

---

Reproductive Ecology of the Common Garter Snake *Thamnophis sirtalis* at the Northern Limit of Its Range

Author(s): Karl W. Larsen, Patrick T. Gregory and Rita Antoniak

Source: *The American Midland Naturalist*, Apr., 1993, Vol. 129, No. 2 (Apr., 1993), pp. 336-345

Published by: The University of Notre Dame

Stable URL: <https://www.jstor.org/stable/2426514>

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



is collaborating with JSTOR to digitize, preserve and extend access to *The American Midland Naturalist*

JSTOR

## Reproductive Ecology of the Common Garter Snake *Thamnophis sirtalis* at the Northern Limit of Its Range

KARL W. LARSEN,<sup>1</sup> PATRICK T. GREGORY

*Department of Biology, University of Victoria, Victoria, British Columbia, Canada V8W 2Y2*

AND

RITA ANTONIAK

*P.O. Box 524, Fort Smith, Northwest Territories, Canada X0E 0P0*

**ABSTRACT.**—The common garter snake, *Thamnophis sirtalis*, ranges farther N than any other North American reptile. We examined the reproductive ecology of this species near its extreme northern limit in Wood Buffalo National Park (WBNP, 59°49'N, 112°W, Northwest Territories, Canada). Our data suggest that individual females in this population rarely gave birth in 2 successive yr. Parturition normally occurred away from the den, in summer habitat, with the females subsequently migrating back to the hibernaculum. These life cycle features were similar to those reported for another northern population in Manitoba (50°30'N, 97°53'W) and may be a consequence of the climate and the distance between summer and winter habitat. However, there were important differences in the reproductive characteristics of WBNP and Manitoba populations. Most strikingly, female snakes at WBNP matured at larger body sizes ( $\geq 570$  mm SVL) than Manitoba snakes ( $\geq 527$  mm SVL). Also, mean litter size for WBNP females was smaller than for Manitoba females (12.5 vs. 18.8 offspring/litter, respectively), but WBNP neonates were considerably larger than Manitoba neonates (191 vs. 154 mm SVL, respectively). Whether these differences between cold-climate populations of *T. sirtalis* are genetic or environmental in origin remains to be determined. Regardless, these two populations differ substantially in demography, indicating that there is no single suite of life history traits that characterizes northern *T. sirtalis*.

### INTRODUCTION

Wide-ranging species of animals often show geographic variation in demographic characteristics, including reproductive traits (*e.g.*, Leggett and Carscadden, 1978; Healey and Heard, 1984; Hemelaar, 1988; Ritke, 1990; Leslie, 1990), either because of environmental influences or presumably adaptive genetic differences. Part of this variation may result from the constraints placed on populations inhabiting extreme environments. For example, reptiles inhabiting high latitudes are faced with a long winter season in which activity is completely impossible, as well as a short cool summer. In fact, far northern environments rank among the most rigorous anywhere for reptiles. Species that occur at relatively high latitudes therefore may be expected to differ in their reproductive ecology from conspecifics living in more benign environments.

Data on the reproductive ecology of reptile species occupying harsh, northern areas (*e.g.*, central Canada) are scarce. For example, Fitch (1985) reviewed clutch (litter) size for North American reptiles and found no consistent latitudinal trends, but he had little information on those species that range relatively far N on the continent. One notable example was the common garter snake, *Thamnophis sirtalis*. This species is the most northerly distributed reptile in North America, with a range extending from extreme southern Florida (sub-

<sup>1</sup> Present address: Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

tropical, 25°N) to the southern Northwest Territories (subarctic, 60°N). Its ecology has been studied extensively in the more southerly parts of its range (reviewed by Fitch, 1965), but there has been only one study of a northern population (the Interlake region of Manitoba, 50°30'N, 97°53'W—Gregory, 1977), and that population was located well S of the most northerly point of the species' range.

In this article we describe the reproductive ecology of a population of *Thamnophis sirtalis* near the northern limit of the species' range, at Wood Buffalo National Park (WBNP) in northern Alberta (59°49'N, 112°W). The snakes in this population do not emerge from hibernation until at least mid-April (Larsen, 1986; Parks Canada staff, pers. comm.). Sub-zero temperatures may occur sporadically throughout the summer (Larsen, 1987), and maximum daily temperatures may drop below 0 C as early as late September (Environment Canada, 1982). In addition to coping with the short, cool summer, snakes in this population also undergo an annual migration (>3.75 km) between summer (marshland) and winter (hibernaculum) habitats (Larsen, 1987). Migration away from the hibernaculum may not commence for 2–3 wk after initial emergence (Macartney *et al.*, 1989; Larsen, 1986), and snakes may return to the dens as early as late July, with most arrivals occurring in late August (Larsen, 1987). Thus, the active season away from the hibernaculum may be as short as 14 wk in some years.

