THE ECOLOGY OF GARTER SNAKES, *THAMNOPHIS SIRTALIS* AND *T. ELEGANS* IN SOUTHEASTERN BRITISH COLUMBIA

by

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ABSTRACT

Explaining patterns of life history variation within a wide-ranging species requires comparative ecological data from populations in different parts of the species' range. Two species of garter snakes, *Thamnophis sirtalis* and *T. elegans*, have been studied in a variety of environments, and the sample of populations from which patterns can be discerned is greater than for most other snakes. I used mark-recapture to document the body size, growth, reproduction, and other aspects of the ecology of each of these species at Creston, in southeastern British Columbia, during 1986 and 1987, and I examined variation between these populations and those in other regions.

Adult body size in both *T. sirtalis* and *T. elegans* at Creston is small compared to many other populations. Whether higher adult mortality, slower growth, smaller asymptotic size, or a combination of factors causes this difference is not known. In *T. elegans*, small female size accounts for the relatively small litter size (7-8 young). In *T. sirtalis*, however, female size is insufficient to explain differences in litter size between snakes at Creston (7-8 young) and other locations. Food availability and local adaptation are possible causes of these differences. Within each species at Creston, females reach larger maximum sizes than males, and females are heavier, with wider, longer heads than males of similar body length. Both sexes exhibit a decrease in relative head size with increasing body size.

Garter snakes at Creston do not overwinter communally, and the long-distance migrations between winter and summer habitats observed in other populations apparently do not occur. The abundance of suitable overwintering sites adjacent to feeding areas may explain the relatively limited seasonal movements of snakes at this location. Variation in movements among individuals was extensive, ranging from less than 50 m to over 2000 m between captures within a 30-day period, with *T. elegans* probably moving longer distances than *T. sirtalis*. Small snakes and gravid females were probably more sedentary than other individuals.

The diet of *T. sirtalis* consisted of primarily (80%) earthworms, amphibians and small mammals, and that of *T. elegans* almost exclusively (90%) slugs and small mammals. Although neither the diet nor the overall proportion of snakes with food was particularly unusual, dramatic shifts in the type and size of prey eaten occurred as snakes grew larger. Large snakes ate relatively larger prey, and tended to eat a wider range of prey types and sizes than small snakes. The largest *T. elegans*, however, excluded small prey (slugs) from their diet, and instead specialized almost completely on small mammals. This may maximize feeding efficiency, and may be associated with adaptations for handling large, active prey.

The extent of ecological variation among populations of each species is at least as great as the variation between each species. Both *T. sirtalis* and *T. elegans* exhibit flexibility in their life histories: *Thamnophis sirtalis*, in particular, may be able to make phenotypic or genotypic (or both) adjustments to local conditions, thereby allowing it to persist under a wide range of environmental conditions.

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INTRODUCTION

Variation in the life history traits of a species suggests that differences exist in the constraints under which different populations live. Theories put forward to explain life history variation have proliferated (see Rose 1983 for a review), but have so far explained little. A major reason for the lack of success is insufficient knowledge of the patterns; before asking *why* patterns exist, it is first necessary to document more fully *what* patterns exist. Patterns within species are less influenced by genetic differences than those among species. Therefore, a potentially productive approach to the study of life history variation is to compare populations of a single species in different parts of its geographic range.

Squamate reptiles (lizards and snakes) often exhibit striking intraspecific variation in life history, and lizards in particular have been the subject of many comparative studies. Large differences in growth rates, clutch or litter size, and even reproductive mode (egg-laying *vs.* live-bearing) have been documented within lizard species (Ballinger 1983). The degree of variation within species of snakes is still poorly known, largely because of the methodological difficulties of studying them, associated with their usually cryptic nature (Parker and Plummer 1987).

Two species of garter snakes, *Thamnophis sirtalis* and *T. elegans*, are good candidates among snakes for studies of intraspecific life history variation. *Thamnophis sirtalis* has the widest range of any snake in North America north of Mexico, extending from the east to the west coast, and from the Northwest Territories to southern Texas and Florida (Fitch 1980). *Thamnophis elegans* ranges across much the western part of the continent, and extends from central British Columbia and Alberta to southern Arizona and New Mexico (Fitch 1983). A large number of previous studies have documented the ecology of one or both of these species in different parts of their range: northern Alberta (Larsen 1986), Manitoba (Gregory 1977), south-central British Columbia (Gregory, unpublished data), Washington (Hebard 1950), Oregon (Stewart 1968), northern California (Kephart 1981), southern California (White and Kolb 1974), Michigan (Carpenter 1952a, 1952b), and Kansas (Fitch 1965). Few other snake species have been studied in such a variety of locations, but the sample size of populations for which life history and ecology are well known is still relatively small. This study adds another "point" to the sample of populations from which patterns of variation can be drawn.

The objectives of my study were:

1) To document in detail the pattern of growth and reproduction of *T. sirtalis* and *T. elegans* at Creston, in southeastern British Columbia, and make preliminary comparisons of the life history traits of garter snakes in this area with those in other regions.

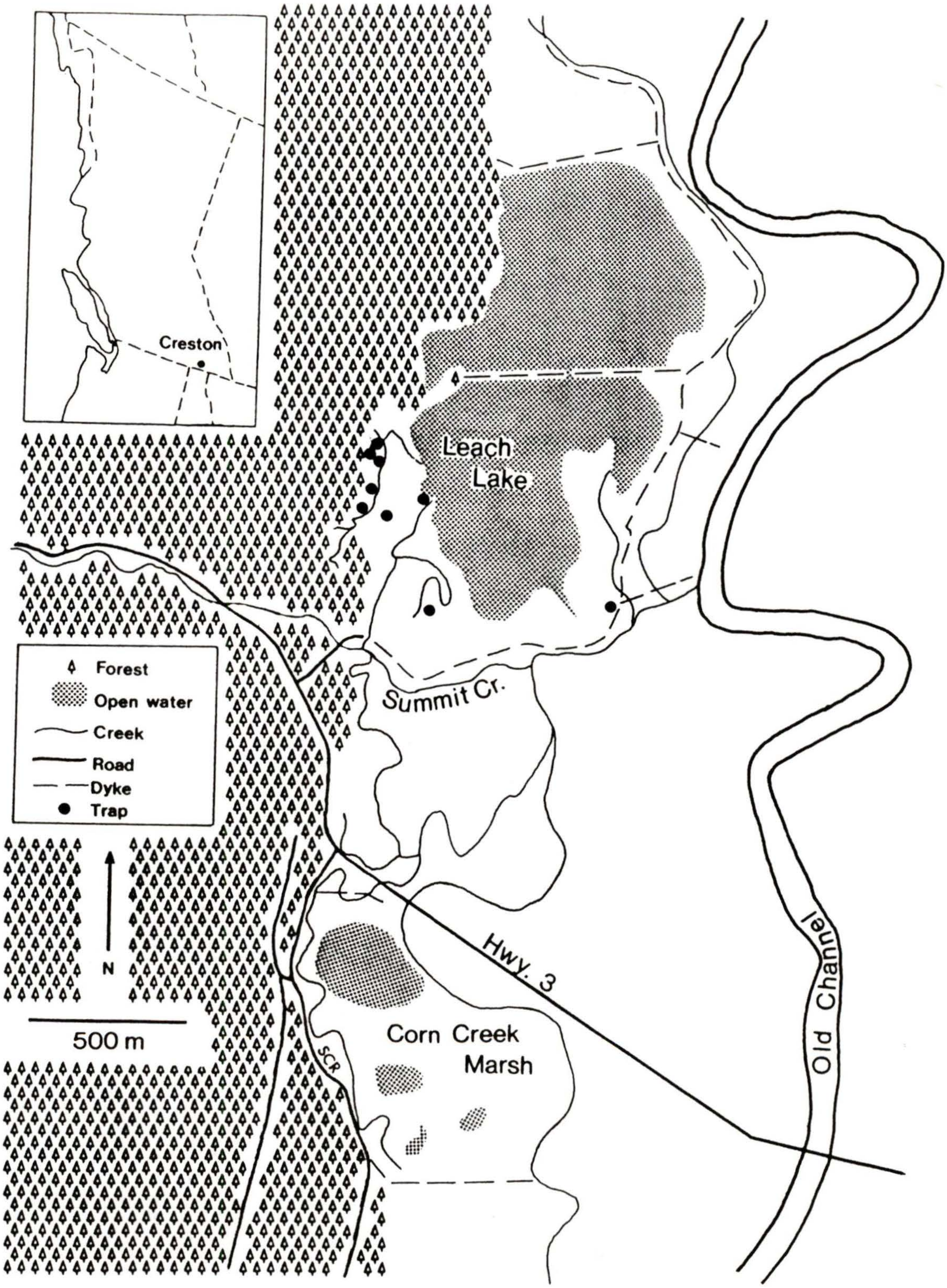
2) To document additional aspects of the ecology of these two species so that their life histories can be interpreted in the light of other ecological processes.

METHODS

Study area

The study site was on the west side of the Creston Valley, 10 km west of Creston (49^{o} 6' N, 116^{o} 31' W; 600 m; see Fig. 1). The Creston Valley is a wide alluvial floodplain created by annual overflow of the Kootenay River, but recent extensive flood control measures have stabilized water levels so that flooding no longer occurs, and much of the valley has been turned over to agriculture. Most of

Figure 1. Map of the study area, with location of Creston inset. The eastern limit of forest corresponds with the abrupt increase in elevation at the west side of the valley. SCR = Summit Creek Road.

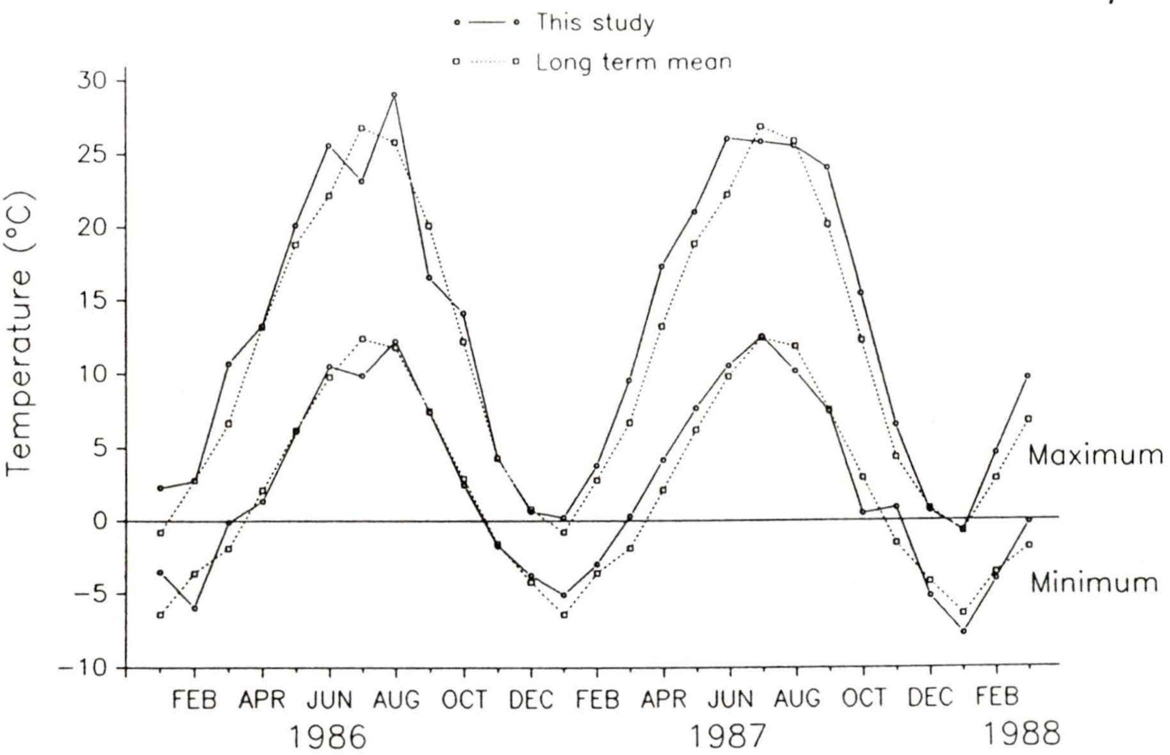

Creston
Leach Lake
Summit Cr.
Forest
Open water
Creek
Road
Dyke
Trap
N
500 m
Hwy. 3
Old Channel
SCR
Corn Creek Marsh

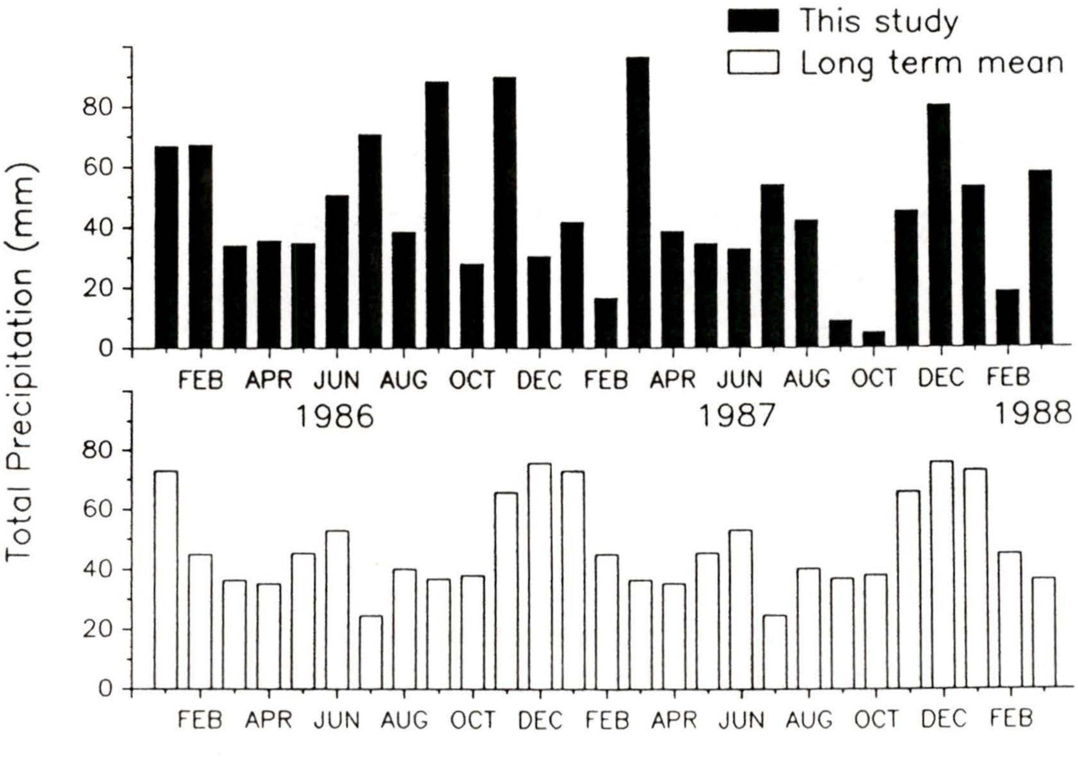
the remaining natural habitat occurs within the 6900 hectare Creston Valley Wildlife Management Area (CVWMA). Water levels within the Management Area are regulated by a system of dykes and other control structures, primarily to maintain wetland habitat for waterfowl.

Both species of garter snakes are found throughout the CVWMA, but my study was concentrated in two regions near Summit Creek: Leach Lake Unit to the north and Corn Creek Marsh to the south (Fig. 1). I selected these two areas after preliminary reconnaissance of the CVWMA suggested that these regions contained large numbers of snakes in relatively undisturbed habitats. Leach Lake Unit contains extensive areas of open water, along with tracts of reed-grass (*Phragmites* sp.), marsh habitats with cattails (*Typha* sp.), and scattered meadows dominated by grasses and sedges. Corn Creek Marsh is characterized by wet meadows and marshes, with bulrushes (*Scirpus* sp.) and cattails being the major plant types. Both regions are part of the valley floor proper, and are bordered along their west sides by steep hillsides forested mainly with Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*).

The climate at Creston is relatively mild, with warm summers, cool winters and abundant precipitation (Fig. 2). Mean daily maximum temperatures range from an average of -0.8° C in January to 26.8° C in July; mean daily minima vary from -6.4° C to 12.4° C. The extreme maximum and minimum recorded temperatures are 39.4° C and -32.8° C, respectively. Mean annual precipitation is 568 mm, most of which falls in winter (Fig. 2). There are 1916 degree days above 5° C annually, and the frost free period is 160 days long (all climate information from Environment Canada 1982a,b,c). During the two years of this study, weather patterns were not especially unusual, but 1987 was slightly warmer and drier than average (Fig. 2).

Figure 2. Temperature (mean daily maximum and minimum) and precipitation patterns at Creston. Records during the period of this study are from the Environment Canada weather station at Creston. Long term means are taken over a 67-69 year period, and are from Environment Canada (1982a).


This study
Long term mean
Temperature (°C)
30
25
20
15
10
5
0
−5
−10
Maximum
Minimum
FEB APR JUN AUG OCT DEC FEB APR JUN AUG OCT DEC FEB
1986
1987
1988


This study
Long term mean
Total Precipitation (mm)
80
60
40
20
0
FEB APR JUN AUG OCT DEC FEB APR JUN AUG OCT DEC FEB
1986
1987
1988
80
60
40
20
0
FEB APR JUN AUG OCT DEC FEB APR JUN AUG OCT DEC FEB

General methods

I collected snakes both by hand and in traps, from late April to early October 1986 and from late March to late September 1987. Snakes were almost always processed in the field (see below) and released immediately at the site of capture. I concentrated my search effort in the most productive areas, and did not attempt to randomize or standardize searches.

The traps were loosely based on the design of Campbell and Christman (1982), and consisted of a + shaped drift fence made of aluminum screening (40 cm high, with each arm 5 m long), with an aluminum screen funnel trap at the distal end of each arm. The mesh size of the screen was sufficiently small (2 mm) to prevent escape of the smallest snakes, and each funnel trap was covered with cardboard to prevent overheating of captured snakes. Nine such trap arrangements were constructed (three in 1986, six in 1987), all in Leach Lake Unit (Fig. 1). I placed five traps close to the west side of the valley in areas of high snake abundance to maximize capture success, and four others farther east in areas of lower abundance to obtain additional information on movements. I checked all traps regularly (usually daily), and removed, processed, and released all snakes.

Regardless of the method of capture, I processed snakes in the following manner. I measured snout-vent length (SVL) to the nearest mm by stretching the snake along a metre stick, and body mass to the nearest g using a hand-held Pesola spring balance. I determined sex either visually by examining the shape of the tail, or by forced eversion of the hemipenes in small snakes; in cases of doubt, I probed for hemipenes (Schaefer 1934). I also determined whether a snake had recently fed by palpating the stomach area, and I noted the stage of ecdysis (skin-shedding), plus evidence of injury or other distinguishing features. Finally, I marked each snake individually by removing a unique combination of subcaudal scutes (Blanchard and Finster 1933) with a small pair of scissors, so that recaptured snakes could be identified.

I estimated the number of garter snakes inhabiting the study area in the fall of 1986 using the Peterson index (Ricker 1975):

$\hat{N} = Mn/m$, where

$\hat{N}$ = estimated population size,

M = number of marked snakes released in the fall (September-October) of 1986,

m = number of snakes marked in fall 1986 recaptured in 1987 (prior to August),

n = total number of snakes captured in 1987 (prior to August).

I calculated lower and upper 95% confidence limits by the formula $1/\hat{N} \pm 2SE(1/\hat{N})$, where $SE(1/\hat{N}) = M(n-M)/(M^2n^3)$. The assumptions of the Peterson index are probably met for this study so long as no recruitment into the population occurs during the sampling periods.

Body size and growth

I examined the distribution of body sizes (SVL) of each species by constructing size-frequency histograms of all snakes captured in spring (March-April) and fall (September-October). Individuals of the same age may exhibit "peaks" in the distribution during these periods. I also examined the relationship between body mass and SVL, using only measurements of individuals that did not contain food. Variation due to the temporary increase in mass of recently-fed snakes was therefore eliminated. Only data from the first capture of each individual were used in this analysis.

Starting in 1987, I measured the heads of most snakes to the nearest 0.1 mm using Vernier calipers. Variation in head morphology may be related to dietary differences (Vitt 1987); gape is of particular interest because it limits the maximum size of prey that can be swallowed (Pough and Groves 1983). I therefore measured two distances associated with gape on each snake: 1) maximum head width, and 2) maximum head length (the distance from the anterior margin of the cranium to the posterior margin of the mandible). The latter measurement always was taken from the snake's right side. When examining ontogenetic variation in head size relative to body size, I used body length (SVL minus head length) as the measure of body size because of the lack of independence between SVL and head length.

Growth in seasonal environments is most easily compared among populations in terms of the increase in size of individuals during one year. I estimated absolute annual growth by calculating the increase in SVL of snakes first captured in spring (or the previous fall), and subsequently captured in fall (or the following spring). I assumed that growth during the winter was minimal. I calculated regressions of annual growth (mm/year) on SVL at first capture to obtain the coefficients of the following equation:

$$GR = a - bSVL,$$ where

GR = growth during one year, and a and b are regression constants. The model assumes that growth rate decreases in a linear fashion as snakes become larger, and I assessed this assumption by visually inspecting scatter plots of growth *vs*. SVL. Asymptotic size is predicted by this model by the ratio -a/b, and I also obtained a field estimate of asymptotic size by calculating the mean of the 10 largest snakes of each sex.

Because of small sample sizes, I was able to describe annual growth for male *T. elegans* only. I therefore estimated daily growth rate (mm/day) by determining the increase in SVL of all snakes captured two or more times within a year. Intervals of less than 60 days between captures were excluded from this analysis because small increments of growth could be obscured by measurement error, which was approximately ±5 mm. Analysis of daily growth was otherwise identical to the analysis of annual growth described above.

I examined the degree to which growth varied among seasons by calculating the mean growth rate (mm/day) of snakes in various sex/reproductive categories within each of four two-month periods. All snakes captured twice during any 7-60 day interval were used in this analysis, and I assigned each snake to a two-month period on the basis of the mean date of the first and second capture dates. The resulting seasonal patterns should be treated with caution, because measurement error is potentially great over short time intervals (see above). However, this error should be fairly evenly distributed among seasons, so that general comparisons can be made.

Reproduction

I considered a female to be gravid if it had a distended abdomen with ova or embryos that could be felt externally; post-partum females usually had an emaciated appearance, with lateral skin folds on either side of the body. The size of the smallest reproductive females approximated size at sexual maturity. I assessed male maturity by examining cloacal smears taken from males in the spring and fall of 1987. By examining fluid palpated from the posterior third of the body, I was able to determine if the vas deferens contained mature spermatozoa, which are readily visible under 400X power of a compound microscope. When using this technique, the absence of spermatozoa in a cloacal smear is not evidence of immaturity, because it was possible to observe no sperm even if they were present in the vas deferens. However, consistent lack of sperm in males below a certain size should approximate the size at which sexual maturity is reached. An additional estimate of size at maturity for both males and females was obtained from the smallest individuals captured in courtship activity.

In addition to size at maturity, I examined three other aspects of reproduction: litter size, size of young, and reproductive effort of females (see below). I determined the litter size of free-ranging females by counting the number of ova detectable by palpation. This technique becomes less reliable in the later stages of gestation (late July and August) because individual ova become less distinct as the embryos develop. I therefore did not count ova in females captured after mid-July.

Starting in July, I held gravid females outdoors in clear plastic shoeboxes, shaded from the sun. Water was available at all times, but no food was offered. Preliminary evidence suggested that free-ranging females feed little, if at all, from July until parturition in August. I measured the SVL and mass of each snake approximately weekly until parturition. After parturition, I sexed, marked, measured and weighed each neonate to the nearest 0.1 g using a triple beam balance. I also determined the combined mass of all young in the litter, and the mass of the post-partum female. I estimated relative reproductive effort by three ratios, using the abbreviations of Larsen (1986): 1) relative clutch mass (RCM1) = total mass of litter/mass of the female prior to parturition; 2) relative clutch mass (RCM2) = total mass of litter/mass of the female after parturition; 3) relative weight loss (RWL) = total mass lost through parturition/mass of female prior to parturition. For the purposes of statistical analysis, I considered only RCM2, because it is the only ratio in which female mass and litter mass are independent (Shine 1980). The other measures are included to facilitate comparisons with other studies. Finally, within 24 hours after parturition, I released each female and her litter, usually at the capture site of the female.

Overwintering

I located potential overwintering sites by searching for snakes in the early spring (March) of 1987. In addition, I constructed three artificial hibernacula in a meadow west of Leach Lake during the summer of 1987. Although preliminary observations suggested that snakes normally overwintered on rocky hillsides, I was unable to dig holes of sufficient depth in such areas. Each hibernaculum was 1 m^2 by 1 m deep, and was filled with large rocks from a nearby talus slope. A PVC pipe placed in the center of each hibernaculum allowed temperature readings to be taken at the bottom; this was done between 0900h and 1300h at approximately three-week intervals during the winter of 1987-1988. Shaded air temperature at 1.5 m above the surface was recorded concurrently with hibernaculum temperature.

In addition to providing information on sub-surface thermal conditions, the purpose of constructing the three hibernacula was to determine whether snakes would select such sites for overwintering, and whether snakes would survive if forced to overwinter there. I examined the hypothesis that conspecifics or their odours may attract snakes to overwintering sites (Parker and Brown 1980) by "baiting" one hibernaculum between late August and mid-September with 38 *T. sirtalis* and 90 *T. elegans*. Most of these snakes were captured in the vicinity of the hibernaculum, and I simply released and allowed each snake to descend within it. A second hibernaculum was left undisturbed to serve as a "control". At the third, I forced snakes to overwinter by enclosing the hibernaculum within a 1 m high aluminum screen fence on 20 September. I then released eleven snakes (six *T. sirtalis* and five *T. elegans*) inside the fence. In February 1988, I dismantled all hibernacula and searched for overwintering snakes within each.

Movements

Because the Leach Lake portion of the study area was more thoroughly searched than the Corn Creek Marsh Unit, I restricted the analysis of movements to snakes captured in the former area. I recorded the approximate location of each snake captured using a system of coordinates drawn on three maps (scales: 1:500; 1:2 500; 1:20 000). The distance between coordinates on the latter map was 50 m, and therefore the overall accuracy of movements was ±50 m. Most movements, however, were within the area covered by the map with the smallest scale (with an inter-coordinate distance of 10 m), and were accurate to ±10 m.

I used SAS (1985) procedures to calculate: 1) the distance between two coordinates (i.e. capture locations) in a north or south direction; 2) the distance between coordinates in an east or west direction; and 3) the straight line distance between each coordinate. I used trigonometry to calculate the direction of travel using distances 1) and 2). In comparisons of the distance and direction moved by snakes at different times of the year, I included only records of movements that occurred within a 30-day period. To test the validity of this procedure, I examined a scatter plot of distance between captures *vs.* time interval between captures (maximum 30 days) to determine if the two were correlated.

I determined the home range size of individual snakes captured at least three times in different locations on different days. Both within-year and between-year records were included in the analysis, which was performed using the Minimum Convex Polygon method of Jennrich and Turner (1969). Gregory *et al.* (1987) suggested that this method is the best available, although it underestimates home range size when the number of capture locations is small. I determined the area of each polygon by this method using McPAAL, a micro-computer program for the analysis of animal locations (Stuwe 1987).

Feeding

I estimated feeding frequency by tabulating the proportion of individuals containing food using the first capture of all individuals plus subsequent recaptures at least seven days apart. In this way, I reduced the potential bias caused by short-term disturbances to normal feeding behaviour. An important presumption when inferring feeding frequency directly from the proportion of snakes with food is that the length of time a prey item is detectable in the stomach does not vary among individuals and among prey items (see Discussion: Feeding).

If a snake contained food, I forced it anteriorly into the buccal cavity for identification. In 1986, I allowed most snakes to reswallow their food, and therefore was able to identify only the most recently eaten food item(s). In 1987, I removed and preserved the stomach contents of most snakes, thereby permitting enumeration and identification of all prey items that had not reached too advanced a stage of digestion.

I determined diet diversity, or dietary niche breadth, for different size classes of snakes using the formula given by Levins (1968):

$$B_i = \frac{(\Sigma N_{ij})^2}{\Sigma N_{ij}^2}$$

where N_{ij} = the number of items of food type j eaten by snakes in the i^{th} size class.

I examined the relationship between prey size and snake SVL by measuring the maximum width and mass of all removed prey items that had not reached too advanced a stage of digestion. For one prey type, the meadow vole *Microtus pennsylvanicus*, I increased the sample of prey sizes by using *M. pennsylvanicus* tail length as an index of maximum width. From a series of 76 voles (mostly dead) collected from snakes, funnel traps, small mammal traps, and roads, I calculated a regression equation (width = 9.128 + 0.286tail; $r^2 = 0.74$). I used this equation to predict the width of 36 additional voles eaten by snakes from which I removed only the vole's tail.

Statistical analyses

Statistical analyses followed Zar (1984), and I used SAS (1985) to summarize and analyze many of the data. I compared differences between means using Student's *t*-test for independent samples, and compared the slopes of two regression lines either by means of a modified *t*-test (Zar 1984:292) or an analysis of covariance (SAS 1985). I also used analysis of covariance to compare more than two regression lines. Adjusted means were compared only if slopes were homogeneous. I used analysis of variance to assess variation in body size among litters of captive-born snakes, and X^2 analysis (corrected for continuity) to compare sex ratios against an expected 1:1 ratio. Finally, I compared proportions using 2X2 contingency tables (X^2, corrected for continuity), and calculated confidence limits for proportions after Zar (1984:378). A minimum rejection level of alpha = 0.05 was used in all statistical tests.

RESULTS

Numbers

During this study, I captured and marked just over 3100 garter snakes, of which approximately one-third were *T. sirtalis*, and two-thirds were *T. elegans*. Table 1 summarizes the number of original captures plus recaptures (after any time interval) of each species. Despite the large number of individuals captured, most snakes were never seen again; only 19.5% and 25.2% of all captures of *T. sirtalis* and *T. elegans*, respectively, were of previously marked individuals. The maximum number of captures of any one individual was seven, and the interval between captures ranged from one day to 16 months.

About 17% of all snakes were captured in the nine traps at Leach Lake Unit. I captured more snakes in the traps closest to the west edge of the valley, corresponding to the greater number of captures by hand in this area than elsewhere. I discovered that large snakes could avoid the traps by crawling over the fence, but even when pursued by me, they seldom did so. In addition, 26 snakes were killed in traps because of insufficient protection from the sun, and predation by beetles and small mammals.

The approximate number of *T. sirtalis* in the study area during the fall of 1986 (based on the Peterson index described in General methods) was 3340 individuals, with lower and upper 95% confidence limits of 2321-5955 individuals, respectively. Approximately 5520 (4344-7571) individual *T. elegans* were in the study area during this period. Density estimates of 1.7 (*T. sirtalis*) and 2.8 (*T. elegans*) snakes per ha are based on an area of 2000 ha, the maximum area in which snakes were captured. Actual densities within the study area during the fall of 1986 probably varied

Table 1. Summary of original captures and recaptures of snakes marked during any previous period. Under each heading, F refers to females, M refers to males.

T. sirtalis

Month	1986				1987				1986+1987
	Original		Recapture		Original		Recapture		
	F	M	F	M	F	M	F	M	
March	-	-	-	-	6	132	3	42	183
April	16	19	0	0	34	42	8	21	140
May	75	73	3	6	60	27	11	8	263
June	21	30	3	3	63	32	10	6	168
July	70	43	17	4	64	35	24	23	280
August	19	27	6	6	21	42	4	16	142
September	34	37	9	12	9	20	8	6	135
October	14	22	2	3	-	-	-	-	41
Total	249	251	40	34	257	330	68	122	1352

T. elegans

Month	1986				1987				1986+1987
	Original		Recapture		Original		Recapture		
	F	M	F	M	F	M	F	M	
March	-	-	-	-	4	71	2	38	115
April	20	68	2	8	25	100	10	82	315
May	116	160	10	51	129	104	41	44	660
June	49	42	3	7	80	40	17	19	259
July	47	78	18	11	68	41	42	22	328
August	91	102	16	21	176	81	29	33	450
Sept.	105	156	37	54	51	69	21	30	525
October	17	17	8	6	-	-	-	-	48
Total	445	623	94	158	433	506	162	268	2700

between two orders of magnitude above and below these estimates. For example, much lower densities occurred in areas of open water, and much higher densities occurred around overwintering sites.

Annual cycle

The annual cycle of activity of each species at Creston is summarized in Fig. 3. The earliest capture date for both species was 17 March 1987; *T. sirtalis* were observed on 13 March 1987 (L.W. Schalla, personal communication), and a large group of "garter snakes" (species unknown) was observed on 14 March 1987 by local residents. Mating occurs in both spring and fall, but more commonly in spring. Although I observed actual copulation only twice (*T. sirtalis*, 28 March; *T. elegans*, 14 April), I observed courtship activity 27 times in spring, and two times in fall (Fig. 3). Courtship activity always consisted of one to six males (usually three to four) pursuing a single female.

I first captured gravid females in early May, and found them regularly until early August, the period during which parturition occurred (Fig. 3). The timing of parturition was probably more variable in *T. elegans* than in *T. sirtalis*, as I observed gravid females of the former species for as long as two weeks after the first *T. elegans* neonates had appeared. The latest date of capture for both species was 8 October; some individuals are probably active for a few weeks after this date.

Body size and growth

The distribution of body sizes (SVL) of all *T. sirtalis* and *T. elegans* captured in spring and fall of each year are presented in Figs. 4 and 5, respectively. In almost all samples, females reached larger maximum sizes than males. Within each sex, distinct peaks corresponding to different size (age) classes are not obvious, except in

Figure 3. Summary of the annual cycle of *T. sirtalis* and *T. elegans* at Creston based on field observations during 1986 and 1987. Upper and lower dashed lines denote the earliest and latest dates of field work, respectively; therefore, the duration of the overwintering period is approximate. The number of courtship groups observed per week corresponds with the scale above each bar.

