Movement patterns of free-ranging and translocated snakes (*Pituophis catenifer deserticola* and *Coluber constrictor mormon*) in southwestern Canada

by

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Abstract

Understanding animal movement is essential for effective wildlife stewardship. In this thesis, I used radiotelemetry to investigate the spatial ecology of two colubrid species in British Columbia, Canada.

In the first chapter, I evaluated the short-term effects of a mitigation translocation on Great Basin gophersnakes (*Pituophis catenifer deserticola*) following the destruction of their natural hibernacula. Although translocations are increasingly used to reduce the impacts of habitat loss, outcomes are rarely monitored, and research suggests they often lead to elevated stress, movement, and mortality. In this study, however, translocated individuals exhibited active season movements and survival rates comparable to those of reference snakes from the same study area. Sex-specific movements aligned with expected mate-seeking patterns, suggesting this natural behaviour was preserved post-translocation. Despite the loss of their original hibernacula, some gophersnakes (7/10) located alternative overwintering sites, demonstrating unexpected resiliency. I propose that the minimal impact of translocation in this case was due in part to most individuals being moved within their historical natural range, as well as a soft release as a social group in the spring.

In the second chapter, I describe the movement ecology of Western Yellow-bellied racers (*Coluber constrictor mormon*), presenting the first radiotelemetry study on this subspecies since the 1970s (Brown & Parker, 1976), and the first ever in Canada. Racers in this northern population had larger home ranges (10.5 ha, $N = 20$, vs. 1.45 ha, $N = 8$ in Utah) and did not exhibit the spring migratory behaviour reported in conspecifics from Utah. These differences align with previous findings that northern snake populations may have larger spatial requirements than populations at the range core, and, accordingly, data from both is essential to accurately describe species' natural history and guide wildlife stewardship.

Together, these studies highlight the importance of using data drawn from local populations to inform conservation strategies and demonstrate the utility of movement ecology in both evaluating mitigation outcomes and guiding the management of northern snake populations.

Keywords: movement ecology, northern range limit, radiotelemetry, Great Basin gophersnakes, Western Yellow-bellied racers, *Pituophis catenifer deserticola*, *Coluber constrictor mormon*, mitigation, translocation

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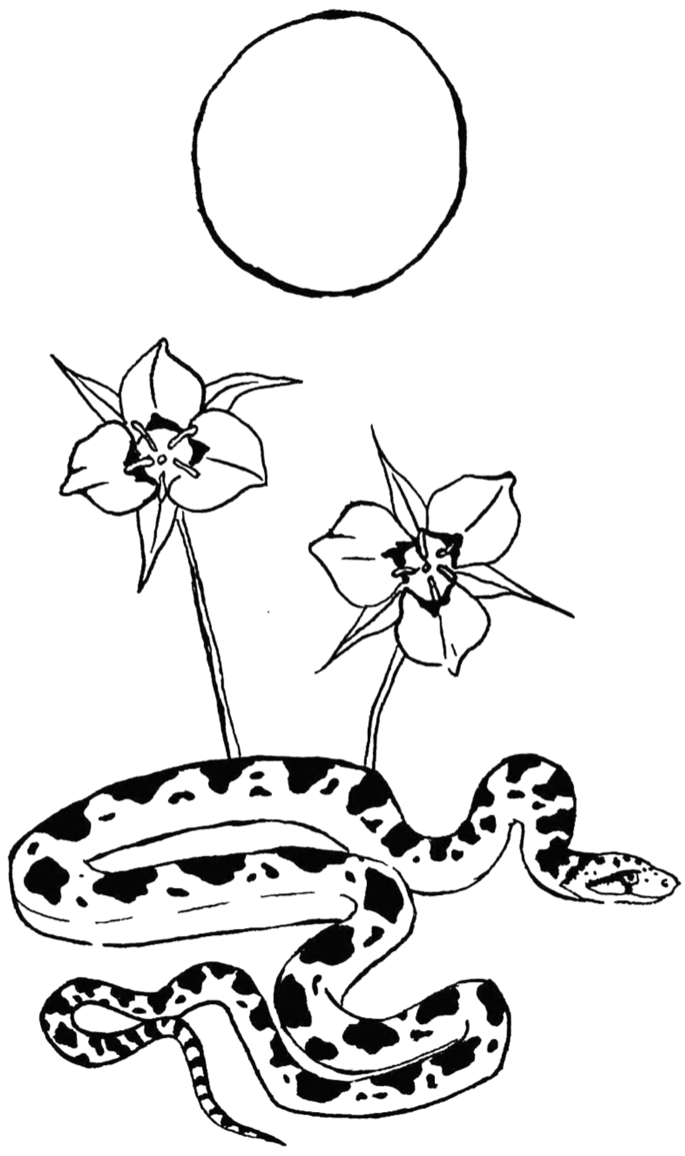
Note: In Chapters 2 and 3, I use plural pronouns to reflect the contributions of everyone involved in this thesis.



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CHAPTER 1

Introduction to the thesis

Animal Movement

Animal movement, the study of the occurrence of animals over space and time, has broad applications in ecology, conservation, and wildlife management. Animals move across the landscape to optimize access to resources (Bailleul et al., 2013), for mating opportunities (Sugita et al., 2009; Schaller et al., 2010), to escape predation (Avgar et al., 2014), and to avoid inhospitable climates. For example, Fowler's toads (*Anaxyrus fowleri*) regulate their body temperature by adjusting their depth within sand dunes in response to fluctuating ground temperatures (Forget-Klein & Green, 2021). Understanding animal movements is fundamental to comprehending behaviour and natural history, which in turn guides effective habitat conservation and species recovery strategies. Moreover, movement data can also be used as a tool in evaluating the effectiveness of conservation and mitigation actions, such as translocations, by assessing whether manipulated individuals exhibit normal movement patterns (Butler et al., 2005; DeGregorio et al., 2017).

Various approaches exist for quantifying animal movement. For instance, trajectories—sequences of consecutive location points with timestamps—are used to calculate metrics such as movement rate (trajectory over time), sinuosity (straightness of a trajectory), and recursiveness (number of times a location is revisited). Peripheral location points can be used to calculate areas and generate values like home range, which is the area an animal regularly lives and moves in (Powell & Mitchell, 2012; Van Moorter et al., 2016). Quantifying animal movement provides crucial insight into how individuals and populations interact with their environment. It allows researchers to identify movement patterns that vary according to factors such as sex, age, body size, habitat type, and geographic location within the species' range. Movement data can provide a baseline from which we can assess how animals respond to disturbance and adapt to environmental changes, making it a valuable tool for both ecological research and conservation planning.

Animal Movement at Northern Latitudes

Animals in northern climates will adapt their movement patterns to cope with environmental stressors. Many northern species undergo seasonal migrations to escape inhospitable winters (Alerstam & Bäckman, 2018). Migration distances vary both within and between species (Rouse, 2006). For example, migratory birds travel large distances between northern breeding grounds and southern winter ranges (Winger et al., 2018), while some northern snakes undergo shorter migrations between active season home ranges and winter refuges (Gienger & Beck, 2011; Gomez et al., 2015; Howarth et al., 2025; Shine & Mason, 2004).

The effect of local temperature on movement patterns is especially evident in ectothermic reptiles, such as snakes, as their summer active period—when above-ground temperatures are warm enough for foraging, mating, and gestation—varies significantly by latitude. Shorter active seasons at higher latitudes can significantly influence population-level movement, resulting in snake populations at the northern periphery exhibiting different migration distances, movement patterns, and home range sizes than snake populations farther south (Martino et al., 2012). The timing of migrations to (ingress) and from (egress) winter dens also may vary depending on environmental conditions as well as the size and species of the snake (Dyugmedzhiev et al., 2019). This variation underscores the importance of local climate in shaping movement patterns across populations of wide-ranging snake species.

Threats to Grassland-Adapted Snakes at Northern Latitudes

The southern interior of British Columbia, Canada, is the northern range limit for several species of North American grassland-adapted snakes including the Great Basin gophersnake (*Pituophis catenifer deserticola*) (Figure 1.1) and the Western Yellow-bellied racer (*Coluber constrictor mormon*) (Figure 1.2), both of which are threatened in Canada (COSEWIC 2013, 2015a). Because of their extremely limited range within the country, northern grassland snakes are heavily impacted by habitat loss. In Canada, most of the suitable grassland habitat in the province remains on unprotected crown and private lands (Environment Canada, 2014; Haney & Sarell, 2007), leaving snake species that are dependent on these ecosystems highly vulnerable to urban and industrial development (COSEWIC 2013, 2015a; Woo-Durand et al., 2020). Along with the actual loss of habitat, the development of grasslands presents other impacts to snakes, with roads causing significant mortality (Breininger et al., 2012; Eye et al., 2018), particularly during periods of migration (Neumann & Mebert, 2011). Persecution by humans and the destruction of habitat features such as egg-laying sites and hibernacula are additional threats present in anthropogenic landscapes (Olson et al., 2015; Takats, 2002).

Study Site

The Thompson region of British Columbia is situated in the dry interior of the province. There are nine biogeoclimatic zones in the Thompson region, including a grassland ecosystem, Bunchgrass zone (BG), that supports several snake species (COSEWIC, 2013, 2015a, 2015b; Ministry of Environment, n.d.). Our research took place in the lower grasslands, also known as the Thompson Very Dry Hot Bunchgrass Biogeoclimatic zone (BGxh2). The terrain is hilly and ranges in elevation from 335 to 700m (Vyse et al., 2000). Bluebunch wheatgrass (*Pseudoroegneria spicata*) and Big sagebrush (*Artemisia tridentata*) are the predominant native vegetative species (Wikeem & Wikeem, 2004).

This study took place in the Lac du Bois Grasslands Protected Area (hereafter Lac du Bois), one of the largest protected grasslands in the province (Ministry of Sustainable Resource Management & Ministry of Water, Land and Air Protection, 2004). Lac du Bois was established in 1996 and covers 15,207 ha of grasslands and dry forests (Vyse et al., 2000). The climate is hot and dry (Wikeem & Wikeem, 2004), with March and April receiving the lowest precipitation (Figure 1.3). Lac du Bois is situated immediately north of the city of Kamloops, and all our field research occurred in Kamloops city limits, within 3km of the Bachelor Bike Trails (LAT: 50.724151, LON: -120.402297). Due to its accessibility, the study area was frequented by hikers, dogs, and mountain bikers. Three threatened snake species, the Great Basin gophersnake (*P. c. deserticola*), Western Yellow-bellied racer (*C. c. mormon*), and Western rattlesnake (*Crotalus oreganus*), are known to inhabit the low-elevation grasslands in Lac du Bois (COSEWIC 2013, 2015a, 2015b).

Figure 1.1. Pictured is an adult Great Basin gophersnake (*Pituophis catenifer deserticola*). Photo by Maria Collins.

Figure 1.2. Pictured is an adult Western Yellow-bellied racer (*Coluber constrictor mormon*) that is partially concealed by vegetation. Photo by Maria Collins.

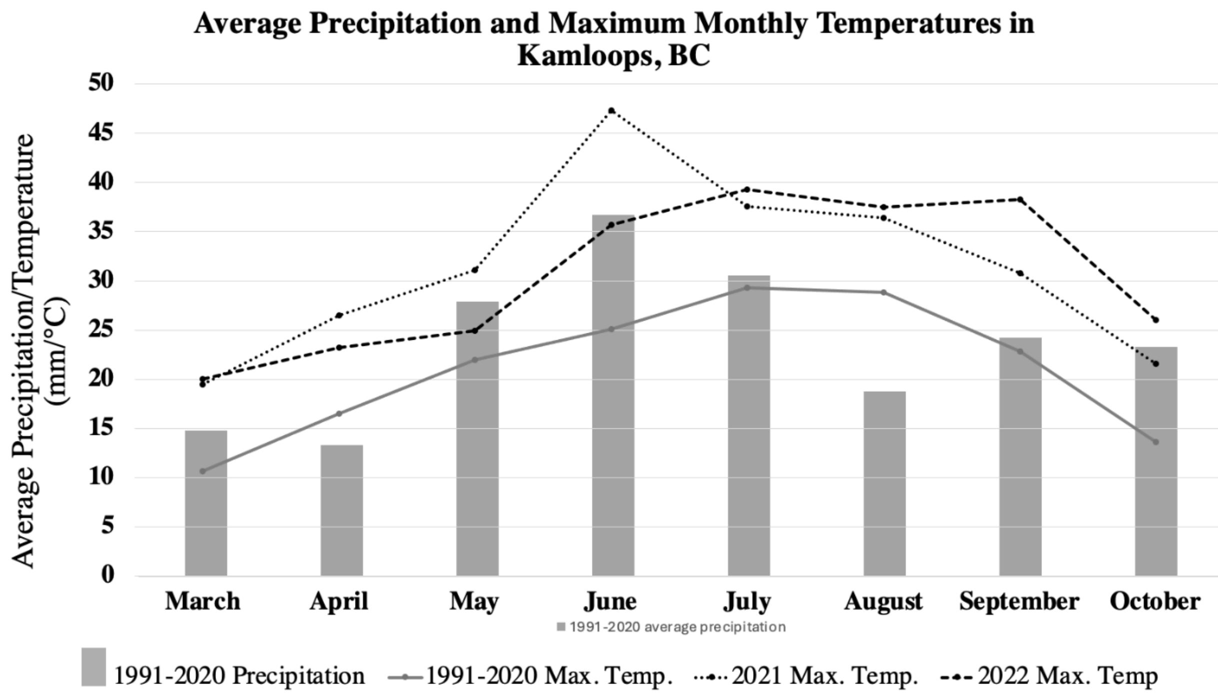

Figure 1.3. Graph of average monthly precipitation and maximum temperatures in Kamloops, BC. The bars and solid line represent the 30-year historical norms (1991-2021) of precipitation and average maximum temperature, and the dotted and dashed lines represent maximum temperatures in 2021 and 2022 respectively. Climate data were sourced from: climate.weather.gc.ca and kamloops.weatherstats.ca.

