyoos, B.C.) is marked with a white square. Inset provided by Hobbs and Sarell (2013).

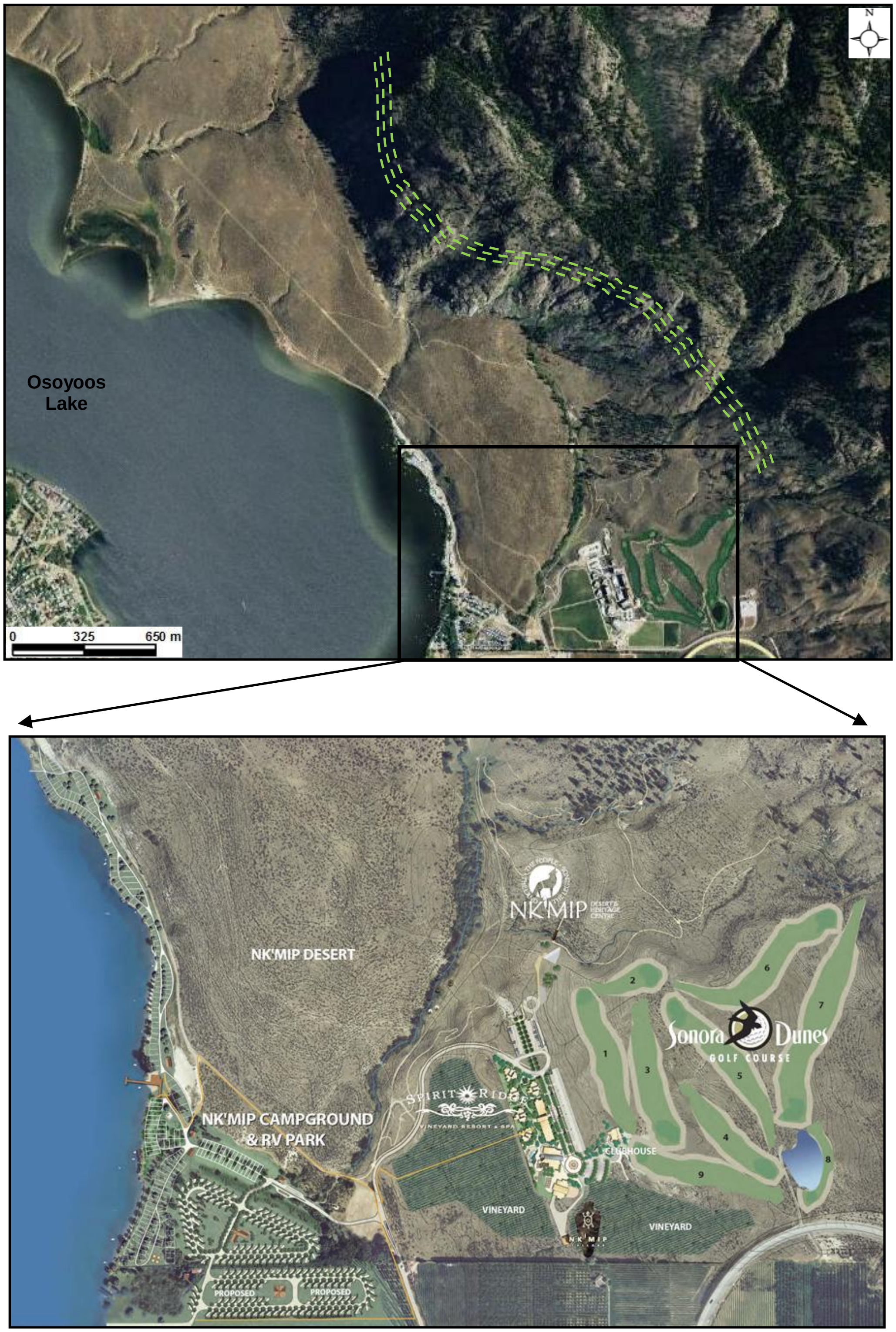

Figure 1.2. Study area in Osoyoos, B.C.. Green dotted shading represents area of hibernacula sites along the hillside. Inset shows areas of human disturbance including a campground, winery, resort, golf course, visitor's centre, walking trails, and roads. Map used with permission from Bellstar Hotels & Resorts Ltd (http://www.spiritridge.ca/nkmip.html).

of two main regions: (1) the lower elevation (300 - 400 m) shrub-steppe habitat and mountain slopes (approximately 270 ha) located within the Bunchgrass and Ponderosa Pine biogeoclimatic zones of B.C. (Lloyd et al. 1990), and (2) the higher elevation (900 - 1200 m) dry forests in the eastern mountains of the Interior Douglas-fir biogeoclimatic zone (Lloyd et al. 1990). These high-elevation forests comprised approximately 650 ha of potential habitat used by snakes in this study. Hibernacula lined the eastern slopes between the two regions (Figure 1.2).

The low elevations contained primarily antelope-brush (*Purshia tridentata*) and big-sagebrush (*Artemisia tridentata*) whereas the mountain slopes consisted of steep cliffs, talus, rock slides and rock outcrops (Figure 1.3). Open ponderosa pine (*Pinus ponderosa*) stands were also found on the mountain slopes and in the valley edges. The upper forests consisted primarily of Douglas-fir (*Pseudotsuga menziesii*) stands (Figure 1.3).

Landscape development and human activity was concentrated in the southern portions of the study area. Development included a large-scale visitor’s facility (the Nk'Mip Desert Cultural Centre), walking trails, condominium resort, golf course, winery, vineyards, a large campground, associated roads and parking lots, and a two-lane highway. These attractions result in tens of thousands of visitors annually (Stringam, pers. comm.). I hereafter refer to these general areas of the landscape as 'disturbed' (Figures 1.4 and 1.5). In contrast to this area, the northern and eastern portions of the study area were characterized by restricted or limited human access. There was no land development and little or no human presence in these areas. I refer to these areas as 'undisturbed' (Figure 1.6). A herd of five feral horses graze throughout the OIR, and low numbers of cattle have grazed all of the area in the past.

Long-term data-set

My study is part of a long-term research program started in 2002 on the OIR, through a partnership between the Canadian Wildlife Service and the Osoyoos Indian Band. The ongoing research on the OIR rattlesnake population focuses on the use of mark-recapture techniques to estimate population size, density, health and survivorship. Radio-telemetry studies began in 2004 and are used to study the spatial ecology of the snakes, identify important habitat features on the OIR, and assess the effectiveness of management

Figure 1.3. Examples of low elevation shrub-steppe habitat (A), high elevation Douglas-fir stands in the eastern mountains (B), and rock slides and talus on the steep mountain slopes (C). Photos by E. Lomas.

Figure 1.4. An oblique view of the east side of Osoyoos, B.C., with part of the study's disturbed landscape outlined in the foreground. Photo by E. Lomas.

Figure 1.5. Examples of disturbed areas within the study site, including a campground (A), trampled shrub-steppe and power-substation construction (with highway in background) (B), and golf course fairway (C). Photos by E. Lomas.

Figure 1.6. Examples of undisturbed landscapes within the study area. Photos by E. Lomas.

techniques such as snake-exclusion fencing and short-distance translocation (e.g. Brown 2006).

The research partnership also provides an outlet for public outreach and educational programs through the Nk'Mip Desert Cultural Centre. Outreach programs continue to create awareness and understanding of snake conservation and the Centre remains a regional resource on this topic.

Where applicable, the analyses and results presented in this thesis include data from my field years (2010 and 2011) as well as mark-recapture data from 2002 to 2009, and radio-telemetry data from 2004 to 2009, and 2012.

Chronology of disturbance

The intensity of anthropogenic disturbances in the study area has shifted over the ten years of this study. However, even though use of the landscape has diversified in the most recent years, many aspects of the main sources of disturbance have been present on the site for the study's duration (Bower, pers. comm.; Holm, pers. comm.). When mark-recapture of the snakes began in 2002, a campground was well established, a winery had been constructed and services (water, electric lines, gravel roads, etc.) had been installed, resulting in substantial landscape development. In July 2002 walking trails were laid with gravel and a smaller version of the Nk'Mip Desert Cultural Centre and parking lot were located approximately 40 m from the current structure that opened in 2006. The radio-telemetry portion of the study began in 2004, after the construction of the Spirit Ridge Resort show centre in 2003. The construction of the associated Spirit Ridge hotel and condominium buildings was ongoing until 2008, with the first phase of buildings completed in 2005. The Sonora Dunes golf course construction was completed in 2004.

In general, rattlesnakes in the study area likely encounter a greater degree of disturbance now than they did in the earlier years of the study. This is an important aspect to account for in the analysis and interpretation of the data presented in this thesis. However, as outlined above, the core developed areas and disturbance sources were actually initiated in the early years of the study, if not before its initiation. In addition, the active construction of these buildings and roads added other aspects of disturbance not present in later years. These include noise and vibration, additional machinery and people, and large areas of broken ground. Finally, the quantification of disturbance categories and disturbance ratings outlined in Chapters 2 and 3 takes yearly variations into account, since the ratings rely on specific distances to disturbance sources that were actually present each year.

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CHAPTER 2: BODY CHARACTERISTICS AND BEHAVIOUR OF THE NORTHERN PACIFIC RATTLESNAKE IN NATURAL AND DISTURBED LANDSCAPES

INTRODUCTION

Habitat loss and alteration are among the greatest threats to wildlife (Wilcove et al. 1998, Gibbons et al. 2000, Hanski 2005). The effects of habitat loss and alteration on animal populations can take the form of direct and indirect impacts. The former are more easily detected, and may include the complete removal of habitat and the immediate extirpation of a species from a location it previously inhabited. Examples of such direct impacts are urban sprawl, draining of wetlands, and agriculture (Theobald et al. 1997, Tilman et al. 2001, Fahrig 2007, Coristine and Kerr 2011). However, the indirect effects of habitat alteration may be equally serious but less easily detected. In some cases, animals may still remain present in disturbed areas, but in smaller or declining numbers (Theobald et al. 1997). Recruitment and eventually the persistence of the population may be compromised (Burkey 1995). Loss of important habitat features, restrictions or increases in movement, and disturbance simply through human presence may produce impacts that only detailed research can reveal.

Indirect effects of habitat alteration on wildlife are especially important to understand in areas peripheral to urban development. Often, animals remain present in these sites through long-term site fidelity or mitigation attempts (e.g. wildlife corridors, habitat patches). While some remaining species may take advantage of modified habitat and thrive in developed areas (e.g. the house mouse, *Mus musculus*, and raccoon, *Procyon lotor*), it is unclear for others whether any benefits exist and whether the potential benefits outweigh the costs (Theobald et al. 1997). Individuals that reside in or near urbanized landscapes are exposed to various forms of potential disturbance: human presence (Burger 2001, 2007), noise (Bowles 1995), barriers to movement (Mader 1984, Shine et al. 2004), increased predation (Pike et al. 2010), changes in prey density or composition (Jenkins and Peterson 2005), increased disease (Theobald et al. 1997), and increased metabolic rates or stress levels (Gabrielsen and Smith 1995). As urbanization and human-use of wilderness areas increases, it is important to quantify their effects in order to fully understand the magnitude of the impact, and to develop proper management and mitigation techniques.

Many studies concerning the indirect effects of disturbance on wildlife have focused on birds and mammals (Boyle and Samson 1985, Burger 2007), however the effects on reptiles also warrant attention. Currently, reptiles are experiencing worldwide population declines due in large part to habitat loss and degradation (Gibbons et al. 2000, Reading et al. 2010). These unique animals are likely especially vulnerable to human-specific habitat disturbances as they are limited in their movement capabilities and experience possible added constraints of ectothermy (Huey 1983, Reinert 1993, Parent and Weatherhead 2000). As with other taxa, the effects of development that result in immediate extirpation of populations are much more readily detected than indirect effects that may take longer to manifest themselves on those individuals that manage (at least in the short term) to persist.

As for most venomous snakes, the persistence of rattlesnakes in the face of human disturbance is a challenging goal. Human disturbance has the potential to cause behavioural changes in rattlesnakes (Parent and Weatherhead 2000), and these changes may affect accessibility to mates, foraging time, and basking regimes (especially important for gravid females - Macartney et al. 1988). Proximity to disturbance in the long-term may result in lower body condition, slower growth rates, reduced fecundity, and shorter and lower body condition offspring (Jenkins et al. 2009). Body size, condition, and growth rate changes may affect over-winter survival and selection (Ashton 2001), resulting in adverse changes in population demographics and traits over time. Any or all of these indirect effects from disturbance may destabilize rattlesnake populations.

Urban development and habitat alteration have placed the Northern Pacific Rattlesnake (*Crotalus oreganus oreganus*) on the list of threatened species in Canada (COSEWIC 2004). Although a precise estimate of the population size of these animals is not easily had, it has been estimated that there were once fewer than 5,000 individual rattlesnakes surviving within British Columbia, Canada, and that the population is likely still declining (Didiuk et al. 2004). The limited range of the Northern Pacific Rattlesnake in this province makes the situation more grave: the animals are restricted to only four dry valleys in the south-central area of the province (Didiuk et al. 2004, Matsuda et al. 2006). The valleys are also popular travel destinations and the cities and towns associated with them are experiencing rapid growth through urbanization, tourism, and agriculture (Didiuk et al. 2004). In addition to persecution by the public, these animals face increasing difficulties navigating routes from hibernacula to their summer ranges due to altered land use and roads (Bertram et al. 2001, Didiuk et al. 2004).

Although no studies to date have deliberately assessed the potential indirect effects of human disturbance on *C. o. oreganus* in British Columbia, many have revealed characteristics of these northern populations that likely make them more susceptible to alterations in their environment. These characteristics include delayed sexual maturity (Macartney 1985), primarily triennial or longer parturition (Macartney 1985), slower growth (Macartney 1985), smaller size (Ashton 2001), lengthy migrations (Gomez 2007; Gosling, pers. comm.), and a shorter foraging season compared to southern *C. oreganus* populations. Although the persistence of rattlesnakes along the periphery of development is seen as a desirable management goal, our lack of knowledge of how the indirect effects of such development may be impacting the animals needs addressing.

Using radio-telemetry and a ten year mark-recapture data set, I examined the body characteristics and behaviour of a population of Northern Pacific Rattlesnakes in both disturbed and undisturbed (i.e. areas where snakes never or rarely encounter humans) sites in Osoyoos, British Columbia. The specific objectives for this study were to: (1) test for differences in mass, length and body condition between rattlesnakes residing in disturbed and undisturbed sites, (2) examine differences in growth rates, weight changes over the active season, and weight losses over hibernation between the two samples of snakes, and (3) compare exposure risk and the behaviour of snakes in disturbed and undisturbed landscapes. I predicted that snakes found in highly disturbed sites would be shorter (and presumably younger) on average than snakes in unaltered habitat due to the possibility of more frequent road kill and persecution of larger snakes. I also predicted that these animals would have lower body condition due to less time spent foraging and more time spent moving or hiding from disturbances. Such behavioural changes could interfere with biological processes such as thermoregulation and consume valuable energy stores, causing negative effects on snake growth (Beaupre 1995). Consequently, snakes residing in highly disturbed sites would be expected to grow more slowly, gain less weight over the active season, and lose more weight overwinter than other snakes. I also predicted that snakes in disturbed sites would be less exposed from cover objects, on average, and spend less time basking due to increased use of cover near perceived predation risks (e.g. humans; Greene 1988).

METHODS

Study area

The study took place on the Osoyoos Indian Reserve (OIR) in the extreme southern Okanagan valley of British Columbia, Canada (119.4° W, 49.28° N). The approximately 900 ha study area was bordered by the town of Osoyoos to the south and south-west, Osoyoos Lake to the west, Anarchist Mountain (elev. 1491 m) to the east, and the remaining OIR to the north (See Figure 1.2). See Chapter 1 for a more detailed description.

Mark-recapture

From 2002 to 2011, rattlesnakes were captured primarily in one of the following three ways: (1) at the dens as snakes emerged in the spring, (2) by active searches or incidental captures throughout the active season and study area, or (3) by residents or staff of local businesses who turned the snakes over to researchers. Snakes were either marked and measured on site, or transported to a nearby facility on the OIR. Sex was determined by probing for hemipenal pouches, and reproductive condition was assessed by palpating the ventral surface of female snakes for detectable follicles or embryos**.** Weight measurements were taken to the nearest gram on an electronic balance or Pesola scale. Both vent-tail length (VTL) and snout-vent length (SVL) were measured electronically from a digital image using the computer program Sigma Scan Pro 5 (Systat Software Inc. 2011) or ImageJ version 1.45s (Rasband 2011). To reduce measurement error, the same researcher measured all snakes whenever possible within a given year, and an average of three measurements within 0.1 cm was used as the final length value. Snakes were also often measured by hand using a flexible measuring tape while the animal was held partly in a plastic tube by a second researcher. Similarly, hand measurements were taken by the same researcher whenever possible and the mean of at least two separate measurements within 0.5 cm was recorded. Electronic length measurements were used in all the analyses, but manual measurements were substituted for a subset of snakes whenever digital images were unavailable. A Wilcoxon Signed-Rank test of a subsample of snakes (n = 35) measured through both methods revealed no significant differences in lengths (P = 0.08), and either type of measurement was not predominantly applied to any one category of snake. All snakes (except neonates and small juveniles) were implanted with a sterile passive integrated transponder (PIT) tag (Biomark Inc. Model TX1411SSL). Tags were inserted subcutaneously in the posterior 1/3 of the body using an implanter gun (Biomark Inc. MK25) or single-use plastic syringe-style implanter (Biomark Inc. MK7). Each snake's three most proximal rattle segments were painted a unique three colour combination for identification in the field and in case the PIT tag failed to respond. Snakes were released at their point of capture 4 - 24 hours after initial capture, unless processed on site. Those found on roads or in campsites were relocated to a maximum of 50 m away to avoid added stress or conflict with campground users. A previous study on this rattlesnake population found that although relocations up to 500 m away did not usually prevent snakes from returning to the initial capture locations, there was no evidence of body condition, behavior, or mortality rate changes in relocated animals (Brown et al. 2009).

Radio-telemetry

From 2004 to 2011, rattlesnakes were captured both by direct search effort at the hibernacula in March and April, and through incidental encounters during the active season. Snakes suitable for telemetry were transported to nearby veterinary clinics and surgically implanted with radio transmitters in their colemic cavities (Holohil Systems Inc., SB-2T 5.0g or SI-2T 9.0g) following procedures described by Reinert and Cundall (1982) with modifications by Reinert (1992). Pharmaceutical procedures followed Brown et al. (2009). Transmitters weighed on average 2.1% of total snake body mass (range: 0.97 - 3.81%). Animals were held for approximately 48 hours following surgery for observation and rehydration before being released at their capture site. Adult males were preferentially used, as female snakes restrict their movements or otherwise alter their behaviours when gravid (Macartney and Gregory 1988). Transmitters were removed at the end of their battery life (approximately 12 months for SB-2T, and 24 months for SI-2T), or in the spring following the hibernation period.

Each telemetered snake was located approximately every two to three days during the active season (mid April to mid October) with the exception of 2007, when snakes were located approximately once per week. A 3-element yagi antenna and a portable radio-telemetry receiver (AVM Instrument Co., model LA12-Q and Communications Specialists Inc., model R-1000) were used to track the snakes. Data collected at each telemetry location included Universal Transverse Mercator (UTM) coordinates using a handheld geographical positioning (GPS) unit (Garmin Ltd., GPS Map 76s), macro and micro habitat, air and ground temperature, distance from last position, distance to nearest urban structure, evidence of shedding events, percent of body exposed from cover objects, body positioning, and behaviour.

In order to monitor health and weight changes, snakes were recaptured every one to two months to measure weight and length. Otherwise, care was taken to locate the animals from at least 2 m away without triggering any movement or other response by the animal. If animals were visually disturbed, this was noted so that the datum could be excluded from behavioural analyses.

Quantifying exposure to disturbance

At each capture and telemetry location, the animals were classified as 'disturbed-site' or 'undisturbed-site' snakes based on the area where they were captured. Disturbed-site snakes were those found within 100 m of a potential source of human disturbance (e.g. campsite, walking trail, road), whereas undisturbed-site snakes were snakes found at distances greater than 100 m from disturbance. I also included a third category of snakes termed ‘mountain’. Although rattlesnakes that travelled up the eastern mountains of the study site could be classified as undisturbed-site snakes according the above criteria, they were instead grouped separately for the following reasons: they foraged in a unique biogeoclimatic zone and vegetation (see Chapter 1), they tended to be larger than all other snakes, the sample size was small (N = 6), and it was not possible to catch them for weight measurements regularly or during the required time windows due to their remote locations.

Different sections of the study area were further classified under a disturbance rating (DR), similar to that used in Parent and Weatherhead (2000). The study area was divided into 17 sections (e.g. resort, campground, riparian zone) based on known major foraging and movement locations of snakes. Boundaries of these sections were defined by naturally-occurring or anthropogenic structures (e.g. gullies, creeks, fences), although not all such boundaries were necessarily barriers to snake movement. Each snake was assigned a DR from 0 to 4 based on the region that the majority (at least 50 %) of its home range fell within and this region's proximity to the nearest source of human activity or development. For snakes captured in the mark-recapture program, I assigned snakes to a DR only if they had been captured at least twice within the DR. A DR of 0 represented an area where access to the general public was restricted and there was no land development (e.g. in the northern regions of the study area (see Figures 1.2 and 1.6). The DR gradient continued up to 4, which represented the most drastically transformed landscapes and heavily-frequented regions (e.g. campground, residential, see Figures 1.4 and 1.5). Specifically, the DRs were defined based on distances (d) to the nearest source of disturbance as follows: $d > 200$ m = DR0; $100 \text{ m} < d > 200$ m = DR1; $50 \text{ m} < d > 100$ m = DR2; $10 < d > 50$ m = DR3; $d < 10$ m = DR4.