Herein we report on the sites and timing of parturition in our study population, and how these conditions may be related to the climatic and geographical conditions experienced by the snakes. We examine specific reproductive characteristics, such as the relationship of female (mother) size to reproductive maturity and fecundity, frequency of reproduction, litter size, neonate size, sex ratio and body mass loss due to parturition. Survivorship data are reported elsewhere (Larsen and Gregory, 1989).

At the outset, we expected that snakes at WBNP would have similar reproductive characteristics to consubspecifics in Manitoba which show a similar annual cycle and occupy similar habitats in an area with a comparable climate. Gregory (1977) found that Manitoba snakes produced large litters and experienced high annual mortality, especially in winter; he interpreted this as an example of *r*-selection in a rigorous environment. However, alternative 'solutions' to the same environmental 'problems' may exist. Thus, in this study, we test the generality of Gregory's (1977) characterization of life-history traits of northern *Thamnophis sirtalis*.

#### METHODS

We conducted the main portion of this study from spring 1983 to autumn 1985 near Fort Smith, Northwest Territories, Canada, along the NE border of Wood Buffalo National Park (WBNP, *see* map in Larsen, 1987). A few additional data were collected in 1986. The reproductive histories of mature females were followed by repeated capture of marked individuals. Because it was difficult to locate snakes during midsummer in WBNP, we collected many of the data when the females were either emerging from or returning to a hibernaculum (Salt River Den, SRD, *cf.*, Larsen, 1987). All snakes were measured (snout-vent length, SVL), weighed and individually marked by clipping subcaudal scutes (Blanchard and Finster, 1933). Snakes (both sexes) that had returned to the SRD in the autumn would, on occasion, be repeatedly recaptured in the immediate vicinity of the hibernaculum entrance, prior to their final regress into hibernation. Therefore, only dates of capture for those females found beyond a 20-m radius of the den were considered as *bona fide* 'dates of return.' On no occasion was a snake that we found at the hibernaculum subsequently found outside this perimeter in the same autumn.

We considered emaciated female snakes (low body mass compared with other females of

similar SVL with longitudinal folds of skin along the body) to be postpartum (*cf.*, Macartney and Gregory, 1988). Their appearance was identical to that of captive postpartum females (*see below*). Emaciation could also characterize malnourished snakes, but the only snakes we found in this condition were mature females late in the summer when parturition occurred. When postpartum females were found at the hibernaculum, we assumed that they would be incapable of reproducing again in the subsequent summer (*cf.*, Macartney and Gregory, 1988) because: (1) accumulation of fat reserves is necessary for reproduction (Crews and Gartska, 1982); (2) the hibernaculum is remote from any known source of food (Larsen, 1987); (3) once females arrived at the hibernaculum they apparently remained there until the next spring, when mating occurred.

Reproductive females were identified by catching them while they were gravid in summer, by noting the presence of a copulatory plug (Devine, 1975), or by observing them in courtship. Gravid females were identified by abdominal palpation of developing eggs. We avoided making inferences about reproductive condition from mass/SVL ratios of female snakes caught in spring because relative body mass of reproductive females may vary significantly from year to year (Whittier and Crews, 1990).

Because the study population is small and legally protected, we were unable to sacrifice and dissect snakes to obtain data on female sexual maturity and other aspects of reproduction. We obtained litter data by capturing and holding gravid females in summer until parturition. Gravid females were held in individual containers at room temperature ( $\approx 20$  C), but each female had access to a heat source (light bulb) during daylight hours. Since free-ranging gravid *Thamnophis* rarely feed (Gregory and Stewart, 1975; Larsen, 1986; Farr, 1988), we did not feed the captive females. Water was provided *ad lib.*, and each female was weighed at least every 3 days. Females and their progeny were weighed individually within 2 days of parturition, at which time offspring SVL also was recorded. Sex was determined by everting the hemipenes of males (Gregory, 1983). In some cases, litters were composed of only live offspring, whereas others contained dead offspring and/or undeveloped ova ('yolks'). We report both sets of figures, but our analyses of litter size are based on the total of the three counts, as recommended by Farr and Gregory (1991) and Gregory *et al.* (1992). Size and sex of neonates captured in the wild were also recorded. Mass of wild-caught neonates was not recorded, as it was impossible to determine if the offspring had already fed.

