THE UNIVERSITY OF MANITOBA

OVERWINTERING POPULATIONS AND HOMING OF THE RED-SIDED GARTER SNAKE (*THAMNOPHIS SIRTALIS PARIETALIS*) AT A NORTHERN LATITUDE

by

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ABSTRACT

Thamnophis sirtalis parietalis overwinters communally in limestone sinks in the Interlake of Manitoba. During the fall of 1969 and spring and fall of 1970, marking experiments were conducted at three dens to determine population sizes and composition, growth rates, and the fidelity of homing to specific hibernacula. Behavioural observations were also made. Data analysis suggested that populations may number in the thousands and that population structure and growth rate are similar to those of the same species further south. Homing to dens was shown to occur. In addition, between the winters of 1969-70 and 1970-71, the den populations apparently decreased in size, the sex ratio shifted in value, and growth was less than expected.

ACKNOWLEDGEMENTS

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INTRODUCTION

The garter snakes (*Thamnophis*) represent the most abundant and widespread genus of snakes in North America. The most widely distributed of these, *Thamnophis sirtalis*, occupies a geographic range (Fig. 1) which exceeds in area that of any other North American species of snake (Fitch, 1965), even extending into the Northwest Territories at Fort Smith near the Alberta border (Logier and Toner, 1961).

Thamnophis sirtalis parietalis, the red-sided garter snake, is the nominal form occurring in Manitoba (Fig. 1). In the eastern part of the province and in northwestern Ontario it merges with *T. s. sirtalis* to form a transition zone (Fitch, 1965; Logier, 1958).

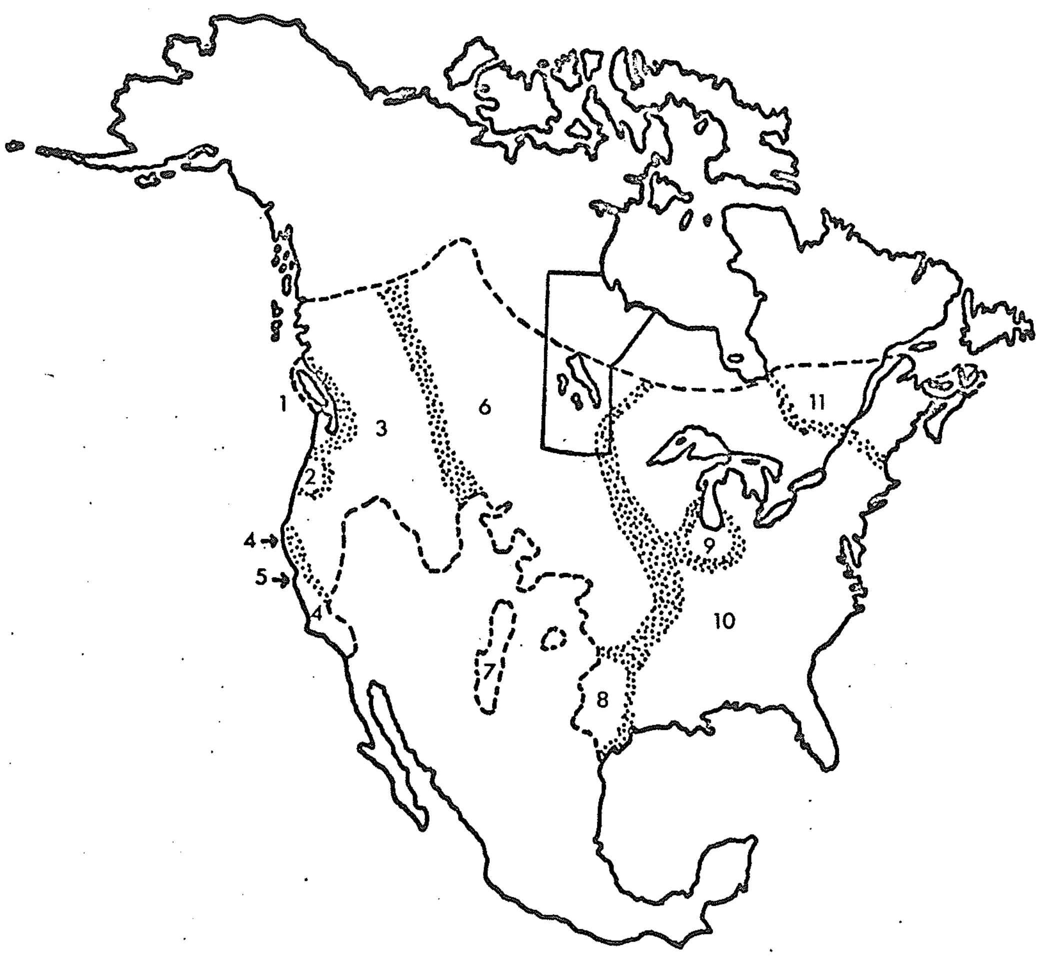
Of the five snake species inhabiting Manitoba, *Thamnophis sirtalis* is the commonest, being particularly abundant in the Interlake region. This species dens communally overwinter, and large concentrations of individuals, often numbering in the thousands, may be found at or near den sites or hibernacula each spring and fall. Dens are common throughout much of the Interlake in the form of "sinks" in the limestone bedrock.

The snakes are also in evidence as they move away from the dens in spring and to them in the autumn. This movement, especially in the latter case, appears to be of the order of

Fig. 1. Map of North America Showing Geographic Range of *Thamnophis sirtalis*.

Range indicated by dashed line and areas of intergradation between subspecies by stippling; Manitoba shown by solid line.

1. *T. s. pickeringi*, 2. *T. s. concinnus*, 3. *T. s. fitchi*, 4. *T. s. infernalis*, 5. *T. s. tetrataenia*, 6. *T. s. parietalis*, 7. *T. s. ornata*, 8. *T. s. annectens*, 9. *T. s. semifasciata*, 10. *T. s. sirtalis*, 11. *T. s. pallidula*. From Fitch (1965: 504).



1
2
3
4
4
5
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7
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9
10
11

a mass migration. The consistent day-to-day directional orientation of all the snakes on, for example, a particular road suggests that individuals may home to the same hibernaculum every year.

The basic outline of the annual cycle of the red-sided garter snake in Manitoba has been described by Aleksiuk and Stewart (1971). Prior to my study, however, no data were available regarding population sizes, age and growth, or movement patterns for this species in the province. The objectives of this study, therefore, were to observe and describe the behaviour of the snakes during the active periods around the dens, to determine the composition and size of overwintering populations using these hibernacula, and to discover whether migration and homing to specific dens are real phenomena. In addition, data on growth were collected and an attempt was made to obtain information about the pattern of dispersal of snakes from the dens in the summer.

METHODS AND MATERIALS

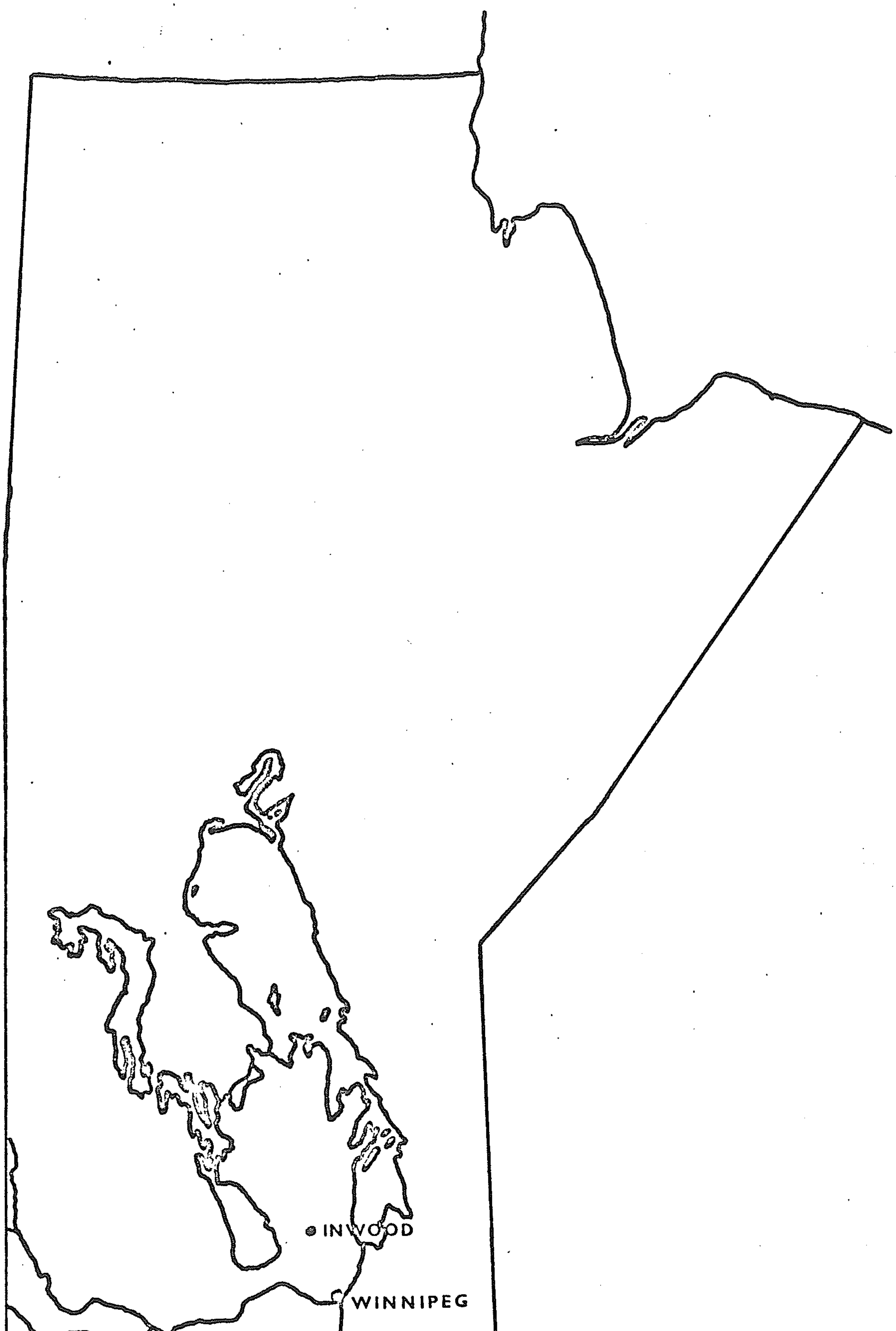
A. THE STUDY AREA

The work on which this study is based was carried out in the Interlake district of Manitoba, in an area centred around the town of Inwood (Fig. 2), about 71 kilometres north-northwest of Winnipeg. This particular site was chosen on the basis of observations of large numbers of snakes in spring and fall both on roads and in known hibernacula within a mile of the town.

The area consists of long, low, forested limestone ridges of northwest-southeast orientation, separated by belts of lower lying land usually occupied by marsh and less commonly by aspen woodland or small lakes and ponds. Much of the natural aspen forest of the ridges has been cleared and replaced by pastureland and grainfields. The hibernacula are most commonly sinks in the limestone bedrock of these ridges. Apparently they are the result of collapse of the overlying limestone and topsoil into caverns in the bedrock.

The formation of sinks is a relatively common occurrence in the Inwood area. They are highly fissured and in some instances lead to the formation of small caves. Because of the many cracks and openings, snakes have access to subterranean levels to escape freezing winter temperatures. In some cases, the bedrock may be fissured but no sink formed. Where such places are exposed, more potential hibernacula occur. Three dens were chosen for the purposes of this study. The location

Fig. 2. Map of Manitoba Showing Location of Study Area.


INWOOD
WINNIPEG

of each with respect to Inwood is shown in Figure 3.

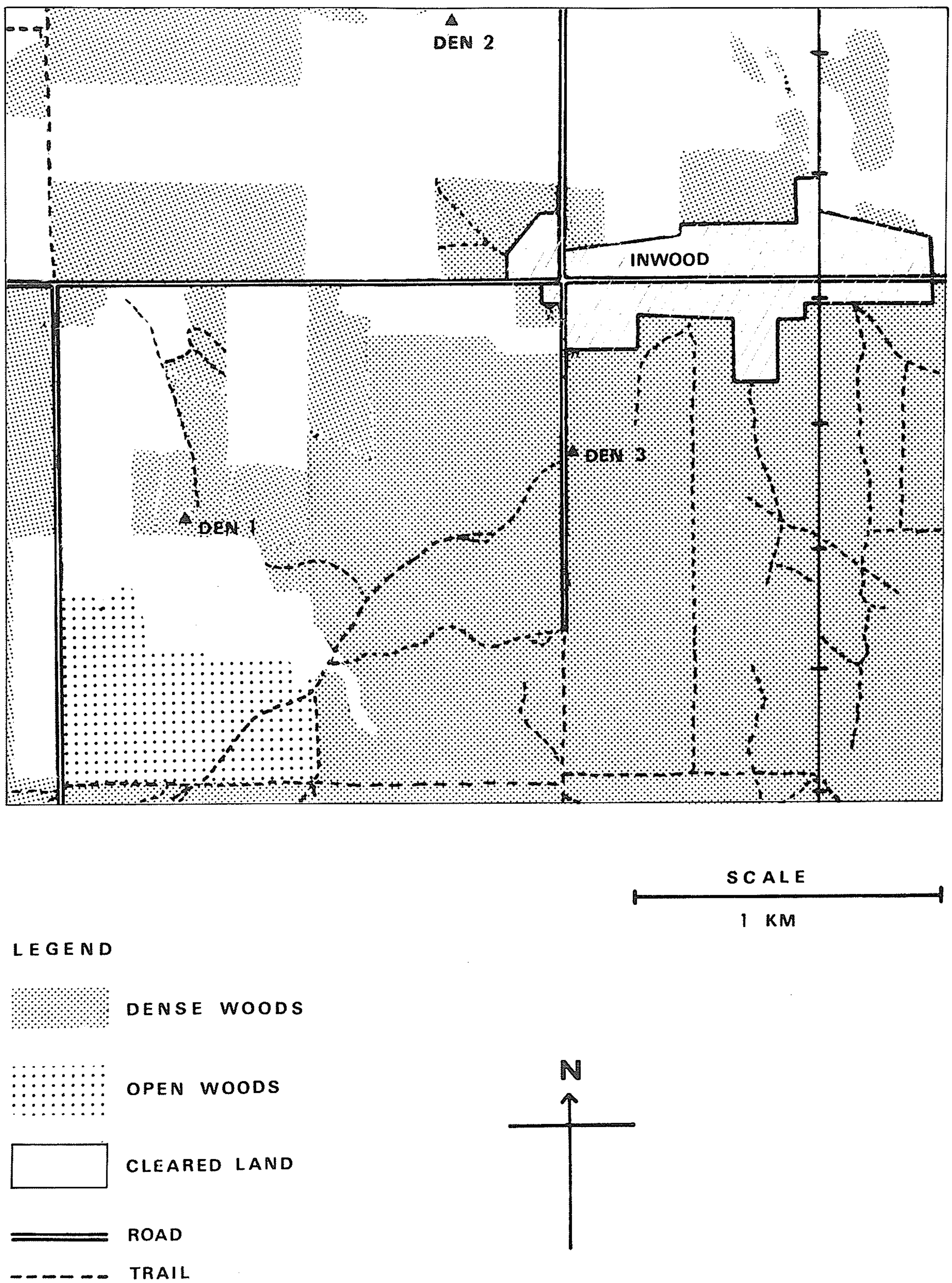
Den one consists of a large, oval-shaped limestone sink about 7.5 metres in length by four metres wide. The bottom of this bowl-like depression is well-fissured and littered with broken-up pieces of rock. This den is mainly surrounded by moderately thick aspen woods but with a clearing on the north side.

Den two consists in part of a circular, boulder-filled sink surrounded by hawthorn bushes. This is continuous some distance to the west with the rocks at the base of an east-west fence line between two pasture fields. Four small sinks which form an arc to the west in the more northerly of the two fields are also considered to comprise part of the same hibernaculum.

Den three is represented by a series of small holes in the ground on either side of a gravel driveway. A few bigger, sink-like holes are present on the south side in a dense stand of scrubby trees. The vegetation is mainly aspen and scrub oak.

Photographs of these three dens are shown in Figures 4, 5, and 6.

Fig. 3. Map of Inwood Area Showing Locations of Dens Studied.



DEN 2
INWOOD
DEN 3
DEN 1
SCALE
1 KM
LEGEND
DENSE WOODS
OPEN WOODS
CLEARED LAND
ROAD
TRAIL
N

Fig. 4. Photograph of Den One.

Fig. 5. Photograph of Den Two.

Fig. 6. Photograph of Den Three.

B. METHODS

During the autumn of 1969, between September 10 and October 19 inclusive, samples of snakes were taken by hand from den one on an almost daily basis and from den two on occasion. Sample size was usually determined by the maximum number of animals which could be handled in the time available. In the case of den one, this number was generally collected after four circuits of the sink. Each new snake was sexed, measured (snout-vent and total length) to the nearest five millimetres, weighed in grams, and individually marked by the clipping of subcaudal scutes after the method of Blanchard and Finster (1933). All recaptures were noted and measured. After the processing of the snakes in each sample, they were released, ideally on the same day as they were caught. In some instances, however, due to technical problems, all or part of a sample had to be taken back to the laboratory to be examined. These animals would then be released at a later date (most often the next day) after that day's sample was taken. This technique presents a minor problem in the use of the Jolly population estimate to be discussed below. It was deemed justifiable, however, in view of the fact that it was desired to mark as many snakes as possible in order to demonstrate homing or the lack of it, here considered the primary objective.

The same sampling method as outlined above was employed at den one in the spring of 1970 from April 26 to June 6, with the addition of increased sampling at den two during the same period. Sampling was also initiated at den three and snakes encountered away from dens were occasionally marked.

In the summer of 1970, much of the area within 16 kilometres of Inwood, particularly to the south (since this appeared to be the main direction of dispersal from den one), was searched for snakes by foot and car. Most of the snakes encountered before the beginning of fall activity at the dens were given an individual mark.