Overview of the Pipeline Disturbance

A unique research opportunity emerged following a large-scale disturbance in Lac du Bois, where the impact of industrial development on snake habitat prompted a large mitigation project. In October 2020, the Trans Mountain Expansion Project (TMEP) encountered a significant conservation challenge when it discovered three snake hibernacula (hereafter Disturbed Dens 1, 2, 3) along an old pipeline that had been in place since the 1960s (Kheraj, 2015; Trans Mountain, 2021). Because the hibernacula were located on the old pipeline and directly impeded the construction of the pipeline expansion, TMEP was granted permission to destroy the three dens pending the salvage and relocation of all resident snakes (Heinrich, 2020). Three species of snakes, Great Basin gophersnake, Western Yellow-bellied racer, and Western rattlesnake, were present in these dens. All are federally listed as threatened (COSEWIC 2013, 2015a, 2015b) and classified as ‘at risk’ by the Province of BC (Ministry of Environment and Climate Change Strategy, 2023). The capture of the impacted snakes began on September 21, 2020, with snakes recovered early in the process being relocated to nearby natural dens (12 gophersnakes, 13 racers, 10 rattlesnakes) by TMEP contractors (Heinrich, 2020; see Table 1.1). When above-ground temperatures were deemed too cold for the safe relocation of the snakes to natural dens, all further excavated snakes (Table 1.1) were transferred to a regional wildlife rehabilitation centre (BC Wildlife Park) in Kamloops. Following protocols developed at the Wildlife Park, snakes were kept in cool, dark conditions to mimic natural overwintering environment until spring 2021 (~7 months). In total, 93 snakes (37 gophersnakes and 56 racers) were overwintered in this fashion. Although the destruction of the dens represented an unfortunate loss of overwintering habitat, the translocation and temporary captivity of these snakes provided a rare, large-scale opportunity to study their post-release behaviour and adaptation in an altered landscape. This initiative included two years of funded research to evaluate the immediate impacts of the mitigation on the disturbed snake populations.

Table 1.1. Summary of a reptile salvage conducted at three disturbed hibernacula in Lac du Bois from September 21 to October 16, 2020 (Heinrich, 2020).

Species	Disturbed hibernacula #	Outcomes		
		Released at alternative natural den	Transported to BC Wildlife Park	Mortality
Western Yellow-bellied racer	1	13	44	2
	2	0	1	0
	3	0	11	0
Great Basin gophersnake	1	10	20	0
	2	1	5	1
	3	1	12	1
Western rattlesnake	1	10	0	0
	2	0	0	0
	3	0	0	0
Totals		35	93	4

Study Species

Great Basin Gophersnakes

Gophersnakes (*Pituophis catenifer*) are oviparous constrictors that range throughout western North America (COSEWIC, 2013). The Great Basin gophersnake (*P.c. deserticola*) is one of two *P. catenifer* subspecies found in Canada, along with the Bullsnake (*P.c. sayi*), and is the only extant subspecies in British Columbia (COSEWIC, 2013). In British Columbia, gophersnakes occupy four distinct populations in the dry southern interior of the province (Matsuda et al., 2006; Southern Interior Reptile and Amphibian Recovery Team, 2008). The three southern populations may be interconnected through populations in the United States, while the northernmost population—Thompson-Fraser—appears isolated (Southern Interior Reptile and Amphibian Recovery Team, 2008).

Gophersnakes hunt small mammals and, opportunistically, small birds and reptiles; they forage in open grassland and in riparian areas within the grassland (McAllister & Maida, 2016; Matsuda et al., 2006; Rodriguez-Robles, 1998). Great Basin gophersnakes demonstrate sexual dimorphism: males typically have longer snout-vent-lengths, and accordingly are heavier, than females (Williams et al., 2014). Gophersnakes lay eggs underground or in shelters, and prefer loose, sandy soil on south facing slopes (Matsuda et al., 2006; Southern Interior Reptile and Amphibian Recovery Team, 2008). Gravid females take advantage of pre-existing natural refuges (e.g. rodent burrows, talus, rock fissures) and anthropogenic substrates, such as wood, for oviposition (Southern Interior Reptile and Amphibian Recovery Team, 2008). Gophersnakes lay eggs in late June and early July (Matsuda et al., 2006; Williams et al., 2014). At the northern range limit, females reach reproductive maturity at a minimum age of five years, with a mean age of 7.3 ± 2.13 years based on skeletochronology ($N = 16$) (Petersen et al., 2024).

In British Columbia, the primary threat to gophersnakes is habitat loss (Southern Interior Reptile and Amphibian Recovery Team, 2008). Because gophersnakes occupy large home ranges and require connectivity between hibernacula, egg-laying sites, and summer foraging sites, the species is highly vulnerable to habitat loss and fragmentation (Bertram et al., 2001; Shewchuk, 1996; Williams et al., 2012). Unfortunately, much of the best habitat for gophersnakes—low elevation valley bottoms—coincide with prime areas for agriculture and urban development (Southern Interior Reptile and Amphibian Recovery Team, 2008).

Western Yellow-bellied Racer

Racers (*Coluber constrictor*) are slender, quick snakes that feed on invertebrates and small vertebrates (Shewchuck & Austin, 2001). Their diet varies depending on the size of the individual (Halstead et al., 2008; King, 2002), the subspecies, and home range size (Fleet et al., 2009). Racers use vision and olfaction to actively hunt prey (Halstead et al., 2008). They are generally considered opportunistic predators, though racers in Florida demonstrated prey selection at the species level, positively selecting for frogs and negatively selecting for toads regardless of abundance (Halstead et al., 2008). Female racers are larger than males (Shewchuk & Austin, 2001), and this sexual dimorphism may reflect differences in diet, as larger females can consume bigger prey than their male counterparts. Racers are oviparous, laying their eggs in late spring (May-June) in underground refuges, which are often communal and may be shared with other snake species (Matsuda et al., 2006). Racers use a variety of substrates for oviposition sites, such as loose soil, talus, large rocks, rotting wood or vegetative matter, and make use of rodent burrows (COSEWIC, 2015a).

Racers are one of the few snake species in North America with a transcontinental distribution, ranging from the west to the east coast, and from southern Canada to Central America (Burbrink et al., 2008). This vast range, which spans multiple ecosystems and geographic barriers to genetic flow (e.g. Rocky Mountains), has led to considerable genetic and ecological diversity among racer populations (Burbrink et al., 2008). Of the 11 subspecies of racer, the Western Yellow-bellied racer (*C. c. mormon,* hereafter WY racer) is the only subspecies found west of the Rocky Mountains (Burbrink et al., 2008). In Canada, WY racers are found in British Columbia, where they are distributed between five population areas. The largest of these areas are the Thompson-Fraser, where this study occurred, and the Okanagan-Similkameen areas (Dulisse, 2007; Environment Canada, 2014). The southern four areas are contiguous with the American species range, while the northernmost area—Thompson-Fraser—is completely isolated (Racer Management Team Working Group, 2013).

In 2015, WY racers were designated threatened in Canada (COSEWIC, 2015a) and a 2023 reassessment reaffirmed this listing (Ministry of Environment and Climate Change Strategy, 2023). Roads are the primary known threat to the species (Racer Management Team Working Group, 2013), contributing to both direct mortality and habitat fragmentation. The racer's diurnal and highly active nature may increase encounters with roads and fencing compared to more sedentary species (Eye et al., 2018). Since road construction and traffic volume are forecast to increase in the province the threat posed by roads to racer population viability is expected to remain high (Racer Management Team Working Group, 2013).

Residential, commercial, and agricultural development on WY racer habitat is also of concern. Urban developments and intensive commercial agriculture heavily fragment the landscape and degrade or remove key habitat features such as dens, egg-laying sites, and foraging grounds (Racer Management Team Working Group, 2013). The one historic study on WY racers (Utah: Brown & Parker, 1976) demonstrated yearly site fidelity, which if present in Canada would exacerbate the threat of habitat fragmentation (Racer Management Team Working Group, 2013), since this could indicate an inability to switch to a different habitat feature should access to the old one be cut off. Environment Canada (2014) estimates a population loss of 10-45% has already occurred in British Columbia, due to a significant decline of grassland habitat (52% Northern Okanagan basin, 29% Southern Okanagan basin, 23% Thompson basin) (Racer Management Team Working Group, 2013). Currently, it is challenging and risky to design effective mitigation strategies for WY racers with our limited knowledge of the natural history (e.g. movement patterns, timing of denning and oviposition, recruitment) of the species in Canada.

Research Objectives

The objective of this thesis was to study the movement behaviour of two threatened snake species in southwestern British Columbia. I principally used movement data collected through radiotelemetry to (1) assess the impacts of a mitigation effort, and (2) collect information on the movement ecology and natural history of two threatened snakes.

In Chapter 2, I use movement metrics and survival rates to assess the effects of a mitigation—removal from the wild, artificial overwintering, translocation—on a population of Great Basin gophersnakes for two years following a disturbance (detailed above). I predicted that if the mitigation affected snakes, then disturbed snakes would have different movement behaviour and survival rates than conspecific reference snakes from the same study area.

In Chapter 3, I examine the movement ecology of the Western Yellow-bellied racer at the northern edge of its range. Using two seasons of radiotelemetry data, I quantify key movement and space use metrics and compare them to the Utah population studied by Brown and Parker (1976). Given this chapter provides the first radiotelemetry study on this subspecies since the Brown and

Parker paper, it offers substantial new insight into the natural history and movement behaviour of this wide-ranging but understudied snake at the periphery of its distribution.

In Chapter 4, I distill the lessons learned from our radiotelemetry of two relatively understudied snake species and outline recommendations to guide future tracking work. I also critically evaluate the mitigation strategy described in Chapter 2 (i.e. translocation to an artificial den) and identify several priority areas for further research that would support more species- and region-specific mitigation strategies in the future.

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CHAPTER 2

Responses of Great Basin gophersnakes (*Pituophis catenifer deserticola*) to translocation after the loss of three hibernacula

Introduction

As human activity continues to fragment and degrade natural landscapes, efforts to minimize harm to wildlife are prompting the search for effective mitigation strategies. Among these, wildlife translocation (the deliberate movement of animals from one location to another) has emerged as a key approach to reduce direct harm to wildlife during habitat disturbance (Bradley et al., 2022). These interventions are known to as "mitigation translocations" and differ in several important ways from translocation for conservation.

Conservation translocations aim to reintroduce or reinforce wildlife populations as part of broader species recovery efforts (Berger-Tal et al., 2020; Novak et al., 2021). These translocations typically are well planned, tailored to the species and local environment, and often include some form of follow-up monitoring (Berger-Tal et al., 2020; McAdie, 2018; McFarlane et al., 2006). In Canada, conservation translocations frequently are implemented or recommended for at-risk wildlife, including 12% of bird species, 24% of reptile species, and 33% of terrestrial mammal species (Swan et al., 2018). Notable, high-profile examples include the Wood bison (*Bison bison athabascae*) and the Vancouver Island marmot (*Marmota vancouverensis*) (McAdie, 2018; McFarlane et al., 2006).

In contrast, mitigation translocations generally are reactive and used to relocate animals away from areas undergoing human-caused disturbances (Germano et al., 2015). Rather than contributing directly to species recovery, these translocations aim to minimize immediate harm to the affected animals. They are often constrained by tight timelines, and as a result receive limited planning and post-release monitoring (Germano et al., 2015; Stuparyk et al., 2018). With human development impacting a growing number of wildlife species, mitigation translocations are becoming increasingly common (Bradley et al., 2022; Larson et al., 2024; Massei et al., 2010; Nash et al., 2020). Yet, despite their frequency, their effectiveness remains poorly understood due to a lack of follow-up studies (Massei et al., 2010; Miller et al., 2014). Although the outcomes of many mitigation translocations are undocumented, available data suggest poor outcomes and generally lower success rates compared to conservation translocations (Bradley et al., 2022; Germano et al., 2015; Sullivan et al., 2015). Improving success in mitigation translocations likely will require adopting principles already established in conservation, such as rigorous planning and consistent post-release monitoring.

Several factors in general influence the outcome of a wildlife translocation, regardless of whether it was for mitigation or conservation. Perhaps most importantly, well-planned translocations, tailored to the species' specific needs, generally have higher success rates (Cornelis et al., 2021; Germano et al., 2015). For this reason, translocations that result from human-wildlife conflict (often occurring unexpectedly and without prior planning) tend to have the lowest success rates (Germano & Bishop, 2008; Stuparyk et al., 2018). Chronic stress experienced by wildlife during and immediately after a translocation can also impact the outcome, with elevated mortality during the first few months after release (establishment phase) observed in several avian translocations (Dickens et al., 2010). The primary stressors affecting animals during and after translocation include capture and handling, prolonged captivity, transport, and release into an unfamiliar environment (Dickens et al., 2010). Survival rates during the establishment phase can significantly impact long-term translocation success (Dickens et al., 2010). Finally, translocation distance, particularly whether the animal is moved within or outside of its home range, can impact outcome. Animals that are translocated within their home range (short-distance translocation) have better survival outcomes than animals moved outside of their home range (long-distance translocation) (Choquette et al., 2023; Cornelis et al., 2021; Skikne et al., 2020; Villaseñor et al., 2013).

For snakes, mitigation translocations occur far more often than conservation translocations. This is largely due to negative perceptions of snakes as dangerous or undesirable that lead to high rates of conflict with humans (Barve et al., 2013; Butler et al., 2005; Devan-Song et al., 2016; Nash et al., 2020; Walker et al., 2009). Although precise figures are lacking, it is estimated that thousands of snakes are translocated each year from residential or commercial areas to alternative ‘suitable habitats’ (Barve et al., 2013; Butler et al., 2005; Devan-Song et al., 2016). A less common but still impactful type of mitigation translocation occurs when entire denning snake populations are relocated to protect them from immediate and direct impacts (Nash et al., 2020; Walker et al., 2009).

The tactic of translocating entire snake populations is often considered when development threatens known communal hibernacula, as the destruction of these sites can place entire populations at immediate risk of mass mortality unless alternate overwintering sites are present and accessible. While such efforts have occasionally succeeded, such as the relocation of a Timber rattlesnake (*Crotalus horridus*) population in Kansas (Walker et al., 2009), the broader literature urges caution, as mitigation translocations of snakes frequently result in poor survival outcomes (Barve et al., 2013; Devan-Song et al., 2016; Germano & Bishop, 2008; Sullivan et al., 2015). A tendency for snakes to disperse post-translocation elevates mortality risks due to predation and vehicle collisions (Barve et al., 2013; Bonnet et al., 1999; Devan-Song et al., 2016; Lee & Park, 2012; Nowak et al., 2002; Reinert & Rupert, 1999).

Germano & Bishop (2008) found only 41% of reptile and amphibian translocations reported successful recruitment, and a more recent review by Cornelis et al. (2021) found the establishment of self-sustaining populations of snakes was 73% after translocation within the home range and 37% after translocation outside of the home range. Overall, the history of dubious translocation outcomes warrants more rigorous post-release monitoring and reporting on all forms of translocation, but particularly those performed for mitigation purposes.

