

NATURAL HISTORY OF THE PLAINS GARTER SNAKE
(*Thamnophis radix*) AT THE NORTHERN LIMIT OF ITS RANGE IN
ALBERTA, CANADA

by

Kryisia Tuttle
Bachelor of Science, University of Victoria, 2004
Bachelor of Arts, University of Calgary, 2002

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

MASTER OF SCIENCE

in the Department of Biology

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ABSTRACT

Natural history is a cornerstone of both theoretical and applied ecology, and provides the context for comparative and experimental studies. I studied the natural history of the Plains Garter Snake (*Thamnophis radix*) near the northern limit of its range in Miquelon Lake Provincial Park, Alberta, Canada. As is typical of garter snakes, *T. radix* at Miquelon were sexually dimorphic as adults – females grew faster, reached larger sizes and had relatively shorter tails than males. Mating occurred in spring and females gave birth in August; litter size ranged from 8-50 and was correlated with size of female. These snakes were generalist predators, but fed mainly on anurans when small, adding mammals and other prey as they grew. Despite sexual size dimorphism, I found no difference in diet between adult males and females. Feeding frequency was low overall (22%), especially in gravid females. In summer, snakes were found mainly near cover on south-facing field edges or in marshes, but not in forests, and moved relatively little. However, movement distances increased in fall as snakes sought hibernating sites. Snakes hibernated for up to eight months, either individually or in pairs, in rodent burrows. This study also revealed the importance of radiotelemetry when studying movements of small, secretive animals, as there were significant differences between the results obtained through opportunistic captures versus telemetry; habitat descriptions from opportunistic captures therefore were biased, although they still captured some elements of microhabitat use by *T. radix*. The data from this study will be important for comparative studies of the ecology of garter snakes and for the management of this species on the human-altered landscape surrounding Miquelon Lake.

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CHAPTER 1 – INTRODUCTION AND BACKGROUND FOR STUDY

Natural-history studies typically focus on quantitative descriptions of animals in their natural environments (Greene, 1986; Arnold 2003), whereas life-history studies are concerned with patterns of resource allocation toward different functions of an organism, such as growth or reproduction, as well as the conditions that lead to the evolution of certain demographic traits (Roff, 1992). In tandem, natural-history and life-history studies contribute to the answers to fundamental questions in ecology such as: 1) What factors limit the distribution and abundance of organisms? and 2) How and why do demographic and other ecological traits vary among individuals, populations, and species (Roff, 1992)? In turn, answers to such questions are relevant to conservation and management of the world's biotic diversity. For species that have not been well described, natural-history studies are especially important for laying the groundwork for future experimental or hypothesis-driven research.

Garter snakes (Genus *Thamnophis*, Family Colubridae, Order Squamata) are a radiation of approximately 30 species of viviparous terrestrial snakes, endemic to North America, and are among the most intensively studied species of snakes (Rossman et al. 1996). They range from the Atlantic to the Pacific, across a wide diversity of habitats, from Mexico to Canada, and reach the highest latitudes of any North American snakes. Past studies have resulted in a substantial accumulation of information on the natural history of several species of *Thamnophis* (Rossman et al., 1996). Two important general patterns have emerged from these studies: (1) most species are diurnal active foragers with generalist diets; (2) seasonal activity patterns in cooler climates typically consist of winter hibernation, mating upon emergence in the spring, movement to summer foraging areas, where young usually are born, and return to the den site in the fall. However, there is also tremendous spatial and temporal variation in details of the ecology of garter snakes; this ecological plasticity may be an important part of the success of these snakes as a group (Seigel, 1996; Burghardt and Krause, 1999).

Canada has 6 species of garter snake, all reaching the northern limits of their ranges in the southern or mid-latitude areas of the country (Gregory, 2007). This is potentially interesting because northern populations presumably exemplify the extreme of the species in terms of survival abilities in cold climates. The marked seasonality and cold

winters in most parts of Canada mean that snakes populating these areas exhibit an annual cycle with pronounced seasonal activity patterns that are restricted to certain times of the year; such patterns may be very different from the activity patterns of more southern populations of the same species. Thus, studying populations of snakes near the species' range limit could contribute significantly to our understanding of how populations respond to different environments and the factors that may limit the distribution and abundance of these animals.

The most widespread and northerly species of garter snake is the Common Garter Snake (*Thamnophis sirtalis*), which reaches slightly north of 60 degrees latitude in the Northwest Territories, Canada (Larsen, 1986). Because of this wide distribution and the species' frequent local abundance, most research on the ecology and life history of high-latitude temperate-zone garter snakes have focused on populations of *T. sirtalis* (Carpenter, 1952a; Fitch, 1965; Gregory, 1971, 1974, 1977a; Gregory and Stewart, 1975; Larsen, 1986; Gregory and Larsen, 1993; Shine et al., 2001a, 2001b). Northern populations of this species are noteworthy for their communal hibernation behaviour and the extensive migrations they make between summer wetland habitats and winter den sites (Gregory, 1977a; Larsen, 1987). This seasonal pattern is herein termed the '*sirtalis*' model, because it is often the dominant paradigm used to characterize the ecology of northern garter snakes. Other northern species of garter snakes, however, have not been observed as frequently to engage in such behaviours, suggesting either that they are understudied or that they use the landscape in different ways and therefore may have different ecological requirements and subsequently exhibit different seasonal activity patterns (Gregory, 1977b, 1984a). Thus, studies of the natural history and ecology of other garter snake species may address both important theoretical questions and practical issues in conservation not answered by single-species approaches.

The Plains Garter Snake (*Thamnophis radix*) offers an opportunity to test the generality of the '*sirtalis* model' of seasonal patterns of garter snakes in a thermally challenging environment. *Thamnophis radix* is closely related to and often syntopic with *T. sirtalis*, although it is more restricted in its range (Rossman et al., 1996; Russell and Bauer, 2000). Although several aspects of the ecology of *T. radix* have been studied elsewhere (Heckrotte, 1961, 1975; Jordan, 1967; Chiszar et al., 1976a, 1976b; Arnold &

Bennett, 1984; Yeager & Burghardt, 1991; Stanford, 2002; Walley et al., 2003; see Chapter 2 and 3 for additional references), the Plains Garter Snake is relatively unstudied in Alberta and other parts of its Canadian range (Gregory, 1977b; Hart, 1979; Lawson and Secoy, 1990). This lack of knowledge of fundamental aspects of a species' ecology contributes to its vulnerability to population decline and range contraction, should it become threatened by habitat loss or other anthropogenic disturbances in the future.

The general purpose of my study was to outline the natural history and ecology of a population of Plains Garter Snakes, *Thamnophis radix*, at Miquelon Lake Provincial Park (MLPP) in central Alberta, and contribute to our developing knowledge of the ecology of snakes, especially in northern environments. My primary objective was to describe basic life-history characteristics of these snakes (e.g. morphometric traits, growth, fertility) to provide the basis for future work on their population ecology. A second objective was to collect data on food habits of these snakes because dietary patterns often influence other life-history traits (e.g. growth, reproduction), as well as use of habitat (Reinert, 1993). My final objective was to identify the macrohabitats used by Plains Garter Snakes (both summer and winter) and to determine the specific microhabitat features that snakes use within those macrohabitats. I used both opportunistic surveys and radiotelemetry to document the spatial ecology of snakes and to determine their patterns of seasonal movement and resource use.

STUDY SPECIES

The Plains Garter Snake (*Thamnophis radix*) is a medium-sized, diurnal, viviparous snake, with two recognized subspecies (Western Plains Garter Snake, *T. radix haydeni* and Eastern Plains Garter Snake, *T. radix radix*; see summary by Rossman et al., 1996; Walley et al., 2003; Fig.1). These snakes are found in the prairie regions of the Great Plains of North America (Fig.2), ranging from New Mexico to Indiana, and north to the Canadian prairies (Alberta, Saskatchewan and Manitoba). These snakes have a broad habitat preference, although they are strongly grassland-associated, and in the summer are commonly found near wetlands (e.g. ponds, marshes, river valleys; Jordan, 1967; Gregory, 1977b). *Thamnophis radix*, like some of its congeners, has been reported to use communal hibernacula, although this aspect of their ecology remains very poorly studied (Gregory, 1977b; Dalrymple and Reichenbach, 1981).



Figure 1. Plains Garter Snake (*Thamnophis radix*) from Miquelon Lake Provincial Park, Alberta. Photo by K. Tuttle.

Thamnophis radix has been reported to reach high densities compared to other species of garter snake (Rossman et al., 1996; Dalrymple and Reichenbach, 1981), making it an attractive subject for study. Plains Garter Snakes also have been documented to coexist with humans in urban populations (e.g. farmsteads, city parks and trash heaps), but whether such populations are stable remains in question. Isolated populations in Illinois and Ohio have been listed as threatened or endangered, and management plans have been developed and implemented (Dalrymple and Reichenbach, 1984; King and Stanford, 2006). Currently in Canada, *T. radix* is listed as a common species; however, certain populations and associated hibernacula have been identified as threatened (e.g. in decline or disappeared; Russell and Bauer, 2000; Gregory, 2007). There are several populations of Plains Garter Snake at the northern limit of the species' range in Alberta, but many of them are small or reported to be experiencing decline (Russell & Bauer, 2000). Thus, a study of the ecology of the species in Alberta is timely.

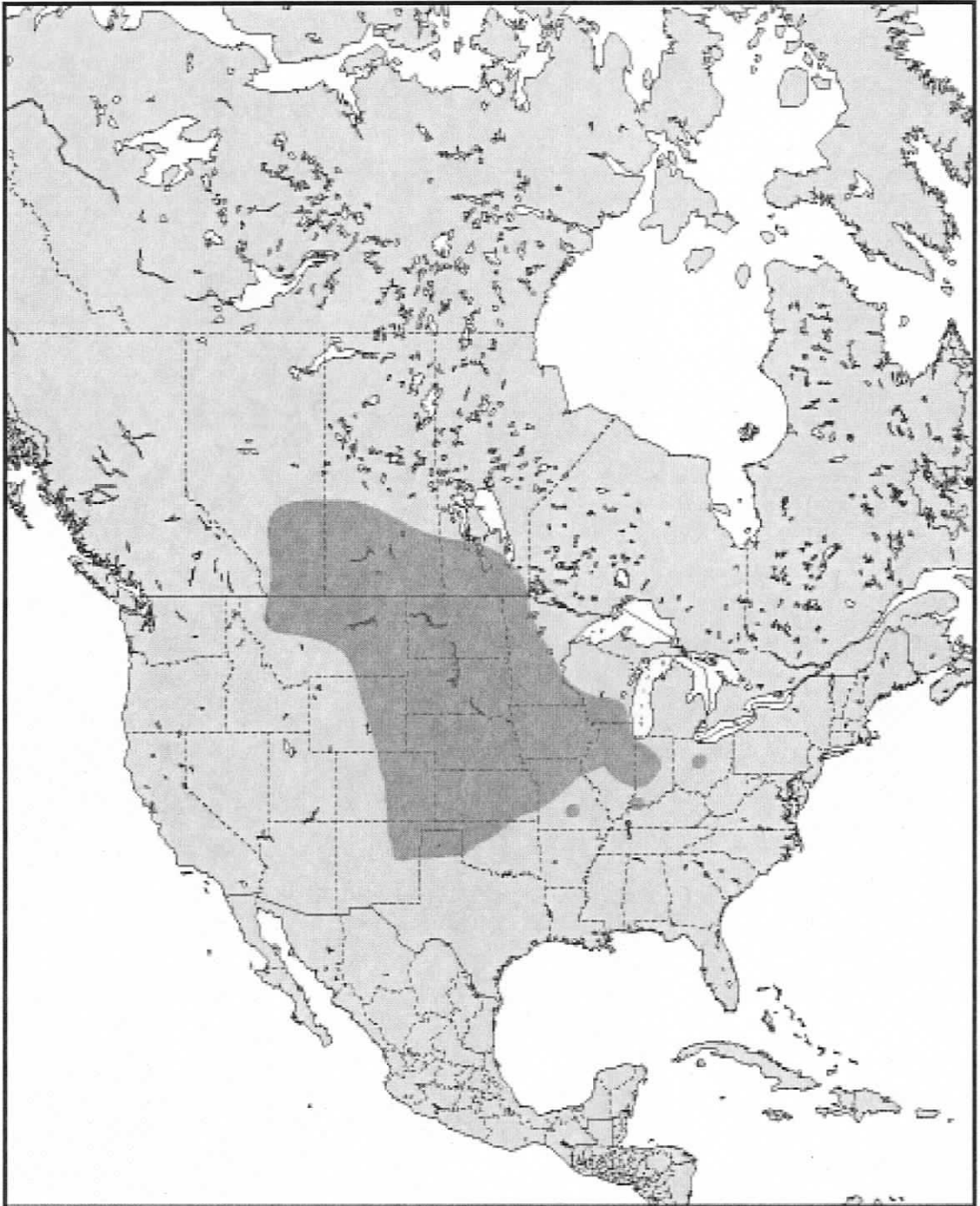


Figure 2. Approximate distribution (grey shaded area) of Plains Garter Snakes (*Thamnophis radix*) in North America. Redrawn largely from Russell and Bauer (2000).

STUDY AREA

General – The study site was Miquelon Lake Provincial Park (MLPP), 60km south east of Edmonton, Alberta (53°21'N, 112°55'W, elevation 763 m; Fig.3). This 836-hectare park is designated as a recreational and protected habitat, most of which is anthropogenically disturbed to varying degrees. There are numerous natural pathways, paved roads, as well as recreational picnic and campground areas interspersed throughout the park. The park experiences heavy recreational use in the summer months of July and August. In 2006, the park was closed to the public for renovations, but experienced heavy construction traffic and land alterations. Major land uses adjacent to the park include farming (e.g. cultivation of wheat, barley and canola and cattle grazing), and natural gas and oil development.

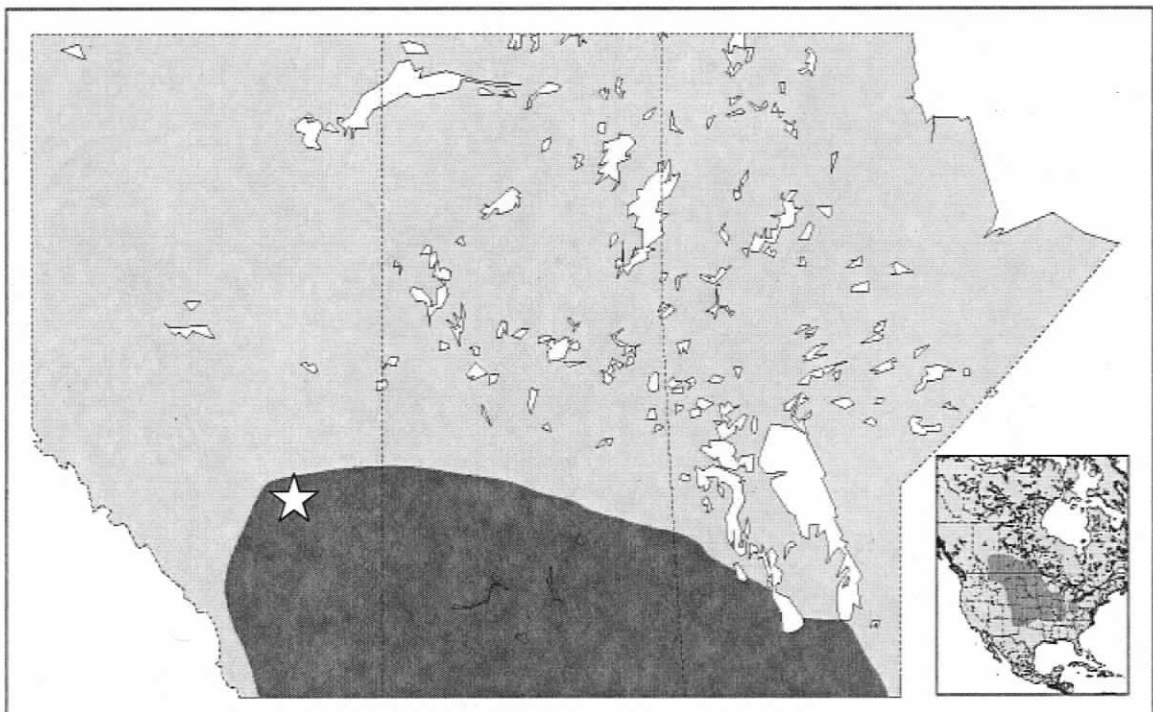


Figure 3. Approximate Canadian distribution of Plains Garter Snakes (*Thamnophis radix*) in Alberta (AB), Saskatchewan (SK) and Manitoba (MB). Shaded area = range; white star = location of study area, Miquelon Lake Provincial Park, Alberta. Inset: map of North American range of *T. radix* (same source as Fig.2).

Biophysical Region and Climate - The study area lies within the Interior Plains region of North America (NRC, 2006). Within Alberta, it is classified as the Central Parkland Natural Sub-region, within the Grassland Ecoclimatic regime. The landscape is characterized by undulating till plains and hummocky uplands, mostly cultivated but with some native parkland and grassland habitats remaining. Five to ten per cent of this region is classified as non-peat accumulating wetlands, and numerous marshes, ponds and saline lakes are interspersed throughout the Miquelon area. Mean annual precipitation is 450 mm, with 330 mm of it falling during the growing season (27th May to 5th September, average of 102 frost-free days; Environment Canada, 2006). Temperature variation can be extreme, with air temperatures reaching 36°C in the summer (April to September average = 12°C) and dropping below -30°C in the winter (October to March average = -7°C). During 2005, the snow-free period was from 29th April to 9th October, and received more rainfall than average. The summer of 2006 was much drier and warmer, more typical of the seasonal conditions. The last day of snow that year occurred on May 3rd 2006 (personal observation).

Habitat and Wildlife - Broad-leaved forest patches cover most of the study area, including mixed and pure stands of trembling aspen and balsam poplar (*Populus tremuloides*, *Populus balsamifera*). Woody understory is largely dominated by beaked hazelnut (*Corylus cornuta*), prickly rose (*Rosa acicularis*), saskatoon (*Amelanchier alnifolia*) and Canada buffaloberry (*Shepherdia canadensis*). Annual and perennial herbaceous species comprise the forest floor (Johnson et al., 1995). Prairie grasslands, which border most of the forest patches, are dominated by grasses (Family Poaceae) and other introduced and native grassland-associated species such as wild vetch (*Vicia americana*), yellow sweet-clover (*Melilotus officinalis*), Canada thistle (*Cirsium arvense*), and Canada goldenrod (*Solidago canadensis*). Marsh and wetland areas are mainly comprised of sedges (Family Cyperaceae), common cattail (*Typha latifolia*), stinging nettle (*Urtica dioica*), common duckweed (*Lemna minor*), and several willow species (Genus *Salix*).

Many resident and migratory wildlife species have been reported in the Miquelon area. The ranges of both the Plains Garter Snake (*Thamnophis radix*) and Common Garter Snake (*Thamnophis sirtalis*) include this area (Russell and Bauer, 2000), but I

detected only *T. radix* during the study period. This parkland region of Alberta represents the northern range limit for *T. radix*, with the Miquelon Lake population being one of several of the most northerly locations. Two species of anurans and one salamander species (Wood Frog, *Rana sylvatica*; Boreal Chorus Frog, *Pseudacris maculata*; and Tiger Salamander, *Ambystoma tigrinum*) occur in the park (personal observation). Bird species common to the park include numerous migratory waterfowl and songbirds, as well as resident predatory species, including hawks (Red-tailed hawk, *Buteo jamaicensis*; Swainson's hawk, *B. swainsoni*; Rough-legged hawk, *B. lagopus*), owls (Great Horned Owl, *Bubo virginianus*; Great Grey Owl, *Strix nebulosa*), and crows (*Corvus brachyrhynchos*). Larger mammals commonly inhabiting the parkland area include beavers (*Castor canadensis*), muskrats (*Ondatra zibethicus*), coyotes (*Canis latrans*), porcupines (*Erethizon dorsatum*), skunk (*Mephitis mephitis*), deer (Mule deer, *Odocoileus hemionus*; White-tailed deer, *Odocoileus virginianus*), moose (*Alces alces*), and black bears (*Ursus americanus*).

GENERAL SAMPLING PROCEDURES

I conducted this study in 2005 and 2006, but some analyses also included data collected periodically by P. Gregory in 1990, 1995-98, and 2004. The two main field seasons ranged from 25th April to 10th October in 2005, and 29th April to 25th August in 2006. I outlined a four-square kilometer section of MLPP to comprise the study area, using previous knowledge of snake locations, aerial photographs and fenced park boundaries (1:10,000, Alberta Map and Airphoto Ref. Library).

I used three techniques to search for and capture snakes. First, I captured snakes opportunistically by hand, both in the open and under natural cover, while searching on foot both within the park and the surrounding area. I searched for snakes mainly between the hours of 0730 to 2100, with some variation due to weather and logistical time constraints (for search effort methodology, see macrohabitat section in Chapter 4). Second, artificial cover objects (ACOs) of various types (e.g. wood boards, asphalt roof tiles, sheets of metal, etc.) were placed in various habitats to enhance capture success. Last, radiotelemetry was used to track a total of 10 female snakes to determine seasonal habitat use (for methodology, see radiotelemetry section in Chapter 4).

I recorded all sightings of snakes, even if the capture was not successful, as well as any dead snakes I found. At each sighting or capture location, I recorded UTM coordinate position and accuracy using a handheld GPS (Global Positioning System, Model Garmin GPS 72 personal navigator), date, time of day, substrate temperature (T_s) with a shaded alcohol thermometer, and weather conditions (e.g. sun, partly cloudy, overcast, rain, wind). Time of day was calculated based on a 24 hour clock.

All statistical analyses were done with SAS, version 9.1 (SAS Institute, 2006). All tests were assessed as significant between $\alpha = 0.05$ to 0.25, depending on the extent of exploratory or detailed data analysis. Detailed descriptions of analyses are given in relevant sections.

CAPTURES, RECAPTURES AND ACTIVITY SEASON

Captures – Observations of Plains Garter Snakes were made on 643 occasions from 1990 to 2006, both inside and outside the boundaries of Miquelon Lake Provincial Park. Ninety-one snakes were spotted but not captured (estimated size categories: 8 neonate, 32 juvenile, 51 adult), all in 2005 and 2006. The remaining observations consisted of 524 live captures and 28 dead specimens (Table 1). Of these, 57 occurred from 1990 to 2004; the remaining 495 occurred in 2005 and 2006, over a total search time of ~2700 person-hours (0.18 snakes/hour). Of the 552 records, 367 (66%) were original captures and 185 (34%) were recaptures. Of the recaptures, 36% (N = 67) of snakes were recaptured only once, and 64% (N = 118) were captured multiple times, ranging from 2 to 9. Time between consecutive captures ranged from 1 to 112 days. Overall, more female snakes were captured than male snakes (209 females, 158 males, sex ratio = 1.32:1); however, there was no statistically significant difference between proportions of male and female recaptures ($\chi^2_1 = 3.302$, $P = 0.069$). I captured large snakes more frequently than small snakes (265 adults, 83 juveniles and 17 neonates). Sex and sizes of two snakes captured in 1990 were not determined.

Table 1. Number of days and Plains Garter Snake (*Thamnophis radix*) captures in each year sampled at Miquelon Lake Provincial Park, Alberta, 1990-2006.

Year	# of days with captures	# of recaptures	# of new captures	Total # of captures
1990	1	0	3	3
1995	4	0	16	16
1996	1	0	10	10
1997	1	0	3	3
1998	5	2	18	20
2004	2	0	5	5
2005	52	36	127	163
2006	63	147	185	332
Total	129	185	367	552

Activity – I captured snakes from 0730 h until 2100 h, with the most frequent capture times occurring in midmorning (1030 h) and early evening (1700-1900 h; Fig.4). Snakes were typically encountered above ground, when ambient temperatures (taken in shade on

the ground; Fig.5) were 18 to 30 degrees Celsius, but microhabitat temperatures were likely considerably less variable. The exception to this was in the early spring and late fall, when several snakes were captured at lower temperatures. The majority of snake captures were made in May and June (44%, N = 243) or July and August (40%, N = 220) months, with the month of June having the highest number of captures (30%, N = 162). More dead snakes were found (i.e. road kill) in the fall months, especially in September of 2005 ($\chi^2_2 = 66.49$, $P < 0.0001$). Adults appeared earlier in the season than juveniles, and neonates were captured only in late August and early September. Month had no effect on the proportion of males or females captured ($\chi^2_4 = 1.4668$, $P = 0.48$).

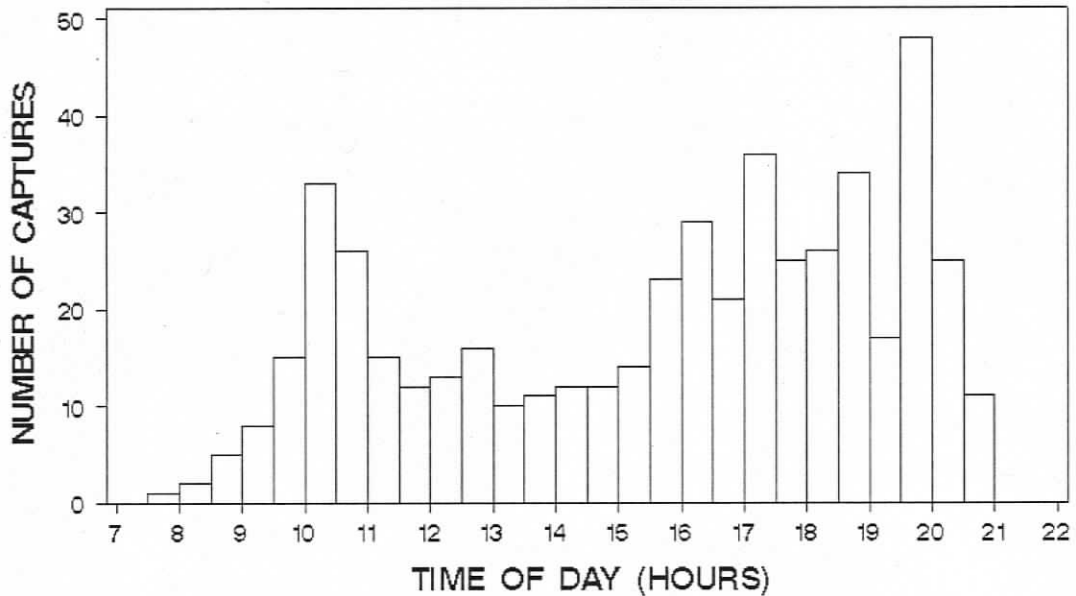


Figure 4. Bimodal frequency distribution of opportunistic captures of Plains Garter Snakes (*Thamnophis radix*) by time of day at Miquelon Lake Provincial Park, Alberta, 1995-2006.

I observed snakes exhibiting a variety of different pre-capture activities, including basking in the open (58.1%, N=303), concealed beneath cover (31.8%, N=166), moving (9.8%, N=51), and swimming (0.3%, N=2). When basking or concealed under cover, snakes were positioned as either coiled (60.1%, N=282) or stretched out (39.9%, N=187). There was a significant relationship between position found (i.e. coiled vs. stretched) and snake behaviour (i.e. basking in the open or concealed), with more snakes stretched when basking and more snakes coiled when under cover ($\chi^2_1 = 82.9714$, $P < 0.001$). Snakes also

were frequently found in aggregations (39.9%, N=219), group size ranging from 2-13 snakes. I did not measure distances between snakes (snakes touching vs. separated) because snakes generally moved too quickly. Of the snakes found in groups, 51.5% (N=113) were aggregated under ACOs and 48.5% (N=106) were aggregated (within half of a metre of one another) but in the open.