From August 25 to August 30 inclusive, a ring of 23 fairly evenly spaced live-traps was established around den one about 30 - 40 metres from its perimeter. These traps were modifications of the design of Fitch (1951). They were checked nearly every day from August 31 through October 22. Hand samples from the den itself were taken less frequently. All new snakes caught were marked. No marking was done at the other two dens although they were periodically checked for homing snakes.

The entire area within a mile of Inwood, particularly to the west where most of the dens are located, was scoured during a twelve week period beginning about August 19. Virtually every snake encountered in any of seven dens known in Inwood or its vicinity, and any snakes found elsewhere, were examined for marks. In this way it was felt that if any snakes marked at the dens before dispersal in the spring of 1970 returned to the Inwood area to hibernate, a significant number of them should be found and the proportion of these returning to the same hibernacula should be an indication of the extent of actual homing.

Estimates of the sizes of the male and female overwintering populations at den one in 1969-70 were made by the Petersen method (Robson and Regier, 1968). These were based on re-captures, in the spring of 1970, of animals marked in the autumn of 1969. No meaningful estimate was possible at den two because of the low number of recaptures. In the spring of 1970, samples of male snakes at den one were large enough that near-daily population estimates based on a slight modification of Jolly's (1965) model could be made. In no other instance were the samples of sufficient size or the recaptures numerous enough to allow the use of this method.

In the analysis of the size frequency distributions of the den populations, maximum separation of overlapping groups was achieved by plotting the cumulative per cent frequency for each size interval on probability paper and then finding inflexion points as described by Cassie (1954). Growth data obtained from measurements of returning snakes in the fall of 1970 were analysed by Walford plots (Walford, 1946).

RESULTS

A. SPRING ACTIVITY

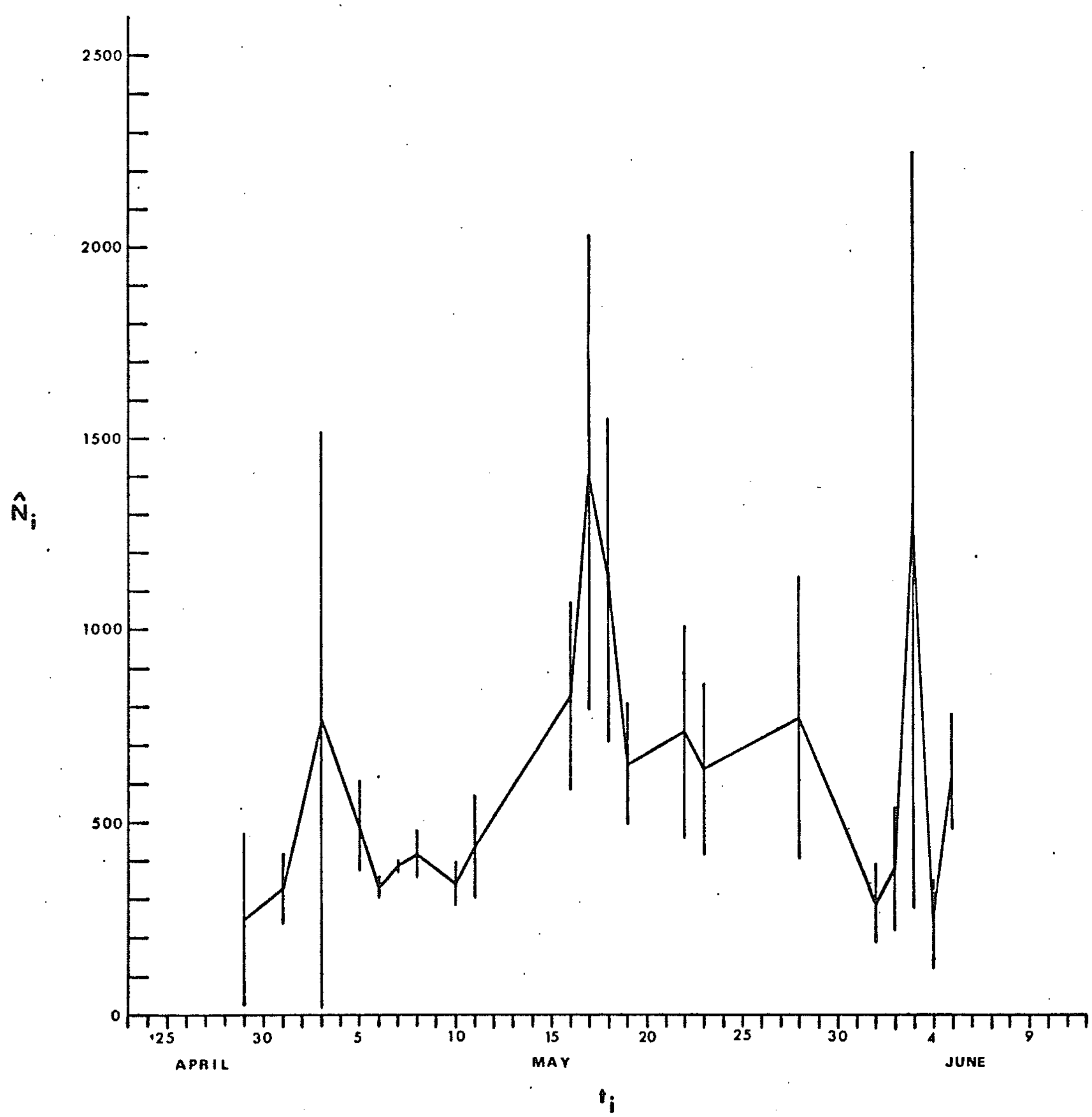
i. Numbers:

During the spring of 1970, in the course of sampling at three dens, 1159 individual snakes, including 107 from the previous fall, were caught, Taking into account the number of times each of these was recaptured later on in the spring, a total of 1708 captures was made. Of these, 1445 (924 individuals) were made at den one, 170 (155) at den two, and 93 (80) at den three. The observed sex ratios were 15.4♂♂:1♀, 50.7:1, and 25.7:1 at dens one, two, and three respectively. At den one a single female was recaptured on one occasion, whereas 520 recaptures involving 317 different individuals were made for males. Many of these males were caught more than twice, up to eight times at the extreme, and over quite variable periods of time as long as 35 days in duration. At dens two and three no females were recaptured. Fifteen males were recaptured once each at den two, while at den three 13 recaptures involving 12 different males were made.

Jolly (1965) estimates of the number of <u>active</u> male snakes present at den one were made on an almost daily basis. These estimates, along with their standard errors, are presented in Figure 7.

From May 6 through June 5, 35 snakes were caught and marked away from dens. This total included eleven males and

Fig. 7. Change in Size of Population of Active Male Snakes at Den One During Spring 1970. Vertical lines indicate population estimates $\pm$ standard errors. t_i = i^{th} sampling occasion or date of sample. $\hat{N}_i$ = estimate of population size at t_i. Based on method of Jolly (1965).


2500
2000
1500
1000
500
0
$\hat{N}_i$
25
30
5
10
15
20
25
30
4
9
APRIL
MAY
JUNE
t_i

24 females. None were subsequently recaptured.

ii. Emergence:

In 1970, snakes were first observed at den one on April 25 when the bottom of the sink contained a pool of snow meltwater. By the following day the den was dry, although water occasionally trickled in until April 30. Most of the snow in exposed places in the area had disappeared by this time, but occasional snowfall left light cover on the ground until May 12. May 2 and May 7 were the first dates of observation of snakes at dens two and three respectively.

iii. Mating:

The most obvious activity connected with spring emergence was that of mating. At den one in 1970, sporadic mating was noted as early as April 29. Mating activity was intense from May 8 until about May 28 and peaked around the middle of the month. Sporadic mating continued until June 2.

Little detailed observation of breeding was made at dens two and three. Indications were that mating covered the period from May 7 to June 6 at den two with no discernible peak in activity. Animals at den three first showed mating behaviour on May 18 and this activity apparently peaked on June 2.

Mating activity seemed to be most intense on warm, sunny days but was observed at air temperatures as low as 4.5^{o}C. at den one. For the most part it consisted of mating "balls". These large aggregations of snakes were usually composed of one female and varying numbers of males, possibly up to 100 on occasion, all attempting to mate with the female. In one instance, on May 19, near the height of the breeding season, a group of males at den one was observed trying to copulate with a dead female. On one occasion at den three, where collecting was difficult because of the dense stand of trees, it was found that catching male snakes was simplified by removing a female found at the edge of the trees, waiting quietly, and picking up all the males attracted to the spot. Four days later it was still possible to make a fair catch of males by waiting at the same place. At den one, on particularly favourable days near the middle of May, with little concealing vegetation present, the bottom of the sink was seen to be strewn with large mating clusters. Similar activity was observed at dens two and three but on a somewhat smaller scale.

iv. Predation:

Large numbers of dead and badly injured snakes, both marked and unmarked, were frequently found at the den sites, especially den one, in the spring. These exhibited various types of wounds but most commonly had pieces of the dorsal musculature pecked out, were headless, or had large holes in the abdominal wall through which the entrails protruded. In one instance, when two such dead snakes were found at den one, a crow was seen flying away on approach to the den. Stewart (pers. comm.) has seen crows attack snakes at den two and I watched two crows attack and kill a garter snake on a road in mid-August of 1970. In the latter case, the birds simply pecked at the snake for a few minutes and then flew off. Upon examination, the snake was found to be in very much the same condition as the spring kills around the dens. The incidence of this sort of mortality seemed to diminish with the growth of the ground vegetation.

v. Dispersal:

Snakes were first noted to wander from the sink at den one on April 29. By May 6 there was a pronounced increase in the extent and intensity of this activity. This wandering trend continued through the remainder of the spring. One long-distance movement of a snake was recorded for the spring season. The animal was a female originally marked on September 11, 1969 at den one and recovered dead on June 2, 1970 near den two.

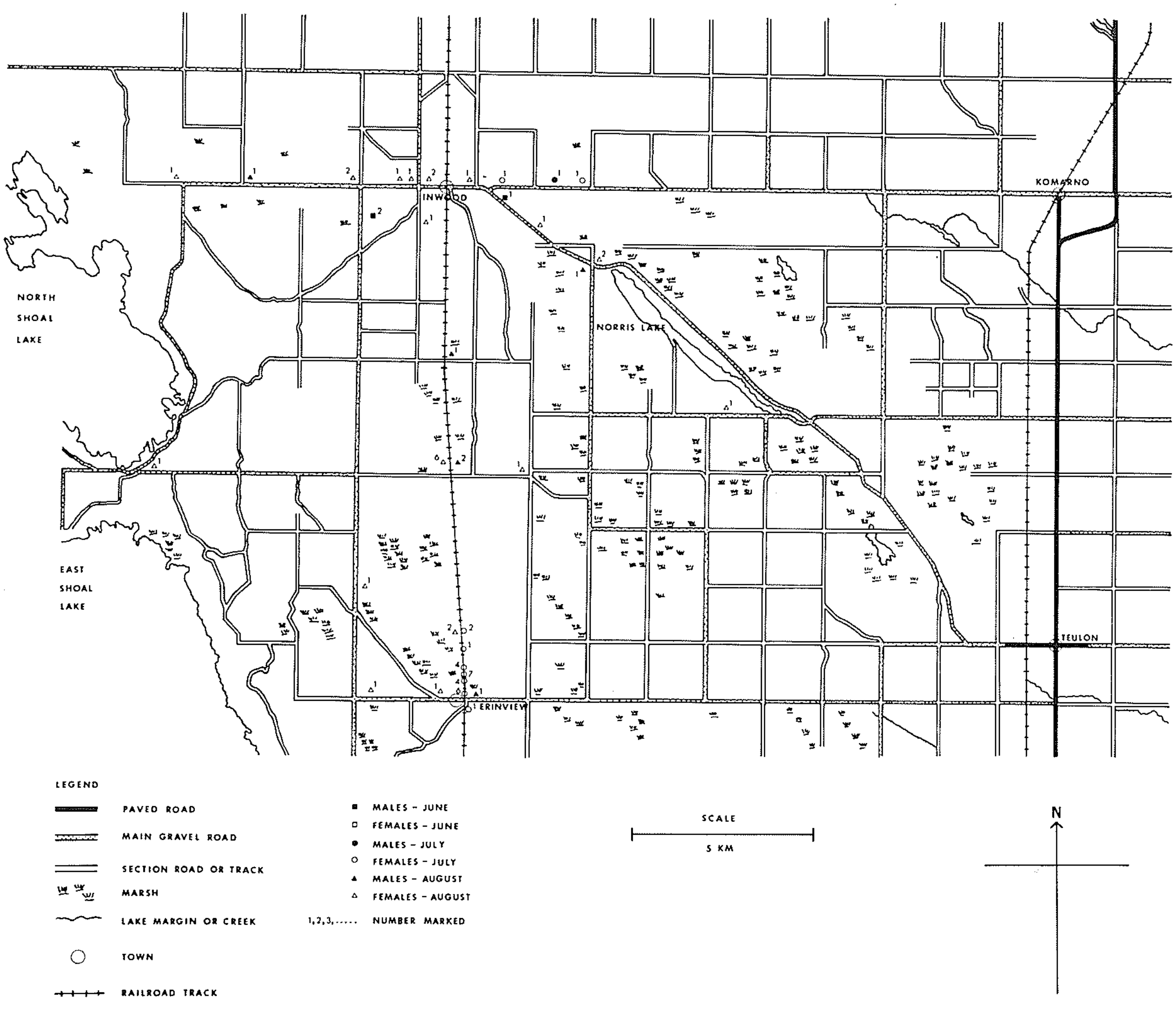
B. SUMMER OBSERVATIONS

Sixty-four snakes were caught and marked during the period from June 26 through August 24 in 1970. No previously marked snakes were found all summer. The locations of the summer captures are shown in Figure 8. By far the greatest number of snakes was found along the railroad track between Inwood and Erinview, although road catches were not uncommon in the latter part of the season.

Females were more frequently encountered than males, comprising 79.7 per cent of the total marked. Of 33 females captured along the railroad embankment, 31 (93.9%) were apparently gravid while only two of the 18 (11.1%) found on roads were recognized as such. Occasional gravid females were noted on roads until August 31 but I did not mark them. The autumn "migration" was under way by this time and a thorough search for homing snakes took priority. Seventeen of the 18 females (95%) found on roads and marked, including the two gravid ones, were captured on or after August 19, whereas all those from the railroad track area were caught up to and including August 19. No snakes were seen in the latter habitat after this date.

Thirteen male snakes were marked in the summer. Eight of these (61.5%) were found on roads, three (23.1%) in the vicinity of the railroad track, and two (15.4%) at den one early in the summer.

Fig. 8. Map of Inwood Area Showing Capture Locations of Snakes Marked During Summer 1970.



NORTH
SHOAL
LAKE
EAST
SHOAL
LAKE
INWOOD
NORRIS LAKE
KOMARNO
TEULON
ERINVIEW
LEGEND
PAVED ROAD
MAIN GRAVEL ROAD
SECTION ROAD OR TRACK
MARSH
LAKE MARGIN OR CREEK
TOWN
RAILROAD TRACK
MALES - JUNE
FEMALES - JUNE
MALES - JULY
FEMALES - JULY
MALES - AUGUST
FEMALES - AUGUST
1,2,3,..... NUMBER MARKED
SCALE
5 KM
N

For a considerable part of the distance between Inwood and Erinview, the railroad track passes through an extensive marshy area which is interspersed with higher "islands" of scrubby woods or aspen parkland. This seemed to be the favoured habitat along the track. Most of the animals found in this situation were basking at the side of the railroad embankment or were under cover such as boards beside the track or under the rails themselves. A cursory search of the marsh proper and the adjacent woods revealed no snakes. Two of the females marked along the stretch of track from Erinview to about one mile north were later recovered dead and two more were recaptured alive. All four were still in essentially the same place as when originally caught, the longest interval between first capture and recovery being eleven days and the shortest one day.

Snakes other than those discussed above were seen occasionally in the summer, particularly on roads, but these were usually either dead or escaped capture.

C. AUTUMN ACTIVITY

i. Numbers:

In the fall of 1969, at dens one and two, 1226 captures of snakes were made. This total involved 1045 individuals. At den one, the sex ratio was 1.86♂♂:1♀ and multiple recaptures occurred in both sexes. In the males, 775 captures were made involving 639 different snakes, while in the females the corresponding figures were 386 and 342. At den two, the sex ratio was 1.20♂♂:1♀. Thirty-five male snakes and 29 females were caught. In addition, there was a single recapture (a female).

In 1970, samples were taken at den one only. A combination of trap and hand samples resulted in a total catch of 378 individuals, including 51 returnees from the previous denning season. The total number of captures involving these animals was 419, animals caught twice or more in one day being counted only once for that day. The male:female ratio in this sample was 1.05:1 and multiple recaptures occurred again in both sexes. In the males, 227 captures were comprised of 194 indivuals while 184 females made up 192 captures.

In considering the trap and hand samples of 1970 separately, only one individual (a female) was caught twice on different days in the traps, whereas there were 18 (14 males, 4 females) instances of recapture in the hand samples. The observed sex ratios were 1.13♂♂:1♀ (total of 231 animals) in the traps and 1.12:1 (170 animals) at the den proper. Seven snakes caught in the traps had been originally captured at the den while fifteen snakes were in the reverse situation. In both cases, males comprised the majority (six and 13 respectively) of the snakes involved.