This study evaluated the impact of mitigation translocation on Great Basin gophersnakes (*Pituophis catenifer deserticola*) after the destruction of their overwintering dens in a protected grassland. We used radiotelemetry to monitor the behaviour and survival rates of translocated snakes following their removal and later release at newly created dens (see below). We also conducted telemetry on wild-caught conspecifics, which served as a reference group of snakes occupying the same habitat and conditions. Being restricted to a two-year monitoring period, we focused on short-term survival and behavioural outcomes rather than long-term recruitment and population establishment. We considered ‘success’ to be patterns of movement behaviour and survival in translocated snakes indistinguishable from those of reference snakes—a lack of similarity in movement metrics between the translocated and reference animals would infer some shift in natural behaviors. Additionally, if natural behaviours were largely retained, then we expected to see sex-specific differences in active season movement patterns of translocated snakes to resemble those observed in a previous empirical study on *P. c. deserticola* at their northern limit, where males moved significantly more than females in spring, while females exhibited greater movement than males in summer and fall (White, 2008). We also followed the benchmark of 50% yearly survival used by Choquette et al. (2023) to aid in the overall evaluation of success two years post-translocation.

Methods

Study Site

Our study site, Lac du Bois Grassland Protected Area (hereafter Lac du Bois), covers 15, 207 ha of grasslands and dry forests in south-central British Columbia, Canada, immediately north of the city of Kamloops, British Columbia, Canada (LAT: 50.724151, LON: -120.402297) (Vyse et al., 2000). The lower grasslands ecosystem, where the study took place, is characterized by hilly terrain with elevations ranging from 335 to 700 m (Vyse et al., 2000), dominated by Bluebunch wheatgrass (*Pseudoroegneria spicata*) and Big sagebrush (*Artemisia tridentata*) (Wikeem & Wikeem, 2004). In the summer, the region experiences a hot, dry climate (Wikeem & Wikeem, 2004) making it susceptible to extreme heat and drought events (White et al., 2023). Typically, the hottest months are July and August, where average daily temperatures are 21.5 ± 1.6°C and 20.9 ± 1.2°C respectively (Environment and Climate Change Canada, 2024). In winter, average daily temperatures drop below freezing, with December averaging -2.7 ± 3.0°C and January -2.8 ± 3.4°C (Environment and Climate Change Canada, 2024; see Chapter 1, Figure 1.3 for details). The lower grasslands of Lac du Bois support communal snake dens, some known before (Bertram et al., 2001) and others discovered during our research (McKelvey, 2024). Additionally, several snake dens were newly detected in the buried rock created by an oil pipeline installed in the 1950s (Kheraj, 2015 – see below). Three snake species federally listed as threatened, Great Basin gophersnake (*P. c. deserticola*), Western Yellow-bellied racer (*Coluber constrictor mormon*), and Western rattlesnake (*Crotalus oreganus*), are known to inhabit these dens (COSEWIC 2013, 2015a, 2015b).

Disturbance and Mitigation

Disturbance to the Lac du Bois landscape and several snake dens within its boundaries occurred with the expansion of an existing oil pipeline (Trans Mountain Expansion Project, hereafter TMEP) from 2020-2022. Three previously undocumented snake dens were identified on the pipeline right-of-way in the fall of 2020 during pre-construction surveys (Heinrich, 2020). Because the dens obstructed progress on the pipeline expansion, TMEP was authorized to demolish them following the relocation of all resident snakes (Heinrich, 2020). To mitigate the immediate risk posed by the loss of these hibernacula on the cusp of winter, 37 gophersnakes and 56 racers were salvaged from the site and temporarily relocated to the BC Wildlife Park in Kamloops (Heinrich, 2020; see Chapter 1, Table 1.1 for details), where they were kept in artificial overwintering conditions for seven months. At this point our research team became informed of the mitigation efforts, and subsequently was involved in plans to monitor the spring release of the snakes.

Two artificial dens (hereafter Artificial Dens 1 and 2) were constructed by TMEP to offset the loss of the disturbed hibernacula. The largest of these, Artificial Den 1, was built ~50m south of Disturbed Den 1 and was completed in April 2021. Artificial Den 2, built ~30m southwest of Disturbed Den 2 and ~300m southeast of Disturbed Den 3, was completed later that summer (Figure 2.1). The release of the captive snakes was planned to coincide with the spring egress at natural dens in Lac du Bois (late March-early May). For this reason, the delayed completion of Artificial Den 2 prevented its use as a re-introduction site, and Artificial Den 1 served as the release site for all snakes that were held overwinter. On May 1st, 2021, the displaced snakes were translocated to the newly constructed artificial hibernaculum located between 50 to 1500 meters from their original hibernation sites.

We released the snakes in a controlled manner ('soft release' (Sacerdote-Velat et al., 2014)) by installing a 1.8m mesh fence around the Artificial Den 1 entrance, burying the base of it 10 cm in the substrate. After construction of the fence on April 29, the captive snakes were released into the fenced enclosure circling Artificial Den 1 on May 1. The fence was removed five days later (May 5).

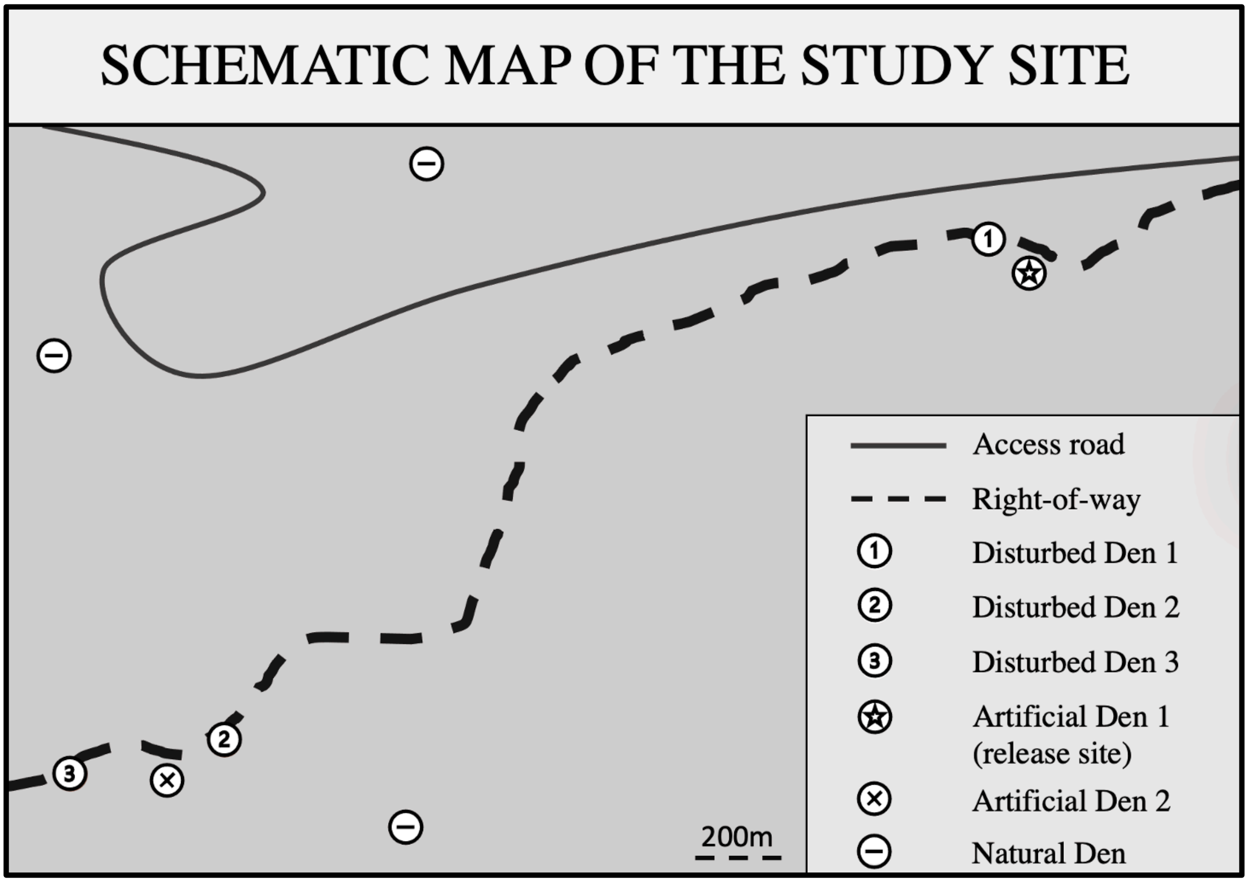

Figure 2.1. Schematic map of the study site showing the pipeline right-of-way, an access road closed to public vehicles, three disturbed dens, and two artificial dens. Artificial Den 1 was the spring 2021 release site for snakes held at the BC Wildlife Park. Natural den locations as shown are only approximate, in keeping with the sensitive conservation status of snake hibernacula in British Columbia. They are shown here to convey the spatial arrangement of artificial and natural dens on the study landscape.

Telemetry

Prior to their release at Artificial Den 1, relatively heavier gophersnakes were selected to ensure transmitters with relatively long lifespans (i.e. larger batteries) could be surgically implanted (i.e. transmitter weight ≤ 4% of body mass). Gophersnakes from each of the three destroyed dens, categorized by translocation distance as either ‘short distance’ (within home range) or ‘long distance’ (outside home range), were included. Over half of the sample (4♀, 7♂) came from Disturbed Den 1 and were moved a short distance (49m) to Artificial Den 1, while the remaining gophersnakes (4♀, 2♂) came from Disturbed Dens 2 and 3 and therefore were translocated a long distance to Artificial Den 1 (>1,300 m, beyond typical home ranges of 5–25 ha: Bertram et al., 2001; Shewchuk, 1996; Williams et al., 2012). Hereafter, snakes removed from the wild, overwintered in captivity, and translocated to Artificial Den 1 are collectively referred to as ‘translocated’ snakes, and are analyzed together and by distance category (short or long). To source a reference sample of free-ranging gophersnakes, we surveyed known natural dens during egress (April–May) and opportunistically captured suitably-sized snakes during the summer (June–August), resulting in 15 reference snakes (7♀, 8♂) in 2021.

In the spring of the second year of our study (2022) we constructed circular fences around both Artificial Dens 1 and 2 to detect any snakes that may have overwintered there. At this time, we also surveyed all known dens on the Lac du Bois landscape (McKelvey, 2024), including those sites where we had followed our 2021 telemetered snakes (translocated and reference) into hibernation. In 2022, we added to our telemetry sample two recaptured, translocated gophersnakes (1♀, 1♂) that were not tracked in the previous year, along with an additional 10 reference snakes (1♀, 9♂). Several recaptured snakes (3 translocated (short distance); 2 reference) tracked in 2021 were selected for a second consecutive year of telemetry in 2022.

In the fall, we intensified tracking efforts to recover transmitters from snakes before hibernation. When a snake appeared to have reached a putative den, we increased monitoring frequency, sometimes up to several times a day, to capture the animal before it went underground for the season. Snakes then were brought in for transmitter removal by a veterinarian. If retrieval was impossible in the fall, we monitored the overwintering site in the spring to catch snakes as they emerged from the den.

We followed a radio-transmitter implantation procedure modified from the methodology of Reinert and Cundall (1982). We used radio transmitters that weighed 3.8g and 5.2g (Holohil model SB-2T) with estimated 6-month and 12-month lifespans respectively. Snakes were anesthetized with isoflurane and transmitters surgically were inserted ~55% of the snout-to-vent length of the animal, posterior from the head. Each transmitter was sutured to intercostal muscles to prevent movement, and the antenna was positioned subcutaneously toward the tail using a catheter. After each surgery, we administered meloxicam (NSAID, DIN: 02240463, Boehringer Ingelheim) and ceftazidime (antibiotic, DIN: 00886971, Fresenius Kabi Canada ltd) doses based on the snake's weight. For snakes tracked in consecutive years, transmitter removal and re-implantation were performed during the same surgery.

Using radiotelemetry, we relocated snakes every 1–5 days throughout the active season (May to October). At each relocation, we recorded coordinates with a Garmin® handheld GPS. Female snakes were captured approximately every two weeks and held briefly to palpate for eggs. We recorded all mortalities among telemetry snakes, determining the cause of death, when possible, through physical examination. When possible, we tracked snakes to putative hibernation sites. When above-ground temperatures reached freezing temperatures, we assume that the last location an animal was tracked to was the selected overwintering site.

Movement Analyses

To quantify summer movements, we calculated five movement parameters using telemetry data: *mean distance travelled per day, mean distance travelled per movement, movement speed, sinuosity,* and *recursiveness* (Rstudio, Version 1.4.1717). Mean daily distance (m/day) was calculated as the distance between successive relocations relative to the time elapsed. Mean distance per movement (m) was calculated as the average distance between relocations, excluding those that occurred less than 24 h or more than 72 h apart; movements under 5 m were also excluded to account for GPS error margins (White, 2008). Movement speed (m/h) was calculated by dividing movement distance (excluding movements <5 m) by the time elapsed between relocations. Sinuosity (ranging from 0 for a straight path to 1 for a highly curved or circular path) provided a measure of path straightness (Benhamou, 2004). Recursiveness represented revisits to locations, defined as returns within 2 m of a prior GPS point after leaving for at least 24 h (Smith et al., 2021). Hereafter, all reported mean values are followed by ±1 standard error of the mean.

During the summer, telemetry snakes found on the pipeline right-of-way by TMEP environmental contractors were required to be translocated 100-500 m in the direction in which they were travelling. To prevent these translocations from skewing our movement analyses, we obtained the date, time, and GPS locations before and after each translocation event. Each translocation triggered a new tracking session, labelled with the snake's ID. To avoid inflating sample size with the addition of tracking session IDs, movement parameters were calculated for each tracking session ID and later combined into a single movement parameter per snake by taking the weighted mean of each session, with weights based on the number of relocations per session.

Statistical Analyses

We conducted a multivariate analysis of covariance (MANCOVA) using all five-movement metrics to examine the effects and interactions of year (2021/2022), sex (male/female), and translocation status (translocated/reference). We also included the factor 'season', following White (2008), we grouped movement data into three sub-seasons: 'spring' (egress to oviposition, April–June), 'summer' (oviposition to ingress, July–August), and 'fall' (ingress period, September–October). In the MANCOVA model, season was nested within year. To allow comparison across metrics measured on different scales, all movement data were centered and scaled prior to analysis. Additionally, because some metrics were asymmetrically distributed, we applied log transformations to sinuosity and recursiveness before running the MANCOVA. We used Pillai's trace as the multivariate test statistic because it is less sensitive to assumption violations, and it reduces the likelihood of Type I errors. We followed-up the MANCOVA with univariate analyses of variance (ANOVA) models for each movement metric testing the same independent variables. Additionally, we conducted supplementary two-way analyses of variance on the 2021 data to further explore the effects of sex and translocation distance (long vs. short) on each movement metric. For all analyses, when significant effects were detected, we conducted *post hoc* comparisons using Tukey's Honestly Significant Difference (HDS) test to determine which groups differed from one another.

