Natural History of Common Gartersnakes (*Thamnophis sirtalis*) in East-Central British Columbia

by

Jillian McAllister
Bachelor of Natural Resource Science, Thompson Rivers University, 2015

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

Supervisory Committee

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Abstract

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Widely distributed species typically exhibit variation in various aspects of their ecology throughout their range. Such variation offers opportunities for fundamental studies in evolution, including local adaptation, biogeographic rules, distributional limits, and speciation. Geographic variation also limits our ability to extrapolate from one population to another, making site-specific knowledge of ecology essential for wildlife management and conservation. I studied the natural history of Common Gartersnakes (*Thamnophis sirtalis*) at two sites in east-central British Columbia, where active seasons are short and cool. I used opportunistic sampling of snakes to study general features of their ecology and radiotelemetry to study movements and habitat selection, including hibernating sites. In September, snakes move from summer habitats to hibernating sites and then emerge from hibernation in April or May. Adult female *T. sirtalis* overwintered with 0 to 16 other adults in inconspicuous underground hollows, typically in forested habitats, near water and/or coarse woody debris; this is distinct from the large-scale communal hibernation seen in other northern populations. Hibernacula were typically distant from summer habitat (mean = 1485 ± 937 m SD, n = 8, range = 148-2657 m). Under the assumption that snakes exhibit site fidelity to hibernacula in consecutive years, I estimated the cumulative distance moved over the entire active season to be 7011 ± 3756 m SD (n = 9, range = 3510-15015 m). Gravid female snakes moved at significantly lower rates, followed more tortuous paths, and inhabited areas that were more open-canopied than their nongravid counterparts (n = 13). Nongravid snakes used locations with a higher percentage of ground cover than gravid snakes. Mating occurred in early spring near the hibernacula and parturition in early to mid August in summer habitat;

litter size ranged from 3 to 25 and was not significantly correlated with the size of the female. Adult snakes preyed exclusively on adult Western Toads (*Anaxyrus boreas*) and juvenile snakes fed on leeches and metamorphosing toads. Through the identification of migratory routes, relevant summer and winter habitat characteristics, and hibernation sites, my study contributes to the protection and conservation of northern reptiles, which are particularly vulnerable to population declines compared to southern populations due to the restrictive cold climate.

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Acknowledgments

Thank you to my supervisor, Dr. Pat Gregory, for sharing your wealth of knowledge and for all of the editorial feedback – my writing has benefited greatly from your mentoring. I admire your enthusiasm for reptiles and amphibians and feel honoured to be the final graduate student of 'Canada's undisputed snake god' (from Matsuda et al. 2006).

This research was funded by an industrial scholarship from the Natural Sciences and Engineering Research Council (NSERC) in collaboration with my industrial sponsor, LGL Limited Environmental Research Associates. LGL provided valuable logistical support in the lending of equipment, the provision of living arrangements, and for keeping my assistants and me safe while out in the field with regular safety check-ins.

Thank you to my committee members, Dr. Geraldine Allen, Dr. Brian Starzomski, and Virgil Hawkes, for your time, advice, and encouragement. Thank you to my field assistants (Melanie Horne, Mac McAllister, and Chloe Swabey) for your genuine interest, dedication to data collection and radiotelemetry, and for enduring long hours of hard work, especially when your boots were filled with marsh water. Thanks to Dr. Janet Jones and everyone else at the Valemount Veterinary Clinic for your meticulous care of the gartersnakes brought in for surgery. Thanks to Dr. David Sedgeman for providing helpful consultation. Thank you to the Valemount locals who welcomed me into the community: Todd Culham, Graham Woolsey, and Bill and Beth Russell.

Thank you to my mom (Kim McAllister) and sisters (Lisa, Katie, and Marlee McAllister) for your love and support, for visiting me when I was on the other side of the province for long seasons of fieldwork, and for making yourselves available when I was able to come home. A special thank you to my mom for accepting my love of snakes and amphibians from an early age and for encouraging me to be an environmentally conscious person. Thank you to my dad for taking me hiking, biking, and camping in the great outdoors at a young age and for sharing with me your enthusiasm for nature. Thank you to the Conlin family (Fran, Kev, and the rest) for feeding me and providing wonderfully fun distractions when I needed it most. Last, I would like to thank Kicker Conlin for being an exceptionally supportive and thoughtful partner.

Chapter 1 - General Introduction and Background for Study

Species with broad geographic distributions are often considered to be adaptive generalists that are tolerant of a wide-range of conditions (e.g. Housefly, *Musca domestica,* Kjærsgaard et al. 2014*;* Cougar, *Puma concolor*, DeAngelo et al. 2011*;* American Crow, *Corvus brachyrhynchos*, Withey and Marzluff 2008). They often vary morphologically across their distribution (Tesche and Hodges 2015) and may exhibit considerable differences in life histories (Gregory and Larsen 1993, Antonovics 2006).

Geographic variation is frequently attributed to environmental clines (Alves and Bélo 2002). Gradients in latitude and elevation can create conditions in which different populations experience different selective forces (Arthur and Kettle 2001, Zamora-Camacho et al. 2014). For example, Bergmann's rule claims that as latitude increases animals are larger than conspecifics or close relatives in warmer climes. This has been shown in mammals, birds, and turtles, but is not consistent in amphibians, lizards, and snakes (Atkinson 1994, Ashton and Feldman 2003, Adams and Church 2008, Zamora-Camacho et al. 2014). Another rule, the temperature-size rule, states that ectothermic species in colder climates often grow to larger adult body sizes than conspecifics in warmer climes (Atkinson 1994). Laboratory experiments have shown that the majority of ectotherms grow more slowly but to larger adult sizes at low rearing-temperatures, whereas growth is faster at higher temperatures but results in smaller adult body sizes (Atkinson 1994). However, Angilletta and Dunham (2003) found that growth efficiency was either positively related to, or independent of, temperature. The hypotheses proposed to explain the temperature-size rule are contentious and are reviewed by Atkinson and Sibly (1997).

Populations at the extremes of a species' distribution are often referred to as peripheral populations. These populations are often considered especially vulnerable to decline and extinction, particularly given the effects of human development, causing fragmentation and climate change (Lesica and Allendorf 1995). Geographic variation of widely distributed species and peripheral populations likely plays a role in speciation. Parapatric speciation involves geographically continuous populations that experience non-random mating and differences in gene flow between groups within the population caused by a disparity in selective pressures brought about by distinct habitats (Endler 1977, Antonovics 2006). Marginal populations also offer opportunities to study the factors that limit geographic distribution. The preservation of critical habitat for peripheral populations is important to the long-term conservation of widespread species through the maintenance of genetic diversity.

To conserve important habitats, studies must be conducted to evaluate habitat quality and their importance to fitness. Studies of habitat selection are often paired with studies of movement due to the interconnectivity of these two phenomena (Charland and Gregory 1995, Constible et al. 2010, Croak et al. 2013). Many species migrate to obtain necessary resources for various life stages or seasonal conditions (Berger 2004, Gilg and Yoccoz 2010). Although there are trade-offs related to migration (Nicholson et al. 1997), ultimately the benefits of movement (e.g. access to overwintering habitat) must outweigh the costs (e.g. energetic expenditure). Determining the timing and route of migration of a species is important to determining seasonal patterns of habitat use, thereby providing fundamental information for conservation (Baldwin et al. 2006).

Gartersnakes (Genus *Thamnophis*, Family Colubridae, Order Squamata) comprise a widely distributed genus of snakes with about 30 species. They are often considered generalists with respect to habitat and diet, but some are specialists (e.g. *Thamnophis scaliger*; Reguera et al. 2011). These non-venomous snakes are primarily diurnal and all are viviparous (see Chapter 5). The Common Gartersnake (*Thamnophis sirtalis*) is the most widespread species in the genus, ranging from the Atlantic to the Pacific Oceans and reaching higher latitudes (southern Northwest Territories) than any other species of reptile in North America (Rossman et al. 1996; Figure 1-1). Because of its frequently high abundance, *Thamnophis sirtalis* is one of the most thoroughly studied species of snakes (Shine et al. 2006; Figure 1-2). Although considered a generalist species, it is most often associated with wetlands and riparian habitats, feeding mainly on anuran amphibians (Kephart and Arnold 1982, Gregory and Nelson 1991, Halliday 2016). Throughout its range, *T. sirtalis* exhibits considerable geographic variation in colour, diet, body size, movement patterns, litter and offspring size, and seasonal activity cycles (Gregory and Larsen 1993, Rossman et al. 1996). This plasticity makes it a species whose ecology cannot easily be generalized, so that extrapolations from one population to another can be risky (cf. Constible et al. 2010). Thus, management and conservation programs for particular populations will often depend on site-specific knowledge. For example, in Narcisse, Manitoba, large communal hibernacula used by gartersnakes are afforded protection through the designation of a Wildlife Management Area (Province of Manitoba 2017). In Alberta, a conservation project aimed to protect so-called 'nuisance' gartersnakes successfully relocated snakes that may have otherwise been destroyed (Takats 2002).

Figure 1-1. Distribution map of the Common Gartersnake (*Thamnophis sirtalis*), including 12 subspecies, from the International Union for Conservation of Nature (NatureServe and IUCN 2015). The asterisk (*) identifies the study location.

Northern populations of Common Gartersnakes face particular climate-related challenges. The active season for gartersnakes is highly restricted in the north compared to more southerly latitudes (Fitch 1965, Gregory 2009). This restricted active season limits the amount of time that animals have to forage, grow, and reproduce, which may lead to reduced productivity or lower population density. Furthermore, because northern winters are cold, hibernation sites are particularly crucial habitats for high-latitude populations. Northern populations of Common Gartersnakes have been intensively studied in the Interlake region of central Manitoba (Gregory and Stewart 1975, Gregory 1977, Shine et al. 2001) and, to a lesser extent, in northern Alberta (Larsen 1987, Larsen and Gregory 1989), but populations in east-central British Columbia have not been studied in detail (but see Hawkes and Tuttle 2010, Swan et al. 2015).

Figure 1-2. Common Gartersnake (*Thamnophis sirtalis*) captured in east-central British Columbia (photograph taken by Jillian McAllister).

My overall objective in this study was to characterize the movement and habitat use of Common Gartersnakes (*Thamnophis sirtalis*) at two disturbed sites (Cranberry Marsh and Kinbasket Reservoir) near Valemount in east-central British Columbia (BC). One particular focus of this study was to determine seasonal habitat use and movement patterns between summer habitat and hibernation sites, which are both critical for conservation. Based on studies of other northern populations of Common Gartersnakes (Gregory and Stewart 1975, Gregory 1984a, Larsen 1986, Shine et al. 2001), I predicted that snakes would hibernate communally. Due to the constraints of pregnancy (Prestt 1971, Farr 1988, Gregory et al. 1999), I predicted that pregnant snakes would have limited summer movements compared to non-pregnant snakes and that they would use habitat that favoured basking to accelerate development of their offspring. I anticipated that the diet of snakes in my study area would consist mainly of amphibians, following preliminary results from previous studies at the site (Hawkes and Tuttle 2010, Boyle 2012), and that their summer habitats would be near areas of amphibian abundance (Kephart 1982, Gregory 1984b, Larsen 1987). I also collected data on body size and litter size and estimated growth rates from mark-recapture data, for comparison with other studies (Fitch 1965, Gregory 1977, Larsen et al. 1993). Previous studies have shown that northern Common Gartersnakes in western Canada are larger-bodied compared to more southerly populations (Larsen 1987, Larsen and Gregory 1988), they produce relatively small litters of large offspring (Fitch 1965, Fitch 1985, Farr 1988, Gregory and Larsen 1996), and they reach reproductive maturity within 2-3 years (Fitch 1965), comparable to conspecifics elsewhere.

Study Area

Biophysical Region and Climate

I conducted my study in east-central British Columbia, Canada at two sites centred around the village of Valemount (52°49'52" N, 119°15'51" W): the Kinbasket Reservoir and Cranberry Marsh. The area is part of the Columbia Watershed and lies within the Rocky Mountain Trench, bordered by the Columbia Mountains to the west and the Rocky Mountains to the east. The region has a continental climate with approximately 60-80 frost-free days per year (Government of Canada 1981).

My research was part of a 10-year study conducted by LGL Limited on behalf of BC Hydro that has confirmed that the Kinbasket Reservoir drawdown zone (the area over which water level fluctuates) is valuable summer habitat for Common Gartersnakes, the only reptile species that is widespread within the reservoir (Hawkes and Tuttle 2010). Several studies have been conducted around the Kinbasket Reservoir to determine the effects of dam operations on plant and wildlife species (Hawkes and Tuttle 2010, Boyle 2012, Swan et al. 2015). The Kinbasket Reservoir drawdown zone (DDZ) is 11.5 km southeast of Valemount and its water level fluctuates as a result of the Mica Dam operations, the northernmost hydroelectric dam in the Columbia Watershed. The DDZ includes a series of ponds within wetland matrices suitable for amphibians and reptiles, in close proximity to woodlands, rocky outcrops, and other habitat such as piles of coarse woody debris that are ideal for shelter and basking. I surveyed a northern portion of the DDZ, called the Valemount Peatland (52°45'18" N, 119°9'9" W) that covers approximately 550 hectares and ranges from 740 to 755 m above sea level (ASL). In the Kinbasket Reservoir, frogs and toads rely on the ponds in the DDZ for breeding (Swan et al. 2015). Therefore immense losses in productivity are possible if water levels rise too quickly, exposing vulnerable tadpoles to increased predation by fish that inhabit the reservoir.

I also surveyed Cranberry Marsh (52°48'54" N, 119°14'49" W) based on the presence of wetland and riparian habitat types, presumably suitable for Common Gartersnakes (Larsen 1987, Rossman et al. 1996). Cranberry Marsh, also known as the R.W. Starratt Wildlife Management Area, is a reclaimed wetland 2 km south of the Village of Valemount and immediately east of a major provincial highway. It serves as a stopover for many migratory bird species and supports both snake and amphibian populations. Cranberry Marsh is entirely surrounded by roads (including a railroad) and is adjacent to both residential and industrial developments. Both sites are moderately disturbed, whether by recreational use, railway, or hydroelectric reservoir operations. Forestry practices are evident at Cranberry Marsh and the Kinbasket Reservoir, but the Kinbasket has more recent logging and apparent plans for future logging (pers. obs. of timber development and block layout upland from the DDZ).

Habitat and Wildlife

Lower elevations in the study area are typically classified as interior cedar-hemlock (ICH) or sub-boreal spruce (SBS) biogeoclimatic zones, ranging from approximately 750-1000 m in altitude. Spruce (*Picea*), cedar (*Thuja*), and hemlock (*Tsuga*) are the most common conifers, whereas birch (*Betula*), aspen (*Populus*), and willow (*Salix*) are the most common deciduous trees.

Common Gartersnakes are the only reptile species reported at my study sites. The distribution of another gartersnake, the Western Terrestrial Gartersnake (*Thamnophis elegans*), overlaps my study area, but I did not observe this species over two years of fieldwork nor has it been recorded in previous years of research at the Kinbasket Reservoir (Hawkes and Tuttle 2010).

Potential predators of Common Gartersnakes in the study area include, but are not limited to, muskrats (*Ondatra zibethicus*), river otters (*Lontra canadensis*), and several avian species, including Great Blue Herons (*Ardea herodius*), Bald Eagles (*Haliaeetus leucocephalus*) and American Crows (*Corvus brachyrhynchos*). The diet of *T. sirtalis* may include earthworms, small mammals, amphibians, fish, and even birds (Kephart and Arnold 1982, Gregory and Nelson 1991, Rossman et al. 1996). Small mammals present in the study area include Meadow Voles (*Microtus pennsylvanicus*) and shrews (*Sorex cinerus, S. hoyi, S. vagrans;* Hawkes and Tuttle 2010). I also observed red-sided shiners (*Cyprinella lutrensis*) and sucker fish (*Catostomos sp.*) in the Kinbasket Reservoir. Long-toed Salamanders (*Ambystoma macrodactylum*), Columbia Spotted Frogs (*Rana luteiventris*), and Western Toads (*Anaxyrus boreas*) make up the amphibian fauna of my study area (Hawkes and Tuttle 2010).

General Methodology

I collected data over two field seasons to determine annual movement patterns, habitat use, and other aspects of the ecology of these populations. I used radiotelemetry to track female snakes in the active seasons of 2016 and 2017 to identify both summer and winter critical habitats at the two sites. I determined the distribution and habitat use of Common Gartersnakes. I also observed all reproductive stages of female snakes (courtship, gestation, parturition) and characterized the habitats used at each phase. Finally, I compared the habitat selection, movement patterns, and hibernation of gravid (pregnant) and nongravid snakes.

In addition to tracking snakes via radiotelemetry, I captured snakes opportunistically while doing visual surveys. Such captures afforded me the opportunity to record other natural-history data from these snakes (morphometrics, presence and type of food in gut, reproductive condition and litter size in pregnant females, habitat characteristics at capture site, and, for recaptured snakes, growth); collectively, these captures also provided rough estimates of temporal activity patterns of snakes.

Chapter 2 - Movements of Common Gartersnakes (*Thamnophis sirtalis*) in East-Central British Columbia

Introduction

Because essential resources may be physically separated on the landscape, vagile animals typically move from one location to another as needs change, resulting in seasonal movement patterns, including migration (Berger 2004, Gilg and Yoccoz 2010). Such needs include food, cover, and appropriate habitat for breeding, rearing young, and overwintering (Madsen and Shine 1996, Raynor et al. 2012). Studies of movement help to address broad questions in ecology, but also provide specific local knowledge, which, because all landscapes differ, is required for effective management (Constible et al. 2010). Studies of movement are commonly linked with studies of habitat use and habitat selection (Charland and Gregory 1995, Baldwin et al. 2006, Croak et al. 2013) and can identify the timing or seasonality of habitat requirements (Milakovic et al. 2012, Kluender et al. 2017). This is important for land management because knowing when and where animals move allows development of effective conservation measures, such as altering impact levels in specific habitats at specific times.

Movement patterns not only vary among species but can also vary among conspecific populations (geographic variation) and within populations (between sexes and among size classes). Differences in movement patterns among populations of the same species are likely related to differences in resource distribution and the physical features of the landscape (Macartney et al. 1988, Gomez et al. 2015, Vanek and Wasko 2017). Within populations, however, variation in movement patterns reflects differences among individuals, including differences among age/size groups, between the sexes, between reproductive and non-reproductive adults, and between other life-history stages with different habitat requirements. For example, young Common Gartersnakes (*Thamnophis sirtalis*) in Manitoba do not use the communal hibernation sites that are used by adults and presumably hibernate at other sites that affect their pre-hibernation movement patterns (Gregory 1974, Gregory 1977, Gregory and Stewart 1975). In some species of snakes, mate-searching males may move more than females in the mating season (Gregory et al. 1987, Putman et al. 2013, Bauder et al. 2016).

Perhaps the best studied of intrapopulation variations in patterns of movements of snakes is that due to pregnancy in females of viviparous species (Reinert and Kodrich 1982, Charland and Gregory 1995, Webb and Shine 1997, Roth and Greene 2006). For snakes in cool climates, viviparity is presumably advantageous because the pregnant female can use her own thermoregulatory behaviour to accelerate embryo development over the relatively short, cool active season ('Cold-Climate Hypothesis'; Shine 1983, Shine 1985, Shine 1987, Gregory 2009). Pregnancy has numerous ecological consequences that result in tradeoffs that constrain movement (Seigel et al. 1987, Charland 1995, Gregory et al. 1999, Gregory 2009). The reduced speed and endurance of gravid snakes is attributable to both the weight of the litter (Brodie 1989) and physiological effects of pregnancy (Gregory 2009), such as reduced locomotor function (Seigel et al. 1987), which may increase the risk of predation. Furthermore, because gravid females prioritize thermoregulation over other activities (Charland and Gregory 1990, Gregory et al. 1999, Brown and Weatherhead 2000), they are more likely to be found in the open compared to non-gravid females (Gregory and Tuttle 2016), which further increases their risk of predation. This thermal prioritization, in combination with reduced locomotor function, helps to explain why gravid females tend to remain near escape cover and avoid crossing wide openings with low cover (Charland and Gregory 1995). Moreover, a reduced rate of feeding, particularly late in gestation, exaggerates the difference in movements between gravid and nongravid snakes (Gregory and Stewart 1975, Gregory et al. 1999), as nongravid females and males spend more time moving while foraging than gravid snakes. These combined factors typically result in lower overall movements and smaller home range sizes in gravid snakes compared to males and nongravid females (Gregory et al. 1987, but see Roth and Greene 2006).

Although some snakes are nonmigratory, inhabiting the same area throughout the year (Lawson 1994, Gomez et al. 2015), others exhibit seasonal migrations related to resource availability (Larsen 1987, Glaudas et al. 2006). In snakes, relatively long-distance seasonal migrations, which are more common in northern populations than southern ones (Fitch 1965, Brown and Parker 1976, Larsen 1987), are mainly associated with movements between the summer habitat and the hibernating site. One hypothesis for this geographic trend is that northern snakes must hibernate deep underground to escape the extreme and prolonged cold and sufficiently deep sites often may be scarce or localized and remote from the summer habitat, necessitating seasonal migration (Gregory 1984a, Larsen and Gregory 1988); more southerly snakes require relatively shallow sites, which are presumably more abundant and widespread (Lawson 1994). The pattern of snake migration may vary in a number of ways. Some snakes migrate in a unidirectional movement between two seasonal centres, where the migratory corridor is used only for travelling (Gregory 1984a). Other snakes follow a circular migration and do not remain in a specific area through the active season but instead follow a path that eventually leads back to their starting point (e.g. their hibernating site; Macartney 1985, Larsen 1987).

Common Gartersnakes (*Thamnophis sirtalis*) are viviparous colubrid snakes that typically inhabit wetlands and riparian habitats (Larsen 1987, Rossman et al. 1996, Friesen et al. 2017). Their geographic distribution reaches farther north than any other reptile in North America (Larsen 1987, Rossman et al. 1996). East-central British Columbia (BC) has a continental climate with long, cold winters and therefore snakes require suitable overwintering sites to avoid freezing temperatures (see Chapter 4) and typically migrate seasonally to and from these sites. The migratory path of Common Gartersnakes can cover up to approximately 18 km, round trip, from the hibernaculum to summer habitat (Gregory and Stewart 1975, Larsen 1987). These snakes use solar and pheromone cues for orientation (Gregory et al. 1987, Macartney et al. 1988, Lawson 1994).

My aim in this study was to describe and quantify the annual movements of Common Gartersnakes (*Thamnophis sirtalis*) in east-central BC. I predicted that adult snakes would undertake relatively long-distance migrations to and from summer habitat, similar to migrations observed in other northern populations (Gregory and Stewart 1975, Larsen 1987). I expected that gravid snakes would move at significantly lower rates than nongravid females prior to parturition but that postpartum and nongravid snakes would move at similar rates. I also expected males and nongravid females to move at similar rates, higher than that of gravid females.

Methods

Study Area

My study area was located in east-central British Columbia (BC), where extremely cold winters and short, relatively cool summers are typical. I conducted my study of snake movements at two disturbed sites, the Kinbasket Reservoir (KR) and Cranberry Marsh (CM), near Valemount, BC. The Kinbasket Reservoir drawdown zone (DDZ) is 11.5 km southeast of Valemount and is the area over which water level fluctuates as a result of the operations of the Mica Dam, the northernmost hydroelectric dam in the Columbia Watershed. The DDZ includes a series of ponds within wetland matrices suitable for amphibians and reptiles, in close proximity to woodlands, rocky outcrops, and other habitat features such as piles of coarse woody debris that are ideal for basking and escape cover. I surveyed a northern portion of the DDZ, called the Valemount Peatland (52°45'18" N, 119°9'9" W), that covers approximately 550 hectares and ranges from 740 to 755 m above sea level (ASL). Cranberry Marsh (52°48'54" N, 119°14'49" W), also known as the R.W. Starratt Wildlife Management Area, is a reclaimed wetland 2 km south of the Village of Valemount and immediately east of a major provincial highway. It serves as a stopover for many migratory bird species and supports both snake and amphibian populations. Cranberry Marsh covers approximately 320 hectares and ranges from 786 to 795 m ASL.

General Survey Procedure

With the aid of a research assistant, I conducted visual encounter surveys (VESs) over two active seasons (May-October 2016, April-September 2017) along the perimeters of ponds and the transition areas between wetlands and woodlands; snakes commonly use such edges (Blouin-Demers and Weatherhead 2001, Carfagno et al. 2005, Dixon-MacCallum et al. 2017). The visual encounter survey is a standard method in wildlife research used to determine species composition and species richness, as well as estimate relative abundance; such surveys have been used in several other studies focused on amphibians and reptiles (Hartmann et al. 2005, Guyer and Donnelly 2012, Rahman et al. 2013, Swan et al. 2015). In 2016, I also tried a random transect design, but discontinued this method part way through the field season as it was not productive (n = 0 observations) and the landscape presented repeated problems such as impassable features along the transects (e.g. bodies of water). In another attempt to increase detection rates, I placed artificial cover objects (ACOs) along wetland edges. I used roofing felt, a heavy-duty black material, cut into 1 m × 1 m squares and placed approximately 20 m apart along 500 m transects. I allowed two weeks for the snakes to begin using the ACOs and checked them at various times during various weather conditions. The use of ACOs is a common method for sampling snake populations (Engelstoft and Ovaska 2000, Harvey and Weatherhead 2006, Wilkinson et al. 2007, Halliday and Blouin-Demers 2015). However, this method was also not productive (n = 0 observations) and was discontinued part way through the 2016 active season.

The University of Victoria Animal Care Committee (protocol 2016-018 and amendment 2016-018(2)) and the Province of British Columbia approved my research protocols. I opportunistically captured snakes by hand, following the University of Victoria Animal Care Committee Standard Operating Procedure #HP2002 (Capture, Handling, and Measurement of Non-Venomous Snakes in the Field). I determined sex by probing for hemipenes with a lubricated ball-tipped probe that I sterilized with alcohol between uses to minimize the potential for pathogen transfer among snakes (Reed and Tucker 2012). I assessed whether female snakes were gravid or nongravid by gently massaging the abdomen to detect oviducal eggs (Farr and Gregory 1991, Boyle 2012, Reed and Tucker 2012). If I detected eggs, I recorded the apparent number of them as an estimation of litter size. I did not assess male reproductive condition, as it is typically determined via dissection (e.g. Gregory 1977). I collected standard morphometric data including mass, measured to the nearest 0.25 g with a Pesola spring scale, and snout-vent length (SVL), to the nearest mm, with a folding ruler. So as not to count the same individual multiple times and thus avoid pseudoreplication in my statistical analyses, I marked each snake (> 40 g) for future recognition by clipping unique combinations of subcaudal scutes (Blanchard and Finster 1933).

Radiotelemetry

I used ground-based, very high frequency (VHF) radiotelemetry to track the movement patterns of adult female Common Gartersnakes at the Kinbasket Reservoir and Cranberry Marsh. I chose to use only adult female snakes because they are typically larger than males (Gregory 1977, Krause et al. 2003), thus reducing the ratio of transmitter mass to snake mass and thereby reducing potential impacts of the transmitter on the health and behaviour of snakes. Most male *T. sirtalis* are too small to receive the radiotelemetry transmitters I selected for my study.

In 2016, between June 16 – July 26, I captured ten adult female gartersnakes suitable for radiotelemetry and tracked them from approximately June 16 to October 8. In 2017, I replaced the transmitters in five of the original ten snakes and tracked them from April 9 to September 11, so that I could compare the movements of these individuals between years. I also captured five additional female snakes in 2017 that I tracked for approximately the same period of time. Transmitter implantation and removal surgeries were performed by a veterinarian at the Valemount Veterinary Clinic and, on one occasion, by a veterinarian at the British Columbia Wildlife Park in Kamloops, BC. Transportation of snakes to and from veterinary clinics followed University of Victoria Animal Care Committee standard operating procedure #GL2001 (Moving Squamate Reptiles (Lizards and Snakes) Between Field and Laboratory). Pre-surgery, snakes were held captive for an average of 3.85 ± 4.42 days SD.

To reduce the impact of the transmitter on snakes, I used the smallest radio-transmitters possible to achieve my study objectives, while also ensuring sufficient battery life for recapture of individuals the following spring to surgically remove or replace transmitters. I used SB-2 model radio-transmitters (Holohil Systems Ltd., Ontario, Canada) with a standard battery life of 10 months and a range of 6-12 months. Transmitters were 5.0 g in weight, 19 mm long, and 9.5 mm in diameter with a whip antenna approximately 15 cm long. These transmitters weighed no more than 4% of any snake's body mass (mean = 2.1 ± 0.7% SD) and were tested prior to implantation and again prior to release at the snakes' capture locations to ensure proper function. Radio-transmitters were surgically implanted in the coelomic cavity following methods described in Reinert and Cundall (1982), with a few modifications (Wilson 2013). Surgeons’ hands and incision sites on snakes were washed with Betadine microbicidal cleanser before and after surgery. All surgical instruments were steam autoclaved or soaked in cold sterilization solution when there were not enough autoclaved packs available. Pre-surgery, transmitters were soaked for a minimum of 2 hours in

Germiphene solution, and then thoroughly rinsed with sterile saline. Each snake was placed on a clean towel over a heating pad during surgery. Surgical anesthesia was achieved with isoflurane, following the protocol established at Thompson Rivers University in Kamloops, BC by Robina Manfield, RAHT, RLAT. Isoflurane was administered through an inhalation chamber. Anesthesia began at 0.5% isoflurane then increased at 0.5% intervals after each breath, reaching a maximum of 4.0% isoflurane. When the snake was sufficiently anesthetized, a 2-cm incision was made, anterior to the gonads, between the first and second dorsal scale rows through to the costocutaneous and lateral squamoscutali muscles. Then an incision was made through the ventral abdominal muscles just below the costal cartilages. The radio-transmitter was placed through the incisions into the coelomic cavity. Two small (5 mm) incisions were made, approximately 10 cm and 15 cm, respectively, posterior to the transmitter; curved haemostats were inserted subcutaneously into these incisions to pull the flexible whip antenna along the body until the entire antenna was positioned beneath the skin. The incisions were then closed with sutures and liquid bandage. As the incision sites were sutured, the anesthesia was terminated to accelerate recovery. Small-size (-5”; 3/0,4/0 Monocryl) monofilament, absorbable suture material was used throughout. Each snake was given a post-operative dose of subcutaneous lactated Ringer's solution (20-40 ml), Ceftazidime (antibiotic, 25 mg/kg SC) and Metacam (NSAID, acting as an analgesic, 0.5 mg/kg SC).

Replacement and removal surgeries followed the same anesthetic, pharmaceutical, and sterilization methods used for implantation. Each transmitter was easily palpated at the original point of insertion, after which a shallow, longitudinal incision was made through the skin between the second and third lateral scale rows. Scissors were used to make an incision in the peritoneum and the transmitter was gently massaged until it lined up with the incision where it could then be grasped with curved haemostats to remove it. In replacement surgeries, the new sterilized transmitter was then inserted into the coelomic cavity following procedures described above. In removal surgeries, instead of implanting a new transmitter, the incision was then closed.

I monitored snakes for a minimum of 24 hours after surgery, during which they were housed in ventilated plastic containers with tight-fitting lids. I provided cover objects, water in a shallow dish, and maintained a heat gradient with a heating pad beneath one end of the container. On average, I monitored snakes for 37 ± 12 hours SD post-surgery, following which the snakes were released at their original capture sites. I kept two individuals for an additional 9 h and 35 h, respectively, as a precaution due to (1) a somewhat reduced defensive reaction and (2) an additional surgical procedure (one snake had bone exposed on her tail when we recaptured her after hibernation and the veterinarian advised surgery to close the wound).

I located newly transmitter-equipped snakes the day following release to ensure that the transmitter was not inhibiting movement, that the snakes were exhibiting apparently normal behaviour, and that the surgical incision site was healing (e.g. stitches were not torn out, snake was not bleeding, incision site did not appear infected). I used a Lotek Wireless Biotracker receiver and a 3-element folding Yagi antenna to locate individuals once every 3.59 ± 6.83 SD days, on average. The variation in the length of intervals between locations was a result of occasional equipment malfunction, tracking issues (such as challenging topography or signal interference), and unavoidable constraints due to weather and safety concerns (e.g. lightning storms over several days in the region). Ultimately, radio-equipped snakes were located as often as feasibly possible to provide the most accurate, in-depth description of their movement patterns and habitat utilization.

When I located a radio-equipped snake, I recorded behavioural data (see General Survey Methods), as well as the distance moved by the snake since the previous location, with Universal Transverse Mercator coordinates (UTM, NAD 83). I recaptured individual snakes approximately once per active season to record SVL and mass and to ensure that surgical sites were in good condition. Otherwise, I disrupted snakes as infrequently as possible to avoid influencing their behaviour. I ceased capture of snakes approximately one month prior to hibernation to avoid interference with hibernation behaviour (Harvey and Weatherhead 2006). At the end of the 2016 active season, I followed radio-equipped snakes from their summer habitats to their hibernating sites (see Chapter 4).