In addition to litter sizes and mass, and mass and SVL of individual offspring, we calculated two indices of relative mass loss [ $RML_1 = (\text{prepartum mass} - \text{postpartum mass}) / \text{prepartum mass}$ ;  $RML_2 = (\text{prepartum mass} - \text{postpartum mass}) / \text{postpartum mass}$ ] and relative clutch mass ( $RCM = \text{total mass of clutch} / \text{postpartum mass of female}$ ). Ratios present problems for statistical analysis (Sokal and Rohlf, 1981), especially when numerator and denominator share a common term, as in RCM (Shine, 1980), and alternative ways of expressing them may be preferable (*cf.*, Brodie, 1989). However, we calculated these indices here simply for comparison with other published figures.

Statistical tests followed methods outlined by Sokal and Rohlf (1981); results were considered significant at  $\alpha = 0.05$ . All analyses were performed using PC SAS version 6.03.

## RESULTS

### FEMALE CHARACTERISTICS

*Movements and timing of parturition.*—We obtained litter data from 23 gravid females (all years combined). Nineteen of these females were captured by a marsh 3.75 km from the hibernaculum during the last 2 wk of July. Most (14) of these 19 females were found

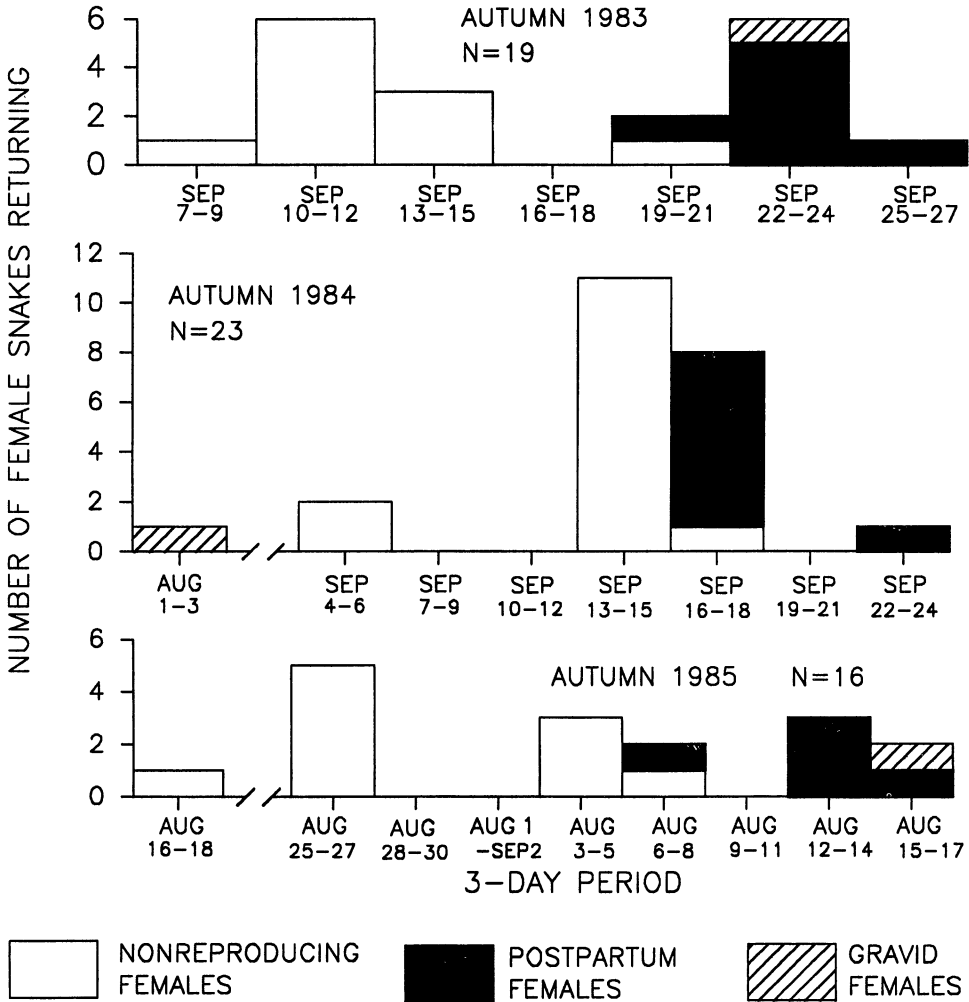


FIG. 1.—Autumn arrival dates of adult females captured as they approached the Salt River Den. In all three years, nonreproducing females ( $n_1$ ) arrived significantly earlier than postpartum females ( $n_2$ ) (Wilcoxon rank-sum tests: 1983:  $U_s = 105$ ,  $n_1 = 11$ ,  $n_2 = 7$ ; 1984:  $U_s = 144$ ,  $n_1 = 14$ ,  $n_2 = 8$ ; 1985:  $U_s = 74$ ,  $n_1 = 9$ ,  $n_2 = 6$ ; all  $P < 0.001$ )