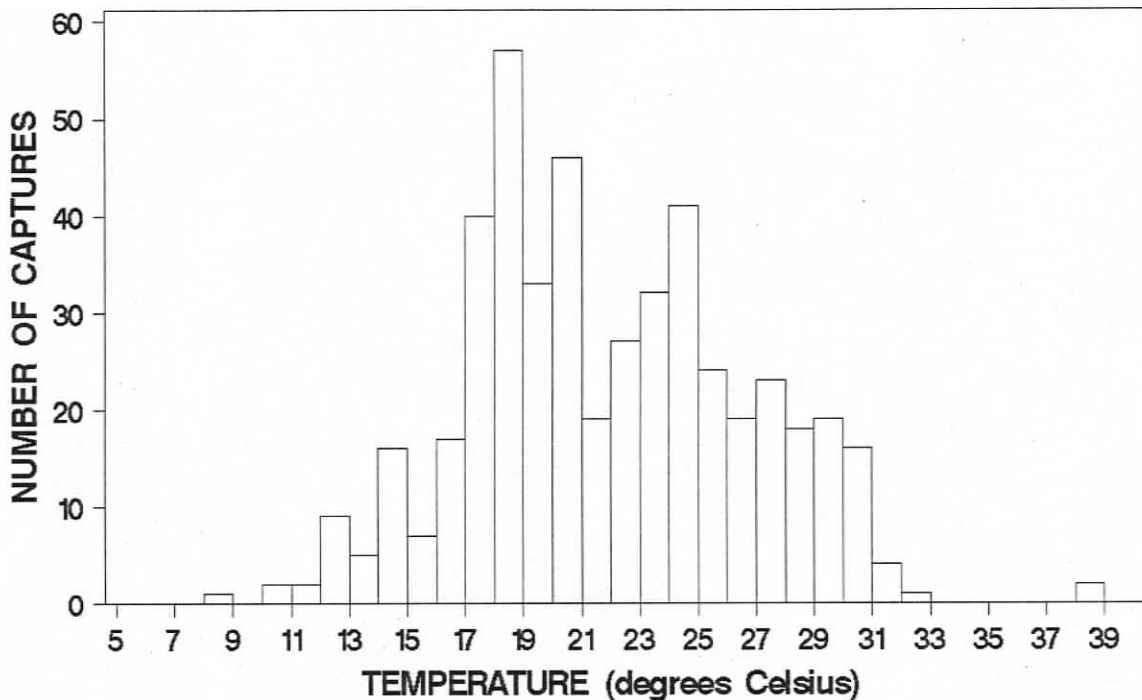


Figure 5. Frequency distribution of opportunistic captures of Plains Garter Snakes (*Thamnophis radix*) by substrate temperature (degrees Celsius) at Miquelon Lake Provincial Park, Alberta, 1995-2006.

DISCUSSION

The capture of snakes in the wild is the result of an interaction between search methods, external factors of the environment and internal factors of individual snakes. The restricted period of this study and the sometimes long intervals between original capture and recapture made mark-recapture estimation of population size at MLPP impractical. Both season and size of snake influenced my capture rates: more snakes were captured in the spring and the proportion of younger snakes captured was low compared to adults. The sex ratios presented in this study also deviated from the usual unbiased sex ratio of snakes at birth (Parker and Plummer, 1987). Biased sex ratios of

subadults and adults could be due to differential mortality of the sexes or differential capture rates of males and females.

Adult snakes were both easier to capture, as well as more easily spotted, than juveniles at MLPP. This probably does not reflect actual frequencies, because given a stable population, younger age classes should be numerically predominant (Parker and Plummer, 1987). However, the resulting ratio of mature to immature snakes was similar to other snake studies (Stanford, 2002). Additionally, as in other studies (Gregory, 1977a; Charland & Gregory, 1995; Bonnet and Naulleau, 1996), gravid females were more easily seen, potentially inflating the likelihood of female captures in this study. Due to differences in size and reproductive activities, male and female snakes likely have differential survival rates. Larger body size has been associated with an increased chance of survival during an attempted predation event (Gregory and Gregory, 2006), but conversely also may make an individual easier to spot and capture. However, in addition to being larger, females when gravid typically have reduced locomotory abilities and must spend more time thermoregulating, potentially increasing their susceptibility to predators (Seigel et al., 1987). To examine the size and sex capture ratios in more depth, a long-term, mark-recapture study with increased capture effort is required.

Snake captures were not evenly distributed throughout the seasons, and differences in capture rates were most likely related to thermal conditions and activities of snakes. As predicted, most captures were in the spring, made at times of the day that were ideal for snakes to be openly basking (i.e. mid-morning and later afternoon). This was presumably due to emergence and mating activities, as well as daily temperatures that fell within an ideal range for snakes (Gregory, 1984c). During the summer, when temperatures were on average much higher, snakes were increasingly more difficult to catch. This was likely influenced by the increased vegetation in the area providing shelter sites for snakes, as well as a decrease of conspicuously basking snakes. This population exhibited a shorter active season than reports of populations at more southerly latitudes (King and Stanford, 2006). It is unknown how lower temperatures or a shorter season affect individual growth, reproduction or survivorship, although they are likely to be negative.

The pattern of spring emergence by communally hibernating Common Garter Snakes is well known (Gregory, 1974; Shine et al., 2001b). Typically, males emerge first and

wait for females, which emerge slightly later, and mating occurs in the vicinity of the den site. Although I did not observe any mass spring aggregations of snakes, emergence dates of *Thamnophis radix* were similar to those reported for other populations of garter snakes (Hart, 1979; Macartney et al., 1989; Graves and Duvall, 1990; personal observation of *T. sirtalis* den site 60 km away from MLPP). It has been suggested that ambient temperatures and thermal gradients within a hibernaculum are potential triggers for emergence from hibernation (Gregory, 1982; Macartney et al., 1989). Daily low temperatures at this time of the year ranged from - 5 to 10 degrees Celsius, suggesting that this species has the ability to tolerate or be active at low temperatures, similar to the temperature regime tolerated by *Thamnophis sirtalis* (Hawley and Aleksiuik, 1975; Reichenbach and Dalrymple, 1986; Shine et al. 2001b).

The routine behaviour of *Thamnophis radix* was like that of 'typical' garter snakes in general. For example, as ectotherms, attaining preferred body temperatures through thermoregulation (i.e. basking) was an important activity for these snakes, and I frequently observed basking behaviour (i.e. stretched at higher temperatures or coiled at lower temperatures). I observed such behaviour across all sizes and sexes of snakes, suggesting that thermoregulation plays an important physiological role for a range of activities, including spring emergence, digestion, pregnancy, foraging or escaping from predators (Arnold and Bennet, 1984; Gregory, 1984c; Peterson et al., 1993). Although I measured ground temperature in the shade at each capture site, such measurements are imperfect indicators of the actual body temperatures of snakes (Peterson, 1987). Furthermore, different body temperatures may characterize different activities (e.g. digestion, foraging, reproduction; Lilliwite, 1987), so the temperatures I recorded give only a crude initial glimpse into the temperature relationships of these animals. Studies using temperature-sensitive radio-telemetry and measurements of effective ambient temperature using physical models (Peterson, 1987; Blouin-Demers and Weatherhead, 2001b) are needed to determine the thermoregulatory capabilities and limits of these northern snakes.

CHAPTER 2 –POPULATION PROFILE OF THE PLAINS GARTER SNAKE (*Thamnophis radix*) IN CENTRAL ALBERTA: SEXUAL DIMORPHISM, GROWTH AND REPRODUCTION.

INTRODUCTION

Variation in nature is a precursor for evolution, and the study of differences in life histories of animals in their natural surroundings is a fundamental part of wildlife ecology (reviewed in Roff, 1992; Stearns, 1992). Pronounced geographic variation in life-history traits is often present in species with large ranges (Gregory and Larsen, 1993; Sorci et al., 1996), especially when a species' range extends across different habitat and temperature regimes. The ideal study would examine diversity in life-history traits across geographically separated populations; however, certain life-history traits (e.g. individual survivorship and mortality rates) are difficult to estimate for species without detailed, long-term studies. By contrast, short-term studies of body size, growth and reproduction can provide an important opening into the analysis and understanding of a species' life-history variation, as well highlight the environmental factors affecting the plasticity of life-history traits.

Body size influences many aspects of an animal's ecology and is closely tied to life-history characteristics such as probability of survival and measures of reproductive success (Sauer and Slade, 1987; Barbault, 1988). The widespread occurrence of sexual size dimorphism (SSD) further suggests that the two sexes often differ in aspects of their life-history strategies because size differences will have different ecological consequences for survival and/or reproductive fitness of males and females (Shine, 1993). Growth to a particular body size may determine an animal's future ability to secure and exploit resources, such as food, space or mates. Reproductive characteristics, such as breeding frequency or litter size, are also affected by body size. Examining the trade-offs between growth and reproduction is an important step towards understanding the various components of a species' life-history strategy (Stearns, 1989, Shine, 2003) and of the plasticity seen in many species, both within and between populations.

The secretive nature of snakes, as well as their low population densities, has made detailed life-history studies difficult to conduct (Turner, 1977; Parker and Plummer, 1987). Despite these shortcomings, several studies have provided valuable ecological

information for the management and conservation of particular species, as well as contributed to knowledge of life-history evolution, both in general and in snakes in particular (Parker and Plummer, 1987; Brown and Weatherhead, 1999; Blouin-Demers et al., 2002; Stanford and King, 2004). Life-history characteristics often vary among different conspecific populations of snakes (Seigel and Fitch, 1985; Parker and Plummer, 1987; Gregory and Larsen, 1993); these variable traits include body size, growth and maturation, and reproduction (Bronikowski and Arnold, 1999; Gregory and Larsen, 1993). Plasticity in such traits may be an important aspect of the general adaptability of wide-ranging species of snakes; documentation of the extent of this geographic variation in their life-history traits is therefore important.

The natricines (Family Colubridae, Subfamily Natricinae) include some of the most comprehensively studied snakes, such as the garter snakes and water snakes of North America (Rossman et al., 1996; Gibbons and Dorcas, 2004). That said, the ‘*sirtalis*’ model, based on studies of the Common Garter Snake (*Thamnophis sirtalis*), dominates the literature on the life history of garter snakes inhabiting northern regions, not to mention the literature on snakes in general (Carpenter, 1952a; Fitch, 1965; Gregory, 1971, 1974, 1977a; Larsen, 1986; Larsen and Gregory, 1989; Gregory and Larsen, 1993, 1996; Shine et al., 2001b). Although other species of *Thamnophis* have been studied in varying depth (Gregory, 1984a; Farr and Gregory, 1991; Brodie, 1993; Wayne, 1999; Gregory and Gregory, 2006), we know relatively little about the life histories of several species, including some that are geographically widespread.

Plains Garter Snakes (*Thamnophis radix*) are medium-sized snakes that range over a wide geographic area from New Mexico to Illinois and north to central Alberta, Canada, sometimes occurring in high densities, which makes them attractive for population studies (Seibert, 1950; Dalrymple and Reichenbach, 1981). Nonetheless, there have been relatively few studies of the population ecology of this species (reviewed by Walley et al., 2003) and none at higher latitudes, where we might expect potential range-limiting factors, such as length of active season, to have a significant influence on life-history traits. Here, I describe patterns of sexual size dimorphism, growth and population size structure, and reproductive traits of females in a population of *Thamnophis radix* near the species’ northern distributional limit in central Alberta. I predict that the short growing

season at this high latitude should result in lower growth rates of snakes compared to more southerly populations and that, because postpartum females will have less time available for replenishing their reproductive stores, females will be less likely to reproduce in consecutive years. However, because snakes that grow slowly could still grow for longer and reach large sizes and have large litters, I make no specific predictions about latitudinal trends in litter size. I also briefly report on the potential sources of mortality for this species at this study site. Finally, the mark-recapture data collected in this study (see also Chapter 1) provide a basis for the future study of population size dynamics and survivorship of *Thamnophis radix* at Miquelon Lake Provincial Park.

METHODS

Body size & growth – I collected data on body size and other morphological measures in the summers of 2005 and 2006; added to this was a smaller data set collected by P. Gregory in various years from 1990 to 2004. I opportunistically captured snakes by hand and gave each an individual mark for future recognition by clipping subcaudal scutes in unique patterns (Brown and Parker, 1976a). I determined the sex of each snake by probing for hemipenes in juveniles and adults (Schaefer, 1934) and attempting to evert hemipenes in neonates (Gregory, 1983). I recorded the following measurements for each snake: snout-vent length (SVL), tail length (TL), head length (HL), head width (HW) and body mass (BM). I measured SVL and TL to the nearest 5 mm by stretching snakes along a metre stick. HL was measured to the nearest 1 mm using metric calipers. To measure HW, I used a metric inking template; HW was the smallest hole through which the snake's head would fit without forcing. I weighed snakes to the nearest gram using sliding Pesola® hand-held spring scales of varying sizes. General body condition of snakes was recorded including number, type and location of injuries. I also gently palpated each snake to force regurgitation of any food items it contained (see Chapter 3). Snakes were released between 5 to 10 minutes after capture. Snakes that were recaptured after a period of one week or more were remeasured.

I identified three size classes (neonate, juvenile, and adult) using snout vent length, reproductive condition for females, and time of the year. Neonates were less than 200 mm in snout-vent length, and captured during the latter part of the summer season (i.e.

recently born in August). Juveniles (200 to 350 mm for males and 200 to 400 mm for females) were distinguished from adults (> 350 mm for males and > 400 mm for females) based on the minimum sizes of courting males and gravid females (Stanford, 2002; Walley et al., 2003). Because of allometric relationships, I log-transformed all morphometric data before analysis (Gregory, 2004a). I directly compared the snout-vent lengths of males and females using ANOVA. However, because tail length, head dimensions and body mass all vary with body length, I used SVL as a covariate in ANCOVA when comparing the sexes for these variables. Prior to ANCOVA, I tested for homogeneity of slopes.

An annual active season of 152 days was determined by the earliest (2 May) and latest (30 September) observed capture dates. To examine growth in snakes, I used only the snakes captured in 2005 and 2006, and only if the recaptures were separated by a period of 15 days or more. For snakes that were captured in the same year, I calculated growth interval as the number of days between original capture and recapture (for individuals that were captured multiple times in the same season, I used the interval between the first and last capture). Because snakes were assumed to grow only during the active season (Macartney et al., 1990), to determine growth interval for snakes captured in two subsequent years, I had to subtract the length of the inactive period (213 days) from the number of days between original capture and recapture. I defined growth (mm) as the absolute change in SVL between captures, and divided growth by the interval (time) to get growth rate (mm/day):

$$\text{Growth rate (mm/day)} = (\text{SVL}_{\text{Final}} - \text{SVL}_{\text{Initial}}) / \text{time interval}$$

Due to my small sample size, I pooled within- and between-year captures for analyses of growth. I used ANCOVA to test for differences between male, gravid and non-gravid female growth rates, using growth rate as the response variable, sex/reproductive condition as a factor and SVL as the covariate.

Reproduction – I determined reproductive condition (i.e. gravid, non-gravid, post-partum) of wild caught females via abdominal palpation for eggs, which also allowed me to count eggs. Palpation of females for egg counts has been shown to be a reasonable method for estimating litter size in garter snakes (Farr and Gregory, 1991). To obtain

additional information on litter size, sex-ratio and offspring size, in the summer of 2005, I captured 8 gravid females and held them in captivity (5 to 12 weeks) until parturition. These snakes were housed individually in 20-litre plastic aquaria and were provided with shelter, water and food (3 fish every two days). The housing room was not thermally regulated, but snakes had constant access to a heat source, with a heating blanket placed under one end of each aquarium. After parturition, neonate snakes were measured (SVL, TL, HL, and HW), weighed and marked and then released at the mother's capture site within two days of birth; I also measured and weighed any stillborn offspring. Gregory et al. (1992) included counts and weights of yolks in their study; however, undeveloped yolks were difficult to differentiate as separate individuals in my litters and were not included in any of the counts. Morphological differences between sexes and families for neonate snakes were analyzed using 2-factor ANCOVA (morphological trait as the dependent variable, sex as a fixed factor, family as a random factor, and female SVL as a covariate). Linear regressions were used to analyze relationships between size of female, size of offspring and litter size. I used logistic regression to examine the probability of a female being gravid in relation to body size.

Mortality – Observations of predation events were recorded with respect to location, time of day, estimated size of snake, and predator type. All road-killed snakes were processed in the same way as live snakes and preserved in 70% ethanol for future study.

Statistics – All analyses were done with SAS 9.1 and used a rejection level of $\alpha = 0.05$. All statistics are presented as mean \pm SD.

RESULTS

Body size – I obtained measurements from 363 (207 female, 156 male) *Thamnophis radix*. Of these, 290 were adults, 56 were juveniles and 17 were neonates (Table 2). The smallest snake was 151 mm SVL and the largest snake captured was 740 mm SVL. Very few snakes less than 250 mm SVL were captured; most males were in the 350-550 mm SVL range and most females ranged from 500-700 mm SVL (Fig.6).

Table 2. Comparative body measurements (SVL = snout-vent length, TL = tail length, HL = head length, HW = head width, M = body mass, N = sample size) for three size classes of Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 1995-2006. Means \pm SD are shown above the ranges. M = male, F = female, NG = non-gravid, G = gravid. Neonates < 200 mm, juvenile males = 200-350 mm, juvenile females = 200-400 mm, adult males > 350 mm, and adult females > 400 mm.

SIZE	SEX	N	SVL (mm)	TL (mm)	HL (mm)	HW (mm)	M (g)
Neonate	F	11	169.9 \pm 14.1 (151 - 195)	57.9 \pm 30.3 (44 - 143)	6.44 \pm 0.35 (5.9 - 7.0)	4.6 \pm 0.27 (4.4 - 5.0)	2.4 \pm 0.97 (1.3 - 4.5)
	M	6	185.5 \pm 6.7 (176 - 196)	48.8 \pm 6.4 (42 - 56)	6.3 \pm 0.95 (5.1 - 7.4)	4.63 \pm 0.25 (4.5 - 5.0)	2.3 \pm 0.62 (1.8 - 3.4)
Juvenile	F	36	308.9 \pm 54.1 (210 - 400)	83.9 \pm 19.2 (49 - 120)	9.0 \pm 1.9 (6.6 - 11.3)	6.9 \pm 1.1 (5.0 - 10)	15.1 \pm 12 (3.0 - 55)
	M	20	280 \pm 51.9 (207 - 350)	79 \pm 15.2 (54 - 98)	8.3 \pm 1.6 (6.3 - 10.7)	6.2 \pm 0.9 (4.5 - 7.5)	10.7 \pm 5.7 (2.8 - 23)
Adult	F (NG)	75	530.7 \pm 97.5 (404 - 760)	133.4 \pm 30.1 (36 - 232)	14.4 \pm 3.4 (9.1 - 26.2)	9.8 \pm 1.8 (7 - 14)	73.9 \pm 42.2 (26 - 187)
	F (G)	85	624.3 \pm 77.2 (460 - 780)	150.2 \pm 31.6 (65 - 209)	16.2 \pm 2.7 (10 - 22)	11.6 \pm 1.5 (9 - 14)	133.7 \pm 47.9 (53 - 260)
	M	130	463.7 \pm 64.8 (355 - 635)	136.1 \pm 28.0 (19 - 194)	12.0 \pm 1.9 (8.1 - 18.3)	8.6 \pm 1.1 (6.5 - 12)	43.9 \pm 17.8 (18 - 95)

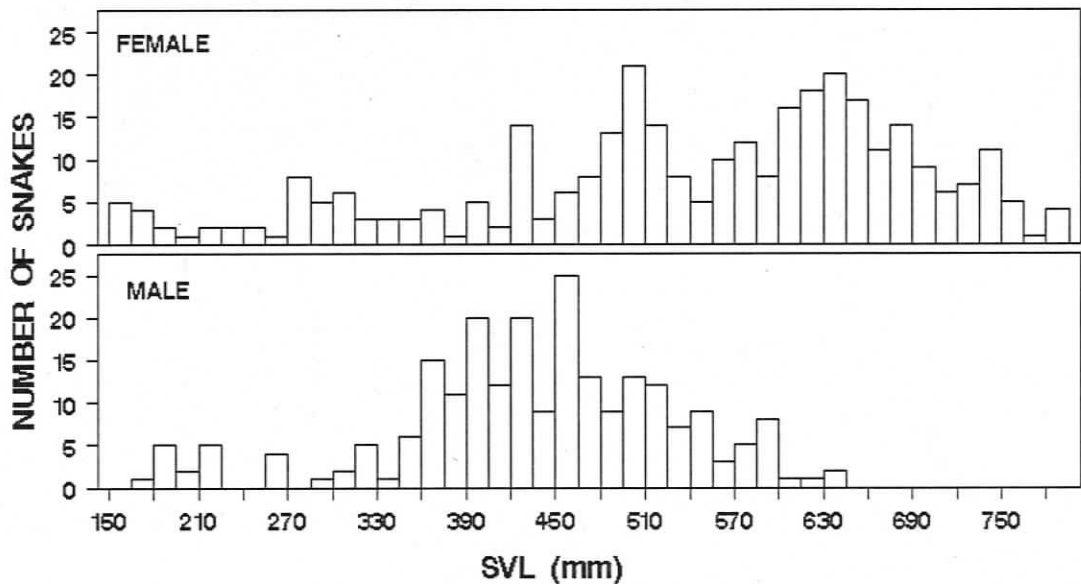


Figure 6. Body size distribution of female and male Plains Garter Snakes (*Thamnophis radix*; females = 207; males = 156) captured at Miquelon Lake Provincial Park, Alberta, 1995-2006.

Overall, females were larger than males in body length and head dimensions (Fig.7). Adult females were significantly longer (SVL) than males (ANOVA, $F_{1,361} = 33.19$, $P < 0.0001$). Females also had longer and wider heads than males relative to body length (ANCOVA; HL – $F_{1,310} = 20.69$, $P < 0.0001$; HW – $F_{1,310} = 39.11$, $P < 0.0001$; SVL as covariate, slopes homogeneous; Fig.8 and 9).

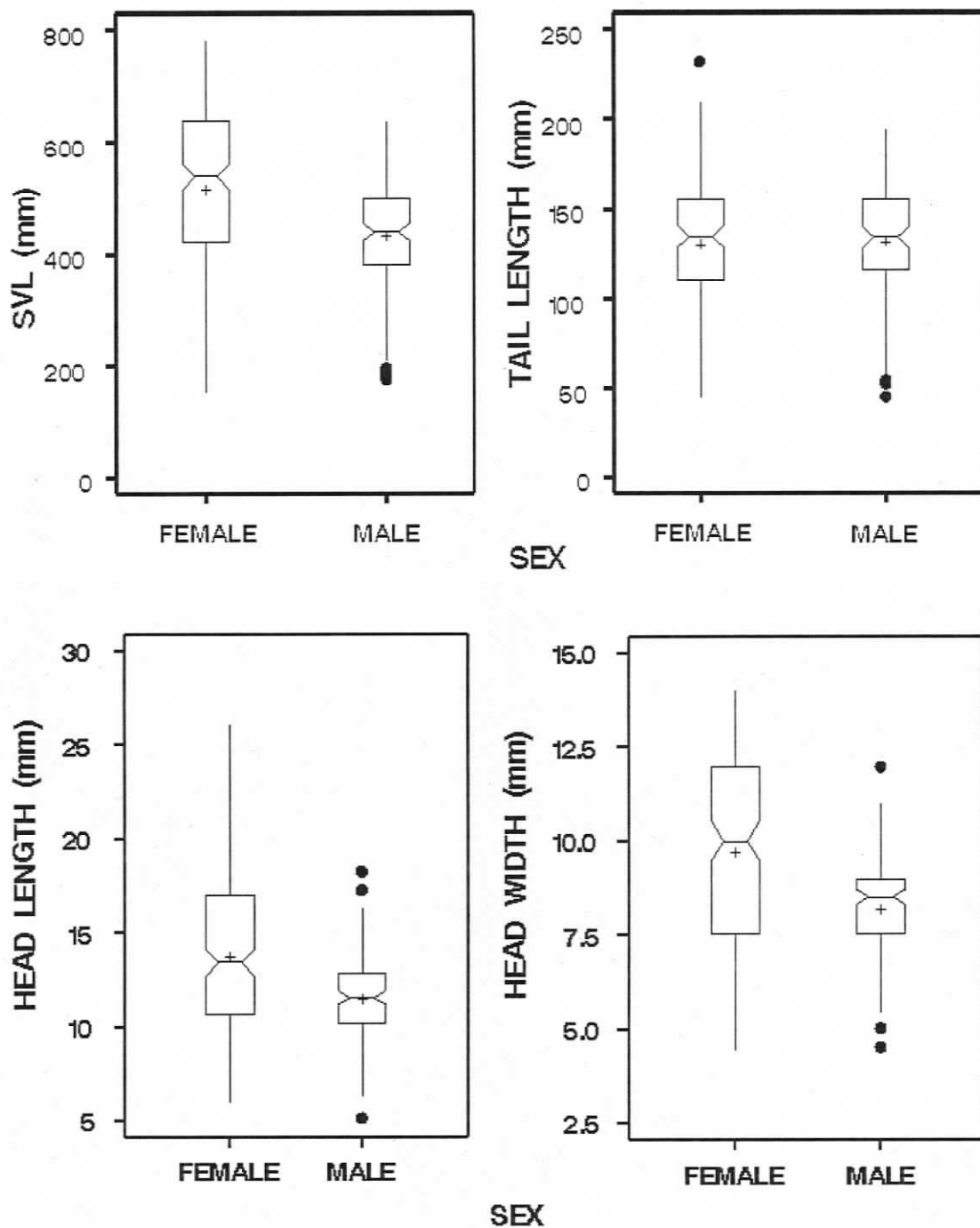


Figure 7. Box and whisker plots of snout-vent lengths (SVL, mm), tail lengths (TL, mm) and head dimensions (HL and HW, mm) for female and male Plains Garter Snakes (*Thamnophis radix*) captured at Miquelon Lake Provincial Park, Alberta, 1995-2006. Horizontal line in each box is the median, the mean shown as a positive sign. Upper and lower boundaries of the boxes represent the 25th and 75th percentiles. Whiskers of boxes or black dots represent the extreme values. Sample size: females = 207, males = 156.

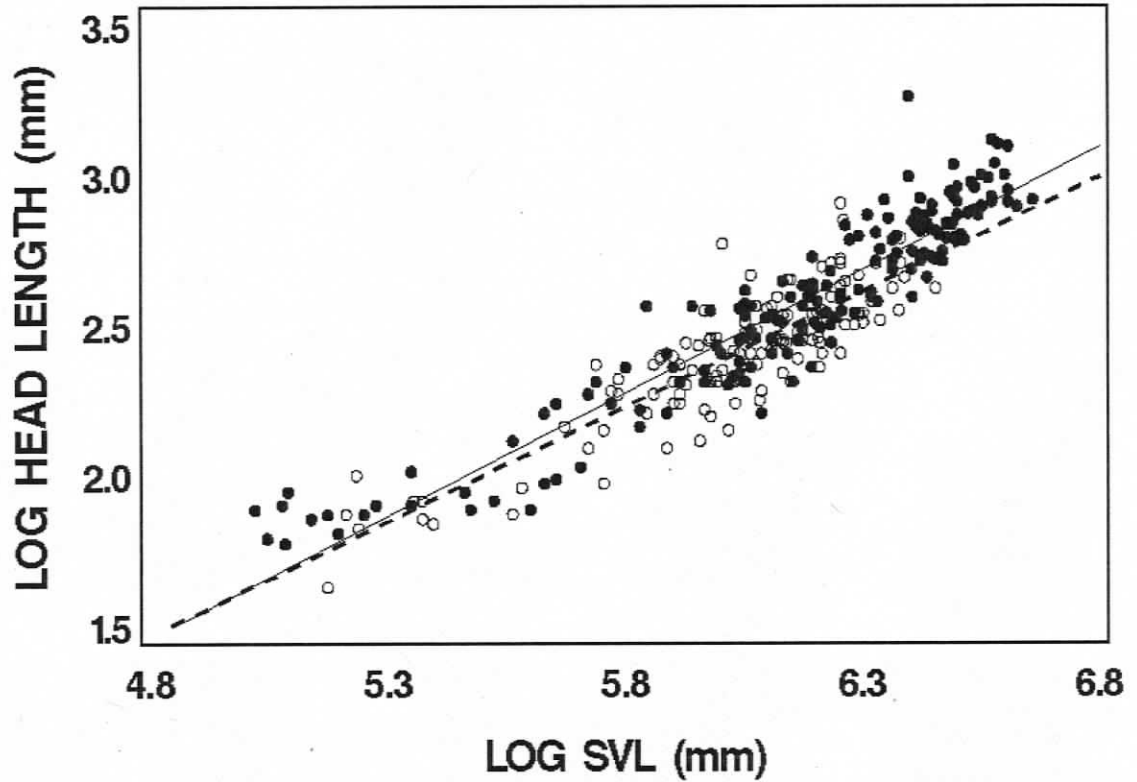


Figure 8. Relationship between log head length (HL, mm) and log body size (SVL, mm) for Plains Garter Snakes (*Thamnophis radix*) covering the range of sizes encountered at Miquelon Lake Provincial Park, Alberta, 1995-2006. Females = filled circles (thin solid line: $Y = -2.47 + 0.82X$), males = open circles (dashed line: $Y = -2.19 + 0.76X$).