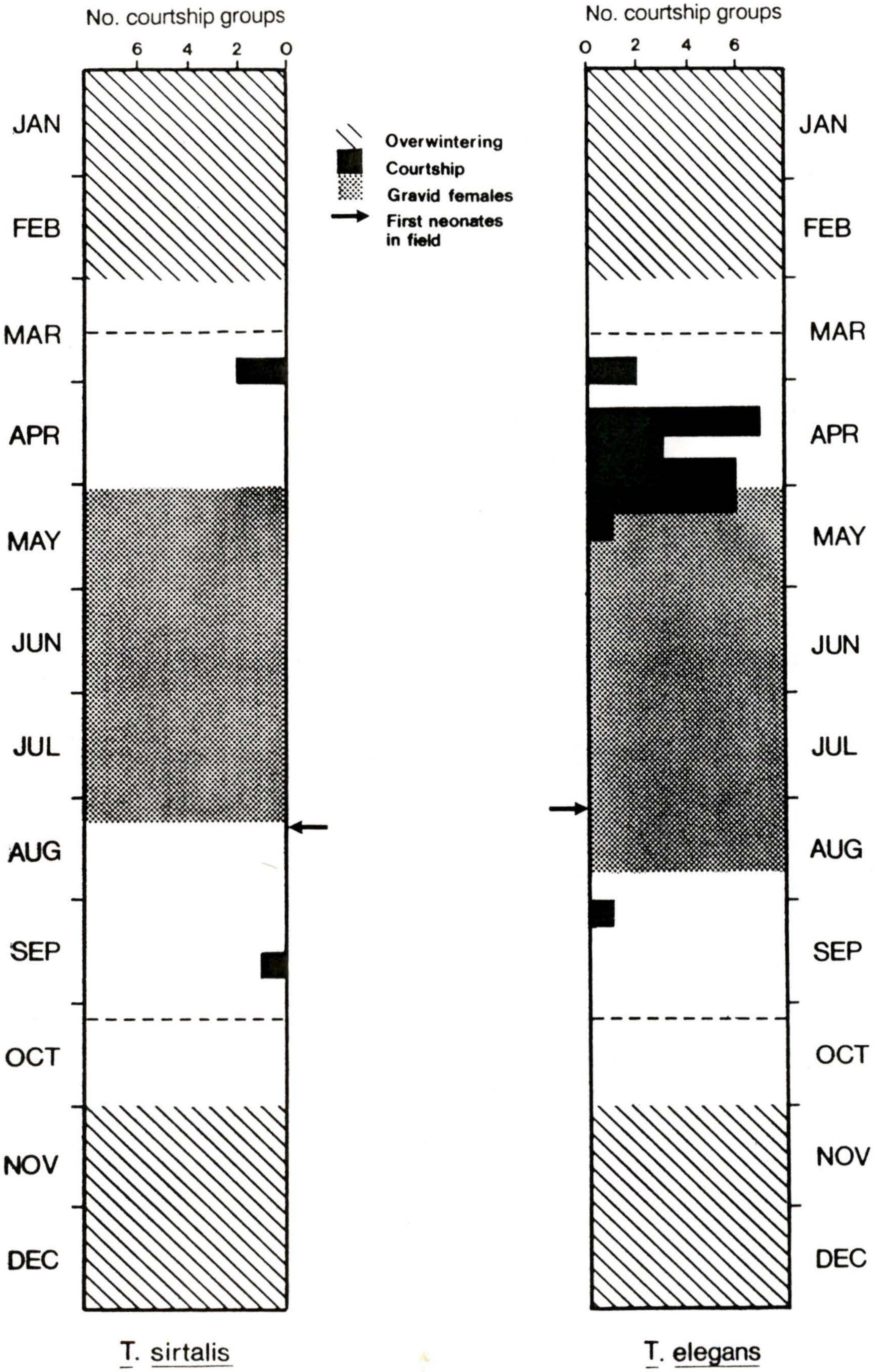

No. courtship groups
6
4
2
0
No. courtship groups
0
2
4
6
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
Overwintering
Courtship
Gravid females
First neonates in field
T. sirtalis
T. elegans

Figure 4. Size-frequency histograms of all *T. sirtalis* captured during spring and fall of 1986 and 1987. Males are above the horizontal axis; females below. Spring = March-April; Fall = September-October.

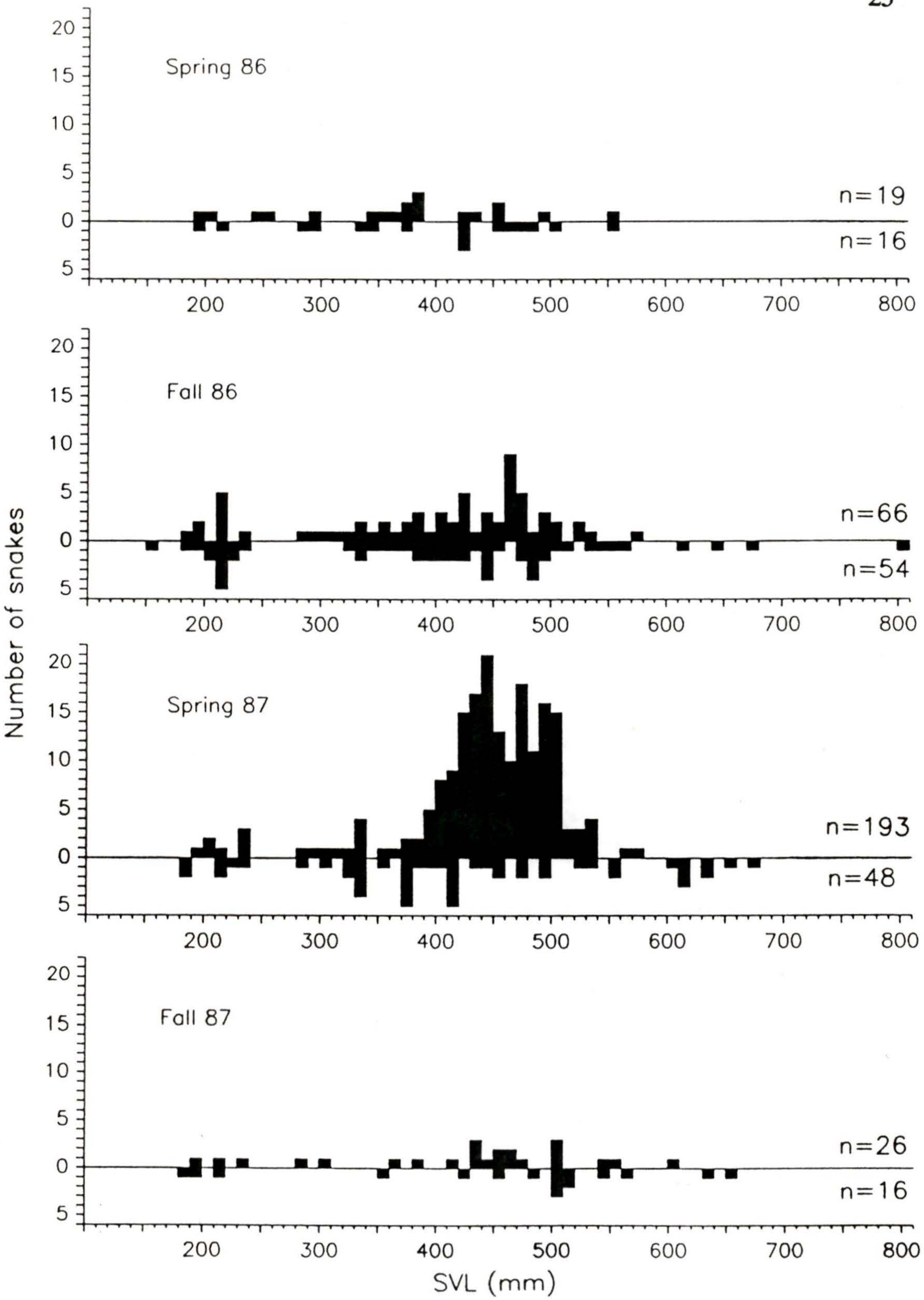
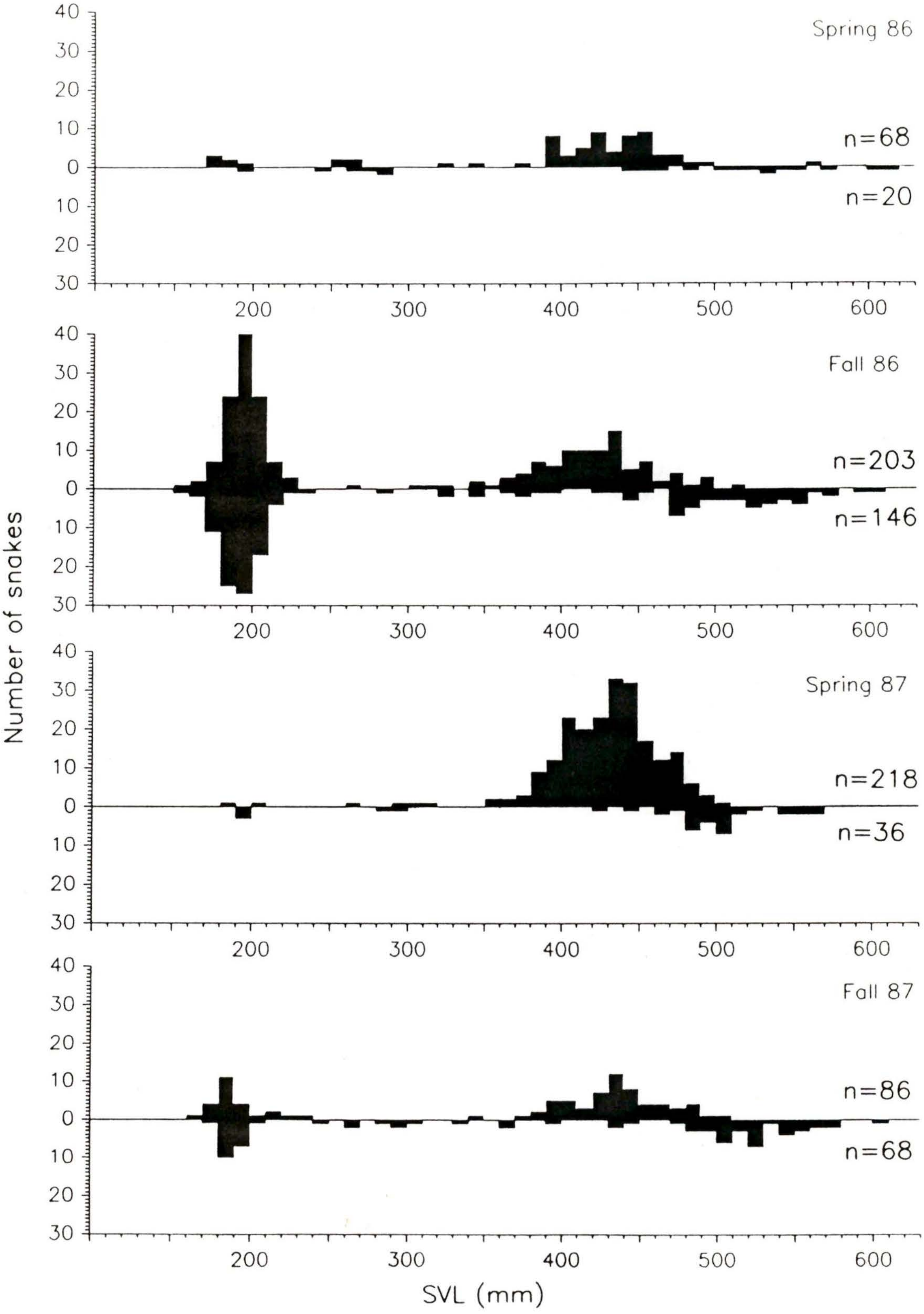

Spring 86
n=19
n=16
Fall 86
n=66
n=54
Spring 87
n=193
n=48
Fall 87
n=26
n=16
Number of snakes
20
15
10
5
0
5
200
300
400
500
600
700
800
SVL (mm)

Figure 5. Size-frequency histograms of all *T. elegans* captured during spring and fall of 1986 and 1987. Males are above the horizontal axis; females below. Spring = March-April; Fall = September-October.


Spring 86
n=68
n=20
Fall 86
n=203
n=146
Spring 87
n=218
n=36
Fall 87
n=86
n=68
40
30
20
10
0
10
20
30
200
300
400
500
600
Number of snakes
SVL (mm)

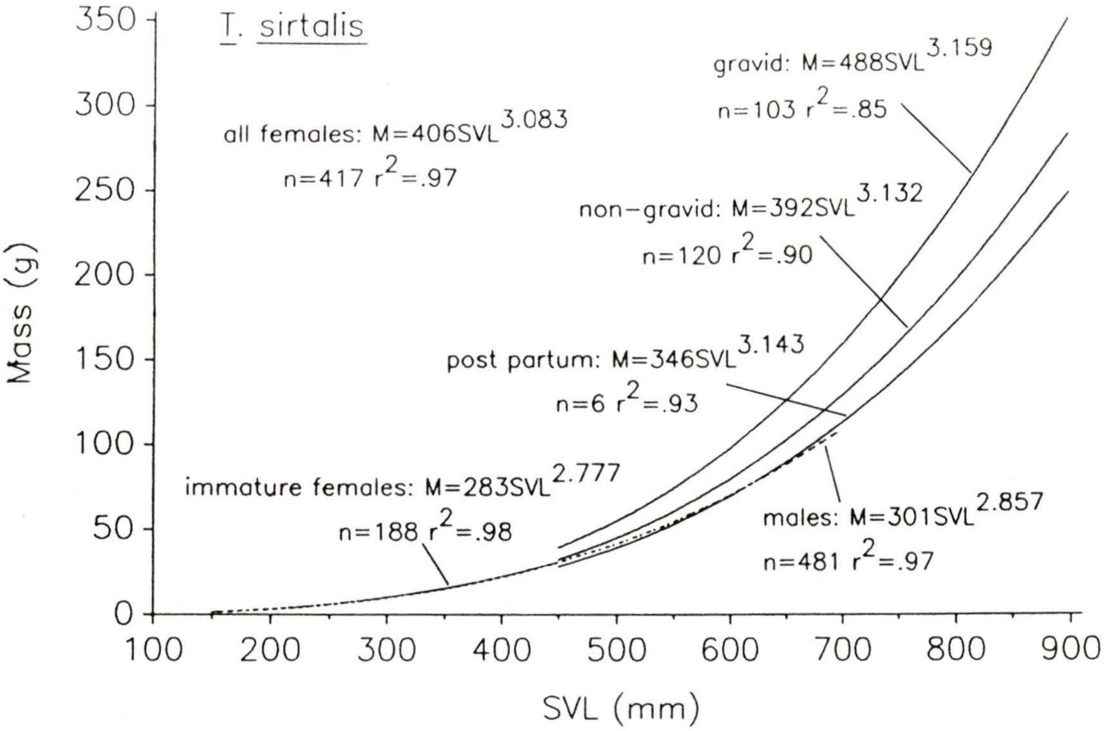
the smallest snakes. In both species, the latter group occurred at around 200 mm SVL, corresponding to snakes born in August of the current year (in fall samples) or previous year (in spring samples). A second size class around 280-340 mm SVL may be present in the spring 1987 sample of *T. sirtalis*, corresponding to snakes that had completed one full year of growth. In general, most female *T. sirtalis* captured were between 350 and 650 mm SVL; most males were between 350 and 550 mm SVL. There may be more than one peak in the male size distribution, but such peaks are indistinct.

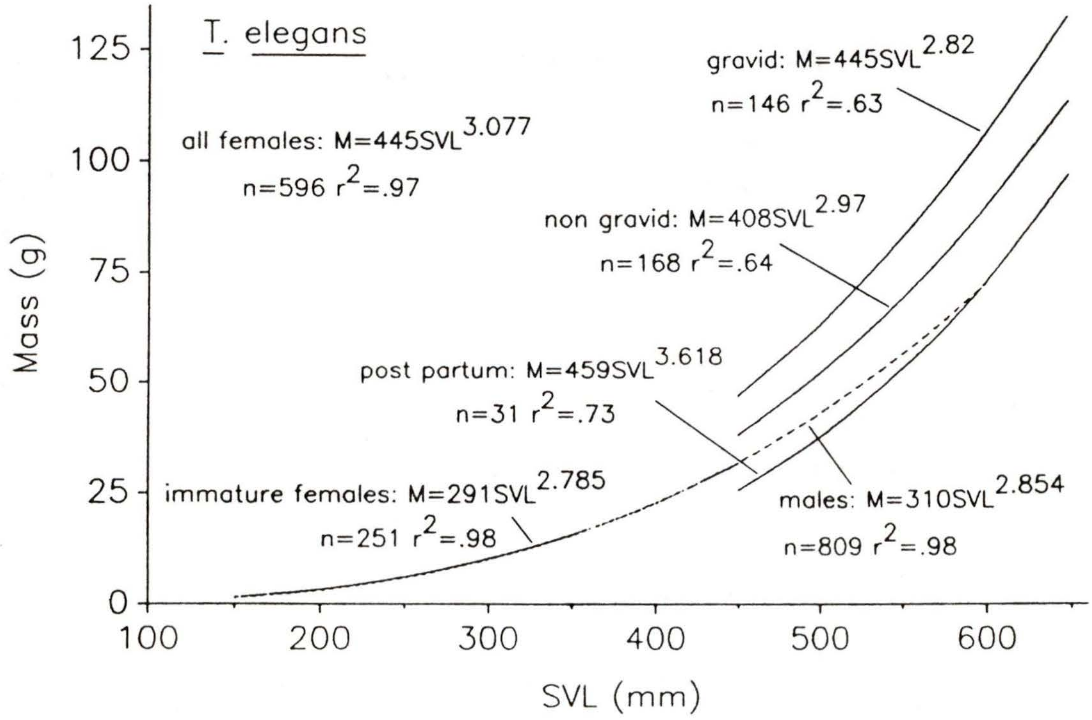
In addition to neonates (which were numerous in fall samples), *T. elegans* may exhibit a size class between 240 and 320 mm in spring samples. Very few individuals in this size range were captured, however, making further interpretation difficult. Excluding neonates, most male *T. elegans* were between 350 and 500 mm SVL, while most female *T. elegans* were between 400 and 550 mm SVL.

The largest snake captured during the entire study was a gravid female *T. sirtalis* (910 mm SVL, 434 g). This snake was 75 mm longer and 140 g heavier than the next largest snake (also a female *T. sirtalis*), and was much larger than the largest male of this species (605 mm SVL, 79 g). The largest female and male *T. elegans* captured were 620 mm SVL (130 g) and 570 mm SVL (41 g), respectively; another male was shorter (525 mm SVL), but heavier (58 g).

The relationship between SVL and mass in both species is exponential (Fig. 6). Regression exponents of the equations for all females and all males were significantly different in both species (*T. sirtalis*: $t = 149.2$; df $= 894$; $p < .001$; *T. elegans*: $t = 154.0$; df $= 1401$; $p < .001$). Among mature females (greater than 450 mm SVL; see Results:Reproduction), differences associated with reproductive condition

Figure 6. Relationship between body mass and SVL for *T. sirtalis* and *T. elegans* (original captures only). Only individuals that did not contain food were included in each analysis. The equations were derived from linear regressions of ln mass (M, in grams) on ln SVL (in metres). The exponent of each regression was significantly different from 0 ($p < .001$). Note the differences in scales between the two species.


T. sirtalis
gravid: $M=488SVL^{3.159}$
$n=103$ $r^2=.85$
all females: $M=406SVL^{3.083}$
$n=417$ $r^2=.97$
non-gravid: $M=392SVL^{3.132}$
$n=120$ $r^2=.90$
post partum: $M=346SVL^{3.143}$
$n=6$ $r^2=.93$
immature females: $M=283SVL^{2.777}$
$n=188$ $r^2=.98$
males: $M=301SVL^{2.857}$
$n=481$ $r^2=.97$
Mass (g)
0
50
100
150
200
250
300
350
SVL (mm)
100
200
300
400
500
600
700
800
900

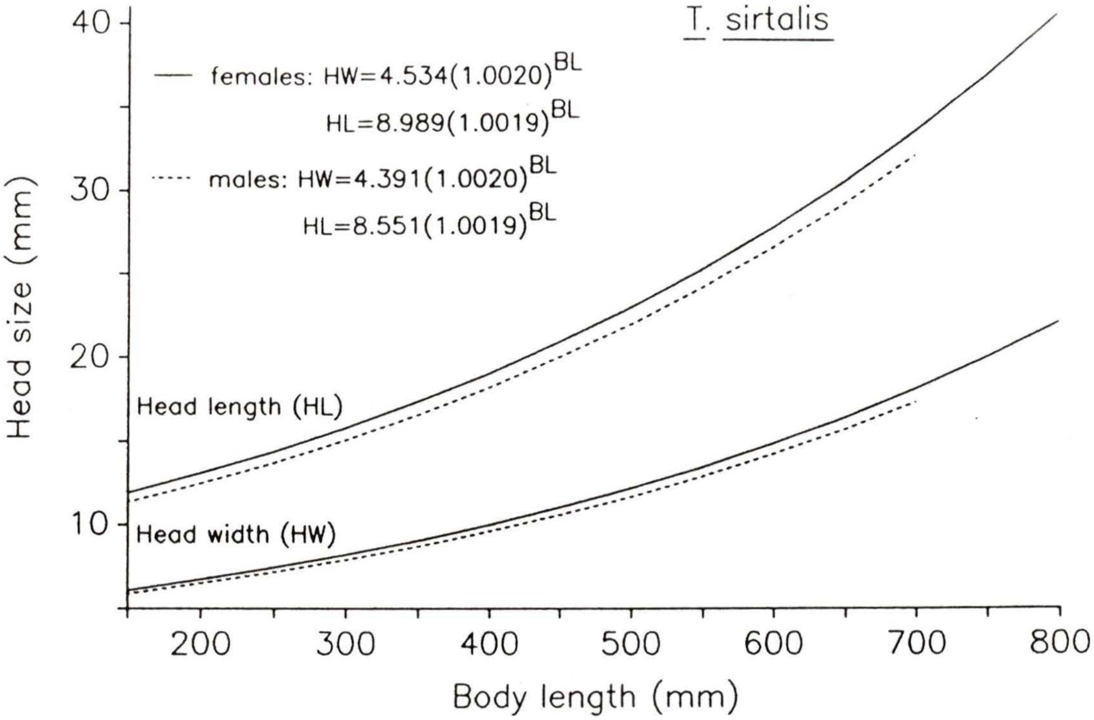

T. elegans
gravid: $M=445SVL^{2.82}$
$n=146$ $r^2=.63$
all females: $M=445SVL^{3.077}$
$n=596$ $r^2=.97$
non gravid: $M=408SVL^{2.97}$
$n=168$ $r^2=.64$
post partum: $M=459SVL^{3.618}$
$n=31$ $r^2=.73$
immature females: $M=291SVL^{2.785}$
$n=251$ $r^2=.98$
males: $M=310SVL^{2.854}$
$n=809$ $r^2=.98$
Mass (g)
0
25
50
75
100
125
SVL (mm)
100
200
300
400
500
600

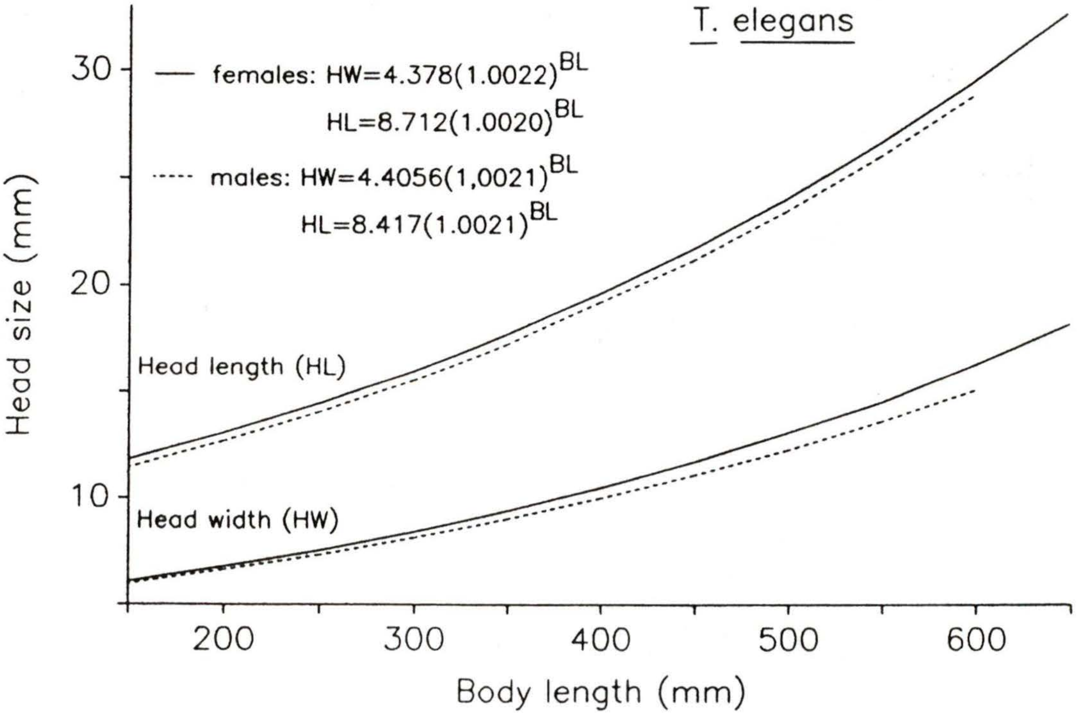
were apparent. Although the slopes of the ln-ln transformed mass-SVL relationships did not differ significantly (*T. sirtalis*: $F = 0.01$, $df = 2{,}223$, $p > .05$; *T. elegans*: $F = 1.63$, $df = 2{,}339$, $p > .05$), the mean mass adjusted for SVL did vary among the three reproductive classes (*T. sirtalis*: $F = 61.25$, $df = 2{,}225$, $p < .001$; *T. elegans*: $F = 143.13$, $df = 2{,}341$; $p < .001$). In general, non-gravid females weighed less than gravid females, but more than post-partum females, of similar length.

The relationships between head size and body length (BL) for free-ranging and captive born snakes combined were best described by transformed regressions of ln head size on body length. Marked non-linearity was evident in untransformed regressions, with small and large snakes having relatively larger heads than predicted by a regression of head size on body length. For *T. sirtalis*, head width (HW) $= 4.412(1.0020)^{BL}$ ($r^2 = 0.96$, $n = 676$), and head length (HL) $= 8.661(1.0019)^{BL}$ ($r^2 = 0.97$, $n = 676$). For *T. elegans*, $HW = 4.334(1.0022)^{BL}$ ($r^2 = 0.95$, $n = 700$), and $HL = 8.497(1.0021)^{BL}$ ($r^2 = 0.98$, $n = 700$). In all cases, relative head size decreased as snakes became larger. For example, *T. sirtalis* having body lengths of 200 mm and 400 mm had predicted head lengths of 6.4% and 4.7% of body length, respectively.

In addition to size-related variation, sexual dimorphism in relative head size was evident in both species, with females tending to have relatively larger heads than males. This dimorphism was not clear from either direct examination of females and males, or from scatter plots of head width (or head length) *vs.* body length. I have therefore presented the relationships for males and females separately (Fig. 7), and compared the sexes using analysis of covariance.

Figure 7. Relationship between head size (width and length) and body length (BL) in *T. sirtalis* and *T. elegans*. Note the differences in scales between each species. Sample sizes for both head width (HW) and head length (HL) are: 387 female, 289 male *T. sirtalis*, 364 female, 334 male *T. elegans*,and include both captive-born and free-ranging snakes. The equations are derived from linear regressions of ln HW on BL and ln HL on BL, and in all cases, $.94 < r^2 < .98$, $p < .001$.


T. sirtalis
— females: HW=4.534(1.0020)^BL
HL=8.989(1.0019)^BL
---- males: HW=4.391(1.0020)^BL
HL=8.551(1.0019)^BL
Head length (HL)
Head width (HW)
Head size (mm)
10
20
30
40
200
300
400
500
600
700
800
Body length (mm)


T. elegans
— females: HW=4.378(1.0022)^BL
HL=8.712(1.0020)^BL
---- males: HW=4.4056(1,0021)^BL
HL=8.417(1.0021)^BL
Head length (HL)
Head width (HW)
Head size (mm)
10
20
30
200
300
400
500
600
Body length (mm)

At all body lengths, female *T. sirtalis* had relatively wider and longer heads than males. The slopes of the transformed regressions for the two sexes did not differ significantly (HW: $t=0.44$, df=672, $p>.05$; HL: $t=0.51$, df=672, $p>.05$), but intercepts were significantly higher for females (HW: $t=2.39$, df=672, $p<.05$; HL: $t=5.27$, df=672, $p<.001$).

In *T. elegans*, as in *T. sirtalis*, females had relatively longer heads than males. Although there were no differences in slopes ($t=0.50$, df=695, $p>.05$), the intercept was significantly higher in females than in males ($t=4.49$, df=695, $p<.001$). In contrast, the slope of the head width-body length relationship was significantly higher in females than in males ($t=3.58$, df=695, $p<.001$). This suggests that although the heads of male and female *T. elegans* did not differ in relative width at birth (see Results: Litter characteristics), the heads of females became relatively wider than males as body length increased.

The relationship between annual growth (GR) and SVL in male *T. elegans*, based on recaptures of snakes before and after one active season, was $GR = 107.05\text{-}0.21SVL$ (Fig. 8). The slope of this relationship was significantly different from zero ($t=9.80$, df= 15, $p<.01$), but the regression did not account for much of the variation in growth ($r^2=0.40$). I was unable to estimate annual growth for female *T. elegans* and both sexes of *T. sirtalis* because they were rarely captured and recaptured one active season apart (maximum number of such records = 4 for any one group).

Larger numbers of recaptures within a single active season permitted the estimation of daily growth rates (mm/day) for all groups except female *T. sirtalis* (Fig. 9; Table 2). Two male *T. sirtalis* and one female and one male *T. elegans* each

Figure 8. Relationship between annual growth and SVL at first capture in male *T. elegans*. Points represent growth of individuals first captured in spring (or the previous fall) and subsequently captured in fall (or the following spring). Regression statistics appear in the text.

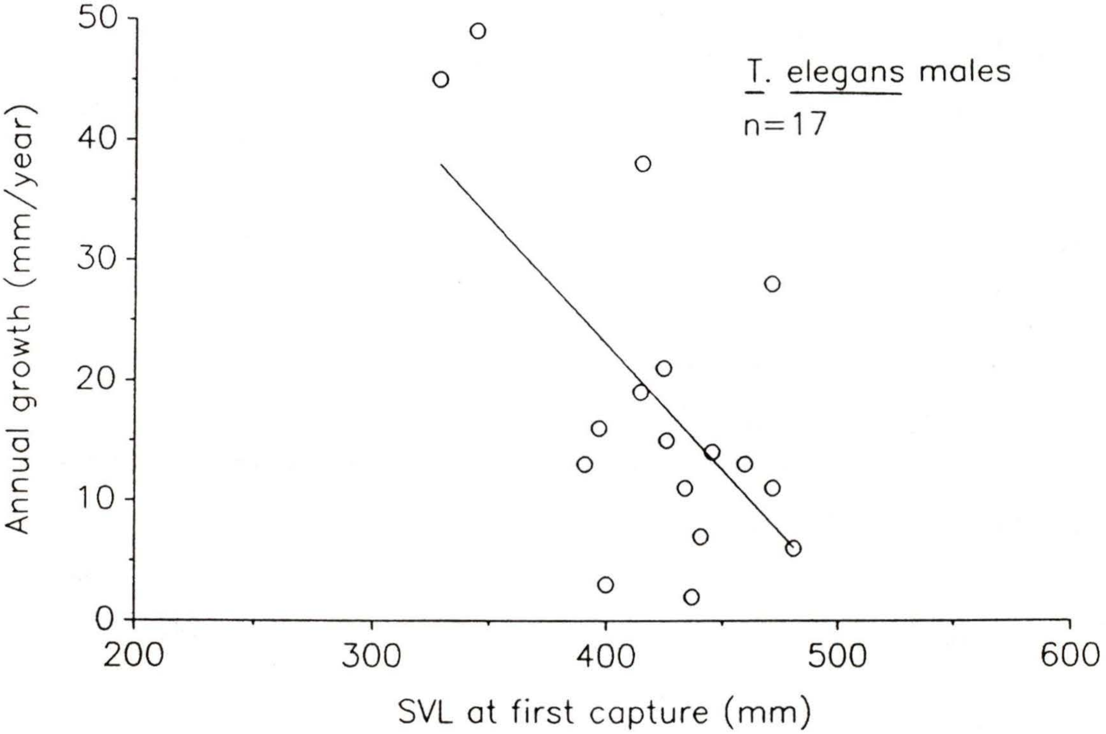

T. elegans males
n=17
Annual growth (mm/year)
0
10
20
30
40
50
SVL at first capture (mm)
200
300
400
500
600

Figure 9. Relationship between daily growth rate and SVL at first capture in *T. sirtalis* and *T. elegans*. Points represent growth of individuals captured two or more times within a year, with a minimum interval between captures of at least 60 days. Regression statistics appear in Table 2.

