

The Effect of Harvesting on Denning  
Populations of the Red-sided Garter Snake  
(Thamnophis sirtalis parietalis)  
in the Interlake Region of Manitoba

by

Stuart Macmillan

A practicum submitted in partial fulfillment of  
the requirements for the degree of  
Master of Natural Resources Management

Natural Resources Institute  
University of Manitoba

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## ABSTRACT

The effects of harvesting on the denning populations of red-sided garter snakes (Thamnophis sirtalis parietalis) in Manitoba's Interlake region were evaluated through a mark-recapture study. Additionally, the potential for re-establishing populations at extirpated dens was examined through a transplantation experiment.

The annual harvest rapidly reduces population size through reduction of the sub-adult component of the population and degradation of den structure. Den populations can withstand little more than 5 years of harvest pressure before reduction to non-harvestable numbers. Extirpated dens show little sign of repopulation decades after disturbance, and transplantation as a means of repopulation may not be feasible. Unexploited dens become subject to harvest pressure as entry to the industry increases, resulting in a decrease in the number of harvestable dens.

Although the red-sided garter snake is not endangered as a species, the phenomenon of large denning aggregations in Manitoba may be. Current management practices are inappropriate as the character of the industry has changed in the last decade due to an increase in the number of harvesters. As a result, the number of large denning populations has de-

creased. Red-sided garter snakes may not be economically exploitable and manageable, for the cost of an effective management scheme may greatly exceed the economic return of continued exploitation. It is recommended that the harvest be terminated immediately, the remaining large denning aggregations be assigned threatened status, and research be initiated to evaluate the status of the remaining large denning aggregations.

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The administrative staff at the Natural Resources Institute, Mrs. Emilie Novotny and Ms. Christine Hofer, deserve special thanks for their cheerful support and professionalism.

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I dedicate this research to my parents, who instilled within me a sense of their own appreciation for the intrinsic value of our natural heritage.

## CONTENTS

|                            |     |
|----------------------------|-----|
| ABSTRACT . . . . .         | i   |
| ACKNOWLEDGEMENTS . . . . . | iii |

| <u>Chapter</u>                               | <u>page</u> |
|----------------------------------------------|-------------|
| I. INTRODUCTION . . . . .                    | 1           |
| Background Statement . . . . .               | 1           |
| Problem Statement . . . . .                  | 10          |
| Research Objectives . . . . .                | 10          |
| Definitions . . . . .                        | 11          |
| II. REVIEW OF RELATED LITERATURE . . . . .   | 13          |
| Introduction . . . . .                       | 13          |
| Review of Methods . . . . .                  | 15          |
| Capture Methods . . . . .                    | 15          |
| Marking Methods . . . . .                    | 16          |
| Uses of Mark-Recapture Data . . . . .        | 18          |
| Summary . . . . .                            | 22          |
| III. MATERIALS AND METHODS . . . . .         | 24          |
| The Study Area . . . . .                     | 24          |
| Data Collection . . . . .                    | 26          |
| Treatment of Objectives . . . . .            | 26          |
| IV. RESULTS . . . . .                        | 30          |
| Sampling Program . . . . .                   | 30          |
| Population Estimates . . . . .               | 31          |
| Population Composition . . . . .             | 33          |
| Sex Ratios . . . . .                         | 38          |
| Homing and Wandering . . . . .               | 40          |
| Growth . . . . .                             | 44          |
| Harvest . . . . .                            | 47          |
| Transplantation . . . . .                    | 47          |
| V. DISCUSSION . . . . .                      | 51          |
| Population Estimates . . . . .               | 51          |
| Fall . . . . .                               | 51          |
| Spring . . . . .                             | 52          |
| Growth, Reproduction, and Maturity . . . . . | 52          |
| Population Composition . . . . .             | 56          |

|                                               |             |
|-----------------------------------------------|-------------|
| Sex Ratios . . . . .                          | 58          |
| Den Fidelity and Wandering . . . . .          | 60          |
| Transplantation . . . . .                     | 62          |
| Effect of Harvest . . . . .                   | 65          |
| VI. CONCLUSIONS AND RECOMMENDATIONS . . . . . | 67          |
| Conclusions . . . . .                         | 67          |
| Recommendations . . . . .                     | 70          |
| LITERATURE CITED . . . . .                    | 71          |
| PERSONAL COMMUNICATIONS . . . . .             | 76          |
| <u>Appendix</u>                               | <u>page</u> |
| A. MARKING METHOD . . . . .                   | 77          |
| B. SAMPLE RECORDS . . . . .                   | 80          |