To assess whether survival rates during the summer active period differed between groups, we conducted two χ^2 tests of independence. First, we compared survival outcomes (survived vs. died) at the end of each active season (2021 & 2022) between reference and translocated snakes. Second, to evaluate whether the distance of translocation influenced survival in the first year

(2021), we ran a separate χ^2 test comparing three groups: reference snakes, snakes translocated short distances, and snakes translocated long distances during the first year of the study.

Results

Over the study period, from April 2021 to October 2022, we tracked 44 individual gophersnakes (Table 2.1). Five snakes (4 translocated + 1 reference) were tracked in both 2021 and 2022, while 39 snakes were tracked for one year (16 translocated + 23 reference), giving 49 individual-year records. In 2021, each snake was relocated an average of 51 (±3.5) times over 123.5 (±8.0) days, while in 2022, the average was 43.7 (±3.5) relocations over 129.5 (±9.8) days.

Movement Behaviour

Across both active seasons, telemetered snakes (N = 49) travelled on average 25.4 m/day (±1.73), 88.8 m/movement (±5.80), and 2.43 m/h (±0.17). Snakes tended to travel in relatively straight paths (x^- sinuosity = 0.14 ±0.01) and revisited sites on average 1.27 times (±0.04). For a detailed breakdown of movement metrics by year, sex, and translocation status, see Appendix B.

Translocated snakes exhibited few significant differences across five movement metrics when compared to reference snakes during both active seasons (2021 and 2022) following their release at the artificial den in 2021. The multivariate analysis revealed significant effects of sex, year, and season on overall movement patterns, but no effect of translocation (Table 2.2).

Univariate analyses provided further details (Table 2.3). Daily distance travelled, movement rate, path sinuosity, and site recursiveness varied between years, while distance travelled per day, per movement, and movement rate differed between sexes. Most *post hoc* comparisons were not statistically significant (P > 0.07), but a few key differences remained. Hourly movement rates were higher in 2021 (t = 2.67, P = 0.01), and males generally travelled more per movement (t = -2,37, P = 0.02) and at faster rates (t = -2.55, P = 0.01) than females (Figure 2.2). Specifically, snakes in 2021 moved on average 0.73 m more per hour than in 2022, and males moved on average 29.7 m farther per movement and 0.62 m faster per hour than females. Although movement rate initially appeared to differ between translocated and reference snakes in the univariate analysis (Table 2.3), this effect was not supported *post hoc* (P = 0.14).

Table 2.1. Summary of Great Basin gophersnakes tracked in the Lac du Bois protected area, British Columbia, Canada, using radiotelemetry in 2021 and 2022, categorized by sex, translocation status and distance, and year(s) tracked. Snakes tracked in both years are listed separately under "Both years (2021 & 2022)".

Year	**Translocation Status**	**Female**	**Male**	**Total**
Year 1 (2021) only	Translocated short distance	2	6	8
	Translocated long distance	4	2	6
	Reference	6	7	13
Year 2 (2022) only	Translocated (unknown distance)	1	1	2
	Reference	1	9	10
Both years (2021 & 2022)	Translocated short distance	2	1	3
	Reference	1	1	2

Table 2.2. Multivariate effects of sex, translocation status, year, and season (nested within year) on five standardized movement metrics (1. Distance travelled per day; 2. Distance travelled per movement; 3. Movement rate; 4. Sinuosity; 5. Recursiveness). Sinuosity and recursiveness were log-transformed. Pillai's trace was used to demonstrate the degree to which groups differed across multiple dependent variables simultaneously (larger values indicate stronger group differences (ranges 0–1)). *F*-values, degrees of freedom (df_1, df_2), and adjusted *P*-values are also reported.

Predictor	Pillai Trace	*F*-value (df_1, df_2)	*P*-value
Sex	0.16	3.19 (5, 82)	**0.01***
Status	0.10	1.90 (5, 82)	0.1
Year	0.20	4.09 (5, 82)	**0.002****
Year:Season	0.38	1.78 (20, 340)	**0.02***

Table 2.3. Results of univariate ANOVAs for each movement metrics following a multivariate analysis of variance (MANCOVA). Each model tested the effect of predictors (factors) on individual response variables included in the MANCOVA. The *F*-values, degrees of freedom (df1, df2), and associated *P*-values are reported for each response variable. Only movement metrics and predictors that were statistically significant ($P < 0.05$) are presented in this table. For the non-significant predictors, see Appendix C.

Metric	Predictor	*F*-value (df1, df2)	*P*-value
Distance travelled per day (m/day)	Sex	5.82 (1, 86)	**0.02***
	Year	6.62 (1, 86)	**0.01***
Distance travelled per movement (m)	Sex	14.46 (1, 86)	**0.001*****
Movement rate (m/h)	Sex	6.00 (1, 86)	**0.02***
	Status	3.98 (1, 86)	**0.05***
	Year	10.08 (1, 86)	**0.002****
Sinuosity	Year	4.49 (1, 86)	**0.04***
	Year:Season	3.92 (4, 86)	**0.006****
Recursiveness	Year	4.90 (1, 86)	**0.03***

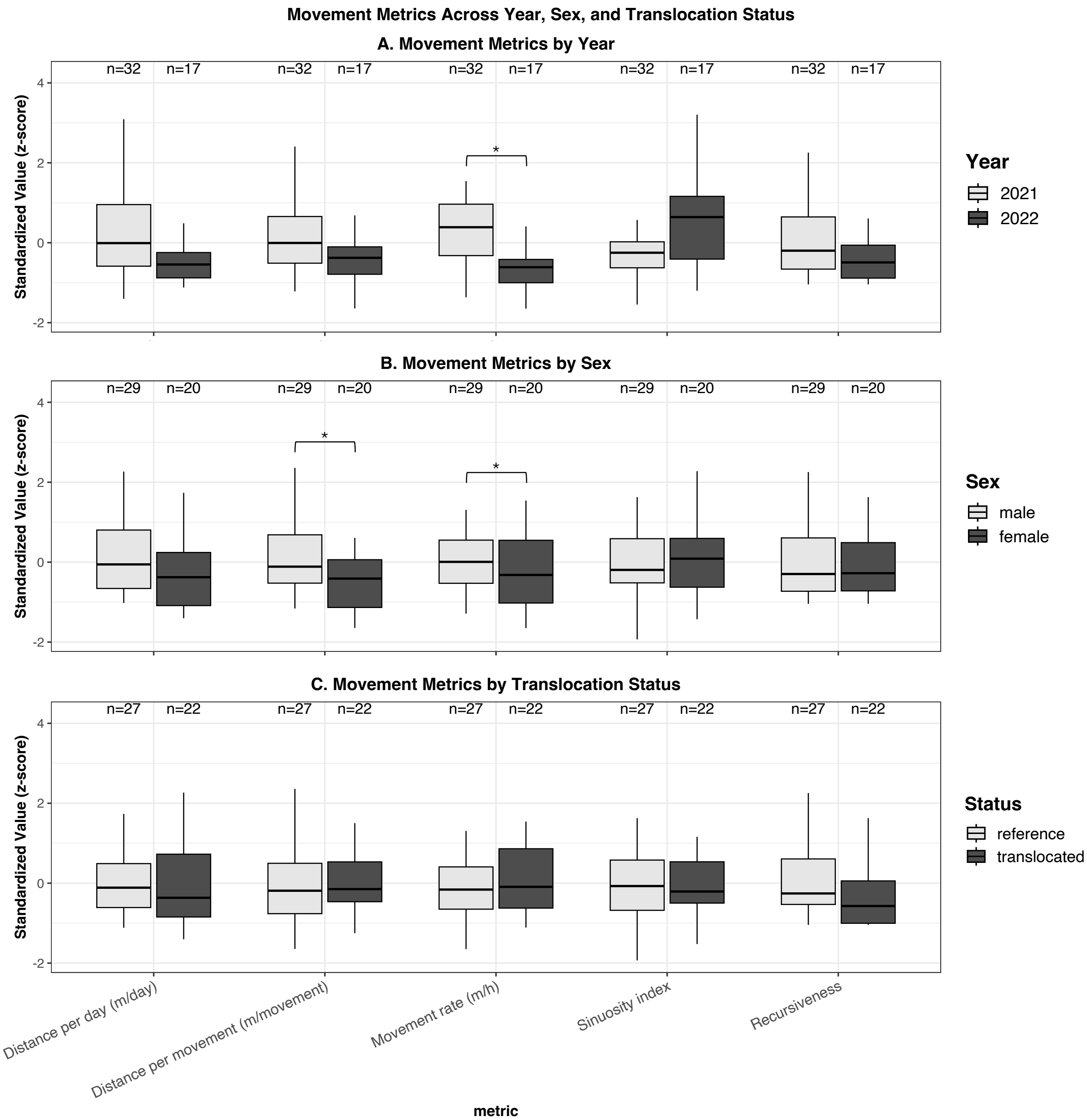

Figure 2.2. Boxplots of standardized movement metrics for Great Basin gophersnakes by (A) year, (B) sex, and (C) translocation status. Metrics include distance per day, distance per movement, movement rate, sinuosity index, and recursiveness. Values were standardized as z-scores, calculated as the number of standard deviations each observation deviated from the mean for that metric, to allow comparison across variables with different scales. Sample sizes are shown above each box. Brackets and asterisks indicate pairwise group differences that remained significant following *post hoc* analyses.

Among translocated snakes during the first year (2021), those moved longer distances (outside of the species' typical home range) had significantly different daily movement and rates of site revisits than those translocated shorter distances (Table 2.4). *Post hoc* tests indicated that within the translocated population males moved significantly more per day than females in both the long-distance (difference = 20.3, t = -2.20, P = 0.05) and short-distance groups (difference = 16.0, t = -2.40, P = 0.03). The effect of translocation distance was not significant within either sex (all $P > 0.09$), although male snakes in the long-distance group tended to move more than those in the short-distance group (difference = 15.6, t = 1.83, P = 0.091). The largest contrast was between long-distance males and short-distance females, where movement differed on average by 31.65 meters per day (t = −2.29, P = 0.02). *Post hoc* revealed a weak trend toward higher revisitation rates in short-distance translocated snakes compared to long-distance ones (difference = 0.27, t = -1.86, P = 0.07), but this difference was not statistically significant. Neither sex nor the interaction between sex and translocation distance had a significant effect, and pairwise comparisons within sex and translocation groups further confirmed a lack of strong differences (all $P > 0.1$).

Survival of Telemetered Snakes

Survival was not significantly related to translocation status in 2021 or 2022 (Table 2.5). Translocation distance (short or long) also was not related to survival rates in 2021 (χ^2 (1, N = 32) = 0.87, P = 0.64), though sample sizes were small. In 2021, one (female) out of 15 reference snakes and three (2 female, 1 male) out of 17 translocated snakes died, with all mortalities occurring in June (χ^2 (1, N = 32) = 0.88, P = 0.35). In 2022, three (all males) out of 12 reference snakes and two (1 female, 1 male) out of five translocated died (χ^2 (1, N = 17) = 0.05, P = 0.83). A third of the deaths were from predation, a third were road mortalities, and a third from unknown causes. Overall the observed mortality rate of the telemetered translocated snakes (4/19 = 21%) was well below the 50% annual survival benchmark set out by Choquette et al. (2023).

Table 2.4. Results of two-way ANOVAs examining the effects of sex and translocation distance (long vs. short) on individual movement metrics in 2021. The degrees of freedom (df1, df2), *F*-values, and *P*-values for each movement metric are presented. Only movement metrics and predictors that were statistically significant ($P < 0.05$) are presented. For the non-significant predictors, see Appendix D.

Metric	$\bar{x}$, SE, n	Predictor	*F*-value (df1, df2)	*P*-value
Distance travelled per day (m/day)	26.2, 3.28, 17	Translocation distance	5.82 (1, 14)	**0.03***
		Sex	7.61 (1, 14)	**0.02***
Recursiveness	1.26, 0.07, 17	Translocation distance	4.34 (1, 14)	0.056.
		Sex	0.13 (1, 14)	0.73

Table 2.5. The yearly average tracking periods of Great Basin gophersnakes in our study, with $\bar{x}$ days, SE, and sample sizes, presented. Under the column "test result", the results of χ^2 tests comparing the annual survival of reference and translocated (short- and long-distance) is shown, including χ^2 test statistics, degrees freedom and P-values.

Year	Average tracking period ($\bar{x}$ days ± SE)	Status	Outcome		Test result
			Survived tracking period	Died during tracking period	
2021	123.5 ± 8.0	Reference	14	1	χ^2 (1) = 0.88, P = 0.35
		Translocated	14	3	
2022	129.5 ± 9.8	Reference	9	3	χ^2 (1) = 0.05, P = 0.83
		Translocated	4	1	

Reproduction

Over two spring seasons, we observed four instances of translocated males mating: in one of those cases the mating occurred with a translocated female. One reference male was recorded mating with two reference females, and based on recapture palpation only one of these females was recorded as becoming gravid later that summer. Among the telemetry females in 2021, two out of seven reference females were confirmed gravid and showed postpartum characteristics on June 30 and July 4, and one out of eight translocated females was gravid but was killed in June before she could oviposit. No telemetry females (0/5) were detected becoming gravid in 2022.

Locating New Dens

During the fall following the disturbance and mitigation (2021), we tracked 10 translocated gophersnakes into ingress. Three translocated snakes originally from Disturbed Den 1 (short-distance translocation) were located in the fall at Artificial Den 1, the spring release site for all translocated snakes. One of these snakes was known to locate Artificial Den 1 independently, while the two others were intentionally moved to Artificial Den 1 by TMEP contractors to seed the den. The remaining translocated snakes (n = 7) found presumably alternative overwintering sites elsewhere on the landscape—four of those snakes were captured the following summer, indicating they survived hibernation. These alternative den sites were on average 416.9m (± 130.0) from Artificial Den 1. Four out of the seven snakes (3 short-distance, 1 long-distance) overwintered within 300m of Artificial Den 1, while three snakes (1 short-distance, 2 long-distance) overwintered 632.9m, 741.1m and 921.4m from the spring release site respectively.

Discussion

Overall, this study found no significant impact of translocation on snake movement behaviour or survival over the two years following the initial disturbance. This included an absence of high or abnormal movement rates, factors known to increase predation risk (Bonnet et al., 1999; Butler et al., 2005; Cornelis et al., 2021; Nash et al., 2020), and low annual survival rates (<50% per year, Choquette et al., 2023). Our sample sizes and metrics were adequate to reveal that males moved significantly more per day, more per movement, and at a faster rate (m/h) than females (Table 2.3), particularly in the spring (Appendix E), indicating that "natural" mate seeking behaviour (Williams et al., 2012) was still being expressed by both reference and translocated snakes. Thus, we feel reasonably confident that the lack of differences we detected in movement metrics between translocated and reference snakes reveal relatively unaltered behaviour due to the mitigation efforts within the context of summer movement patterns.