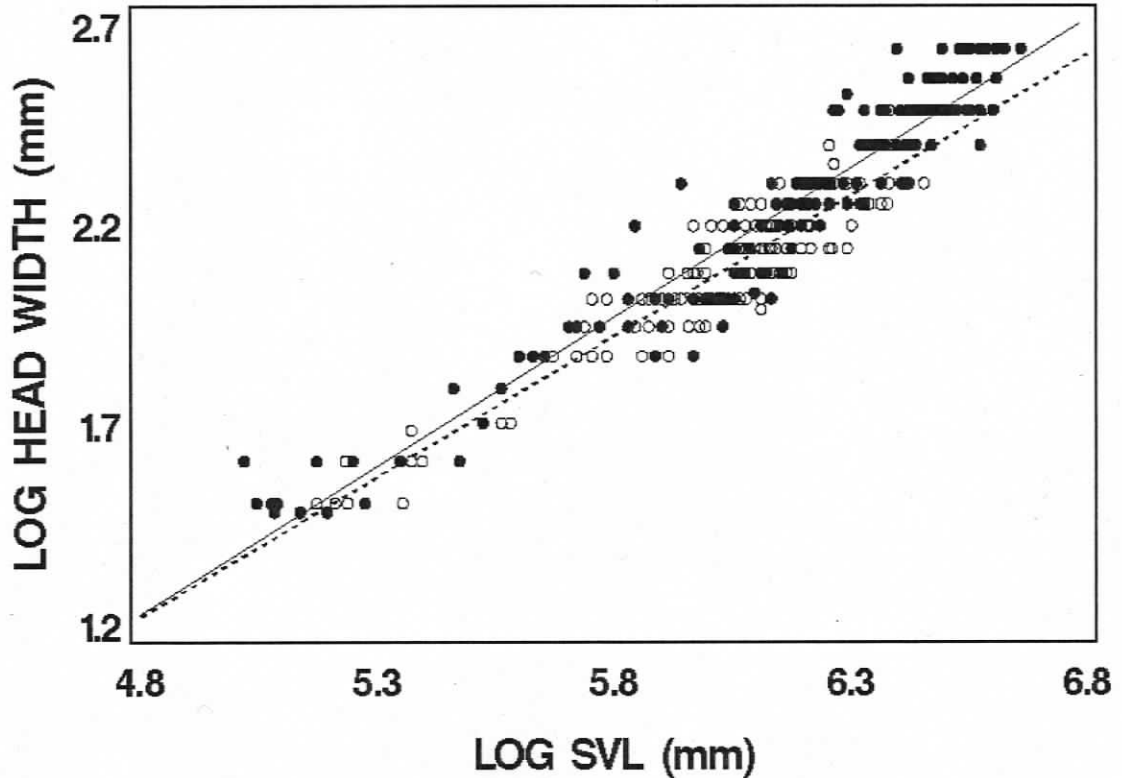


Figure 9. Relationship between log head width (HW, mm) and log body size (SVL, mm) for Plains Garter Snakes (*Thamnophis radix*) covering the range of sizes encountered at Miquelon Lake Provincial Park, Alberta, 1995-2006. Females = filled circles (thin solid line: $Y = -2.35 + 0.75X$), males = open circles (dashed line: $Y = -2.16 + 0.70X$).

To compare tail lengths between the sexes, I used only snakes that had intact tails (i.e. no previous tail loss injury; $N = 254$). There was a positive significant linear relationship between body size and tail size ($r^2 = 0.83$, $P < 0.0001$). I found a significant heterogeneity of slopes between the sexes in tail length ($F_{1, 250} = 35.36$, $P < 0.0001$; steeper slope in males; Fig. 10). I then removed smaller snakes (< 400 mm SVL) and analyzed large snakes separately. Among large snakes, I found that males had relatively longer tails than females (ANCOVA; $F_{1, 130} = 51.68$, $P < 0.0001$, SVL as covariate, slopes homogeneous).

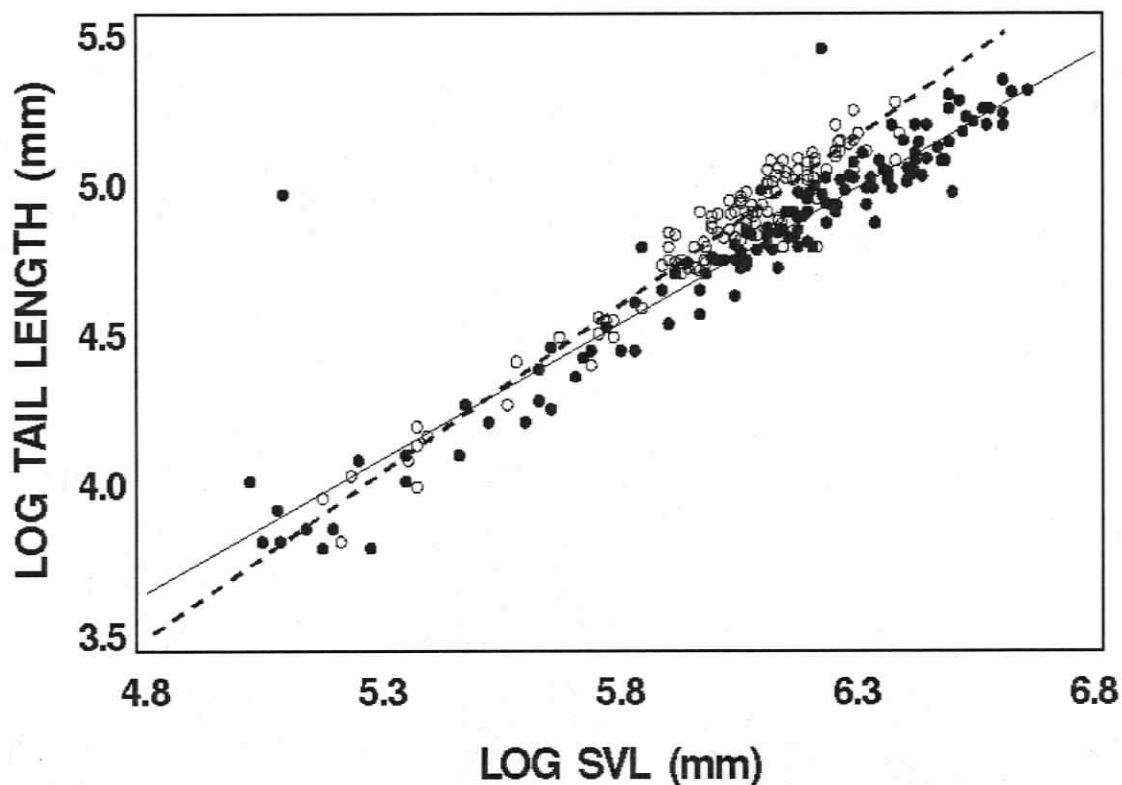


Figure 10. Relationship between log tail length (TL, mm) and log body size (SVL, mm) for female and male Plains Garter Snakes (*Thamnophis radix*) covering the range of sizes encountered at Miquelon Lake Provincial Park, Alberta, 1995-2006. Females = filled circles (solid line: $Y = -0.68 + 0.89X$), males = open circles (dashed line: $Y = -1.87 + 1.11X$).

Because female mass is greatly affected by reproductive status, I tested for differences in body mass among males, reproductive and non-reproductive females. I compared the slopes of each group and found homogeneity of slopes between males and non-gravid females ($F_{1, 272} = 0.53$, $P = 0.47$), and heterogeneity of slopes between the previous two and gravid females ($F_{2, 354} = 75.11$, $P < 0.0001$; steeper slope in males and non-gravid females than gravid females; Fig. 11). I found no difference between males and non-gravid females in body mass (ANCOVA; $F_{1, 272} = 3.85$, $P = 0.049$). However, gravid females had larger body mass than both non-gravid females and males (ANOVA; $F_{2, 354} = 88.51$, $P < 0.001$; Least Squares Means, $P < 0.001$).

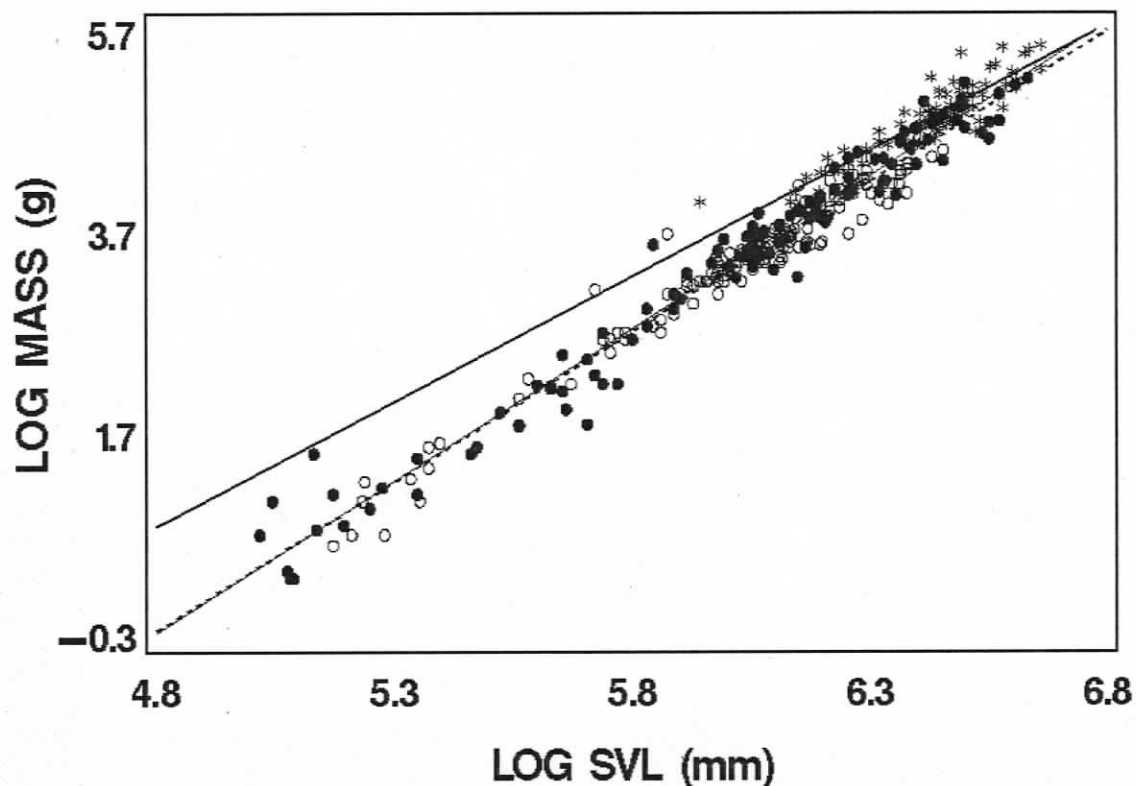


Figure 11. Relationship between log body mass (g) and log body size (SVL, mm) for Plains Garter Snakes (*Thamnophis radix*) covering the range of sizes encountered at Miquelon Lake Provincial Park, Alberta, 1995-2006. Non-gravid females = filled circles (thin solid line: $Y = -14.86 + 3.04X$), gravid females = stars (thick solid line: $Y = -11.20 + 2.49X$), males = open circles (dashed line: $Y = -14.59 + 2.984X$).

Growth – I calculated growth measurements for 50 recaptures of snakes in 2005-06 (males = 20, female = 30). Because short intervals between capture and recapture may not reveal any growth, I used intervals that were 15 days or greater. Both sexes exhibited a decreased rate of growth with increasing size of snake (Fig.12). The average (\pm SD) daily growth rate of males (1.25 ± 1.08 mm/day, $N = 20$) was lower than that of females (1.29 ± 0.81 mm/day, $N = 18$). The growth rate of gravid females was lower than both males and non-gravid females (0.96 ± 0.71 mm/day, $N = 12$). I found heterogeneity of slopes for growth between males, non-gravid and gravid females ($F_{2, 44} = 1.79$, $P = 0.018$; steeper slope in males than both female groups). When I grouped gravid and non-gravid females, there was still heterogeneity of slopes between the sexes ($F_{1, 46} = 5.26$, $P = 0.03$; steeper slope in males than females). Females grew significantly faster than males (ANOVA, $F_{1, 47} = 3.87$, $P = 0.048$).

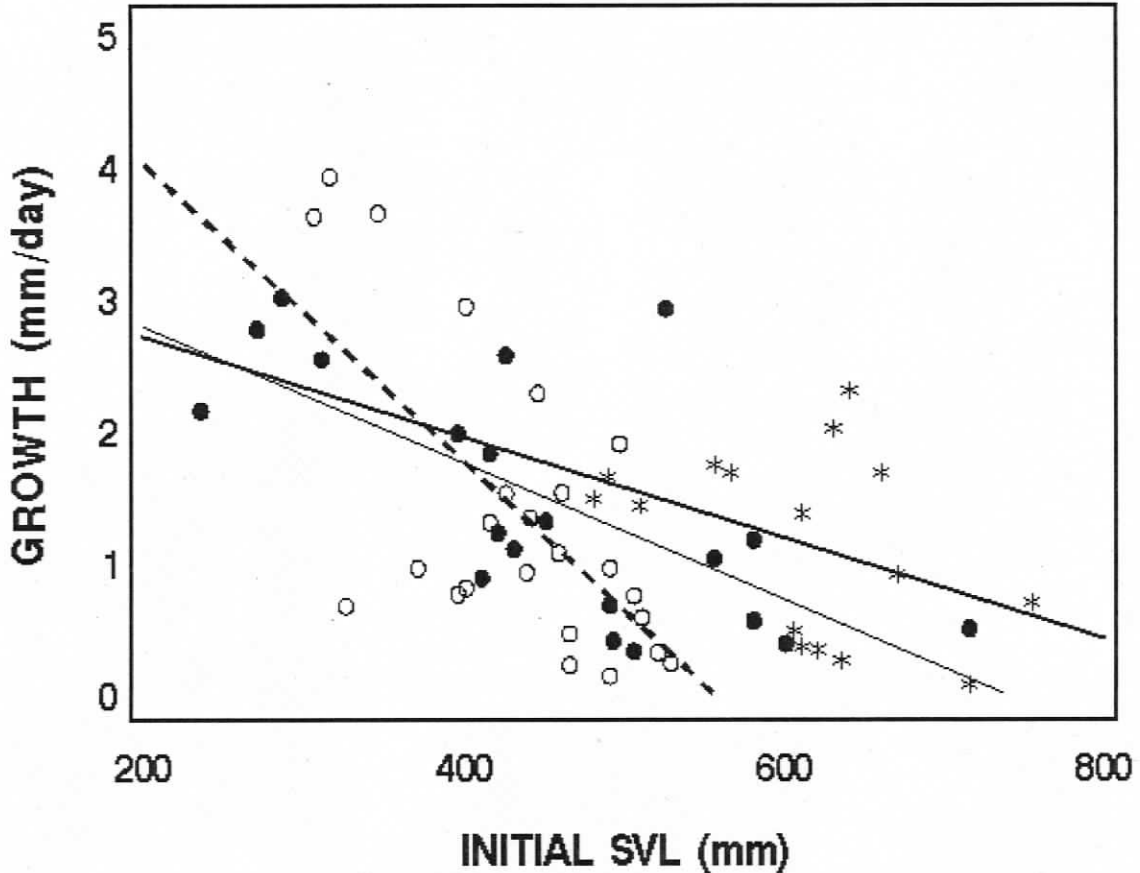


Figure 12. Growth per day (mm) as a function of size (SVL, mm) for male and female Plains Garter Snakes (*Thamnophis radix*) captured at Miquelon Lake Provincial Park, Alberta, 2005-2006. Data are for individual snakes recaptured at least 15 days after first capture (N = 50). Non-gravid females = filled circles (thin solid line: $Y = 3.82 - 0.005X$, N = 18), gravid females = stars (thick solid line: $Y = 5.96 - 0.008X$, N = 12), males = open circles (dashed line: $Y = 6.25 - 0.011X$, N = 20).

Reproduction – Although I obtained slight circumstantial evidence that *T. radix* at MLPP mate in spring, I focus here on female reproductive cycles only and on only the last two stages of the typical four stages in the cycle (vitellogenesis, courtship and mating, pregnancy, parturition). I observed four incidents of apparent courting, all in early May and all consisting of a female and one or two smaller males. Females were captured with eggs in their abdomen from May 10 to August 23. In the wild, based on evidence of wild-caught neonates and post-partum females, parturition likely commenced in late July or early August and continued into late August.

In 2005 and 2006, 81 (43%) of the females I captured were gravid, even though 149 (80%) were of reproductive size (> 400 mm, N = 187). In 2005, 13 females (18%) were

gravid, with 59 (82%) of reproductive size ($N = 72$). In 2006, 68 females (59%) were gravid, whereas 90 (78%) were of reproductive size ($N = 115$). Recapture records showed that only 2 of 11 females were gravid in two consecutive years. Both of these females had larger litters in the second year (19 to 25 and 15 to 43), and showed growth in SVL between the years (35 and 75 mm respectively).

I found a significant relationship between reproductive state and body size, using logistic regression ($\chi^2_1 = 71.97$, $P < 0.001$; Fig.13), with the probability of being pregnant increasing with SVL of snake. Litter size of wild-caught females averaged 23 ± 7.45 and ranged from 7 to 50 offspring. Females averaged 620 mm SVL, with the smallest 380 mm SVL (litter size = 14) and the largest 780 mm (litter size = 37). There was a positive significant linear relationship between size of female and litter size ($r^2 = 0.39$, $P < 0.0001$; Fig.14).

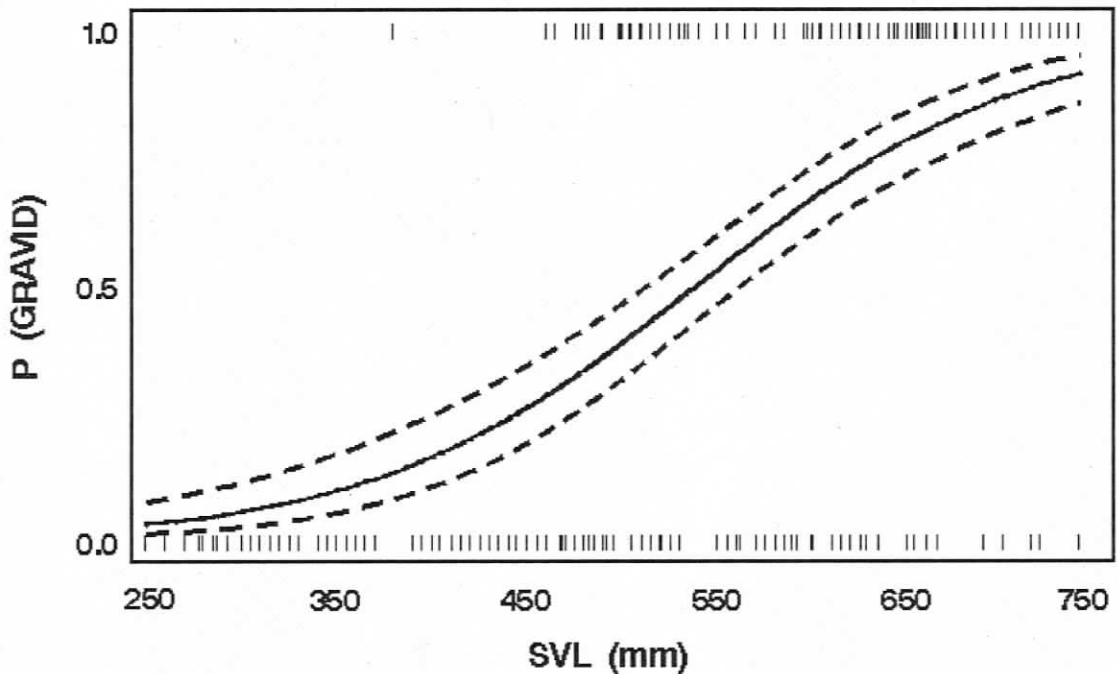


Figure 13. Probability of female Plains Garter Snakes (*Thamnophis radix*) being gravid versus size of snakes (SVL, mm) at Miquelon Lake Provincial Park, Alberta, 1995-2006. Vertical lines at top = gravid females ($N = 85$), vertical lines at bottom = non-gravid females ($N = 122$). Solid line represents predicted values from logistic regression of presence/absence of being gravid against size. Dotted lines represent 95% confidence limits on predicted values.

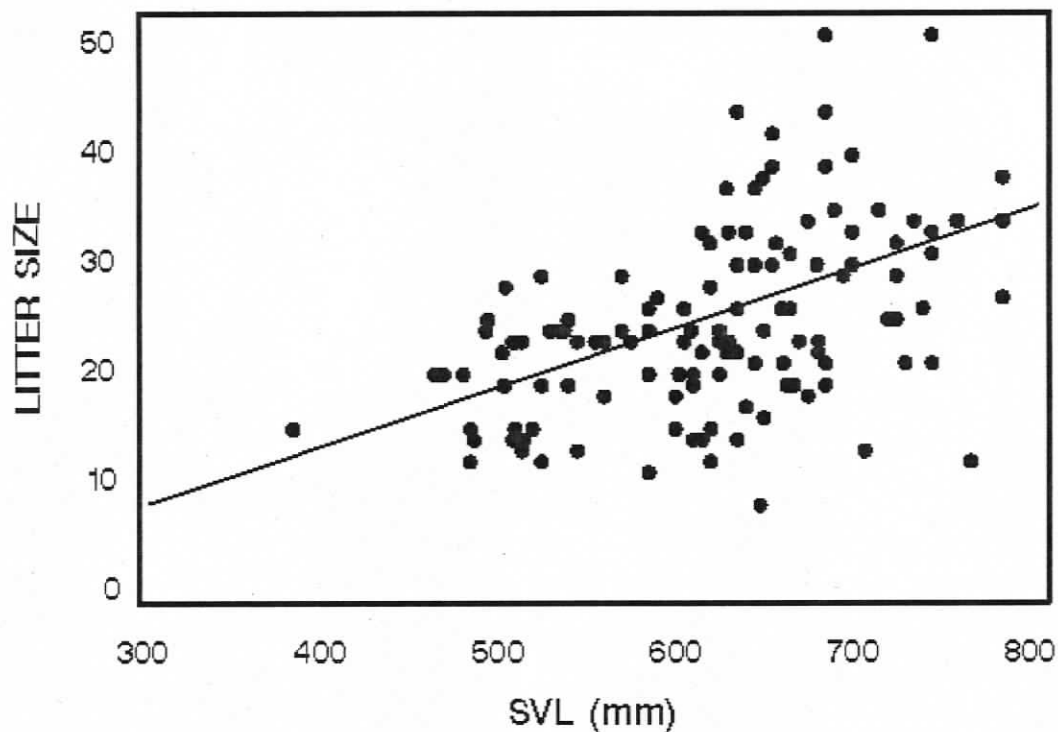


Figure 14. Estimated litter size versus female size (SVL, mm) for Plains Garter Snakes (*Thamnophis radix*; N = 85) at Miquelon Lake Provincial Park, Alberta, 1995-2006. Solid line represents regression equation: $Y = -9.1082 + 0.0543X$.

I collected 8 gravid females (mated in the wild) that gave birth in captivity to a total of 170 offspring (136 live and 34 dead) from August 15 to September 13, 2005. Captive females ranged in size from 620 to 740 mm SVL (average = 695 ± 42.0 SD mm). On average (\pm SD), each female lost 84 ± 19.6 g of mass during parturition. Litter size in captivity ranged from 9-42 with a mean of 27 young. For all eight litters pooled (N = 170), when I tested the sex ratio (female: male = 1:1.13) against a 1:1 null hypothesis I found no significant difference ($\chi^2_1 = 0.59$, $P = 0.44$). Average size of offspring was not correlated with litter size ($r = 0.35$, $P = 0.40$) or size of female parent ($r = -0.24$, $P = 0.56$).

Overall, average (\pm SD) offspring snout-vent length was 159.6 ± 12.1 mm (range 125-180 mm, N = 170; Table 3). The smallest wild-captured snake was 151 mm SVL (August 2006), compared to the smallest captive-born snake of 125 mm SVL (August 2005). No significant differences were found between the sexes of newly born garter

snakes (ANOVA) in either snout-vent length ($F_{1,162} = 0.59$, $P = 0.44$), head length ($F_{1,162} = 0.20$, $P = 0.66$), head width ($F_{1,162} = 0.76$, $P = 0.38$), or body mass ($F_{1,162} = 2.83$, $P = 0.09$; Table 3). However, male snakes had significantly longer tails than females ($F_{1,162} = 103.25$, $P < 0.0001$). No significant interactions were found between female SVL and size of offspring. There was no sex effect on morphological traits, but there were significant differences between the litters in all morphological traits of offspring (2-way ANOVA): SVL ($F_{6,162} = 65.2$, $P < 0.001$), TL ($F_{6,162} = 7.0$, $P < 0.001$), mass ($F_{6,162} = 85.9$, $P < 0.001$), HL ($F_{6,162} = 6.2$, $P < 0.001$) and HW ($F_{6,162} = 11.5$, $P < 0.001$).

Table 3. Comparative body measurements of neonatal male and female Plains Garter Snakes (*Thamnophis radix*) born in captivity at Miquelon Lake Provincial Park, Alberta in 2005. Means \pm SD are shown above the ranges. SVL = snout-vent length, TL = tail length, HL = head length, HW = head width, M = body mass, N = sample size.

SEX	SVL (mm)	TL (mm)	HL (mm)	HW (mm)	M (g)
Male	158.78 \pm 12.6	47.93 \pm 4.3	5.58 \pm 0.34	4.32 \pm 0.17	1.62 \pm 0.42
N = 90	(125-180)	(29-58)	(4.9-6.4)	(4.0-5.0)	(0.5-2.5)
Female	160.5 \pm 11.5	42.51 \pm 3.1	5.6 \pm 0.38	4.3 \pm 0.19	1.69 \pm 0.45
N = 80	(130-179)	(36-52)	(4.6-7.2)	(4.0-5.0)	(0.6-2.5)

Mortality – Evidence of predation on Plains Garter Snakes was rarely observed at MLPP. One gravid female snake was found dead with her abdomen ripped open (unknown cause) and one report of a hawk taking a snake from a gravel road was made in July 2005. All other evidence of mortality (27 individuals) was related to vehicles and park maintenance equipment. Plains Garter Snakes frequently showed evidence of injury. These injuries (N = 129 individuals) consisted of stumped tails (N = 60), scars (N = 90), lacerations (N = 4), and healed bone fractures (N = 3). The frequency of injury increased with increasing size of snake ($\chi^2_1 = 16.71$, $P < 0.001$; Fig. 15). When included as factors in a logistic regression, neither sex ($\chi^2_1 = 2.74$, $P = 0.098$) nor reproductive status ($\chi^2_1 = 0.98$, $P = 0.322$) had an effect on probability of injury.

