THE UNIVERSITY OF MANITOBA

LIFE HISTORY PARAMETERS OF A POPULATION OF RED-SIDED GARTER SNAKES (*THAMNOPHIS SIRTALIS PARIETALIS*) ADAPTED TO A RIGOROUS AND FLUCTUATING ENVIRONMENT

by

PATRICK THOMAS GREGORY

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DEPARTMENT OF ZOOLOGY

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FALL, 1973

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PATRICK THOMAS GREGORY

A dissertation submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

The red-sided garter snake, *Thamnophis sirtalis parietalis*, approaches the northern limit of its range in the Interlake of Manitoba, Canada. Although the climate is extreme and variable, the species is abundant in this region. The main objective of this study was to explain this abundance in ecological terms.

Denning populations of *T. sirtalis* are large, but susceptible to great fluctuation in size. Population declines may occur because of reproductive failure in response to poor weather conditions, rather than because of variable survivorship of adults. Growth of juvenile snakes is sufficiently rapid that first reproduction usually takes place in the second year of life. Reproductive potential is apparently higher than in more southerly populations, although considerable loss of potential may take place during gestation. It is suggested that *T. sirtalis* resembles an "r-selected" species throughout its range and that the characteristics of such species are particularly well-developed in the Interlake populations.

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TABLE OF CONTENTS

PAGE

ABSTRACT i

ACKNOWLEDGEMENTS ii

LIST OF FIGURES v

LIST OF TABLES viii

INTRODUCTION 1

MATERIALS AND METHODS 5

A. THE STUDY AREA 5

B. METHODS 11

RESULTS 16

A. SUMMER ECOLOGY 16

i. Dispersal 16

ii. Food 18

B. GROWTH 24

C. POPULATION CHARACTERISTICS 27

i. Population Dynamics 27

a. Tests of Assumptions 27

b. Population Size and Survivorship Estimates . 29

ii. Population Structure 31

D. REPRODUCTION IN FEMALES 36

i. Potential Fecundity 36

ii. Development of Young and Realized Fecundity ... 40

iii. Reproductive Cycle 47

E. REPRODUCTION IN MALES 51

PAGE

DISCUSSION 55

A. SUMMER ECOLOGY 55

i. Dispersal 55

ii. Food 57

B. GROWTH 60

C. POPULATION CHARACTERISTICS 63

i. Structure and Numbers 63

ii. Population Dynamics 65

D. REPRODUCTION 73

i. Potential Fecundity 73

ii. Development of Young 76

iii. Reproductive Cycles 79

E. LIFE HISTORY STRATEGY 83

LITERATURE CITED 92

LIST OF FIGURES

FIGURE		PAGE
1	Map of North America showing distribution of *Thamnophis sirtalis* and study area in Manitoba	2
2	Photograph of typical marsh in Interlake	6
3	Map of Inwood area showing distribution of known dens	7
4	Photograph of den one	8
5	Winnipeg weather records for 1972	10
6	Distances and directions of dispersal of snakes from Inwood dens	17
7	Frequency of occurrence of food types found in snakes in summer 1971	19
8	Frequency of occurrence of food types found in snakes in summer 1972	20
9	Percentage of snake stomachs containing food throughout summer	23
10	Walford plots of growth of both sexes for 1970, 1971, and 1972	26
11	Changes in numbers $(\hat{N})$ of male snakes at den one from fall 1969 to fall 1972	32

FIGURE PAGE

12 Size frequency distributions of male snakes at den one from fall 1969 to spring 1973 33

13 Size frequency distribution of female snakes at den one from fall 1969 to spring 1973 34

14 Regressions of potential brood size on size of female for females overwintering just prior to 1972 and 1973 breeding seasons 39

15 Distribution of potentially reproductive and non-reproductive individuals in mated and non-mated categories of dispersing females in spring 1972 41

16 Embryonic development and times of birth in female snakes from summer 1972 43

17 Regression of number of normal young on number of ovulation scars for females from summer 1972 44

18 A. Regression of brood size on size of females for females from summer 1972 and theoretical regression for denning females in spring 1972. B. Average size of young in brood vs. size of female 46

19 Weight of testes/S-V length of animal for males throughout active season of 1972 52

FIGURE PAGE

20 Average number of organs/animal containing sperm for testes, epididymes, and vasa deferentia from males caught in summer 1972 53

LIST OF TABLES

TABLE PAGE

I A. Number of instances of snakes containing more than one individual of a particular prey type

B. Number of instances of snakes containing more than one prey type 21

II Population size changes and survivorship in overwintering populations at den one, fall 1969 to fall 1972 30

III Percentages of reproductive females in different size groups for overwintering seasons of 1971-72 and 1972-73 37

IV Sex ratios of 14 intact broods from summer of 1972 and estimate of proportion ($\hat{P}$) of males in total sample with estimated standard error 48

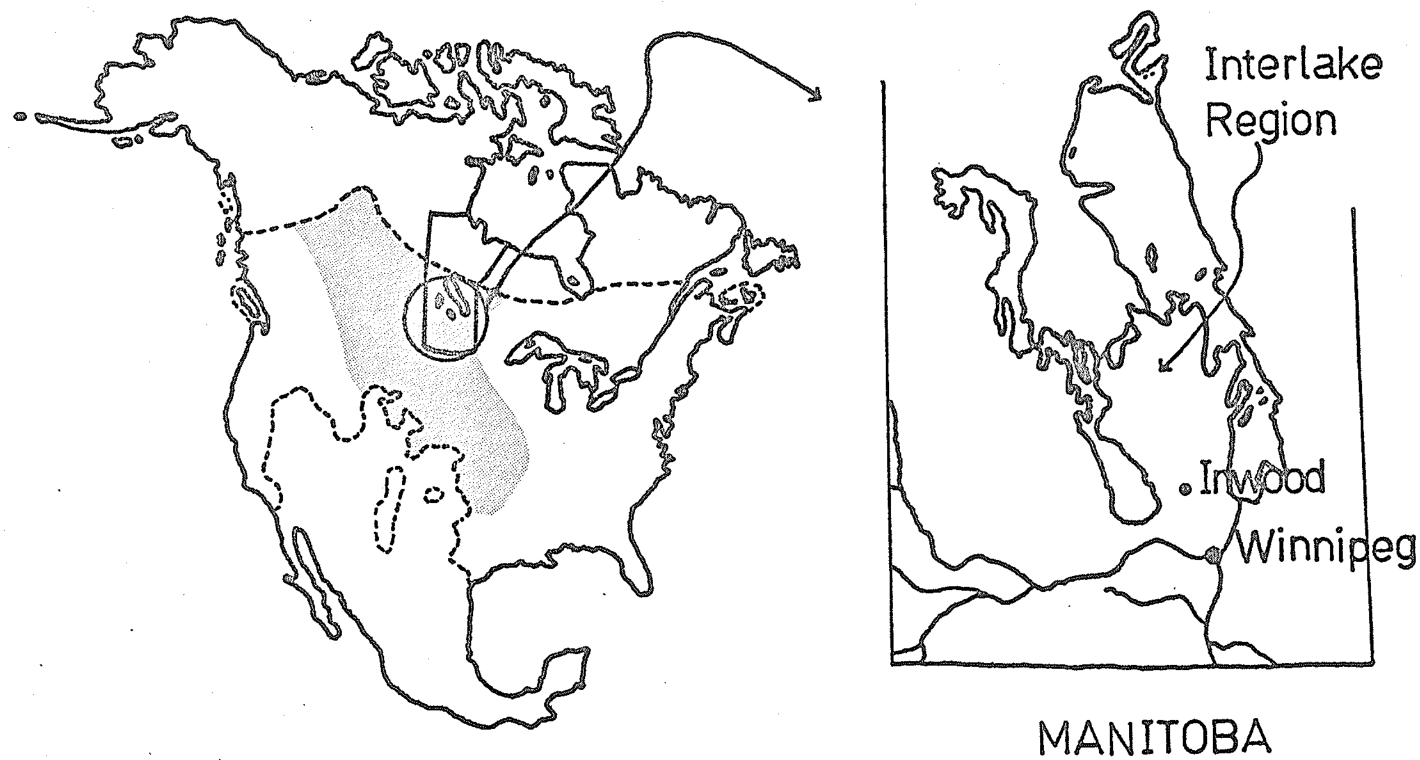
INTRODUCTION

The climate in the Interlake region of Manitoba is a distinctly rigorous one for a reptile, the long winter resulting in a very short growing season during which daily variations in temperature may be quite severe. The red-sided garter snake, *Thamnophis sirtalis parietalis*, approaches the northern limit of its distribution in this area (Fig. 1). The short growing season is apparently reflected in the annual cycle of these snakes. Six or more months of the year are spent in hibernation and only about three seem to be spent away from hibernacula (Gregory, 1971). In more southerly areas, the growing season is longer (Carpenter, 1952a; Platt, 1970).

Despite this, *T. sirtalis* appears to be a very abundant species in the Interlake, although large fluctuations in population size seem to take place. Young snakes are rarely seen, but the adults are particularly evident in spring and fall because of their habit of overwintering in large communal aggregations at traditional hibernacula or dens. The snakes are active in the vicinity of the dens for as much as one and one-half or two months each spring and fall. These den populations may number in the thousands in some cases (Gregory, 1971). This impression

Fig. 1 Map of North America showing distribution of *Thamnophis sirtalis* and study area in Manitoba.

Dotted line indicates range of *T. sirtalis* and shaded area range of subspecies *parietalis* (after Fitch, 1965: 504).


Interlake
Region
Inwood
Winnipeg
MANITOBA

of abundance is further reinforced at these times of year by the mass migrations that the snakes undertake when dispersing to marshes in the summer and returning in the fall. Neither such large overwintering populations nor such large-scale movements are known for the same species at lower latitudes.

These considerations suggest that the Interlake red-sided garter snake populations might represent a system for the study of ecological adaptation to a northern and nearly limiting environment. The relative wealth of literature (Carpenter, 1952b; Fitch, 1965; Platt, 1970) concerning the ecology of the species further south provides a suitable basis for comparison. Also, the presence of large, virtually non-interchanging populations at discrete denning areas (Gregory, 1971) affords a unique opportunity to investigate in detail the long-term population dynamics of this species. The following questions were of particular interest in this study:

1. Do population sizes fluctuate as greatly as appears to be the case? This has often been felt to be a characteristic of northern animal populations but it may well apply to *T. sirtalis* in general (Fitch, 1965; Platt, 1970). Do any changes in survivorship, fecundity, and sex or age composition accompany such

fluctuations and what might be their causes?

2. Are growth, fecundity, and age of first reproduction comparable with those of more southerly populations? Are such differences as might occur related to differences in reproductive strategies of the kinds shown for lizards (Tinkle, 1969; Tinkle *et al*, 1970)?
3. Does reproduction in individual females follow a cycle of two or more years as is the case for many species of snakes inhabiting high altitude or latitude localities (Rahn, 1942; St. Girons, 1957; Prestt, 1971)?

In addition to answering the above questions, a further objective of this study was to gather information concerning various aspects of the previously uninvestigated summer phase of the annual cycle of this species in the Interlake. The main points of interest were distances and direction of summer dispersal and food habits.

MATERIALS AND METHODS

A. THE STUDY AREA

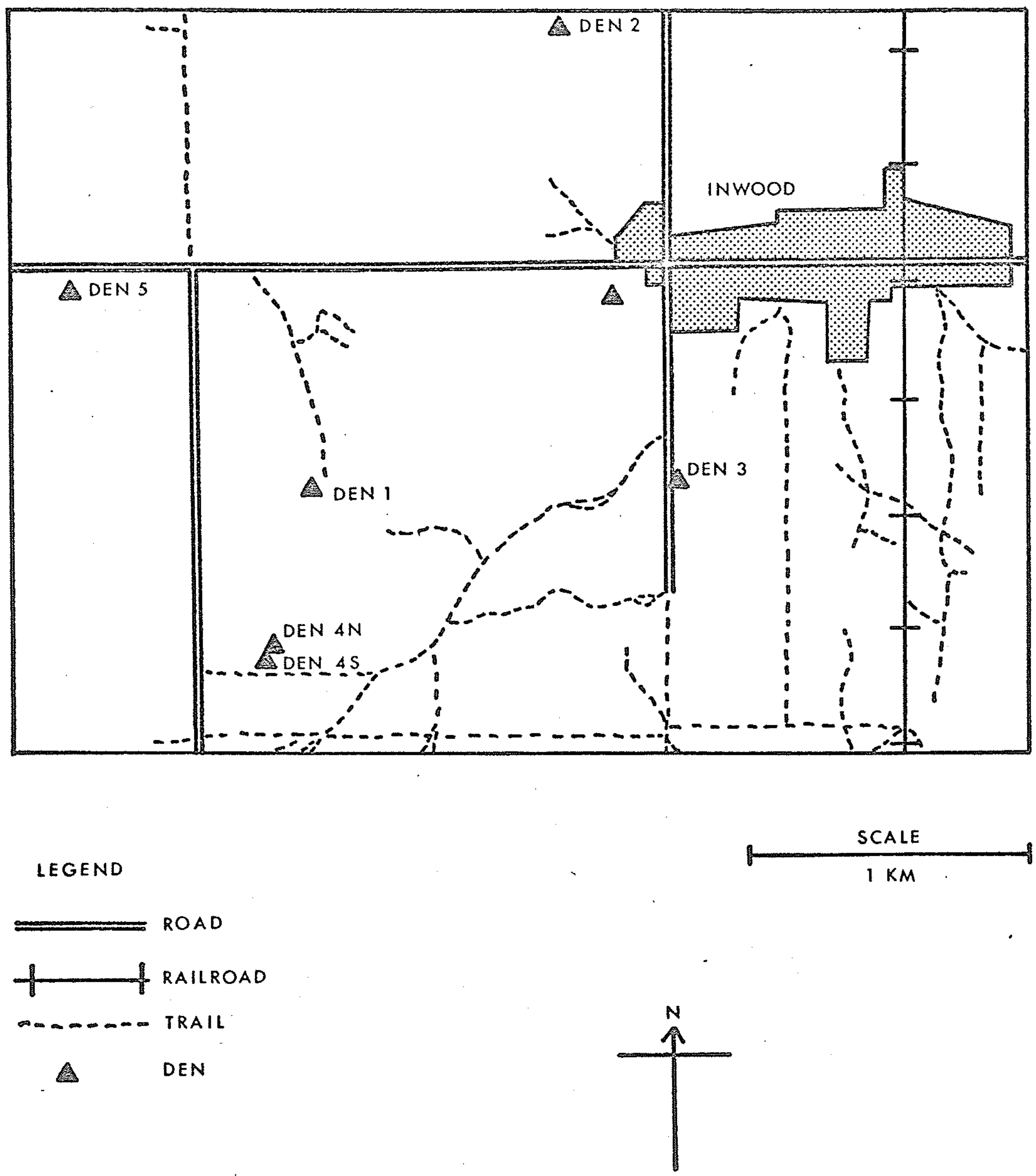
This study was carried out in the Interlake region of Manitoba, in an area centred around the town of Inwood, about 71 km. northwest of Winnipeg (Fig. 1). This is the same study site as described in Gregory (1971).

The area consists of a system of alternating linear ridges and depressions oriented in a northwest-southeast direction. The depressions are mainly occupied by marshes (Fig. 2), with small lakes or ponds in the middle of the larger marshes. The ridges are forested and consist of fissured limestone outcrop which often slumps into subterranean caves forming "sinks" and providing access underground. *T. sirtalis* uses these sinks as dens.

Inwood lies on one of the more southerly of these ridges. The area immediately around the town is dotted with hibernacula of varying sizes (Fig. 3), several of these apparently having been used for many years. An example of such a hibernaculum, and the one which has been studied most intensively, is den one (Fig. 3). This den consists of a large, oval-shaped limestone sink about 20 m. in length by 12 m. wide and 3 m. deep (Fig. 4). The bottom of this bowl-like depression is well-fissured and littered with broken-up pieces of rock.

Fig. 2 Photograph of typical marsh in Interlake.

Fig. 3 Map of Inwood area showing distribution of known dens.

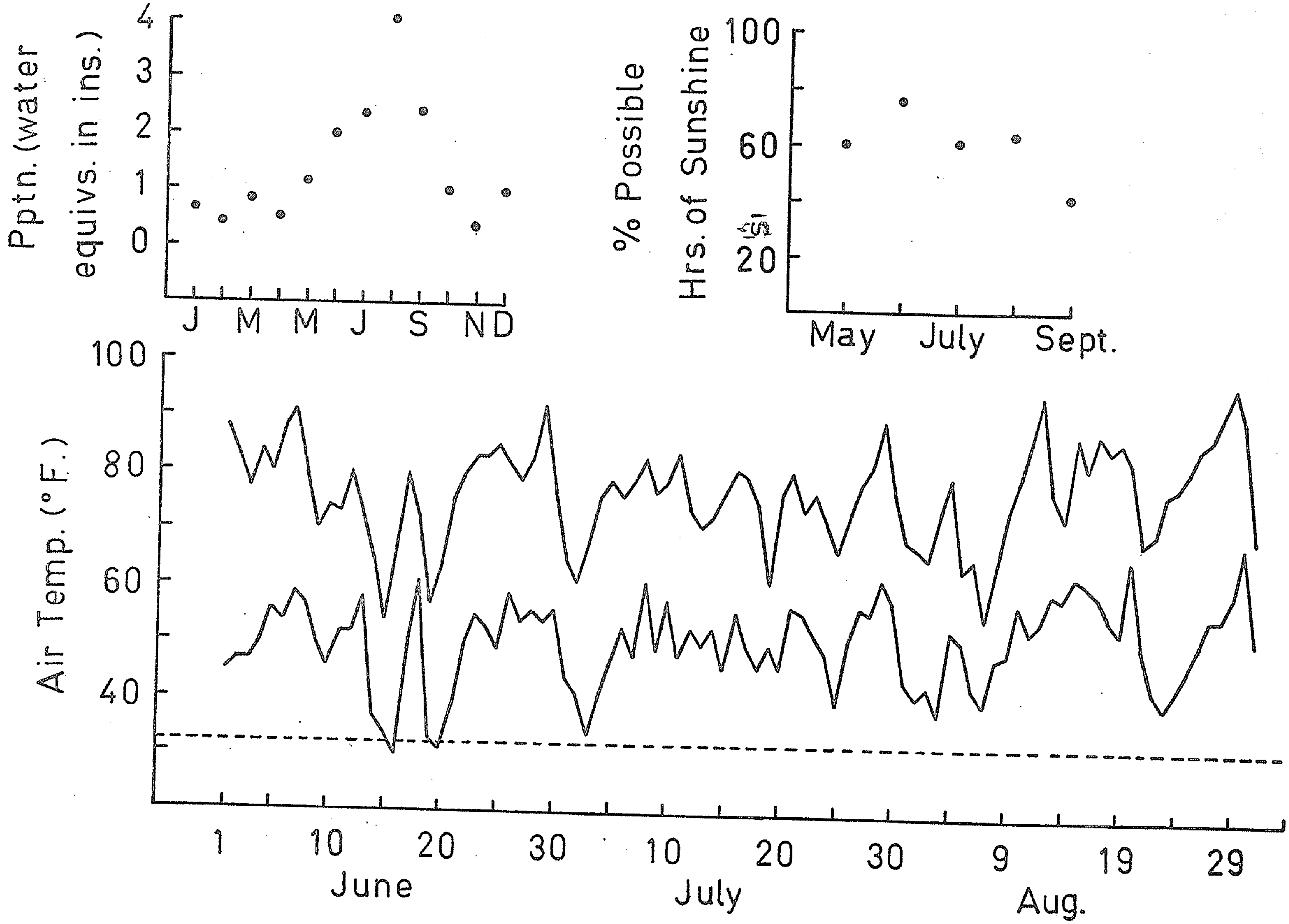


DEN 2
INWOOD
DEN 5
DEN 3
DEN 1
DEN 4N
DEN 4S
SCALE
1 KM
LEGEND
ROAD
RAILROAD
TRAIL
DEN
N

Fig. 4 Photograph of den one.