I was not able to follow snakes to their hibernacula for a second year due to the limited battery power of the radio-transmitters. If I had allowed snakes to enter hibernation with transmitters still implanted, the transmitters would have lost power 1-2 months prior to spring emergence (thus losing all individuals with implanted transmitters). Therefore, I recaptured radio-equipped individuals in the second week of September 2017 to surgically remove the transmitters.

I mapped the known locations of radio-tracked snakes using Google Earth Pro. To describe the movement patterns of the snakes, I analyzed multiple parameters, as follows:

Cumulative Distance Moved - I estimated this parameter for each snake using the distance between consecutive known locations; this does not reveal the exact path taken or speed of travel.

Maximum Displacement - I identified the two most widely separated locations along the path of an individual and calculated the straight-line distance (m) between the points, based on UTM coordinates I measured in the field.

Net Displacement - I calculated the straight-line distance (m) between the initial point of capture and the final location of each snake using UTM coordinates I measured in the field.

Tortuosity Ratio - I calculated the ratio of the cumulative distance moved to the net displacement, which provided an index of linearity of each snake's path.

Movement Rate - I calculated the approximate movement rate by dividing the distance moved per interval (m) by the amount of time per interval (h).

I compared values of these parameters between snakes at the Kinbasket Reservoir and Cranberry Marsh, as well as between gravid and nongravid snakes.

Recaptures

During VES, I recorded occasional movements of non-radio-tagged snakes through opportunistic recapture, identifying them by their individual marks. I estimated the distance moved by opportunistically recaptured snakes with the same methodology I used for radio-tagged snakes. However, because these snakes usually had significantly longer intervals between captures compared to radio-tracked snakes (mean for opportunistic captures = 81.62 ± 144.37 days SD, $n = 20$, $W = 388$, $P < 0.001$), I analyzed only their average movement rate (distance moved in m/day). I also gained additional information on habitat use and growth from these recaptures (see Chapters 3 and 5).

Statistical Analysis

I tested all data for normality with Shapiro-Wilks tests (Royston 1982). Most data were non-normally distributed, but I could not find appropriate transformations for all cases, so instead I ranked the non-normal data and analyzed the ranked values (Rayner and Best 2013). Because I radio-tracked several of the snakes over two years, I conducted an analysis of variance (ANOVA) on ranks, with year as a random factor, for each movement parameter. Due to a relatively small sample size, I decided to include both years of data for each individual instead of removing half of the data for snakes I tracked over two years. Although this repeated measures design does not recognize the individual, the differences I observed between years suggested that year was a more suitable random effect than individual snake. I determined whether the movement patterns I observed were statistically different based on reproductive status or study site. I also used these tests to compare movement rates of gravid females before and after parturition. I tested whether the size of snakes influenced their average movement rate. For simple, two-sample comparisons of non-normal data I used Wilcoxon sign-rank tests. To reflect the exploratory nature of my study I used a relatively liberal statistical threshold of $P = 0.10$ throughout, but present actual p-values for all tests. I present average values as arithmetic means with standard deviations (SD) throughout.

Results

Radiotelemetry

Over two years of data collection, I captured a total of 15 adult female snakes that I selected for radiotelemetry and for which I recorded 590 locations (average = 39 ± 22 locations SD, including repeat locations). I tracked snakes from 07:00 to 20:00 h (95% of locations were between 07:30 and 18:30). On average I tracked each individual for 83 ± 26 days SD in 2016 and 76 ± 53 days SD in 2017 (Table 2-1). The average snout-vent length of radio-tagged snakes was 782 ± 88 mm SD and the average mass was 253 ± 77 g SD. Average SVL and average mass were calculated from 1-3 measurements per individual over an average of 190 ± 153 days SD. Most snakes changed reproductive status from one year to the next (i.e. snakes that were gravid in year one were nongravid in year two, or vice-versa; Table 2-1).

Of the ten snakes I captured in 2016, one was preyed upon near the end of summer. In early spring 2017, I lost three snakes from 2016 due to depleted transmitter batteries. I searched for these individuals persistently through 2017 by checking the same areas that they inhabited in the previous active season, haphazardly scanning, and returning to their hibernacula, in hopes of removing their transmitters, unfortunately without any success. One of the snakes I added in 2017 was tracked only one day before she completely disappeared. I continued to scan for her signal up to the end of the active season, similar to the three individuals with dead batteries, again without any success. This new individual had been basking on the side of a major highway, so it is very possible she was hit by a car and/or picked up and carried off by a bird or other highly mobile predator/scavenger. It is also possible that the transmitter malfunctioned immediately after her release, though unlikely given my rigorous testing protocol. Two other snakes in 2017 were preyed upon: one was decapitated, whereas the other was fully consumed, with only the transmitter remaining. Another snake that I began tracking in 2016 went missing part way through the 2017 active season. Up until her disappearance, her movement patterns had been drastically different from 2016. I continued to search for the remainder of the active season, and surveyed her hibernating site near the end of the summer, without any trace of her signal. It is possible that topographical features could have blocked the signal or that she was preyed upon and the transmitter was destroyed or carried out of range.

Table 2-1. Summary of radio-tracked snakes, Season indicates the active season(s) during which snakes were tracked (those tracked over two active seasons were also located once in December 2016), Days Tracked is the number of days during the active season of each year the snake was tracked, * = lost, ** = confirmed dead, CM = Cranberry Marsh, KR = Kinbasket Reservoir, SVL = snout-vent length (mm), G = gravid, NG = nongravid, U = unknown reproductive status. Snake E was omitted from analyses due to the very low number of days tracked.

Snake ID	Site	Average SVL (mm)	Average Mass (g)	Season	Days Tracked	Reproductive State
Snake C**	KR	834	265	S17	43	G
Snake G*	KR	725.5	182	S16/S17	110/27	NG/U
Snake H	KR	800	215	S17	102	NG
Snake N*	KR	927.5	428	S16/S17	76/79	G/NG
Snake P	KR	833	293	S17	94	G
Snake R	KR	815	224.5	S16/S17	72/153	G/NG
Snake S	KR	852	264.5	S16/S17	80/153	NG/G
Snake A*	CM	848.5	298	S16/S17	105/34	G/NG
Snake B**	CM	794	325	S16/S17	106/44	G/NG
Snake E*	CM	667	197	S17	1	G
Snake J**	CM	795	291	S16	22	G
Snake L*	CM	638	131	S16/S17	105/23	G/NG
Snake O*	CM	708	217.5	S16	77	NG
Snake T*	CM	632	149	S17	88	NG
Snake V	CM	855	334	S16/S17	77/151	NG/NG

Snakes that I radio-tracked at the Kinbasket Reservoir typically used the drawdown zone (DDZ, the area over which water fluctuates as a result of hydroelectric reservoir operations) for summer habitat. They moved upland, crossing a gravel road, to overwintering sites in late summer or early fall, gaining considerable elevation (101-153 m) and exhibiting fairly linear movement patterns along their migration path. In 2017 snakes continued to show fairly linear migration movements and most used the same general areas as in 2016, including the DDZ, and the same upland wetland as a stopover point to and from hibernating sites (Figure 2-1). Two of the reservoir snakes (Snakes R & N) that were gravid in 2016 but non-reproductive in 2017 used upland habitat at a much higher rate in the second year of tracking. One of these snakes did not descend into the DDZ, as she had done the previous year, but instead traversed the slope much farther south than any other radio-tracked snake (1809 m from any other snake observation). Two other snakes at the Kinbasket that I tracked in 2017 (Snakes P & H) were located exclusively or primarily upland from the DDZ, with 0 and 1 locations in the DDZ, respectively. Near the end of the summer of 2017, snakes at the reservoir appeared to be moving back towards the same area in which I located hibernacula in 2016 (see Chapter 4). However, because I had to remove transmitters before the end of the active season, there was no way to determine whether snakes were actually returning to the same hibernating site.

Figure 2-1. Seasonal movements of a radio-tagged female snake during the 2017 active season at the Kinbasket Reservoir. Labelling (e.g. S-01) indicates the individual snake with the code letter (Snake S) and the location number (location 01; Google Earth Pro 2017).

At Cranberry Marsh, some of the snakes that I tracked had relatively short migratory paths (Snakes L & B), whereas others moved across the entire marsh from summer to winter habitats (Snakes O & V; Figure 2-2). At least one individual at Cranberry Marsh crossed the adjacent highway. The topography at Cranberry Marsh is much less varied than that of the Kinbasket Reservoir (CM: 786-795 m elevation; KR: 754-914 m elevation), which led to a significant elevational difference between the migratory paths of snakes from each site (Two Sample t-test (equal variances): $t = 11.109$, $df = 7$, $P < 0.001$).

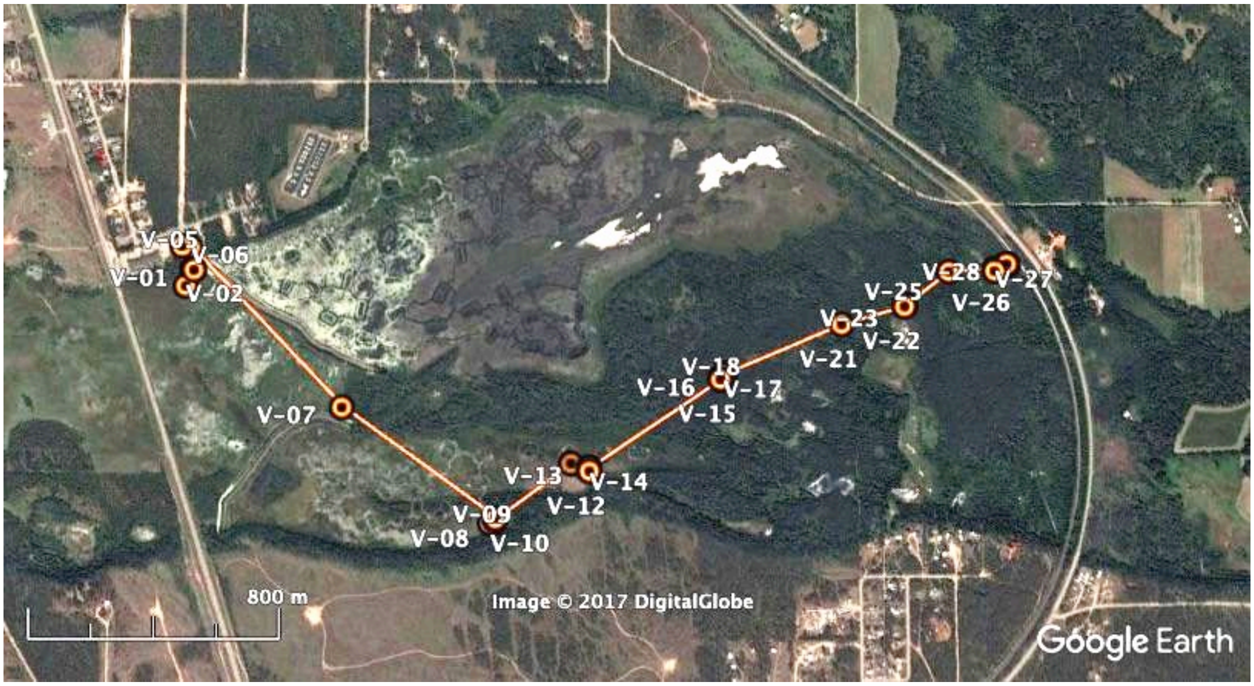

Figure 2-2. Seasonal movements of a radio-tagged female snake during the 2017 active season at Cranberry Marsh. Labelling (e.g. V-01) indicates the individual snake with the code letter (Snake V) and the location number (location 01; Google Earth Pro 2017).

Figure 2-3 shows the somewhat episodic nature of the movements of these animals, characterized by periods of stasis alternating with substantial movements. Overall, the curves are approximately parallel, suggesting there are not any gross differences in the rate of movement among snakes. However, for the 2016 data, the trendline slopes for nongravid snakes were steeper than those of gravid snakes, suggesting that nongravid snakes moved at a greater rate than gravid snakes (Welch Two Sample t-test (unequal variances): $t = -2.5195$, $df = 3$, $P = 0.08$). For many of the snakes I tracked, movements were reduced in the early season (all snakes were captured opportunistically away from their hibernating sites in 2016). The extended periods of stasis were more pronounced in gravid snakes and occurred just prior to parturition, which occurs in the first two weeks of August (see Chapter 5). I observed two parturition events in 2016 and used the average date (August 8/9) as the estimated parturition date for nongravid females so I could compare movements of gravid and nongravid snakes before and after parturition (see Chapter 5). For gravid snakes that I did not observe giving birth, I inferred the parturition date as that which immediately followed the period of extended stasis (Figure 2-4). The two stars in Figure 2-4 mark parturition events I observed, whereas the circle indicates an estimated date of parturition for a gravid female I did not observe giving birth.

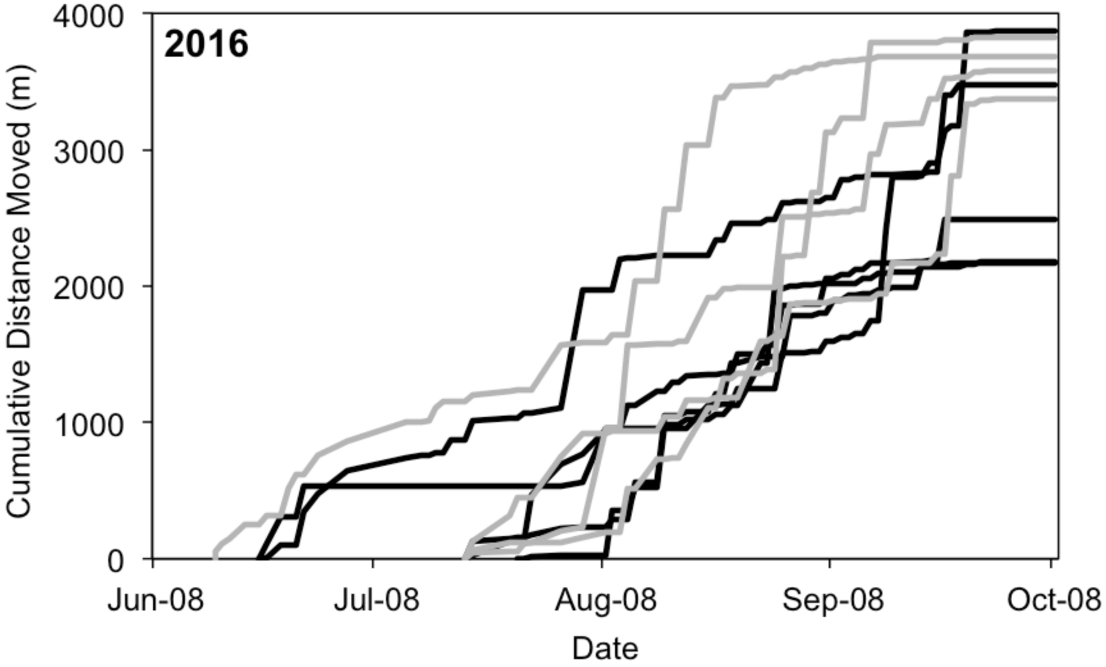

Figure 2-3. Cumulative distance graph of radio-tracked snakes over the 2016 active season. Grey lines represent nongravid snakes (n = 4) and black lines represent gravid snakes (n = 6).

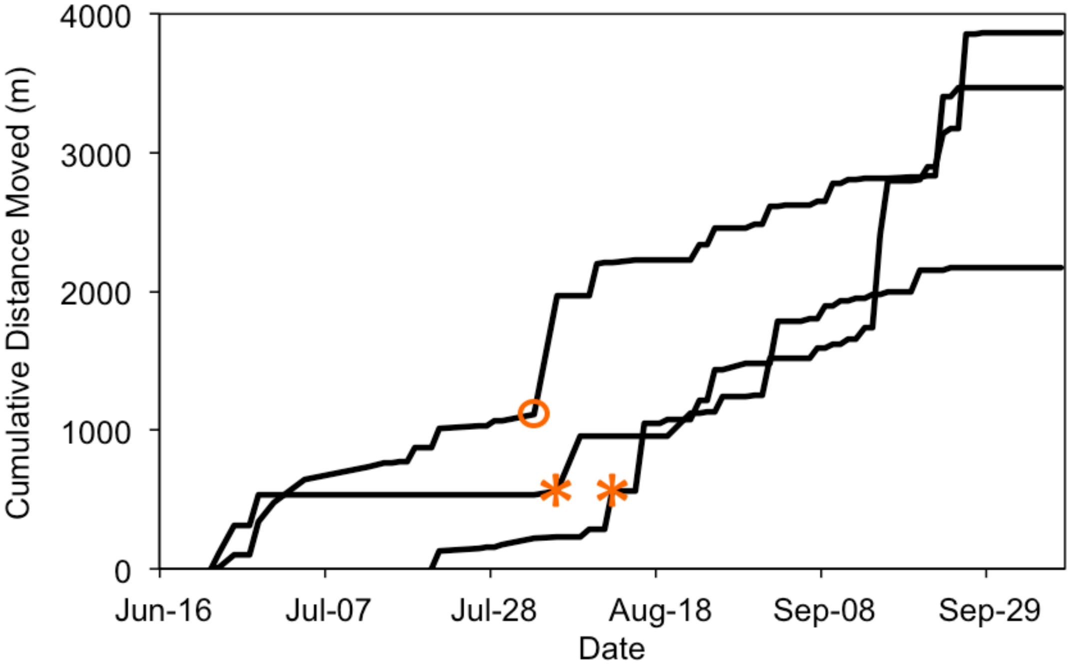

Figure 2-4. Cumulative distance graph of select gravid radio-tracked snakes over the 2016 active season. Orange stars represent the observed dates of parturition (August 5, 2016 and August 12, 2016) whereas the orange circle represents an estimated date of parturition.

In 2017, one individual moved twice as far as other snakes that were tracked for the same period of time (Figure 2-5). This individual was also the only snake I tracked in both years that did not produce offspring. Aside from this unusual individual, the cumulative distance curves are approximately parallel, as seen in 2016, suggesting that there are no gross differences in the average movement rate of these snakes. For snakes that I tracked from spring emergence to the beginning of September (n = 3), the average cumulative distance moved was 7662 ± 3521 m SD. Under the assumption that snakes return to the same hibernacula in consecutive years (and that they would do so in a straight line from their last capture location), I estimate that the cumulative distance moved over one full active season would be 7011 ± 3756 m SD.

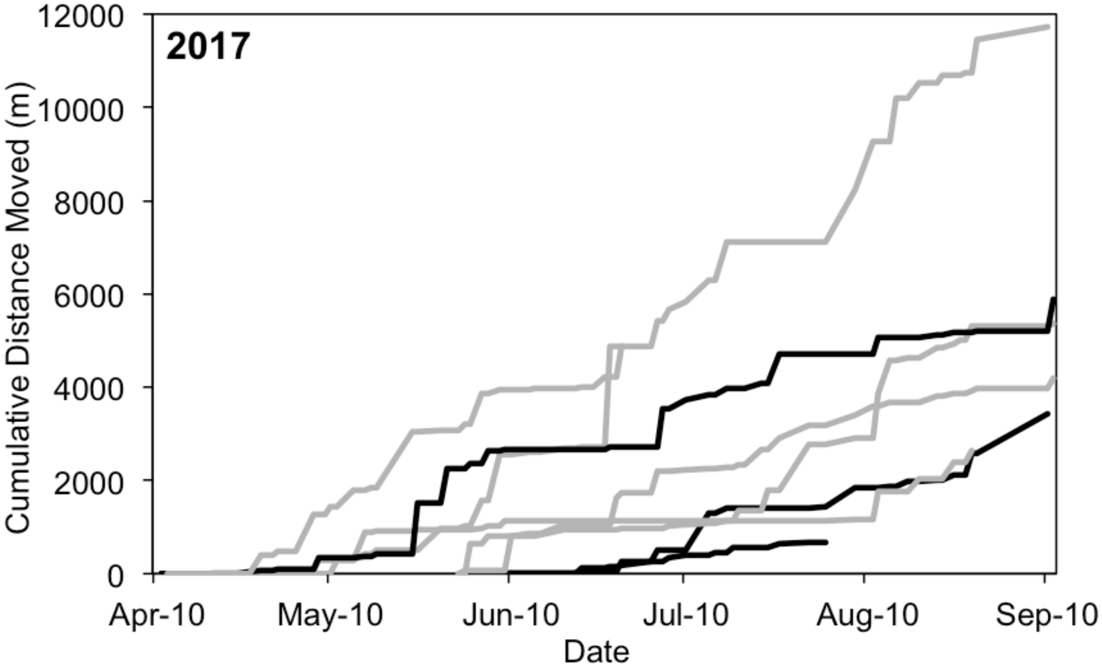

Figure 2-5. Cumulative distance graph of radio-tracked snakes over the 2017 active season (excluding individuals that were lost early in the spring). Grey lines represent nongravid snakes and black lines represent gravid snakes.

Each of the four movement parameters I examined were statistically similar between snakes at the Kinbasket Reservoir and those at Cranberry Marsh (ANOVA; maximum displacement, $F_{1,18} = 0.30$, $P = 0.58$; net displacement, $F_{1,18} = 0.01$, $P = 0.90$; tortuosity ratio, $F_{1,18} = 0.12$, $P = 0.72$; average movement rate; $F_{1,18} = 0.36$, $P = 0.55$). Net displacement was significantly lower in gravid snakes compared to nongravid snakes (ANOVA, $F_{1,18} = 1.32$, $P = 0.08$, Figure 2-6), as was average movement rate (ANOVA, $F_{1,18} = 2.70$, $P = 0.09$, Figure 2-7). Tortuosity ratio, on the other hand, was higher in gravid snakes compared to nongravid snakes (ANOVA, $F_{1,18} = 3.81$, $P = 0.06$, Figure 2-7). However, maximum displacement did not differ based on reproductive status (ANOVA, $F_{1,18} = 1.32$, $P = 0.26$, Figure 2-6).

To determine whether my non-significant results were due to a lack of statistical power, I conducted post-hoc power analyses using G*Power software (Version 3.1.9.3). I set power $(1-\beta) = 0.8$ and $\alpha = 0.1$ for a two-tailed test. For maximum displacement and net displacement between study sites, the power I calculated was low (0.13 and 0.10, respectively). However, to detect a large effect (effect size = 0.8, Cohen's threshold) of study site on these parameters, the required sample size would be very large (616 and

2346, respectively), suggesting it is unlikely that the non-significant result are due to the small sample size. The power of my test of study site on the tortuosity ratio of snakes was considerably higher (0.65) and suggested a sample size of 32 to detect a large effect. This indicates that it may be worth future investigation if the recommended sample size can be obtained.

Six gravid females returned to the same areas with open canopies and high percentage cover at least once (e.g. piles of coarse woody debris), whereas nongravid snakes generally moved in a more unidirectional pattern and did not return to habitats (aside from those along their migratory path). Overall, the snakes I radio-tracked exhibited some highly unidirectional movement, but a few individuals made frequent zigzag-like movements. Most notably, two individuals that used the same hibernaculum at Cranberry Marsh made tortuous movements. One of these snakes' migratory paths seemed to follow a figure-eight pattern with few unidirectional movements, whereas the other seemed to follow a more circular path with some zigzagging around the centre of her summer habitat. The distance between the summer habitat and hibernaculum of this snake was considerably less than that of the other snakes (see Chapter 4). One individual at the Kinbasket Reservoir returned to the same pile of logs multiple times over two years regardless of her reproductive condition.

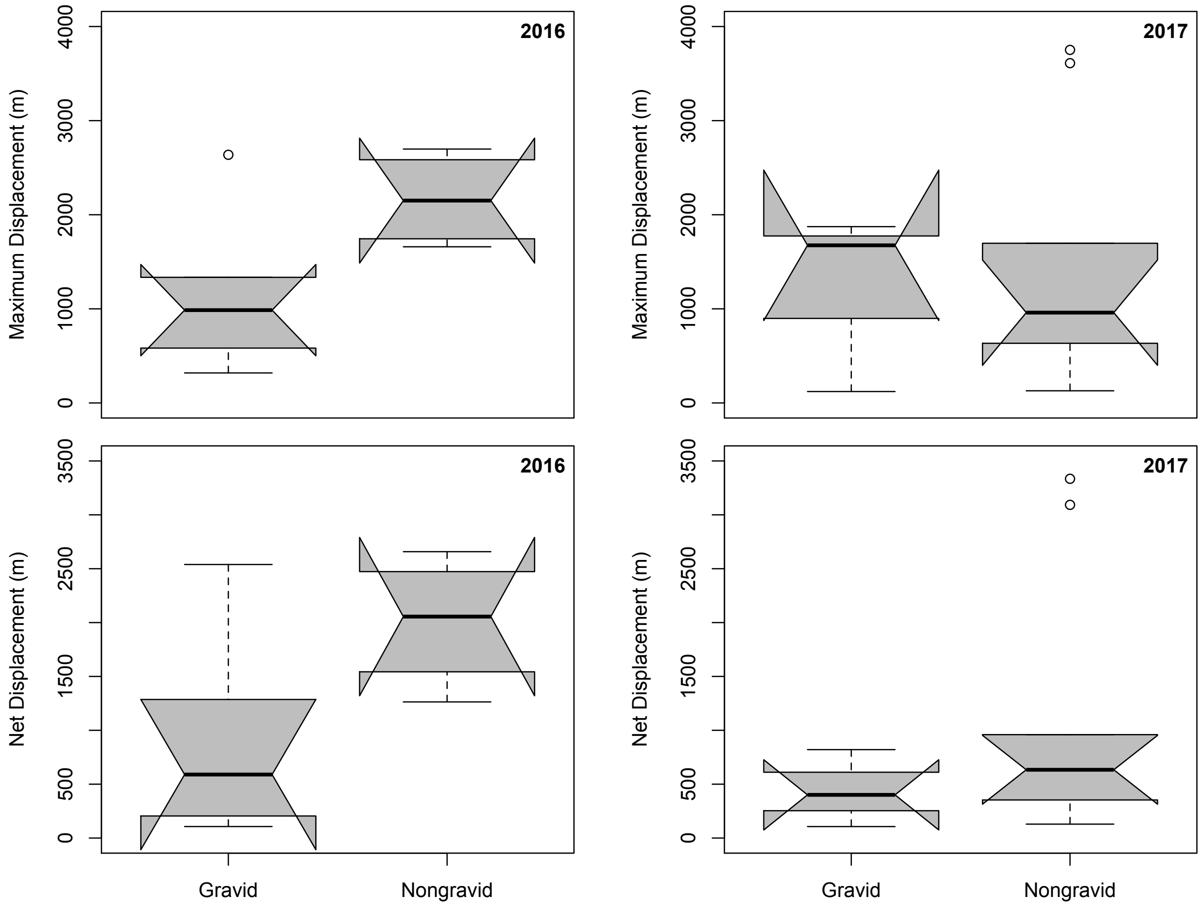

Figure 2-6. Box and whisker plots of maximum displacement (m) and net displacement (m) of radio-tracked gravid (2016 n = 6, 2017 n = 3) and nongravid (2016 n = 4, 2017 n = 9) snakes. Grey boxes cover the second and third quartiles and the centre lines represent the medians. Whiskers represent the first and fourth quartiles. Notches that do not overlap strongly suggest a statistical difference.

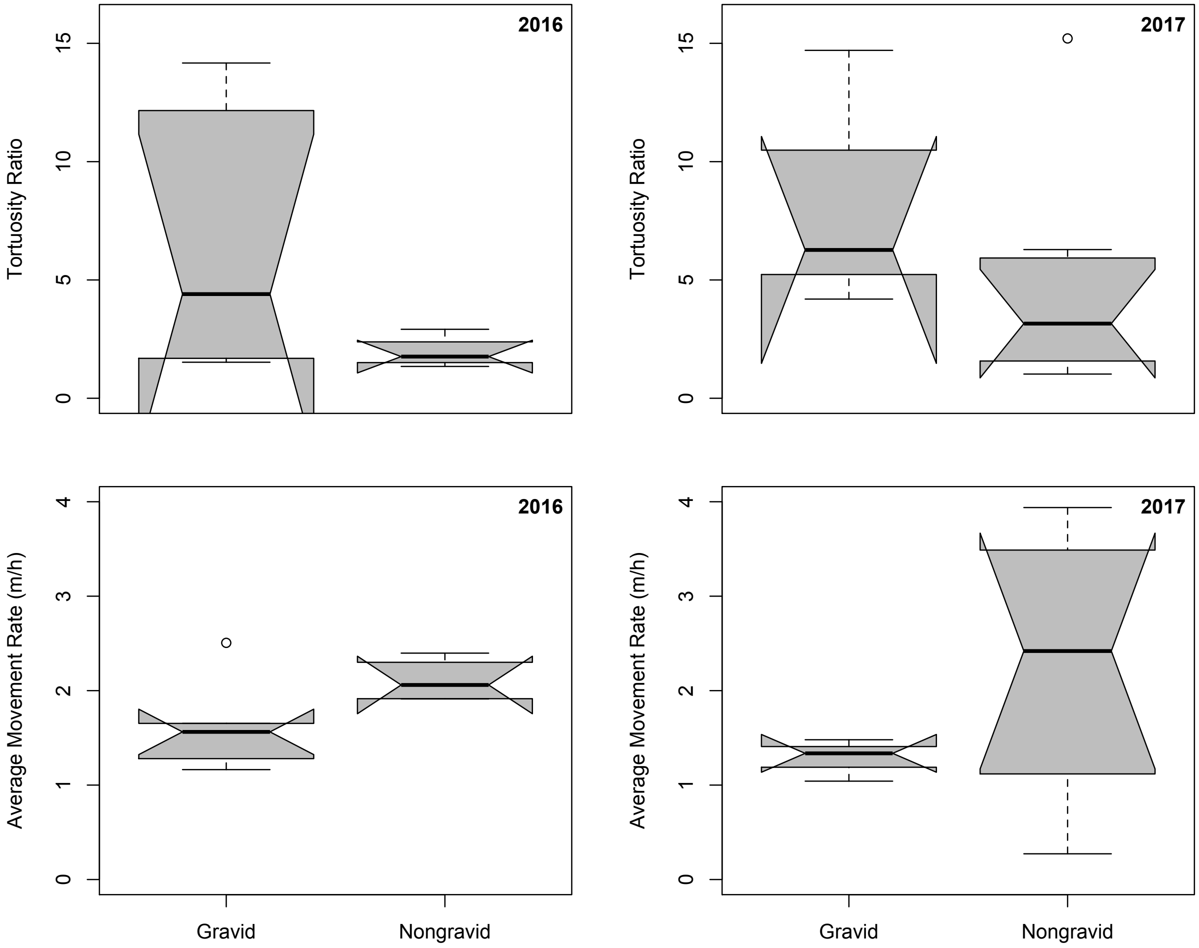

Figure 2-7. Box and whisker plots of tortuosity ratio and average movement rate (m/h) of radio-tracked gravid (2016 n = 6, 2017 n = 3) and nongravid (2016 n = 4, 2017 n = 9) snakes. Grey boxes cover the second and third quartiles and the centre lines represent the medians. Whiskers represent the first and fourth quartiles. Notches that do not overlap strongly suggest a statistical difference.

Figure 2-8 shows no effect of size on average movement rate in 2016, but in 2017 a difference is evident in the average movement rates of gravid and nongravid snakes as their size (SVL) increases; however, this difference was non-significant ($F_{1,21} = 2.72$, P = 0.11). In 2016, the equation for radio-tagged gravid snakes was **y = -0.0001x + 1.7416** and the equation for nongravid snakes was **y = -0.0003x + 2.4017**. In 2017, the equation for radio-tagged gravid snakes was **y = 0.0021x + 0.0599** and the equation for nongravid snakes was **y = 0.012x - 7.365**. The 2017 data suggest that large nongravid females have higher rates of movement compared to similarly sized gravid snakes and that as size increases, average movement rates of nongravid females increase.

