ECOLOGY OF THE COMMON GARTER SNAKE, *THAMNOPHIS SIRTALIS*, AT THE NORTHERN LIMIT OF ITS RANGE

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ABSTRACT

Population ecologists concern themselves with two fundamental, and related, kinds of questions. How (and why) do life history traits vary in different environments? What factors limit the distribution and abundance of a species? The answers to such questions depend, on part, on an understanding of patterns in nature, but patterns need to be described before they can be analyzed. The aim of this study was to document the annual cycle and life history characteristics of a wide-ranging species at the edge of its range and compare them with the ecology of the same species in contrasting environments elsewhere.

The common garter snake, *Thamnophis sirtalis*, is the most widely distributed snake species in North America, ranging further north than any other reptile on the continent. This species has been well studied in several geographic locations, but never at its northern limit. From 1983 to 1985, the ecology of *T. sirtalis* was examined near Fort Smith, Northwest Territories, the known northern limit of the species. The study centred around the Salt River den, in Wood Buffalo National Park (WBNP).

The active season in WBNP is short, and weather conditions during that period are sometimes harsh. Garter snakes in the Salt River den begin emerging very early in the spring (mid to late April), when snow cover is still prevalent. Body temperatures as low as 0.5°C were recorded for emerging snakes. The total period of activity at the den (emergence and mating) was quite short, with the vast majority of the population having dispersed by the second week in May.

The distance from the Salt River den to the nearest summer habitat (marshes) is approximately 3.75 km. Mark-recapture and biotelemetry studies indicated that snakes undertake an annual migration to and from this area, presumably in search of food (which is predominantly frogs). One snake completed a round-trip of over 15 km in 1984. Migrations such as this may be costly, both in terms of the time taken to complete the journey between the den and marsh (9 to 13 days for two radio-tracked snakes) and the energy expended. The time taken to migrate to the marshes in the summer is also affected by variable weather conditions.

Growth of snakes was measured by changes in length of recaptured snakes. A paucity of growth records for immature snakes prevented the construction of formal growth curves. However, analysis revealed that growth of adults was similar to that of the same species in Manitoba, but considerably less than that of Kansas snakes. Male and female snakes in WBNP reach sizes that, on average, are larger than those reported elsewhere. The reason for this is unknown.

Only five mature females were recaptured frequently enough to permit interpretation of their reproductive history. However,these few data suggest that females do not reproduce annually, in contrast to the situation in warmer environments. Females may fail to reproduce every year because of the shortness of the season. Birth occurs late in the summer (late August), and most postparturient females are probably unable to feed prior to hibernation. Hence, one (or possibly more) summer(s) may be spent re-attaining reproductive condition, and low annual recruitment is a possible consequence of the short active season. Although gravid females in Wood Buffalo National Park were much larger than those in Manitoba and British Columbia populations, there was not a corresponding increase in litter size (mean=11.6 in WBNP). No clear interpretation of this is possible at present.

Surface and subsurface temperatures were measured in the Salt River den, and in a nearby control. Temperatures in the former were warmer and more stable through winter, implying that only certain sites can function as overwintering facilities. The temperature of a hibernating snake (measured through telemetry) remained in the 2-6 °C range during winter. Emergence patterns of the snakes in the spring were not strongly correlated with a reversal in the surface/subsurface temperature gradient.

It is not possible to conclude, from this study, what determines the northern limit of *T. sirtalis*, but the leading potential factors are length of active season and availability of hibernating sites.

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DEDICATION

This thesis is dedicated to my parents, Leona and Walter Larsen, who did not share my enthusiasm for reptiles and amphibians, but nevertheless tolerated and encouraged my interest.

INTRODUCTION

What are the factors responsible for the patterns seen in nature? In recent years, numerous researchers have attempted to predict how life-history traits should vary in different environments (see Stearns, 1976 and Rose, 1983 for reviews). Unfortunately, the collection of empirical data on life-history variation has not kept pace with the proliferation of theoretical models. This is an undesirable situation, for natural history provides the basis for theory, and thus is essential for the formulation of testable hypotheses (Greene, 1986). Patterns of varying life-histories may be sought through long-term studies of a relatively monotypic group of organisms (i.e. a 'species') under a variety of environmental conditions, such as wide-ranging geographic locations. In this manner, differences in life-histories, should they exist, may be realized and interpreted, with phylogenetic effects being minimized, providing the basis for more analytic approaches. Such studies may reveal the precise manner(s) in which organisms are limited in distribution and abundance.

Reptiles, as ectotherms, likely are prohibited from colonizing high latitudes by climate. However, the exact manner in which climate limits their range and abundance is often unclear. For example, the specific factors restricting the distribution of any species of snake are unknown. Short summers may severely restrict the length of the activity season. This in turn may significantly influence demography; growth may be limited, which may in turn lead to reduced reproductive output of individuals, lower population recruitment, and reduced ability of the population to respond to declines in numbers. Long, cold winters also pose great challenges to survival, and suitable hibernation sites are critical (Gregory, 1982).

The relative importance of these factors in limiting snake distributions remains to be seen. However, any assessment of them will depend on an understanding of the basic ecology and life cycle of snakes at high latitudes.

The common garter snake, *Thamnophis sirtalis*, is the widest ranging snake species in North America. One subspecies *(T. s. parietalis)* ranges further north than any other North American reptile. *Thamnophis sirtalis* is also probably the most studied snake in North America. Its ecology has been examined in numerous parts of its range (e.g. Michigan- Carpenter, 1952a and b; Kansas- Fitch, 1965; Manitoba- Aleksiuk and Gregory, 1974 and Gregory 1977; California- Kephart, 1981). However, it has never been studied near the northern limit of its distribution. The objective of this study was to examine the annual cycle and life history of *T. sirtalis* near the northern limit of its range (Fort Smith, N.W.T.). I asked several specific questions, all of which were related to the presumed problems posed by short summers and long winters:

1. How does the annual growth rate of *T. sirtalis* at its northern limit compare with that reported in more southerly localities? Lower growth rates might have important demographic consequences, especially if sexual maturity is delayed.

2. What movement patterns are exhibited by snakes during the summer months ('active season')? Previous studies have suggested that long-distance migration between hibernating sites and summer habitats is common in northern populations, and that it may reflect a shortage of suitable hibernating sites (Gregory, 1984a).

3. What are the reproductive characteristics of the northernmost populations of *T. sirtalis*? Areas of special concern were the frequency with which sexually mature females give birth, and the size of litters relative to those reported for more southerly populations. Such data (along with estimates of mortality) are of obvious importance in determining if low recruitment rates are limiting northern populations.

4. What are the physical properties associated with snake hibernacula, and how abundant are hibernacula? A scarcity of suitable overwintering facilities would inhibit populations from colonizing new areas.

In addition to answering these major questions, I collected data on other aspects of the ecology of these snakes, such as population size and structure, and feeding habits.

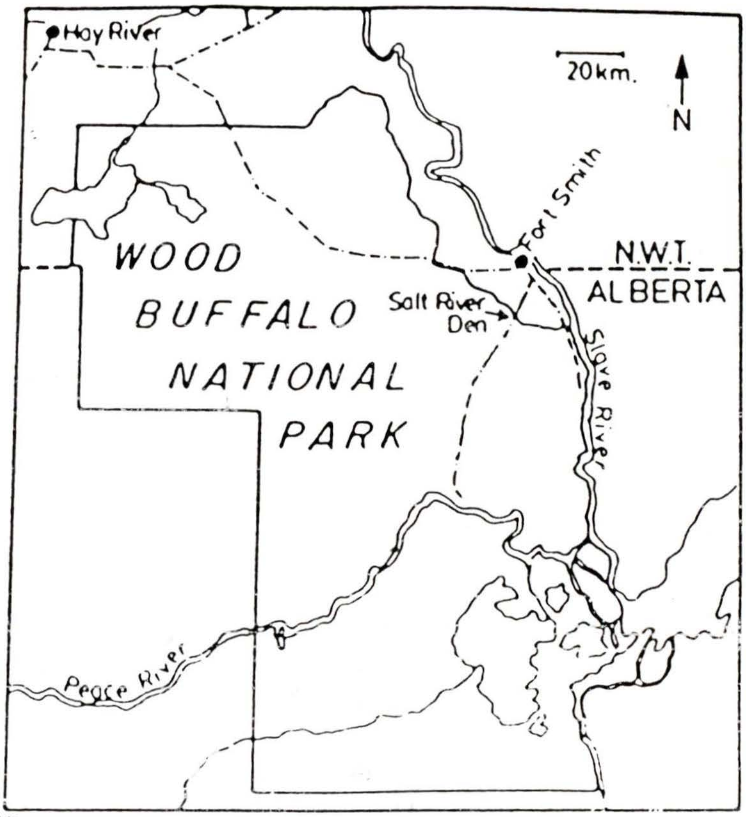
THE STUDY AREA

General

Communal denning of temperate zone snakes has been documented for a number of species. Such dens (or hibernacula) may house from a few individuals to several thousand snakes, as has been observed in the Interlake region of Manitoba (Gregory, 1977). Also, denning snakes often show a strong tendency to return to the same den year after year ('den fidelity'). This provides the researcher with repeated access to a large number of individuals, a situation very desirable when conducting population studies.

Although communal garter snake dens are known at several sites in the northern part of the range, most are inaccessible. This study focused on the Salt River den (SRD) in Wood Buffalo National Park (WBNP) on the Alberta-Northwest Territories border. The SRD was, until this study, the most northerly overwintering site known for *T. sirtalis*. It is easily reached by road from Fort Smith, N.W.T., approximately 24 km north of the den (Figure 1). During the course of the study other hibernacula were located in the general region, including one in the N.W.T., but they received comparatively less attention.

Figure 1: Range of *Thamnophis sirtalis* (after Stebbins, 1985). * indicates some examples of where the ecology of the species has been (or is being) studied: central British Columbia (Chilcotin) - Gregory, 1984a; Manitoba - Gregory, 1977; Michigan - Carpenter, 1952a and b; northern California - Kephart, 1981; Kansas - Fitch, 1965. Inset shows Wood Buffalo National Park and location of the Salt River den.


Hay River
20km.
N
Fort Smith
N.W.T.
ALBERTA
Salt River Den
Slave River
WOOD BUFFALO NATIONAL PARK
Peace River

Climate

The climate in the Fort Smith/WBNP area is continental sub-arctic, with short, dry summers and long, cold winters. Figure 2 compares the mean monthly temperatures of Fort Smith to a sample of other locations where the ecology of *T. sirtalis* has been studied. Above-freezing temperatures arrive in Fort Smith later in the year than in these other areas. Temperatures in Fort Smith also drop off much sooner in the fall, with a mean temperature of 0°C being reached near the start of October. Also, the actual temperatures experienced in the area during the course of the summer are, on average, lower than in other areas of the species' range, and are more variable (Table 1). During 1985, for example, there were incidences of frost during each of the summer months (personal observation).

Thus, the 'quality' of the active period available to snake populations near Fort Smith is relatively unfavourable when compared to that found further south. This 'quality' is perhaps better expressed as growing degree-days (degree-days above 5°C Environment Canada, Atmospheric Environment Service, 1982b). As Figure 3 indicates, total growing degree-days in the Fort Smith area varied during this study. Summers were warmer than normal, at least in midsummer, in 1983 and 1984, but cooler than usual in 1985.

Table 1: Long-term temperature statistics (May-September) for various sites of research on *Thamnophis sirtalis*.

mean=mean daily temperature, S.D.=standard deviation, C.V.=coefficient of variation [(S.D./mean)100]; Source: Environment Canada, Atmospheric Environment Service, 1982a.

location	mean	S.D.	C.V.
Vernon, Okanangan Valley (British Columbia)	16.6	1.4	8.4
Williams Lake (Chilcotin, British Columbia)	12.5	1.6	12.8
Winnipeg (Manitoba)	15.7	1.8	11.5
Fort Smith (N.W.T.)	11.8	1.6	13.6

Geophysical and Biotic Characteristics:

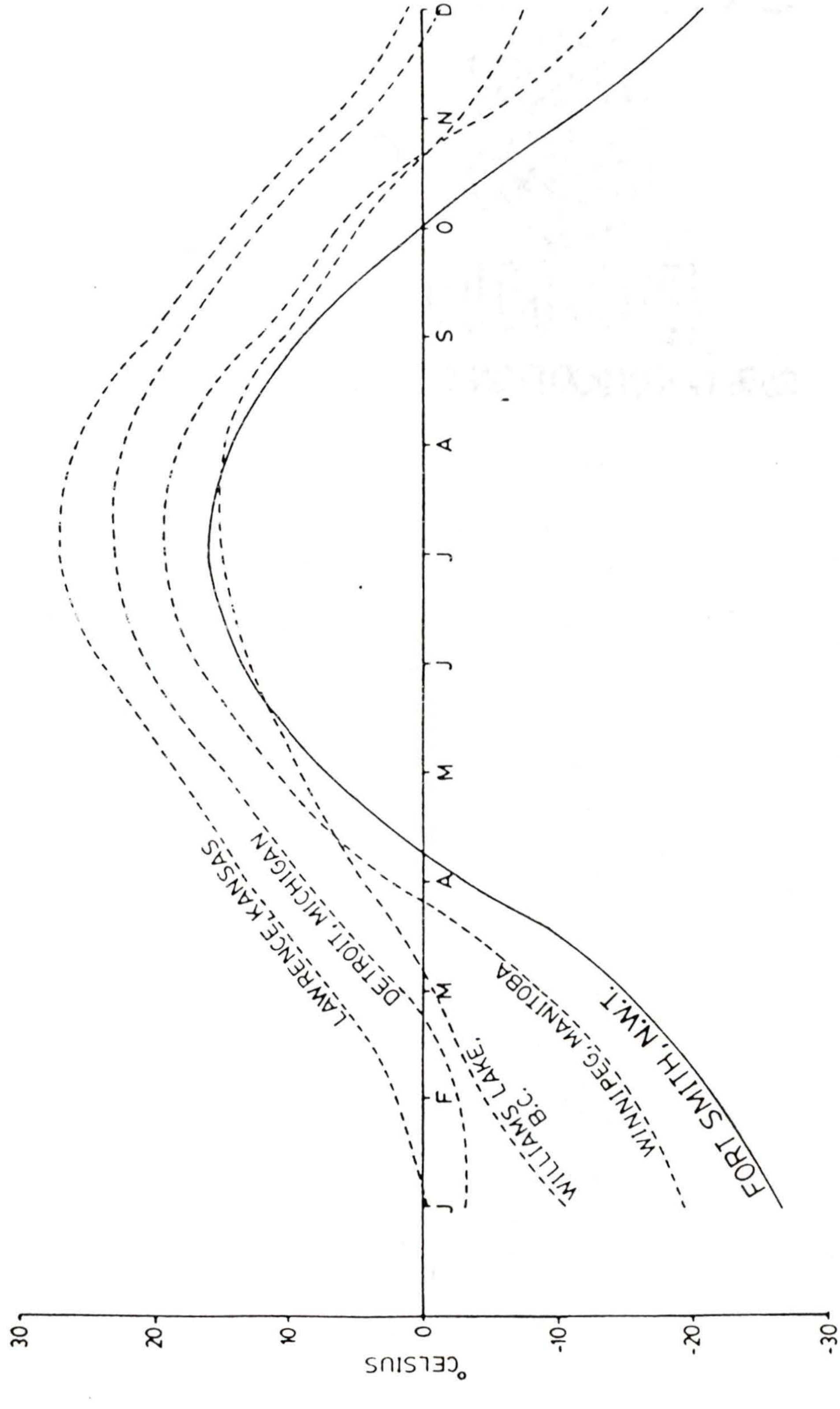
WBNP lies within the Interior Plains region of North America (Cobus and Church, 1977). However, unlike the southern portions of the Canadian prairie provinces, which are covered by grassland, most of WBNP is boreal forest, or a transition zone dominated by poplars *(Populus)*. Interspersed on this basic physiography are several secondary landscape features. A band of karst topography extends across the park, and within it caves, sinkholes and other karst structures are quite common. The SRD (Figure 4) consists of a collapsed sinkhole, similar to the snake dens described by Gregory (1977) in Manitoba. Numerous cracks and openings in the rock allow snakes to get underground, presumably below the frostline. All other dens found in the area were associated with sinkholes, fissures, or some other type of karst feature.

Because of the flat surface of the land, much of WBNP is poorly drained. WBNP also lies within the zone of discontinuous permafrost, which also contributes to the presence of saturated soils (Brown, 1960). This in turn leads to the formation of muskeg, sedge meadows, extensive fields of dwarf birch *(Betula nana)* and other similar communities. Most of the surface water in the karstland is saline, a result of underground salt springs (Cobus and Church, 1977).

The faunal composition of the area is that typical of the boreal forest (Larsen, 1980).

Figure 2: Comparison of the mean monthly temperatures of locations where the ecology of *Thamnophis sirtalis* has been studied.

(sources: Environment Canada, Atmospheric Environment Service, 1982a, for William's Lake, Winnipeg and Fort Smith data; National Oceanic and Atmospheric Administration, 1974, for Kansas and Detroit data).


°CELSIUS
30
20
10
0
-10
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F
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J
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S
O
N
D
FORT SMITH, N.W.T.
WINNIPEG, MANITOBA
WILLIAMS LAKE, B.C.
DETROIT, MICHIGAN
LAWRENCE, KANSAS

Figure 3: Total growing degree-days for Fort Smith, during each year of the study.

Also shown is the 30-year norm for the area (source: Environment Canada, Atmospheric Environment Service, 1982b).

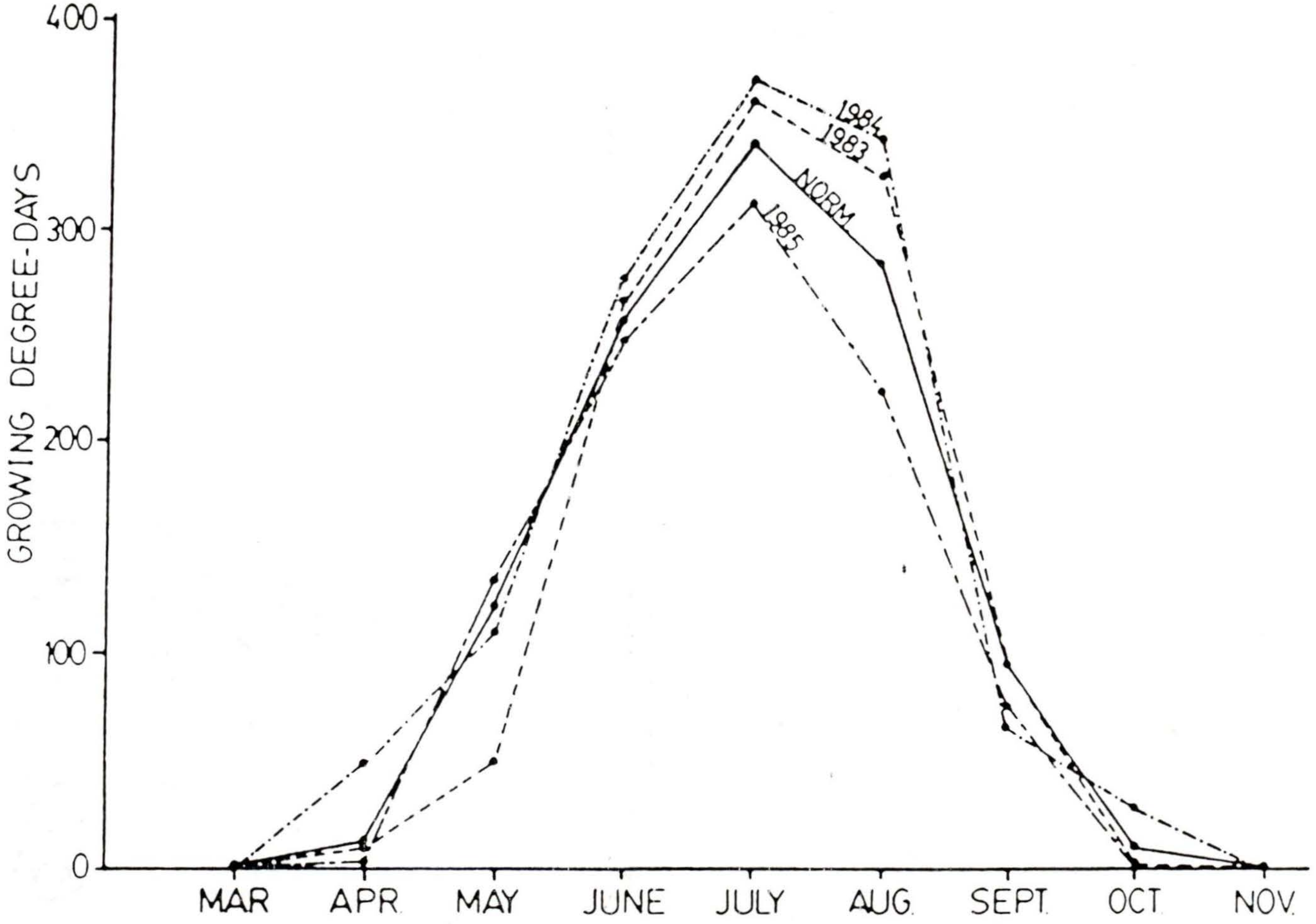

400
300
200
100
0
GROWING DEGREE-DAYS
MAR
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
1984
1983
NORM
1985

Figure 4: Photograph of Salt River den (SRD) in spring.