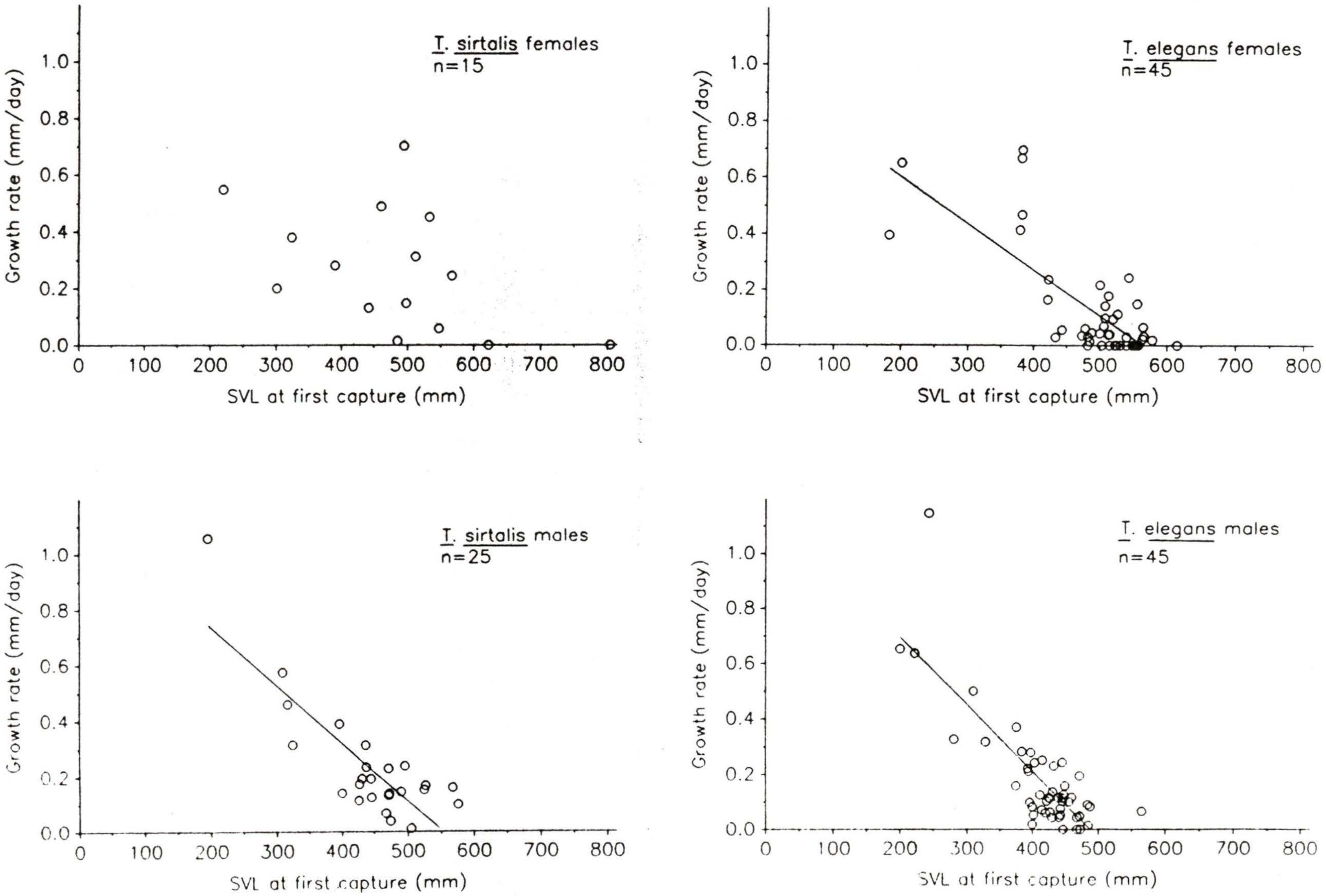

T. sirtalis females
n=15
T. elegans females
n=45
T. sirtalis males
n=25
T. elegans males
n=45
Growth rate (mm/day)
0.0
0.2
0.4
0.6
0.8
1.0
SVL at first capture (mm)
0
100
200
300
400
500
600
700
800

Table 2. Summary of regression equations of growth rate in mm/day (GR) on SVL at first capture in mm, based on the growth of snakes captured twice within a year, with the interval between captures at least 60 days. The right-most column contains the mean and median SVL of the 10 largest individuals captured.

	n	Regression equation	r^2	Estimated maximum SVL (mm)	10 largest (mm)	
					mean	median
T. sirtalis						
Females	15	$GR=0.625-0.0007SVL^{+}$	0.23	---	780	761
Males	25	$GR=1.151-0.0021SVL^{*}$	0.68	554	578	577
T. elegans						
Females	45	$GR=0.932-0.0016SVL^{*}$	0.57	565	608	605
Males	45	$GR=1.306-0.0027SVL^{*}$	0.65	478	518	513

+ $.10<p<.05$
* $p<.001$

occur twice in this analysis. The growth of female *T. sirtalis* was extremely variable, and possible non-linearity in the relationship between growth and SVL in the other three groups was suggested by the much higher than predicted growth rates of some small snakes (Fig. 9). In *T. elegans*, the slope of the regression was significantly lower in females than in males ($t = 18.41$; $df = 86$; $p < .05$). Female *T. elegans* grew increasingly more quickly than males as SVL increased. Females of both species reached larger asymptotic sizes than males, although the predicted asymptotic size was probably underestimated in all groups (Table 2).

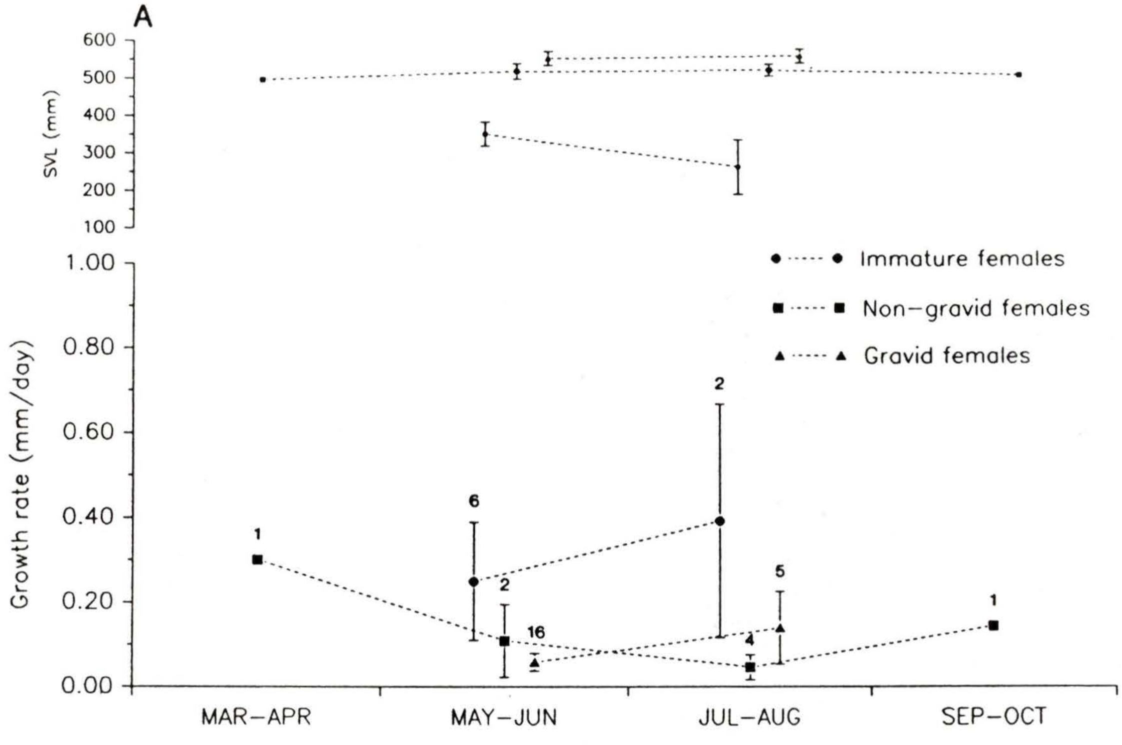
Since much variation in growth was not explained by variation in body size (maximum $r^2 = 0.68$, Table 2), I examined two other sources of variation: time of year and reproductive status. Sample sizes were small, particularly for *T. sirtalis*, and variation within seasons was large, making interpretation difficult. In *T. elegans*, and possibly *T. sirtalis*, growth was slow in spring, but no consistent pattern was apparent during the remainder of the year (Figs. 10 and 11). Gravid female *T. elegans* appeared to grow more slowly than non-gravid females (Fig. 11). No such trend was evident for *T. sirtalis*, but variation was great.

Reproduction

Sexual maturity

The smallest gravid female *T. sirtalis* and *T. elegans* captured during this study were 445 mm SVL and 420 mm SVL, respectively. I captured many smaller females in the period during which their reproductive condition could be assessed (15 May to 15 August); none of these were either gravid or post-partum (Fig. 12). The vast majority of reproductive females were greater than 450 mm in both species, and the range of SVLs of both reproductive and non-reproductive females was greater in *T. sirtalis*. I captured only one female *T. sirtalis* (555 mm SVL) involved in courtship

Figure 10. Growth of *T. sirtalis* females (A) and males (B) compared among seasons. Immature females are less than 450 mm SVL; immature males are less than 400 mm SVL (see Results: Reproduction). Mean growth rates were calculated for all individuals captured twice during any 7-60 day interval, and each record was assigned to a two month period on the basis of the mean date of the first and second capture dates. Because differences in mean growth rate among seasons may be due to differences in mean SVL, the mean SVL for each group is plotted above growth rate. All symbols are means ± 1 standard error (SE), and the numbers above each symbol are sample sizes.


A
SVL (mm)
600
500
400
300
200
100
Growth rate (mm/day)
1.00
0.80
0.60
0.40
0.20
0.00
Immature females
Non−gravid females
Gravid females
1
6
2
16
2
4
5
1
MAR−APR
MAY−JUN
JUL−AUG
SEP−OCT

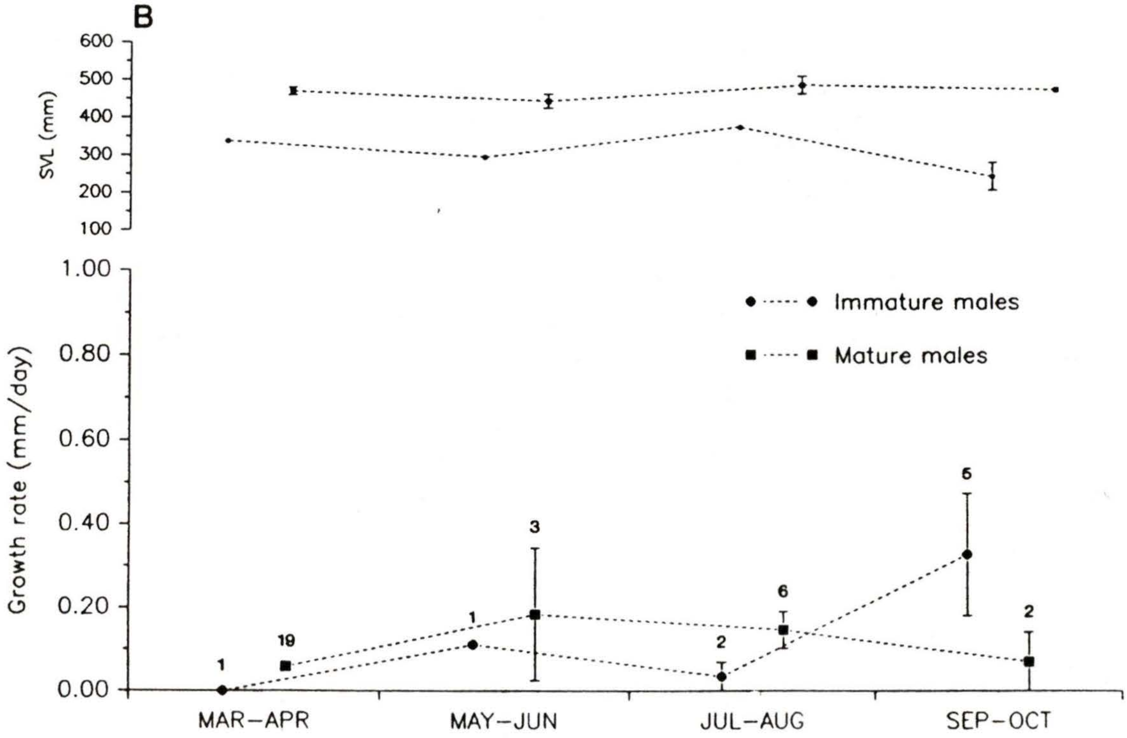

B
SVL (mm)
600
500
400
300
200
100
Growth rate (mm/day)
1.00
0.80
0.60
0.40
0.20
0.00
Immature males
Mature males
1
19
1
3
2
6
5
2
MAR−APR
MAY−JUN
JUL−AUG
SEP−OCT

Figure 11. Growth of *T. elegans* females (A) and males (B) compared among seasons. Immature females are less than 450 mm SVL; immature males are less than 400 mm SVL (see Results: Reproduction). Mean growth rates were calculated for all individuals captured twice during any 7-60 day interval, and each record was assigned to a two month period on the basis of the mean date of the first and second capture dates. Because differences in mean growth rate among seasons may be due to differences in mean SVL, the mean SVL for each group is plotted above growth rate. All symbols are means ± 1 SE, and the numbers above each symbol are sample sizes.

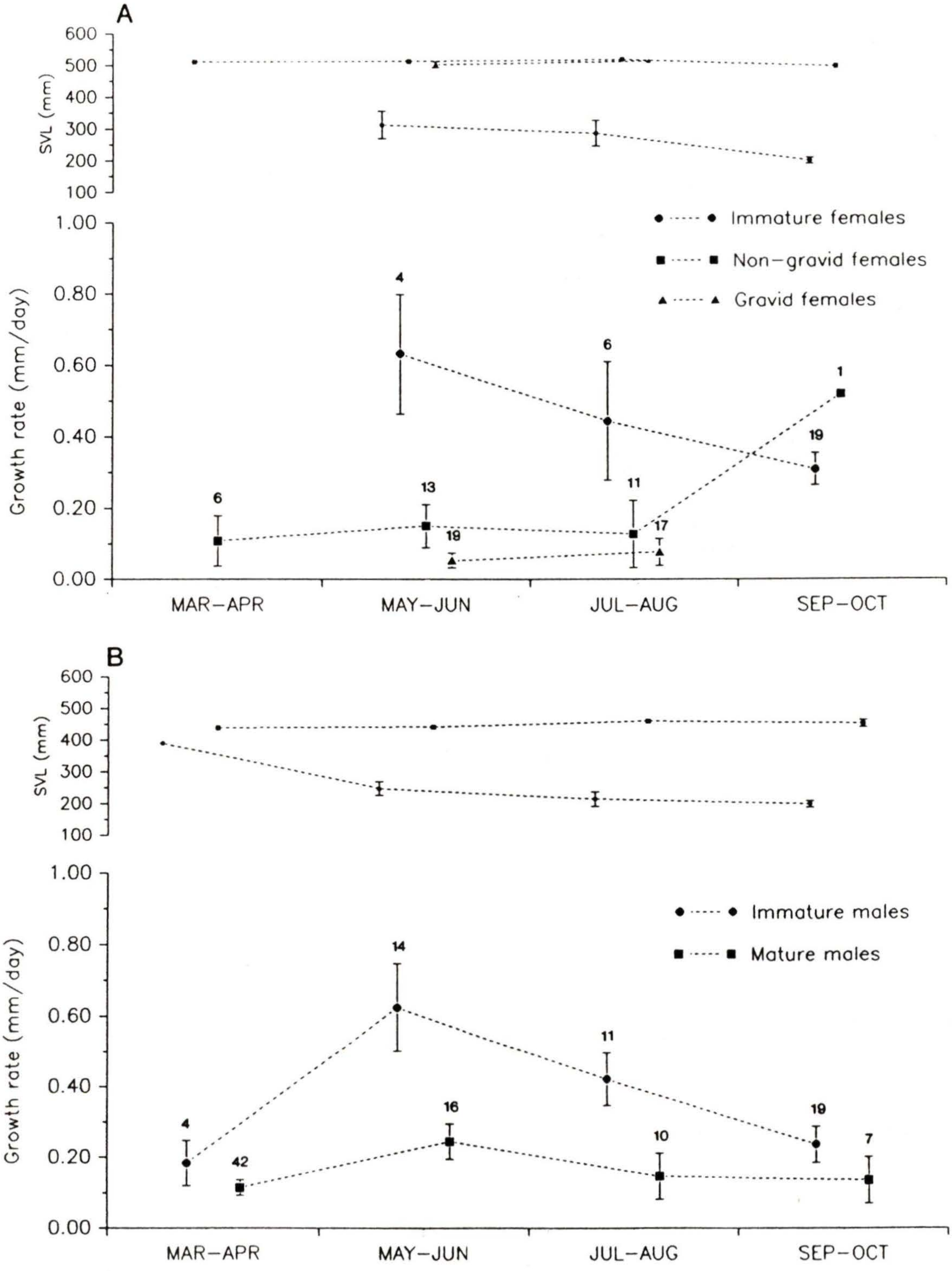
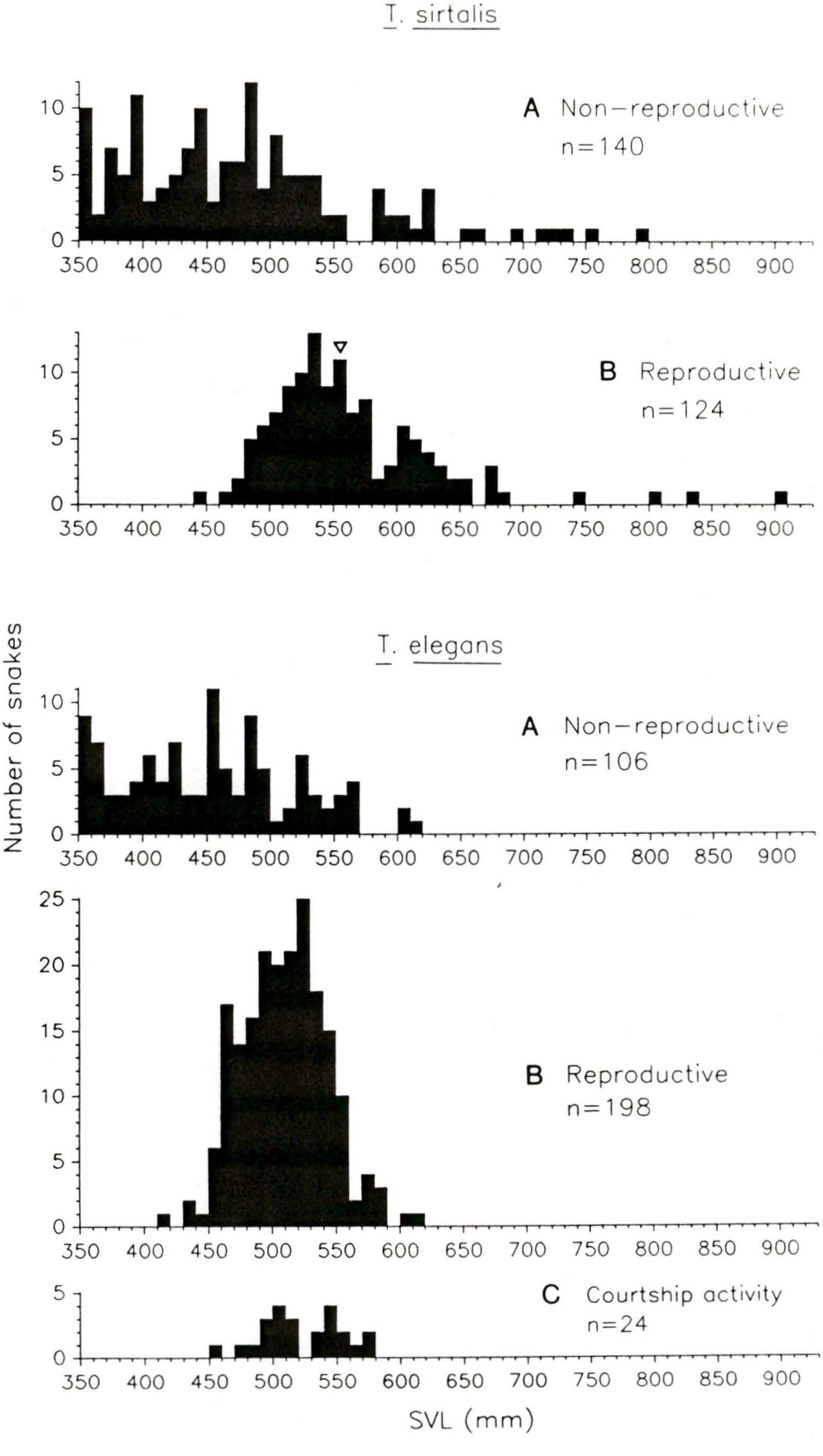

A
SVL (mm)
600
500
400
300
200
100
Growth rate (mm/day)
1.00
0.80
0.60
0.40
0.20
0.00
● ····· ● Immature females
■ ····· ■ Non-gravid females
▲ ····· ▲ Gravid females
4
6
1
19
6
13
19
11
17
MAR–APR
MAY–JUN
JUL–AUG
SEP–OCT
B
SVL (mm)
600
500
400
300
200
100
Growth rate (mm/day)
1.00
0.80
0.60
0.40
0.20
0.00
● ····· ● Immature males
■ ····· ■ Mature males
14
11
16
4
42
10
19
7
MAR–APR
MAY–JUN
JUL–AUG
SEP–OCT

Figure 12. Body sizes of a) non-reproductive, and b) reproductive females captured between 15 May and 15 August. Only original captures are shown, and reproductive females are defined as those that were gravid or post-partum at the time of capture. Also illustrated for *T. elegans* are c) the SVLs of females captured while being courted by males. Triangle denotes a single female *T. sirtalis* captured while being courted by males.


T. sirtalis
A Non−reproductive
n=140
B Reproductive
n=124
T. elegans
A Non−reproductive
n=106
B Reproductive
n=198
C Courtship activity
n=24
Number of snakes
SVL (mm)
0
5
10
15
20
25
350
400
450
500
550
600
650
700
750
800
850
900

activity; of 24 female *T. elegans* captured while being courted by males, the smallest was 460 mm SVL.

The size at sexual maturity in males is between 350 and 400 mm SVL (Fig. 13). In *T. elegans*, and possibly *T. sirtalis*, there may be a delay in behavioural maturity once physiological maturity is reached. As suggested in Fig. 13, the majority of males observed courting females were larger than the smallest males found to contain sperm. For the purposes of future comparisons of movements and feeding frequency, I shall consider male and female size at maturity to be 400 and 450 mm SVL, respectively.

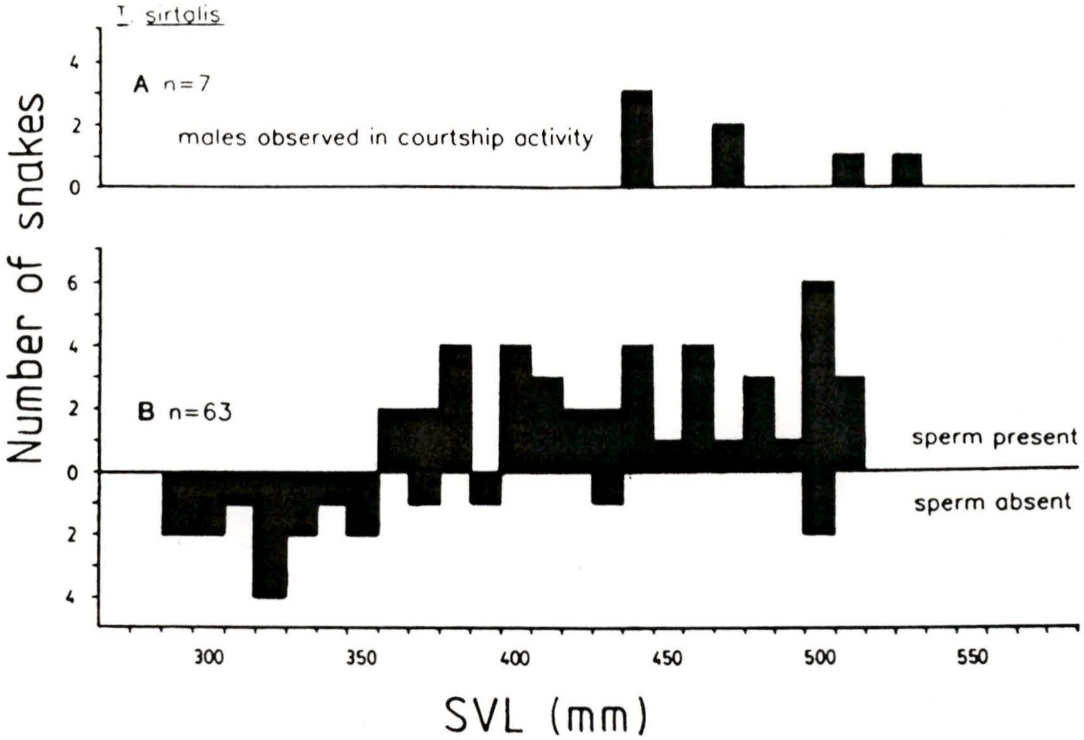
Litter statistics

A total of 35 females (13 *T. sirtalis*, 22 *T. elegans*) gave birth in captivity during this study. One female of each species produced a litter consisting of only stillborn young and undeveloped yolky masses (unfertilized ova); these litters are not included in subsequent analyses. All the 33 remaining litters contained live young, but five of 12 *T. sirtalis* litters, and one of 21 *T. elegans* litters, also contained some stillborn young (Table 3). Unfertilized ova (from one to three in number) were present in four litters (Table 3). In addition, one *T. sirtalis* litter (parturition 13 August 1986), and two *T. elegans* litters (parturition 9 and 19 August 1987) each contained a neonate with a spinal deformity. In each case, the deformity was in the form of kinks along the back or tail, and each neonate was apparently healthy in all other respects.

Litter size

The litter sizes of the two species were similar, averaging around 7.5 young per litter (Table 4). Litter size was significantly correlated with SVL of both captive

Figure 13. Body sizes of: (A) all males observed in courtship activity, and (B) all males whose cloacal smears were examined for the presence or absence of sperm before 15 May and after 15 August 1987. In (B), individuals that contained sperm are shown above the horizontal axis and individuals that did not contain sperm are below the axis.


T. sirtalis
Number of snakes
A n=7
males observed in courtship activity
B n=63
sperm present
sperm absent
0
2
4
6
300
350
400
450
500
550
SVL (mm)

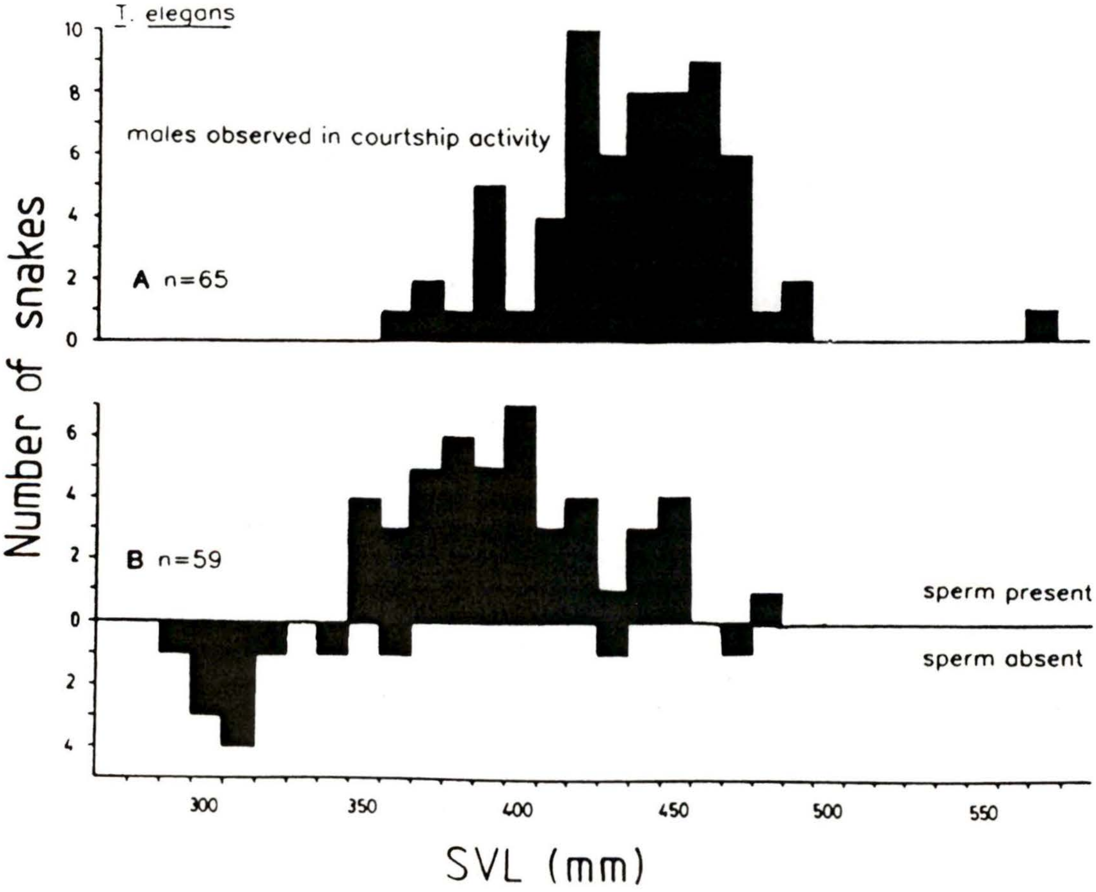

T. elegans
Number of snakes
10
8
6
4
2
0
males observed in courtship activity
A n=65
B n=59
sperm present
sperm absent
300
350
400
450
500
550
SVL (mm)

Table 3. Summary of data obtained from gravid females held in captivity until parturition (PART.). For litter mass and number of young, both live and dead young are included in the total; the number of dead young is in parentheses.

DATE OF PART.	DAYS HELD	SVL (mm)	MASS BEFORE PART. (g)	MASS AFTER PART. (g)	LITTER MASS (g)	NUMBER OF YOUNG
T. sirtalis						
21AUG87	46	492	46.4	26.0	9.8	5(4)
14AUG87	10	495	59.6	34.5	17.6	7
03SEP87	59	506	41.5	33.3	5.2	2(1)
22AUG87	49	513	59.2	34.7	18.5	8
01AUG87	26	528	53.3	31.5	14.0	5
13AUG86	10	532	55.6	41.5	10.4	*4
22AUG87	47	558	57.2	38.7	14.2	5
20AUG87	45	561	64.8	46.9	10.8	*5(3)
18AUG87	14	592	83.4	61.3	20.7	7(2)
07AUG87	32	602	77.7	53.6	17.7	7
08AUG87	3	607	88.0	50.2	24.9	11
21AUG87	35	749	191.4	119.2	61.2	21(1)
T. elegans						
29AUG87	57	460	48.1	21.1	17.3	8(1)
20AUG86	17	464	56.9	32.0	16.7	*8
15AUG87	3	465	38.6	24.7	10.9	5
18AUG87	6	473	54.2	28.2	14.0	6
03SEP87	62	482	61.4	30.8	18.7	8
17AUG86	4	497	74.6	39.5	21.5	10
01SEP87	57	497	41.6	31.5	7.5	3
25AUG86	12	502	66.3	36.9	18.9	9
22AUG87	18	503	62.2	35.2	19.9	5
05SEP87	63	506	72.2	40.2	20.1	6
17AUG87	5	507	58.8	38.2	10.8	*3
26AUG87	51	513	81.0	39.8	25.0	10
06AUG87	2	514	78.2	39.8	23.7	7
01AUG87	4	525	95.7	51.3	24.9	8
25AUG86	5	531	74.6	41.8	28.2	10
09AUG87	5	532	90.9	41.8	29.6	8
19AUG87	11	533	81.5	46.0	22.9	8
24AUG87	16	533	79.0	39.5	23.4	11
22AUG86	9	537	63.9	36.7	19.5	7
17AUG86	14	541	65.3	40.9	15.3	6
26AUG86	12	570	115.1	55.6	33.4	11

* undeveloped ova present

Table 4. Litter characteristics of Creston garter snakes. Litter size is based on 33 females held in captivity until parturition and 205 free-ranging females palpated in the field; yearly means are for combined samples. Neonate size and reproductive effort are based on litters of the 33 captive females. RCM1 = litter mass/female mass *before* parturition; RCM2 = litter mass/female mass *after* parturition; RWL = total mass lost through parturition/female mass before parturition.

		T. sirtalis		*T. elegans*
	n	$\bar{X}$±SD (Range)	n	$\bar{X}$±SD (Range)
Litter size:				
Captive	12	7.25±4.88 (2-21)	21	7.48±2.32 (3-11)
Free-ranging	85	7.52±2.56 (3-17)	120	7.56±2.08 (3-13)
1986	45	7.18±2.63	41	7.90±1.97
1987	52	7.75±3.14	100	7.40±2.15
Neonate size:				
SVL (mm)	85	183.0±11.9 (150-200)	157	176.1±10.7 (152-201)
Mass (g)	87	2.59±0.39 (1.7-3.3)	157	2.70±0.59 (2.7-4.5)
Reproductive effort:				
Litter mass (g)	12	18.75±14.41 (5.2-61.2)	21	20.10±6.42 (7.5-33.4)
RCM1	12	0.241±0.060 (0.125-0.320)	21	0.287±0.047 (0.180-0.378)
RCM2	12	0.379±0.124 (0.156-0.533)	21	0.534±0.132 (0.238-0.820)
RWL	12	0.343±0.082 (0.198-0.440)	21	0.448±0.072 (0.243-0.561)

and free-ranging *T. sirtalis*, but the correlation in *T. elegans* was significant for free-ranging females only (Fig. 14). A comparison of the mean litter sizes of free-ranging and captive female *T. sirtalis* via analysis of covariance was not possible due to heterogeneity of slopes of the litter size-female SVL regression ($t = 3.28$, df = 93, $p < .01$), but no major differences were apparent (Fig. 14). In *T. elegans*, neither the slopes ($t = 0.01$, df = 137, $p > .05$), nor the adjusted mean litter sizes ($t = 0.03$, df = 138, $p > .05$) differed significantly between captive and free-ranging females.