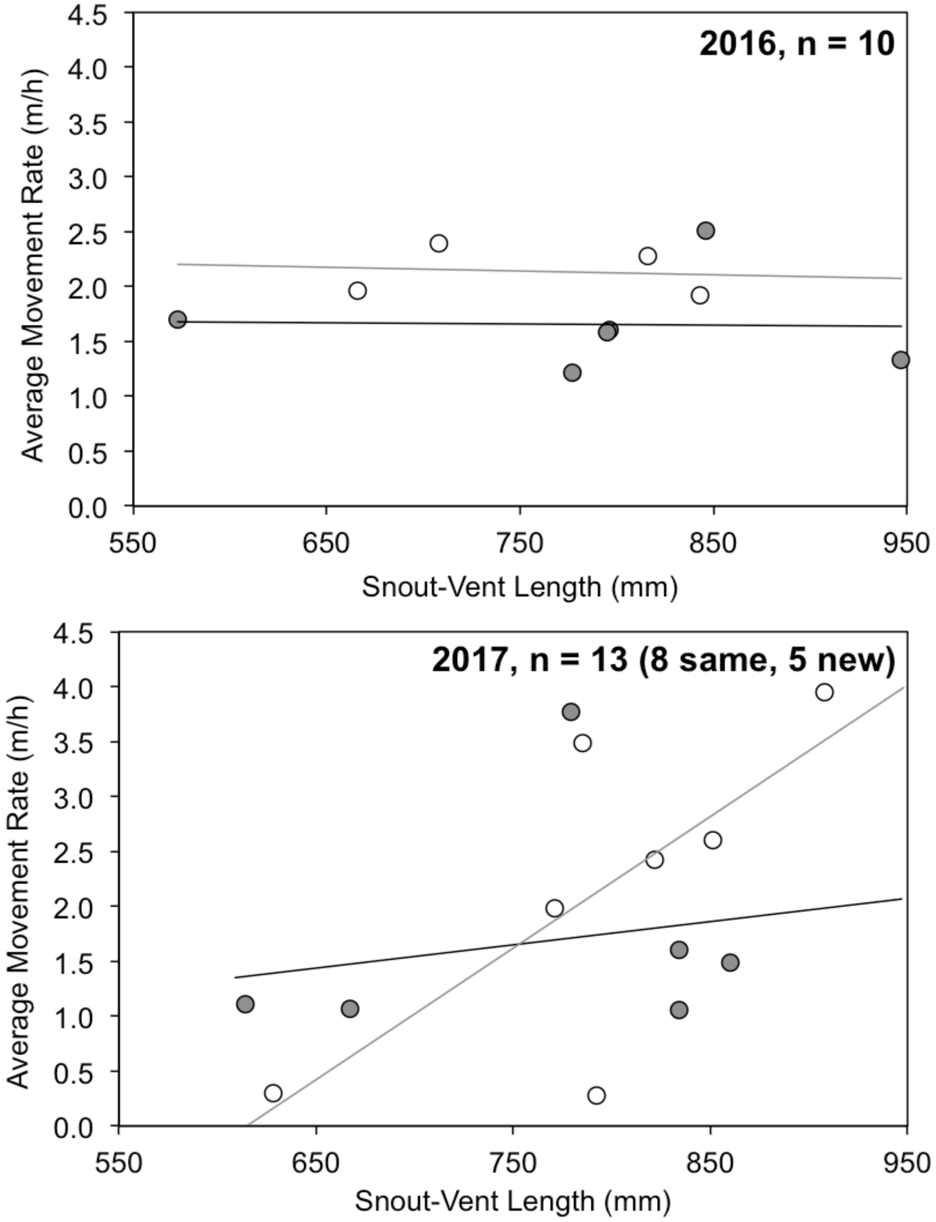

Figure 2-8. Average movement rate (m/h) versus size (snout-vent length, millimetres) by radio-tracked gravid (*grey* circles) and nongravid (*white* circles) female snakes in 2016 (*top*) and 2017 (*bottom*).

Movement rates of gravid and nongravid females prior to parturition were significantly different ($F_{1, 217} = 3.78$, $P = 0.05$; Figure 2-9). Movements after parturition, however, were not significantly different between the two groups ($F_{1, 224} = 2.32$, $P = 0.12$). I did not detect any differences between study sites for pre- or post-parturition movements.

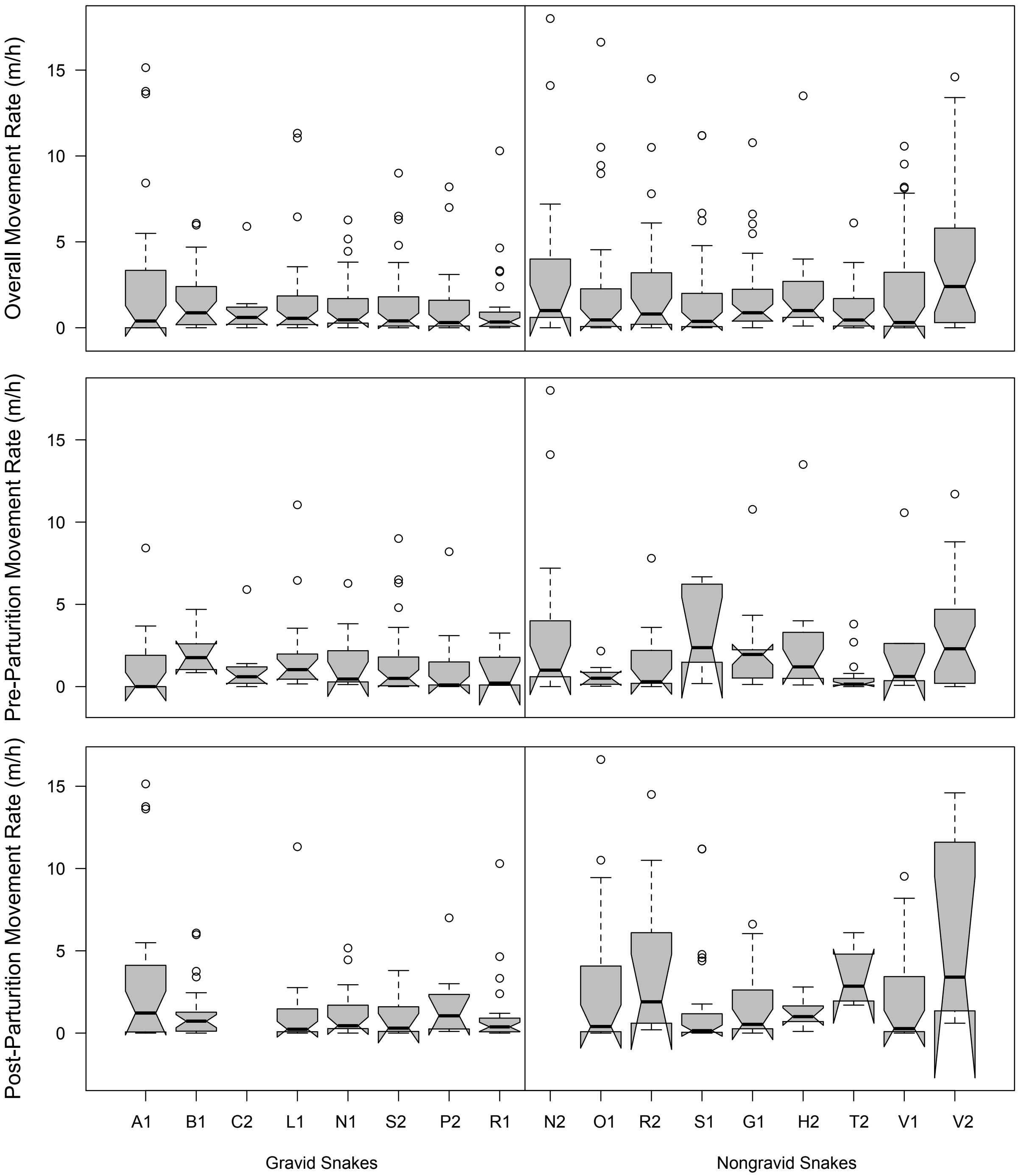

Figure 2-9. Box and Whisker plot of movement rate (metres/hour) of individual snakes, gravid or nongravid, overall (*top*), pre-parturition (*middle*), and post-parturition (*bottom*; parturition = giving birth, or the estimated date of giving birth). Grey boxes cover the second and third quartiles and the centre lines represent the medians. Whiskers represent the first and fourth quartiles. Notches that do not overlap strongly suggest a statistical difference. Letter and number combinations indicate an individual snake and the year that they were tracked. For example, A1 = Snake A movement rate during Year 1 (2016). A blank indicates that the snake was either preyed upon or was lost.

Recaptures

I made few recaptures over the course of the study, despite extensive surveying and the inclusion of captures from 2015 at the Kinbasket Reservoir from a long-term research project by BC Hydro that was made available to me (Table 2-2). I had five recaptures in 2016 (10% of all captures) and 23 recaptures in 2017 (21% of all captures). The five recaptures during 2016 were of four individuals (2 males, 2 females) over intervals of 2 to 46 days and movements ranging from 8 m to 479 m, equating to movement rates of 0.02 m/h to 5.90 m/h, respectively. The individual that I recaptured twice (Snake L) was selected as a snake for radiotelemetry after the second recapture (prior to that point, I had yet to receive the radio-transmitters).

Table 2-2. Movement summary of opportunistically recaptured snakes in 2016 and 2017. Average values reported are the arithmetic mean ± standard deviation.

Year	Recapture	Average Time Between Locations (Days)	Average Distance Moved (m)	Average Movement Rate (m/h)
2016 (n = 5)	1st (n = 4)	17.93 ± 20.11	224.09 ± 246.32	1.63 ± 2.85
	2nd (n = 1)	5.04 ± 0	120.91 ± 0	1.28 ± 0
2017 (n = 23)	1st (n = 16)	97.58 ± 158.04	363.08 ± 651.46	0.91 ± 2.87
	2nd (n = 6)	7.13 ± 5.85	8.26 ± 2.86	0.11 ± 0.12
	3rd (n = 1)	15.97 ± 0	14.89 ± 0	0.04 ± 0

In my second field season, 2017, I recaptured 16 snakes total (9 males, 7 females), five individuals twice, and one individual three times, for a total of 23 recaptures. All but one of the snakes that were recaptured multiple times were gravid females at a single location inhabited by one of my radio-equipped snakes at Cranberry Marsh (see Chapter 3). Three of the snakes I recaptured in 2017 were originally captured in the spring or summer of 2016, whereas the rest were from 2017. For first recaptures, the average interval was 97.58 ± 158.04 days SD, the average distance moved was 363.08 ± 651.46 m SD, and the average movement rate was 0.91 ± 2.87 m/h SD. For second recaptures, the average interval between captures was much shorter than the first interval at 7.13 ± 5.85 days SD, the average distance moved was 8.26 ± 2.86 m SD, and the average movement rate was 0.11 ± 0.12 m/h SD. The longest distance moved by an opportunistically recaptured snake was 2363 m, with the initial capture at a hibernaculum and the recapture in a wetland used as summer habitat at Cranberry Marsh. The longest interval between locations for opportunistically captured snakes was 452 days. Overall, intervals between opportunistic recaptures were significantly longer than the intervals for radio-tagged snakes (W = 388, P < 0.0001).

Recaptured males moved at a significantly higher rate compared to female snakes I recaptured (W = 22, P = 0.03; Figure 2-10). One male from the 2016 season had a much higher movement rate than other opportunistically recaptured males. This individual was found with a radio-tagged snake, a nongravid female, at two consecutive locations along her migratory route over a three-day period in late summer. Even when I removed this individual from the analysis, the results were still significant (W = 22, P = 0.06).

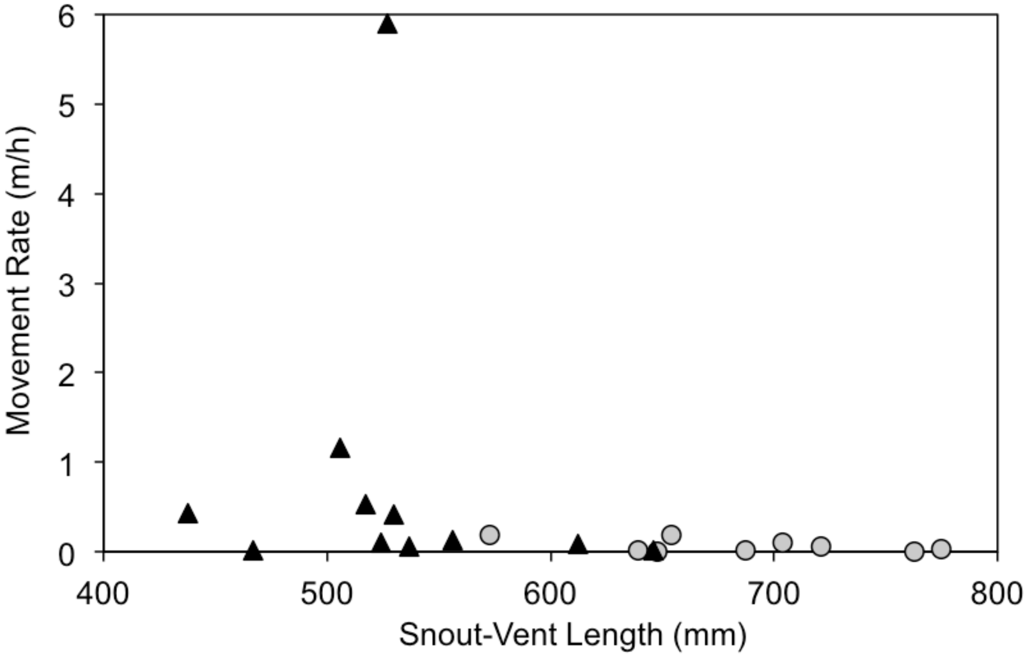

Figure 2-10. Snout-vent length (SVL; millimetres) versus movement rate (metres per hour) of opportunistically captured snakes over the 2016 and 2017 active seasons. Males = *black* triangles (n = 11), females = *grey* circles (n = 9, 8 gravid + 1 nongravid).

Discussion

My radiotelemetry study showed that adult female Common Gartersnakes in my study area make migratory movements that are similar to that of other populations at northern latitudes in that they are highly directional (Gregory and Stewart 1975, Larsen 1987). They also moved from their overwintering sites to summer foraging habitat, without returning to the hibernaculum in the summer, as seen by Larsen (1987) and Shine et al. (2001). The pattern of migration differed among individuals, with some following a circular or loop-like migration (Macartney 1985, Larsen 1987) and others following relatively narrow migration corridors that connected their summer and winter habitats (Gregory 1984a). The timing of migratory movements by snakes in my study area was also somewhat comparable to that of other populations near the northern extent of the species' range. Larsen (1987) reported returns of Common Gartersnakes in northern Alberta to the hibernaculum between late July and late August. This range is notably earlier than for the snakes in my study area, which arrived at their hibernacula between mid-September and early October. This is likely a function of the more northerly latitude of the Alberta study area, because temperature generally decreases with increased latitude and snakes would presumably require safe overwintering refuge earlier in the year due to lower overnight temperatures.

Statistical differences between the elevations gained during migration at each site can be explained by the significant difference in topography between sites. Although the higher elevation habitat is not available at CM, it is nonetheless interesting that the KR snakes utilize hibernacula that require a migratory path upslope to their overwintering habitat as opposed to a comparatively flat journey taken by the CM snakes. Despite this difference in the landscape, the similarity between the movement patterns of snakes at CM and KR suggests that these two populations of snakes have similar migration and that they can be combined for analyses.

The extended periods of stasis I observed by radio-tracked snakes early in the 2016 active season could be a resting period after migration, as I captured all of these snakes away from their respective hibernacula. Alternatively, this stasis could be a period of reorientation and resting after undergoing transmitter-implantation surgery. Regardless of the reason for the stasis, this period was more exaggerated for gravid females than for nongravid females. Including males in future radiotelemetry studies could potentially help to explain this pattern. The shorter periods of inactivity that I observed are likely attributed to digestion, ecdysis, or bouts of poor weather (Larsen 1987, Reinert 1992, Plummer and Congdon 1994).

Consistent with reports in the literature (Seigel et al. 1987, Charland and Gregory 1995), gravid snakes moved at significantly lower rates than nongravid females. Behavioural differences are often observed between gravid and nongravid viviparous snakes, presumably due to differences in their thermoregulatory requirements (Charland and Gregory 1990). Nongravid snakes that I radio-tracked typically moved at higher rates as their body size (SVL) increased and moved more than gravid snakes of a similar size. This is likely related to the differing thermoregulatory and energetic requirements of snakes in the two reproductive states. Because gravid viviparous snakes are known to thermoregulate more precisely than nongravid snakes (Charland 1995, Gregory et al. 1999, Brown and Weatherhead 2000, Gregory 2009, Gregory and Tuttle 2016), they should spend more time basking with movements generally limited to shuttling between preferred basking sites. Nongravid snakes, on the other hand, should have higher foraging rates compared to gravid snakes (Gregory et al. 1987, Gregory et al. 1999), which typically involve more widespread movements. The reason(s) for the lack of relationship between body size and average movement rate in the snakes I tracked in 2016 remains unclear, although it is possibly a function of the slightly smaller sample size attained in 2016.

The statistical difference in the tortuosity ratio (an index of linearity) between gravid and nongravid snakes indicates that gravid snakes take a more convoluted path over the course of the active season. However, this does not mean that they are more likely to remain in the same general area compared to nongravid snakes, as there was no significant difference in net or maximum displacement (the distance between the two most widely separated points along the path of a snake). However, the two gravid snakes that shared a hibernaculum at CM (see Chapter 4) likely made fewer unidirectional movements simply due to the close proximity of their hibernaculum to their summer habitats. The difference in tortuosity between gravid and nongravid snakes appears to be related to the return of gravid individuals to safe basking habitat (e.g. piles of coarse woody debris). The use of log piles as cover by gravid snakes has been reported by Larsen et al. (1993), who also identified a log pile as a site of parturition; however, I did not detect any evidence of snakes giving birth in this type of habitat (see Chapter 5).

Radiotelemetry studies require the assumption that the animals being radio-tracked are not significantly impacted by either the weight of the transmitter or the frequent presence of the surveyors. Through my selection of only the largest females and caution when approaching during radio-tracking, I believe that this assumption holds true. However, a recurrent limitation of my research is the relatively small sample size. This is partly a function of the challenge to locate and capture snakes but is also related to the size constraints of radiotelemetry transmitters. Radio-transmitters that are small enough to be considered suitable for most snakes captured during my research have battery power too low to meet the objectives of my study. Therefore I was restricted to only the largest females, which were often few and far between.

One issue frequently associated with radiotelemetry studies is that of autocorrelation (Richards et al. 1994, Aarts et al. 2008). Because animals usually move in a non-random fashion each location is not independent of the previous or the subsequent location (DeSolla et al. 1999). Autocorrelation may exist in either spatial or temporal form and can represent a positive or negative relationship (Dray et al. 2010, Millspaugh et al. 2012). Although there have been numerous methods developed to remove autocorrelation by altering data prior to analysis, DeSolla et al. (1999) point out the potential loss of biological relevance that may result from the elimination of autocorrelated data.

Future research should consider further study of the movement patterns of male snakes in my study area, to determine whether they are consistent with males in other populations (Shine et al. 2001) and to make an accurate comparison of movements between the sexes. When comparing males and females, researchers should incorporate reproductive status as well as the different periods associated with reproductive activities for each sex (Macartney et al. 1988). For some species, such as the Broad-Headed Snake (*Hoplocephalus bungaroides*), movement patterns are similar between the sexes (Webb and Shine 1997, Croak et al. 2013). Other snake species have more complicated or unclear trends in the movement rates of males and females. For example, Hyslop et al.

(2014) identified male-biased movement rates in Eastern Indigo Snakes (*Drymarchon couperi*) throughout the active season; however, Bauder et al. (2016) reported male-biased movements for *D. couperi* only during the breeding season. This difference between studies may result from geographic variation or perhaps annual variation in climate or resource availability that could potentially increase or decrease movements. Putman et al. (2013) also observed a significant difference in movements between the sexes based on the season, but for Western Rattlesnakes (*Crotalus oreganus*), with males moving greater distances that were attributed to mate searching. Movement rates can also depend on the body size of an individual. Roth and Greene (2006) found the movement patterns of Northern Watersnakes (*Nerodia sipedon*) differed based on body size for females, with size positively associated with movement, but this correlation was not evident in males. Clearly there are various trends that appear in the movement ecology of snakes, but none seem to occur with any great consistency (Gregory et al. 1987). This emphasizes the importance of studying individual populations and considering how different groups within a population may utilize the landscape differently.

Some of the most common issues involved with VES include bias in the detection of specimens because not all individuals are detected at the same rate (e.g. gravid females are more likely to be found in open areas and juveniles are more likely to utilize cover; Gregory and Tuttle 2016). Detection rates may also vary based on habitat type (e.g. easier to see animals in habitats with low vegetative cover than in those with high cover). Cover was abundant at both study sites and snakes were not frequently observed by chance. This may have caused my sample to be biased towards adult snakes, particularly gravid females.

Studies of movement are important to understanding the ecology of a species and are crucial to consider in the management of lands and resources. In hydroelectric reservoirs water levels can be adjusted to manipulate habitat availability in the drawdown zone (DDZ) adjacent to the reservoir. Furthermore, the development of mitigation structures may help to reduce road mortality, particularly during periods of migration (Glista et al. 2008, Jochimsen et al. 2014, Colley et al. 2017). Studies of movement can also provide home range estimates that contribute to knowledge of the space and resources required by a species (Macartney et al. 1988, Hagen and Bull 2011, Croak et al. 2013). This is particularly important given the increasing fragmentation of the landscape from forestry practices, roads, and residential development.

Chapter 3 - Habitat Use by Common Gartersnakes (*Thamnophis sirtalis*) in East-Central British Columbia

Introduction

Determining how and when animals use different habitats is central to understanding their ecology and initiating conservation actions (Semlitsch and Bodie 2003, Davidson-Watts et al. 2006, Indermaur and Schmidt 2011, Miller et al. 2012). Potentially important habitat characteristics for various species include physical structure (e.g. vegetation), cover, water, food, and places to breed (Broquet et al. 2002, Baldwin et al. 2006, Raynor et al. 2012, Yandow et al. 2015). Where seasonally harsh conditions (e.g. extreme temperatures) are encountered, sites suitable for estivation or hibernation may also be key habitat requirements (Burger et al. 2012; see Chapter 4). Thus, the habitat requirements of wide-ranging species should be expected to vary over their range in response to variation in climate and other factors.

Detailed characterization of a species' habitats (e.g. for reproduction or hibernation) is particularly important when habitats are disturbed or altered by humans (Baldwin et al. 2006, Bonin 2012, Swan et al. 2015). Natural resource development and residential sprawl can affect wildlife populations through an alteration in the quality or accessibility of habitats (Miller et al. 2012, Browne and Paszkowski 2014). These changes in habitat may lead to increased mortality (e.g. road mortality, Jochimsen et al. 2014), a reduction in food availability (Andriolo et al. 2013) and an increase in intraspecific and/or interspecific competition (Boström-Einarsson et al. 2014). Hydroelectric reservoir operations clearly impact aquatic habitats (Harnish et al. 2014) and result in habitat loss for species that normally would use the habitats flooded during reservoir construction (Andriolo et al. 2013), but they also affect the ecological communities that inhabit their altered shorelines by causing water levels to fluctuate unnaturally (Palmeirim et al. 2014, Swan et al. 2015, Storck-Tonon and Peres 2017). Resource managers should be aware of the location of critical habitats around reservoirs and the timing of habitat use so they can make responsible conservation decisions.

Habitat evaluation studies are frequently conducted to assess the requirements of a species, which are presumably related to increased fitness (i.e. survival and reproduction;

Halliday and Blouin-Demers 2016). Habitat management can then alter the availability or quality of habitats in order to increase the prevalence of a target species. The two most common types of habitat evaluation studies differ in the type of information they provide. Habitat use studies offer information on the realized habitats of animals but not on the choices made by the animals about the habitats they use (e.g. Reinert and Kodrich 1982). Habitat selection studies, on the other hand, use indicators of choice to infer an animal's selection of resources and conditions (e.g. Row and Blouin-Demers 2006). Use-availability designs are the most widely used for birds and mammals; they compare the proportion of available habitat with the proportion used by the study animals (Garshelis 2000, Thomas and Taylor 2006). Habitat selection is indicated by non-random use of available habitats; if animals use a certain habitat at a disproportionate rate compared to its availability, then it is concluded that habitat is either selected (used proportionately more than available) or not selected, or even avoided (used proportionately less than available). For these kinds of studies, it is assumed that all habitats are equally available to all individuals and a proxy must be used for selection, such as the amount of time spent in a particular habitat (Garshelis 2000, Buskirk and Millspaugh 2006). Another approach to investigate habitat selection is the site attribute design (Garshelis 2000). Instead of analyzing the amount of time an animal spends in a particular habitat, as done in use-availability studies, site attribute studies compare numerous variables at used and corresponding randomly chosen unused sites to determine the variables influencing selection of one habitat over another (Flores and Eddleman 1995, Wilkinson et al. 2007, Raynor et al. 2012, Beatty et al. 2016).

Like other animals, snakes do not use habitats randomly, but use some habitats preferentially and avoid others (Reinert 1993, Charland and Gregory 1995, Blouin-Demers and Weatherhead 2001, Harvey and Weatherhead 2006). The structural characteristics of vegetation (e.g. canopy cover), rather than vegetative species composition, have been shown to affect habitat selection by snakes (Reinert 1984, Gienger and Beck 2011). Thermoregulatory characteristics of habitats (e.g. basking sites; Row and Blouin-Demers 2006, Gienger and Beck 2011) are also particularly important to snakes because their movement rate, digestive rate, and reproductive efficiency are dependent on achieving an optimal body temperature (Stevenson et al. 1985, Peterson et al. 1993, but see Brown and Weatherhead 2000). Other important habitat variables include suitable cover resources (Dixon-MacCallum et al. 2017) and prey availability (Madsen and Shine 1996, Hyslop et al. 2014). Aggregations of gravid snakes occur in some populations (Gregory 1975, Larsen and Gregory 1988) and may reveal critically important habitats for successful recruitment and for consideration in conservation planning. This is especially important for northern populations that are restricted to short, relatively cool summers and may hibernate for up to 8 months of the year (Gregory 1977).

Common Gartersnakes (*Thamnophis sirtalis*) are the most northerly-distributed reptile in North America and have a wide geographic distribution (Rossman et al. 1996). They are typically considered generalists in their diet and habitat selection but are usually associated with wetlands and riparian habitats where they feed primarily on anuran amphibians (Kephart and Arnold 1982, Gregory and Nelson 1991). Snakes in northern populations undertake relatively long-distance migrations between summer and winter habitats (Gregory and Stewart 1975, Larsen 1987). In this study, I investigate habitat use and selection by gartersnakes towards the northern extent of their geographic range at two study sites in east-central British Columbia: the Kinbasket Reservoir and Cranberry Marsh. Though Common Gartersnakes have been thoroughly studied in other parts of their geographic range, their habitat use and selection in this part of their distribution was largely unknown.

Study Objectives

The objective of this study was to measure the use and selection of habitat by Common Gartersnakes in east-central British Columbia. I predicted that gravid snakes, because of their thermoregulatory requirements, would use habitat with more open canopy that provides more opportunities for basking (Charland and Gregory 1995, Row and Blouin-Demers 2006, Halliday and Blouin-Demers 2015). I expected that gravid snakes would be more frequently observed than nongravid snakes near woody debris because their reduced locomotor ability necessitates remaining near ready escape shelter (Seigel et al. 1987). I also expected low to moderate cover height and high percentage of potential cover to be associated with the presence of gravid snakes because this combination should provide adequate shelter as well as basking opportunities. Last, because snakes exhibit reduced feeding when gravid (Gregory et al. 1999), I predicted that gravid snakes would be less likely than nongravid snakes to be found near water, where their amphibian prey are most abundant.

Methods

I conducted my study of habitat use at two sites in east-central British Columbia, the Kinbasket Reservoir and Cranberry Marsh. The Kinbasket Reservoir (52°45'18" N, 119°9'9" W) is a hydroelectric reservoir in the Columbia Watershed that has a drawdown zone (DDZ, the area over which water fluctuates) made up of a series of ponds in a wetland matrix. The DDZ is gradually inundated through the summer as a result of the seasonal operations of the Mica Dam. My second site, Cranberry Marsh (52°48'54" N, 119°14'49" W), is the remnant of a drained flat-bottomed lake that has been reclaimed as waterfowl habitat by Ducks Unlimited and is a popular recreation site for hiking, biking, and canoeing. It is bordered by a provincial highway, a railroad, and is adjacent to both industrial and residential developments.

I collected data on habitat use from snakes I captured opportunistically during visual encounter surveys (VES, see Chapter 2) and from snakes I tracked using radiotelemetry (see Chapter 2 for details on radio-tagged snakes, surgical methods, and radiotelemetry protocols). The first approach has the advantage of including all classes of snakes (i.e. juveniles and adults of both sexes), but is limited by the necessity to detect snakes visually. My VES method is also biased to the margins of waterbodies and habitat edges where I concentrated my searches for snakes, so can reveal only a subset of potential patterns of habitat use. Radiotelemetry, on the other hand, allows for the determination of habitats used by snakes, even when the snakes are hidden and are outside the areas included in VES. However, for logistical reasons, radiotelemetry is usually limited to a small sample size that is typically made up of only the largest individuals (females in this case). I compared the percentage of snake observations in each habitat type (listed in Table 3-1) between the two survey methods and tested for associations using the Pearson Chi-squared test.

I opportunistically captured snakes by hand, following Animal Care Committee Standard Operating Procedure #HP2002 (Capture, Handling, and Measurement of Non-Venomous Snakes in the Field), recorded standard data on each individual (sex, snout-vent length, weight, reproductive state if female), and marked each individual by clipping a unique combination of subcaudal scutes for future identification (Blanchard and Finster 1933). Recognition of individual snakes also allowed me to avoid pseudoreplication in statistical analyses through counting the same snake more than once (see Chapter 2 for detailed procedures). For each opportunistic snake capture I categorized the habitat type and measured average cover height and percentage cover (Table 3-1; Cooperrider 1986, Gray-Lovich and Lovich 2012). I also recorded habitat data for snakes that were merely observed (e.g. snakes that evaded capture). Although these data provide information on habitat use, they do not offer any indication of habitat choice.

I used ground-based, very high frequency (VHF) radiotelemetry to track the movements of adult female Common Gartersnakes at the two sites. To determine the criteria by which snakes select certain habitats over others, I chose an analysis that involves the comparison of used plots paired with nearby random plots. When I located a radio-tagged snake in 2017, I collected habitat variables in a 1 m × 1 m area centred on the snake (Table 3-1), while disrupting the snake as little as feasibly possible. To select a random plot to pair with the used plot, I chose a distance from 20-30 m (within the daily movement range for *T. sirtalis* (Lawson 1991), but far enough away from the used plot to incorporate habitat heterogeneity) and a bearing from 1°-360° using a random number generator. I then walked the random distance along the random bearing to create the random plot (again, 1 m × 1 m). Because I selected random plots only when I located a radio-tagged snake, the paired plots were not independent of one another; however, each pair was independent of every other pair for each individual snake (n = 7). I then collected data on the same variables at the random plots as those at locations where I observed snakes. To avoid repeat measurements of the same habitat for snakes that remained in one place over several days, I defined a change in location as a minimum movement of 3 m and measured habitat variables again for each snake once it had made at least this minimum movement. When I relocated a radio-tagged snake I recorded the date, time, UTM coordinates (NAD 83), physical structure of the site, and habitat type. Physical structure refers to the presence, abundance, and spatial arrangement of relevant entities within a habitat (McCoy and Bell 1991). For snakes, physical structure includes rock, vegetation type (forbs, shrubs, trees, etc.), leaf litter, and cover (including coarse woody debris, CWD) as well as distance to logs, trees, and bodies of water (Reinert 1984, Gienger and Beck 2011). I quantified physical structure by measuring these variables, as well as vegetation height and canopy cover. I based my four habitat categories on vegetation structure (Gray-Lovich and Lovich 2012). I categorized habitats with a high canopy as forests, those with lower canopies and dominant shrub cover as scrub, and open-canopy habitats with grass and sedge as the main cover as either fields or wetlands, the difference being that the latter were permanently or temporarily saturated with water. I removed observations of snakes that were found on roads from my habitat analysis because I could not characterize the habitat for these observations.

I analyzed the data from radio-tagged snakes in two main ways. The first method compares the proportions of 'successes' and 'failures' for binary habitat variables at used plots vs. random plots. The second method involves habitat modeling of the continuous variables and canopy cover. I conducted separate analyses for each individual because I could not incorporate individuals as a factor in a combined analysis with unequal sample sizes. I used R (R Core Team 2012) for all analyses and used a somewhat liberal criterion of $P = 0.10$ as a statistical threshold of significance. I conducted data exploration and tested for normality with Shapiro-Wilks tests.