METHODS AND MATERIALS

General

This study was conducted from Spring 1983 to Autumn 1985, and consisted of two main components: sampling of snakes at the den in the spring and fall, and searching for snakes in other habitats during the summer. At the den, I captured snakes by hand. During the field season of 1984, I attempted to circle the SRD with drift fences and funnel traps (Fitch, 1951) in order to increase the probability of capturing dispersing or returning individuals. I was forced to abandon this approach because of constant damage inflicted on the fences by large mammals (*Bison bison* and *Ursus americanus*).

During spring emergence, I remained in the immediate vicinity of the den on most of the days when the snakes were active. When first captured, each snake was initially sexed by probing for hemipenial pouches (Schaefer, 1934) or, in the case of juveniles and neonates, by using Gregory's (1983) method. An individual mark was assigned to each snake by clipping a unique combination of subcaudal scutes (Blanchard and Finster, 1933). Also at this time, and at all subsequent recaptures, I measured the snout-vent length (SVL) of each snake, usually to within the nearest 5 mm. Similarly, the weight of each snake was measured using a Pesola spring scale, graduated in 2-g intervals. In order to avoid unnecessary recaptures of the same individuals during the same emergence period, I marked the dorsal stripe of each 'processed' snake with a small dot, using a waterproof felt pen. This allowed me to determine whether or not a snake had been previously captured, without disturbing the animal.

Generally, I avoided disturbing mating groups, preferring to wait until after the female(s) had copulated. If possible, I would capture and process an emerging female before she became engaged in mating. This apparently had little effect on the behaviour of the snakes, as both males and females were observed copulating shortly after they had been measured and marked.

During the spring of 1985, I periodically arrived at the den early in the morning, before the snakes had begun emerging. At this time I searched under cover-objects and in the leaf litter, to determine if any snakes had remained on the surface overnight. Cloacal temperatures of snakes were taken using a Schultheis quick-reading pocket thermometer. Air temperatures were measured at chest height, with the thermometer shielded from direct sunlight and/or wind. Substrate temperatures also were taken with the thermometer shielded.

During the summer months of 1983, I searched for snakes in a wide variety of directions and habitats. In 1984 and 1985 this searching became restricted to areas where snakes had been more frequently encountered. Snakes captured in the field were processed in the same manner as those captured at the SRD.

Population Dynamics

Estimates of the number of male snakes at the SRD was made using the Jolly-Seber method of multiple mark/recapture analysis (Seber, 1982); too few females were captured for their numbers to be estimated using this technique. The Jolly-

Seber analysis provides estimates of recruitment and survivorship as well as population size. Gregory (1977) discusses the degree to which assumptions of this analysis are met when the technique is applied to a denning population of *Thamnophis:*. Essentially, his arguments and provisions hold true for this study: dispersal of marked snakes can be considered complete between sample times, and the mark assigned to each snake was permanent and likely did not affect the survival chances or catchability of the bearer. Another assumption of the method is that every marked animal has the same probability of being sampled at a given sampling period; this will be true only if individual snakes return to the SRD each fall. Although the degree to which the WBNP snakes exhibited den fidelity was not tested directly (as only one den was intensively sampled), there was little reason to suspect that it would differ significantly from that in Manitoba, where Gregory (1977) calculated that approximately 96% of denning snakes returned to their den of origin. Furthermore, during the second and third years of this study, the vast majority of older male snakes at the SRD had been found there previously.

Although the Jolly-Seber analysis could not be applied to females, simple Petersen estimates (Seber, 1982) were made of the number of females entering the den each fall; i.e. the females captured at the den each fall were considered 'marked', and the population estimate was then calculated based on the proportion of these marks in the subsequent spring sample. Use of the Petersen estimate is appropriate in this case, as recruitment does not occur between the sampling periods (Gregory, 1977). Petersen estimates also were made for male snakes.

In species in which parental care is undeveloped, survival rates between mature and immature animals are often significantly different (Pianka, 1983). Although age-specific mortality in *Thamnophis* has not been determined, it is quite likely that immature individuals (<400 mm SVL, see Results) suffer higher mortality. Therefore, all immature snakes captured at the SRD were omitted from the analyses of population size, even though they represented a very small number of snakes.

I analyzed the relative proportions of the sexes using autumn samples. During this time period, I noted no obvious behavioural differences between the males and females (as reported by Gregory, 1984a, for Manitoba *Thamnophis*), implying that samples taken during this time could be considered random. One exception to this was gravid females returning to the den. These females would continue to bask at the den until parturition, thus increasing their likelihood of being captured. However, there were never more than a few gravid females at the den each fall, so any bias their presence might introduce was minimal. Neonates at the den in the fall were excluded from sex composition analysis, as their occurrence was attributable solely to the presence of their mother. I estimated the standard errors of the proportions of males using the method described by Cochran (1963:51) and used by Gregory (1977). Fall sex ratios were tested against a theoretical 1:1 sex ratio, using chi-square goodness of fit (Zar, 1974) and a rejection level of alpha= 0.05.

Movements

I obtained some information on the movements of the snakes from the SRD through the recapture of marked individuals. However, more detailed information on migration and movement patterns was acquired through biotelemetry. Snakes were equipped with surgically-implanted radiotransmitters which were capable of transmitting a signal over several hundred m, depending on terrain, for approximately four months. This eliminated the need for intermittent recapture of the tracked snakes, thus minimizing disturbance to the animals (subsequent findings revealed that simply recapturing the transmitter-equipped snakes during the course of the summer would, in itself, have been very difficult if not impossible). Unfortunately, a consequence of choosing a transmitter with a relatively long 'life' was that the final transmitter/battery assemblage (6 g., 30x18 mm.) could be implanted safely only in the largest snakes. Choosing smaller subjects would have increased greatly the likelihood of the transmitter implantation affecting the movements, normal behaviour and/or survivorship of the individuals concerned.

My first attempts at following transmitter-equipped snakes demonstrated that simultaneous tracking of more than two individuals was not feasible, because of: (1) available manpower and telemetry equipment, (2) the great distances snakes were capable of moving in a relatively short time, (3) the inaccessibility of the region surrounding the SRD, and (4) the poor signal quality when the snakes moved through forests or other heavily vegetated areas. As a result of these and the aforementioned constraints, I radio-tracked two large female snakes during the 1984 active season, and a third large female in 1985.

Snakes chosen for biotelemetric study were captured shortly after they emerged from the SRD, and transported to Fort Smith where they were equipped with the transmitters (SM1, AVM Instrument Co.). The transmitters were potted in a 1:1 paraffin-beeswax mixture, and then waterproofed with two coats of liquid plastic (Plasti Dip, Plasti Dip International - after Jansen, 1982). Surgical anesthesia was induced by supplying halothane (Fluothane B.P., Ayerst Laboratories) through a head mask, with the concentration of gas regulated using an oxygen tank, a flow meter and a Mark IV vapourizer (Cyprane Ltd). The time taken for the snakes to reach a surgical state of anesthesia (using the criteria of Bonath, 1979) ranged from 25 to 55 minutes. The surgical procedure was similar to that of Reinert and Cundall (1983): The transmitter was implanted extraperitoneally in the lower abdomen, and the antenna was threaded under the skin anteriorly, using a slim metal sleeve. Incisions were closed using nylon sutures. Following closure, the halothane was turned off but the snake was maintained on oxygen until recovery (about 15 minutes).

After surgery, I held the animals in captivity for two to three days, to permit at least some recuperation from the surgery and to ensure that the transmitter was functioning normally. Each snake was released at the den during the late afternoon, when the declining ambient temperatures would force it to retreat into the den and remain there for the night. I commenced tracking the following morning, when the snakes emerged from the den.

Upon their departure from the SRD, the transmitter-equipped snakes were followed on foot, using a hand-held, collapsible antenna and a portable receiver (LA12-D2, AVM Instrument Co.). I made every attempt to observe the snakes from a distance, using binoculars when possible, in order to minimize disturbance. Because of the highly directional, and hence predictable, movements of the snakes, it was often possible to move ahead, secure a good vantage point, and then observe the animal as it moved along its course. Generally, the position of each snake was determined throughout the day, either by making periodic checks or, on occasion, through constant monitoring. Using flagging ribbon, I also marked the route used by each snake. This allowed the path to be retraced and traversed for mapping purposes. When the snakes appeared to have ended their daily movements, I placed a maximum-minimum recording thermometer on the ground, near the snake. This provided me with some information on the overnight temperatures experienced during the migration.

This tracking procedure was followed as long as was possible. Eventually, however, the migrating snakes reached a system of interconnected marshes and ponds, and I could no longer track the snakes on foot; canoeing was also impractical. At this point the position of each animal was periodically determined by attaching antennas to the wing struts of a small airplane (Cessna-185 float plane) and flying a close grid pattern over the marshes, at approximately 45 m above ground level. Once the signal was located, I was able to obtain the approximate location of the snake by triangulating on known landmarks.

Diet

Snakes captured during the summer and fall periods were examined for gut contents by gently palpating any stomach contents into the oral cavity, where identification of prey type was usually possible. Following this, the food was palpated back into the stomach of the animal. In this manner, data on prey selection often could be obtained without depriving the snake of the meal. Because gut contents usually were not removed from the snake, several stomach contents were not identified to species, but only to a general category (e.g. anurans). Some data on prey type were also obtained by dissecting road-killed snakes.

I carried out an informal examination of the types and sizes of prey that would be taken by captive snakes of various sizes, including young snakes born in captivity. I did not actually feed gravid females (see Reproduction below), but only noted their response to the scent of the prey.

Growth

Linear relationships between the weights and lengths of the male and female snakes were obtained using log-log transformations. Tests for differences in the slopes and intercepts of the regressions followed Zar (1974), with a rejection level of alpha=0.05.

I used changes in the lengths of recaptured snakes to represent growth. Length is less subject than weight to temporary variation, which may be caused by the presence or absence of food or water in the gut or, in the case of mature females, by reproductive condition. In fact, it was not uncommon to encounter a snake that had substantially increased its length over the past year while apparently maintaining its original weight. Because the vast majority of snakes were marked and recaptured at the SRD, most records represented growth over one active season, or a multiple thereof.

I obtained very few growth records for juvenile and neonate snakes. Thus, constructing a particular growth curve (e.g. Von Bertalanffy, logistic, Gompertz - see Kaufmann, 1981) would have required that adult growth patterns be extrapolated to young snakes, an untestable assumption. Also, the very few repeated growth records of younger snakes (i.e. resulting from a long series of successive recaptures) that I did collect were somewhat limited in value, as it was impossible to attach a definite age to these individuals. Therefore, I confined my examination of growth to analysis of Walford plots (Ricker, 1975) of changes in size of adults, as employed by Gregory (1977). This involved plotting the length of an animal at the end of an active season (SVL_{t+1}) as a function of its length at the start of the season (SVL_t) Predicted asymptotic size was taken as the point at which $SVL_t=SVL_{t+1}$. Walford plots were compared among sexes and years by Zar's method (1974:228-230) with a rejection level of alpha= 0.05.

Reproduction

I obtained information on litter sizes by capturing gravid females during the later part of the summer (after July 1) and housing them in aquariums until parturition. Light bulbs were positioned above the aquariums, and females frequently basked in the heat. Captive gravid females were not fed, in order not to influence litter characteristics, such as size of young (gravid females feed very little in the later stages of gestation, Gregory and Stewart, 1975), but they were supplied with fresh water *ad libitum*. When the females were being maintained in captivity for an extended period of time, I recorded their weight every few days until parturition. The most recent weight measurement was used in the calculation of relative weight loss and clutch mass. Statistical analysis of neonate size (ANOVA) and sex ratios (chi-square) followed Zar (1974). All tests were carried out at a 0.05 rejection level. Estimating the overall proportion of male neonates was done using the method described by Cochran (1963:64-67).

Following parturition, I measured and weighed both the mother and the offspring. The neonates also were sexed (Gregory, 1983) and measured. Following this, I released the mother, along with her litter, at the site of her capture.

I also attempted to determine reproductive condition by noting the physical state of each sexually mature female. Females that had recently given birth could be identified by their emaciated appearance (e.g. abdominal folds of skin) and low weight in relation to their length. Conversely, females were inferred to be capable of reproducing during the upcoming active season if they appeared robust and/or if they were courted by males in the spring. The presence of the gelatinous copulatory 'plug' (Devine, 1977) also indicated that the female had mated recently and therefore was likely to become gravid.

Because the study population is small and protected by the boundaries of WBNP, I could not sacrifice and dissect snakes to obtain data on reproduction. I did, however, collect some information, such as litter size and condition of unborn young, by dissecting snakes found dead in the field.

Characteristics of the Hibernaculum

I examined the thermal conditions of the SRD by placing a 3 m long cable, containing thermistors (UUT43J1, Fenwell Electronics) at 0.5. m intervals, into a narrow rock crevice near the entrance to the den. The most proximal thermistor was positioned at the ground surface and, using trigonometry, the positions of the others were calculated to be 0.8 m and 1.9 m from the surface, respectively. Telethermometer probes were placed into another karst opening approximately 50 m away (reference site), which superficially resembled a den, but was not used by the snakes for hibernation. The respective depths of these probes were at the surface, 0.75 m and 1.5 m. On February 16, 1985, these telethermometers were replaced with thermistor probes similar to that in the SRD. A 8022B multimeter (John Fluke Mfg. Co. Inc.) was used to take readings from the thermistor probes throughout winter, and temperatures were determined from a conversion table.

Finally, during the fall of 1984, temperature-sensitive radio transmitters (SM1, AVM Instrument Co.) were surgically implanted in two large females, following the procedure described above (see Movements) and the snakes released at the den. Over the course of the ensuing hibernation period, the signal pulse rates of these transmitters were timed periodically, and then converted into temperatures using previously established calibration curves.

RESULTS

Spring Behaviour

Male snakes emerged from hibernation earlier than females. During the three years of this study, males were first observed above ground from the second to third week of April (WBNP staff, personal communications). At this time, most of the SRD area was still covered with snow, except for the immediate vicinity of the main den entrance. Early emerging snakes remained very close to the entrance, and usually appeared for only a few hours during mid-day, before returning underground.

Extremely low body temperatures were recorded for several of these snakes: On May 6, 1983, newly-emerged snakes displayed cloacal temperatures as low as 0.5°C (air temperature was 1.5°C). I took similar body temperature readings on April 30, 1985, when the air temperature was 8°C. Once on the surface and exposed to sunlight, however, snakes were capable of attaining body temperatures much higher than ambient. For example, on May 4, 1983, four snakes near the SRD had cloacal temperatures of 14.4, 10.2, 10.4 and 10.6 °C, despite an air temperature of 2°C. Substrate temperature where the snakes were basking was 6.4°C. The following day cloacal temperatures as high as 25°C were measured (air temperature was 8°C). Female snakes (and mating) were first noted each year on May 4, 1983, April 9, 1984 (R. Lewis, personal communication), and April 30, 1985. Maximum temperatures recorded on these days at the Fort Smith airport were, respectively, 3.0, 13.2 and 13.5 °C. As the den was not visited on a regular basis prior to my arrival each spring, it is very likely that snakes were at least emerging, and possibly mating, before these dates.

Female snakes, unlike males, remained in the vicinity of the den only briefly, leaving soon after having copulated. Occasionally, I would recapture a dispersing female a short distance away from the den, particularly if the snake had emerged during the later part of the day, and was forced to spend the night near the den. However, no female was captured emerging from the SRD more than once during any spring period. Males, on the other hand were caught repeatedly, sometimes over a period of two or three weeks (see below).

Occasionally, I found emerging snakes covered with dirt, giving them a light grey colour. This was especially common in large females, but no exact numbers were recorded. I also found snakes emerging from the den with very wet skin, particularly in early spring. The source of this water was presumably melting snow. Nevertheless, some of the snakes at the den may have been dehydrated. During the spring, several small cavities near the SRD remained filled with ice, and during mid-day a thin layer of meltwater would form on the surface; on several occasions, a snake I was pursuing would fall into one of these holes, and it often paused to drink before moving off the ice.

Mating activity at the SRD reached a peak for only two or three days during the early part of May (i.e several females being courted simultaneously). Following this, the number of observed females dropped drastically, with only one or two emerging daily. My last records of females being courted at the den each year were May 25 (1983), May 13 (1984) and May 12 (1985); however, two females were observed with copulatory plugs at the marsh on August 10, 1985. Males, although remaining at the den longer, also decreased steadily in numbers after the early part of May. I last observed males at the SRD on May 31 (1983), June 5 (1984) and May 16 (1985), but these were the extreme cases (i.e. only one or two males were present on those dates). Snakes that had been born at the den in the previous fall tended to appear almost synchronously after most of the adults had departed.

Population Dynamics and Structure

The results of the Jolly-Seber and Petersen population estimates are shown in Table 2, along with estimates of survivorship and recruitment for the adult male snakes. The small sample sizes resulted in rather large standard errors. There is some suggestion of a slight increase in the numbers of both sexes, but the confidence limits are large.

A strongly unimodal distribution of body sizes of males was observed each spring, with the majority of males falling in the 475 to 650 mm SVL range (Figure 5). Figure 6 shows the corresponding size-frequency distribution for the female snakes at the den. The number of females captured each spring was always much less than the number of males. Immature snakes (<400 mm SVL, see Reproduction) in the denning population were represented by a few juveniles (snakes at least one year old, but still not mature), and those neonates born at the den the previous fall.

Superimposed on the histograms in Figures 5 and 6 are the proportions of snakes *first encountered* at the den during each of the three spring periods. As

Table 2: Estimates of adult population parameters at the SRD.

N=population size, ß=survivorship, Ø=recruitment.

	period	Peterson estimate		Jolly estimate					
		$\hat{N}$	S.E.($\hat{N}$)	$\hat{N}$	S.E.($\hat{N}$)	Ø	S.E.(Ø)	ß	S.E.(ß)
males	fall 1983	301.7	36.3	236.1	38.3	0.676	0.069		
	spring 1984			281.6	25.9	0.940	0.098	59.7	28.7
	fall 1984	418	40.45	338.7	51.0	0.773	0.091	121.0	25.9
	spring 1985			338.0	88.5	0.815	0.220	62.0	33.7
females	fall 1983	150	39.5						
	fall 1984	248.4	53.1						

seen in Figure 5, the males first encountered in the spring of 1983 formed a decreasing proportion of the denning population during the following two years. Of the 237 males marked at emergence in 1983, 100 were recaptured at the den in the spring of 1984. During the spring of 1985, 74 males were captured that had marks dating back to spring 1983, and of these roughly half (40/74) had been captured for the third consecutive spring (i.e. had been recaptured in the both spring periods of 1984 and 1985). By the spring of 1985, males that originally had been marked during the spring of 1983 constituted the majority of the larger males at the den, but made up only a small percentage of the total male population. The same trend appears in Figure 6, in which females first captured in 1983 form a small proportion of the denning females in 1984 and 1985. During the spring periods of 1984 and 1985, the majority of 'new', unmarked males at the den fell into the 450 to 550 range (Figure 5). Similar interpretations may be made of the female population (Figure 6), although they are less reliable, because of the relatively small sample sizes.

On two occasions, a male snake that had been marked at another hibernaculum (approximately 1 km away) was recaptured at the SRD. One of these males had been marked earlier in the same spring.