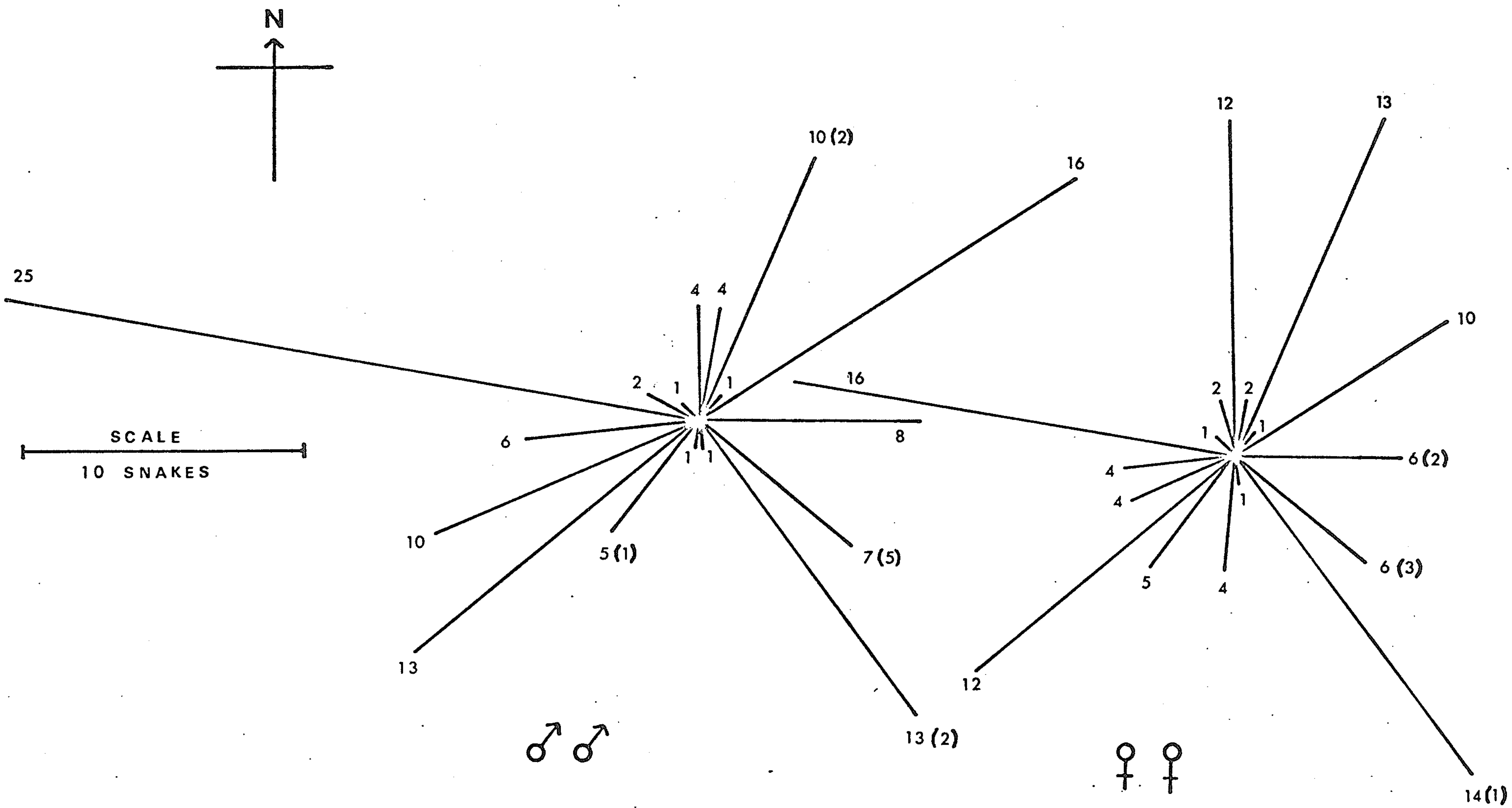
ii. Movement to the Dens and Retirement into Hibernation:

Snakes were first seen in large numbers on the roads, including those in and about Inwood, on August 19 in 1970. The first appearance of snakes at den one occurred on August 31 and movement to the dens was virtually over by the beginning of October in both 1969 and 1970. This was evidenced by a decline in the number of road observations at this time and also, in 1970, by a decrease in the number of catches in the traps around den one. Occasional sightings and captures, however, indicated some movement until the middle of the month in both years. After this time, the snakes seemed to have gone underground to stay until spring, although on November 1 in 1969, one female was found at den one, two snakes were found at den three, and a fourth animal was discovered at another den in the town of Inwood.

The ring of traps around den one was used as an indicator of the direction of approach of the snakes to the den. Figure 9 depicts the number of individual snakes caught at each trap. Animals caught at the den and then later in the season in traps, and recaptures of animals originally caught in traps, are not shown. This figure

Fig. 9. Direction of Immigration of Snakes to Den One in Autumn 1970.

Based on first captures of snakes originally caught in traps (escapees and unsexed dead animals not included). Centre point represents approximate centre of den.


N
SCALE
10 SNAKES
25
10 (2)
16
4 4
2 1 1
6
8
1 1
10
5 (1)
7 (5)
13
13 (2)
♂ ♂
12
13
10
2 2
1 1
16
6 (2)
4
4
1
5
4
6 (3)
12
14 (1)
♀ ♀

therefore represents the original captures of snakes seen for the first time, in the autumn of 1970, in traps.

iii. Gravid Females and Autumn Mating at the Dens:

On October 15, 1970, two gravid females were caught at den one. They were taken back to the laboratory and four days later one of them produced 24 live young. These young, which were not sexed, had a mean snout-vent length of 154.4 millimetres with a standard deviation of 4.73 millimetres. This female and her brood were subsequently released at den one, but the second female was kept in a cage in a laboratory in the winter of 1970. This individual bore a few dead young in early November.

An instance of autumn mating was noted at den one on September 6, 1970. This consisted of a pair of snakes rather than a "ball".

iv. *Thamnophis radix* at the Dens:

On September 28, 1970, three female western plains garter snakes, *Thamnophis radix haydeni*, were found at den one. From this date until October 16, 14 individuals (three males, eleven females) were caught. Eleven of these were caught in the traps and three at the den proper. Only one, a female, was recaptured alive. A second female was recovered dead, apparently frozen. No plains garter snakes had been observed at a den in the Inwood area before and few were seen on the roads in the district, most of them being found further east near the towns of Komarno and Teulon. *T. radix* was also noted in a few smaller dens in and around Inwood subsequent to the original discovery, but none were seen at dens two and three. The most likely explanation of the sudden appearance of plains garter snakes in the study area is that the species is undergoing a minor range extension.

D. POPULATION SIZE AND COMPOSITION

i. Population Estimates:

Petersen estimates (Robson and Regier, 1968) for the winter of 1969-70 indicate that 5585 males (standard error = 463.56) and 2720 females (S. E. = 949.28), for a total of about 8305 snakes, hibernated at den one. The numbers of recaptures of males and females were 99 and seven respectively. In the autumn of 1970, it was quite obvious that the populations at all the dens were very much smaller than they had been the previous year, although no size estimates are available.

ii. Population Composition:

Figures 10 and 11 show the size frequency distributions of animals measured at den one during three sampling seasons. Snakes found dead are omitted, but animals measured in addition to the regular samples are included. In each histogram, the snakes are represented by ten millimetre intervals of snout-vent length. Measurements were considered to be accurate within ± five millimetres.

Table I summarizes the breakdown of these frequency distributions into approximate size classes which are probably representative of different age groups or combinations of age groups. In all cases, a probability paper plot was used as a guideline for division, although the problem of obvious overlapping of size units occurred only in the autumn 1969

Fig. 10. Size Frequency Distributions of Male Snakes at Den One in Fall 1969, Spring 1970, and Fall 1970.

N = total sample size, n = number of individuals in each size interval,

S-V = snout-vent.

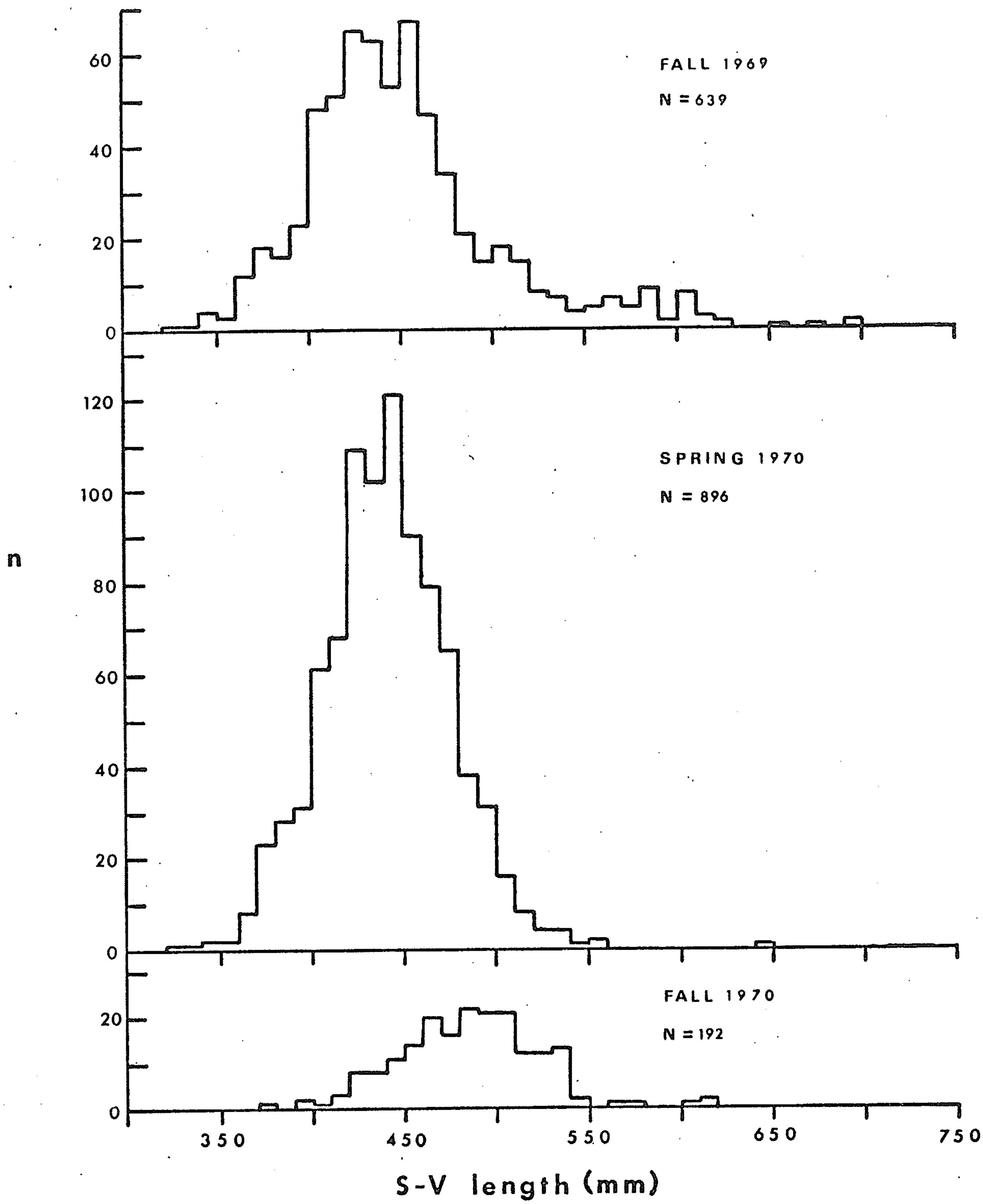
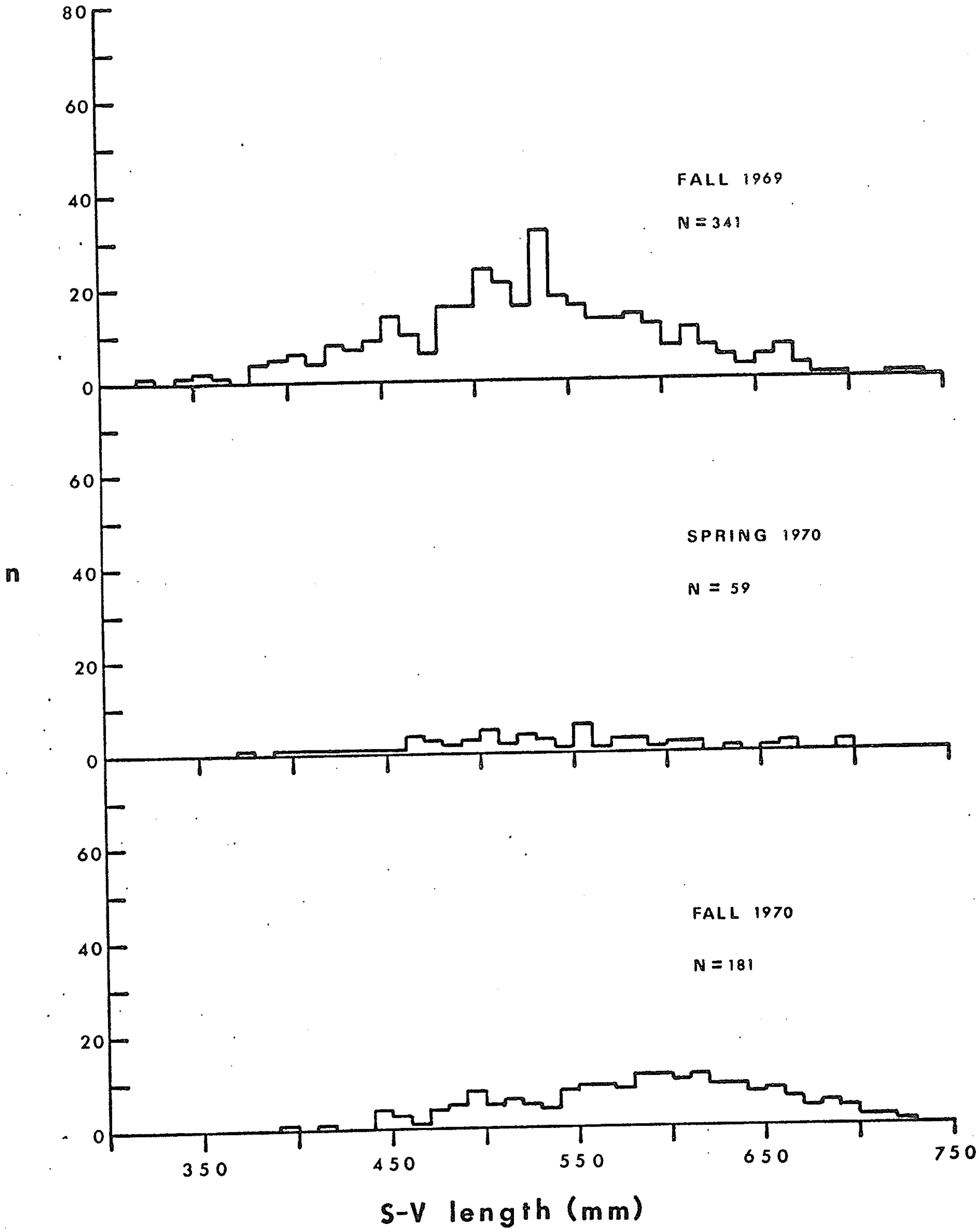

FALL 1969
N = 639
SPRING 1970
N = 896
FALL 1970
N = 192
n
0
20
40
60
80
100
120
350
450
550
650
750
S-V length (mm)

Fig. 11. Size Frequency Distributions of Female Snakes at Den One in Fall 1969, Spring 1970, and Fall 1970.

Symbols as in Figure 10.



FALL 1969
N = 341
SPRING 1970
N = 59
FALL 1970
N = 181
n
80
60
40
20
0
350
450
550
650
750
S-V length (mm)

Table I. Analysis of Size Frequency Distributions of Both Sexes at Den One in Fall 1969, Spring 1970, and Fall 1970. Except where otherwise indicated, means and standard deviations are approximations from histograms.

Males

Fall 1969				Spring 1970				Fall 1970			
Range (in mm.)	No. Animals (% of pop.)	Mean (in mm.)	Standard deviation (in mm.)	Range (in mm.)	No. Animals (% of pop.)	Mean (in mm.)	Standard deviation (in mm.)	Range (in mm.)	No. Animals (% of pop.)	Mean (in mm.)	Standard deviation (in mm.)
	[A]575 (90.0%)	[A]440	[A]40 <---------->	321-560	895 (99.8%)	440.8	33.9	371-580	189 (98.4%)	482.5	35.1
321-630	[A]45 (7.0%)	[A]555	[A]27								
	[A]15 (2.4%)	[A]610	[A]10 <----------	----------	----------	----------	---------->	601-620	3 (0.6%)	[B]613.3	[B]7.6
				641-650	1 (0.2%)	[B]650	[B]0				
651-700	4 (0.6%)	[B]682.5	[B]20.2								
Σ	639 (100%)				896 (100%)				192 (100%)		

Females

Fall 1969				Spring 1970				Fall 1970			
Range (in mm.)	No. Animals (% of pop.)	Mean (in mm.)	Standard deviation (in mm.)	Range (in mm.)	No. Animals (% of pop.)	Mean (in mm.)	Standard deviation (in mm.)	Range (in mm.)	No. Animals (% of pop.)	Mean (in mm.)	Standard deviation (in mm.)
	[A]333 (97.7%)	[A]520	[A]70 <---------->	371-700	59 (100%)	530.8	73.0	391-730	181 (100%)	582.7	68.8
321-700	[A] 6 (1.8%)	[A]680	[A]12								
721-740	2 (0.5%)	[B]735	[B] 5								
Σ	341 (100%)				59 (100%)				181 (100%)		

[A] approximate values obtained by method of Cassie (1954).

[B] values calculated from actual measurements of snakes.

<---> indicates t-test shows no significant difference between means of groups at 0.05 level of probability (Snedecor and Cochran, 1967: 114 - 116).

sample (Fig. 12). In two instances, females in the spring and fall of 1970, no breakdown at all was possible. The data in Table I are arranged so that the most similar size groups in the three seasons, as indicated by t-tests on their means (Snedecor and Cochran, 1967: 114-116), are aligned across the table.

The size frequency distributions for each sex are similar for the autumn of 1969 and spring of 1970, but are different between the sexes. Figure 13 shows the same type of analysis for snakes from dens two and three. Separation is approximate in these cases but in general they are comparable to the subdivisions made in the larger den one samples from the same periods.