The extreme climate prevalent at this latitude in Manitoba is indicated by meteorological records for the city of Winnipeg, which has slightly milder weather (Weir, 1960). In the years from 1969 to 1972 inclusive, the greatest number of consecutive days free of killing frost (i.e. air temperature $\leq -1.4^{o}C.$) was 137 days and in 1969 this period was only 95 days. The longest frost-free period in those four years was 109 days. In addition, the variation in air temperature both within and among days is very great, even during the summer (Fig. 5). The percentage of possible sunshine is high during the summer and annual precipitation is generally low (Fig. 5).

Fig. 5 Winnipeg weather records for 1972.



Pptn. (water equivs. in ins.)
4
3
2
1
0
J
M
M
J
S
ND
% Possible Hrs. of Sunshine
100
60
20
May
July
Sept.
Air Temp. (° F.)
100
80
60
40
1
10
20
30
10
20
30
9
19
29
June
July
Aug.

B. METHODS

Every spring and fall from autumn 1969 to spring 1973 inclusive, samples of snakes were taken by hand from den one on an almost daily basis. Each previously uncaught snake was sexed, measured (snout-vent length, S-V) to the nearest five mm., and individually marked by removing subcaudal scutes after the method of Blanchard and Finster (1933), using the code described in Gregory (1971). All recaptures were noted and measured. Analysis of population structure was based on the size frequency distributions obtained for each sex. Average lengths were calculated for individuals measured more than once in a given fall or spring. Separation into size groups representative of different age classes was attempted by means of the method of Cassie (1954).

Two methods making use of the marked snakes were chosen to assess the sizes of the denning populations. Separate estimates were made for each sex. Simple Petersen indices (Robson and Regier, 1968) of the number of snakes entering the den every fall were calculated by considering each fall as a marking period and the subsequent spring as a recapturing period. The use of this estimator was possible because there was no recruitment between sampling times.

The multiple-recapture Jolly (1965) model allowing both death and recruitment was also used since the number of successive sampling periods (eight) and the sample sizes obtainable appeared sufficiently large that meaningful estimates could be expected, at least for the males. In addition to providing estimates of both spring and fall population sizes, the Jolly model also allows the calculation of estimates of survivorship between sampling periods and their variances. The possible problem of unequal catchability due to some animals switching from den to den in different years was assessed by calculating the percentage den-fidelity of marked snakes caught at all dens one summer or more after original marking as in Gregory (1971). Unequal catchability of marked animals at den one was tested using the method of Leslie (1958).

Growth was analyzed on the basis of the increase in snout-vent length shown by marked snakes found at dens in two successive overwintering periods. Since all the snakes at dens are adults (Gregory, 1971) and since a definite age in years could be attached to only a few individuals, the Walford (1946) type of analysis was employed. Growth rates among years were compared by analysis of covariance.

Estimates of potential fecundity in denning populations were obtained in 1972 and 1973 by taking samples of female snakes from the vicinity of Inwood and measuring the lengths of all the ova in their ovaries to the nearest 0.1 mm.; no snakes were taken from den one. These data were then broken into size groups by probability paper analysis (Cassie, 1954) and estimates of number of mature eggs per size of female were obtained. These figures were checked for accuracy by comparing the sizes of the remaining ova with those of immature eggs left in the ovaries of females that had ovulated later in the spring. Reproductive potentials in the two years were compared by analysis of covariance.

Realized fecundity was calculated by correlating the number of mature eggs ovulated (as indicated by the number of ovulation scars in the ovaries) with the number of apparently viable young *in utero*. These data were taken from females in advanced stages of gestation in the summer of 1972. Additional information was obtained from gravid females kept in an outdoor enclosure at the University of Manitoba in the summer of 1972 and allowed to give birth in the laboratory before being sacrificed. The young of these snakes were measured (S-V length to nearest mm.) and sexed by dissection.

Females dissected throughout the active season of 1972 and during the spring of 1973 were checked for presence of copulatory plugs in their cloacae and sperm in their oviducts to determine if they had recently mated. Examination of the reproductive tract also allowed determinations of times of ovulation, stages of embryonic development (Zehr, 1962), and times of birth. Females with obvious signs of recent gestation (ovulation scars, uterine scars) were examined in 1972 and the spring of 1973 in order to compare the state of development of their reproductive tracts with previously non-gravid females and thereby determine whether annual breeding takes place.

In order to complement the study of reproduction in females, males were also collected throughout the active season of 1972. These were checked for presence of sperm in each testis, epididymis, and vas deferens and a plot was made of mgm. testes/mm. S-V length vs. time, for the entire period, after the method of Fox (1952, 1954).

Information on distances and directions of summer dispersal was obtained by driving roads and searching marshes up to 20 km. in all directions from Inwood during the summers of 1971 and 1972. Most unmarked snakes caught were measured and marked and recaptures noted and measured. Reciprocal information, in the form of summer-marked snakes overwintering at dens around Inwood, was also obtained. Most snakes caught and marked during both summers were palpated and forced to regurgitate their stomach contents. This technique allowed a frequency-of-occurrence type of food analysis. It was also occasionally used on snakes caught at dens.

RESULTS

A. SUMMER ECOLOGY

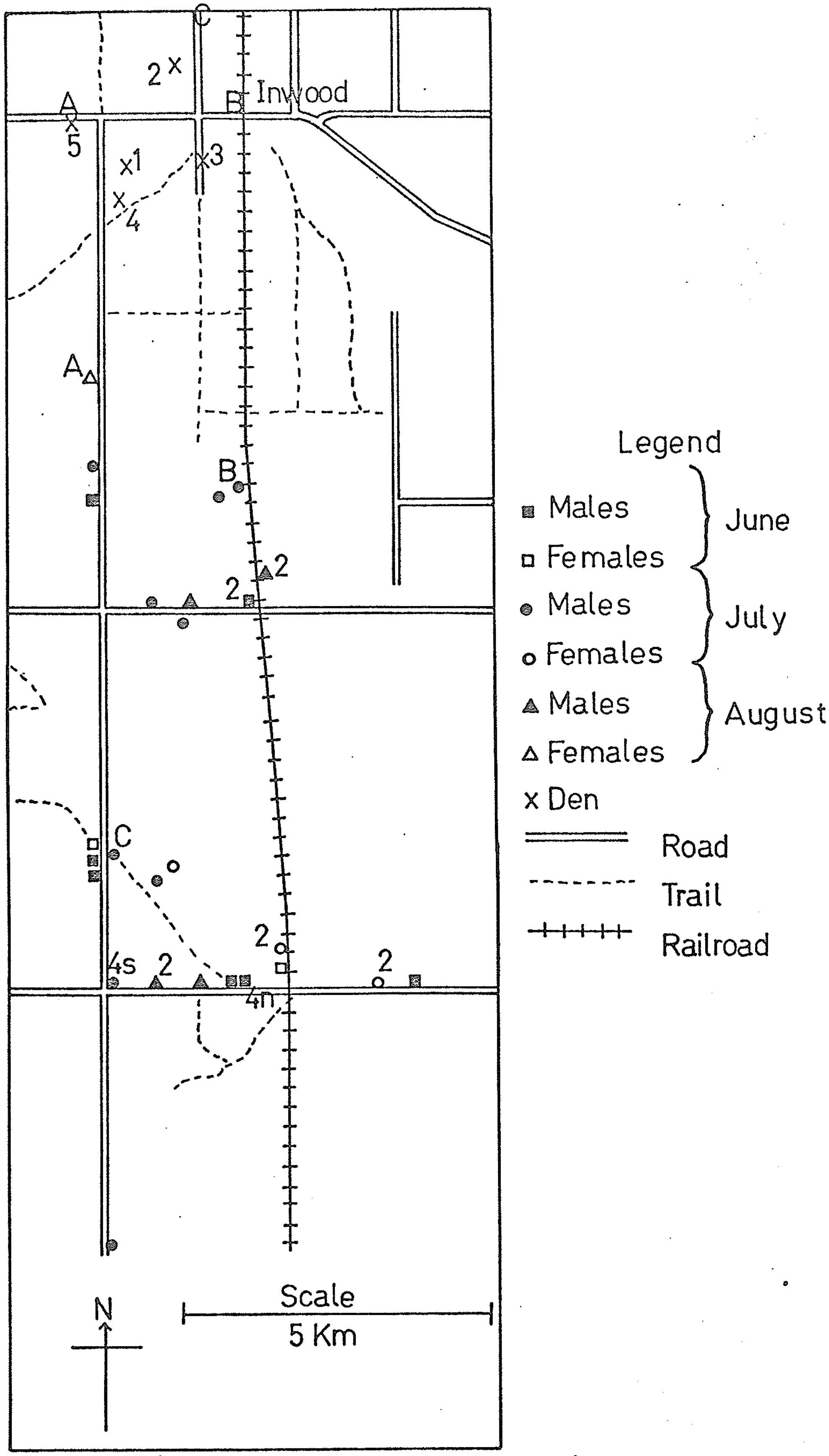
i. Dispersal

Information on distance and direction of dispersal from dens in summer was obtained from a total of 26 marked snakes, including both live and dead specimens, found in 1971 and 1972. Twenty of these were snakes originally marked at dens and recovered in the summer while the remaining six were summer-marked and recovered in the Inwood area during denning periods. Three animals in this second group were not caught at actual dens (A, B, C in Fig. 6). On the basis of capture history, 16 of the remaining 23 snakes were animals from den one, five were from den two, and one each were from den four north and south.

In all but four instances, these snakes were recovered in the summer or denning period immediately following last capture. The other four, all den-marked snakes, were recovered during the second summer following marking. One male was recorded in the denning periods both immediately before and after its summer capture.

All of the recorded movements were in a southerly direction from the Inwood area. The shortest straight-line movement was measured at approximately 4.3 km. and the longest at about 17.7 km.; the average distance moved was

Fig. 6 Distances and directions of dispersal of snakes from Inwood dens.
Nos. indicate den of origin; unnumbered individuals are from den one. Snakes A, B, C are from points A, B, C to north.



C
2 X
Inwood
B
A
5
X1
X3
X
4
A
B
2
2
2
C
2
2
4s
2
4n
2
Legend
Males
Females
June
Males
Females
July
Males
Females
August
X Den
Road
Trail
Railroad
N
Scale
5 Km

about 10.7 km. (S.E. = 0.73). No differences in distance or direction of movement were noted among months or between sexes. These results, lumped for both years, are summarized in Figure 6.

Road-counts of dispersing and returning snakes were occasionally made in spring and fall in the Inwood area. Most were made on east-west roads since these seemed to be most heavily used by the snakes. In spring, it was noted that virtually all snakes were moving south, whereas in fall all were moving north. The relatively few snakes seen on north-south roads were not very consistent in the directions in which they were moving.

ii. Food

During two summers of this study, a total of 1059 stomach examinations were made: 598 in 1971 and 461 in 1972. Most of these yielded no stomach contents. In those stomachs that did contain food, every anuran species occurring in the Interlake was represented along with a variety of other vertebrates and invertebrates. The wood frog (*Rana sylvatica*) was by far the most frequently recorded food item. Although most snakes with food in their stomachs contained a single prey item only, individuals containing two or more food items were occasionally found. These results are summarized in Figures 7 and 8 and Table I.

Fig. 7 Frequency of occurrence of food types found in snakes in summer 1971.

SUMMER 1971

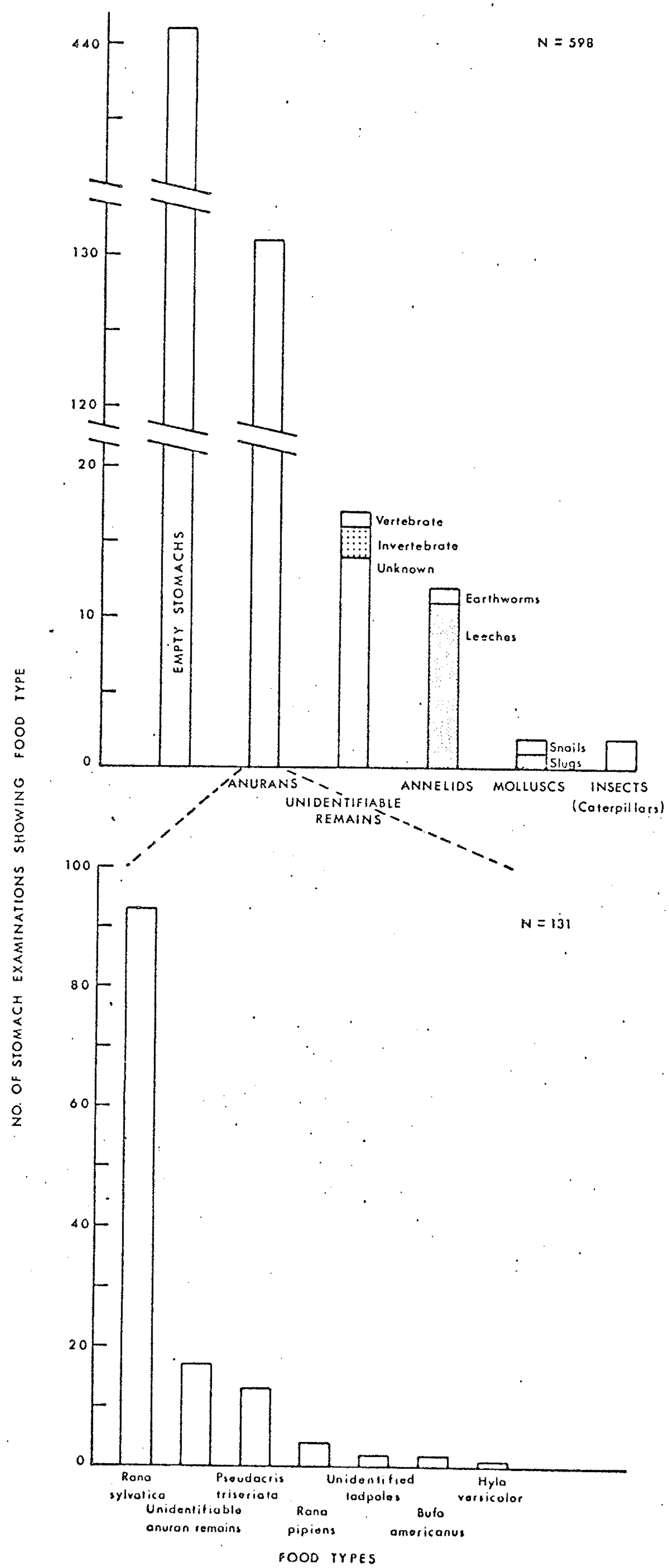

N = 598
440
130
120
20
10
0
EMPTY STOMACHS
Vertebrate
Invertebrate
Unknown
Earthworms
Leeches
Snails
Slugs
ANURANS
UNIDENTIFIABLE
REMAINS
ANNELIDS
MOLLUSCS
INSECTS
(Caterpillars)
NO. OF STOMACH EXAMINATIONS SHOWING FOOD TYPE
100
80
60
40
20
0
N = 131
Rana
sylvatica
Unidentifiable
anuran remains
Pseudacris
triseriata
Rana
pipiens
Unidentified
tadpoles
Bufo
americanus
Hyla
versicolor
FOOD TYPES

Fig. 8 Frequency of occurrence of food types found in snakes in summer 1972.