Male survivorship figures were quite high (Table 2), particularly for the overwintering periods. Mortality was concentrated in the active season. Only four dead snakes were located at the SRD, and with one exception the deaths appeared to have been the result of snakes being exposed to freezing temperatures (one individual was beaten with a rock by a human visitor to the den). However,

Figure 5: Population structure of male *Thamnophis sirtalis* captured at the SRD each spring.

Superimposed on each histogram are the number of snakes first captured each spring. ■, ▨, and □ represent snakes first captured in 1983, 1984 and 1985 respectively (e.g. in 1985, nine snakes were captured in the 520-530 mm interval; of these, two were originally captured at the den in 1984, and one was originally captured at the den in 1983.

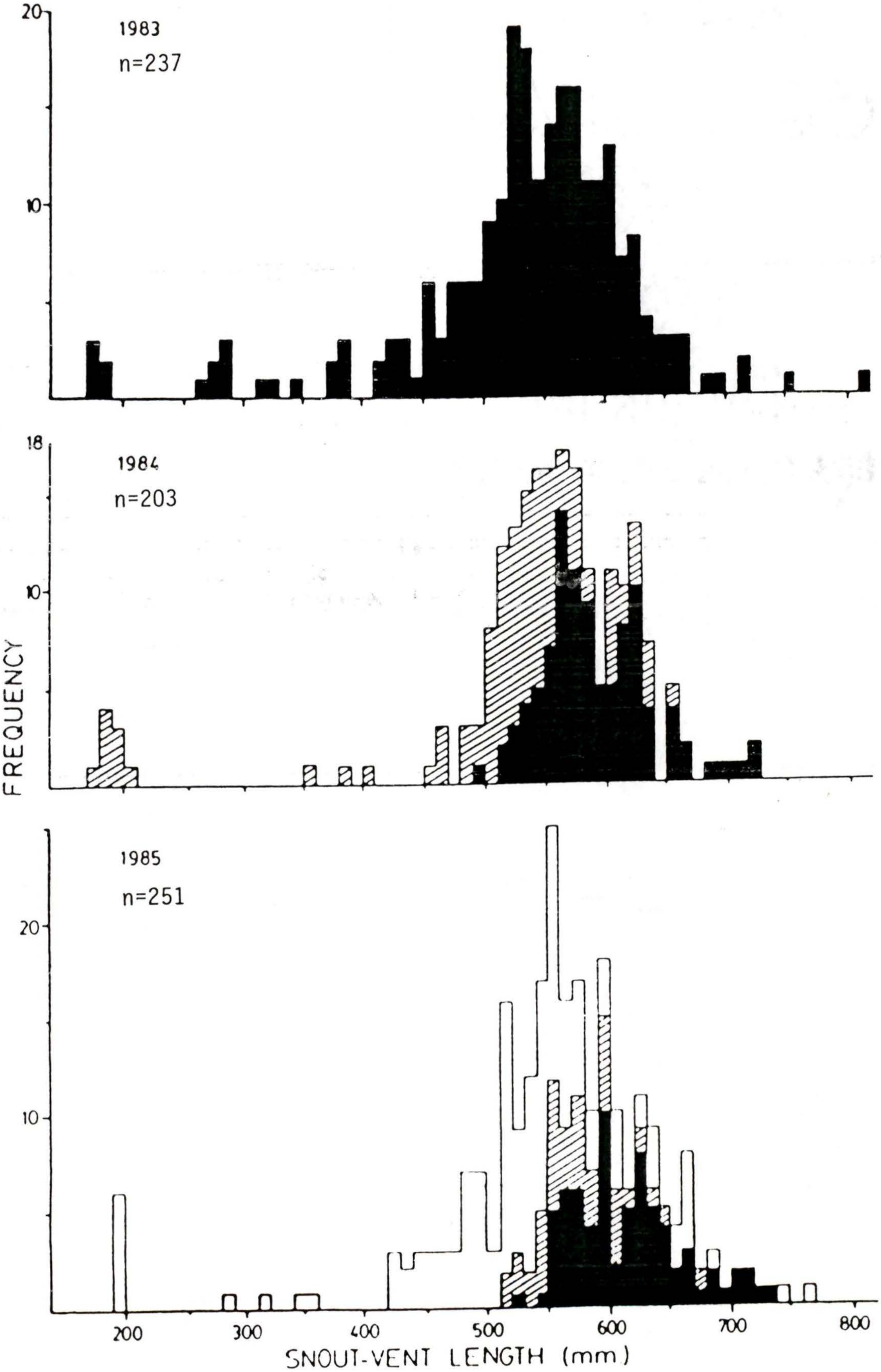
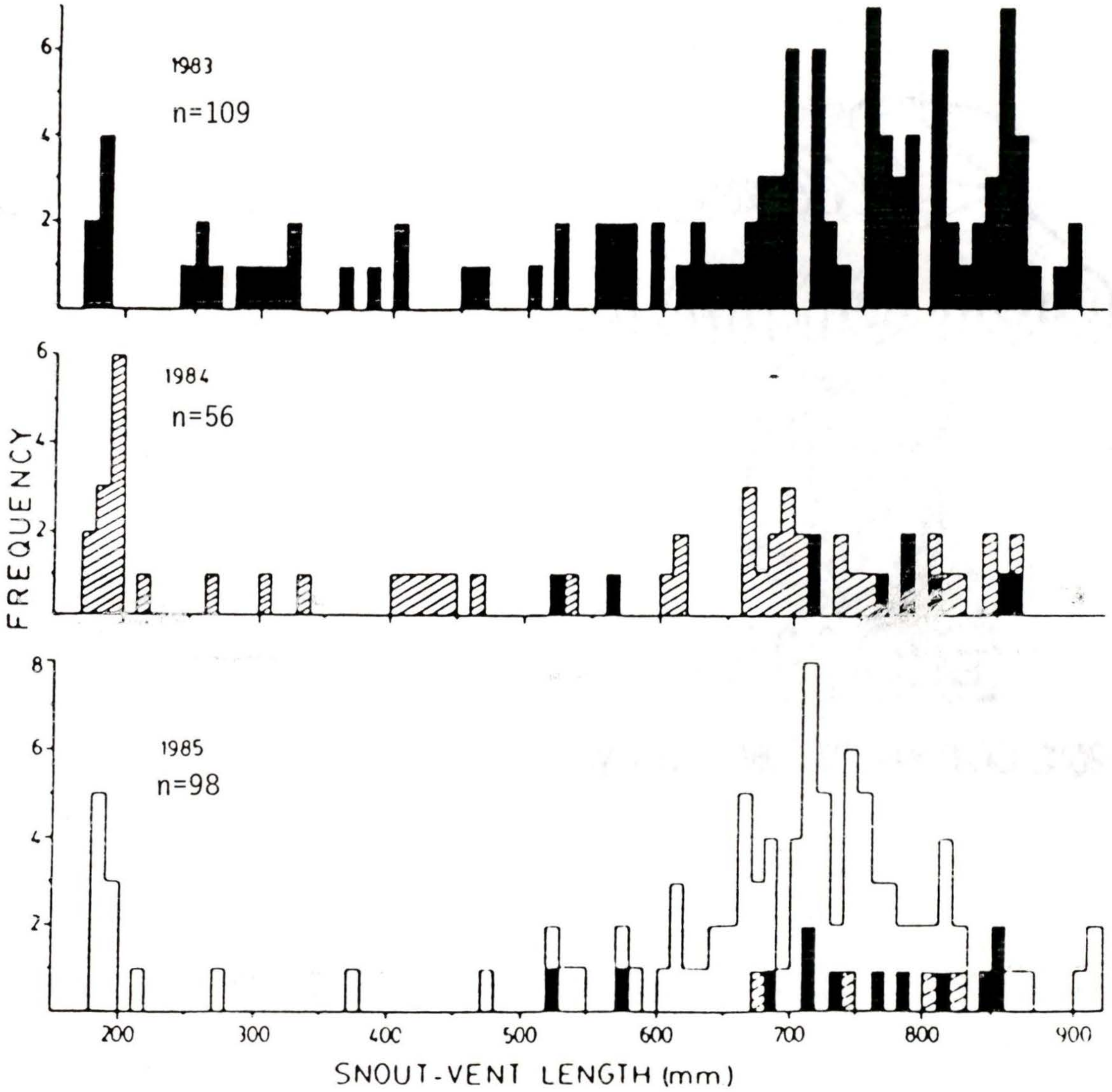

1983
n=237
20
10
1984
n=203
18
10
FREQUENCY
1985
n=251
20
10
200
300
400
500
600
700
800
SNOUT-VENT LENGTH (mm)

Figure 6: Population structure of female *Thamnophis sirtalis* captured at the SRD each spring.

(see Figure 4 for further explanation of figure).


1983
n=109
1984
n=56
1985
n=98
FREQUENCY
SNOUT-VENT LENGTH (mm)
200
300
400
500
600
700
800
900
2
4
6
8

predation seemed more common at other denning areas in WBNP. In one instance, I found seven dead male snakes at a den downstream of the SRD. The only external injuries were small punctures in the region of the neck, suggesting a small mammalian carnivore had been responsible for the killings. Several of the bodies were draped over small shrubs and branches. At a third den, I routinely found several snakes, usually with the flesh cleanly removed from a portion of the body. Whether these snakes had died of exposure (as with the snakes at the SRD) and the bodies been scavenged, or actual predation had occurred was impossible to determine. On one occasion, I observed a weasel *(Mustela erminiea)* at this den; a second weasel was seen at the SRD.

Instances of mortality observed away from the dens included two separate sightings of predation on snakes by red-tailed hawks, *(Buteo regalis)* by R. Lewis (personal communication) and myself. I also discovered three partially-eaten carcasses in a patch of open ground, away from any known hibernaculum, as well as a dead snake at the the feeding perch of a bald eagle *(Haliaeetus leucocephalus)*, which was near the SRD. A radio-tracked snake emerged one morning from its overnight retreat with flesh missing from a portion of the tail. (see Movements and Migration). Roadkills were not uncommon, particularly in the fall when the animals were migrating back to the dens. Gravid females were especially susceptible to this, because of their tendency to bask on the road.

I attempted to determine if adult size influenced survivorship, in the following manner: The population of adult males (>400 mm SVL) that were captured at the SRD during fall 1983 or spring 1984 was divided into three size categories, based on snout-vent length (400-530 mm, 535-575 mm, and 580-815 mm). I then tabulated the number of snakes in each group that were recaptured at least once during the remaining two years of the study. These figures, therefore, represented relative *minimum* survivorship over one year in each of the three groups (assuming adult size had no effect on catchability). Differences between the figures were significant (chi-square=8.93, 3 df, $0.025<P<0.05$), with the greatest proportion of recaptured individuals coming from the largest SVL category. This might suggest that larger males have higher survivorship. However, when the same sample of males was divided into two, four or five size categories, observed differences were not significant, although in each case the largest size class did have the greatest proportion of recaptures.

The proportions of males at the den were .583 (S.E. =.064), .591 (S.E.=.043) and .655 (S.E.=.089) for the autumn periods of 1983, 1984 and 1985, respectively. Only in the fall of 1984 did the sex ratio significantly differ from 1:1 (chi-square=4.36, df=1, $0.025<P<0.05$).

Movements and Migration

Localized movements at the den

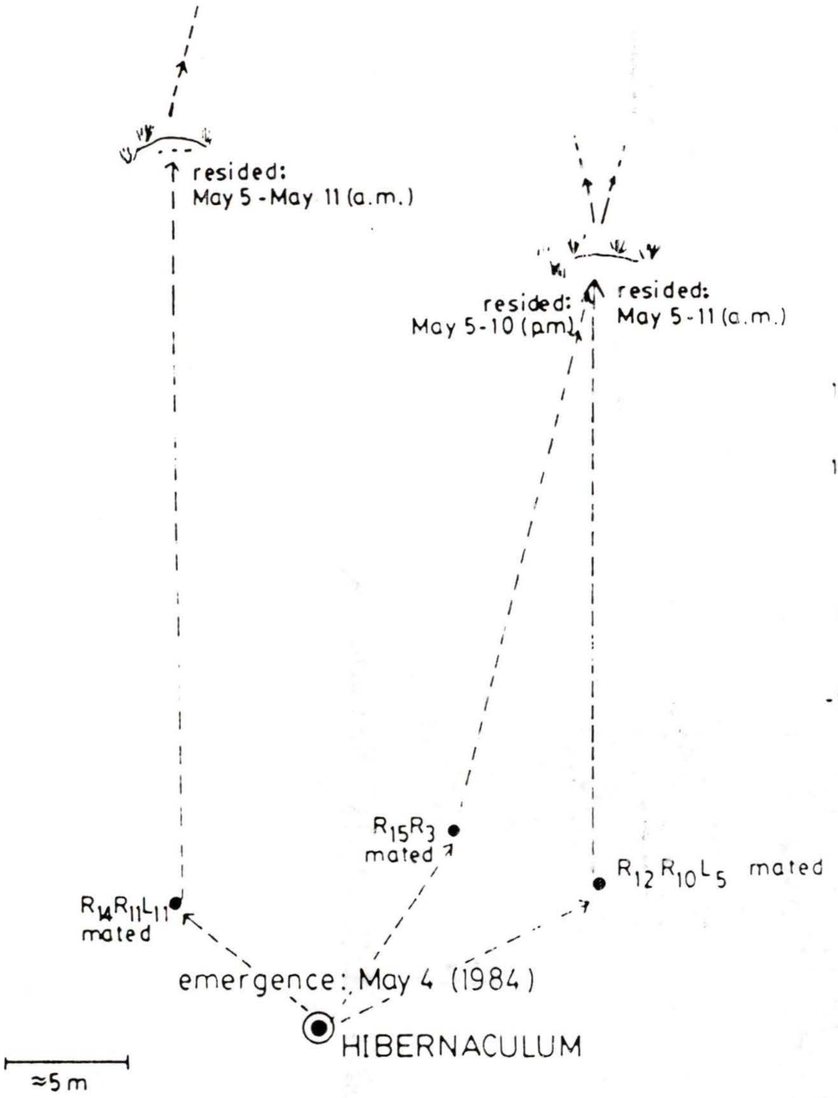
During the early stages of emergence, most males remained very close to the major openings of the den. As the spring warming trend continued, the male snakes would gradually 'fan out' during mid-day, but return to the den when the afternoon temperature began to fall. This pattern continued until the overnight temperatures became less severe (i.e. remained above freezing). At this point some of the males continued to retreat into the den each night, but an increasing number spent the night outside. In 1985, I first found a male overnighting outside the den on May 6, and by May 12 it appeared that a large number of males were choosing to remain on the surface. A few were found under logs and rocks, but many had simply curled up under accumulations of leaf litter.

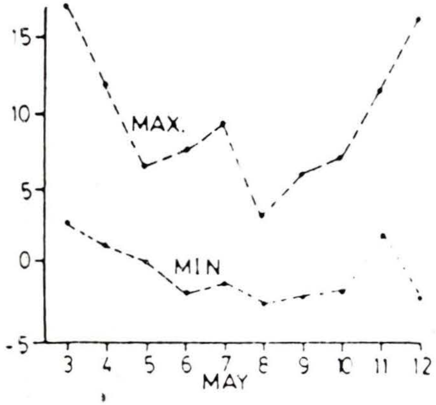
During the later (and warmer) part of spring emergence, when females were emerging, I often found males 20 m or more away from the den. Approximately 50 m from the SRD was a small limestone outcrop that seemed to function as a 'satellite den', i.e a small number of individuals (males and females) hibernated there each winter. However, during spring emergence, males from the SRD often took up temporary residency at this site. It was not unusual to find a snake at the outcrop on one day, and back at the SRD the next. Mating was occasionally observed in these peripheral areas, although it was not nearly as frequent as in the immediate vicinity of the den. Males appeared to move about freely; there was no indication that certain males remained on the periphery of the den area permanently.

Very few movements of females were recorded near the SRD, as most were observed for only a short time before they left the area. Several earthen mounds (origin unknown, about 0.25 m high and 2 m long) were located approximately 20 m from the SRD. They were used often as an overnight retreat by dispersing females. The usual trend was for these females to emerge from the den, mate, spend the first night at these mounds (entering and exiting them through numerous small openings), and then move out of the vicinity of the den the next day. On several occasions this trend was interrupted by a relapse of cold weather, which would delay the departure of the females (Figure 7).

Figure 7: Localized movements of three female *Thamnophis sirtalis* which emerged from the SRD on May 4, 1984.

All three females copulated shortly after emerging. However, low temperatures (inset) forced them to remain near the den for several days, a behaviour atypical for females.


resided:
May 5 - May 11 (a.m.)
resided:
May 5-10 (pm)
resided:
May 5-11 (a.m.)
R14R11L11
mated
R15R3
mated
R12R10L5 mated
emergence: May 4 (1984)
HIBERNACULUM
≈5 m


15
10
5
0
-5
MAX.
MIN
3
4
5
6
7
8
9
10
11
12
MAY

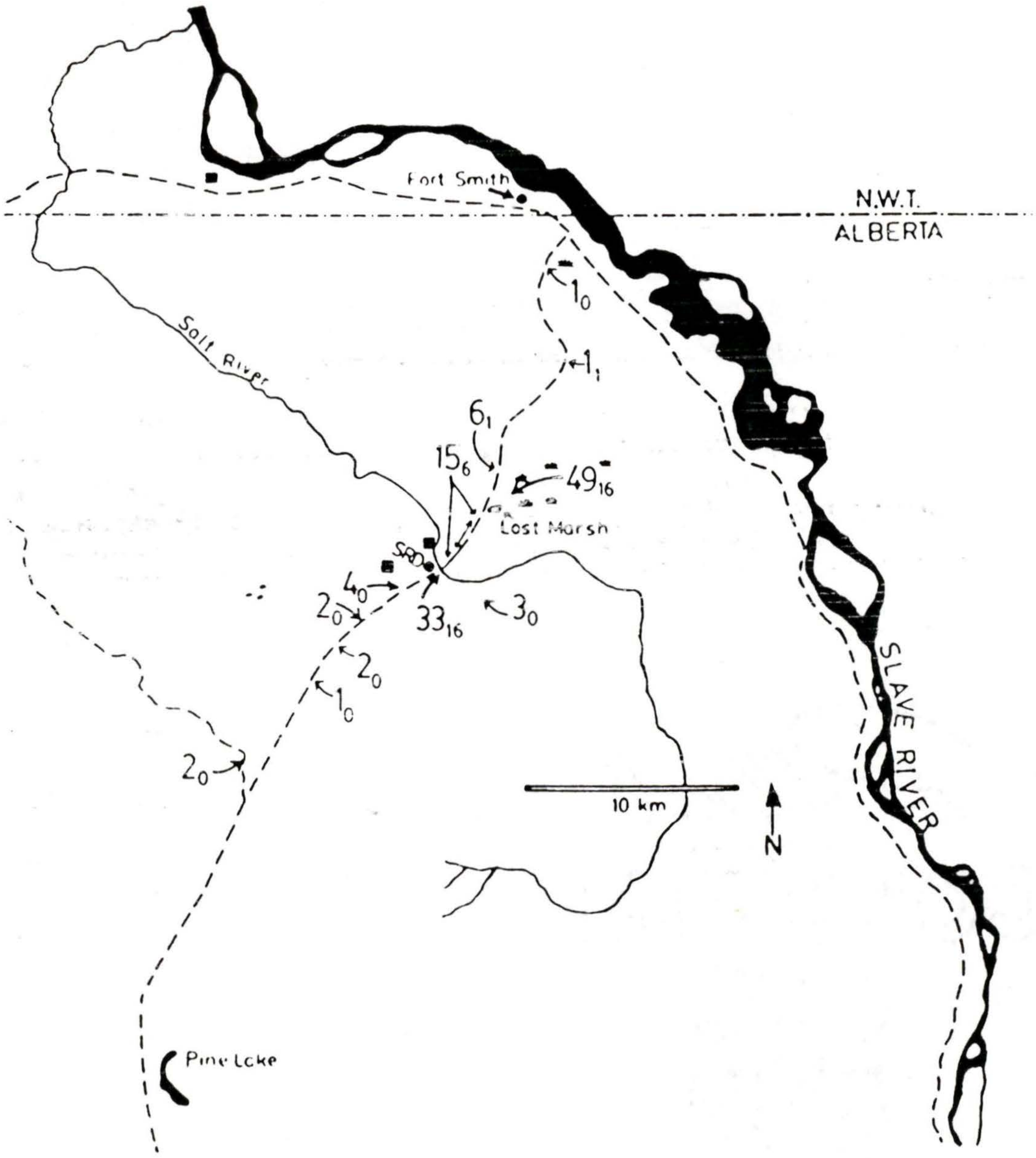
Migratory movements

Although recoveries of marked snakes (alive or dead) away from the den were few, the majority of them occurred at a complex of freshwater ponds and marshes, approximately 3.75 km NE of the SRD. Aerial reconnaissance indicated this was the closest freshwater marsh habitat to the SRD (aside from a few very small, often temporary, ponds). The first marsh in this complex ('Lost Marsh') was bordered along one edge by the only road in the region. Consequently, the chance of locating snakes during the summer months was high at this spot, relative to other areas that I searched. In fact, along a 60 km portion of the road (Fort Smith to Pine Lake) sightings of snakes were prevalent only in the proximities of Lost Marsh and the SRD (Figure 8). Only one snake that had been marked at the SRD was found elsewhere: This male had been last observed at the SRD on May 16, 1983, and was subsequently found, as a roadkill, on September 3, 1983 approximately 11 km northeast of the SRD.