Mass, length, and body condition

I compared mass and length (SVL) between DRs using two-factor Analysis of Variance (ANOVA) with DR and year as treatments for each variable, along with an interaction term. I compared the relationship between rattlesnake mass and SVL among DRs and years using Analysis of Covariance (ANCOVA). Following Parent and Weatherhead (2000), Shine et al. (2001) and Brown et al. (2009), I used the residuals from the regression between mass and SVL as an index of body condition. I tested for differences and interactions in the body condition scores between DRs and years using ANOVA.

Weight changes

Active season

I calculated the percent weight change for telemetered disturbed-site, undisturbed-site, and mountain snakes from egress (April/May) to ingress (September/October) of the same year. To supplement the analysis and investigate the potential effects of carrying a transmitter, I also included snakes from the long-term mark-recapture data set that had been captured and weighed in both the spring and fall, and were assumed to be from only disturbed areas. I used an ANOVA with area (disturbed/undisturbed/mountain/mark-recapture) and year as treatments with an interaction term to determine if snakes from different sites gained or lost significantly different percentages of weight over the season.

Over-winter

I used weight measurements at fall ingress and at the following year's spring egress to compare differences in percent weight loss over the winter hibernation period between disturbed-site, undisturbed-site, and mountain telemetered snakes. Mark-recapture snakes from disturbed areas caught at both sampling periods also were included as a comparison. Mass percent changes were compared among snakes using a two-factor ANOVA with area and year as treatments along with an interaction term.

Growth

I estimated growth rates by dividing the change in SVL between captures in consecutive years by the number of days between the captures during which snakes could potentially be active (April 1st to October 31st). I did not include days spent in hibernation since the minimal growth occurring over-winter may not be reliably detected (Macartney et al. 1990). I used ANOVA to test for differences in growth rates between undisturbed-site, disturbed-site, and mountain snakes. Comparisons have shown that although different snake-measuring techniques may produce correlated estimates, the estimates themselves may differ significantly (Bertram and Larsen 2004). Since analysis of growth requires not only accurate, but precise measurements, I used snakes caught only during the 2010 and 2011 field seasons for this analysis. I was able to minimize human error in SVL measurements and keep them precise during those years by using measurements I had performed personally and with one method.

I calculated shedding rates by counting the number of molts per year (identified by new, unpainted rattle segments since the snake's rattle was last painted). Snakes with broken distal rattle segments were excluded from the analysis. I compared shedding rates among areas and between years using a generalized linear model with Poisson errors for zero-truncated count data (Zuur et al. 2009).

Exposure and behaviour

Whenever telemetered snakes were located, their exposure was scored on a scale of 0 to 5 based on the percent of body exposed from cover objects (0 = 0% exposed; 1 = 1 - 24%; 2 = 25 - 49%; 3 = 50 - 74%; 4 = 75 - 99%; 5 = 100%). Concurrently, behaviour was classified as concealed (< 25% of body exposed), basking (≥ 25 % of body exposed), moving, or mating.

In order to account for the potential effects of temperature on snake exposure and behaviour, I followed the methods of Parent and Weatherhead (2000) to classify each snake telemetry point as cool (< 22.9 °C), warm (≥ 22.9 °C and ≤ 31.4 °C), or hot (> 31.4 °C) using the 25% and 75% quartile divisions of all substrate temperatures measured at the tracked locations (range 6.2 °C - 47.0 °C).

I used snakes as the sample unit (instead of radio-locations) to avoid problems of non-independence (Aebischer et al. 1993). To do this, I calculated the mean exposure of individual snakes from a minimum of three observations within each substrate temperature and area combination (e.g. hot, disturbed; Parent and Weatherhead 2000). Mean exposure was then used as the response variable in a two-factor ANOVA with substrate temperature class (cool, warm, or hot) and area (undisturbed-site, disturbed-site, den) as treatments. Similarly, the mean percent of telemetry points documented for each behaviour (at least three) was calculated per individual snake within each temperature and area combination. The behaviour classification percentages, however, are proportions. Since a snake may be doing one of only four activities, they are not independent (Aebischer et al.1993). To account for this, I log-ratio transformed each percentage using the geometric mean as the denominator, as described in Aitchison (1986) and Kucera and Malmgren (1998). I tested for differences in behaviour on the transformed data using two-factor ANOVAs for each behaviour category, with substrate temperature class (cool, warm, or hot) and area (undisturbed-site, disturbed-site, den) as treatments, and the mean percent of telemetry points as the response variable.

Statistical considerations

Neonates and juveniles under 35 cm (SVL) were removed from the data set in order to account for differences in movement capabilities, human error in length measurements, and the inability to permanently mark the animals (via PIT tag or rattle coding) due to their small size. Further, only males and non-gravid females were included in the analyses, since gravid females weigh more for their length than non-gravid females which may restrict their movements and behaviour (Macartney and Gregory 1988, Parent and Weatherhead 2000). Snakes with discernible food items in their stomachs were removed from the mass and body condition analyses.

To control for the potentially confounding effects of weather and seasonal migratory patterns, only data collected during the foraging seasons were used in the analyses, with the exception of exposure and behaviour. I defined the foraging season as the period occurring between egress (movement from overwinter hibernacula toward summer range) and ingress (movement from summer range toward hibernacula). Egress was deemed complete on May 15th based on the movements of snakes I personally tracked during 2010 and 2011. By this date, each telemetered snake had reached the low elevation shrub-steppe from their hibernaculum and any straight-line, long-distance movements of 50 m or more had ended for at least four days. Ingress dates varied much more among snakes and years, but generally occurred in mid-September of each year when snakes were within at least 30 m of their respective hibernaculum (Parent and Weatherhead 2000).

To avoid pseudoreplication in the mark-recapture analyses, I used only one capture record (at random) for a snake caught in the same DR more than once within the same year (Coates et al. 2009). All analyses were performed using the statistical program R version 2.12.1 (R Development Core Team 2011). Data were tested for normality by visual examination of histograms and bar-and-whisker plots, and the Kolmogorov-Smirnov goodness of fit test (Zar 1999). Homogeneity of variances between groups was tested using the Fligner-Killeen test (Conover et al. 1981, Crawley 2007). Non-normal and non-homogenous data were transformed for parametric tests. A p-value of ≤ 0.05 was used to guide statistical interpretation of the results. Tukey's Honestly Significant Difference (HSD) test was used for post-hoc multiple comparisons (Crawley 2007). Means are reported as ± 1 SE unless otherwise stated.

RESULTS

Mark-recapture

From 2002 to 2011, 1850 rattlesnake captures or identified sightings were documented by researchers in the study area. Of those, 841 were previously untagged animals. After removing multiple captures of individual snakes within years, a total of 623 adult males and non-gravid females with complete mass and length data were captured during the foraging season and used in the mass, length, and body condition analyses. One hundred and seventy one rattlesnakes were caught in undisturbed sites, and 452 in disturbed areas. More specifically, 66 animals were found in DR0, 105 in DR1, 116 in DR2, 140 in DR3, and 196 in DR4.

Radio-telemetry

From 2004 to 2011, 104 rattlesnakes were tracked using radio-telemetry. Of these, 25 were tracked over two years, resulting in a total of 129 full or partial active seasons represented. Due to mortality, transmitter failures and other complications, not all snakes were tracked over a full season. Radio-tracked snakes were mostly adult males (n = 101 males, n = 4 non-gravid females). On average, males measured 72.90 cm in length (SVL) and weighed 272.56 g (range: 62.0 cm - 98.5 cm; 166 g - 761 g). Females were 61.75 cm and 174.75g on average (range: 59.0 cm - 65.5 cm; 145 g - 209 g). Telemetered snakes were relocated on average 54 times (range: 1 - 209 times) over the course of each foraging season.

From the data set, 87 rattlesnakes were incorporated into the exposure and behaviour analyses due to complications that required removal of other transmitters or otherwise produced too few behavioural observations within each treatment category. A total of 4030 telemetry locations were used in the exposure analyses: 2521 locations in undisturbed sites, 1091 locations in disturbed sites, and 417 locations at den sites. A total of 4039 locations were used in the behaviour analyses: 2529 locations in undisturbed sites, 1092 locations in disturbed sites, and 417 locations at den sites.

Mass, length, and body condition

Mass and SVL values were $\log_{10}$-transformed prior to analysis to meet assumptions of normality. Rattlesnakes captured in DR0 were heavier but not necessarily longer than snakes in all other DRs (Figure 2.1). The ANOVA showed a significant effect of DR for both mass and SVL when all years were combined (mass: $F_{4,617} = 7.80$, $P < 0.0001$; SVL: $F_{4,617} = 9.42$, $P < 0.0001$). Specifically, snakes in DR0 were heavier and longer on average than snakes in all other DRs (mass: $P < 0.0001$; SVL: $P < 0.02$ in all cases), except in DR4 where snake length did not differ ($P = 0.12$).

The ANOVA for mass assessing differences between DRs and incorporating year was similar to the pooled model, and showed a significant effect of DR, year, and the interaction term (DR: $F_{4,581} = 8.77$, $P < 0.0001$; year: $F_{9,581} = 7.67$, $P < 0.0001$; DR x year: $F_{27,581} = 1.62$, $P = 0.02$). Pairwise comparisons showed that most significant differences in snake masses between DRs occurred between 2010 or 2011 and other years. Overall, masses in 2010 and 2011 were both significantly lower than in 2005 ($P < 0.03$), 2007 ($P < 0.01$), and 2008 ($P < 0.001$). Masses in 2011 were also lower than in 2006 ($P = 0.01$), and masses were lower in 2004 than in 2005 ($P = 0.03$). The ANOVA for SVL between DR and year also showed an effect of DR, year, and the interaction term (DR: $F_{4,581} = 10.03$, $P < 0.0001$; year: $F_{9,581} = 3.15$, $P = 0.001$; DR × year: $F_{27,581} = 1.76$, $P = 0.01$). The significant interactions between DR and year reflect the fact that not all DRs are represented evenly throughout the years of the study. Snakes in DR0 were not included in years 2002, 2003, 2004 and 2010, either due to low sample size or not meeting the criteria to be included in this analysis (see Methods).

I found a strong relationship between rattlesnake mass and SVL ($\log_{10}\text{mass[g]} = 2.62 \cdot \log_{10}\text{SVL [cm]} - 2.47$, $r^2 = 0.78$, $F_{1,621} = 2210$, $P < 0.0001$; Figure 2.2). These relationships within each DR are shown in Figure 2.3: the relationship between mass and SVL was significantly different between DR0 and two of the other categories, DR2 ($P = 0.01$) and DR4 ($P < 0.0001$).

Disturbance ratings did have an effect on rattlesnake body condition (residuals) ($F_{4,617} = 19.68$, $P < 0.0001$; Figure 2.4). Those snakes in the most disturbed areas had lower (and negative) body condition compared to snakes in lesser-disturbed sites. Tukey's HSD post-hoc tests showed specifically that snakes in DR4 had significantly lower body condition than snakes in all other DRs (DR0: $P < 0.0001$; DR1: $P < 0.0001$; DR2: $P = 0.002$; DR3:

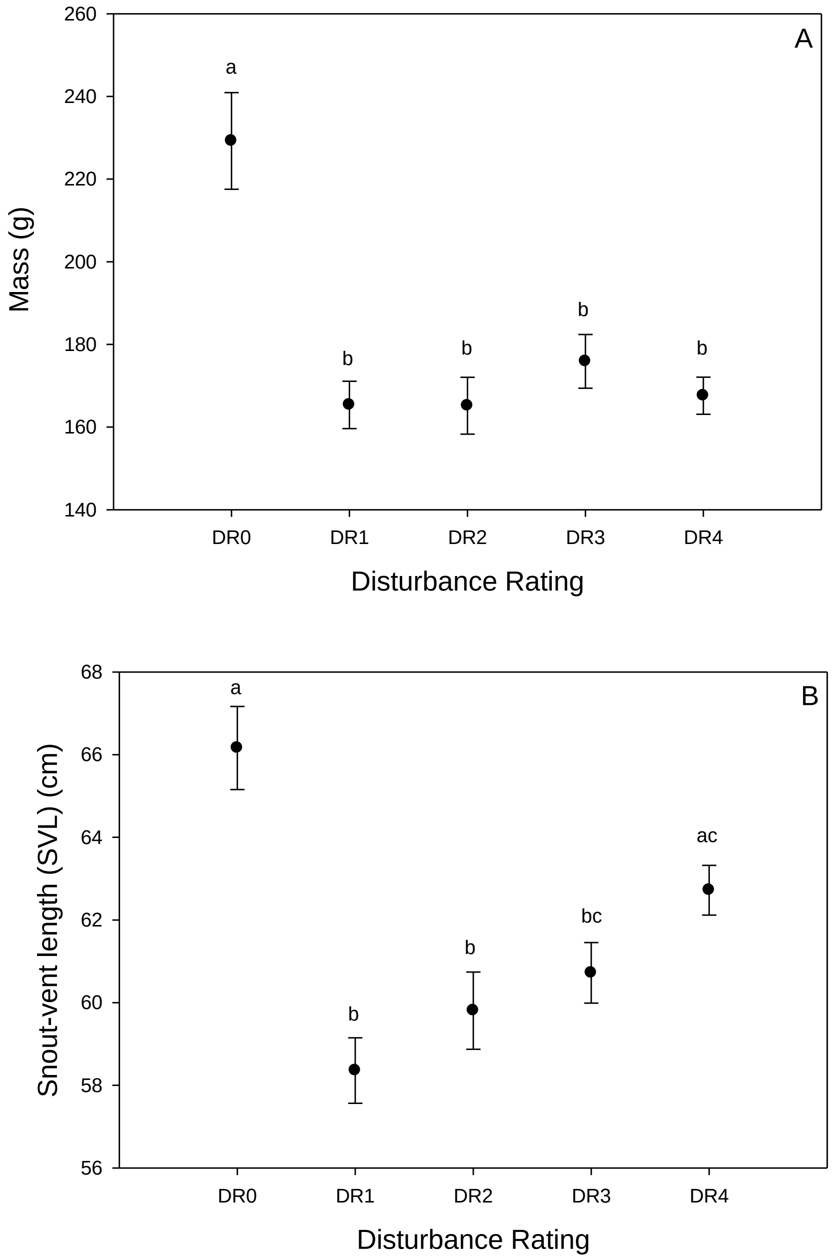

Figure 2.1. Comparison of the mean mass (A) and snout-vent length (B) ± 1 SE of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada, between 2002 and 2011. N = 66 (DR0), 105 (DR1), 116 (DR2), 140 (DR3), 196 (DR4). Means with different letters indicate a significant difference between DRs at $\alpha = 0.05$.

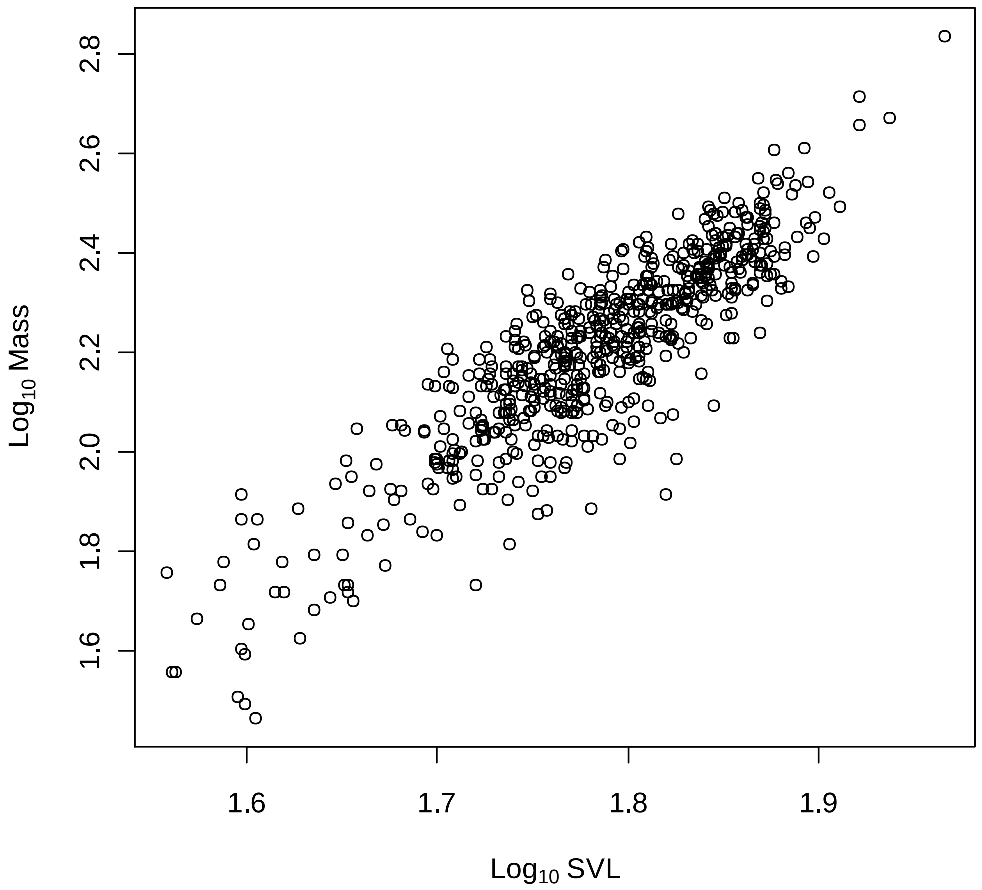

Figure 2.2. The relationship between $\log_{10}$ snout-vent length (cm) and $\log_{10}$ mass (g) for male and non-gravid female Northern Pacific Rattlesnakes captured on the study site in Osoyoos, British Columbia, Canada, between 2002 and 2011.

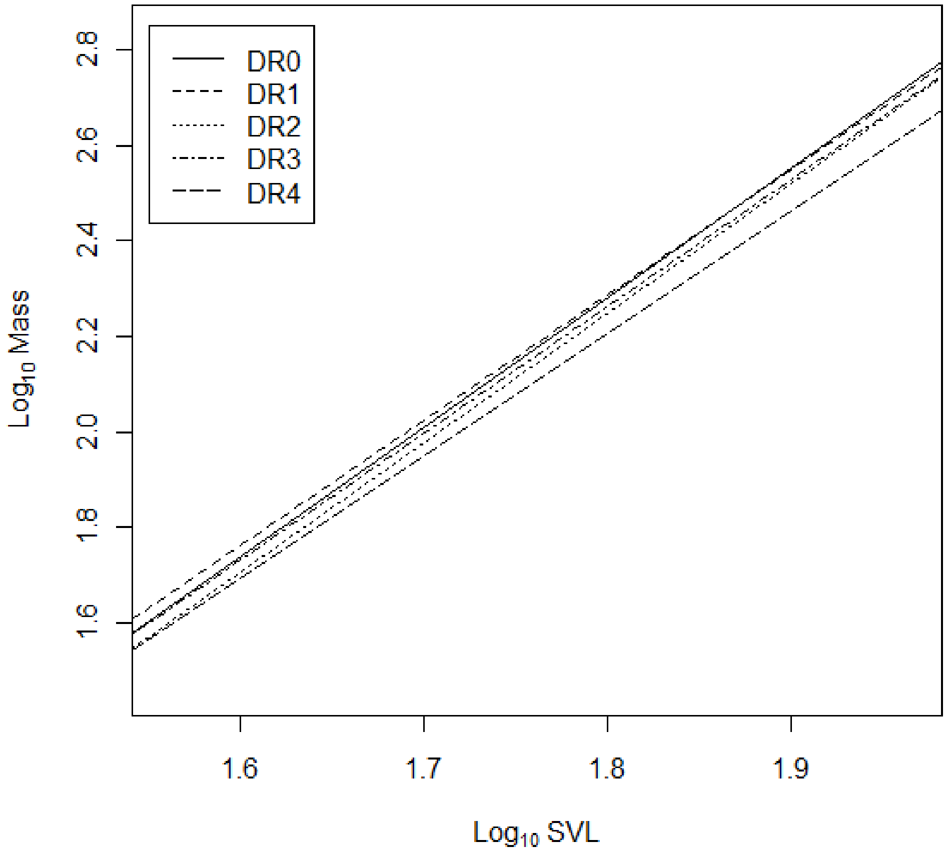

Figure 2.3. Log-log linear regression of mass (g) on snout-vent length (SVL) (cm) for male and non-gravid female Northern Pacific Rattlesnakes captured in different disturbance ratings (DRs) on the study site in Osoyoos, British Columbia, Canada, between 2002 and 2011.

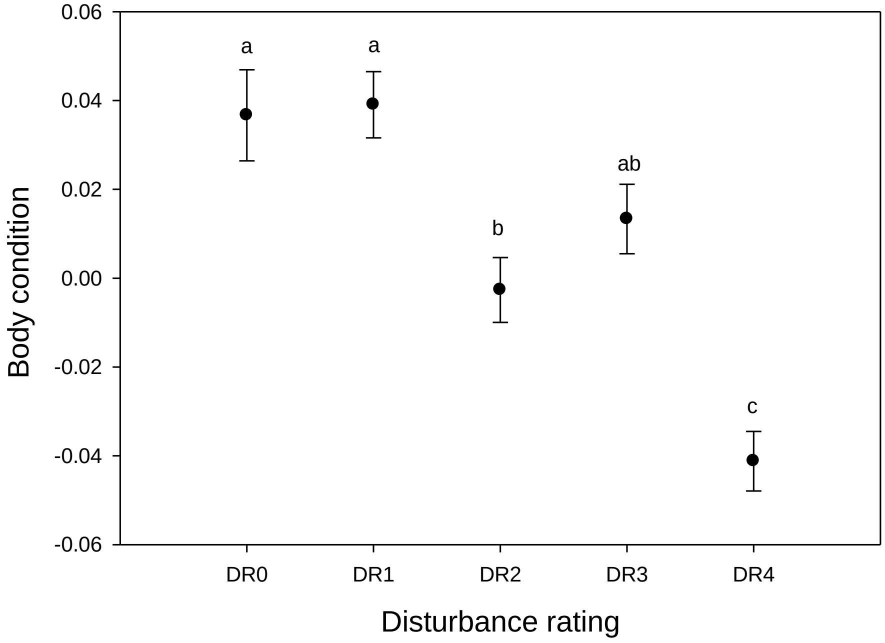

Figure 2.4. Comparison of mean body condition scores (residuals from the regression of mass on snout-vent length) ± 1 SE of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada, between 2002 and 2011. N = 66 (DR0), 105 (DR1), 116 (DR2), 140 (DR3), 196 (DR4). Means with different letters indicate a significant difference between DRs at $\alpha = 0.05$.