## LIST OF FIGURES

| FIGURE                                                                                              | PAGE |
|-----------------------------------------------------------------------------------------------------|------|
| 1. Red-sided Garter Snake Range .....                                                               | 2    |
| 2. Red-sided Garter Snake Harvest<br>History, Manitoba (1972-1986) .....                            | 5    |
| 3. Red-sided Garter Snake Harvest<br>History, Manitoba (1972-1986):<br>Harvest per Unit Efort ..... | 8    |
| 4. The Study Area .....                                                                             | 25   |
| 5. Population Composition - Den 1<br>Spring 1985 & 1986 .....                                       | 34   |
| 6. Population Composition - Den 1<br>Fall 1985 & 1986 .....                                         | 35   |
| 7. Population Composition - Den 2<br>Spring 1985 & 1986 .....                                       | 36   |
| 8. Population Composition - Den 2<br>Fall 1985 & 1986 .....                                         | 37   |
| 9. Walford Plot of Growth, 1985 and 1986<br>(male data only) .....                                  | 46   |
| A-1. The Marking Method .....                                                                       | 79   |

# LIST OF TABLES

| TABLE                                                                                                | PAGE  |
|------------------------------------------------------------------------------------------------------|-------|
| 1. History of the Frog and Snake<br>Harvest in Manitoba, 1972-1986 .....                             | 7     |
| 2. Jolly Population Estimates<br>Den 2 Spring 1986 .....                                             | 32    |
| 3. Population Estimates - Males and<br>Females Fall 1985 .....                                       | 32    |
| 4. Proportion of Population Male:<br>1985-1986 .....                                                 | 39    |
| 5. Degree of Homing Exhibited in<br>the Study Area (Dens 1 and 2<br>Combined - method 1) .....       | 41    |
| 6. Degree of Wandering Exhibited<br>by Populations in Fall - 1985<br>and 1986 .....                  | 42    |
| 7. Size Frequency Distribution of<br>Wandering Snakes in the Study<br>Area - Males (1985-1986) ..... | 42    |
| 8. Mean Growth by Snout-Vent Length<br>Group - Dens 1 & 2 Combined (Males Only) .....                | 45    |
| 9. Sample Record - Den 2<br>(Fall 1985 - Harvest) .....                                              | 48    |
| 10. Transplantation Sampling Data<br>Den 4 - 1986 .....                                              | 50    |
| B-1 to B-8. Sample Records - Dens 1 & 2<br>Spring and Fall (1985 & 1986) .....                       | 81-88 |

## Chapter I

### INTRODUCTION

The semi-annual accumulations of red-sided garter snakes (Thamnophis sirtalis parietalis) at hibernacula in Manitoba's Interlake region (Figure 1) are renowned internationally as unique natural phenomena representing one of the worlds' largest concentrations of reptiles. There is concern that the annual harvest of the snakes may be leading to depletion of many major dens, however little information is available upon which to evaluate these concerns. Consequently, this research was initiated by the Wildlife Branch, Manitoba Department of Natural Resources, to provide information regarding effects of the annual harvest on denning populations of red-sided garter snakes in Manitoba.

#### 1.1 BACKGROUND STATEMENT

Red-sided garter snakes range throughout southern Manitoba and are the most common species of snake in the province. They tend to frequent moist, marshy areas during summer, but over-winter communally at dens which allow the snakes to enter the ground and hibernate beneath the frost line. Interlake dens usually occur in limestone sinks, however they may also occur in rock cracks and shallow depressions.