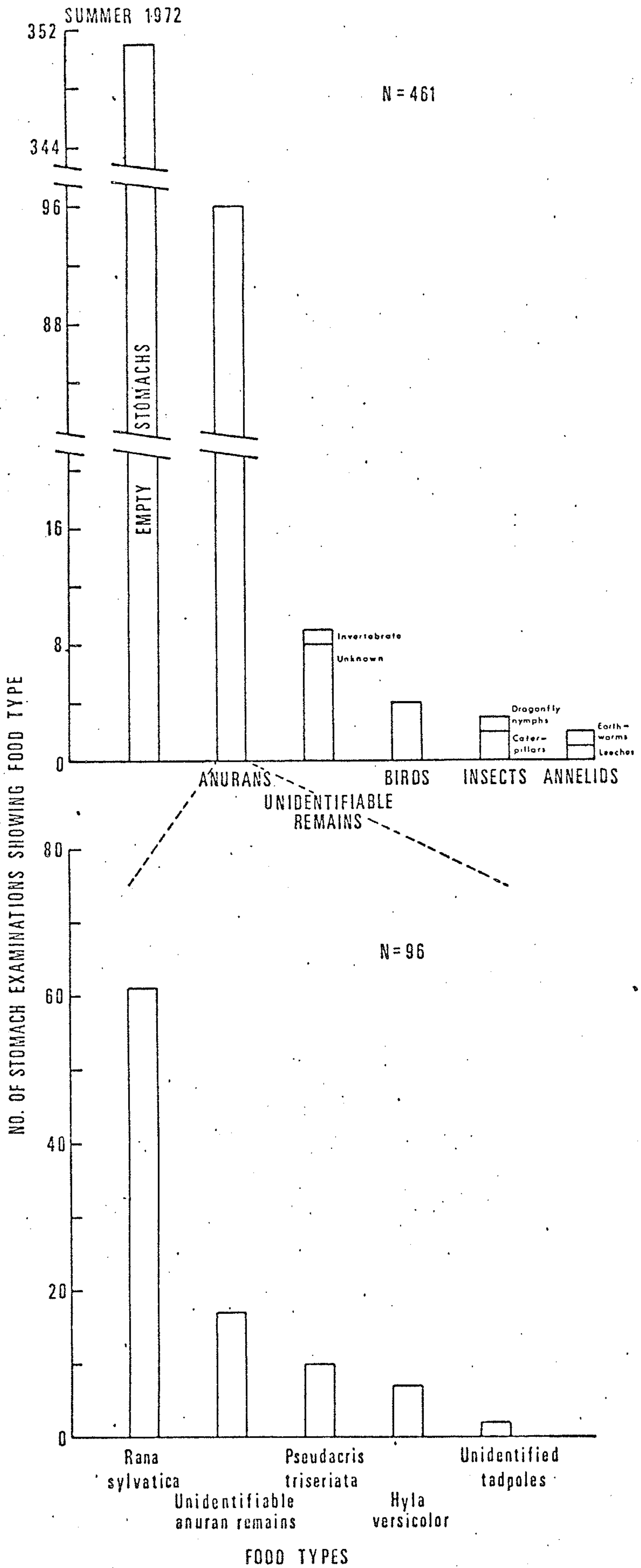

SUMMER 1972
N = 461
352
344
96
88
16
8
0
STOMACHS
EMPTY
Invertebrate
Unknown
Dragonfly nymphs
Cater-pillars
Earth-worms
Leeches
ANURANS
BIRDS
INSECTS
ANNELIDS
UNIDENTIFIABLE REMAINS
NO. OF STOMACH EXAMINATIONS SHOWING FOOD TYPE
N = 96
80
60
40
20
0
Rana sylvatica
Unidentifiable anuran remains
Pseudacris triseriata
Hyla versicolor
Unidentified tadpoles
FOOD TYPES

Table I

A. Number of instances of snakes containing more than one individual of a particular prey type

	Size of Group				
Type of Prey	2	3	4	5	36
Tadpoles				1	1
Rana sylvatica	8	4	1		
Leeches	1	1	1		
Pseudacris triseriata	1	1			
Rana pipiens	1				
Sparrow Chicks	1				

plus one snake with several snails and unidentifiable vertebrate remains

B. Number of instances of snakes containing more than one prey type

Type of Prey	Vert. Remains	Slug	Invert. Remains	Cater- pillar	Leech	*Hyla versicolor*
Rana sylvatica			1	3	1	1
Anuran remains		1	1	1		
Snails	1					

plus one snake with a wood frog, a leech, and a tadpole

No differences in foods taken were found between snakes of different sizes, although the chorus frog (*Pseudacris triseriata*) occurred only in snakes with a snout-vent length of 500 mm. or less. No attempt was made to measure size of prey for correlation with size of snake. The types of food eaten by the two sexes were similar and no temporal pattern of prey species taken was evident, nor was there any difference between the two years. The percentage of stomachs containing food was highest in early to mid-summer with a gradual decline in late summer (Fig. 9). Females that were obviously gravid showed a consistently greater proportion of empty stomachs than did the remainder of the population, and this proportion declined to zero earlier in this group (Fig. 9B). Other females and males showed no differences.

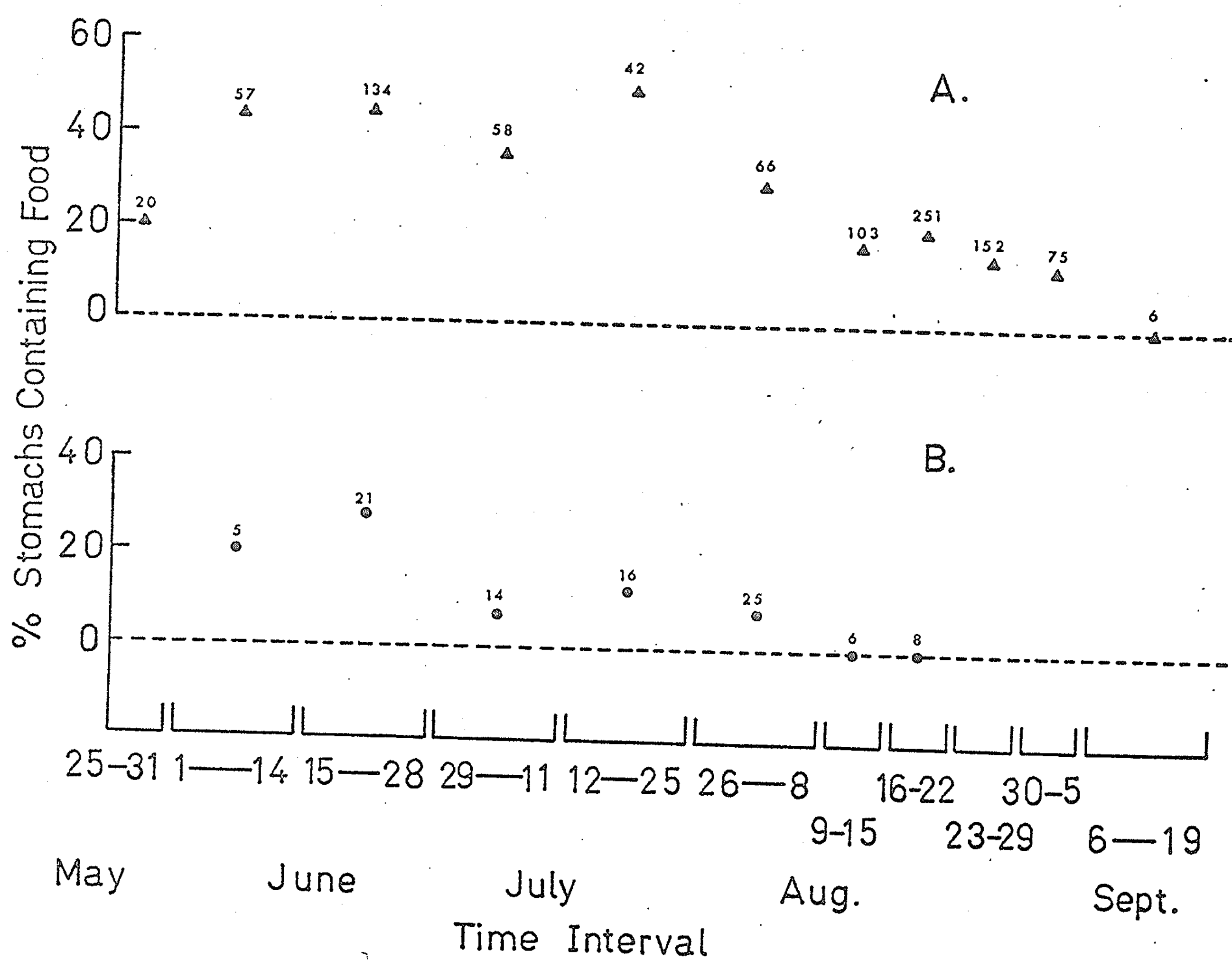
During this study, 307 stomach examinations were made at den one: 92 in fall 1971, 37 in spring 1972, and 178 in fall 1972. Only five of these, all from snakes captured from August 28 to September 7 inclusive in 1972, yielded stomach contents. Three snakes contained a wood frog each, one of them in company with a lady beetle (Coleoptera), one contained unidentifiable anuran remains, and the fifth contained totally unidentifiable remains.

Fig. 9 Percentage of snake stomachs containing food throughout summer.

A. All snakes except obviously gravid females.

B. Obviously gravid females.

All points placed at mid-points of time intervals. Nos. indicate sample sizes.



% Stomachs Containing Food
60
40
20
0
A.
20
57
134
58
42
66
103
251
152
75
6
40
20
0
B.
5
21
14
16
25
6
8
25–31
1—14
15—28
29—11
12—25
26—8
9-15
16-22
23-29
30-5
6—19
May
June
July
Aug.
Sept.
Time Interval

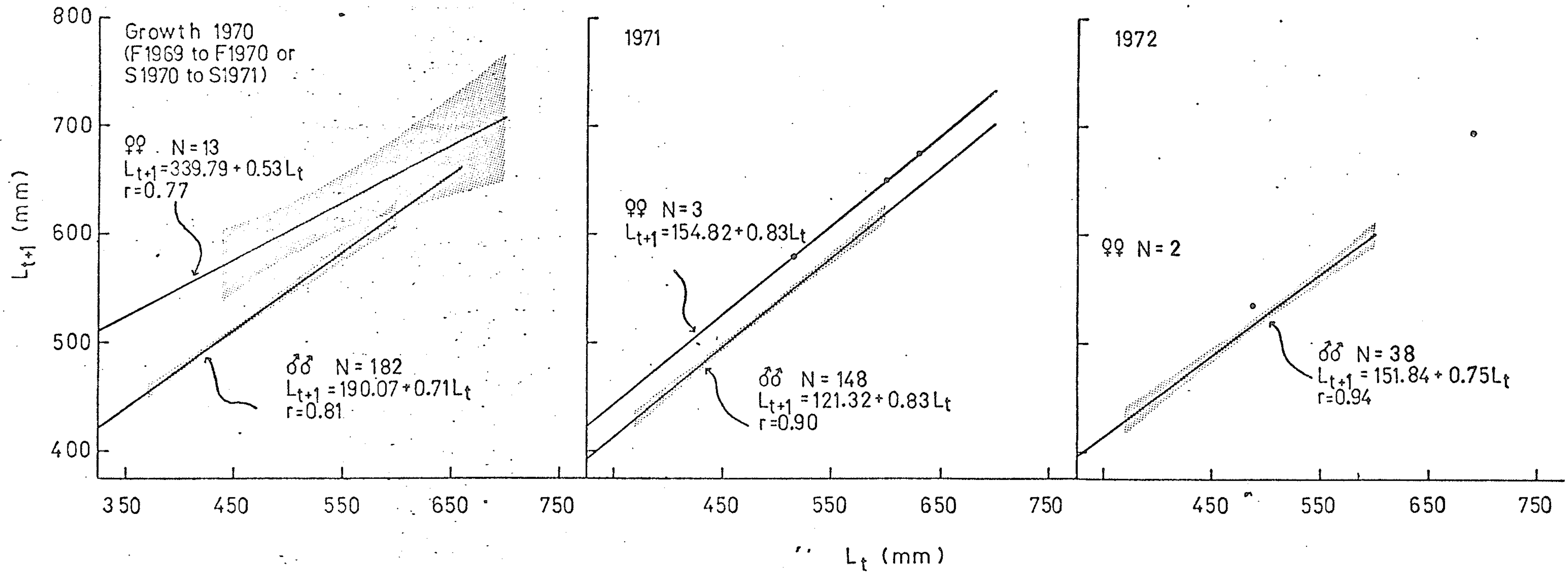
B. GROWTH

Annual growth was measured through the use of increments of snout-vent lengths of individual marked snakes found at dens in the Inwood area in two successive overwintering seasons. In the case of the males, the time intervals used were fall-to-fall and spring-to-spring, the former being chosen where both were available for a given snake in a particular year. This was done to minimize the effects on the growth analysis of the growth spurt which seemed to take place in spring shortly after emergence. This growth was detected through the repeated capture of individual snakes at den one in spring; the increase in length was sometimes as much as 20 mm. and appeared to be the only part of the annual growth occurring at the den sites. In the case of females, for which many fewer data were obtained, this phenomenon was ignored and the time interval considered was overwintering period-to-overwintering period except where the preferred intervals were available. In all instances, the figures used were averages of all the times the particular animal was measured in a given spring or fall.

A total of 368 such growth measurements were obtained for males: 182 for 1970, 148 for 1971, and 38 for 1972. Only 18 in all were obtained for females: 13, three, and two for 1970, 1971 and 1972 respectively. Several individuals contributed to more than one year through repeated annual recaptures. The data were plotted in the form L_{t+1} vs. L_t (L = S-V length in mm., t = year) and the linear regressions of L_{t+1} on L_t were calculated along with the 95% confidence limits about their means. These plots are shown in Figure 10. The confidence belts are missing for females in 1971 and 1972 since, in the first case, the nearly perfect correlation of the three points resulted in misleadingly narrow confidence limits and, in the second case, only two points were available.

Comparisons of growth rates were attempted by applying the analysis of covariance to the regressions for each sex separately. The 1972 data for the females were not used in this analysis. In the case of the males, one of the assumptions for the analysis of covariance, that of homogeneity of within-group variances, was not satisfied, Bartlett's chi-square being barely significant at the 0.05 level. The differences among the adjusted means of the three groups were, however, highly significant ($p < 0.01$), suggesting that the lines were probably different. Bartlett's chi-square also indicated significant heterogeneity of within-group variances ($p = 0.01$) for the females, invalidating the analysis.

Fig. 10 Walford plots of growth of both sexes for 1970, 1971, and 1972. Dots indicate measurements of females; shaded areas are 95% confidence belts about means of regressions. F = fall, S = spring.


Growth 1970
(F1969 to F1970 or
S1970 to S1971)
♀♀ N = 13
L_{t+1} = 339.79 + 0.53 L_t
r = 0.77
♂♂ N = 182
L_{t+1} = 190.07 + 0.71 L_t
r = 0.81
1971
♀♀ N = 3
L_{t+1} = 154.82 + 0.83 L_t
♂♂ N = 148
L_{t+1} = 121.32 + 0.83 L_t
r = 0.90
1972
♀♀ N = 2
♂♂ N = 38
L_{t+1} = 151.84 + 0.75 L_t
r = 0.94
L_{t+1} (mm)
L_t (mm)
800
700
600
500
400
350
450
550
650
750

C. POPULATION CHARACTERISTICS

i. Population Dynamics

a. Tests of Assumptions

There are four assumptions for the use of mark-recapture methods for estimating population sizes:

1. All animals, marked and unmarked, have the same chance of being caught in any sample.
2. All animals, marked and unmarked, are subject to the same survival rate.
3. All animals that leave the population do so permanently.
4. The marked animals disperse completely in the population between the time of release and the time of the next sample.

In the use of certain estimators, such as the Petersen index, a fifth assumption is that there is no recruitment between original marking and recapturing. This was discussed in the Methods section.

Not all of these assumptions are testable, but most can be assessed at least indirectly. Assumption four, which is really a corollary of assumption one, is almost certainly satisfied in this situation since the area over which the sampled population is dispersed (i.e. the den) is small. Recently marked animals have been captured at all parts of the den. Assumption two is also likely to be satisfied because the population being dealt with is all adult (Gregory, 1971) and differential survival rates in animal populations usually occur between adults and young rather than among mature age groups. The mark itself should not cause a differential survival rate since it is inconspicuous and does not appear to impair the snakes in any way (Gregory, 1971).

Assumption three is also a corollary of assumption one in that animals which temporarily leave the population are uncatchable during their absence. If they leave permanently, they essentially add to the mortality figures. During the course of this study, 610 instances were recorded of male snakes returning to dens in the Inwood area in denning periods subsequent to the one in which they were originally marked. Of these, 586 (96.1%) represented returns to the den of origin. In the case of females, the equivalent figures were 30 and 29 (96.7%). No animals were recorded as switching from one den to another and then switching back again. Assumption three has almost certainly been satisfied in this instance.

It is obviously not possible to make a complete test of the validity of assumption one since the catchability of uncaught animals cannot be assessed. Leslie's (1958) test, however, can be used to test for equal catchability of marked animals on the basis of individual capture histories over the whole experiment. Dr. A. N. Arnason of the Computer Science Department of this University performed this test on my data and found that catchability of males varied by not more than about 25% of the mean. Carothers (1973) feels that equal catchability is unattainable in natural populations, but the degree of variability obtained in this study is not considered adequate to invalidate the use of mark-recapture methods as a means of estimating population size. Leslie's test could not be done on the female data because they were so few in number.

b. Population Size and Survivorship Estimates

The Jolly (1965) model was applied to the male data from den one. It was not possible to do this for the females because of the small sample sizes obtained, due to their low probability of capture in spring (Gregory, 1971). The recruitment estimates ($\hat{B}_i$) which it is possible to calculate from the Jolly model were not made since $\hat{B}_i$ is not generally considered to be a very accurate estimator. Petersen estimates of the sizes of the populations entering the den each fall were made for both sexes. All of these results are shown in Table II.

The population at den one apparently dropped from a high level in 1969-70 to about half that size for the next two winters. The estimates for 1972-73 are of little value since the standard errors associated with them are

Table II: Population Size Changes and Survivorship in Overwintering Populations at Den One, Fall 1969 to Fall 1972

	i	Number caught & marked n_i	Number of n_i released s_i	$n_{i+1,i}$	m_i	R_i	z_i	Population Size (Jolly) $\hat{N}_i$	S.E. $(\hat{N}_i)$	Population Size (Petersen) $\hat{N}_iP$	S.E. $(\hat{N}_iP)$	Survivorship to next sampling period $\hat{\phi}_i$	S.E. $(\hat{\phi}_i)$
Males	Fall 1969	640	638	100	-	168	-	-	-	5544.22	476.80	0.615	0.059
	Spring 1970	869	868		100	202	68	3407.45	420.00	-	-	0.616	0.092
	Fall 1970	90	90	29	25	32	245	2570.42	570.81	2762.07	415.14	0.588	0.092
	Spring 1971	890	890		238	158	39	1711.61	153.78	-	-	0.470	0.056
	Fall 1971	221	221	66	56	67	141	2056.39	321.85	2832.82	280.17	0.512	0.091
	Spring 1972	846	845		199	50	9	1492.77	238.56	-	-	0.702	0.259
	Fall 1972	130	130	8	17	8	42	5347.86	2285.49	5248.75	1775.13	-	-
	Spring 1973	323	323		50	-	-	-		-	-	-	-
Females	Fall 1969	341	339	7						2712.00	948.66		
	Spring 1970	56	56										
	Fall 1970	80	78	4						1462.50	693.08		
	Spring 1971	75	72										
	Fall 1971	198	198	8						1732.50	564.80		
	Spring 1972	70	70										
	Fall 1972	122	122	3						976.00	520.83		
	Spring 1973	24	24										

$$\hat{N}_i = \frac{n_i}{m_i}\hat{M}_i \quad \text{where } \hat{M}_i = \frac{s_i Z_i}{R_i} + m_i$$

$$\hat{N}_iP = \frac{s_i\, n_{i+1}}{n_{i+1,i}}$$

$$\hat{\phi}_i = \hat{M}_{i+1}/\hat{M}_i - m_i + s_i$$

All notations as in Jolly (1965), except for $\hat{N}_iP$ (Petersen estimate).