$P < 0.0001$; Figure 2.4). Snakes in DR2 also had significantly lower body condition than snakes in DR0 ($P = 0.04$) and DR1 ($P < 0.01$).

When year was included in the ANOVA, the same differences between DRs were observed, as well as differences between years, but there was no interaction effect (DR: $F_{4,581} = 22.65$, $P < 0.0001$; year: $F_{9,581} = 10.92$, $P < 0.0001$; DR × year: $F_{27,581} = 1.14$, $P = 0.29$). The only significant differences among years occurred between 2010, 2011 and other years. Snakes had lower body condition overall in 2011 than in all other years except 2002 and 2010 ($P < 0.03$ in all cases; Figure 2.5). Condition was also lower in 2010 than in 2005, 2007, and 2008 ($P < 0.01$ in all cases). As in the mass and SVL analyses, there were disproportionate captures of snakes in different DRs between years.

Percent change in mass values were $\log_{10}$-transformed prior to analysis to meet assumptions of normality. Seventy-four snakes were used in the analysis: disturbed-site telemetered ($n = 17$), undisturbed-site telemetered ($n = 43$), mountain telemetered ($n = 6$) and disturbed-site mark-recapture ($n = 8$).

Weight changes

Active season

There was a significant effect of snake location on percent weight change ($F_{3,70} = 6.15$, $P < 0.001$; Figure 2.6; Table 1), but not of year ($F_{5,70} = 2.10$, $P = 0.08$). On average, disturbed-site snakes lost weight over the active season, whereas other groups gained weight. Tukey's HSD post-hoc tests revealed that the percent change in mass of disturbed-site snakes was significantly different from undisturbed-site snakes ($P = 0.02$) and mountain snakes ($P = 0.001$), but not disturbed-site mark-recapture snakes ($P = 0.28$). No other significant differences were observed between groups.

Over-winter

Percent weight change over the hibernation period between snakes in different areas and years was not significant ($F_{12,24} = 1.03$, $P = 0.45$). The trends showed that snakes from disturbed sites lost on average a similar percentage of weight as snakes from other areas (Figure 2.7; Table 1).

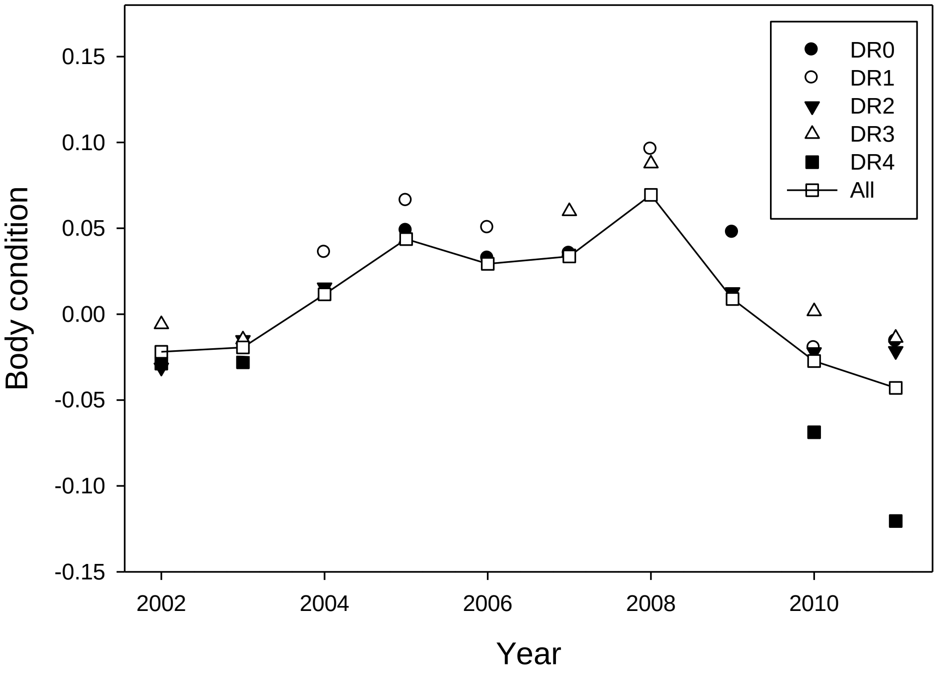

Figure 2.5. The trend in mean body condition scores (residuals from the regression of mass on snout-vent length) over the years of the study (2002- 2011) of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada.

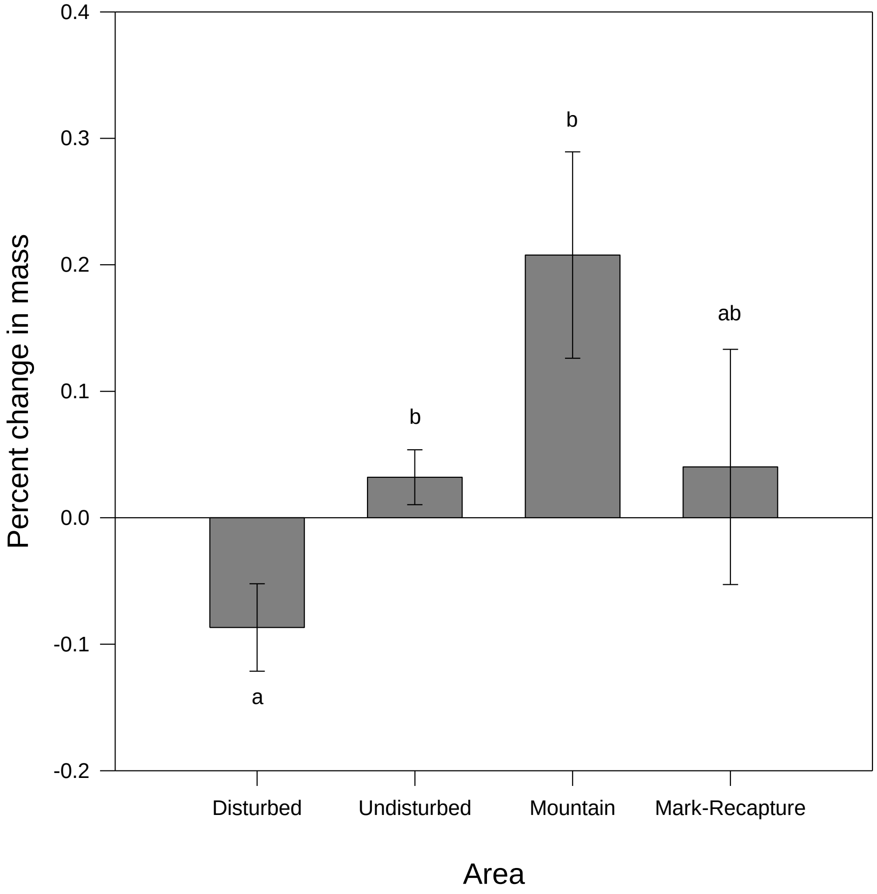

Figure 2.6. Comparison of percent change in mass (± 1 SE) over the active season (May to October) of male and non-gravid female Northern Pacific Rattlesnakes within different treatment areas on the study site in Osoyoos, British Columbia, Canada, between 2004 and 2011. Different letters indicate a significant difference in percent change in mass between treatments at $\alpha = 0.05$.

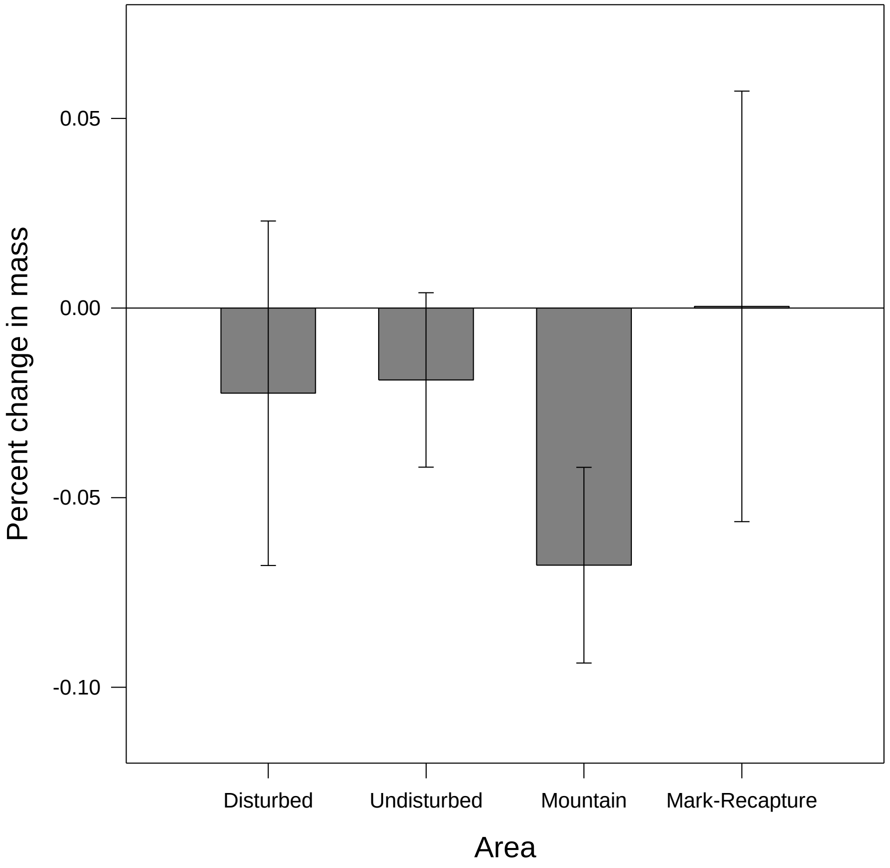

Figure 2.7. Comparison of percent change in mass (± 1 SE) over hibernation (October to April) of male and non-gravid female Northern Pacific Rattlesnakes on the study site in Osoyoos, British Columbia, Canada, between 2004-2011. Snakes were grouped into treatment areas based on where they resided during the previous active season.

Growth

There was an effect of location on rattlesnake growth ($F_{2,17} = 9.16$, $P < 0.01$), but not year ($F_{2,17} = 2.00$, $P = 0.17$), so years were combined. Post-hoc tests revealed that snakes that travelled up the mountain (n = 5) grew at faster rates than snakes in all other areas ($P < 0.01$ in all cases; Table 1). There was no difference in growth rates between snakes in disturbed (n = 11) and undisturbed (n = 6) sites ($P = 0.99$; Table 1).

There were no significant differences in shedding rates among snakes in different areas ($P = 0.36$; Table 1) or years ($P = 0.12$). However, snakes in disturbed (n = 18) sites were never observed to shed more than once in a year, whereas snakes in undisturbed (n = 47) sites shed one or two times per year.

Exposure and behaviour

There was a significant effect of substrate temperature class ($F_{2,340} = 23.84$, $P < 0.0001$) and area ($F_{2,340} = 32.51$, $P < 0.0001$) on exposure. Specifically, pair-wise comparisons showed that snakes were less visible overall in hot substrates ($P < 0.0001$ in all cases; Figure 2.8) and at den sites ($P < 0.0001$ in all cases; Figure 2.8). No differences were observed between disturbed-site and undisturbed-site snakes within any temperature class or over all temperatures ($P = 0.83$; Table 1). Thus, the mean exposure of rattlesnakes varied significantly with substrate temperature, but did not change significantly with disturbance category.

The results assessing the effects of disturbance on rattlesnake behaviour were similar to the exposure results. The models for each behaviour were significant (basking $F_{4,340} = 6.73$, $P < 0.0001$; concealed $F_{4,340} = 21.05$, $P < 0.0001$; moving $F_{4,340} = 11.00$, $P < 0.0001$; mating $F_{4,340} = 8.19$, $P < 0.0001$). Differences were seen between hot and other substrates for basking ($P < 0.01$), concealed ($P < 0.01$) and mating ($P < 0.01$); snakes spent less time basking or mating and more time concealed on hot substrates (Figure 2.9). More snakes were also observed moving on warm substrates ($P = 0.01$). There were significant differences in behaviour between snakes at den sites and other areas in all cases ($P < 0.0001$). Although snakes were never observed mating in disturbed landscapes when it was hot, there were no significant differences in any snake behaviours between disturbed and undisturbed sites

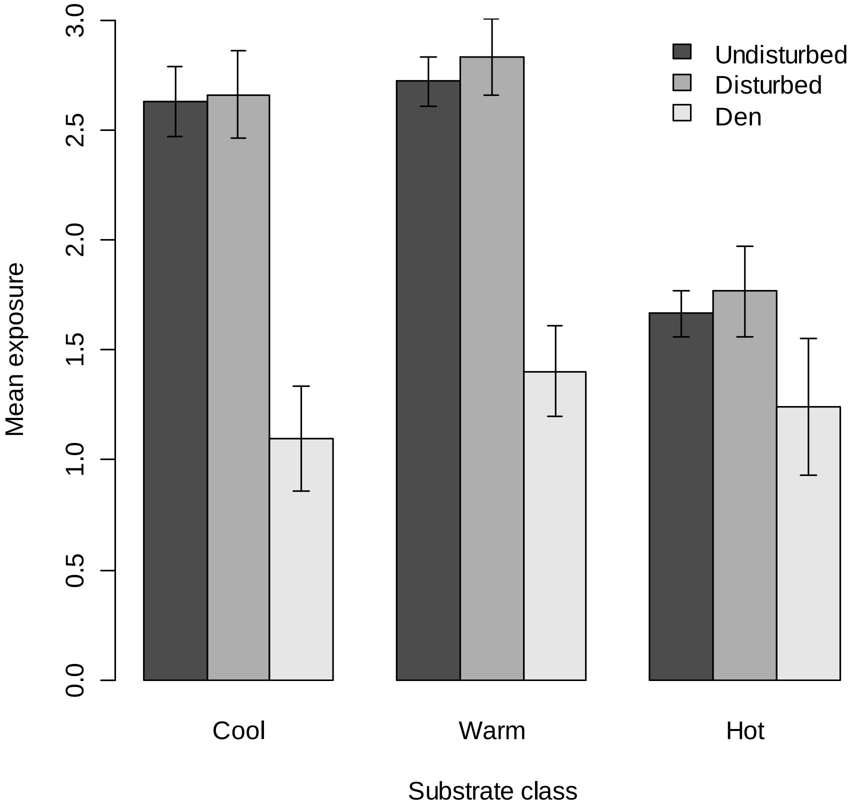

Figure 2.8. Mean percent of exposure (± 1 SE) of male and non gravid female Northern Pacific Rattlesnakes within treatment areas and substrate temperature classes on the study site in Osoyoos, British Columbia, Canada, between 2004 and 2011. Substrate temperatures were cool (< 22 ˚C), warm (≥ 22.9 ˚C and ≤ 31.4 ˚C), and hot (> 31.4 ˚C).

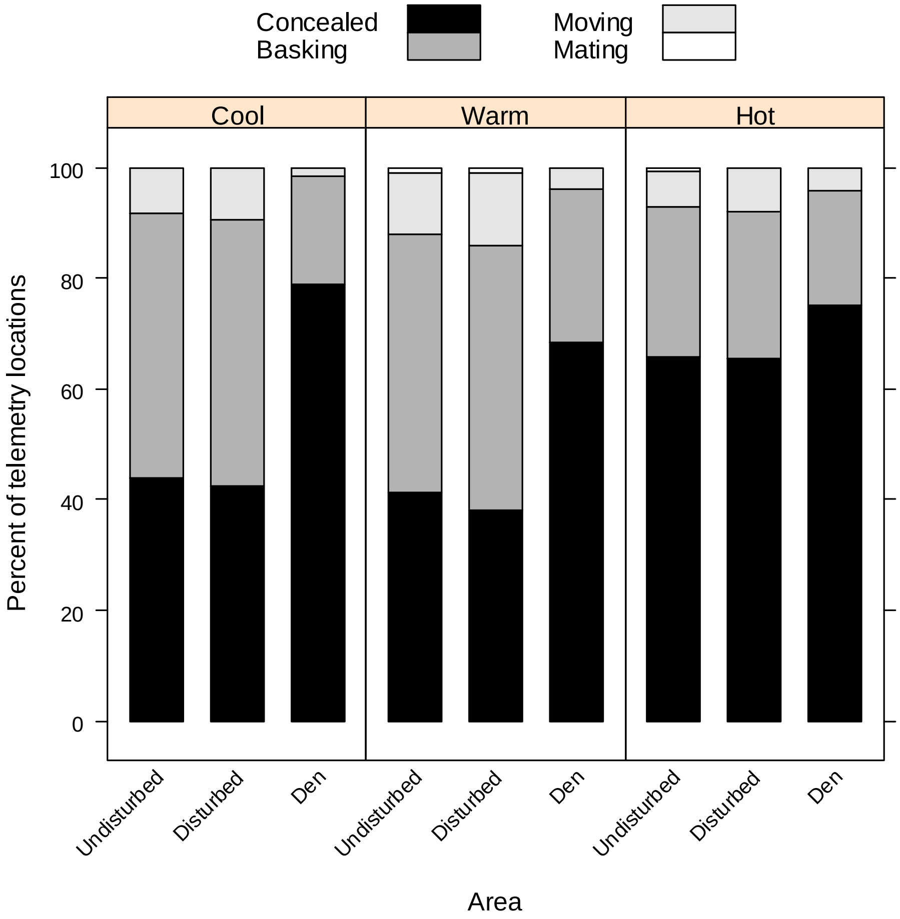

Figure 2.9. Comparison of the mean percent of telemetry locations where male and non-gravid female Northern Pacific Rattlesnakes in Osoyoos, British Columbia, Canada were found concealed, basking, moving, or mating between 2004 and 2011. Behavioural observations are grouped within temperature substrate classes and treatment areas.

within any of the substrate temperatures ($P > 0.19$). Thus, although observed behaviour did vary significantly with substrate temperature and at den sites, my disturbance categories did not appear to be linked to snake behaviour.

Summary

Table 2.1. Summary of relative mean characteristics for Northern Pacific Rattlesnakes in disturbed, undisturbed and mountain areas of the study site in Osoyoos, B.C.. Different superscript letters indicate significantly different values at $P < 0.05$. Standard errors for means are shown in parentheses.

Characteristic	Trend with increasing disturbance	Disturbed-site	Undisturbed-site	Mountain	Figure
Relative body condition	Decreasing	Low	High	High	2.4
Percent weight change					
Active season	Increasing weight loss	0.91 (0.03)^{a}	1.03 (0.02)^{b}	1.21 (0.08)^{b}	2.6
Over-winter	Similar	0.98 (0.05)	0.98 (0.02)	0.93 (0.03)	2.7
Growth (cm/yr)	Similar (although 'Mountain' snakes grew faster)	0.01 (0.002)^{a}	0.01 (0.002)^{a}	0.02 (0.005)^{b}	--
Shedding (sheds/yr)	Decreasing (not significant)	1.00 (0.00)	1.28 (0.07)	1.25 (0.16)	--
Exposure (%)	Similar	52.8 (0.03)	51.1 (0.03)	--	2.8
Behaviour	Similar	--	--	--	2.9

DISCUSSION

As predicted, disturbance had a negative effect on rattlesnake size, body condition and weight gain. However, my predictions of changes to growth rate, exposure risk and behaviour in disturbed locations were not supported. Taken together, the results suggest that indirect disturbance, as measured in this study, has a consistent negative effect on certain body characteristics of rattlesnakes, but not on snake behaviour. These observations suggest negative consequences for the rattlesnakes in this population inhabiting disturbed habitat.

Responses in body characteristics to disturbance

Rattlesnakes residing in the undisturbed areas were heavier, but not necessarily longer than snakes in disturbed areas, as I had predicted. This pattern matches the decreasing trend seen in body condition as disturbance increased; as predicted, it appears that for a given length, a snake in a highly disturbed location of my study area was more likely to have poorer body condition than a snake of similar length living in relatively undisturbed habitat. Disturbed-site snakes also lost more weight over the foraging season, as predicted, but not over winter. The over-winter weight losses I observed (2.5 - 10 %) are consistent with those reported for this species previously in B.C. (2.3 - 20.0 %; Macartney 1985). Weight loss over the foraging season, however, has not previously been recorded (with the exception of weight loss through desiccation at the den just prior to or post-hibernation (Macartney 1985)). Indeed, other studies on *C. o. oreganus* at other sites within B.C. have revealed only weight gains or consistent weights for males and non-gravid females over the foraging season (Macartney 1985; Gosling, pers. comm.). My prediction of lower growth and shedding rates in disturbed-site snakes was not supported in the data from the last two years of the study. However, an interesting and unexpected observation came from the subset of snakes that traveled higher into the mountains; although this sample size was small, these snakes tended to be larger, gained greater amounts of weight over the active season, and grew at faster rates than all other groups of snakes.

Similar to this study in both methods and results, Parent & Weatherhead (2000) found no difference in growth rates between disturbed and undisturbed Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) in a provincial park in Ontario, Canada.