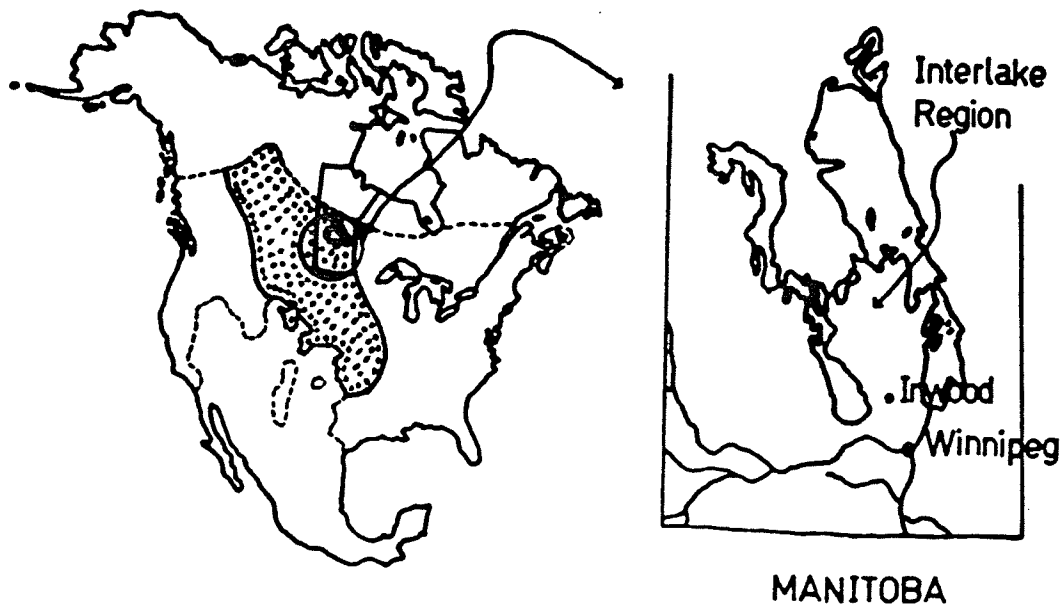


Figure 1: Red-sided Garter Snake Range

(broken line indicates range of *T. sirtalis*,  
 shaded area shows range of subspecies *parietalis*,  
 inset of study area: after Gregory 1977:12)

In southwestern Manitoba, major dens occur in the shale outcrops of creek and river valleys, while in the Duck Mountains they may be found in limestone bedrock exposed on the steeper side hills.

Large aggregations of snakes occur at den sites in spring and fall, making the populations particularly vulnerable to environmental and human pressures at these times. Market demand for garter snakes prompted exploitation of Manitoba's snake dens through development of the annual harvest industry which currently supplies snakes to American biological supply warehouses.

The structure of the industry is such that pickers, usually composed of family groups, harvest snakes from dens and sell them to a smaller contingent of buyers. The buyers purchase the snakes from pickers for approximately 40-50 cents each (regardless of size or sex), and then sell the snakes to American biological supply warehouses with a profit margin sometimes as low as the monetary exchange rate. The biological supply warehouses market the snakes to individuals or pet stores for \$5.00 to \$10.00 each, depending on sex and reproductive state (gravid females fetch a higher price) (Lemberger pers. comm. 1986). Pet stores commonly sell the snakes (sometimes back to Manitobans) for upwards of \$20.00 each.

Snake harvesting was unregulated until 1972, when provincial legislation established a one month fall picking season (picking is prohibited in spring to prevent disruption of mating activities) and required pickers and buyers to purchase amphibian and reptile collecting permits (Koonz pers. comm.). The legislation thus provided for annual monitoring of the harvest (Figure 2). In 1975, due to a perceived reduction in snake numbers, the season was reduced to one week but, under pressure from increasing numbers of pickers and buyers, the season was extended to two weeks in 1982.

Management of the red-sided garter snake in Manitoba is currently at a primitive level, with the harvest restricted only by season length. Commercial harvesters may operate anywhere (except in the Narcisse Wildlife Management Area) through two active weeks of the fall aggregation period. Although it is illegal to possess snakes before the season begins, many pickers begin harvesting at least a week early (Hallam, pers. comm. 1987). There are no limits on number, sex, or size of snakes harvested.

