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Food Habits of the Plains Garter Snake (*Thamnophis radix*) at the Northern Limit of Its Range

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Abstract.—The North American genus *Thamnophis* is a widely distributed and abundant group of snakes. Previous research has indicated that most garter snakes are generalist predators that largely consume anurans, with some degree of geographic and temporal plasticity in response to resource variation. We studied the dietary habits of the Plains Garter Snake, *Thamnophis radix*, based on stomach contents from 548 animals collected in the field from 1995–2006 at the northern limit of the species' range in central Alberta, Canada. Feeding frequency overall was low (22%) and was highest in spring and early summer. Diet was composed mainly of anurans (85%), especially Wood Frogs (*Rana sylvatica*) and Boreal Chorus Frogs (*Pseudacris maculata*), and occasionally invertebrates (10%) and small mammals (5%). Small snakes (<200 mm) began feeding shortly after birth and consumed mainly smaller frogs. Larger snakes ate a wider range of prey sizes and types, but frogs still constituted the majority of prey consumed. Despite sexual size dimorphism, males and females ate prey of the same size and type; however, gravid females contained food less frequently than both males and nongravid females. This study adds to the growing number of dietary studies on *T. radix* and provides additional evidence for the ecological plasticity of *Thamnophis* species. Further studies are needed to examine how important these snakes are as components of wetland food chains.

Foraging is a critical aspect of an animal's ecology, because success or failure in securing food resources has obvious consequences for survival, growth, and reproduction (Sih, 1993). Patterns of resource use are influenced by many factors, such as habitat and prey availability, and diet may be linked to the evolution of life-history traits (Arnold, 1993; Greene, 1997). The food habits of a species also are an important part of food web dynamics, especially in animals that forage across the boundaries of ecosystems (e.g., aquatic-terrestrial interface) and facilitate the transfer of nutrients between them (Polis et al., 1997; Huxel and McCann, 1998).

Natricines, a widespread group of New World and Old World snakes, frequently forage in both aquatic and terrestrial environments. The New World garter snakes (*Thamnophis*) exhibit an especially notable evolutionary diversification into a variety of habitats and associated feeding habits (Greene, 1983, 1997; Rossman et al., 1996). As a group, garter snakes consume a wide range of prey types (Drummond, 1983). Some species are specialist predators on a primary prey (e.g., *Thamnophis couchi*, *Thamnophis melanogaster*), whereas others generalize their diets (e.g., *Thamnophis sirtalis*, *Thamnophis elegans*) and consume multiple prey types (Rossman et al., 1996). A generalist foraging strategy presumably reflects high diversity of prey types or patchy abundance of prey in a particular environment (Carpenter, 1952; Gregory, 1977a, 1978, 1984). In general, diets of garter snakes consist of amphibians (especially anurans), fish, invertebrates, and occasional mammals and birds (Rossman et al., 1996). Most garter snakes are also active foragers, rather than sit-and-wait predators (MacArthur and Pianka, 1966); hence, 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 trade-offs often contribute to variation in resource acquisition within populations, with important consequences for population dynamics (Lomnicki, 1988).

Previous studies of feeding habits of *Thamnophis* have investigated several of the factors that may influence variation in dietary habits, such as phylogeny (Arnold, 1981), prey availability (Kephart and Arnold, 1982; de Queiroz et al., 2001; Matthews et al., 2002), and body size (Arnold, 1993; Lind and Welsh, 1994). Most research has focused on a few well-studied species such as *T. sirtalis* and *T. elegans* (Rossman et al., 1996). Both of these species typically have broad diets and show considerable inter-population variation (Gregory and Stewart, 1975; Kephart and Arnold 1982; Larsen, 1986; Bronikowski and Arnold, 1999). Diets of other

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species of garter snakes have not been studied as extensively, and it is generally unknown whether they exhibit the same tendencies of variation and plasticity seen in *T. sirtalis* and *T. elegans*. Such plasticity should be especially important for species that reach high latitudes, where prey diversity may be reduced and where short, variable active seasons limit the time available for feeding. Thus, the study of feeding habits of northern snakes can make an important contribution to our understanding of how a species' natural history is shaped by extreme environments. In this study, we investigate the feeding habits of another widely distributed species, the Plains Garter Snake (*Thamnophis radix*), near the northern limit of its range in central Alberta, Canada.