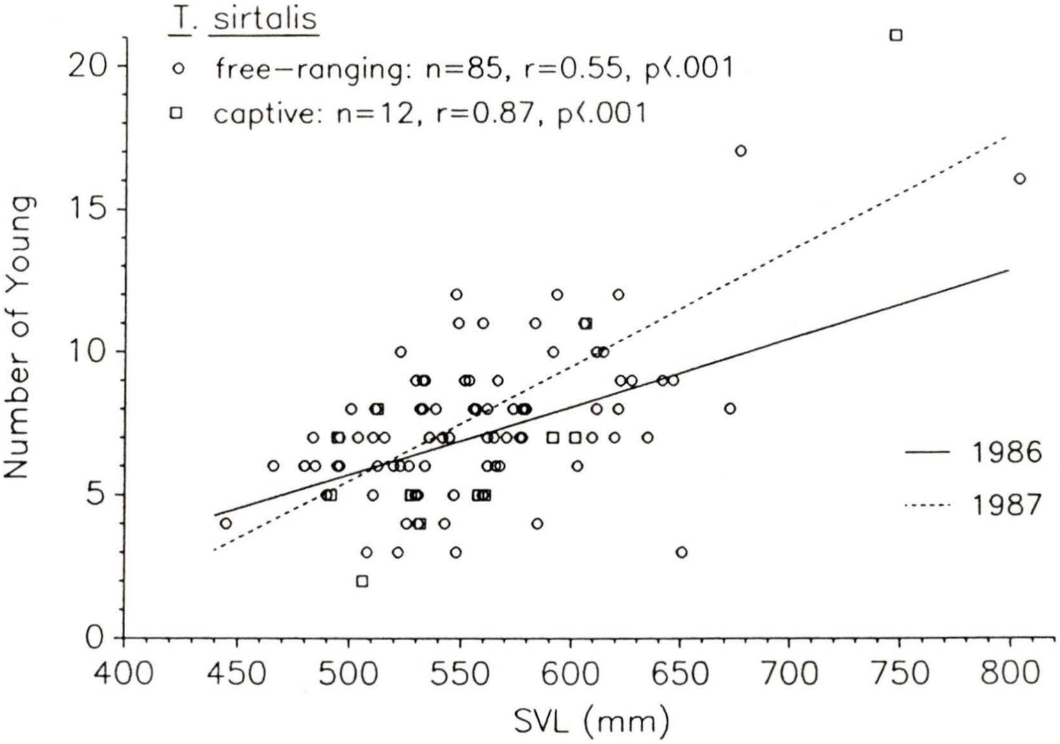
The slope of the relationship between litter size and SVL of combined free-ranging and captive *T. sirtalis* varied significantly between years ($t = 2.03$, df = 93, $p < .05$; Fig. 14). The unadjusted mean litter size in 1986, however, was not significantly different from 1987 ($t = 1.23$, df = 95, $p > .05$). In *T. elegans*, none of slope ($t = 0.30$, df = 138, $p > .05$), adjusted mean litter size ($t = 1.32$, df = 138, $p > .05$), or unadjusted mean litter size ($t = 1.44$, df = 139, $p > .05$) differed significantly between years.

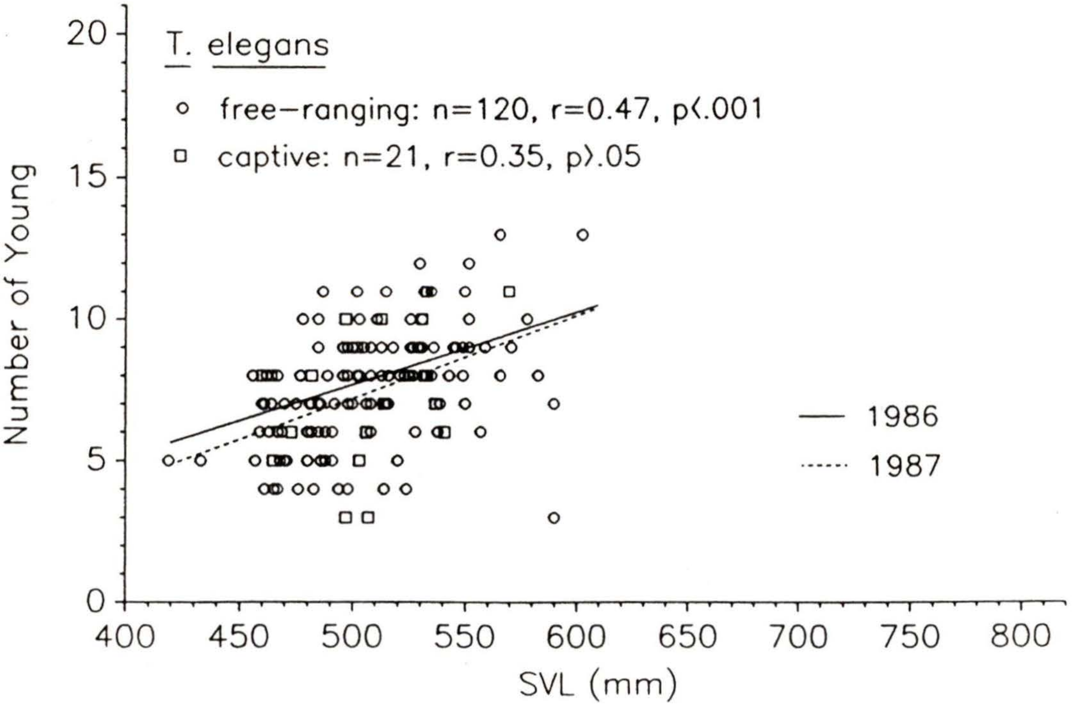
The sex ratio of all captive litters combined was male-biased in each species (37:48 for *T. sirtalis*, 70:84 for *T. elegans*). These ratios did not, however, differ statistically from an expected 1:1 sex ratio (*T. sirtalis*: $X^2_c = 1.18$, df = 1, $p > .05$; *T. elegans*: $X^2_c = 1.10$, df = 1, $p > .05$).

Neonate size

Thamnophis sirtalis and *T. elegans* were born at lengths of approximately 183 and 176 mm SVL, respectively (Table 4). Variation in neonate SVL was significant among litters of both species ($F = 29.3$, df = 11,73, $p < .001$ for *T. sirtalis*; $F = 27.7$, df = 20,136, $p < .001$ for *T. elegans*). One source of this variation may be the SVL of the mother. Mean neonate size in each litter was significantly correlated with the

Figure 14. Relationship between litter size (LS) and SVL of the mother based on palpation of free-ranging females (original captures only), and on litters born to captive females. Regressions for each year are for both groups combined.
For *T. sirtalis*:
$LS = -6.140 + 0.023SVL$ in 1986 ($n = 45$, $r^2 = .28$, $p < .001$),
$LS = -14.536 + 0.040SVL$ in 1987 ($n = 52$, $r^2 = .50$, $p < .001$).
For *T. elegans*:
$LS = -5.059 + 0.025SVL$ in 1986 ($n = 41$, $r^2 = .13$, $p < .05$),
$LS = -7.307 + 0.029SVL$ in 1987 ($n = 100$, $r^2 = .23$, $p < .001$).


T. sirtalis
○ free–ranging: n=85, r=0.55, p<.001
□ captive: n=12, r=0.87, p<.001
Number of Young
0
5
10
15
20
400
450
500
550
600
650
700
750
800
SVL (mm)
— 1986
----- 1987


T. elegans
○ free–ranging: n=120, r=0.47, p<.001
□ captive: n=21, r=0.35, p>.05
Number of Young
0
5
10
15
20
400
450
500
550
600
650
700
750
800
SVL (mm)
— 1986
----- 1987

mother's SVL in *T. elegans* ($r = 0.56$, $n = 21$, $p < .01$) but not *T. sirtalis* ($r = 0.54$, $n = 12$, $p > .05$). As with SVL, there was significant variation in neonate mass among litters (*T. sirtalis*: $F = 9.2$, $df = 11,71$, $p < .001$; *T. elegans*: $F = 62.4$, $df = 20,136$, $p < .001$). Longer females tended to produce heavier young, the correlation being significant for *T. elegans* ($r = 0.45$, $n = 21$, $p < .05$) but not *T. sirtalis* ($r = 0.40$, $n = 12$, $p > .05$).

Although female and male neonates of neither species differed significantly in body mass (Table 5), differences in body size and head size were apparent. In both species, SVL and body length of males was greater than females, although the difference was nonsignificant in *T. sirtalis* (Table 5). In contrast, female neonates of both species tended to have longer heads than males, particularly when body length was adjusted by analysis of covariance (Table 5, Fig. 15). Female *T. sirtalis*, but not *T. elegans*, also had relatively wider heads than males (Table 5, Fig. 15). In neither species did the slope of the relationship between body size and head size differ between the sexes.

Reproductive effort

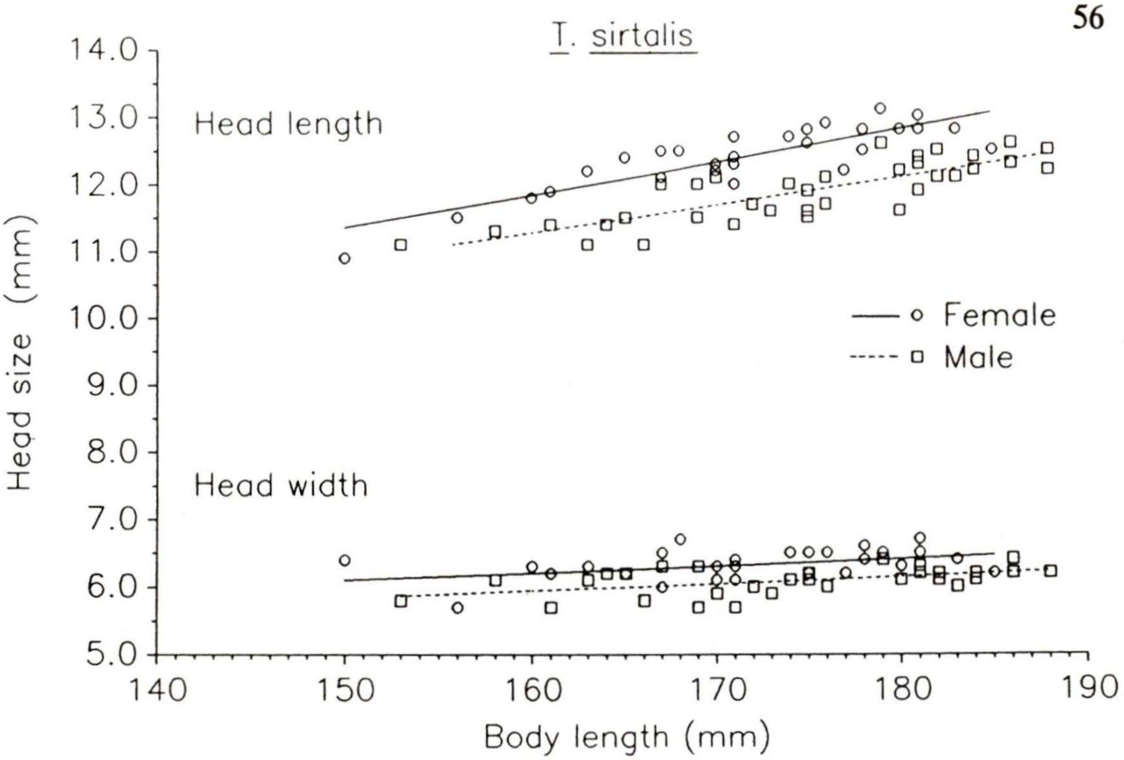
In both *T. sirtalis* and *T. elegans*, longer females produced litters having greater total mass than smaller females (*T. sirtalis*: $r = 0.89$, $n = 12$, $p < .001$; *T. elegans*: $r = 0.65$. $n = 21$, $p < .01$). In contrast, *relative* reproductive effort (RCM2) was not significantly correlated with female SVL in either species (*T. sirtalis*: $r = 0.26$, $n = 12$, $p > .05$; *T. elegans*: $r = 0.01$, $n = 21$, $p > .05$). Following the example of Ford and Killebrew (1983), I also calculated the relative reproductive effort per progeny (RCM2/litter size) for each female. This value was negatively correlated with female SVL in both species (*T. sirtalis*: $r = 0.86$, $n = 12$, $p < .001$; *T. elegans*: $r = 0.44$, $n = 21$, $p < .05$). Therefore, longer females invested relatively less energy in each offspring.

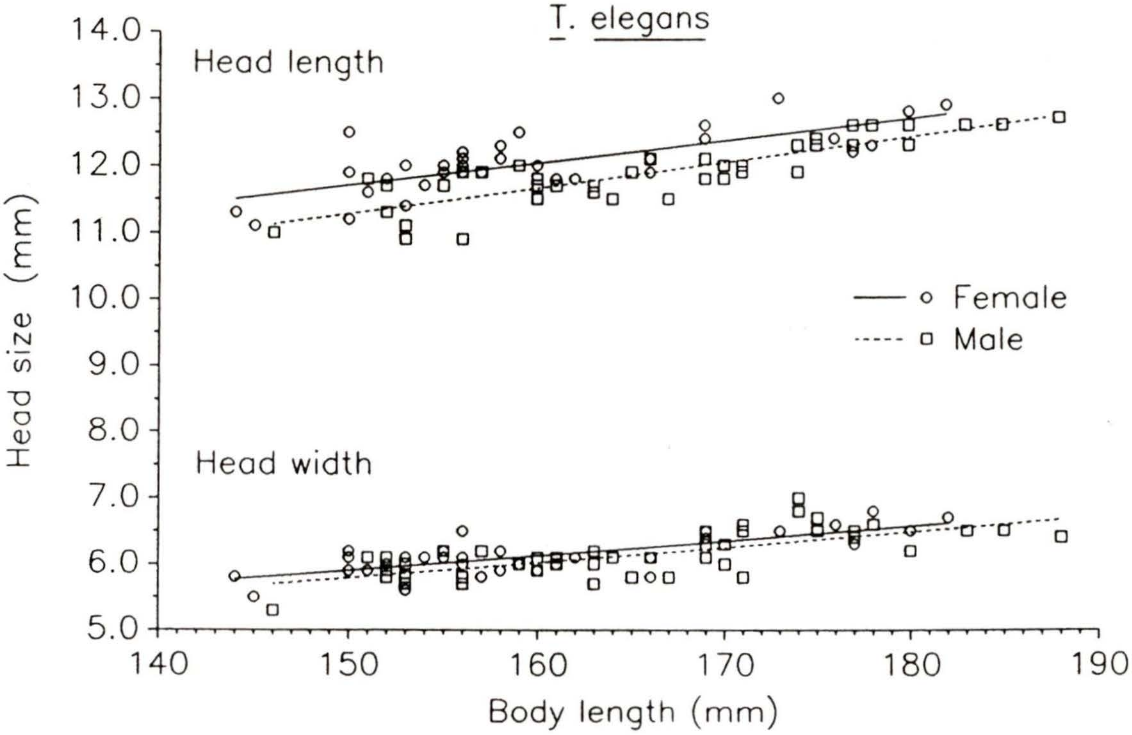
Table 5. Comparison of female and male neonates: body size and head size. For body size (SVL, body length, and mass), independent sample *t*-tests were used to compare sexes. For head size (width and length), differences between means were adjusted for differences in body length using analysis of covariance, and *t*-tests were performed on adjusted means. No significant between-sex differences in the relationship between body length and head size were found in either species.

	T. sirtalis		*T. elegans*	
	n	$\bar{X}$±SD	n	$\bar{X}$±SD
SVL (mm)				
female	37	181.0±12.1	70	174.0±10.5
male	48	184.5±11.7	84	178.2±10.2*
Body length (mm)				
female	29	171.4±8.3	34	160.2±10.1
male	35	174.7±8.9	46	165.6±10.3*
Mass (g)				
female	37	2.56±0.38	70	2.64±0.57
male	48	2.63±0.39	84	2.74±0.60
Head width (mm)				
female	29	6.32±0.22	34	6.13±0.30
male	35	6.09±0.19*	46	6.15±0.34
Head length (mm)				
female	29	12.40±0.47	34	12.04±0.45
male	35	11.88±0.45*	46	11.87±0.46*

* significant difference between the sexes ($p<.05$)

Figure 15. Relationship between head size and body length in captive-born garter snakes. For both head width and head length, n = 29 female and 35 male *T. sirtalis*; n = 34 female and 46 male *T. elegans*.


T. sirtalis
Head length
Head width
Head size (mm)
Body length (mm)
Female
Male
14.0
13.0
12.0
11.0
10.0
9.0
8.0
7.0
6.0
5.0
140
150
160
170
180
190


T. elegans
Head length
Head width
Head size (mm)
Body length (mm)
Female
Male
14.0
13.0
12.0
11.0
10.0
9.0
8.0
7.0
6.0
5.0
140
150
160
170
180
190

Reproductive frequency

The frequency with which individual females reproduced once they reached maturity is largely unknown, because too few females were captured in both 1986 and 1987 during periods in which their reproductive status could be assessed. Despite the large number of females captured in 1986, few were recaptured in 1987. However, the reproductive status of four mature female *T. sirtalis* is known for both years: two were gravid in both years, and two were non-gravid in both years. A fifth female was immature in 1986 (375 mm SVL) and probably mature in 1987 (460 mm SVL), but did not reproduce in 1987. A single mature female *T. elegans* whose reproductive status could be assessed in both years was gravid in 1986 but not in 1987.

Overwintering

Suitable overwintering sites for both *T. sirtalis* and *T. elegans* appeared to be abundant, but were associated with particular topographic features. All the 211 snakes captured in March 1987 were on or adjacent to the hillsides at the west edge of the valley from Leach Lake to Corn Creek Marsh (Fig. 1). I also searched for snakes on the valley floor at this time, but found none. Capture locations were widely but patchily distributed, and I found snakes singly or in groups ranging in size from two to 42 individuals. The areas that appeared to be used as overwintering sites included rocky talus slopes, fractured bedrock, and a roadbed (Summit Creek Road) along the west side of Corn Creek Marsh. Many snakes observed in early spring were covered in dried mud, suggesting that conditions within some hibernacula were moist.

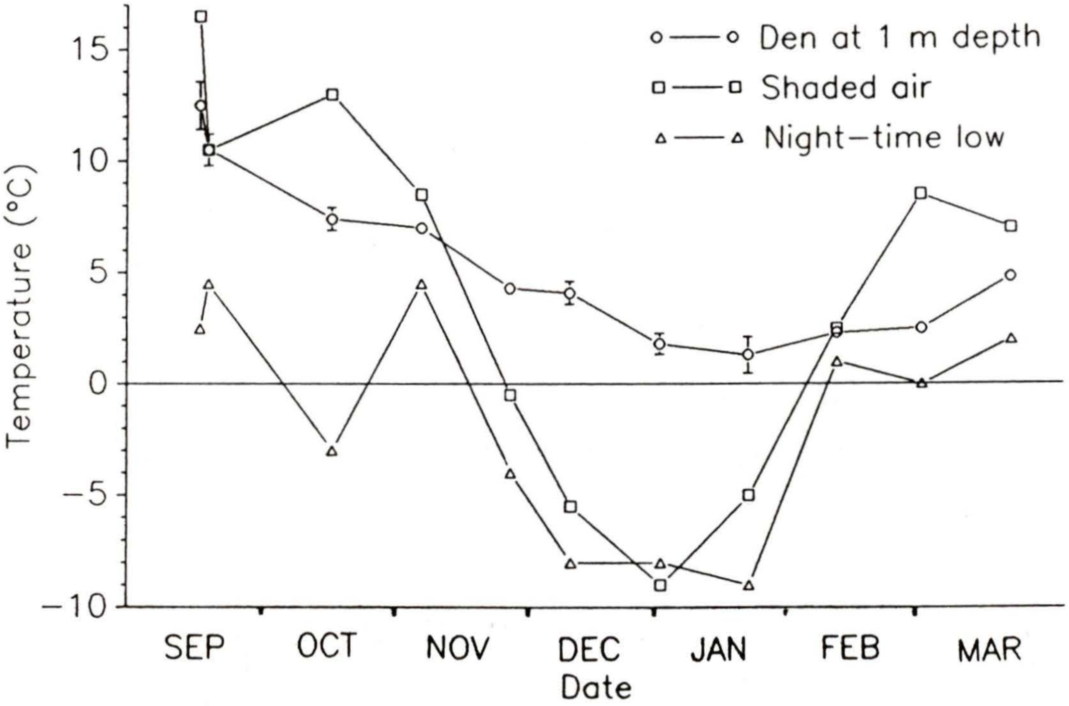
I found one discrete communal den in a large talus slope 300 m west of the valley floor, and 100 m higher in elevation. I captured 89 *T. elegans* (8 females, 81 males) ranging in size from 355 to 510 mm SVL at this location between 30 March and 22 April 1987. *Thamnophis sirtalis* were never observed at the den *per se*, but they were captured in other areas less than 100 m away. Less discrete communal overwintering occurred at Summit Creek Road, with approximately 100 individuals of each species captured along a 50 m stretch of road in the spring of 1987. I observed courtship activity at each of these locations (and others), and males greatly outnumbered females during this time (Table 1).

In the late summer and fall of 1987, I frequently observed both *T. sirtalis* and *T. elegans* basking on the rocks I had piled on the three artificial hibernacula. Neonate *T. elegans*, which were abundant in the surrounding area, were observed most frequently.

The temperatures at the bottom of the three artificial hibernacula constructed in 1987 steadily declined in the fall and winter, then rose in spring (Fig. 16). Within a given day, temperatures in the three dens varied by no more than 2.5° C, and the lowest recorded den temperature was 0.8° C (24 January). Standing water at the bottom of the dens was first detected in late January, and water levels in all dens increased to almost surface level by spring.

Upon excavation of the three dens on 18-19 February, one snake (*T. sirtalis* male, 285 mm SVL) was found in the fenced den, 80 cm below the surface. Its cloacal temperature (3.7° C, measured with a Schultheis quick-reading thermometer) was higher than the temperature at the bottom of the den (2.5° C), and higher than air temperature at the surface (1.5° C). None of the other 10 snakes placed in this den were found, and no snakes were found in either of the two unfenced dens.

Figure 16. Temperatures of artificial hibernacula during the winter of 1987-1988. Den temperatures are means ± 1 standard deviation (SD) for the three hibernacula (two in March because the PVC pipe in one was not replaced after excavation on 19 February). Shaded air temperature at 1.5 m above the surface was measured concurrently with den temperatures, and night-time low is the minimum air temperature recorded at the Environment Canada weather station at Creston.


Den at 1 m depth
Shaded air
Night–time low
Temperature (°C)
15
10
5
0
–5
–10
SEP
OCT
NOV
DEC
JAN
FEB
MAR
Date

Movements

General

I obtained 584 measurements of distance between captures of individuals at Leach Lake during both years combined, with some snakes appearing more than once in this total. No movement was recorded in 128 of these records, and the interval between successive captures of an individual ranged from one day to 16 months.

The overall mean distances (± 1 SD) between captures of female and male *T. sirtalis* were 98±177 m (n=53) and 114±183 m (n=89), respectively. Mean distances between captures of female and male *T. elegans* were 146±183 m (n=175) and 153±360 m (n=267), respectively. The maximum recorded distances moved by *T. sirtalis* were 950 m (female, 465 mm SVL), and 1000 m (male, 505 mm SVL). Both of these movements are based on recaptures in different years, and spanned the periods of July to June and October to June, respectively. The maximum distances moved by *T. elegans* were considerably greater: 2400 m (female, 480 mm SVL), and 2750 m (male, 415 mm SVL). Both of these latter movements occurred within one active season. The rate at which individuals moved varied considerably; maxima were 137 m in one day for *T. sirtalis* (male, 400 mm SVL) and 2100 m in seven days for *T. elegans* (female, 355 mm SVL). Both of these movements occurred in early June.

Seasonal and individual variation in movements

A scatter plot of distance between captures *vs*. time interval between captures (over a maximum interval of 30 days) suggested no correlation between the two variables. I therefore examined seasonal and individual variation in movements based on the distance between captures within a 30-day period.

Movements of many garter snakes within a 30 day period in early spring were apparently short, and I often recaptured the same individuals around overwintering areas more than once during this time. Starting in late April and early May, I captured snakes in these areas less frequently, and instead captured them increasingly often on the valley floor. Somewhat longer movements (500 m to 2000 m) in a south-eastward direction were recorded for a few individuals (Figs. 17, 18). Each of these records corresponded to movements away from overwintering areas towards the valley floor. No directionality was evident during the summer months, and most movements within a 30 day period were less than 100 m (Figs. 17, 18). In the fall, individuals (primarily adult males) were once again common around overwintering areas, and less common on the valley floor. During September of both years, I observed four individuals on the hillsides that may have been "migrating". All were facing uphill (west), and were moving in the open.

Differences in the movements within a 30-day period made by individuals of each sex and reproductive status are shown in Fig. 19 (*T. sirtalis*) and Fig. 20 (*T. elegans*). Mature males showed the only consistent trend towards long-distance movements (in late spring and early summer), moving in excess of 2 km within 30 days in the case of *T. elegans*. Mature females may undergo similar movements, but few records for this group were obtained. Gravid females and immature males and females appeared to be relatively sedentary, but data are sparse, except for neonate *T. elegans*. Following parturition in August, neonates of this species were frequently recaptured; rarely had they moved more than 50 m (Fig. 20).

Gravid females formed aggregations of a few to over 20 individuals, especially during the latter part of gestation (July and early August). The highest density was recorded on 19 July 1987, when I captured 22 gravid females

Figure 17. Seasonal pattern of movement of *T. sirtalis* based on successive captures of individuals at intervals of 1-30 days. For each of the five time periods illustrated, the first capture of each individual is standardized to a single common point, represented by a filled circle. The second capture of each individual is represented by an open circle; half-filled circles represent overlapping second captures of two individuals.

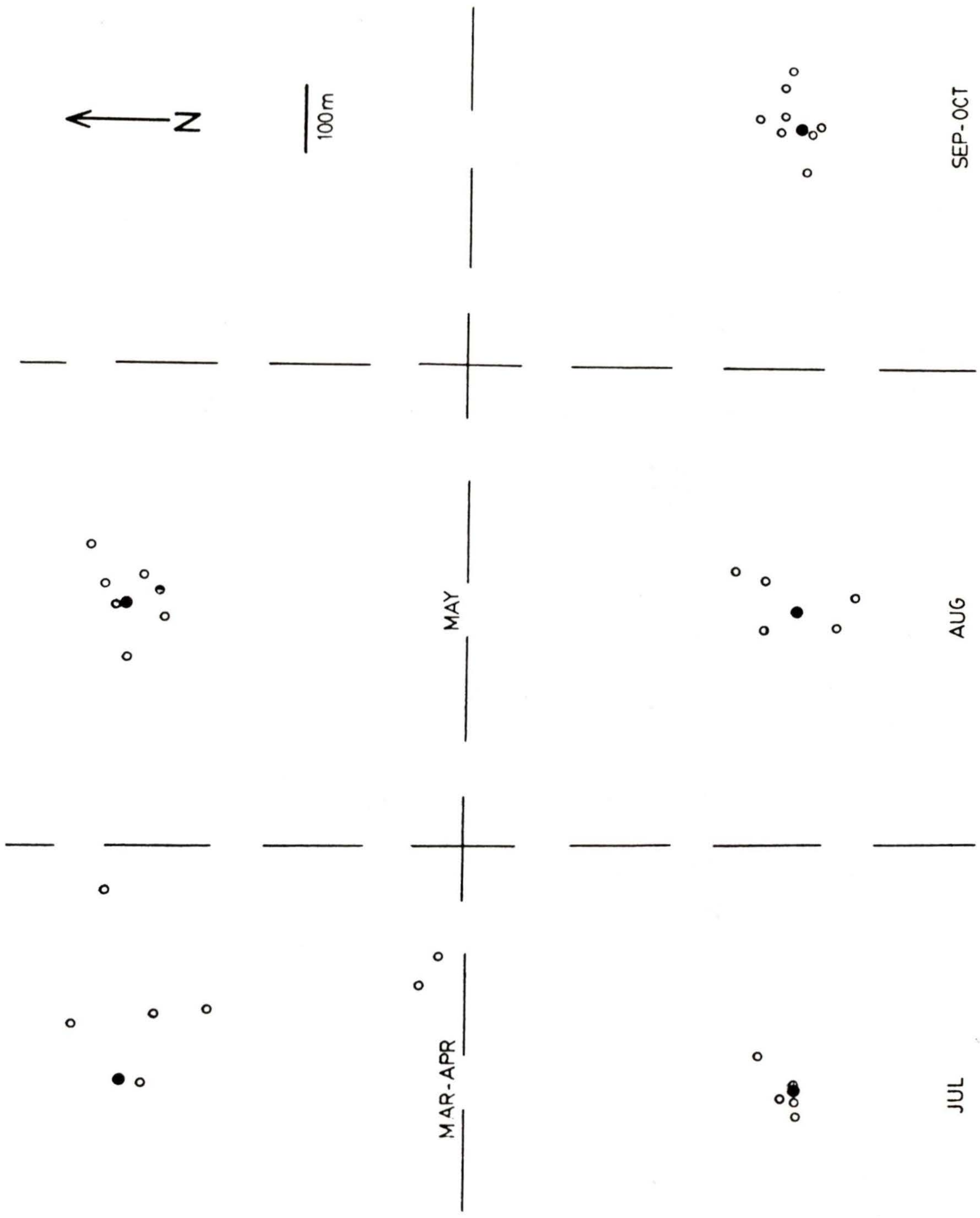

N
100 m
SEP-OCT
MAY
AUG
MAR-APR
JUL

Figure 18. Seasonal pattern of movement of *T. elegans* based on successive captures of individuals at intervals of 1-30 days. For each of the six time periods illustrated, the first capture of each individual is standardized to a single common point, represented by a filled circle. The second capture of each individual is represented by an open circle; half-filled circles represent overlapping second captures of two individuals.

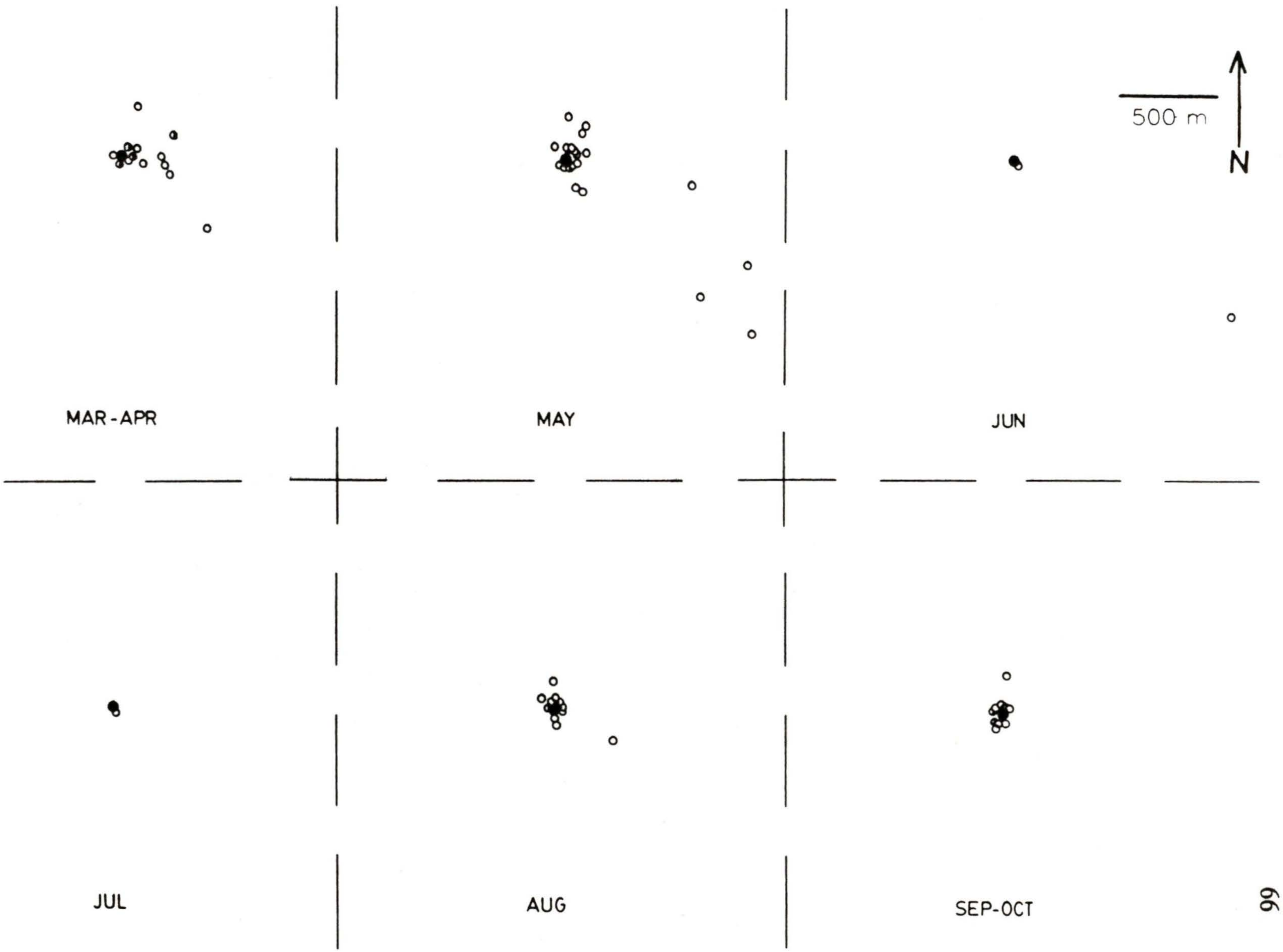

500 m
N
MAR-APR
MAY
JUN
JUL
AUG
SEP-OCT

Figure 19. Movements of *T. sirtalis* of each sex and reproductive status. Data are from successive captures of individuals at intervals of 1-30 days; distance moved is plotted against the mean of the first and second capture dates of each individual.