Analyses of Paired Plots

For the three binomial habitat variables measured at each pair of used and random plots, I constructed 2 × 2 contingency tables for each individual. I calculated the proportion of 'successes' (1) and 'failures' (0) for each variable for each individual (Agresti 1996). I categorized canopy cover into two fields: open (1) and closed (0). For distance to CWD, I categorized plots as either greater than 2 m away (0) or less than or equal to 2 m (1). This distance is presumably short enough so a snake could easily take refuge beneath the CWD in the case that a predator was approaching. Last, I classified plots based on the proximity to water, either greater than 5 m from water (0) or less than or equal to 5 m from water (1), based on the frequent detection of amphibians within this buffer area. I then graphed the proportion of 'successes' for each variable at random plots against the proportion of 'successes' at the used plots for gravid and nongravid snakes, separately. These graphs provide a visual comparison of the paired plots for each individual as well as an opportunity to look for trends in the data based on reproductive status. Because the data are matched pairs, the samples are statistically dependent and therefore unsuitable for Fisher's exact test (Agresti 1996). I instead conducted McNemar tests for each habitat variable for each snake to test for symmetry in the contingency tables and to detect differences between the paired random and used plots (Agresti 1996). Because my sample sizes were fairly small, I used the mid-p variant of the McNemar test suggested by Fagerland et al. (2013) using the R package 'exact2x2' (Fay et al. 2018). The mid-p variant of the McNemar test provides a balance between overly conservative exact tests and liberal asymptotic methods (Fagerland et al. 2013).

Table 3-1. Habitat variables collected at each snake capture location for visual encounter surveys (VES) and/or at each radio-tagged snake location and random associated plot for radiotelemetry (RT).

Variable	Type	Unit	Description	Method(s)
Canopy Cover	Binomial	Open (1) or Closed (0)	Tree canopy cover immediately above plot	RT
Distance to CWD	Binomial	≤2 m (1) or >2 m (0)	Distance from plot to CWD	RT
Distance to Water	Binomial	≤5 m (1) or >5 m (0)	Distance from plot to water	RT
Habitat Type	Categorical	Forest, wetland, scrub, field	General habitat in which plot is located	RT & VES
Cover Height	Continuous	mm	Average height of vegetation in plot	RT & VES
Percentage Cover	Continuous	%	Percentage cover available from vegetation in plot	RT & VES

Univariate Analysis of Paired Plots

Percentage cover and cover height data were primarily non-normal so I conducted non-parametric paired Wilcoxon rank-sign tests. Because the data were binned into relatively few classes, R could not compute exact p-values for the paired Wilcoxon sign-rank tests, so I used the wilcox.exact() function in the package 'exactRankTests' (Hothorn and Hornik 2017), which provided similar results and no changes in terms of significance vs. non-significance. I therefore report the statistics for the initial Wilcoxon tests.

Matched-Pair Logistic Regression Modelling

Matched-pair logistic regression (MPLR) is a type of logistic regression modelling that handles matched binary data (Hosmer and Lemeshow 2000). For this paired study, the case represents the used point where snake capture or observation took place (case/used = 1) and the control is the associated random point (control/random = 0). Because used and random plots are paired and therefore not independent, standard logistic regression cannot be used for their analysis (Manly et al. 2002). Matched-pairs logistic regression is more appropriate (and more powerful) than standard logistic regression for paired designs because it tests the differences between the paired data points.

I used the clogit() function from the 'survival' package in R (R Core Team 2012) to model the paired habitat data. I used the strata argument to identify pairs by plot number and included three habitat variables: percentage cover, cover height, and canopy cover (open = 1 or closed = 0). I fitted matched-pair logistic regression models to each of the seven individual snakes I radio-tracked in 2017.

I used the AICc() function in the 'MuMIn' package (Barton 2018) to compute second-order Akaike's information criterion (AIC_c) for model selection. Burnham and Anderson (2002) recommend the use of AIC_c for small sample sizes to avoid overfitting models. Because AIC_c approaches Akaike's information criterion (AIC) as sample size increases, AIC_c should be used regardless of sample size. I tested models based on AIC_c, and considered the model with the minimum AIC_c to be the best model and those within two of the minimum value to be supported as candidate models (Burnham and Anderson 2004). I calculated odds ratios and 95% confidence limits from estimates and compared models within each set.

The methods typically used to validate standard logistic regression models are inappropriate for matched-pair logistic regression models because, in the latter, the response variable always has a value of one. Steyerberg et al. (2001) reviewed methods of internal validation for logistic regression and found that bootstrapping produced the most reliable estimates of performance. Bootstrapping is a method with diverse functions that can be used to quantify uncertainty of a result by estimating standard error of a coefficient or a confidence interval for a coefficient (Steyerberg et al. 2001). It involves randomly sampling an original set of data with replacement to create new datasets for which statistics of interest may be calculated. To conduct bootstrapping to assess the fit of my global models I used the boot() function in the ‘boot’ package (Canty and Ripley 2017). I initially ran 999 iterations and found that several of the models would not converge. I then adjusted the code, using the tryCatch() function to determine at what level of iteration the models would begin to result in non-convergence. This number was very low (<5 iterations for most models), which led me to pursue other methods of model validation. I had intended to compare the bootstrapped estimates and standard errors to the original values. I would have considered the model to have a good fit if the bootstrapped estimates and standard errors overlapped that of the original model (adapted from Steyerberg et al. 2001). Because I was unable to validate my models using this method, I tried cross-validation, the second-ranked method reviewed by Steyerberg et al. (2001). Cross-validation is an extension of the split sample-method in which a model is developed from a randomly chosen portion (often 50%) of the data and then tested using the remaining data, and vice-versa. The resulting average is interpreted as a measure of performance. This method produces low bias and low variability, but is not appropriate for all performance measures (Steyerberg et al. 2001). Cross-validation also resulted in non-convergence of models and was therefore not successful in validating the matched-pair logistic regression models. Therefore, I present my model results with the caveat that they are based on a limited sample size and have not undergone internal validation.

Results

I recorded habitat use from 166 opportunistically captured snakes and from the locations of radio-tagged snakes (n = 449 observations, not including repeat locations) in 2016 and 2017. The habitat type in which an observation occurred was significantly associated with the sampling method (Pearson's Chi-squared test, $X^2 = 26.70$, df = 3, $P < 0.0001$). I captured snakes opportunistically most frequently in wetland habitats, whereas radio-tagged snakes were most commonly found in forests (Figure 3-1). Compared to radiotelemetry observations, opportunistic captures were more frequent in field habitat but less so in scrub habitat. Three opportunistically captured snakes at Cranberry Marsh were located at least once in open, deep-water habitats (>50 cm), a habitat that was not utilized by snakes that I tracked at the reservoir. I frequently found snakes at the Kinbasket Reservoir within a long stretch of transitional habitat between wetland and scrub where CWD had piled up as a result of hydroelectric reservoir fluctuations.

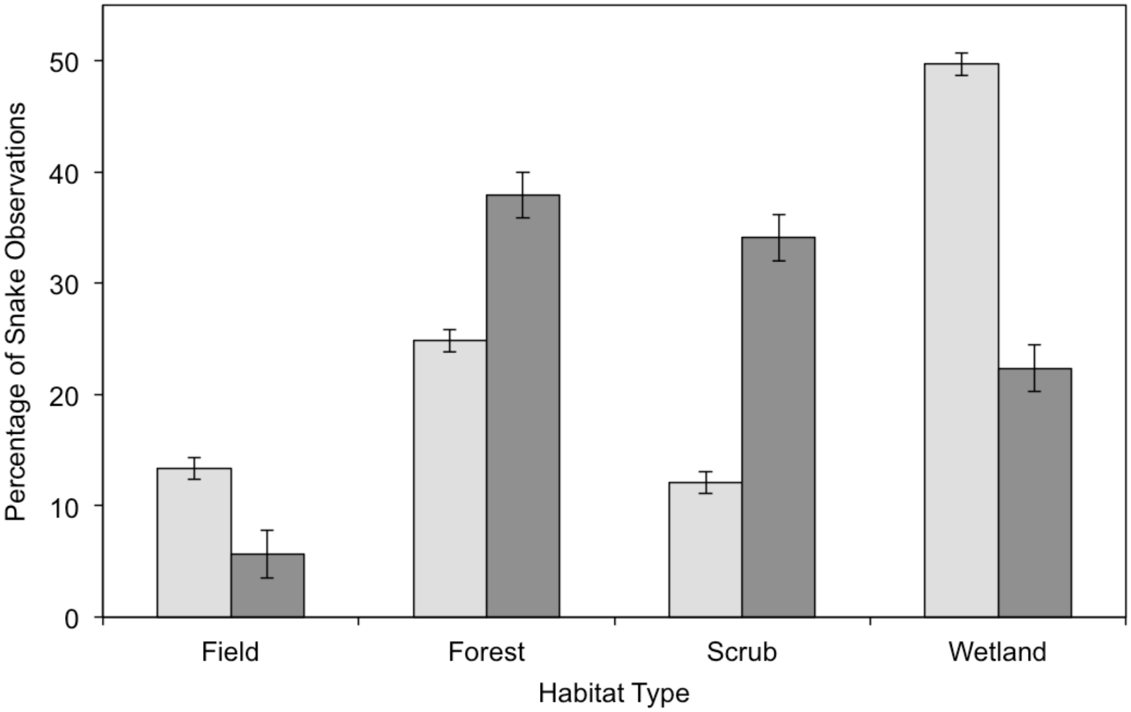

Figure 3-1. Percentage of snake observations in habitat types for visual encounter surveys (opportunistic captures = *light grey*, n = 156) and radiotelemetry (observations minus repeat locations = *dark grey*, n = 444). Error bars = 95% confidence intervals.

Fifty-three of 502 total radiotelemetry relocations were repeat locations (≤ 3 m from the previous location) by 12 of the 15 snakes (i.e. three individuals were never found in the same spot over consecutive relocations). Repeat relocations occurred primarily in mid to late summer (July-September), and ranged from 1-8 times per location per individual (average = 1.51 ± 1.33 SD) over 1-35 days (average = 4.76 ± 5.99 SD; Figure 3-2). The two longest sedentary periods occurred in the month of July by snakes using artificial cover (35 days beneath a tarp covering a compost pile and 14 days inside a pile of plywood and yard waste).

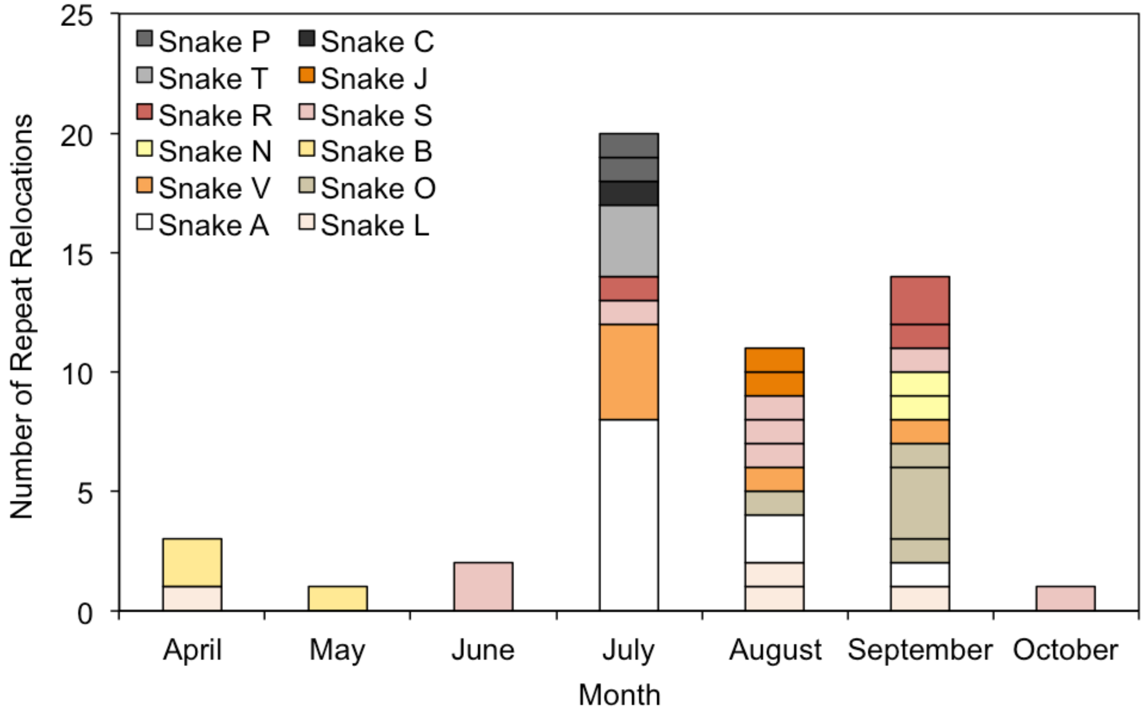

Figure 3-2. Monthly number of repeat, or consecutive, relocations of radio-tagged female snakes in the same location (≤ 3 m from the previous location) from 2016-2017. Colours in legend represent individual snakes.

Analyses of Paired Plots

Gravid females used areas with more open canopy than nongravid females (Figure 3-3). For nongravid females that were located in close proximity to gravid snakes, this general trend was less evident. Two of the nongravid females I radio-tracked were repeatedly observed within a few metres of gravid individuals and therefore overlapped gravid snakes in their habitat choices. The availability and use of CWD differed between study sites. Observations of habitat use by snakes within 2 m of CWD were less frequent at Cranberry Marsh (Snakes T & V; Figure 3-4) than at the Kinbasket Reservoir. Proximity of the plots to water did not indicate habitat preference or avoidance and did not differ between study sites or reproductive states (Figure 3-5). Because rocks were rarely present in used or random plots (4% and 6%, respectively), I removed this variable from my analysis (76% of total presence of rock in the plots was attributed to just two individuals). For the remaining habitat variables, I calculated exact 95% binomial confidence intervals using the number of 'successes' and the total number of plots (or 'attempts') for random plots and used plots for each individual (Fagan 1999; Figure 3-3–Figure 3-5).

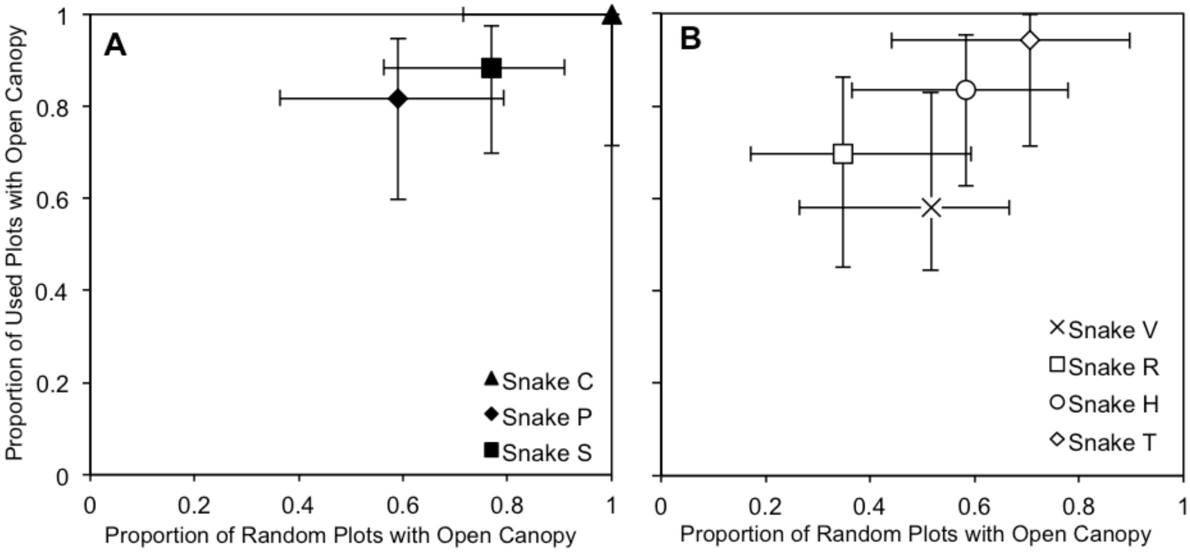

Figure 3-3. Proportion of habitats with open canopy at random locations versus locations where radio-tracked (**A**) gravid (*black*) and (**B**) nongravid (*white*) snakes were observed in 2017. Error bars = exact 95% binomial confidence intervals.

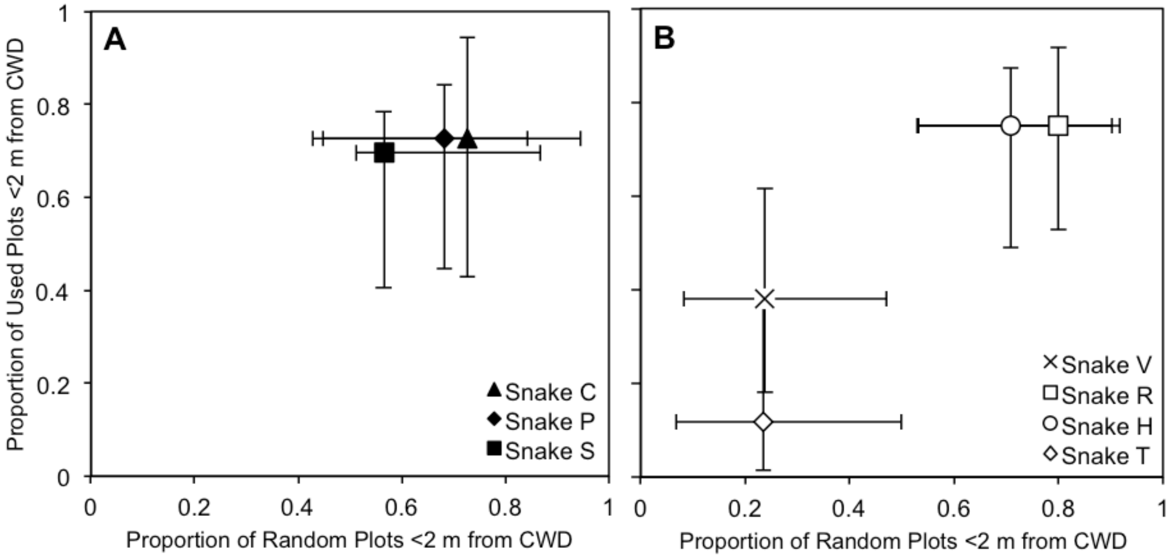

Figure 3-4. Proportion of habitats within 2 metres of coarse woody debris (CWD) at random locations versus locations where (**A**) gravid (*black*) and (**B**) nongravid (*white*) radio-tracked snakes were observed in 2017. Error bars = exact 95% binomial confidence intervals.

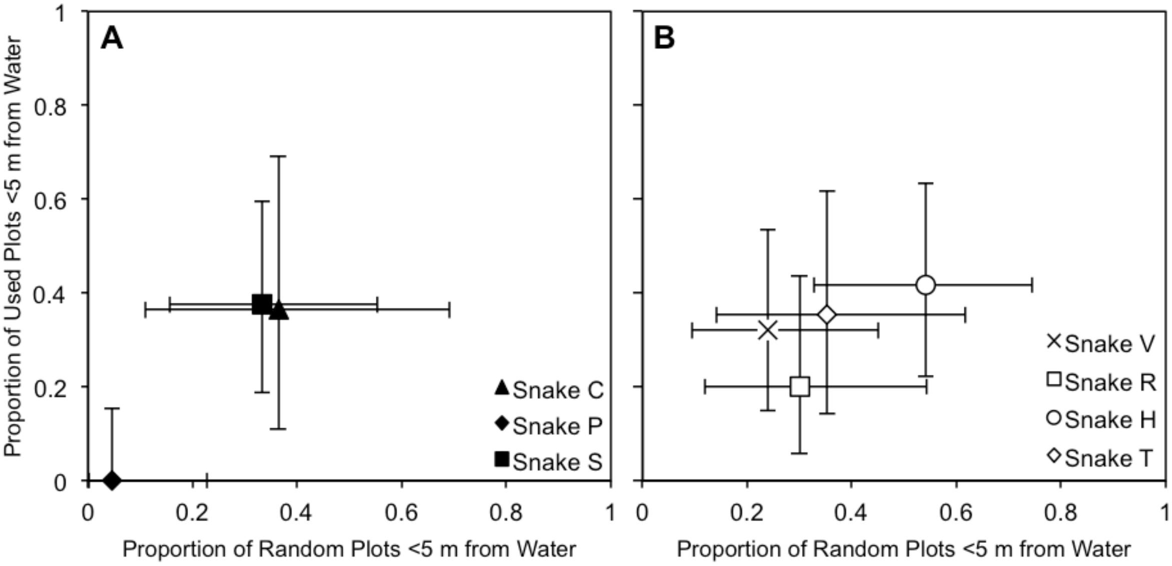

Figure 3-5. Proportion of habitats within 5 metres of water at random locations versus locations where (**A**) gravid (*black*) and (**B**) nongravid (*white*) radio-tracked snakes were observed in 2017. Error bars = exact 95% binomial confidence intervals.

Used and random plots for each individual were shown to have similar cover heights and percentage cover through McNemar tests (Table 3-2). Canopy cover was significantly different between used and random plots for two nongravid snakes and one gravid snake (Table 3-2). These individuals used open-canopy habitats even when closed-canopy habitats were nearby. Results shown as ‘NA’ are due to consistent habitat conditions for all pairs. For example, pairs of used and random plots for Snake T were always both within 5 m of water or farther than 5 m from water. In other words, none of the pairs differed in this characteristic.

Univariate Analysis of Paired Plots

Nongravid snakes used plots with significantly higher percentage cover than the associated random plots (e.g. Snake V, n = 21, W = 215, P = 0.004; Figure 3-6). The average cover height at the plots used by nongravid snakes was similar to that of the random plots (e.g. Snake V, n = 25, W = 144, P = 0.62) with the exception of one snake that used plots with significantly lower cover height than random plots (n = 11, W = 15, P = 0.05; Snake T, Figure 3-6). Gravid snakes used plots with percentage cover similar to associated random plots (e.g. Snake S, n = 21, W = 103, P = 0.67), as was also true for cover height (e.g. Snake S, n = 23, W = 108, P = 0.36; Figure 3-6). Contrary to my prediction of high potential cover in areas used by gravid snakes, areas inhabited by nongravid snakes had higher potential cover than areas where gravid snakes were found. Gravid snakes were found in areas with lower cover height than in areas used by nongravid snakes (though these differences were not evident between used and random plots).

Table 3-2. McNemar's Chi-squared test results (P-values and McNemar's chi-squared X^2) for habitat variables from paired plots of radio-tagged snakes.

	Nongravid Snakes				Gravid Snakes		
Variable	V	H	R	T	C	P	S
Distance to CWD	P = 0.37 $X^2 = 0.8$	P = 1 $X^2 = 0$	P = 1 $X^2 = 0$	P = 0.61 $X^2 = 0.25$	P = 1 $X^2 = 0$	P = 1 $X^2 = 0$	P = 0.37 $X^2 = 0.8$
Distance to Water	P = 0.61 $X^2 = 0.25$	P = 1 $X^2 = 0$	P = 0.61 $X^2 = 0.25$	P = NA X^2 = NaN	P = 1 $X^2 = 0$	P = 1 $X^2 = 0$	P = 1 $X^2 = 0$
Canopy Cover	P = 0.12 $X^2 = 2.2$	P = 0.10 $X^2 = 2.5$	P = 0.03 $X^2 = 4$	P = 0.21 $X^2 = 1.5$	P = NA X^2 = NaN	P = 0.07 $X^2 = 3.2$	P = 0.24 $X^2 = 1.3$

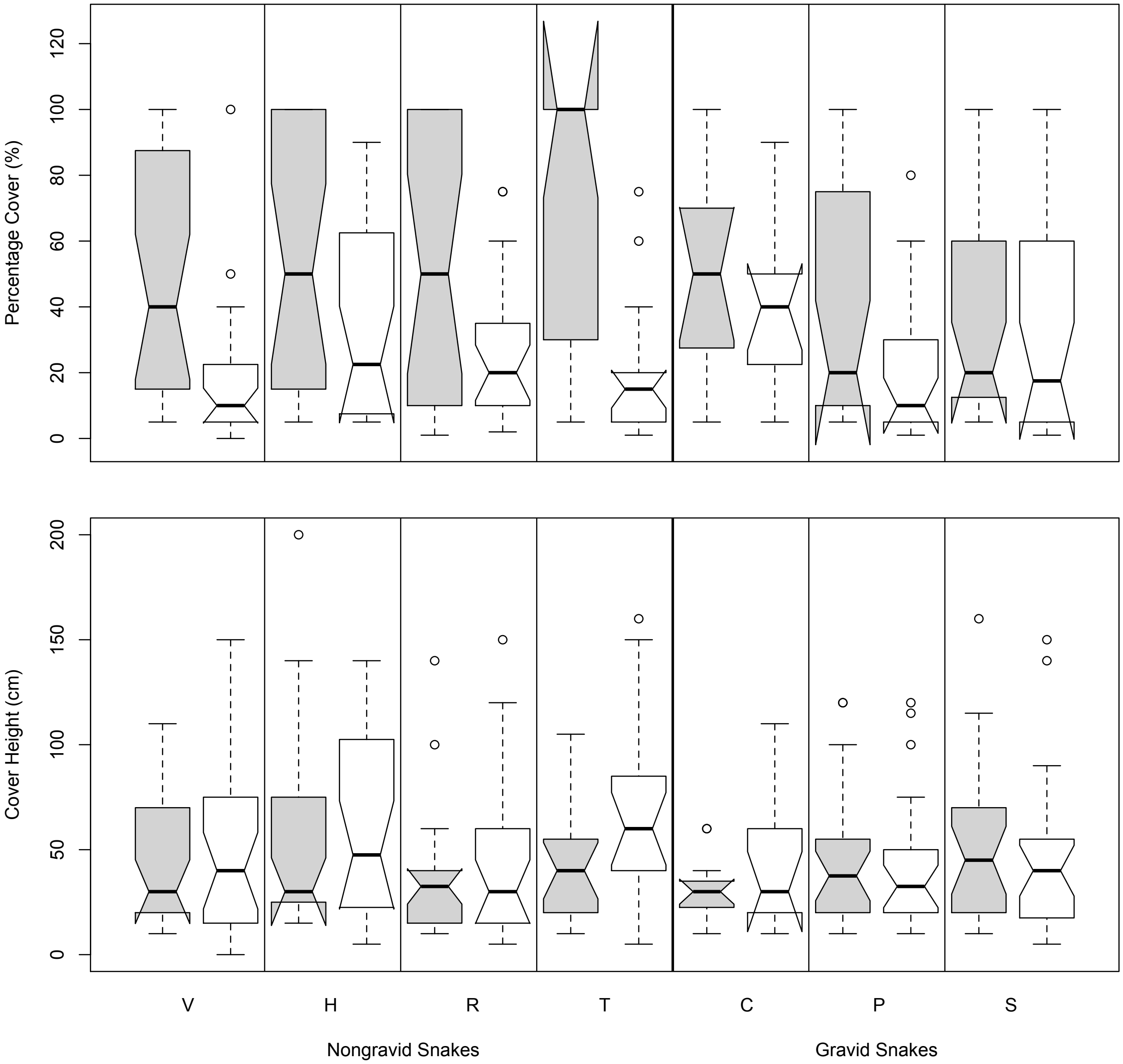

Figure 3-6. Box and whisker plots for percentage cover (%) and cover height (cm) at used (*grey*) and random (*white*) sites for each radio-tagged snake. Boxes cover the second and third quartiles and the centre lines represent the medians. Whiskers represent the first and fourth quartiles. Notches that do not overlap strongly suggest a statistical difference.

Matched-Pair Logistic Regression Modelling

Percentage cover was significantly greater in used than random plots for all nongravid females but one. However, cover height was statistically lower at random sites compared to used sites for this individual, but for none of the other snakes (Table 3-3). For canopy closure, univariate models for gravid females would not converge and therefore were omitted from the individuals' analyses. For the snakes for which convergence was achieved, the trend for canopy was similar to that for percentage cover.

For global models, I included all three variables plus an interaction between percentage cover and cover height for each individual (Table 3-4).

Table 3-3. P-values for variables fitted in univariate matched-pair logistic regression models for each radio-tracked snake. For certain individuals, the canopy variable was similar throughout and caused the model to not converge. I therefore omitted canopy from the analysis for these individuals ('omit'). Positive estimates are indicated by (+) and negative estimates are indicated by (-).

	Nongravid Snakes				Gravid Snakes		
Variable	V	H	R	T	C	P	S
Percentage Cover	0.024 (+)	0.087 (+)	0.038 (+)	0.135 (+)	0.298 (+)	0.140 (+)	0.714 (+)
Cover Height	0.594 (-)	0.658 (-)	0.379 (-)	0.091 (-)	0.333 (-)	0.722 (+)	1.000 (-)
Canopy Cover	0.068 (+)	0.079 (+)	0.049 (+)	0.142 (+)	omit	omit	omit

Table 3-4. Coefficient estimates, standard errors, z-values, and p-values for each global matched-pair logistic regression model, for each individual snake (n = 7).

Snake	Variable	Coefficient	Standard Error	Z-value	P-value
V (n = 52, 26 pairs)	Percentage Cover	0.079	0.042	1.861	0.062*
	Cover Height	0.021	0.019	1.073	0.283
	Canopy Cover	3.944	3.181	1.240	0.215
	Percentage Cover × Cover Height	-0.00076	0.00065	-1.174	0.240
H (n = 48, 24 pairs)	Percentage Cover	0.085	0.039	2.147	0.031*
	Cover Height	0.039	0.021	1.815	0.069*
	Canopy Cover	1.831	1.203	1.521	0.128
	Percentage Cover × Cover Height	-0.00099	0.00044	-2.23	0.025*
R (n = 44, 22 pairs)	Percentage Cover	8.99E-02	5.85E-02	1.537	0.124
	Cover Height	3.97E-02	4.21E-02	0.944	0.345
	Canopy Cover	2.96E+00	1.58E+00	1.870	0.061*
	Percentage Cover × Cover Height	-1.46E-03	1.41E-03	-1.037	0.299
T (n = 34, 17 pairs)	Percentage Cover	2.30e-01	2.41e-01	0.955	0.340
	Cover Height	7.97e-03	3.45e-02	0.231	0.818
	Canopy Cover	-1.35e+00	2.73e+00	-0.494	0.621
	Percentage Cover × Cover Height	-1.21e-03	3.09e-03	-0.393	0.695
C (n = 22, 11 pairs)	Percentage Cover	0.045	0.034	1.325	0.185
	Cover Height	-0.0050	0.038	-0.130	0.897
	Percentage Cover × Cover Height	-0.00038	0.00058	-0.649	0.516
P (n = 44, 22 pairs)	Percentage Cover	0.095	0.049	1.921	0.054*
	Cover Height	0.079	0.050	1.570	0.116
	Percentage Cover × Cover Height	-0.0020	0.0011	-1.734	0.082*
S (n = 48, 24 pairs)	Percentage Cover	6.72e-03	1.80e-02	0.372	0.710
	Cover Height	-4.49e-03	1.21e-02	0.369	0.712
	Percentage Cover × Cover Height	-6.89e-05	3.61e-04	-0.191	0.849

I selected candidate models for each snake based on AIC$_c$ values within two of the model with the best fit for each individual (Table 3-5; Burnham and Anderson 2002). Neither cover height nor canopy cover was selected as a standalone variable in any of the best models. Percentage cover appeared to be the most important habitat characteristic for radio-tagged snakes.

The best candidate models differed among individuals (Table 3-6). Cover height was included as a variable for the best models of only two snakes, individuals that were repeatedly observed within 1 m of each other. Percentage cover was the most important variable for habitat selection and was included in each individual's best candidate model (Table 3-6). Consistent with my previous results, the models of nongravid female habitat selection typically included more significant variables than models for gravid females.

Table 3-5. Candidate matched-pair logistic regression models and Akaike's Information Criterion, corrected for small samples (AIC$_c$) for individual radio-tracked snakes. An asterisk (*) indicates the model with the best fit and bold AIC$_c$ values are within two of the model with the best fit.

	Nongravid Snakes				Gravid Snakes		
Model	V	H	R	T	C	P	S
Percentage Cover × Cover Height + Canopy Cover	29.60	**26.78***	26.08	16.55	-	-	-
Percentage Cover × Cover Height	31.56	**26.88**	29.06	13.34	20.94	**25.01***	38.93
Percentage Cover + Cover Height	30.33	33.87	26.88	11.06	**17.45**	32.43	36.32
Percentage Cover + Canopy Cover	**25.91***	30.12	**21.64***	**10.29**	-	-	-
Percentage Cover	28.05	31.94	25.42	**8.48***	**16.20***	30.00	**33.93***
Cover Height	39.30	35.25	31.85	21.19	**16.59**	32.57	**34.07**
Canopy Cover	34.53	31.60	26.50	22.92	-	-	-

Table 3-6. Best candidate models based on Akaike's Information Criterion, corrected for small sample sizes (AIC$_c$) for each radio-tracked snake.