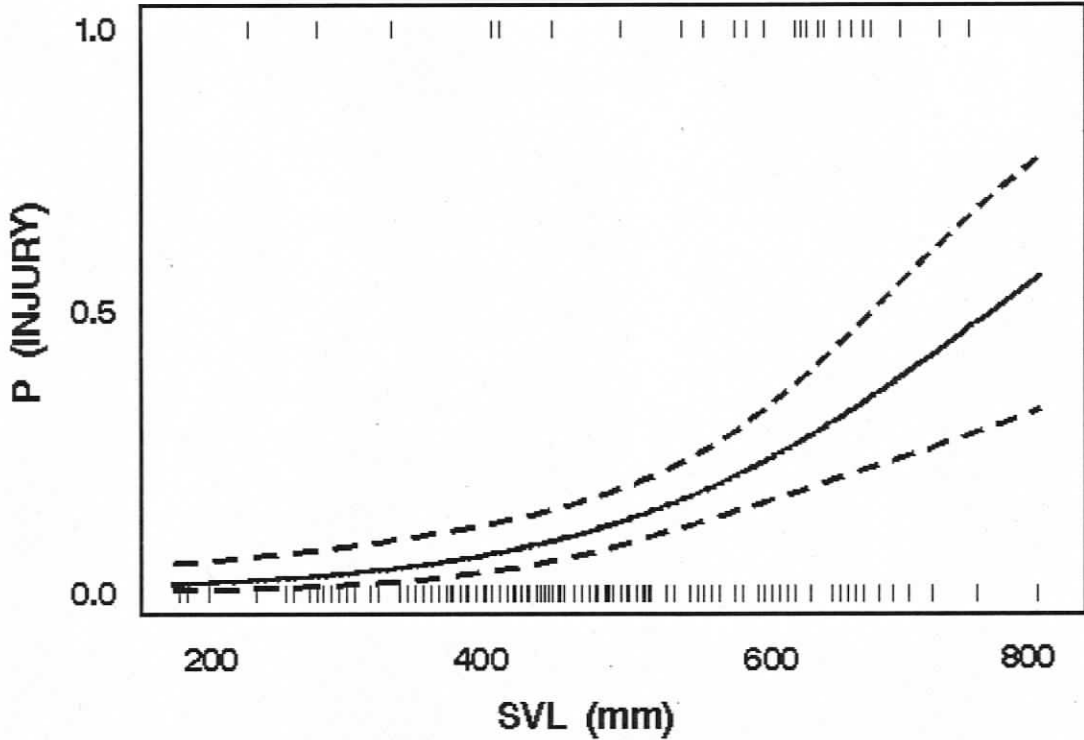


Figure 15. Probability of observing an injury versus size (SVL, mm) of Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 1995-2006. Vertical lines at top = injured snakes (N = 129), vertical lines at bottom = non-injured snakes (N = 190). Solid line represents predicted values from logistic regression of presence/absence of injury against size. Dotted lines represent 95% confidence limits on predicted values.

DISCUSSION

My study shows that body size is an important ecological trait in the natural history of *Thamnophis radix*, as it influences other life-history traits (e.g. growth, fertility). Comparison between my study and others show variation throughout this species' range, indicating the potential plasticity associated with this trait. Geographic variation in body size (and correlated traits) has been observed among conspecific snake populations (Gregory and Larsen, 1993, 1996; Shine, 1991; King, 1989a, 1997; Pearson et al., 2002). Not surprisingly, given the wide geographic range occupied by *T. radix*, there is inter-population variation in body size of snakes. The size-frequency distributions of snakes at MLPP differed from those reported for *T. radix* elsewhere (Cline, 2000; Stanford, 2002); snakes of both sexes had larger body sizes than populations in the south. Average size of neonate snakes at MLPP also appeared to be greater than the reported sizes from more southerly populations (Cline, 2000; Stanford, 2002).

Size differences between males and females have been documented for many taxonomic groups, and sexual-size dimorphism (SSD; Emlen and Oring, 1977; Shine, 1989) is thought to result from divergent selection pressures on males and females, likely due to either sexual competition (Shine, 1993, 1994), parental investment (Emlen and Oring, 1977), or patterns of resource use (Schoener, 1974; Pearson et al., 2002; Luselli, 2006). In species of snakes in which males compete for females, males are typically larger than females; however, in species which lack male combat, the female is typically larger (Shine, 1993). Plains Garter Snakes at MLPP exhibited no obvious male-to-male combat, and consistent with previous studies of natricine snakes (Gregory, 1977a, 2004a; Larsen, 1986; Madsen and Shine, 1993; Brown and Weatherhead, 1999; Stanford and King, 2004), I found clear evidence of sexual size dimorphism: females were longer than males, had relatively bigger heads, and had relatively shorter tails.

Reproductive success of a female is determined by the number of offspring produced and the subsequent survival of those offspring, and because parental care is not common in snakes, a females' investment in offspring is entirely through the allocation of resources to the eggs or developing embryos (Andrews, 1982). In viviparous species, larger females have an increased ability to accommodate more embryos in their body cavities; thus larger sizes of females are selectively advantageous. For *T. radix* at MLPP, there was clear evidence of a positive relationship between size of female and litter size. This link between size and reproductive output is a well-documented phenomenon in female natricines (Fitch, 1965, 1981; Gregory & Larsen, 1993; Gignac & Gregory 2005).

As is typical of snakes in general, male *Thamnophis radix* had proportionally longer tails than females. Dimorphism in tail length was the only sexually dimorphic trait that was established at birth and remained throughout life (excluding snakes with tail injuries). This is consistent with what is seen in other natricines snakes (King et al., 1999; Gregory, 2004a), and is generally attributed to one of three hypotheses (King, 1989b): morphological constraint – longer tail in males to accommodate copulatory organs and muscles; reproductive output – females allocate resources to growth of body length to increase reproductive output, resulting in a shorter tail; male mating ability – males use their tails as aids in courtship and mating, resulting in selection for a longer tail (Shine et al., 1999; Shine et al., 2000b).

Why are head dimensions sexually dimorphic in Plains Garter Snakes? Smaller head size in males may begin as a hormone-based influence (Shine and Crews, 1988), and develop into a dietary divergence between the sexes based on selection (Shine, 1991a, 1991b). Snakes are gape-limited predators – head size influences the size of prey a snake can consume. Because females need food resources to grow to large sizes for increased reproductive output, a larger head may facilitate larger meals (more energy). Although larger Plains Garter Snakes eat larger prey, there was little evidence of sexual differences in diet at MLPP (see Chapter 3).

Despite numerous studies of sexual dimorphism in snakes, most information on this phenomenon comes from studies of adults and very little from examination of younger age groups. For example, inclusion of smaller snakes in such analyses is important because it may illuminate the process by which SSD arises (King et al., 1999). Data from my captive-born snakes suggest that males and females are similar in most size traits at birth, and that sexual dimorphism in *T. radix* arises later in life. Although not fully understood, it has been suggested that the development of these dimorphisms may be a function of age or of differential rates of early growth (Andrews, 1982; Halliday and Verrell, 1988; Badyaev, 2002). An explicit examination of growth patterns of young snakes is required to more fully understand these patterns. This could be accomplished either through experimental studies using captive animals or mark-recapture studies focusing on young snakes.

Garter snakes typically continue to grow over their life span, rapidly as juveniles and at a slower rate after reproductive maturity (Rossman et al., 1996). Factors affecting growth (Andrews, 1982) are likely to be both intrinsic (e.g. phylogeny, maternal effects, sex) and extrinsic (e.g. food, temperature). Sex is the most obvious factor affecting the growth rates of *Thamnophis radix*. Andrews (1982) outlined two possible patterns of growth in juveniles that lead to SSD in adults. Juvenile males and females might have the same growth rates until the smaller of the two sexes stops or slows growth, while the other continues to grow to the larger size. Alternatively, juveniles might grow at different rates early in life, ultimately resulting in adult size differences. Most natricines, including *T. radix* from my study, support the latter pattern of ontogenetic growth and SSD: males and females are similar sizes at birth (King et al., 1999), but females grow

faster, and reach larger adult sizes (Carpenter, 1952b; Fitch, 1981; Shine, 1993; Luiselli, et al., 1997; Gregory, 2004a). Studies of *T. radix* in Illinois have reported similar growth rates between neonate males and females, with sexual differences arising at around 11 months of life (Seibert and Hagen, 1947; Cline, 2000; Stanford, 2002).

Environmental temperatures are likely to have a great influence on growth in ectotherms, including snakes, especially at northern latitudes where there is significant variation in seasonal extremes. A trend of reduced annual growth and delayed sexual maturity with increasing latitude has been observed in other species of reptiles (Christiansen and Moll, 1973; Ferguson and Brockman, 1980; Macartney et al., 1990). Higher annual growth rate in southern populations is perhaps a function of the longer growing season at lower latitudes. Larsen (1986) reported lower annual growth in a northern population of *T. sirtalis* than the growth rates reported by Fitch (1965) in Kansas. Autumn and De Nardo (1995) showed that lizard growth rates decreased when individuals were prevented from thermoregulating. This suggests that lower temperatures and a shorter growing season are presumably in part responsible for the lower rates of growth seen in Plains Garter Snakes in Alberta compared to southern populations (Stanford, 2002), although both of these factors require further examination.

Availability of prey also likely affects growth, especially in temperate-zone environments, where food resources must be secured by growing snakes in a short period of time. Bronikowski and Arnold (1999) found that prey availability was the primary factor affecting variation in growth rates of Western Terrestrial Garter Snakes (*T. elegans*) in California. In an experimental study of *T. elegans*, Gregory and Prelypchan (1994) found variation in growth in response to food intake in juveniles. Other studies also have found relationships between food resources and growth in snakes other than garter snakes (Ford and Seigel, 1994; Luiselli et al., 1997; Lindell, 1997; Taylor et al., 2005). Further examination of the dietary differences between *T. radix* populations (e.g. available prey resources at each site) may help to clarify the role of food availability in affecting the growth, reproduction and other life-history traits of these snakes.

Both growth and reproduction are energetically costly; as such, the first time an animal reproduces often involves an inherent tradeoff between these two traits (Bernardo, 1993, Ford and Seigel, 1994). In order to maximize fitness, animals are predicted to

grow to optimum (usually larger) sizes before reproducing (Smith and Fretwell, 1974). In species that exhibit SSD as adults, males and females usually mature at different sizes (Shine, 1993, Bonnet et al., 1998a). Reproductive success increases with body size (Shine, 1980); therefore, all else being equal, female Plains Garter Snakes should be expected to allocate resources to growth in the first few years of life and to delay maturation until a later age and larger size.

Demographic studies have shown that female garter snakes usually start reproducing at around age two or three (Gregory and Larsen, 1993; Bronikowski and Arnold, 1999; Stanford, 2002). At MLPP, without age-related data, size at sexual maturity was roughly determined from my records of the smallest observed copulating male (350 mm SVL) and also from the smallest female captured with embryos (380 mm SVL). My size data corresponded with sexual maturation results from other studies of *T. radix* in Illinois (males: 325-370 mm SVL, females: 380-400 mm SVL; King et al., 1999; Stanford, 2002). However, because of the strong likelihood of geographic variance in growth rates in a species like *T. radix*, my conclusions about reproductive maturation in these snakes are only estimates that need to be confirmed by further investigation involving age and size correlations (Waye, 1999).

Female garter snakes may breed annually, biennially, or even less frequently (Gregory and Larsen, 1993; Rossman et al., 1996). Depending on body condition, which is likely a result of the preceding year's accumulated resources, a female may not have the resources to breed in two subsequent years (Naulleau and Bonnet, 1996; Bonnet et al., 1998b). Furthermore, females in better condition may give birth earlier, buying themselves more time to feed and replenish their reserves and making it more likely that they will reproduce in successive years (Macartney and Gregory, 1988; Bonnet et al., 2001; Gregory, 2006). The low proportion of gravid females I found compared to the proportion of females of reproductive size within the population, together with the low frequency of annual reproduction (2 snakes), suggest that *T. radix* likely reproduce biennially at MLPP. Other species of snakes, including female *T. sirtalis* reproduce less than annually at similar latitudes (Gregory, 1977a; Larsen, 1986).

Low reproductive output is generally associated with northern areas, as the short growing seasons likely contribute to slower growth rates and less frequent reproduction

(Luiselli et al., 1997). Larsen (1986) found lower reproductive output in high-latitude female *T. sirtalis* compared to southern populations. At MLPP, the average litter sizes observed (23) were slightly larger than for other populations of this species: Illinois (18.4 and 17, Stanford, 2002 and Rossman et al., 1996); Kansas (9.0-11.9, Seigel and Fitch, 1985); Ohio (15.2, Reichenbach and Dalrymple, 1986); Colorado (11.6, Rossman et al., 1996); Nebraska (20.6, Lesch and Fawcett, 1978); and Manitoba (29.5, Gregory, 1977b). My data also suggest that *T. radix* produce some of the largest litters compared to the average litter sizes documented in other species, such as *T. sirtalis* (18 - Carpenter, 1952a; 13.5 - Fitch, 1965; 11.6 - Larsen, 1986). Female snakes may exhibit significant phenotypic plasticity in litter size in response to varying environments; however, without adjusting for body size (Gregory and Larsen, 1993, 1996), latitudinal inter-population comparisons are equivocal. For example, females may compensate for reduced frequency of breeding by having larger litters. Conversely, females in northern environments may simply grow for longer periods before reproducing, and therefore be larger at maturity and have correspondingly larger litters.

At northern latitudes, thermal constraints and a short growing season are imposed on animals and timing of reproduction is important to allow the production of offspring before winter and under the best available conditions for growth and survival (Duvall et al., 1982; Seigel and Fitch, 1985; Seigel et al., 2000). At MLPP, birth took place during August and September. In Manitoba, Gregory (1977b) reported parturition dates for both *T. radix* and *T. sirtalis* from early August on. I observed later parturition times than those reported in other studies of *T. radix* (Stanford, 2002). These differences are likely a result of latitudinal and corresponding temperature differences between northern and southern populations. Female Plains Garter Snakes at higher latitudes may face lower temperatures, and are therefore more likely to retain their eggs because of longer embryonic development times (Peterson, et al., 1993; Charland, 1995). This pattern comes with an explicit reproductive tradeoff: longer gestation allows for development of embryos, but late parturition dates decrease the time for neonate snakes to feed and grow before the onset of winter – both influencing survivorship.

Survival and mortality rates for snakes in the wild are difficult to quantify because of their low densities and secretive nature (Parker and Plummer, 1987), but should be

possible using long-term data sets and modern methods of mark-recapture analysis (Lind et al., 2005). Because mortality patterns are likely to have an effect on other life-history traits, they merit study. For example, mortality rates of different age classes may influence the reproductive strategy of snakes (Luiselli et al., 1997; Bonnet et al., 2002). If mortality is high for older age classes, then females may adapt by having large litter sizes in case they have only one chance to reproduce, but if adult mortality is low, then females may spread out reproduction, with fewer offspring at any given time. Such 'bet hedging' strategies (Slatkin, 1974; Simons, 2007) may additionally vary by geographic location, and may be particularly important in populations at the edges of their ranges.

Although there was little evidence of predation on garter snakes at MLPP, this is undoubtedly observational bias. Other studies have identified avian species as the most likely predators of snakes (Mushinsky and Miller, 1993; Shine et al., 2001b). Hawks and crows were the most likely predators present at this site (personal observation, 2005). Snakes may be vulnerable to predation while foraging in areas without cover, while thermoregulating during pregnancy or after eating, or while moving from one location to the next (Seigel et al., 1987). Injuries in Plains Garter Snakes provided evidence that interactions between snakes and their predators likely occur. Mortality from predation also is likely higher for neonate and juvenile snakes (Jayne and Bennett, 1990, Bronikowski and Arnold, 1999; Shine et al., 2001a; Stanford and King, 2004); which may have partially accounted for the lower injury rates of smaller snakes. That is, larger snakes are older, and therefore have a higher chance of being injured, but they also should be more able to withstand predator attacks and escape with an injury, rather than being killed (Gregory and Isaac, 2005).

Snakes in northern regions also sometimes experience high mortality rates during hibernation (Shine et al., 2001a; Shine and Mason, 2004). Shine et al. (2001a) found that communally denning snakes suffered from several sources of mortality associated with hibernation: 1) predation by corvids during spring emergence; 2) suffocation during winter; or 3) death from unknown causes, possibly due to low body condition or advanced age. Over-wintering mortality was presumed to occur at MLPP, as three of five females radio-tracked did not emerge in the spring (see Chapter 4). However, the potential negative effects of radio-transmitters on the survival of these snakes may have

also been a factor (Weatherhead and Blouin-Demers, 2004). Further demographic studies of Plains Garter Snakes should include measures of mortality (e.g. predation, over-winter deaths), as well as examine the repercussions of non-lethal injuries to the survival of individual snakes (Willis et al., 1982).

The results of my study support what is currently known about sexual size dimorphism, growth and reproduction in snakes in general, but also provide important life-history details for a northern population of *Thamnophis radix* that help to fill the natural-history gap in our knowledge of this species at this latitude. Living in temperate climates, snakes exhibit trade-offs between life-history traits (e.g. growth and reproduction) that may differ from those of southern populations. Further demographic studies on northern populations of this species are required to give a more complete picture of intra- and inter-population variation in life histories of Plains Garter Snakes.

CHAPTER 3 – FOOD HABITS OF THE PLAINS GARTER SNAKE (*Thamnophis radix*) AT MIQUELON LAKE PROVINCIAL PARK, ALBERTA, CANADA

INTRODUCTION

Diet is an important component of an animal's ecology, because success or failure in securing food resources has significant consequences for survival, growth or reproduction (Sih, 1993). Patterns of food resource utilization are influenced by many factors, such as phylogeny, habitat, and prey availability, and studies of diet may provide valuable insight into the evolution of life-history traits (Arnold, 1993; Greene, 1997). Many predators generalize their diets to accommodate the variety of prey types or the patchy abundance of food within a particular environment, whereas others are highly specialized on a few types of prey (Drummond, 1983). The food habits of a species are also an important part of food web dynamics, and in many cases animals act as vectors in the transfer of nutrients between ecosystems (Polis et al., 1997; Huxel and McCann, 1998).

Natricines, a widespread group of new- and old-world snakes, have been extensively studied with regard to their dietary ecology and frequently forage in both aquatic and terrestrial milieus. Among natricines, the new world garter snakes (genus *Thamnophis*) exhibit an especially notable evolutionary diversification into a variety of habitats, thought to be associated with a variety of prey resources and feeding habits (Greene, 1983, 1997). As a group, garter snakes have a wide range of dietary habits (Drummond, 1983). Based on foraging strategies and the types of food eaten, some are specialist predators on a primary prey (e.g. *T. couchi* and *T. melanogaster*), whereas others are more generalized (e.g. *T. sirtalis* and *T. elegans*) and consume multiple prey types (Carpenter, 1952a; Gregory, 1977a, 1978; Arnold, 1981; Drummond, 1983). In general, diets of garter snakes consist of anurans, fish or invertebrates, and occasional mammals, birds and other prey species (Rossman et al., 1996). Most garter snakes are also active foragers (versus sit and wait predators; MacArthur and Pianka, 1966), so they must balance the need for energy from food intake, the energy required to search for and capture prey, and the increased risk of the snake's own exposure to predators while actively foraging. Such tradeoffs often contribute to intraspecific variation among populations, depending on some combination of genetic, spatial and temporal factors, and

this variation in resource acquisition likely has important evolutionary consequences for population dynamics (Lomnicki, 1988; Stearns, 1989).

Previous studies of *Thamnophis* have investigated several of the factors that may influence variation in dietary habits, such as phylogeny (Arnold, 1971, 1981), prey availability (Kephart & Arnold, 1982; de Queiroz et al., 2001; Matthews et al., 2002), and body size (Arnold, 1993; Lind & Welsh, 1994). Most research has focused on a few well-studied species (Rossman et al., 1996), such as the Common Garter Snake (*Thamnophis sirtalis*) and the Western Garter Snake (*T. elegans*). Both of these species typically have broad diets and show considerable inter-population variation (Fitch, 1965; Carpenter 1952a; Gregory & Stewart, 1975; Kephart & Arnold 1982; Larsen, 1986; Bronikowski and Arnold, 1999; Nelson & Gregory, 2000). Other garter snakes species have not been as extensively studied in terms of diet, and it is unknown whether they exhibit the same tendencies of variation and plasticity seen in *T. sirtalis* and *T. elegans*. In particular, at high latitudes, diet of a species may be constrained by reduced diversity of prey and their habitats, and food intake may be limited by short active seasons. Thus, the study of feeding habits of northern snakes can make an important contribution to our understanding of how a species' life history is shaped by extreme environments.

As part of a larger study on the natural history of *Thamnophis radix*, I examined the dietary habits of these snakes near the northern limit of their range in central Alberta. General reports from field guides indicate that Plains Garter Snakes appear to be very similar in diet to other semi-aquatic garter snakes (Rossman et al., 1996; Russell and Bauer, 2000; Walley et al., 2003). Limited dietary information is available from Ohio (Reichenbach and Dalrymple, 1986), Illinois (King and Stanford 2006), Nebraska (Lesch and Fawcett, 1978), Missouri (Seigel, 1984) and Manitoba (Gregory, 1977b; Hart, 1979). Together, these studies highlight the potential for geographic variation in diet among populations. However, limited information is available on the differences between the food habits of northern and southern populations of this species.

My main objectives were as follows: 1) to determine the types of prey eaten by *T. radix* at Miquelon Lake, and thus whether they are generalist or specialist predators; 2) to describe seasonal dietary patterns, including variation due to snake size (i.e. ontogeny), sex, or reproductive state; and 3) to compare the diet of *T. radix* at Miquelon Lake to

literature reports for this species, as well as with reported diets of other species of *Thamnophis*. I predicted that: (1) given the high abundance of frogs at the study site, snakes would consume mainly anurans as prey, at least when adult; (2) given the very wide size range exhibited by *T. radix* from birth to adulthood, prey size would vary ontogenetically; (3) given the locomotory and other costs of reproduction (Seigel et al., 1987), that pregnant females would have a lower frequency of feeding than other snakes (Gregory et al., 1999).

METHODS

I collected snakes by hand in the summers of 2005 and 2006, but also used additional data collected by P. Gregory at Miquelon Lake Provincial Park (MLPP) from 1995-2004. Each snake was measured (snout-vent length, SVL) and given a unique identifying mark by clipping subcaudal scales (see Chapter 2). Reproductive condition and state of ecdysis (i.e. shedding or not) were also noted. I examined stomach contents of each captured snake by gently inducing regurgitation of food items. Prey items observed were counted and classified as invertebrate, anuran, mammalian or unknown. Items were further identified to species, where possible, or recorded as digested. Digested items were excluded from all size analyses because I could not estimate size of prey in those cases. When possible, I determined the direction of ingestion of prey items, either by direct observation of recently swallowed items or by noting which end of the regurgitated prey was digested. I also measured the body length of all anuran and mammalian prey items along a metre stick to the nearest mm. After identifying, counting and measuring prey, I gently palpated them back into stomachs of snakes when possible. This allowed data on diet to be collected without depriving a snake of a meal and interfering with its natural energy intake. I indexed frequency of feeding by proportion of snakes with food in their stomachs.

To reduce pseudoreplication, and because digestion rates were unknown, recently recaptured individuals (e.g. recaptures under 30 days) were not included in the analyses if the first capture yielded stomach contents. I did not study foraging behaviour, largely because very few observations were made of snakes attacking prey in the field. I also did not measure relative prey abundance at the site, but kept notes and grid references of prey

seen in the field. However, in captivity, I incidentally observed feeding behaviour while measuring food intake of eight gravid females housed individually in a heated cabin (see Chapter 2). These snakes were offered three goldfish in a glass bowl, every other day until parturition (up to 2 months); they had constant access to heat (e.g. heating pad) at one end of the tank, and water and shelter.

Analysis of the data consisted mainly of correlations, χ^2 -contingency tables or logistic regressions. All means are given with \pm standard deviation and a rejection level of $\alpha = 0.05$ was used in all statistical tests. I used a slightly different size classification for snakes than the one used in Chapter 2: neonates (< 200 mm); juveniles (200-400 mm); adults (> 400 mm). I was more conservative with the minimum size cut-off for adults; both males and females were considered adults when > 400 mm SVL. To test for differences in prey size between the sexes or months, I used an ANCOVA of prey size by sex or month, with SVL as a covariate to account for sexual size dimorphism (see Chapter 2).

RESULTS

Dietary analysis – Of the 548 snakes captured from 1995 to 2006, 122 snakes had stomach contents (feeding frequency = 22.3%). Between 2005 and 2006, there was no difference in frequency of feeding, prey type or prey size; thus, data were pooled for most analyses. I did not test for differences between the years 1995-2004 because of the patchiness of the data. The number of prey items per capture ranged from 1-10 (mean = 1.56 ± 1.30 SD, $N = 106$), but the majority of snakes contained only one (71.7%) or two (15.1%) prey items in their gut (Fig.16). Only thirteen snakes contained more than two prey items: eleven snakes with three or more frogs, one with 4 nestling rodents, and one with ten large earthworms. No snakes contained more than one type of prey. The number of prey eaten was influenced by size class of snake, with adult snakes having more prey items in their stomachs (χ^2 contingency table, $\chi^2_{10} = 22.23$, $P = 0.0034$).

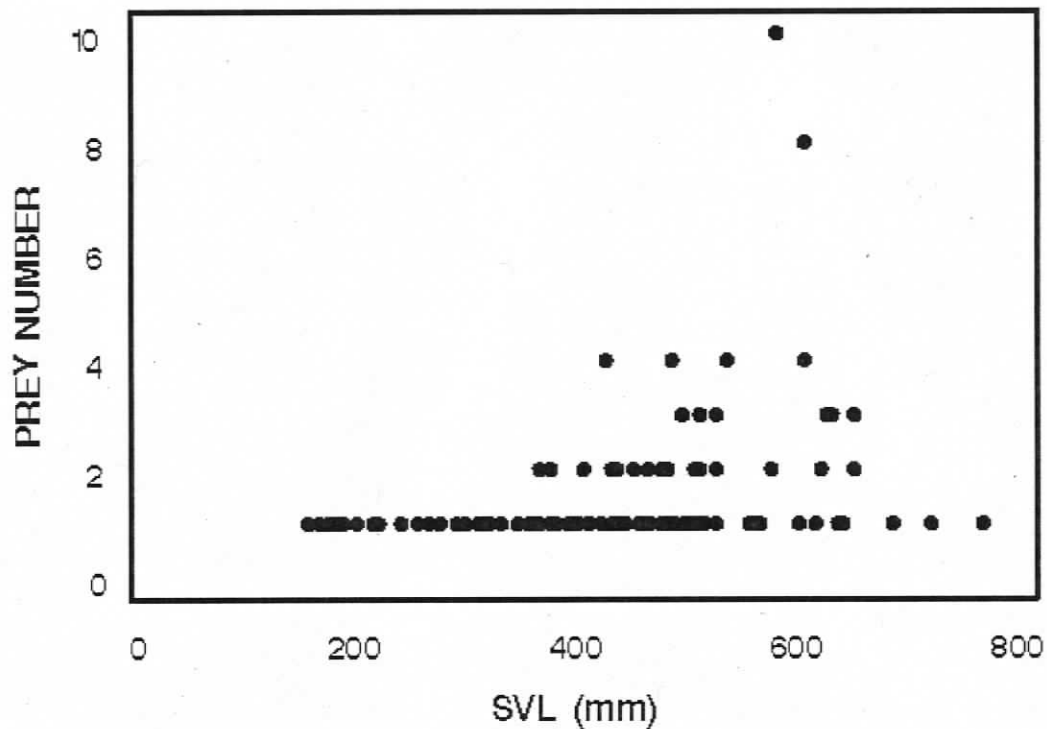


Figure 16. Number of prey in stomach as a function of snake size (SVL, mm) of Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 2005-2006. Each dot represents an individual snake with x prey item(s) in its stomach ($r = 0.31$, $N = 106$, $P = 0.0006$).