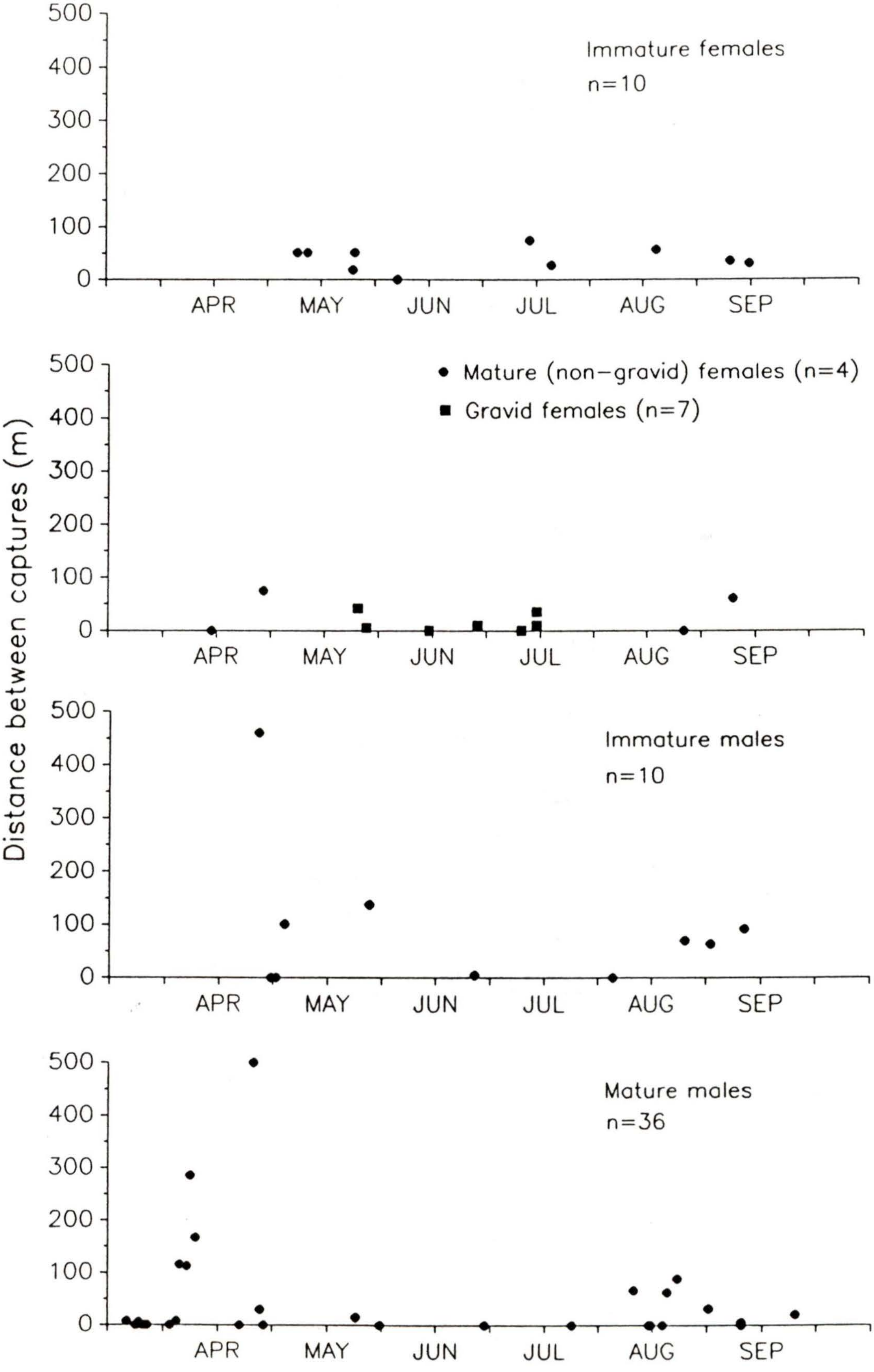
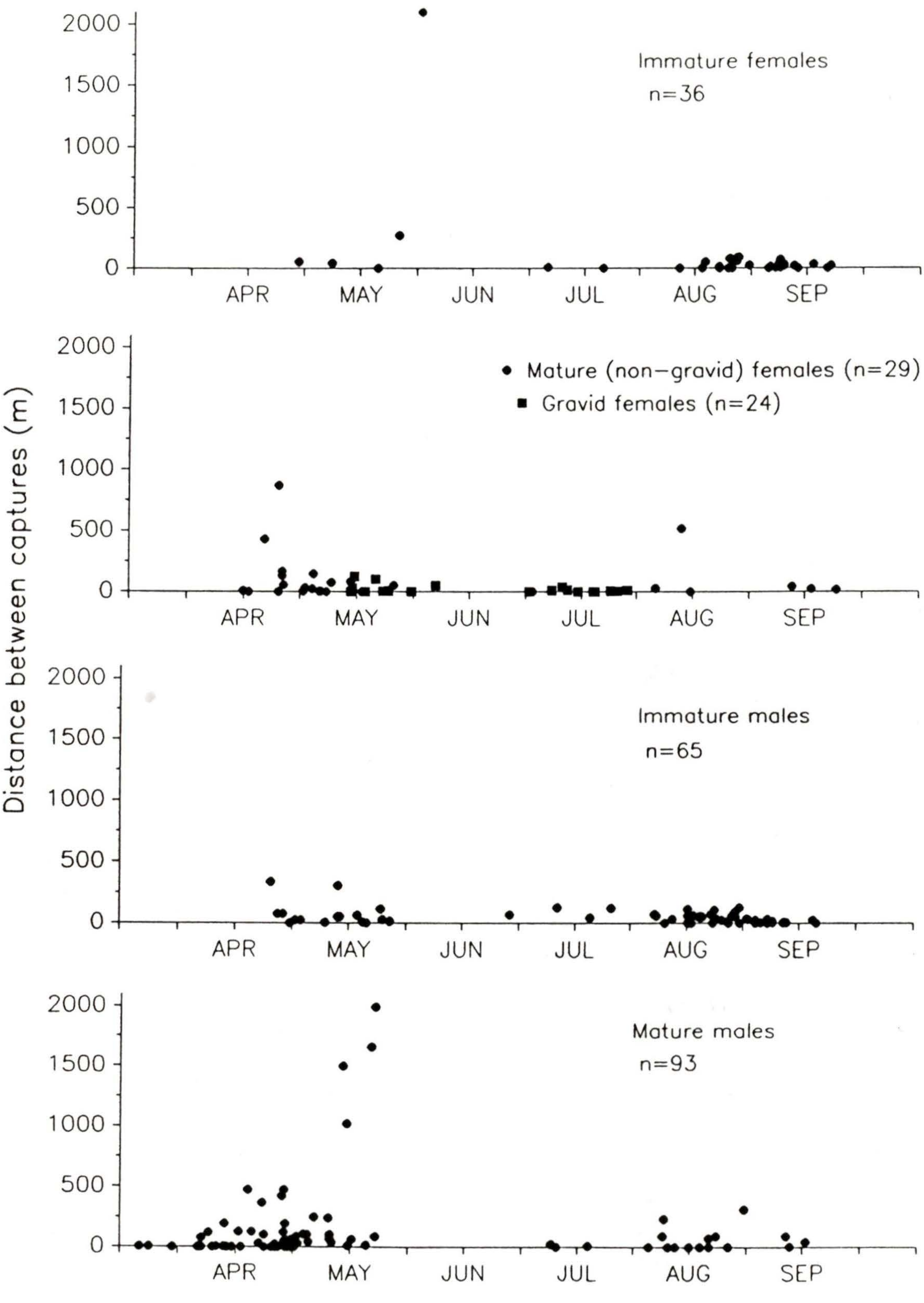

Distance between captures (m)
0
100
200
300
400
500
APR
MAY
JUN
JUL
AUG
SEP
Immature females
n=10
● Mature (non-gravid) females (n=4)
■ Gravid females (n=7)
Immature males
n=10
Mature males
n=36

Figure 20. Movements of *T. elegans* of each sex and reproductive status. Data are from successive captures of individuals at intervals of 1-30 days; distance moved is plotted against the mean of the first and second capture dates of each individual.


Distance between captures (m)
2000
1500
1000
500
0
APR
MAY
JUN
JUL
AUG
SEP
Immature females
n=36
Mature (non-gravid) females (n=29)
Gravid females (n=24)
Immature males
n=65
Mature males
n=93

(11 *T. sirtalis*, 11 *T. elegans*) along a 50 m stretch of Summit Creek Road. I captured several individual females repeatedly over periods of up to two months in this area and at other locations west of Leach Lake. All but two of the sites used by gravid females were near known overwintering areas. The exceptions were two sites used by small groups of gravid *T. sirtalis*; one occurred on a roadbed south of Leach Lake, and the other was near the shore of Old Channel (Fig. 1). I did not visit either of these locations in spring, and it is not known if they were also used as overwintering sites.

Home range size

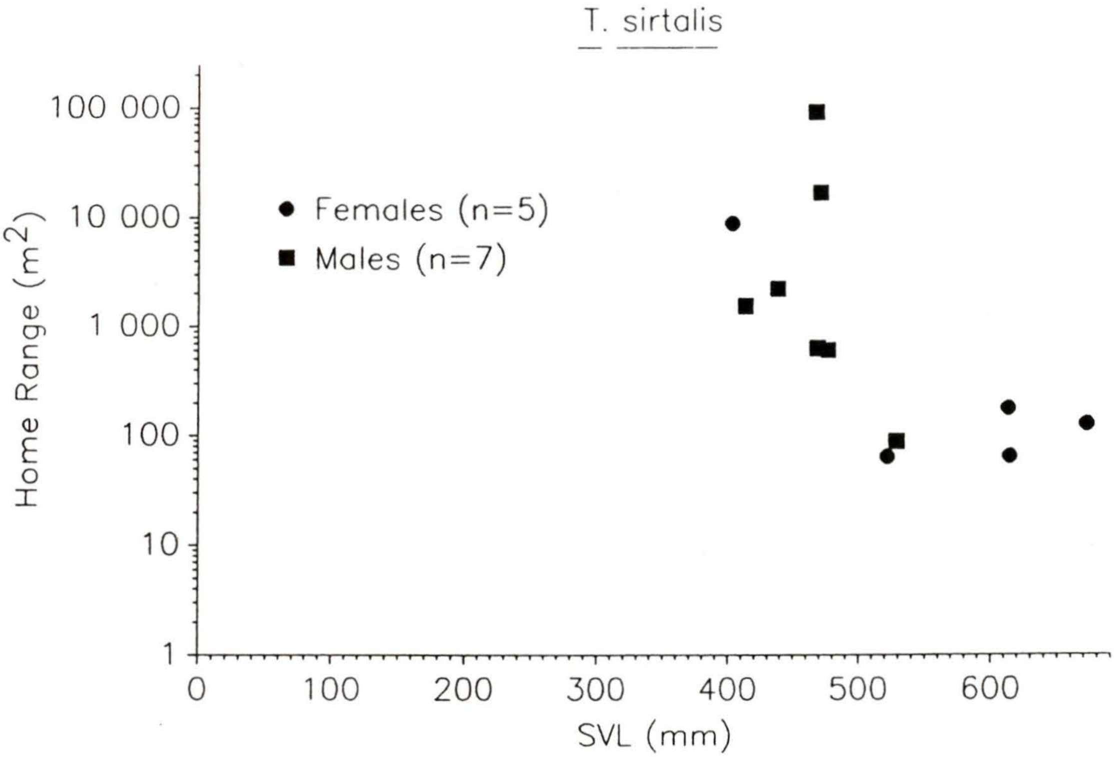
I captured a total of 96 snakes four or more times each during 1986-1987. Calculations of home range size required that each individual move at least twice; this condition was satisfied for 59 snakes. As shown in Fig. 21, variation in home range size was great, especially among larger individuals. Male *T. sirtalis* tended to have larger home ranges than females, although the difference between sexes was not significant in either *T. sirtalis* ($t = 0.93$; df = 10, $p > .05$) or *T. elegans* ($t = 0.53$, df = 45, $p > .05$). The home ranges of small *T. elegans* appeared to be relatively limited (Fig. 21). The three mature female *T. elegans* with the smallest home ranges (all captures within a year) were all gravid at each capture, corresponding with the observations of aggregation behaviour in gravid females described above.

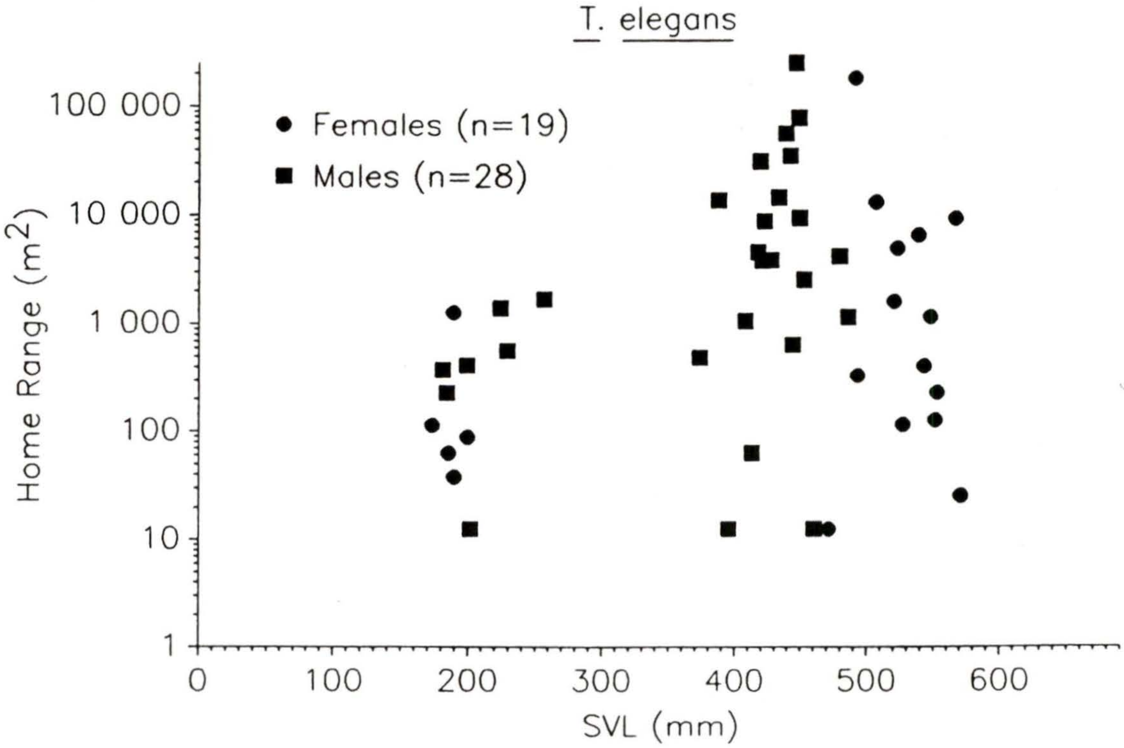
Feeding

Frequency

Most snakes captured during this study did not contain food in their stomachs. The percentage of snakes (first captures plus subsequent recaptures at least seven days apart) that contained food was 15.8% (200/1269) for *T. sirtalis*, and 26.7% (685/2492) for *T. elegans*.

Figure 21. Relationship between home range size and SVL for *T. sirtalis* and *T. elegans*. Only snakes captured at least three times in different locations on different days were used to calculate home range size, using the Minimum Convex Polygon method (Jennrich and Turner 1969).


T. sirtalis
● Females (n=5)
■ Males (n=7)
Home Range (m^2)
100 000
10 000
1 000
100
10
1
0
100
200
300
400
500
600
SVL (mm)

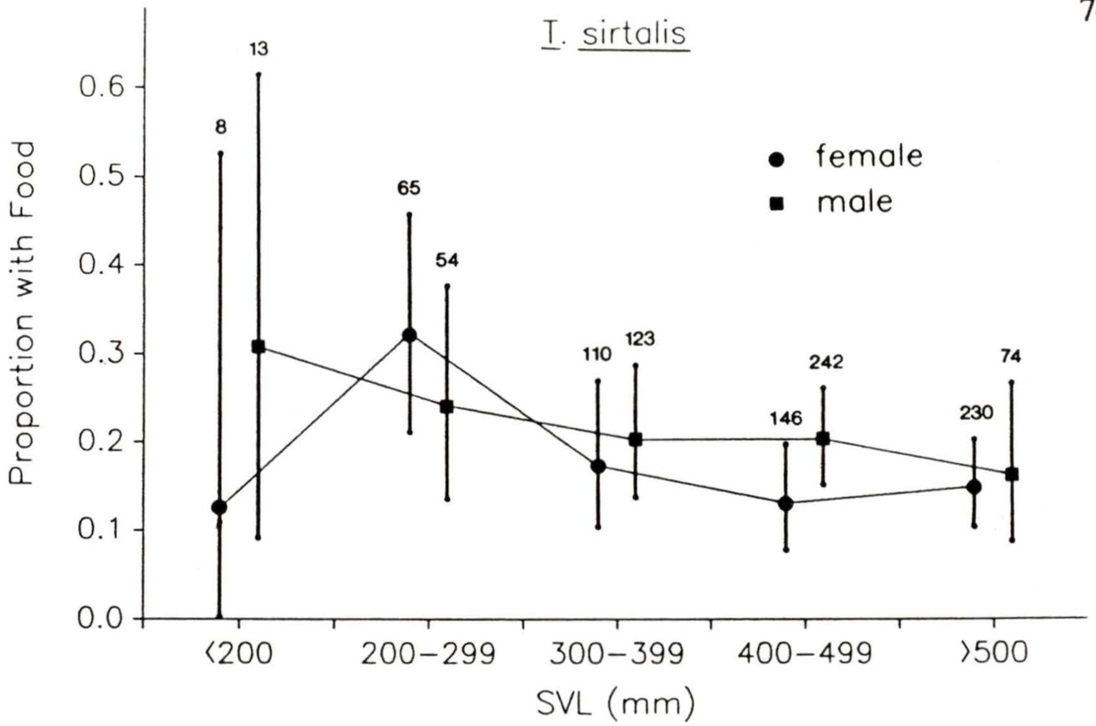

T. elegans
● Females (n=19)
■ Males (n=28)
Home Range (m^2)
100 000
10 000
1 000
100
10
1
0
100
200
300
400
500
600
SVL (mm)

Stage of ecdysis appeared to affect feeding frequency. Several days prior to ecdysis, the eyes of snakes became cloudy; this condition disappeared a few days prior to ecdysis, at which time the skin became loose and easily peeled. Of snakes captured with cloudy eyes, only 9% (11/122, *T. sirtalis*) and 15% (38/255, *T. elegans*) contained food. Only 6% (3/47) of *T. sirtalis*, and 6% (8/141) of *T. elegans* with loose skin contained food. Snakes that had recently shed (lustrous, clean-looking skin), contained food somewhat more frequently: 16% (47/286) for *T. sirtalis*, and 34% (188/559) for *T. elegans*.

In addition to ecdysis, body size and time of year were associated with variation in feeding frequency. The overall proportion of snakes containing food was higher in small snakes than large ones (Fig. 22), but the trend was clear only for *T. elegans*. The proportion of small *T. elegans* (< 300 mm) with food was particularly high, around 0.50 in both females and males. In different months, the proportion of *T. sirtalis* with food ranged from 0.00 to 0.40 (Fig. 23). Gravid females fed only during the first half of gestation (May-June), mature males fed little from July onward, and immature individuals showed little seasonal variation. In *T. elegans*, the proportion of snakes with food in different months varied from 0.00 to 0.55 (Fig. 24). Non-gravid females and mature males exhibited a fairly distinct peak in feeding in mid-summer; the latter group fed little from August onward. Immature *T. elegans* frequently contained food from May through to September, with the exception of July, a month of somewhat decreased feeding activity. Gravid female *T. elegans* fed very little, and, as with *T. sirtalis*, only during the early stages of gestation.

I observed actual feeding by snakes twice during this study, both times in late summer. I encountered a female *T. elegans* (465 mm SVL) while it was swallowing an adult vole (*Microtus pennsylvanicus*, 21 mm wide, 29 g). Almost half of the vole

Figure 22. Proportion of garter snakes captured from April to October that contained food in their stomachs. Vertical bars are 95% confidence intervals for a binomial distribution, and the numbers above each bar are sample sizes.


T. sirtalis
Proportion with Food
0.0
0.1
0.2
0.3
0.4
0.5
0.6
● female
■ male
8
13
65
54
110
123
146
242
230
74
<200
200-299
300-399
400-499
>500
SVL (mm)

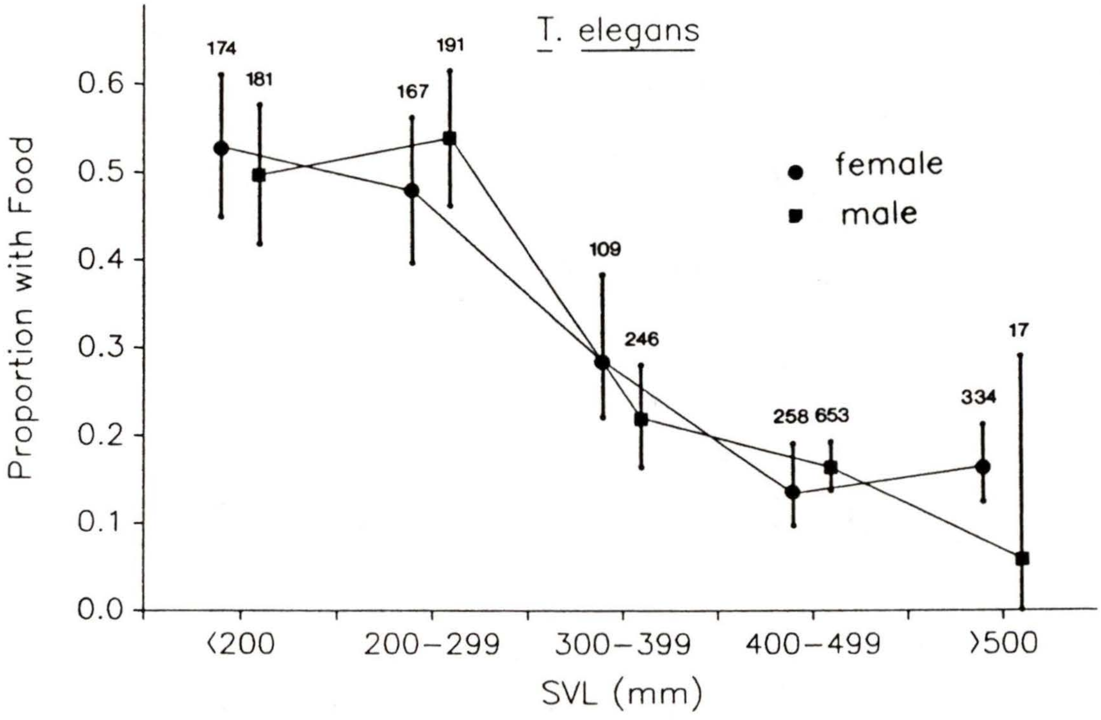

T. elegans
Proportion with Food
0.0
0.1
0.2
0.3
0.4
0.5
0.6
● female
■ male
174
181
167
191
109
246
258
653
334
17
<200
200-299
300-399
400-499
>500
SVL (mm)

Figure 23. Proportion of *T. sirtalis* that contained food in their stomachs compared among months. Immature females are less than 450 mm SVL; immature males are less than 400 mm SVL (see Results: Reproduction). Vertical bars are 95% confidence intervals for binomial distributions, and the numbers above each bar are sample sizes.

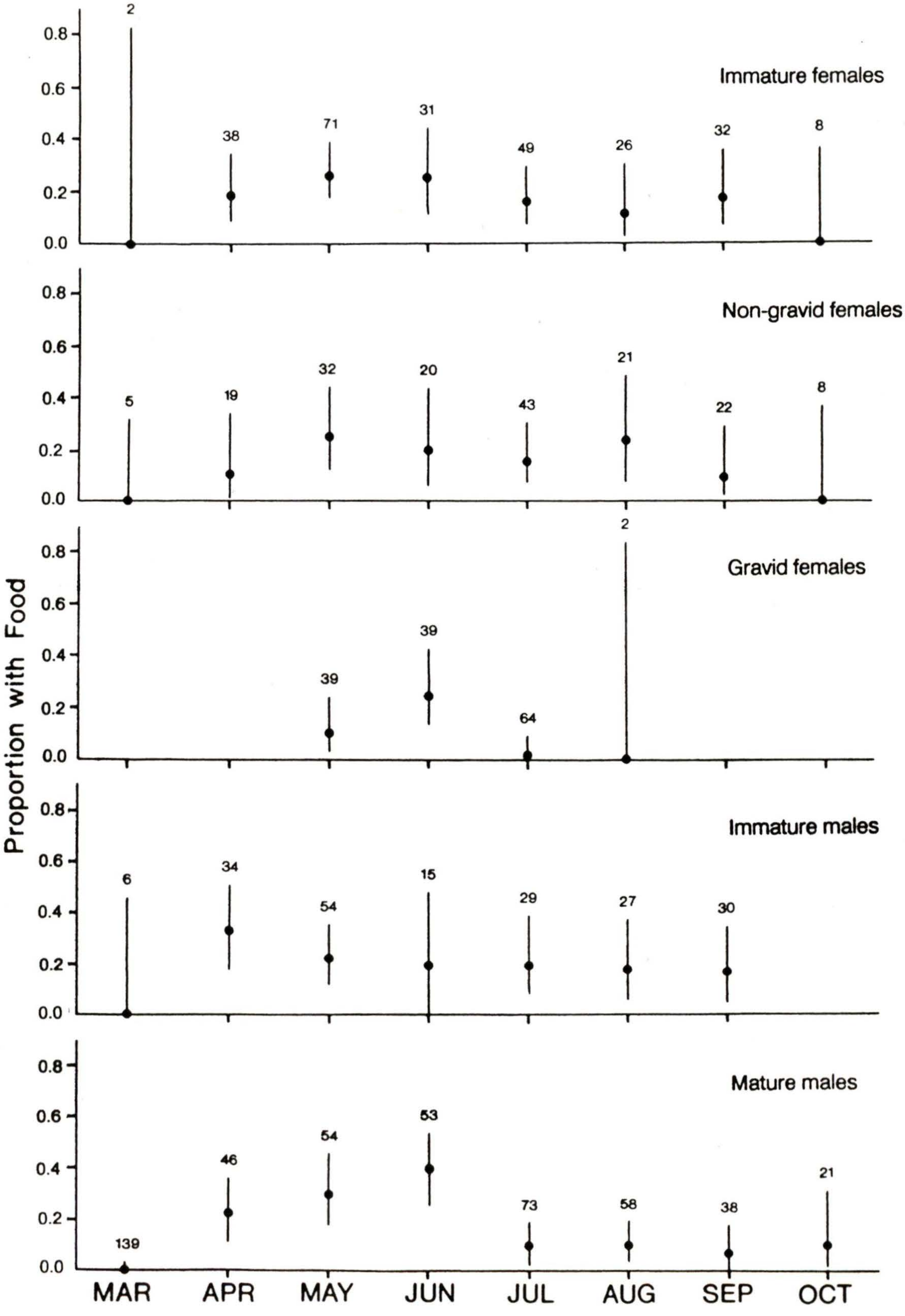
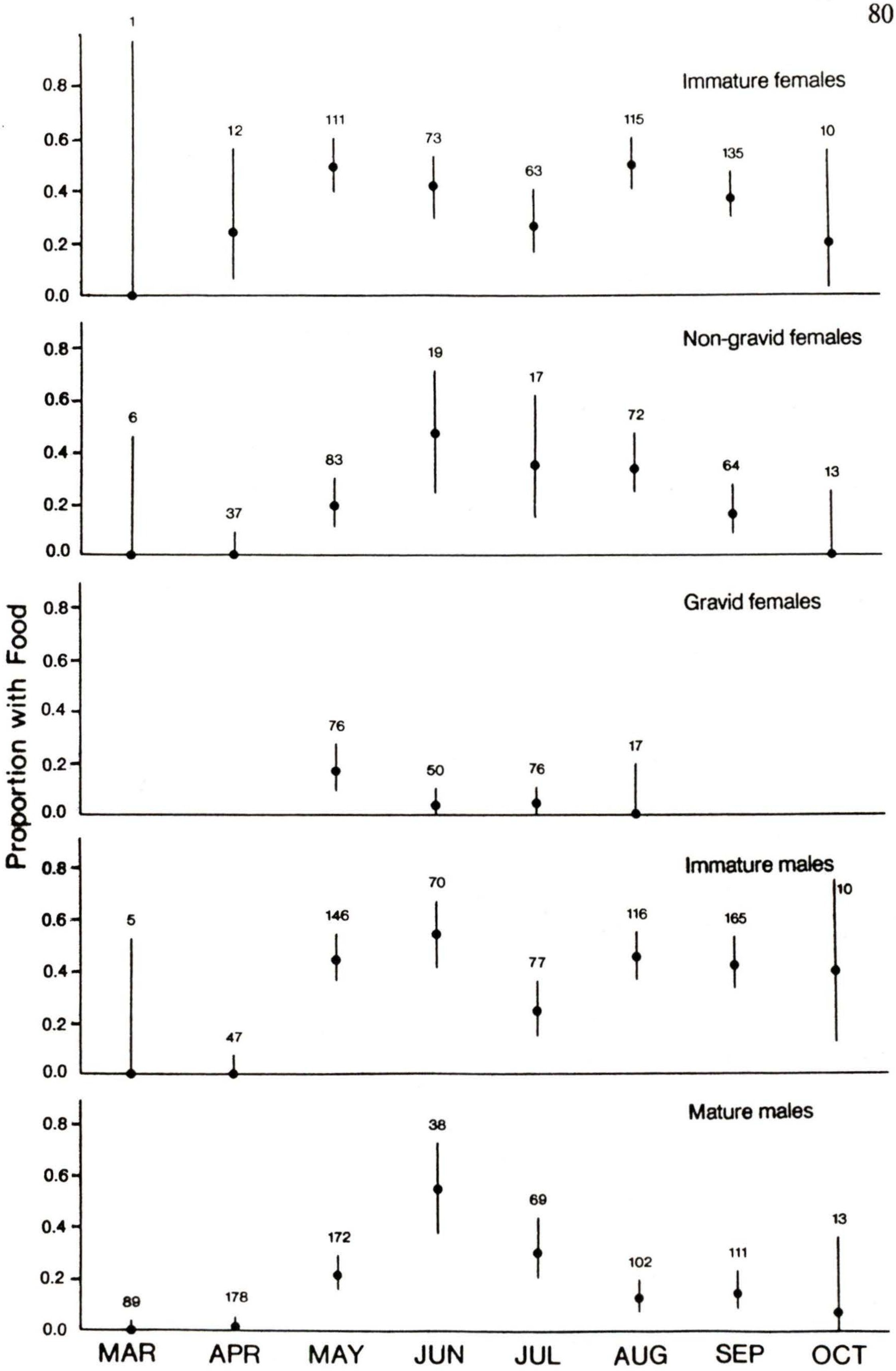

Proportion with Food
Immature females
Non-gravid females
Gravid females
Immature males
Mature males
0.0
0.2
0.4
0.6
0.8
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
2
38
71
31
49
26
32
8
5
19
32
20
43
21
22
8
39
39
64
2
6
34
54
15
29
27
30
139
46
54
53
73
58
38
21

Figure 24. Proportion of *T. elegans* that contained food in their stomachs compared among months. Immature females are less than 450 mm SVL; immature males are less than 400 mm SVL (see Results: Reproduction). Vertical bars are 95% confidence intervals for binomial distributions, and the numbers above each bar are sample sizes.


Proportion with Food
Immature females
1
12
111
73
63
115
135
10
Non-gravid females
6
37
83
19
17
72
64
13
Gravid females
76
50
76
17
Immature males
5
47
146
70
77
116
165
10
Mature males
89
178
172
38
69
102
111
13
0.0
0.2
0.4
0.6
0.8
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT

was inside the snake's mouth when first observed, and the vole was not completely ingested (head first) until 94 minutes later. I also encountered a male *T. elegans* (425 mm SVL), swallowing a nestling vole (12 mm wide, 5.5 g) tail first. This vole was completely swallowed 11 minutes later. In neither case did the snake use its body to restrain its prey.

Food type

A list of the frequency all food types found in snakes is presented in Table 6. Not included in this table are six food items that were not completely swallowed. I captured six *T. sirtalis* with a bullhead (*Ictalurus melas*) or a vole (*M. pennsylvanicus*) lodged in its alimentary tract. The prey was held fast by pectoral spines, in the case of bullheads, or incisors, in the case of voles. In addition, five *T. sirtalis* and three *T. elegans* contained mammals that were probably dead when encountered, as indicated by the presence of Dipteran eggs, larvae or pupae on the mammal.

Three *T. sirtalis* and 15 *T. elegans* contained two prey types each; no snakes contained more than two prey types. Each of the three *T. sirtalis* with two prey types contained worms, and the other prey type was a slug, an amphibian, or a mammal. Similarly, all of the 15 *T. elegans* containing two prey types shared one (slugs), and the other prey type was a mammal (eight cases), a worm, a snail, or an amphibian.

Although each species consumed a variety of different kinds of prey, the diet of each was dominated by a few major prey types (Table 6). Earthworms, mammals, and amphibians together accounted for over 80% of all items eaten by *T. sirtalis*, while *T. elegans* consumed almost exclusively (90%) slugs and mammals. In addition, the proportion of major prey types in the diet changed as snakes became larger (Fig. 25). Small *T. sirtalis* ingested earthworms exclusively; these were

Table 6. Diet of garter snakes at Creston, based on stomach palpations of 200 *T. sirtalis* and 685 *T. elegans* that contained food.