Several possible explanations exist for why active season movement metrics and survival rates appeared similar in both translocated and referenced snakes. Perhaps most importantly, in the first year following the disturbance, a small majority (11/17) of the impacted telemetry sample were translocated within or near their home range (short-distance translocation). A systematic review of snake translocations by Choquette et al. (2023) found that minimizing the translocation distance of wild snakes was correlated with a positive survival outcome. Similarly, Cornelis et al. (2021) found that 47% of long-distance translocations failed compared to just 20% of short-distance translocations. Within the translocated population, we observed significant differences in daily movement rates and site revisits (Table 2.4); however, movement behaviours in this species are strongly tied to sex, which confounds the effects of other variables such as translocation distance and complicates interpretation of their independent influences. While there appear to be some differences in movement between long- and short-distance translocated snakes, potentially reflecting divergent translocation outcomes, the influence of sex and the limited sample size make it difficult to draw firm conclusions.

The impacts of the translocations also may have been tempered through the 'soft release', another practise shown to improve snake translocation outcomes (Choquette et al., 2023). Allowing animals to acclimated to their new environment, typically in an enclosure, before full release appears to improve outcomes across terrestrial taxa and particularly is effective in reptile translocations (Resende et al., 2021). Soft releases also may be especially beneficial when working with wild-caught individuals (Tetzlaff et al., 2019).

Another action that may have reduced translocation effects in this study was releasing snakes as a social group, a practice shown to improve post-release movement outcomes in snakes (Choquette et al., 2023). Releasing animals in large and socially functional groups has demonstrated benefits in highly social taxa such as elephants (Goldenberg et al., 2019). While the mechanisms by which group release benefits less social animals like snakes are less well understood, possible explanations include reduced stress due to the presence of conspecifics and familiar scent cues that may decrease dispersal or homing behaviour (Choquette et al., 2023).

Beyond the scope of our research on the effects of a mitigation translocation, our results demonstrated some year effects on snake movement (Tables 2.2 & 2.3). While the underlying cause remains unclear, the contrast between years highlights the extent to which movement patterns can fluctuate within the same population. Perhaps the most logical explanation for the year effects is the variations in local weather during the two years of our study. An extreme heat event (White et al., 2023) during the first field season (2021) occurred a few months after the translocated snakes were reintroduced to the landscape (see Chapter 1, Figure 1.3); this may have influenced physiology and behaviour in ways that were difficult to quantify in an *in situ* study. A small number of *ex situ* studies examining the impacts of simulated heatwaves on snakes have demonstrated that exposure to short periods of extreme heat can lead to reduced body mass, elevated stress levels, and altered drinking behaviour (Dezetter et al., 2022; Stahlschmidt et al., 2017). However, there is a lack of *in situ* research examining how extreme heat events affect snakes in the wild, and how the physiological effects of heatwaves may manifest as altered behaviours. We offer a few speculations on how the extreme and prolonged 2021 heatwave may have influenced our study population.

Firstly, it is plausible that the heatwave affected the movement patterns of both reference and translocated snakes over the relatively short period of our study, causing both to move atypically and potentially obscuring any differences attributable to translocation. Additionally, we recorded a notably low rate of gravid females within the telemetry population, and this trend was consistent among both translocated and reference females, suggesting that translocation was not a contributing factor. Throughout our study, only ≈ 18% (3/17) of telemetry females were observed gravid, a rate substantially lower than the ≈90% (17/19) rate previously reported for gophersnakes in British Columbia (Williams et al., 2014). Although speculative, it is possible that physiological stress experienced during the first field season influenced reproductive output at our site. Further long-term monitoring of the Lac du Bois population under typical environmental conditions would be required to assess whether the yearly variation in movement and low rate of gravid females we observed were temporary responses to environmental stressors or if low recruitment and variable movement patterns are persistent characteristics of this site.

One of the more understated outcomes of our research was the very poor return rates of snakes to the artificial den (1/17) from where they were released. At the same time, our data demonstrated the ability of at least some snakes to find alternative overwintering sites, suggesting a capacity to compensate for the loss of the traditional hibernacula. Gophersnakes are known to switch hibernacula between years (Williams et al., 2012), and this flexibility could explain the adoption of alternative sites. While there is no direct evidence that adult snakes use scent trailing to locate hibernacula in the same way as reported for juveniles (Brown & Maclean, 1983; Burger, 1989; Muellman et al., 2018; Reinert & Zappalorti, 1988), it is possible that displaced adults follow the scent trails of other snakes in the fall to locate overwintering sites they have never previously visited.

Unfortunately, we were unable to conduct a parallel study on the racers and rattlesnakes that were simultaneously impacted by the same disturbance in our study area. Most racers were too slender to carry transmitters that allowed longer-term tracking (see Chapter 3), and as mentioned in Chapter 1, rattlesnakes upon excavation were relocated to natural hibernacula without marking or tagging (see Chapter 1, Table 1.1). Rattlesnakes in our study region rely exclusively on communal dens that they demonstrate high fidelity towards (Gomez et al., 2015; Gienger & Beck, 2011). Conversely, gophersnakes and racers appear to use a wider range of hibernating sites in our study region (McKelvey, 2024; Williams et al., 2012) that spans co-hibernation with rattlesnakes to individual dens. These differences in natural history across taxa suggest possible different responses to hibernacula alterations or outright losses.

Additional data need to be collected across a wider range of species and locations before large scale mitigation translocations, such as the one described in this study, can be automatically adopted as a default strategy for addressing the loss of overwintering habitats. Admittedly, for the mitigation described herein, earlier and more extensive consultation with herpetologists and translocation experts could have strengthened the mitigation approach and research program (Cornelis et al., 2021; Germano et al., 2015). However, current development permits do not always mandate or facilitate such consultation, and even when they do, urgent decisions—in this case, the excavation of snake hibernacula on the cusp of winter—still may take place without previous knowledge. Expecting extensive consultation and research in every scenario often is impractical, particularly in time-sensitive situations. It is therefore critical to develop and disseminate species- and region-specific research on translocations, ensuring future mitigations are effective and consistent no matter the level of expertise available.

Conclusions and Management Recommendations

Mitigation translocations should be carefully planned with expert consultation whenever possible to improve success rates and minimize unintended consequences. One of the most important considerations is translocation distance—short-distance translocations within an individual's home range are preferable to long-distance relocations as they reduce the risk of increased movement, and subsequently heightened mortality. Additionally, soft-release strategies, where animals are given time to acclimate to their release site, have shown promise in improving site fidelity and reducing stress. Similarly, the potential benefits of releasing snakes in social groups warrant further exploration, as some evidence suggests that maintaining familiar conspecifics can ease the transition into a new environment.

Follow-up monitoring of translocated animals is essential for two key reasons. First, because many animals exhibit site fidelity, translocated individuals may attempt to return to their original location, potentially exposing themselves to immediate harm. If habitat disturbances persist, ongoing monitoring is necessary to ensure the translocated animals do not return to the hazardous areas from which they were relocated. Second, it should become standard practice to document and publish the outcomes of at least a subset of translocated individuals, contributing to a broader understanding of best practices in mitigation translocations. Without post-release data, it is impossible to determine whether translocations are successful or if adjustments are needed to improve future efforts. Further research is required to examine species- and region-specific factors that may improve translocation outcomes.

Ultimately, mitigation translocations should not be mistaken for well-planned conservation actions, such as the reintroduction of a species following extirpation. However, by integrating strategic planning, follow-up monitoring, and the publication of research on successes and failures, mitigation translocations could extend beyond short-term conflict resolution and contribute meaningfully to species conservation.

Additional suggestions for 'best management practices' are presented in Chapter 4

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CHAPTER 3

Distinct movement ecology in a northern population of Western Yellow-bellied racers (*Coluber constrictor mormon*): Further evidence of divergent behaviour in snakes at range limits

Introduction

Natural history, the study of natural patterns through observation, remains a cornerstone of modern ecology (Tosa et al., 2021). However, the natural history of many cryptic and endangered species remains understudied, particularly at their range limits, where abundance often is lower (Eckert et al., 2008; Lessica and Allendorf, 1995; Luiselli, 2006). For these peripheral populations, region-specific natural history is essential to inform management, particularly because data from core populations may not reflect local ecological pressures (Safriel et al., 1994). This issue becomes especially important in wide-ranging species, as extreme variations in local ecological pressures can impact morphology and behaviour at the population level.

Presumed ecological effects on populations in temperate zones are believed to result from relatively shorter summers and harsher winters. The significant survival pressures posed by temperate winters, including low food availability and prolonged cold exposure (Townsend et al., 1999; Korslund & Steen, 2006), drive adaptations in morphology and behaviour. For example, mammals, birds, and turtles tend to have larger body sizes the farther they are from the equator (Bergmann's Rule (Bergmann, 1847)) while squamates are larger near the equator (Ashton & Feldman, 2003; Blackburn et al., 1999). In addition to morphology, distinct local climates across latitudes can shape movement patterns and seasonal behaviours (Avgar et al., 2013; Singh et al., 2012).

For ectothermic reptiles, whose activity is tightly constrained by temperature, northern environmental pressures have particularly strong implications for movement ecology. In Canada, all native reptiles occur at the northern limit of their ranges and experience distinct environmental constraints such as colder temperatures and shorter active seasons. Consequently, the movement ecology of these extreme-northern populations has been shown to differ considerably from that of conspecifics farther south, with some northern reptiles occupying larger home ranges (Martino et al., 2012). Ideally, knowledge from populations from the center of the species' range should be integrated with comparable northern research to reveal key similarities and differences across latitudes.

The Western Yellow-bellied racer (Serpentes: *Coluber constrictor mormon,* hereafter WY racer) is an oviparous snake found relatively far north (southwestern Canada), where it largely occupies semi-arid grasslands below 900m in elevation (Dulisse, 2007; Racer Management Team Working Group, 2013). Due to their limited distribution within Canada (Figure 3.1), and the high human impact in these regions, WY racers have recently become federally listed as threatened (COSEWIC, 2015; Ministry of Environment and Climate Change Strategy, 2023). Despite this, there is a scarcity of formal research on WY racers across their range; this paucity of data hinders effective management and conservation efforts of the species. Most of what is known about the movement ecology of WY racer comes from a single telemetry study conducted in Utah in 1976 (Brown & Parker, 1976). Those authors observed that WY racers used communal dens, exhibited den fidelity, and migrated in the spring from their hibernacula to a summer active range. Although more recent research examined the snake's diet (Shewchuck & Austin, 2001) and road mortality (Spruyt, 2023) in Canada, these studies relied on dead specimens or single-capture individuals, offering little insight into movement ecology. Thus, gathering data on the movement patterns and natural history of WY racers in Canada remains a high conservation priority (Environment Canada, 2014).

Despite a recognized need for movement data on racers in the north, a major obstacle is the difficulty of obtaining a large sample of wild-caught individuals suitable for telemetry. Their natural scarcity, coupled with their less predictable and often solitary overwintering habits (McKelvey, 2024; Wong, 2025) make it hard to locate the animals during spring emergence. In contrast, sympatric species like the Western rattlesnake (*Crotalus oreganus*), that frequently use communal dens, can be captured in large numbers during spring and fall when individuals are visible at hibernacula—a feature that has supported decades of detailed ecological research (Harvey & Larsen, 2020; Howarth et al., 2025; Kirk et al., 2021; Macartney, 1985; Putman et al., 2016). To this end, current snake surveying methods (Ministry of Environment, Lands and Parks,

1988) in Canada often are based on the more predictable emergence behaviour of communal denning species (e.g. *C. oreganus*) and thus are poorly suited to detecting racers.

This study became feasible due to extensive industrial damage that temporarily displaced snakes, allowing for mitigative work while providing animals suitable for telemetry. This chapter details a two-year radiotelemetry study of WY racers at their northern limit in southwestern Canada. In doing so, it provides the first detailed overview of WY racer movement behaviour and natural history at their northern range limit, and the first such study on the subspecies since Brown and Parker (1976). Guiding our research were two primary objectives: (1) To use radiotelemetry to characterize the summer movement behaviour and space use of Western Yellow-bellied racers, and (2) to compare this element of the animal's ecology with those reported for conspecifics in Utah.

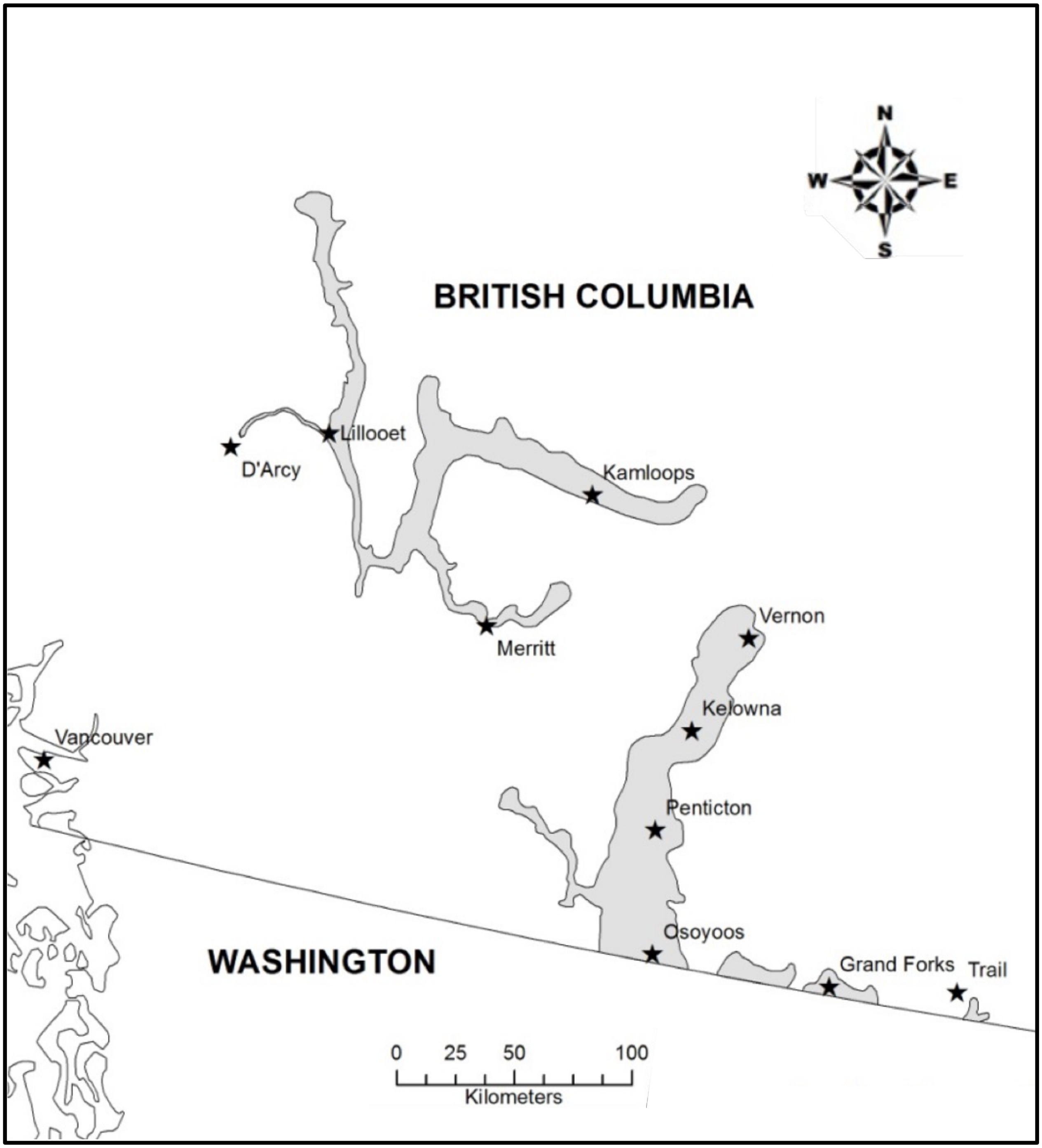

Fig. 3.1. Distribution of *Coluber constrictor mormon* in southwestern Canada. Cities and towns that overlap with or are near the *C. constrictor* range are indicated with a star. Source: Environment and Climate Change Canada (2015).