Formulae for estimated variances of $\hat{N}_i$ and $\hat{\phi}_i$ in Jolly (1965), for $\hat{N}_iP$ in Robson and Regier (1968).

very large, probably because of the small values of $n_{i+1,i}$, m_i, and R_i (Table II). Survivorship of the males was fairly similar in all years and for the summer and winter periods within each year. Again, the final estimate is a poor one.

Figure 11 shows the changes in the male population graphically. The 95% confidence limits shown are assymetrical because they are calculated on the basis of the estimated standard error of $1/\hat{N}$ which is more normally distributed than $\hat{N}$ (Ricker, 1958). The estimated standard error of $1/\hat{N}$ in the Jolly estimator is $\sqrt{\hat{V}(\hat{N}_i)/\hat{N}_i^4}$ (Arnason, pers. comm.) and in the Petersen $\sqrt{n_{i+1,i}(n_{i+1} - n_{i+1,i})/s_i^2 \, n_{i+1}^3}$ (Ricker, 1958), using the notation of Jolly (1965).

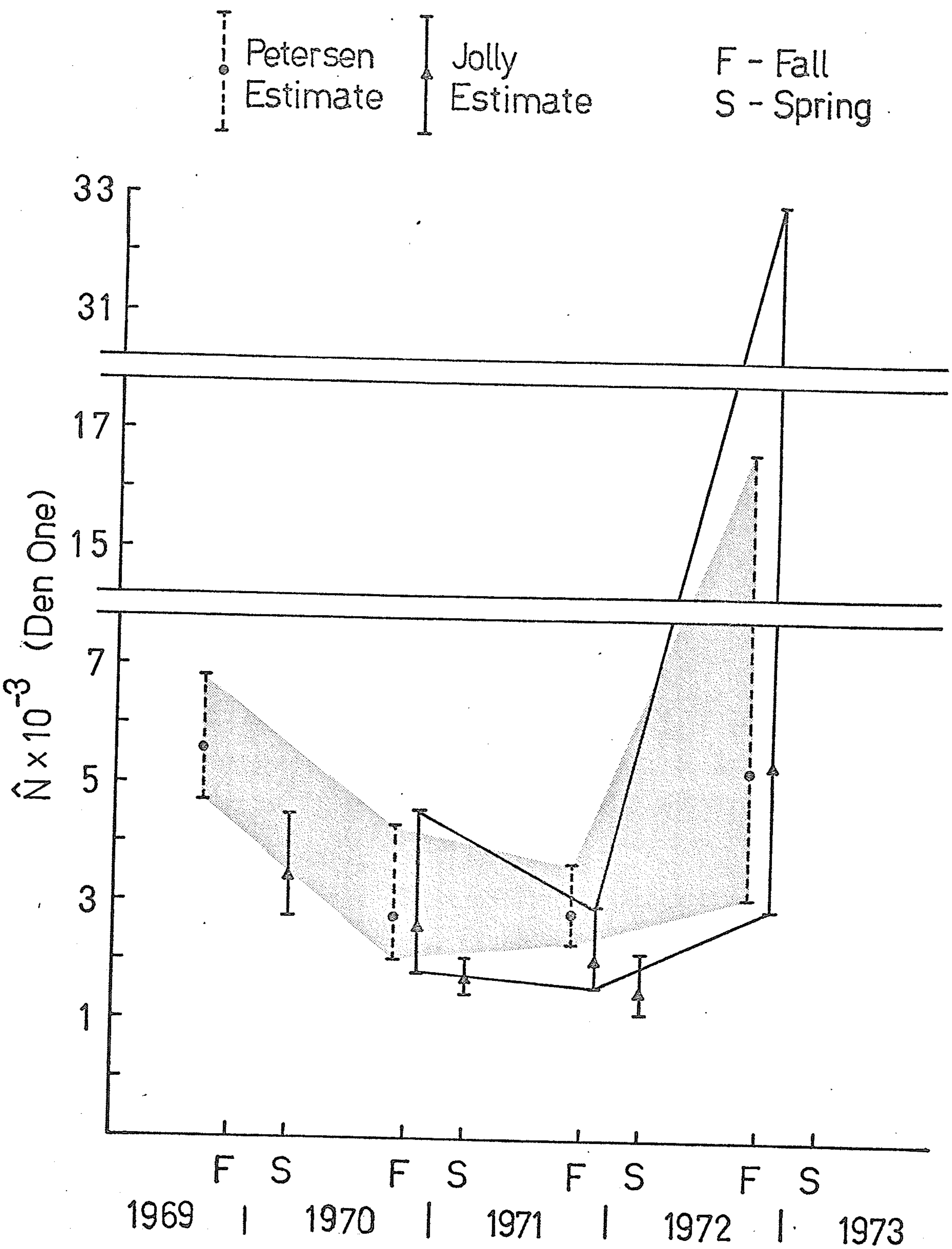
ii. Population Structure

Figures 12 and 13 show the size frequency distributions of animals measured at den one during the eight sampling periods of this study. In each case, the animals shown are only those measured in regular sampling for the purpose of population size estimation and they are grouped into intervals of ten mm. S-V length.

The degree of overlap of size classes was found to be very great, particularly in the highly variable females. Attempted separation using the method of Cassie (1954) was

Fig. 11 Changes in numbers ($\hat{N}$) of male snakes at den one from fall 1969 to fall 1972.

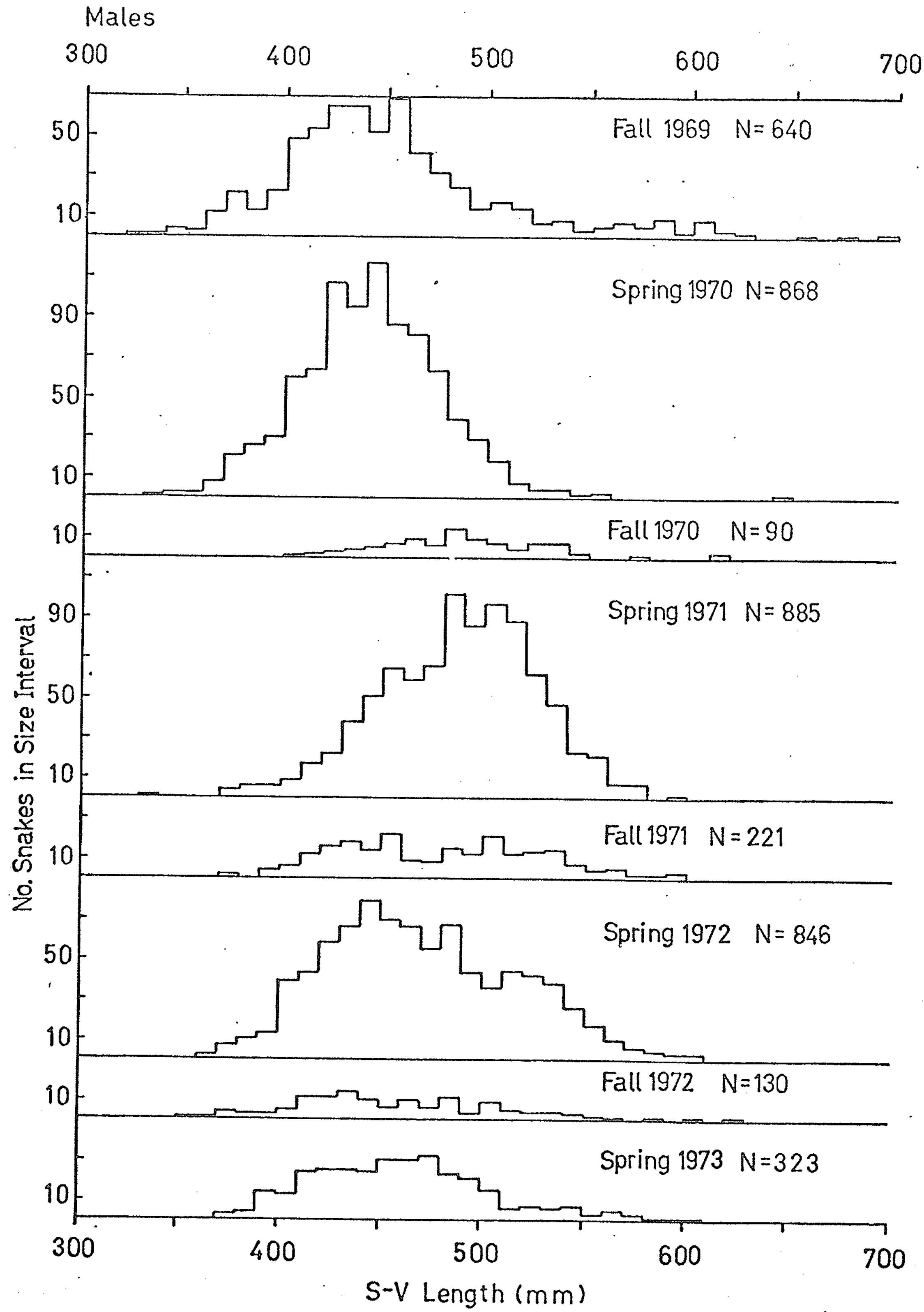
Enclosed areas represent annual population changes on a fall-to-fall basis. Vertical lines are 95% confidence limits about estimates.



Petersen Estimate
Jolly Estimate
F - Fall
S - Spring
33
31
17
15
7
5
3
1
N̂ × 10^-3 (Den One)
F S F S F S F S
1969 | 1970 | 1971 | 1972 | 1973

Fig. 12 Size frequency distributions of male snakes at den one from fall 1969 to spring 1973.

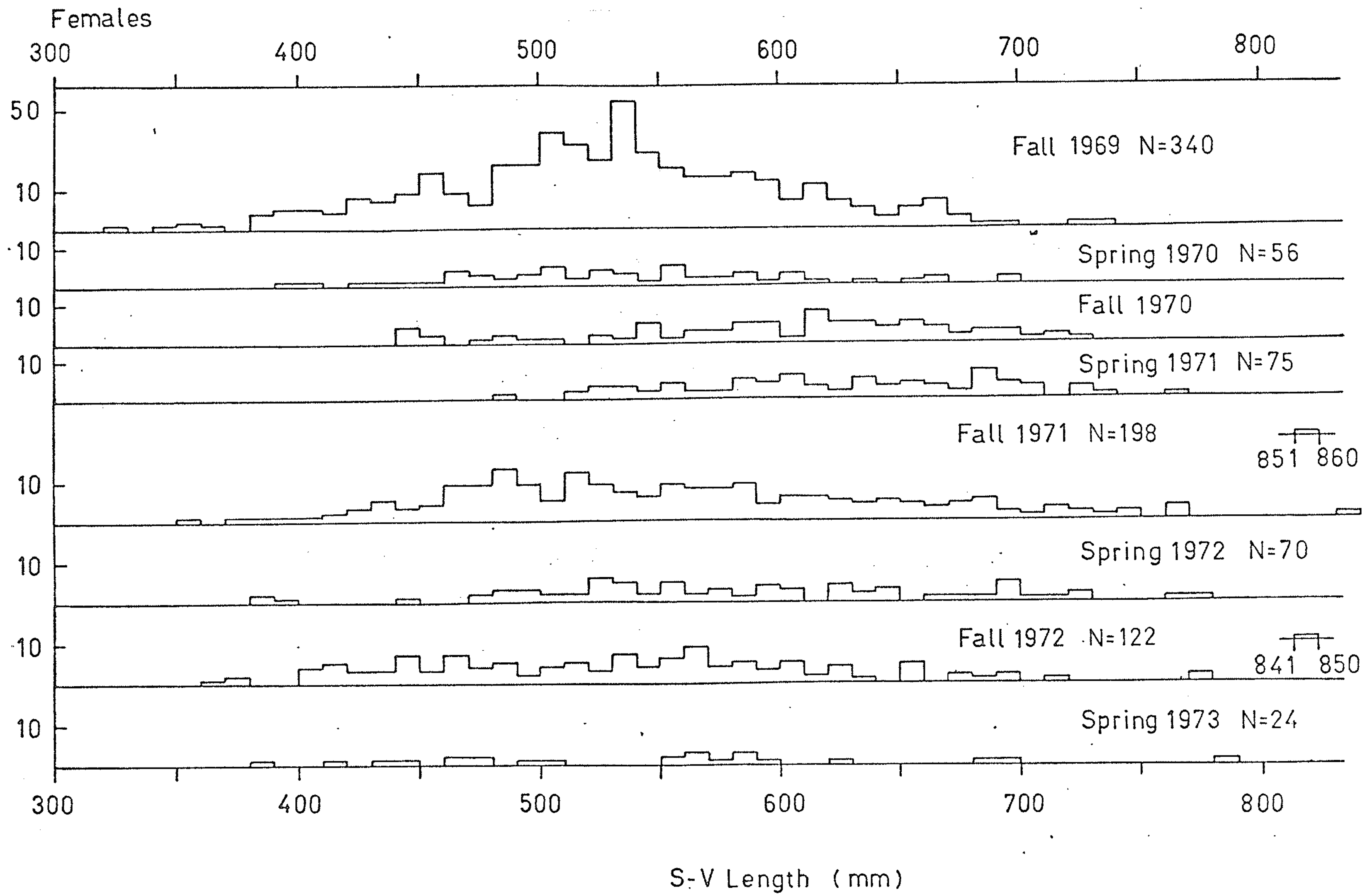
Animals grouped into intervals of 10 mm. S-V length.



Males
300
400
500
600
700
Fall 1969 N= 640
Spring 1970 N=868
Fall 1970 N=90
Spring 1971 N= 885
Fall 1971 N=221
Spring 1972 N= 846
Fall 1972 N=130
Spring 1973 N=323
50
10
90
No. Snakes in Size Interval
S-V Length (mm)

Fig. 13 Size frequency distributions of female snakes at den one from fall 1969 to spring 1973.

Animals grouped into intervals of 10 mm. S-V length.



Females
300
400
500
600
700
800
50
10
Fall 1969 N=340
10
Spring 1970 N=56
10
Fall 1970
10
Spring 1971 N=75
10
Fall 1971 N=198
851 860
10
Spring 1972 N=70
10
Fall 1972 N=122
841 850
10
Spring 1973 N=24
S-V Length (mm)

found to be unsatisfactory. Only the youngest, or second-year age group (Gregory, 1971) could be separated out in each case, and only in the males was it very clear. The mean size of the youngest males was about 440-450 mm. S-V length and of the youngest females about 520-530 mm. The second-year snakes constituted the dominant age-group in each instance except for the fall of 1970 and spring of 1971.

Sex ratios of the denning populations were calculated for each autumn. This was accomplished by using the Petersen estimates for each sex. Standard errors of the ratios obtained were estimated by applying the population estimates and their variances to the formula for variance of a ratio given by Overman and Clark (1960: p. 109). The male: female ratios were 2.04:1 (S.E. = 0.74), 1.89:1 (S.E. = 0.94), 1.64:1 (S.E. = 0.56), and 5.38:1 (S.E. = 3.40) for 1969, 1970, 1971, and 1972 respectively.

D. REPRODUCTION IN FEMALES

i. Potential Fecundity

Potential fecundity for the year of 1972 was estimated from dissections of 64 female snakes collected in late April and May from roads within three km. of Inwood and from dens throughout the entire spring. Reproductive potential for 1973 was assessed on the basis of 40 females from dens in the fall of 1972 and 20 from dens in the spring of 1973. Other female snakes were found in the vicinity of Inwood during the fall of 1972, but I felt that as long as snakes were not found at actual dens at this time of year, the possibility of further development remained and their reproductive potential might not be properly assessed. These snakes were therefore not included in the following analysis.

In both years, smaller females tended to be non-reproductive (Table III). Potentially reproductive females were generally those that contained ova greater than three to four mm. in length. Agreement was good between separations of egg size groups based on frequency analysis and conclusions reached from dissections of females that had ovulated later in 1972. Very large females tended to have larger ova in both immature and mature categories than did smaller snakes. Ovarian eggs were generally white and elliptical in shape.

Table III: Percentages of reproductive females in different size groups for overwintering seasons of 1971-72 and 1972-73.