Our main objectives were (1) to determine the types of prey eaten and, thus, whether *T. radix* at this site is a generalist or specialist predator; (2) to describe intrapopulation dietary patterns of *T. radix*, including variation relating to snake size (i.e., ontogeny), season, sex, or reproductive state; and (3) to compare the diet of *T. radix* at our study site with literature reports for this species from elsewhere within its range. We 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 wide size range exhibited by *T. radix* from birth to adulthood, prey size would vary ontogenetically; and (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 sex or size groups (Gregory et al., 1999).

Materials and Methods

This study took place at Miquelon Lake Provincial Park, 60 km southeast of Edmonton, Alberta (53°21′N, 112°55′W, elevation 763 m). The study area lies within the Grassland Ecoclimatic Region, and the natural landscape is characterized by aspen parkland, prairie grassland, and non–peat-accumulating wetland habitats (NRC, 2006). The park itself is designated as recreational and protected habitat, but the surrounding area is anthropogenically disturbed; major land uses adjacent to the park include farming and natural gas and oil development.

We surveyed the study area on foot and collected snakes by hand during the active season (early May to end of September) from 1995–2006. From 1995–2004, data collection was infrequent, but we studied the population intensively in 2005 and 2006. We measured each captured snake (snout–vent length, SVL, to the nearest 1 mm) and gave it a unique identifying mark by clipping subcaudal scales (Blanchard and Finster, 1933). We broadly classified snakes as young-of-year (<200 mm), juveniles (200–400 mm), or adults (>400 mm), based on birth sizes and minimum sizes of courting males and gravid females. We also recorded sex, reproductive condition (gravid or not), and state of ecdysis (e.g., about to shed, as evidenced by cloudy eyes or venter).

We gently induced regurgitation of stomach contents of each captured snake by abdominal palpation. We counted and classified prey items as invertebrate, anuran, mammalian, or unknown; we further identified anuran prey by species. Partially or completely digested items were excluded from all analyses involving size of prey. When possible, we determined the direction of ingestion of prey items, either by direct observation of recently swallowed items as they were regurgitated or by noting which end of the regurgitated prey was digested. We also measured the body length of all anuran (snout-urostyle length) and mammalian (excluding tail) prey items along a meter stick to the nearest millimeter. After identifying, counting, and measuring prey, we 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. We 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 (i.e., recaptures under 30 days) were not included in the analyses if the previous capture yielded stomach contents.

We did all statistical analyses using SAS 9.1 (SAS Institute, Cary, NC, 2003). Analysis of the data consisted mainly of correlation tests, χ^2-contingency tables, logistic regressions, and analysis of covariance (ANCOVA), with a rejection level of $\alpha = 0.05$. In each case, we ensured that assumptions of the analysis were met (e.g., homogeneity of slopes in ANCOVA). All means are presented with ±standard deviation (SD).

Results

Diet Composition.—Of the 548 capture records from 1995–2006, 122 had stomach contents (feeding frequency = 22.3%). Because of the paucity of data (11 sample days and 7 food items) from 1995–2004, we could not compare diet from early and late in the study. Furthermore, there were no differences between the years 2005 and 2006 for any aspect of feeding that we studied; thus, we pooled data across all years. We identified 167 of the 183 prey items in

TABLE 1. 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. Young-of-year < 200 mm, juvenile = 200–400 mm, adult > 400 mm (N = 122).

	Stomach contents				
Size class	Frog	Mammal	Worm	Leech	Unidentified
Young-of-year	9 (90%)	–	1 (10%)	–	–
Juvenile	37 (97%)	–	1 (3%)	–	–
Adult	57 (77%)	5 (7%)	8 (11%)	1 (1%)	3 (4%)

stomachs (Table 1). Snakes primarily ate anurans (87%), followed by invertebrates (9%), and small rodents (4%). Of the two anuran species consumed (including both larval and metamorphosed forms), Wood Frog (*Rana sylvatica*) (81%) were eaten with a greater frequency than Boreal Chorus Frog (*Pseudacris maculata*) (19%; χ^2_1 = 38.53, P < 0.0001, N = 106). *Rana sylvatica* were observed virtually every day that we looked for snakes, although frog observations ceased in late September. *Pseudacris maculata* were frequently heard in spring but not seen as frequently as *R. sylvatica*. The small mammals taken were nestling rodents (N = 8), likely either voles (*Microtus* or *Myodes*) or mice (*Peromyscus*). We 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-end first. All eight rodent prey items were swallowed head first.