Methods

Study Site and Disturbance

We studied the WY racer near its northern periphery, inside the Lac du Bois Protected Area in the Thompson region of British Columbia, Canada (LAT 50.724161, LONG -120.402250). Here the climate in the summer is hot and dry while winter temperatures drop well below freezing (Wikeem & Wikeem, 2004). The hottest months are July (average: 21.5 ± 1.6 °C) and August (average: 20.9 ± 1.2 °C), while the coldest are December (average: –2.7 ± 3.0 °C) and January (average: –2.8 ± 3.4 °C) (Environment and Climate Change Canada, 2024). The dominant native plant species are Bluebunch wheatgrass (*Pseudoroegneria spicata*) and Big sagebrush (*Artemisia tridentata*) (Wikeem & Wikeem, 2004). See Chapter 1 for a more detailed description of the habitat.

In November 2021, a pipeline expansion project across western Canada (Trans Mountain, 2021) excavated three snake hibernacula in Lac du Bois, with WY racers being recovered from each site. The ensuing mitigation work resulted in 56 WY racers being held overwinter at the nearby BC Wildlife Park under conditions intended to mimic natural hibernation. This sample furnished sufficient numbers of large animals that were suitable for radiotelemetry (see *Telemetry* below). All racers (telemetered or not) were released at an artificial den approximately 50-1500m from the three original hibernacula in the ensuing spring (April/May 2021; see Chapter 2 for details about the mitigation).

To minimize concern about using the displaced racers to collect natural history data, we collected simultaneous data on unmanipulated ('reference') racers occupying the same landscape (see below). This enabled us to conduct statistical comparisons between the two groups of snakes, potentially detecting differences in movement behaviour and allowing improved interpretation of the data.

Telemetry

To obtain summer movement data in 2021, we selected 11 relatively large racers (9♀, 2♂) for telemetry from those snakes housed overwinter in captivity. We paired this sample with eight undisturbed 'reference' snakes (6♀, 2♂) in 2021 from neighbouring dens in the same study area. We conducted telemetry again the following summer (2022) on a new sample population of five racers (4 reference ♀, 1 disturbed ♂) captured from the same study area.

Snakes selected for telemetry were transported to nearby veterinary clinics for surgical implantation of transmitters. We used a revised version of the surgical methodology of Reinert and Cundall (1982): an incision was made at roughly 55% of the snout-vent-length (SVL) of the snake through which a transmitter (weighing <4% of the snake's body weight) was inserted into the body cavity. Prior to the procedure, the snake was anesthetized with isoflurane gas, and following the surgery, the snake was given meloxicam (NSAID, DIN: 02240463, Boehringer Ingelheim) and ceftazidime (antibiotic, DIN: 00886971, Fresenius Kabi Canada ltd). The average weight of male and female telemetry snakes at the time of surgery was 89.0 g (SE = ±3.5, n = 5), and 129.8g (SE = ±8.2, n =19), respectively. On the largest snakes we used heavier transmitters (SB-2T; Holohil Systems Ltd, Carp, Ontario, Canada) to maximize life span (est. 6-month and 12-month batteries); snakes below 190 g were outfitted with lighter transmitters (BD-2; Holohil Systems Ltd, Carp, Ontario, Canada) with projected lifespans of 60 and 90 days.

We relocated telemetry snakes once every 1-5 days, occasionally longer when a snake could not be found, recording UTM coordinates for each new location, defined as following a movement exceeding 5 m.

Movement Rates

To measure movement rates during the active season, we calculated three parameters (Rstudio, Version 1.4.1717). *Mean distance travelled per day* was the distance between relocations relative to the time elapsed. *Sinuosity* was a measure of path straightness (ranging from 0 for a straight path to 1 for a highly curved or circular path—Benhamou, 2004). Finally, *recursiveness* measured site revisits, defined as returns within 2m of a prior GPS point after leaving for at least 24 h (Smith et al., 2021).

Home Range

To estimate the summer range of the racers, we used the minimum convex polygon (hereafter MCP) method because of its frequent, historical use in the literature on *C. constrictor* (Brown & Parker, 1976; Gardiner et al., 2013; Fleet et al., 2009; Martino et al., 2012). However, since the MCP model assumes the entire area within the peripheral points is used (Worton, 1995), random excursions can lead to overestimations of space use. We addressed these overestimations using two approaches: (1) recalculating MCP home ranges after removing 5% of outliers to minimize the influence of random excursions (Fey et al., 2021; Fleet et al., 2009), and (2) introducing a new index, the *minimum area occupied* (hereafter MAO), a reflection of the area used by a snake based on the total area covered by its traversed paths. Unlike the MCP model, which assumes uniform use of space within its boundaries, MAO assumes that snakes follow specific paths, leaving large portions of the landscape within the peripheral points unused. We calculated MAO by summing the snake's traversed path and adding a 0.5 m buffer on either side, with the total area of this buffered path representing the MAO. The MCP model also has been criticized (Crane et al., 2021) for being highly influenced by sampling time and effort (Worton, 1995). To account for this, we excluded snakes with fewer than 20 tracking days (n = 1♀ + 1♂) and greater than 100 (n = 2♀) tracking days from the grouped home range and MAO analyses.

The MCP home range and MAO also serve as small-scale analogues of two widely used metrics in species at risk assessments: Extent of Occurrence and Area of Occupancy. The Extent of Occurrence metric is defined as a polygon encompassing a species' entire distribution, including areas that may be unsuitable and/or unoccupied, while Area of Occupancy represents the portion of the Extent of Occurrence that is actually occupied (COSEWIC, 2024). Similarly, MCP home range is analogous to Extent of Occurrence at the individual level, capturing the broadest area used by an animal, whereas MAO reflects the space actively utilized within that range, making it conceptually comparable to Area of Occupancy.

Migration

Following Brown and Parker (1976) we defined spring migration as a period of long, straight movements immediately after egress that were distinct from shorter more tortuous movements during the rest of the active season. We tested if this behaviour existed in our population by plotting distance travelled per day (calculated between successive locations of each snake) against time of year and testing the significance of this relationship. Snakes that we began tracking after June 1st (n = 5) were excluded from these analyses as they may have already completed their outbound migratory movements (if there was one) before tracking began.

Statistical Analyses

To compare the movement behaviour of males and females, we used two-way analysis of variance tests (ANOVA). Throughout our analyses, we also used ANOVA tests to compare the movements of the manipulated and reference snakes. When no significant differences were detected between manipulated and reference groups (α = 0.05), these groups were combined for subsequent reporting. Where we found significant differences, we ran Tukey's Honestly Significant Difference (HDS) *post hoc* tests. Hereafter, all mean values reported on telemetry statistics in the methods and results are followed by ±1 standard error of the mean.

Results

Over the two active seasons, we radio-tracked 24 WY racers. In 2021, our telemetry snakes (6 reference ♀, 2 reference ♂, 9 manipulated ♀, 2 manipulated ♂) were tracked for an average of 55.8 (±9.2) days between May and October. In 2022, the smaller sample of snakes (3 reference ♀, 1 reference ♂, 1 manipulated ♀) were followed for an average of 73.0 (±10.1) days between May and August. Since we found few significant differences (all $P > 0.1$) between reference and disturbed snakes in 2021 [the exception being straighter paths in reference snakes (n = 8) compared to manipulated snakes (n = 10) in 2021 ($F_{1,15}$ = 5.70, P = 0.03*)] we combined the snakes from both the manipulated population and natural reference dens when reporting on the behaviour and movements of WY racers in this study. During our fieldwork, two out of 24 telemetry snakes died, both in 2021. The first mortality (May 27th) was likely from predation, and the second (June 20th) was of unknown causes.

Active Season Movement and Space Use

WY racers tracked at our site ($N = 24$) had high average daily movement rates (43.3 m/day ±3.57) and travelled in paths that were generally straight (x^{-} sinuosity index = 0.156 ±0.01). Average recursiveness rates were 1.19 ±0.06, indicating that snakes typically visited each site on the landscape only once, though there was a fair amount of variance in this metric between individuals, particularly between males. A breakdown of movement metrics by year and sex can be found in Table 3.1.

Across both years, average space use for racers ($N = 20$, after excluding snakes with fewer than 20 or more than 100 tracking days) was 10.5 ha (±2.72) for MCP 100%, which included all relocation points, and 6.16 ha (±1.38) for MCP 95%, which excluded the outermost 5% of relocations. Mean MAO was 0.178 (±0.02). Detailed values by year and sex are provided in Table 3.2. Minimum convex polygon home ranges were considerably larger than minimum area occupied values in both years of the study (Figure 3.1)—on average, MAO represented just 3% of the MCP (95%) values for females and 4% for males (Table 3.2).

In 2021, across all measures of movement behaviour and space use there were no significant differences between males and females (all $P > 0.3$) (Table 3.1 and 3.2). Due to the small male sample size ($n = 1$), statistical comparisons between sexes were impossible for 2022.

Two large female racers that were tracked for over 100 days during the 2021 active season, but excluded from the home range models, travelled on average 48.1 m/day (±2.8) and occupied home ranges of 29.6 and 46.2 ha, respectively.

Migration

For most snakes, daily movements were not markedly elevated at the start of the active season, possibly indicating an absence of spring migration. In most cases ($n = 19$), a regression analysis of daily travel distances over time revealed no significant trend. One snake, however, showed a long, directed movement early in the season, with a strong inverse relationship between daily travel distance and time ($\beta = -1.95 \times 10^{-5}$, $t(14) = -3.43$, $P = 0.004$, $R^2 = 0.46$).

Table 3.1. Mean (± SE) values for daily distance travelled, path sinuosity, and site recursiveness, grouped by sex and year. Results of two-way ANOVAs are presented to test for the effects of sex and status (manipulated vs. reference) on each movement metric during the first year (2021). *Post hoc* testing indicated that manipulated snakes moved in significantly more sinuous paths than reference snakes (diff. = 0.05, t = 2.5, P = 0.03) in 2021. No other P-values were statistically significant (all $P > 0.1$).

Metric	Year	Sex	$\bar{x}$, SE, n	Predictor	F-value (df1, df2)	P-value
Distance travelled per day (m/day)	2021	female	43.6, 5.32, 15	status	1.39 (1, 16)	0.26
		male	51.9, 5.40, 4	sex	0.47 (1, 16)	0.51
	2022	female	33.8, 2.78, 4			
		male	42.2, NA, 1			
Sinuosity	2021	female	0.15, 0.02, 14	status	5.70 (1, 15)	**0.03***
		male	0.18, 0.02, 4	sex	1.17 (1, 15)	0.30
	2022	female	0.15, 0.02, 4			
		male	0.16, NA, 1			
Recursiveness	2021	female	1.15, 0.04, 15	status	1.84 (1, 16)	0.19
		male	1.26, 0.26, 4	sex	0.44 (1, 16)	0.52
	2022	female	1.31, 0.18, 4			
		male	1, NA, 1			

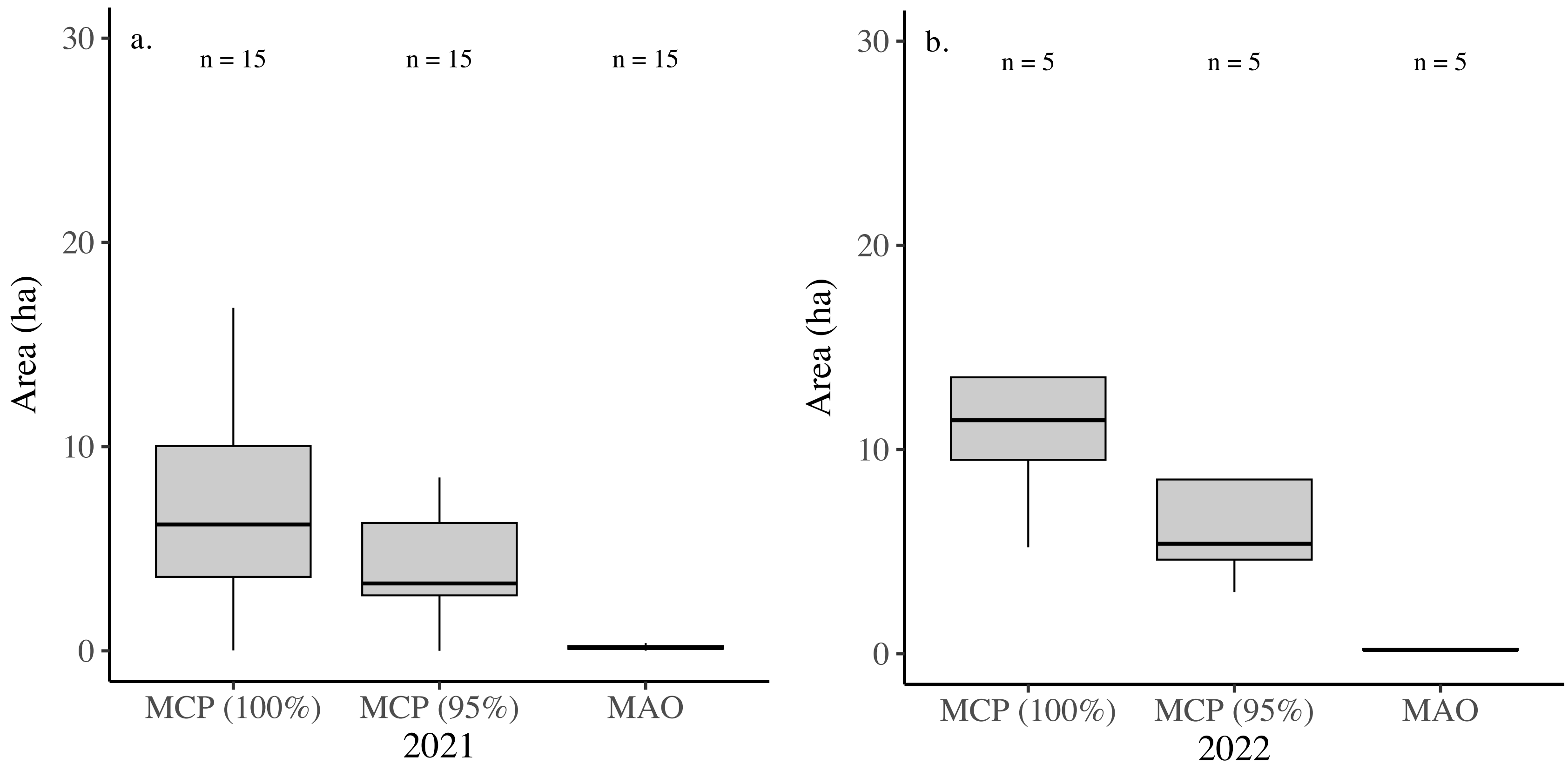

Figure. 3.2. Box plots illustrating racer space use in 2021 (a.) and 2022 (b.). The x-axis references three area use metrics: MCP home range with 100% of data points, MCP home range with 95% of data points, and minimum area occupied (MAO). The y-axis shows area in hectares (ha).