	Number of snakes (%)			
Prey type	*T. sirtalis*		*T. elegans*	
Earthworm	108	(53.2)	9	(1.3)
Leech	8	(3.9)	1	(0.1)
Snail	0	(0.0)	5	(0.7)
Slug	2	(1.0)	488	(69.7)
Fish	[a]2	(1.0)	[a]1	(0.1)
Amphibian	[b]19	(9.4)	[c]1	(0.1)
Reptile	0	(0.0)	[d]3	(0.4)
Bird	[e]1	(0.5)	0	(0.0)
Mammal	[f]39	(19.2)	[f]141	(20.1)
Unidentified	24	(11.8)	51	(7.3)
Total	203	(100.0)	700	(100.0)

[a] Cottidae

[b] *Ambystoma macrodactylum, Bufo boreas, Hyla regilla, Rana pretiosa*

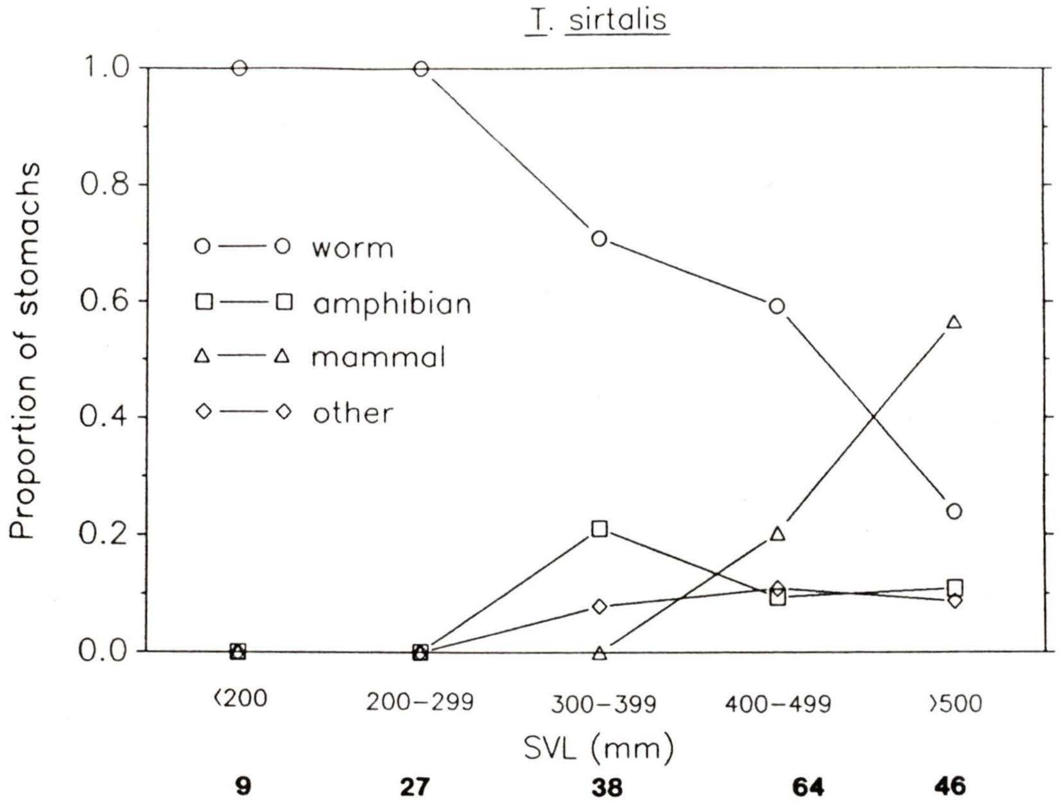
[c] *A. macrodactylum*

[d] *T. sirtalis, Elgaria coerulea*

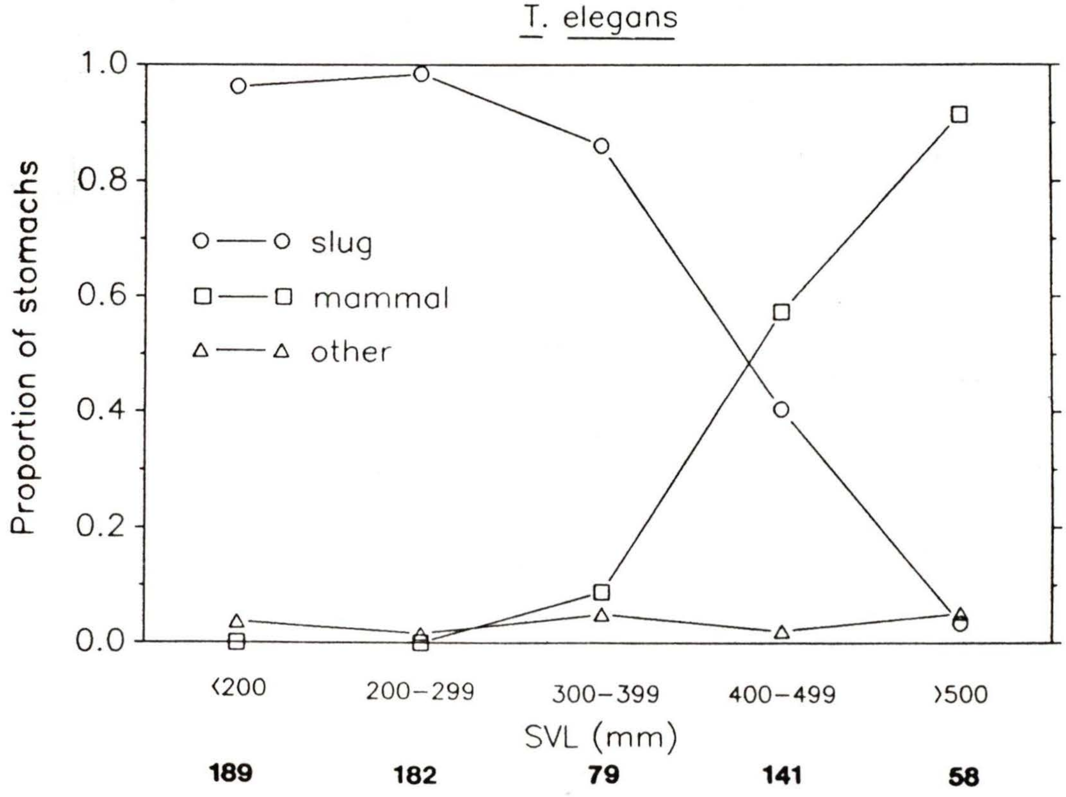
[e] Fringillidae (probably a ground-nesting sparrow)

[f] *Microtus pennsylvanicus, Sorex vagrans* and unidentified

Figure 25. Ontogenetic changes in garter snake diets. Numbers below each size class indicate the total number of snakes in that class that contained food.



T. sirtalis



T. elegans

gradually replaced by mammals as the dominant food type. In *T. elegans* there was a nearly complete shift from slugs to mammals. I also detected sexual differences in diet of large snakes (over 400 mm SVL), with large females containing mammals more often than large males ($X^2_c = 16.8$, $df = 1$, $p < .001$ for *T. sirtalis*; $X^2_c = 21.7$, $df = 1$, $p < .001$ for *T. elegans*). In *T. sirtalis*, 56% (29/52) of large females, and 17% (11/63) of large males that contained food had eaten mammals. The comparable figures for *T. elegans* were 86% (82/95) with mammals for females, and 50% (50/101) with mammals for males. Diet diversity with respect to prey type was low in small snakes, and increased with increasing SVL (Fig. 26). The largest size class of *T. elegans*, however, had a relatively low diet diversity, due primarily to the near exclusion of slugs from the diet.

Stomach contents

I removed the stomach contents from 39 *T. sirtalis* and 125 *T. elegans* in 1987, yielding a total of 81 and 357 measurable prey items, respectively. The number of prey items per individual ranged from 1-12 (*T. sirtalis*) and from 1-35 (*T. elegans*). *T. elegans* exhibited pronounced variation among size classes, with individuals in the middle size range having a mean number of prey items five times greater than the largest size class (Fig. 27).

In both species, the range and maximum size of prey eaten increased as snakes became larger (Figs. 28, 29). In the largest *T. elegans*, the lower limit of prey size changed: Small prey items (slugs and earthworms, respectively) were virtually excluded from the diet (Figs. 28, 29). The largest mammal removed from a stomach was a *Microtus pennsylvanicus*, 21 mm wide, with a mass of 28.8 g. This vole (eaten by a *T. elegans*) was much smaller than the maximum size of *M. pennsylvanicus* in this area: Of 28 voles found dead or captured in traps, several were considerably

Figure 26. Ontogenetic changes in the diversity of the diet of *T. sirtalis* and *T. elegans*. $B_i = (\Sigma N_{ij})^2 / \Sigma N_{ij}^2$, where N_{ij} = the number of items of food type j eaten by snakes in the i^{th} size class.

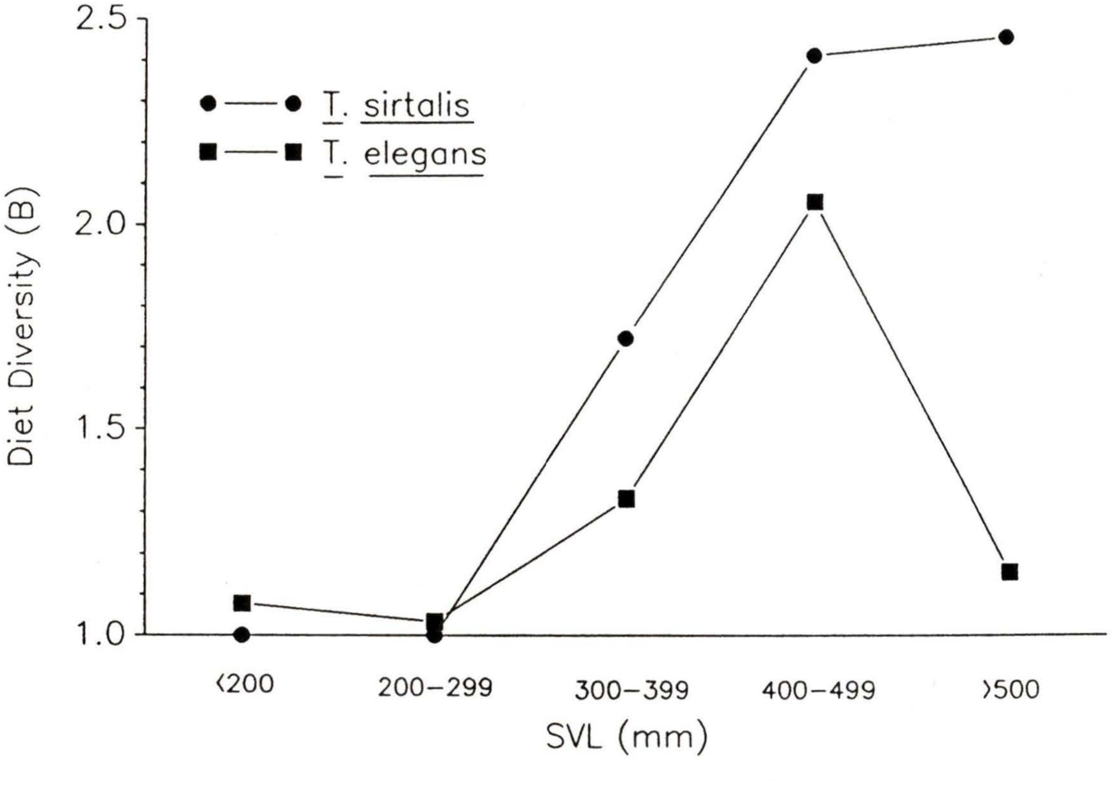
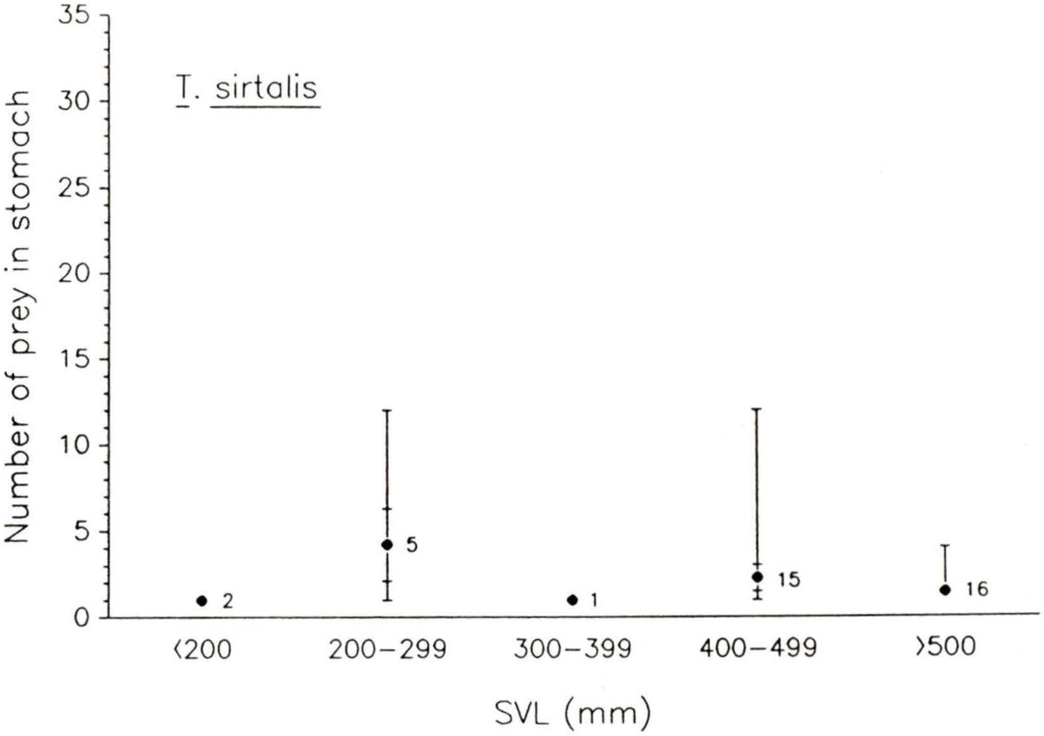

2.5
2.0
1.5
1.0
Diet Diversity (B)
● — ● T. sirtalis
■ — ■ T. elegans
<200
200–299
300–399
400–499
>500
SVL (mm)

Figure 27. Number of prey items removed from the stomachs of *T. sirtalis* and *T. elegans* in different size classes. Only snakes that contained one or more prey items are included. Symbols are means, outer vertical bars are ranges, and inner vertical bars (when visible) are one SD. Numbers beside each point are number of stomachs.


T. sirtalis
Number of prey in stomach
35
30
25
20
15
10
5
0
2
5
1
15
16
<200
200–299
300–399
400–499
>500
SVL (mm)

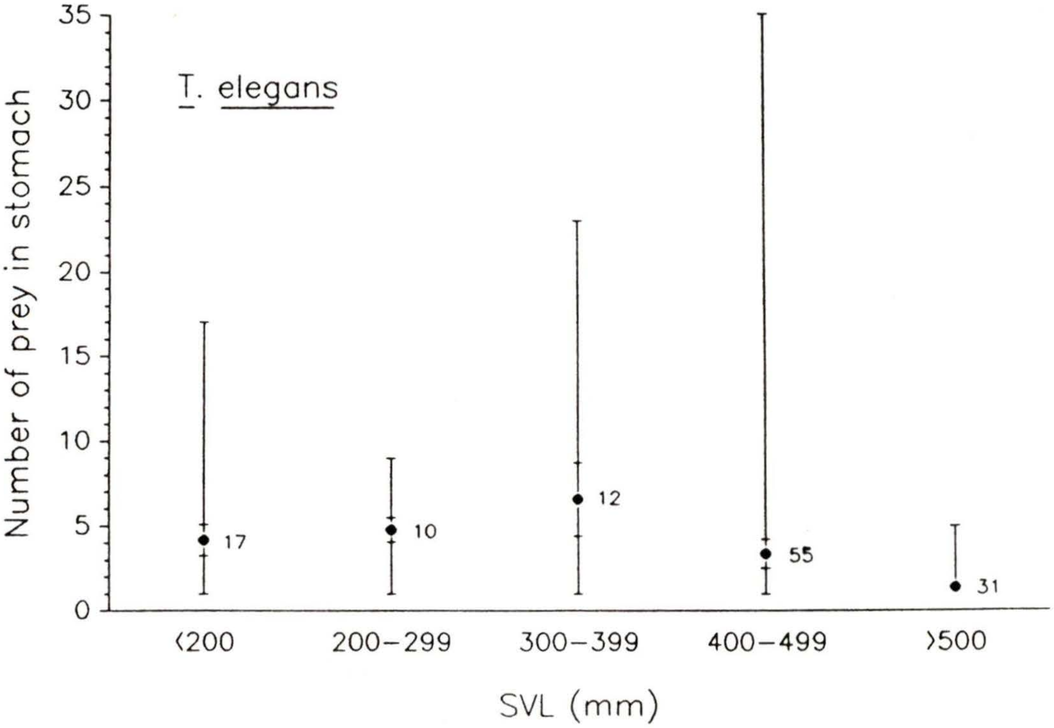

T. elegans
Number of prey in stomach
35
30
25
20
15
10
5
0
17
10
12
55
31
<200
200–299
300–399
400–499
>500
SVL (mm)

Figure 28. Ontogenetic changes in the size of prey eaten by *T. sirtalis*.
Solid = earthworms
Hatched = amphibians
Open = mammals
Dotted = other

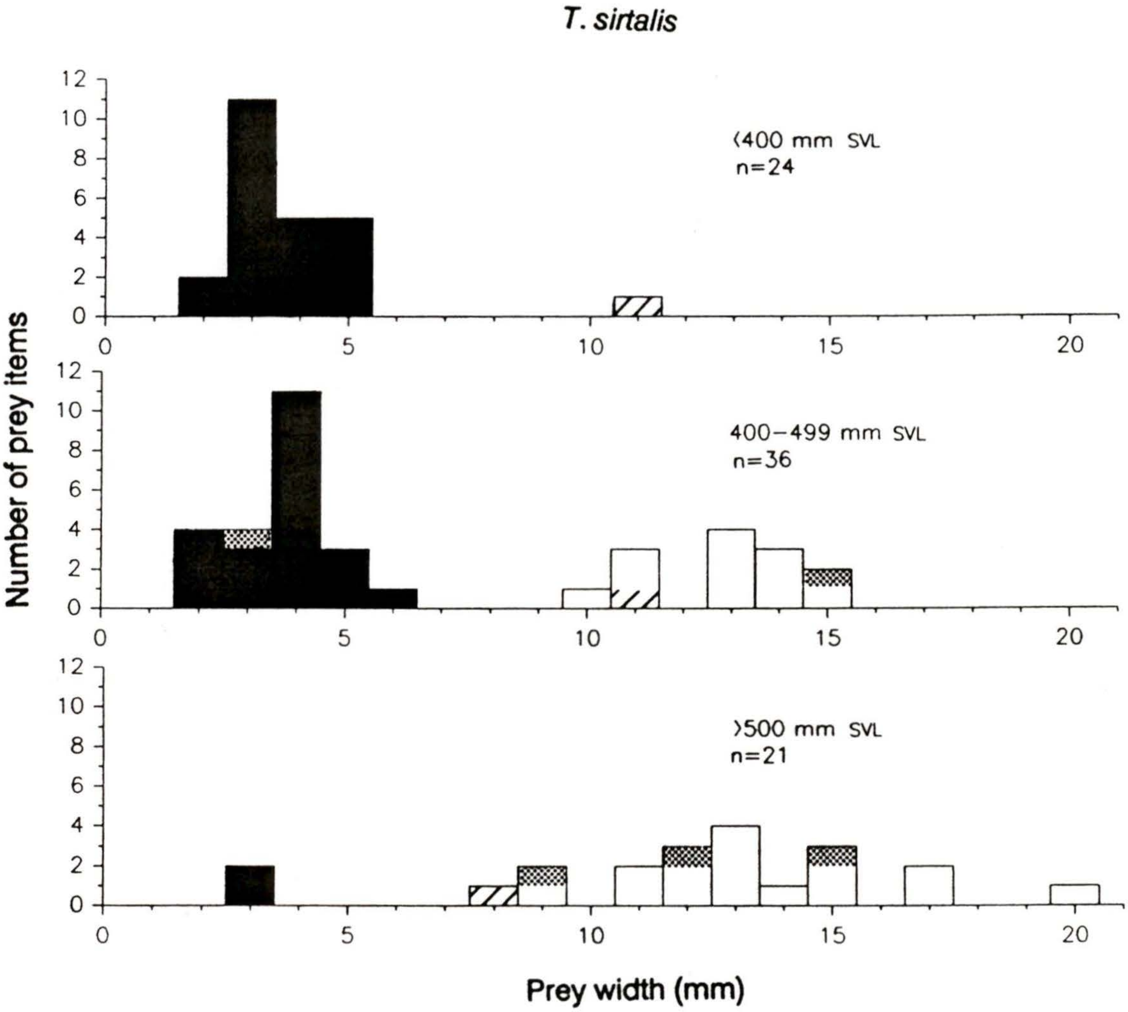
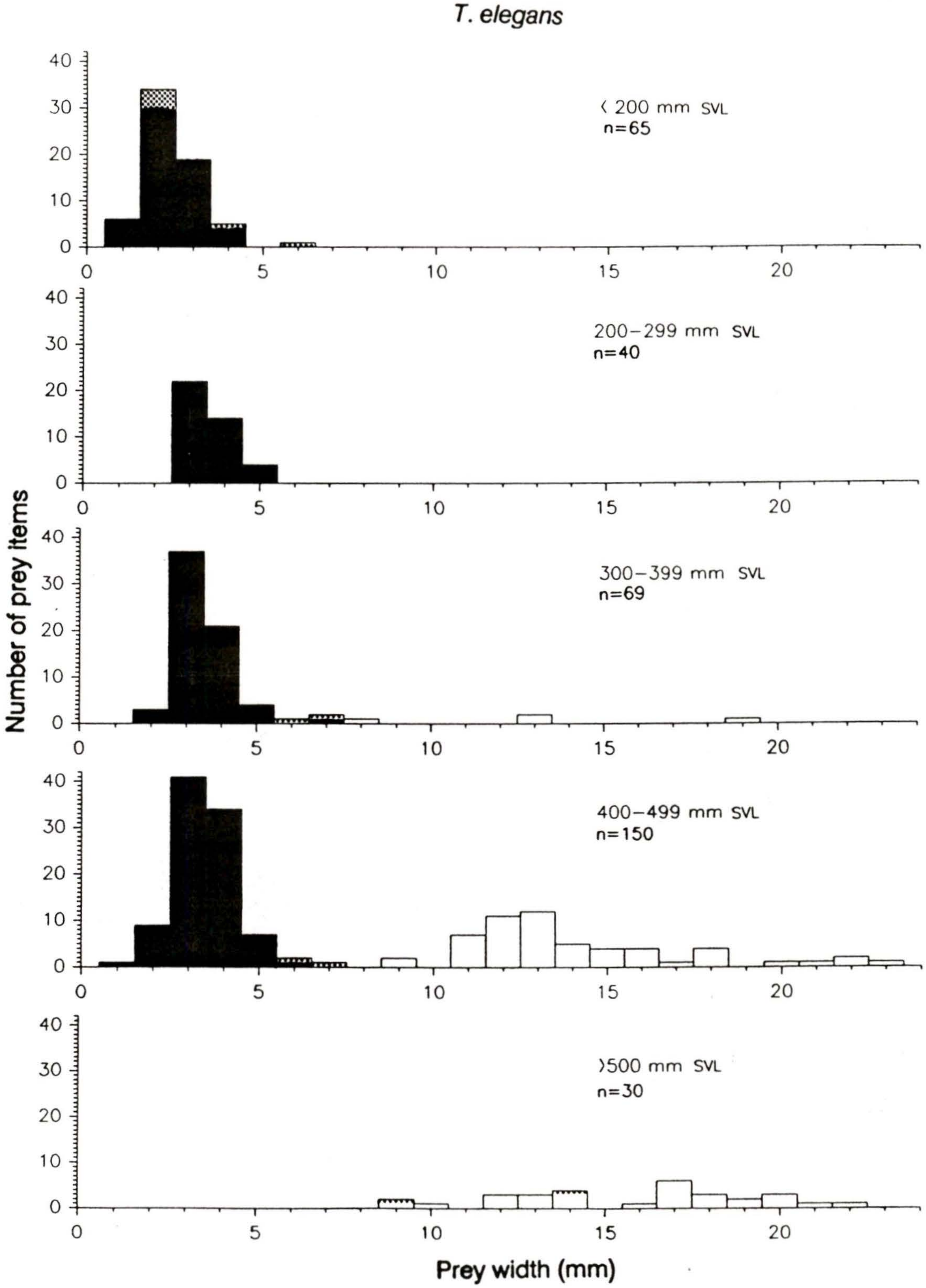

T. sirtalis
Number of prey items
<400 mm SVL
n=24
400–499 mm SVL
n=36
>500 mm SVL
n=21
0
2
4
6
8
10
12
0
5
10
15
20
Prey width (mm)

Figure 29. Ontogenetic changes in the size of prey eaten by *T. elegans*.
Solid = slugs
Open = mammals
Dotted = other


T. elegans
Number of prey items
Prey width (mm)
0
10
20
30
40
0
5
10
15
20
< 200 mm SVL
n=65
200–299 mm SVL
n=40
300–399 mm SVL
n=69
400–499 mm SVL
n=150
>500 mm SVL
n=30

larger (up to 26 mm wide, 52.0 g). In fact, most of the mammals eaten by both species were *Microtus* nestlings less than 5 g in mass.

I expressed relative prey size using the ratio of prey width to snake head width. The relative width of prey items eaten by *T. sirtalis* varied from 0.2 to 1.5 times head width (Fig. 30). *Thamnophis elegans* ate prey ranging in width from 0.1 to 2.2 times head width (Fig. 31). In both species, larger snakes tended to eat relatively larger prey than small snakes, but the differences were not as great as in the case of absolute prey size.

In addition to eating fewer larger prey, and a wider range of prey sizes, larger snakes tended to have a greater mass of food in their stomachs at one time (Fig. 32), although the range of masses of stomach contents was great (from less than one g to almost 30 g). Relative mass of stomach contents (stomach content mass/mass of snake without food) followed a similar pattern in the case of *T. elegans*, but in *T. sirtalis*, snakes of all sizes tended to contain a similar range of relative masses of food in their stomach (Fig. 33).

Figure 30. Ontogenetic changes in the relative size of prey (prey width/snake head width) eaten by *T. sirtalis*.
Solid = earthworms
Open = mammals
Dotted = other

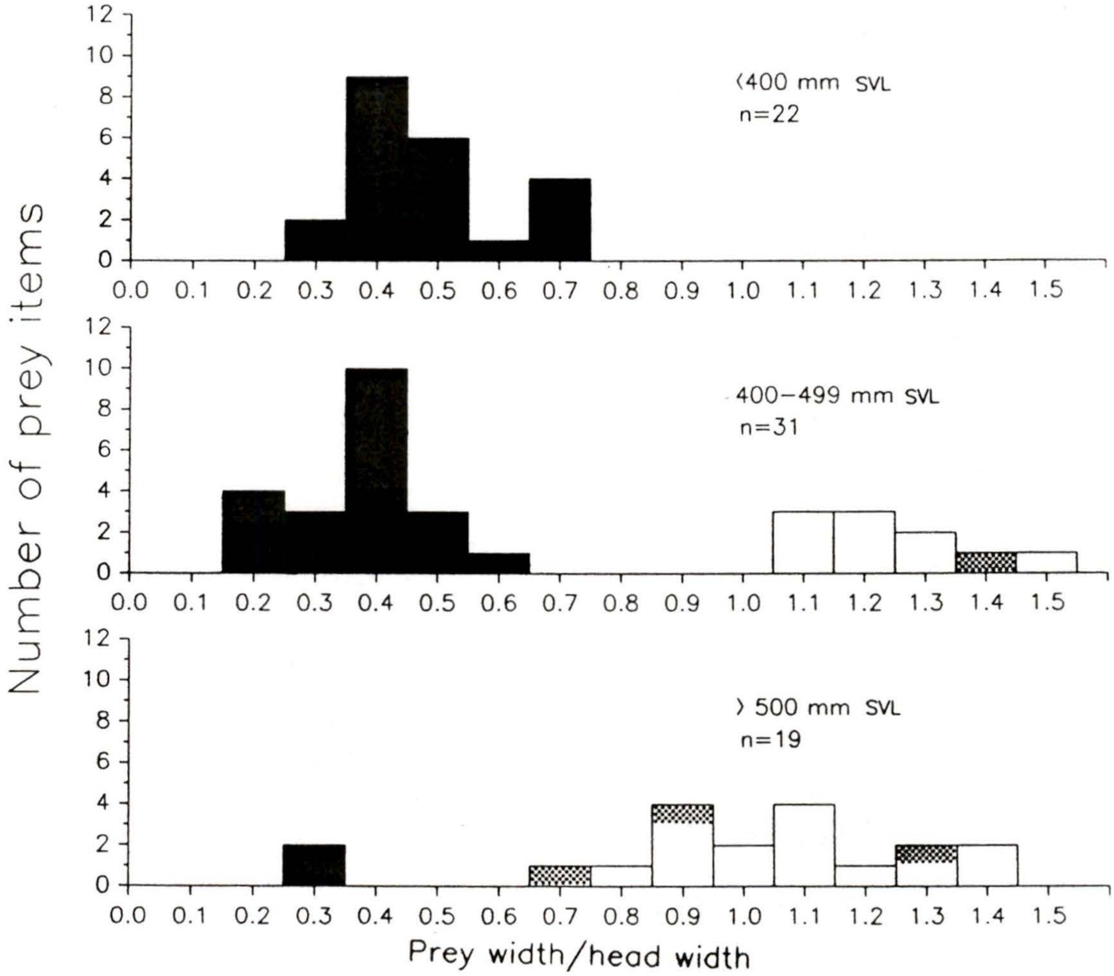

Number of prey items
12
10
8
6
4
2
0
(400 mm SVL
n=22
400–499 mm SVL
n=31
) 500 mm SVL
n=19
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
1.5
Prey width/head width

Figure 31. Ontogenetic changes in the relative size of prey (prey width/snake head width) eaten by *T. elegans*.
Solid = slugs
Open = mammals
Dotted = other

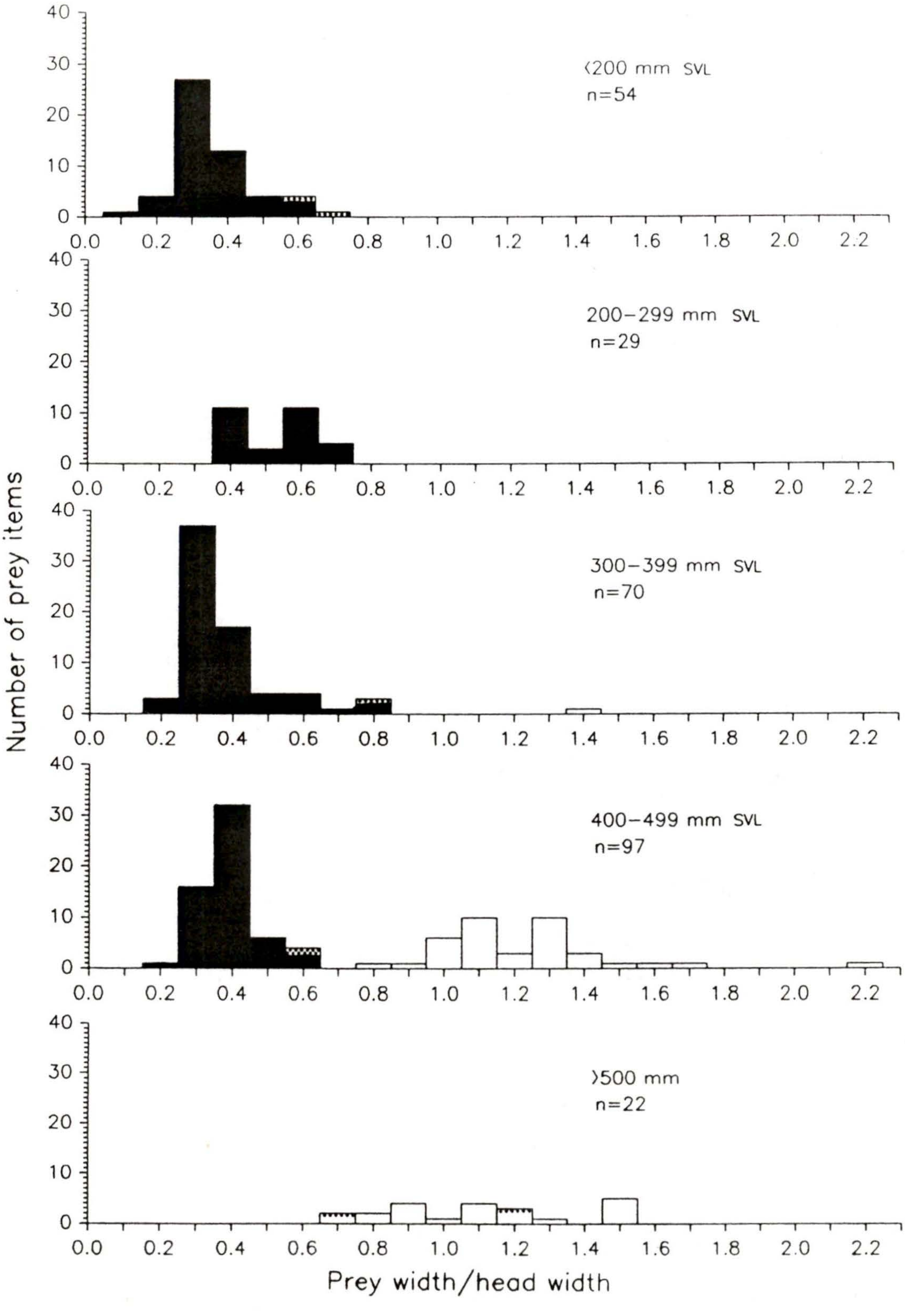
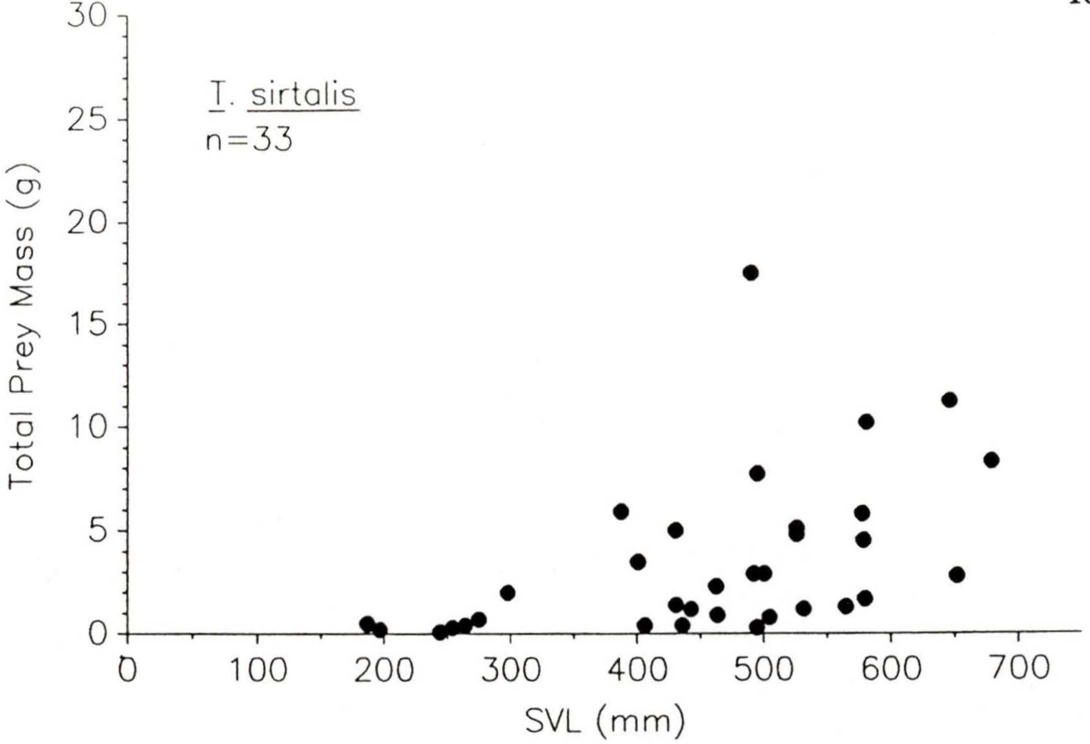

Number of prey items
Prey width/head width
<200 mm SVL
n=54
200–299 mm SVL
n=29
300–399 mm SVL
n=70
400–499 mm SVL
n=97
>500 mm
n=22
0
10
20
30
40
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2

Figure 32. Ontogenetic changes in the total mass of food in the stomach of *T. sirtalis* and *T. elegans*.