For the autumn of 1970, a different picture is presented for den one. Females, as in the previous year, are more highly variant in size than the males, but in both sexes the youngest separable group has a larger mean size. Those snakes marked during the 1969-70 overwintering period which fell into the youngest size group at the time of marking, and were recaptured the following denning season, still fell into the youngest separable size group in the fall of 1970, although they had undergone a full season of growth. The distributions of the size groups in the two denning seasons are dissimilar.

Fig. 12. Probability Paper Plots of Size Interval Against Cumulative per cent Frequency of Occurrence for Each Sex at Den One in Fall 1969.
x's represent cumulative normal plot and ·'s represent fitted points. I = inflexion point, m = mean, s = standard deviation. Based on method of Cassie (1954) and fall 1969 data from Figures 10 and 11.

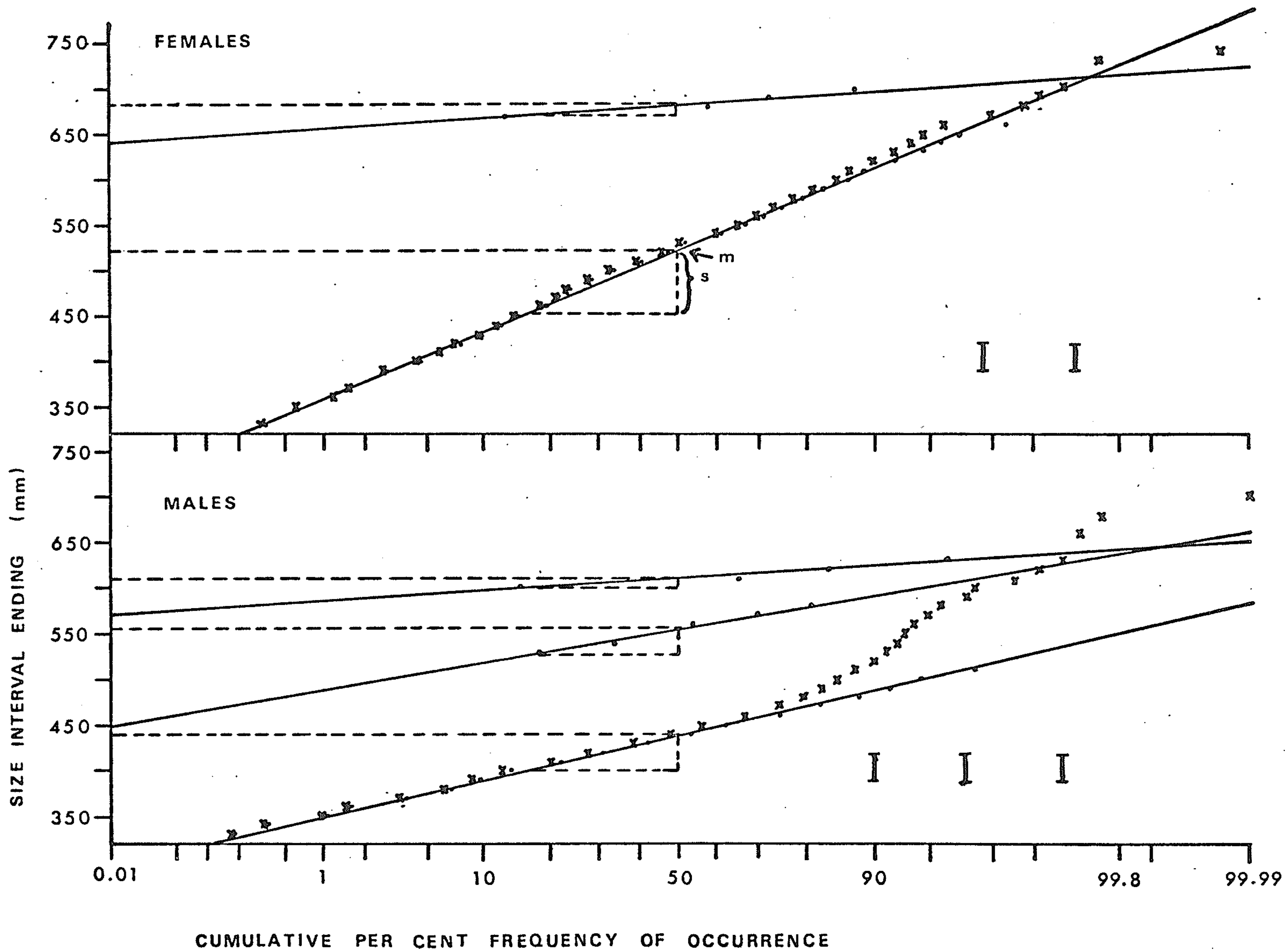
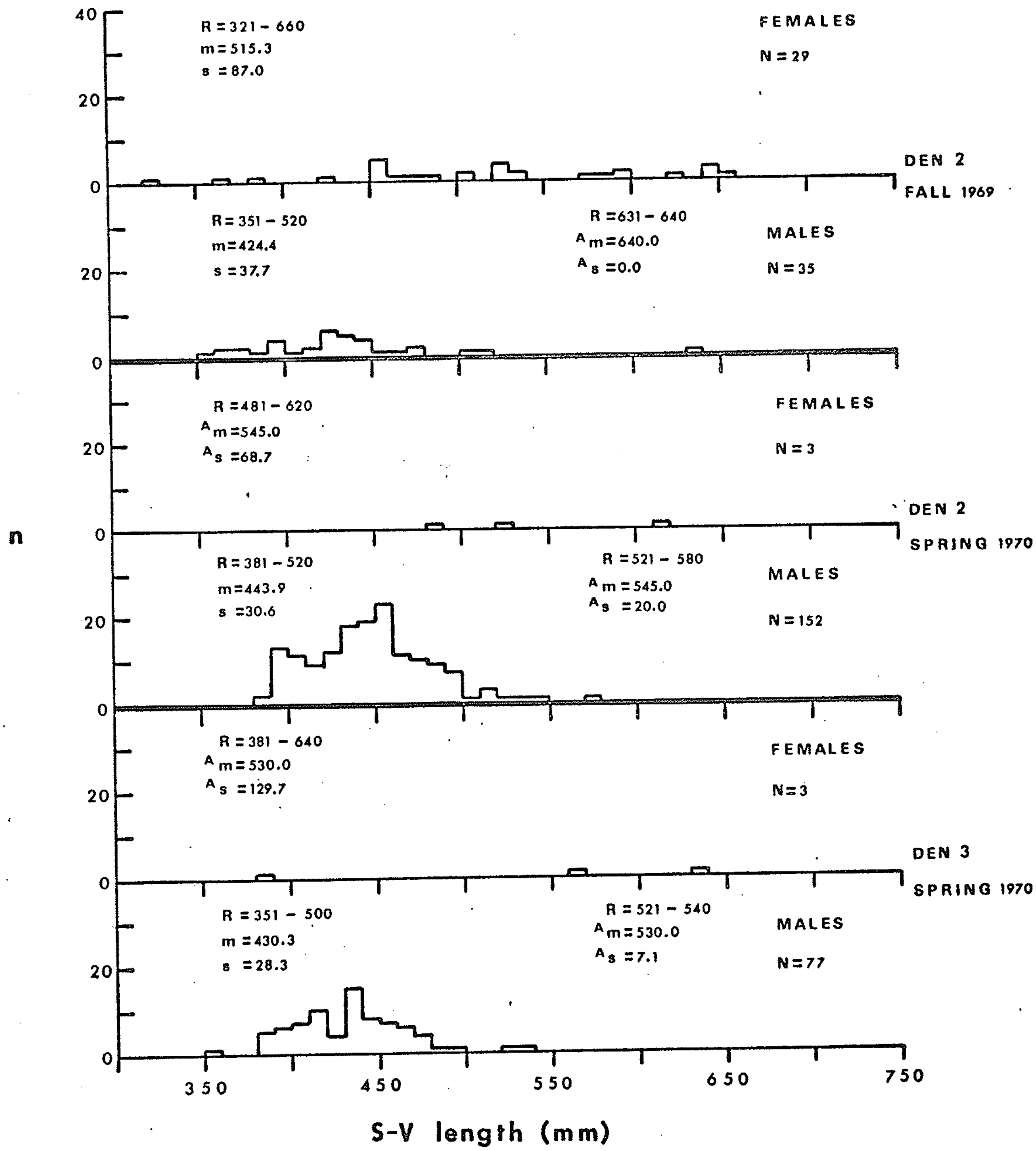

FEMALES
MALES
750
650
550
450
350
m
s
SIZE INTERVAL ENDING (mm)
0.01
1
10
50
90
99.8
99.99
CUMULATIVE PER CENT FREQUENCY OF OCCURRENCE

Fig. 13. Size Frequency Distributions of Both Sexes at Dens Two and Three in Fall 1969 and Spring 1970.

R = range; other symbols as in Figures 10, 11, and 12. A. values calculated from actual measurements of snakes.



R = 321 – 660
m = 515.3
s = 87.0
FEMALES
N = 29
DEN 2
FALL 1969
R = 351 – 520
m = 424.4
s = 37.7
R = 631 – 640
Am = 640.0
As = 0.0
MALES
N = 35
R = 481 – 620
Am = 545.0
As = 68.7
FEMALES
N = 3
DEN 2
SPRING 1970
R = 381 – 520
m = 443.9
s = 30.6
R = 521 – 580
Am = 545.0
As = 20.0
MALES
N = 152
R = 381 – 640
Am = 530.0
As = 129.7
FEMALES
N = 3
DEN 3
SPRING 1970
R = 351 – 500
m = 430.3
s = 28.3
R = 521 – 540
Am = 530.0
As = 7.1
MALES
N = 77
n
0
20
40
350
450
550
650
750
S-V length (mm)

E. GROWTH

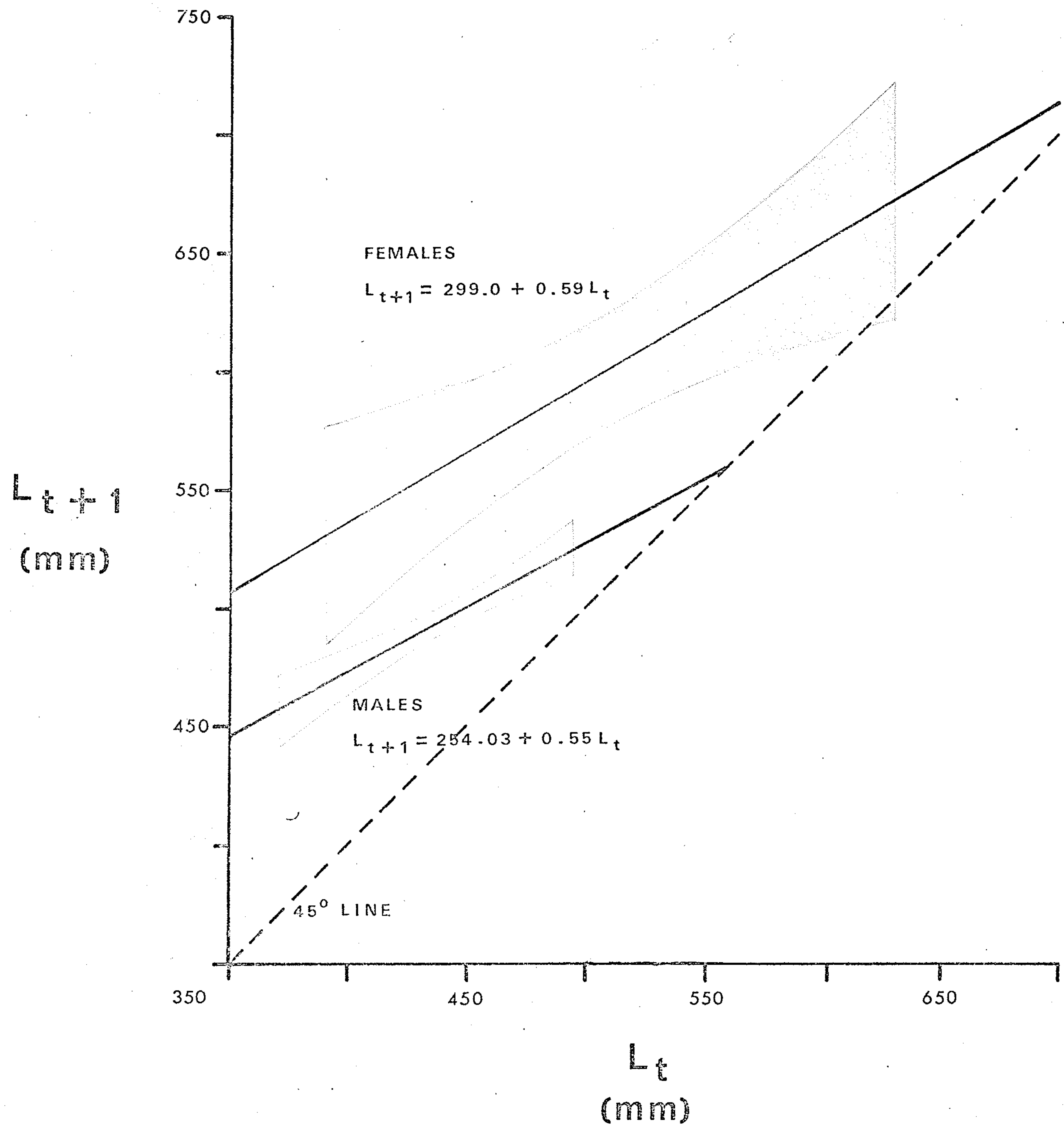
No growth was measurable in snakes throughout the period spent in the vicinity of the dens. Because of this, the change in length of individuals marked in 1969-70 and recaptured in the autumn of 1970 represents annual growth.

All but three males of the 58 recovered snakes (49 males, nine females) were measured. Of these, one male was probably misidentified and this snake was excluded from the following analysis. All of the animals recovered and measured, regardless of which den they were originally caught at, were lumped together and then divided according to sex. This was justified on the basis that no real differences in the structures of the populations at the three dens in 1969-70 were detectable from the data at hand.

Plots of length in 1969-70 (L_t) versus length in the fall of 1970 (L_{t+1}) were made for each sex. These were based on individual measurements. Tests of the regressions of L_{t+1} on L_t against a slope of one resulted in t-values of 4.82 (43 df) and 2.82 (7 df) for males and females respectively. This indicated a significant difference at the 0.01 level for males and at the 0.05 level for females. The calculated regression lines and the 95 per cent confidence bands for the intervals in which measurements were obtained are shown in Figure 14.

Fig. 14. Growth Rates of Both Sexes for Summer 1970 and the 95 per cent Confidence Bands About Their Means.

Shaded areas represent 95 per cent confidence bands. L_t = S-V length in 1969-70 denning season, L_{t+1} = S-V length in fall 1970.



750
650
550
450
350
450
550
650
FEMALES
L t+1 = 299.0 + 0.59 L t
MALES
L t+1 = 254.03 + 0.55 L t
45° LINE
L t+1 (mm)
L t (mm)

An analysis of covariance was carried out to determine whether or not there were any differences between the sexes. Bartlett's chi-square test for the homogeneity of within-group variances resulted in a value of 3.53 (1 df), indicating a non-significant difference in the variances of the measurements of males and females. The slopes of the regression lines calculated for each group are not significantly different since a test of the homogeneity of within-group regression coefficients gave a value of F at 0.098 (1, 50 df). A test of significant differences between the adjusted group L_{t+1} means resulted in an F-value of 57.57 (1, 51 df), indicating a significant difference at the 0.01 level between the L_{t+1}-intercepts of the two lines.

All the animals involved in this analysis were well within the ranges of length of the youngest size group in their respective sexes (Table I) when originally measured in 1969-70. The mean original length of the 45 males was 441.58 millimetres (standard deviation = 28.55). This is not significantly different from the 440 millimetre mean obtained from the fall 1969 data when compared by a t-test for independent samples with unequal variances (Snedecor and Cochran, 1967: 114-116). Similarly, in the females, no difference was found between the mean of 503.89 millimetres (s = 74.62) and the 520 millimetre average from the autumn of 1969. The average measurements of the two groups when recaptured a year later, however, were significantly smaller at the 0.01 level than the next oldest size groups in the fall of 1969 (Table I). The mean lengths of the males and females when recaptured were 495.98 millimetres (s = 24.21) and 598.33 millimetres (s = 52.80) respectively.

F. HOMING

In the fall of 1969 and spring of 1970 a total of 1830 snakes (1437 males, 393 females) were marked and released at den one. This sum includes 29 males and three females which were caught and marked in the spring season in the immediate vicinity of, but not actually at, the den. Of all these, 47 males and eleven females were known to have died from various causes prior to and during dispersal from the den in spring, 1970. The maximum possible number of marked animals able to return in the fall was therefore 1390 males and 382 females. At dens two and three, maxima of 217 (185 males, 32 females) and 80 (77 males, three females) marked snakes respectively were still available for recapture in the autumn of 1970. The grand total of all these figures resulted in a marked pool of 1652 males and 417 females from which to draw evidence of homing to specific hibernacula.

During the fall of 1970, over 350 male snakes and 300 females were caught and examined in the vicinity of Inwood. This sample included 49 males and nine females which had been marked the previous denning season. Only one marked snake, a male, was not found at the den at which it was originally caught, despite an intensive search which covered seven different known hibernacula. This individual, however, was only about eight-tenths of a kilometre from its point of origin (den one) when it was caught on September 15. It was not recovered again after its release on September 17, so that whether or not it homed or whether it stayed at the den near which it was found remain unknown.

A combination of trap and hand samples at den one in the fall of 1970 resulted in the capture of 51 live, previously marked snakes. In addition, four other returnees, three of them males, were found at den one. Two of the males were recovered dead in traps. The third male was found alive, along with the remaining female, at the den itself, although no sample was attempted on that day. Two homing males were found alive at den two but no animals marked at den three were recaptured.