The movement of snakes back towards the hibernacula began during late summer. Snakes that had returned to the SRD were first observed on August 23 (1983), August 7 (1984) and July 23 (1985), although most arrivals were not recorded until somewhat later (late August), at which point snakes were frequently seen crossing the road near the den. A strong directional movement was evident at this time: Out of 31 snakes sighted on the road before they had been disturbed, 29 (94%) were travelling in a westerly direction. Most of the live snakes and roadkills were found on the road within a 200 m section near the SRD. A similar movement 'corridor' existed approximately seven km NE from the SRD, where snakes were regularly observed crossing the road. Snakes at this location

Figure 8: Map of study area in WBNP, indicating the total numbers of snakes captured or observed away from the vicinity of the Salt River den (SRD) during the three years of the study.

The majority of these snakes were captured either near Lost Marsh (49), on the road (--) between Lost Marsh and the SRD (15), or on the road adjacent to the SRD (33). Subscripts indicate the number of snakes in each subsample that were also captured at the Salt River Den. Not indicated are those snakes captured in the vicinity of other known dens (■).


Fort Smith
N.W.T.
ALBERTA
1_0
1_1
Salt River
6_1
15_6
49_{16}
Lost Marsh
SRO
4_0
2_0
33_{16}
3_0
2_0
1_0
SLAVE RIVER
2_0
10 km
N
Pine Lake

were possibly returning to a hibernaculum other than the SRD, but attempts to find the den failed.

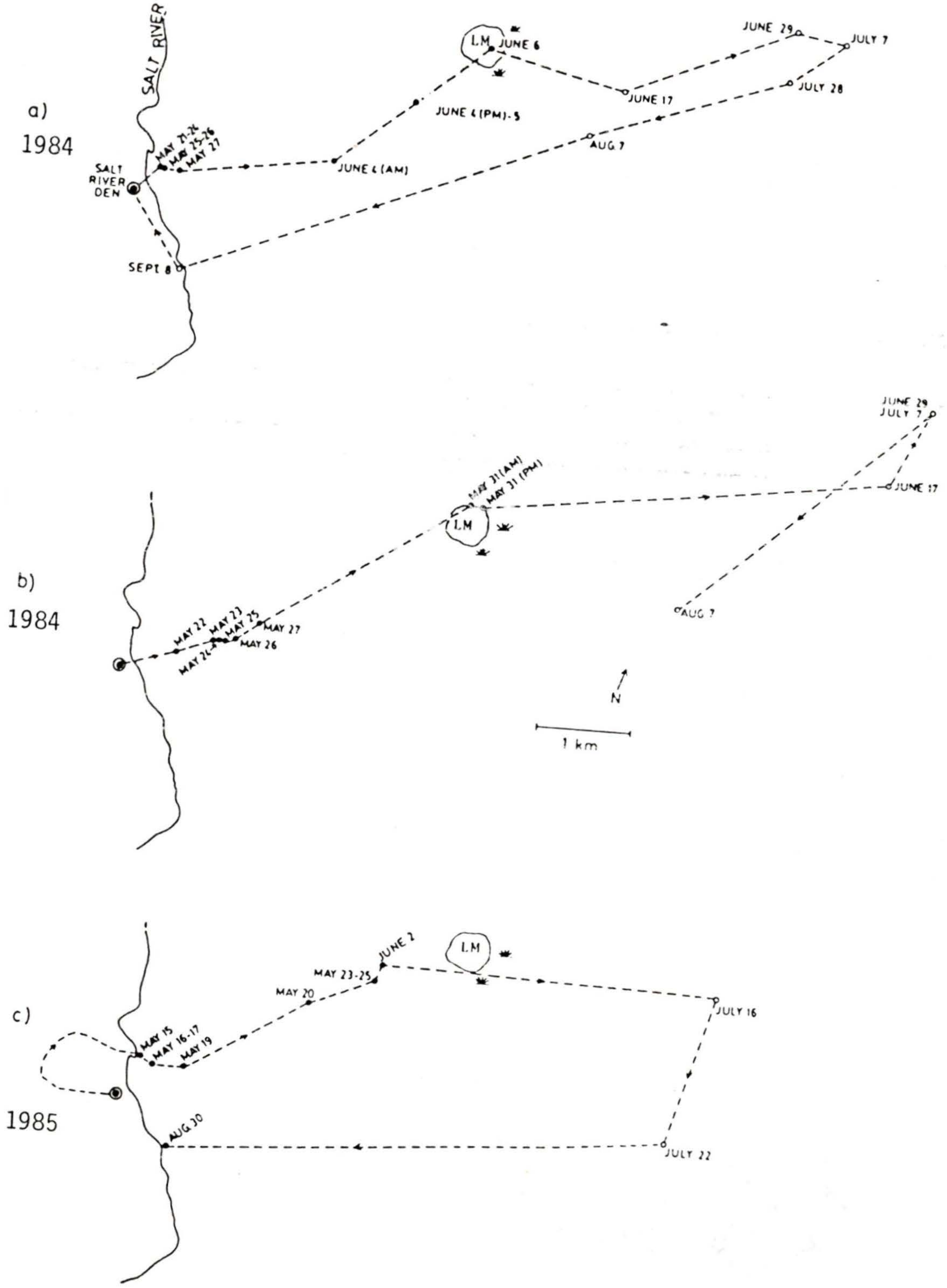
Movements recorded for the three radio-tracked females are presented in Figure 9. The signals (and positions) of two of the snakes were lost towards the end of the active season, possibly because of transmitter failure. Both females tracked in 1984 (Figure 9a,b) followed very similar routes in the spring, proceeding along a north-easterly bearing from the den. The third female, which I tracked during 1985 (Figure 9c), initially left the den in a westerly direction, but during the first day it appeared to 'correct' this movement, leading it to the same route used by the two females in 1984.

As I was following the snakes on foot, their daily movement and behaviour became quite predictable. In the morning, the snakes would emerge from their overnight retreats, and spend a period of time basking in the early hours of sunlight. If weather conditions were adverse, then they would remain at this site throughout the day. In extreme cases (e.g. cold and rain) the snakes sometimes remained out of sight for several days. When 'good' weather prevailed, the animals would resume travelling. Migrating females never hesitated to enter standing water (spring snowmelt) along their route, and once in the water, they did not deviate significantly from their previous bearing. One female, which was observed encountering the Salt River, swam submerged across the river (approximately nine m), climbed up the vertical riverbank, paused for a few minutes, and then continued along its previous direction.

Generally speaking, it was not uncommon in the morning to find one or more males near a female during the early part of its migration. For example, on May

Figure 9: Movements of radio-tracked *Thamnophis sirtalis* females.

All three females left the SRD and moved in the direction of marshland. Lost Marsh (LM on Figure 9a), the closest marsh to the den, is indicated on each diagram. ● =sighting on ground, ○ =location determined from aircraft.


a)
1984
SALT RIVER
SALT RIVER DEN
MAY 21-24
MAY 25-26
MAY 27
JUNE 4 (AM)
JUNE 4 (PM)-5
L.M
JUNE 6
JUNE 17
JUNE 29
JULY 7
JULY 28
AUG 7
SEPT 8
b)
1984
MAY 22
MAY 23
MAY 24
MAY 25
MAY 26
MAY 27
MAY 31 (AM)
MAY 31 (PM)
L.M
JUNE 17
JUNE 29
JULY 7
AUG 7
N
1 km
c)
1985
MAY 15
MAY 16-17
MAY 19
MAY 20
MAY 23-25
JUNE 2
L.M
JULY 16
JULY 22
AUG 30

22, 1983, three males were near a transmitter-equipped female. Interestingly, on May 24, one of these males was recaptured within 10 m of the female, which had moved approximately 360 m during the two-day interval.

The distance travelled by a moving snake, over the course of one day, varied considerably, ranging from less than 50 m to over one km. In most cases this movement was inferred from two or more periodic checks of the snake's position. Because of this, it was usually impossible to determine exactly how long the snake had been moving. Occasionally it was possible to monitor movements constantly over a longer period of time; this resulted in recorded movements of 1060 m in five hours, 1120 m in 6.3 hours, and 630 m in 3.5 hours. These figures do not represent *continual* motion for, as described below, daily movement patterns involved periods in which the snake was stationary.

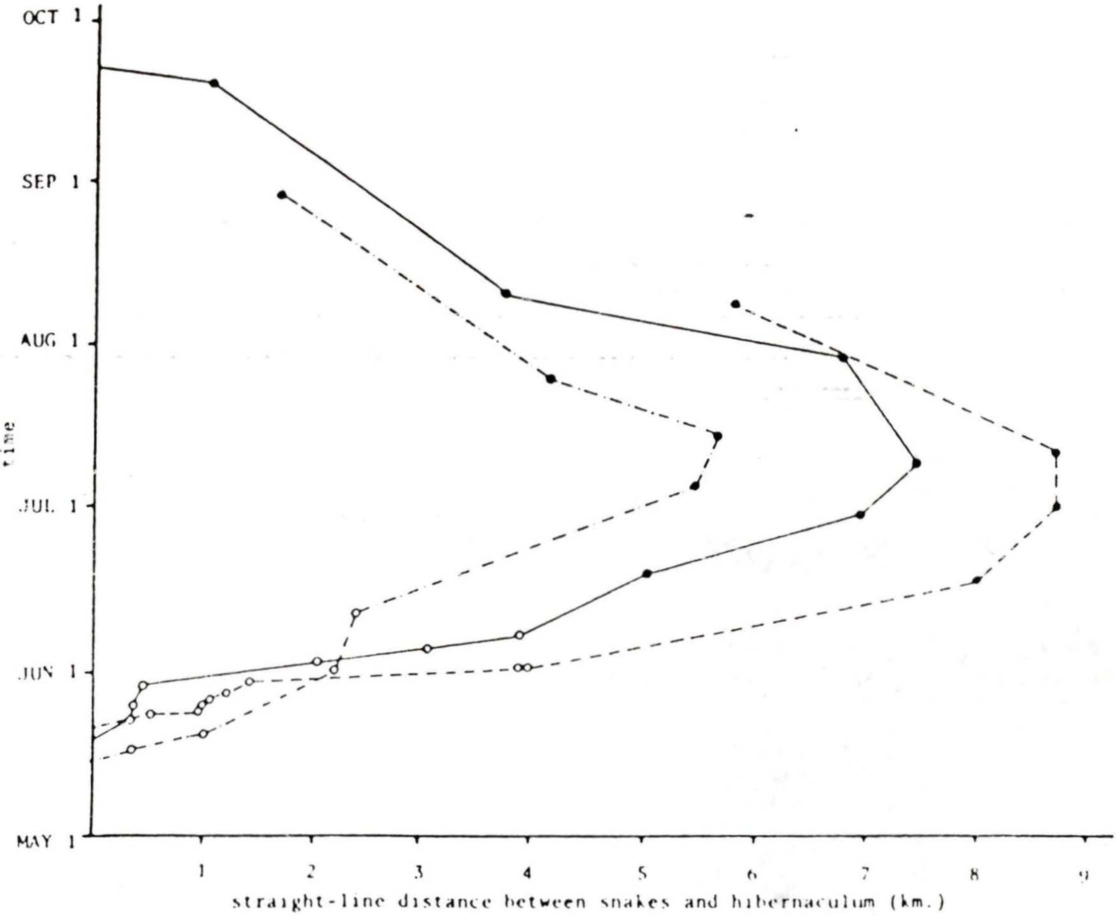
The distance moved by a snake was not clearly correlated with any particular weather condition (e.g. maximum temperature, hours of direct sunlight, etc.), but overall weather patterns did seem to affect migrating snakes. For example, on May 23, 1984, I observed a female emerging from her overnight retreat (a large log) with flesh missing from the dorsal portion of her tail, exposing several vertebrae. As this had happened overnight, the probable explanation was that a small animal (possibly *Sorex*) had attacked the snake. The cold overnight conditions (recorded surface minimum was 1.5°C) suggested that the snake may have been too sluggish to avoid the attack. On the afternoon of May 31, 1984, the same female was basking on a large grassy patch at Lost Marsh, when a cold rain began and the temperature never exceeded 9° C. The female failed to select and/or locate an overnight retreat, and consequently spent the night laying outstretched on the grass. During the next few days the maximum temperature recorded at the marsh was 4.5°C, and one evening a slight snowfall occurred. The snake made no significant shifts in its position, even when its cloacal body temperature (5°C) was taken. During this time period the snake appeared to be quite visible to any would-be predators. It was not until June 4 that moderate temperatures (a high of 16°C) resumed, at which point the female coiled up under a nearby clump of dead grass.

A discrete behavioural sequence was observed while the snakes were travelling: After having moved for a certain distance (ranging from a few to 100+ m), the female would come to a halt, and raise the head off the ground. The duration of this 'pause' varied (timed pauses ranged from 54 sec to just over 6 min), and tongue-flicking was noticeably absent. Following this, the snake would lower its head to the ground, and resume movement and tongue-flicking. This pattern would repeat itself until some time late in the day, when the snake would stop and assume a basking (coiled) position in the sun. When the sun got too low to provide good basking conditions, the snake would begin searching the immediate area, apparently for an overnight retreat. This searching was often quite extensive, lasting up to 45 minutes. When an appropriate site was found (the criterion used was not evident), the snake would enter it. These sites included brush piles, logs, tree root systems and, when the snake was in a bog, clumps of willows or grass.

After I was no longer able to follow snakes on foot and had to switch to aircraft, it became impossible to record daily, or even weekly, movement patterns. However, aerial searches revealed that the snakes did not establish a summer-long occupancy of a particular site. Although I documented the actual return to the den of only one of the three females, all three snakes displayed a 'looping' migratory movement (Figure 10). This pattern took them through the marshes, where food presumably was abundant, throughout most of the summer. In late summer, however, their movement appeared to be directed back towards the SRD (Figures 9 and 10).

Figure 10: Straight-line distance of radio-tracked snakes from den during the course of their migrations.

All three females appeared to start their return to the den during late July. ○ =sighting on ground, ● =location determined from aircraft.


OCT 1
SEP 1
AUG 1
JUL 1
JUN 1
MAY 1
time
1
2
3
4
5
6
7
8
9
straight-line distance between snakes and hibernaculum (km.)

Feeding

Sixty-five snakes were captured at or near the marshes during the period of July 15 to August 31 (all years combined). Of these, only 17 (26%) produced prey items when palpated (or, in the case of roadkills, dissected). No stomach contents were found in 10 snakes caught at the marsh on earlier dates, or in 3 snakes captured at the marsh in September. Of all the snakes caught returning to the den in the fall, only one individual produced stomach contents (see below). Each snake that had fed contained only one prey item.

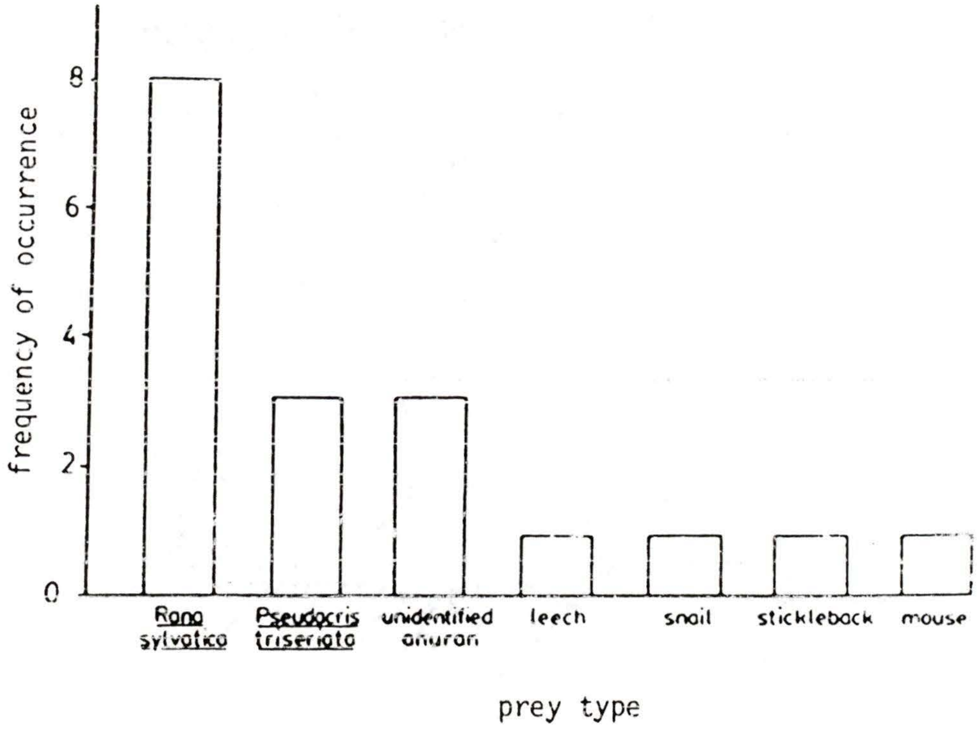
Wood frogs *(Rana sylvatica)* were the most frequently recorded food item, followed by the smaller chorus frogs *(Pseudacris triseriata)* and unidentified anurans (Figure 11). All of the wood and chorus frogs were metamorphosed individuals. Other prey items found were 1 snail, 1 leech, 1 stickleback *(Culaea inconstans)*, and 1 mouse *(Peromyscus maniculatus)*. I observed two of these prey items being eaten by the snakes. On one occasion I located a large, nongravid female preying on a small wood frog by following the sound of the frog's distress call. I also witnessed another snake, its head protruding from the water, as it was swallowing a leech.

No stomach contents were taken from gravid females (n=11), even though most were captured within a few m of the marsh. In captivity, however, gravid females were very responsive to the scent of a prey species; places in the cage where frogs or fish had been rubbed were thoroughly investigated, with frequent tongue-flicking.

Four of the snakes that yielded stomach contents were small (<400 mm SVL), and one was a neonate. The latter contained a newly-metamorphosed chorus frog, while the larger juveniles had preyed upon newly-metamorphosed wood frogs.

Figure 11: Frequency of prey items found in WBNP *Thamnophis sirtalis*

No more than one prey item was found in any one snake (N=18).


frequency of occurrence
8
6
4
2
0
Rana sylvatica
Pseudacris triseriata
unidentified anuran
leech
snail
stickleback
mouse
prey type

Prey abundance appeared to be heavily biased towards wood frogs, which were very common near any freshwater body. These frogs were sighted very rarely in the areas that the radio-tracked snakes travelled through *en route* to Lost Marsh (although *Pseudacris* was occasionally heard calling from some of the deeper pools of water on the forest floor). However, wood frogs were extremely abundant in and around the freshwater marshes. Once a radio-tracked snake had reached Lost Marsh, I was often able to see several wood frogs sitting within two m of a snake, although no radio-tracked snake was observed feeding. Wood frogs also were abundant later in the summer, especially when the tadpoles were just completing metamorphosis. The numbers of these small frogs had dropped quite considerably by the time most of the snakes apparently were giving birth (late August -see Reproduction). My first observations of climax metamorphic (Duellman and Trueb, 1986) wood frogs were on July 22 (1983), July 6 (1984) and July 8 (1985).