S-V	Spring 1972			Fall 1972			Spring 1973			Total		
Length (mm.)	R	NR	%R	R	NR	%R	R	NR	%R	R	NR	%R
- 400		1	0.0					2	0.0		3	0.0
401 - 450	1	2	33.3		3	0.0	3	5	0.0	1	10	9.1
451 - 500	9	5	64.3	3	4	42.9	1	2	33.3	13	11	54.2
501 - 550	19		100.0	8	2	80.0	5	1	83.3	32	3	91.4
551 - 600	11		100.0	6	2	75.0	3		100.0	20	2	90.9
601 - 650	9		100.0	7	1	87.5				16	1	94.1
651 - 700	5		100.0	3		100.0	1	100.0	100.0	9		100.0
701 -	2		100.0	1		100.0				3		100.0

R = potentially reproductive

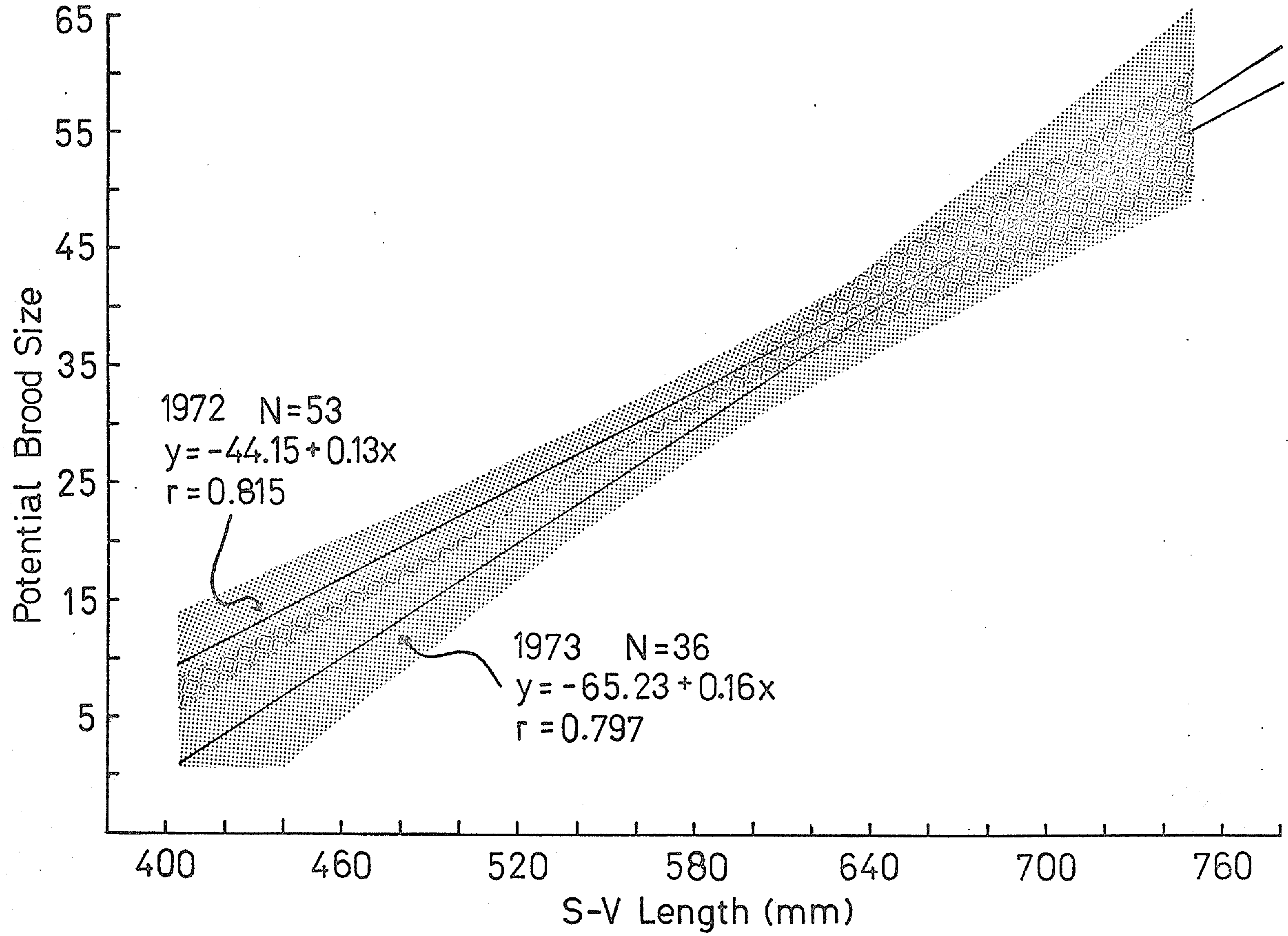
NR = non-reproductive

Of the 94 potentially reproductive females collected, 89 were completely examined: 53 in spring 1972, 26 in fall 1972, and ten in spring 1973. The fall 1972 and spring 1973 samples were combined for the purpose of estimating reproductive potential for 1973. Potential brood size was plotted against snout-vent length of female for both years and the correlation was high in both cases. In comparing the two resultant straight line regressions, the assumptions of the analysis of covariance were completely satisfied, but the difference between the adjusted means of the two groups was just significant at $p = 0.05$. The two lines with the 95% confidence bands about their means are shown in Figure 14.

Of the 64 female snakes in the 1972 spring sample, 24 were obtained from roads. These females were presumably dispersing from dens for the summer. Of the 24, 16 showed evidence of recent mating in the form of live sperm in one or both oviducts. All 16 were judged to be potentially reproductive on the basis of the examination of their ovaries. Of the other eight animals, none of which showed any evidence of recent mating at all, four appeared to contain mature ova. In addition to the snakes from the denning area, seven more females, all captured in the presumed summer habitat, were dissected during the month of May in 1972. Four of these were sexually mature and

Fig. 14 Regressions of potential brood size on size of female for females overwintering just prior to 1972 and 1973 breeding seasons.

Shaded areas represent 95% confidence bands about means of regressions.


1972 N=53
y=-44.15+0.13x
r=0.815
1973 N=36
y=-65.23+0.16x
r=0.797
Potential Brood Size
65
55
45
35
25
15
5
400
460
520
580
640
700
760
S-V Length (mm)

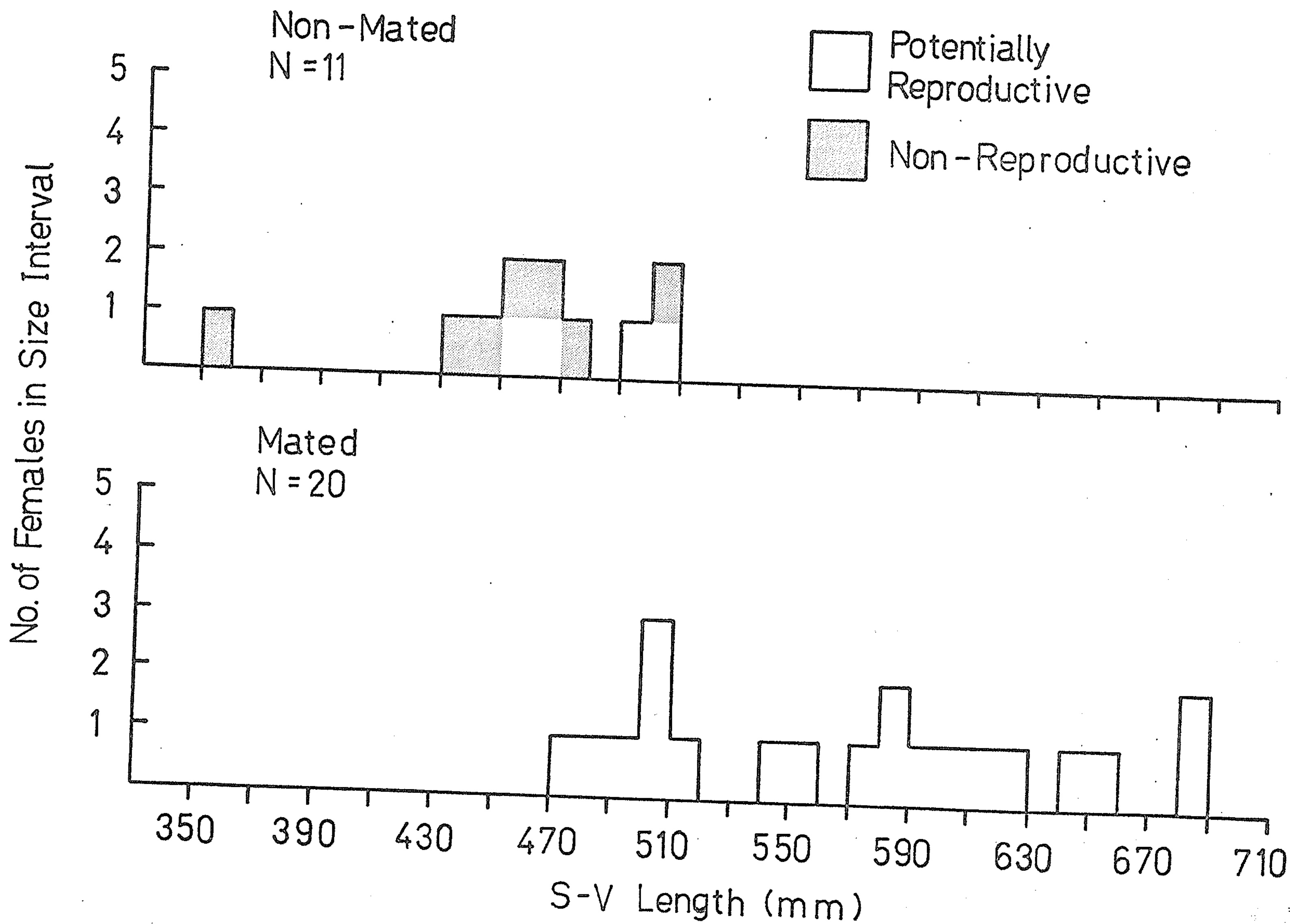
had mated, while the other three were not in reproductive condition and had apparently not mated. The distributions of sizes of all the animals in the mated and non-mated categories are shown in Figure 15.

ii. Development of Young and Realized Fecundity

In 1972, ovulation was first observed to have occurred in a female collected at a den on May 17 and dissected on May 24. It was next observed in a single female on June 1 and was commonly seen to have occurred from June 16 on. Ovulated eggs were yolky, somewhat round in shape, and much larger than the normal ovarian eggs. One snake dissected in June of 1972 had mature ovarian eggs containing yolk but had not yet ovulated. The appearance of eggs in oviducts was simultaneous with the appearance of fleshy yellow ovulation scars in the ovaries.

The very early stages of embryonic development were not distinguished in this study and females bearing embryos at these stages were simply noted as having ovulated. Females with embryos well enough advanced that their stages of development could be readily identified began appearing in samples on June 17. All gravid females were caught in summer areas, and none in the Inwood area. The earliest births recorded were on about July 28 when five broods were produced by females *in transit* from the field to the

Fig. 15 Distribution of potentially reproductive and non-reproductive individuals in mated and non-mated categories of dispersing females in spring 1972.



Non-Mated
N = 11
Mated
N = 20
Potentially Reproductive
Non-Reproductive
No. of Females in Size Interval
1
2
3
4
5
350
390
430
470
510
550
590
630
670
710
S-V Length (mm)

laboratory. Births continued well into September, but all of these were from females that had been kept in laboratory conditions since the end of July. Post-partum females first began appearing in the summer areas on August 9.

Figure 16 shows the embryonic development of these animals based on findings from dissections of 47 females. The stages shown are those of Zehr (1962) and the dates are generally those when the animals were dissected except in instances where the snakes were killed and frozen shortly after capture. Where exact dates were not known, the mid-point of the time interval over which the event must have occurred was used. Post-partum females are shown in this figure only if they were captured away from the denning area.

Realized fecundity was lower than potential fecundity, particularly in smaller females. Most gravid females had fewer eggs in their oviducts than ovulation scars in their ovaries and it was apparent that eggs from the right ovary often entered the left oviduct and *vice versa*. In many cases, eggs seemed to fail to develop at all *in utero*, or small, malformed embryos accompanied other normal-looking embryos.

The regression of number of apparently normal young on number of ovulation scars was calculated for 16 female snakes from the summer of 1972 (Fig. 17). The correlation was very high. All of these were snakes dissected in

Fig. 16 Embryonic development and times of birth in female snakes from summer 1972.

° = snakes caught in summer areas

| = captive specimens.

Nos. indicate sample sizes greater than one.

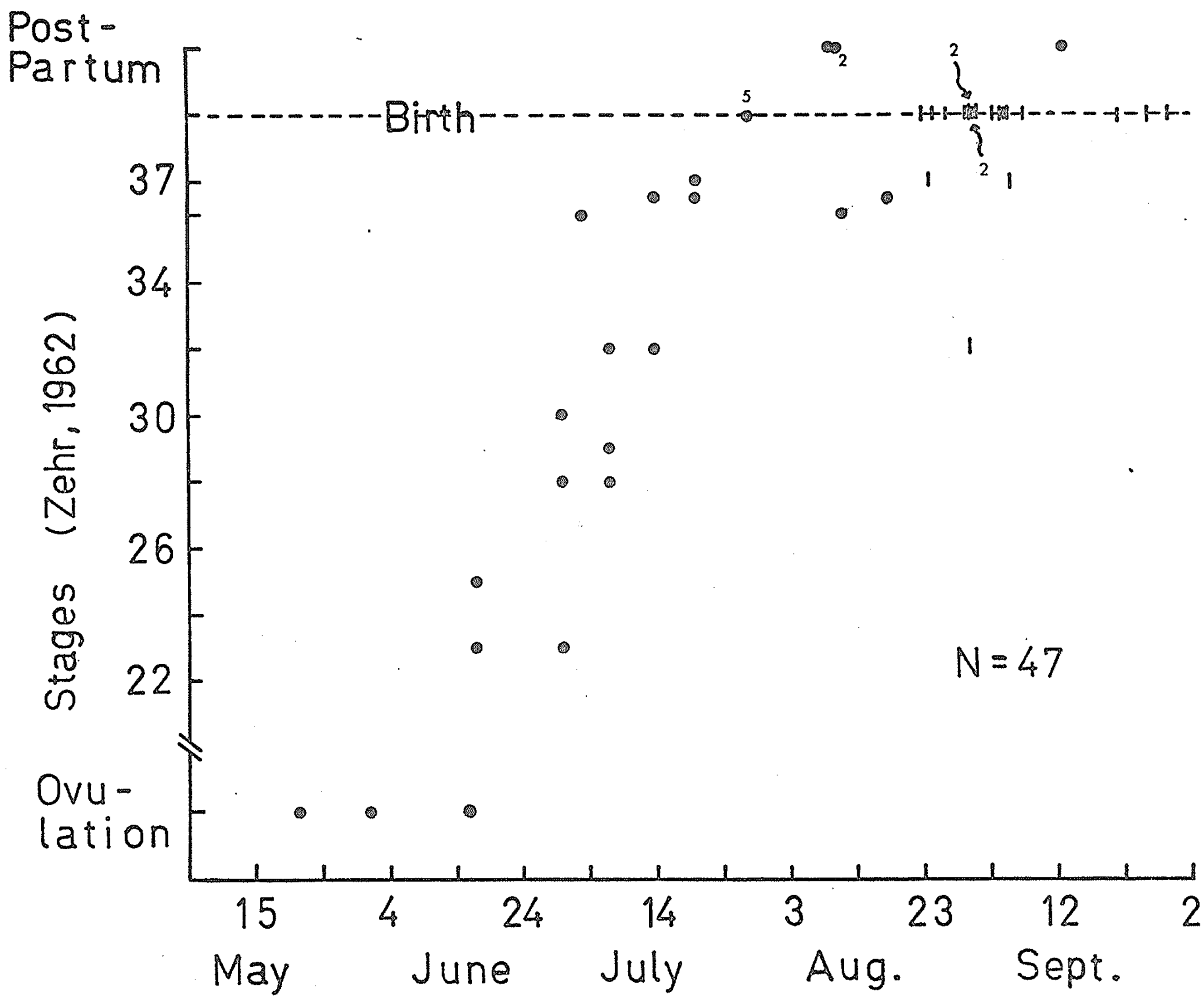
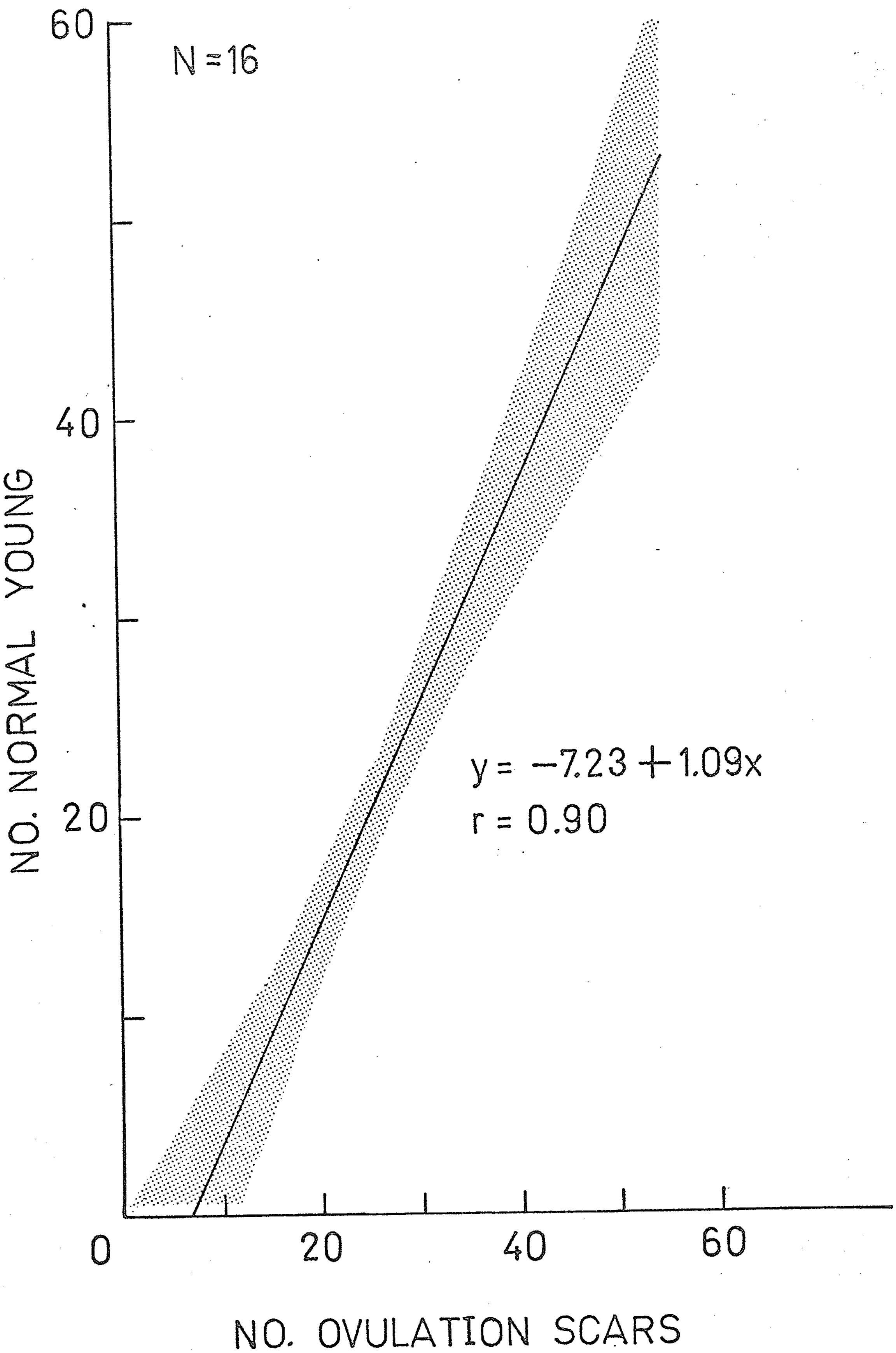

Post-
Partum
Birth
37
34
30
26
22
Stages (Zehr, 1962)
Ovu-
lation
N=47
15
May
4
June
24
14
July
3
Aug.
23
12
Sept.
2

Fig. 17 Regression of number of normal young on number of ovulation scars for females from summer 1972. Shaded area represents 95% confidence band about mean of regression.