Snake pickers have one week's grace at the end of the season to sell their snakes to buyers. Once dealers in the U.S. find their markets saturated, however, they no longer purchase snakes from buyers; and buyers stop purchasing from pickers. Harvesting beyond market demand is not unknown, as dealers and pickers were left with surplus snakes in fall 1985.

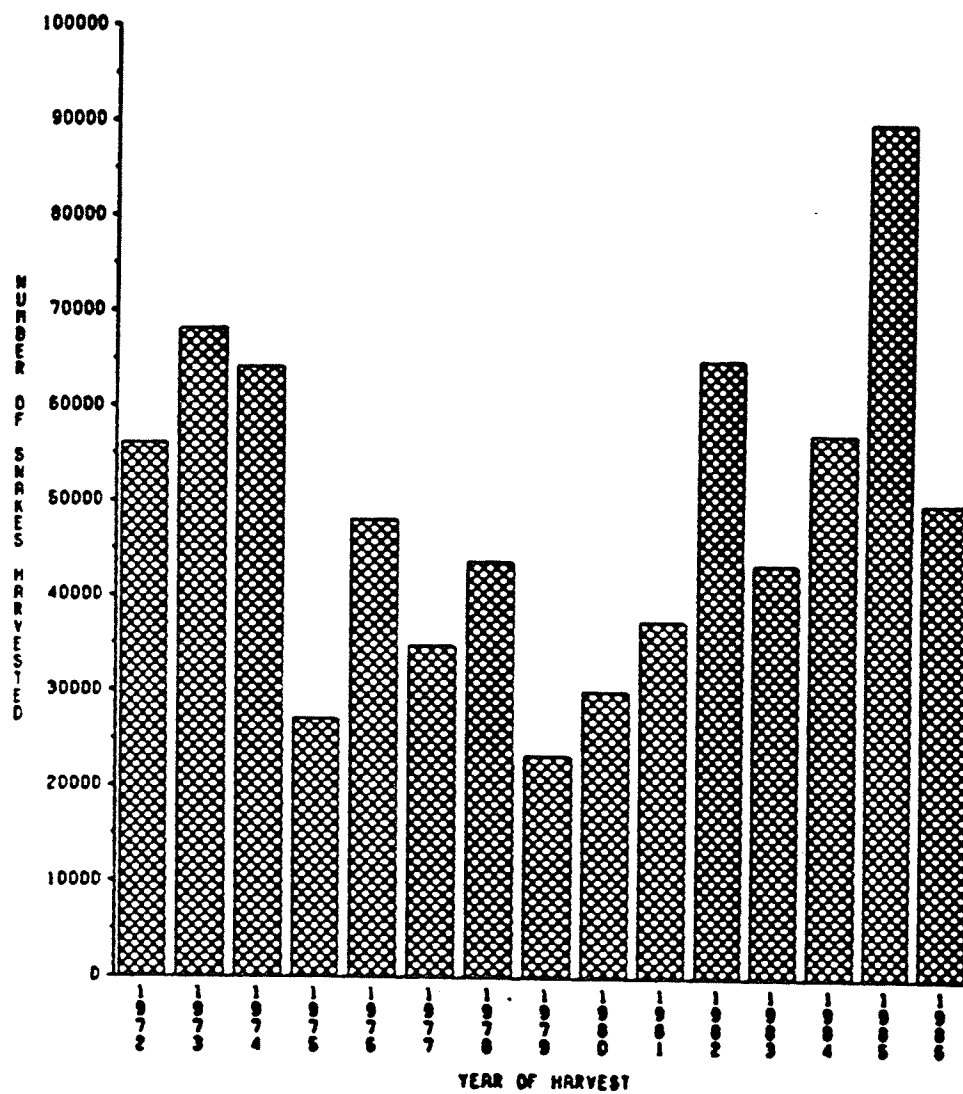


Figure 2: Red-sided Garter Snake Harvest History,  
Manitoba (1972 - 1986)

Surplus snakes released alive and not suffering vertebral damage or internal injury from handling may survive if released near hibernacula. In fall 1985, 5000 such snakes were reportedly released at a limestone quarry near Inwood, Manitoba, which had previously supported few snakes. Very few snakes were found in spring 1986 at the quarry. Mortality may have been extensive due to unfamiliarity with the environment and subsequent freezing at the onset of winter. The true magnitude of the harvest, then, is likely greater than that reflected by export permits.