I also intermittently saw chorus frogs throughout the summer, although in numbers far below wood frogs. This could have been because chorus frogs are smaller, and thus more cryptic. If, however, spring choruses are used as an indication of the relative abundance of the two species, then wood frogs were substantially more numerous than chorus frogs. I regularly observed toads *(Bufo hemiophrys)* in certain areas of the park, but never in the marshland near the SRD. Leopard frogs *(Rana pipiens)*, which have been reported in WBNP, were never seen throughout my study.

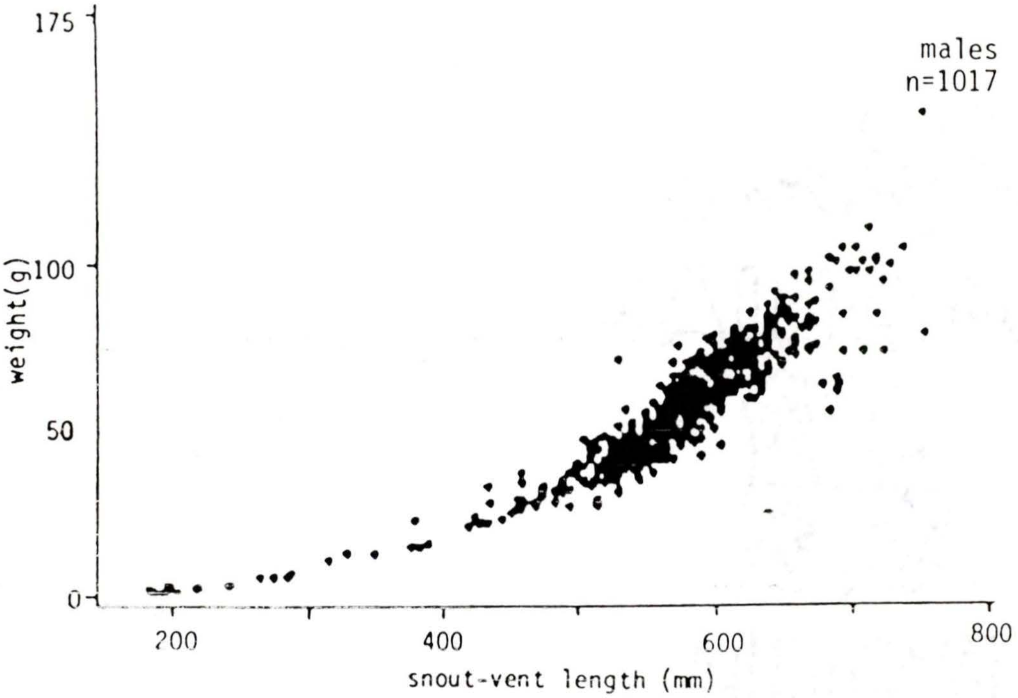
Captive juvenile snakes easily subdued and devoured newly-metamorphosed wood frogs. Captive neonate snakes, on the other hand, appeared incapable of feeding on the small frogs. They often grasped the frog, and occasionally would swallow part or all of a limb, but eventually they would abandon the attempt. Large chorus frogs and dead, newly-metamorphosed wood frogs posed identical problems to the neonates. However, captive neonates did feed on immature chorus frogs and small sticklebacks. Insects (orthopterans and coleopterans) did not elicit any response. Captive adult snakes fed readily on wood frogs, chorus frogs, sticklebacks and toads. Earthworms, which do not occur in WBNP (personal observation; W. Fender, personal communication), were offered to several captive snakes of various sizes. In some cases the earthworms were investigated by the snakes, but they were never eaten.

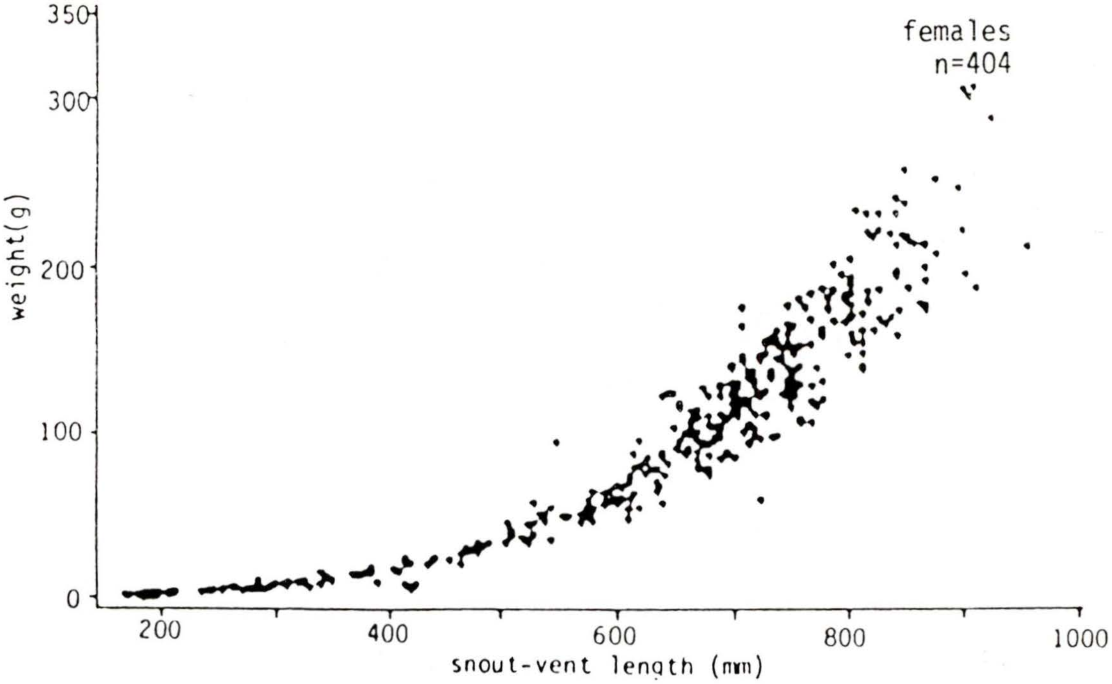
Growth

The equations best describing exponential weight-length relationships of all the snakes encountered in WBNP (Figure 12) were (LOG WT) = 2.76(LOG SVL)-13.632 for males (n=1421) and (LOG WT) = 2.976(LOG SVL)-14.805 for females (n=404), where LOG = natural log, WT = weight expressed in g and SVL is expressed in mm. Significant differences existed between the slopes (t=1.96, df=1417, $P<0.001$) and between intercepts (t=12.71, df=1418, $P<0.001$). However, the validity of the latter conclusion is somewhat questionable, as the test assumes homogeneity of the regression coefficients (Zar, 1974). As indicated in Figure 12, snakes of a given length often varied in weight, especially in the larger size classes.

Relatively large sample sizes of male growth over the 1983 and 1984 active seasons allowed separate Walford plots of the two years to be calculated. Slopes and intercepts of these two lines were not significantly different (slopes: t=1.90,

Figure 12: Weight-length relationships for male and female *Thamnophis sirtalis* in WBNP


175
100
50
0
weight(g)
males
n=1017
200
400
600
800
snout-vent length (mm)

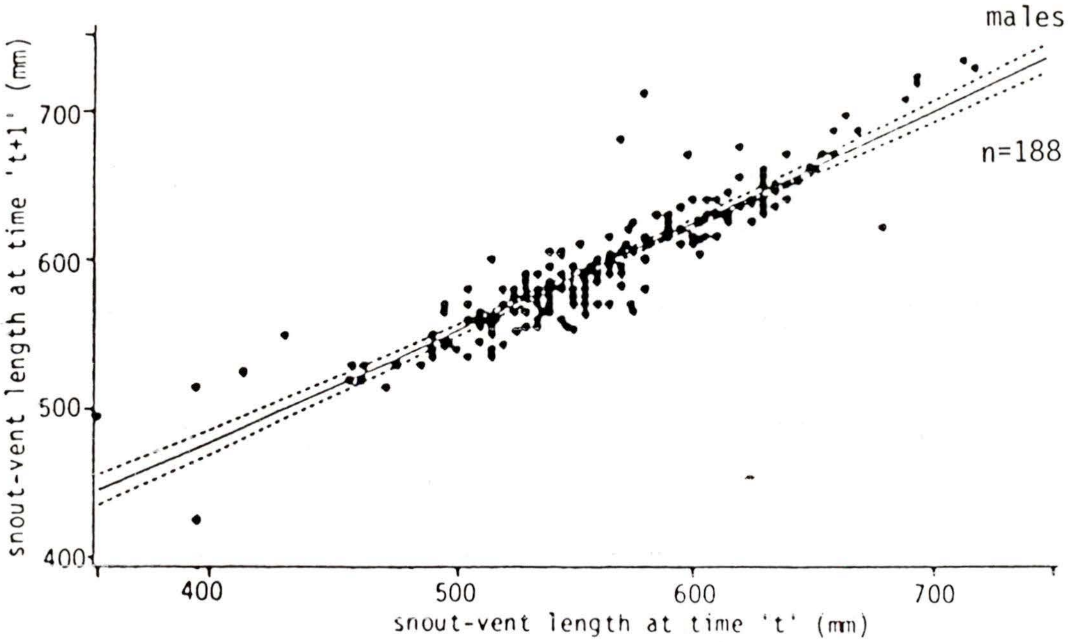

350
300
200
100
0
weight(g)
females
n=404
200
400
600
800
1000
snout-vent length (mm)

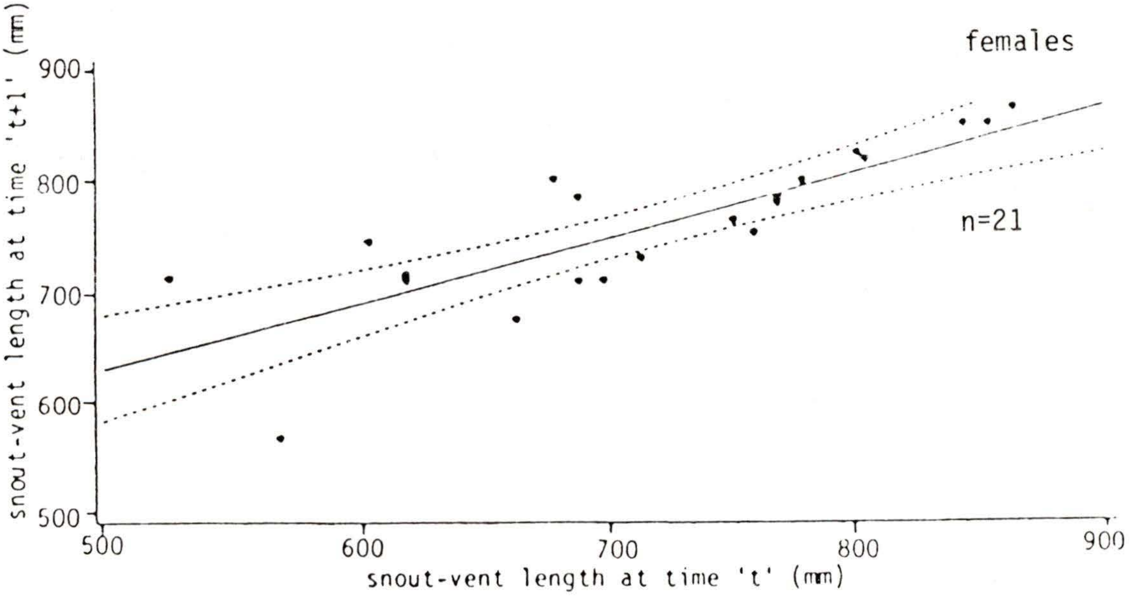
df=162, $0.05<P<0.10$; intercepts: t=0.958, df=163, $0.20<P<0.50$). Hence, I combined male growth records from 1983 and 1984, along with a smaller number of observations from 1985. I pooled all female growth records, although the relatively small numbers of annual recaptures precluded any year-to-year statistical comparison. The resultant Walford plots for both male and female growth appear in Figure 13. The linear equations for these relationships were $SVL_{t+1}=0.715\ SVL_t+194.88$ (for males) and $SVL_{t+1}=0.603\ SVL_t+331.22$ (for females). The difference between the slopes of these lines was nonsignificant (t=1.97, df=206, $0.05<P<0.10$). However, the intercepts were significantly different (t=8.11, df=207, $P<0.001$).

During this study, I obtained no growth records for snakes that had been originally captured as neonates. However, while on a field trip to WBNP in 1986, an adult male (540 mm SVL) was recaptured at the SRD on September 7. This snake had been previously captured on August 25, 1983, when it was a neonate (175 mm SVL).

Figure 13: Walford plots for *Thamnophis sirtalis* in WBNP.

Dotted lines represent 95% confidence limits on estimated value.


males
n=188
snout-vent length at time 't+1' (mm)
700
600
500
400
400
500
600
700
snout-vent length at time 't' (mm)


females
n=21
snout-vent length at time 't+1' (mm)
900
800
700
600
500
500
600
700
800
900
snout-vent length at time 't' (mm)

Reproduction

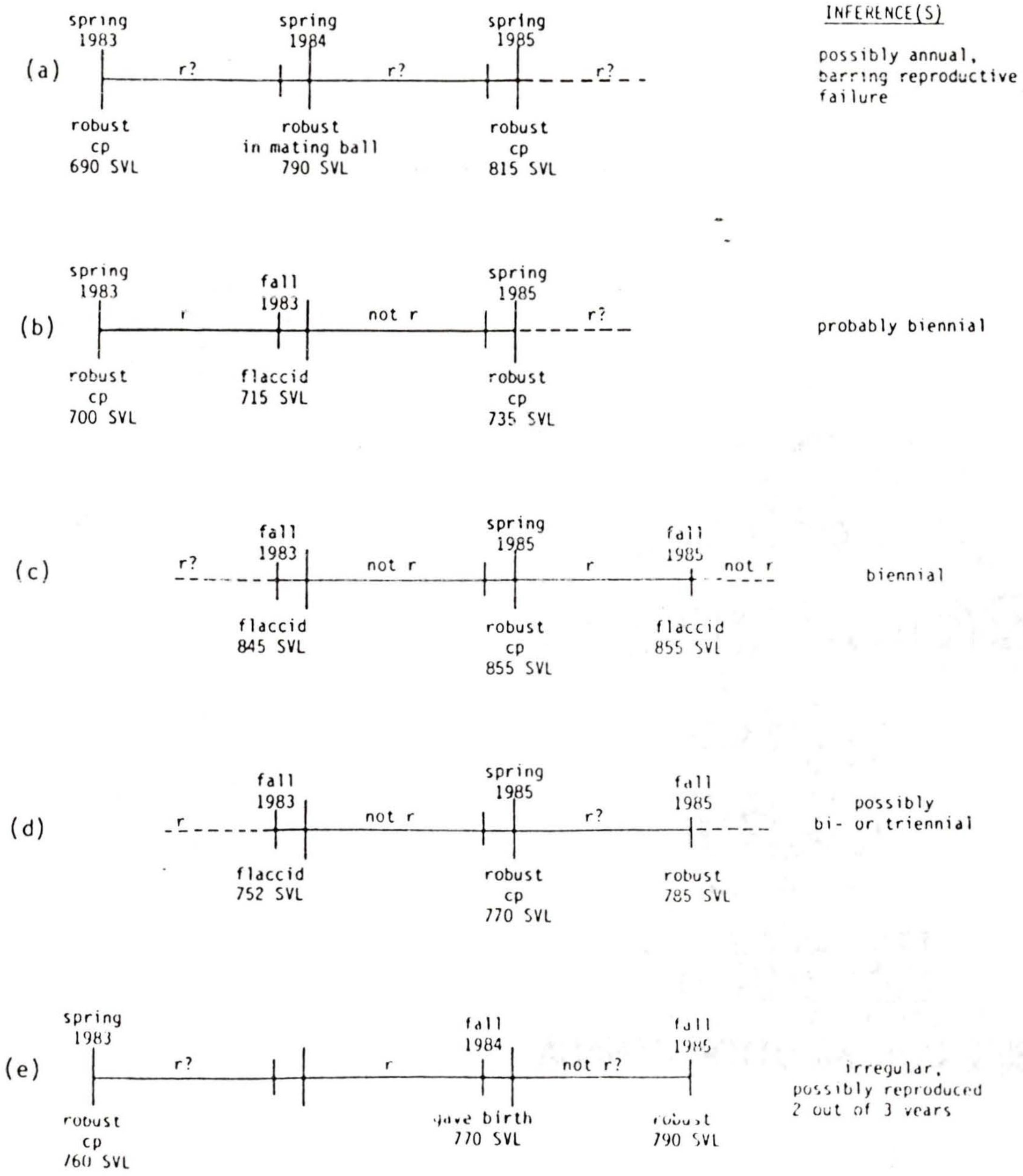
The smallest gravid female that I observed during the study was 640 mm SVL, with a prepartum weight of 89 g. However, at the den I captured a female of 570 mm SVL with a copulatory plug, and an even smaller female (535 mm SVL) was observed being courted by males. The smallest male I actually observed in copulation was 490 mm SVL, although slightly smaller males (460 mm<SVL<490 mm) were occasionally captured in mating balls.

Only five females were recaptured frequently enough to permit some interpretation of their reproductive histories (Figure 14), but the evidence was weak. There was little similarity among individuals in this small sample. One female (Figure 14a) may have reproduced each year of this study, but the fact that the snake grew substantially each year perhaps indicates otherwise (assuming that there is an energetic tradeoff between reproduction and growth). However, each of the remaining four females (Figure 14b, c, d, and e) almost certainly skipped at least one year between successive reproductions.

Gravid females were seen at both the marsh and the den. Each summer, gravid females were located near a loose pile of logs and other debris beside Lost Marsh. Others were found dead on the road nearby. The total numbers observed here each summer were one (1983), three (1984) and seven (1985). One of these snakes was captured on August 2 (1984); all others were found during the last two weeks of July. All of these females were captured and held for litter data, so it was impossible to determine if they would have remained at the marsh until parturition. Neonates, however, were observed in the marsh each August. One female that gave birth in captivity was released at Lost Marsh (where she had

Figure 14: Reproductive histories of five female snakes, inferred from observations made at times of capture.

r=probably reproduced, r?=possibly reproduced


INFERENCE(S)
(a)
spring 1983
spring 1984
spring 1985
r?
r?
r?
robust cp 690 SVL
robust in mating ball 790 SVL
robust cp 815 SVL
possibly annual, barring reproductive failure
(b)
spring 1983
fall 1983
spring 1985
r
not r
r?
robust cp 700 SVL
flaccid 715 SVL
robust cp 735 SVL
probably biennial
(c)
fall 1983
spring 1985
fall 1985
r?
not r
r
not r
flaccid 845 SVL
robust cp 855 SVL
flaccid 855 SVL
biennial
(d)
fall 1983
spring 1985
fall 1985
r
not r
r?
flaccid 752 SVL
robust cp 770 SVL
robust 785 SVL
possibly bi- or triennial
(e)
spring 1983
fall 1984
fall 1985
r?
r
not r?
robust cp 760 SVL
gave birth 770 SVL
robust 790 SVL
irregular, possibly reproduced 2 out of 3 years

been captured originally) on August 15, 1984. During the spring of 1985 she was recaptured at the SRD. This was the only documented case of a postparturient female travelling back to the SRD from the marsh.. Compared to robust females, postparturient snakes were relatively scarce at the den, both in fall and spring samples.

I observed gravid females near the SRD from July 23 (1985) to September 13 (1985), although the majority of them appeared during the later part of August. Total numbers (alive and dead) of gravid females seen in this area were three (1983), five (1984) and six (1985). Again, most of these snakes were roadkills or were captured and held for litter data. During 1985, I left two gravid females at the den; they continued to bask for two days, and then disappeared. Although these particular females were never actually recovered in a postparturient condition, neonates were frequently found at the den in the fall, indicating that parturition did occur in the area. In fact, another female was actually captured at the den as she was giving birth on August 25, 1985 (see Table 3).

On August 23, 1983, I found a gravid female (730 mm SVL) on the road, approximately half way between the SRD and Lost Marsh. This snake had been run over by a vehicle recently, and died shortly after I discovered her. She apparently had been run over during parturition, as two neonates, one squashed and another alive, were located nearby. Sixteen dead, but fully developed young were present in the female.

Eighteen captive females gave birth to intact litters (i.e. composed of all live, healthy-looking young). The mean size of these litters was 11.56 (S.E.=0.886), with a range of 5 to 21 (Table 3). Also included in Table 3 is the relative weight

Table 3: Reproductive data on 18 intact broods of WBNP *T. sirtalis*, born in captivity.