However, unlike my study, they did not detect a decrease in body condition as disturbance increased. These contrasting results may be explained in two ways: First, the intensity of disturbance in a provincial park likely is relatively dampened compared to an area with urban development. Parent and Weatherhead (2000) reported that disturbance was “moderate” and development was limited to campgrounds and three hiking trails. Some of the anthropogenic alterations within my study area are quite conspicuous. In addition to a large campground and walking trails, development included parking lots, buildings, vineyards, and areas cleared of native vegetation. These may affect more drastic landscape changes in terms of prey availability, thermoregulation opportunities, and cover. Second, Parent and Weatherhead (2000) stated they could not be entirely certain that a snake classified as 'disturbed' would stay within the disturbed area and it was therefore possible that some individuals spent time between captures in less-disturbed locations. Admittedly, this is also a possibility in my study for snakes followed solely through mark-recapture. However, there are several reasons to suggest otherwise: (1) I assigned snakes to a disturbance rating (DR) category only if they had been captured at least twice within that DR, (2) rattlesnakes within my study area are known to demonstrate high fidelity to specific foraging locations (Brown 2006; Lomas, unpublished data), as have rattlesnakes in other regions (e.g. Sealy 2002, Travsky and Beauvais 2004, Jenkins and Peterson 2005, Gomez 2007), (3) the greater over-season weight loss observed in telemetry snakes in disturbed sites (where telemetry confirms site fidelity) compliments the lower body condition results observed in the mark-recapture data, and (4) by using finer scale DRs, I was able to show that although snakes in proximate DRs may not show large differences in body condition (perhaps a consequence of the movement of snakes between adjacent, similar DRs), there were notable differences between disturbance extremes (i.e. DR0 and DR4) .

The results of my research show similarities and differences with a study conducted on *C. oreganus* in Idaho by Jenkins et al. (2009). In that study, disturbance to the animals was related to the form of livestock grazing and wildfire occurring on the landscape. Akin to my results, individuals in Idaho from the most disturbed area had lower body condition. They were also shorter, grew slower, shed less, had lower fecundity, and had shorter and lower body condition offspring compared to other populations. Although I detected lower body condition and greater over-season weight loss, I did not observe any differences in growth;

however my analysis was limited to data from across only two years (to ensure consistency in measurements - see Methods). Thus, any differences attributable to disturbance types may have been overshadowed by seasonal variations in weather and prey abundance (Macartney et al. 1990, Madsen and Shine 2000). In addition, it is widely known that larger snakes grow more slowly (Macartney et al. 1990, Coates et al. 2009). By using mainly larger snakes (through necessity) for my telemetry study, my data from these animals may have been biased. Further, although disturbed-site snakes were never observed to shed more than once in a season, I found no significant differences in shedding rates. However, rattlesnakes at their northern range limits may only shed once or twice a season compared to their more southern relatives due to the relatively shorter growing season (Macartney 1985). Shedding frequency therefore may not be a suitable variable to assess the effects of disturbance at this latitude.

Behavioural responses to disturbance

Contrary to my expectations, rattlesnakes residing in disturbed and undisturbed areas did not appear to differ in behaviour or amount of exposure from cover objects. Snake exposure and behaviour did vary with substrate temperature and at den sites, which is not surprising for a hibernating ectotherm.

Parent and Weatherhead (2000) also found that male and non-gravid female Eastern Massasauga Rattlesnakes did not differ in their exposure in relation to distance to disturbance. Gravid females were also included in their study, however, and they were observed to be less visible as disturbance increased. This may be explained by the fact that gravid rattlesnakes limit their food intake and movement during gestation (Macartney and Gregory 1988, Graves and Duvall 1993), so increased use of cover by gravid snakes in disturbed areas may not result in foraging costs to them (Parent and Weatherhead 2000).

Male and non-gravid female rattlesnakes in my study did not alter their behaviour and use of cover objects in disturbed areas because they may (1) fail to perceive disturbed landscapes as high-risk areas, (2) have become desensitized to potential threats through recurring human presence, (3) respond behaviourally to disturbance similarly to snakes that rarely encounter people (e.g. Prior and Weatherhead 1994), or (4) perceive disturbed areas as high-risk, but any benefits from reducing exposure or changing behaviour in disturbed areas may not be worth the costs of reduced activity (Lima and Dill 1990). For males and non-gravid females, altering behaviour and use of cover objects in disturbed landscapes may interfere with the needs of thermoregulation, foraging, and mate-seeking (Ydenberg and Dill 1986, Parent and Weatherhead 2000, Rodríguez-prieto et al. 2010).

Direct and indirect effects of disturbance

Changes to population demographics through disturbance can be attributed to direct or indirect effects, or a combination thereof. The physical presence of buildings and people, coupled with habitat alteration, could directly affect animal movement behaviour (e.g. McLellan and Shackleton 1988) and survival of certain age classes due to road mortality (Andrews and Gibbons 2005). In turn, activities such as thermoregulation (Attum and Eason 2006) and foraging opportunities (Gander and Ingold 1997, Weatherhead and Blouin-demers 2004) could be indirectly affected. Reduction of a snake’s foraging activity budget may result in energy limitation, slower growth rates, and smaller size (Beaupre 1995).

I hypothesized that rattlesnakes in this study would have lower body condition due to less time spent foraging as well as increased energy expenditure from more time spent moving or hiding from disturbances. However, I did not observe the changes in behaviour to support this. The difference in body condition and weight gain that I observed may instead be attributable to other indirect effects of human disturbance and habitat alteration, such as a change in prey availability. A study of Western Diamond-backed Rattlesnakes (*Crotalus atrox*) fed supplementary in the field supports this hypothesis: the supplemented snakes did not change their movement patterns, but gained mass faster, had better body condition following reproduction, and grew faster than unfed snakes (Taylor et al. 2005). Jenkins and Peterson (2005) found that disturbed landscapes had fewer prey, lower prey biomass, and fewer large prey items. Consequently, they found that Great Basin Rattlesnakes (*Crotalus o. lutosus*) in undisturbed areas experienced greater biomass of small mammals in their home range and as a result gained more weight. Although small mammal densities are notoriously variable over time, other studies have also documented declines of small mammal populations in disturbed areas (Parmenter and MacMahon 1983), including sagebrush steppe habitat similar to my study area (e.g. McGee 1982). Nearby in the South-Central Okanagan, Sullivan and Sullivan (2006) found that undisturbed sagebrush habitats held the highest overall small mammal abundances, second only to abandoned hay fields. Human-altered habitats, such as orchards and hedgerows had the lowest abundance of small mammals (Sullivan and Sullivan 2006). In the South Okanagan, Melaschenko (2010) noted that deer mice (*Peromyscus maniculatus*) and western harvest mice (*Reithrodontomys megalotis*) selected shrubs and avoided bare ground, whereas Great Basin pocket mice (*Perognathus parvus*) avoided shrubs and selected for bare ground. All three species, however, rely on shrubs for food; pocket mice can subsist on a diet of only seeds (MacMillen 1964), whereas deer mice and harvest mice also forage on arthropods found near shrubs (Harris 1984). This indicates that although a combination of native shrubs and natural bare ground is likely important for prey species, the presence of antelope brush or sagebrush may be needed to support a diverse prey base for rattlesnakes.

The greater body condition, weight gain and growth seen in the telemetered mountain snakes may also be explained by prey availability and diversity. These snakes travelled through ponderosa pine forests, which in addition to containing higher numbers of prey species than in orchards (but less than in sagebrush) also is known to provide habitat for a larger potential prey species: the Northwestern Chipmunk (*Tamias amoenus*) (Sullivan and Sullivan 2006). Aside from sagebrush habitats, captures of chipmunks in any other habitat type in the valley have been negligible (Sullivan and Sullivan 2006). Northern Pacific Rattlesnakes at other locations in B.C. have also used upper-elevation Douglas-fir habitat when available; Gomez (2007) noted that use of this habitat by the snakes was significantly greater than the use of other available habitat types, suggesting that Douglas-fir forests are associated with important resources required by these rattlesnakes. As in this study, the identity of the resource(s) remains unknown.

Implications for conservation

This is the first study to examine disturbance effects on the Northern Pacific Rattlesnake in British Columbia. I found that snakes in disturbed landscapes did not alter their behaviour, but had greater weight loss and poorer body condition compared to undisturbed snakes. As energy limited systems (Jenkins and Peterson 2005), rattlesnakes experiencing low weight gain may suffer delayed maturity and reduced fecundity (Taylor et al. 2005). Body condition is strongly correlated with main body reserves and fat bodies

(Bonnet and Naulleau 1996). Poor body condition has the potential to lower reproductive threshold (Madsen and Shine 1999, Taylor et al. 2005), and reduce litter size and offspring body condition (Jenkins et al. 2009; but see Taylor et al. 2005). Perhaps most importantly, poor body condition has the potential to lower survival (Shine et al. 2001, Kissner and Weatherhead 2005). Recent work to investigate survivorship within the study area, however, has shown overall annual survival to be relatively high (between 70 % and 98 % between 2002 and 2012, except in one outlier year of 38 %, based on an estimated population of 1300 individuals**;** Bishop et al. 2012, unpubl. data). These survival estimates included snakes from all disturbance ratings. The only other comparable survivorship rates in B.C. were documented in the 1980s at a different site in the Okanagan, where Macartney (1985) found overwinter survivorship (1981-1982) to be 97% for males (n = 31) (100% excluding yearlings) and 86% for females (n = 42) (89% excluding yearlings). Survival was higher than in some years of my study, but Macartney's rates fall within the ranges calculated for my study area (although his sample sizes were smaller). The comparable survival rates imply that despite poor condition, the Osoyoos rattlesnake population appears to be relatively stable, at least in terms of survival. Although this is an encouraging finding, declines in body condition of snakes in all disturbance ratings in recent years (see Figure 2.5) is cause for concern. Rattlesnakes are long-lived animals (Klauber 1972), and changes in survivorship due to increased stressors in recent years may not be apparent for several years. Additionally, rattlesnake densities at the site were found to be low (approximately 2.6 snakes per hectare; Bishop et al. 2012, unpubl. data). Presently, information on recruitment and population trends over time is lacking, as well as survivorship among individual disturbance ratings. Caution should be exercised when interpreting rattlesnake survival rates in disturbed areas. Delayed sexual maturity, long inter-birth intervals, and low juvenile growth rates have been noted in these animals in B.C. (Macartney 1985, Didiuk et al. 2004). Poor body condition, weight gain, and low population densities, when coupled with the above, could eventually affect population age, genetic structure, and exacerbate population decline (Bertram et al. 2001, Didiuk et al. 2004).

Managers and policy-makers should understand that altering habitat might not only affect snakes directly through human presence, habitat fragmentation, and road mortality. Although it remains to be tested, indirect effects of disturbance on prey abundance and diversity might also be critical to the perseverance of the snake population. In addition to investigating disturbance effects on juveniles and gravid females (not included here), further studies should examine fecundity, neonate survival, micro-habitat differences, and prey diversity and abundance in disturbed and undisturbed areas. If warranted, habitat or vegetation alteration and re-establishment may be used to increase cover and prey abundance for rattlesnakes in human-altered landscapes.

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CHAPTER 3: SPATIAL ECOLOGY OF THE NORTHERN PACIFIC RATTLESNAKE IN NATURAL AND HUMAN-DISTURBED LANDSCAPES: HOME RANGE AND MOVEMENT PATTERNS

INTRODUCTION

As urbanization increases worldwide, an increasing number of threats face animal populations remaining on once natural landscapes (Marzluff et al. 2001, Wikelski and Cooke 2006, May 2010). Habitat loss and fragmentation are some of the greatest contributors to species' declines, extirpations and extinctions (Theobald et al. 1997, Wilcove et al. 1998, Gibbons et al. 2000, Krebs 2001, Clark et al. 2010, Coristine and Kerr 2011). However, the more subtle effects of habitat degradation and human disturbance on animals living peripheral to urban centers are less well-understood. Shifts in normal behaviour patterns may cause disruptions in daily activities that have little to no influence on lifetime fitness (Lima and Dill 1990), but conversely, disturbance of essential behaviours, or continual disturbance may result in serious consequences for the individual, and ultimately, the population (Taylor and Knight 2003, Clark et al. 2010). These generally poorly-documented effects are of concern to wildlife managers, since animal populations in marginal urban habitat often already are in decline from the more direct consequences of habitat loss.

The degree to which a population is affected by urbanization will depend on the ability of individual organisms to navigate fragmented habitat and respond to associated disturbances (Webb and Shine 1997). An animal's natural movement pattern reflects both the behaviour and ecology of the species; it corresponds to an individual's need to find prey, mates, shelter and other resources (Gregory et al. 1987), in addition to avoiding competition (Fahrig 2007). Movement can be costly due to energetic requirements and increased predation risks (Gregory et al. 1987, Norrdahl and Korpimaki 1998, Bowler and Benton 2005, Fahrig 2007, Salo et al. 2008). Thus, in theory, animals move only when necessity requires it (Gibbons and Semlitsch 1987, Gregory et al. 1987, Laundré et al. 2001). Adjustments to movement patterns due to habitat disturbances can therefore represent additional costs and risks for individuals (Murphy and Curatolo 1987, Gabrielsen and Smith 1995).

Reptiles (particularly in temperate zones) may be especially vulnerable to fragmentation and disturbances due to the physiological constraints of ectothermy that restrict them to certain microhabitat features and activity periods (Huey 1983, Reinert 1993, Parent and Weatherhead 2000). Snakes in these areas present a unique conservation challenge due to their seasonal habitat requirements and limited movement capabilities. Navigation of anthropogenic landscapes, and the search for new migration pathways and summer habitat may impact the energy and time available for essential life-history behaviours such as foraging and mate searching (Murphy and Curatolo 1987, Secor and Nagy 1994), while also increasing predation risks (Bonnet et al. 1999, Webb et al. 2003). Habitat degradation may also reduce accessibility or quality of important habitat features, which are necessary for thermoregulation (Reinert 1993, Pike et al. 2010). Regulation of body temperature is essential for development, growth, behaviour, reproduction, digestion, immune function, foraging, defensive behaviour, and immediate survival (Peterson et al. 1993). Fragmented landscapes can comprise barriers to movement that prevent accessibility to mates, resulting in interrupted gene flow and inbreeding depression (Prior et al. 1997, Ujvari et al. 2006, Clark et al. 2010). Severe habitat degradation may cause changes in prey density or composition (Jenkins and Peterson 2005), compounding the effects of changes in movement patterns. Road mortality is an additional and severe consequence of habitat fragmentation (Rosen and Lowe 1994, Bonnet et al. 1999, Andrews and Gibbons 2005). Direct persecution by humans and associated animals, such as feral cats, can also be a source of high snake mortality in modified landscapes (Whitaker and Shine 2000, Didiuk et al. 2004). Ultimately at the population level, negative consequences of individuals' reduced energy budgets, combined with potential losses in genetic diversity, and high mortality may result in extirpations of species in highly fragmented areas (Clark et al. 2010).

The Northern Pacific Rattlesnake (*Crotalus oreganus oreganus*) is sensitive to human activities due to habitat loss, fragmentation, persecution, and a restricted range in British Columbia, Canada (Bertram et al. 2001, Didiuk et al. 2004). It is consequently a designated species-at-risk at both the provincial and federal level (COSEWIC 2004). The dry southern valleys this snake inhabits in B.C. are experiencing rapid growth from urban development, tourism and agriculture. Although studies thus far have identified life history traits and the general spatial ecology of rattlesnakes in British Columbia (e.g. Macartney 1985, Gomez

2007), none have compared fine scale differences in movement patterns and home ranges between snakes residing in urbanized and natural areas. If snake movements are altered or impeded in modified landscapes, their reproductive successes, foraging opportunities and survival may be compromised. Thus, simple population estimates alone are inadequate to assess the recovery of rattlesnakes in British Columbia, and detailed research is required to investigate the longevity of the population.

I used radio-telemetry to compare the spatial ecology of Northern Pacific Rattlesnakes in both natural and human-disturbed landscapes in Osoyoos, British Columbia. The specific objectives were to test for differences between sites in (1) home range size and attributes, and (2) movement patterns**.** Due to the physical presence of humans, barriers, and other anthropogenic features that snakes may perceive as barriers to movement in disturbed habitat, I predicted that rattlesnakes in these areas would have smaller home range sizes and display shorter maximum distances from hibernacula. I predicted that snakes in disturbed sites would have greater movement rates, greater total distances moved, and more convoluted movement patterns (greater tortuosity) due to greater difficulty in locating features necessary for thermoregulation.

METHODS

Study area

The study took place on the Osoyoos Indian Reserve (OIR) in the extreme southern Okanagan valley of British Columbia, Canada (119.4° W, 49.28° N). The approximately 900 ha study area was bordered by the town of Osoyoos to the south and south-west, Osoyoos Lake to the west, Anarchist Mountain (elev. 1491 m) to the east, and the remaining OIR to the north (See Figure 1.2). See Chapter 1 for a more detailed description.

Radio-telemetry

From 2006 to 2012, rattlesnakes were captured both by direct search effort in April and May at hibernacula, and through incidental encounters during the active season. Adult males were preferentially selected for telemetry, as female snakes have been shown to restrict their movements or otherwise alter their behaviours if gravid (Macartney and Gregory 1988). These animals were transported to a nearby veterinary clinic and implanted with transmitters (Holohil Ltd., SB-2T 5.0g or SI-2T 9.0g) following procedures described by Reinert and Cundall (1982) with modifications by Reinert (1992). Pharmaceutical procedures followed Brown et al. (2009). Transmitters weighed on average 2.2% of total snake body mass (range: 0.97 - 3.81%). Telemetered animals were held for approximately 48 hours following surgery for observation and rehydration before being released at their capture site. Transmitters were removed at the end of their battery life (approximately 12 months for SB-2T, and 24 months for SI-2T), or in the spring following the study period through capture of the animals and their return to the veterinary clinic.

Each telemetered snake was located approximately every two to three days during the active season (April to October), with the exception of 2007, when snakes were located approximately once per week. A 3-element yagi antenna and a portable radio-telemetry receiver (AVM Instrument Co., model LA12-Q and Communications Specialists Inc., model R-1000) were used to track the snakes.

Snakes were briefly recaptured every one to two months to monitor health and check for signs of surgery implications. Otherwise, care was taken to locate the animals from at least 2 m away without triggering any movement or other disturbance to the animal.

Quantifying disturbance

Landscape development and human activity was concentrated in the southern portions of the study area. Development included a large-scale visitor’s facility (Nk'Mip Desert Cultural Centre), walking trails, condominium resort, golf course, winery, vineyards, a large campground, associated roads and parking lots, and a major highway. These attractions result in tens of thousands of visitors annually (Stringam, pers. comm.). I hereafter refer to these general areas of the landscape as 'disturbed'. In contrast, the northern portions of the study area were characterized by restricted or limited human access and no land development. I hereafter refer to these areas as 'undisturbed'.

Different sections of the study area were further classified under a disturbance rating (DR), similar to that used in Parent and Weatherhead (2000). The study area was divided into 17 sections (e.g. resort, campground, riparian zone) based on known major foraging and movement locations of snakes. Boundaries of these sections were defined by naturally-occurring or anthropogenic structures (e.g. gullies, creeks, fences), although not all such boundaries were necessarily barriers to snake movement. Each snake was assigned a DR from 0 to 4 based on the region that the majority of its home range fell within and this region's proximity to the nearest source of human activity or development. A DR of 0 represented an area where access to the general public was restricted and there was no land development (e.g. in the northern regions of the study area (see Figures 1.2 and 1.6). The DR gradient continued up to 4, which represented the most drastically transformed landscapes and heavily-frequented regions (e.g. campground, residential, see Figures 1.2 and 1.3). Specifically, the DRs were defined based on distances (d) to the nearest source of disturbance as follows: $d > 200$ m = DR0; $100 \text{ m} < d > 200$ m = DR1; $50 \text{ m} < d > 100$ m = DR2; $10 < d > 50$ m = DR3; $d < 10$ m = DR4.

Some rattlesnakes traveled up the eastern mountains of the study site and were grouped separately from those classified under DRs. These 'mountain' snakes were not included in the analyses presented herein because they foraged in unique biogeoclimatic zones and vegetation, tracking intervals were sporadic due to the terrain, few radio-locations were obtained, and sample size was small (N = 6). However, wherever mean values could be calculated for range parameters, these were included in graphs for comparison with DR snakes and to complement previous work (see Chapter 2).

Seasonal movement

The full activity season (April to October) was divided into three subseasons in order to account for seasonal weather patterns and snake migratory movements to and from winter hibernacula: egress (movement from hibernacula to foraging grounds), foraging, and ingress (movement from foraging grounds back to hibernacula). I defined the foraging season as beginning when a snake's straight-line movements away from its hibernaculum were less than 50 m, and/or more than four days spanned between a snake movement. Likewise, the foraging season ended when snakes began straight-line movements of 50 m or more towards hibernacula in the autumn. Subseason cut-off dates were calculated individually for each snake.

Periods of mating and ecdysis undoubtedly influence a snake's movement patterns (Gibbons and Semlitsch 1987, Gillingham 1987); however, it was not always possible to positively determine the occurrence or timing of a mating or shedding event for each individual. Male snakes often are more active than females during the mating season (late summer and early fall) due to mate-searching behaviour (Gregory et al. 1987). Because this study did not aim to describe differences between the sexes (only one rattlesnake included in the study was female), and all males were of similar size (and presumably age and sexual maturity level), demarcation of the mating period each year was deemed unnecessary. Due to increased cryptic behaviour during ecdysis, often indistinguishable changes in movement behaviour, and a protocol of minimal disturbance by researchers, it was not possible to consistently identify ecdysis periods. However, previous work has shown no significant differences in shedding frequency between snakes across all areas of the study site (see Chapter 2), and males of this species in B.C. generally shed over a similar month-long period (July; Macartney et al. 1990). Thus I am confident comparisons of movement metrics including periods of ecdysis are warranted.