The number of prey items per capture ranged from 1–10 (mean = 1.56 ± 1.30, N = 106, 16 digested items excluded), but the majority of snakes contained only one (71.7%) or two (15.1%) prey items in their gut (Fig. 1). Only 13 snakes contained more than two prey items: 11 with three or more frogs; one with four nestling rodents; and one with 10 large earthworms. No snakes contained more than one type of prey. The number of prey eaten was significantly influenced by size of snake (r = 0.31, P = 0.0006).

Ontogenetic Shifts in Diet.—Snakes of different sizes ate a changing diversity of prey types (Fig. 2) and prey of different sizes (Fig. 3). Young-of-year snakes ate only small prey, which restricted them to the smaller of the frog species, *P. maculata*. Juveniles ate mainly frogs of both species and occasionally small earthworms. Adult snakes ate all prey types, including frogs of all sizes, annelids, and small mammals; hence, the general pattern was increasing diet diversity with size of snake. Mammalian prey were taken by only the largest snakes (>555 mm SVL), which also ate the widest range of prey sizes and continued to include smaller food items in their diets. Sex had no significant effect on the type of prey taken (χ^2_2 = 2.32, P = 0.31), although four of the five snakes with mammalian prey in their stomachs were female. We found no significant variation in prey size among months (AN-

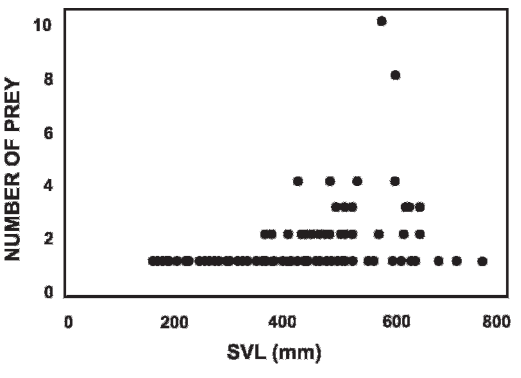

FIG. 1. Number of prey items in stomach as a function of snake size (SVL, mm) of Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 2005–2006. Each dot represents a capture record (N = 106).

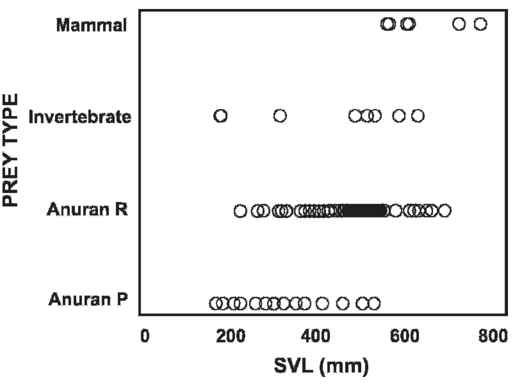

FIG. 2. Prey type versus size of snake (SVL, mm) at Miquelon Lake Provincial Park, Alberta, 1995–2006. Each circle represents an individual snake with a type of prey item (N = 106). Anuran P = *Pseudacris maculata*; Anuran R = *Rana sylvatica*; Invertebrate = earthworm or leech; Mammal = nestling vole or mouse.

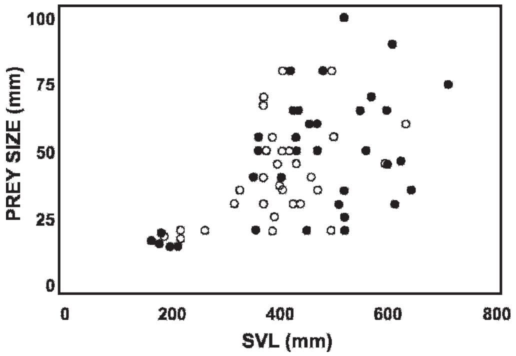

FIG. 3. Prey size (body length, mm) as a function of snake size (SVL, mm) at Miquelon Lake Provincial Park, Alberta, 2005–2006 (r = 0.50, P < 0.0001, N = 67). Each dot represents an individual prey item (anuran or mammalian only); females = filled circles, males = open circles.

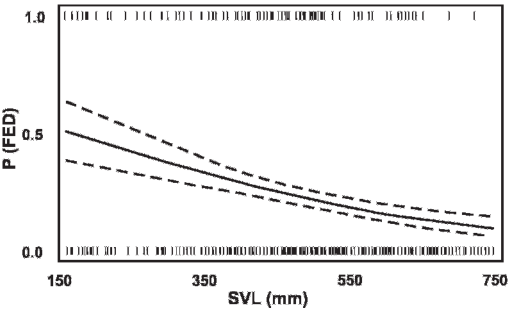

FIG. 4. Probability of food present in stomach versus size (SVL, mm) of Plains Garter Snakes (*Thamnophis radix*) at Miquelon Lake Provincial Park, Alberta, 1995–2006. Vertical lines at top = snakes with food (N = 122), vertical lines at bottom = snakes without food (N = 426). Solid line represents predicted values from logistic regression of presence/absence of food against size. Dotted lines represent 95% confidence limits on predicted values.