Snake	Variable	Coef.	Std. Error	Z-value	P-value	Odds	95% CI	Odds Ratio
V	Percentage Cover	0.042	0.018	2.355	0.019	1.043	1.01, 1.08	0.51
	Canopy Cover	2.830	1.821	1.554	0.120	16.93	0.48, 600.	0.94
H	Percentage Cover	0.085	0.040	2.147	0.032	1.089	1.01, 1.18	0.52
	Cover Height	0.039	0.022	1.815	0.070	1.040	1.00, 1.08	0.51
	Canopy Cover	1.831	1.204	1.521	0.128	6.240	0.59, 66.0	0.86
	Percentage Cover × Cover Height	-0.001	0.000	-2.231	0.026	0.999	0.99, 1.00	0.50
R	Percentage Cover	0.043	0.023	1.854	0.064	1.044	0.99, 1.09	0.51
	Canopy Cover	2.480	1.257	1.973	0.049	11.94	1.01, 140.	0.92
T	Percentage Cover	0.127	0.085	1.496	0.135	1.136	0.96, 1.34	0.53
C	Percentage Cover	0.020	0.019	1.041	0.298	1.020	0.98, 1.06	0.51
P	Percentage Cover	0.095	0.050	1.921	0.055	1.100	1.00, 1.21	0.52
	Cover Height	0.079	0.050	1.570	0.116	1.082	0.98, 1.19	0.52
	Percentage Cover × Cover Height	-0.002	0.001	-1.734	0.083	0.998	0.99, 1.00	0.50
S	Percentage Cover	0.004	0.011	0.367	0.714	1.004	0.98, 1.02	0.50

Discussion

Gravid and nongravid Common Gartersnakes use habitat differently, presumably because of the physiological effects associated with pregnancy (Seigel et al. 1987, Charland 1995, Charland and Gregory 1995). Gravid Common Gartersnakes in my study used habitats that were more open-canopied than habitats used by nongravid snakes, consistent with increased basking opportunities in open-canopy areas (Tuttle and Gregory 2016). This distinction is also evident in other species of snakes (Reinert 1993). Gravid Broad-Headed Snakes (*Hoplocephalus bungaroides*) in Australia use exposed cliff habitats more than nongravid snakes (Webb and Shine 1997). Likewise, gravid Rat Snakes (*Pantherophis obsoletus*) in Ontario use habitat edges more than nongravid females (Blouin-demers and Weatherhead 2001). Edge habitats offer an area of open canopy for basking opportunities and also provide ample cover from predators (Burger et al. 2004). Edge habitats, such as the transition zone between wetland and scrub at the Kinbasket Reservoir, are important for gravid snakes given their reduced mobility, their increased risk of predation, and their prioritization of thermoregulation (Seigel et al. 1987, Charland and Gregory 1995, Tuttle and Gregory 2016). Although the transitional area at the Kinbasket Reservoir offers abundant cover in the form of CWD, my study does not suggest that distance to CWD differs between gravid and nongravid snakes. Future work should involve testing a wider range of distances with various types of cover (not just CWD).

Common Gartersnakes are reported to meander along the edges of ponds while foraging (Drummond 1983). Because snakes feed at a reduced rate when gravid (Gregory et al. 1999), nongravid snakes should be observed near water more frequently than gravid snakes. However, the distance to water was not correlated with either the absence or presence of gravid or nongravid snakes in my study area. The ponds at my study sites have shorelines that may be too steep to provide the shallow areas in which *T. sirtalis* would be capable of handling prey (Drummond 1983). Because snakes eat infrequently their habitat should be more reflective of activities other than hunting such as basking or hiding. As with the distance to CWD, it is possible that the distance I selected as a threshold of closeness to water was not suitable for identifying a difference in habitat selection between gravid and nongravid snakes.

Though the McNemar Tests indicated no clear difference between habitat selection of gravid and nongravid snakes, the paired Wilcoxon signed-rank tests suggested that nongravid snakes in my study area occupied more heterogeneous habitats with respect to percentage cover and cover height than the relatively homogeneous habitats in which gravid snakes were found. This is shown by the differences between used and random plots for snakes in each reproductive status (i.e. nongravid paired plots are more distinct than gravid pairs).

Percentage cover was included in the best candidate MPLR model for each snake. The prevalence of this variable is likely related to anti-predator behaviour (Greene 1988). By selecting areas with high percentage cover, there are presumably more effective refuge sites that would provide protection from potential predators (Greene 1988). The best MPLR models for nongravid snakes typically included more variables than those for gravid snakes. The smaller number of significant variables in the MPLR models of gravid snakes might be a result of the limited explanatory variables included due to failure of models with canopy closure to converge for gravid snakes.

The relatively long-term use of anthropogenic cover by Common Gartersnakes at Cranberry Marsh corresponded with the final stages of gestation (see Chapter 5). Use of man-made cover (compost/yard waste) has also been observed in other species. Grass Snakes (*Natrix natrix*) in Sweden used anthropogenic heat sources (e.g. piles of yard waste or livestock manure) for nesting sites, allowing the species to extend their northern distribution beyond that of any other oviparous reptile (Löwenborg et al. 2010). However, the extended stasis in my study was not strictly limited to gravid snakes, so there must be other causal factors aside from those associated with reproduction. Some snake species temporarily adopt nocturnal patterns of activity during periods of high temperatures (Blem and Blem 1990, DeGregorio et al. 2015), but this has not been reported in studies of Common Gartersnakes (though anecdotal observations have been recorded). Because I did not track snakes at night I cannot say whether these snakes were truly sedentary, remaining in the same location, or if they shifted to nocturnal activity and repeatedly returned to the same anthropogenic cover for daytime hours. Regardless of whether these periods were truly sedentary, the extended use of anthropogenic cover seems to suggest the value of this cover type. But a more focused study on the use of anthropogenic cover is required to definitively rate its importance to Common Gartersnakes in east-central BC.

One assumption of habitat evaluation studies is that the area we consider to be ‘available habitat’ is truly available to all individuals and that availability does not vary through the course of the study (though studies of seasonal habitat use address this weakness; Browne and Paszkowski 2014, Hyslop et al. 2014). Researchers should be careful to avoid mistaking habitat use for habitat selection, because although they are both related to the spatial distribution of animals they differ in that habitat selection is the process by which an animal chooses the habitat components it will use (Hall et al. 1997). Garshelis (2000) provides a comprehensive review of the issues embedded in habitat evaluation studies. Both habitat use and habitat selection studies are frequently plagued by sample bias with respect to detection, which may differ depending on habitat characteristics (e.g. animals are more difficult to see in habitats with thick vegetation than those with sparse vegetation). For studies that utilize radiotelemetry methods, technological constraints such as transmitter size may introduce biases in the species, sex, age, and size of animal that will be sampled. Furthermore, signal interference and certain habitat types may bias where and when a radio-tagged animal can be detected (e.g. deep ravines or rocky areas often impede radiotelemetry signals and may prevent detection in these habitats).

Because most of the areas I surveyed had very high potential cover (vegetation, coarse woody debris, etc.) I likely was often unable to detect snakes during VES. This issue of detection is nicely demonstrated with radiotelemetry, during which I was able to locate snakes that were underground, in very high vegetation, or well camouflaged. The issue of detection as well as the intensive time required to track individuals resulted in a relatively low sample size, a common characteristic of radiotelemetry studies (Constible et al. 2010, Croak et al. 2013). The difference in the proportion of various habitats used between VES and radiotelemetry methods indicates that radiotelemetry is a valuable tool for studying the habitat and behaviour of these relatively small, secretive animals. Furthermore, the number of relevant habitat variables that I collected was limited. These issues reduced the statistical power of my analysis but nevertheless my study provides a basis for a more in-depth approach for future study in east-central BC.

Like most animals, Common Gartersnakes used habitat non-randomly. Gravid females inhabited areas with an open canopy that were more homogeneous than areas frequented by nongravid snakes exclusively. Some nongravid females were repeatedly found in close proximity to gravid snakes and therefore overlapped in their habitat choices; however, nongravid snakes selected habitat with higher percentage cover and lower cover height than random associated plots. The use of radiotelemetry allowed for an adequate preliminary description of gravid and nongravid female habitat selection; however, further study of male and juvenile gartersnakes in east-central BC is needed for a comprehensive understanding of the habitat characteristics selected by Common Gartersnakes.

Chapter 4 - Hibernation Ecology of Common Gartersnakes (*Thamnophis sirtalis*) in East-Central British Columbia

Introduction

For animals that reach high latitudes, length and severity of winter are important potential limiting factors, but endotherms and ectotherms, because of their differing physiologies, are affected in different ways. Although some high-latitude mammals hibernate (Robbins et al. 2012), others, by virtue of their endothermy, remain active in winter (Sheriff et al. 2009), as do some birds (Lait and Burg 2013; Conover et al. 2015). However, most species of birds that spend their summers at high latitudes migrate long distances to warmer climes to avoid winter; their endothermic physiology allows the high levels of activity required for such energetically costly movements (Newton and Dale 1996, Gilg and Yoccoz 2010).

Ectothermic vertebrates, such as amphibians and reptiles, do not generate significant body heat and therefore cannot sustain activity in freezing temperatures. They also are not sufficiently mobile to be able to migrate long distances to avoid winter conditions. Amphibians and reptiles are generally capable of some degree of supercooling for short-term survival in cold conditions, but ultimately must find some sort of shelter (den, hibernating site, or hibernaculum) to pass the winter (Gregory 1982, Churchill and Storey 1992a, Voituron et al. 2005). Requirements for hibernating sites vary among species. For example, some species such as Wood Frogs (*Lithobates sylvaticus*) and Painted Turtle hatchlings (*Chrysemys picta*) are freeze-tolerant and can survive in relatively cold hibernacula (Schmid 1982, Churchill and Storey 1992b, Krivoruchko and Storey 2010, Larson et al. 2014). Non-freeze-tolerant species, however, must find sufficiently deep hibernacula to avoid freezing. For example, Northern Leopard Frogs (*Lithobates pipiens*) and adult Painted Turtles (*Chrysemys picta*) hibernate underwater in near anoxic conditions to avoid freezing temperatures (Hermes-Lima and Storey 1998, St. Clair and Gregory 1990) and terrestrial hibernators such as snakes must reach depths below the frost line to avoid lethal temperatures (Gregory 1982, Macartney et al. 1989, Gienger and Beck 2011).

Availability of suitable hibernating sites is critical to the survival of snakes at northern latitudes, which may spend over half the year at these sites (Gregory 1977).

Although some species are capable of excavating their own hibernacula in loose substrates (e.g. Northern Pinesnakes, *Pituophis melanoleucus*, Burger et al. 2012), most snakes depend on existing underground hollows or burrows (Carpenter 1952, Lang 1971, Gregory 1984a, Williams et al. 2015). Many snake species are known to return to the same hibernating sites in consecutive years, with return rates often in the 90-100% range (Lang 1971, Gregory and Stewart 1975, Gregory 1977, Harvey and Weatherhead 2006, Gienger and Beck 2011). This stresses the importance of the preservation of sites in which snakes have successfully overwintered. Nonetheless, unusually low temperatures or lighter than average snowfall (reducing insulation of hibernacula) may result in freezing temperatures within the hibernaculum that can cause severe winter mortality (Shine and Mason 2004).

Important physical features that characterize sites around snake hibernacula include, but are not limited to, canopy closure, slope, aspect, and rock size (Harvey and Weatherhead 2006, Gienger and Beck 2011). Massasauga Rattlesnakes (*Sistrurus catenatus*) in Ontario use hibernacula in forests, whereas conspecifics at more southern latitudes overwinter in open-canopy wetlands (Reinert and Kodrich 1982, Harvey and Weatherhead 2006); the explanation for this geographical difference is currently unknown and requires further investigation. A study of rattlesnakes in Washington State reported higher temperatures in hibernacula compared to nearby random sites, which were superficially similar but were not used as overwintering habitat (Gienger and Beck 2011). Hibernacula were located on less steep slopes with more south-facing orientations and intermediate-sized rocks compared to unused sites (Gienger and Beck 2011). Surface temperatures on south-facing sites are often higher because they typically receive more solar radiation than do north-facing sites and therefore provide important basking opportunities after emergence (Hamilton and Nowak 2009, Gienger and Beck 2011, Bonan 2016). Reference sites that superficially resembled gartersnake hibernacula in northern Alberta reached lethal sub-zero temperatures and had a much wider range of temperatures compared to nearby hibernacula used by gartersnakes (Larsen 1986, Macartney et al. 1989). Research that characterizes the physical properties of suitable hibernacula can contribute to the conservation of species, which may be especially important for populations that are already challenged by a limited active season.

Although Common Gartersnakes (*Thamnophis sirtalis*) are well studied and well known for their large-scale communal hibernation in the northern part of their range (Gregory and Stewart 1975, Gregory 1984a, Larsen 1986), their hibernation ecology has not been studied in east-central British Columbia (BC), where the active season for snakes is limited to approximately 60-80 frost-free days per year (Government of Canada 1981). Typical hibernacula for populations at similar latitudes consist of limestone sinkholes in karst topography (Gregory and Stewart 1975, Larsen 1987, Shine et al. 2001). The Rocky Mountains are known to contain an abundance of soluble rock, some of which is karst (Bradford 1997); however, detailed maps showing locations of karst have yet to be developed for this region. In one location in central BC, Common Gartersnakes hibernate in grassland habitat in a large, rocky mound full of cavities (Gregory 1984a). Common Gartersnakes hibernate underwater in some cases (Carpenter 1953, Costanzo 1989), but overwinter mortality from drowning when hibernacula are flooded is an associated risk (Gregory 1977, Shine and Mason 2004). The objective of this study was to describe the hibernation ecology of Common Gartersnakes at two sites near Valemount in east-central BC (the Kinbasket Reservoir and Cranberry Marsh), including thermal and other physical characteristics of hibernating sites, sizes of hibernating aggregations of snakes, and the timing and duration of the hibernation period. I anticipated that Common Gartersnakes in my study area would follow the pattern of large-scale communal hibernation seen in most other northern populations of *T. sirtalis* and that sites used as hibernacula would be warmer than randomly selected sites nearby.

I also tested whether postpartum females differed in the timing of their return to hibernacula in fall compared to other females. Snakes typically feed at a low rate when gravid, especially in the late stages of gestation, either due to reduced locomotive capabilities or lack of internal space (Prestt 1971, Larsen 1986, Farr 1988, Gregory et al. 1999) and therefore are in poor body condition postpartum (Madsen and Shine 1992, Luiselli et al. 1996, Harvey and Weatherhead 2011). Thus, postpartum snakes might be forced to forage later into the summer to regain mass lost in gestation, either to increase their prospects for overwinter survival or to improve their chances to reproduce again the following year, and, as a result, return to hibernacula later than other snakes.

Methods

My study area consists of two study sites, the Kinbasket Reservoir (KR) and Cranberry Marsh (CM), near Valemount, BC, which is at the convergence of the Rocky, Cariboo, and Monashee Mountain ranges. The Kinbasket Reservoir (52°45'18" N, 119°9'9" W) is part of a hydroelectric operation that inundates the drawdown zone (DDZ) via prevention of water flow at the Mica Dam. In the summer, while energy demand is low, water is retained in the reservoir and then during the winter water is allowed to flow through the generators at the Mica Dam to produce electricity to meet the increased seasonal demand. The northernmost portion of the DDZ is a 550 ha wetland that includes over 40 ponds and is bordered along the west by a scrub habitat that transitions into a mixed forest leading upslope towards the base of Canoe Mountain. Kinbasket Reservoir is not only disrupted by cycles of inundation but is also downslope from a forest service road. My second study site, Cranberry Marsh (52°48'54" N, 119°14'49" W), is a reclaimed wetland just south of the Village of Valemount that has shallow open water, wetlands, and mixed conifer-deciduous forests. Cranberry Marsh is bordered by a railway and provincial highway, is in close proximity to residential development, and is frequented by hikers and cyclists.

In 2016 I captured nine adult female snakes at Cranberry Marsh and the Kinbasket Reservoir that I subsequently tracked using radiotelemetry (see Chapter 2 for a detailed description of surgical procedures, information on individual snakes, and tracking protocols). In late June 2016 I had only captured two snakes large enough for radiotelemetry. So when a local resident let me know there was a large snake in their garden I decided to capture the snake (Snake A) for radiotelemetry based on the possibility that the snake had come from Cranberry Marsh (approximately 3 km away). At the end of the 2016 active season, I followed snakes from their summer habitats to their hibernating sites (see Chapter 2). I deemed snakes to have entered hibernation once they remained in the same location for one week without any movement and stayed underground during the warmest part of the day. I did not excavate suspected or actual hibernacula; in fact, I disturbed overwintering sites as little as possible. I recorded relevant physical surface features including canopy cover, slope, aspect, and rock size to characterize each hibernation site. I also recorded percentage cover, cover height, distance to coarse woody debris (CWD), and distance to water at each site to help quantify the structural characteristics of used overwintering sites. I also recorded the number of individuals observed within 10 m of each hibernation site to estimate the number of snakes overwintering in each hibernaculum. In mid-December of 2016, I returned to the hibernation sites to confirm, via radiotelemetry, that the snakes had remained in their respective hibernacula and had not selected different sites after my departure in the fall.

Because thermal properties of dens are especially important to ectotherms, I used two methods to assess the thermal quality of confirmed hibernacula for comparison with nearby random sites. To choose random sites, I selected a random bearing (1-360°) and distance (20-40 m away) with a random number generator and then searched for a potential entrance/exit hole that could potentially lead to a suitable hollow for overwintering. For my first approach, I placed temperature loggers (Onset HOBO Tidbit v2) in known hibernacula and random associated sites ($n = 5$ pairs) at the end of the 2016 active season to determine whether subsurface temperatures differed between used and random sites through the winter months. I placed the data loggers within each entrance (10 cm underground), positioned so that they did not obstruct passage of snakes. Temperature readings were recorded every 0.5 hours from October 3, 2016 to June 1, 2017. To analyze each snake separately, I calculated daily average temperatures for random sites and hibernacula and then conducted paired t-tests. To compare individual snakes, I calculated the differences within each pair (used – random) and ran an analysis of variance (ANOVA). For my second approach, I took infrared photographs in December 2016 (FLIR C2 Compact Thermal Imaging System, FLIR Systems Inc.) centred on the apparent entrance of the underground hollow (or presumed hollow, for random sites) to compare surface temperatures. For the thermal imagery data, I used the temperature from the centre of the image in my comparison of surface temperature of known hibernacula and random sites. Because each random site was associated with a particular hibernation site, for each approach I used paired t-tests to compare used and random sites for each individual.

For confirmed hibernacula, I measured the linear distance between the site and the nearest summer habitat to provide an estimate of minimum migration distance. I defined summer habitats as wetland areas with amphibian prey present. I then compared this value to the tracked distance and determined whether snakes moved to or from the nearest wetland. Financial and other constraints prevented me from following radio-tagged snakes back to overwintering sites in fall 2017 to determine overwintering site fidelity. Therefore, to predict site fidelity for radio-tagged snakes whose 2016-2017 hibernacula locations were known, I graphed the distances of each snake location through the 2017 active season from their previous hibernaculum to show any suggestion of return.

Results

Via radiotelemetry, I located eight hibernacula (CM = 4, KR = 4), one of which was shared by two radio-tracked snakes (Figure 4-1A - blue circle). At Cranberry Marsh hibernacula were spread across the landscape, whereas at Kinbasket Reservoir all four hibernacula were in the same drainage, and three of the sites were within 200 m of each other (Figure 4-1B).

Hibernacula were relatively inconspicuous, most without obvious entrances or obvious basking habitat nearby (such as rocks). At some hibernacula, I found small holes (~2.5 cm diameter) beneath layers of leaf litter (up to 10 cm deep) that presumably were the entrance/exit holes of the hibernacula. Hibernating sites were in forested habitats, with one exception, the site used by two of the snakes I tracked, which was located on the edge of an artificial dike in a wetland with no canopy (Figure 4-2).

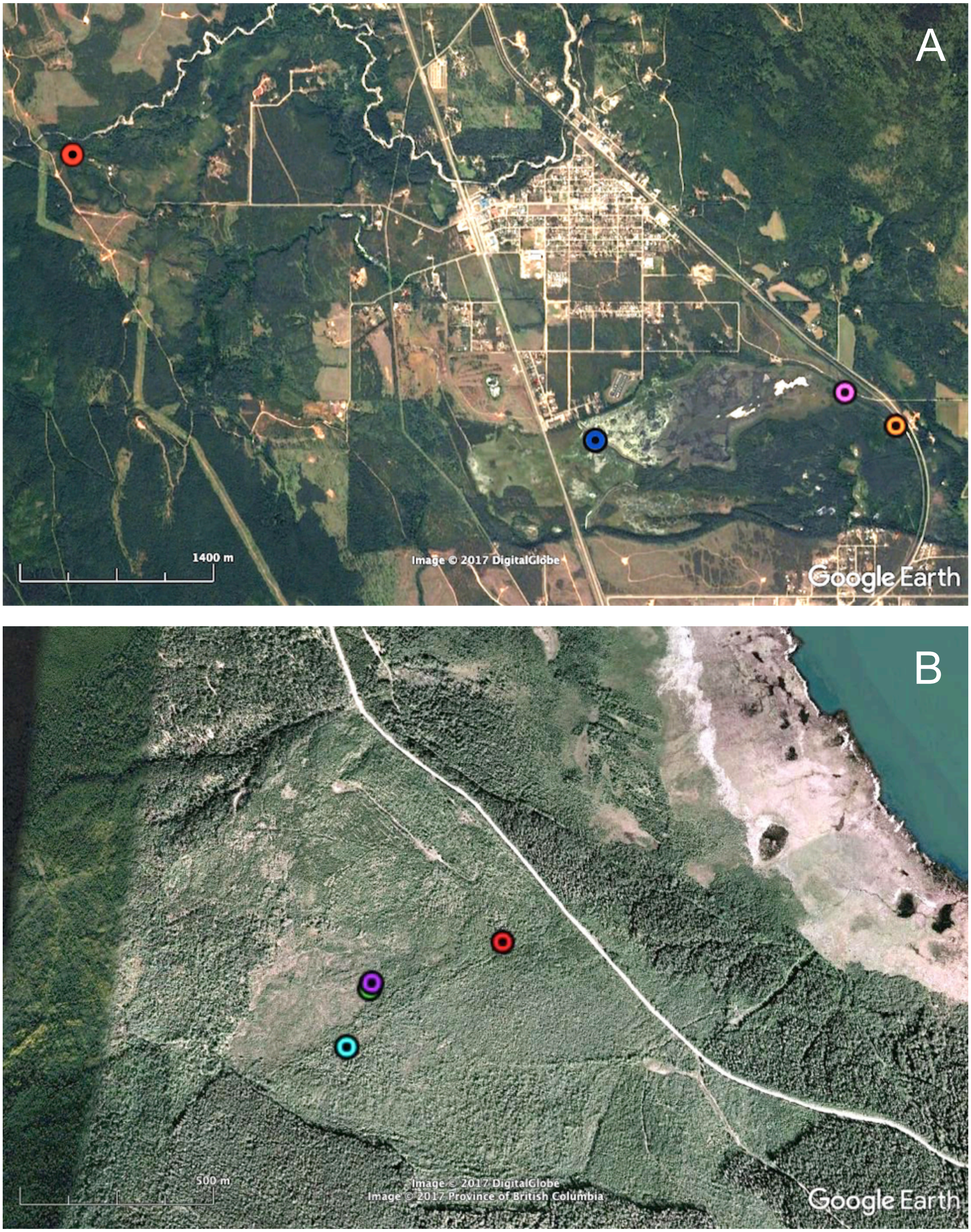

Figure 4-1. Locations of hibernacula used by adult female snakes at (**A**) Cranberry Marsh and (**B**) the Kinbasket Reservoir for the winter of 2016-2017.

Figure 4-2. Example hibernacula (marked by white squares) used by radio-tagged female snakes over the winter of 2016-2017.

The snakes that I tracked hibernated in relatively small groups, with 2-16 other snakes, or, in one case, alone (Table 4-1). I did not observe any juvenile snakes (< 400 mm SVL) at any of the eight hibernacula, but I observed juveniles upland from the DDZ at the Kinbasket Reservoir during the migration period (late August to September). These juveniles were on the forest service road that bisects the migratory path of the adult snakes that I tracked at that site. In 2015, juvenile snakes were captured late in August in the DDZ. Most snakes hibernated a considerable distance from their summer habitats (n = 9, mean = 1485 ± 937 m SD, range = 148-2657 m) and none overwintered in the DDZ of the Kinbasket Reservoir. At Cranberry Marsh, two snakes migrated past wetlands with basking habitat and anuran prey that were far closer (approximately 2010 m and 1465 m closer) to their respective hibernacula than the summer habitats that they used.

Hibernacula at the Kinbasket Reservoir were located at considerably higher elevations than those at Cranberry Marsh (t = 8.58, df = 3, P = 0.003). None of the hibernation sites had greater than 50% canopy closure (Table 4-1). Hibernacula were located on slopes less than or equal to 20%, with one exception, the hibernaculum used by Snake A. This individual was also consistently different in movements and summer habitat use (see Chapters 2 and 3). The aspect of hibernacula differed between sites, with those at the Kinbasket Reservoir facing NE (18° - 90°) and sites at Cranberry Marsh facing SW (200° - 240°), with Snake A once again being an exception (32°). Close proximity to water and coarse woody debris (CWD) were common characteristics across hibernacula. Surface temperatures of used and random sites recorded in mid-December with infrared photography were not statistically different (Figure 4-3; $t = -1.04$, $df = 7$, $P = 0.33$).

Table 4-1. Characteristics of hibernacula used by radio-tagged female snakes at Cranberry Marsh and Kinbasket Reservoir over the winter of 2016-2017. Surface temperature was recorded with a thermal camera (FLIR C2 Compact Thermal Imaging System, FLIR Systems Inc.) on December 22, 2016. The difference reported is the temperature of the used site minus that of the random. Note: two radio-tagged snakes shared a single hibernaculum.

Snake (Site)	Elevation (m)	Canopy (%)	Slope (%)	Aspect (°)	Vegetative Cover (%)	Surface Temperature Difference (°C)	Other Snakes
B & L (CM)	786	0	5	200	60	+1.0	3
V (CM)	793	50	5	240	25	-0.9	7
O (CM)	790	25	15	200	70	-0.2	16
A (CM)	792	35	45	32	10	-0.4	0
S (KR)	907	25	10	18	10	-2.1	2
R (KR)	855	40	20	70	60	-2.6	2
G (KR)	894	25	10	45	10	-1.3	7
N (KR)	891	30	15	90	15	+2.0	4

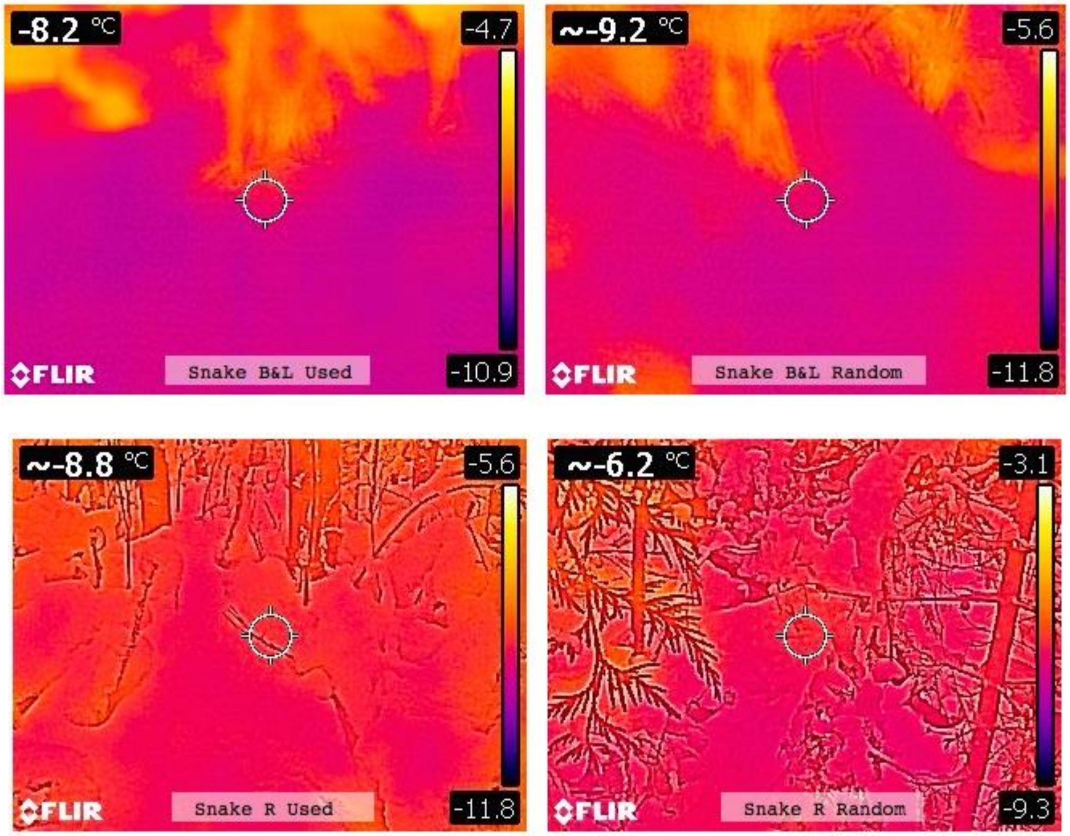

Figure 4-3. Thermal/infrared images of used hibernacula (Snakes B & L: *top left* and Snake R: *bottom left*) and random associated sites (Snakes B & L: top *right* and Snake R: *bottom right*) taken December 22, 2016 with a thermal camera (FLIR C2 Compact Thermal Imaging System, FLIR Systems Inc.).

Subsurface temperatures of hibernacula were typically higher than those at the random sites through the winter months. In June 2017 when I went to collect the data loggers, the one at the random site for Snakes B & L was missing from the hollow where I had placed it in the fall; I presume an animal grabbed the twine that I had attached to the logger and carried it away. The hibernating site used by Snake G was significantly warmer than its paired random site ($t = 9.05$, $df = 243$, $P < 2.2e-16$), as also was the case for Snake R ($t = 9.02$, $df = 243$, $P < 2.2e-16$) and Snake O ($t = 16.52$, $df = 243$, $P < 2.2e-16$; Figure 4-4). Conversely, I found no difference between the hibernating site and paired random site for Snake A ($t = -0.83$, $df = 243$, $P = 0.40$; Figure 4-4).