basking near a pile of logs which apparently provided shelter. All gravid females captured at the marsh were taken into captivity; thus we could not determine whether they would have moved elsewhere prior to parturition. However, parturition at the log pile did occur, as an average of 26 neonates were captured at this site in mid- to late August of each year. Because of the numerous cover objects afforded by the log pile as well as the dense vegetation alongside it, the neonates captured there likely represented only a fraction of those present. In contrast, very little cover is available at the hibernaculum in the spring, making detection of neonates relatively simple (Larsen and Gregory, 1989). However, only a small number of neonates were found at the hibernaculum each spring ( $\leq 20$ ). Coincidentally, only six

TABLE 1.—Summary of data from 23 captive-born litters of *Thamnophis sirtalis* from Wood Buffalo National Park. SVL = snout-vent length of mother (mm), LITSIZE = litter size, using all litters (n = 23) and using only those litters in which all neonates were alive and not malformed (“intact,” n = 11). RML<sub>1</sub> and RML<sub>2</sub> = relative mass loss (see text), RCM = relative clutch mass (see text)

Variable	n	Mean (SD)	Range
SVL	23	745 (75.9)	640–915
LITSIZE (all litters)	23	12.5 (4.95)	5–25
LITSIZE (“intact” only)	11	9.6 (1.86)	5–12
RML <sub>1</sub>	18	0.36 (0.08)	0.24–0.53
RML <sub>2</sub>	18	0.58 (0.20)	0.31–1.13
RCM	17	0.20 (0.05)	0.13–0.32

gravid females were observed at the hibernaculum in autumn (one as early as 2 August 1984). Four of these females were captured and held for litter data.

Parturition dates for the captive females over the 3 yr ranged from 15 August to 11 September, with a mean of 27 August (all years pooled). There was no significant correlation between date of birth and the number of days the gravid female spent in captivity (n = 23, r = 0.045, P > 0.839). Two females at the hibernaculum were still gravid on 15 September 1986, despite the fact that subzero nighttime temperatures are the norm at this time of year (Environment Canada, 1982); we do not know if these two individuals produced young that year because we did not attempt to hold them in captivity. Another two gravid females collected in early September of 1986 had not given birth by 18 October and were released at the den. Whether these two snakes entered hibernation with unborn young is not known.

Twelve females that had given birth in captivity were marked and released at their point of capture, along with their progeny. One of these females (released on 14 August 1984) was recaptured at the hibernaculum the ensuing spring, indicating a movement of 3.2 km prior to hibernation. Eleven postpartum females and their young were released at the hibernaculum because of the imminence of winter.

The arrival times of adult females at the SRD each autumn varied somewhat, but despite the small samples, a clear distinction existed in arrival times between females we classified as nonreproducing and postpartum. In each year, the former arrived at the hibernaculum significantly earlier than the latter (Fig. 1). Thirty-eight nongravid, adult females were captured away from hibernacula during the months of June and July; eight of these females were recaptured at the SRD in the subsequent autumn, and all arrived prior to the appearance of the first postpartum female.

*Minimum reproductive size of females.*—The smallest of 25 gravid females observed during this study was 640 mm SVL, with a prepartum mass of 89 g. However, at the hibernaculum, we captured a female of 570 mm with a copulatory plug. We therefore considered adult females to be  $\geq 570$  mm SVL. Although a smaller female (535 mm) was observed in a mating aggregation, actual copulation was not seen.