Snakes were found with food in their stomachs only from May through to September. When I tested for variation in frequency of feeding day of the active season (with May 3 set to day 1) using logistic regression (treating presence-absence of stomach contents as the binomial dependent variable), there was a weak relationship indicating a higher frequency of feeding earlier in the sampling season (Wald $\chi^2_1 = 3.843$, $P = 0.0499$). To test for seasonal differences in the prey sizes consumed, I used an ANCOVA, given that food size may vary with SVL. I found no significant relationship between in prey size among months (ANCOVA, $F_{4, 60} = 1.81$, $P = 0.14$; slopes homogeneous).

Snakes ate a variety of different prey types and I identified 167 of the 183 prey items found in their stomachs (Table 4). Snakes primarily ate anurans (85%), followed by invertebrates (10%; earthworms and leeches, 9.5% & 0.5% respectively), and small rodents (5%). Sixteen food items were too digested to be identified. Of the two anuran species consumed ($N = 130$, including both larval and metamorphosed forms), *Rana sylvatica* (81%) were eaten with a greater frequency than *Pseudacris maculata* (19%).

When I tested the ratio of frog types against a 1:1 null hypothesis there was a significant difference ($\chi^2_1 = 38.53$, $P < 0.0001$, $N = 106$). I made only one observation of foraging behaviour: a juvenile foraging for tadpoles in a shallow open marsh. *Rana sylvatica* were observed virtually everyday that I looked for snakes, although frog observations ceased in late September. *Pseudacris maculata* were frequently heard in the spring months, but not seen as frequently as Wood Frogs. The small mammals in snakes were nestling rodents ($N = 8$), likely either voles or mice. I determined the direction of ingestion for 143 of the anuran and mammalian prey items. Of these, 106 (74%) were swallowed head first, and 37 (26%) were swallowed hind first. All eight rodent prey items were swallowed head first.

Table 4. Summary of stomach contents of Plains Garter Snakes (*Thamnophis radix*) by size class at Miquelon Lake Provincial Park, Alberta, 1995-2006. Shown are the numbers of snakes containing a prey type, with the percentages of that prey type per size class given in parentheses (%). Neonate < 200 mm, Juvenile = 200-400 mm, Adult > 400 mm.

Size class	Stomach contents				
	Frog	Mammal	Worm	Leech	Unidentified
Neonate	9 (90%)	0	1 (10%)	0	-
Juvenile	37 (97%)	0	1 (3%)	0	-
Adult	59 (74%)	6 (7%)	10 (12%)	1 (1%)	5 (6%)

At MLPP, snakes showed shifts in frequency of feeding and in type and size of prey ingested with body size (presumably ontogenetic). Using logistic regression, frequency of feeding was significantly related to SVL, with the probability of having stomach contents decreasing with increasing size of snake ($\chi^2_1 = 27.41$, $P < 0.0001$; Fig.17). To eliminate any effect of reproductive status on this relationship, I removed gravid females from the analysis, but the relationship remained unchanged ($\chi^2_1 = 6.35$, $P = 0.01$). Neonates had the highest proportion of stomachs with food (33.3%), followed by juveniles (27.2%) and adults (11.7%).

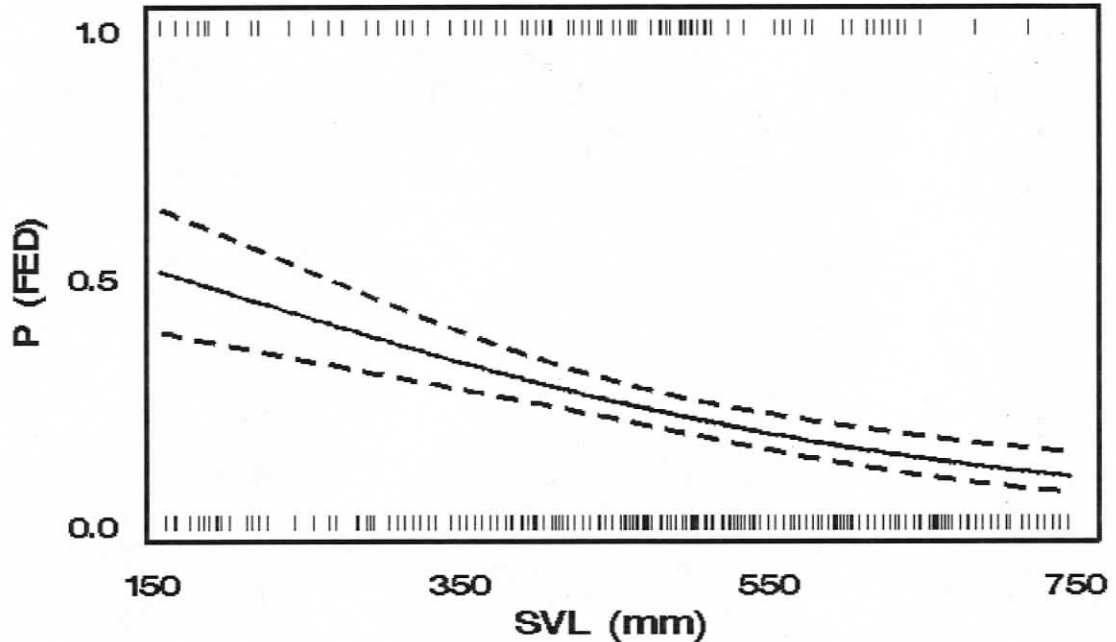


Figure 17. Probability of food present in stomach versus size (SVL, mm) of Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 1995-2006. Vertical lines at top = snakes with food (N = 122), vertical lines at bottom = snakes without food (N = 426). Solid line represents predicted values from logistic regression of presence/absence of food against size. Dotted lines represent 95% confidence limits on predicted values.

Snakes of different sizes also ate a changing diversity of prey types (Fig.18) and prey of different sizes (Fig.19). Neonate snakes (i.e. born that year) ate only prey of smaller sizes, which restricted them to the smaller of the frog species, *Pseudacris maculata*, and small earthworms. Juveniles ate mainly frogs of both species, and occasional small earthworms. Adult snakes ate all prey types, including frogs of all sizes, annelids and small mammals, so the general pattern was increasing diet diversity with size of snake. Mammalian prey were taken by only the largest snakes (> 555 mm SVL). Large snakes also ate the widest range of prey sizes and continued to include smaller food items in their diets.

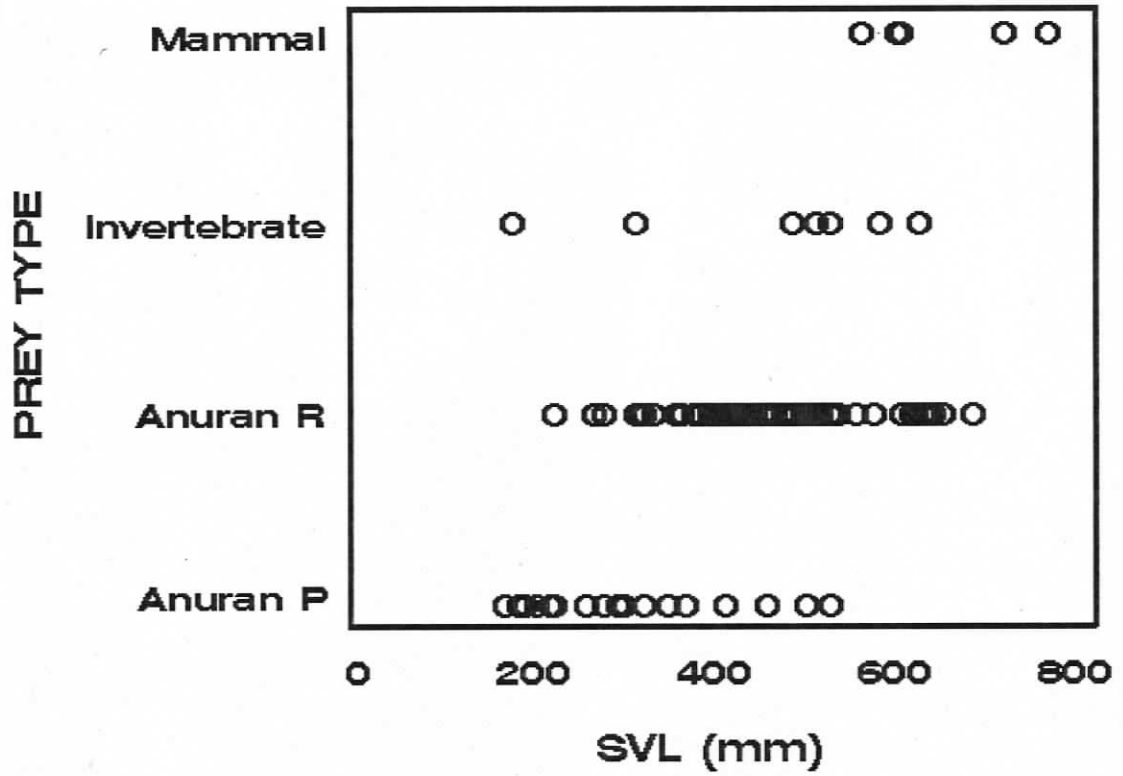


Figure 18. Prey type versus size of snake (SVL, mm) for Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta 1995-2006. Each circle represents an individual snake with a type of prey item (N = 106). Anuran P = *Pseudacris maculata*; Anuran R = *Rana sylvatica*; Invertebrate = earthworm or leech; Mammal = nestling vole or mouse.

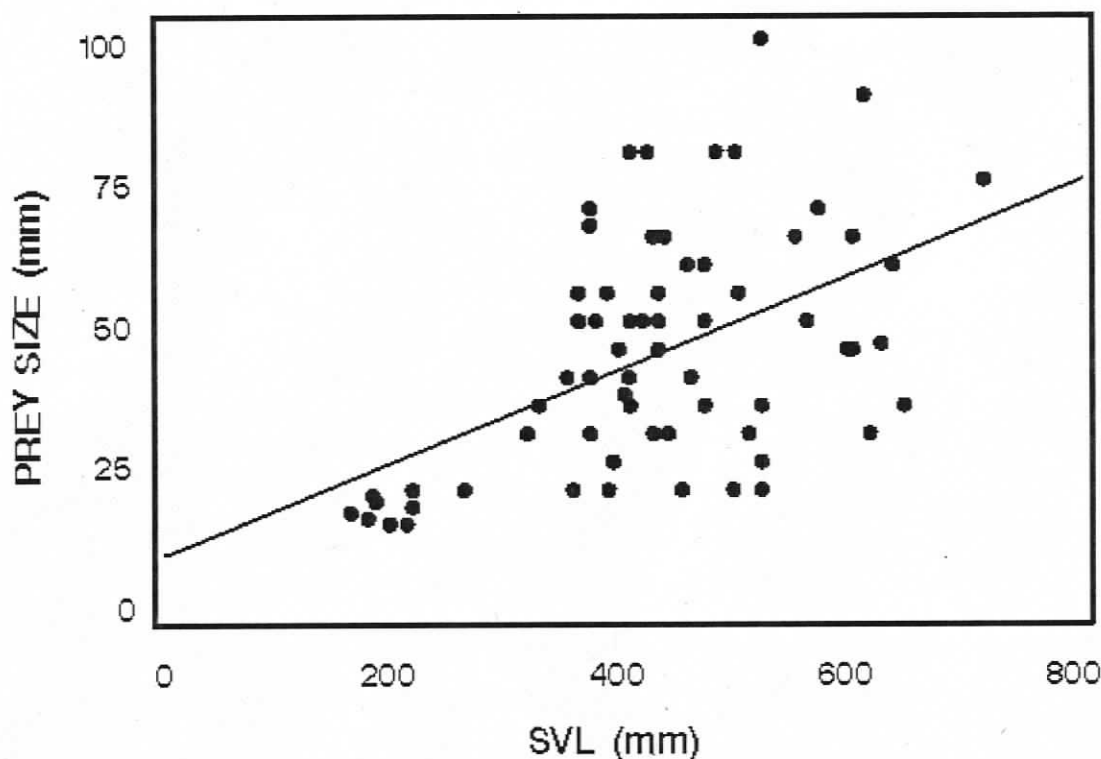


Figure 19. Prey size (e.g. body length, mm) as a function of snake size (SVL, mm) for Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 2005-2006 ($r^2 = 0.4982$, $P < 0.0001$, $N = 67$). Each dot represents an individual vertebrate prey item (anuran or mammalian only). Solid line represents regression equation: $Y = 8.5329 + 0.08302X$.

Overall, there was no significant difference in feeding between the sexes ($\chi^2_1 = 1.815$, $P = 0.1779$). However, because of possible size-based sex differences and effects of reproductive state (i.e. gravid vs non-gravid), I tested gravid females, non-gravid females, all females combined, and males separately for each analysis. Frequency of feeding differed significantly among males ($N = 57/227$), non-gravid females ($N = 46/154$) and gravid females ($N = 19/167$; $\chi^2_2 = 17.65$, $P < 0.0001$). There were no differences in frequency of feeding between males and non-gravid females ($\chi^2_1 = 1.0539$, $P = 0.3046$), but males contained prey more often than gravid females ($\chi^2_1 = 11.655$, $P = 0.0006$). The comparison of female snakes of differing reproductive condition showed that non-gravid females ate more frequently ($\chi^2_1 = 16.967$, $P < 0.0001$) and ate larger prey items ($\chi^2_2 = 10.17$, $P = 0.0062$) than gravid females. This relationship did not change when I included only mature females (defined as females >380 mm SVL, see Chapter 2). Sex had no

significant effect on the type of prey taken ($\chi^2_2 = 2.319$, $P = 0.314$), although 4 of the 5 snakes with mammalian prey in their stomachs were female. Males and females did not differ in the size of prey consumed (ANCOVA with SVL as covariate, $F_{1,63} = 0.02$, $P = 0.90$; slopes homogeneous).

Finally, I compared the food habits of snakes according to their state of ecdysis (shedding or not). There was a significant relationship between feeding and state of ecdysis, whereby snakes that were shedding or about to shed had a lower frequency of feeding than snakes that were freshly shed ($\chi^2_1 = 14.13$, $P = 0.0002$).

DISCUSSION

Diet of *Thamnophis radix* at MLPP varies with particular life-history traits (e.g. body size and reproductive condition; see Chapter 2) and influences other ecological patterns (e.g. habitat use; see Chapter 4). My main general findings are: anurans (85%) appear to be the most important component of diet for these snakes; males and non-reproductive females show little difference in diet; and prey size increases with snake size, but large snakes continue to eat smaller items. As this study site represents the northern limit of this species' range, results from my study provide much needed information for inter-population geographic comparisons of the dietary ecology of this species.

The evolution of ectothermy allows reptiles to tolerate periods of fluctuating feeding frequency (Pough, 1980), and the frequency with which a snake feeds may vary among individual snakes (e.g. size, reproductive status, ecdysis) or according to environmental conditions (e.g. locality, season, prey availability). The frequency of snakes with food in their stomachs is possibly a crude index of feeding frequency because opportunistic searching leads to catches of mainly those snakes that are active on the surface. However, assuming that active snakes comprise a representative sample, the data I collected on feeding frequency (22%) are within the range seen in other studies of snakes and suggest moreover that small, growing snakes feed at a higher rate than larger snakes and that pregnant females have reduced food intake compared to non-gravid snakes. Frequency of snakes with food ranges widely in the literature (5 to 100%; Shine, 1977). In other studies of *Thamnophis radix*, frequency of feeding ranges from 20 to 57% (Jordan, 1967; Gregory, 1977b; Hart, 1979). However, without measuring prey

availabilities or correcting for influential variables such as size and reproductive condition, it is impossible to determine if these differences among studies are real. If they are, they might reflect inter-site variation in productivity, with consequent effects on life-history traits and demography, but this is untested.

Snakes of different sizes will often feed at different frequencies, and such variation has been shown to be related to growth demands and biological restraints (Andrews, 1982; Mushinsky, 1987). Previous studies of growth have shown that garter snakes typically increase rapidly in size for approximately the first 1 to 3 years of life, after which growth slows (Scudder-Davis and Burghardt, 1987; Stanford, 2002; see Discussion from Chapter 2). My data on differences in feeding frequency relating to size suggest that snakes decrease the frequency of feeding as they reach larger sizes. Reproductive condition did not affect this trend, despite the fact that females decreased feeding while gravid. Thus, the high frequency of feeding observed for smaller snakes at MLPP is possibly due to increased energy requirements associated with growth, necessitating the increased consumption of food (Mushinsky, 1987). Nearly half of neonates were captured with food in their stomachs, a large proportion compared to the overall population feeding frequency of only 20%. This suggests the importance of snakes feeding in the same year as birth, rather than relying on endogenous yolk, before entering hibernation (Andrews, 1982; Gregory, personal communication). It would be advantageous for newborn snakes to feed early in life, thereby maximizing growth and increasing their potential for early sexual maturity. A lower frequency of feeding observed in larger-sized snakes was also consistent with the prediction that once adult size has been attained energy requirements are likely to decrease, and therefore, food consumption becomes a requirement only for maintenance and reproduction.

Size-based differences in diet should not be tested without consideration of sex because, in most species of snakes, females and males are different in size (Shine, 1991b). Garter snakes are sexually dimorphic species, with females being the larger sex (Rossman et al., 1996); thus, the sexes may differ in diet simply because they differ in both SVL and relative head size. A few studies of diet in garter snakes have found sex-based differences, particularly in the form of partitioning of food resources (Fitch, 1981; Shine, 1991b), but there are also several that support no dietary differences between the

sexes (de Queiroz et al., 2001). Even when I controlled for the size differences, I found no differences in the diets of males and females at MLPP, except possibly for the greater consumption of small mammals by large females (albeit based on a small sample). Only when reproductive status of females was factored into the analysis did I find any difference in diet between the sexes.

Numerous studies have found reduced levels of feeding in pregnant snakes (Seigel et al., 1987; Gregory and Skebo, 1998; Gregory et al., 1999; Gregory, 2001; Gignac and Gregory, 2005). Such anorexia may due to: 1) physical constraints of lack of space since embryos take up a large amount of the body cavity during later stages of pregnancy and may conflict with digestion processes; 2) constraints on locomotion because of the additional weight of the developing embryos, reducing the female's ability to capture prey and/or escape from predators while foraging (Shine, 1980; Charland and Gregory, 1995); 3) conflicts with other, more immediately pressing requirements such as thermoregulation. I detected no difference in feeding frequency between males and non-gravid females, but gravid females of the same size decreased their feeding noticeably from both males and non-gravid females. Additionally, when the prey sizes of gravid and non-gravid females were compared, non-gravid females ate larger prey items, supporting the idea that feeding is constrained by reproduction.

By contrast with my wild-caught reproductive females, all eight of my captive females ate consistently while gravid, suggesting that physical restriction was not the only constraint for these snakes. By providing both food and heat for snakes, I potentially reduced costs that wild gravid females would have to contend with, such as time spent on thermoregulation (as opposed to foraging). However, without comparing these data to captive feeding of non-gravid snakes, I cannot conclude that gravid snakes do not have reduced feeding (Gregory et al., 1999). The interaction between feeding, thermoregulation and reproductive ecology in female snakes is an important area for further study.

Shedding snakes at MLPP had food in their stomachs significantly less often than did freshly shed snakes. Studies on captive snakes have revealed a decreased frequency of feeding both before and during shedding, varying with temperature, injury or other demographic factors (King and Turmo, 1997). A decrease in feeding, both prior to and

during shedding, is thought to be either from indirect effects of physiological changes (i.e. hormone levels) or from the potential direct effects of visual impairment (i.e. blue-eyed state; King and Turmo, 1997). Although garter snakes rely heavily on chemoreception in searching for prey, as diurnal species they also employ vision to capture prey, especially when prey move (Drummond, 1985); thus, a decreased feeding frequency during shedding may be due to an inability to see effectively. Similarly, ecdysis leading to visual impairment may also leave a snake vulnerable to predators, thus contributing to decreased frequency of feeding due to low levels of activity associated with avoiding predators.

Seasonal shifts in diet are an important component of a species' ecology (Shine, 1977). My results suggest that season influenced frequency of feeding, and that the shifts observed may have reflected two factors: 1) snake activity patterns, and 2) prey availabilities. At MLPP, snakes fed mostly from late May through late August, with overall feeding declining throughout the season, a similar pattern to that reported in other studies (Gregory and Stewart, 1975; Reichenbach and Dalrymple, 1986). Snakes likely feed at a high frequency in spring because they are in relatively poor condition when they emerge from hibernation (Shine et al., 2001a; Shine & Mason, 2004). All snakes ceased eating by late September, presumably in preparation for hibernation, but also perhaps because of decreased food availability (Gregory and Stewart, 1975). During the summer, feeding in *T. radix* may reflect changes in prey availability (Kephart, 1982). Seasonal fluctuations in diet in response to prey availability are common in other species, such as nest predation during the early spring in Black Rat Snakes (Weatherhead et al., 2003), higher insect predation in Racers during the summer (Shewchuk and Austin, 2001), or temporal variation in the diet of *Thamnophis elegans* paralleling the occurrence of toads in response to changes in water levels between years (Kephart and Arnold, 1982).

Thamnophis radix have been reported to eat a wide variety of food types (Jordan, 1967; Lesch and Fawcett, 1978; Walley et al., 2003), a trend very similar to the generalist diets of other species garter snakes (Rossman et al., 1996). At MLPP, the diet of *T. radix* included several different prey types (e.g. anurans, earthworms, leeches and nestling mammals), and is broadly comparable to those reported in other studies (Table 5). However, diet of *T. radix* at this site also differed in some ways from those reported in

other parts of their ranges. In particular, studies elsewhere have reported additional items such as fish (Jordan, 1967), fledgling birds (Sawin et al., 2003), gastropods (Seigel, 1984) and other amphibians (Dalrymple and Reichenbach, 1981; Seigel, 1984). The variety of prey types eaten by *T. radix* lends support to the presence of significant intraspecific geographic variation in dietary habits of this species, as well as its potential for behavioral plasticity.

Table 5. Summary of diets of Plains Garter Snakes (*Thamnophis radix*) populations in various parts of its range. Shown are the number of snakes containing a prey type or the presence of a prey type (X) where numbers were not reported (primary prey type in bold). Totals include number of snakes captured. Anurans and Urodeles include both larval and adult stages. Province or state for the study is shown below the date.

Prey Type	Jordan 1967 Minnesota	Gregory 1977b Manitoba	Hart 1979 Manitoba	Dalrymple & Reichenbach 1981 Ohio	Seigel 1984 Missouri	Present study 2007 Alberta
Anurans	X	5	98	X	X	102
Urodeles	-	-	-	-	X	-
Mammals	-	-	2	-	X	6
Fish	X	-	-	-	X	-
Birds	-	-	-	-	-	-
Annelids	X	1	17	X	X	13
Gastropods	-	-	2	-	X	-
Unidentified	-	1	-	-	-	6
Total	-	21	210	-	-	548

The predominant prey type for a population appears to depend on the locality, although without measuring relative prey availabilities, comparison among populations is not possible. Arnold (1981) found similar geographic variation between the dietary behaviours of coastal and inland populations of *Thamnophis elegans*. For *Thamnophis radix*, anurans were components of the diet at all sites, but not necessarily always the primary food item. At MLPP, Wood Frogs (*Rana sylvatica*) were the most commonly found dietary items, followed by Boreal Chorus Frogs (*Pseudacris maculata*) and this likely was related to the relative availability of anuran prey species at this site. Perhaps, in addition to being more abundant than Chorus Frogs, the larger size of Wood Frogs makes them a more energetically preferable food item (Perz and Purdy, 2001). In Manitoba, near the same latitude as MLPP, both Hart (1979) and Gregory (1977b) reported *R. sylvatica* as the primary prey item, with other anurans (e.g. *R. pipiens*,

Pseudacris triseriata, *Hyla versicolor*, and *Bufo* species) eaten less frequently. Southern populations of *T. radix* have also been reported to consume predominantly small anurans (Dalrymple and Reichenbach, 1981; Seigel, 1984). The overall high frequency of anurans in the diet of snakes may be a function of abundance or availability, or the relative ease of capture and manipulation of frogs compared to other prey species (e.g. fish, birds and mice).

Despite several fish species occurring in the ponds and lakes at MLPP, no fish were found in any snakes there. *Thamnophis radix* has been reported to eat minnows (Jordan, 1967), but is not generally considered a piscivorous species, like *T. elegans* or *T. couchii* (Lind and Welsh, 1994; Drummond, 1983). Large body sizes have been related to both endurance and a snake's ability to maintain appropriate body temperatures while diving for fish (Peterson, 1987; Gregory and Nelson, 1991; Nelson & Gregory 2000). At this site, snakes attained similar sizes to other species of garter snake that have been reported to eat fish (Halloy and Burghardt, 1990; Lind and Welsh, 1994), so it is unlikely that body size was an influential factor. Snakes in my study also voraciously attacked fish when fed them in captivity (e.g. use of open mouth fishing, personal observation). The reason for the lack of fish in the diet of *T. radix* at MLPP is therefore unclear.

Are Plains Garter Snakes, therefore, generalist or specialist predators? On the one hand, with a diet largely focused on anurans, the evidence may support the conclusion that *Thamnophis radix* is moderately specialized. There have been no published reports of populations of *T. radix* existing on diets that exclude amphibians. Consequently, the distribution of Plains Garter Snakes may be a function of the presence of amphibians (Matthews et al., 2002). On the other hand, *T. radix* has also been reported to eat a wide variety of prey species (Jordan, 1967; Hart, 1979; Seigel, 1984), such as invertebrates, mammals and birds, which supports the conclusion that these snakes are generalists. Furthermore, if different amphibian species and anuran life stages are considered to be different prey types, the diet is even more general. Most likely, diet in this species is a function of prey availability at a particular site.

At MLPP, Plains Garter Snakes also consumed different sizes of prey. Differences in the types and sizes of prey eaten by a snake may be due to a combination of physiological (e.g. endurance), morphological (e.g. gape size), or preferential factors (reviewed by

Mushinsky, 1987; Shine, 1991a; Arnold, 1993). Ecological factors such as prey availability, seasonal differences, habitat structure, environmental temperature or exposure to predators may also influence this relationship (Mushinsky 1987; Krause and Burghardt, 2001). Size-based or ontogenetic shifts between prey types have been documented in several species of snakes, including *Nerodia* (Mushinsky et al., 1982), *Thamnophis* (Fitch, 1965; Seigel, 1984; Garcia and Drummond, 1988; Lind and Welsh, 1994), *Natrix* (Gregory and Isaac, 2004), and sea snakes (Voris and Moffett, 1981).

Snakes are gape-limited predators because they swallow their prey whole, and therefore size of prey that can be eaten is partially dependent on size of snake (Forsman, 1996). Increases in size of prey consumed, as well as in the variance in prey size, seem to be common patterns in snakes (Shine, 1991a). Arnold (1993) described two main patterns of ontogenetic shifts in dietary habits of snakes: (1) as snakes grow in size they eat larger prey while continuing to include prey of all sizes; and (2) larger snakes exclude smaller prey items from their diet as they increase in size. My results suggest that Plains Garter Snakes exhibited an increase in the upper size limit of prey as snake size increased. Neonate Plains Garter Snakes (<200 mm), which were likely constrained by their size, were found to consume only small prey. However, *T. radix* continued to eat smaller prey even as large adults, a pattern seen in other species of snakes (Shine, 1977; Voris and Moffett, 1981; Mushinsky et al., 1982). Arnold (1993) suggested that the alternative pattern (2 above) is most common in piscivorous snakes, which may account for large *T. radix* continuing to prey upon small sized prey, since there was no evidence of fish in the diets of snakes at MLPP. Such evidence of ontogenetic shifts in diet highlights the likely importance of multiple prey types of varying sizes in an area for fulfilling a population's dietary needs.