Home range parameters

To investigate home range attributes, I calculated a series of metrics, namely home range size (MCP and KD), core area of use (CA), range width (RW), range length (RL), range shape (RS), and maximum distance from hibernacula (MDH). See Table 3.1 for definitions and measurement descriptions. I imported spatial data into the GIS software ArcView 3.2 and ArcMap 10.0 and analyzed them using the Animal Movement Analysis Extension (Hooge and Eichenlaub 1997), Longest Straight Line Extension v. 1.3a (Jenness 2007), and the Bounding Containers script (Patterson 2010). I calculated all range parameters for both the full activity season and the foraging subseason, with the exception of MDH, which was measured over the full season only.

Measurements of home range can be greatly affected by sample size and the choice of estimator (Nilsen et al. 2008, Boyle et al. 2009, Harless et al. 2010). Due to the limitations associated with either method, I measured both 100% minimum convex polygons (MCPs) and 95% kernel density estimators (KDs) to make comparisons among sites. An MCP is calculated by drawing the smallest possible polygon around all known locations for an

Table 3.1. Parameter descriptions and calculation methods used to describe home range attributes of telemetered Northern Pacific Rattlesnakes. Each parameter was measured for both the full active season and the foraging season.

Home range Parameter	Abbr.	Description	Calculation notes
Home range (100% minimum convex polygon) (m^2)	MCP	Home range calculated by drawing the smallest possible convex polygon using all telemetry locations for an animal. Measured using the Animal Movement Analysis Extension for ArcView 3.2 (Hooge and Eichenlaub 1997).	Included relocations less than 10 m apart as 0 m (non-significant) movements.
Home range (95% kernel density) (m^2)	KD	Home range calculated using kernel estimators. Measured using the Animal Movement Analysis Extension for ArcView 3.2 (Hooge and Eichenlaub 1997).	Included relocations less than 10 m apart as 0 m (non-significant) movements.
Core area (m^2)	CA	50% kernel density of a snake's home range. Measured using the Animal Movement Analysis Extension for ArcView (Hooge and Eichenlaub 1997).	Included relocations less than 10 m apart as 0 m (non-significant) movements.
Range width (m)	RW	Maximum distance across the width of a snake's dispersion of radiolocations. Measured using the Arc GIS Bounding Containers script in ArcMap 10.0 (Patterson 2010).	Did not include relocations less than 10 m apart.
Range length (m)	RL	The longest straight line that is completely contained within a snake's home range (Roth and Greene 2006, Rouse 2006, Jenness 2007). Measured using the ArcView 3.2 extension Longest Straight Line v. 1.3a (Jenness 2007). For many snakes, RL = MDH.	Did not include relocations less than 10 m apart.
Range shape	RS	Ratio of range width to range length (RW:RL), representing the range shape. A value of one represents a circular home range shape; lower values approach a more linear shape (Rouse 2006).	
Maximum distance from hibernacula (m)	MDH	Maximum Euclidean distance between a snake's hibernaculum and any tracking event.	Did not include relocations less than 10 m apart.

individual animal (Hayne 1949). It is one of the most commonly used home range calculation methods (Burgman and Fox 2003, Row and Blouin-Demers 2006, Nilsen et al. 2008, Laver and Kelly 2008). The use of MCPs has been recommended to calculate home range sizes of herpetofauna and its common use in the snake literature facilitates comparisons of my results to other studies (Pearson et al. 2005, Row and Blouin-Demers 2006). However, MCPs may include areas not actually used by the animal, and do not take into account patterns of temporal and spatial selection within the home range (Worton 1987, Burgman and Fox 2003, Row and Blouin-Demers 2006). Because kernel estimators do take into account these patterns of intensity (Worton 1987, 1989), I used 95% KDs as an additional estimate of home range size, and 50% KD as an estimate of core area of use (Tiebout and Cary 1987). I used the least-squares cross-validation (LSCV) method to calculate the smoothing factor (*h*) for both 95% and 50% KDs. Although the LSCV method is recommended by many and is accurate for many situations (Worton 1989, Seaman and Powell 1996, Row and Blouin-Demers 2006), it may produce wide ranges of *h* and consequently affect the calculated home range sizes (Hemson et al. 2005, Row and Blouin-Demers 2006, Wauters et al. 2007).

Movement parameters

To investigate snake movement patterns I calculated total distance moved (TDM), maximum distance between consecutive relocations (MAD), minimum distance between consecutive relocations (MID), mean distance between consecutive relocations (MED), movement frequency (MF), mean movement rate (MMR), mean movement distance (MMD), set movement time (SMT), and fractal dimension or tortuosity (FD) for my telemetered snakes. See Table 3.2 for definitions and measurement descriptions. I calculated these movement parameters for each of the subseasons (egress, foraging, and ingress). Since the snakes were located intermittently, these movement parameters represent minimum values.

The metrics MAD, MID, and MED were calculated using data where the average interval between relocations was between 24 and 72 hours, in order to standardize the measurements. Including larger tracking intervals would have inflated the size of the distances moved, not to mention the probability that a snake relocated between locations. For SMT, an arbitrary value of 45 - 55m was used to calculate the length of time it took a snake to travel a set distance.

Table 3.2. Parameter descriptions and calculation methods used to describe movement pattern attributes of telemetered Northern Pacific Rattlesnakes. Each parameter was calculated for the full active season and within each subseason (egress, foraging, ingress).

Movement parameter	Abbr.	Description	Calculation notes
Total distance moved (m)	TDM	Cumulative sum of Euclidean distances between sequential relocations. Represents minimum distance moved.	Did not include relocations less than 10 m apart.
Maximum distance between consecutive relocations (m)	MAD	Maximum distance between any two sequential relocations in a set time frame (24-72 hrs).	Did not include relocations less than 10 m apart.
Minimum distance between consecutive relocations (m)	MID	Minimum distance between any two sequential relocations in a set time frame (24-72 hrs).	Did not include relocations less than 10 m apart.
Mean distance between consecutive relocations (m)	MED	Mean distance between all sequential relocation pairs in a set time frame (24-72 hrs).	Did not include relocations less than 10 m apart.
Movement frequency	MF	Proportion of tracking events resulting in a movement greater than 10m.	Included relocations less than 10 m apart.
Mean movement rate (m/d)	MMR	Mean distance moved per day. Distance traveled between two relocations divided by the number of days in between, measured across sequential pairs of tracking events (Diffendorfer et al. 2005). Mean rate calculated from sequential pairs.	Included relocations less than 10 m apart as 0 m (non-significant) movements.
Mean movement distance (m/d)	MMD	Mean distance traveled per movement, standardized by number of days between relocations. Mean rate calculated from sequential pairs. This metric is similar to movement rate, but excludes non-significant movements (Mitrovich et al. 2009).	Did not include relocations less than 10 m apart.
Set movement time (d)	SMT	Mean number of days between relocations of a set distance (45 to 55m).	Did not include relocations less than 10 m apart.
Fractal dimension (tortuosity)	FD	Estimate of tortuosity or crookedness of a movement path, measured using the program Fractal v. 5.20 (Nams 1996). The estimate lies between a minimum value of one to a maximum of two: One represents a straight path, and two represents a path so tortuous as to completely cover a plane.	Included relocations less than 10 m apart as 0 m (non-significant) movements.

The FractalMean estimator (Nams 2006) within the program Fractal v. 5.20 (V.O. Nams, Nova Scotia Agricultural College, Truro, NS, Canada) was used to calculate the fractal dimension (FD) or tortuosity of each animal's movement path. This is essentially a quantification of the 'crookedness' of the movement pattern. This index can range in value from 1 (straight path) to 2 (a path so tortuous as to completely cover a plane) (Nams 1996, 2006).

Statistical analyses

Analyses were performed using the program R v. 2.12.1 (R Development Core Team 2011). Data were tested for normality by visual examination of histograms and bar-and-whisker plots, and the Kolmogorov-Smirnov goodness-of-fit test (Zar 1999). Homogeneity of variances between groups was tested where necessary using the Fligner-Killeen test (Conover et al. 1981, Crawley 2007). Non-normal and non-homogenous data were transformed for parametric tests. A p-value of ≤ 0.05 was used to guide statistical interpretation of the results. Tukey's honestly significant difference (HSD) test was used for post-hoc multiple comparisons where appropriate (Crawley 2007). Means are reported as ± 1 SE unless otherwise stated.

Rattlesnakes were excluded from analyses if they were tracked for less than 75% of the active season or for less than 110 days or 20 fixes. However, partial datasets were included in subseason analyses where appropriate. If a snake was captured and implanted away from its hibernaculum, the hibernaculum location was added into the dataset in order to complete home range calculations. Likewise, if a snake was removed from the study before the end of the season (e.g. due to predation or road-kill), its hibernaculum location was added in to complete the dataset. If a snake had to be translocated greater than 40 m away by researchers because of safety concerns (i.e. proximity to other people) it was excluded from analyses. The locations of snakes found preyed upon were removed from the dataset since it was not possible to determine if a snake had been moved from its previous location by a predator.

Consecutive radiolocations less than 10 m apart were not included in all movement and range parameter calculations, since GPS error at any location was up to 5m (see Tables 3.1 and 3.2). Calculations of home range sizes (MCP and KD), mean movement rate (MMR), and fractal dimension (FD) included relocations less than 10 m apart as non-significant movements (i.e. the relocation distance was reset to 0 m) to account for temporal and intensity patterns within a range.

Most snakes were tracked for only one active season, but some individuals were tracked over two to three years. I treated all range parameters for each snake in each year it was tracked as independent. Simulation studies have shown that treating successive years and seasons of data from the same individual as independent should not bias results as long as the intra-subject variance is greater than or equal to the between-subject variance (Leger and Didrichsons 1994). Or, in the case presented here, as long as the magnitude of differences in range and movement parameters across seasons demonstrated by an individual animal are similar to (or larger than) the variation among all of the animals observed within a single season (Pearson et al. 2005). I tested this by comparing the two variances using an F-test, following Crawley (2007). Wherever full data sets were available for each snake, my data fulfilled this assumption.

Body size and sampling effort

I ran preliminary analyses using univariate one-way ANOVAs to check for differences in body mass, body size, and sampling effort (length of tracking season and number of radiolocations) between disturbance ratings (DRs).

Home range and movement

I compared each home range parameter among DRs and years using ANOVA for the full active season and foraging subseason separately, with the exception of maximum distance from hibernaculum (MDH) which was measured for the full season only.

I compared movement parameters among subseasons (egress, foraging, and ingress) and between DRs and years using mixed-effects models for repeated measures, with the restricted maximum likelihood (REML) method under the R package *nlme* (Pinheiro et al. 2008). I checked for normality and homogeneity in the models by visual inspections of plots of residuals against fitted values. I treated DR and year as fixed variables and individual study animal and subseason as random effects (to account for variation in snake behaviour among individuals and within subseasons, and uneven sample sizes among subseasons). Furthermore, I used univariate two-factor ANOVAs to compare each movement parameter between DRs and years within the forging season alone, since this season formed the most complete dataset and it excluded migratory movements. I also compared total distance moved (TDM) among DRs and years for the full active season using ANOVA.

Temperature effects

I used logistic regression to investigate whether DRs and temperature had an influence on snake movement. I fit a regression with binomial errors using a generalized linear model (GLM) function, as outlined in Crawley (2007). I used Wald's χ^2 statistic to assess the association of a variable with snake movement. The probability of snake movement was used as the response variable, with 'no movement' and 'movement' (> 10m relocation) representing the binary responses. The explanatory variables were maximum daily temperature of the town of Osoyoos for the snake's last radio-location, and DR category. Temperature data were taken from the National Climate Data and Information Archive (Environment Canada 2012).

To avoid compounding effects of migration patterns during egress and ingress, I tested for the effects of temperature during the foraging subseason only, and standardized the data using only relocations up to 48 hours apart. All years were pooled in the analysis.

RESULTS

Radio-telemetry

From April 2006 to October 2012, 90 rattlesnakes were tracked for at least one year. Fifty-four rattlesnakes were tracked for at least 75% of the active season and met the minimum criteria for inclusion into the analyses presented here. Eight of the 54 individuals were tracked over two years, and one was tracked over three years. The few rattlesnakes that resided in DR4 did not do so for the entire duration of the active season, so those snakes were placed within DR3 (where they resided when not in DR4). All snakes were male, with the exception of one non-gravid female tracked in DR3 in 2010. Table 3.3 provides a summary

Table 3.3. Summary of sample sizes, body sizes at start of study, number of radiolocations and tracking duration for Northern Pacific Rattlesnakes used in this study. Eight of the 54 individuals were tracked over two years, and one was tracked over three years. Standard deviations given in parentheses after mean values.

Site	Number	Mean snout-vent length (cm)	Range of snout-vent lengths (cm)	Mean body mass (g)	Range of snake body mass (g)	Mean number of radiolocations included in analyses	Range of radio-locations included in analyses	Mean length of tracking season (days)	Range of tracking season (days)
DR0									
Males	21	73.5 (4.2)	63.5-81.0	259.4 (35.0)	197.0- 337.0	44.4 (15.8)	10- 59	137.1 (22.5)	85-174
DR1									
Males	11	70.5 (4.6)	59.0- 76.0	253.8 (32.0)	190.0- 285.0	31.7 (14.5)	11-57	118.5 (27.9)	57- 151
DR2									
Males	5	68.8 (2.8)	66.5- 73.5	243.2 (43.4)	202.0- 310.0	49.6 (10.0)	37-63	137.8 (20.0)	116- 156
DR3									
Males	16	69.7 (6.5)	62.0- 90.2	243.2 (51.9)	151.0-381.0	40.4 (9.9)	21-58	126.2 (23.6)	76- 160
Female	1	65.5	---	209.0	---	53	---	110	---
Average	54	71.2 (5.2)	59.0- 90.2	251.0 (40.6)	151.0- 381.0	41.3 (14.2)	10-63	129.6 (24.3)	57- 174

of rattlesnake size and tracking duration within each DR and overall. Of the 54 rattlesnakes used in the analyses, seven died during the study: five were preyed upon, one was killed on a road, and one was believed to have been killed by humans.

Body size and sampling effort

Body sizes and sampling effort were equal across all areas of the study site. There was no difference in body mass or SVL between DRs (mass: $F_{3,41} = 1.05$, $P = 0.38$; SVL: $F_{3,41} = 1.75$, $P = 0.17$). There were also no differences in the number of radiolocations or the length of the tracking season between DRs (locations: $F_{3,41} = 1.49$, $P = 0.23$; season: $F_{3,41} = 0.99$, $P = 0.41$).

Home range parameters

Home range: 100% minimum convex polygon (MCP)

Rattlesnake home range sizes tended to be greater in the least disturbed areas, but otherwise were relatively similar. There was a significant effect of DR on MCP, but no effect of year or the interaction term (DR: $F_{3,26} = 3.24$, $P = 0.04$; year: $F_{5,26} = 0.52$, $P = 0.76$; DR × year: $F_{4,26} = 0.72$, $P = 0.59$). However, Tukey’s HSD post-hoc test showed no significant differences between any pairs of DRs, with only marginal differences between DR0 and all other DRs ($P > 0.07$ in all cases; Figure 3.1 A). Average MCP over the active season was 20.0 ± 12.1 (SD) ha.

Within the foraging subseason, ANOVA showed no effect of DR, year, or the interaction term on MCP (DR: $F_{3,29} = 1.52$, $P = 0.23$, Figure 3.1 B; year: $F_{6,29} = 1.21$, $P = 0.33$; DR × year: $F_{6,29} = 0.66$, $P = 0.68$). Average MCP over the foraging season was 9.5 ± 7.9 (SD) ha.

Home range: 95% kernel density (KD)

Trends in rattlesnake home range size between DRs, calculated using the KD method, were similar to those shown for the MCP method. The exception was in DR1, where snakes had much larger range sizes relative to other DRs for the KD method. Overall, sizes

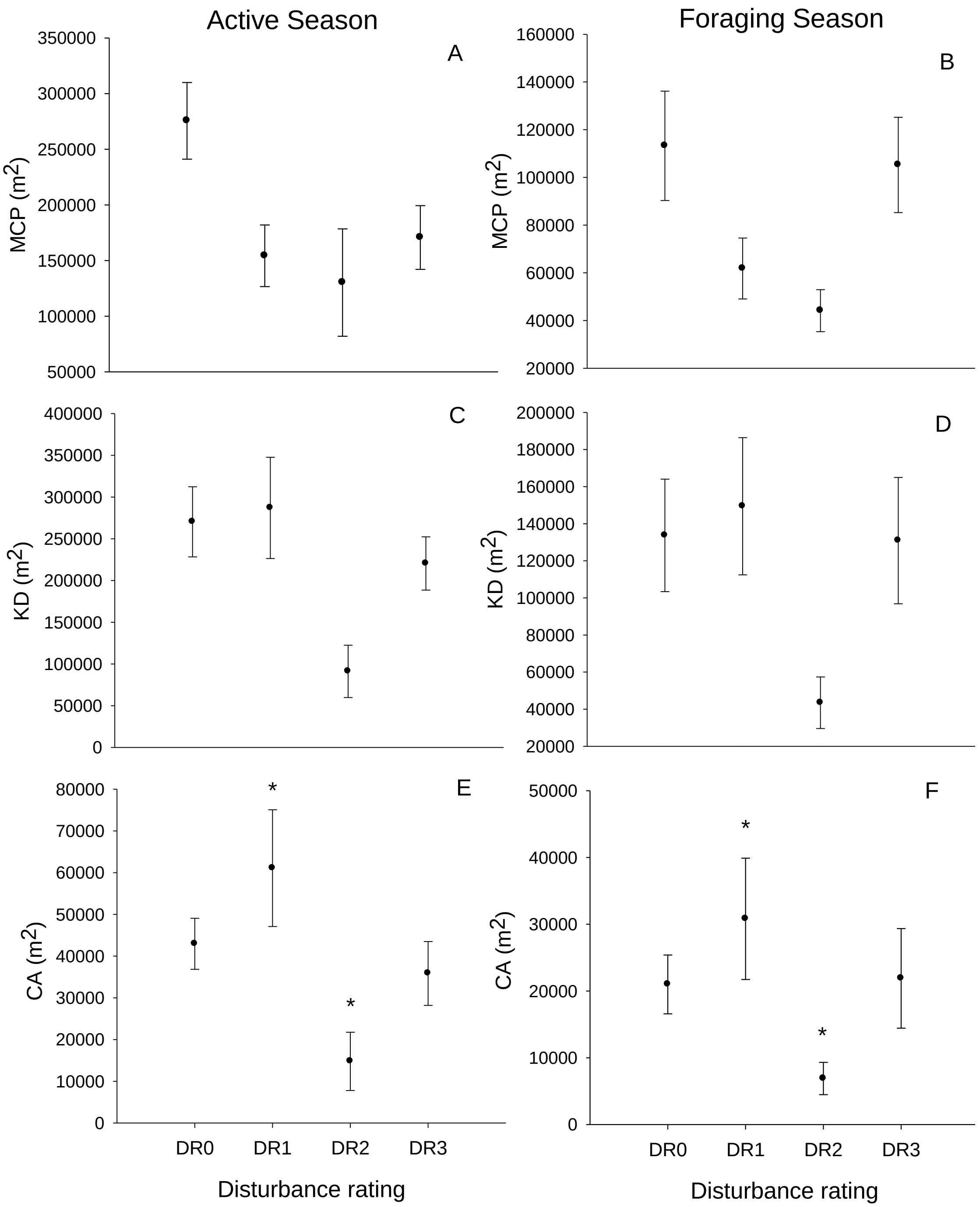

Figure 3.1. Mean ± 1 SE of 100% minimum convex polygon (MCP) home range estimate, 95% kernel density (KD) home range estimate, and core area (CA) for the full active season and foraging subseason of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada, between 2006 and 2012. Active season N: 14 (DR0), 7 (DR1), 5 (DR2), 13 (DR3). Foraging N: 17 (DR0), 7 (DR1), 5 (DR2), 16 (DR3). Means with asterisks (*) indicate a significant difference between DRs at α = 0.05.

remained larger in the least disturbed areas. ANOVA showed a marginally significant effect of DR, and no effect of year, or the interaction term on KD for the active season (DR: $F_{3,26}$ = 2.74, P = 0.06; year: $F_{5,26}$ = 1.70, P = 0.17; DR × year: $F_{4,26}$ = 0.80, P = 0.54). Tukey's HSD post-hoc test showed no significant differences between DR pairs (P > 0.07 in all cases; Figure 3.1 C). Average KD over the active season was 23.36 ± 14.48 (SD) ha.

Within the foraging subseason, there was no effect of DR, or the interaction term on KD, but there was an effect of year (DR: $F_{3,29}$ = 1.40, P = 0.26, Figure 3.1 D; year: $F_{6,29}$ = 4.20, P < 0.01; DR × year: $F_{6,29}$ = 1.49, P = 0.22). Post-hoc tests showed that KD was significantly greater in 2008 than in 2006 (P = 0.02), 2009 (P = 0.04), and 2011 (P = 0.01). However, only two observations in 2008 met the criteria to be included for foraging season KD analyses, and the differences may be observed due to unbalanced data among years. Average KD over the foraging season was 12.5 ± 11.9 (SD) ha.

Core area (CA)

Core area sizes followed the same pattern as KD home ranges; the rattlesnakes' core area of use tended to be larger in the least disturbed areas (DR0 and DR1). ANOVA showed an effect of DR and year on CA, but not the interaction term (DR: $F_{3,26}$ = 3.99, P = 0.02; year: $F_{5,26}$ = 2.59, P = 0.05; DR × year: $F_{4,26}$ = 1.62, P = 0.20). Tukey's HSD tests revealed that CA in DR1 was greater than in DR2 (P = 0.01; Figure 3.1 E), but no significant differences between years (P > 0.07 in all cases).