*Frequency of reproduction by individual females.*—Twenty-four adult females were captured in 2 consecutive yr of the study, and all of them gave birth in at least one of those years (based on finding them gravid or postpartum). However, only three of these 24 females reproduced 2 yr in a row. One female that was captured upon emergence 3 yr in a row appeared capable of reproduction each year (*i.e.*, robust condition, copulatory plug, presence in mating ball), but the large growth increments recorded for this individual each summer suggest that she did not reproduce in any of those years, assuming a tradeoff between

TABLE 2.—Comparison of reproductive characteristics of *Thamnophis sirtalis* from Wood Buffalo National Park (WBNP) and the Interlake region of Manitoba. Statistics given are  $\bar{x}$  (top row),  $n$  and  $SD$  (middle row), and range (bottom row). Estimated litter size\* for a 600-mm SVL female was determined using the regression of litter size on SVL of mothers for each population, respectively. Additional data to that used by Gregory (1977) was used in the calculations for Manitoba snakes. na = not available

Location	SVL of mothers (mm)	Litter size		Neonate SVL (mm)	Neonate mass (g)	Prop. of males
		$\bar{x}$	600 mm*			
WBNP, Alberta	745	12.5	4.7*	191	2.6	0.55
	(23, 75.9)	(23, 4.9)		(284, 9.3)	(187, 0.4)	
	(640–915)	(5–25)		(146–214)	(0.95–3.80)	
Interlake, Manitoba	583	18.8	19.7*	154	na	0.47
	(30, 62.0)	(30, 8.1)		(207, 9.9)		
	(514–800)	(7–50)		(117–175)		

reproduction and growth. However, this assumption is risky, especially given the difficulty in measuring tradeoffs in natural populations (Reznick, 1985).

Approximately 36% of the individual adult females captured at the hibernaculum each autumn were considered postpartum (1983—11/28; 1984—12/34; 1985—8/24). These measurements exclude females that were released by us at the hibernaculum (*see above*). We were unable to obtain analogous figures for the spring emergence periods because adult females do not remain in the vicinity of the hibernaculum at this time, making their capture unlikely.

#### LITTER CHARACTERISTICS

*Litter size.*—Mean litter size was 12.5 ( $SD = 4.85$ ,  $n = 23$ ), with a range of 5 to 25 (Table 1). The relationship between the SVL of the mothers and their respective litter sizes was positive and significant [ $LITTER\ SIZE = 0.054(SVL) - 27.731$ ;  $n = 23$ ,  $r^2 = 0.714$ ,  $P < 0.0001$ ].

*Neonate size.*—There were no significant differences between the mean SVLs of male and female neonates, nor between those of captive-born and wild-born neonates (2-way ANOVA, all  $P > 0.50$ ); hence the lengths of 284 neonates were pooled for a mean SVL of 191 mm (Table 2). Similarly, the average mass of 187 captive-born neonates was 2.62 g (Table 2).

TABLE 3.—Correlation coefficients between SVL of mother and various potential measurements of reproductive effort. NCML = mass of non-clutch matter due to parturition, CML = clutch (litter) mass loss due to parturition, and TML = total mass loss due to parturition (CML + NCML). *See* Methods and Materials in text for definition of  $RML_1$ ,  $RML_2$ , and RCM. For each pair combination, Pearson correlation coefficients are given in bold type, and their respective probability values and sample size appear below them. \*Statistical significance at  $P \leq 0.05$

	NCML	CML	TML	$RML_1$	$RML_2$	RCM
SVL of mother	0.140	<b>0.802*</b>	<b>0.697*</b>	-0.101	-0.268	0.276
	0.59, 17	0.01, 17	<0.01, 17	0.65, 23	0.28, 18	0.28, 17
CML	-0.036					
	0.89, 17					



*Neonate sex ratio.*—We simultaneously tested differences in sex ratio among litters and departure of the overall sex ratio of all captive-born offspring from 1:1 using a chi-square heterogeneity test. There was no significant difference in sex ratio among litters (chi square = 8.4,  $df = 16$ ,  $0.95 < P < 0.975$ ), nor did the overall sex ratio of captive-born offspring (109 males: 88 females) differ significantly from 1:1 (chi square = 1.108,  $df = 1$ ,  $0.25 < P < 0.50$ ). The relative proportions of male and female neonates born in captivity and those encountered in the wild were not significantly different (chi square = 1.206,  $df = 1$ ,  $P = 0.272$ ). The proportion of male neonates in the combined samples was 0.53.

*Mass loss due to parturition.*—Summary statistics for  $RML_1$ ,  $RML_2$  and RCM values appear in Table 1. None of these three estimates of 'reproductive effort' was correlated with the SVL of the mother (Table 3). The total mass lost by the females consisted of two components: (1) litter or clutch mass, and (2) other matter, primarily fluids. Total mass loss was always greater than the mass of the litter, and both were strongly correlated with the SVL of the mother (Table 3); however, the difference between total mass loss and litter mass varied widely, in no obvious pattern, among individuals. Consequently there was no correlation between the two components of mass loss (Table 3).