The results of this study suggest that Plains Garter Snakes may play an important role as predators in the aquatic and terrestrial food chains associated with wetland-grassland systems. Due to the high frequency of anurans in their diets, it is also likely that these snakes are highly dependent on wetlands to satisfy their foraging needs. Future studies could expand on this theme by using modern techniques such as stable-isotope analysis (Peterson and Fry, 1987; Post, 2002; Kupfer et al., 2006) to determine how important snakes are as agents of nutrient transfer between aquatic and terrestrial environments.

Additional studies could explore the potential negative impacts of dependence on amphibians in snakes, including: (1) the effects of declining amphibian food resources (Blaustein and Wake, 1990); and (2) amphibians as vectors of harmful chemicals (e.g. pesticides; Relyea et al., 2005). The latter issue is especially significant to Alberta's anuran populations because of the province's reliance on agriculture and consequent use of a variety of herbicides and pesticides.

CHAPTER 4 – HABITAT USE AND MOVEMENTS OF THE PLAINS GARTER SNAKE (*Thamnophis radix*) AT THE NORTHERN LIMIT OF ITS RANGE IN ALBERTA, CANADA

INTRODUCTION

The environment can be viewed as a patchwork of habitats, within which organisms are constrained to particular areas in which they must procure specific resources in order to gain nourishment, grow and reproduce (Morris, 1987, 2003). Additionally, animals may require different habitats for different functions, and when such habitats are spatially separated, animals must move between them (MacArthur & Pianka, 1966; Baker, 1978; Dingle, 1980; Gregory et al., 1987). Thus, the study of habitat use and movements is a fundamental area of research in wildlife ecology and crucial for management and conservation of species in the world's increasingly anthropogenically altered ecosystems.

Habitat has been broadly defined as the resources and conditions of a given landscape (Hall et al., 1997). Heterogeneity of the landscape and varying resources are precursors for habitat selection, a process by which an animal preferentially occupies a non-random area and set of conditions (Morris, 2003). Recently, studies of habitat selection have focused on the comparison of what aspects of habitat an animal uses compared to what is available in the greater landscape (Manly et al., 2002). This can occur at several different scales (Johnson, 1980), and ideally a study would examine use at both coarse and fine scales. Many studies also examine the movements of animals through different habitats as a tool to predict use over time (Gregory et al., 1987). Animals presumably move in response to resource variation across the landscape (Dingle, 1980). Examination of the variation that occurs among individuals, populations and species can be used not only to predict animal occurrence, temporally and seasonally, but also to highlight life-history strategies of animals based on the trade-offs with which they are faced.

Snakes are ectotherms; thus, their use of habitats is affected not only by the abundance of critical resources (e.g. food, shelter, basking sites), but also by temperature (Gibbons & Semlitsch, 1987). This is especially true in the temperate zone, where seasonal temperature variation can be extreme. In such environments, winter is a particular challenge and snakes need to find over-wintering sites (hibernacula) that

provide access underground, below the frost level (Fitch 1965; Gregory, 1982; Gregory, 1984b; Macartney et al., 1989). In summer, by contrast, snakes require habitats that provide adequate food, cover, and appropriate conditions for breeding (Charland & Gregory, 1995; Blouin-Demers & Weatherhead, 2001c). Frequently, hibernacula, breeding grounds and summer foraging sites are located in widely separated areas, thus requiring snakes to undertake seasonal movements between them (Gregory & Stewart, 1975; King & Duvall, 1990; Shine et al., 2001b). If multiple habitats are required for survival of snakes in a particular landscape, then determining their movements among habitats, and their fitness-related uses of different habitats, is essential to understanding their conservation needs.

Although studies of habitat utilization have been conducted on northern species of garter snakes (Gregory, 1984a; Larsen, 1986; Charland and Gregory, 1995), most work has been done on populations of the Common Garter Snake (*Thamnophis sirtalis*) in central Manitoba and northern Alberta (Gregory, 1974, 1977a; Larsen, 1986; Shine et al., 2001b). Northern populations of this species are noteworthy for their communal hibernation behaviour and the extensive migrations they make between summer wetland habitats and winter den sites (i.e. the '*sirtalis*' model). Other northern species of garter snakes, however, have not been observed as frequently to engage in such behaviours, suggesting either that they are understudied or that they use the landscape in different ways and therefore may have different habitat/ecological requirements. Because garter snakes occupy such a wide diversity of habitats, ranging from wetlands and prairies to forests and estuaries (Rossman et al., 1996), results from single-species models may be only partially relevant to other populations or species that have yet to be examined. Thus, studies of the habitat use and movements of additional species may address important theoretical life-history and ecological questions, as well as have practical applications within conservation biology, as management action usually requires species-specific and site-specific information.

The Plains Garter Snake (*Thamnophis radix*) is distributed over a wide geographic area, from New Mexico to Indiana and north to central Alberta, Canada (Rossman et al., 1996). This medium-sized species is similar to *T. sirtalis* in several life-history traits (e.g. body size, growth; see Chapter 2) and in diet (e.g. generalist predators; see Chapter

3); however, little is known about its habitat requirements (e.g. summer habitats, nature or availability of hibernation sites) or spatial ecology. Given the severe winter conditions faced by snakes at higher latitudes, the seasonal patterns and habits of *T. radix* are of particular interest in Alberta, where we might expect potential range-limiting factors such as length of active season to have a significant influence on life-history traits. Thus, *T. radix* provides an opportunity to test the generality of the 'sirtalis model' of habitat use and movement patterns of garter snakes in a thermally challenging environment.

In this study, I quantified the habitat use and movement patterns of a population of *Thamnophis radix* near the northern limit of the species' distribution in central Alberta, Canada. Radiotelemetry is an effective method for obtaining information on habitat utilization, activity patterns and movements of cryptic and secretive species like snakes (Reinert, 1984, 1992). Data from radiotelemetry also allowed me to test, via comparison, how effective data from opportunistic captures are at describing habitat use by animals (Rettie and Mcloughlin, 1999). This portion of my study had three main objectives: (1) to identify both the landscapes and microhabitat features used by snakes; (2) to examine the extent of seasonal movement patterns; and (3) to determine the types and locations of hibernation sites. Because of the cooler climate at this latitude, I expected thermoregulation to be particularly important for *T. radix*; thus, thermal qualities of a habitat were predicted to affect habitat use. Specifically, I predicted that snakes in the summer would occupy open sites that provided both foraging opportunities and shelter from predators. I also compared my results for *T. radix* to other literature reports for this species, as well as to the 'sirtalis' model.

METHODS

Movement – I determined movement patterns of snakes in two ways: (1) by recapture of previously marked snakes (see Chapter 1 for details of snake capture, measurement and marking); and (2) by tracking radio-tagged snakes using radio-telemetry (Weatherhead & Hoysak, 1989; Ujvari & Korsos, 2000). I used the mark-recapture method on opportunistic captures in 2005 and 2006 to determine distance moved per day and total distance moved per season and compared values between sex, size, and reproductive categories of snakes. I used radiotelemetry for three main purposes: (1) to track snakes in

their daily use of habitat; (2) to determine seasonal movement patterns; and (3) to identify and locate winter hibernating sites.

In 2005 and 2006, I collected five female snakes (snout-vent length >600mm, mass >100g) each year for radiotelemetry. Males were not used as they were too small for the size of transmitter used. Radio-transmitters were surgically implanted in the peritoneal cavity, with the whip antenna threaded back under the skin, by two different veterinary surgeons, following the procedure described by Reinert and Cundall (1982). Snakes were anesthetized with 3-4% Isoflurane®, and heart and respiration rates were monitored throughout the procedure until snakes recovered. Radio-transmitters (Model SB-2, Holohil Systems Ltd., Ontario, Canada) weighed 5 grams, including battery and antenna, thereby comprising < 5% of each snake's body mass, a standard maximum ratio for acceptable reduction of the impact of the transmitter on the snake's activity (Ujvari and Korsos, 2000). Snakes were kept for three days post-surgery and then released at the original capture site. The transmitters were calibrated before use by the manufacturer and produced pulsed signals in the 148-152 MHz range. They had a functional field range of approximately 200 m with a handheld receiver (Communications Specialists Model R-1000) and Yagi antenna. At a closer distance (e.g. 20 m), the Yagi antenna was removed and a smaller antenna was used to locate the snake. At the end of the study, transmitters were removed using a similar surgical procedure, and snakes were released at their last capture location.

In 2005, radio-tracking commenced the first day after release (September 5th) and continued until October 6th when snakes were concealed under ground for several days in a row. The transmitters were left in the snakes over the winter so that movements in 2006 back to summer habitats could be determined. In spring 2006, however, only one snake was recovered; that snake was tracked from spring emergence until June 13th, when she was recaptured for removal of her radio-transmitter. Radio-tracking of five additional females (same surgical procedure as previous summer) began on July 1st and concluded on August 18th 2006.

Radio-tagged snakes were located daily, if possible. To avoid disturbing these snakes and affecting their immediately subsequent movement patterns, only visual contact was made with them if they were in the open (Rettie and McLoughlin, 1999). For each snake

location, I recorded UTM coordinate position with a handheld GPS (Garmin Ltd.), snake posture and activity (e.g. concealed, basking, moving), time of day, and weather conditions.

I defined a movement as: distance moved (> 25 m) between two capture (i.e. opportunistic) or observed (i.e. radiotelemetry) locations. I further defined seasonal long-distance movements as: a series of consecutive movements over a period of time (e.g. several days), occurring in either the spring (May 1st to May 30th) or fall (September 1st to October 6th); and either beginning or ending at a den site. Summer movements occurred during the months of June, July and August. Average (\pm SD) distances moved per day and season (e.g. in one year) were estimated for both recaptured and radio-tagged snakes, as straight-line distances between measured locations (Harris et al., 1990). For opportunistic captures, I separately compared movements (dependent variable) between sex and reproductive categories (factors) using ANOVA.

Hibernation sites – Hibernation sites were determined for five females using radiotelemetry. The den sites I located were not excavated or disturbed, but simply marked with stakes and flagging tape for the duration of the study period. Data were collected on den site areas in the same manner as for microhabitat plots (see below), although not analyzed due to small sample size ($N = 4$).

Macrohabitat types – To determine the characteristics of the habitat available in the study area, I mapped a 4 km² section of Miquelon Lake Provincial Park (MLPP) using aerial photo enlargements (scale 1:10,000). A grid with 1 cm² cells representing 10 m x 10 m, was superimposed on the photograph, oriented along a north-south axis, and 50 grid intersection points were randomly selected using a random numbers table to be my 'available' locations. I then systematically sampled these available sites in May, July and September, and outlined four macrohabitat types that were represented proportionally as: MARSH (20%), FIELD (26%), FOREST (52%) and SCRUB (2%). None of these habitats changed over the active season (e.g. a marsh drying up into a field). Forest (e.g. aspen groves) was defined as any area that had trees greater than 5 m tall in an arc of at least 180 degrees around that point. Scrub was similarly defined, but with trees 2-5 m tall. Field (e.g. prairie grassland) was defined by the absence of Forest and Scrub characteristics. Marsh (including marshes, ponds, bogs and lakes) was defined as any

location in or within 5 m of standing water. These four types were adopted based on the vegetation types at MLPP and following classification systems used in other studies (Charland & Gregory, 1995; Fig.20).



Figure 20. Four habitat types outlined in the landscape at Miquelon Lake Provincial Park, Alberta, 2005-2006. Top left = FIELD; top right = FOREST; bottom left = MARSH; bottom right = SCRUB.

In May and June 2005, I undertook wide-ranging searches of snakes throughout the various habitats. Search effort over the area was kept as even as possible. Very few snakes were found in the forest habitat type, so I reduced my search time in the forest to only an hour per day for the rest of the year (randomly chosen between 0700 and 2100). For the remainder of 2005 and the spring of 2006, my searching was more opportunistic in fields, marshes and along scrub edges, and focused on areas where snakes had been encountered more frequently. Sightings of snakes, shed skins and capture locations were deemed as 'used' sites, and classified as one of the four major habitat types. Snakes that were recaptured within two weeks in the same habitat were left out of the analysis. In July and August 2006, I conducted timed searches across the four different habitats in rough proportion to their availability (FIELD = 2.5 hrs, FOREST = 5 hrs, MARSH = 2

hrs, SCRUB = 0.5 hr). I determined my success at opportunistic captures in the four habitats by comparing the number of snakes captured per unit time spent searching in each habitat.

To explore these data I used chi-square tests to compare the proportion of used sites (i.e. snake locations) with the proportion of the 4 available macrohabitat types (e.g. 50 habitat plots) for both opportunistic captures and radiotelemetry locations. I used chi-square to test for differences between habitats used by opportunistically captured snakes differing by sex (males, females), body size (same size categories as Chapter 3; neonates < 200 mm, juveniles = 200-400 mm, adults > 400 mm SVL), reproductive condition (gravid vs. non-gravid females; based on palpation for presence of eggs in abdomen), and season (spring, summer, fall; see movement section for dates). Data for 2005 and 2006 were pooled and rejection values were set at $\alpha = 0.05$.

I also used logistic regression to test for differences between used and available locations. I treated locations as values of a binary dependent variable (1 = used, 0 = available), and habitat types as the independent categorical variable (FIELD, FOREST, MARSH, SCRUB). These categories of habitat type were represented as dummy variables (i.e. values of 0 or 1); SCRUB, the 'reference' category, was represented by a value of 0 for each of the dummy variables (Manly et al., 2000). The estimated coefficient indicated the direction of association of snakes with each habitat type, and the likelihood ratio test indicated the statistical significance of that association.

Microhabitat sampling locations – At each snake location, both opportunistic and radiotelemetry, I also described and sampled the microhabitat. Location was described as either natural or disturbed, based on the degree of anthropogenic alteration and proximity to human structures (< 5 m). Starting at the location at which I first sighted a snake, habitat variables were measured along four 10-m transects placed in the cardinal directions (0 m for each transect marks the centre capture location), using string, tent pegs and a handheld compass. Capture sites within 25 m of one another were considered the same location, and habitat features therefore were not re-surveyed (King & Duvall, 1990; Block et al., 1998; Rettie & McLoughlin, 1999; Ashton, 2003), but repeat locations were re-sampled if 1 month or more had elapsed since the last measurements. For radiotelemetry, habitat was sampled repeatedly for each snake, but only if the snake

moved more than 25 m between locations or if more than 4 weeks had passed with the snake using the same location. For every capture location ('used'), a random location ('available') was sampled to create matched-paired sites as a basis for comparisons of use versus available habitat (Hosmer and Lemeshow, 2000; Compton et al. 2002). Each paired random plot was located 50 m away from the capture location, in a random direction selected using a random numbers table and a compass, and was visually searched to confirm absence of snakes prior to taking measurements.

I used previous studies on snakes as guides to habitat variables likely to be relevant to habitat selection by *T. radix* (Reinert, 1984; Gregory, 1984a; Lind and Welsh, 1994; Charland and Gregory, 1995; Matthews et al., 2002). However, because mine was the first study of habitat use by Plains Garter Snakes in Alberta, I also chose variables to cover as many aspects of habitat as possible.

The following variables were measured at each of the capture and random locations (name used in the analysis):

Canopy cover – Canopy cover (%CANOPY), an index of shade coverage for an area with trees (> 2 m tall), was measured using a concave spherical densitometer (Model-C). Four readings, one in each cardinal direction, were taken at the 0 m mark. Each value was multiplied by 1.04, allowing for overstory density to be estimated as a percentage (Lemmon, 1956).

Woody vegetation – Tree cover (%TREE) was determined by measuring the total distance intercepted by trees (> 2 m tree/bush) along the distance of each transect using a metre stick and converted to a percentage. Height of the forest canopy (TREEHT) was measured (to the nearest m) using a clinometer (Suunto PM 5/1520). Shrub cover (< 2 m bush, %SHRUB) was determined the same way as for tree cover. Dominant tree and bush species along each transect were recorded.

Ground vegetation – Ground vegetation cover (%GRASS, %SEDGE, %FORVEG – forest floor vegetation) was determined by measuring the total distance intercepted by live vegetation along the distance of each transect and converting to a percentage. Height of ground vegetation (< 2 m; VEGHT) was measured using a metre stick at 3 sites per transect and calculated by averaging (sites selected using a random numbers table). The dominant plant species along each transect were recorded and then classified as either short (< 0.5 m) or tall (> 0.5 m) vegetation (%TALL, %SHORT). Coverage for each of these groups along each transect was measured with a metre stick and converted to a percentage.

Litter – Litter cover (%LITTER) was determined by measuring the total distance intercepted by dead plant material along the distance of the transect using a metre stick and converted to a percentage. Litter depth (LITTERD) was measured using a metre stick at 3 sites per transect and then averaged (sites selected using a random numbers table). The composition of the litter (e.g. grass, leaf, or sedge) also was recorded.

Coarse woody debris (CWD) – This was determined by counting the number of logs greater than 0.1 m in width (LOGN). The width of each piece of wood debris was measured at the point where it intersected each transect, and then all widths were added together to give the total percentage coverage (%CWD).

Substrate cover – When the substrate was something other than vegetation, litter or cwd (e.g. rock/cement or soil), I measured its distance using a metre stick along each transect and converted to percentage cover (%ROCK, %SOIL).

Aspect – The general aspect of each transect was measured in degrees with a compass at the 0 m mark. A measurement of 180° indicates a southerly aspect.

Slope – The general slope of each transect was measured in degrees with a clinometer (Suunto PM 5/1520).

Proximities to habitat features – Distances to various habitat features and anthropogenic structures were determined, using a hip-belt measuring tape. Measurement began at the 0 m mark and stopped at the closest feature within a 50 m radius. Distances greater than 50 m were not measured and left out of the analysis (due to frequency of private property). Species of vegetation and types of structures were also recorded. Distance to nearest log (LOG), bush (BUSH), tree (CT), standing water (WATER), marsh (MARSH), forest edge (FOREST), artificial and natural cover (ACO, VCO), human structures (HS) and roads/paths (ROAD, PATH) were all measured.

Microhabitat analysis – To analyze microhabitat use such as substrate types, cover types and disturbances to locations, I used chi-square tests for proportions to examine any differences between used and available sites. To avoid pseudoreplication, I used a reduced data set (i.e. means of the four transects treated as variables) for analyses. Because aspect is an angular variable, with the lowest possible value (0°) identical to the highest possible (360°), I had to treat it differently from the other variables. I categorized values of aspect into quadrants representing NE = DIR1, SE = DIR2, SW = DIR3, NW = DIR4. These categories were represented as dummy variables that replaced aspect value. I tested all habitat variables for normality using normal distribution curves and Shapiro

tests ($P < 0.10$). None were normal, even after transformation (arcsine – % cover, logarithmic – distances); thus, I used non-parametric tests for subsequent analyses.

I conducted preliminary exploratory data analyses to further reduce my data set and selected only variables most likely to account for the differences between snake and random locations. I tested each variable with a paired Wilcoxon signed-rank test and retained variables whose test P-value was < 0.25 for use in the multivariate tests (Hosmer and Lemeshow, 2000). I then ran a univariate paired (conditional) logistic regression test for each variable and retained all variables that showed some association (using $P < 0.25$ as a selection criterion) with the outcome (used vs. available). Of sets of highly correlated variables (Spearman's $Rho > 0.7$), only one member was included in the models to avoid masking the effects of important variables (Reinert, 1992). To decide which of the two correlated variables to retain, I compared the P-values from the paired logistic regressions and kept the variable that had the higher significance value. After these eliminations, the ratio of number of variables to sample size was 0.09 (15 habitat variables and 172 plots for opportunistic; 8 habitat variables and 86 plots for radiotelemetry), which satisfied the theoretical proposed maximum value of 10% (Peduzzi et al., 1996). All variables retained at that point were used in multivariate tests.

To analyze microhabitat use based on multiple habitat variables, I used paired (matched-pairs or conditional) logistic regression, in which each snake location is compared to its paired random location (Compton et al., 2002; Manly et al., 2002; Keating and Cherry, 2004). Logistic regression is a more robust technique than compositional analysis (Aebischer, 1993) or discriminant function analysis (Block et al., 1998), as it allows the use of categorical variables (e.g. aspect). In paired logistic regression, the estimated coefficients are interpreted as in standard logistic regression using maximum likelihood methods (Hosmer and Lemeshow, 2000). The sign of the coefficient indicates the direction of the relationship for the variable relative to what is available. I used *a posteriori* forwards, backwards and stepwise selection processes and found that backwards provided the best model. I tested global and best-fit models for goodness-of-fit with Hosmer and Lemeshow statistics ($P < 0.05$; Burnham & Anderson, 2002).

RESULTS

Movements of opportunistically captured snakes – Fifty-eight of 67 recaptured snakes (males = 24, females = 34) had changed locations within one active season ($N_{2005} = 8$, $N_{2006} = 50$). The average total distance moved per snake was 396.3 ± 485.9 SD m, with a maximum distance moved by one snake in a season of 2132 m. When I controlled for the time interval between moves, snakes moved, on average, 19.3 ± 55.8 SD m/day (range = 0.6 to 426 m). Overall, I found no significant relationship between size of snake and either distances moved per day (ANOVA, $F_{1,56} = 0.78$, $P = 0.38$) or total distance moved per season (ANOVA, $F_{1,56} = 2.77$, $P = 0.10$). There were no significant differences between the sexes (ANOVA, $F_{1,55} = 0.14$, $P = 0.71$) or reproductive states (males included with non-gravid females; ANOVA, $F_{1,55} = 0.19$, $P = 0.83$) in distances moved per day (Fig.21).

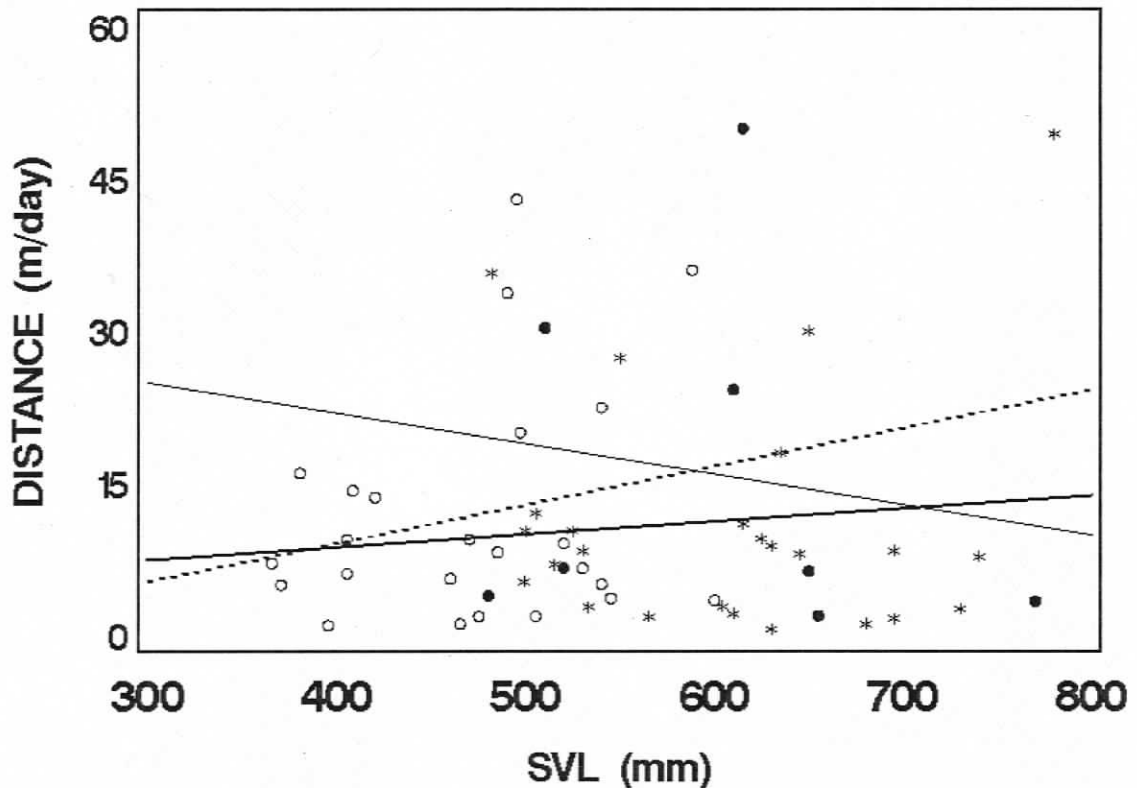


Figure 21. Distance moved (m/day) as a function of size (SVL, mm) for opportunistic captured Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 2005-2006. Data are for individual snakes recaptured at least 25 m from first capture location ($N = 58$). Non-gravid females = filled circles (thin solid line: $Y = 33.8 - 0.03X$, $N = 8$), gravid females = stars (thick solid line: $Y = 3.55 + 0.01X$, $N = 26$), males = open circles (dashed line: $Y = -6.05 + 0.04X$, $N = 24$).

Movements of radio-tagged snakes – The 10 radio-tracked female *Thamnophis radix* changed locations on 95 (33%) of the 288 snake-days of monitoring. Almost all movements occurred during the daytime hours; snakes were frequently found in nocturnal retreat sites on consecutive evening and morning observations. Snakes concealed themselves in various types of retreat sites (e.g. under buildings, cracks in cement, holes in the ground) 77% of the time and were seen basking on the remaining observation occasions. Although I observed a higher frequency of movements in 2006 (54.7%), I did not test for differences between years because snakes were not tracked at the same time of the year in 2005 as in 2006. Thus, I pooled data from the two years for most of the analyses.

Total distance moved for all ten females combined was over 7500 m. This covered a substantial area of MLPP since there was basically no range overlap between any of the radio-tagged snakes. The average distance moved per day was 26.1 ± 76.2 SD m (range = 25-450 m, N = 288), whereas the average distance moved to a new location was 79.1 ± 116.1 SD m (N = 95). The longest distance moved by a snake during a single season was 2192 m during August 2006. The same snake also exhibited the longest single-day movement (750 m on August 6th), while traveling a distance of 1220m over a period of seven days, through 5 different habitats.

Female Plains Garter Snakes exhibited a bimodal pattern of seasonal activity (i.e. movement frequency – $\chi^2_2 = 20.3$, $P < 0.0001$), with snakes moving more frequently in early May (43.2%) and September (45.3%) than during summer (11.6%; June, July and August). Long-distance movements were recorded for five snakes in September of 2005 and one snake in May of 2006 (Table 6). The average long-distance movement distance was 607 m (N = 6). In 2005, all five snakes were highly directional in moving towards hibernation sites from early September to mid-October. All snakes moved away from marsh habitat into either field or scrub habitat where den sites were located. In May 2006, one female moved away from the over-wintering site over a period of approximately one week, following the same path she used to get to the hibernation site in 2005. She moved from field to marsh habitat and then remained localized in that marsh until she was captured on June 13th 2006.

Table 6. Radiotelemetry and movement data for ten female Plains Garter Snakes (*Thamnophis radix*) tracked in 2005 and 2006 at Miquelon Lake Provincial Park, Alberta.