60
N = 16
40
20
0
20
40
60
NO. NORMAL YOUNG
y = −7.23 + 1.09x
r = 0.90
NO. OVULATION SCARS

various stages of mid-gestation. Snakes which had just given birth were not used since there appeared to be some disintegration of ovulation scars by this time, and although the presence of some of them could be detected, I did not feel that a reliable count of them could be made.

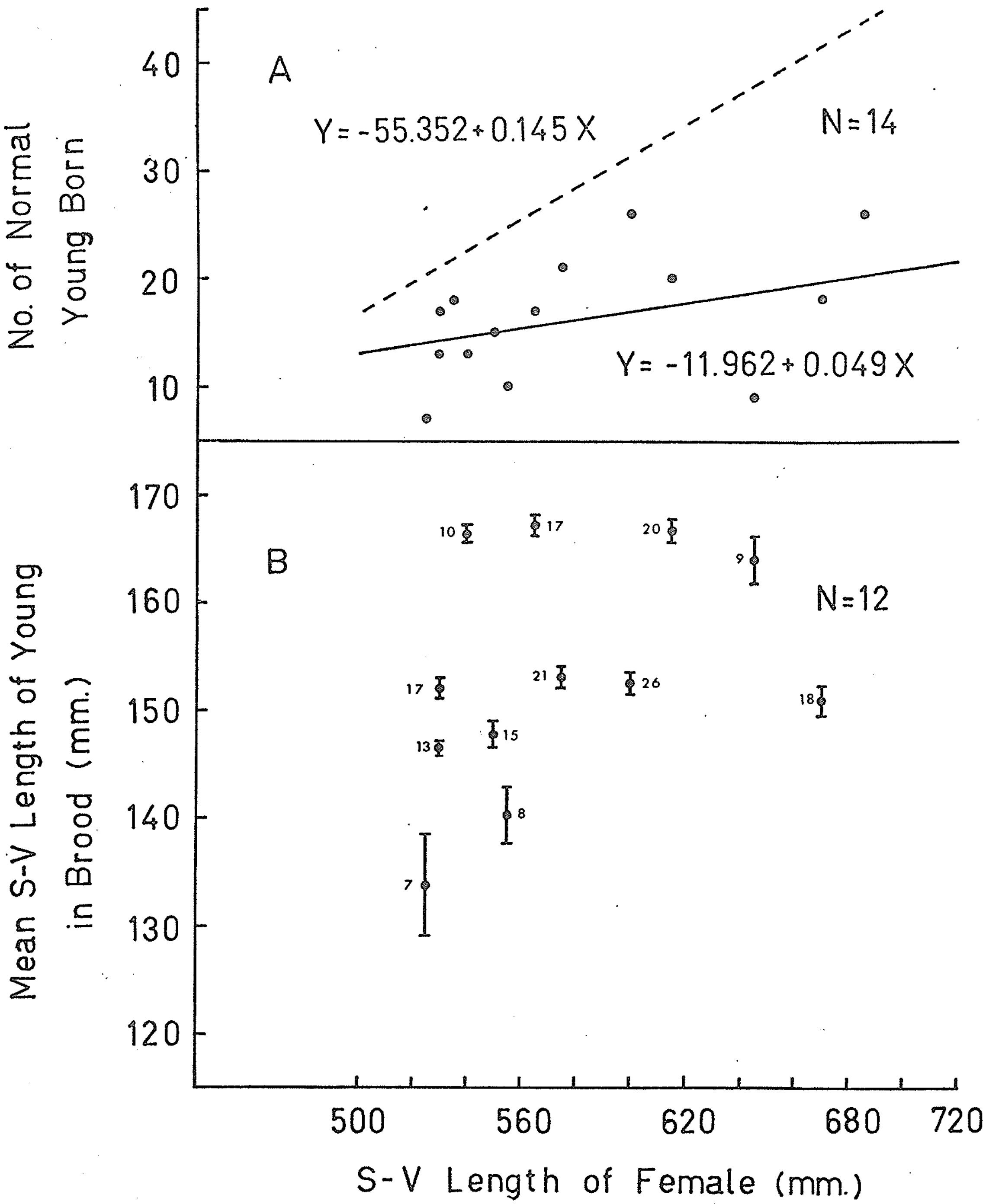
Twenty-two female snakes used in this study gave birth in 1972. Three broods were born in improperly closed containers and some of the young snakes escaped, making these litters of little value for sex ratio determinations. Another five broods were born *in transit* such that three of them were mixed together in one container and the other two in another. The remaining 14 were all born in individual containers and complete examination could be made of them. In most cases, a number of apparently normal young were born dead; this number was quite variable and some of these young were in poor condition. Several litters contained as many as three deformed young, all of which were also born dead. The mean number of normal young, both live and dead, of the 14 complete and separate broods was 16.43 (S.E. = 1.54), larger litters tending to come from larger females (Fig. 18A). For comparative purposes, the dotted line in Figure 18A represents the theoretical regression of brood size on size of female for females in spring 1972. This line is an extrapolation of data for 1972 presented in Figure 14 based on the known

Fig. 18 A. Regression of brood size on size of females for females from summer 1972 and theoretical regression for denning females in spring 1973.

Solid line and dots represent summer females, dotted line spring females.

B. Average size of young in brood vs. size of female.

Vertical lines are ± 1 S.E. about mean. Nos. represent sample size.



A
B
Y= -55.352 + 0.145 X
N=14
Y= -11.962 + 0.049 X
N=12
No. of Normal Young Born
Mean S-V Length of Young in Brood (mm.)
S-V Length of Female (mm.)
40
30
20
10
170
160
150
140
130
120
500
560
620
680
720
10
17
20
9
21
26
18
17
13
15
8
7

loss of reproductive potential during gestation (Fig. 17).

The total sex ratio of the five litters born *in transit* was 57 ♂♂: 54 ♀♀ plus one unsexed. Table IV summarizes the results of the sex ratio determination performed on the 14 intact broods using the method for estimation of proportions in cluster sampling (Cochran, 1963: 64 - 67). All the normal-looking young were used in this analysis except for one unsexed animal.

Ninety-one males and 91 females from the 14 litters were measured. The average snout-vent length of the males was 154.88 mm. (S.E. = 1.15) and of the females 154.00 (S.E. = 1.03). A t-test on the means of the two groups revealed no significant difference between them. Larger young tended to come from larger females (Fig. 18B), but the correlation was not high.

ii. Reproductive Cycle

It was not possible to trace the development of the female reproductive tract in this study. Females in all states of reproductive readiness were found in all months. Even in June, the immediately post-dispersal part of the year, apparently mature but unmated females were found away from dens. It was not known, however, how long ago these snakes had dispersed from their dens and how much growth had taken place in that time.

Table IV: Sex ratios of 14 intact broods from summer of 1972 and estimate of proportion ($\hat{P}$) of males in total sample with estimated standard error.

Litter No.	No. Normal Young X_i	No. ♂♂ Y_i	No. ♀♀	
1	26	15	11	
2	20	11	9	
3	25	9	16	+ 1 unsexed
4	17	6	11	
5	18	6	12	
6	9	3	6	
7	7	5	2	
8	13	7	6	
9	10	6	4	
10	21	9	12	
11	18	9	9	
12	17	8	9	
13	13	5	8	
14	15	8	7	
	229	107	122	

$$\hat{P}♂♂ = \sum_{i=1}^{14} Y_i \Big/ \sum_{i=1}^{14} X_i = {}^{107}/_{229} = 0.4672$$

$$S.\hat{E}.\ (\hat{P}) \doteq \sqrt{\frac{\{\Sigma\ Y_i^2 + \hat{P}^2\ \Sigma\ X_i^2 - 2\hat{P}\ \Sigma\ Y_i\ X_i\}}{n\ (n-1)\ \bar{X}^2}}$$

$\doteq 0.0280$ where $n = 14$ (Cochran, 1963:64-67).

Mating in these snakes was most evident at dens in spring in the form of mating "balls" (Gregory, 1971)and generally covered a period of a month to a month and a half. Twenty-seven females, however, were caught in late summer or fall of 1972 containing sperm in their oviducts. In all cases but one (a post-partum female) the ovaries were in reproductive or near-reproductive condition. Fourteen snakes bore totally non-motile sperm and about half of the sperm complement of another one was non-motile. In all other cases, and in the spring examinations, the sperm all seemed to be completely motile. Other information bearing on late summer mating came from snakes with copulatory plugs. Two snakes caught in August of 1971 possessed these as did one of the females containing sperm in August of 1972.

Quantitative fat body measurements were not made in this study, but it was observed that potentially reproductive females generally had large amounts of fat covering the abdominal viscera ventrally, while immediately post-partum or immature females had little or no fat.

Fourteen post-partum females were examined: 13 in late summer and fall of 1972 and one in spring 1973. In general, there appeared to be a direct relationship between reproductive readiness and condition of the fat body. Three of the post-partum females were judged to be reproductive, two of them having large fat bodies. The third had a relatively small fat body, but also had a correspondingly low reproductive potential (three mature ova). The remaining eleven post-partum females were all non-reproductive at the time of examination and only one had a large fat body, although the fat body appeared to be somewhat enlarged in two. Three individuals caught in early August had ova apparently approaching maturity. Post-partum females accounted for five of the six non-reproductive females in the 501 - 650 mm. interval shown in the totals column of Table III.

E. REPRODUCTION IN MALES

A total sample of 118 male snakes was examined in 1972. Most of the animals collected in spring and early summer came from a den in which emergence and dispersal were particularly late. No attempt was made to collect already dispersed males until all den activity had ceased. Den samples were again taken when snakes began returning to hibernacula in late summer.

Total weight of testes per snout-vent length of animal was low in spring, rising to a level amost four times that of spring by mid-July (Fig. 19). Thereafter, testis weight declined gradually until it again reached the spring level by September.

For each of testis, epididymis, and vas deferens, the average number containing sperm per animal was calculated for each sample day (Fig. 20). Most animals had no sperm in their testes during spring, but the average number of testes containing sperm per animal rose gradually through the second half of June and in July. Throughout August, most males had sperm in both testes. This was more or less coincident with the decline in the ratio of weight of testes to length of animal. By fall, most males had no sperm in either testis.

The epididymis was often difficult to locate precisely and the resultant picture is not clear. Figure 20 indicates that sperm were most commonly found in the epididymis at

Fig. 19 Weight of testes/S-V length of animal for males throughout active season of 1972.

All points are means for particular sample day; vertical lines are ± 1 S.E. about mean. Nos. indicate sample sizes greater than one. Triangles = snakes caught at dens; circles = snakes caught elsewhere.

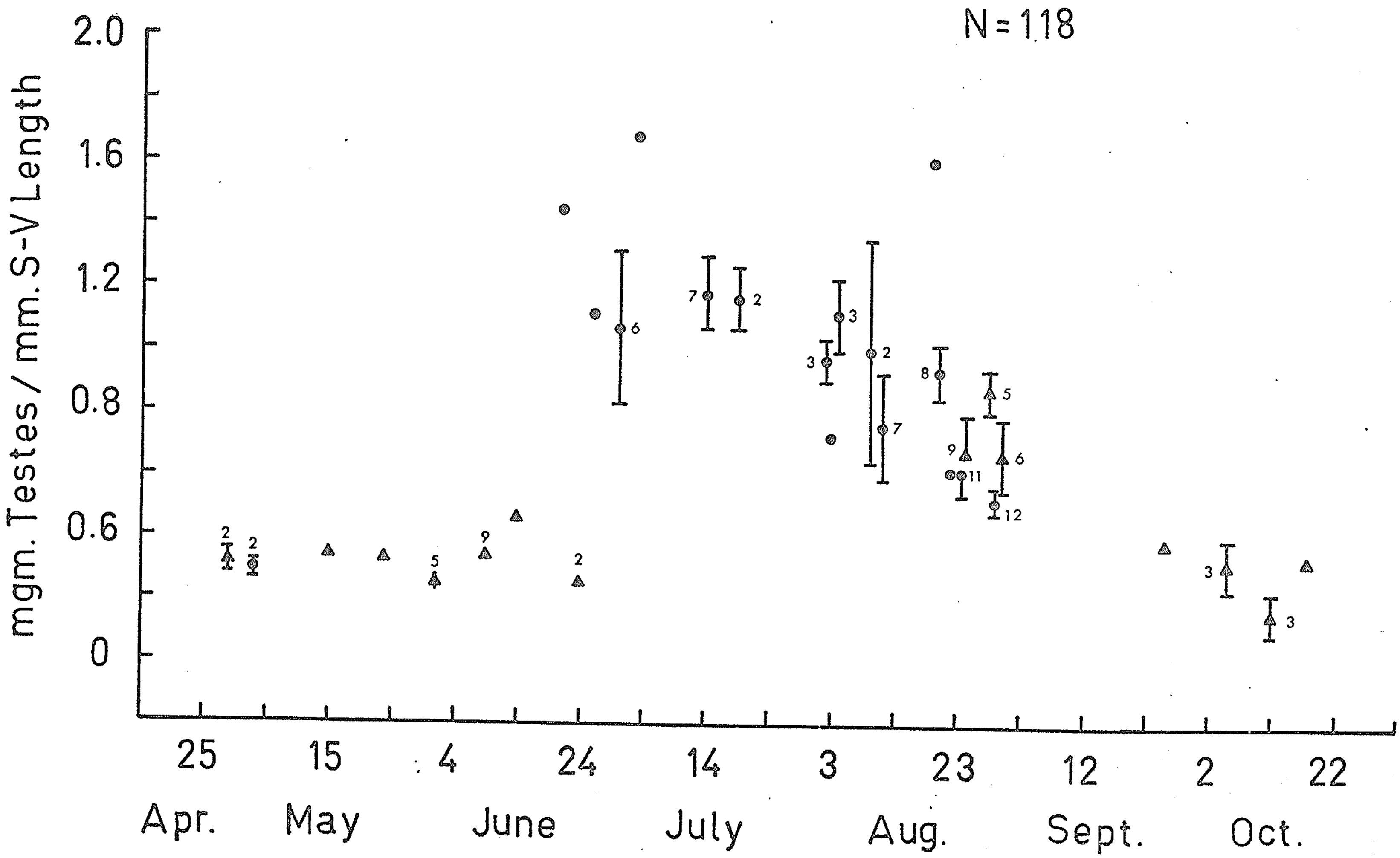
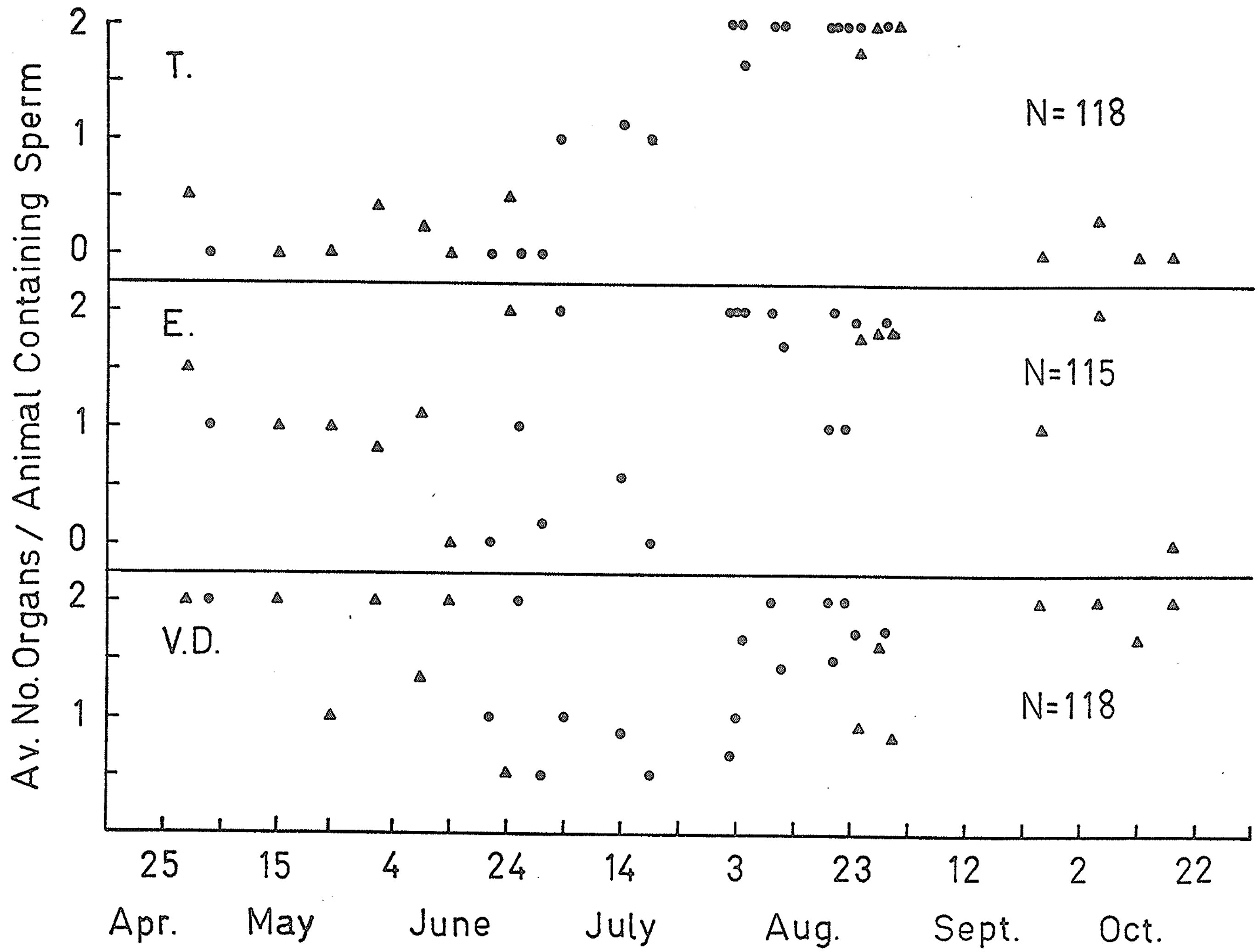

N = 118
mgm. Testes / mm. S-V Length
2.0
1.6
1.2
0.8
0.6
0
25
15
4
24
14
3
23
12
2
22
Apr.
May
June
July
Aug.
Sept.
Oct.