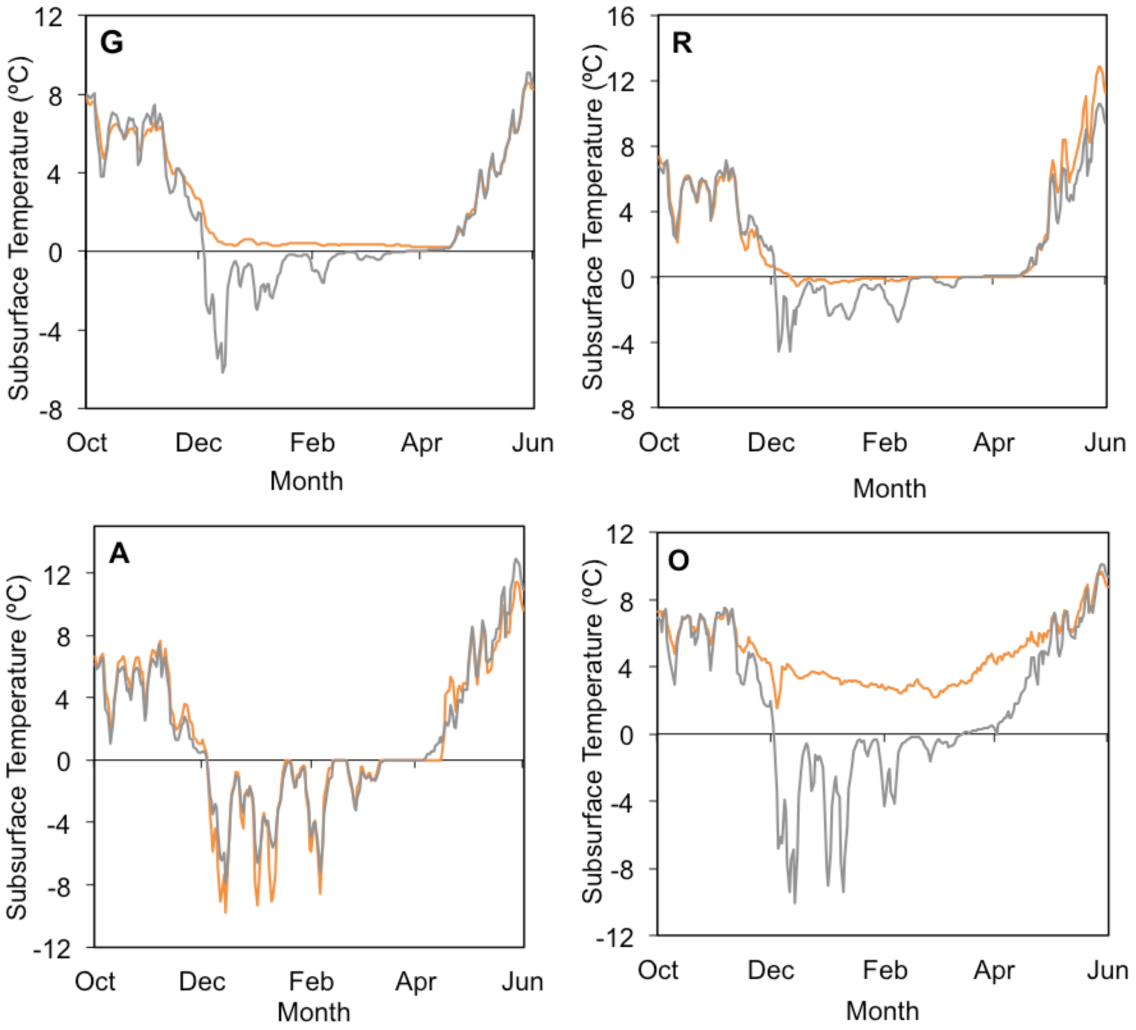

Figure 4-4. Daily average subsurface temperatures (10 cm deep) at hibernating sites (*orange*) used by adult female snakes and nearby associated random sites (*grey*). Snake G = *top left,* Snake R = *top right,* Snake A = *bottom left,* Snake O = *bottom right.*

Radio-tracked snakes arrived at their hibernacula between September 13 and 30, 2016. They entered hibernation between September 20 and October 8, 2016 (Figure 4-5). Although most snakes did not move a detectable distance during the hibernation period, when I returned to my study sites in December 2016, two of the nine snakes had moved, both at the reservoir site (9 m and 26 m, respectively). The snake that moved 9 m likely did so underground, as her hibernaculum was located immediately beside a stream that flowed below the surface for approximately 10 m from the point that I had originally designated as her hibernating site. The individual that moved 26 m was the last snake to enter hibernation. One snake at Cranberry Marsh remained underground at the hibernaculum well into the spring, without moving or ever coming to the surface (Snake O; Figure 4-5). She presumably died over the winter. I attempted recovery to confirm this presumption, but the transmitter was inaccessible, underground beneath a mature spruce tree. Alternatively, the snake may have remained in hibernation well into the spring while the transmitter battery lost power and then emerged without my knowledge when I could no longer detect the signal from her transmitter. Snakes emerged from hibernation between April 10 and May 10, 2017, for an average duration of hibernation of 207.9 ± 11.7 days SD (n = 8, range: 193 - 224). The duration of hibernation of postpartum snakes and non-reproductive female snakes was similar (t = -0.02, df = 5, P = 0.98), though the range was wider for postpartum snakes (Figure 4-6).

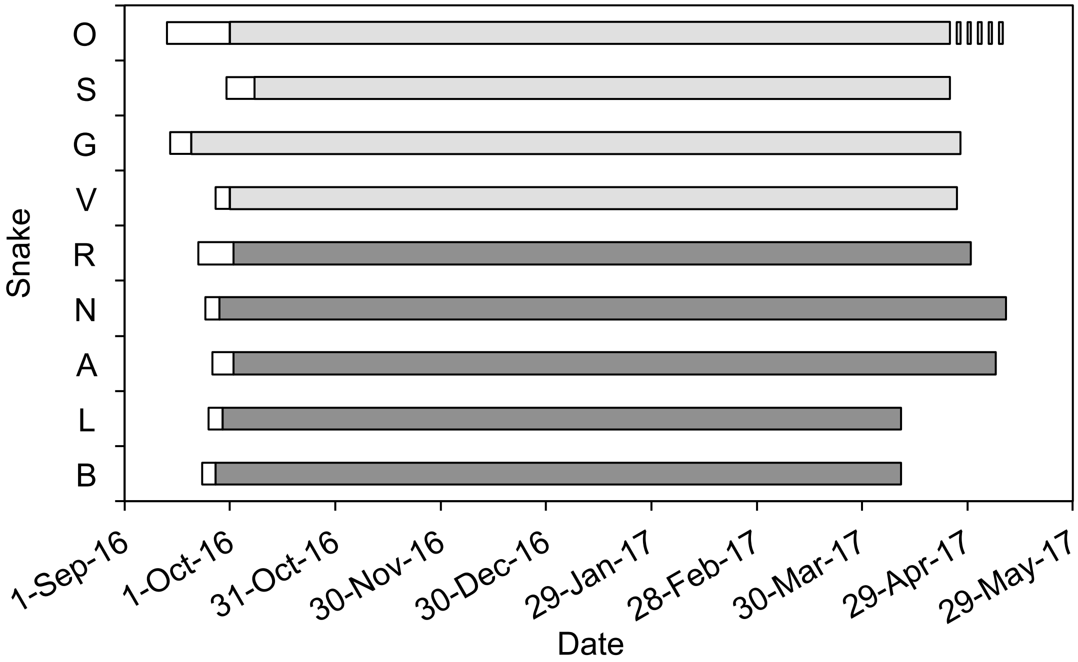

Figure 4-5. Hibernation timeline of female snakes. The *white* bar indicates when the individual arrived at its hibernaculum and how long it remained active there before entering hibernation. The length of the grey bar represents the duration of hibernation, ending at spring emergence. Postpartum snakes = *dark grey*, other snakes = *light grey*. The dashed bar represents failure to detect emergence.

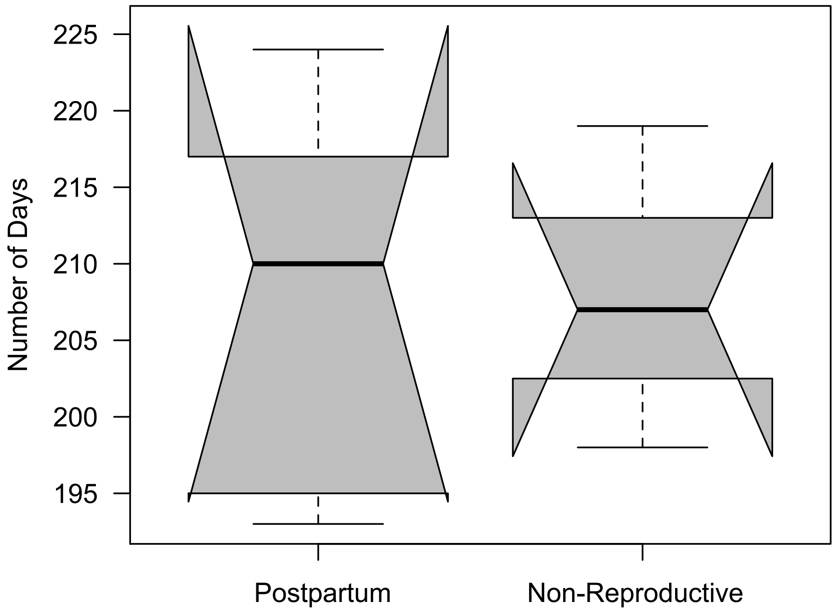

Figure 4-6. Box and whisker plots of the number of days radio-tracked postpartum and non-reproductive female snakes remained in hibernation at Cranberry Marsh and Kinbasket Reservoir over the winter of 2016-2017. Grey boxes cover the second and third quartiles and the centre lines represent the medians. Whiskers represent the first and fourth quartiles. Notches that do not overlap strongly suggest a statistical difference.

Of the three individuals that I tracked over nearly two full active seasons, two appeared to be returning to the general location of their respective previous hibernacula when they were captured to have their transmitters removed (Figure 4-7). Snake R and Snake S were 350 m and 421 m from their respective 2016 hibernating sites in the second week of September 2017 when they were captured for transmitter removal surgeries. The prominent downward spike in the red line in Figure 4-7 is from Snake R passing her hibernaculum on the way to the DDZ for a brief, 10-day period at the beginning of August before returning upslope towards the hibernaculum she used in 2016. Contrary to the first two snakes, Snake V did not appear to be returning to the hibernaculum she used in 2016. In the second week of September 2017, when she was captured for transmitter removal, she was 2354 m from her location on the same date in 2016 and 3334 m from her previously used hibernaculum (Figure 4-7), nearly the farthest that I had recorded her from her previous hibernating site.

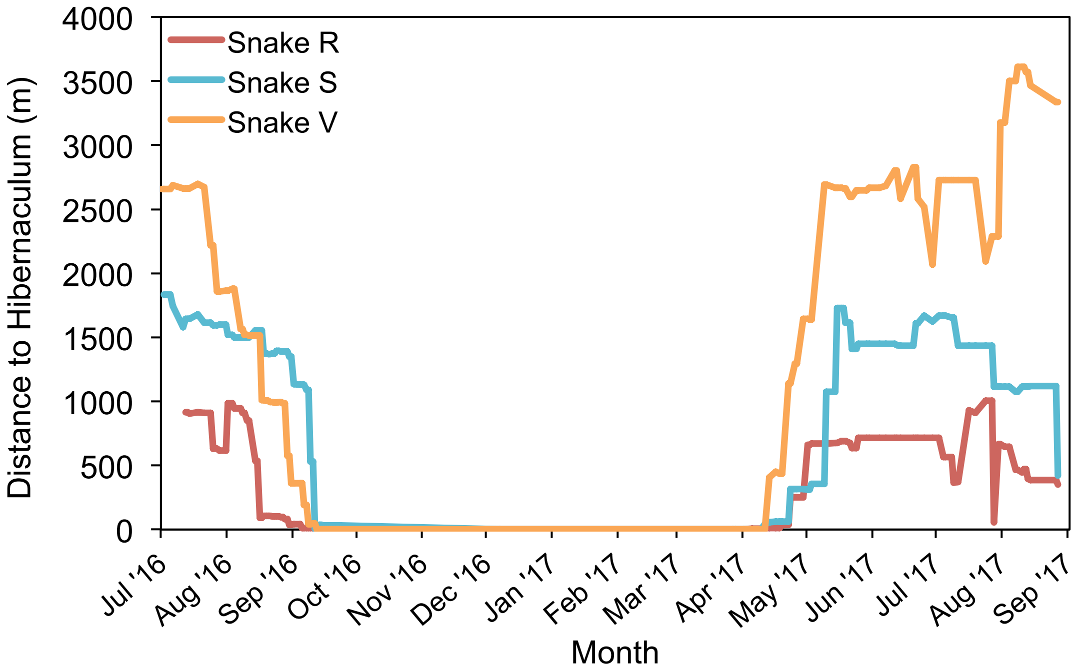

Figure 4-7. Distance from the hibernaculum, in metres, for three female snakes from July 2016 to September 2017 at the Kinbasket Reservoir (Snakes R & S, *red* and *blue*, respectively) and Cranberry Marsh (Snake V, *orange*).

Discussion

The hibernation ecology of Common Gartersnakes in my study area is clearly distinct from that of southern populations, but also is notably different from other northern populations of this species. In the southern portions of its range the Common Gartersnake not only has a longer active season, it typically can find sufficiently deep hibernacula within or near its summer habitat, obviating the need for significant migrations between summer habitat and hibernaculum (Carpenter 1952, Fitch 1965, Lawson 1994). In the extreme southern part of its range, this species is active year-round without any need to enter hibernation (Dalrymple et al. 1991). By contrast, at higher latitudes, hibernation is obligatory and suitable sites for avoiding cold may be in limited supply and not necessarily near the summer habitat, necessitating migrations between the summer habitat and hibernaculum. Although I recorded migratory behaviour in Common Gartersnakes in the Valemount area, the distances moved fall well short of those seen in some other northern populations. For example, Gregory and Stewart (1975) found that *T. sirtalis* in Manitoba moved an average of 10.7 ± 0.73 km SE (standard error, n = 23) between summer and winter habitat and reported a maximum distance of 17.7 km. A distance of over 15 km was reported for a female *T. sirtalis* in northern Alberta (Larsen 1987). Furthermore, although I found evidence of communal hibernation, I did not find examples of the very large hibernating aggregations that characterize other northern populations of this species (Gregory and Stewart 1975, Gregory 1984a, Larsen 1986).

Throughout its wide range, the Common Gartersnake is often the earliest snake species to emerge from hibernation in spring and the last to enter hibernation in fall (Carpenter 1952, Fitch 1965, Macartney et al. 1989). In the northern reaches of its range, the Common Gartersnake demonstrates a particularly impressive tolerance to cold (Joy and Crews 1987). Common Gartersnakes cannot maintain a supercooled state for very long periods (Costanzo et al. 1988), but they are capable of surviving short periods of sub-zero temperatures and may freeze up to 40% of their extracellular body fluids without suffering any permanent damage (Churchill and Storey 1992a, Hermes-Lima and Storey 1993). They can withstand these conditions due to metabolic and enzymatic adaptations (Storey 2006). These tactics are effective in situations where snakes are away from the hibernacula during brief periods of sub-zero temperatures (e.g. spring nights, late fall during or prior to migration, or unseasonably cool summer nights), but they do not provide long-term protection (e.g. in a poorly insulated hibernaculum).

In northern Alberta, the earliest date snakes were observed post-hibernation was mid-April and the return to hibernacula began as early as late July, with most snakes migrating in late August (Larsen 1986, Larsen 1987). The timing of hibernation by snakes in my study area was similar to that seen in other northern populations of *T. sirtalis* (Aleksiuk 1976). Every individual I radio-tracked entered hibernation by the second week of October and emerged in April or early May the following year, approximating seven months in hibernation. Although postpartum females foraged after parturition to regain fat stores (see Chapter 5), they left their summer foraging habitat for winter hibernacula at about the same time as snakes that had not reproduced that active season. There is, however, some evidence for delayed migrations by postpartum females in other northern populations of Common Gartersnakes as well as other snake species (Prestt 1971, Gregory and Stewart 1975, see Chapter 5). This additional time spent in summer habitats to forage after parturition may increase the risk of exposure to cold weather late in the active season.

Although neonate and juvenile snakes are more difficult to sample because of their small size and secretive behaviour (Gregory 1984a), these age groups of snakes are clearly absent from many communal hibernacula (Gregory 1977, Costanzo 1986, Larsen et al. 1993, Shine and Mason 2004; but see Gregory 1984a). The location of the overwintering sites used by neonates and juveniles is unknown in many populations (Larsen and Hare 1992). It is possible that the absence of these snakes at hibernacula is due to their selection of underground hollows with smaller entrances that are not available to adult snakes and that may be located closer to summer habitat (Lang 1971, Gregory 1977, Larsen and Gregory 1989). Lang (1971) noted that although gartersnakes were abundant in his study area in Minnesota, adults were rarely observed at the ant mound (*Formica spp.*) hibernacula used by young gartersnakes alongside adult Red-Bellied Snakes (*Storeria occipitomaculata*) and Green Snakes (*Opheodrys vernalis*). Ant mounds have also been reported as suitable hibernacula for juvenile gartersnakes in Manitoba (Criddle 1937). Juveniles potentially follow pheromone trails of other snakes later in life to locate communal overwintering habitats (Gregory 1977, Reinert and

Zappalorti 1988, Lawson 1994). Further research is required to characterize the hibernation ecology of juvenile gartersnakes in my study area and, specifically, confirm whether they utilize the Kinbasket Reservoir DDZ in the winter months. This information could help reduce the potential of drowning juvenile snakes by ensuring the inundation of the DDZ is not too early in the spring.

Despite the fact that I was not able to verify hibernating site fidelity in my study area, two of the three snakes that I tracked to the end of the 2017 field season and whose previous hibernation sites were known were moving towards their previously used hibernacula when I stopped tracking them. The question of den fidelity therefore remains an open one for further study, but, based on my limited observations, it is a viable hypothesis.

Although some northern snake populations exhibit impressive large-scale communal hibernation, with hundreds to thousands of individuals, the snakes in my study area do not. The hibernation ecology of the Common Gartersnakes I studied shows a greater resemblance to that of a close relative, the Plains Gartersnake (*Thamnophis radix;* Tuttle 2007*)*, than other populations of *T. sirtalis* at similar latitudes (Gregory and Stewart 1975, Larsen and Gregory 1988). Plains Gartersnakes in central Alberta hibernate in pairs or individually in rodent burrows (Tuttle 2007). The reason(s) for this striking difference are currently unclear, in part because the root cause(s) of large-scale communal hibernation are unknown. Northern populations of *T. sirtalis* hibernate communally more frequently than southern populations (Fitch 1965), so it is reasonable to expect that the duration and severity of low temperatures are the principal drivers. As the climate changes towards cooler means, the frost line is able to permeate deeper underground and therefore only very deep hollows are suitable for overwintering. Hibernating site fidelity and communal hibernation are likely explained by a scarcity of suitable hibernating sites, which presumably requires long-distance migration from summer habitats to overwintering habitats (Gregory 1984a, Larsen 1989). An alternative, or perhaps additional or exaptive, explanation for communal hibernation is that it is part of a breeding strategy to increase mating success in areas with restricted active seasons, permitting more time for foraging rather than searching for conspecifics with which to breed (Gregory 1977). The reasons for this divergence from the norm may be due to an abundance of suitable hibernacula in the Valemount area or possibly a spatial limitation due to the size of the underground hollows created in this landscape apparently lacking features of karst topography (e.g. sinkholes). Alternatively, there is potential for research and publication bias, since large-scale communal hibernation is a fascinating spectacle of snake ecology that readily garners attention. Northern snake populations that do not demonstrate large-scale communal hibernation may have lower population densities or are simply left out of the publication spotlight or perhaps not even studied due to lack of awareness (i.e. large aggregations of snakes are more conspicuous than individual snakes or small aggregations).

The physical characteristics of the hibernacula I located were distinct from those used by other northern populations that are typically closely associated with karst topography or other rock formations. The close proximity of hibernacula to moving bodies of water and moderately degraded coarse woody debris (CWD) indicates that these features are likely the source of suitable underground hollows. As water flows past, and carries away soil particles, it leaves a small hollow in which snakes may retreat overwinter, and likely also warms the surrounding substrate. Likewise, decomposing CWD may provide access to underground tunnel networks, originally resulting from tree root systems or buried CWD that have since degraded. Moisture levels are important considerations in the selection of hibernacula because not only freezing temperatures, but also desiccation and drowning, are serious threats to snakes during hibernation, with up to 50% mortality rates having been recorded (Gregory 1977, Costanzo 1989, Shine and Mason 2004). Therefore, selecting hibernacula underground near bodies of water (streams, pools) and other sources of moisture (CWD) should be beneficial to survival. Common Gartersnakes have been shown to hibernate fully submerged underwater (Costanzo 1986, 1989), but because of the inaccessibility of the underground hollows used by snakes in my study I could not determine whether snakes hibernated in air or water.

Subsurface temperatures of randomly chosen sites were typically lower (in some cases, much lower) than in used hibernacula. Temperatures at hibernacula have been shown to influence the selection of overwintering sites by snakes (Gienger and Beck 2011). However, the surface temperatures I collected with thermal images do not suggest site selection is based on higher surface temperatures. The hibernacula at the Kinbasket Reservoir site were all located along the same drainage topography. There is currently some ongoing research regarding geothermal activity in the Valemount area; this information could be used to assess the value of this resource to snake hibernation. Anecdotal reports from local residents of observations of gartersnakes on the frozen surface of Cranberry Marsh in the midst of winter raise questions regarding the impact of this geothermal activity on gartersnakes. Shine and Mason (2004) suggest that mortality from winterkill is considerably higher than mortality that occurs during the active season from predation and roadkills. If so, conservation measures taken directly at the hibernacula should have a much greater impact on increasing survival than those taken to protect snakes during their seasonal migrations. My study highlights the importance of radiotelemetry in studies of small, cryptic animals, especially when the location of critical habitats like hibernacula is a primary goal. The hibernating sites I located with radiotelemetry were highly inconspicuous and would not have been detectable otherwise.

Chapter 5 - Gartersnake Miscellanea and the Value of Natural History

Introduction

Natural-history studies focus on the ethology and ecology of animals in their natural setting (Greene 1994). Such studies not only contribute to the conservation of species but also reveal natural patterns of variation that may underlie evolutionary potential, constrain theory to realistic parameter values, and provide the context for interpretation of experimental results (Arnold 2003).

In studies that require significant time and effort to acquire samples, it is important to collect as much useful data as possible, not only for the study at hand, but also to provide background and preliminary hypotheses for future studies (Gregory 2012). Although the initial focus of my study of Common Gartersnakes in the Valemount area was on movements, habitat, and hibernacula, through the observation and capture of snakes I had the opportunity to collect data on diet, growth, and reproduction. These data may be relevant to conservation and, via comparison with other populations, contribute to studies of geographic variation.

Simple observations of snakes can help define daily and seasonal patterns of activity (Dalrymple et al. 1991, Roth and Greene 2006, Croak et al. 2013), but multiple additional data can be obtained when a snake is captured and in the hand (Gregory 2012). For example, measurement of body size and other morphometric variables can reveal sexual size dimorphism that may suggest hypotheses about sexual selection (King 1989, Friesen et al. 2017). Body size has multiple effects on an animal's ecology (Barbault 1988), including demographic traits such as survivorship and, in females, reproductive output (Madsen and Shine 1992, Luiselli et al. 1996). Thus, measurements of body size collectively provide important data on population structure; abdominal palpation of pregnant female snakes yields estimates of litter size (Farr and Gregory 1991). Prey eaten by snakes often can be sampled fairly readily and build up a picture of diet that has obvious links to habitat use (Carpenter 1952, Kephart 1982). If snakes are individually marked, then recaptures can be used for supplementary movement data and analyses of growth. Recaptures of marked animals also form the basis for estimates of population size and survivorship, at least if sampling intensity is sufficiently high (Larsen and Gregory 1989, Shine and Mason 2004).

My study area surrounds the village of Valemount (52.8312° N, 119.2643° W) in British Columbia (BC) and consists of two disturbed study sites: the Kinbasket Reservoir, and Cranberry Marsh. Both sites are affected by human development and include forested areas that have been harvested. The Kinbasket Reservoir (KR) is a hydroelectric reservoir that fluctuates unnaturally, inundating the adjacent wetlands in the summer. The area over which the reservoir water fluctuates is called the drawdown zone (DDZ). Cranberry Marsh (CM) is a popular recreation site that is bordered by a provincial highway, a railroad, and both residential and industrial developments. Both study sites support a variety of wildlife such as waterfowl, mammals, amphibians, and snakes, specifically the Common Gartersnake.

The Common Gartersnake (*Thamnophis sirtalis*) is a nonvenomous colubrid snake that is the most northerly distributed reptile in North America (Rossman et al. 1996). Common Gartersnakes consume a wide range of prey types throughout their broad geographic range, including amphibians, earthworms, leeches, small mammals, and fish (Fitch 1965, Kephart and Arnold 1982, Gregory 1984b, Farr 1988, Halliday 2016). They are viviparous and typically exhibit female-biased sexual dimorphism (Larsen 1987, Rossman et al. 1996, Friesen et al. 2017), although the degree of dimorphism varies among populations (Krause et al. 2003, Friesen et al. 2017).

Because of its wide latitudinal range, *T. sirtalis* offers the opportunity to test life-history hypotheses based on the presumed influence of short high-latitude active seasons on demographic traits such as litter size, litter frequency, and growth rate. Because a shorter active season means there is less time available to forage, determining prey composition and the frequency of feeding may help to reveal how this widely-distributed snake is successful at high latitudes.

I collected natural-history data on Common Gartersnakes in east-central BC both for their site-specific value and for comparison with other populations. I predicted snakes would be detected most frequently in July based on the high daily average temperatures that allow for increased activity for these ectotherms (Jones 1986). Futhermore, given the importance of temperature in the development of embryos, gravid snakes should bask during warm periods (Charland and Gregory 1995). I also predicted that snakes would follow a bimodal pattern of daily activity in July, with peaks in mid-morning and late-afternoon (Reichenbach and Dalrymple 1986). I anticipated that the primary prey of Common Gartersnakes in my study area would be anuran amphibians, but would also include small mammals and earthworms. Because gartersnakes are opportunistic predators, I expected their diet would follow the abundance of prey species (Kephart and Arnold 1982). I expected to find significant sexual dimorphism in SVL (female-biased) and relative tail length (male-biased). I predicted that mean litter sizes would be similar to that of other northern populations and that litter size would be positively correlated with the body size of the mother.

Methods

I conducted visual encounter surveys (VESs) in 2016 and 2017 at the Kinbasket Reservoir and Cranberry Marsh (see Chapter 2 for VES details). I also radio-tracked adult female snakes at these sites from 2016-2017 (see Chapter 2 for details on surgical procedures, number of snakes, and tracking protocols). I was provided with supplementary VES data for snakes, toads, and frogs from 2015 at the Kinbasket Reservoir, part of a long-term study of the DDZ conducted by LGL Limited Environmental Consultants on behalf of BC Hydro.

I captured snakes by hand, following Animal Care Committee Standard Operating Procedure #HP2002 (Capture, Handling, and Measurement of Non-Venomous Snakes in the Field). To prevent pseudoreplication by counting the same individuals multiple times, I marked each snake (> 40 g) for future recognition by clipping a unique combination of subcaudal scutes (Blanchard and Finster 1933). I recorded the time and UTM coordinates (NAD 83) after each snake observation and instances when two or more snakes were in close proximity to one another (0-10 m). I palpated the stomach of each snake I captured to check if it had recently eaten, and if it had, I induced regurgitation by gently massaging the snake’s abdomen (Carpenter 1952). I quickly identified the prey and then re-fed the snake its prey by carefully massaging the prey back into the snake's stomach. Some snakes readily regurgitated stomach contents when captured, thereby simplifying the procedure. I also surveyed anuran amphibians (adults, metamorphs, and tadpoles), which, based on published literature (Kephart and Arnold 1982, Gregory 1984b, Farr 1988, Halliday 2016), I expected to be the main prey of snakes.

Given the direct effects of weather on the detectability of many terrestrial ectotherms (Jones 1986), I recorded weather data at 1 m above the ground, in the shade, including air temperature, relative humidity, cloud cover, precipitation, wind speed, and wind direction (Mitchell 2012) for each survey with a Kestrel 4250 handheld weather station. To compare daily average temperatures between years I used data from the weather station closest to my study sites (approximately 6.5 km and 16 km north of CM and KR, respectively). The Wildfire Management Branch within the BC Ministry of Forests, Lands, and Natural Resource Operations (FLNRO) operates this station (ID#

194). I accessed these data via the BC Station Data tool on the Pacific Climate Impacts Consortium website (pacificclimate.org).

I collected standard morphometric data from each captured snake, including mass (to nearest 0.25 g, with Pesola spring scales), snout-vent length, tail length, and head width (each to nearest mm). For snakes that I recaptured after two weeks or longer, I re-measured SVL and mass. I re-captured radio-tagged snakes approximately once per active season to collect morphometric data to estimate growth. I calculated the intervals between captures and checked for differences in interval length between the opportunistic captures and radiotelemetry check-ups (see Chapter 2). Because the data were primarily opportunistic, intervals between captures varied widely and measurements were taken at different times of the active season under different conditions (postprandial, pre-parturition, etc.).

I used changes in SVL between the first and last capture of each snake to estimate growth constants and asymptotic sizes for males and females separately, by fitting the data for each sex to the von Bertalanffy growth model, which is commonly used to describe growth in reptiles (Andrews 1982, Tuttle and Gregory 2012). I used Fabens' (1965) version of the von Bertalanffy model to estimate these parameters via non-linear regression by regressing the size of each snake at the end of the inter-capture interval ($SVL_{t+\Delta t}$) against the size at initial capture (SVL_t) and length of interval (Δt) expressed as proportion of a snake-year, viz.

$$\mathbf{SVL_{t+\Delta t} = SVL_{\infty} - (SVL_{\infty} - SVL_{t}) * e^{(-k*\Delta t)}}$$

where SVL_{∞} (asymptotic length) and k (growth constant = rate of growth from current size to asymptotic size). I calculated 95% confidence limits for each parameter estimate. Finally, I used the Fabens' equation recursively to calculate annual size-specific growth increments, starting from estimated size at birth and then used these values to construct the growth curve for each sex.

I determined sex by probing the base of the tail of each snake for presence of hemipenes (Fitch 1960, Reed and Tucker 2012) with a lubricated ball-tipped probe that I sterilized between uses to minimize the potential for pathogen transfer among snakes (Reed and Tucker 2012). I assessed whether females were gravid (pregnant) or nongravid (not pregnant) by gently massaging the abdomen to detect oviducal eggs (Farr and Gregory 1991, Gregory et al. 1992). If I detected eggs, I recorded the number as an estimate of litter size. For a few snakes I confirmed as gravid, it was unclear how many oviducal eggs were present and I therefore removed these individuals from the litter size analysis. I did not assess male reproductive condition, as it is typically determined via dissection (e.g. Gregory 1977). I avoided disrupting all reproductive events (courting, copulation, and parturition) to avoid influencing behaviour in ways that could potentially reduce productivity.

Results

In 2016, I surveyed from May to September and in 2017 from April to August. In both years I detected the most snakes in July (2016 = 27 and 2017 = 36; Figure 5-1). Nearly all captures in April 2017 were at hibernacula, shortly after emergence (see Chapter 4). The spring and early fall of 2017 were cooler than 2016 but the late summer of 2017 was warmer (Figure 5-2). In 2016, I recorded the most snake observations (captures and visuals combined) between 10:00AM and 11:00AM (Figure 5-3). In 2017, a bimodal pattern emerged in my snake observations, with peaks from 10:00AM to 11:00AM and from 2:00PM to 3:00PM, with near-equal number of observations (Figure 5-4).

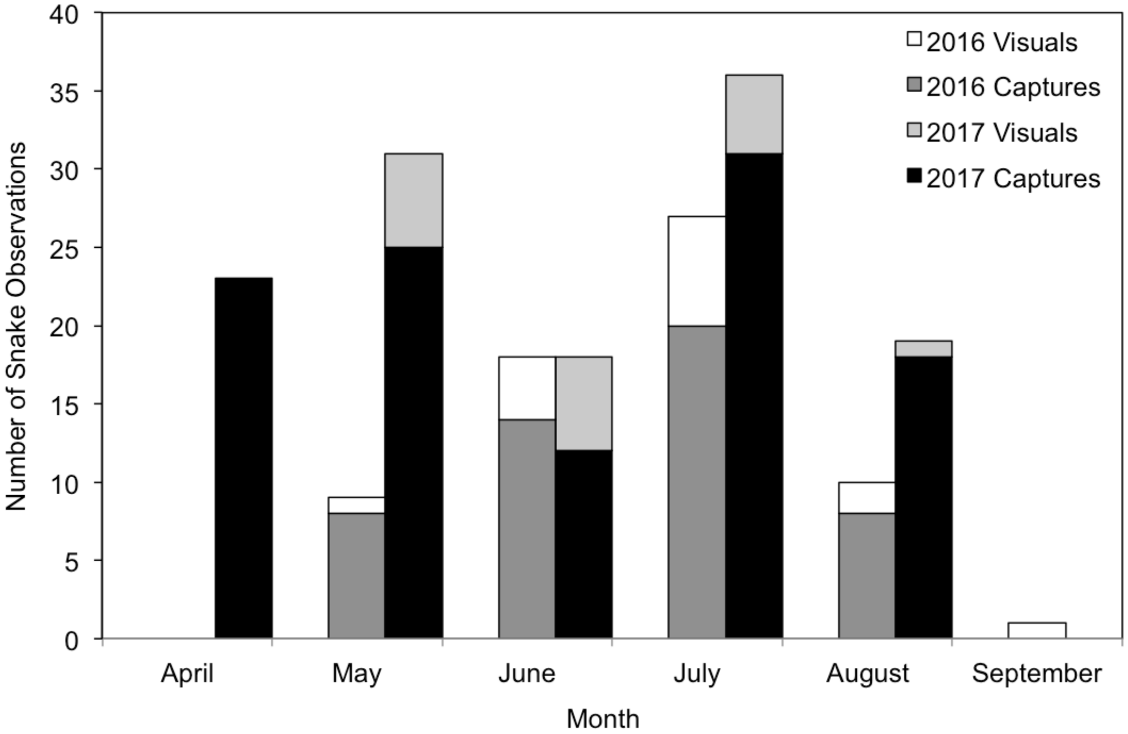

Figure 5-1. Distribution of opportunistic observations of snakes by month from 2016-2017. Visual observations (2016 = *white*, 2017 = *light grey*), captures (2016 = *medium grey*, 2017 = *black*). Surveys were not conducted in April 2016 or September 2017.