Snake ID	SVL (mm)	Total distance moved per seasonal period (m)			# new locations	# movements	# days tracked	Mean distance per move (m)	Maximum distance between successive locations (m)
		Spring	Summer	Fall					
1	740	-	-	430	4	6	8	71.7	300
2	620	-	-	558	8	10	24	55.8	242
3	665	-	-	553	7	8	24	69.1	209
4	735	-	-	287	6	7	13	41.1	140
5	695	706	-	1108	23	23	51	78.9	357
6	645	-	364	-	9	9	43	40.4	61
7	660	-	699	-	5	6	33	116.5	350
8	695	-	157	-	4	4	12	39.3	76
9	740	-	458	-	6	8	41	57.3	158
10	680	-	2192	-	12	14	30	156.6	750

Snakes traversed several potential 'risky' habitats, including open fields (~800 m across with low shrub cover; N = 3), gravel roads (~10 m across; N = 5), paved roads (~20 m across; N = 5), and a busy construction yard (~500 m length; N = 4). I documented 10 incidents, in 9 of the 10 tracked snakes, of road crossing, which occurred both in the summer foraging season and when snakes were moving to their hibernacula. However, these crossings occurred only in one direction, and I did not document any incidents of snakes crossing back over the same road.

Hibernation sites – Based on telemetry data, movements towards hibernacula occurred primarily in September, with most activity stopping in mid-October. Because of snowfall and the need to terminate the 2005 field season, I could not determine the exact dates on which snakes entered their hibernacula. I found no evidence of large communal hibernacula in the MLPP area in either 2005 or 2006. Instead, snakes were tracked to den sites which consisted of holes in the ground, three snakes alone at their sites and two snakes sharing a single site (Fig. 22). Holes in which the snakes were last located were assumed to be pre-existing mammal burrows, indistinguishable above ground from many of the burrows used by snakes during the active season. Sites were a minimum distance of 500 m apart and all occurred within habitats used in summer these snakes (Table 7).

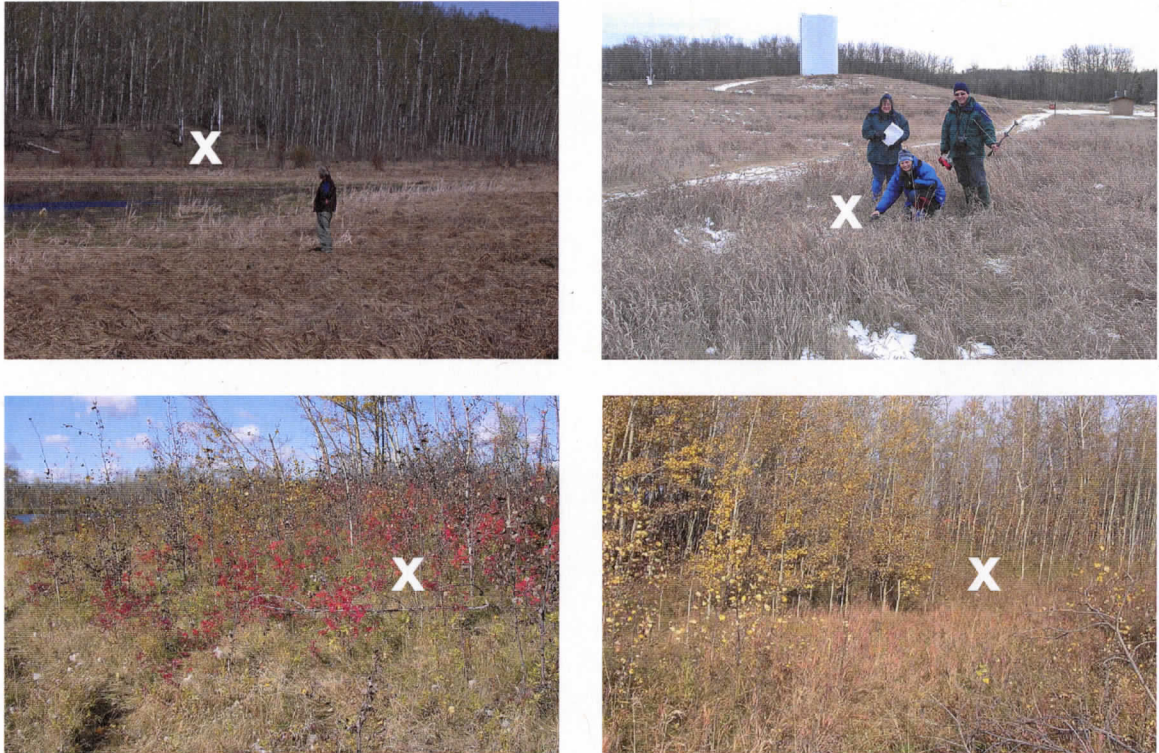


Figure 22. Den sites used by five female Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, October 2005 to May 2006. X marks the location of the den site. Top left = SCRUB #1; top right = FIELD #4/5; bottom left = FIELD #3; bottom right = FIELD #2. Numbers refer to the snake that used that location (see Table 7).

Snakes were located in mid-February 2006 to determine if final hibernation sites corresponded to the last known locations in October 2005. I was able to locate only two of the snakes at their last known sites and unable to locate signals for the remaining three snakes; transmitter failure was assumed. In total, four transmitters failed over the winter and only one snake was known to have emerged from hibernation in 2006. Tracking of this female resumed on May 2nd 2006 and continued until mid-June.

Table 7. Key characteristics of over-wintering sites for five female Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 2005.

Habitat Type	Coverage (%)			Distance to nearest (m)			Slope	Aspect
	Canopy	Shrub	Litter	Edge	Marsh	Cover		
SCRUB #1	0	90	95	4.8	30	4.8	40°	E
SCRUB #2	20	20	95	0.8	>50	2.8	25°	SE
FIELD #3	0	30	95	3.4	15	1.8	20°	S
FIELD #4/5	0	5	100	>50	>50	0	-	-

Other potential hibernation sites located within the boundaries of the park included foundations of several buildings and several natural hillsides. These sites were identified only as potential areas where snakes could have spent the winter months, based on the capture and recapture of 5 snakes at the same location in both the late fall and following spring. Additionally, in the very early spring snakes were frequently captured at the same location on subsequent days.

Macrohabitat Use – Macrohabitat use was determined for both opportunistically captured snakes (N = 205) and radio-tracked snakes (N = 91) in 2005 and 2006 (Fig.23). Thirty-six of the opportunistic captures were on paved roads, for which habitat could not be defined, and these cases were therefore left out of the analysis. Approximately 60% of all snake locations occurred in Fields and 21% occurred in Marshes, whereas these two habitat types made up only 26% and 20% of the available landscape. I captured the most snakes in field habitats, even after factoring in the time spent searching the 4 habitat types (Fig. 24).

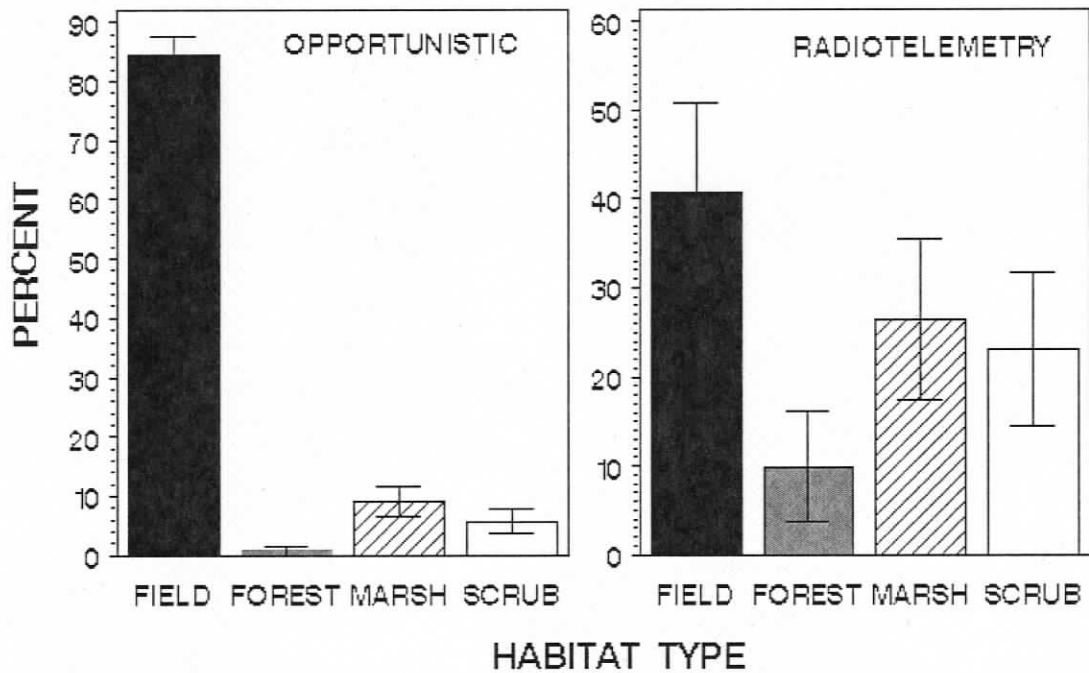


Figure 23. Frequency of snake captures in the macrohabitat types observed for opportunistic searching (N = 205) or radiotelemetry (N = 91) for Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 2005-2006. Error bars = 95% confidence intervals.

I found no difference in habitat use between different size categories of snakes ($\chi^2_6 = 11.6$, $P = 0.07$). However, I found a significant sex differences in habitats used by snakes ($\chi^2_3 = 7.99$, $P = 0.046$), with females located in fields more often than males. Because reproductive condition may affect a female's use of habitat, I also tested for differences gravid and non-gravid females, but found no significant difference ($\chi^2_3 = 4.49$, $P = 0.21$). The presence of food in a snake's stomach made no difference in the types of habitats used ($\chi^2_3 = 2.23$, $P = 0.53$). However, number of captures in different habitats was significantly related to season ($\chi^2_6 = 18.01$, $P = 0.006$), with snakes captured more frequently in fields and marshes in the summer, and scrub in the fall.

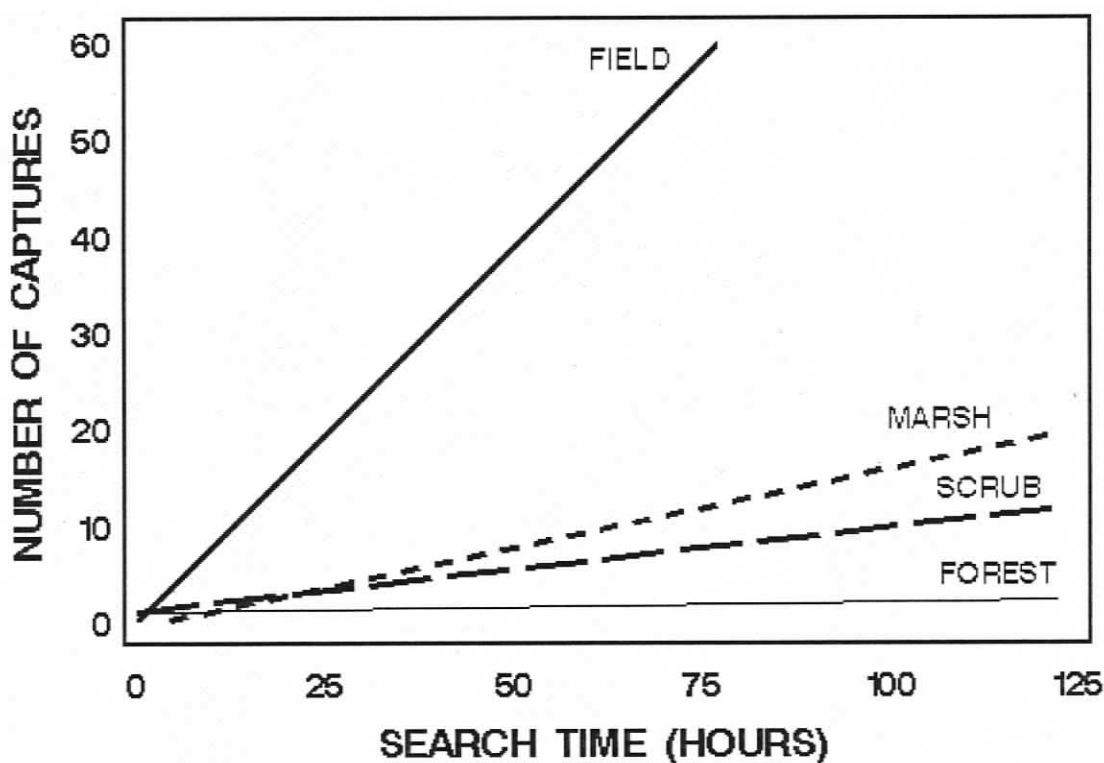


Figure 24. Number of opportunistic captures in the macrohabitat types by time spent searching ($N = 57$) for Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, July and August 2006.

Based on my exploratory chi-square tests, habitat type was significantly different between used and available sites for both opportunistic ($\chi^2_3 = 43.08$, $P < 0.0001$) and telemetry ($\chi^2_3 = 17.63$, $P = 0.0005$) snake locations. When opportunistic and telemetry data were pooled together there was still a difference between what snakes used versus what was available to them ($\chi^2_3 = 74.69$, $P < 0.0001$). However, because there was a

significant difference between the frequency of habitats recorded for opportunistic captures and radiotelemetry locations ($\chi^2_4 = 126.69$, $P < 0.0001$), I kept these two sets of data separate for the remaining analyses. When I analyzed each group using logistic regression to determine the direction of the relationship between habitat type and use, opportunistically captured snakes were positively associated with fields and marshes, and both groups were negatively associated with forests (Table 8).

Table 8. Logistic regression analysis of macrohabitat use for Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 2005-2006. The sign of the coefficient indicates the snake's relationship with the habitat category. Negative values indicate avoidance and positive values indicate selection relative to other habitats. The test statistic (P) shows whether the habitat type is significantly associated with the probability of use.

Habitat	Df	Coefficient	SE	χ^2	P
Opportunistic captures (N = 205) Log likelihood ratio = 69.37					
FIELD	1	1.7434	0.3051	32.6428	< 0.001
FOREST	1	-2.6415	0.4917	28.859	< 0.001
MARSH	1	0.6128	0.3388	3.2704	0.0705
Radiotelemetry locations (N = 91) Log likelihood ratio = 19.61					
FIELD	1	0.4642	0.3011	2.3778	0.1231
FOREST	1	-1.429	0.3436	17.3017	< 0.001
MARSH	1	0.2937	0.3309	0.788	0.3747

Microhabitat use – I characterized the microhabitat at a total of 263 used locations (172 opportunistic captures and 91 radio-tracked snakes) and 263 matched available locations. Snakes were found at both natural (N = 124) and anthropogenically altered sites (e.g. buildings, lawns, garbage heaps, paved and grass pathways, N = 139), and this was not significantly different from a 1:1 ratio ($\chi^2_1 = 0.86$, $P = 0.36$). One gravid female spent over a month on a man-made gravel bank, which was sparsely covered with 0.5 m tall weeds. Exploratory data analysis showed that Plains Garter Snakes tended to occur in microhabitats that were relatively sunnier and near some form of cover, either vegetative (VCO) or artificial (ACO; Fig. 25). Used locations were also closer to roads than available sites, especially later in the active season.

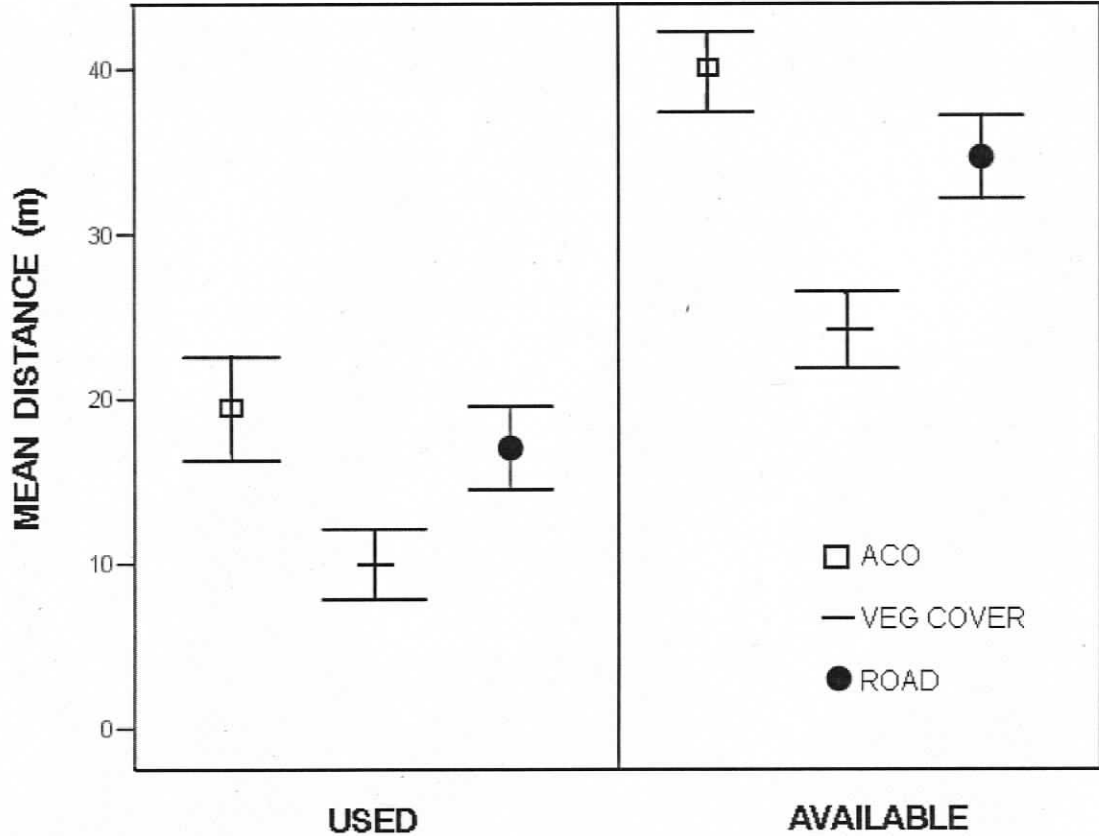


Figure 25. Mean and 95% confidence intervals for distances to habitat features in sites used and available for Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 2005-2006. Square = artificial cover objects; line = natural vegetative cover; circle = road (gravel or paved).

I often found snakes under cover. Vegetative cover usually involved some form of distinctive edge habitat, including tall grass (50.3%, N = 150), bush banks (40.9%, N = 122) or marsh reeds (1.3%, N = 4). Common bushes that snakes used as cover were Prickly Rose, Saskatoonberry and Canada Buffaloberry. Coarse woody debris was also used in a few cases, including one log that was found with 13 snakes in it (7.4%, N = 22). Common artificial cover types (ACO) used by snakes included thin wood boards (85.6%, N = 137) and metal sheets or pipes (11.9%, N = 19; Fig. 26). I found a significant negative relationship between artificial cover use and body size, using logistic regression ($\chi^2_1 = 71.97$, $P < 0.001$; Fig.27).

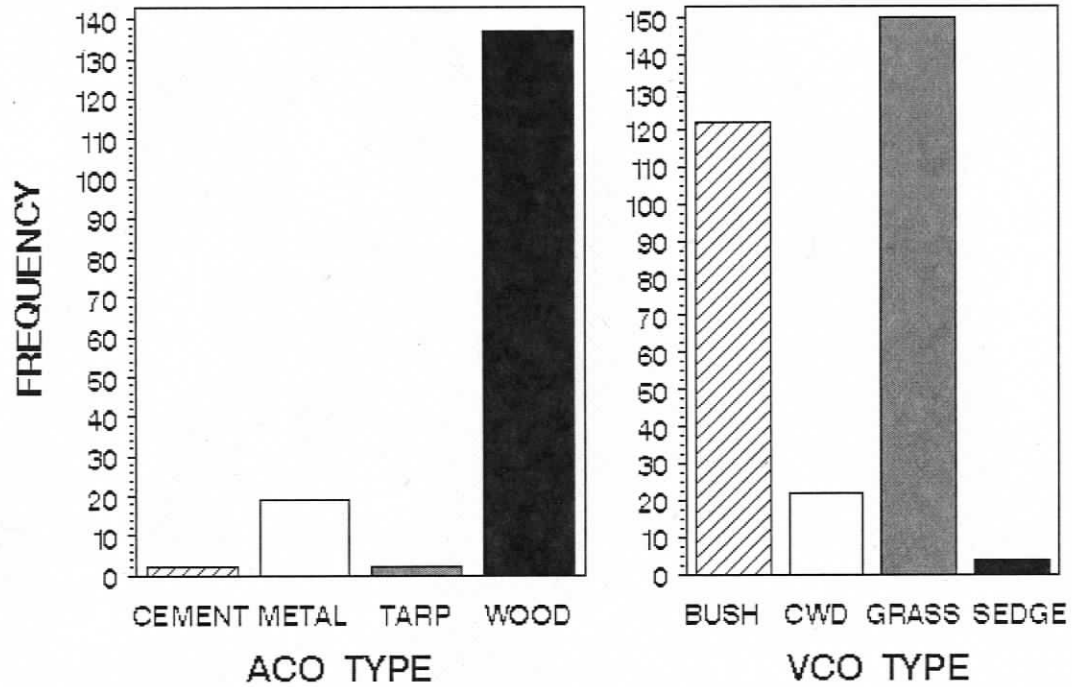


Figure 26. Frequency of Plains Garter Snakes (*Thamnophis radix*) associated with artificial (ACO) and natural vegetative (VCO) cover types at Miquelon Lake Provincial Park, Alberta, 2005-2006. ACO type includes all snakes captured directly under an object. VCO type includes all snakes under or within 0.5 m of a vegetation cover type. CWD = coarse woody debris.

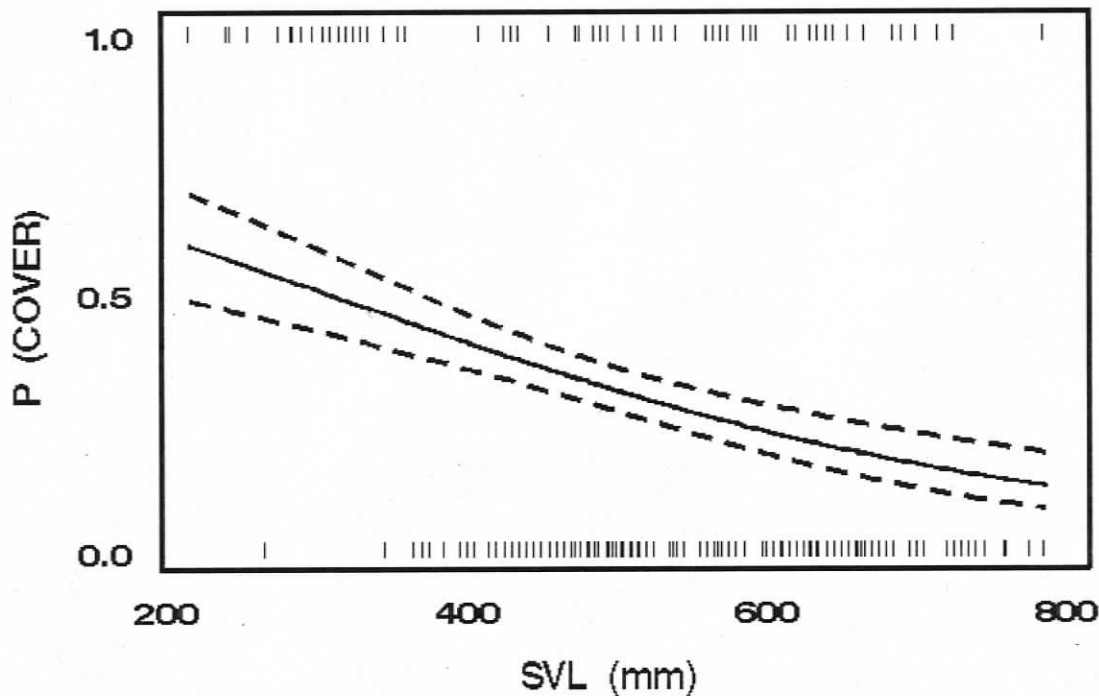


Figure 27. Probability of observing a snake under an artificial cover object versus size of snake (SVL, mm) for Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 1995-2006. Vertical lines at top = snakes under cover (N = 161), vertical lines at bottom = snakes out in open (N = 339). Solid line represents predicted values from logistic regression of presence/absence of cover against size. Dotted lines represent 95% confidence limits on predicted values. Data include opportunistic captures only and recaptures are included only where a snake used more than one cover object in a season.

Paired logistic regression of microhabitat use – Because my samples were of adequate size, I kept opportunistic and radiotelemetry separate for the logistic analysis of microhabitat. I used P-values (< 0.25) from Wilcoxon signed rank tests as selection criteria for the microhabitat variables, and dropped 5 variables (PATH, LITTERD, LOG, %TALL, %SHORT) from the analysis of both the opportunistic capture and radiotelemetry analysis. I then ran a univariate paired logistic regression for each variable, and eliminated the ones that showed no differences between used and available sites ($P > 0.25$): opportunistic (DIR-SW, and distance to WATER, CT) and radiotelemetry (%GRASS, %LITTER, %SHRUB, %CWD, LOGN, DIR-SW, DIR-NW, and distance to BUSH, FOREST, WATER, ROAD).

Due to correlations between several habitat variables ($R > 0.7$), I further eliminated 9 opportunistic variables (%CANOPY, %TREE, TREEHT, VEGHT, LOGN, %LITTER,

%SHRUB, and distance to PATH, HS) and 8 radiotelemetry variables (%CANOPY, %TREE, TREEHT, VEGHT, %SEDGE and distance to CT, HS, ACO). To determine which correlated variable to remove, I used the P-values from the univariate paired logistic regression, and kept the variable with the lower value. Overall, I retained 15 variables from opportunistic captures and 7 variables from radiotelemetry for further multiple regression analysis (Table 9).

Table 9. Associated habitat features identified from univariate conditional logistic regression tests ($P < 0.25$ selection criteria) for the occurrence of Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 2005-2006.

Parameter	Habitat Characteristic	Analysis of Max. Likelihood Estimates			
		Coefficient	SE	WALD χ^2	P
Opportunistic (15 habitat features, 172 habitat plots)					
GRASS	%Cover	0.00557	0.00335	2.7619	0.0965
SEDGE	%Cover	-0.0348	0.0123	7.9667	0.0048
FORVEG	%Cover	-0.0263	0.00855	9.431	0.0021
SOIL	%Cover	0.0195	0.0114	2.8967	0.0888
ROCK	%Cover	0.0375	0.0108	12.0221	0.0005
CWD	%Cover	-0.593	0.2719	4.7555	0.0292
SLOPE	Slope	0.096	0.0215	20.0149	< 0.001
DIR – SE	Aspect	1.5596	0.3306	22.257	< 0.001
DIR – NW	Aspect	-0.6968	0.5473	1.6207	0.203
BUSH	Proximity	-0.0223	0.0114	3.8273	0.0504
FOREST	Proximity	-0.0458	0.0109	17.7841	< 0.001
VCO	Proximity	-0.1318	0.0239	30.5016	< 0.001
ACO	Proximity	0.1371	0.0369	13.7662	0.0002
ROAD	Proximity	-0.0429	0.0116	13.6251	0.0002
MARSH	Proximity	0.0146	0.0117	1.5594	0.2118
Radiotelemetry (7 habitat features, 86 habitat plots)					
FORVEG	%Cover	-0.0545	0.0219	6.2058	0.0127
SOIL	%Cover	0.0325	0.0156	4.3334	0.0374
ROCK	%Cover	0.0652	0.0476	1.8768	0.1707
SLOPE	Slope	0.1936	0.0558	12.033	0.0005
DIR – SE	Aspect	1.2365	0.04103	9.0839	0.0026
VCO	Proximity	0.0583	0.0239	5.9355	0.0148
MARSH	Proximity	0.0448	0.0202	4.9146	0.0266

Snakes located by opportunistic searching were associated with sites characterized by a higher percentage of grass, sedge, soil or rock coverage (indicated by positive coefficients, Table 9). Sloped, southeast-facing hillsides were also positively associated with use by snakes. Snakes were not associated with habitat features related to forest (e.g. canopy coverage, trees or forest floor vegetation) or human structures (e.g. roads,

buildings or paths). Opportunistically captured snakes also used sites that were closer to marshes and artificial cover. The ten female snakes followed by radiotelemetry were associated with similar habitat features to the opportunistic snakes (Table 9).