T. sirtalis
n=33
Total Prey Mass (g)
0
5
10
15
20
25
30
SVL (mm)
0
100
200
300
400
500
600
700

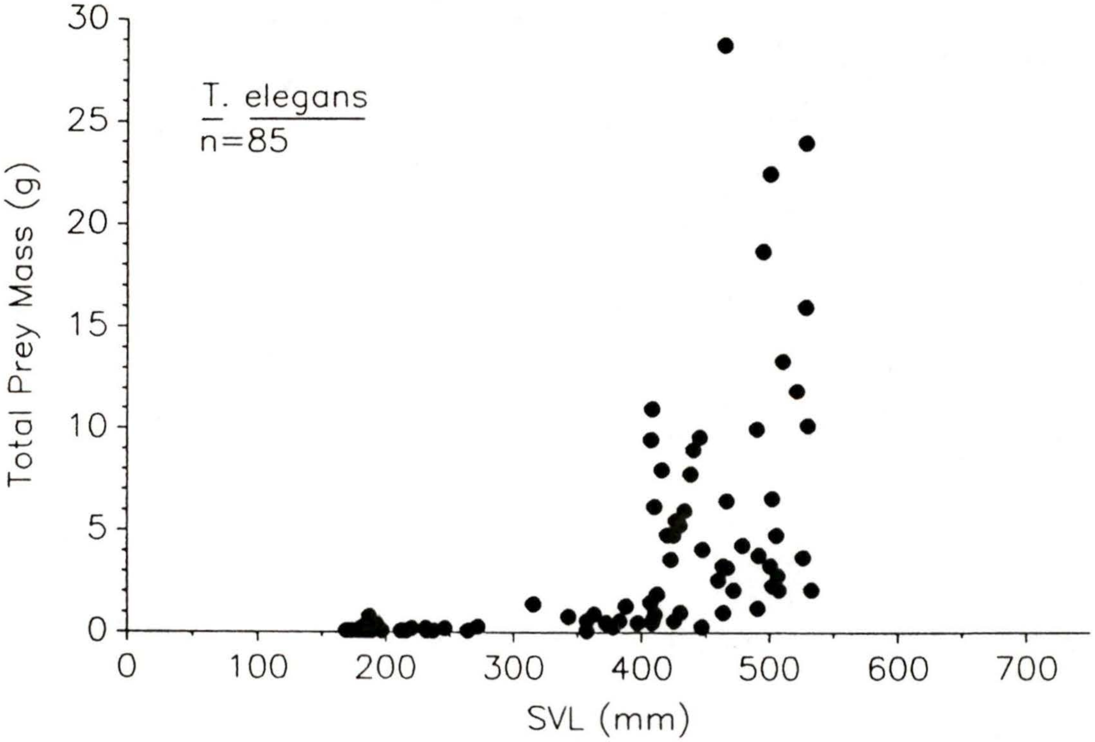
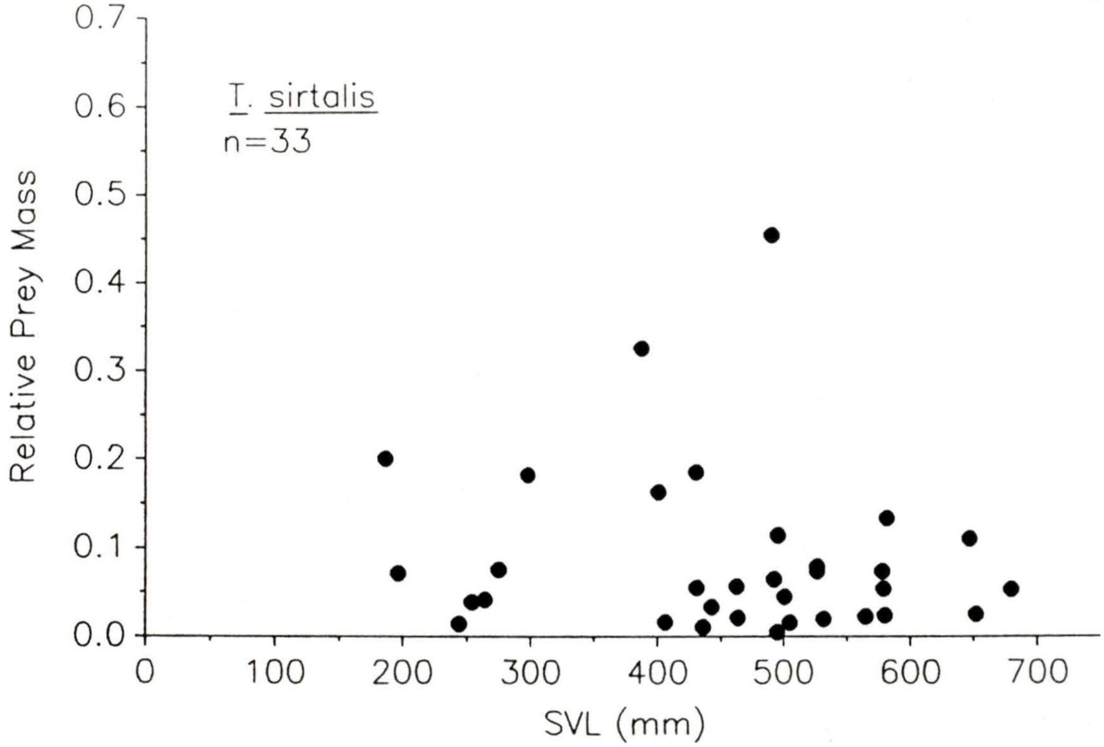
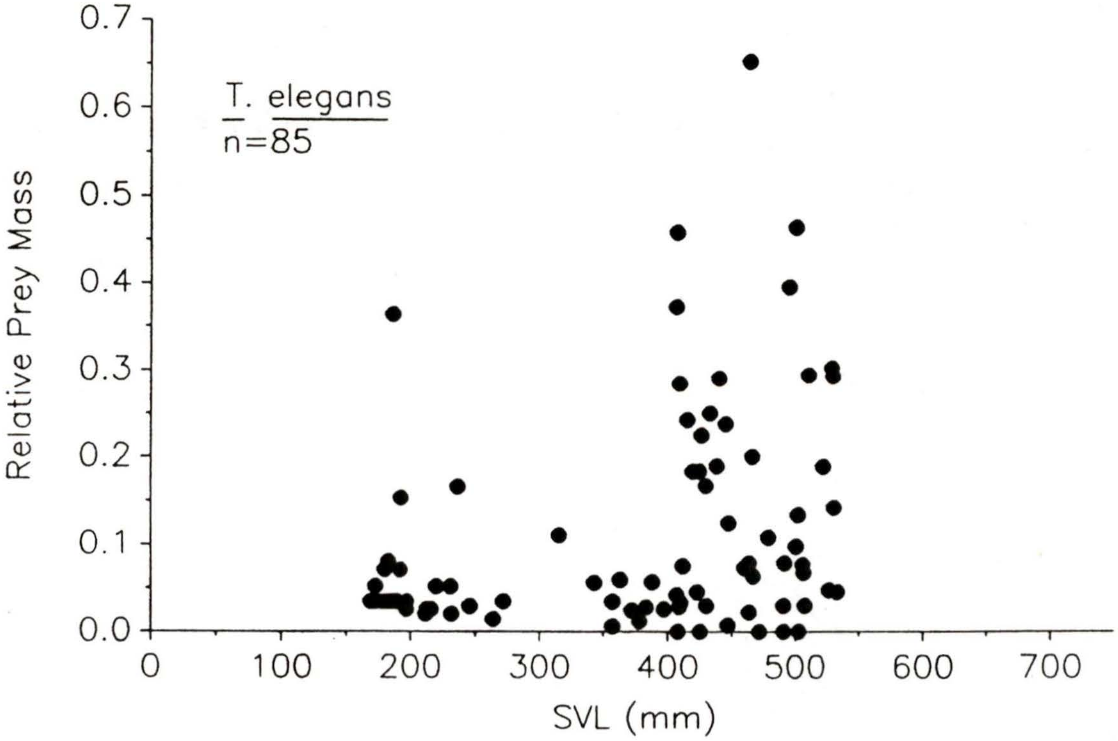

T. elegans
n=85
Total Prey Mass (g)
0
5
10
15
20
25
30
SVL (mm)
0
100
200
300
400
500
600
700

Figure 33. Ontogenetic changes in the relative mass of prey (total mass of all prey/mass of snake without food) in the stomach of *T. sirtalis* and *T. elegans*.


T. sirtalis
n=33
Relative Prey Mass
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0
100
200
300
400
500
600
700
SVL (mm)


T. elegans
n=85
Relative Prey Mass
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0
100
200
300
400
500
600
700
SVL (mm)

DISCUSSION

Annual cycle

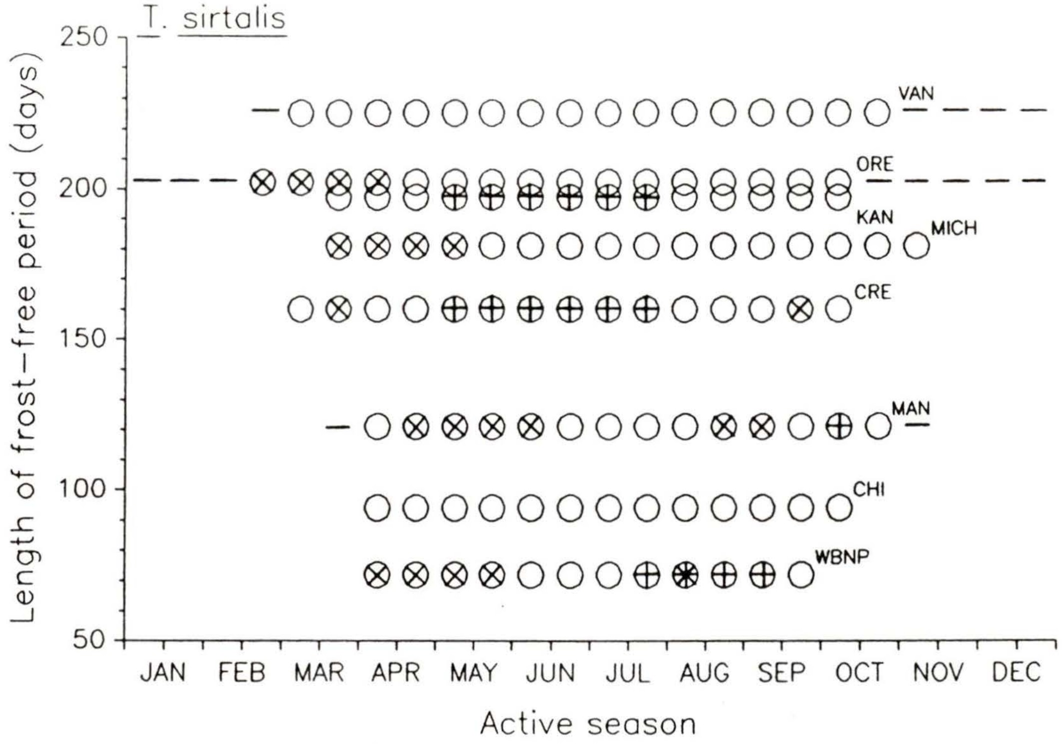
The influence of length of active season on the ecology of *T. sirtalis* and *T. elegans* in different parts of their ranges is potentially large; snakes inhabiting regions with long, cold winters may be limited in the time available for growth and reproduction each year (Gregory 1982). Conversely, such limitations may be relaxed in populations inhabiting more benign environments. I have attempted to summarize information on the timing of activity, mating, and gestation for Creston garter snakes plus seven other populations of *T. sirtalis*, and four other populations of *T. elegans* in Fig. 34. These data are incomplete, and are subject to differences in the detail with which the annual cycle in each population was reported. At Creston, the length of the frost free period (a crude measure of climatic severity) is intermediate compared to locations of previous studies (Fig. 34). The approximate period during which garter snakes are active at Creston (7 months) is greater than for populations inhabiting more severe climates, whereas garter snakes inhabiting milder climates are active for slightly longer periods each year (Fig. 34).

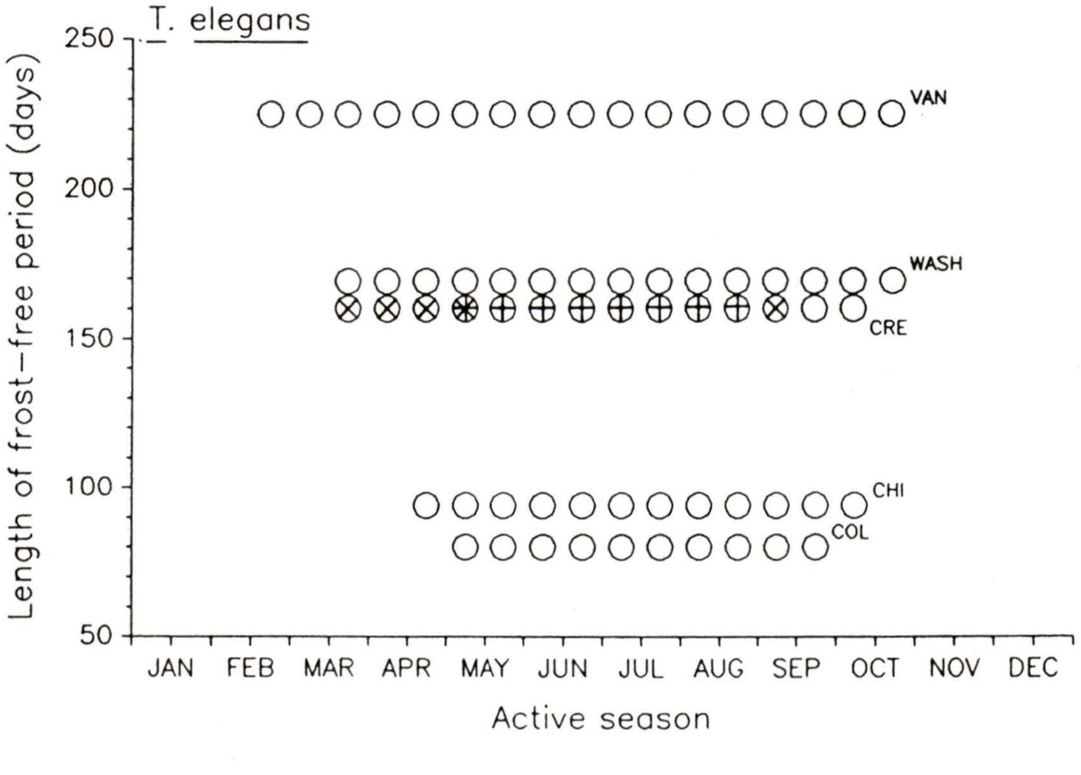
Other characteristics of the annual cycle of *T. sirtalis* and *T. elegans* at Creston are probably not unusual compared to other populations. The occurrence of fall courtship and/or mating has been observed in a number of populations of *T. sirtalis* (Blanchard and Blanchard 1941; Fox 1955; Fitch 1965; see also Fig. 34) and one population of *T. elegans* (Kephart 1981). Brown *et al.* (1974) found sperm in cloacal smears of hibernating female *T. elegans* in Utah, suggesting the presence of fall mating in that population as well. The phenomenon is not easily explained. Hormonal studies have suggested that a period of winter dormancy is required to

Figure 34. Summary of the annual cycle of *T. sirtalis* and *T. elegans* in different locations. Circles represent half-month periods during which snakes are regularly active; dashes represent periods during which snakes were observed, but are probably not regularly active.
X = courtship or mating observed
\+ = gravid females observed
✳ = both

Locations:
VAN = S. Vancouver Island (Gregory, unpublished data)
ORE = W. Oregon (Stewart 1965)
KAN = Kansas (Fitch 1965)
MICH = Michigan (Carpenter 1952a, Blanchard and Blanchard 1941)
CRE = Creston
MAN = Manitoba (Aleksiuk and Gregory 1974; Gregory 1974 and unpublished data)
CHI = Chilcotin (Gregory, unpublished data)
WBNP = Wood Buffalo National Park, N. Alberta (Larsen 1986)
WASH = E. Washington (Peterson 1982)
COL = N. Colorado (Scott 1978)

Sources of lengths of frost-free periods are Environment Canada (1982c) and National Oceanic and Atmospheric Administration (1974).


T. sirtalis
Length of frost-free period (days)
250
200
150
100
50
VAN
ORE
KAN
MICH
CRE
MAN
CHI
WBNP
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
Active season


T. elegans
Length of frost-free period (days)
250
200
150
100
50
VAN
WASH
CRE
CHI
COL
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
Active season

initiate mating activity in both female (Bona-Gallo and Licht 1983) and male (Garstka *et al.* 1982) *T. sirtalis*. Aleksiuk and Gregory (1974) suggested that fall mating may be induced by a period of cool weather, but this was not the case for either of the observations in this study. An ultimate benefit, for females, at least, may be the release from having to locate a mate in spring. This may be more important in populations where communal overwintering is uncommon (such as Creston), but too few data are available to compare the frequency of fall mating in communally *vs*. non-communally overwintering populations.

Body size and growth

The average adult body size of *T. sirtalis* at Creston appears to be among the smallest of several populations for which body size data are available. I compared the size-frequency distributions of males and females among seven populations: Creston snakes were generally smaller than four (Wood Buffalo National Park (WBNP) in northern Alberta, Larsen 1986; Chilcotin region of B.C., Gregory 1984 and personal communication; Manitoba, Gregory 1977; Kansas, Fitch 1965), and similar to three (northern California, Kephart 1981; southern California, White and Kolb 1974; Michigan, Carpenter 1952a). There are fewer populations of *T. elegans* for which similar data are available: adults at Creston appear to be smaller than those in the Chilcotin (Gregory 1984), and similar to those in northern (Kephart 1981) and southern (White and Kolb 1974) California. I also compared the maximum body sizes among several populations (Table 7), providing further support for the observation that adult snakes at Creston are relatively small.

Although the trends in body mass are probably similar to SVL, the smaller SVLs of Creston *T. sirtalis* may be partly compensated by increased stoutness (mass relative to SVL). Both females and males at Creston tend to be heavier at a given

Table 7. Summary of the size of the largest individuals in various populations of garter snakes. Values are the mean, median, and range (SVL, in mm) of the 10 largest individuals reported in each study. Most values are derived from size-frequency histograms, and are therefore only approximate.

	FEMALE			MALE		
LOCATION	MEAN	MEDIAN	RANGE	MEAN	MEDIAN	RANGE
T. sirtalis						
WBNP[1]	913	895	875-915	715	-	715-815
Kansas[2]	895	-	----950	579	-	----680
Manitoba[3]	789	-	----790	672	-	----695
Creston	780	761	720-910	578	577	556-607
W. Oregon[4]	-	-	----890	-	-	----590
Puget Sound[5]	-	-	----740	-	-	----540
N. Calif.[6]	685	675	675-725	565	575	525-625
1800 m	610	625	575-675	535	575	525-625
2055 m	560	575	575-625	495	525	475-525
Michigan[7]	-	-	----715	-	-	----600
T. elegans						
Chilcotin[8]	683	688	638-713	628	638	613-638
N. Calif.[6]	635	625	625-675	595	575	575-625
1555 m	635	625	625-675	595	575	575-625
2055 m	545	525	525-575	475	475	-------
Creston	608	605	596-620	518	513	505-568
Puget Sound[5]	-	-	----615	-	-	----510

Sources:

1 Larsen 1986
2 Fitch 1965 (and summary in Larsen 1986)
3 Gregory 1977 (and summary in Larsen 1986)
4 Stewart 1968
5 Hebard 1950
6 Kephart 1981
7 Carpenter 1952a
8 Gregory 1984

SVL than at WBNP (see Larsen 1986: Fig. 12). Although Fitch (1965: Fig. 1) does not differentiate between sexes, the mass-SVL relationship of Kansas *T. sirtalis* suggests that this population also contains relatively lighter individuals. The mass-SVL relationship of both *T. sirtalis* and *T. elegans* in northern California (Kephart 1981: Figs. 30 and 31) are similar to Creston. Andren (1982) suggested that food availability accounted for the pronounced differences in the mass-SVL relationships of *Vipera berus* between two populations, and between two years in a single population. In both comparisons, higher food availability was associated with increased stoutness in both males and females. Whether or not a similar explanation accounts for variation among populations of *T. sirtalis* is unknown.

A complex of factors may be responsible for the relatively small body sizes of garter snakes at Creston. Growth rate may be lower, either because of environmental constraints (e.g. food limitation) or genetic reduction in growth potential. Asymptotic size, which has a strong genetic component, may also be lower at Creston. Superimposed upon the pattern of growth and asymptotic size are patterns of mortality: perhaps fewer adults live to reach large sizes at Creston than elsewhere, despite similarities in growth and asymptotic size.

The importance of mortality is impossible to evaluate without comparative survivorship data; sources of adult mortality in other populations include freezing during winter (Gregory 1977) and predation (Fitch 1965). I found no evidence suggesting that either of these sources of mortality are particularly severe at Creston, but information was limited.

The roles of growth and asymptotic size in the observed body size differences are also difficult to evaluate. The large amount of variation (e.g. Fig. 9) makes it difficult to characterize the "typical" pattern of growth at one location, particularly if growth varies among years (Gregory 1977). The model used to describe growth may, in fact, be inappropriate. In this study, both the growth rates of small snakes, and asymptotic size, probably were underestimated. Differences in techniques for measuring growth also confound comparisons among studies.

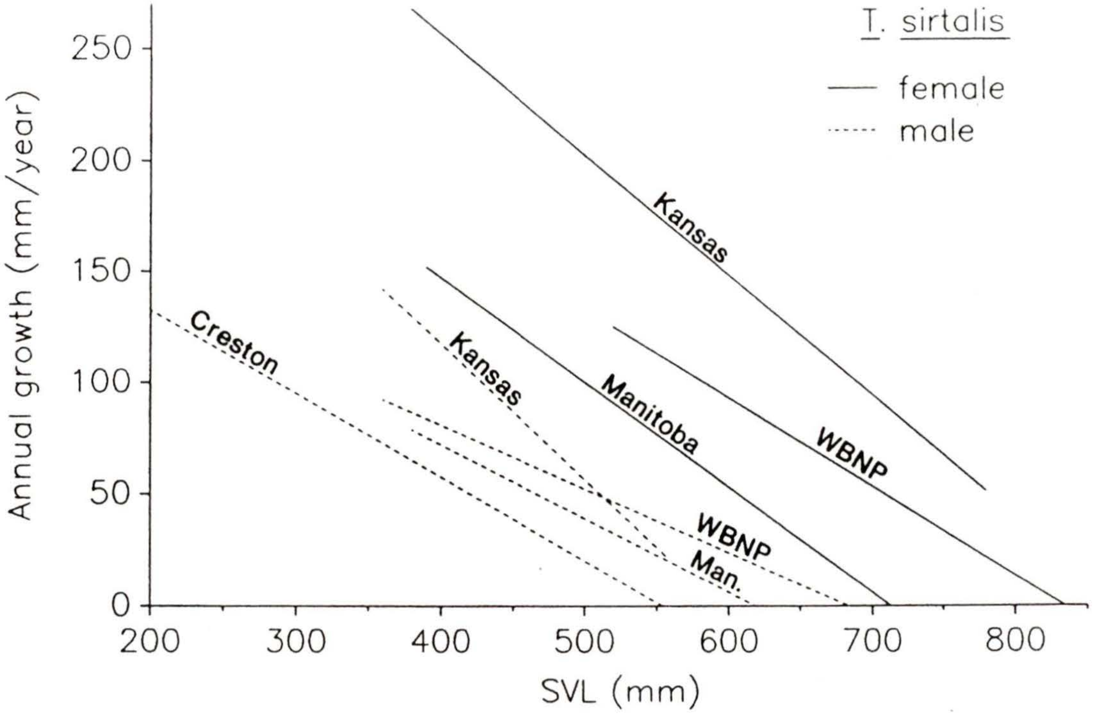
I nonetheless attempted to compare the pattern of growth of *T. sirtalis* and *T. elegans* at Creston with other populations by plotting growth curves for studies with similar methodologies (repeated measurements of individual snakes at intervals of one active season). Although reliable annual growth data for Creston snakes are not available, I extrapolated daily growth to annual growth by multiplying the regression constants of the growth equations (Table 2) by the mean time period during which growth data were obtained in each year (180 days). The large seasonal component of variation makes such an extrapolation tenuous, because if a higher proportion of individual growth records were measured during months of rapid growth, the "average" annual growth would be overestimated, and vice versa.

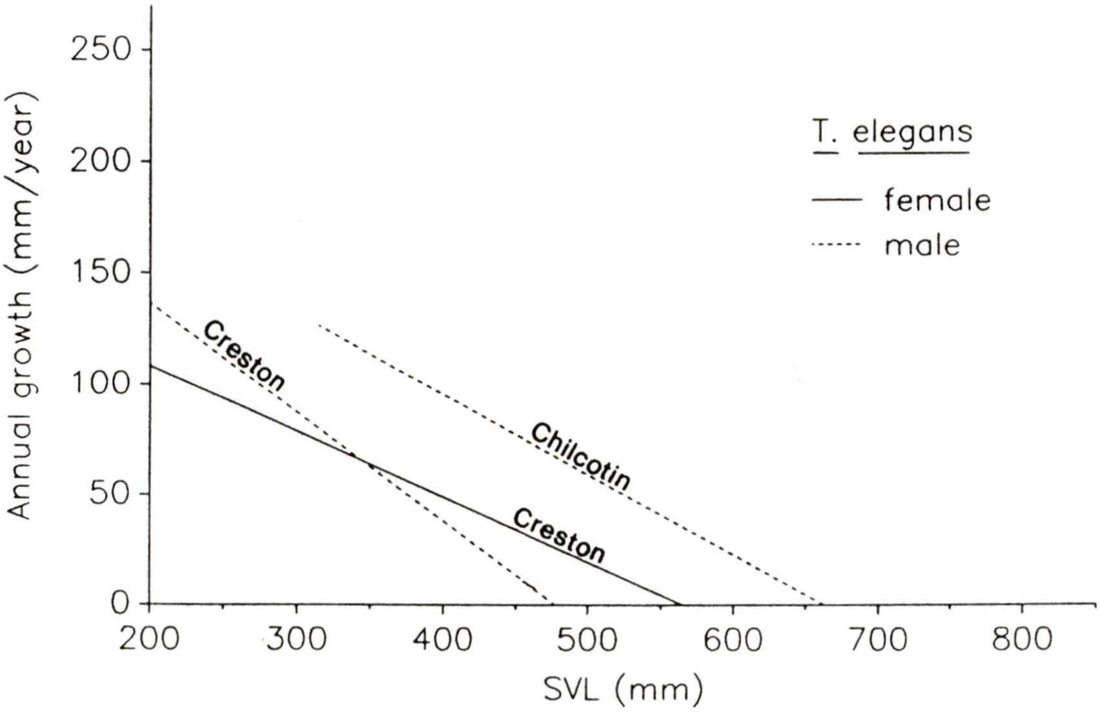
It appears that, subject to the cautions noted above, both *T. sirtalis* and *T. elegans* grow more slowly at Creston than at the other locations for which comparative data are available (Fig. 35). More striking is the apparent degree of variation among different populations. *T. sirtalis* in Kansas, in particular, seem to grow very quickly at most sizes. Fitch (1965) suggested that differences in apparent food availability caused *T. sirtalis* in eastern Kansas to grow more quickly than individuals in a nearby population. It seems unlikely that a similar explanation accounts for the apparently slower growth of Creston *Thamnophis*, since food availability at Creston does not appear to be particularly low (see Discussion: Feeding). Without detailed information on actual food availability at Creston and

Figure 35. Relationship between annual growth and SVL at first capture in different populations of garter snakes. Only the range of SVLs for which growth data were available are included. See text for further details.

Sources:

Kansas: Larsen (1986), using data from Fitch (1965) and Fitch (unpublished data),
WBNP: Larsen (1986),
Manitoba: Gregory (1977),
Chilcotin: Gregory (unpublished data).


T. sirtalis
female
male
Annual growth (mm/year)
250
200
150
100
50
0
200
300
400
500
600
700
800
SVL (mm)
Kansas
Creston
Kansas
Manitoba
WBNP
WBNP
Man.


T. elegans
female
male
Annual growth (mm/year)
250
200
150
100
50
0
200
300
400
500
600
700
800
SVL (mm)
Creston
Chilcotin
Creston

other locations, it is impossible to draw any firm conclusions. It is possible that innate, genetically-based reduction in growth rate has occurred in Creston garter snakes, as has been documented within some lizard species (e.g. *Sceloporus*, Ferguson and Brockman 1980). The hypothesis that length of active season may limit growth in some snake populations (Platt 1984) is not supported, but further data on growth rates, especially of small snakes, are badly needed.

In contrast to SVL and mass, there are no head size measurements for other populations of *T. sirtalis* or *T. elegans* to compare with those from Creston. Fitch (1965:499-500) noticed the relatively large heads of newborn *T. sirtalis*, and also the relatively wide, "triangular" shaped heads of large female *T. sirtalis*. The ontogenetic decrease in head size relative to body size probably is common in snakes, and has been documented in water snakes (*Nerodia*, Nakamura and Smith 1960), worm snakes (*Carphophis*, Clark 1970), and several other species (Vitt and Vangilder 1983). When considering the possible ecological significance of this trend, it is important to recognize that although the relative width of a snake's head decreases with increasing body length, the maximum cross-sectional area of an object that can be swallowed increases relative to body length. Therefore, the reduction in relative head size should not be expected to result in a reduction in relative prey size. Furthermore, Rossman (1980) documented an increase in the length of the jaws and jaw suspension apparatus relative to skull length in *Nerodia rhombifera*. The magnitude of this increase was much greater (up to 30% in some characters) than the approximately 5% decrease in head length relative to body length observed in this study. On the basis of skull bone morphology, Rossman (1980) predicted an increase in relative prey size during ontogeny, a prediction that is supported by the results of this study.

The importance of the small but significant sexual dimorphism in garter snake head sizes is unclear. Clark (1970) found that relative head width was greater in male than in female *Carphophis*, and Vitt and Vangilder (1983) found that males had relatively larger gapes than females in *Liophis poecilogyras* and *Waglerophis merremii*. Each of these trends are in a direction opposite to that obtained in this study. Whether or not such dimorphisms have an ecological basis probably awaits more detailed examination of the relationship between head size and prey size in female and male snakes.

Reproduction

Variation in reproductive characteristics among populations of *T. sirtalis* and *T. elegans* is better documented than variation in growth and body size. Tables 8 and 9 summarize information from various studies for a range of locations, making it possible to assess the relative position of Creston populations.

The size at which females at Creston become sexually mature is smaller than in populations composed of relatively large individuals (e.g. WBNP, Kansas, Chilcotin), while males at Creston appear to mature at a size similar to most other populations except WBNP. If the age at which female reproduction can occur does not vary among populations, then slower juvenile growth could explain the small size of mature females at Creston. Growth of juvenile garter snakes is virtually unknown, however, making it impossible to evaluate this hypothesis. An alternative explanation is that females at Creston mature earlier than elsewhere, a characteristic that may be advantageous if adult mortality greatly exceeds juvenile mortality (Stearns 1976). An improved understanding of patterns of survivorship and growth are required to test these ideas in these species.

Table 8. Summary of reproductive characteristics of *T. sirtalis* from different locations, ordered from north to south. Unless otherwise noted, size at maturity is based on the SVL of the smallest gravid female and the smallest courting male, reported in each study. In the four right-most columns, the mean is presented, with sample size in parentheses. See Table 9 for sources.

LOCATION	FEMALE MATURITY (mm)	MALE MATURITY (mm)	LITTER SIZE	NEONATE SVL (mm)	NEONATE MASS (g)	RCM1
WBNP[1]	640	+490	11.6 (18)	191.2 (284)	2.62 (187)	0.19 (16)
Chilcotin[2]	-	-	13.8 (7)	199.1 (29)	2.99 (29)	-
N. Okanagan[3]	520	-	9.3 (21)	182.0 -	2.35 -	0.25 -
Manitoba[4]	425	-	16.4 (14)	154.4 (182)-	-	-
Creston	445	360	7.3 (12)	183.0 (85)	2.59 (87)	0.24 (12)
Puget Sound[5]	^435	^390	-	159.0 (68)	-	-
W. Oregon[6]	435	+360	11.3 (7)	184.2 (67)	-	-
New Hampshire[7]	-	-	*12.9 (104)	-	-	-
Michigan[8]	425	+390	*18.0 (20)	-	-	-
Chicago area[9]	-	-	-	-	-	0.32 (11)
N. Calif.[10]	470	-	*7.6 (29)	-	-	-
1800 m	-	-	*5.8 (5)	-	-	-
2055 m	-	-	*5.3 (8)	-	-	-
Missouri[11]	-	-	13.4 (19)	-	-	-
Kansas[12]	505	390	13.5 (11)	167.9 (151)	1.88 (151)	0.24 -

+ smallest male reported to contain sperm
^ method not stated
* from palpations of free-ranging females or dissections; all other litter sizes from births to captive females

Table 9. Summary of reproductive characteristics of *T. elegans* from different locations, ordered from north to south. Unless otherwise noted, size at maturity is based on the SVL of the smallest gravid female and the smallest male from which sperm was palpated in each study. In the four right-most columns, the mean is presented, with sample size in parentheses.