RWL=relative weight loss, RCM_1=relative clutch mass (clutch mass/preparturient weight of female), RCM_2=relative clutch mass (clutch mass/postparturient weight of female), days=number of days gravid female was in captivity prior to giving birth.

SVL of mother (mm)	RWL	RCM_1	RCM_2	size of litter	days	date of birth
640	0.416	0.196	0.336	8	15	15 AUG 85
640	0.258	0.129	0.173	5	1	16 AUG 85
655	0.445	0.212	0.382	10	27	27 AUG 85
675	0.531	0.166	0.355	10	39	29 AUG 85
690	0.401	0.251	0.420	11	1	5 SEP 85
710	0.241	0.210	0.277	11	2	26 AUG 83
710	0.367	0.175	0.277	10	29	18 AUG 85
710	0.266	0.123	0.168	8	20	19 AUG 85
725	0.388	-	-	11	5	10 SEP 86*
740	-	-	-	10	0	25 AUG 85
740	0.393	0.206	0.340	12	26	16 AUG 85
750	0.444	0.204	0.366	15	35	25 AUG 85
750	0.345	0.249	0.379	13	5	21 AUG 84
780	0.309	0.160	0.231	12	12	28 AUG 85
780	0.326	0.167	0.248	10	8	15 AUG 84
805	0.320	0.153	0.224	12	24	24 AUG 84
840	0.327	0.220	0.327	21	3	18 AUG 84
905	0.357	0.191	0.298	19	26	28 AUG 85

---

mean RWL =0.361 (S.E.=0.018)

mean RCM_1=0.188 (S.E.=0.009)

mean RCM_2=0.300 (S.E.=0.019)

mean litter size=11.56 (S.E.=0.886)

*data supplied by R. Antoniak

lost at parturition and the relative mass of each litter. The SVL of the mother was strongly correlated with litter size (Pearson's correlation coefficient =0.83, P>0.001). Not included in Table 3 are four litters that contained deformed young (spinal abnormalities) and/or stillborns, and three litters which were completely stillborn. The dates of birth of these litters appear in Table 4.

Reproductive abnormalities were observed in the field: I found three dead neonates near one another at the SRD, on August 28, 1985, and one roadkilled female (found on September 2, 1985) contained two unborn young that had obvious spinal deformities. Also, two gravid females which were collected on September 2 and 4, 1986 had not given birth by October 18, and were released at the den (K. and R. Antoniak, personal communication). Whether these two snake entered hibernation with unborn young is not known.

Body lengths of the neonates born in captivity varied significantly among the 18 intact litters (F=14.62, df=16,180, P<.0005). The mean SVL and mean weight of the neonates in each litter were poorly correlated with the SVL of the mother [Pearson's correlation coefficients of -0.034 (P>0.892) and 0.205 (P>0.445), respectively]. Little difference in mean SVL was found between male and female neonates, and between captive-born and wild-born neonates (Figure 15). Therefore, the lengths of all normal neonates were pooled, to give a mean SVL of 191.15 mm (S.E.=0.535, n=284). The average weight of 187 neonates (those weighed on a precision scale) was 2.62 g (S.E.=0.028).

Sex ratios of captive-born litters varied somewhat (Figure 16), although not significantly (heterogeneity chi-square=8.40, df=16, 0.975<P<0.95); the pooled sex

Table 4: Data on litters born in captivity which contained stillborn or deformed young.

days=number of days gravid female was in captivity prior to giving birth.

SVL of mother (mm)	RWL	status of litter	days	date of birth
695	0.404	9 live young, including 4 with spinal deformities	11	3 SEP 83
700	0.391	1 live young, 11 stillborns	17	11 SEP 83
725	0.385	3 live young, 6 stillborns	34	4 SEP 84
845	0.336	17 stillborns	18	8 SEP 83
915	0.386	25 stillborns	17	5 SEP 85

ratio of these litters was not significantly different from 1:1 (chi-square=1.018, df=1, 0.25<P<0.50). There was no significant difference between the proportions of males in neonates born in captivity and neonates encountered in the wild (Z=0.897, 0.20<P<0.50). Thus, these samples were pooled to give an overall estimated proportion of male neonates of 0.547 (S.E.=0.029, n=284).

Characteristics of the Hibernaculum

The data from the temperature probes installed at the SRD indicated that subterranean temperatures never fell below 0°C. (Figure 17). During late fall and through the winter, the temperature difference between the surface and the most distal probe was minuscule. By mid-April the snow cover on the ground disappeared and surface temperatures increased rapidly, while subsurface temperatures responded more slowly. This situation existed throughout the course of the summer, and it was not until early fall that a decrease in ground and underground temperatures occurred.

A distinctly different temperature profile was recorded at the reference site, where snakes did not hibernate. Although the thermistor depths at this location were comparable to those of the SRD, temperatures well below zero were recorded for the winter period; also, surface temperatures in this location appeared more responsive to changes in ambient temperatures (Figure 17). During the spring and summer, surface temperatures at the SRD were below that recorded at the reference site. However, spring and summer underground temperatures were greater in the SRD than at the reference site.

Figure 15: Average SVLs for various categories of WBNP neonates.

Vertical lines equal ±1 S.E. about the mean. ♂♂ and ♀♀ = all (captive+born in wild) male and female neonates, respectively; c.b. = captive born neonates; b.w. =neonates born in the wild; 'combined' = all neonates combined.

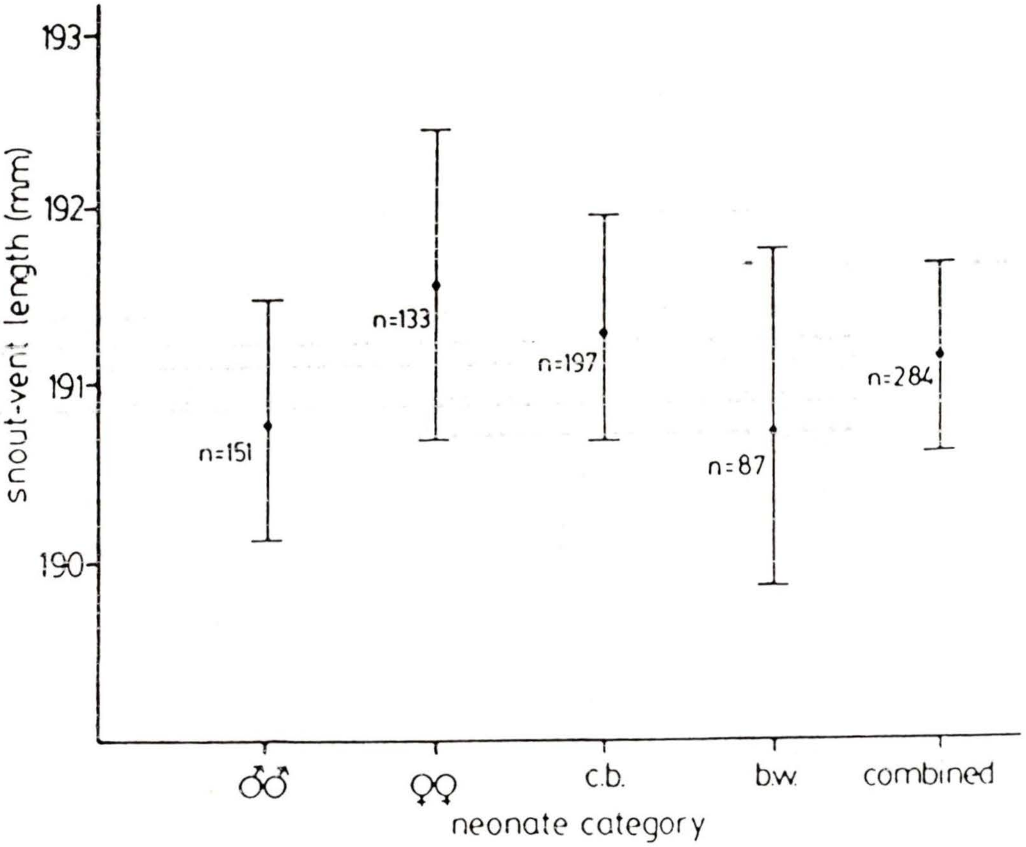

193
192
191
190
snout-vent length (mm)
n=151
n=133
n=197
n=87
n=284
♂♂
♀♀
c.b.
b.w.
combined
neonate category

Figure 16: Number of male neonates occurring in intact litters (from Table 3)

The enclosed numbers represent an overlap of data points. Dotted line represents a theoretical 1:1 sex ratio.

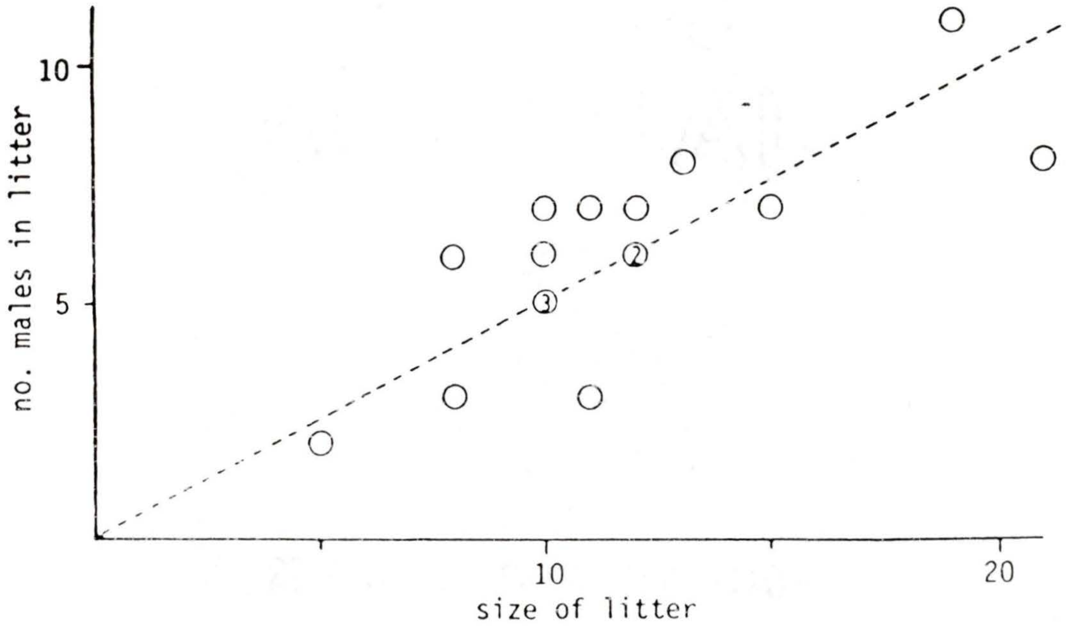
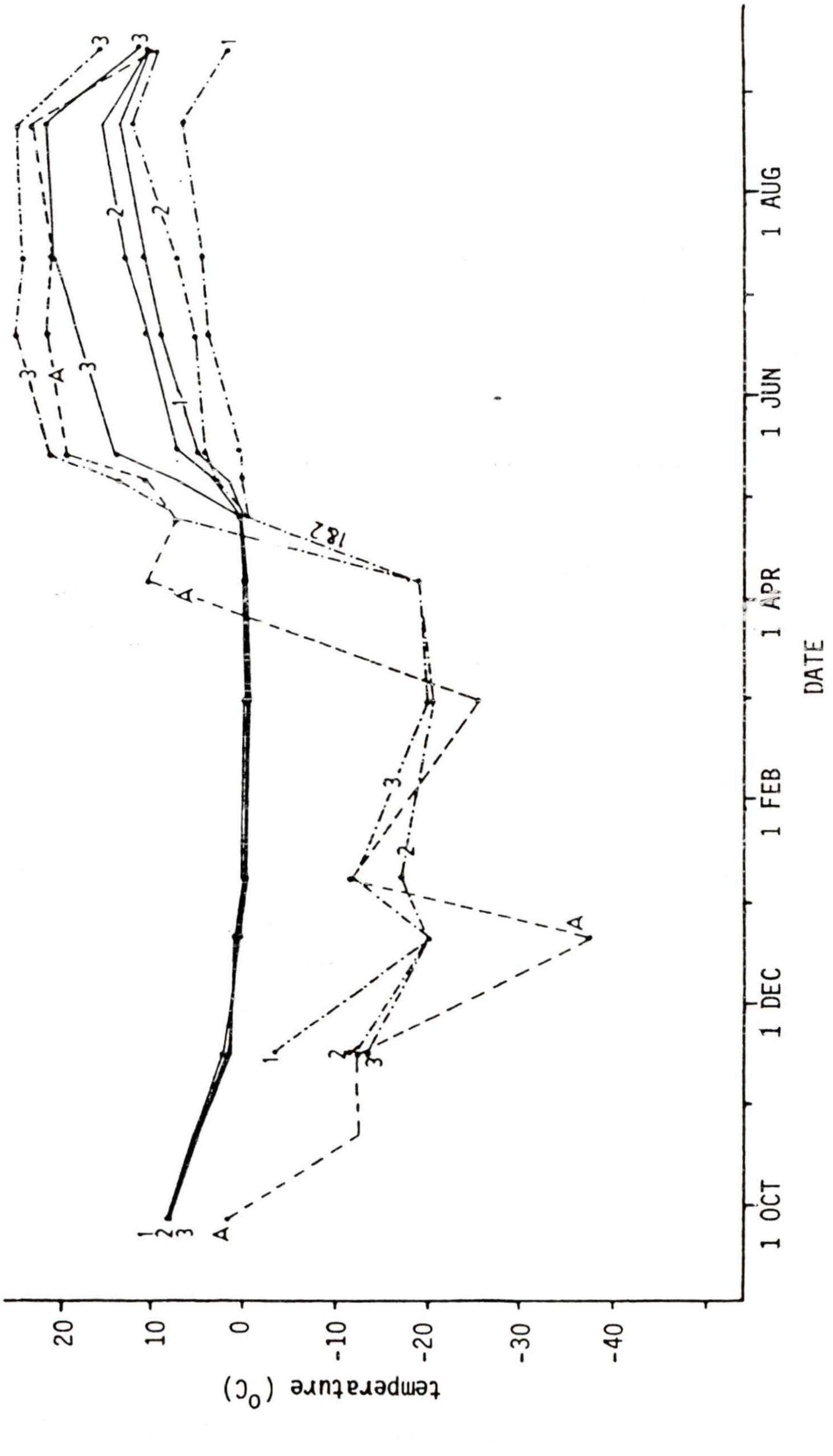

no. males in litter
10
5
size of litter
10
20
3
2

Figure 17: Surface and underground temperatures recorded at the SRD and at nearby reference site.

Solid lines = temperatures at SRD, broken/dotted line = temperatures at reference site. For both sites, probe 3 =surface temperatures, probe 1 =temperatures at greatest depth, and probe 2 =temperatures at intermediate area (see Methods for precise depths). Also indicated is air temperature ('A' and broken line) at the two sites.


temperature (°C)
20
10
0
-10
-20
-30
-40
DATE
1 OCT
1 DEC
1 FEB
1 APR
1 JUN
1 AUG
1
2
3
A
1&2

An interesting characteristic of the den was the formation of 'air vents' in the snow during winter. Several of these vents developed above the major openings of the SRD, and they were apparently caused by relatively warm subterranean air rising out of the ground. Presumably, the warm air melted the snow, which then recrystallized, forming mounds about 25-30 cm high and wide. A pocket thermometer lowered into two of these vents in mid-February, 1985, indicated temperatures of 0 and -2°C. while the ambient temperature was -23°C. Vegetation near these vents was laden with ice crystals, apparently caused by moist air rising out of the vents. A mist from the vents was visible on particularly cold winter days (J. Saquet and R. Antoniak, personal communication). Air vents were not observed at the reference site.

Only one of the two snakes implanted with temperature-sensitive transmitters during the fall of 1984 was monitored until emergence. The signal from one transmitter grew fainter during the course of the winter, and was eventually lost. This transmitter also gave rather erratic readings during the later part of the winter, and as it was never recovered and recalibrated, its readings were considered unreliable and are not presented here. However, the second transmitter gave strong signals throughout the winter, and when the snake emerged in the spring, the transmitter was removed and recalibrated, which verified the previous calibration readings.

Figure 18 presents the recorded body temperatures of the hibernating snake, and compares them to the temperatures recorded by the SRD probe. The snake maintained a body temperature several degrees above that recorded by the deepest probe, and never fell below 4°C.

During the first few months of the hibernation period, significant shifts in the signal sources of the two transmitter-equipped snakes were detected, implying the snakes were moving about while in the den. Horizontal displacement of the snakes was estimated to be approximately 15 m. Both snakes eventually settled down below a den opening other than the one they had originally entered.

Figure 19 compares the number of snakes emerging during the spring of 1985 with air temperatures and temperatures recorded from the underground probe at the SRD. Major peaks of emergence seemed to follow a sudden increase in temperature, particularly surface temperature. The gradient 'reversal' (i.e. that point at which surface temperatures begin to exceed subsurface temperatures) occurred prior to the point at which snakes emerged *en masse*.

Figure 18: Body temperatures recorded for a hibernating *Thamnophis sirtalis* (S) during the winter of 1984-1985.

Also shown are temperatures recorded by the temperature probes inserted in the SRD (1,2,3) and air temperature (A) (as in Figure 17).