COVA, $F_{4,60}$ = 1.81, P = 0.14; SVL as covariate, slopes homogeneous).

Feeding Frequency.—In addition to ontogenetic shifts in type and size of prey ingested, snakes at Miquelon Lake showed shifts with body size in frequency of feeding. Frequency of feeding was significantly related to SVL, with the probability of having stomach contents decreasing with increasing size of snake (logistic regression, χ^2_1 = 27.41, P < 0.0001; Fig. 4). To eliminate any effect of reproductive status on this relationship (see Feeding during Pregnancy below), we removed gravid females from the analysis, but the relationship remained unchanged (χ^2_1 = 6.35, P = 0.01). Young-of-year had the highest proportion of stomachs with food (33.3%), followed by juveniles (27.2%) and adults (11.7%). Overall, there was no significant difference in feeding frequency between the sexes (χ^2_1 = 1.82, P = 0.18). This did not change when we removed gravid females from the analysis (χ^2_1 = 1.05, P = 0.30). However, snakes that were shedding or about to shed had a lower frequency of feeding than snakes that had recently shed (χ^2_1 = 14.13, P = 0.0002, N = 106).

Snakes were found with food in their stomachs from May to September, inclusive. However, logistic regression of presence/absence of food against time (day of season, with 3 May set to day 1) showed that frequency of feeding was higher early in the season (χ^2_1 = 3.84, P = 0.0499; Hosmer and Lemeshow χ^2_8 = 7.54, P = 0.48, N = 106).

Feeding during Pregnancy.—Because of possible effects of reproductive state on feeding, we separated our sample into gravid females, nongravid females, and males for further comparison. Frequency of feeding differed significantly among males (57/227), nongravid females (46/154), and gravid females (19/167; χ^2_2 = 17.65, P < 0.0001, N = 548). Although there were no differences in frequency of feeding between males and nongravid females (see above), males contained prey more often than gravid females (χ^2_1 = 11.66, P = 0.0006). The comparison of female snakes of differing reproductive condition showed that nongravid females ate more frequently (χ^2_1 = 16.97, P < 0.0001) and ate larger prey items (χ^2_1 = 10.17, P = 0.006; small-sized prey <25 mm, large-sized prey ≥25 mm) than did gravid females. This relationship did not change when we restricted the analysis to mature females only (defined as females >400 mm SVL, based on the smallest gravid female we found; unpubl. data).

DISCUSSION

Diet Composition.—*Thamnophis radix* has been reported to eat a wide variety of food types (Jordan, 1967; Walley et al., 2003; M. E. Lesch and J. D. Fawcett, 1978, unpubl. data), a trend very similar to the generalist diets of other garter snakes (Arnold, 1981; Rossman et al., 1996). Although the predominant prey type consumed by *T. radix* varies among localities (Table 2), meaningful interpopulation comparison is misleading without data on relative prey availabilities. Anurans seem to be typical components of the diet but not necessarily always the primary food item. Perhaps they are increasingly important prey as one proceeds northward. Nonetheless, the diet of *T. radix* at Miquelon Lake included several different prey types and was broadly comparable to those reported in other studies (Table 2), although surveys elsewhere have reported additional

TABLE 2. Summary of diets of Plains Garter Snake (*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). Total is the number of snakes sampled. 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 and Reichenbach 1981 Ohio	Seigel 1984 Missouri	Present study Alberta
Anurans	X	**5**	**98**	**X**	**X**	**102**
Urodeles	–	–	–	–	X	–
Mammals	–	–	2	–	X	6
Fish	X	–	–	–	X	–
Annelids	**X**	1	17	X	X	13
Gastropods	–	–	2	–	X	–
Unidentified	–	1	–	–	–	16
Total	–	21	210	–	–	548

items such as fish (Jordan, 1967), fledgling birds (Sawin et al., 2003), gastropods (Seigel, 1984), and salamanders (Dalrymple and Reichenbach, 1981; Seigel, 1984). The variety of prey types eaten by *T. radix* indicates significant intraspecific geographic variation in diet, as well as potential for behavioral plasticity.