The character of the harvest industry has changed in the last decade as entry into the industry has increased (Table 1). In the early 1970's, few people were picking snakes in Manitoba, evidenced by the drop in sales of amphibian-reptile collecting permits when the frog population declined in the middle of the decade. These individuals spread their harvest effort amongst several dens. Today, however, large groups of harvesters concentrate on single dens for entire days, thereby increasing harvest effort at individual den locations. At the same time, harvest per unit effort has decreased dramatically, indicating a reduction in the number of snakes available for harvest (Figure 3).

Apparently, dens can sustain little more than five continuous years of intense harvesting pressure. Dens near Gypsumville, Lundar, and Ericksdale have previously supported large numbers of snakes but currently, after seven or eight years of harvesting, support too few snakes to warrant

Table 1: History of Frog and Snake Harvest in Manitoba  
1972 - 1986

| Year | Licence Sales |            | Harvest            |                | Snake Harvest/<br>Unit Effort* |
|------|---------------|------------|--------------------|----------------|--------------------------------|
|      | Family        | Individual | Snakes<br>(indiv.) | Frogs<br>(lbs) |                                |
| 1972 | 78            | 204        | 56,000             | 109,796        | 14,000                         |
| 1973 | 119           | 42         | 68,000             | 26,272         | 17,000                         |
| 1974 | 117           | 58         | 64,000             | 43,868         | 16,000                         |
| 1975 | 169           | 37         | 27,000             | 12,980         | 27,000                         |
| 1976 | 7             | 13         | 48,000             | 0              | 48,000                         |
| 1977 | 1             | 1          | 34,745             | 0              | 34,745                         |
| 1978 | 8             | 2          | 43,667             | 0              | 8,734                          |
| 1979 | 10            | 4          | 23,220             | 0              | 3,318                          |
| 1980 | 1             | 2          | 30,000             | 0              | 20,000                         |
| 1981 | 12            | 14         | 37,409             | 0              | 2,878                          |
| 1982 | 17            | 20         | 64,992             | 0              | 1,757                          |
| 1983 | 41            | 31         | 43,440             | 2,911          | 790                            |
| 1984 | 55            | 55         | 57,245             | 13,058         | 774                            |
| 1985 | 77            | 72         | 90,080             | 30,162         | 969                            |
| 1986 | 52            | 28         | 52,000             | ?              | 847                            |

\*Effort = total licences sold for snake harvest; harvest adjusted to a two week season.  
(licences sold for snake harvest assumed to be 2 before 1977; half of yearly increase in licence sales after 1982 is assumed entry into snake industry).

Sources: Doug Tuck - Supervisor, Wildlife and Fisheries Licencing,  
Manitoba Department of Natural Resources.  
Catherine Hummelt - Wildlife Analyst, Wildlife Branch,  
Manitoba Department of Natural Resources.