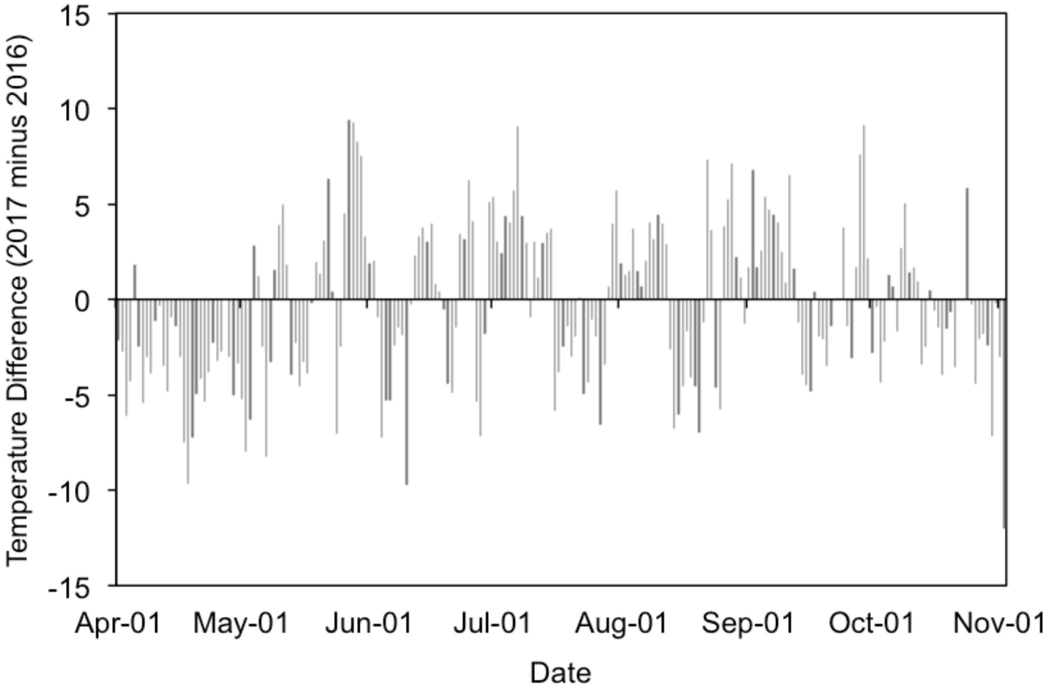

Figure 5-2. Differences between daily average temperatures (°C) in 2017 versus 2016 (2017 minus 2016). Weather station: FLNRO-WMB (station ID 194) from the Pacific Climate Impacts Consortium website. Grey bars in the positive portion along the y-axis indicate that 2017 was warmer during that time whereas grey bars in the negative portion of the y-axis indicate that 2017 was cooler than 2016 for those days.

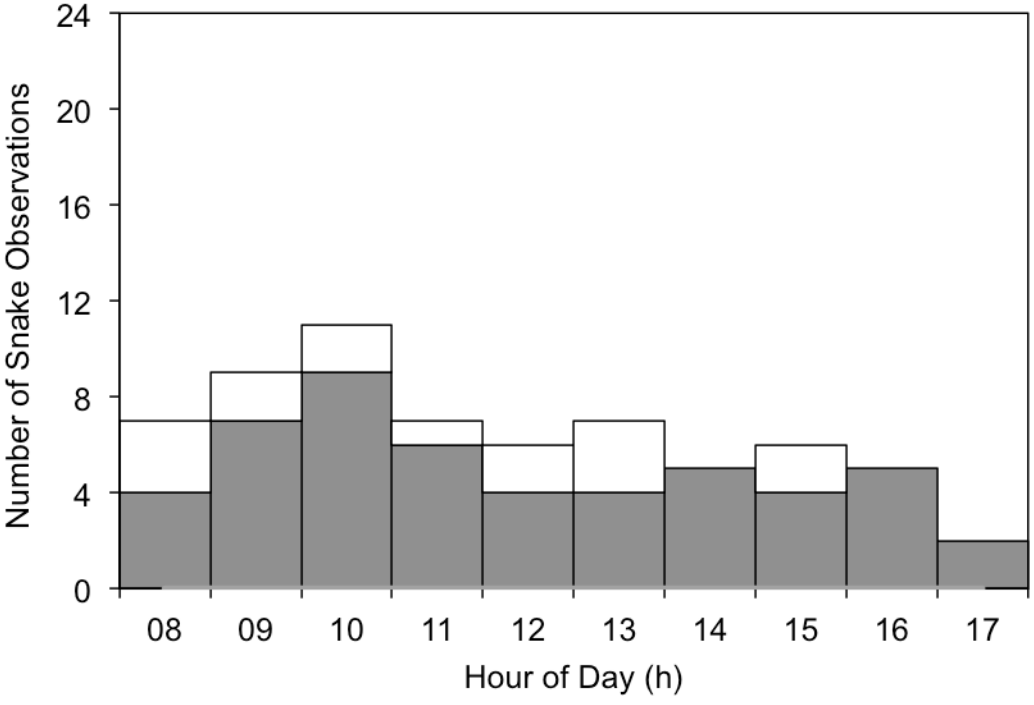

Figure 5-3. Distribution of opportunistic observations of snakes in 2016 by hour of day. Visuals = 18 (*white*), captures = 109 (*grey*).

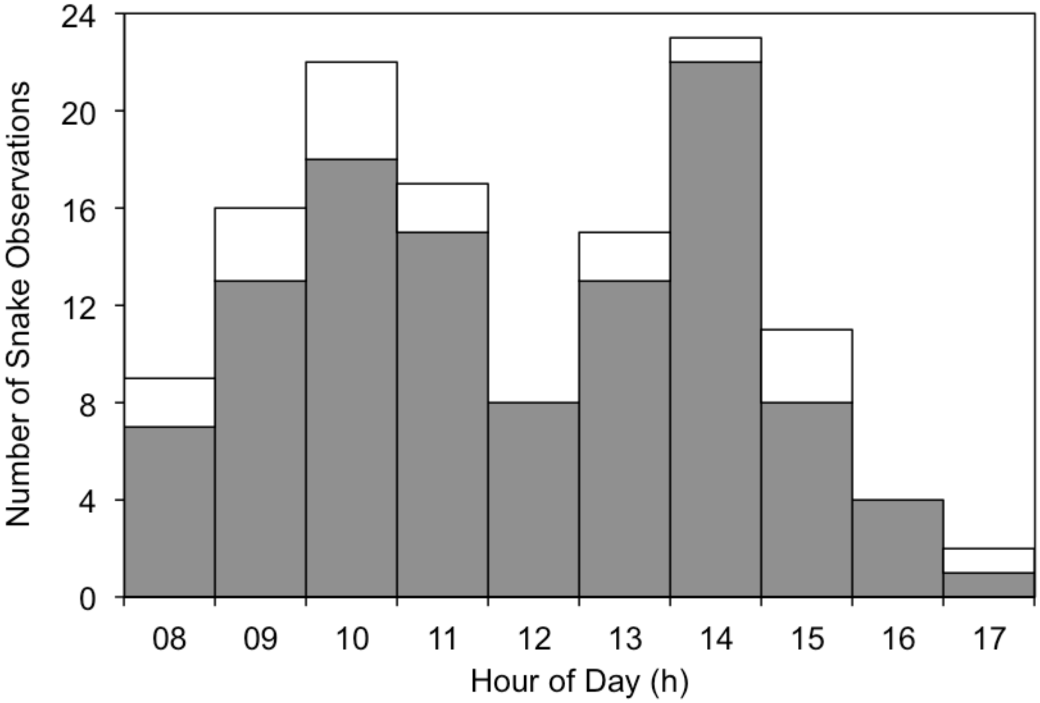

Figure 5-4. Distribution of opportunistic observations of snakes in 2017 by hour of day. Visuals = 15 (*white*), captures = 50 (*grey*).

Most of the time, I captured snakes individually but occasionally I observed two or more snakes in close proximity to each other (0-10 m). I observed male and female snakes together most frequently in early spring and late summer (Figure 5-5). I witnessed males right beside or on top of radio-tagged females during these periods, without obvious signs of courtship. In July, females spent the most time with other females (both gravid and nongravid). Juveniles were rarely observed together, nor were juveniles and adults (Figure 5-5).

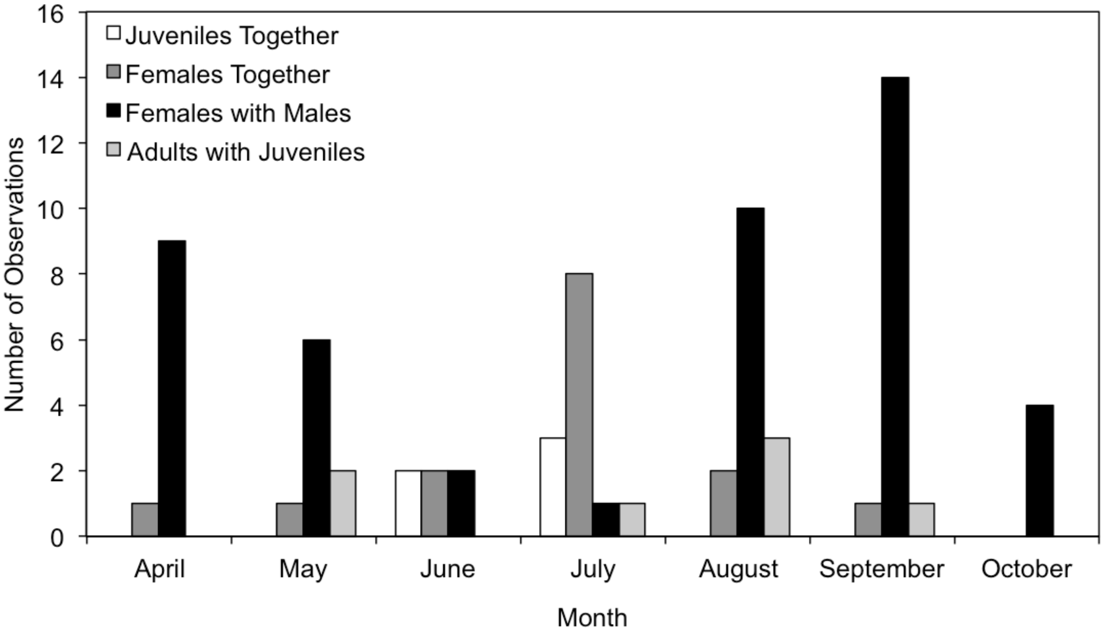

Figure 5-5. Number of observations of snakes in close proximity with other conspecifics (0-10 m) from 2015-2017. *White* bars = juveniles with juveniles, *dark grey* bars = females with females, *black* bars = females with males, and *light grey* bars = adults with juveniles.

During radio-tracking, I made four observations of radio-equipped snakes feeding on Western Toads (*Anaxyrus boreas*), two head-first and two hind legs-first. I also noted five instances when radio-equipped snakes, based on visible abdominal bulges, had obviously eaten prey recently; however, for all but one of these I did not induce regurgitation of prey. The one radio-tracked individual in which I did induce regurgitation was the first observation of the sort and I subsequently deemed the procedure an unnecessary additional stress on the radio-tagged animals. Adult Western Toads were the only prey item I detected in the stomachs of adult Common Gartersnakes. At the Kinbasket Reservoir, I captured juvenile snakes that had consumed metamorphic toads and leeches.

Of the 196 snake captures between 2015 and 2017, 47 had stomach contents (23%, adults and juveniles combined). The number of snakes with food peaked in July for juvenile snakes (Figure 5-6), coincident with the peak of metamorphic toad observations. Most adult snakes with stomach contents were captured in August, which did not align with when I observed the highest number of adult Western Toads (Figure 5-6 and Figure 5-7). I detected adult toads in much greater numbers in May, during their breeding season, than the rest of the active season. None of the snakes captured in April (n = 23) had stomach contents, although the only snake captured in September (n = 1) did have stomach contents (not shown in figures). The greatest percentage of snakes I captured with stomach contents was in August (48% of all captures in that month; Figure 5-8). I never detected more than one prey item in any adult snake. However, juvenile snakes contained up to five, albeit much smaller, prey items (metamorphosing toads) in their gut.

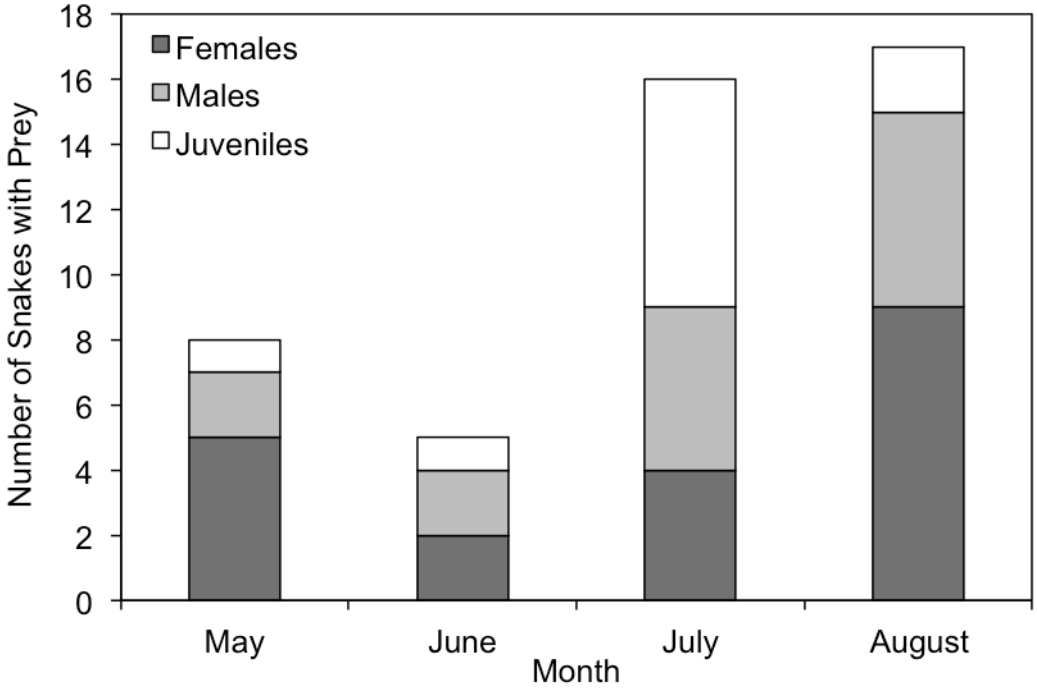

Figure 5-6. Number of snakes found with prey in their gastrointestinal tract 2015-2017 in my study area (n = 47, 28% of all captures). Females = *dark grey*, males = *light grey*, juveniles = *white*.

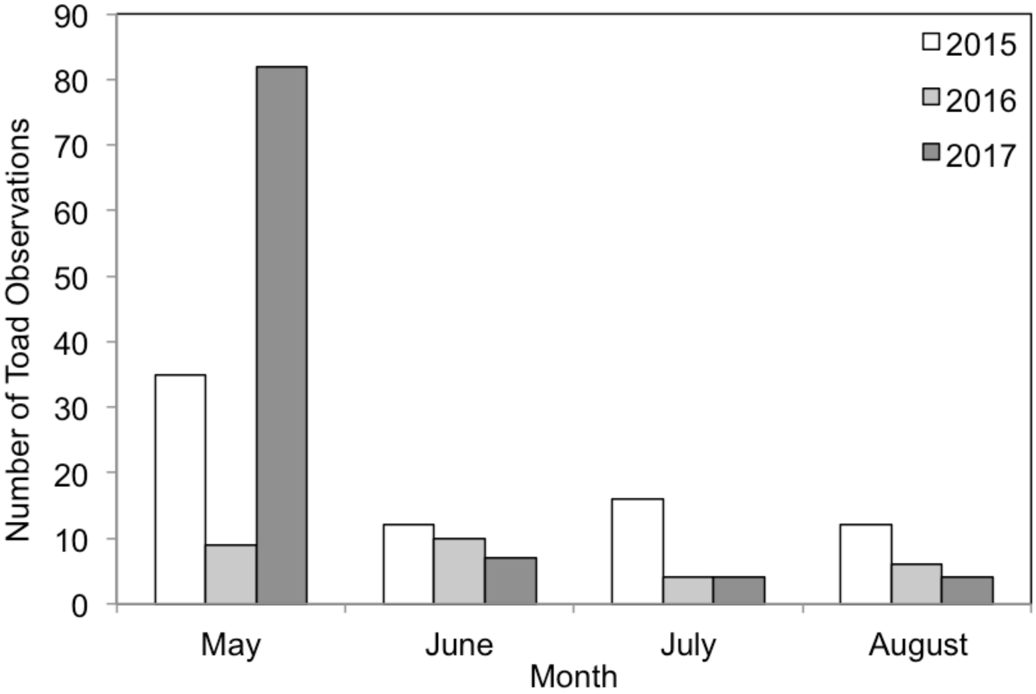

Figure 5-7. Observations of Western Toads (*Anaxyrus boreas*) by month in my study area from 2015-2017 (2015 = *white*, 2016 = *light grey*, 2017 = *dark grey*, n = 201 total).

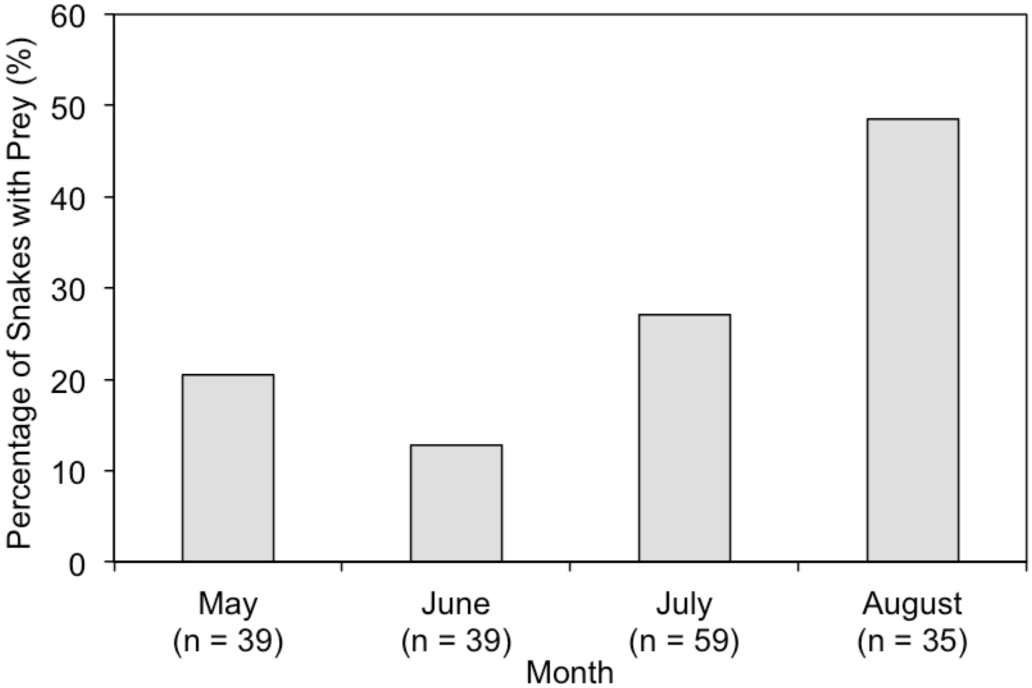

Figure 5-8. Percentage of snakes (adults and juveniles combined) captured with detectable stomach contents each month (2015-2017 combined).

The highest number of Western Toad observations occurred in 2015, likely a product of the increased time spent surveying around ponds in the Kinbasket Reservoir (weekly instead of biweekly; Table 5-1). The high number of visual observations of adult Western Toads in 2017 can be attributed to a single mating event during which I witnessed over 30 mating pairs in one pond, all within 10-15m². Western Toad observations (including visuals) decreased from 2015 to 2016, then peaked in 2017, whereas the total number of Columbia Spotted Frog observations peaked in 2015, decreased drastically in 2016, and increased slightly in 2017 (Table 5-1). Metamorphosing toads (developmental stages 42-44; Gosner 1960) were observed in greatest numbers in early July in 2016 and mid to late July in 2017.

Table 5-1. Observations of adult and juvenile amphibians from 2015 to 2017 in my study area.

Species	Type of Observation	Age Class	2015	2016	2017
Western Toad *(Anaxyrus boreas)*	Capture	Adult	51	20	20
		Juvenile	7	34	1
	Visual	Adult	20	1	61
		Juvenile	2	9	0
	Dead	Adult	2	9	17
		Juvenile	0	2	0
Total			**82**	**75**	**99**
Columbia Spotted Frog *(Rana luteiventris)*	Capture	Adult	75	33	48
		Juvenile	63	16	29
	Visual	Adult	61	56	55
		Juvenile	44	4	25
	Dead	Adult	3	1	3
		Juvenile	0	3	0
Total			**246**	**113**	**160**

I measured 166 snakes (56 female, 55 male, and 55 of unknown sex) from 2015-2017. Of the 55 unknowns, 49 were juveniles, and 6 were neonates (Figure 5-9). The largest snake I captured was a gravid female that was 947 mm SVL and 512 g in mass. The largest male was 646 mm SVL and 86 g. The smallest snake captured over the three years was 159 mm SVL and 2.5 g (Table 5-2). Very few neonates, or young-of-year, were captured (n = 6) and all but the smallest one were between 190 mm and 198 mm

SVL. The smallest gravid female I captured was 573 mm SVL (average = 743 ± 87 mm SD).

Table 5-2. Measurements of snakes captured from 2015-2017. Means and standard deviations are given above the ranges. SVL = snout-vent length.

Size/Sex	n	SVL (mm)	Tail (mm)	Mass (g)	Head Width (mm)
Neonate	6	188.8 ± 14.9 (159 - 198)	60.7 ± 7.0 (52 - 70)	5.8 ± 1.9 (2.5 - 7.8)	5.156 (5.156 - 5.156)
Juvenile	49	278.3 ± 55.7 (203 - 392)	90.8 ± 23.3 (60 - 180)	11.9 ± 5.8 (3.8 - 24.2)	6.170 ± 0.793 (5.080 - 7.544)
Adult Male	55	522.7 ± 65.3 (405 - 646)	174.5 ± 28.9 (88 - 260)	55.6 ± 20.2 (25 - 115)	9.726 ± 1.202 (7.544 - 12.07)
Adult Female (Nongravid)	36	640.9 ± 112.5 (440 - 843)	187.2 ± 36.3 (93 - 240)	151.6 ± 99.0 (28 - 378)	12.57 ± 2.78 (8.33 - 18.26)
Adult Female (Gravid)	20	743.3 ± 87.2 (573 - 947)	205.6 ± 26.3 (143 - 248)	250.5 ± 91.8 (108 - 512)	15.805 ± 1.450 (13.487 - 19.050)

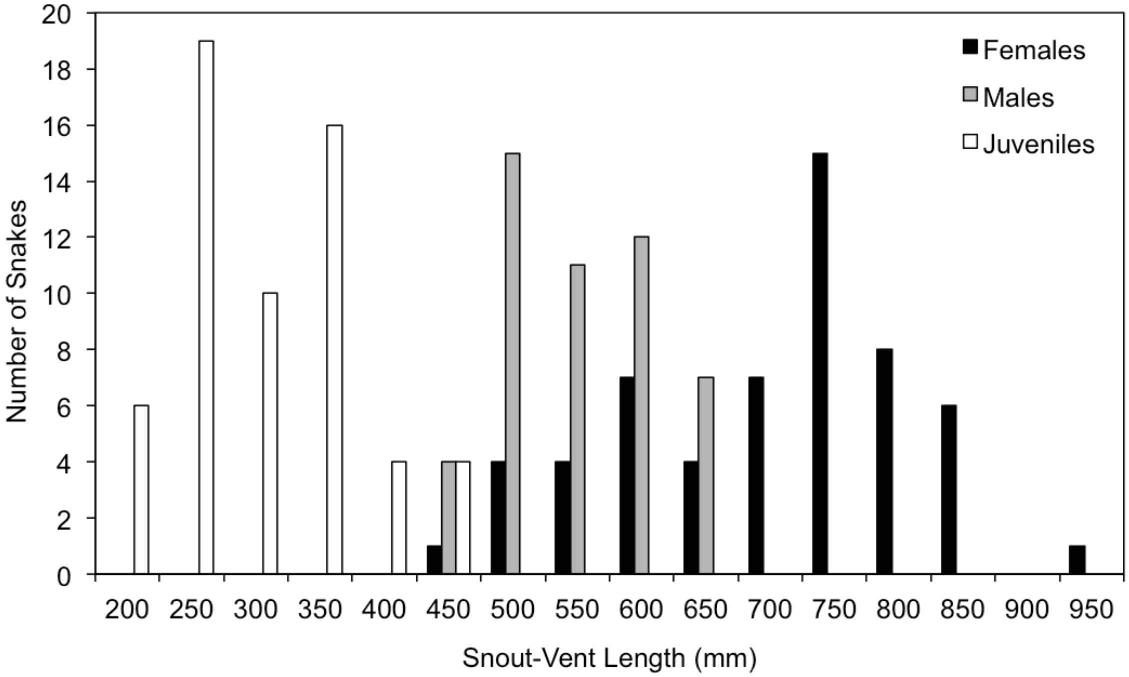

Figure 5-9. Size frequency distribution of female, male, and juvenile snakes from 2015-2017. Upper limits of bins shown along x-axis. Females = *black*, males = *grey*, juveniles = *white*.

Overall, females were larger than males in mass, length, and head width (Figure 5-10). Because the mass of a female snake varies depending on reproductive status, I compared the mass of gravid females, nongravid females, males, and juveniles (Figure

5-11). The log(mass)-log(length) (y vs. x) relationship for all the snakes I measured (n = 165, one missing mass measurement) is best described by the equation **y = 2.81x - 5.84**.

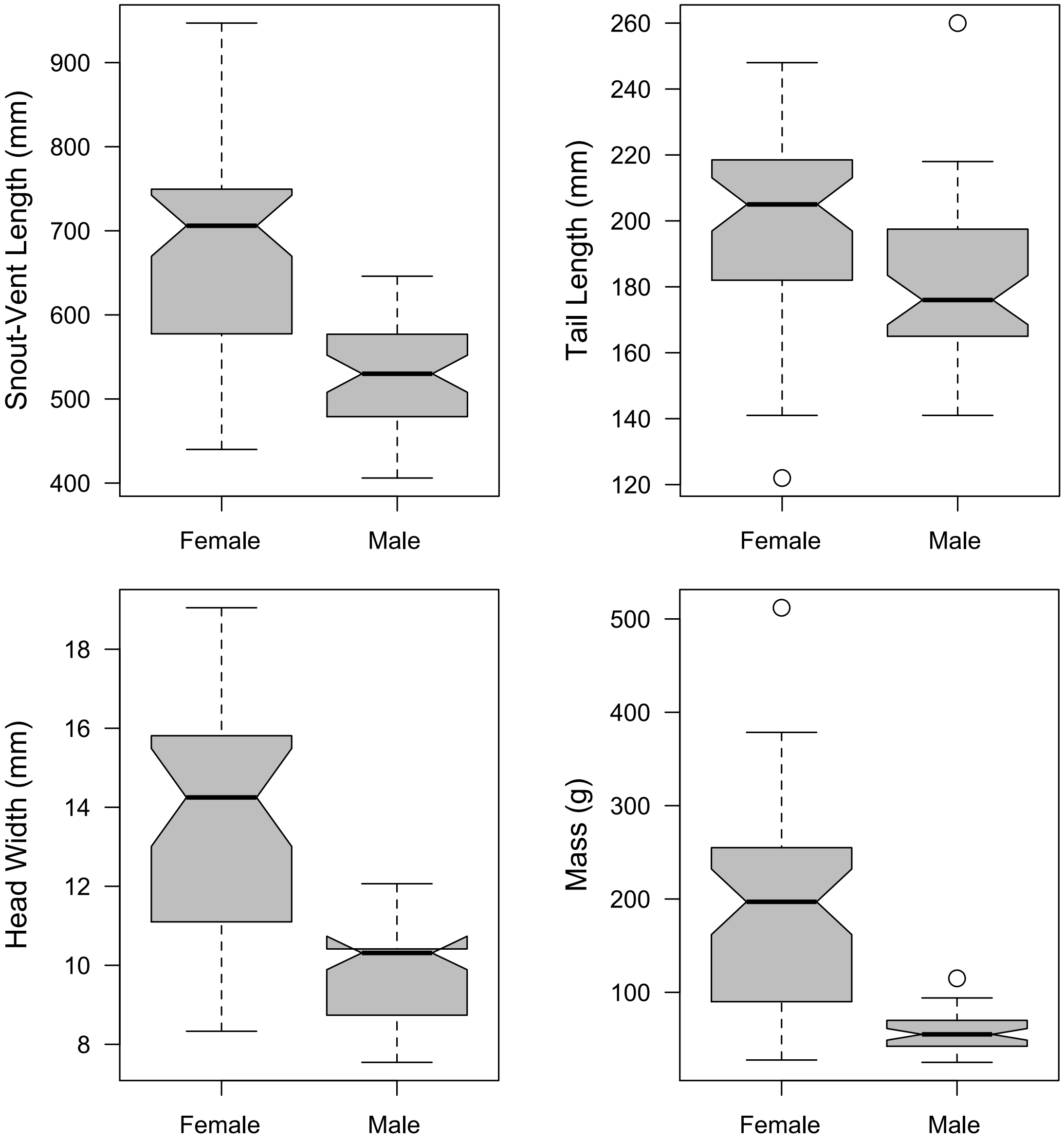

Figure 5-10. Box and whisker plots of snout-vent length (mm), tail length (mm), head width (mm), and mass (g) of female and male snakes. The grey box covers the second and third quartiles and the centre lines represent the medians. Whiskers represent the first and fourth quartiles. Notches that do not overlap strongly suggest a statistical difference.

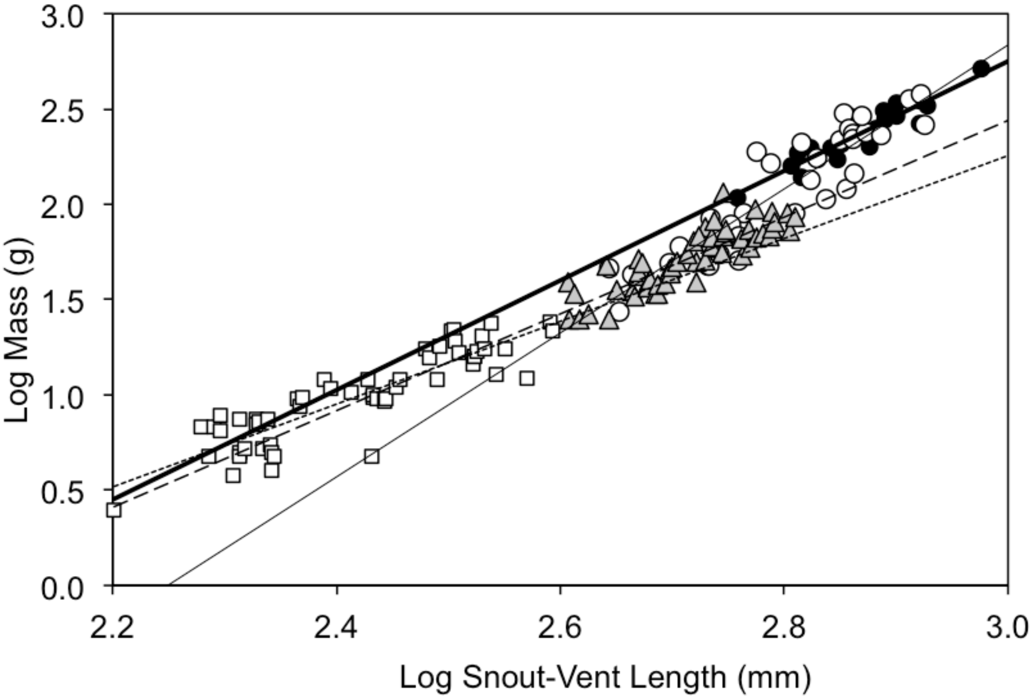

Figure 5-11. Log mass (g) as a function of log snout-vent length (mm) of snakes captured from 2015-2017. Gravid females = *black* circles (thick solid line, $y = 2.88x - 5.88$, $R^2 = 0.87$, $P < 0.0001$), nongravid females = *white* circles (thin solid line, $y = 3.78x - 8.50$, $R^2 = 0.84$, $P < 0.0001$), males = *grey* triangles (dashed line, $y = 2.54x - 5.17$, $R^2 = 0.74$, $P < 0.0001$), juveniles = *white* squares (dotted line, $y = 2.17x - 4.26$, $R^2 = 0.78$, $P < 0.0001$).