Table 3.2. Summary of space use metrics by year, including mean, SE, and sample size (n). Space use metrics include only individuals tracked for 20–100 days (mean ± SE: 49.1 ± 5.63 days). Results of two-way ANOVAs are presented to test for the effects of sex and status (manipulated vs. reference) on each movement metric during the first year (2021). No *P*-values were statistically significant (all $P > 0.1$).

Metric	Year	Sex	$\bar{x}$, SE, n	Predictor	*F*-value (df1, df2)	*P*-value
MCP home range (100%) (ha)	2021	female	11.4, 4.42, 12	status	2.44 (1, 14)	0.14
		male	4.60, 1.10, 3	sex	0.62 (1, 14)	0.45
	2022	female	12.0, 3.06, 4			
		male	11.4, N/A, 1			
MCP home range (95%) (ha)	2021	female	5.96, 2.08, 12	status	1.99 (1, 14)	0.18
		male	4.44, 1.17, 3	sex	0.13 (1, 14)	0.72
	2022	female	8.79, 2.75, 4			
		male	3.02, N/A, 1			
Minimum area occupied (MAO) (ha)	2021	female	0.18, 0.03, 12	status	2.67 (1, 12)	0.12
		male	0.15, 0.06, 3	sex	0.20 (1, 12)	0.66
	2022	female	0.20, 0.02, 4			
		male	0.23, N/A, 1			

Discussion

Our radiotelemetry data provided valuable insight into the summer movements and ecology of WY racers at their northern limit. Consistent with studies of other *C. constrictor* subspecies (Carfagno & Weatherhead, 2008), we found little difference in movement patterns and home range sizes between males and females. Additionally, the movements of WY racers in our study appeared largely unaffected by the major disturbance in the area during the study period. Further details on the impact of this disturbance and related mitigation efforts for Great Basin gophersnakes (*Pituophis catenifer deserticola*) are presented in Chapter 2.

Home range estimates of WY racers in our population were substantially larger than conspecifics in Utah, with snakes (N = 20) in our study averaging MCP (100%) home ranges of 10.5 ha (± 2.72; see Table 3.2 for more details) compared to just 1.45 ha (N = 8) in Utah (Brown & Parker, 1976). Home range size varies significantly between racer subspecies: WY racers in Utah occupy significantly smaller average home ranges than Tan racers (*C. c. etheridgei*) and Southern Black racers (*C .c. priapus*), two subspecies found farther south (Fleet et al., 2009). Comparisons between our data and that from Brown and Parker's (1976) study suggest that home range size also may vary between racer populations of the same sub-species, particularly those at range extremities where animals face different ecological pressures compared to populations at the range core. Similarly, Eastern Yellow-bellied racers (*C. c. flaviventris*) and Bullsnakes (*Pituophis catenifer sayi*) at their northern limit in Saskatchewan, Canada, also occupied larger home ranges than their southern conspecifics (Martino et al., 2012). A positive correlation between home range size and latitude has been observed in avian and mammalian taxa as well (e.g. *Richmondena cardinalis* – Dow, 1969; *Felis rufus, Canis latrans, Ursus americanus* – Gompper and Gittleman, 1991; *Capreolus capreolus* – Morellet et al., 2013). The considerable variation in home range sizes across latitudes has important conservation implications for northern snake populations, which may require larger conservation areas than populations at the range core especially if overwintering and summer foraging habitats are separated by substantial distances.

Another key difference between our study population and the population in Utah is the absence of a spring migration period in our study. WY racers in Utah travelled in directed paths at the start of the season, migrating from large communal dens to small active season ranges (Brown

& Parker, 1976). In contrast, most snakes in our study (19/20) did not appear to travel in directed paths at the start of the summer but wandered over a much larger area during the active season.

Less accentuated movements early in the active season, along with greater home range sizes, likely reflect the combination of factors influencing racer movements at their northern limits. Brown and Parker (1976) hypothesized that a refuging model, where dispersal is driven by intraspecific competition and constrained by the energetic costs of movement, shaped the migratory behaviour of racers in Utah over the active season. If this model holds in our northern population, then a low population density may negate the need for lengthy migrations from the hibernacula. Indeed, low snake densities, and consequently lower levels of competition, have been observed at northern latitudes (Luiselli, 2006), supporting the idea that reduced spring migration at our site may be consistent with the refuging model.

Low population density at northern range limits may also drive racers to cover greater areas in search of mates during the spring, expanding their active season range. Additionally, the abundance, seasonality, and patchiness of prey at these sites may contribute to increased movement during the summer. In British Columbia, racer diet composition has been observed to shift seasonally with prey availability—insects are less abundant in spring—which may prompt movements between foraging habitats (Shewchuk et al., 2001).

Finally, snakes that den communally tend to migrate long distances between active season ranges and winter hibernacula, whereas snakes that hibernate singly or with small groups are more likely to overwinter within or near the active season home range (Gregory, 1984). The Utah racers were sourced from large communal dens (e.g., 272 racers captured during one egress at the largest den—Brown & Parker, 1976), and their migratory behaviour aligns with this pattern. In contrast, at our site, racers emerged primarily from small hibernacula shared with other snake species (*P. c. deserticola* and *C. oreganus*)—during a single spring egress, five racers emerged from hibernacula containing fewer than five snakes in total, thirteen from hibernacula with five to ten, and only two from a hibernaculum with more than twenty individuals of any species (McKelvey, 2024). Smaller aggregations at hibernacula likely reduce both intra- and interspecific competition upon emergence. With competition low, migration may offer little advantage, and snakes at our site appear to transition directly into active season behaviour.

Conclusions and Management Recommendations

Our data indicate that Western Yellow-bellied racers at their northern range limit travel long distances per day and occupy large areas during the summer active season. This extensive movement likely reflects the broad spatial distribution of key resources across the landscape, low population density, and low rates of intraspecific competition. Racers have diverse seasonal requirements, including access to foraging grounds, overwintering sites, and oviposition sites for gravid females. At northern sites, the abundance and patchiness of these critical resources likely are key factors shaping local movement patterns.

These patterns may differ substantially from those observed in more central populations (i.e. Utah), where resource availability is generally higher, climatic constraints are milder, and competition more intense (Luiselli, 2006). As a result, the movement behaviour and spatial requirements of snakes, and other taxa, at the edge of their ranges may differ markedly from those at the core, often trending larger (Dow, 1969; Gompper and Gittleman, 1991; Martino et al., 2012; Morellet et al., 2013).

Improved methods for quantifying snake space use would greatly benefit future research and management. In this study, the minimum convex polygon (MCP) method was useful for comparison with previous studies. However, the MCP method often overestimates actual space use, especially for northern snakes, which tend to concentrate their activity in discrete centres connected by narrow movement corridors (Gardiner et al., 2013).

Home range and MAO also serve as small-scale analogues of the species level conservation metrics Extent of Occurrence and Area of Occupancy. Two species may have similar Extent of Occurrence, but if one is a habitat generalist and the other a specialist, their Area of Occupancy, and consequently their response to habitat disturbance, will differ greatly. The same principle can be applied at the population level using home range and MAO. Our study population of racers had large home ranges, but likely relied on a limited number of spatially dispersed habitats such as hibernacula and seasonal foraging areas, that was reflected in the much smaller MAO values.

Finer scale movement-based models like Brownian bridge (BBMM) methods can help identify these functionally important areas of the landscape. Where disturbance is unavoidable, mitigation efforts should consider preserving the smaller, high-use areas within the home range, to ensure that access to essential habitat features and movement corridors remains intact.

Overall, this study suggests that snakes at the northern edge of their range occupy large home ranges, relative to conspecifics at the range core, but likely rely on limited and spatially dispersed resources within the home range. The distinct spatial ecology expressed by peripheral, far-northern snake populations has important implications for conservation planning and highlights the need for strategies informed by local data. Relying on movement data from central populations risks underestimating the spatial needs of snakes at range limits. While traditional home range estimators such as minimum convex polygons offer a useful starting point for describing space use, effective conservation will require a deeper understanding of the location, abundance, and connectivity of critical habitats. Tailoring conservation efforts to region-specific movement ecology is essential to supporting the long-term persistence of snakes at the edges of their ranges.

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CHAPTER 4

Conclusions and management recommendations

This thesis investigated the movement behaviour of two threatened snake species, Great Basin gophersnakes (*Pituophis catenifer deserticola*) and Western Yellow-bellied racers (*Coluber constrictor mormon*), in southwestern British Columbia. The first objective was to evaluate the effects of a mitigation involving translocation, which I addressed by comparing the movement behaviour and survival rates of translocated gophersnakes with undisturbed reference conspecifics from the same area. The second objective was to collect data on the movement ecology and general natural history of both species, with particular emphasis on racer movement. This was achieved through two seasons of radiotelemetry, and the results represent the first radiotelemetry study of *C. c. mormon* since the 1970s (Brown & Parker, 1976), and the first such study conducted at the northern edge of its range.

Below, I present the main findings of this research:

1. **Translocation had no detectable short-term impact on gophersnakes.** Over two years of monitoring, translocated individuals showed no significant differences in movement or survival compared to reference snakes, suggesting that translocation can be successful under suitable conditions.

2. **Seven out of ten gophersnakes that were tracked to ingress appeared to independently locate alternate overwintering sites** following the destruction of three large hibernacula within the study area. This finding supports growing evidence (McKelvey, 2024; Williams et al., 2012; Wong, 2025) that both gophersnakes and racers exhibit flexible, generalist denning strategies, in contrast to the strong fidelity to communal hibernacula observed in *Crotalus* and *Thamnophis* (Gomez et al., 2015; Gienger & Beck, 2011; Shine & Mason, 2004).

3. **The annual proportion of gravid female gophersnakes at Lac du Bois (≈ 18% across both years; N = 17) was low** relative to previous studies of the species in British Columbia (≈90%; N = 19; Williams et al., 2014). Both translocated and reference females showed very limited reproductive output during the study period. I speculate that an extreme heat event (White et al., 2023) during the first year of the study may have contributed to suppressed reproduction.

4. **Racers at their northern limit demonstrated distinct movement behaviour**, including notably larger home ranges than a central population in Utah. This is consistent with prior studies suggesting that some snake species, and other avian and mammalian taxa, at northern peripheries occupy larger areas during the summer active period than their southern counterparts (Dow, 1969; Gompper and Gittleman, 1991; Koprowski et al., 2008; Martino et al., 2012).

5. **Racers had large home ranges but occupied only a small portion of that space**, suggesting a reliance on patchy, seasonal resources dispersed across the landscape. To identify these critical habitats and movement corridors, future research and management should look to more precise movement models such as Brownian Bridge approaches.

Recommendations for Future Radiotelemetry

Based on my findings, and previous research demonstrating that spatial requirements are greater at range limits across several taxa (Dow, 1969; Gompper and Gittleman, 1991; Koprowski et al., 2008; Martino et al., 2012), I recommend more research on the movement ecology of snakes at the far northern limits of their ranges. Existing work in British Columbia has focused primarily on a few taxa, such as *Crotalus oreganus* and *Thamnophis* spp., which typically overwinter in large communal hibernacula. While this research has been instrumental, especially for the conservation of the threatened Western Rattlesnake (*C. oreganus*) in Canada, it has left several other at-risk species underrepresented in the literature. These include our study species (*P. c. deserticola* and *C. c. mormon*), as well as the Rubber boa (*Charina bottae*), which is of special concern in the province (Collins, in progress).

To address the underrepresentation of these species, survey methods should be adapted to reflect our growing understanding of the more cryptic and solitary denning behaviours exhibited by some of the province's snakes. For gophersnakes and racers, I recommend targeting a broader range of habitats during egress surveys, including not only traditional rattlesnake hibernacula, but also rodent burrows and anthropogenic substrates (McKelvey, 2024; White, 2008). Expanding the search radius around known hibernacula may also improve detection, as gophersnakes and racers were often found farther from den entrances than rattlesnakes (personal observation). Increasing revisit frequency to hibernacula could further improve capture numbers. However, where possible, fencing around hibernacula during egress may be even more effective than simply increasing visits to unfenced sites. Previous studies have used fencing to capture *C. constrictor* and *P. catenifer* during egress; some reported higher capture rates when fencing was used (Parker & Brown, 1973), while others did not report on its effectiveness (Gardiner et al., 2013). At my study site, McKelvey (2024) used a fence around an artificial den to capture seven snakes (three gophersnakes, four racers) during spring emergence. Overall, fencing could be a promising survey method that warrants further exploration.

I also believe it is possible to increase a telemetry sample by taking advantage of natural mate-seeking behaviour if tracking begins early in the spring, before mating. If snakes are tracked frequently and left undisturbed, they can lead researchers to additional individuals via mate-seeking behaviour later in the season. In the first year of this study, this approach resulted in the capture of three racers and six gophersnakes of suitable size for telemetry.