Known homing occurred, therefore, in two of the three dens studied, although all the females and 46 of the 48 males involved were from den one. Per cent recoveries of marked snakes from the previous season, including the single possible non-homer originally from den one, were very low for all dens combined (2.96% for males, 2.15% for females). Homing success of all the males recovered was 97.95 per cent while that of the females was 100.00 per cent; for the combined sexes it was 98.27 per cent.

DISCUSSION

A. THE ANNUAL CYCLE

The annual cycle of *Thamnophis sirtalis* in the Interlake of Manitoba consists of two main phases: a dormant overwintering phase and an active summer phase. Vincent (unpubl. data) has demonstrated that temperature is the most important factor involved in inducing both the onset of hibernation and emergence in the spring. In both these seasons, however, there is a period during which snakes are active in the immediate vicinity of their dens. Submergence and re-appearance, therefore, seem to be gradual, rather than sudden, processes when considered on a populational basis.

In the spring, snakes begin to emerge by the end of April. At this time, sinks such as that at den one of this study may be partly flooded with snow meltwater. This would at first seem to represent a potential danger to the hibernating animals, but findings of Carpenter (1953) tend to suggest that snakes may fairly often pass the winter under water in tunnels, etc. in the ground. Also, the greatly depressed metabolic activity of the snakes (Aleksiuk, 1970) would minimize the likelihood of drowning. In the case of hibernacula in the Interlake, there may also be subterranean air cavities in which the animals could locate themselves.

In early spring, activity seems at first to be confined to a few individuals and to the warmest parts of sunny days.

At night, the animals go back underground into the dens. As the season progresses, more snakes emerge and remain above ground longer. Some begin movement away from the dens. The exact timing of spring activities probably depends on temperatures in the microclimate of the den. These temperatures will be influenced by cover in the vicinity of the den through its shading effect and its action as a snow trap. For example, in 1970, snakes at den three were among the last to emerge. In the autumn, the sequence of events is reversed, activity around the dens decreasing with the advent of cooler weather.

Blanchard and Blanchard (1941) have outlined the courtship and mating behaviour of *T. s. sirtalis* in Michigan and Munro (1948) has briefly noted that of *T. s. parietalis* from Arkansas. In the Interlake of Manitoba, copulation most frequently takes the form of the mating "balls" previously described in this paper and alluded to by Blanchard and Blanchard (1941). Snake balls have been observed by other authors in the past, among them Finneran (1949) for *T. butleri*, Fox (1955) for *T. s. tetrataenia*, and Gardner (1955, 1957) for an unidentified species of garter snake. I have also noted the same sort of behaviour in spring in *T. s. sirtalis* at a den near the outskirts of Toronto, Ontario. None of these, however, is of the order of magnitude of the mating activity at large dens in the Interlake.

In this study, fall mating was observed only once, although its occurrence was recorded frequently by Blanchard and Blanchard (1941) for *T. s. sirtalis* and Fox (1954) indicates that autumn is the usual breeding time of *T. s. tetrataenia* near San Francisco. Blanchard and Blanchard (1941) suggested that in such cases the sperm "hibernate" with the female, fertilization occurring the following spring. Rahn (1942) showed that this is the usual situation in *Crotalus v. viridis* in Wyoming.

Male snakes apparently recognize the females by odour (Fitch, 1965). In this study, the attraction of males at den three to a spot formerly occupied by a female supports this view. Similarly, Stewart (pers. comm.) recalls holding a large female at the edge of den one in spring and attracting large numbers of males from some distance. Carpenter (1952a) reports releasing a female *T. s. sirtalis* at the peak of the breeding season and then watching two males released shortly thereafter follow exactly the same path, one of them eventually courting her. Observations of this kind are common in the literature.

Blanchard and Blanchard (1941) found that copulation in *T. s. sirtalis* occurs in sunny weather and when the air temperature is above 15.5^{o}C. They also state that in early spring, unconsummated courtship, which they claim is often confused with actual copulation, is common at cooler temperatures. In this study, courtship was observed when the air temperature was as low as 4.5^{o}C., although it was not noted whether mating took place. It would seem, however, that it could have since, according to Vincent (pers. comm.), as long as the weather is sunny and the ambient temperature 4^{o}C. or higher, snakes in the Interlake may be capable of maintaining a body temperature of 15^{o}C or more.

After mating, the females leave the dens for their summer habitat while the males stay around for a variable number of days to copulate with unmated emerging females. There are four lines of evidence which support this idea:

1. Blanchard and Blanchard (1941) state that the males of *T. s. sirtalis* generally mate several times whereas the females become intolerant of courtship after mating.

2. In this study, of all the females collected at three dens in the spring of 1970 only one was recaptured and then after the short time of three days. Both captures of this snake were made before May 1 when emergence was only beginning and conditions probably were not yet favourable enough for the animals to leave the den. On May 1, this snake was recovered dead. In addition, the total spring catch was heavily biased in favour of males. For example, at den one in the spring of 1970 the observed sex ratio was 15.4:1 as compared to 1.86:1 for the same population in the fall of 1969. This would seem to indicate that the females do not

remain around the den long enough after emergence and mating, which quickly follows, to make up any substantial proportion of the catch.

3. Between May 6 and June 5, 1970, 24 of the 35 snakes found away from dens and marked were females.

4. Males caught at den one in the spring period included several multiple recaptures. The length of time a given male spends at the den may depend upon his mating success; competition for a mate is obviously keen.

Throughout most of the spring activity period, emergence from hibernation and dispersal from the dens seem to occur simultaneously. There is, however, a peak period before which more snakes emerge than leave and after which the opposite is true. Figure 7 suggests that the peak at den one in 1970 cccurred on May 17, which is about coincident with what was subjectively considered to be the height of the breeding season. The two aberrant high peaks, on May 3 and June 3, which do not fit into this increase-decrease picture have large standard errors and are the result of low recapture rates on these days, leading to positive biases in the population estimates (Platt, 1969).

The activities described for the spring of 1970 at den one occurred on the average about a month later than they do in garter snake populations in warmer climates further south. For example, Blanchard and Blanchard (1941) recorded the usual mating period of *T. s. sirtalis* in Michigan as being from early April to early May, occasionally beginning in late March. Fox (1955) has noted mating of *T. s. tetrataenia* in California in March and April and Gardner (1955) observed garter snake balls in Connecticut in mid-April. In the latter case the species was not named but was probably *T. s. sirtalis*. Presumably, emergence times are also earlier in these areas.

After mating, the snakes disperse to their summer habitat. If it can be assumed that snakes normally restrict themselves to a relatively small home range in the summer, as Stickel and Cope (1947) suggest is usual in many species, the direction of return of individuals to den one (Fig. 9) should approximate the direction of dispersal since homing appears to be a real phenomenon. In either sex, the directional breakdown is apparently random, although the possibility of a slight northeast-southwest orientation exists in the males. It is also possible that these results, rather than indicating anything about the pattern of summer dispersal in the snakes, simply represent migration routes since there is obvious orientation of the snakes during movement to the dens in the fall. Nothing is known about summer habitat and home ranges of the Inwood snakes.

The best source of snakes in the summer of 1970 was the large marsh near Erinview. This area is similar to what Fitch (1965) describes as the most preferred habitat of the species in Kansas. The findings of Aleksiuk and Stewart (1971) from the few stomachs they examined indicate that anurans and occasional small fish are the predominant food items in the Interlake. Such a diet is compatible with the type of prey available in this marsh. The adjacent drier wooded areas also provide places to which the snakes can withdraw. No evidence was found, however, that snakes inhabited a similar, but smaller, marshy pond about one kilometre south-west of den one, even though food was abundant and adjacent dry woods available. The parameters important in the definition of "typical" summer habitat of this species in Manitoba have yet to be discovered.

The collection of snakes marked in the summer of 1970, although not based on any type of regular sampling, is useful in indicating something of the pattern of summer activity in these animals. With respect to the females, there is a fairly obvious division of activity into two phases. During the first phase, the feeding period, most of the females marked were found in the vicinity of the marsh and most were gravid. All of these were either basking on the railroad embankment or were under cover adjacent to it. Stewart (1965) implies that gravid females may bask more than other snakes as an aid to the development of the young, so that the artificial site afforded by the railroad is presumably attractive to them.

The second phase slightly overlaps the first and represents the beginnings of movement back to the hibernacula, most of the animals being found on roads. Very few gravid females were seen in this last part of the summer. It would appear, therefore, that the females produce their young at about the middle of August and usually before they begin moving back to the denning sites. Fitch (1965) refers to several records of birth in the species from the literature, citing late July or early August as the usual date in Kansas. He also implies that at more northern latitudes the young are born somewhat later in the season, making the suggested time of birth of these snakes in Manitoba reasonable.

In 1970, males were seen less commonly than females all summer and no two-phase activity pattern was discernible. Presumably, males and non-gravid females also inhabit the area of the marsh in summer but because of a lesser need to bask are more likely to be found in the marsh proper or the adjacent woods. The density of the cover in this habitat would make sighting and capture of these animals by hand difficult. In addition, males may have larger home ranges than do females. Fitch (1965) concludes that this is the case in Kansas. Males would therefore be more inclined to wander throughout the summer and be caught on roads. Data obtained by Seibert and Hagen (1947), however, for two species of *Thamnophis (radix* and *s. sirtalis)* and *Opheodrys* in Illinois indicate that the females wander more than the males and Carpenter's (1952a) study revealed no differences in movement between the sexes for three species of *Thamnophis* in Michigan.

Observations for the summer of 1970 indicate that movement back to the dens begins in mid-August but that snakes may not appear at the actual hibernacula until two weeks later. In contrast to the spring, there does not appear to be any differential activity of the sexes in the fall. Samples taken at the dens at this time may more accurately reflect population characteristics such as sex ratios than do samples taken upon emergence. For example, the ratio of 1.86♂♂:1♀ observed at den one in the fall of 1969 is much closer to the 2.05:1 value suggested by the Petersen population estimates than is the 15.4:1 figure obtained for the spring of 1970. Occasional wandering some distance from the den after initial arrival is indicated, particularly in the males, by trap-catches of animals caught earlier in the season at the hibernaculum proper. Twice as many animals, however, were first caught in the traps and then in the den, suggesting generally restricted movement at this time.

B. POPULATION COMPOSITION AND CHANGES

The samples taken at den one in the fall of 1970 were different in several respects from those in 1969-70, reflecting important population changes. The most obvious of these was the major decline in the size of the over-wintering population. In addition to this the sex ratio apparently shifted from nearly 2♂♂:1♀ to close to 1:1.

The size frequency distributions of the samples taken at den one in the two denning seasons (Figs. 10 and 11) provide indications of the types of changes in population size and structure which took place. For either sex, the distributions for the fall of 1969 and spring of 1970 show considerable agreement, but in each case the less abundant size groups are better represented in the fall samples. It was therefore decided to accept the size class breakdowns derived for the fall animals (Table I) as being representative of the population overwintering at den one in 1969-70. Measurements of snakes collected at den one in the fall of 1968 (Cook, unpubl. data) suggest a similar structure for that year.

The age of the youngest size class in these samples is questionable. According to Fitch (1965), 15-month old males in Kansas average about 450 millimetres in snout-vent length and females around 550 millimetres. These figures are in close agreement with my data, so that the youngest size group in each sex in the fall 1969 sample is considered to represent second year snakes (about 13-14 months old) with successive size classes representing successive years. There are fewer older groups than Fitch found. These older snakes, especially the females, seem to be generally larger in size than the corresponding animals from Fitch's analysis, although they are less abundant in terms of numbers of individuals. Carpenter's (1952b) seasonal size distributions are consistent with Fitch's observations but the growth curves presented by him are apparently in disagreement with his own data. They would place the 450 millimetre males and 550 millimetre females well into their third year of growth. This is an unlikely situation in the Interlake since the necessary intermediate sizes to represent second year snakes in the spring and fall are not known. Measurements of red-sided garter snakes collected by Cook (unpubl. data) at a den in Saskatchewan in the spring of 1961 do not show the presence of a group in the 270 - 330 millimetre size range, although obvious young-of-the-year are present in the 200 - 270 millimetre interval.

The distributions obtained for the fall of 1970 are radically different from those of the season before. In each sex, the youngest separable size group lies between the youngest and next older group from the previous season in length and consists, at least in part, of animals concluded to have been second year snakes in 1969-70. This suggests that the population decline was partly linked with a failure of recruitment or very low recruitment of second year snakes, possibly indicating a reproductive failure in 1969.

In 1969, although average summer temperatures were not particularly low, precipitation was well above normal. Fitch (1965) says that rainfall is often beneficial in that it allows improved survival of prey items such as frogs. Excessive rain, however, might be very harmful in that it would have a cooling effect on gravid females, since they are largely dependent on radiant energy for maintenance of body temperatures (Stewart, 1965). Since Zehr (1962) has shown that lower temperatures have a retarding effect on the development of embryos of *T. s. sirtalis*, this possibly explains the postulated failure in reproduction.

The shift in the sex ratio at den one between 1969-70 and 1970-71 remains unexplained. It is possibly related to the population decline. In addition, no explanation is available as to the bias towards males in the sex ratios.

Based on the size frequency data presented in this paper and observations at the dens, very few or no young-of-the-year of either sex occur at communal hibernacula in the area studied. Any young born at the earliest possible date in the season would not likely be more than about 270 - 280 millimetres long by autumn (Fitch, 1965; Cook, unpubl. data) and no snakes of this size have been seen at any of the large dens around Inwood. If the youngest snakes at the dens in the fall are 13 to 14 months of age, they would be about 21 months old upon emergence in the spring. According to Fitch (1965), this is the age when they usually first mate in Kansas. In other words, the snakes that den communally in the Interlake are virtually all of breeding age in the spring. I suggest that the main benefit of communal denning is that it confers a reproductive advantage on the population since it is very difficult for any potentially breeding female to go unmated in such a situation. As far as is known, this habit is unique to the adult members of this single species in Manitoba.

C. GROWTH

The annual growth of the red-sided garter snake in Manitoba appears to be completely confined to the three months of June, July, and August. Growth data for the species in other parts of its range are available in Burt (1928), Seibert and Hagen (1947), Carpenter (1952b), and Fitch (1965), the latter two being most comprehensive. Carpenter and Fitch agree that both sexes grow most rapidly during the first year and that females maintain a greater growth rate than males in subsequent years. Although no young snakes were involved in the current analysis, the significantly different intercepts obtained for the partial growth plots (Fig. 14) indicate a similar situation in Manitoba. Once this difference is attained, the growth rates of the two sexes decline with age at approximately the same rate (i.e. the slopes of the two lines are not significantly different). As is common to all such studies to date, however, there is great individual variation in the rate of growth.

A comparison of size frequency data with those of Fitch (1965) suggests that the snakes in Manitoba grow at least as much in a year as do those in Kansas. According to Fitch, the active period in Kansas extends from April to October inclusive. How much of this time is involved in major growth is not mentioned. Carpenter (1952b) states that significant growth is limited to the five months from May through September in Michigan (i.e. between the spring and fall denning phases). It would seem then that the garter snakes in the Interlake have considerably less time annually to make up the same amount of growth as members of the same species further south. It is possible that major growth in the study area is restricted to a period of time as short as two and one half months (early June to mid-August).

Growth in the summer of 1970 was apparently reduced relative to that suggested by the 1969-70 size frequency distributions. The failure of at least the second-year snakes of 1969-70 to reach their expected size in 1970-71, as shown by measurements of homing snakes, is likely tied in with population changes over the same period, but no interpretation is immediately forthcoming.

D. HOMING

Annual homing, or fidelity of individual snakes to specific dens, has apparently been demonstrated in this study. Considering the low levels of the den populations in the fall of 1970, recovery of previously marked animals was good. The one snake found away from its point of origin was caught relatively early in the season and may well have been stopped *en route*. Otherwise, homing success of the recaptured snakes was perfect.

In other species of snakes, Woodbury *et al* (1951) have demonstrated that most of the individuals in a mixed species den in Utah return year after year, although Hirth (1966) states that this is the only major den in the area. Preston's (1964) study suggested that *Crotalus viridis oreganus* in British Columbia tends to be den-specific even where several dens are fairly close together. Lang's (1969) work indicated that *Storeria occipitomaculata* in Minnesota has a strong tendency to return to the same hibernaculum, with very little interchange between dens occurring. In addition, he (pers. comm.) found that interchange was greatest between the most closely spaced dens. Fitch (1965), however, did not record a particularly high degree of fidelity of *T. sirtalis* to hibernacula in Kansas, but in this case the dens are closely spaced along limestone outcrops so that the high rate of exchange agrees with Lang's observations.

In this study, none of the dens examined were less than eight-tenths of a kilometre from any other known hibernaculum. This close grouping effect has therefore been undetected.

The simplest explanation of the survival value of homing is that it ensures that each individual will have a place to pass the winter. In many situations this is no doubt true. In the Inwood area, however, there does not seem to be a dearth of good hibernating sites and many sinks are apparently unused. Although these sinks may conceivably be lacking in some unknown quality vital to survival, this is not apparent on casual examination. Since unused sinks seem to remain unused for successive years, the habits of homing and communal denning may be linked. Together they would function to ensure a large breeding population every year at each den.

CONCLUSIONS

1. Adults of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake of Manitoba hibernate in communal dens which are most often in the form of sinks in the limestone bedrock. Populations using these hibernacula may number in the thousands, males being more abundant than females.
2. Populations at the dens in the fall of 1970 were lower than in the previous year, presumably because of a reproductive failure in 1969. Coincident with this, at least at one den, was an apparent shift toward a more balanced sex ratio. Growth of second year snakes from the winter of 1969-70 was less than expected during the summer of 1970.
3. The dormant phase of the life cycle is longer and the active season shorter in these populations than in the same species at lower latitudes. Emergence and mating are later and the onset of hibernation earlier. The young are in general born somewhat later in the year. Despite the brevity of the period of feeding, growth appears to be at least as great as in more southerly populations.
4. The period of dormancy is approximately from mid-October to mid-April. Upon emergence in the spring, mating

occurs, peaking about mid-May. Females mate once and then disperse to the summer habitat, whereas males mate several times prior to abandoning the den. Dispersal appears to be random in both sexes and takes place until early June.