There was a positive linear relationship between tail length and snout-vent length ($R^2 = 0.78$, $P < 0.0001$); I removed snakes with stubbed tails ($n = 7$), likely caused by failed predation attempts, from this analysis (Figure 5-12). Two snakes had relatively longer tails than others with the same SVL. For adult snakes I found that the relative tail length of males was significantly greater than that of females (ANCOVA of log(tail length) between the sexes; $F_{1,95} = 22.3$, $P < 0.0001$, with log(SVL) as covariate; homogeneous slopes). For males, tail length was an average of 33.5% of their SVL (± 4.6% SD) whereas females had tails that were, on average, only 28.9% of their SVL (± 4.3% SD).

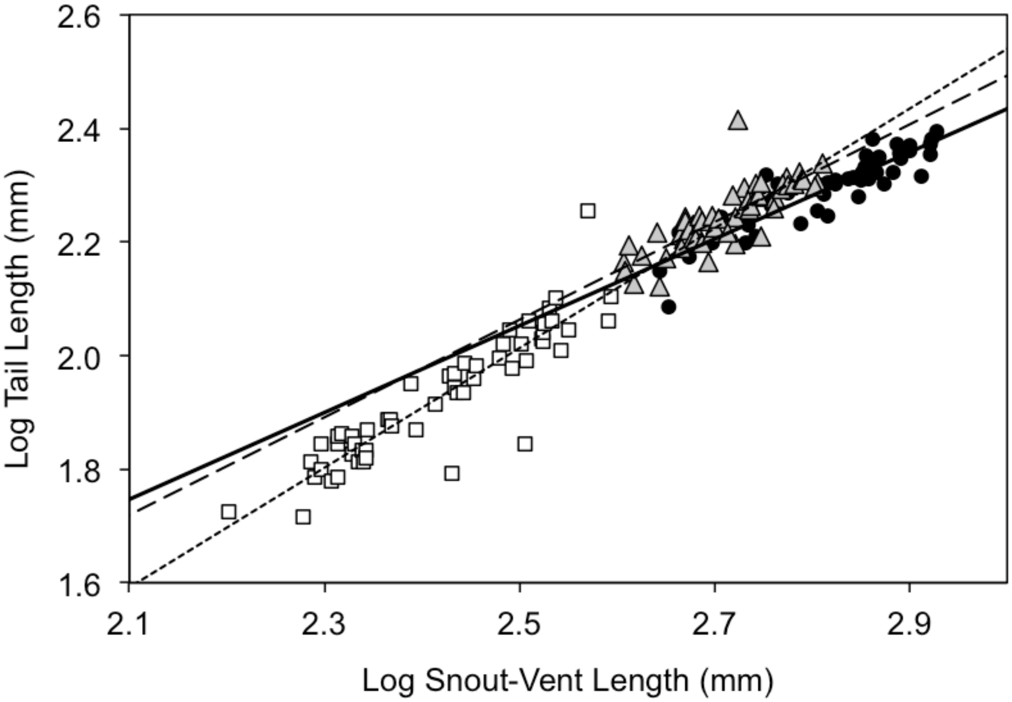

Figure 5-12. Log tail length (mm) as a function of log snout-vent length (mm) of snakes captured from 2016-2017. Females (gravid + nongravid) = *black* circles (solid line, $y = 0.7641x + 0.1422$, $R^2 = 0.81$, $P < 0.0001$), males = *grey* triangles (dashed line, $y = 0.8594x - 0.0856$, $R^2 = 0.59$, $P < 0.0001$), juveniles = *white* squares (dotted line, $y = 1.0536x - 0.6209$, $R^2 = 0.82$, $P < 0.0001$).

Head widths differed significantly between the sexes, reproductive states, and age classes (Figure 5-13 and Figure 5-14). Females had wider heads than males relative to SVL (ANCOVA; $F_{1,72}$=, P00001, SVL as covariate, slopes heterogeneous). Adults had wider heads than juveniles relative to SVL (ANCOVA of log(head width); $F_{1,107} = 11.53$, $P = 0.0009$, log(SVL) as covariate; slopes heterogeneous $F_{1,106} = 82.41$, $P < 0.0001$). The head widths of males and females also differed in relation to SVL, with females having relatively larger heads than males (ANCOVA of log(head width); $F_{1,83} = 29.57$, $P < 0.0001$; log(SVL) as covariate; slopes homogeneous).

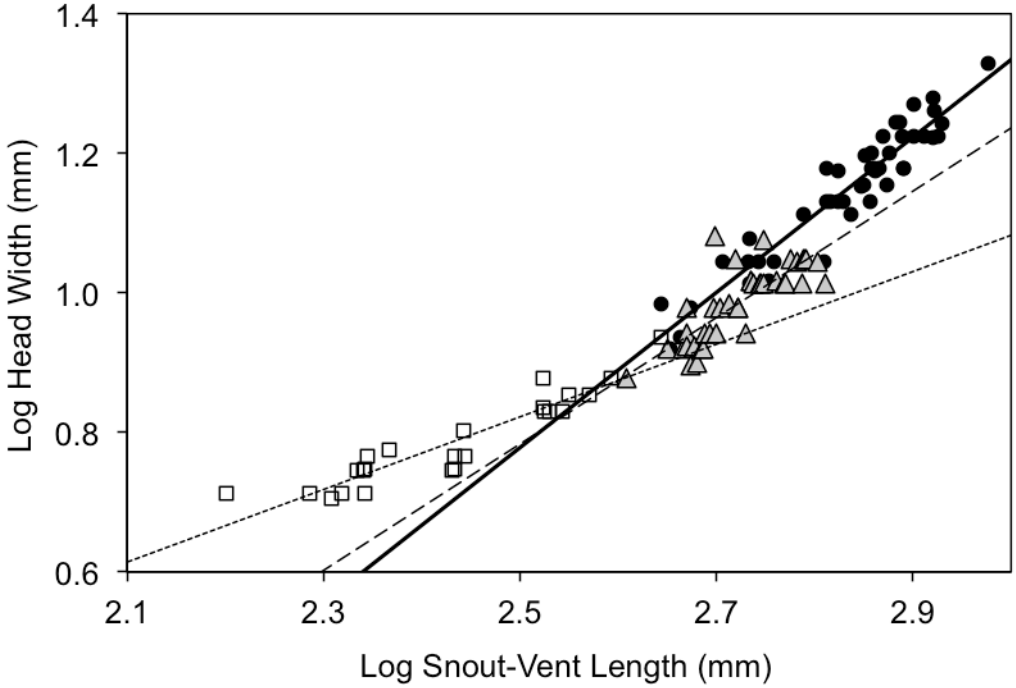

Figure 5-13. Log head width (mm) as a function of log snout-vent length (mm) for snakes in 2016 and 2017. Females (gravid + nongravid) = *black* circles (solid line, y = 1.1123x - 2.0027, $R^2 = 0.90$, $P < 0.0001$), males = *grey* triangles (dashed line, y = 0.9059x - 1.4815, $R^2 = 0.63$, $P < 0.0001$), juveniles = *white* squares (dotted line, y = 0.5206x - 0.4791, $R^2 = 0.86$, $P < 0.0001$).

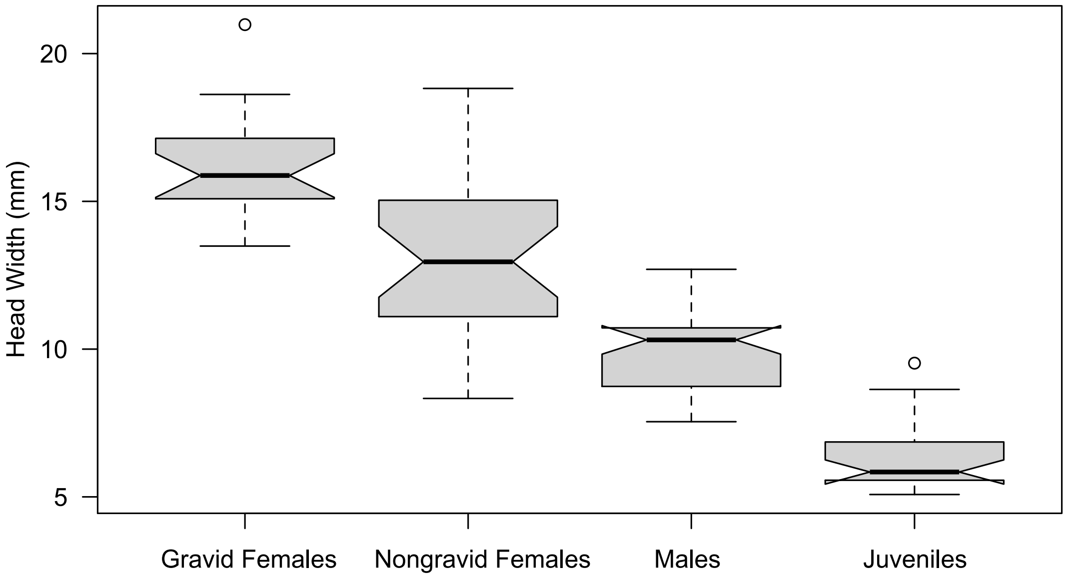

Figure 5-14. Box and whisker plots of head width (mm) of gravid and nongravid females, males, and juveniles. The grey box covers the second and third quartiles and the centre lines represent the medians. Whiskers represent the first and fourth quartiles. Notches that do not overlap strongly suggest a statistical difference.

I made five recaptures in 2016 (10% of all captures, males = 2, females = 2) and 23 recaptures in 2017 (21% of all captures, males = 9, females = 7). These values include snakes marked in 2015 (n = 7) as part of a long-term study of the Kinbasket Reservoir DDZ. One recapture in 2016, six recaptures in 2017, and 11 radio-tagged snakes provided growth data. Male and nongravid female snakes tended to increase steadily in SVL over time, whereas snakes that were initially gravid when captured had negligible growth (Figure 5-15). One individual seemed to decrease in length, likely due to measurement error, possibly related to the fact that this snake was in a very late stage of gestation when first measured and therefore was more easily handled for measurements.

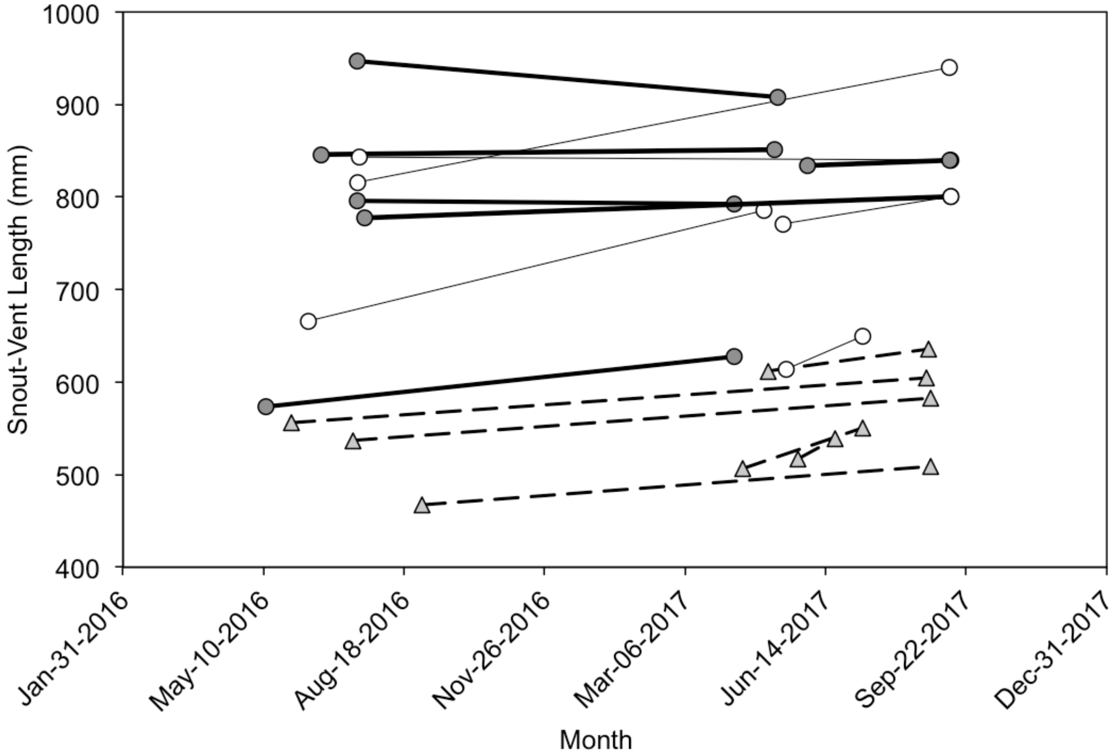

Figure 5-15. Growth of snout-vent length from 2016-2017 for opportunistically recaptured and radio-tagged snakes. Gravid females = *grey* circles (thick solid line), nongravid females = *white* circles (thin solid line), males = *grey* triangles (dashed line).

I estimated the length of the growing season based on the earliest and latest observations of activity by radio-tracked snakes over 30 m away from their respective hibernacula (April 10 - September 16). Thus, the annual active season was 159 days long. I treated the active season as a 'snake-year' in constructing growth curves (i.e. the inactive part of the year was considered non-time; Tuttle and Gregory 2012).

The confidence intervals I calculated for the parameter estimates of the nonlinear regression of Fabens' (1965) equation are quite wide, a reflection of the relatively small sample size (Table 5-3), which also explains the negative values for lower confidence limits of growth constant estimates. The von Bertalanffy mean growth curves show that although male snakes have a higher *k*, females have a higher growth rate overall due to the higher asymptotic size for females (Figure 5-16). Based on these estimates, males reach an asymptotic length around 600 mm SVL at 2 years, whereas females level out near 900 mm in 4 years and reach maturity at 2 years.

Table 5-3. Confidence limits (95%) of parameter estimates from nonlinear regression of Fabens' (1965) equation.

Sex	CI (k)	CI (SVLasym)
Female	-0.0645 - 0.9063	761.76 - 1038.66
Male	-1.0146 - 3.0019	497.18 - 724.17

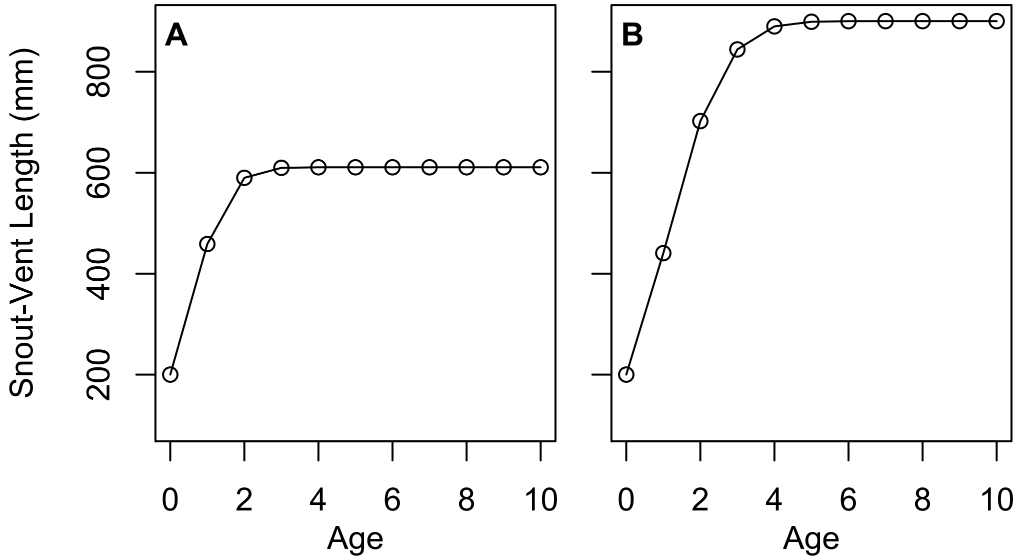

Figure 5-16. Von Bertalanffy growth curves for (**A**) male and (**B**) female snakes captured in 2016 and 2017. Size at birth (200 mm) is based on my measurements (n = 6) and observations of neonate snakes.

In late April of 2017 I observed a radio-tagged snake (Snake S) mating with a single male, dragging him behind her, tail end first. One week later I observed another radio-tagged snake (Snake R) being courted by a single male, lined up side-by-side while the male rubbed his chin along her body, which is typical courtship behaviour

(Gillingham and Dickinson 1980, Gillingham 1987). I searched each of the surrounding areas for additional males but found no other individuals. Both of these events occurred within 40 m of the females' respective hibernating sites, in small clearings (5 m × 5 m) in moderate-canopied mixed forests. Snake S was later confirmed as gravid, but Snake R was not despite being examined in mid July when pregnancy should have been obvious; each had been the opposite reproductive condition the year prior (i.e. Snake S was not gravid in 2016, but Snake R was).

I captured 56 adult females, of which 21 (37.5%) were gravid (2015 n = 2, 2016 n = 9, 2017 n = 10). Gravid snakes in my study area ranged from 640 mm SVL to 947 mm SVL (747.24 ± 78.58 mm SD). Litter size ranged from 3 to 25 (12.6 ± 6.2 SD). Figure 5-17 shows the litter size was not significantly correlated with the SVL of the mother ($y = 0.032x - 10.926$, $R^2 = 0.103$, $P = 0.18$).

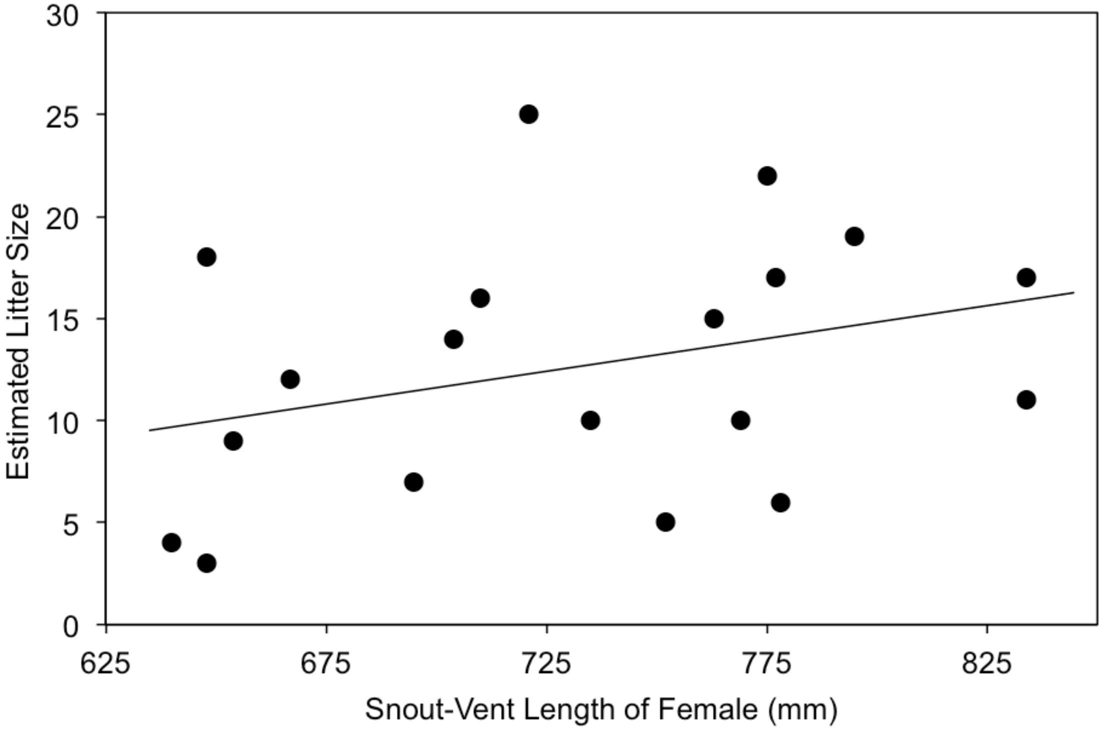

Figure 5-17. Litter size (number of ova) as a function of the snout-vent length (mm) of female snakes (n = 19) from 2015-2017.

I could not estimate litter size for two of the gravid females I captured but later confirmed their reproductive condition through the observation of parturition in both individuals on August 5 2016 and August 12 2016, respectively. Both of these were radio-tagged snakes. Each snake was in habitat with a high percentage of shrub cover, on mossy substrate, within 10 m of a water source. One was in fairly open canopy of aspen poles and the other was in very open canopy, beside willow shrubs. I observed two and ten neonates born, respectively, including one stillbirth in the larger litter. In 2017, I did not observe any parturition events and therefore had to estimate the date of parturition from other observations. One radio-tagged snake was very clearly in late gestation in early August, but when I next saw her aboveground on August 14, she was noticeably emaciated and had clearly given birth. The next time I located her (3 days later) she was in the midst of consuming an adult male Western Toad.

None of the snakes that I tracked reproduced in both years. One individual (Snake V), which I tracked for two full years did not reproduce in either year, despite observations of her with males lined up beside her in courtship posture. This same individual moved significantly farther than any other snake in her second non-breeding year and used different habitats than the previous year (see Chapters 1-3). She also had one of the highest growth rates of any individual.

Discussion

Snakes at northern latitudes are presumably limited by long, cold winters during which they have no time available to reproduce, forage, and grow (Gregory 2009). However, despite the restricted active season and cooler climate in east-central British Columbia, snakes in my study area have life-histories comparable to conspecifics in the south (Fitch 1965, Farr 1988). They do not grow at considerably lower rates nor do they have a significantly lower reproductive output (Fitch 1965, Fitch 1985, Farr 1988, Dunlap and Lang 1990). Wetlands in my study area, and others at northern latitudes appear to be highly productive and support large amphibian populations (Moore 2001, Swan et al. 2015), which implies high prey availability for *T. sirtalis*. The Common Gartersnakes in my study area also appear to have similar feeding ecology to that of more southerly populations (Carpenter 1952, Fitch 1965, Kephart and Arnold 1982, Gregory 1984b).

Common Gartersnakes are opportunistic feeders whose diets may vary drastically from year to year depending on prey abundance (Kephart and Arnold 1982). Dietary studies of Common Gartersnakes have identified earthworms (Carpenter 1952) and anuran amphibians (Fitch 1965, Gregory and Stewart 1975, Kephart and Arnold 1982, Gregory 1984b) as their primary prey. Although gartersnakes are known to prey upon spotted frogs (Reaser and Dexter 1996, McAllister et al. 2004), they were not observed as predators of the spotted frogs in my study area. Columbia Spotted Frogs are strongly associated with bodies of water, and remain at or close to breeding ponds throughout the year (Bull and Hayes 2001, Pilliod et al. 2002), areas where I frequently observed gartersnakes. Thus it is unclear why Columbia Spotted Frogs were never observed as prey. It is possible that the slow movements and large size of the Western Toad make it a preferred prey to snakes. This study supports previous research done in the Valemount area concluding that Western Toads are the primary prey species of Common Gartersnakes (Hawkes and Tuttle 2010, Boyle 2012).

The difference between the timing of Western Toad observations and the temporal pattern of captures of snakes that had eaten can be explained by the reproductive strategy of toads and amphibians in general. Amphibians are often most detectable during early spring, when they are mating at breeding ponds. After the surge of activity, many amphibians, including the Western Toad, move to different habitat (Browne and Paszkowski 2014). The timing of the maximum number of juvenile snakes with prey contents aligns with the emergence of metamorphosing Western Toads. Amphibians at this life stage are particularly vulnerable during the last Gosner (1960) stages of development (stages 42-44) when they shift from aquatic to terrestrial habitats (Arnold and Wassersug 1978). Because I induced regurgitation of prey only in snakes in which I could feel the prey within the snake's abdomen, soft or smaller prey items were likely left undetected. For radio-tagged snakes, I recorded when they had obvious bulges, so they may have been feeding at a greater rate on smaller prey that would be left undetected due to my efforts to disrupt them as little as possible. It is also possible that snakes in my study area consume other prey types such as small mammals, which were frequently observed at the study sites, or earthworms, which were not observed at the study sites but are present in Valemount (pers. obs.). Future studies should utilize multiple methods to analyze diet such as scat analysis using DNA barcoding (Valentini et al. 2009) and stable isotope analysis (Gillespie 2013).

As is typical of the species, Common Gartersnakes in my study area were sexually dimorphic in size (Fitch 1965, Rossman et al. 1996, Friesen et al. 2017), with females reaching larger body sizes (SVL) than males. The sexes were also dimorphic with respect to relative head width and relative tail length. As snakes are gape-limited predators (Cundall and Greene 2000), the ontogenetic changes in head size and the difference in head size between the sexes presumably means that prey availability or prey accessibility varies widely for snakes of different sizes and sexes. Male snakes in my study area had relatively longer tails than females, following the typical pattern in snakes (Fitch 1965, Weatherhead et al. 1995, King et al. 1999). Shine et al. (1999) provide two explanations of this trend: (1) larger tails of males are able to house larger hemipenes (copulatory organs) and (2) during copulation, males with shortened tails (from predation) have largely reduced reproductive success. King (1989) conducted a thorough analysis of these hypotheses and others, indicating that for male snakes, relatively longer tails play an important role in courtship.

Although my estimates of growth parameters had wide confidence intervals, the resulting growth curves are similar to those seen in other northern populations of

T.sirtalis (Larsen 1986, Larsen et al. 1993) and are not considerably different from that of southern populations (Fitch 1965). This implies that snake growth is not constrained by the relatively cool, short active season at high latitudes; however, more intensive studies with standardized measurement intervals are required to confirm this suggestion. An increased sample size would improve the precision of estimates of growth patterns for the snakes in my study area. Additionally, capturing and measuring individuals at the hibernaculum on an annual basis would help to standardize their physiological condition so that comparison between measurements of an individual when gravid and another measurement of the same individual postpartum would be avoided. It is also important to note that growth rates of *T. sirtalis* can vary considerably among populations and years, presumably in relation to food supply (Fitch 1965, Kephart 1982, Scudder-Davis and Burghardt 1987); therefore, studies of growth should span several years to reduce the effects of annual variation.

The populations I studied have larger average snout-vent lengths than gartersnakes in southeastern British Columbia (female range = 350 – 650 mm SVL, male range = 350 – 550 mm SVL; Farr 1988; but see southern Okanagan snakes; Gregory and Larsen 1993), central Manitoba (female average = 520 – 530 mm SVL, male average = 440 – 450 mm SVL; Gregory 1977) and Ontario (female range = 236 – 641 mm SVL, male range = 222 – 617 mm SVL, Maillet et al. 2015), but are comparable to populations in northern Alberta (female range = 640 – 915 mm SVL; Larsen 1986). Gartersnake SVLs may vary geographically as well as annually (Fitch 1999).

Female snakes in my study area were not documented as reproducing in successive years, perhaps following a biennial reproductive schedule, as observed in northern Alberta (Larsen 1986), but annual reproduction is seen in *T. sirtalis* in Kansas (Fitch 1965). The biennial reproductive trend for female snakes is well documented in rattlesnakes (Seigel and Ford 1987, Schuett et al. 2011), but is not consistent in Common Gartersnakes. Reproduction of female snakes in the north is likely constrained by the short period available to feed between parturition and the beginning of winter (Gregory 2009). If they have not succeeded in regaining at least some of the stored energy used to reproduce, they will likely have a higher risk of winter mortality and may not be capable of reproducing the following year (Gregory 2009). Although snakes in the north may reproduce less frequently than those in the south, there is currently no unambiguous evidence to confirm it.

Though spring is the primary breeding season for Common Gartersnakes, some studies offer evidence of sexual activity in the fall (Fitch 1965, Whittier and Crews 1986, Mendonca and Crews 1989). Although I frequently observed males and females together in the late summer and fall, there was no clear evidence of fall mating at my study sites. The close proximity of males and females could be attributed to the return to hibernacula, in that male and female snakes could have been observed together along the migration route simply because they were returning to the same hibernating site.

In Canada, the litter size for *T. sirtalis* ranges from 9 to 30 (17.00 ± 6.44 SD; Gregory and Larsen 1996) and averages 7.50 ± 2.56 SD in BC (range = 3-17; Farr 1988). Litters considerably larger in number are observed in southern populations but with smaller offspring (Fitch 1965). This trade-off in reduced neonate size for increased number of neonates per litter is also evident in eastern populations of *T. sirtalis* in Canada compared to that of western populations (Gregory and Larsen 1993). Average litter size in my study area is higher than that reported by Farr (1988) but is similar to the mean litter size and neonate size in northern Alberta (12.5 ± 4.85 SD; Larsen et al. 1993). The minimum SVL of a gravid female in my study was the same as for the population studied in northern Alberta, but I did not find a significant correlation between litter size and SVL of the female, as seen in other populations (Gregory and Larsen 1993).

The similarities between the life-histories of northern and southern populations of Common Gartersnakes are intriguing, given the restricted active season at high latitudes as well as the relatively cool summers and cold winters. The high abundance of prey and comparable growth rates indicate that the snakes in my study area are not likely at a disadvantage in terms of food availability when compared to their southern counterparts. Although snakes at northern latitudes often succumb to winter mortality (Joy and Crews 1989, Shine and Mason 2004), evidence is currently lacking on the impacts of this mortality. Future studies that focus on the factors limiting geographic distribution will likely help contribute to an explanation of the similarities between the life-histories of northern and southern populations.

Major Conclusions

Because of annual variation in weather and other environmental features, my two-year study offers a mere snapshot in time of the natural history of Common Gartersnakes in east-central British Columbia. Furthermore, the relatively small sample size limits the extrapolation potential of my research. Nonetheless, it yields important information that can contribute to the management and conservation of *T. sirtalis*. My study offers a comparison of the natural history of *T. sirtalis* in east-central BC to that of other populations of conspecifics at northern and southern latitudes. This provides a fundamental basis for investigating the factors that influence intraspecific variation. However, to develop effective conservation measures, studies of populations should be conducted over longer periods of time.

The major conclusions from my study of the natural history of Common Gartersnakes in east-central British Columbia are:

(1) Common Gartersnakes in the Valemount area undertake relatively long-distance migrations between winter and summer habitats, which is commonly seen in other northern populations of *T. sirtalis*. The pattern of migration varies among individuals and typically spans shorter distances compared to other *T. sirtalis* at northern latitudes, but greater distances than those moved by southern conspecifics. The rate of movement of gravid snakes increases after parturition but is overall less than that of nongravid females. Understanding how and when snakes move allows for the development of mitigation to reduce the rates of road mortality.

(2) Conclusions about habitat use differed according to methodology, with radio-tagged snakes inhabiting forested areas most frequently, but opportunistically observed snakes being recorded most often in wetland habitats. Gravid snakes (and nongravid snakes that were observed with gravid snakes) used habitats with open canopies more frequently than nongravid snakes in general. High percentage ground cover and open canopy cover were the most important habitat characteristics for nongravid snakes, based on matched-pair logistic regression modelling. Annual variation in habitat use is evident for some individuals. Because large females were the only snakes suitable for radiotelemetry methods, future studies should also consider males and juveniles.

(3) Hibernation by *T. sirtalis* in my study area is similar to other northern populations in timing and duration but the physical characteristics of hibernacula and the small sizes of overwintering aggregations are different from other northern populations and seem to be most similar to those seen in a congener, the Plains Gartersnake (*Thamnophis radix*), in central Alberta. The lack of large-scale communal hibernation suggests that the availability of suitable hibernacula is not limited in my study area. By determining the locations of hibernating sites, I increased the ease with which future snake research in my study area may be conducted because snakes are more easily observed and/or captured during spring and fall at the hibernaculum (Gregory 1984a). This assumes overwintering site fidelity of snakes in this population, which requires further study and would contribute to our understanding of the importance of these habitats.

(4) Adult Common Gartersnakes near Valemount consume adult Western Toads, but not Columbia Spotted Frogs, despite the inclusion of the latter in diets of snakes in other populations. Sexual size dimorphism was consistent with other populations of *T. sirtalis*, with females reaching greater lengths with higher overall growth rates. Gravid females gave birth in early to mid August and often foraged immediately afterwards so that they had fed prior to hibernation. Female Common Gartersnakes did not reproduce in successive years, possibly a result of the limited active season; the biennial trend of female reproduction is well established in other snake species, but is not consistent in *T. sirtalis*.

Recommendations

(1) I recommend the protection of forested habitat at both the Kinbasket Reservoir and Cranberry Marsh because most hibernacula and migratory routes I located were in forested habitats. Previous research suggests that the protection of hibernacula is more effective than conservation efforts in summer habitat or merely along the migratory route (Shine et al. 2001).

(2) Traffic signs (e.g. 'Please Give Snakes a Brake') should be posted along the West Canoe Forest Service Road at the 2 km and 6 km markers to help mitigate snake road mortality. The signs should also include peak migration times ('April – May' and 'August – September').

(3) Future studies should investigate the natural history of juveniles and males to account for any variation in ecology based on age class or sex. As a precautionary measure, I recommend ensuring the inundation of the Kinbasket Reservoir DDZ does not occur until mid-May to help reduce the risk of drowning snakes that are hibernating.

(4) Investigation of potential geothermal activity at these study sites could help explain how snakes select suitable overwintering sites and may reveal the factors influencing the distribution of reptiles at northern latitudes.

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