#### DISCUSSION

The ecology of *Thamnophis sirtalis* is similar in WBNP to that reported for the Interlake region of Manitoba (50°30'N, 97°53'W—Gregory, 1975, 1977), but it contrasts sharply with the ecology of the same species in more southerly regions (*e.g.*, Fitch, 1965). Both WBNP and the Interlake are characterized by long, cold winters and the snakes in both places hibernate communally in limestone sinks, and migrate several kilometres each spring to large marshes where they feed on frogs. In this study we found that the phenology of reproductive events is also similar in the two populations. However, our data also reveal significant differences in life history traits between these two populations.

In both WBNP and the Interlake, mating takes place mainly at the hibernaculum during spring emergence. After mating, females abandon the hibernaculum for the summer habitat, while males remain in wait for more emerging females (Crews and Gartska, 1982; Gregory, 1984; Larsen, 1986). In both areas, reproducing females apparently remain in the summer habitat until they give birth because gravid females and neonates are rarely seen at the hibernacula (this study; Gregory, 1977; MacMillan, 1988). Although gravid females occasionally use hibernacula in other migratory populations of *Thamnophis*, there is a general tendency for females not to return to the hibernaculum until they have given birth (Gregory, 1984). At WBNP, in fact, postpartum females arrive at the hibernaculum later than other females.

Gravid *Thamnophis sirtalis* rarely feed in the field, especially later in gestation (Larsen, 1986; Farr, 1988). Why then do they not usually return to give birth at the den, where they and their offspring would have assured hibernation quarters? Perhaps the problem is that neither mother nor offspring would be able to feed between parturition and entrance into hibernation. Further, the offspring as well as the female would be faced with the long, presumably risky migration in the ensuing spring. The mobility of gravid females is also reduced (Seigel *et al.*, 1987; Shine, 1980), so that returning to the hibernaculum prior to parturition may be a relatively dangerous and energetically expensive tactic. If neonates are able to find suitable hibernating sites near the summer habitat, as has been suggested elsewhere (Gregory, 1977; Larsen and Gregory, 1989; Larsen and Hare, 1992), then the advantages to giving birth in summer habitat seem substantial. Offspring may be able to spend some time feeding prior to winter, thus perhaps increasing their overwinter survivorship (*cf.*, Völkl, 1989), and they can begin feeding immediately in the spring without a



long migration. The late parturition dates shown by WBNP females suggest that they had little time to feed before beginning their lengthy migration, but returning to the hibernaculum before parturition would provide them with even less opportunity for foraging. It is therefore not surprising that individual females in WBNP normally bear their litters away from the hibernaculum, and that they rarely reproduce in successive years.

Extended reproductive cycles also are seen in females in nonmigratory populations of snakes. Although latitudinal trends in frequency of reproduction have been seen in viperids, with longer reproductive cycles in more northerly (or higher altitude) populations (*e.g.*, Saint Girons and Kramer, 1963; Macartney and Gregory, 1988), long migrations have not been reported in these populations. In these and other cases, productivity and prey availability may affect reproductive frequency (Seigel and Ford, 1987). For example, Fitch (1965) reported that some adult females in a southern population of *Thamnophis sirtalis* (Kansas) failed to breed every year. Thus, extended reproductive cycles also may occur in temperate and montane areas in more southerly regions.

Despite the overall similarity of the annual cycle and general ecology of *Thamnophis sirtalis* in WBNP and Manitoba, these two populations differ strikingly, especially in demographic variables (Table 2). Snakes at WBNP are larger (Larsen and Gregory, 1989) and females begin reproducing at a larger size than do Manitoba females. Whether WBNP snakes grow faster or grow larger and mature later is not known. Furthermore, litter sizes of WBNP snakes are relatively smaller but the young are much larger. In fact, neonates from WBNP are larger than those reported in the literature for any other population of *T. sirtalis*. Differences between populations in adult body size, litter size, neonate size and sex ratio (Table 2) could reflect phenotypic responses to contrasting environmental conditions that we did not measure (*e.g.*, food availability, Ford and Seigel, 1989; temperature, Burger *et al.*, 1987). However, these differences may also reflect fundamentally different reproductive strategies that are responses to variations in lifetime patterns of mortality (Stearns, 1976). Annual survivorship of adult males in WBNP is higher than that of adult males in Manitoba (67% and 34%, respectively—Gregory, 1977; Larsen and Gregory, 1989); however, we lack critical data on mortality rates of juveniles and adult females to evaluate properly the demographic differences between WBNP and Manitoba snakes.