As we predicted at the outset of this study, the main prey of *T. radix* at Miquelon Lake were anurans. Wood Frogs were the most commonly eaten prey, perhaps because they were more abundant than Boreal Chorus Frogs, but perhaps also because their larger size makes them an energetically preferable food item (Perz and Purdy, 2001). The overall high frequency of anurans in the diet of Plains Garter Snakes at this site presumably reflects both their relative abundance and the relative ease with which frogs can be captured and eaten compared to other types of prey (e.g., birds, rodents, fish). For example, adult rodents are potentially dangerous prey for garter snakes and may require specialized handling (Gregory et al., 1980). Thus, it is not surprising that we found only nestling rodents in our samples; even so, snakes raiding rodent nests may face hazards from mothers defending their litters (Hoyer and Stewart, 2000), which may explain the overall low occurrence of rodents as prey in our study.

The absence of fish from the diet of *T. radix* at Miquelon Lake is puzzling because this species has been reported to eat minnows elsewhere (Jordan, 1967) and several small fish species occur in the ponds and lakes in our study site. Furthermore, gravid snakes that we kept in the laboratory ate fish readily (KNT, unpubl. data). Although some species of garter snakes are highly piscivorous (e.g., *T. couchi*; Lind and Welsh, 1994), less-specialized generalist species may not feed on fish unless they are extremely abundant or otherwise easily caught (Gregory and Nelson, 1991). Thus, we hypothesize that *T. radix* do not eat fish at Miquelon Lake mainly because fish are not readily available prey there.

Although small soft-bodied prey, such as worms and leeches, can be more difficult to detect by palpation than other prey, we do not believe that they are underrepresented in our sample because we attempted to induce regurgitation even when initial palpation did not clearly indicate that a prey item was present. Furthermore, in previous studies of food habits of garter snakes, we have found such prey in high frequency (e.g., Gregory, 1984). Thus, we conclude that *T. radix* at Miquelon Lake feeds on such prey to a minor extent. Again, relatively low availability of such prey at higher latitudes might account for this.

Ontogenetic Shifts in Diet.—As *T. radix* at Miquelon Lake grew, they consumed different sizes and types of prey. Such ontogenetic shifts in diet have been documented in numerous species of snakes (Arnold, 1993), including *Thamnophis* (Fitch, 1965; Seigel, 1984; Macias Garcia and Drummond, 1988; Lind and Welsh, 1994) and other genera of natricines (e.g., *Nerodia*—Mushinsky et al., 1982; *Natrix*—Luiselli et al., 1997; Gregory and Isaac, 2004). Because they swallow their prey whole, snakes are gape-limited predators. Therefore, maximum size of prey that can be eaten varies with size of snake (Shine, 1991a; Forsman, 1996). Arnold (1993) described two main patterns of ontogenetic shifts in the dietary habits of snakes: (1) larger snakes exclude smaller prey items from their diet as they increase in size; and (2) as snakes grow in size they eat larger prey while continuing to include prey of all sizes. The first pattern is typical of piscivorous snakes (Arnold, 1993), whereas the second characterizes more generalist predators; our data clearly fit the latter pattern (Fig. 3) and highlight the likely importance of multiple prey types of varying sizes for fulfilling a population's dietary needs.

Feeding Frequency.—Ectothermy allows reptiles to tolerate periods of low food intake (Pough, 1980), and the frequency with which an individual snake feeds may vary according to its physiological state (e.g., growing, gravid, shedding) or environmental conditions (e.g., season, prey availability). The frequency of snakes with food in their stomachs is possibly a crude index of feeding frequency because opportunistic searching has unknown biases, but our sample included snakes that were active on the surface and presumably foraging, as well as those found basking in the open or hiding under cover. Whatever bias may be present, our estimate of feeding frequency (22%) is toward the lower end of the range seen in other studies of snakes (5–100%; Shine, 1977). In other studies of *T. radix*, frequency of feeding ranges from 20–57% (Jordan, 1967; Gregory, 1977b; Hart, 1979). However, without measuring prey availability or correcting for influential variables such as size and reproductive condition, it is impossible to determine whether these differences among studies are real. If they are, they might reflect intersite variation in productivity, with consequent effects on life-history traits and demography. The consequences for snakes at our site might include reduced growth rate (hence, later maturation) and reduced frequency of reproduction for females, especially if they are capital breeders like other northern garter snakes (Gregory, 2006).