5. The preferred summer habitat has not been precisely defined, but marshes seem to be important. Feeding and growth are restricted to June, July, and August. Growth is faster in females. The young are likely born in mid- to late August, with movement back to the dens beginning at about the same time.
6. Snakes appear at the dens around the beginning of September and movement to the hibernacula is virtually over by the end of the month. Mating may occasionally occur but is not common.
7. Annual homing to specific hibernacula occurs.
8. It is felt that communal denning may confer a reproductive advantage on this species in the Interlake and that fidelity to particular hibernacula in successive years acts to maintain adequate breeding populations at the dens.

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APPENDIX A: The Study Area

The following description of the landform and vegetation of the study area is based on the provincial government's summary of these features edited by Weir (1960) and on personal observations.

The area lies in what is known as the Manitoba Lowland and represents part of the floor of glacial Lake Agassiz of which the two large lakes, Manitoba and Winnipeg, and other smaller lakes, are remnants. The altitude is between 255 and 270 metres above sea level with local relief generally under 7.5 metres due to the nearly horizontal Palaeozoic bedrock. This results in poor drainage and the formation of large marshy areas around the shores of the existing lakes. Inwood lies at the southern end of a network of marshes which extends throughout the Interlake district.

The physiography is gently undulating till plain, specifically Interlake-Westlake Plain, with a micro-relief consisting of long ridges of a northwest-southeast orientation, the marshes mentioned above lying between these. The limy dolomite bedrock of Silurian age is characteristic of that along the whole central part of the Interlake. This bedrock is overlain by degraded Rendzina soil of shallow profile strewn with glacial drift surface deposits in the form of rocks of a predominantly limestone nature.

The vegetation is broadleaf forest, mainly aspen, on the ridges, but with some willow and burr oak and frequent meadowlike clearings of woodland grasses and forbs. Much of the land has now been given over to pasture and grainfields.

APPENDIX B: The Marking Method

The marking method employed in this study was that of clipping subcaudal scutes as described by Blanchard and Finster (1933), although a different coding system was followed and ventral scutes were also used.

The first two subcaudal scutes (Fig. B1) behind the anal plate on either side of the tail (i.e. R_1, R_2, L_1, L_2) were not used except as marks designating the location at which the animal was originally found. Additional location marks were obtained by clipping the right or left side of particular ventral scutes. A few examples of this type of identification tag are shown below:

0 - no location mark (den one),

R_2 - R_2 clipped (den two),

L_1 - L_1 clipped (den three),

V_{L3} - left side of V_3 clipped (traps around den one).

In addition to these, each snake was given an individual mark using subcaudals three to 20 on each side in differing combinations. The numbering scheme used was very simple:

L_3 to L_{11} - digits one to nine,

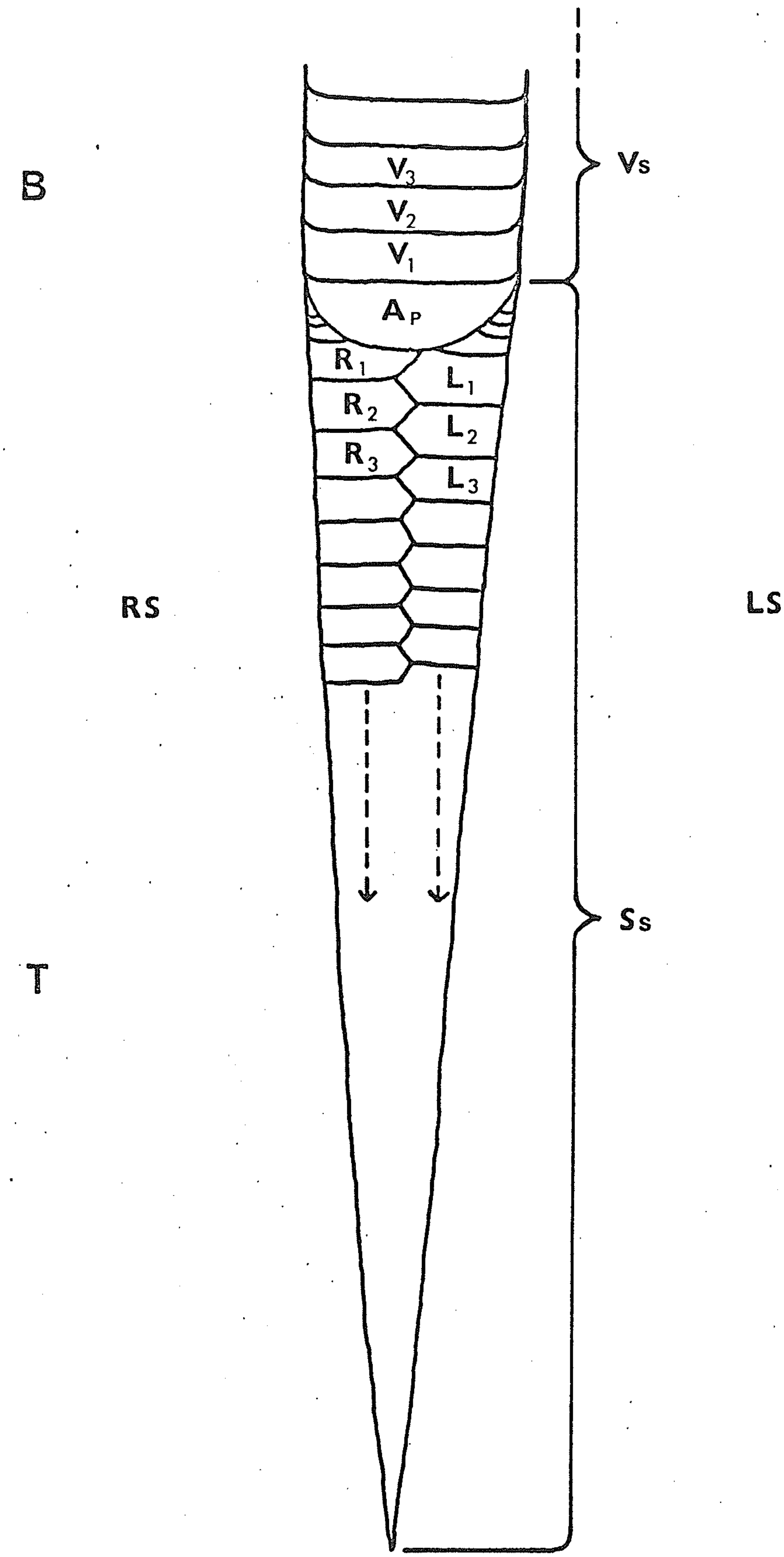
R_3 to R_{11} - tens from ten to ninety,

R_{12} to R_{20} - hundreds from one hundred to nine hundred,

L_{12} to L_{21} - thousands from one thousand to ten thousand.

An example of a fully marked snake would be 0 - $L_{12}R_{15}R_6L_3$, which represents the 1441st. snake marked at den one.

Fig. B1. Diagram of Ventral View of Posterior Portion of Body and Tail of Garter Snake. Note: for the sake of uniformity, L_1 is always considered to be the first complete subcaudal scute on the left side adjacent to and slightly below the first subcaudal on the right side. Ap = anal plate, B = body, LS = left side of snake, RS = right side of snake, Ss = subcaudal scutes, T = tail, Vs = ventral scutes.


B
RS
T
V3
V2
V1
AP
R1
R2
R3
L1
L2
L3
Vs
LS
Ss

This system allows the individual marking of a very large number of animals. Stumping of the tail, which is quite common, is not considered to be a serious hindrance to the usefulness of the method as experience suggests that only rarely does stumping occur anterior to the 25th. pair of subcaudal scutes.

A pair of corneal scissors was used in removing the scutes. The cut was made deep enough that the dermis below the scute was also removed to ensure a minimal rate of regeneration. In the case of the subcaudals, an attempt was made to cut away the entire scute, while in the ventrals a piece about as big as the largest subcaudal was removed from the far side. Bleeding from the wound was common, but healing was rapid. The major precautions that had to be taken were to make sure that the tail muscle, and sometimes the hemipenes in males, were not too severely cut and that the internal organs were not damaged in the clipping of ventral scutes.

To test for ill effects of the marking method and the wounds thus formed, 26 snakes (18 males, eight females) were marked on December 21, 1969 and kept in laboratory conditions during the winter of 1969-70. Of these, three males and two females were maintained in cages at room temperature while the remainder were held in a coldroom at 4^{o}C. to more closely approximate conditions in the field.

The test snakes appeared to show no abnormal behaviour when compared with several unmarked snakes kept under the same conditions. No differences were observed between the animals in the two temperature regimes with respect to healing of the wounds and scale regeneration. Covering of the wounds by scar tissue was apparently effected within two weeks in most cases. The snakes in the coldroom had all died by early March in 1970, presumably because the temperature was not low enough to keep them as inactive as was required since they were not fed during the test period. The marks, however, were still easily readable at the time of death. By the end of October, 1970, the last of the caged snakes had died, the marks still clearly visible. In no case was death judged to be a result of marking, unmarked snakes dying at about the same rate.

In the field, snakes marked late in the fall still looked freshly marked upon emergence in the spring. In active snakes, regeneration was rapid, but animals marked in the fall of 1969 were still identifiable at the same time the next year. Some regeneration had taken place, a small scute having replaced the scar tissue. In some of the snakes, regeneration was fairly well advanced and these individuals probably could not have been distinguished by an inexperienced person. In view of this, I do not feel that marks more than two years old are likely to be of continuing value in studies of this type.

This method of marking has been used by several workers and has generally been found to be satisfactory. Regeneration times present a problem. Conant (1948) states that the scars on a marked black rat snake (*Elaphe o. obsoleta*) in the Philadelphia Zoological Garden had regenerated so far after three years that identification was possible only after close examination. Fitch (1963), however, working with the same species, indicates that regeneration is relatively rapid in this snake and that marks may be intelligible for longer periods in other species. Also, Gilreath and Blanchard, cited by Conant (1948), reported that a recaptured ring-necked snake (*Diadophis punctatus edwardsii*) still had visible marks after 13 years. Records of this sort must be rare, however, and I contend that remarking of individuals recaptured after one year, as was experimented with in this study, will help to yield the maximum amount of useful information.

APPENDIX C: A Modification of the Jolly Estimator

The stochastic model developed by Jolly (1965) has formed the basis for one of the most general and flexible multiple-recapture population estimators to date. In addition, estimates of survival and recruitment into the population can be obtained and the model is applicable to situations where the population is heterogeneous, consisting of different classes of animals behaving in different ways. The main stipulation is that each animal caught must be marked in a unique manner or in such fashion that its complete capture history can be recorded. Otherwise, the assumptions underlying the use of this method, with the exception that recruitment of new animals is allowable, are similar to those of most other methods. They are:

1. All animals, marked and unmarked, are equally catchable.
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.

The procedures involved in the application of this model to various situations are discussed in Jolly's (1965) paper. The reader is referred to that work for definitions of most of the symbols used, but those directly relevant to this discussion are shown below:

n_i - the number of animals in the i^{th} sample, m_i of them having been previously marked,

s_i - the number of animals released from the i^{th} sample, or, the number of animals released at time i,

R_i - the number of the s_i animals that are caught subsequently,

Z_i - the number of animals marked before time i which are not caught in the i^{th} sample but are caught subsequently.

The general method requires that successive samples of animals be taken and that any new individuals be marked prior to release. The use of the Jolly estimator was not a primary objective of this study, but the sampling procedure employed was such that it could be implemented. It was thought that its application where possible might reveal something about patterns of activity of the snakes at hibernacula. Experience suggests that the Jolly estimator is of value only where the sampling intensity is high and where there are as few zeroes as possible in the table of recaptures, especially near the diagonal side. According to this, the method could only be applied with any sort of meaning to the male snakes at den number one in the spring of 1970.

Although no statistical tests were applied to the assumptions of the model, there is no reason to suspect that they were in any way violated except for number three. In this respect, it is important to note that the population being estimated is not the total number of males using the den but the number on the surface of the ground and active on a given day. Therefore, if any snakes tended to come out on alternate days or in some other such pattern, assumption number three would not be completely adhered to. This, however, is not likely to be an important source of error in this case.

The major problem involved in fitting the model to the data in question is caused by the fact that, as described in the Methods section, some samples were taken back to the laboratory and then released after subsequent samples were taken. The exact methods outlined by Jolly (1965) cannot be used since they require that the period of captivity be short relative to the time between samples, but this obstacle can be overcome by a slight modification. The fact that corresponding values of n_i and s_i are sometimes quite different, because of the sampling and release timing used, is not serious since Jolly (1965) states in a discussion of his model that there is no absolute necessity for n_i and s_i to be interdependent, only random. The difficulty lies in developing proper values of Z_i and R_i. To do this, it is first necessary to examine the relationship

$$\hat{M}_i - m_i / Z_i = s_i/R_i$$

which is used to estimate the number of marked animals, M_i, in the population at time i. In each fraction, note that the denominator represents a particular subset of the numerator. Keeping this in mind, the equation above can be validly worded as:

$$\frac{\text{no. of animals handled and marked before } i\text{, but not at } i}{\text{no. of } (\hat{M}_i - m_i) \text{ caught again after } i} \quad \frac{(\hat{M}_i - m_i)}{(Z_i)}$$

$$= \frac{\text{no. of animals released at } i}{\text{no of } s_i \text{ caught and released again after } i} \quad \frac{(s_i)}{(R_i)}$$

Obviously, from the above, Z_i is related to the capture date of a particular sample and is obtained in the normal fashion by dividing the recaptures according to the dates at which they were last captured (Tables CI and CII). The R_i, however, are related to the release dates of the samples and a separate table of recaptures (Table CIII) is necessary. The recaptures in this instance are placed opposite their release dates rather than their capture dates, and are divided according to the dates at which they were last released. Tables CI and CIII are identical for the last part of the spring season when samples were released on the same day as caught.

One additional category of animals is necessary before any estimates can be made. These, which I will call the M^R_i are animals that have been handled before time i but which are not released until after the i^{th} or a later sample is taken. The total number of marked animals in the population at the time of the i^{th} sample is therefore M_i (the number of marks at large) + M^R_i (the number of captive marks). When release is effected on the same day as capture, $M^R_i = 0$, but when, as in this case, the two are not always coincident, M^R_i

Table CI Table of n_{ij} Based on Capture Dates.

n_{ij} - number in i^{th} sample last captured in j^{th} sample (1 _ j _ i-1).

	Date		n_i																												
1	Apr.	26	13	1																											
2		27	1	0	2																										
3		29	42	2	0	3																									
4		30	3	0	0	0	4																								
5	May	1	66	1	1	6	0	5																							
6		2	98	1	0	11	3	1	6																						
7		3	25	0	0	1	0	0	0	7																					
8		5	39	1	0	1	0	5	8	0	8																				
9		6	101	2	0	8	0	16	19	3	1	9																			
10		7	211	0	0	4	0	18	24	9	11	54	10																		
11		8	76	0	0	1	0	1	3	0	3	5	44	11																	
12		9	8	0	0	0	0	0	0	0	1	1	1	0	12																
13		10	61	0	0	1	0	1	2	1	3	3	22	9	0	13															
14		11	34	0	0	1	0	1	1	1	1	2	7	3	0	4	14														
15		12	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	15													
16		16	63	0	0	0	0	1	2	1	0	0	6	3	0	3	3	0	16												
17		17	40	0	0	0	0	0	0	0	1	1	4	0	0	2	0	0	2	17											
18		18	51	0	0	0	0	0	0	0	0	0	2	3	0	1	1	0	2	2	18										
19		19	105	0	0	0	0	0	1	0	0	1	6	3	1	5	5	0	6	1	3	19									
20		22	47	0	0	0	0	0	0	0	0	1	0	1	0	3	0	0	1	2	3	4	20								
21		23	61	0	0	0	0	0	1	0	0	0	2	2	0	0	0	0	1	1	3	9	1	21							
22		28	53	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	2	0	2	3	4	3	22						
23	June	1	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	4	2	23					
24		2	37	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	1	0	1	1	4	24				
25		3	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	3	1	25			
26		4	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	3	1	1	26		
27		5	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	3	2	0	1	27	
28		6	25	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	2	3	1	4	2	28
$\Sigma = R_i$				7	1	34	3	44	60	15	23	68	96	25	3	20	9	0	15	7	12	22	9	10	5	15	7	2	5	2	

Table CII Table of a_{ij} Based on Capture Dates.

a_{ij} - number in i^{th} sample last caught in j_{th} sample or before.

	Date		n_i																												
1	Apr.	26	13	1																											
2		27	1	0	2																										
3		29	42	2	2	3																									
4		30	3	0	0	0	4																								
5	May	1	66	1	2	8	8	5																							
6		2	98	1	1	12	15	16	6																						
7		3	25	0	0	1	1	1	1	7																					
8		5	39	1	1	2	2	7	15	15	8																				
9		6	101	2	2	10	10	26	45	48	49	9																			
10		7	211	0	0	4	4	22	46	55	66	120	10																		
11		8	76	0	0	1	1	2	5	5	8	13	57	11																	
12		9	8	0	0	0	0	0	0	0	1	2	3	3	12																
13		10	61	0	0	1	1	2	4	5	8	11	33	42	42	13															
14		11	34	0	0	1	1	2	3	4	5	7	14	17	17	21	14														
15		12	4	0	0	0	0	0	0	0	0	0	0	0	0	1	1	15													
16		16	63	0	0	0	0	1	3	4	4	4	10	13	13	16	19	19	16												
17		17	40	0	0	0	0	0	0	0	1	2	6	6	6	8	8	8	10	17											
18		18	51	0	0	0	0	0	0	0	0	0	2	5	5	6	7	7	9	11	18										
19		19	105	0	0	0	0	0	1	1	1	2	8	11	12	17	22	22	28	29	32	19									
20		22	47	0	0	0	0	0	0	0	0	1	1	2	2	5	5	5	6	8	11	15	20								
21		23	61	0	0	0	0	0	1	1	1	1	3	5	5	5	5	5	6	7	10	19	20	21							
22		28	53	0	0	0	0	0	0	0	1	1	2	2	3	4	4	4	6	6	8	11	15	18	22						
23	June	1	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	4	8	10	23					
24		2	37	0	0	0	0	0	0	0	1	1	2	2	3	3	3	3	3	4	5	6	6	7	8	12	24				
25		3	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	5	6	25			
26		4	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	3	6	7	8	26		
27		5	30	0	00	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	3	6	8	8	9	27	
28		6	25	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	2	3	3	5	8	9	13	15	28
Σ	$= Z_{i+1}$			7	6	40	35	63	123	123	97	45	84	106	67	66	74	55	60	56	35	42	31	23	18	21	22	16	12		

will sometimes be greater than zero. In other words, $\hat{M}_i + M^R_i - m_i / Z_i = s_i / R_i$ and $\hat{M}_i = \frac{s_i Z_i}{R_i} + m_i - M^R_i$.