Relative clutch mass values for Manitoba snakes are not available for comparison with our WBNP data. However, our measurements, albeit highly variable, are comparable to the values reported for *Thamnophis sirtalis* by Seigel *et al.* (1986) for Kansas populations ( $\bar{x} = 0.27 \pm 0.05$  SD,  $n = 18$ ). Saint Girons and Naulleau (1981) noted that RCM varied widely among individual vipers (*Vipera*), and they associated this with the differential feeding success of females during vitellogenesis. We are skeptical about the usefulness of RCM values as an index of reproductive effort (Seigel and Fitch, 1984; Seigel *et al.*, 1986) because, as our data show, the additional mass acquired during pregnancy consists of more than just the progeny (Table 3). This point was also raised by Brodie (1989). Relative mass loss (RML) seems a more complete, if imperfect, measure for generating interspecific comparisons; unfortunately, the failure of previous authors to report RML figures makes it impossible to draw comparisons at this time.

It is apparent from this study that no obvious suite of reproductive characteristics clearly typifies northern populations of *Thamnophis sirtalis*; additional data on other northern populations will be required before the presence or absence of latitudinal or other geographic trends can be clearly shown. Our data show that populations which inhabit superficially similar habitats may exhibit profound differences as well as similarities when studied in detail. Ultimately, experimental work will be necessary to understand the variation. Interpretations will be limited, however, if a solid empirical database does not exist.

*Acknowledgments.*—This research could not have been accomplished without the logistic support of Parks Canada (Prairie Region), the staff and employees of Wood Buffalo National Park, and the Renewable Resources Program at Arctic College (Thebacha Campus), Fort Smith, Northwest Territories. Kari Nelson made valuable comments on the manuscript as did two anonymous reviewers. Jim 'Bocephus' Hare provided the senior author with insightful commentary on the occurrence of northern limits in species' distributions. Funds were provided by an Operating Grant and a Northern Supplement to PTG from the Natural Sciences and Engineering Research Council of Canada.

## LITERATURE CITED

- BLANCHARD, F. N. AND E. B. FINSTER. 1933. A method of marking living snakes for future recognition, with a discussion of some problems and results. *Ecology*, **14**:334–347.
- BRODIE, E. D., III. 1989. Behavioral modification as a means of reducing the cost of reproduction. *Am. Nat.*, **134**:225–238.
- BURGER, J., R. T. ZAPPALORTI AND M. GOCHFELD. 1987. Developmental effects of incubation temperature on hatchling pine snake *Pituophis melanoleucus*. *Comp. Biochem. Physiol.*, **87A**: 727–732.
- CREWS, D. AND W. R. GARTSKA. 1982. The ecological physiology of a garter snake. *Sci. Am.*, **247**: 158–168.
- DEVINE, M. C. 1975. Copulatory plugs in snakes: enforced chastity. *Science*, **187**:844–845.
- ENVIRONMENT CANADA, ATMOSPHERIC ENVIRONMENT SERVICE. 1982. Canadian climate normals: temperature and precipitation, Vol. 1, 3 and 4. Ottawa.
- FARR, D. R. 1988. The ecology of snakes, *Thamnophis elegans* and *T. sirtalis* in southeastern British Columbia. M.Sc. Thesis, University of Victoria, Victoria, British Columbia. 141 p.
- AND P. T. GREGORY. 1991. Sources of variation in estimating litter characteristics of snakes, *Thamnophis elegans*. *J. Herpetol.*, **25**:261–267.
- FITCH, H. S. 1965. An ecological study of the garter snake, *Thamnophis sirtalis*. *Univ. Kans. Publ. Mus. Nat. Hist.*, **15**:493–564.
- . 1985. Variation in clutch and litter size in New World reptiles. *Univ. Kans. Mus. Nat. Hist. Misc. Publ. No. 76*. Lawrence, Kansas. 76 p.
- FORD, N. B. AND R. A. SEIGEL. 1989. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. *Ecology*, **70**:1768–1774.
- GREGORY, P. T. 1975. Aggregations of gravid snakes in Manitoba, Canada. *Copeia* **1975**:185–186.
- . 1977. Life-history parameters of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in an extreme environment, the Interlake region of Manitoba. *Publ. Zool. No. 13. Natl. Mus. Nat. Sci.* 44 p.
- . 1983. Identification of sex of small snakes in the field. *Herpetol. Rev.*, **14**:42–43.
- . 1984. Communal denning in snakes, p. 57–75. In: R. A. Seigel, L. E. Hunt, J. L. Knight, L. L. Malaret and N. L. Zuschlag (eds.). *Vertebrate ecology and systematics—a tribute to Henry S. Fitch. Univ. Kans. Mus. Nat. Hist. Spec. Publ. 10.*
- , K. W. LARSEN AND D. R. FARR. 1992. Snake litter size = live young + dead young + yolks. *Herpetol. J.*, **2**:65–71.
- AND K. W. STEWART. 1975. Long-distance dispersal and feeding strategy of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake of Manitoba. *Can. J. Zool.*, **53**: 238–245.
- HEALEY, M. C. AND W. R. HEARD. 1984. Inter- and intra-population variation in the fecundity of chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. *Can. J. Fish. Aquat. Sci.*, **41**:476–483.
- HEMELAAR, A. 1988. Age, growth and other population characteristics of *Bufo bufo* from different latitudes and altitudes. *J. Herpetol.*, **22**:369–388.
- LARSEN, K. W. 1986. Ecology of the common garter snake, *Thamnophis sirtalis*, at the northern limit of its range. M.Sc. Thesis, University of Victoria, Victoria, British Columbia. 112 p.
- . 1987. Movements and behavior of migratory garter snakes, *Thamnophis sirtalis*. *Can. J. Zool.*, **65**:2241–2247.