Fig. 20 Average number of organs/animal containing sperm for testes, epididymes, and vasa deferentia from males caught in summer 1972. T. = testis, E. = epididymis, and V.D. = vas deferens. Other symbols and sample sizes same as in Fig. 19.



Av. No. Organs / Animal Containing Sperm
T.
N= 118
E.
N=115
V.D.
N=118
25
15
4
24
14
3
23
12
2
22
Apr.
May
June
July
Aug.
Sept.
Oct.

the same time as they were in the testis (i.e. August). The snakes tended to have sperm in their epididymes fairly frequently in spring and fall and less so in early summer.

Almost all vasa deferentia examined in spring and fall contained sperm, but this average dropped during early summer, rising again when sperm also became common in the testes in August.

As in the case of several females which had mated in late summer or fall of 1972, some of the males collected at this time of year also contained non-motile sperm in their reproductive tracts.

DISCUSSION

A. SUMMER ECOLOGY

i. Dispersal

The results of this study concerning direction of summer dispersal of snakes from dens are at variance with my previous results (Gregory, 1971). In that study, direction of dispersal was assessed on the basis of distributions of catches of snakes returning to dens in fall in traps placed in a ring around den one. It was tentatively concluded on this basis that dispersal in both sexes was of a random nature. This is obviously not the case. The strong correlation between directions of movements of snakes on roads in spring and fall and the distribution of recaptures indicates that these animals move south for the summer, returning north again in the fall. The incorrect conclusions reached in the earlier study may have been due to the fact that the traps were placed too close to the den to give any valid indication of direction of dispersal.

Little information is available in the literature regarding directed movements of snakes, although the work of Hirth *et al* (1969) with three species of snakes in Utah indicates fairly strong directional orientation in each. The significance of the directed movements of

T. sirtalis in the Interlake of Manitoba is unclear, particularly when one considers that many large marshes inhabited by snakes are closer to, but in other directions from, Inwood.

Summer dispersal in the Interlake populations is also noteworthy because of the very large distances involved. Fitch (1965) found that males of *T. sirtalis* in Kansas moved an average of 1745 feet (about 532 metres) and females 1138 feet (about 347 metres) between their summer habitat and hibernacula. Studies of other species of snakes (Fitch, 1960, 1963; Hirth *et al*, 1969; Prestt, 1971) have shown that distances as great as those recorded here are rare, although Hirth *et al* reported the movement of one whipsnake (*Masticophis*) over a distance of at least 16.8 kilometres from one den to another during the course of one summer. Other species (Platt, 1969) apparently hibernate in or very near their summer ranges. Platt (pers. comm.) also found this to be the case in the populations of *T. sirtalis* he studied.

In view of the work done with other snake populations, it is surprising to find such long distances of dispersal as an apparently normal life history feature. The areas to which these snakes disperse are large marsh belts. It is likely that the partitioning of the necessary resources among all the snakes from the Inwood dens requires a very large area. This also helps explain the large variation in dispersal distances found in this study. There is no obvious explanation, however, for the fact that the few small marshes and ponds a short distance south of Inwood seem to be virtually uninhabited by snakes, despite the presence of the usual prey species (Figs. 7 and 8).

ii. Food

Fitch (1965) summarized the literature on food habits of *T. sirtalis*, including his own and Carpenter's (1952b) findings, and concluded that the species was relatively stable in its food habits throughout its range. In most areas, either earthworms or frogs appear to be the dominant food items taken. Frogs are the most frequently eaten food in the Interlake. I did not find any food types that were not recorded in Fitch's summary.

Figures 7 and 8 show that *Rana sylvatica* is the most frequent frog species found in stomachs. This species is probably the most common of all the anurans found in the Interlake except for *Pseudacris triseriata*. My data indicate that *T. sirtalis* in this area normally eats only one prey item at a time, multiple occurrences of a single prey species and single occurrences of two or more prey species being rare (Table I).

Most of the stomach examinations made in this study produced no food. Similar findings were obtained by Carpenter (1952b) for three species of *Thamnophis* and Platt (1969) for two species of *Heterodon* when they used the palpation method and by Prestt (1971) for *Vipera berus* on the basis of post-mortem examinations. Like Carpenter, I feel that the palpation method of obtaining stomach contents is an effective one and gives reliable, complete results.

Significant feeding seems to occur only during the months of June, July, and August (Fig. 9). During this time, the snakes are either in their summer habitat or moving between hibernacula and summer areas. Feeding is most intense in early to mid- summer. This is not surprising since the snakes are in near starvation condition following spring emergence (Aleksiuk and Stewart, 1971) and may have spent as much as 35 days or more at the den in frantic mating activity prior to dispersing (Gregory, 1971). Of the usual prey items taken, only *Pseudacris* has been seen near any den and no feeding occurs at dens. The five snakes found at den one with food in their stomachs were almost certainly recent arrivals just completing their fall migration.

Gravid females apparently feed very little, at least during late gestation. This may be, as Volsøe (1944) suggests for *Vipera berus* in Denmark, because the added bulk of the developing embryos reduces their ability to catch prey. It might, however, be simply due to a lack of internal space since the embryos take up almost the entire body cavity in females that I have examined in late stages of gestation. In any case, the abdominal fat body appears to fulfill the function of food supply in gravid and other non-feeding *Vipera berus* in England (Prestt, 1971) and I have found that the fat bodies of gravid *T. sirtalis* from my study area are almost completely reduced during gestation. Prestt (1971) also showed that gravid *Vipera berus* do not feed at all during gestation, but actively feed after parturition in the vicinity of their hibernacula. At least some female *T. sirtalis* in my study area must feed following parturition since post-partum females with partially developed and large fat bodies were found in fall 1972.

B. GROWTH

Previous growth studies of *T. sirtalis* (Carpenter, 1952a; Fitch, 1965; Platt, 1970) have shown that females grow faster than males and that great individual variation exists in growth rates. In both sexes, the rate of growth decreases with age. My data are in agreement with this and indicate that females are more variable than males (Fig. 10).

It is difficult to compare the growth of adult *T. sirtalis* from the Interlake of Manitoba with that of adults from other parts of the range because of the scarcity of formal growth analyses in the literature. Fitch (1965) has described the growth of the species in Kansas, based to a large extent on relatively short-term recaptures. His description of populations inhabiting the University of Kansas Natural History Reservation seems to suggest annual growth rates similar to those shown by adult snakes in my study. Carpenter's (1952a) scatter plot data for *T. sirtalis* in Michigan also agree with my results in terms of annual growth, but his growth curves are not in agreement since they indicate a much slower rate of growth. The reasons for this apparent conflict in Carpenter's paper are not clear. Platt (1970) obtained annual growth rates for *T. sirtalis* in Kansas which are higher than any reported elsewhere.

Growth in *T. sirtalis* appears to be subject to much variation. In this study, growth rates of the males, and presumably of the females, were somewhat different in every year. Both Fitch (1965) and Platt (1970) found that growth rates were greater in higher rainfall years, presumably because of the beneficial effects on the amphibian populations preyed upon by the snakes. In the Interlake region, rainfall was not notably different in any of the years of the study. Although other factors may have been important, the reasons for these different growth rates are not obvious.

In a similar vein, Fitch (1965) found a two-fold difference in growth rates between individuals in two populations of *T. sirtalis* in separate localities in Kansas. This difference appeared to be related to food supply. Obviously, the potential for a great deal of variation exists and it is possible that *T. sirtalis* in Manitoba might be able to grow as much in the three months it has available for major growth as do populations in, for example, Michigan, in five months (Carpenter, 1952a). Attempts to compare growth rates of this species in widely separated geographic localities are probably futile unless detailed information on the factors affecting growth in the different areas is available.

Growth rates of subadult snakes in the populations under study are also difficult to assess because little is known about this stage of life. It is not even known how long an active feeding season they have available for growth. It appears however, that they are at least capable of growing from an average size of about 154 mm. S-V length at birth to 200 - 300 mm. by May of the following year (Gregory, 1971).

By the end of their first full summer of growth, young males and females reach sizes roughly equivalent to those of the smallest denning snakes. Females again appear to show the greatest variability. These sizes are regularly achieved by second-year snakes, at least in the males, (Figs. 12 and 13) and are similar to those described for snakes entering their second winter by Carpenter (1952a) and Fitch (1965), but smaller than those in Platt's (1970) study.

C. POPULATION CHARACTERISTICS

i. Structure and Numbers

Single-species aggregations of denning snakes of the large sizes cited in this study have not been reported elsewhere. Although some authors believe that all or most estimators (and their variances) based on mark-recapture methods are open to question (Manly, 1971; Eisenberg, 1972; Roff, 1973a, 1973b), the results of Carothers (1973) suggest that the Jolly (1965) model gives fairly accurate estimates, particularly at high sampling intensities. I agree with Eisenberg's (1972) assertion that adherence to the assumptions of the model is too often overlooked in studies of this type, but I feel that due attention was paid to them in this study and that they were met adequately. Roff (1973b) even doubts the validity of the statistical tests available for assessing the assumptions. It would seem, nevertheless, on the basis of the sample sizes obtained and the degree of accuracy attained by Carothers (1973), that the results obtained in this study are realistic and are certainly indicators of at least relative population sizes. The good agreement obtained between the Jolly and Petersen estimates is not surprising since the former is simply an extension of the latter and high correlation of the two is to be expected.

Little information concerning size structures of denning populations of *T. sirtalis* is available in the literature. The size-frequency distributions shown by Fitch (1965) are similar to mine (Figs. 12 and 13), especially for the males. The second-year snakes are particularly alike, although a larger variance is probably attached to the female sizes in my study than in Fitch's. The degree of overlap of size groups is so great that it is impossible for me to determine how many age groups of each sex exist. Presumably at least four are present, since individuals of both sexes have been found at dens three years after original marking. Fitch feels that females may live to seven years or more in Kansas.

In contrast to the situation in the Interlake, large dens in Riding Mountain National Park in Manitoba and in Saskatchewan (Cook, pers. comm.) also contain juvenile snakes. Among other species of snakes, both Volsøe (1944) and Prestt (1971) found young *Vipera berus* hibernating with adults, but Parker and Brown (pers. comm.) felt that young of three species in Utah generally denned elsewhere in their first few years. Other authors do not specifically consider this question.

The sex ratios of the adult populations in this study, assuming that all adults den at the large communal hibernacula, are heavily biased towards males. Platt (1970) also found an excess of male *T. sirtalis* in his study. Fitch (1965) found the opposite to be the case in Kansas and Carpenter's (1952b) population estimates also indicated that females may be more numerous than males. The approximately 1:1 sex ratio at birth obtained for the snakes in my study is in general agreement with Carpenter (1952b), Martof (1954), and Fitch (1965), although all found a slight excess of males. Platt (1970), however, found that the primary sex ratio of the *T. sirtalis* populations he studied was heavily biased in favour of males. The reduction of the relative number of females from 1:1 in the Interlake population estimates is probably due to differential juvenile mortality and/or catchability of the two sexes. An added cause of mortality for older females may be that gravid females tend to bask more than other snakes. This heavy dependence on radiant energy (Vincent, 1971) for maintaining body temperatures and presumably optimal conditions for development of young would make gravid females more susceptible to predation.

ii. Population Dynamics

One common characteristic of animals living in areas of variable or unpredictable climate is variability in population size (Pianka, 1970). The populations of *T. sirtalis* under study appear to be no exception. While good population size estimates with relatively low variances were obtained only for males, it seems certain that the den one population dropped drastically from a high of about 8,000 snakes in 1969-70 to about half that size the following year and that this lower level was maintained in 1971-72. A swing back upward is indicated for 1972-73, but the accuracy of these estimates is poor.

The survivorship figures obtained from the Jolly analysis, strictly speaking, represent probability of survival <u>on the study area</u>. In this instance, however, they are taken as being indicative of population survival since den-fidelity appears to be the rule. Carothers (1973) has shown that the Jolly estimates of survival rate are not biased by unequal catchability. The discussion which follows is not dependent on equal survivorship of males and females, which does not appear to be the case anyway.

The survivorship figures (Table II) are interesting for two reasons. First, overwinter survivorship is relatively low, indicating significant loss of animals during hibernation. Hawley (pers. comm.) found large numbers of dead snakes below ground in a den at which he was working at Narcisse, Manitoba in the spring of 1973. Many of these had apparently been frozen but most had their heads chewed off as if they had been attacked by small mammals. The winter of 1972-73 was one with low snowfall and this lack of insulation might have accounted for the snakes freezing underground. Hirth (1966) found similar rates of overwinter mortality for three species of snakes in Utah and Carpenter (1952b) felt that the young of three species of garter snakes in Michigan might be subject to high winter mortality. Carpenter in fact recorded one definite instance of winter kill in *T. sirtalis*.

The second noteworthy point concerning the calculated survivorship probabilities is that they are similar for summer and winter and for both years. If anything, survivorship was slightly higher in the summer of 1970 than in the summer of 1971. This suggests that the population decline between 1969-70 and 1970-71 was not due to decreased survivorship of adults *per se* but to other causes.

An examination of the size frequency data (Figs. 12 and 13) supports this idea. In all instances except for fall 1970 and spring 1971, which represent the overwintering season of first decline of the population, the second year snakes are the dominant age group in each sex. This is most clearly seen in the males. In fall 1970 and spring 1971, this age group comprised a small part of the population, suggesting that the population decline might have been due to a reproductive failure in 1969, which is when these animals would have been born. Low subsequent survival of the young of that year might also account for the decline.

It has been pointed out that weather, through its effects on populations of prey animals, can greatly influence the amount of food snakes obtain and thereby the amount of energy they have available for reproductive purposes the following Spring (Platt, 1970; Parker and Brown, pers. comm.). Winnipeg weather records for 1968 indicate no abnormal amounts of rainfall or sunshine or exceptional temperature deviations. In 1969, however, June was exceptionally cold. In that month, maximum, minimum, and mean temperatures were all below normal and on two days, June 13 and 20, frost was recorded. In addition to the low June temperatures, July was cooler than usual. Rainfall was high in both months, resulting in further cooling effects. It is likely that these weather conditions had a profound influence on reproduction in that year. By June, the snakes have generally all dispersed from their hibernacula (Gregory, 1971), ovulation should have occurred (Fig. 16), and gravid females should have been incubating their broods. Since gravid females spend much time basking in exposed areas, it is possible that the occurrence of frost so late in June may have resulted in the deaths of many gravid females, and hence of unborn young.

More likely, however, is that development of young was simply interfered with to the extent that total reproduction in that year was low. Fitch (1960) found that gestation periods of *Agkistrodon contortrix* were extended in summers characterized by low temperatures and high cloud cover. Blanchard and Blanchard (1940), Fox (1948), and Zehr (1962) have all shown that embryonic development in *T. sirtalis* is retarded by lower temperatures. Fox's work further suggests that development may be completely arrested under cool conditions.

The generally poor summer of 1969 may also explain the failure of the den one population to rise again in 1971-72. The second-year snakes recruited into the population in that overwintering season were products of the reproductive activities of the 1969-70 den population. Considering the facts that this latter population was large and that the summer of 1970 was not particularly harsh, it might have been expected that reproduction would have been quite successful in 1970, resulting in a population increase in the fall of 1971. It is possible, however, that the cool conditions existing in the early summer of 1969 might have inhibited feeding of the snakes so much that the energy requirements for reproduction the following year were not completely fulfilled. Reproduction in 1970 would therefore have been low and the den population would have been maintained at a low level in 1971-72.

A possible further test of the importance of weather in affecting garter snake numbers might be performed by monitoring the den one population for a few more years. For example, late frost occurred in June of 1972 (Fig. 5) and it may be that this will have an effect on the sizes of denning populations in 1973-74 and/or 1974-75. Weather in general in the summer of 1972 was not as poor as in 1969, however, and little or no effect may be detectable.

Platt's (1970) conclusions that large changes in population sizes of snakes, including *T. sirtalis*, in Kansas may be due mainly to changes in fecundity or survival of young probably apply in the Interlake. Parker and Brown (pers. comm.) arrived at similar conclusions for *Coluber* in Utah. These workers felt that these parameters are influenced by changes in population levels of prey species. Platt in fact monitored the prey populations in addition to the snake populations. The implication in these studies is that weather is an ultimate factor in limiting snake populations since it acts through the prey species. In the Interlake of Manitoba, weather may at least sometimes act as a proximate limiting factor in affecting fecundity and hence snake population levels.

Obviously, weather is a significant factor in determining the abundance of *T. sirtalis* and thereby limiting its range. For example, rainfall is very important in promoting the production of large numbers of prey animals but too much rain, because of the accompanying cloud cover and cooling effects, may severely hinder reproduction of the snakes. For maximum reproductive success in any given year, a balance must be achieved between these two opposing needs. In addition, food supply, through its dependence on weather, might sometimes more directly affect the survivorship of already existing snakes as is implied by Fitch (1965). An extremely dry year could leave the snakes with almost no food and cause them to suffer a high mortality. In my study area, weather itself, particularly temperature, may occasionally play a significant role in directly affecting survivorship of snakes. It is probable that different aspects of weather are important in limiting *T. sirtalis* in different parts of its range. Rainfall is likely most important in the southwestern U.S.A. but temperature is almost certainly the most critical factor in far northern parts of the range.