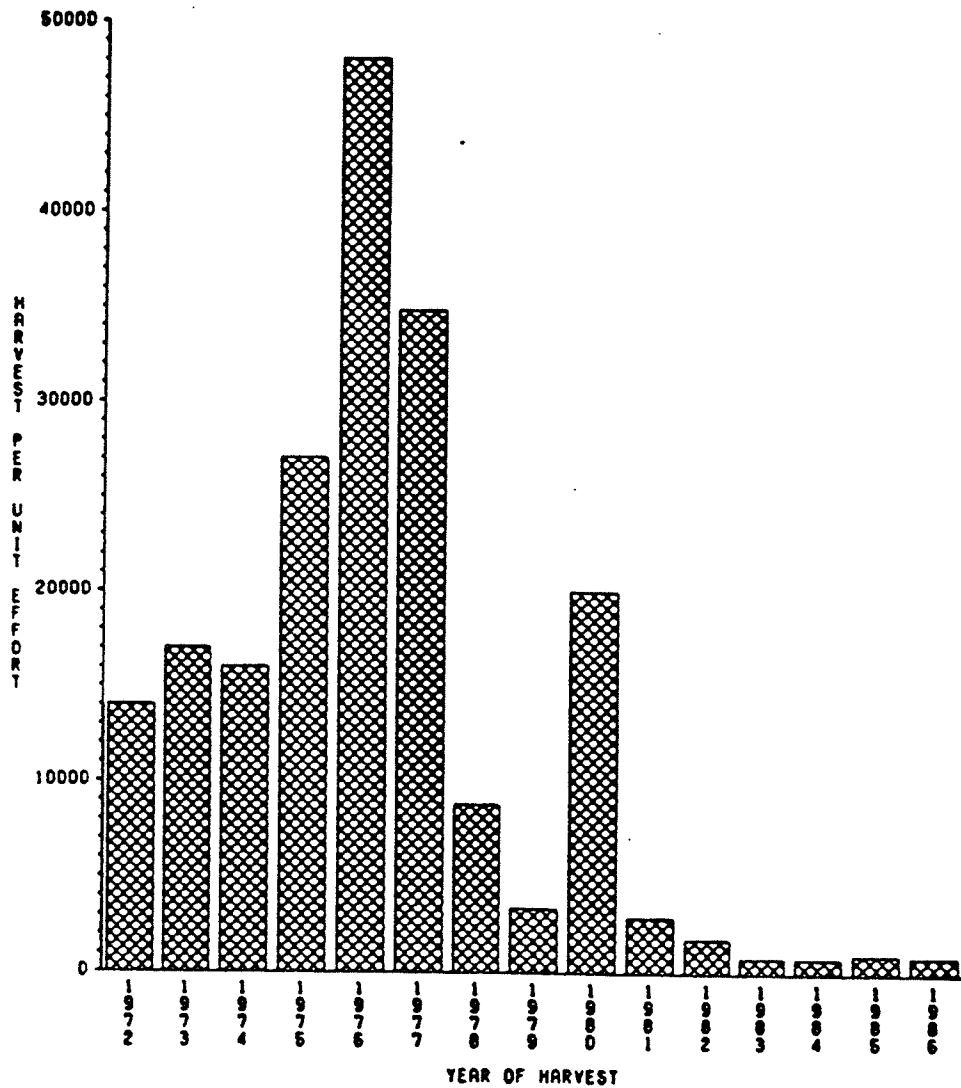


Figure 3: Red-sided Garter Snake Harvest History, Manitoba (1972-1986): Harvest per Unit Effort

attention from pickers (E. Sutherland pers. comm.). Unexploited dens at Highrock Lake, Manitoba, were subjected to harvesting pressure for the first time in 1986 (H.C. Paul, pers. comm.). These developments reflect a trend that is becoming increasingly apparent. Large dens are picked intensively for a few years until reduced to low numbers, and new dens are then continually searched for. Pickers are becoming highly efficient at finding unexploited dens as accessibility to back country is increased via access roads and all-terrain vehicles. As a result, exploitation of remaining dens is proceeding at an increasingly rapid pace.

The goal of the management program is to maintain the annual harvest without harming the integrity of the species. However, the establishment of an effective management program is impaired by three major hindrances to decision making:

1. unpredictable availability of snakes during the picking season (due to weather, etc.);
2. management staff ignorance of dens and snake numbers; and
3. a poor understanding of snake numbers, survival rates, and general biology (Koonz, pers. comm.).

Thus, effects of the harvest and management program are unknown.