There was an effect of DR, but not year or the interaction term on CA during the foraging subseason (DR: $F_{3,29}$ = 2.90, P = 0.05; year: $F_{6,29}$ = 2.07, P = 0.09; DR × year: $F_{5,29}$ = 1.50, P = 0.22). Post-hoc tests revealed that CA in DR1 was greater than in DR2 (P = 0.05; Figure 3.1 F).

Range width (RW)

Range width tended to be greater in the least disturbed site (DR0) compared to other areas, but ANOVA showed no significant effect of year, DR or the interaction term on RW (DR: $F_{3,26}$ = 2.16, P = 0.11; year: $F_{5,26}$ = 0.84, P = 0.53; DR × year: $F_{4,26}$ = 0.59, P = 0.68). Average RW over the active season was 314.52 ± 146.82 (SD) m (Figure 3.2 A).

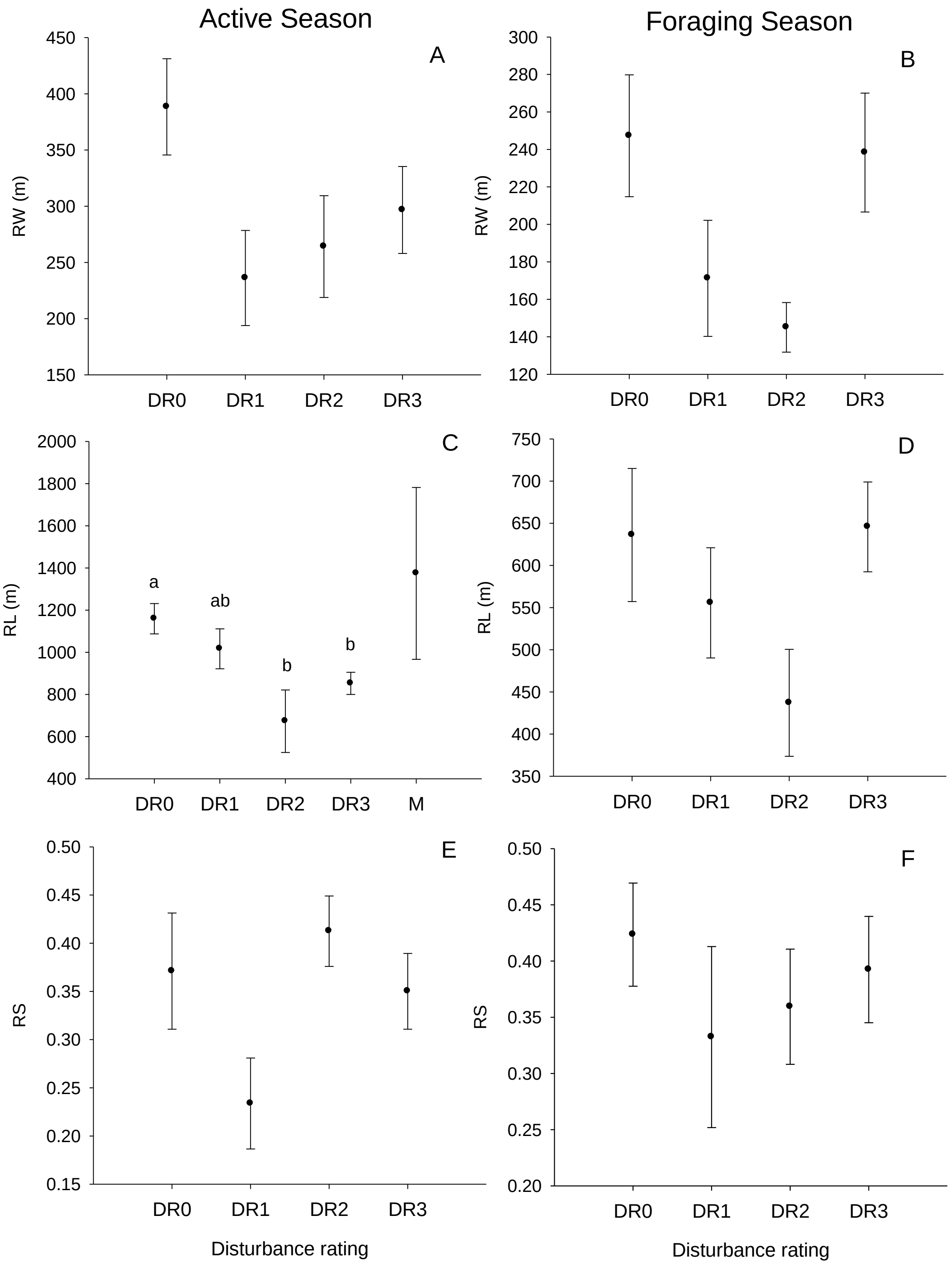

Figure 3.2. Mean ± 1 SE of range width (RW), range length (RL), and range shape (RS) for the full active season and foraging subseason of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) or mountain area (M) on the study site in Osoyoos, British Columbia, Canada, between 2006 and 2012. Active season N = 14 (DR0), 7 (DR1), 5 (DR2),13 (DR3), 7 (M). Foraging N: 17 (DR0), 7 (DR1), 5 (DR2), 16 (DR3), 1 (M). Means with different letters indicate a significant difference between DRs at α = 0.05.

Likewise, there were no significant effects in the foraging subseason ANOVA (DR: $F_{3,29} = 1.40$, $P = 0.26$; year: $F_{6,29} = 0.92$, $P = 0.49$; DR × year: $F_{6,29} = 0.64$, $P = 0.70$). Average RW over the foraging subseason was 220.88 ± 120.20 (SD) m (Figure 3.2 B).

Range length (RL)

The length of rattlesnake ranges decreased with increasing disturbance. There was a significant effect of DR, but not year or the interaction term on RL (DR: $F_{3,26} = 6.05$, $P < 0.01$; year: $F_{5,26} = 0.97$, $P = 0.45$; DR × year: $F_{4,26} = 1.07$, $P = 0.39$). Post-hoc tests indicated that the RL of snakes in DR0 (1159 ± 72 m) was significantly greater than for snakes in DR2 (1017 ± 95 m; $P < 0.01$) and in DR3 (852 ± 56 m; $P = 0.02$; Figure 3.2 C).

ANOVA for foraging subseason showed no effect of DR, year or the interaction term on RL (DR: $F_{3,29} = 0.94$, $P = 0.43$; year: $F_{6,29} = 0.92$, $P = 0.49$; DR × year: $F_{6,29} = 0.43$, $P = 0.86$). Average RL over the foraging subseason was 604.82 ± 254.02 (SD) m (Figure 3.2 D).

Rattlesnakes that traveled up into the eastern mountains tended to have longer range lengths than all other snakes (Figure 3.2 C, D), however they were not included in the analyses due to low sample sizes and sampling effort. Maximum RL detected for ‘mountain’ snakes was 2.7 km.

Range shape (RS)

The shapes of rattlesnake home ranges were relatively uniform among areas. All RS ratios ranged from 0.23 to 0.41, indicating the ranges were closer to a linear shape (RS value of zero) than a circular shape (RS value of one). ANOVA showed no effect of DR, year or the interaction term on RS (DR: $F_{3,25} = 1.37$, $P = 0.28$; year: $F_{5,25} = 1.06$, $P = 0.41$; DR × year: $F_{4,25} = 0.43$, $P = 0.79$). Average RS was 0.34 ± 0.17 (SD) (Figure 3.2 E)

ANOVA showed no significant effect of DR, year or the interaction term on RS in the foraging subseason (DR: $F_{3,29} = 0.42$, $P = 0.74$; year: $F_{6,29} = 0.73$, $P = 0.63$; DR × year: $F_{6,29} = 0.86$, $P = 0.54$). Average RS over the foraging subseason was 0.39 ± 0.18 (SD) (Figure 3.2 F).

Maximum distance from hibernacula (MDH)

Similar to range length, the maximum distance rattlesnakes moved from their hibernacula decreased with increasing disturbance. Rattlesnakes residing in the mountain habitats travelled much farther distances overall. There was an effect of DR, but not year or the interaction term on MDH (DR: $F_{3,37} = 2.78$, $P = 0.05$; year: $F_{6,37} = 1.08$, $P = 0.39$; DR × year: $F_{7,37} = 1.19$, $P = 0.33$). Post-hoc tests revealed that MDH of snakes in DR0 (1042.60 ± 73.18 m) was greater than in DR2 (620.33 ± 168.02 m; $P = 0.03$; Figure 3.3). Maximum MDH detected for 'mountain' snakes was 2.7 km.

Movement parameters

Total distance moved (TDM)

Rattlesnakes traveled greater distances during the foraging subseason than during egress and ingress, as well as in the least disturbed areas, but no discernible trends were observed over the gradient of disturbance. The mixed-effects model showed no effect of any year on TDM ($P > 0.16$ in all cases) and no significant interaction terms ($P > 0.30$ in all cases), so the data were pooled among years and interaction terms were removed from the model (data were log-transformed to meet assumptions of equal variance). Overall, TDM was greater in all DRs within the foraging subseason ($t = 11.36$, df = 49, $P < 0.0001$; Figure 3.4). There was a declining trend in TDM from DR0 through DR2 that approached statistical significance (DR1; $t = -1.83$, df = 39, $P = 0.07$, DR2; $t = -1.84$, df = 39, $P = 0.07$). However, the trend did not hold into DR3, where TDM was similar to that within DR0 ($t = -1.39$, df = 39, $P = 0.17$).

Further analysis for the entire active season (ANOVA) showed a marginal effect of DR, an effect of year, but no interaction effect on TDM (DR: $F_{3,37} = 2.71$, $P = 0.06$; year: $F_{6,37} = 2.60$, $P = 0.03$; DR × year: $F_{7,37} = 0.26$, $P = 0.97$). However, post-hoc tests showed no significant pairwise differences between DRs or years ($P > 0.11$ in all cases). Average TDM was 4191.2 ± 1411.0 (SD) (Figure 3.5).

Within the foraging subseason alone, ANOVA showed no significant effect of DR, year or the interaction term on TDM (DR: $F_{3,30} = 1.16$, $P = 0.34$; year: $F_{6,30} = 2.05$,

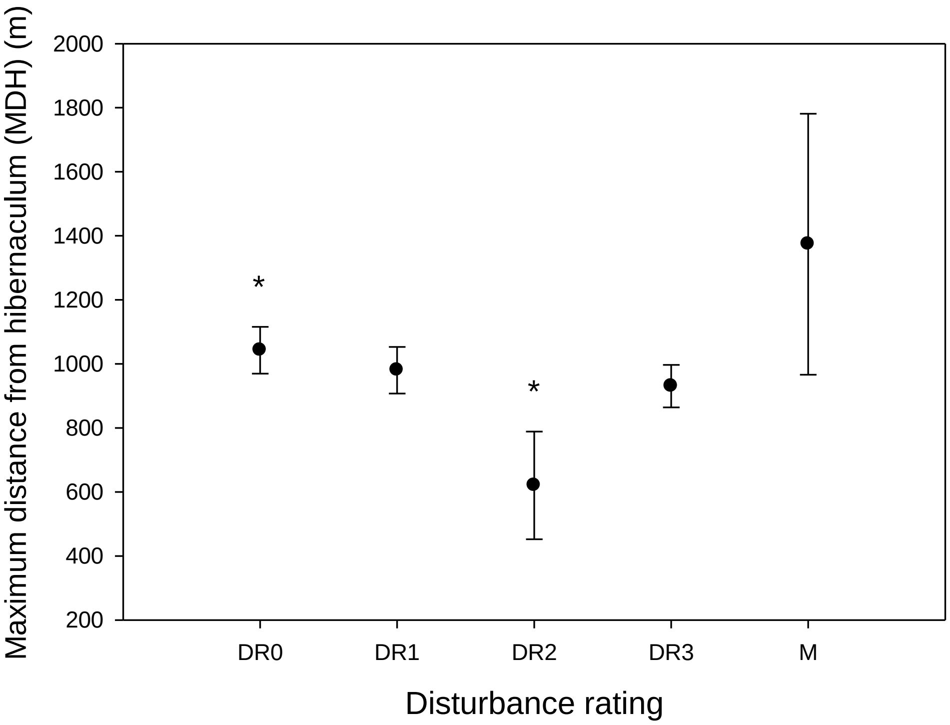

Figure 3.3. Mean ± 1 SE of maximum distance from hibernaculum (MDH) over the full active season of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada, between 2006 and 2012. N = 21 (DR0), 11 (DR1), 5 (DR2), 17 (DR3), 7 (M). Means with asterisks (*) indicate a significant difference between DRs at α = 0.05. Snakes in mountain areas (M) are included for comparison, but were not included in the analyses.

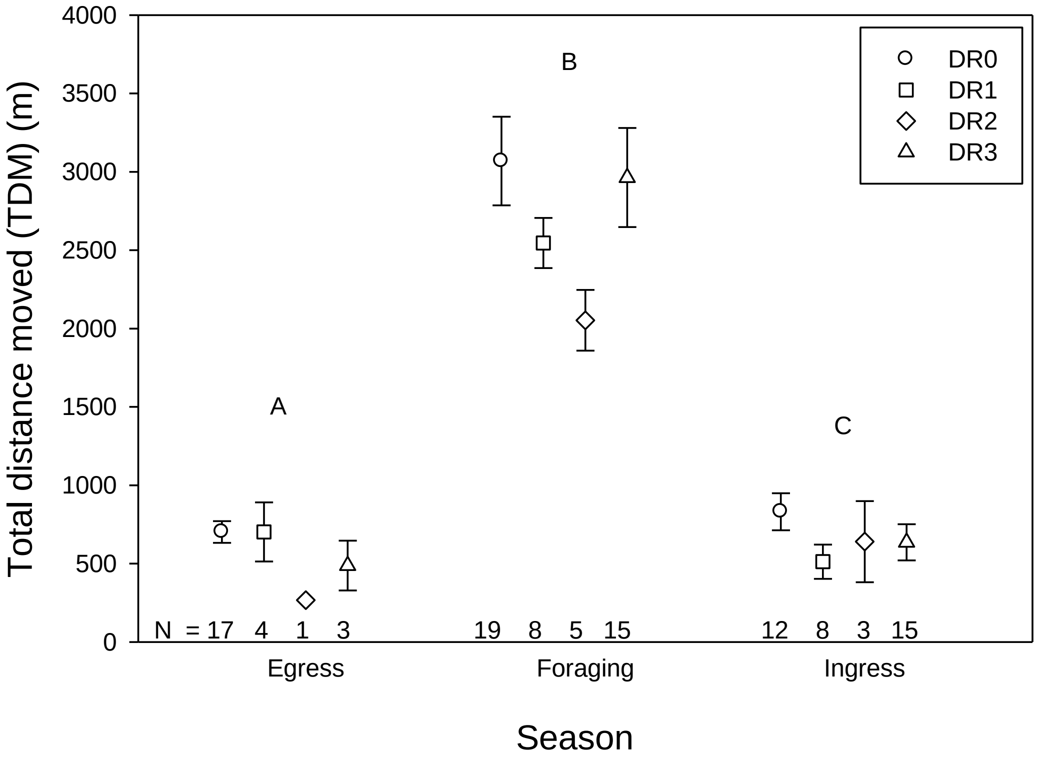

Figure 3.4. Mean ± 1 SE of total distance moved (TDM) among subseasons of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada, between 2006 and 2012. Different uppercase letters indicate a significant difference between subseasons at α=0.05.

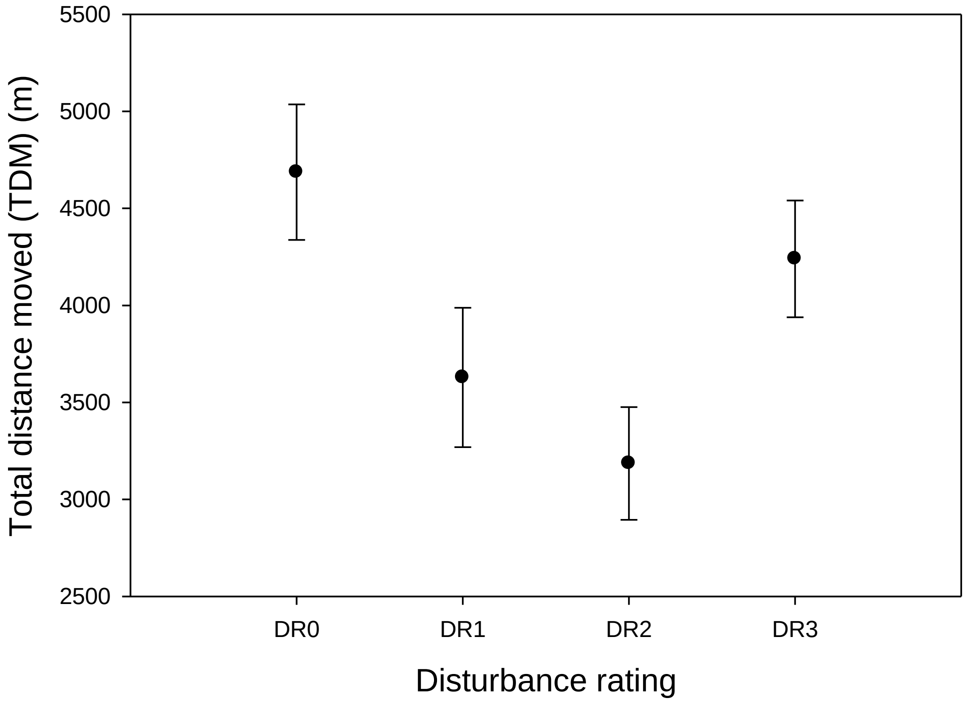

Figure 3.5. Mean ± 1 SE of total distance moved (TDM) over the full active season of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada, between 2006 and 2012. N = 21 (DR0), 11 (DR1), 5 (DR2), 17 (DR3).

P = 0.09; DR × year: $F_{7,30} = 0.43$, P = 0.88). Average TDM over the foraging subseason was 2837.8 ± 1099.4 m (SD) (Figure 3.4).

Maximum distance between consecutive relocations (MAD)

The maximum distances rattlesnakes traveled between relocations were variable, with no trends evident between areas. A mixed-effects model showed no effect of any year on MAD (P > 0.13 in all cases) and no interaction term was fitted due to unbalanced data among DRs and years (data were log-transformed to meet assumptions of equal variance). A pooled model revealed that MAD was significantly greater during the foraging subseason ($t = 2.58$, df = 37, P = 0.01; Figure 3.6). There was no significant effect of DR (P > 0.13 in all cases).

A two-factor ANOVA for the foraging subseason, fitted without an interaction term, revealed an effect of year but not DR on MAD (DR: $F_{3,36} = 1.34$, P = 0.28; year: $F_{6,36} = 2.44$, P = 0.04). Tukey's HSD post-hoc tests showed this was principally caused by MAD in 2006 being marginally shorter than in 2011 (P = 0.06). Average MAD over the foraging season was 348.6 ± 207.9 (SD) m.

Minimum distance between consecutive relocations (MID)

Rattlesnakes traveled greater minimum distances while dispersing from hibernacula in the spring, but no trends were evident between areas. The mixed-effects model showed no effect of any year on MID (P > 0.12 in all cases) and no interaction term was fitted due to unbalanced data among DRs and years (a reciprocal-transformation was used on MID to meet assumptions of equal variance). A pooled model revealed that MID was shorter during the foraging subseasons than during egress (foraging: $t = 2.96$, df = 37, P < 0.01; Figure 3.6). There was no significant effect of DR (P > 0.21 in all cases).

A two-factor ANOVA for the foraging subseason, fitted without an interaction term, revealed no effect of year or DR on MID (DR: $F_{3,36} = 0.90$, P = 0.45; year: $F_{6,36} = 2.06$, P = 0.08). Average MID over the foraging season was 20.1 ± 19.4 (SD) m.