In addition to weather, predation must also be considered as a significant source of mortality. Carpenter (1952b) and Fitch (1965) have documented the important predators on *T. sirtalis* in their study areas. In the Interlake of Manitoba, known predators on this species are crows (Gregory, 1971), owls (Weselowski, pers. comm.), coyotes (Pastuk, pers. comm.) and skunks (Penny, pers. comm.). Road-kills also play a major role in annual mortality in my study area. On the basis of the available literature and personal communications, I find it most likely that *T. sirtalis* is not a preferred food of any single predator species, but an occasional food of many.

D. REPRODUCTION

i. Potential Fecundity

Bragdon (1952) has described the ovary of *T. sirtalis*. In snakes in general, the right ovary is more anteriorly located than the left and is larger, containing more eggs (Betz, 1963a, 1963b). The ovaries of females that I have examined are similar to these descriptions. Previous workers have generally also found different size groups of ova in the ovaries (Cieslak, 1945; Bragdon, 1952; Tinkle, 1962; Betz, 1963b), each presumably representing the potential for a different breeding season.

In most reptiles, reproductive potential varies directly with the size of the female (Tinkle, 1962). The data obtained in this study reveal that this is also true for *T. sirtalis* in the Interlake. Fitch (1965) found similar results for the same species in Kansas, but the correlation did not appear to be as high. Whereas my data show a linear increase in fecundity with increasing body size, Fitch found a levelling off at an age of about four years and perhaps even a decline in very old snakes. It also seems that the reproductive potential is higher at any given body size for Interlake than for Kansas *T. sirtalis*.

It should be noted, however, that Fitch's data were obtained by palpation of gravid females in summer, and mine by dissection of unovulated females in spring. Also, my samples may not have included individuals as old as Fitch's oldest females. My samples did, however, cover the sizes at which he detected the levelling-off effect, indicating that the difference between the two situations is probably real.

The method which I used may slightly overestimate reproductive potential. I feel, however, that any overestimate applied more or less equally to snakes in all size groups and that the high correlation observed between reproductive potential and body size is real. Tinkle *et al* (1970) described a similar situation in the lizard, *Uta stansburiana*, in which the correlation between clutch size and body size was higher in northern than in southern populations.

Carpenter (1952b) and Fitch (1965) found that not all adult female *T. sirtalis* were gravid in any given year. Fitch showed that there was a positive correlation between age group and the proportion of gravid females in that age group. These data, however, were from snakes captured in the summer. Platt (1970) felt that most adult females in the populations he studied were gravid in summer, although a smaller proportion may have reproduced in poor food years.

In general, both Platt and Fitch found that the youngest reproductive females were second-year snakes, as was the case in my study, although Platt found that first-year females in his population of fast-growing snakes could reproduce in good food years. My data (Table III) from denning populations and dispersing snakes suggest that females less than 400 mm. S-V length in spring are not capable of reproduction, but that the percentage of reproductive females increases steadily in larger snakes. Above 500 mm., virtually all females appear to be potentially reproductive. Five of the six females in this size category that were not reproductive had obviously borne young the previous year.

Carpenter (1952b) felt that most of the non-gravid adult females he caught had not mated. My work (Fig. 15) indicates that this may sometimes be the case as far as the smallest potentially reproductive females are concerned. The effect of reproductive maturity of females on mating behaviour has not been studied extensively, but Hawley (pers. comm.) feels that *T. sirtalis* in the Interlake may select for large size in their mates. This being the case, the non-reproductive females, which are almost always small, and the smallest potentially reproductive females may go unmated. The status of the unmated but mature females caught away from dens in the early summer of 1972 is not clear. It is possible that these snakes were early migrants and, though immature at the time of dispersal, had developed to an apparently reproductive condition by the time I caught them.

The reason for the difference in reproductive potential between 1972 and 1973 is unknown. It is possibly related to differences in food supply or weather conditions of which I am unaware.

ii. Development of Young

Yolk deposition in mature eggs of *T. sirtalis* in the Interlake apparently occurs following emergence and prior to ovulation. This is in agreement with Bragdon's (1952) findings that mature ovocytes increase rapidly in volume in spring before they ovulate. Platt (1970) concluded that the abdominal fat body was probably not an important source of nutrients in this development.

Ovulation may occur anytime from mid-May on. Time of ovulation undoubtedly has great bearing on time of birth since this is when gestation presumably begins. The observation that ovulated eggs may enter the oviduct on the opposite side of the body has been made previously (Cieslak, 1945; Betz, 1963a, 1963b). The difference between the number of eggs *in utero* and the number of ovulation scars in the ovaries that was frequently detected in this study, however, seems to be unknown in the literature. Betz (1963a, 1963b) found that yolk masses sometimes undergo resorption *in utero* in *Natrix*. While this may have accounted for some of the differences observed, it is also possible that some eggs may simply have failed to reach the oviduct upon ovulation. Other sources of loss during embryonic development are well-known. Ovulated eggs may fail to be fertilized (Fitch, 1965) or otherwise fail to develop (Cieslak, 1945), embryos may develop abnormally and die (Martof, 1954; Betz, 1963b) or be aborted (Fitch, 1965), or even apparently normal young may be stillborn (Fitch, 1965). Dead young are even sometimes retained in the body following parturition (Betz, 1963a). Observations similar to these were made in this study but it was my impression that loss of eggs upon ovulation, abnormal development, and stillbirths were most important. The significance of this rather high rate of loss is not known although it tended to be greatest in the smallest snakes (Fig. 17). Perhaps small females are sometimes unable to build up sufficient energy reserves to enable them to produce complete litters and meet their apparent reproductive potential.

Birth in the populations of *T. sirtalis* under study may occur anytime from the end of July until the end of September. As previously noted, most of these births were observed in captive females. The later births reported here may be unnatural since many authors have expressed the opinion that captive female snakes may show a retarded gestation. Any retardation in this case, however, was probably not due to the fact that the females were not fed in the later stages of gestation since I have shown that they eat very little at this time anyway (Fig. 9). It also seems likely that at least some female snakes might give birth later in the year because of the variation in timing of activities at different dens. Emergence and dispersal times may vary by as much as a month in my study area. Some dens are not empty until mid- to late June and females from such hibernacula presumably give birth much later than do others. Date of birth probably depends on a multitude of factors including date of spring emergence and dispersal, date of ovulation, and weather, especially temperature and incoming radiant energy.

The degeneration of the ovulation scars by the time of birth, as noted in this study, is in sharp contrast to the findings of Cieslak (1945) and Bragdon (1952). These authors felt that these scars did not regress markedly until after gestation was terminated.

The average litter size obtained in this study does not differ significantly from those observed by Carpenter (1952b), Zehr (1962), Fitch (1965), and Platt (1970). Average number of live young was not calculated because it was not known to what extent the captive conditions might have been responsible for stillbirths. The comparison of the regression of brood size on female body size with that predicting litter sizes for spring females (Fig. 18A) indicates that the method used for calculating potential fecundity tended to overestimate. That is, the amount of annual growth predicted from this figure for females bearing specific numbers of young is much greater than that obtained from the formal growth analysis. The variance about the upper of these two lines has not been calculated but is undoubtedly very great. Average size of the newborn young recorded in this study was somewhat smaller than the figures obtained by Carpenter (1952b), Fitch (1965), and Platt (1970), but larger than those reported by Martof (1954).

iii. Reproductive Cycles

The occurrence of a biennial reproductive cycle in females has been reported for several species of viperid snakes, although it is by no means a univeral phenomenon and its significance is not always clear. Tinkle (1962) has reviewed the literature on reproductive cycles for viperids as has Prestt (1971) more recently for *Vipera berus*. St. Girons (1957) concluded, for *Vipera aspis*, that longer reproductive cycles occur in colder climates because of the short amount of time available for accumulation of energy reserves.

While biennial reproductive cycles have not been previously reported for *T. sirtalis*, females of this species in the Interlake of Manitoba might be expected to be subject to such a cycle in response to the short growing season. Although it has already been shown that some potentially reproductive females may go unmated each year, it appears that most denning females above 500 mm. S-V length are in reproductive condition. This is in contrast to the findings of Rahn (1942), Tinkle (1962), and Prestt (1971). On the basis of presence or absence of ovulation scars, size of ovarian follicles, and size of fat body, these authors found that denning populations of their respective species could be separated into two classes of adult females: reproductive and non-reproductive. The ratio was not 1:1 in each case, but it was clear that a biennial cycle was involved in each case. Prestt (1971) obtained other evidence, including yearly records of individual females.

In this study, obvious post-partum females were occasionally found at dens. Most of these (62.5%) were definitely not in reproductive condition as evidenced by the condition of the fat body and sizes of eggs in the ovaries, while the remainder were. It is obvious, therefore, that females are sometimes incapable of breeding in successive years. Whether or not they are may depend on how early in the summer they bear young and the availability of food to them after this time. Both of these, in turn, may depend heavily on weather. The small number of obviously post-partum females found at dens may indicate that most females are capable of regaining reproductive condition to the point where they can no longer be recognized as post-partum or that they simply do not return to the dens after giving birth. In the latter case, females that have given birth late in the summer may feed so long that they simply do not have time to return. Perhaps as a result of this they die from exposure in the fall or they find other hibernating sites such as might be used by the young-of-year. I have not found hibernacula of the young in the Interlake. These results are therefore inconclusive.

The male reproductive cycle is an annual one. This is not surprising since males are not presented with the energy problems that females are. Maximum testis development occurs in mid-summer coinciding with the appearance of mature sperm. The apparent abrupt rise in weight of tests/S-V length of animal in early summer (Fig. 19) is probably an artifact due to the way in which samples from dens and elsewhere were distributed. Sperm appear to be rapidly evacuated from the testes and are present in the vas deferens throughout most of the year. Males are obviously in reproductive condition before they enter hibernation in fall. These results indicate a male reproductive cycle compatible with the results of the more detailed studies of *Thamnophis* by Cieslak (1945) and Fox (1952, 1954). They also account for the occurrence of late summer and fall mating in these snakes, although its significance is not clear (Aleksiuk and Gregory, in preparation).

The reason for the occurrence of non-motile sperm in the reproductive tracts of males and in mated females in the fall of 1972 is also not clear. No reference is made to this phenomenon in the literature and it is possible that these sperm could have been dead. On the other hand, such sperm might overwinter in this condition and be capacitated the following spring. Why some snakes should have living, motile sperm and others living, non-motile sperm, is however, unanswerable at present.

F. LIFE HISTORY STRATEGY

Throughout the range of the species, population levels of *T. sirtalis* appear to be subject to considerable fluctuation. It has usually been felt that such fluctuations occur in response to variations in weather, either directly or indirectly. In the Interlake of Manitoba, where the climate is extreme and highly variable, population fluctuations of *T. sirtalis* are particularly great and population declines of as much as 50% have been observed to occur. Despite this, the species is very abundant in the Interlake, even during population lows, and is the most common of the four snake species occurring there. Its abundance may be partly explicable in terms of physiological adaptations to this environment (Aleksiuk, 1970; Vincent, 1971; Hoskins and Aleksiuk, 1973a, 1973b), but the ability to regain high numbers following large-scale population decline involves adaptations in the area of life history strategies. Because of differences in environmental severity and stability, and the resultant population effects, populations of *T. sirtalis* in the Interlake and in more southerly regions should exhibit important differences in life history.

The evolution of reproductive patterns in lizards has been reviewed in detail by Tinkle (1969) and Tinkle *et al* (1970). These authors found that lizards, both interspecifically and intraspecifically, could be grouped into two categories:

1. early-maturing, short-lived, and highly fecund;
2. slow-maturing, long-lived, and less fecund. The latter was felt to be characteristic of more temperate zone populations because of the shorter growing season available. These conclusions were reached, however, without reference to environmental instability during the growing season and population response to it. In an animal population which is subject to frequent fluctuation, the ability to build numbers back up again following a decline depends on the attainment of a high intrinsic rate of population increase, r_{max}. As Cole (1954) has pointed out, one of the most effective ways of doing this is to have first reproduction at an early age. The distinction between these two possible types of reproductive strategies, depending on whether or not a population is responding to a variable part of the environment, has recently been demonstrated by the work of Tilley (1973). He found that populations of the salamander, *Desmognathus ochrophaeus*, in fluctuating environments showed an earlier age of maturity than did populations in more stable environments, even though they were not widely separated geographically.

In this study, *T. sirtalis* were usually found to be capable of reproduction by the second year of life, in accordance with the findings of other authors (Carpenter, 1952; Fitch, 1965; Platt, 1970). Although detailed reviews of reproduction in snakes with respect to the evolution of life history patterns have not been made, this appears to represent early attainment of sexual maturity. In view of the species' dramatic response to a highly variable component of the environment, namely weather, it is not surprising that this is a basic life history feature throughout the range of the species.

The particular problem facing *T. sirtalis* in the Interlake, however, is that the growing season is much shorter than it is further south. Adult garter snakes in this area appear to spend only about three months actively feeding and growing each year. This is in contrast to the situation in Michigan, for example, where five months are available (Carpenter, 1952). Platt (pers. comm.) also indicates a longer active season for his populations in Kansas. Given that there is a minimum body size below which reproduction does not occur in females, the growth of first year female *T. sirtalis* in the Interlake must somehow compensate for this shortened season if reproduction is to normally occur in the second year of life. Growth of adult females is less important because these animals are already mature and have presumably made their major contribution to population increase. How this large amount of growth of juveniles is accomplished in the Interlake is unknown since the young are rarely found.

Once adult size and sexual maturity are attained, the Interlake populations are still faced with a much more variable environment than are more southerly populations and are consequently more susceptible to large fluctuations in numbers. They are apparently able to compensate for this and achieve a greater rate of increase than these other populations by maximizing reproductive output in two different ways. The first of these concerns reproductive potential. Females in the Interlake populations, particularly the larger individuals, apparently have a higher reproductive potential than do females in Kansas. Although little difference in average litter sizes of the Interlake and Kansas populations was found in this study, it is not known how potential and actual fecundity are related. It is possible that in some years much more of the existing potential might be realized. Increased litter size, in addition to early age of maturity, would be a significant factor in the attainment of a high r_{max}.

The second means of maximizing reproductive output may simply be an apportioning of more of the annual energy resources to reproduction than to other activities. The habit of communal denning in this species may well have evolved as a means of accomplishing this. *T. sirtalis* is known to overwinter in large numbers in other parts of its range, but the habit is by no means universal. For example, Platt (pers. comm.) has never been able to find large aggregations of hibernating snakes in his study area. In Manitoba, communal denning is particularly well-developed and *T. sirtalis* is the only snake species in the province known to overwinter in such large numbers. While this type of behaviour may be partly governed by the availability of suitable hibernacula, some apparently useable sinks seem to be unutilized in most years. Communal denning may therefore be important in ensuring that the entire breeding population is together in one place during the mating period.

This hypothesis is strengthened when one examines the details of spring emergence in these snakes. The real benefit of communal denning may be conferred by the differential behaviour of the two sexes at this time of year. In an earlier study (Gregory, 1971), I presented evidence that male snakes emerge from the dens in large numbers early in spring and that females emerge a few at a time throughout the entire spring period of about one and a half months. Upon emergence, female snakes are immediately attacked by large numbers of males and mated. After this, the females leave the den, presumably for their summer habitat, while the males remain in the vicinity of the hibernaculum to mate with more emerging females. This would appear to represent a highly effective mating system, with very little likelihood that many mature females will go unmated. The ability of large numbers of males to increase mating effectiveness has not been tested to my knowledge, however. This system has the added advantage that the actual producers in the population, the mature females, spend a minimum of time in an active, non-feeding state at the den and more time in feeding and incubating their broods. As a result of this, the growing season for females, particularly the early emergers, may well be more than three months. The bulk of the population which stays at the den for any length of time is male and therefore somewhat more expendable, especially since they are already in surplus. The staggering of emergence times of the female population, despite the apparent advantages of early dispersal, may also provide for at least partial reproductive success even in the event of a severe cold snap early in the spring. If all the females dispersed early, such a cold period could entirely eliminate reproduction in that year, but the reserve of later emergents may partially compensate for this potential source of loss.

There is possibly an alternative explanation of the differential activity patterns of the two sexes in spring. It may be that the two sexes themselves are following different life history strategies related to their different roles in propagation and population increase. Females may risk exposure to cold snaps in early spring in order to prolong their season of activity and improve their chances of satisfying their annual feeding requirements and successfully reproducing. Males, on the other hand, do not have energy requirements as great as the mature females and might be sacrificing part of their available feeding season in favour of remaining longer in the shelter of the den area. Whatever the explanation of this pattern of spring emergence, it has not been reported elsewhere for *T. sirtalis*.

Evidently, on a population basis, it is advantageous to have all the adult members of the species overwinter in large communal groups, despite the fact that this behaviour necessitates a long return migration to the summer feeding areas and markedly reduces the amount of time available for annual growth. There are no obvious sites suitable for use as hibernacula by large numbers of adult snakes in or near the summer habitat in the Interlake region. On the other hand, there is no advantage accruing to the population in the juvenile snakes hibernating in large numbers. It is in fact probably advantageous for them to remain in the summer habitat where they were born for their first winter since the energy expenditure of the long migration is eliminated.

Being small, they are likely capable of using many small denning sites which the adults would physically be unable to use. Also, this behaviour may actually result in their having a longer active season than the adults by allowing them to feed late into their first fall of life and early in their first spring and may at least partly account for the rapid growth of the first-year snakes. Snakes have rarely been found in the vicinity of marshes in early spring, but most of these have been juveniles, lending support to this idea. In any case, it is obvious that there is a developmental change in behaviour of the Interlake snakes between their first and second winters of life. Its significance is not known, especially since communal dens of *T. sirtalis* in other parts of Manitoba include the young-of-year. Perhaps the difference between these situations is related solely to the distance between den and summer habitat.

On the basis of this study, it is obvious that such differences as may exist among life history strategies of different populations of *T. sirtalis* are not similar to those described for lizards by Tinkle (1969) and Tinkle *et al* (1970). *T. sirtalis* appears to be so sensitive to particularly unpredictable components of the environment that it essentially resembles an "r-selected" species

(Pianka, 1970) throughout its range. Variable population size, rapid development and early maturity, and high r_{max} are all characteristic of such species. Shortening of the available growth season may only serve to exaggerate those characteristics which result in a high r_{max}. Although this appears to be the case in the Interlake populations of *T. sirtalis*, the entire question of what factors affect reproductive strategies of animals in general and of snakes in particular is in need of much further examination.

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