For opportunistic captures, the “best” multiple paired logistic regression model relating snake presence to habitat characteristics included five measures of habitat (Table 10). Snakes were strongly associated with higher percentage cover of sedge vegetation and rocks, on south-east facing slopes. Snakes also appeared not to be associated with forests, as evidenced by the negative coefficient value for areas with a higher percentage of forest floor vegetation. Multiple paired logistic regression for the association of radio-tracked snakes included three measures of habitat (Table 10). Snakes that were radio-tracked were positively associated with sunny slopes near marshes.

Table 10. Multiple conditional logistic regression analysis of microhabitat features for the occurrence of Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 2005-2006.

Capture Type	Habitat Characteristic	Analysis of Max. Likelihood Estimates			
		Parameter	β	SE	P
Opportunistic Captures	Slope	SLOPE	0.1086	0.0299	0.0003
	%Cover	%SEDGE	0.0544	0.0185	0.0032
	Aspect	DIR-SE	0.9459	0.4103	0.0212
	%Cover	%ROCK	0.0313	0.0145	0.0312
	%Cover	%FLOOR	-0.0468	0.148	0.0015
Radiotelemetry	Proximity	DMARSH	0.106	0.0369	0.0041
	Slope	SLOPE	0.2229	0.083	0.0073
	Aspect	DIR-SE	3.0391	1.014	0.0027

DISCUSSION

Because they are ectotherms, snakes at northern latitudes require hibernacula to survive the harsh winter conditions (Aleksiuk, 1976; Gregory, 1982). Thus, the availability of suitably deep hibernation sites may dictate the northern range limits of a species (Gregory, 1982). The phenomenon of communal denning in several species of snakes that inhabit northern latitudes may be a response to limited availability of suitable over-wintering sites (Gregory, 1984b). Den population sizes for garter snakes can vary considerably, from solitary individuals in mammal burrows to large aggregations of snakes in stable, rock cavern structures (Gregory, 1974). The largest aggregations of hibernating snakes in the world occur at the Interlake den sites in Manitoba, from which

thousands of Common Red-sided Garter Snakes (*T. sirtalis parietalis*) emerge every spring and to which they return every fall (Gregory, 1974, 1977a; Shine et al., 2001b). Although Plains Garter Snakes inhabit the same area of Manitoba, and are reported to use the communal dens occasionally (Mason, personal communication), they typically use much smaller dens with fewer individuals at each site (Gregory, 1977b). Plains Garter Snakes in other regions of North America reportedly use rock sinks (Rossman et al., 1996), small mammal burrows (Mason, personal communication, 2005) or crayfish burrows (Dalrymple and Reichenbach, 1981) as hibernacula.

At MLPP, the only hibernation sites definitely located consisted of small pre-existing holes in the ground, possibly dug by small mammals. All sites were covered by varying levels of grass-mat litter, and in close proximity to edge vegetation (Table 7). Three of the sites were located on south-facing slopes, potentially providing ideal thermal conditions for spring emergence activities (Sexton and Hunt, 1980). However, surface habitat features are unlikely to be good predictors of locations of hibernacula at MLPP, because they are not distinct from sites that are generally available within the habitat. The internal environmental conditions of natural hibernacula of *T. radix*, which I could not measure, are likely to be important to the over-wintering survival of snakes. Macartney et al. (1989) compared the thermal profiles of a garter snake den site to a nearby site not used by snakes (based on superficial appearances of similar qualities) and found significant differences, including lethal temperatures at the unused site. Other studies have highlighted stability, depth, and humidity as important internal features of a hibernating site (Costanzo, 1989; Prior and Weatherhead, 1996). At present, I cannot determine the important defining characteristics of hibernating sites for *T. radix* at MLPP.

I did not observe any communal den sites for *T. radix* at MLPP. This deviation from the supposedly "typical" behaviour of garter snakes at northern latitudes could be attributed to a couple of different factors: (1) den sites large enough to provide stable winter habitat for many snakes may not be available in this region; or (2) there is an abundance of small over-wintering sites available (i.e. den sites are not a limiting factor for this population). Regardless of the reason, snakes apparently are able to find a sufficient number of over-wintering sites that provide stability and frost-free microclimates. However, departure from communal hibernation behaviour may have

potential consequences for population ecology, such as increased time and energy spent searching for mates in spring.

Den fidelity has been reported for several species of snakes, including racers (Brown and Parker, 1976b), garter snakes (Fitch, 1965; Gregory and Stewart, 1975; Larsen, 1986) and rattlesnakes (King and Duvall, 1990). Brown and Parker (1976b) reported that racers typically returned to an area that held a series of den sites, rather than using the same hibernacula. It is currently unknown whether *T. radix* at MLPP show fidelity to hibernation sites, but protection of the known existing *T. radix* den sites in Alberta is likely important to ensure population persistence.

In many cases, young snakes are not normally found at the same den sites as adults (MacMillan, 1988; Larsen and Hare, 1992). This may be due to their small size and consequential inability to travel long distances to adult den sites. Or it may simply be that small snakes are less restricted in their choice of hibernacula than adults and have many suitable sites available to them (Gregory, 1977a; Larsen and Hare, 1992). At present, nothing is known about the over-wintering sites of neonate and juvenile Plains Garter Snakes at MLPP. Ant mounds have been suggested as potential over-wintering sites for young snakes (Gregory, 1977b), and although there were plenty of ant mounds at MLPP, visual searches of these sites provided no evidence of young snakes using them for hibernation sites. This lack of data for early-life hibernation remains an obstacle to the overall understanding of the ecology of these snakes.

Timing of spring dispersal from the hibernation sites was unclear for Plains Garter Snakes at MLPP. In the very early spring snakes were frequently captured at the same location on successive days, suggesting that they may remain within the vicinity of the den for a length of time immediately after emergence. Gregory (1977b) found that *T. radix* spent a very short amount of time at the communal den sites where he occasionally observed them in Manitoba. By contrast, *T. sirtalis* has been shown to spend longer periods of time at communal den sites, apparently related to the mating activities that occur during this stage of the active season (Gregory, 1974; Krohmer and Crews, 1989; Shine et al., 2001b). *Thamnophis radix* at MLPP presumably mate in spring as well, but, given the apparent lack of communal denning, may disperse earlier from the den to search for mates. If the probability of finding a mate is greatly reduced when den sites

are spread out over a wide area, snakes may have to move large distances in the spring in order to mate.

At least some hibernation sites at MLPP are located in or near summer habitats of these snakes, which decreases the need to disperse the long distances that have been reported for *T. sirtalis* (Gregory and Stewart, 1975). Nonetheless, I found strong evidence of directed spring and fall movements, through several different habitats, by female Plains Garter Snakes at this site. Such seasonal patterns are common in temperate-zone snakes, including several species of rattlesnake (Gannon and Secoy, 1987; King and Duvall, 1990; Ashton, 2003; Gomez, 2007), colubrids (Hirth et al., 1968; Brown and Parker, 1976b; Weatherhead and Hoysak, 1988; Burger and Zappalorti, 1989), and the well-documented garter snakes (Gregory and Larsen, 1975; Larsen, 1986; Shine et al., 2001b).

Long-distance seasonal migration of snakes appears to occur more often at higher latitudes (Gregory, 1984c). Movements by animals are likely to differ between populations based on how widely spaced resources are from one another (Gibbon and Semlitsch, 1987; Gregory et al., 1987). Gregory and Stewart (1975) found that Manitoba *T. sirtalis* traveled up to 18 km from den sites to summer marsh habitat. In northern Alberta, Larsen (1987) also found long-distance movements in *T. sirtalis*, including round-trip migrations (up to 15 km). Movement is presumably risky and energetically expensive, and long-distance movements likely are undertaken only when there are no other options for satisfying an individual's needs (Gregory and Stewart, 1975). The shorter seasonal movements exhibited by female *T. radix* at MLPP therefore were likely due to the den sites being relatively near summer sites that contained needed resources (e.g. basking sites, foraging areas).

In contrast to fall and spring, movements of radio-tracked female snakes during the summer appeared to be shorter and less frequent, and snakes often stayed in a relatively small area for long periods of time. These observations match those made for other non-migrating garter snakes (Fitch and Shirer, 1971), in which movement distances generally have been reported to be less than 75 meters over a period of several months (Reichenbach and Dalrymple, 1986). Snakes on the surface of the ground spend much of their time in stationary positions (mainly basking; Carpenter, 1952a; Fitch, 1965;

Reichenbach and Dalrymple, 1986), rather than actively moving. Female *T. radix* in my study were frequently observed basking in the same localized area for long periods of time. However, many of these females were gravid during the summer, which has been shown to decrease the frequency and distance moved by a female (Brown and Parker, 1976b; Reinert and Zappalorti, 1988; Charland and Gregory, 1995).

In addition to reproductive state of females, factors such as age, size and sex also may affect movement behaviour of individual snakes (Gibbon and Semlitsch, 1987; Gregory et al., 1987). Such variation probably depends on the distribution of resources across the habitats combined with the specific needs of the individual. Since I radio-tracked only large females, my analysis of intra-population variation was limited, but I also found no relationships between size, sex or reproductive condition and movement patterns for opportunistically captured snakes. However, both large and small snakes appeared capable of moving great distances (refer to Fig.21). One artifact in my data results from measuring distance between captures as the shortest straight line, but it is likely that actual distances traveled were substantially longer. Because snakes are often associated with edge habitat (i.e. in close proximity to cover), it is more likely that a snake would move along a more sheltered route, such as the edge of a field or marsh, rather than cut straight across open ground (Blouin-Demers and Weatherhead, 2001a, 2001c). The wide spatial distribution of snakes observed in and around MLPP, combined with their wide-ranging movements, suggests that large preserved areas that include multiple habitats, both aquatic and terrestrial, are required to ensure population persistence of *T. radix* on the landscape around MLPP.

Animals typically do not use their environments at random, but actively select some sites over others because of particular habitat features (Manly et al., 2002). Non-random use of habitat therefore typically occurs in response to heterogeneous environments, where particular resources are found only in certain areas. Reptiles have been shown to select habitats based on both intrinsic factors, such as body size and reproductive condition (Reinert, 1993), and extrinsic factors such as distribution of prey (Reinert 1993; Blouin-Demers and Weatherhead, 2001a), hibernation sites (Reinert, 1993), temperature (Huey, 1982; Row and Blouin-Demers, 2006) and moisture (Drummond, 1983). Garter snakes are widespread in North America and occupy a wide diversity of habitats

(Rossman et al., 1996). Some species like *T. melanogaster* and *T. couchi* are highly dependent on the presence of water (Drummond, 1983) and are thus restricted in distribution by the presence of aquatic habitats (e.g. marsh, ponds, streams). Conversely, other species like *T. ordinoides* are terrestrial and not dependent on water, and therefore occur in a wider diversity of habitats characterized by other factors such as temperature (Gregory, 1984a). The habitat use of most species of garter snakes is likely affected by a suite of factors, leading to intra- and inter-specific variation depending on geographic location.

What are the key features that describe suitable habitat for Plains Garter Snakes? On a macro-scale, these snakes tended to be located in mainly marsh and field habitats. For example, all of the basking sites were at the edges of marshes or fields and most of the summer retreat sites that I observed for these snakes were hillside holes at the edges of fields. Marsh and field sites were frequently near one another and use of them was proportionally greater than their availability, suggesting some level of resource selection (Manly et al., 2002). Use of marsh during the summer months supports the observation that these snakes have a diet consisting mainly of wetland species (see Chapter 3). Additionally, field habitat with well-defined bush edges offers basking sites with an abundance of cover for protection from predators. Many other species of snakes have been reported to use marsh and field habitats (Drummond, 1983; Bronikowski and Arnold, 1999; Roe et al., 2003, 2004; Burger et al., 2004; Row and Blouin-Demers, 2006). Charland and Gregory (1995) found use of grassland habitats by *T. elegans*, especially in gravid females. In Manitoba, Hart (1979) found that where *T. radix* and *T. sirtalis* were sympatric, *T. radix* occupied warm, open parkland regions with ponds, whereas *T. sirtalis* was associated with cooler closed marshes in aspen forest. As marshes and grassland fields are common throughout the Great Plains of North America, the presence of both of these habitats may be linked to the distribution of *T. radix* (Jordan, 1967).

On a finer scale, microhabitat use by Plains Garter Snakes at MLPP was described by several individual features (Table 9). Most of the relevant habitat variables had been predicted ahead of time to be related to a variety of snake activities, including thermoregulation (e.g. sunny, grass covered hillsides), foraging (e.g. marsh-related

variables) or avoidance of predators (e.g. under cover, thick grass or sedge vegetation). However, habitat variables when examined alone have been shown to have limited predictive power for determining animal use in heterogeneous habitats (Garshelis, 2000). The habitat of an organism is a multidimensional space, and requires a multivariate approach for realistic evaluation of how it is used (Carey, 1981).

The multiple logistic regression of the matched used and available sites emphasizes the non-random use by *T. radix* of sloped hills with a south-easterly aspect, allowing for a high level of sun exposure. However, even at the multivariate level of analysis, slope, aspect and marsh-related vegetation were important habitat variables for snakes both caught opportunistically and located via radiotelemetry. The similarities between my results and other studies suggest the utility of using thermal qualities of sites (e.g. sun exposure – slope and aspect), as well as structural features (e.g. rock or vegetation coverage) for predicting the probability of use of habitats by snakes (Hart, 1979; Gregory, 1984a).

Many ecological studies on reptiles have highlighted temperature as a key influence on habitat use (Huey, 1982; Gregory, 1984a; Peterson, 1993; Pringle et al., 2003). Thermal responses of snakes have been shown to restrict their activities, both spatially and temporally (Nelson and Gregory, 2000), as well as the overall geographic range of a species (Passek and Gillingham, 1997). Vegetation is an important structural characteristic of habitat, and likely has a large impact on the thermal properties of a microhabitat site used by a snake (Reinert and Kodrich, 1982). The relative availability of sun and shade (i.e. canopy closure) has been used to measure thermal suitability in habitats used by Black Rat Snakes (Weatherhead and Charland, 1985), Wood Turtles (Compton et al., 2002) and Milksnakes (Row and Blouin-Demers, 2006). As predicted, Plains Garter Snakes were not often found in forests, even though that habitat was widely available. This suggests that snakes avoided areas with lower temperature regimes (e.g. increased canopy coverage, saturated leaf litter), and used forest-related habitat only when it intersected their movement paths. Row and Blouin-Demers (2006) examined use of habitat in Milksnakes at several spatial scales and found that snakes used areas based on thermal qualities, especially open areas (e.g. fields, rocky outcrops and marshes) with well-defined edges. Avoidance of forest was also a key component of Milksnake habitat

use (Row and Blouin-Demers, 2006). My results for *T. radix* add to the literature supporting the importance of temperature in determining the spatial distribution of snakes; however, specific thermal regimes for this species remain to be studied.

Many studies of habitat use in snakes have found an association between habitat occupancy and prey availability (Shine, 1977; King and Duvall, 1990; Mullin et al., 1998; Perz and Purdy, 2001). As seen in *T. sirtalis* (Gregory, 1974), in the early spring and late fall, *T. radix* at MLPP are occupied with activities associated with hibernation, and prey availability is unlikely to be a significant factor in their use of habitat. However, in the summer, garter snakes must acquire resources to grow, reproduce and survive, and their use of habitat probably reflects both their foraging strategy and diet (Reinert, 1987, 1993; Matthews et al., 2002). Similar to various other habitat features, prey species are not evenly distributed across a landscape, and thus, snakes select areas to occupy based on the abundance or availability of prey. Results from radiotelemetry revealed that *T. radix* spent more time during the summer months in marshes, where their most frequent prey, anurans, were presumably most abundant. However, I did not measure prey abundance or availability in this study; such measurement is required to determine the degree to which habitat selection by snakes is influenced by their prey.

Small snakes, due to their seasonal behaviours, physical constraints (e.g. decreased locomotory ability) and vulnerability to predators, are likely to use habitat differently from adults. For example, there was a clear trend for smaller snakes to be found under cover. The use of artificial cover objects (ACOs) by snakes has been well-documented (Grant et al., 1992; Englestoft & Ovaska, 2000). At MLPP, ACOs that were associated with use by *T. radix* were abundant in the populated regions of the park and included buildings with cracked foundations, sheds, abandoned picnic tables, wood and junk piles, wood boards and even beer bottles on the sides of the roads. These materials seem to be favoured because they afford protection from predators, but they also offer thermal regimes that may be different from ambient temperatures. Smaller snakes are likely more vulnerable to predation, and as a consequence presumably spend more time under cover (Webb and Whiting, 2005).

Gravid females at MLPP tended to be found in warmer field and marsh habitats, often along the edges of dense marsh reeds or in grass patches near banks of raspberry or

prickly rose bushes. Charland and Gregory (1995) found that gravid female *T. sirtalis* and *T. elegans* were associated with microhabitats that contained more rock cover. Huey et al. (1989) found that rocks, due to their thermal qualities, provided both shelter and thermal opportunities to snakes. Rocky sites were not common at MLPP and most were in areas associated with human use; therefore the gravid snakes located at these sites were presumably benefiting enough from thermal qualities to compensate for the presence of humans.

Although studies of habitat use typically focus on natural habitats, garter snakes often are common near human habitations in both rural and urban settings (Stanford, 2002; Burger et al., 2004). The ability to co-exist with humans obviously reduces the likelihood of extinction of these species, but it also can lead to conflicts with humans. Furthermore, the ability of snakes to persist in human-altered landscapes obviously depends on the type and degree of anthropogenic disturbance that they face. The distribution of *T. radix* is largely restricted to the Great Plains, an area that has undergone significant landscape alteration due to agricultural land use (Dahl, 1990). Perhaps thousands of homesteads, farms, towns and human-altered areas litter the Great Plains landscape, and large areas of land that used to be available for animal occupancy are now either unsuitable for snakes or constantly disturbed by human presence. Of particular importance for many semi-aquatic reptiles is the loss of wetlands (Roe et al., 2003). Considering the importance of marsh habitat to *T. radix* at MLPP, the loss of wetlands is likely to have a negative effect on these snakes, and should be investigated in greater detail.

At MLPP, *Thamnophis radix* were frequently found near human structures (e.g. buildings, junk-piles), and inhabiting areas occupied by humans entailed certain risks. For example, snakes were often seen basking at the edges of mowed lawns, and no doubt sometimes were run over by lawnmowers. Roads, especially those with high levels of traffic, also pose significant hazards (Bernardino & Dalrymple, 1992; Ashley & Robinson, 1996; Shine et al., 2004). Forman (2000) and Ritters and Wickham (2003) both estimated that 20% of ecosystems in North America were either completely surrounded by roadways or within 200 meters of a road. Because snakes are ectothermic, paved roads may provide a heat source to them, especially in cooler weather (Huey et al.,

1989; Shine et al., 2004). However, this heat source comes with a tradeoff: no shelter from predators and a high threat of mortality from cars. Roads, or more specifically road sides, also may offer corridor habitat for movements. More likely, though, roads often just happen to intersect areas that snakes use at a high frequency. Evidence for this may be seen in the higher number of road kills often observed in fall, as snakes were moving from their summer habitat to winter den sites (Bonnet et al., 1999). Shine et al. (2004) found that when a road intersected paths of snakes, the snakes typically either crossed straight over or moved parallel to the road, potentially indicating an avoidance of road surfaces. Regardless of reasons for why snakes were found on roads, roads were negative entities of habitat for snakes at MLPP (N = 36 road kills); however, it is unknown how road mortality affects overall population dynamics (Bonnet et al, 1999).

Radiotelemetry has revolutionized the study of movement patterns of snakes and other animals (Ujvari and Korsos, 2000), allowing spatial use of habitats to be measured more precisely through frequent relocations of the same individuals (Fitch and Shirer, 1971; Brown and Parker, 1976b; Peterson, 1987; Reinert, 1984; Macartney et al., 1988). Data from my study show clearly that, compared to radiotelemetric observations, movement data based on opportunistic captures can be significantly biased. Such bias is due to the differential ability of human searchers to find snakes in different habitats, some of which hide animals better than others. By tracking individual female snakes I found that wetland environments were used at a higher frequency than was indicated from opportunistic searching alone (Fig. 23). Nonetheless, on the microhabitat scale, both opportunistic and radio-tracked snakes were associated with similar habitat features. Thus, the greater utility of telemetry compared to opportunistic capture seemed to apply most significantly to the macrohabitat scale.

Despite the utility of radiotelemetry in describing movement patterns of snakes, studies that use it, including mine, inevitably are compromised by small sample size (in terms of number of individuals) and bias towards larger snakes (and to just females in my case). Shine (1987b) showed extensive variation in the many habitat attributes to which one species of snake responded in Australia. Thus, the generality of studies measuring a small number of individuals of the same sex or size is questionable. Furthermore, some of the females I used were gravid (which has been shown to influence daily activity and

habitat use of snakes; Reinert and Zappalorti, 1988), but they were pooled with non-gravid females because of small sample size. In order to achieve an overall picture of this population's movements and use of habitat, as well as to uncover variation due to sex, size, or reproductive condition, future studies on this population should include telemetry data for males and females of varying sizes.

Radiotelemetry observations of use of habitat are also not independent of one another because the same snake is followed over time (Swihart and Slade, 1985) and use of habitat at one location is dependent on a snake's previous location. I used sample location (defined as greater than 25 m from the previous location or after one month had passed at same location), rather than individual female, as the sampling unit. Partly to compensate for both the use of only females for radiotelemetry, as well as autocorrelation of radiotelemetry locations, I also examined habitat use for opportunistically captured snakes. Although opportunistic captures are themselves biased (see above), they nonetheless acted as an informative comparison for the exploratory purposes of this study. The combination of these two kinds of data yielded results that were broadly consistent with each other and with literature observations, strengthening my conclusions about habitat use in Plains Garter Snakes at MLPP.

The Plains Garter Snake can be considered an umbrella species with respect to its use of habitat at the aquatic-terrestrial interface. Like most garter snakes, *T. radix* is a wetland-associated species during the summer months, but it relies on adjacent terrestrial habitats for numerous activities, including hibernation. Thus, protection of garter snake habitat has the potential for multi-species benefits, by expanding the boundaries of wetland habitat to include surrounding terrestrial areas. Furthermore, from a landscape perspective, my results show the extent to which Plains Garter Snakes rely upon healthy wetland habitats in Alberta, strengthening the case for conservation and management of wetland ecosystems.

CONCLUSION

Natural systems vary from year to year, and long-term studies are needed to capture the variation needed to answer important questions about how populations themselves vary, as well as how their ecology responds to changes in the natural environment. Short-term studies such as mine therefore can be nothing more than a snapshot of dynamic processes, but nonetheless can contribute to our understanding of natural history and patterns of life-history variation. In so doing, they also provide essential information for management and conservation of the study species, should such information become necessary in future.

The main conclusions from my study of the natural history and ecology of *Thamnophis radix* at Miquelon Lake Provincial Park were:

- 1) The major features of the population ecology of this species at MLPP are comparable to those observed in other studies of *T. radix* and of *Thamnophis* in general, especially high-latitude populations. However, numerous aspects of the population ecology of snakes at MLPP are unstudied (e.g. survivorship) and those gaps need to be filled before we have a comprehensive picture of the demography of this population and of geographic variation through the species' range.
- 2) Although *Thamnophis radix* at MLPP feed mainly on anurans, they are more generalized predators as adults and, based on comparisons with studies elsewhere in the species' range, apparently are plastic in their food habits in response to resource variation. Reliance on frogs as food, however, underscores this species' potential importance in energy flow within wetlands and between aquatic and terrestrial systems.
- 3) At MLPP, snakes use open field habitats and marshes, but largely avoid forest. Sites used by snakes tend to include sunny hillsides near marshes, and near cover, exemplifying the inherent trade-offs among foraging, thermoregulating and hiding from predators. In winter, snakes depend on small mammal burrows for hibernation. Large-scale communal denning was not observed, suggesting that the availability of suitable hibernation sites is not limited. Although hibernation sites tend to be located within or

near the summer habitats used by these snakes, obviating the need for long seasonal migrations, movements are longer and more frequent in fall and spring, associated with movements to and from hibernacula, than in summer. Thus, in general pattern if not necessarily in physical scale, seasonal movements and habitat use of *T. radix* at MLPP are similar to those of other populations of garter snakes in northern environments.

4) Radio-tracking of female *T. radix* at MLPP revealed important seasonal movements and locations of hibernacula, as well as a higher frequency of use of marsh habitats than was evident from opportunistic captures alone. Because only large female snakes were tracked, further longer-term studies that include collection of data from a larger number of individual snakes of various categories within the population are required.

5) Although the well-documented Common Garter Snake (*Thamnophis sirtalis*) has been used as a model species to describe and predict the ecology of garter snakes in general (Rossman et al., 1996; Seigel, 1996) and northern populations in particular (Gregory, 2007a), my study shows that it is an imperfect model and that variation in the ecology of northern snakes exists between species (in this case) and likely between populations of the same species. Table 11 highlights the major deviations in life history traits and ecological patterns (using both my results and literature values) between these *T. radix* and *T. sirtalis*.

Table 11. Comparative life history and ecology of Common Garter Snakes (*Thamnophis sirtalis*) and Plains Garter Snakes (*Thamnophis radix*).

Ecological or life history trait		<i>Thamnophis sirtalis</i>	<i>Thamnophis radix</i>
Body Size	Sexual dimorphism	Present ^{2,3,4}	Present ^{1,6,7}
	Male SVL (mm)	455 (387-678) ²	463 (355-635) ¹
	Female SVL (mm)	550 (504-950) ²	580 (404-780) ¹
	Neonate SVL (mm)	168 (134-191) ²	159 (151-196) ¹
Reproduction	Mode	Viviparous	Viviparous
	Strategy	Capital Breeder	Capital Breeder
	Female Cycle	Annual/Biennial ^{2,3,4}	Annual/Biennial ^{1,7}
	Litter size	18 ⁸ 13.5 ² 11.6 ⁴	23 ¹ 18.4 ⁷ 29.5 ¹⁰
Food Habits	Diet	Generalist ⁹	Generalist ^{1,9}
	Frequency of feeding	32% ¹⁵	22% ¹ -57% ¹²
	Prey types	Anurans ^{2,3,4}	Anurans ^{1,10,11,12}
		Earthworms ^{2,3,4} Fish ¹³	Earthworms ^{1,10,11,12} Mammals ^{1,10}
Habitat	Hibernacula	Communal ^{3,4}	Solitary ¹
	Den structure	Rock sinks ^{3,4}	Mammal burrows ^{1,9}
	Macrohabitat	Marsh ^{3,4,16}	Field, Marsh ^{1,12}
Movement	Migration	Long distance ^{3,5}	Short distance ¹
	Average distance	10.7 km, 3.75 km	0.6 km ¹
Distribution	Overall range	Widespread ^{2,9}	Great Plains ⁹
	Canadian range	BC, AB, SK, MN ¹⁷ ON, QB, NB, NS ¹⁴ NWT ⁴	AB, SK, MN ^{9, 16}
Temperature	Activity range	-1.5 to 34 °C ¹⁹	5 to 35 °C ^{1,18}

References: 1-This study (2006); 2-Fitch (1965); 3-Gregory (1977a); 4-Larsen (1986); 5-Larsen (1987); 6-Cline (2000); 7-Stanford (2002); 8-Carpenter (1952a); 9-Rossman et al. (1996); 10-Gregory (1977b); 11-Hart (1979); 12-Jordan (1967); 13-Gregory and Nelson (1991); 14-Barnes et al. (2006); 15-Gregory (1984b); 16-Russell and Bauer (2000); 17-Gregory (2007); 18-Heckrotte (1962); 19-Peterson (1987).

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