Mean distance between consecutive relocations (MED)

Mean distances traveled between relocations were highly variable while snakes were

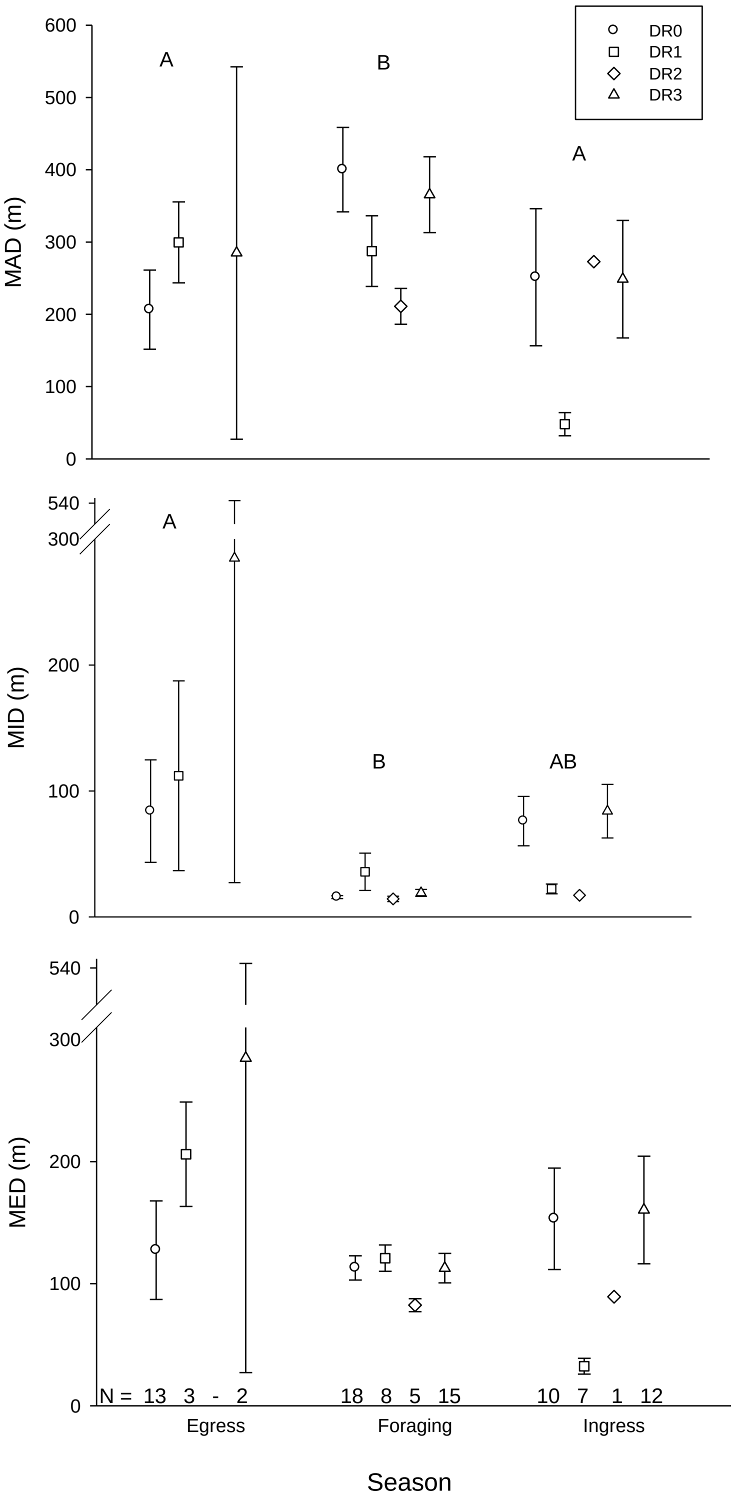

Figure 3.6. Mean ± 1 SE of maximum (MAD), minimum (MID) and mean (MED) distance between consecutive relocations of male and non-gravid female snakes. The snakes are categorized according to the disturbance rating assigned to their capture sites, as well as different periods during the active season. Data were collected from 2006 - 2012. Different uppercase letters indicate a significant difference between subseasons at $\alpha = 0.05$.

moving between hibernacula and foraging grounds, but otherwise were fairly consistent among areas during the foraging season. The mixed-effects model showed no effect of any year on MED ($P > 0.08$ in all cases) and no interaction term was fitted due to unbalanced data among DRs and years (the data were log-transformed to meet assumptions of equal variances). A pooled model revealed no significant differences among subseasons ($P > 0.55$) or DRs ($P > 0.36$; Figure 3.6).

A two-factor ANOVA for the foraging subseason, fitted without an interaction term, revealed no effect of year or DR on MID (DR: $F_{3,36} = 1.13$, $P = 0.35$; year: $F_{6,36} = 1.83$, $P = 0.12$). Average MED over the foraging season was 110.9 ± 40.3 (SD) m.

Movement frequency (MF)

Movement frequency was highly variable while rattlesnakes were traveling to and from hibernacula, but while foraging, movements tended to occur more frequently in the least disturbed areas. The mixed-effects model showed no effect of any year on MF ($P > 0.07$ in all cases) and no significant interaction terms ($P > 0.37$ in all cases), so the data were pooled among years and interaction terms were removed from the model. A pooled model revealed that MF was slightly, but significantly, greater during the foraging and ingress subseasons than during egress (foraging: $t = 2.09$, df = 48, $P = 0.04$; ingress: $t = 4.07$, df = 48, $P < 0.001$; Figure 3.7). There was no significant effect of DR ($P > 0.34$ in all cases).

A two-factor ANOVA for the foraging subseason showed an effect of DR, but not year or the interaction term (DR: $F_{3,29} = 2.91$, $P = 0.05$; year: $F_{5,29} = 2.34$, $P = 0.07$; year × DR: $F_{7,29} = 1.06$, $P = 0.42$). However, post-hoc tests revealed no significant differences between pairwise DR comparisons ($P > 0.07$ in all cases). Average MF over the foraging season was 0.76 ± 0.12 (SD).

Mean movement rate (MMR)

Similar to movement frequency, movement rates were highly variable while rattlesnakes were traveling to and from hibernacula. While foraging, no trends were observed across the gradient of disturbance. The mixed-effects model showed no effect of any year on MMR ($P > 0.07$ in all cases) and no significant interaction terms ($P > 0.39$ in all cases), so the data were

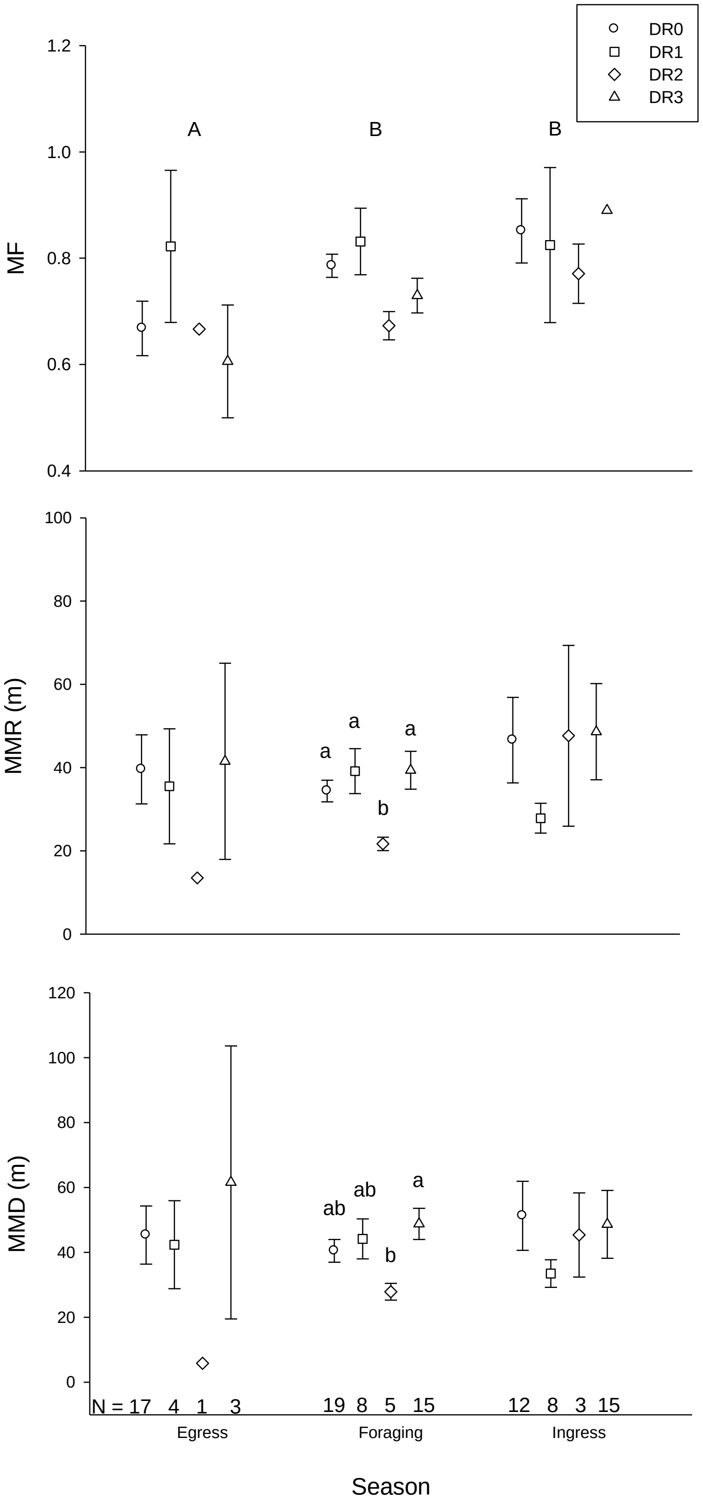

Figure 3.7. Mean ± 1 SE of movement frequency (MF), movement rate (MMR), movement distance (MMD) and set movement time (SMT) among subseasons of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada, between 2006 and 2012. Different uppercase letters indicate a significant difference between subseasons at α = 0.05. Lowercase letters indicate a significant difference between DRs within a subseason.

pooled among years and interaction terms were removed from the model (the data were log-transformed to meet assumptions of equal variances). A pooled model revealed no significant differences among subseasons ($P > 0.15$) or DRs ($P > 0.17$; Figure 3.7).

A two-factor ANOVA for the foraging subseason showed an effect of DR and year, but not the interaction term on MMR (DR: $F_{3,30} = 4.35$, $P = 0.01$; year: $F_{6,30} = 4.34$, $P < 0.01$; year × DR: $F_{7,30} = 0.73$, $P = 0.65$). Post-hoc tests revealed that MMR in DR2 was significantly lower than in DR0 ($P = 0.03$), DR1 ($P = 0.01$) and DR3 ($P < 0.01$) (Figure 3.7). In 2011, MMR was significantly lower than in 2006 ($P = 0.02$) and 2012 ($P = 0.01$).

Mean movement distance (MMD)

Similar to movement rate, mean movement distance was variable while rattlesnakes were traveling to and from hibernacula. No trends were observed across the gradient of disturbance within any subseason. The mixed-effects model showed that MMD was significantly lower in 2007 ($t = -2.65$, df = 10, $P = 0.02$) and lowest in DR2 ($t = -2.56$, df = 39, $P = 0.01$; Figure 3.7), and there was a significant interaction between the ingress subseason and DR2 ($t = 2.18$, df = 43, $P = 0.03$). However, only one snake met the requirements to be included in the analysis within DR2 for the ingress season, and this value was lower than any other observation (Figure 3.7), so a model with no interaction term was also fitted. This revealed no significant differences in MMD among subseasons ($P > 0.09$) or DRs ($P > 0.13$), but the difference in year 2007 remained ($t = -2.48$, df = 10, $P = 0.03$). The data were log-transformed to meet assumptions of equal variances between groups.

A two-factor ANOVA for the foraging subseason showed an effect of DR and year, but not the interaction term on MMD (DR: $F_{3,30} = 3.71$, $P = 0.02$; year: $F_{6,30} = 4.48$, $P < 0.01$; year × DR: $F_{7,30} = 0.62$, $P = 0.74$). Post-hoc tests revealed that MMD in DR2 was significantly lower than in DR3 ($P < 0.01$; Figure 3.7). In 2011, MMD was significantly lower than in 2006 ($P < 0.01$) and 2012 ($P = 0.02$).

Set movement time (SMT)

Since SMT relied on a specific set distance of 45 to 55 m, many snakes were excluded from the analysis and sample size was reduced compared to other analyses (N =

46). During egress, only snakes within DR0 remained in the dataset (N = 5). During ingress, one snake from DR0, two from DR1, and three from DR3 were included. Since the majority of the dataset represents the foraging subseason (N = 35), a mixed-model for repeated measures over subseasons was not performed. Instead, only ANOVA was used for the subseason data. The data were log-transformed to meet assumptions of equal variances between groups.

Generally, it took rattlesnakes less time to move the set distance in areas of least disturbance. There was an effect of DR and year, but not the interaction term on SMT (DR: $F_{3,22} = 4.29$, $P = 0.02$; year: $F_{5,22} = 6.96$, $P < 0.001$; year × DR: $F_{4,22} = 2.12$, $P = 0.11$). Post-hoc tests revealed that SMT in DR1 was significantly shorter than in DR3 ($P = 0.03$; Figure 3.8). The SMT was significantly longer in 2008 and 2012 than in 2009 ($P < 0.04$) and 2010 ($P < 0.03$).

Fractal dimension (FD)

Rattlesnake movement paths were more linear than crooked, with the greatest tortuosity seen during the foraging subseason. The mixed-effects model showed no effect of any year on FD ($P > 0.12$ in all cases) and no interaction term was fitted due to unbalanced data among DRs and years. A pooled model revealed that FD was greatest during the foraging subseason ($t = 7.5$, df = 34, $P < 0.001$; Figure 3.9). There was no significant effect of DR ($P > 0.31$ in all cases). The plot of residuals against fitted values for this model, however, showed evidence of non-homogenous data, and no appropriate transformation of FD resolved the linear trend of the model error, so care should be taken in the interpretation.

A two-factor ANOVA for the foraging subseason showed no significant interaction effect (year × DR; $F_{7,29} = 2.29$, $P = 0.06$). A model fitted without the interaction term showed no significant effect of either year or DR (year: $F_{5,36} = 0.45$, $P = 0.81$; DR: $F_{3,36} = 2.05$, $P = 0.12$).

Temperature effects

Both full and partial season datasets from all years were used in the temperature analyses, with a total sample size of 798 movement events. Logistic regression revealed that

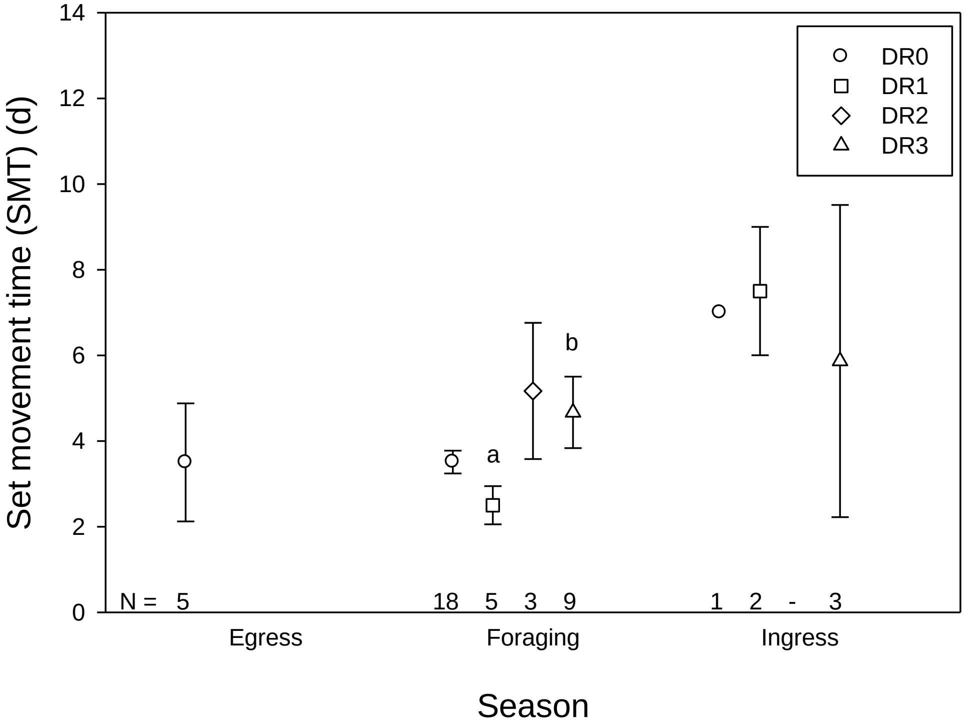

Figure 3.8. Mean ± 1 SE of set movement time (SMT) of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada, between 2006 and 2012. Different lowercase letters indicate a significant difference between DRs within a subseason at α = 0.05.

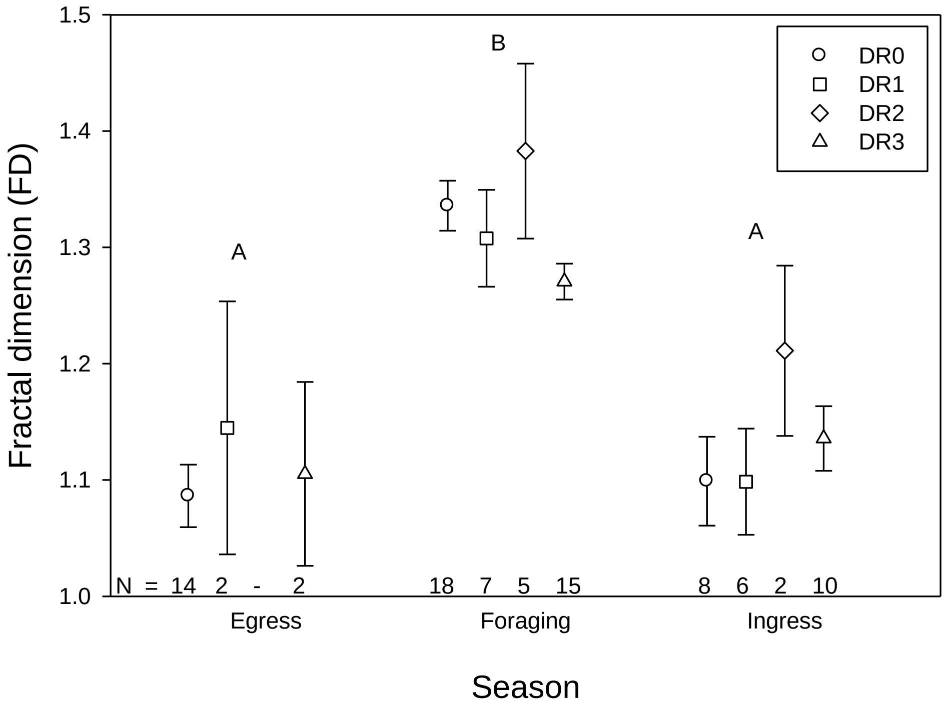

Figure 3.9. Mean ± 1 SE of fractal dimension or tortuosity (FD) of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada, between 2006 and 2012. Different uppercase letters indicate a significant difference between subseasons at $\alpha = 0.05$.

maximum daily temperature was associated with snake movement probability (Wald's χ^2 = 6.4, df = 1, P = 0.01), and there was an overall effect of DR (Wald's χ^2 = 15.9, df = 3, P = 0.001). An interaction between temperature and DR2 shows that temperature was associated mainly with movement in that disturbance category, where the animals were less likely to move at lower temperatures (P = 0.04; Figure 3.10). There was no trend in movement probability over disturbance categories. Overall, snakes in DR0 had a higher probability of having moved in a 48 hour period than snakes in DR1 ($P < 0.001$) and DR3 ($P < 0.01$).

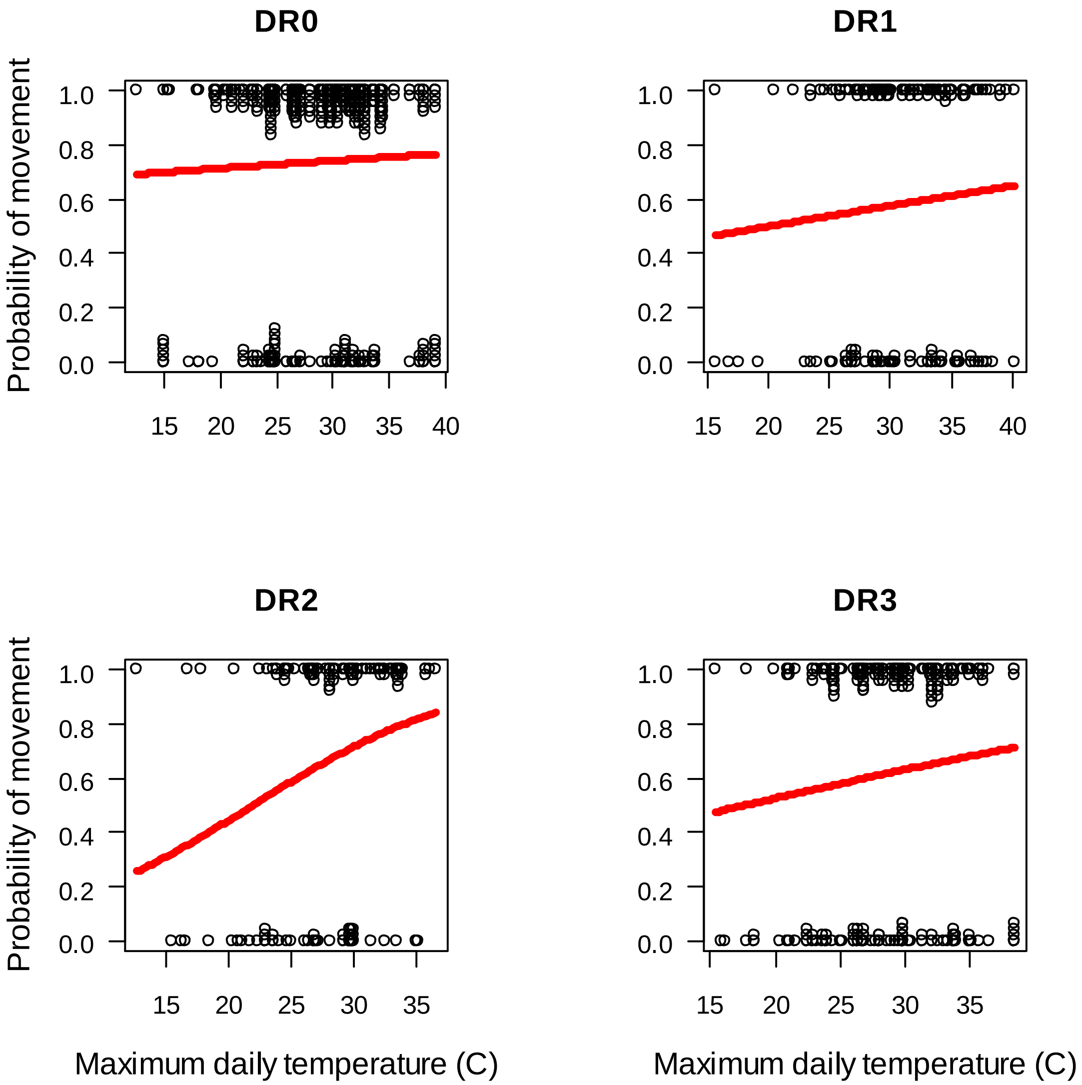

Figure 3.10. Individual relationships for snake movement probability in relation to maximum daily temperature for DR0, DR1, DR2 and DR3 of male and non-gravid female Northern Pacific Rattlesnakes captured within each disturbance rating (DR) on the study site in Osoyoos, British Columbia, Canada, between 2006 and 2012. Points indicate frequency of occurrences of movement and no movement by temperature. Lines represent predicted movement probability.