## 1.2 PROBLEM STATEMENT

The character of the red-sided garter snake harvest in Manitoba has changed in the last decade with increased entry into the industry. Individual dens are subjected to an intense harvesting pressure each fall to satisfy market demand for the snakes. The effect of this pressure on the populations is unknown, although previously occupied dens that had been subjected to years of harvesting no longer support viable populations. It is hypothesized that intense annual harvesting pressure can, over a period of years, reduce individual den populations to levels such that they cannot maintain themselves. However, quantitative data upon which this hypothesis can be tested and upon which management decisions can be based are not available. It is this lack of data that is currently hampering efforts to effectively preserve the large garter snake denning aggregations of Manitoba's Interlake region.

## 1.3 RESEARCH OBJECTIVES

The purpose of this study was to determine the effect of harvesting on the denning population of red-sided garter snakes in Manitoba's Interlake region, with the greater intention of providing information useful in developing a management scheme for the denning areas.

The objectives of this research were:

1. to obtain a population estimate of 2 adjacent dens near Broad Valley, Manitoba;
2. to determine the effects of harvesting on one den population;
3. to initiate a transplant experiment by relocating harvested snakes;
4. to provide baseline information regarding snake numbers, homing, and growth rates; and
5. to make recommendations useful in the development of a red-sided garter snake management strategy.

#### 1.4 DEFINITIONS

The following is a list of terms, and their definitions, used throughout the body of this paper. The definitions apply in all cases excepting those for which the context dictates otherwise (i.e. use of 'season').

Den Fidelity: the degree to which snakes tend to return to the same den each year.

Harvest: the collection of snakes for commercial sale.

Harvester/Picker: an individual who, through purchase of an amphibian-reptile collecting permit, gains the right to collect snakes during the harvest season.

Scutes: lateral plates located on the ventral surface of the snake; clipped to assign a number to snakes allowing re-identification.

Season: refers to the study season (spring 1985,1986; fall 1985,1986).

Wandering: movement of snakes in an area separate from the immediate den environment in fall after migration from summer range; may bring snakes into vicinity of one or more other dens.

## Chapter II

### REVIEW OF RELATED LITERATURE

#### 2.1 INTRODUCTION

Studies on the demographics of snake populations are not prevalent in the literature due to the secretive habits of snake species and their generally low population densities (Parker 1976). However, the large aggregations of red-sided garter snakes in Manitoba's Interlake region provide the opportunity to gather a substantial amount of information about this species.

Gregory (1971, 1974, 1977) conducted the first extensive field study of Manitoba's red-sided garter snake population in the late 1960's and early 1970's. His studies documented times of emergence, mating activities, summer range movements, diet, reproduction, and onset of hibernation, leading to the development of a life history strategy for the population. Later studies in the mid-1970's focussed on specific life-history parameters of the population, such as regulation and physiology of hibernation and reproduction (Aleksiuk and Stewart 1971; Aleksiuk and Gregory 1974), patterns of spring emergence (Gregory 1974), and summer range movements and feeding (Gregory and Stewart 1975). Recent

studies have focussed largely on the hormonal and behavioural regulation of mating behaviour and reproduction in the species (Garstka and Crews 1981; Crews et al. 1984; Friedman and Crews 1985; Garstka et al. 1985; Mason and Crews 1985).

Few studies have focussed specifically on the management of snake populations. In an Ohio State wildlife area, game management practices proved to have a deleterious effect on an endangered non-game species, the prairie garter snake (Thamnophis radix radix) (Dalrymple and Reichenbach 1984). Galligan and Dunson (1979) assessed the status of the timber rattlesnake (Crotalus h. horridus) in Pennsylvania and the impact of commercial exploitation. Many disturbing parallels in the course of events regarding the status of this snake and that of the red-sided garter snake in Manitoba can be found. Higher prices, increased accessibility, and publicity have combined to interest more people in hunting the timber rattlesnake. As a result, many dens have been exterminated and the search for unexploited dens has intensified. Dens can tolerate only five to seven years of hunting. Some of the snakes collected for fairs are released at a later date, but the snakes are maltreated and it is doubtful whether they can survive after release. The timber rattlesnake is considered endangered by the Society for the Study of Amphibians and Reptiles and is rapidly approaching extinction in Pennsylvania (Galligan and Dunson 1979).