Garter snakes typically increase rapidly in size for approximately the first one to three years of life, after which growth slows (Scudder-Davis and Burghardt, 1987; Bronikowski and Arnold, 1999; Stanford, 2002). Our data suggest that snakes decrease their feeding frequency as they grow. The higher frequency of feeding observed for smaller snakes at Miquelon Lake is likely caused by increased energy requirements associated with growth, necessitating increased consumption of food (Andrews, 1982; Mushinsky, 1987). Nearly half of the young-of-year we caught had food in their stomachs, a large proportion compared to the overall population frequency. This further suggests that it is important for snakes to begin feeding shortly after birth, rather than relying on endogenous yolk, before entering hibernation (Andrews, 1982). It also would be advantageous for newborn snakes to feed early in life if by so doing they increase their potential for early sexual maturity. In contrast, larger snakes, which grow much more slowly or not at all, require food only for maintenance and reproduction.

Shedding snakes at Miquelon Lake had food in their stomachs significantly less often than other snakes. Captive snakes reduce their feeding both before and during shedding (King and Turmo, 1997). This decrease in feeding is thought to result either from indirect effects of physiological changes via hormone levels or from the direct effects of visual impairment when snakes are in the ''blue-eyed'' state (King and Turmo, 1997). Although garter snakes rely heavily on chemoreception in searching for prey, as diurnal predators they also employ vision to capture mobile prey (Drummond, 1985); thus, a decreased feeding frequency during shedding may be caused by an inability to see effectively. Visual impairment also may leave a snake vulnerable to predators, thus contributing to decreased frequency of feeding via low levels of activity associated with avoiding predators.

Our results also suggest that frequency of feeding varies seasonally. At our study site, 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., 2001; Shine and Mason, 2004). All snakes ceased eating by late September, presumably in preparation for hibernation, but also perhaps because of decreased food availability.

Because garter snakes are sexually dimorphic in body size and relative head size (females larger; Rossman et al., 1996), size-based comparisons of feeding frequency and diet are potentially confounded with differences between the sexes (Shine, 1991b, 1993). A few studies of diet in garter snakes have found sex-based differences, particularly in the form of food-partitioning (Fitch, 1981; Shine, 1991b), but there also are several that support no dietary differences between the sexes (e.g., de Queiroz et al., 2001). Even when we controlled for size differences, we found no differences in the diets of males and females at Miquelon Lake, except possibly for 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 we find any effect of sex on feeding.

Feeding during Pregnancy.—Numerous studies have found reduced levels of feeding in gravid snakes (Gregory et al., 1999; Gregory and Isaac, 2004). Such anorexia may be caused by (1) physical constraints because embryos take up space in the body cavity (Gregory et al., 1999); (2) constraints on locomotion, reducing the female's ability to capture prey and escape from predators while foraging (Shine, 1980; Charland and Gregory, 1995); or (3) conflicts with other requirements such as thermoregulation (Gregory et al., 1999). We detected no difference in feeding frequency between males and nongravid females, but compared to both males and nongravid females, gravid females of the same size decreased their feeding significantly. In addition, nongravid females ate larger prey items than did gravid females, supporting the idea that feeding is constrained physically by reproduction.

Although gravid females in the field had food in their stomachs at a lower frequency than other snakes, gravid females maintained in captivity during pregnancy ate fish readily when offered (KNT, unpubl. data). However, without comparative data on captive feeding of both gravid and nongravid snakes, we cannot determine whether gravid snakes have a reduced propensity to feed, which has been observed in other species despite easy access to food (Gregory et al., 1999). The interactions among feeding, thermoregulation, and reproduction in female snakes are complex and merit further study.

General Conclusions.—Our study provides the most comprehensive analysis of feeding ecology of *T. radix* to date. Only Hart's (1979) study is comparable in sample size and quantification of diet, but does not go beyond simple enumeration of prey species. It is surprising that so little is known about the feeding ecology of this species because it is so widespread and frequently locally abundant. *Thamnophis radix* is an important candidate species for further study because of geographic variation and plasticity in numerous aspects of its ecology, including feeding, and its occurrence at high latitudes, where it approaches important limiting factors. We hope that our work will spur interest in obtaining comparative data from other sites within the range of this species.

The results of our 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. Because of 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 should explore the potential negative impacts of dependence on amphibians in snakes, including the effects of declining amphibians (Blaustein and Wake, 1990; Roe et al., 2003) and 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 herbicides and pesticides.

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