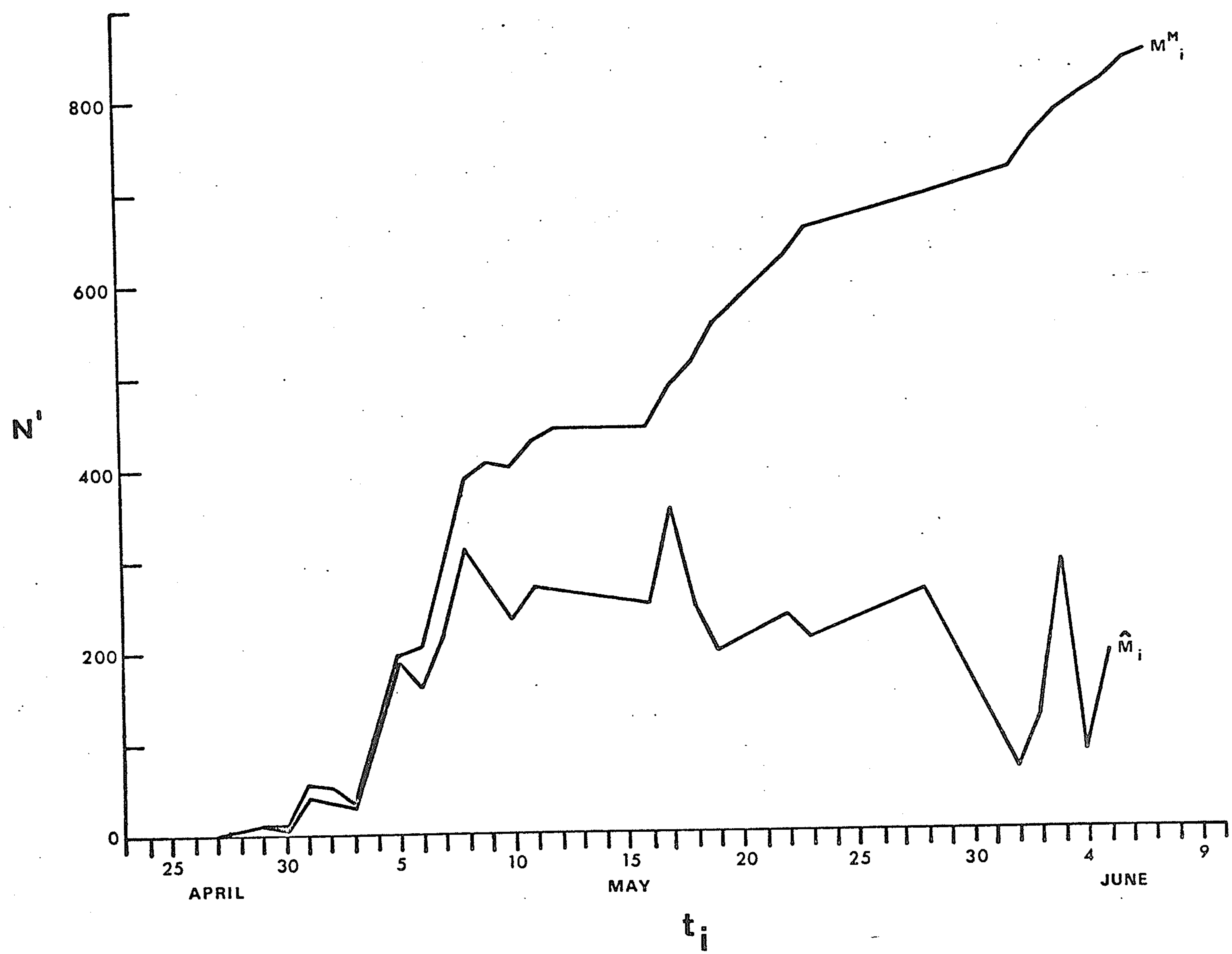
The number of free snakes in the population at time i, N_i, can then be estimated as in the Petersen index (Robson and Regier, 1968) from the relationship, $\hat{N}_i = \hat{M}_i / \hat{\alpha}_i$ where $\hat{\alpha}_i = m_i / n_i$. The remainder of the procedure is as outlined in Jolly (1965).

The justification for using this method to calculate $\hat{M}_i$, and hence $\hat{N}_i$, is in part demonstrated in Figure C1. M^M_i represents the total possible number of spring marks available each sampling day based on dates and numbers of releases and known deaths around the den. Note that the curve of M^M_i rises irregularly throughout the sampling season as more animals are marked. The curve for $\hat{M}_i$ follows that of M^M_i closely during the first part of the season but levels off as the weather gets warmer and snakes begin to leave the den and then finally declines as would be expected. No other method of calculation of R_i, Z_i, and $\hat{M}_i$ makes sense either biologically or mathematically.

Obviously, it would be much better to sample and release animals on the same day. What has been made here is an attempt to show how data not specifically collected for the purpose of using the Jolly estimator can be made sense of. It is important to note that what is being measured in this case is

Fig. C1. Graph Comparing Daily Values of M^{M}_{i} and $\hat{M}_{i}$ for Male Snakes at Den One in Spring 1970.

t_i = date of sample, N' = number of snakes.



N'
800
600
400
200
0
M^M_i
$\hat{M}_i$
25
30
5
10
15
20
25
30
4
9
APRIL
MAY
JUNE
t_i

not the total population size of the den, but the number present and active in the den at time i. By adding $\hat{N}_i$ and M^R_i for any specific i, a better estimate of total active population at time i might be arrived at. There is no reason to believe, however, that the M^R_i would necessarily constitute a part of the population at time i had they been released on the same day as they were caught. On only one day, May 3, would the addition of M^R_i make a significant difference in the estimated population size, and even this would not result in any important change in the overall picture. It is felt, therefore, that in these circumstances, the presentation of the calculated $\hat{N}_i$ as shown is the more sensible course.

APPENDIX D: The Trap

The live-traps used in this study were patterned after the design of Fitch (1951). Each consisted of a cylinder about 30.5 centimetres long by 12 centimetres in diameter constructed from a single piece of .6 centimetre hardware cloth. A funnel made from a similar sized piece of the same material was inserted into each end of the cylinder.

These traps were different in some respects from those described by Fitch. The margins of the cylinders were not turned inwards as he suggested, the funnels being held in place by hook-shaped pins of stout wire, and cellulose acetate doors were not used in the small openings of the funnels. In addition, a 2.7 metre long drift fence was used as a lead into each funnel. These were constructed of window screening about 20 centimetres in height, one end being tapered so that it could be fitted right into the funnel.

These traps were tested and modified during the spring of 1970. Five of them were set up in the area around den one on May 15. They were found to be very effective in catching snakes. As many as 14 at a time were caught near the height of the breeding season in the traps closest to the den. Not all of the new snakes captured were given a mark nor were all recaptures recorded, but from May 16 through June 5, 32 new snakes (29 males, three females) were marked and 35 previously marked male snakes, including one which was trapped at least twice, were handled.

Certain precautions were taken in setting up the traps. It was found necessary to cover the trap proper with branches or some other sort of shading to help weight down the structure and to provide protection from the sun for captured animals. Each trap was usually located well away from active ant mounds as the ants attacked and chewed up any imprisoned snakes. In some instances in the fall of 1970, where the union of funnel and cylinder was imperfect, trapped snakes were found that had managed to get part of the way out via the seam and had then got stuck. These animals were generally badly injured and had to be killed. Such incidents pointed out the need for a tight seal in this part of the trap.

On a few occasions in the fall of 1970, snakes were observed as they followed the drift fences leading into various traps. In one case, the individual was allowed to go right into the trap. The apparatus seemed to be working as expected. No instances of snakes climbing over drift fences or traps were noted and both components were so close to the ground that it is unlikely that many animals went under them. Only once was a snake seen to find its way out of a trap via a funnel.

Besides snakes, other animals such as various insects, rodents, shrews, and small birds were sometimes caught.

APPENDIX E: The Summer Sampling Program

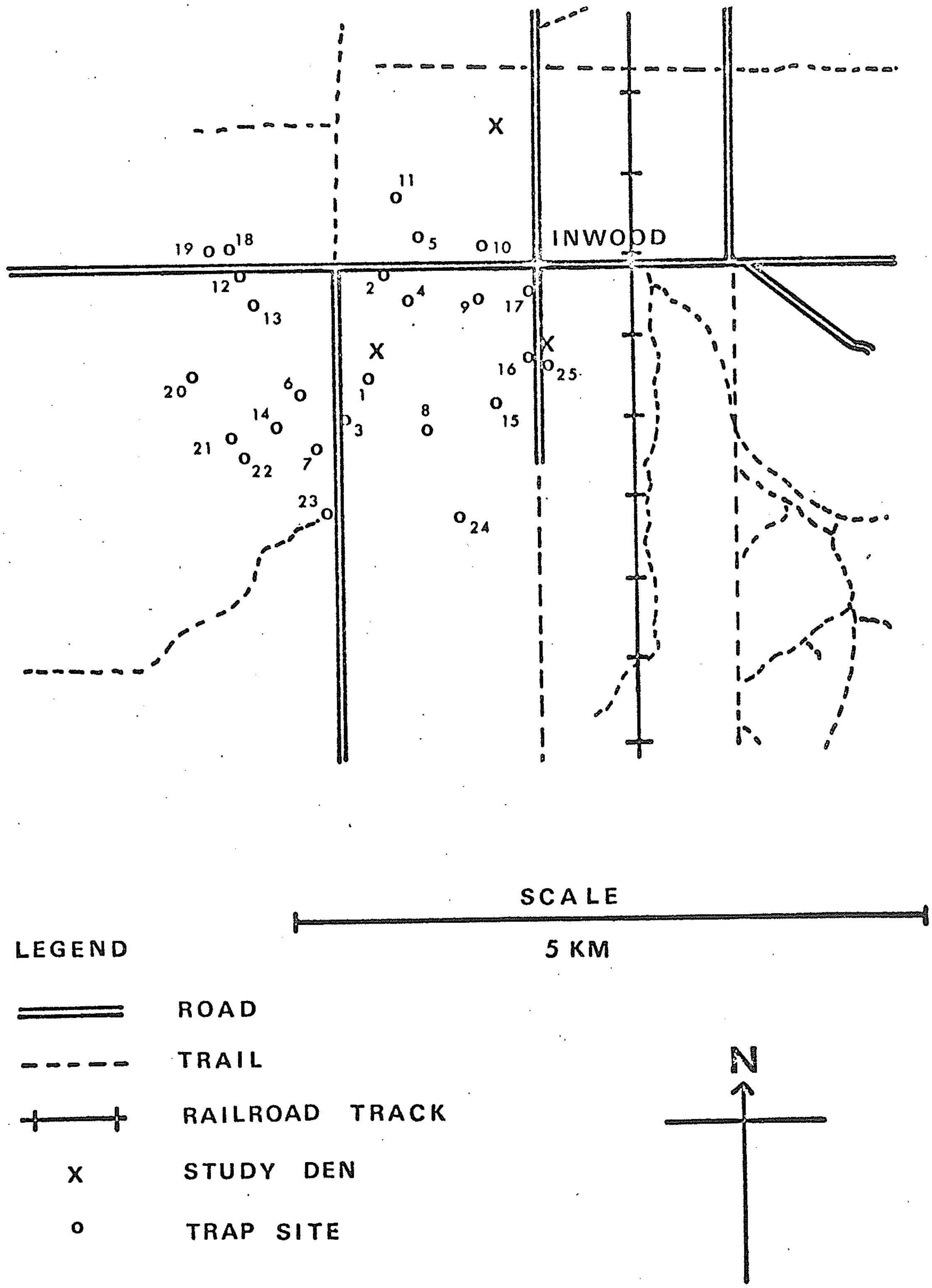
In an attempt to determine the manner of dispersal of snakes from den one and the type of summer habitat preferred, an arbitrary summer sampling plan was established in 1970. Twenty-five of the traps described in Appendix D were distributed over a circular area 1.6 kilometres in radius and centred at den one. All major habitat types in the vicinity of Inwood were included in this scheme. It was desired to set up the traps in a random fashion while allowing for a good coverage of the area at the same time. The following procedure was therefore adopted.

The large circle was broken up into a small central circle about one-third of a kilometre in radius and four concentric rings approximately one-third of a kilometre wide each. The central circle was divided into four quarters and the rings partitioned into similar sized units. The exact positioning of the compartments of any one ring relative to those of the next and the order of numbering them were determined by the use of a random numbers table. Each of these small units was subsequently divided into nine equal-sized subunits.

This subdivision resulted in a central ring of four compartments and outer rings of 12, 20, 28, and 36 compartments, the particular number being proportional to the area involved. It was previously decided that the 25 traps should also be apportioned in relation to the area of each ring so that, beginning with the central circle, one, three, five, seven, and nine traps respectively were used. Having arrived at a definite number of traps per ring, I then randomly distributed them among the numbered compartments, and, within compartments, among the nine numbered subunits. The result was the arrangement shown in Figure EI. A description of each of the trap sites is shown in Table EI.

The traps were checked frequently but irregularly until August 3 and very occasionally thereafter until fall. The plan did not result in the capture of a single snake although insects, shrews, rodents, and even sparrows were caught on occasion.

Fig. E1. Map of Inwood Area Showing Locations of 25 Traps Used in Summer 1970.


INWOOD
11
5
10
19
18
12
2
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17
13
16
25
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6
1
14
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15
21
22
7
23
24
SCALE
5 KM
LEGEND
ROAD
TRAIL
RAILROAD TRACK
X
STUDY DEN
o
TRAP SITE
N

Table EI. Brief Qualitative Descriptions of Trap Sites Used in Summer of 1970.

1. in cherry and poplar scrub island beside a rockpile near edge of a grainfield.
2. on edge of a small island of cherry and some poplar in a grassy field.
3. in open poplar forest near a small marshy pond.
4. in fairly open poplar woods with much cherry in understory.
5. in fairly dense poplar woods with oak, cherry, raspberry, and dogwood understory.
6. in very open poplar woods near edge of an open field.
7. in fairly open poplar woods with many clearings.
8. at edge of a relatively dense poplar stand with much cherry in understory and rockpiles and a large open grainfield immediately to north.
9. in low, fairly open poplar scrub with some tall trees; more trees to west, an open field about 67 metres to north, and dense, low poplar scrub about 67 metres to south.
10. in open, grassy, rock-covered field.
11. in open field with young secondary growth of poplar and piles of slash timber.
12. in poplar scrub area of small trees.

(continued)

Table EI. Brief Qualitative Descriptions of Trap Sites Used in Summer of 1970. (Continued)

13. in very open area of tall poplar trees with understory of secondary poplar growth.
14. at edge of poplar stand just outside border of a dense willow thicket at margin of a large marshy pond.
15. in area of low scrubby poplar (a few trees) interspersed with occasional grassy openings.
16. at edge of fairly open oak-poplar scrub.
17. in roadside ditch with mossy floor; young willows and poplars on either side and fairly open poplar stands at each side of road; cattle grazing area to west.
18. in open poplar forest with some oak and undergrowth of cherry and poplar.
19. in open poplar forest with some oak and mainly hazel understory.
20. in dense poplar woods with heavy undergrowth; many clearings and patches of burr oak in vicinity.
21. in open grassy field interspersed with willow bushes to west of a large marshy pond.
22. in damp, sedge-covered area to south of a large marshy pond; some bushes interspersed throughout vicinity.
23. in fairly open poplar scrub forest (small trees) with sparse undergrowth of forbs, especially raspberry.

(continued)

Table EI. Brief Qualitative Descriptions of Trap Sites Used in Summer of 1970. (Concluded)

24. in open poplar forest with thin undergrowth of various forbs.

25. in dense poplar thicket.