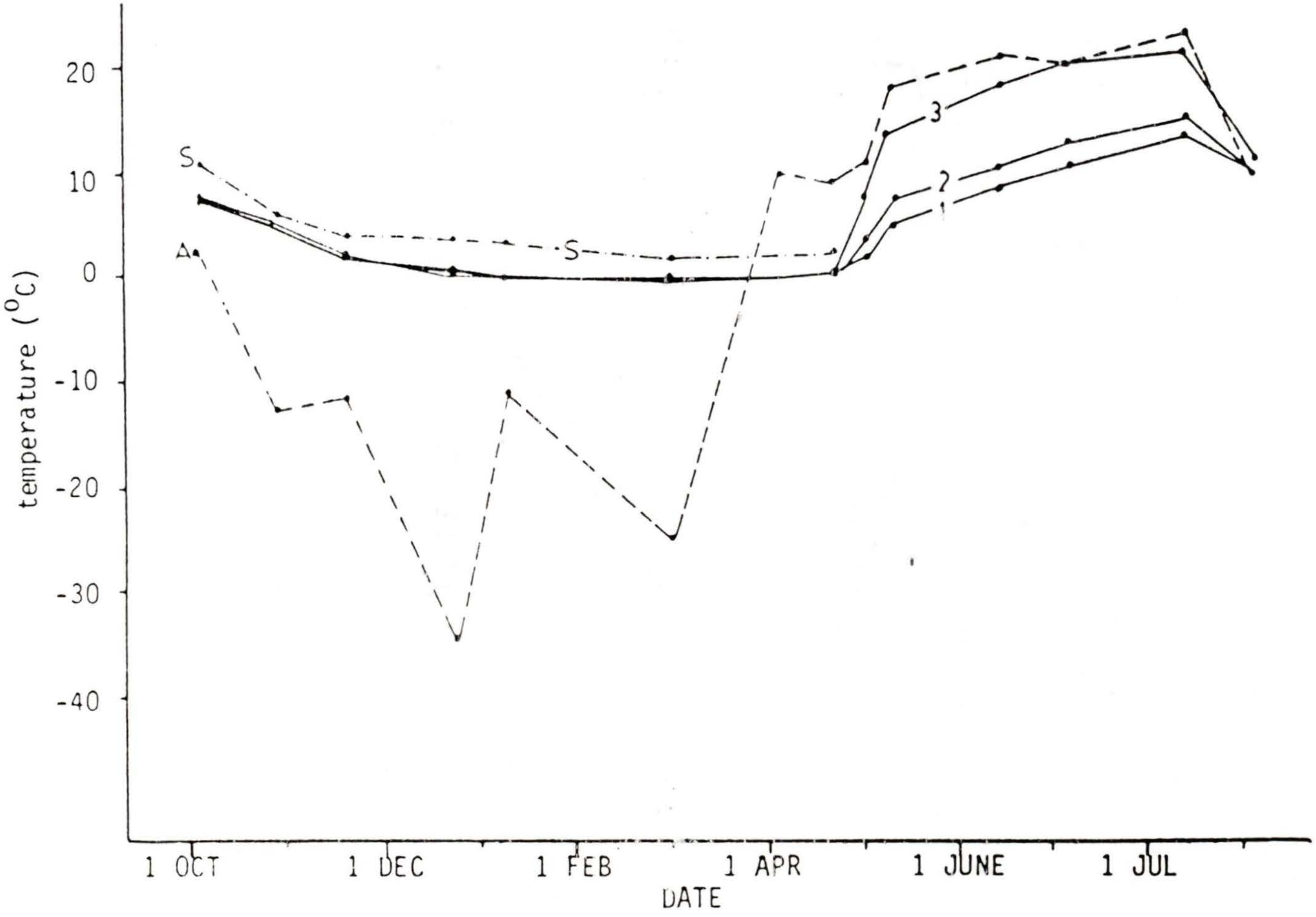
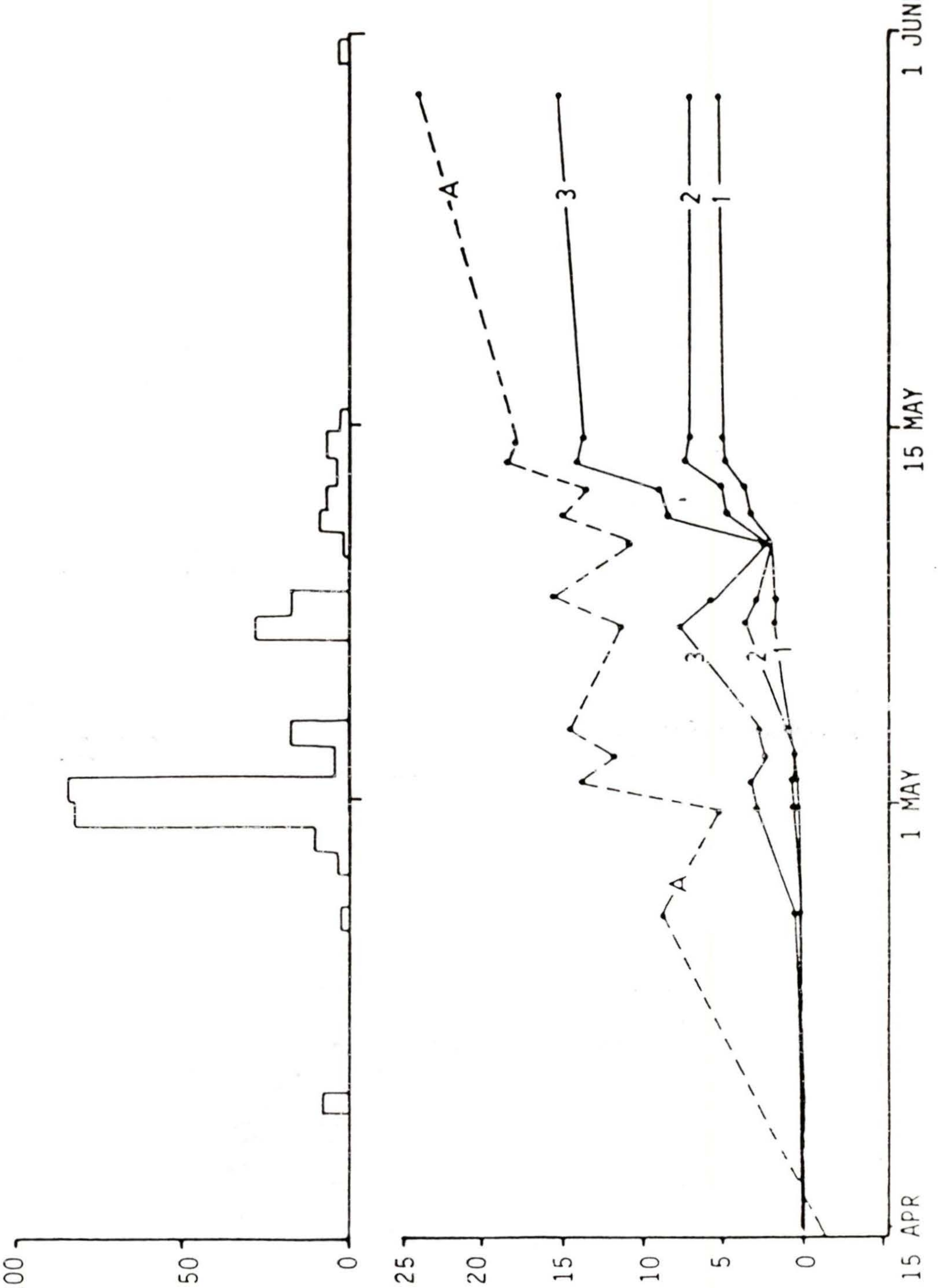

temperature (^{o}C)
20
10
0
-10
-20
-30
-40
S
A
S
3
2
1
1 OCT
1 DEC
1 FEB
1 APR
1 JUNE
1 JUL
DATE

Figure 19: Number of snakes emerging from SRD in the spring of 1985, compared to underground temperature gradient and air temperature.

See Figure 17 for explanation of temperature lines.


no. snakes emerging
from hibernation
100
50
0
temperature (°C)
25
20
15
10
5
0
15 APR
1 MAY
15 MAY
1 JUNE
A
3
2
1

DISCUSSION

Spring Behaviour

The emergence and mating behaviour of snakes at the SRD did not differ substantially from that described for *T. sirtalis* at communal dens in Manitoba (Aleksiuk and Gregory, 1974; Gregory, 1974; Crews and Gartska, 1982). However, the overall length of time that snakes spent at the den in spring was considerably less than that in Manitoba (about six weeks, Gregory, 1974). This may be a reflection of the relatively short active season in WBNP; that is, snakes are forced to trade off time that could be spent near the shelter provided by the den in the cool early spring in favour of foraging or other activities. Alternatively, the short activity season at the den might simply be a function of the size of the den population (i.e. fewer snakes, hence a shorter mating period). Estimates of the size of the denning population studied by Gregory (1977) varied from roughly 4,000 to 8,000 among years.

Some strength is given to the hypothesis that length of potential active season has an important effect on spring behaviour when one considers the body temperatures of early-emerging snakes, and the ambient temperature conditions at the time of their emergence. They are apparently the lowest that have been recorded for any emerging snake. Emergence under cold conditions suggests that time is at a premium for these animals. It is not clear why the cloacal temperatures of these snakes were lower than temperatures recorded underground. Perhaps the snakes spend some time fairly close to the surface before actually emerging, thus exposing themselves to low temperatures. Almost nothing is known about the stimuli and underground movements involved in emergence of snakes from hibernation (see Characteristics of the Hibernaculum).

Population Dynamics and Structure

It is impossible to determine whether or not the SRD population changed in size during the study period, in view of the large variances of the population estimates (Table 2). Correlation between the Jolly-Seber and Petersen estimates for the males is not surprising, given that the two are based on similar principles. Recruitment and survivorship estimates were, however, quite similar for the two fall periods. The most reasonable interpretation of the statistics in Table 2 is that the population was holding steady.

The size-frequency distributions presented in Figures 5 and 6 are similar in shape to those reported for *T. sirtalis* elsewhere (Carpenter 1952a; Fitch 1965; Gregory 1977). The presence of immature snakes at the SRD (albeit in very small numbers) is similar to that reported for the Chilcotin region of British Columbia (*T. sirtalis* and *T. elegans*, Gregory, 1984a), and other sites discussed by Gregory (1977). However, Gregory's (1977) den in Manitoba was devoid of juveniles and neonates. Variations in presence or absence of young at dens are also seen in other species (*Crotalus viridis*, Macartney, 1985; *Vipera berus*, Viitanen, 1967 and Prestt, 1971).

In the case of the Salt River and Chilcotin dens, the presence of neonates results from the return of some gravid females to the den in the later part of the summer, and their subsequent parturition. In the Manitoba dens examined by Gregory (1977), gravid females did not return to the den, hence the absence of neonates. Why this difference exists between denning populations of the same species is not known. It may be caused by local conditions, such as habitat arrangement and type (Gregory 1984a). If summer habitat and hibernacula are relatively close, then presumably there would be very little cost associated with returning to the den for parturition. Benefits to the female may include good basking and escape conditions. On the other hand, if a large distance separates the two habitats, and if being gravid increases vulnerability to predators (Shine, 1980), then a better strategy may be to remain in the summer habitat until parturition. The scarcity of juveniles (i.e. >1 year old) at the den is not as easily explained, since they presumably have had at least one summer to relocate themselves.

Although young snakes were represented in the denning population, the overall proportion of immature snakes was relatively small each year. Under conditions such as those at the SRD, there is a reasonably good chance of locating immature snakes upon emergence, especially in the spring when the ground is barren. Thus, the apparent scarcity of juvenile (and neonate) snakes at the SRD is likely quite real, and is not attributable to ineffective detection (Fitch, 1965). I conclude, therefore, that the majority of immature snakes in WBNP spend their first few years away from the communal dens, as seems to be the case elsewhere (Gregory, 1977). This conclusion implies that survival, at least in the younger age classes, is possible without use of the communal den. This may simply be a function of body size: smaller garter snakes have been shown to hibernate in cavities that are inaccessible to larger members of the population (Lang 1971). Thus, adults perhaps hibernate at communal dens because they are the only sites available for them (Gregory, 1984a, but see Reproduction). A more complicated hypothesis is that the main benefit of communal denning is not winter survival but enhanced reproduction because of the presence of many potential mates upon emergence in spring, when mating occurs. These theories represent two possibilities; a combination of factors may be responsible (see Gregory 1984a).

Such hypotheses are not easily tested. Ideally, immature snakes in WBNP should be followed for the first few years of their life to determine where they hibernate. Existing technology, unfortunately, does not permit this approach. However, more information on the female portion of the denning population would be valuable. It is impossible to determine from the results of this study if females and males using the den for the first time fall into a similar size category. As females reach sexual maturity at a larger size than males (Gregory 1977), they may not use communal hibernacula until they are older than first-time males (assuming the two sexes grow at similar rates when young). This would indicate that survival away from the den is less dependent on size. Additional evidence on this point would come from the demonstration that postparturient females also hibernate at sites other than communal dens (see Reproduction).

Most studies of denning snakes indicate some degree of exchange of individuals among dens, although den fidelity from year to year is often very high (Gregory, 1977, 1984a). The appearance of two males at the SRD, after they were marked at another den, confirms that dens in WBNP are not genetically isolated demes. It is also likely that young snakes do not always return to the den that their parents used, especially if parturition occurs away from the hibernacula (Gregory 1984a). This also would contribute to gene flow between denning populations.

Overwinter survivorship figures for Gregory's (1977) population were relatively lower than the summer estimates, indicating a significant loss of individuals during hibernation. Gregory also reported other cases of high overwinter mortality; in one case, large numbers of dead snakes were found in a den following a winter of light snowfall. Gregory hypothesized that a lack of insulation (snow) may have resulted in the snakes freezing underground. SRD snakes showed relatively high overwinter survivorship, even though low snowfalls were recorded in the Fort Smith region during the winters of 1983-84 and 1984-85 (39.4 cm and 54.5 cm, respectively, compared to a norm of 145.9 cm; Atmospheric Environment Service, Edmonton, Alberta).

Why there was relatively little observed mortality at the SRD during spring emergence is unclear. In Manitoba, crows *(Corvus caurinus)* kill large numbers of snakes each spring (Gregory, 1971), but ravens *(C. corax)*, which are very common in WBNP, seemed to have little effect on the SRD population. The frequent presence of park staff and visitors (and myself) may have deterred some predators from approachng the den, but ravens are not normally disinclined to occupy areas that humans inhabit.

As I was unable to calculate survivorship estimates for the females, it is impossible to determine if survivorship differs between the sexes. However, a significant difference in survivorship between the sexes might be reflected in the sex ratio of adults compared to that of neonates (Gregory, 1977). Parker and Brown (1980) found only a slight difference between the survivorship of male and female *Masticophis*, which showed a 1:1 sex ratio. Conversely, they also found that, over a period of four years, male *Pituophis* averaged 15.7% higher survivorship than females, with a significantly skewed sex ratio towards males occuring only once during their study. However, their sample sizes of *Pituophis* were relatively small. Assuming that the autumn samples were random in this study, then the sex ratio of adult male and female snakes in the SRD was close to 1:1 each year, which is the approximate ratio obtained in other studies of *T. sirtalis* (Gregory, 1977; Carpenter, 1952a; Martof, 1954; Fitch, 1965). As the sex ratio at birth was also close to 1:1, this suggests that adult female survivorship in the SRD population was probably close to that of the adult males, at least during the course of this study. The sex ratio at birth found in this study was approximately the same as that reported by other researchers (Carpenter, 1952a; Martof, 1954; Fitch, 1965; Gregory, 1977). These studies, with the exception of Gregory's work, also indicated a slight skewness towards males at birth.

Differing survival rates may exist within the adult female population, varying with reproductive condition, but the small sample sizes I collected cannot reveal this. Postparturient females that enter hibernation depleted of fat reserves may have a relatively lower chance of surviving the overwintering period. Also, gravid females were occasionally found very late in the fall and, in extreme cases, mortality might have occurred if they were unable to give birth prior to the arrival of cold weather, i.e. if trapped outside the den, survival would be unlikely. Another possibility is that they may enter hibernation with unborn young (see

Reproduction), but the consequences of this are unknown. Shine (1980) has hypothesized that survival of gravid reptiles may be reduced by increased exposure to predators, brought about by the need to bask for longer periods of time in order to complete embryogenesis. If such costs exist, they may be more prevalent in extreme northern areas, where average ambient temperatures are lower, thus necessitating more basking time by snakes.

Movements and Migration

Migratory movements have been reported for several snake species (see Gregory, 1984a, for a review). The direction in which snakes depart from a den also has been shown, in certain cases, to be nearly constant within a population, i.e., most of the snakes leave in the same general direction, with the individuals spreading out at some distance from the den (Viitanen, 1967; Gregory and Stewart, 1975). The recapture of some SRD snakes in the marshes and the movement patterns seen in the fall, coupled with biotelemetry data, indicates that at least a portion, and perhaps all, of the SRD population uses the marshland to the northeast, especially since these marshes are the closest major freshwater habitat to the den.

Gregory and Stewart (1975) reported long-distance (10.7 km average) movements in a denning population of *T. sirtalis* in Manitoba. Carpenter (1952a) and Fitch (1965) also reported seasonal movements of *T. sirtalis* in Michigan and Kansas, respectively, but these distances were considerably less than those observed here (less than 1.2 km). Particularly large movements of individual snakes over one summer have been documented for *T. sirtalis* in Manitoba (17.7

km, Gregory and Stewart, 1975) and for *Crotalus viridis* in Wyoming (average 5.6 km, Duvall *et al*, 1985). However, these were recorded only as one-way movements. The movements shown in Figure 9a appear to be the longest documented *round trip* for any one snake species. This, coupled with the fact that snakes returned to the den by a route different from that used in spring migration, indicates that these animals have complex orientational capabilities.

I am unable to explain why the three radio-tracked snakes continued to move further away from the den once the marshland was reached, as prey (frogs) were readily observed in the more proximate regions. Gregory and Stewart (1975) hypothesized that long-distance migrations of *T. sirtalis* in Manitoba might be caused simply by the partitioning of the necessary resources among all the snakes, which required a very large area. Obviously, knowledge is required of the daily movements and behaviour patterns of the snakes throughout the summer, and the degree to which individuals compete for food. Regardless, the loop-like movement displayed in this study must represent a compromise between feeding strategy and the minimum distance needed to travel.

Extensive migrations are presumably costly, especially if the time taken to complete the movement takes time away from other necessary activities, such as feeding, which appears to be the case in WBNP. Data collected in this study also suggest that adverse spring and fall weather conditions in WBNP may add to this cost, by impeding the progress of the migrating snakes and/or subjecting them to predation or lethal temperatures.

Feeding

Generally, the observations made on the feeding ecology of WBNP *T. sirtalis* are consistent with those recorded for other populations. Several investigators have found similar proportions of snakes with prey (e.g. 26%, Carpenter, 1952a; 37%, Gregory and Stewart, 1975; 25%, Kephart, 1982; 44%, Gregory, 1978), although this proportion may vary in time (Gregory and Stewart, 1975; Kephart and Arnold, 1982). The small number of stomach samples that I recorded is therefore probably due to the small number of snakes examined, rather than any other factor. The absence of food from all but one of the snakes sampled at the den is in accordance with Gregory and Stewart's (1975) study in Manitoba, where food was found in only five out of 270 snakes at a den, during the fall period. In addition, Gregory and Stewart found that gravid females in Manitoba, as in WBNP, rarely contained food, particularly in late summer.

The high incidence of amphibians in the diet of WBNP snakes also agrees with previous studies of *T. sirtalis* (Fitch, 1965; Gregory and Stewart, 1975; Kephart, 1982; Gregory, 1984b). The other prey items found in this study also have been recorded for *T. sirtalis* (e.g. Hamilton, 1951; Carpenter, 1952a). By constrast, earthworms are a common, and sometimes dominant, prey item in many southern populations (Hamilton, 1951; Carpenter, 1952a; Fitch, 1965; Kephart, 1982; Gregory, 1984b), and in some cases are eaten more frequently by smaller snakes (Carpenter, 1952a; Fitch, 1965: Gregory, unpublished). Fitch (1965) observed that neonates in his study area (Kansas) were born after the majority of the newly-metamorphosed frogs had dispersed or had grown too large to swallow, a situation comparable to that in WBNP. However, he found that neonates were able to use earthworms as a food source. This led him to postulate that the absence of earthworms may be important in preventing the successful establishment of a population.

Evidently, the absence of earthworms from the WBNP area has not prevented *T. sirtalis* from colonizing the area, but it is possible that it affects the foraging success and survivorship of young (small) snakes. Even if other sources of food are plentiful (e.g. chorus frogs, leeches), neonates born at the hibernacula may be faced with a formidable, energetically-expensive journey to the nearest food source (marshes). Insects may be preyed upon to some degree by the smaller snakes, but this has yet to be established (but see Hamilton, 1951). On the other hand, neonates born near the marsh appear able to feed prior to hibernation, and would be able to resume feeding earlier in the spring. Thus, they may have an advantage over conspecifics born near the hibernaculum.

Growth

As pointed out by Gregory (1977), it is difficult to compare the growth rates of adult *T. sirtalis* from various parts of its range, due to an absence of a standard approach to growth analysis. Communal denning and the presence of a clearly defined 'growing season' make it possible to obtain growth records at precise intervals. Without these conditions present, researchers in southern parts of the range of *T. sirtalis* often calculate growth rates based on a variety of capture intervals (e.g. Carpenter, 1952b; Fitch, 1965; Kephart, 1981). Obviously, the shorter the capture interval the less likely that extrapolations of yearly growth will be accurate (and the longer the intervals, the less likely that interpolations will be valid). Moreover, one must also realize that observations made over the course of a short study (i.e. 1 to 5 years) reflect a very brief period in the 'lifetime' of a population, and as such probably do not represent the *average* growth rates of the snakes in a population (assuming that such a rate has any biological meaning). Gregory (1977) found significant differences in growth among the years 1970, 1971 and 1972. Fitch (1965) also found a difference in growth rates of *T. sirtalis* populations between years (and between his study sites) in Kansas.

Other factors hampering the modelling of growth of *T. sirtalis* include the interactions of reproduction and growth in females, and the paucity of growth records for garter snakes during the first part of their lives. Until more information is gathered in these areas, attempts to compare growth in different geographic populations of this species can be done only at a very superficial level. Nevertheless, I have attempted a cursory comparison of *T. sirtalis* growth, by calculating Walford plots (based on several years of growth) for Manitoba and Kansas populations (Table 5). Growth records for Kansas were not always representative of one year's growth; therefore, records of reasonable length (>30 days) were used to estimate growth for a theoretical active season of mid April to late October (H. Fitch, personal communication). The Walford plot that resulted from this approach is, therefore, probably not as accurate as those for the Manitoba and WBNP populations (growth records taken at definite, one-season intervals). However, it does indicate that adult snakes of a given length in Kansas will grow more during an active season than will snakes of similar length in Manitoba and WBNP (Figure 20). The Walford plots also predict higher asymptotic sizes for Kansas and WBNP snakes than Manitoba snakes. This prediction correlates well with actual measurements of snakes at those sites. However, the relative proportions of snakes which approach the asymptotic size is higher in WBNP than Kansas (compare Figures 5 and 6 with Figure 8 of Fitch, 1965); this structural difference in the populations is somewhat obscured by by the use of Walford plots.