- AND P. T. GREGORY. 1989. Population size and survivorship of the common garter snake, *Thamnophis sirtalis parietalis*, near the northern limit of its distribution. *Holarct. Ecol.*, **12**: 81–86.
- AND J. F. HARE. 1992. Criddle's riddle: where do young garter snakes hibernate? *Herpetol. Rev.*, **23**:39–41.
- LEGGETT, W. C. AND J. E. CARSCADDEN. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. *J. Fish. Res. Board Can.*, **35**:1469–1478.
- LESLIE, J. F. 1990. Graphical and genetic structure of life-history variation in milkweed bugs (Hemiptera: Lygaeidae: *Oncopeltus*). *Evolution*, **44**:295–304.
- MACARTNEY, J. M. AND P. T. GREGORY. 1988. Reproductive biology of female rattlesnakes (*Crotalus viridis*) in British Columbia. *Copeia*, **1988**:47–57.
- , K. W. LARSEN AND P. T. GREGORY. 1989. Body temperatures and movements of hibernating snakes (*Crotalus* and *Thamnophis*) in relation to changes in the thermal gradient of natural hibernacula. *Can. J. Zool.*, **67**:108–114.
- MACMILLAN, S. 1988. Young of the year red-sided garter snakes (*Thamnophis sirtalis parietalis*) at communal dens in Manitoba's Interlake region. *Herpetol. Rev.*, **19**:8–9.
- REZNICK, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos*, **44**:257–267.
- RITKE, M. E. 1990. Quantitative assessment of variation in litter size of the raccoon *Procyon lotor*. *Am. Midl. Nat.*, **123**:390–398.
- SAINT GIRONS, H. AND E. KRAMER. 1963. Le cycle sexuel chez *Vipera berus* (L) en montagne. *Rev. Suisse Zool.*, **70**:191–221.
- AND G. NAULLEAU. 1981. Poids des nouveau-nes et strategies reproductrices des viperes Europeens. *Rev. Ecol. (Terre et Vie)*, **35**:597–616.
- SEIGEL, R. A. AND H. S. FITCH. 1984. Ecological patterns of relative clutch mass in snakes. *Oecologia*, **61**:293–301.
- , ——— AND N. B. FORD. 1986. Variation in relative clutch mass in snakes among and within species. *Herpetologica*, **42**:179–185.
- AND N. B. FORD. 1987. Reproductive ecology, p. 210–252. In: R. A. Seigel, J. T. Collins and S. S. Novak (eds.). *Snakes: ecology and evolutionary biology*. Macmillan, New York, N.Y.
- , M. M. HUGGINS AND N. B. FORD. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia*, **73**:481–485.
- SHINE, R. 1980. "Costs" of reproduction in reptiles. *Oecologia*, **46**:92–100.
- SOKAL, R. R. AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman and Co., New York. 859 p.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.*, **51**:3–47.
- VÖLKL, W. 1989. Prey density and growth: factors limiting the hibernation success in neonate adders (*Vipera berus* L.) (Reptilia: Serpentes, Viperidae). *Zool. Anz.*, **222**:75–82.
- WHITTIER, J. M. AND D. CREWS. 1990. Body mass and reproduction in female red-sided garter snakes (*Thamnophis sirtalis parietalis*). *Herpetologica*, **46**:219–226.

SUBMITTED 24 SEPTEMBER 1991

ACCEPTED 26 OCTOBER 1992