APPENDIX F: Sample Records

Table FI Sample Record -- Den One (Spring 1970)

Capture Date	Release Date	Both Sexes n_i	Both Sexes $(n_i - m_i)$	Both Sexes m_i	Males n_i	Males $(n_i - m_i)$	Males m_i	Females n_i	Females $(n_i - m_i)$	Females m_i
Apr. 26	Apr. 26	15	15 (1)	0	12	12	0	3	3 (1)	0
	Apr. 29	1	1	0	1	0	0	0	0	0
Apr. 27	Apr. 29	3	3	0	1	1	0	2	2	0
Apr. 29	Apr. 30	45	42 (5)	3	42	40 (4)	2	3	2 (1)	1
Apr. 30	May 1	5	5 (3)	0	3	3 (2)	0	2	2 (1)	0
May 1	May 1	1	0	1	1	0	1	0	0	0
	May 3	68	61 (13)	7	65	58 (13)	7	3	3	0
May 2	May 3	100	84 (6)	16	98	82 (6)	16	2	2	0
May 3	May 5	25	24 (3)	1	25	24 (3)	1	0	0	0
May 5	May 5	1	1	0	1	1	0	0	0	0
	May 6	40	25 (4)	15	38	23 (4)	15	2	2	0
May 6	May 6	102	53 (5)	49	101	52 (5)	49	1	1	0
May 7	May 7	215	95 (11)	120	211	91 (11)	120	4	4	0
May 8	May 8	80	23 (2)	57	76	19 (2)	57	4	4	0
May 9	May 10	10	7 (1)	3	8	5 (1)	3	2	2	0
May 10	May 10	62	20 (3)	42	61	19 (2)	42	1	1 (1)	0
May 11	May 11	34	13 (2)	21	34	13 (2)	21	0	0	0
May 12	May 12	6	5	1	4	3	1	2	2	0
May 16	May 16	69	50 (4)	19	63	44 (2)	19	6	6 (2)	0
May 17	May 17	43	33 (4)	10	40	30 (3)	10	3	3 (1)	0
May 18	May 18	52	41 (5)	11	51	40 (5)	11	1	1	0
May 19	May 19	109	77 (11)	32	105	73 (11)	32	4	4	0

(continued)

Table FI Sample Record -- Den One (Spring 1970) (concluded)

Capture Date	Release Date	Both Sexes n_i	Both Sexes $(n_i - m_i)$	Both Sexes m_i	Males n_i	Males $(n_i - m_i)$	Males m_i	Females n_i	Females $(n_i - m_i)$	Females m_i
May 22	May 22	51	36 (2)	15	47	32 (2)	15	4	4	0
May 23	May 23	65	45 (1)	20	61	41 (1)	20	4	4	0
May 28	May 28	55	37 (4)	18	53	35 (4)	18	2	2	0
June 1	June 1	46	36 (5)	10	45	A35 (5)	10	1	1	0
June 2	June 2	37	25 (3)	12	37	25 (3)	12	0	0	0
June 3	June 3	26	20 (3)	6	26	B20 (3)	6	0	0	0
June 4	June 4	24	16 (2)	8	23	15 (2)	8	1	1	0
June 5	June 5	30	21 (1)	9	30	21 (1)	9	0	0	0
June 6	June 6	25	10 (2)	15	25	10 (2)	15	0	0	0
	Σ	1445	924 (106)	521	1338	868 (99)	520	57	56 (7)	1

n_i = total sample size (dead animals not included).

m_i = numbers of recaptures (from same sampling season) in sample.

$(n_i - m_i)$ = number of new animals in sample (numbers in parentheses indicate animals originally marked in autumn 1969, but first caught in spring 1970 on day i).

A two snakes caught in traps prior to day i.
B one snake caught in trap prior to day i.

Table FII Sample Record -- Den Two (Spring 1970)

Capture Date	Release Date	Both Sexes n_i	Both Sexes $(n_i - m_i)$	Both Sexes m_i	Males n_i	Males $(n_i - m_i)$	Males m_i	Females n_i	Females $(n_i - m_i)$	Females m_i
May 7	May 7	27	27 (1)	0	27	27 (1)	0	0	0	0
May 18	May 18	15	15	0	15	15	0	0	0	0
May 19	May 19	16	13	3	14	11	3	2	2	0
May 22	May 22	23	19	4	22	18	4	1	1	0
June 2	June 2	24	21	3	24	21	3	0	0	0
June 3	June 3	29	28	1	29	28	1	0	0	0
June 6	June 6	36	32	4	36	32	4	0	0	0
	Σ	170	155 (1)	15	167	152 (1)	15	3	3	0

Symbols as in Table FI.

Table FIII Sample Record -- Den Three (Spring 1970)

Capture Date	Release Date	Both Sexes n_i	Both Sexes $(n_i - m_i)$	Both Sexes m_i	Males n_i	Males $(n_i - m_i)$	Males m_i	Females n_i	Females $(n_i - m_i)$	Females n_i
May 7	May 7	3	3	0	3	3	0	0	0	0
May 18	May 18	9	9	0	8	8	0	1	1	0
May 22	May 22	10	10	0	10	10	0	0	0	0
June 2	June 2	41	40	1	39	38	1	2	2	0
June 3	June 3	9	6	3	9	6	3	0	0	0
June 6	June 6	21	12	9	21	12	9	0	0	0
	Σ	93	80	13	90	77	13	3	3	0

Symbols as in Table FI.

Table FIV Record of Snakes Marked in Inwood Area, but Away from Dens (Spring 1970).

Capture Date	Release Date	Both Sexes n_i	Both Sexes $(n_i - m_i)$	Both Sexes m_i	Males n_i	Males $(n_i - m_i)$	Males m_i	Females n_i	Females $(n_i - m_i)$	Females m_i
May 6	May 6	1	1	0	0	0	0	1	1	0
May 7	May 7	17	17	0	5	5	0	12	12	0
May 10	May 10	1	1	0	0	0	0	1	1	0
May 16	May 16	2	2	0	1	1	0	1	1	0
May 17	May 17	1	1	0	1	1	0	0	0	0
May 18	May 18	7	7	0	1	1	0	6	6	0
May 19	May 19	1	1	0	0	0	0	1	1	0
May 22	May 22	1	1	0	0	0	0	1	1	0
May 23	May 23	2	2	0	1	1	0	1	1	0
June 2	June 2	1	1	0	1	1	0	0	0	0
June 5	June 5	1	1	0	1	1	0	0	0	0
	Σ	35	35	0	11	11	0	24	24	0

Symbols as in Table FI.

Table FV Record of Snakes Marked (Summer 1970)

Date	Railroad Track and Vicinity Males	Railroad Track and Vicinity Females	Roads Males	Roads Females	Dens Males	Dens Females
June 26			1	0	2	0
July 7			2	0		
July 22	0	19 (19)				
July 27	0	1	0	1		
Aug. 2	0	5 (4)				
Aug. 5	0	3 (3)				
Aug. 6	2	2 (2)	1	0		
Aug. 13	0	2 (2)	1	0		
Aug. 19	1	1 (1)	1	4 (2)		
Aug. 22			2	9		
Aug. 23			0	2		
Aug. 24			0	2		
Σ	3	33 (31)	8	18 (2)	2	0

Numbers in parentheses indicate numbers obviously gravid.

Recaptures:
- o marked on July 22 - recaptured on August 2
- o marked on August 5 - recaptured on August 6

all along railroad tracks.

Recoveries of dead animals:
- o marked on July 22 - recovered on July 27
- o marked on July 22 - recovered on August 2

all along railroad tracks.

Table FVI Sample Record -- Den One (Fall 1969)

Capture Date	Release Date	Both Sexes n_i	Both Sexes (n_i-m_i)	Both Sexes m_i	Males n_i	Males (n_i-m_i)	Males m_i	Females n_i	Females (n_i-m_i)	Females m_i
Sept. 10	Sept. 10	26	26	0	15	15	0	11	11	0
Sept. 11	Sept. 11	34	33	1	19	19	0	15	14	1
	Sept. 12	22	21	1	16	15	1	6	6	0
Sept. 12	Sept. 12	96	92	4	67	64	3	29	28	1
Sept. 13	Sept 13	73	68	5	54	51	3	19	17	2
Sept. 14	Sept. 14	157	149	8	103	99	4	54	50	4
Sept. 15	Sept. 15	53	45	8	28	23	5	25	22	3
	Sept. 16	3	3	0	1	1	0	2	2	0
Sept. 16	Sept. 16	38	32	6	17	12	5	21	20	1
	Sept. 18	37	37	0	23	23	0	14	14	0
Sept. 17	Sept. 18	46	38	8	28	23	5	18	15	3
Sept. 18	Sept. 19	78	69	9	42	38	A4	36	31	A5
Sept. 19	Sept. 20	71	66	5	41	39	A2	30	B27	3
Sept. 20	Sept. 21	77	62	15	48	37	11	29	25	4
	Sept. 22	47	47	0	40	40	0	7	7	0
Sept. 21	Sept. 22	14	13	1	10	9	1	4	4	0
Sept. 23	Sept. 25	16	14	2	6	5	1	10	9	1
Sept. 25	Sept. 26	1	1	0	1	1	0	0	0	0
Sept. 27	Sept. 28	11	8	3	10	7	3	1	1	0
Sept. 28	Sept. 29	30	25	5	16	15	1	14	10	4
Sept. 29	Sept. 30	12	11	1	8	8	0	4	3	1

(continued)

Table FVI Sample Record -- Den One (Fall 1969) (concluded)

Capture Date	Release Date	Both Sexes n_i	Both Sexes (n_i-m_i)	Both Sexes m_i	Males n_i	Males (n_i-m_i)	Males m_i	Females n_i	Females (n_i-m_i)	Females m_i
Oct. 4	Oct. 5	14	7	7	13	6	7	1	1	0
Oct. 5	Oct. 6	36	21	15	26	15	11	10	6	4
Oct. 6	Oct. 8	16	14	2	10	9	1	6	5	1
Oct. 8	Oct. 9	20	11	9	17	10	7	3	1	2
Oct. 9	Oct. 14	103	61	42	91	52	39	12	9	3
Oct. 11	Oct. 14	3	1	2	2	0	2	1	1	0
Oct. 12	Oct. 12	1	0	1	1	0	1	0	0	0
Oct. 14	Oct. 15	1	1	0	0	0	0	1	1	0
Oct. 18	Oct. 19	9	1	8	9	1	8	0	0	0
Oct. 19	Oct. 20	15	4	11	12	2	10	3	2	1
Oct. 20	Oct. 20	1	0	1	1	0	1	0	0	0
	Σ	1161	981	180	775	639	136	386	342	44

Symbols as in Table FI.

A one animal killed.

B one animal kept in live lab. collection.

Table FVII Sample Record -- Den Two (Fall 1969)

Capture Date	Release Date	Both Sexes n_i	Both Sexes (n_i-m_i)	Both Sexes m_i	Males n_i	Males (n_i-m_i)	Males m_i	Females n_i	Females (n_i-m_i)	Females m_i
Sept. 17	Sept. 20	8	8	0	4	4	0	4	4	0
Sept. 20	Sept. 21	11	11	0	4	4	0	7	7	0
Sept. 23	Sept. 23	43	43	0	25	25	0	18	18	0
Oct. 5	Oct. 6	2	1	1	1	1	0	1	0	1
Oct. 8	Oct. 11	1	1	0	1	1	0	0	0	0
	Σ	65	64	1	35	35	0	30	29	1

Symbols as in Table FI.

Table FVIII Sample Record (Combined Hand and Trap Samples) -- Den One (Fall 1970).

Capture Date	Release Date	Both Sexes n_i	Both Sexes (n_i-m_i)	Both Sexes m_i	Males n_i	Males (n_i-m_i)	Males m_i	Females n_i	Females (n_i-m_i)	Females m_i
Aug. 31	Aug. 31	5	5 (1)	0	1	1 (1)	0	4	4	0
Sept. 2	Sept. 2	2	2	0	2	2	0	0	0	0
Sept. 4	Sept. 4	10	10	0	5	5	0	5	5	0
Sept. 5	Sept. 5	10	10	0	3	3	0	7	7	0
Sept. 6	Sept. 6	16	16 (1)	0	5	5 (1)	0	11	11	0
Sept. 8	Sept. 8	23	23 (4)	0	10	10 (4)	0	13	13	0
Sept. 10	Sept. 10	31	31 (4)	0	12	12 (4)	0	19	19	0
Sept. 14	Sept. 14	21	20 (6)	1	9	8 (5)	1	12	12 (1)	0
Sept. 15	Sept. 15	13	13 (2)	0	7	7 (1)	0	6	6 (1)	0
Sept. 17	Sept. 17	35	31 (3)	4	16	14 (3)	2	19	17	2
Sept. 18	Sept. 18	19	17 (1)	2	6	5 (1)	1	13	12	1
Sept. 19	Sept. 19	53	51 (9)	2	29	29 (8)	0	24	22 (1)	2
Sept. 22	Sept. 22	14	13 (2)	1	7	6 (2)	1	7	7	0
Sept. 26	Sept. 26	12	12 (3)	0	11	11 (2)	0	1	1 (1)	0
Sept. 28	Sept. 28	48	40 (6)	8	31	23 (4)	8	17	17 (2)	0
Sept. 29	Sept. 29	13	12 (1)	1	8	7 (1)	1	5	5	0
Oct. 1	Oct. 1	49	47 (6)	2	33	31 (4)	2	16	16 (2)	0
Oct. 5	Oct. 5	6	5	1	3	2	1	3	3	0

(continued)

Table FVIII Sample Record (Combined Hand and Trap Samples) -- Den One (Fall 1970) (Concluded)

Capture Date	Release Date	Both Sexes n_i	Both Sexes (n_i-m_i)	Both Sexes m_i	Males n_i	Males (n_i-m_i)	Males m_i	Females n_i	Females (n_i-m_i)	Females m_i
Oct. 6	Oct. 6	4	4	0	2	2	0	2	2	0
Oct. 15	Oct. 15	15	9 (2)	6	12	6 (2)	6	3	[A]3	0
	Oct. 20	1	1	0	0	0	0	1	[B]1	0
Oct. 16	Oct. 16	13	3	10	11	2	9	2	1	1
Oct. 22	Oct. 22	6	3	3	4	3	1	2	0	2
	Σ	419	378 (51)	41	227	194 (43)	33	192	184 (8)	8

Numbers in parentheses indicate returning snakes (i.e. from fall 1969 and spring 1970); other symbols as in Table FI.

[A] one gravid female kept in collection.

[B] one gravid female released with 24 young.

Table FIX Trap Sample Record -- Den One (Fall 1970); dead animals not included.

Capture Date	Release Date	Both Sexes n_i	Both Sexes (n_i-m_i)	Both Sexes m_i	Males n_i	Males (n_i-m_i)	Males m_i	Females n_i	Females (n_i-m_i)	Females m_i
Aug. 31	Aug. 31	5	5 (1)	0	1	1 (1)	0	4	4	0
Sept. 2	Sept. 2	2	2	0	2	2	0	0	0	0
Sept. 4	Sept. 4	2	2	0	1	1	0	1	^{A}1	0
Sept. 5	Sept. 5	10	10	0	3	3	0	7	7	0
Sept. 6	Sept. 6	16	16 (1)	0	5	5 (1)	0	11	11	0
Sept. 8	Sept. 8	8	8 (2)	0	3	3 (2)	0	5	5	0
Sept. 10	Sept. 10	11	11 (2)	0	4	4 (2)	0	7	7	0
Sept. 14	Sept. 14	4	4 (2)	0	3	3 (2)	0	1	1	0
Sept. 15	Sept. 15	13	13 (2)	0	7	7 (1)	0	6	6 (1)	0
Sept. 17	Sept. 17	5	5	1	2	2	0	4	3	1
Sept. 18	Sept. 18	19	19 (2)	0	6	^{C}6 (^{C}2)	0	13	^{C}13	0
Sept. 19	Sept. 19	28	28 (2)	0	14	14 (2)	0	14	14	0
Sept. 22	Sept. 22	14	14 (2)	0	7	^{C}7 (2)	0	7	7	0
Sept. 26	Sept. 26	12	12 (3)	0	11	11 (2)	0	1	1 (1)	0
Sept. 28	Sept. 28	12	12	0	8	8	0	4	4	0
Sept. 29	Sept. 29	13	13 (1)	0	8	^{C}8 (1)	0	5	5	0
Oct. 1	Oct. 1	49	49 (7)	0	33	^{D}33 (^{C}5)	0	16	^{B}16 (2)	0
Oct. 5	Oct. 5	6	6	0	3	^{C}3	0	3	3	0
Oct. 6	Oct. 6	1	1	0	1	1	0	0	0	0
Oct. 22	Oct. 22	1	1	0	1	1	0	0	0	0
	Σ	232	231 (27)	1	123	123 (23)	0	109	108 (4)	1

(continued)

Table FIX Trap Sample Record -- Den One (Fall 1970); dead animals not included.

(concluded)

A one snake caught at den proper on same day.

B one snake caught in two different traps on same day.

C one snake previously caught at den proper.

D two snakes previously caught at den proper.

Numbers in parentheses indicate returning snakes (i.e. from fall 1969 and spring 1970); other symbols as in Table FI.

NOTE: capture date in this instance is meant to represent the date on which the traps were checked. In some cases the animals were almost certainly caught prior to this date.

Table FX Hand Sample Record -- Den One (Fall 1970)

Capture Date	Release Date	Both Sexes n_i	Both Sexes (n_i-m_i)	Both Sexes m_i	Males n_i	Males (n_i-m_i)	Males m_i	Females n_i	Females (n_i-m_i)	Females m_i
Sept. 4	Sept. 4	9	9	0	4	4	0	5	[C]5	0
Sept. 8	Sept. 8	15	15 (2)	0	7	7 (2)	0	8	8	0
Sept. 10	Sept. 10	20	20 (2)	0	8	8 (2)	0	12	12	0
Sept. 14	Sept. 14	17	16 (4)	1	6	5 (3)	1	11	11 (1)	0
Sept. 17	Sept. 17	29	28 (4)	1	14	[D]13 ([D]4)	1	15	[D]15	0
Sept. 19	Sept. 19	25	24 (7)	1	15	15 (6)	0	10	[D]9 (1)	1
Sept. 28	Sept. 28	36	33 (7)	3	23	[F]20 ([D]5)	3	13	13 (2)	0
Oct. 6	Oct. 6	3	3	0	1	1	0	2	2	0
Oct. 15	Oct. 15	15	14 (2)	1	12	[AF]11 (2)	1	3	3	0
	Oct. 20	1	1	0	0	0	0	1	[B]1	0
Oct. 16	Oct. 16	13	5 (1)	8	11	[E]4 (1)	7	2	1	1
Oct. 22	Oct. 22	5	2	3	3	2	1	2	0	2
	Σ	188	170 (29)	18	104	90 (25)	14	84	80 (4)	4

Numbers in parentheses indicate returning snakes (i.e. from fall 1969 and spring 1970); other symbols as in Table FI.

A one gravid female kept in collection.

B one gravid female released with 24 young.

C one snake caught in a trap on same day.

D one snake previously caught in a trap.

E two snakes previously caught in traps.

F five snakes previously caught in traps.

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