There is no simple explanation for the large body sizes in the WBNP population. Adult snakes simply may live, on average, longer in WBNP than, for example, in Manitoba (for whatever reasons) and consequently grow larger, but this does not square readily with comparisons of Walford plots (Figure 12). Bergmann's Rule, which states that animals living in colder climates tend to be larger, is meant to apply to homeotherms (Pianka, 1983). However, thermoregulatory advantages might accrue to a basking reptile with an increase in body size (i.e. the benefits gained by increasing thermal inertia outweigh the cost of a lengthier 'warming up' period). Alternatively, larger size might be explained by reproductive advantages if larger females produce more (or larger) young. In the case of mature WBNP females, however, an increase in body size does not lead to an increase in fecundity (see below), and even if it did, it would not explain male gigantism, unless selection for larger females somehow operates on males as well (e.g. larger females may possess a reproductive advantage, but both larger female and male offspring will be produced). Complicating the matter even further is the fact that there is not a clear-cut latitudinal trend in body size of *T. sirtalis* (Table 5). In addition, occasional extremely large individuals are found in many populations that consist of relatively smaller snakes (Gregory, personal

Table 5: Summary of Walford plots for three populations of *T. sirtalis*.

RC=regression coefficient, I-intercept, PAS=predicted asymptotic size, MS=mean size of 10 largest individuals reported in study, r^2= coefficient of determination, and n=size of sample used to generate Walford plot.

	location	n	RC	I	PAS	MS	r^2
males	Kansas[*]	27	0.392	360.77	593	579	0.16
	Manitoba[**]	368	0.672	203.13	619	672	0.72
	WBNP	188	0.715	194.88	684	715	0.83
females	Kansas[*]	46	0.459	473.08	874	895[+]	0.24
	Manitoba[**]	18	0.530	335.25	713	789	0.62
	WBNP	21	0.603	331.22	833	913	0.67

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sources:

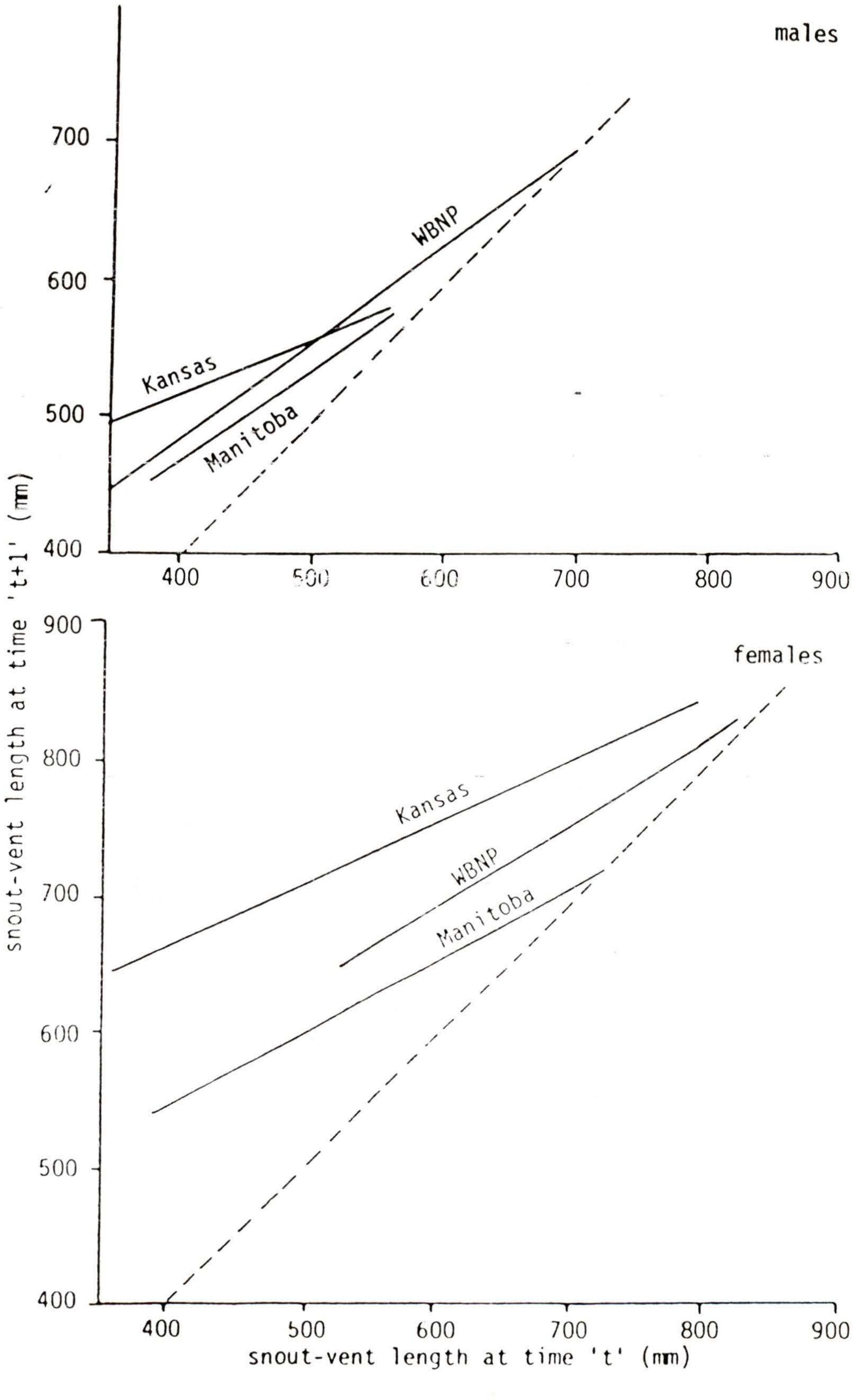
[*] Fitch, unpublished

[**] Gregory, unpublished

[+] extracted from Fitch (1965) and Fitch (unpublished) communication; Farr, personal communication). Body size variation is likely the result of the interplay of multiple factors. Obviously, manipulative and long-term studies are required to explain this variation.

Figure 20: Comparison of Walford plots for populations of *Thamnophis sirtalis* in Kansas, Manitoba and WBNP.

Regression coefficients and intercept values appear in Table 5. Note that the higher the line, the greater the annual growth for snakes of a given size. Dotted line equals the diagonal (i.e. $SVL_t=SVL_{t+1}$).


males
700
600
500
400
400
500
600
700
800
900
WBNP
Kansas
Manitoba
females
900
800
700
600
500
400
400
500
600
700
800
900
Kansas
WBNP
Manitoba
snout-vent length at time 't+1' (mm)
snout-vent length at time 't' (mm)

Reproduction

Several authors have presented reproductive statistics for various populations of *T. sirtalis* (Table 6). The variability among these figures is striking. Some of it is possibly due to differences in technique (e.g. estimating litter sizes through dissection rather than captive parturition), but other factors, such as local variations in food supply, are probably important. Furthermore, reproductive measurements such as clutch size can vary among years as well as among populations (Seigel and Fitch, 1985). Thus, estimates of reproductive traits generated by short-term studies may or may not reflect true population parameters.

Variation due to differences in technique can be eliminated by comparing studies in which data were collected in some standard fashion. Figure 21 does this for data collected in Manitoba, the Okanagan Valley in British Columbia, and WBNP. This figure illustrates three points. First, gravid females in WBNP are larger than most gravid females at the other two sites. Although the smallest female found with a copulatory plug in this study (570 mm SVL) may or may not have been capable of reproducing, it was still larger than the smallest gravid female reported by Gregory (1977) (and by Fitch, 1965, for Kansas *T. sirtalis*). Second, although WBNP females grow larger than Manitoba or Okanagan snakes, they do not produce larger litters. Third, for any given SVL, Manitoba females produce more young than females in the Okanagan, even though SVLs of gravid females at the two sites are similar. These last two points argue strongly that differences in litter size among populations are not simply correlated with variations in body size of gravid females. There are insufficient data at present

Table 6: Reproduction statistics of *T. sirtalis* from various geographical locations.

n=number of litters that mean litter size is based on; RWL=relative weight loss of postparturient females; RCM_1=relative clutch mass (clutch mass/preparturient weight of female.

location	average litter size	n	average SVL of neonate (mm)	average weight of neonate (g)	average RWL	average RCM_1
WBNP	11.56 (0.886)	18	191.5 (0.535)	2.62 (0.028)	0.361 (0.018)	0.188 (0.009)
Manitoba[1]	16.43 (1.54)	14	154.4 (1.09)	-	-	-
Okanagan Valley, B.C.[2]	9.33 (0.811)	21	182.0 (0.82)	2.35 (0.034)	0.447 (0.016)	0.254 (0.020)
Michigan[3]	18	20	-	-	-	-
Kansas[4]	13.8	132	167.9 (0.865)	1.88 (0.029)	-	0.244[5]
New Hampshire[6]	12.9	104				

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sources:

[1] Gregory, 1977

[2] Gregory, Macartney and Larsen, unpublished

[3] Carpenter, 1952a

[4] Fitch, 1965 (found average of 14.5 eggs/gravid female with approximately a 4.6% loss before parturition)

[5] Seigel and Fitch, 1984

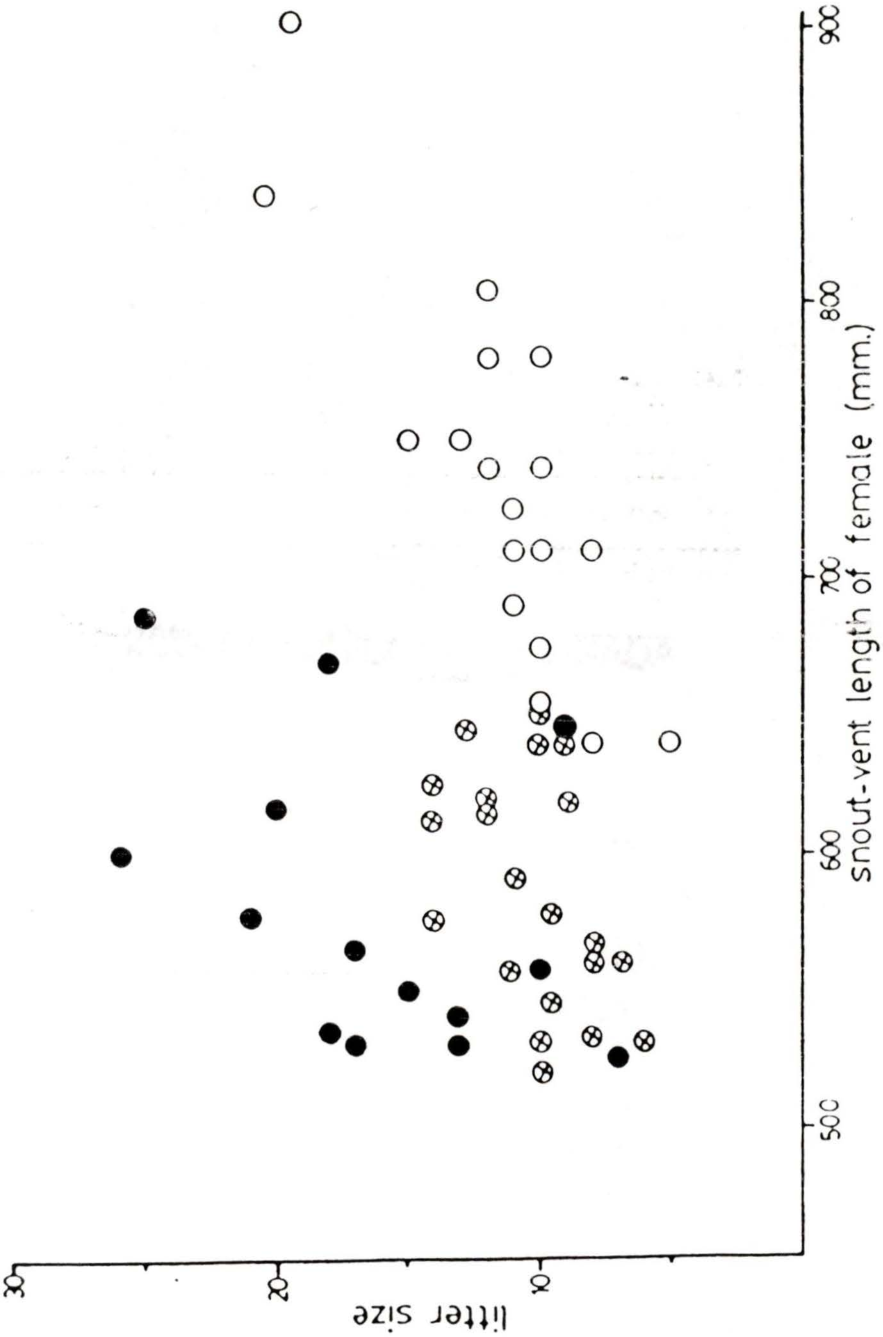
[6] Zehr, 1962 (based on embryo count in sample of gravid females)

to explain these patterns. Also, litter size is just one aspect of reproductive variation. For example, neonates in Manitoba are much smaller than those produced at WBNP (Table 6). The relative advantages (if any) of producing a few, large young versus many, smaller young remain to be determined, despite the attention given to this aspect of life history in the theoretical literature (cf. Stearns, 1976). Other important data, such as age of sexual maturity, are also lacking.

Apparently, WBNP females do not normally reproduce annually (Figure 14). Gregory (1977) suspected that female *T. sirtalis* in Manitoba exhibited biennial reproduction, but this suspicion was based on extremely limited evidence. Fitch (1965), on the other hand, concluded that most mature females in Kansas reproduced annually. Incidences of biennial or longer reproductive cycles of females have often been documented for northern snakes (Saint Girons, 1957; Gregory, 1982; Macartney, 1985). Presumably, deviations from an annual cycle would result if a post-parturient female was unable to feed and attain a reproductive condition prior to the denning period (Gregory, 1977, 1982). Females using the SRD may be especially susceptible to this, given the relatively short active season in WBNP and the long migration required. Those females that give birth at the den immediately before hibernation are almost certainly incapable of reproducing again the next year. Snakes that give birth away from the den and late in summer may be in a similar situation, especially if they must forego feeding to return to the den before winter. Whether females that produce young earlier in the summer are more likely to give birth in consecutive years remains to be seen.

Figure 21: Litter size as a function of SVL for female *Thamnophis sirtalis* from three different populations.

○ =WBNP; ● =Manitoba (Gregory, 1977),⊗=Okanagan Valley, B.C. (Gregory, Macartney and Larsen, unpublished). Only intact litters (containing no stillborn or malformed young) were used in the analysis.


litter size
30
20
10
snout-vent length of female (mm.)
500
600
700
800
900

My data, limited as they are, indicate considerable variability in reproductive frequency of individual females. The factors responsible remain to be determined, but likely involve variations in body size, individual foraging success, and year to year variation in weather. In certain years, some gravid females may fail to produce young (e.g. the two gravid females which had not given birth by October 18, 1986). Perhaps snake embryos can sometimes overwinter successfully *in utero*, but evidence on this is scant and equivocal (Gregory, 1982).

Regardless of the specific cycles involved, if some proportion of sexually mature females do not reproduce every year, there will be a relatively low recruitment rate in the population. If this proportion of non-reproducing females is increased (e.g. active season shortened, as would be the case if populations occurred further north), a point will be reached at which the population is unable to sustain itself. A corresponding increase in the age at which females first reproduce (as may be the case in WBNP, given their large size and relatively slow growth - Figure 20) will not necessarily lower the recruitment rate of a stable population, but will make recovery from occasional population crashes very slow. Although the population using the SRD remained stable during this study, the climate of WBNP (and of points further north) makes it likely that populations experience declines from time to time, as was observed for *T. sirtalis* in Manitoba (Gregory, 1977).

I have previously discussed the question of where neonates hibernate (see Population Structure and Dynamics); it is possible that postparturient females also hibernate away from communal dens. The recorded movement of the one female from the marsh (following parturition in captivity) implies that some postparturient females return to dens. However, there was a scarcity of postparturient females at the den. A strategy of hibernating nearer the marsh following birth might be favourable, because postparturient females could then feed longer into the fall (replace lost fat reserves) and resume feeding earlier in the spring. Whether suitable hibernation sites for small numbers of snakes exist near marshes remains to be determined.

Characteristics of the Hibernaculum

The comparison of the temperature profiles of the SRD and the reference site supports the hypothesis that suitable hibernating sites may be limited in northern areas (Gregory, 1984a), although a more extensive study is needed to test this possibility. Despite a superficial resemblance between the two sites, and the fact that surface temperatures were, as a rule, lower at the SRD, the sub-zero underground temperatures recorded at the reference site would have been fatal to a hibernating snake. The 'air-vents' in the snow above the SRD also suggest relatively high underground temperature conditions. The source of heat is not known; there are no hot springs recorded for this region (R. Lewis, personal communication) and it seems unlikely that the heat would be derived from the collective metabolism of hibernating snakes (cf. Gregory, 1982). Air vents also have been reported at a *T. sirtalis* den on Birch Creek, near the Peace-Athabaska delta (M. Bossenmeier, personal communication), but I do not know if all dens in this region exhibit this phenomenon.

It seems likely that the snake whose body temperature was monitored overwinter hibernated at a depth greater than 1.9 m, since its body temperature was higher than that of the probe at that depth. Alternatively, it could have raised its body temperature somewhat by generating metabolic heat. However, this seems unlikely, especially if conservation of energy resources is an important part of hibernation physiology (Gregory, 1982). Nevertheless, snakes are capable of movement during some, if not all, of the hibernating period. Such movement may allow them to 'sample' the thermal environment underground, and thereby influence when they emerge in spring. Viitanen (1967) hypothesized that entrance and emergence may be correlated with seasonal reversals of the surface-to-subsurface temperature gradient, and recent work by Lang (1971), Sexton and Hunt (1980) and Sexton and Marion (1981) have provided some support for this theory. It has also been demonstrated that snakes, under laboratory conditions, will respond to a gradient reversal by moving to a warmer area (Sexton and Marion, 1981). However, the results of my study, and those of Macartney's (1985) study, suggest that a gradient reversal *per se* does not stimulate the hibernating snakes to emerge. Rather, the animals simply may be investigating and moving towards the higher temperatures that develop nearer the surface in the spring. Admittedly, as Macartney points out, it is not easy to isolate the effects of the gradient reversal from the overall warming trend underground. Conversely, laboratory studies may present an animal with only one particular stimulus, whereas a hibernating snake's 'decision' to emerge may be prompted by the synergistic effects of several factors. There is reason to consider that emergence patterns are not solely dictated by temperature patterns: In autumn, for example, some signal, far removed from a reversal of the subterranean gradient at the SRD, prompts the snakes to migrate several km back to the den. Also, there is a marked difference in the emergence patterns of the sexes (males emerge earlier, and in large numbers, while females emerge later and singly or in small numbers). Thus, endogenous behaviour may be partly responsible for evoking spring emergence.

CONCLUSION

Although this study did not test directly how *T. sirtalis* is limited in distribution, some important correlations are apparent: Reduced annual growth, biennial or longer reproductive cycles of females, and 'costly' long migrations all qualify as likely sources of population limitation for the species, and all probably are caused, in one manner or another, by short summers and long, harsh winters. Throughout my discussion, I have tried to point out areas in which a lack of knowledge precludes any attempt to draw firm conclusions about limiting factors. More detailed natural history observations and experimental tests of specific hypotheses are required. One major weakness of this study was the infrequent capture of female snakes. Improving this situation might supply information on age of sexual maturity, reproductive history and the influences of reproduction on future survivorship. Ensuring capture of all snakes returning to and dispersing from the den would certainly help alleviate this problem. However, as I mentioned in Methods, this procedure is somewhat difficult at the SRD, and might be best applied elsewhere. Experimental manipulation also may also provide clues: For example, construction of artificial dens could reveal if (and how) a scarcity of hibernacula limits colonization of areas and, therefore, population size.

The means by which snakes are limited probably differ between species and among ecological categories (e.g. viviparous versus oviparous snakes), and the presumed demographic consequences of short active seasons, which seem to be borne out by this study, are not necessarily universal. Nevertheless, I hope this study will help provide a basis for future, more specific research, designed to address the problem of limiting factors on snakes.

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Title of Thesis

ECOLOGY OF THE COMMON GARTER SNAKE,

THAMNOPHIS SIRTALIS,

AT THE NORTHERN LIMIT OF ITS RANGE

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