DISCUSSION

My results show that snakes in some disturbed sites had smaller core areas, shorter range lengths, shorter maximum displacements from hibernacula, lower movement rates, and took a greater number of days to travel a given distance than snakes in the least disturbed habitats. Contrary to my expectations, snakes in highly disturbed sites did not necessarily move greater total distances, have greater movement frequencies, higher movement rates, and more convoluted movement patterns (greater tortuosity). The study also revealed differences in range and movement parameters between subseasons and a trend of smaller home range sizes and range widths in disturbed areas. However, the differences and trends observed do not necessarily hold across all disturbance rating groups, suggesting that accurately predicting the magnitude of disturbance effects on rattlesnake spatial ecology will not be straightforward.

Overall, the patterns I observed do not suggest that rattlesnake spatial ecology at my study site is unique from other years and areas in British Columbia. Minimum convex polygon (MCP) home ranges, range lengths (RLs), and range shapes (RSs) measured in this study are consistent with metrics measured in an earlier study on this site. Brown (2006) found MCP area, RL and RS in his control treatment (similar to DR0 in this study) to be 25.1 ± 16.8 ha, 1082 ± 328 m, and 0.33 ± 0.15 m (mean ± SD), respectively. My results revealed a wide range of distances traveled by snakes from hibernacula, which has also been documented at other sites. Generally, males in grassland and shrub-steppe areas have been found to travel under 1.4 km from hibernacula (up to 1.2 km: Macartney 1985; 0.92 - 1.4 km: Bertram et al. 2001; 0.30 - 1.0 km: Gomez 2007), which is consistent with my results. Exceptions do occur however, with rattlesnakes at higher elevations in Ponderosa Pine and Interior Douglas-fir habitats having been documented as far as almost 4 km away from den sites (3.5 km: Gomez 2007; 3.9 km: Gosling, pers. comm.). Larger travel distances were also documented in this study in the ‘mountain’ snake group (up to 2.8 km, with greater distances suspected). It is unclear at this time what drives such large movements into upper-elevation habitats, but changes in prey type and abundance may be one explanation, as prey abundance has been shown to influence habitat use in snakes (Whitaker and Shine 2003, Jenkins and Peterson 2005).

Disturbance effects

Although many studies have investigated rattlesnake spatial ecology throughout North America and in varying habitats, few have examined movement patterns in relation to disturbance. This is the first study to compare disturbance effects on *C. oreganus* range and movement parameters within homogenous habitat and topography.

Given that rattlesnakes in the most heavily disturbed and developed areas may encounter physical barriers to movement, such as buildings and fences, it is not surprising that ranges in these sites tended to be smaller. However, many sites classified as disturbed did not necessarily contain physical obstacles. Instead, the landscape in some areas is interrupted by other permeable (at least in theory) features, such as heavily-used walking trails, golf course fairways, and landscaping. Smaller core areas and range lengths in these areas suggest, then, that rattlesnakes may be (a) treating such developments as physical barriers, and/or (b) responding to disturbances associated with the developments by remaining motionless, as opposed to leaving the area. Remaining motionless has been shown to be a typical rattlesnake response to direct human presence (Prior and Weatherhead 1994). If rattlesnakes reacted to human presence by leaving the area and abandoning otherwise preferred habitat (Brown 1993), then I should have expected to see greater movement frequencies, greater total movement, and higher tortuosity, which I did not. In a similar study investigating human disturbance effects on the Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*), Parent and Weatherhead (2000) found support for the motionless response; gravid females, non-gravid females and males in their study all moved shorter distances and less frequently in human-disturbed sites. Although I did not document such significant differences, I did observe that movement frequency (MF) was lower during the foraging season in the two most disturbed habitat categories. Similarly, after comparing Timber Rattlesnake (*Crotalus horridus*) spatial ecology before, during and after commercial logging operations, Reinert et al. (2011) found no short-term changes in snake behaviour or movement patterns in affected areas. These studies highlight the repeated use of habitat and well-documented high fidelity of rattlesnakes for established activity areas and movement corridors (Sealy 2002, Travsky and Beauvais 2004, Jenkins and Peterson 2005, Brown 2006, Gomez 2007, this study), even potentially in the wake of habitat disturbance.

Implications for conservation

My results suggest that rattlesnakes may be experiencing smaller core range sizes and shorter range lengths in disturbed sites. Overall, however, it appears snakes are not changing their daily movement behaviour. This raises the question of whether smaller ranges will impact individual animals and the population as a whole. The observations of consistent and repeated movement patterns, year after year and between sites, imply that rattlesnake behaviour may be resistant to disturbances and fragmentation. However, in Chapter 2 I showed that snakes in the disturbed areas weighed less overall, had significantly lower body condition, and lost weight throughout the foraging season. This suggests there are negative effects stemming from use of more disturbed areas. Although the precise mechanism for these effects is not clear, my results suggest they are not due to increased movement.

There may be a range of indirect disturbance effects that affect snake condition and weight gain, but not behaviour or movement patterns. One hypothesis is that prey density and quality is reduced in disturbed sites due to poorer natural habitat and food resource quality. Jenkins and Peterson (2005) found that disturbed landscapes had fewer prey, lower prey biomass, and fewer large prey items. Nearer to my sties, in the South-Central Okanagan, Sullivan and Sullivan (2006) found that undisturbed sagebrush habitats held some of the highest overall small mammal abundances and diversities compared to a variety of other habitat types. Small mammal density surveys at my study site would help to clarify this issue, although populations of these animals are notoriously erratic through time and lengthy data sets will likely be needed to identify any linkages. A second hypothesis is that the snakes may be susceptible to disturbances through habitat fragmentation itself, and not necessarily the physical presence of people and buildings. This “edge-exposure” hypothesis states that species, irrespective of population size, are susceptible to the effects of fragmentation because their movement patterns leave them most exposed to edge effects (Woodroffe and Ginsberg 1998, Mitrovich et al. 2009). Human activities in disturbed sites can also modify habitat attributes and change the microclimates within them (Knight and Cole 1991). I did not detect strong differences in movement patterns between sites. My data also showed no clear relationship between temperature, movement probability, and disturbance category. By not altering movement patterns and behaviour, rattlesnakes in disturbed areas may be exposed to microhabitat refuge sites along edges (or within their ranges) that differ in quality or quantity from natural landscapes. If disturbed areas have poorer microhabitat availability, a snake's ability to thermoregulate and forage effectively might be compromised. Control of body temperature through thermoregulation is essential for foraging ability, development, growth, digestion, and immune function (Peterson et al. 1993). In addition to changes in prey composition, edge-adapted predators associated with urban areas and mortality on roads and through persecution place added constraints on this vulnerable species.

Conservation planning

A major constraint of conserving snake species is a lack of basic population estimates over time. Accurate demographic data are difficult and often impractical to collect, especially for cryptic species. In such cases, using knowledge of snake behaviour and spatial ecology can be used as a proxy. For example, Rouse et al. (2011) used knowledge of space use of Eastern Massasauga Rattlesnakes and Eastern Hog-Nosed Snakes to make predictions of the effects of roads on resident populations and provide ways of mitigating for the effects. Similarly, this study provides insight into the longevity of rattlesnakes at similar sites within B.C., in the absence of detailed demographic data.

The behaviour and spatial ecology of rattlesnakes in this study were shown to be fairly consistent across sites of varying disturbances, with some significant differences in core area sizes and range lengths between areas of high and low disturbance. These findings, combined with the continued use of disturbed habitat over each active season, suggest that rattlesnakes at this site may not possess the behavioural plasticity needed to adjust to and avoid the disturbances that will undoubtedly increase as urbanization and habitat fragmentation continue. Increased urbanization will likely increase any edge effects, mating disruptions, persecution events, and interactions with roads.

The key to maintaining rattlesnake populations in urbanized areas may be to decrease edge effects by maintaining high-quality microhabitat refuges that aid in thermoregulation and enhance prey populations. Conservation of the Northern Pacific Rattlesnake will be aided by investigations into prey density and quantification of microhabitat-use across disturbed and natural landscapes. Additionally, since snakes in this study displayed site-fidelity even when disturbances were present, secure fencing along roadsides will be essential to help prevent fatalities along established and future roads. When combined with what is known about snake body condition and weight loss at this site, the results presented here highlight the discrete nature of indirect disturbance effects. The continued presence of animals in urbanized areas as well as their mostly unvarying movement patterns from natural areas may be misleading assessments of population viability.

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CHAPTER 4: CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The overall goal of my thesis was to expand our understanding of how urbanized or disturbed landscapes may affect wildlife. More specifically, I aimed to investigate the indirect effects of anthropogenic disturbances on a population of Northern Pacific Rattlesnakes and, in doing so, contribute information for the future management and recovery of the species in British Columbia and elsewhere. Two main objectives were pursued: (1) examine the body characteristics and behaviour of rattlesnakes in both natural and disturbed areas, and (2) compare the spatial ecology of rattlesnakes between areas.

The major results of my thesis are:

- Rattlesnakes in highly disturbed landscapes had lower body condition (i.e. lower mass given their length) than snakes in other areas. Snakes in the least disturbed regions had the highest body condition.
- Rattlesnakes residing in disturbed areas lost weight on average over the foraging season, whereas snakes in undisturbed and mountain areas gained weight.
- No differences in snake daily behaviour or exposure risk were observed between sites.
- Strong trends in spatial ecology parameters were not apparent across my disturbance rating categories.
- Somewhat unexpectedly, individual rattlesnakes that traveled higher into the mountains tended to be larger, gained greater amounts of weight over the active season, and grew at faster rates than all other groups of snakes residing in both disturbed and undisturbed lower elevation shrub-steppe habitat.

In general, these results bear out my predictions that disturbance would have a negative effect on rattlesnake body condition and weight gain, although I did not observe significant differences in growth rates, exposure risk, or behaviour. Also contrary to my predictions, snakes in highly disturbed sites did not necessarily move greater total distances, have greater movement frequencies, higher movement rates, or display more convoluted movement patterns (greater tortuosity) than snakes in natural landscapes. Overall, however, both the predicted and unexpected results of this study may have significant ramifications for the conservation and persistence of these animals.

Management recommendations

My study has implications for the conservation of Northern Pacific Rattlesnakes in British Columbia, and perhaps snakes elsewhere. The recovery strategy for these animals (Southern Interior Reptile and Amphibian Recovery Team 2008) identified several critical knowledge gaps, namely the need for (1) long-term population monitoring to address population trends and persistence, (2) biological and ecological research to quantify population viability, and (3) threat clarification research to assess the ability of rattlesnakes to adapt to habitat characteristics that have been altered by increased human activity. It is the last two points especially that my study will help to address. Based on the results of this work, I make the following recommendations:

- ***Protect and maintain important prey habitat and refuge sites***

The most striking results seen in my study were the differences in body condition and weight gain observed across the gradient of disturbance (Chapter 2). This study did not investigate the causes for the observed differences, so any explanations remain speculative until further research is conducted. I hypothesized that a) prey density and/or quality may be reduced in disturbed sites, or b) essential microclimates required for thermoregulation may be changed due to landscape modification. In order to support prey populations and maintain microhabitats for snakes, managers may have to provide increased protection and maintenance of native habitat, in this case shrub-steppe vegetation.

Anthropogenic activities can have severe long-term effects on shrub-steppe communities. For example, the antelope-brush/ needle-and-thread grass (*Purshia tridentata/ Hesperostipa comate*) ecosystem in the southern Okanagan Valley has suffered a loss of almost 70% of its original extent from 1800 to 2008 (Iverson 2012). Big sage-brush (*Artemisia tridentata*) communities in the Okanagan Valley have also undergone a significant reduction in extent of occurrence (Lea 2008). Recovery of remaining disturbed shrub-steppe habitat, and thus the small mammal communities that rely upon it, is difficult to accomplish since *Artemisia* and *Purshia* are relatively slow growing plants; indeed, Hales (2011) noted that it could take up to 30 years for *Artemisia* to reach the average stem diameters used by mice as retreat sites in a lower grassland community in B.C. (as measured by Perryman and Olson (2000)). Efforts to increase prey availability for rattlesnakes could include conservation and specific protection of already mature shrub-steppe plants in areas of construction, as well as transplantation of mature plants from healthy populations to disturbed sites.

The protection and recovery of mature shrub-steppe plants may also protect vital microhabitat and refuge sites for rattlesnakes. Microhabitat features can be useful predictors of rattlesnake habitat use (Gomez 2007), and therefore may be associated with essential physiological processes. Microhabitat may play an important role in the ability of rattlesnakes to thermoregulate (Reinert 1993, Pike et al. 2010) and therefore forage effectively, digest prey, and maintain immune function (Peterson et al. 1993). In addition to protecting existing mature shrub-steppe plants, wildlife and land managers could consider replanting or reseeding already disturbed areas with shrubs and other vegetation.

- ***Protect neighbouring habitat***

The home range sizes and maximum distances from hibernacula (MDH) I calculated in this study (Chapter 3) can be used by managers in the area to define the extent of habitat requiring recovery or protection for rattlesnakes. On provincial land with similar habitat and topography to my site, range size, MDH, and range shape values could be used to guide creation of Wildlife Management Areas (WMAs). The data collected from rattlesnakes that travelled up into the eastern mountains of the study area (see Figure 1.2) are particularly important to use for the creation of WMAs. These snakes tended to travel farther than snakes in lower elevations. This may have been due to the fact that the snakes travelling into higher elevations were larger (and therefore can traverse greater distances), there were no artificial or natural barriers to movement (e.g. fencing, lakes), or that the snakes simply traveled farther and in relatively straight lines in search of additional prey types (Duvall et al 1985). The mountain habitat used by snakes in my study was in close proximity to a proposed new development area in the Osoyoos region (“Regal Ridge”). To use this mountain habitat, the snakes that I tracked crossed from the Osoyoos Indian Reserve, into the Anarchist Protected Area, and then into crown (unprotected) land. To my knowledge, this is the first documentation of how snakes from this study site are using these upper-elevation forests, and the data may be useful in future regional planning, such as the extension of protected area notations. In addition, to minimize effects on these ‘mountain’ snakes, resource managers (e.g. forestry and cattle industry) or developers could limit disruptive activities in this mountain area to late autumn, winter, and early spring when rattlesnakes remain in hibernacula. Some sort of action would seem prudent, given that the ‘mountain snakes’ in my study were the largest and most robust of the animals I surveyed.

- ***Use multiple indicators of population stability***

Recent work has shown overall annual survival in my study area to be relatively high (Bishop et al., unpubl. data), which is encouraging for the conservation of the population. However, the poor body condition and weight loss documented in individuals from highly disturbed areas in this study imply less-obvious and negative consequences for the Osoyoos rattlesnake population. As discussed in Chapter 2, poor weight gain (or the opposite - weight loss) may cause delayed maturity and reduced fecundity (Taylor et al. 2005). Poor body condition has the potential to lower reproductive threshold (Madsen and Shine 1999, Taylor et al. 2005), reduce litter size and offspring body condition (Jenkins et al. 2009), and eventually lower survival in snakes (Shine et al. 2001, Kissner and Weatherhead 2005). As development and human-use of habitat increases, managers should avoid relying exclusively on survival estimates as an indicator of population stability. As long-lived animals, changes in survivorship due to more recent disturbances and habitat alteration may not be detectable at this point in time.

In future years, increased numbers of snakes across B.C. and elsewhere will likely be exposed to similar conditions, possibly causing the same poor body condition and weight gain documented in this study.

- ***Promote education***

Persecution by humans is a persistent problem in the conservation of rattlesnakes (Bertram et al. 2001, Didiuk et al. 2004), and my study was no exception. Achieving snake recovery goals will require a multi-faceted research and management approach, and public outreach programs and education can help address the issue of persecution. The provision of snake relocation services in areas of high human-snake interaction can also provide educational opportunities (Bertram et al. 2001). Wildlife managers should consider this aspect when planning for recovery efforts, and allocating resources for conservation.

Limitations and future research priorities

I could not obtain detailed information on all categories of snakes in the study population, which limits the degree to which my data can be extrapolated. Juveniles and gravid females were not implanted with transmitters in this study due to size restrictions and health concerns, a common pattern in many studies of snakes. Animals of different age and reproductive classes, however, may have responded differently to disturbances (e.g. Burger 2007). For example, juveniles or gravid females may have altered their behaviour and movements in the disturbed landscapes. Younger snakes may be especially sensitive to potential predators (e.g. Roth and Johnson 2004, Burger 2007), and therefore may react more significantly to disturbances from humans. Juveniles relying on increased crypsis in disturbed landscapes may suffer fitness costs from reduced foraging or increased avoidance, or lower overwinter survival if body size remains small (Ashton 2001). Future studies would ideally combine behavioural studies of juveniles while also tracking juvenile survival, although current technology (i.e. transmitter size) makes this very difficult. Gravid female Eastern Massasauga Rattlesnakes have been shown to change their behaviour and movement patterns in the face of human disturbance (Parent and Weatherhead 2000). If gravid females are being impacted by disturbance, reproductive success may be affected. While this possibility remains untested in this study, future research could benefit from including gravid females in behaviour and exposure analyses (where it is deemed warranted, given the health risks associated with implantation), as well as reproductive success.

In addition to investigations of different age and reproductive classes, rattlesnake conservation near urban areas could be aided by studies of prey density and prey habitat preferences within disturbed and natural landscapes. Earlier, I hypothesized that prey availability could be responsible for the differences in body condition observed in this study. To investigate this hypothesis, small mammal trapping and microhabitat preference studies will be necessary to piece together a map of prey densities within a mosaic of disturbance regimes. Manipulated feeding experiments with free-ranging snakes would also be powerful tests of whether food levels are affecting individuals in different areas of disturbance.

Combined with prey density studies, research into other sources of indirect disturbance effects that may be influencing snake body condition would be valuable. For example, identification of microhabitat used by rattlesnakes across a disturbance gradient may shed light on whether snakes are able to find and use preferred habitat features in disturbed sites. Although my study did not detect any striking differences in movement and behaviour between disturbance ratings, it is possible that differences in microhabitat-use were occurring at a finer scale than I recorded.

Future studies on this snake population could incorporate adrenal hormone (corticosterone) or stress testing in the study design to help explain why body condition and weight gain were different among disturbance ratings. Human-animal interactions can cause physiological responses and impact the stress physiology of a variety of wildlife species, which might have consequences for individual fitness (French et al. 2011). While increases in stress hormone levels from capture and confinement has been documented in rattlesnakes (e.g. Lutterschmidt et al. 2009), studies of stress responses to lower-level disturbance (e.g. hikers) is sparse in the snake literature, with some suggesting that mere human presence does not cause increased stress levels (e.g. Cottonmouths, *Agkistrodon piscivorus;* Bailey et al. 2009). If the same is true for the rattlesnakes in this study, it would indirectly support the low prey density and microhabitat availability hypotheses mentioned above.

A concern regarding animals residing in disturbed and fragmented habitat is that populations may become genetically isolated (Prior et al. 1997, Ujvari et al. 2006, Clark et al. 2010). Inbreeding depression could be a serious problem for rattlesnake populations that otherwise seem unaffected by disturbance. An investigation into the genetic structure of the snake population was beyond the scope of my research. Future genetic studies would be a novel way of assessing the status and stability of rattlesnake populations in B.C., and would aid in addressing some of the knowledge gaps identified in the rattlesnake recovery strategy.

Conclusions

My results contribute to our understanding of how rattlesnakes may be impacted in discrete ways within disturbed habitat, but the findings can also be applied to other animal populations. Often, reptile, amphibian and mammal species face similar disruptions in semi-developed and urban areas. These include common issues, such as barriers to movement, habitat modification, human disturbance, noise, and pollution (Boyle and Samson 1985, Knight and Cole 1991). Immediate consequences of human-wildlife interactions are well-understood: these include death through road-kill, recreational activities, or persecution. Many immediate behavioural responses of animals to human disturbance are also well understood. For example, marine mammals can demonstrate immediate, but not necessarily lasting responses to approaching humans during the breeding season (Holcomb et al. 2009), bison have greater fleeing probabilities from trucks than from snowmobiles or people on foot (Fortin and Andruskiw 2003), and deer in urban parks change their immediate behaviour in response to a variety of visitor activities (Langbein and Putman 1992). In addition to immediate responses, some long-term effects on individuals have been documented, such as shifts in behaviour patterns over time or decreased productivity (Knight and Cole 1991). While identifying the responses themselves, there are numerous studies that have identified the types of individuals that are most prone to disturbances: males or females, young or old, solitary or in groups, large or small body size (e.g. Madsen 1985, Hamr 1988, Loehr et al. 2005, Keeley and Bechard 2011). However, our knowledge of the long-term impacts of disturbance at the population level remains less clear. My results indicate that monitoring only behavioural changes or even survival rates may not expose more discrete changes in a population experiencing disturbance. Changes in the body condition of individuals, as revealed in this study, may have dire consequences for an animal population in the long-term.

To date, no other studies have focused on the effects of human disturbance on the Northern Pacific Rattlesnake, and few have addressed the topic for rattlesnakes in general. This study can be used as a starting point to further our investigations into such a pertinent issue. I believe that conserving snake populations will require both field research on the animal was well as recognition of the human element. Public awareness and understanding of rattlesnake ecology, combined with the dispelling of common myths that perpetuate persecution, will be a powerful step towards protecting the species. Ultimately, while public outreach will need to remain an integral part of rattlesnake conservation, it cannot replace proactive and directed recovery actions.

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