LOCATION	FEMALE MATURITY (mm)	MALE MATURITY (mm)	LITTER SIZE	NEONATE SVL (mm)	NEONATE MASS (g)	RCM1
Chilcotin[2]	495	-	11.8 (25)	168.2 (254)	2.30 (254)	0.27 (20)
S. Okanagan[2]	560	-	14.5 (11)	187.1 (152)	2.63 (152)	0.30 (11)
Creston	420	345	7.5 (21)	176.1 (157)	2.70 (157)	0.29 (21)
Puget Sound[5]	^460	^380	-	144.0 (81)	-	-
N. Calif.[10]	415	-	*7.8 (73)	-	-	-
1555 m	-	-	*7.8 (22)	-	-	-
2055 m	-	-	*4.9 (15)	-	-	-

^ method not stated

* from palpations of free-ranging females or dissections; all other litter sizes from births to captive females

Sources for Tables 8 and 9:

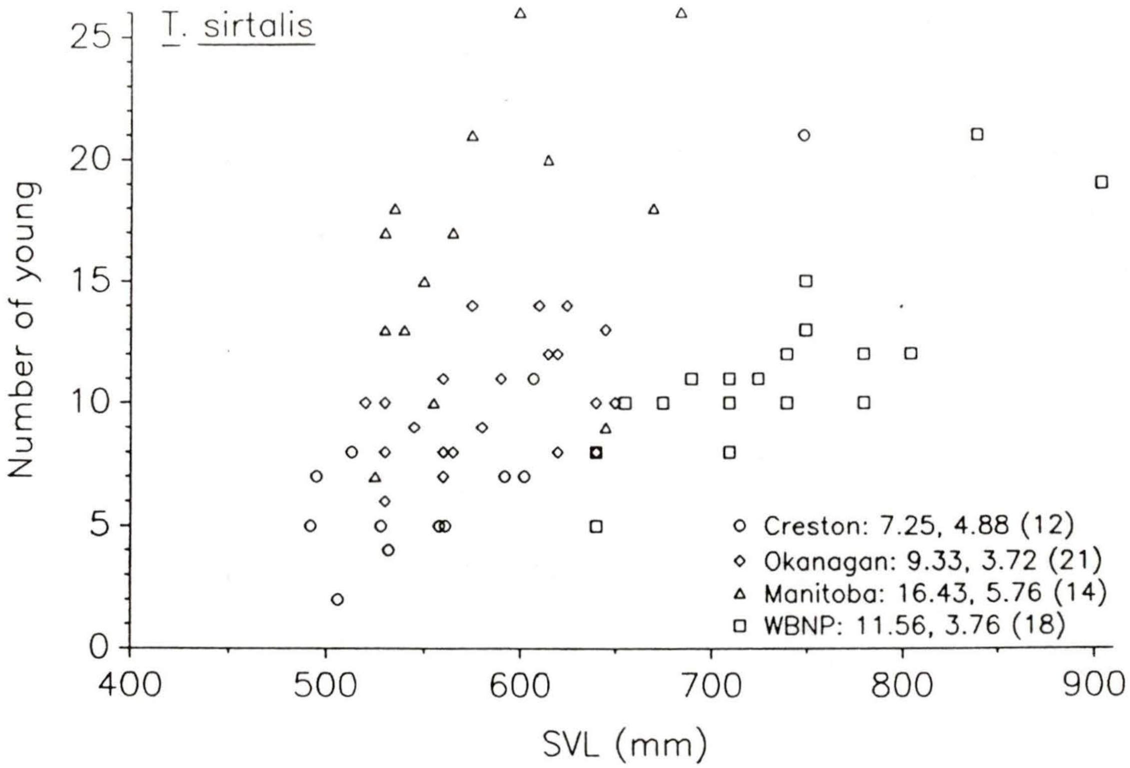
1 Larsen 1986
2 Gregory, unpublished data
3 Gregory, Macartney and Larsen, unpublished data
4 Gregory 1977
5 Hebard 1950
6 Stewart 1968
7 Zehr 1962
8 Carpenter 1952a, b
9 Seigel and Fitch 1984
10 Kephart 1981
11 Seigel and Fitch 1985
12 Fitch 1965

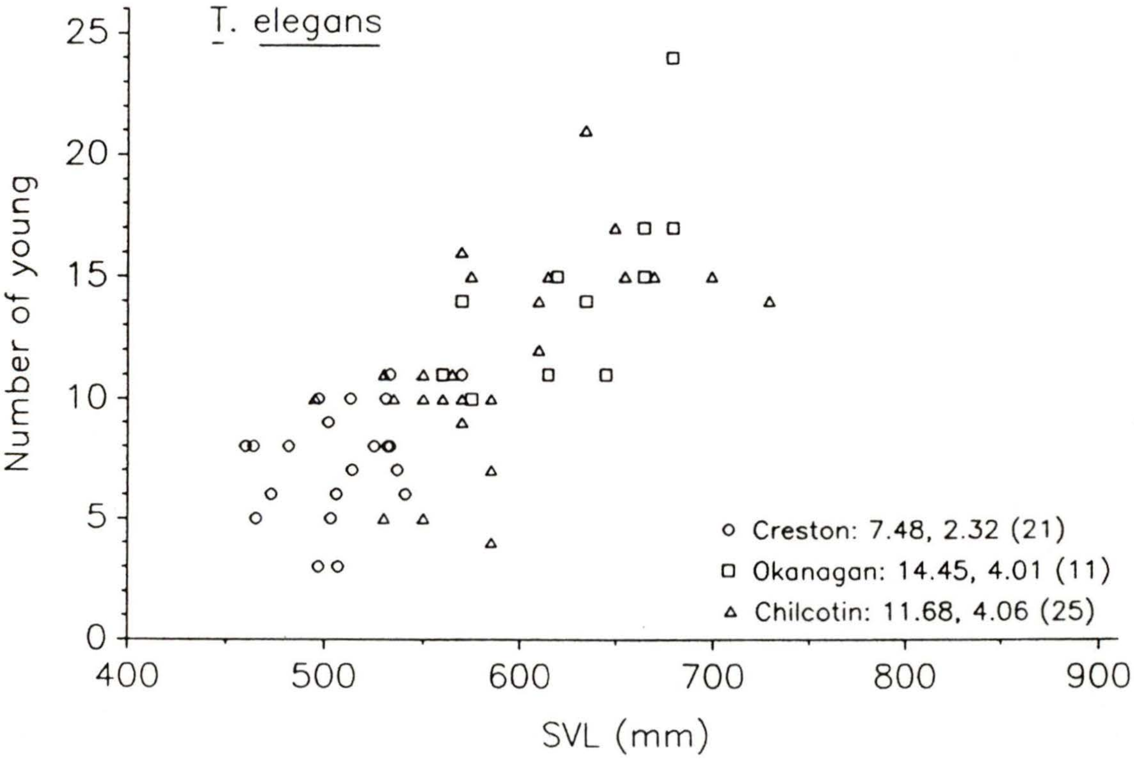
Some of the variation among the other reproductive characteristics listed in Tables 8 and 9 may be caused by differences in methodologies among studies. For example, litter sizes based on palpations of free-ranging females are probably overestimates due to the inclusion of unfertilized ova and embryos that will be resorbed later (Fitch 1965; but see Results: Litter size). It is also possible that variation in neonate size may be increased by differences in the degree of stretching applied when measuring neonate SVL, although the variation persists even when different populations are examined by the same person (P.T. Gregory, personal communication). As demonstrated below, much of the remaining "real" variation may be influenced by the correlation of reproductive characteristics with female body size.

The mean number of young produced by female *T. sirtalis* and *T. elegans* at Creston is small compared to populations in other locations (Tables 8, 9). Furthermore, in all populations of *T. sirtalis* and *T. elegans* examined, litter size increases with increased female SVL (Fitch 1965; Gregory 1977 and unpublished data; Kephart 1981; Larsen 1986; Seigel et al. 1986; this study). Are the relatively small mean litter sizes of *T. sirtalis* and *T. elegans* at Creston caused by the relatively small size of females, or by exogenous environmental factors (e.g. food availability) acting on litter size?

In *T. sirtalis*, body size does not account for much of the litter size differences between Creston females and those from other locations. Comparative litter size-female SVL data for Creston plus three other populations (summarized by Larsen 1986: Fig. 21) are illustrated in Fig. 36. Litter sizes of Manitoba females are larger than those of similar-sized females from the north Okanagan Valley and Creston, while the litters of WBNP females are in fact smaller than their very large body sizes

Figure 36. Relationship between number of young per litter and female SVL in different populations of garter snakes. Each point is the total number of young (live and dead) born to a captive female, and numbers beside each location are mean, SD (sample size). The figure for *T. sirtalis* is modified from Larsen (1986), and includes data from the following sources:
North Okanagan Valley B.C.: Gregory, Macartney and Larsen (unpublished data),
Manitoba: Gregory (1977),
WBNP: Larsen (1986).
T. elegans data for the south Okanagan Valley and the Chilcotin are from Gregory (unpublished data).


T. sirtalis
Number of young
SVL (mm)
0
5
10
15
20
25
400
500
600
700
800
900
○ Creston: 7.25, 4.88 (12)
◇ Okanagan: 9.33, 3.72 (21)
△ Manitoba: 16.43, 5.76 (14)
□ WBNP: 11.56, 3.76 (18)


T. elegans
Number of young
SVL (mm)
0
5
10
15
20
25
400
500
600
700
800
900
○ Creston: 7.48, 2.32 (21)
□ Okanagan: 14.45, 4.01 (11)
△ Chilcotin: 11.68, 4.06 (25)

would suggest. These visual impressions are supported by an analysis of covariance, which indicates significant among-population variation in litter size when female SVL is held constant (F = 27.0, df = 3,60, p < .001); the adjusted mean litter sizes of each of the above populations (in order) are 18.3, 11.7, 10.0 and 6.3. The assumption of homogeneity of slopes in this analysis is satisfied (F = 0.94, df = 3,57, p > .05).

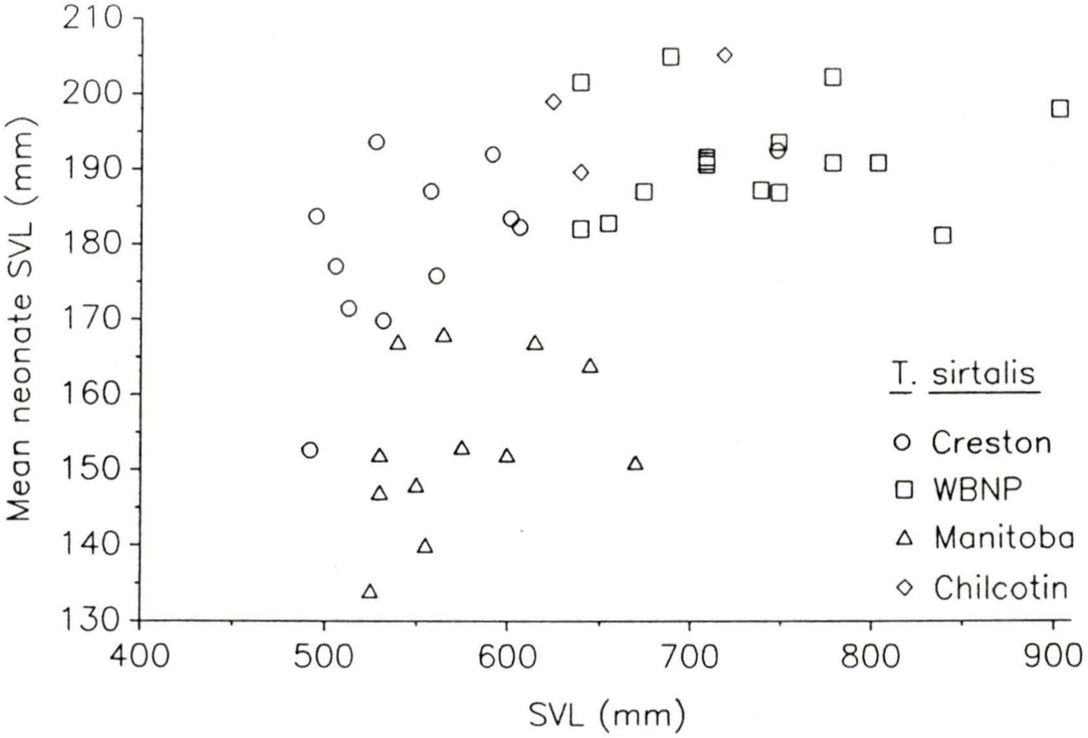
In contrast, variation among the litter sizes of female *T. elegans* at Creston and two other locations (Chilcotin, south Okanagan Valley) appears to be most directly related to differences in body size alone. As suggested by the similarity of litter size-SVL relationships (Fig. 36), the adjusted mean litter sizes of the three populations do not differ significantly (F = 0.78, df = 2,53, p > .05), despite significant differences among unadjusted litter sizes (F = 23.3, df = 2,53, p < .001). As with *T. sirtalis*, the slopes of the three litter size-SVL relationships were not significantly different (F = 0.64, df = 2,51, p > .05). It should be recognized that the lack of apparent size-independent variation in litter size among populations of *T. elegans* is not evidence that such variation does not exist; it may indeed exist in other populations for which no comparative data are yet available.

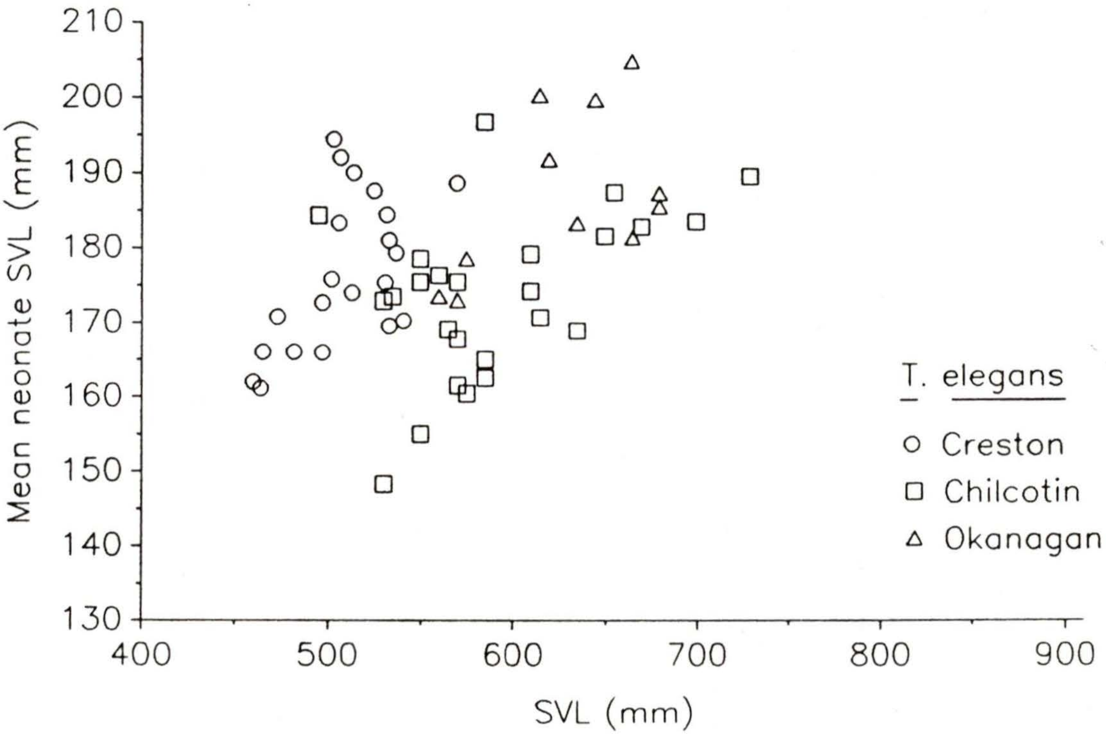
It therefore appears that female *T. elegans* at Creston produce small litters mainly because of their small body size. In *T. sirtalis*, however, body size alone cannot explain litter size variation; females at Creston produce much smaller litters than similar-sized females in Manitoba.

Few other studies of intraspecific variation in litter size of snakes are available for comparison. In *Coluber constrictor*, female size probably accounts for litter size variation: females in Kansas grow more quickly to larger sizes and produce more young than smaller, more slowly growing females in Utah (Brown and Parker 1984). In *Storeria occipitomaculata*, the opposite pattern occurs: females in South Carolina are smaller but produce more young per litter (mean = 9) than the larger females in Michigan (mean = 7 young, Semlitsch and Moran 1984). Clearly, factors other than body size cause litter size variation in snakes. In Kansas, the timing and amount of precipitation (and presumably its effects on food supply) may influence litter size (with body size differences removed) of *T. sirtalis*, with more young being produced in years with wetter springs (Seigel and Fitch 1985). Annual variation in litter size in *Vipera berus* has also been linked to variation in food availability (Andren and Nilson 1983). As mentioned previously, it seems unlikely that *T. sirtalis* at Creston are particularly food-limited. It is therefore likely that other environmental factors besides food availability, and possibly genetic adaptation, account for the smaller litter sizes of Creston females compared to those in Manitoba.

The mean size of *T. sirtalis* and *T. elegans* neonates at Creston is within the range of variation among other populations (Tables 8, 9). There are, however, fewer other populations with which to compare, and the variation in neonate size is less than the variation in litter size. Despite the lack of a significant correlation between female SVL and size at birth within some populations (e.g. Gregory 1977; Larsen 1986; this study), female body size does account for some of the observed differences among populations. Among three populations of *T. sirtalis* for which female size-litter size data are available, neonate size increases or remains constant as female size increases: the smaller females at Creston produce smaller young than the larger females at WBNP or the Chilcotin. In a fourth population (Manitoba), females produce smaller young than similar-sized females at Creston (Fig. 37).

Figure 37. Relationship between neonate SVL and female body size in different populations of garter snakes. Each point is the mean SVL of all live young born to a captive female, and data are from the following sources:
WBNP: Larsen (unpublished data),
Manitoba: Gregory (1977),
Chilcotin, south Okanagan Valley: Gregory (unpublished data).


Mean neonate SVL (mm)
SVL (mm)
130
140
150
160
170
180
190
200
210
400
500
600
700
800
900
T. sirtalis
○ Creston
□ WBNP
△ Manitoba
◇ Chilcotin


Mean neonate SVL (mm)
SVL (mm)
130
140
150
160
170
180
190
200
210
400
500
600
700
800
900
T. elegans
○ Creston
□ Chilcotin
△ Okanagan

Recall that females in Manitoba also produced relatively large numbers of young; possibly the "balance" between optimal number and size of young (Smith and Fretwell 1974) has shifted in this population. Without further information on the interactions among litter size, neonate size and reproductive effort, the pattern will remain unclear.

Among the three populations of *T. elegans* for which similar data are available, neonate size increases with increased female SVL (Fig. 37), and the relatively minor differences in mean size at birth (Table 9) are probably due to differences in the size of females in each population. Neonates in a fourth population (Puget Sound, for which female size-neonate size data are unavailable) are much smaller than neonates at Creston, the Okanagan, or the Chilcotin (Table 9). The SVLs of 44 mature females at Puget Sound are similar to those at Creston (460 to 615 mm, Hebard 1950). It is therefore possible that, as with Manitoba *T. sirtalis*, *T. elegans* at Puget Sound exhibit variation in neonate size unaccounted for by female size.

Limited evidence suggests that annual variation in food availability causes such variation in the size of *T. sirtalis* neonates (Seigel and Fitch 1985), but in general, factors influencing size at birth in snakes are poorly understood (Seigel and Ford 1987:238). In a live-bearing lizard, *Sceloporus jarrovi*, thermal regime in an experimental setting during gestation significantly alters size at birth (Beuchat 1988). Caution should therefore be used when comparing data collected from the litters of female snakes held in captivity under different thermal regimes.

Reproductive effort of snakes is less well documented than litter size or neonate size. Only relative clutch mass (RCM1) is reported in most studies. Both

T. sirtalis (Table 8) and *T. elegans* (Table 9) at Creston have a mean RCM1 that is midway between the extremes for each species. While relative reproductive effort of snakes has recently received much theoretical attention (e.g. Seigel and Fitch 1984), variation within species is poorly documented. No evidence for a relationship between relative reproductive effort and female body size has been found in *T. sirtalis*, *T. elegans*, or any other colubrid species for which sufficient data are available (Seigel *et al.* 1986; but see Hailey and Davies 1987). In *Coluber constrictor*, relative clutch mass (RCM2) is lower in populations composed of larger, faster growing individuals (Brown and Parker 1984). Ballinger (1977) suggested that differences in food availability may contribute to relative reproductive effort variation within certain lizards.

There are no populations of *T. sirtalis* or *T. elegans* for which the frequency of female reproduction is well known. At Creston, many females of both species captured in spring were still emaciated because of reproduction during the previous year, and would likely not have been able to acquire enough energy in time for ovulation in May. Reproduction may therefore not always be possible in successive years. Although annual reproduction does occur in female *T. sirtalis* at Creston, it is probably uncommon in both species at this location. Fitch (1965) suggested that most female *T. sirtalis* in Kansas reproduce annually, while Larsen (1986) concluded that most *T. sirtalis* at WBNP do not reproduce each year. Larsen suggested that the short active season prevented the accumulation of sufficient energy for reproduction in successive years. Active season length may therefore account for the probable lack of annual reproduction in females at Creston.

Overwintering and Movements

The thermal and physical characteristics of the hibernacula I constructed may be less favourable than the actual sites used by snakes in this region. The two unenclosed hibernacula therefore may have been unattractive to snakes. Both sites were used as daily and nightly retreats in the fall, so snakes probably had an opportunity to investigate them, although the cues used by snakes to select overwintering sites are completely unknown (Gregory 1982). It is probably not difficult for snakes to locate sites in talus slopes and rocky outcrops where they can descend to depths of greater than one metre, probably achieving increased protection from freezing temperatures (see Macartney *et al.* in press).

The uncommon occurrence of large communal dens in Creston is similar to populations in regions with similar or milder climates (e.g. Vancouver Island, P. Lawson unpublished; Kansas, Fitch 1965; Michigan, Carpenter 1953). In climatically more extreme regions, overwintering aggregations of thousands of *T. sirtalis* (e.g. WBNP, Larsen 1986; Manitoba, Gregory 1977), and hundreds of *T. elegans* (e.g. Chilcotin, Gregory 1984) occur. Individual adult male (but not female) *T. sirtalis* remain at communal dens for over 30 days following emergence (Gregory 1974), which severely limits the time available for feeding and growth (Gregory and Stewart 1975). It is unlikely that snakes that overwinter alone remain near their overwintering sites for long periods, although limited evidence suggests that adult male *Thamnophis* at Creston are relatively sedentary in early spring (see Results: Movements).

At Creston, the apparent abundance of overwintering sites on rocky hillsides, and their close proximity to summer feeding habitat, apparently eliminates the requirement of long distance seasonal migrations (but see below). In regions with longer and more severe winters, suitable sites are less abundant, often resulting in movements of several kilometres between winter and summer habitats (e.g. WBNP, Larsen 1987; Manitoba, Gregory 1977; Chilcotin, Gregory unpublished observations). Potential costs of such migrations include the time spent moving through food-poor terrain (Gregory 1982) and the risk of predation while travelling through unfamiliar areas (Larsen 1987).

Caution should be used when inferring movements based on the recapture data obtained in this study. The actual distances moved may be greater than such data suggest, because sedentary snakes are more likely to be captured than snakes that move long distances. Home range, too, was probably underestimated because of the small number of capture locations (maximum of five) used in calculating home range size (cf. Jennrich and Turner 1969).

The influence of body size on vagility in snakes is not well known (Macartney *et al.* 1988). In this study, small *T. elegans* apparently moved shorter distances and had smaller home ranges than large *T. elegans*. This may be associated with the relatively low endurance of small garter snakes (Pough 1977) or with differences in foraging behaviour. Slugs (the major prey of small *T. elegans*) probably occur at higher densities than small mammals (the major prey of large *T. elegans*), thereby not requiring small snakes to travel great distances in search of food.

The relatively sedentary nature of female snakes during at least part of gestation has been observed in Manitoba *T. sirtalis* (Gregory 1975), and numerous other species (see Gregory *et al.* 1987 for a review). This may be associated with a higher energetic cost of locomotion, due to the mass of developing embryos within gravid females (Seigel *et al.* 1987). The related occurrence of gravid female aggregations may be caused by attraction to sites with favourable cover and thermoregulatory opportunities. Other explanations include predator deterrence (Shine 1979), and increased probability of escaping while a predator captures another member of the group (Gregory *et al.* 1987).

Feeding

Variation in the proportion of garter snakes captured with food varied as much among months during this study as it does among different studies (in which different months are not grouped separately). The seasonal variation I observed is possibly associated with seasonal variation in prey abundance (Garcia and Drummond 1988), although Seigel (1984) detected no differences in the foraging success of *T. sirtalis* among seasons despite marked variation in prey abundance. Since the time of year during which snakes were sampled varies among studies, comparisons of overall proportions of snakes with food should therefore be made with caution. In *T. sirtalis*, the overall proportion of snakes captured with food in other studies ranges from 18% (Fouquette 1954) to 63% (Lagler and Salyer 1945). In *T. elegans*, the proportion with food varies from 22% (Fleharty 1967) to 41% (Gregory 1978). The proportion of snakes with food for each species in this study is not unusually high or low, and reduced food availability is therefore probably not the source of differences in growth and reproductive characteristics discussed previously.

In order to infer feeding frequency directly from the proportion of snakes captured with food, it is necessary to assume that the length of time a prey item is detectable in the stomach does not vary among individuals and among prey items. This assumption is almost certainly not met. Hamilton (1951) suggested that earthworms were underrepresented in the stomachs of *T. sirtalis* because they were rapidly digested; the same may apply to slugs eaten by *T. elegans*, although their mucous secretions may act to slow digestion. The influence of relative prey size on digestion rate is unclear. Naulleau (1983) and Stevenson *et al.* (1985) found that relative prey mass had little effect on rate of digestion in *Vipera aspis* and *T. elegans*, respectively, but neither study included very small snakes. Skoczylas (1970) suggested that both size and type of prey affected digestion rate in *Natrix natrix*, with relatively larger prey taking longer to digest. In this study, then, it is unlikely that small snakes digested their relatively smaller meals more slowly than large snakes. The actual difference between the feeding frequency of small *vs.* large snakes is probably at least as great as that suggested by the proportion of snakes with food (Fig. 22).

The ontogenetic decrease in the proportion of *T. elegans,* and possibly *T. sirtalis*, captured with food therefore probably represents a decrease in feeding frequency. Although ontogenetic patterns of energy utilization are relatively well known in some reptiles, particularly lizards (Congden *et al.* 1982), variation in energy acquisition is poorly documented, and even less well understood. Decreased feeding rate in large garter snakes (Fig. 22) is probably compensated by an increase in the relative amount of food eaten at one time (Fig. 32). The efficiency with which snakes of different sizes convert food energy into snake mass is poorly known, and varies among studies. Diller and Johnson (1988) documented increased efficiency in small *Crotalus viridis*, a result similar to that of Gehrmann (1971) for *Nerodia erythrogaster*. Dmi'el (1967), however, found decreased production efficiency in small *Spalerosophis cliffordi*, and Ford (1974) found no size-related differences in the efficiency of digestion in captive *Elaphe obsoleta*. Young reptiles possess higher relative metabolic rates than older individuals (Bennett and Dawson 1976), and the pressure to consume relatively large quantities of food is therefore probably great. Not surprisingly, smaller individuals in snake populations appear to have relatively high annual energy intakes (Godley 1980; Diller and Johnson 1988).

The energetic demands of reproduction in mature reptiles, particularly females, involve changes in energy allocation (Congden *et al.* 1982). Female *T. sirtalis* and *T. elegans* at Creston direct a large proportion of their body mass towards offspring, and most of this mass must be obtained prior to gestation. I did not detect unusually high feeding rates in non-gravid females, but the proportion of gravid females found with food was low, particularly in the late stages of gestation. Reduced feeding rates in gravid snakes have been documented in a number of species (see Shine 1980 for a partial list, and Shine 1981 for an example of the opposite), including a Manitoba population of *T. sirtalis* (Gregory and Stewart 1975). Shine (1980) suggested that since gravid females may experience reduced locomotory performance, they may therefore be less capable predators than non-gravid females. Reductions in both speed and endurance have, in fact, been demonstrated in gravid *T. marcianus* (Seigel *et al.* 1987). A possible effect of the decrease in feeding rate of gravid females may be slower growth, as appears to be the case in *T. elegans* (Fig. 11). The "trade-off" between growth and reproduction may be an important influence on size-related life history traits such as litter size and neonate size.

The types of prey eaten by *T. sirtalis* and *T. elegans* at Creston are not unusual, but, as in most populations previously studied, only a fraction of the known prey types for each species was recorded. *T. sirtalis* eats more mammals at this location than elsewhere (cf. Carpenter 1952a; Fitch 1965; Gregory 1978; Nelson 1988), and *T. elegans* consumes fewer fish (cf. Fox 1952; Gregory 1978). Geographic variation in innate prey preference has been documented in both *T. sirtalis* (Dix 1968; Burghardt 1970) and *T. elegans* (Arnold 1977). In *T. elegans*, Drummond and Burghardt (1983) have also documented geographic variation in the behaviour of foraging snakes. Food availability is probably an important source of such variation: Kephart (1982) found that dietary variation among sites in northern California was several times greater than the variation between *T. sirtalis* and *T. elegans* occupying such sites. Clearly, there is much plasticity in the feeding ecology of both species. Detailed studies of the effects of food availability on diet at different locations are required to evaluate this plasticity.

The ontogenetic changes in the diet of *T. sirtalis* at Creston parallel the results of Carpenter (1952a), Fitch (1965), Seigel (1984), and Gregory (unpublished data). In each study, small snakes ate earthworms. The proportion of earthworms in the diet decreased in larger individuals, to be replaced by amphibians and sometimes small mammals. Unlike at Creston, however, large *T. sirtalis* (greater than 400 mm SVL) in Kansas excluded earthworms from the diet altogether (Fitch 1965). This type of ontogenetic shift is similar to that for *T. elegans* at Creston and on Vancouver Island (Gregory unpublished data; see below).

The relatively smaller size of prey eaten by small garter snakes was predicted by Pough (1977), based on their relatively low physiological endurance. Pough obtained support for his prediction using overall mean prey sizes eaten by different size classes of *T. sirtalis* in Kansas; this study provides further evidence that small snakes of this species (but not all species; see Voris and Moffett 1981) eat relatively small prey.

Prey selection in both species is probably correlated with changes in morphology and physiology, rather than energy allocation, during ontogeny. Increases in body size and head size allow larger objects to be swallowed without affecting the minimum size of prey that can be eaten (Pough and Groves 1983). Therefore the range of types and sizes of prey available to snakes increases during ontogeny, and an expansion of the diet is in fact predicted by optimal foraging theory (Pyke *et al.* 1977). Ontogenetic dietary expansion occurs in many snake species (see Godley *et al.* 1984 for a partial list), including other populations of *T. sirtalis* (Carpenter 1952a; Fitch 1965; White and Kolb 1974; Gregory unpublished data) and *T. elegans* (White and Kolb 1974; Gregory unpublished data).

The apparent avoidance of small prey (slugs) by large *T. elegans* is interesting. A similar pattern has been observed in *Nerodia rhombifera* (Plummer and Goy 1984), *Regina alleni* (Godley 1980), *Epicrates striatus* (Henderson *et al.* 1987), some *Vipera* species (Saint Girons 1980), some *Crotalus* species (Mackessy 1988), and other populations of *T. elegans* (Jansen 1981; Gregory, unpublished data). The common theme in all of these cases is a shift from a smaller prey type to a larger prey type, rather than size discrimination within one prey type. These shifts are possibly mediated by ontogenetic shifts in responsiveness to prey odours (Mushinsky and Lotz 1980; Mushinsky *et al.* 1982) and/or behavioural changes affected by experience (Burghardt and Pruitt 1975). *Microtus* may be dangerous prey for garter snakes (personal observations), and the risk of injury while feeding may force specialization on *Microtus* to be delayed until a size large enough to avoid serious injury has been attained. It is possible that greater prey specialization occurs in large *T. elegans* than large *T. sirtalis* because *T. elegans* possesses adaptations such as constricting behaviour (Gregory *et al.* 1980), enlarged teeth at the posterior end of each maxilla (Wright *et al.* 1979), and oral gland secretions that may digest or immobilize prey (Jansen 1987). These adaptations may improve its ability to consume large, active prey. Regardless of proximate cause, specializing on a single larger prey type may reduce the time spent foraging, and the associated risk of predation (Mushinsky 1987). Seigel (1984) suggested that *T. sirtalis* in Missouri maximized their net energy intake by concentrating on frogs instead of earthworms, particularly when frogs were abundant. Perhaps it is not profitable for large *T. elegans* to stop and eat the slugs they encounter, especially if doing so reduces their rate of encountering larger prey such as *Microtus*.

Conclusions

The life history traits of *T. sirtalis* and *T. elegans* at Creston are not unusual. It is possible that garter snakes at this location grow more slowly than those in some other regions, but convincing data are lacking, especially for young snakes. It does appear, however, that adults at Creston are relatively small compared with most other populations, and that small body size accounts for the smaller number of young produced by *T. elegans*. A similar explanation may not hold true for *T. sirtalis*, in which litter size and neonate size variation not associated with body size variation occurs. Perhaps *T. sirtalis* is more flexible in its life history, and is able to adjust its reproductive characteristics according to local conditions to a greater extent than *T. elegans*. Further information from more populations of both species is required to evaluate this hypothesis, but it may partly explain the wider geographic range and greater diversity of habitats occupied by *T. sirtalis* compared with *T. elegans* or any other snake in North America.

Other aspects of the ecology of garter snakes at Creston are also not unique, but this study suggests that an abundance of overwintering sites and their close proximity to summer feeding habitat results in more limited movements at Creston than in many other regions. Evidence also suggests that variation exists in the extent to which individuals of different size and reproductive status move during the course of an active season. A better description of this variation could be obtained using radiotelemetry to follow the movements of different individuals on a daily basis.

The proportion of garter snakes captured that contained food was comparable to previous studies, and reduced food availability is an unlikely source of differences in life history characteristics between populations in Creston and those elsewhere. However, the large amount of variation in feeding frequency within each species at Creston suggests that comparisons among studies are of questionable validity. Future studies would benefit by more detailed assessment of potential food availability within a particular habitat.

Small garter snakes, particularly *T. elegans*, feed more frequently, and consume fewer types of prey of relatively smaller size than large snakes. In these respects and others, small *T. sirtalis* and *T. elegans* are probably ecologically more similar to each other than they are to larger individuals of their own species. Larger body size is accompanied by increased food availability, although, as observed in this study, large *T. elegans* at Creston become small mammal specialists. Energetic considerations, rather than physical limitations, may explain the foraging patterns of large garter snakes.

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