Special attention should be paid to the transmitter properties used for gophersnakes and racers. We recommend transmitters with thin, flexible antennae capped with resin, as firm, sharp-tipped antennae can cause skin perforations. Additionally, anchoring the transmitter with a suture through the ribcage proved successful. As with other constrictors (Bryant et al., 2010), we observed transmitter migration when anchoring stitches were not used, an issue that was resolved by modifying the implantation procedure to include an anchoring suture (see Chapter 2, Methods for more details).

Recommendations for Future Mitigations

To improve the success of mitigation translocations for snakes, I recommend adopting a framework more closely aligned with conservation translocations, which have historically had higher success rates (Cornelis et al., 2021; Germano et al., 2015). In particular, mitigation strategies must be informed by species- and region-specific data. Accordingly, part of the responsibility of a mitigation should be to fund research on understudied species that are, or may be, affected by development or habitat disturbance, as was the case in this study.

The ecological knowledge gained through this research has already produced valuable insights. For example, adult gophersnakes demonstrated an unexpected ability to locate alternate overwintering sites and exhibited low fidelity to the artificial hibernaculum where they were released (McKelvey, 2024), both of which have implications for future mitigation planning. A significant portion of the budget for this mitigation was spent constructing two artificial dens to offset the loss of three natural hibernacula. While the artificial dens satisfied the provincial offset requirements in terms of area and provided survivable overwintering conditions (McKelvey, 2024), neither artificial den was readily adopted and offered negligible benefit to the snakes directly impacted by the disturbance. Based on these findings, we recommend that future efforts to mitigate the loss of overwintering habitat for gophersnakes and racers explore alternative offset strategies. Among those, funded research on the ecology of these understudied species would be of great benefit. I suggest several priority areas for further investigation:

- **Experimental designs** evaluating the effects of treatments such as translocation distance and release strategy (e.g., soft vs. hard release) could substantially improve the outcomes of snake translocations in British Columbia and elsewhere.

- **Characterization of key habitat features**, including hibernacula and oviposition sites, is also needed, particularly for northern egg-laying species, whose requirements may differ from those of better-studied ovoviviparous species like rattlesnakes.

- **Landscape-level studies** on the connectivity of these critical habitats across different sites in the province are needed to determine whether individuals can realistically access alternate sites following disturbance.

Heatwaves as an Emerging Conservation Concern in British Columbia

An unplanned component of this research was an extreme heat event that occurred during the first year of the study (White et al., 2023). I was not equipped to assess its effects on our study population: our snakes were already undergoing an experimental treatment (translocation), and no historical data exist for this population to support comparisons. However, recent work suggests that northern gophersnakes' late reproductive age and short reproductive window make them vulnerable to extreme weather (Petersen et al., 2024), as low recruitment may reduce the likelihood of the population persisting through consecutive adverse years. Although snakes show thermal plasticity early in life, adults are less able to physiologically adjust to abrupt temperature shifts (Aubret & Shine, 2010). Thus, while gradual warming may be tolerated, extreme heat events, which are forecasted to increase in severity (Luo et al., 2024), may pose a serious threat. I observed low reproductive output in our study population during the summer of the heatwave and the year that followed, though no definitive connection to the extreme heat can be made. Nonetheless, these patterns highlight the need for future research on the ecological impacts of extreme heat events on northern snake populations.

Studying the effects of extreme heat events *in situ* is challenging, as heatwaves are difficult to predict in advance. On rare occasions, a baseline has been established prior to a heatwave, allowing researchers to document substantial impacts that would be difficult to study in an *ex situ* setting (Galvez et al., 2023). Because field data on heatwaves are limited, our observations of snake movement and reproduction during the 2021 Pacific Northwest extreme heat event provide a valuable dataset for future comparison. These data could be retrospectively evaluated against findings from future telemetry work at the same site.

Building baseline datasets on snake population ecology across multiple sites in the province would increase the likelihood of studying future heatwaves in real time rather than retrospectively. With climate change accelerating the frequency and intensity of extreme events, establishing these baselines now will improve our ability to evaluate the ecological consequences of future heatwaves.

Conclusions

Understanding how animals move through their environment is critical for effective wildlife stewardship. Movement ecology offers not only key insights into species' natural history, but also practical tools for informing habitat protection, threat mitigation, and species recovery. As demonstrated in this thesis, movement data can be used both in advancing region specific natural history knowledge and to assess the outcomes of mitigation efforts. In doing so, it highlights the value of movement studies in shaping evidence-based strategies for management and conservation.

There remains a clear and pressing need for movement ecology research in Canada, where many at-risk species remain understudied. Snake behaviour, habitat use, and life history traits can differ dramatically across a species' range, particularly in wide ranging taxa. Accordingly, management and conservation strategies for peripheral populations must be informed by data from the regions where they are to be applied. Extrapolating from data collected elsewhere may lead to ineffective, and potentially wasteful, management decisions. To ensure conservation and mitigation actions are ecologically appropriate and have the best chance of success, they must be grounded in region- and species-specific empirical data.

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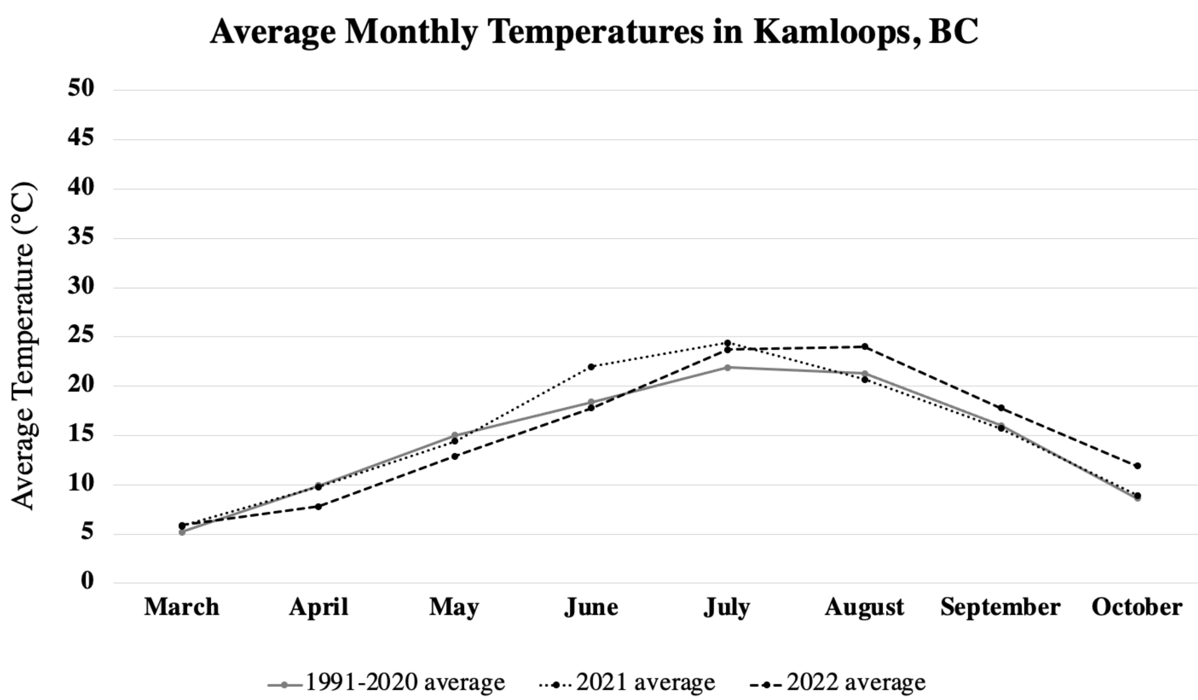
Appendix A

Graph of average monthly temperatures in Kamloops, BC. The solid line represents 30-year historical norms (1991-2021), and the dotted and dashed lines represent 2021 and 2022 respectively. Climate data was sourced from: https://climate.weather.gc.ca/climate_normals/results_1991_2020_e.html?searchType=stnProv&lstProvince=&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=333000000&dispBack=0 AND https://kamloops.weatherstats.ca/charts/temperature-monthly.html



Appendix B

Means ($\bar{x}$), standard errors (SE), and sample sizes (*n*) of movement metrics for Great Basin gophersnakes. The same dataset was summarized three times, each divided by a different factor: (A) year, (B) sex, and (C) translocation status. Metrics include distance per day (m/day), distance per movement (m/movement), movement rate (m/h), sinuosity index, and recursiveness. Values represent unstandardized measurements derived from telemetry data.

Grouping	**Group**	***n***	**Metric**	$\bar{x}$	**SE**
(A) year	2021	32	dist. per day (m/day)	28.34	2.35
			dist. per move. (m/movement)	95.82	7.31
			move. rate (m)	2.85	0.23
			sinuosity index	0.13	0.01
			recursiveness	1.29	0.04
	2022	17	dist. per day (m/day)	19.84	1.65
			dist. per move. (m/movement)	75.58	8.90
			move. rate (m)	1.67	0.14
			sinuosity index	0.16	0.01
			recursiveness	1.22	0.07
(B) sex	female	20	dist. per day (m/day)	23.39	2.97
			dist. per move. (m/movement)	74.66	8.20
			move. rate (m)	2.39	0.35
			sinuosity index	0.14	0.01
			recursiveness	1.24	0.05

	male	29	dist. per day (m/day)	26.77	2.08
			dist. per move. (m/movement)	98.55	7.59
			move. rate (m)	2.45	0.17
			sinuosity index	0.13	0.01
			recursiveness	1.29	0.05
(C) status	reference	27	dist. per day (m/day)	26.16	2.30
			dist. per move. (m/movement)	89.59	8.79
			move. rate (m)	2.35	0.27
			sinuosity index	0.13	0.01
			recursiveness	1.30	0.05
	translocated	22	dist. per day (m/day)	24.45	2.66
			dist. per move. (m/movement)	87.83	7.32
			move. rate (m)	2.52	0.22
			sinuosity index	0.14	0.01
			recursiveness	1.22	0.06

Appendix C

Results of univariate ANOVAs for each movement metrics following a multivariate analysis of variance (MANCOVA). Each model tested the effect of predictors (factors) on individual response variables included in the MANCOVA. The F-values, degrees of freedom (df1, df2), and associated P-values are reported for each response variable. Only movement metrics and predictors that were not statistically significant ($P > 0.05$) are presented in this table. For the significant predictors, see Table 2.3.

Metric	Predictor	F-value (df1, df2)	P-value
Distance travelled per day (m/day)	Status	0.02 (1, 86)	0.89
	Year:Season	0.98 (4, 86)	0.42
Distance travelled per movement (m)	Status	0.2 (1, 86)	0.65
	Year	1.78 (1, 86)	0.19
	Year:Season	2.02 (4, 86)	0.1
Movement rate (m/h)	Year:Season	0.67 (4, 86)	0.61
Sinuosity	Sex	0.13 (1, 86)	0.73
	Status	0.02 (1, 86)	0.88
Recursiveness	Sex	0.06 (1, 86)	0.8
	Status	0.003 (1, 86)	0.96
	Year:Season	1.22 (4, 86)	0.31

Appendix D

Results of two-way ANOVAs examining the effects of sex and translocation distance (long vs. short) on individual movement metrics in 2021. In this table the *F*-values, degrees of freedom (df1, df2), and *P*-values for each movement metric are presented. Only movement metrics and factors that were not statistically significant ($P > 0.05$) are presented in this table. For the significant predictors, see Table 2.4.

Metric	$\bar{x}$, SE, n	Predictors	*F*-value (df1, df2)	*P*-value
Distance travelled per movement (m)	93.8, 8.68, 17	Translocation distance	0.05 (1, 14)	0.84
		Sex	3.76 (1, 14)	0.07
Movement rate	2.77, 0.25, 17	Translocation distance	1.79 (1, 14)	0.2
		Sex	1.08 (1, 14)	0.32
Sinuosity	0.13, 0.01, 17	Translocation distance	0.15 (1, 14)	0.71
		Sex	2.64 (1, 14)	0.13

Appendix E

Results of two-way ANOVAs examining the effects of sex and translocation status ('status') on each movement metric by year when only data from the 'spring' sub-season (April-June) are included. For each test, *F*-values, degrees of freedom (df1, df2), and *P*-values are reported. *Post hoc* notes include adjusted *P*-values, and where significant, corresponding *t*-ratios and group differences and standard error (SE) are provided.

Metric	Year	Factor	*F*-value (df1, df2)	*P*-value	*post hoc* notes
Distance travelled per day (m/day)	2021	status	0.62 (1, 27)	0.4	not significant (*P* = 0.28)
		sex	24.0 (1, 27)	**4.01e-05***	male > female (diff. = 26.31, SE = 5.4, *t* = 4.9, *P* < 0.0001*)
	2022	status	0.1 (1, 14)	0.76	not significant (*P* = 0.48)
		sex	5.4 (1, 14)	**0.04***	male > female (diff. = 12.2, SE = 5.27, *t* = 2.33, *P* < 0.04*)
Distance travelled per movement (m)	2021	status	0.94 (1, 27)	0.34	not significant (*P* = 0.49)
		sex	16.5 (1, 27)	**0.0004***	male > female (diff. = 62.9, SE = 15.6, *t* = 4.06, *P* = 0.0004*)
	2022	status[1]	5.07 (1, 10)	**0.048***	ref. > trans. (diff. = 29.9, SE = 13.3, *t* = 2.25, *P* = 0.048*)
		sex[1]	24.55 (1, 10)	**0.0006***	male > female (diff. = 43.4, SE = 8.76, *t* = 5.04, *P* = 0.0006*)
Movement rate (m/h)	2021	status	0.21 (1, 27)	0.65	not significant (*P* = 0.8)
		sex	8.34 (1, 27)	**0.008***	male > female (diff. = 1.12, SE = 0.39, *t* = 2.89, *P* = 0.008*)
	2022	status[1]	1.08 (1, 12)	0.32	not significant (*P* = 0.32)
		sex[1]	4.58 (1, 12)	0.05.	marginally not significant (*P* = 0.05.)

Sinuosity	2021	status	2.5 (1, 27)	0.13	not significant ($P = 0.56$)
		sex	3.25 (1, 27)	0.08.	marginally not significant ($P = 0.08$.)
	2022	status[1]	1.32 (1, 13)	0.27	non-significant ($P = 0.27$)
		sex[1]	3.99 (1, 13)	0.07.	marginally not significant ($P = 0.07$.)
Recursiveness	2021	status	1.48 (1, 27)	0.24	not significant ($P = 0.25$)
		sex	0.23 (1, 27)	0.64	not significant ($P = 0.64$)
	2022	status	2.72 (1, 14)	0.12	marginally not significant ($P = 0.06$.)
		sex	1.45 (1, 14)	0.25	not significant ($P = 0.25$)

[1] When sample sizes were insufficient for two-way ANOVA, separate one-way ANOVAs were performed for each factor.