## 2.2 REVIEW OF METHODS

Although information in the literature about the specific effects of removal of snakes on denning populations is scarce, a number of studies have investigated population parameters of various snake populations. The research method usually employed in these types of studies is mark and recapture. The following discussion will focus on data collection through mark and recapture. I will examine methods of catching and marking the animals, and discuss the range of information obtainable.

### 2.2.1 Capture Methods

Methods of capturing snakes include erecting fences around dens, placing funnel traps in or near dens, and using a combination of fences and funnel traps.

Fencing a den to catch snakes is most effective when the den mouth is small and discrete (only one entrance into and one exit out of the den) (Brown and Parker 1984). Hirth et al. (1968) used a wire screen to surround the den mouth and captured snakes as they emerged in spring. Parker and Brown (1973) achieved a 95% catch rate by completely encircling a hibernaculum with an aluminum screen wire fence whose base was buried 10-15 cm in sandy soil surrounding the den.

A simplified type of funnel trap suitable for catching reptiles was devised by Fitch (1951). It consists of a wire

mesh cylinder with a funnel shaped opening at each end. Upon entry, a clear plastic acetate door closes behind the animal, preventing escape. These traps can be used without drift fences, but are usually placed where objects like logs, walls, or rock outcrops serve to funnel the animals to the traps. However, the samples may be biased if varied terrain prevents uniform distribution of the traps. Fraker (1970) used funnel traps to capture watersnakes (Natrix sipedon sipedon) but found the method to be relatively inefficient.

The effectiveness of funnel traps is increased when used in conjunction with drift fences. The fences act as a preliminary funnel, directing snakes to the funnel traps instead of to the den opening. Presumably, the combined use of funnel traps and drift fences would ameliorate any bias that may be introduced by varied terrain. Clark (1974) used this method in a study of the western ribbon snake (Thamnophis proximus).

Snakes may also be captured by hand. This method is most efficient when population densities are high and localized and when the species is non-venomous.

#### 2.2.2 Marking Methods

Several methods of marking snakes have been reported in the literature. However, most are variations of three basic methods:

1. caudal scute clipping;
2. ventral scute clipping; and
3. combined caudal and ventral scute clipping.

Blanchard and Finster (1933) developed the first reported method of permanently marking snakes. The method involved snipping a piece from a caudal scute and recording the number of the scute thus marked. A more or less permanent scar is left after healing if most of the scute is removed. The development of this method revolutionized the study of snake populations, in that large numbers of snakes could be processed quickly and efficiently. Previously, complete scute counts and measurements for each snake had to be made before the snake could be recognized upon recapture, making the process slow and laborious (Carpenter 1952). The Blanchard-Finster method has been used successfully to mark thousands of red-sided garter snakes in Manitoba (Gregory and Stewart 1975; Gregory 1977) and has been used in several other studies (Blanchard et al. 1979; Galligan and Dunson 1979).

Other authors have taken the idea of scute clipping and have applied it to the ventral scutes instead of the caudal scutes. Ventral scutes are larger and therefore easier to clip, and data are not lost if tail breakage occurs (Carpenter 1952; Brown and Parker 1976). One modification of the Blanchard-Finster method involves clipping both caudal and ventral scales (Clark 1974), while other methods operate by clipping only ventral scales (Woodbury 1951). Brown and

Parker (1976) simplified the marking scheme by numbering ventrals from the anal scute such that whole number designations resulted rather than the left and right numbered designators as per the Blanchard-Finster method. By removing half of a given ventral with each clip, a combination of only 1-3 clipped scutes enables the labelling of 989 individuals before advancing to the 1000's.

Other more unusual methods of marking snakes include tattooing and branding. Tattooing allows a number to be placed directly on any light-colored surface (such as the chin) but requires a portable battery-operated tattooing outfit suitable for the field (Woodbury 1951). By using a finely-drawn metal wire heated to high temperatures, the scales can be branded in a pattern similar to that of the Blanchard-Finster method (Clark 1971). Under field conditions, this method may be less convenient, but apparently increased survivorship may warrant its use.

### 2.2.3 Uses of Mark-Recapture Data

Mark and recapture data can be used to gain an abundance of information about populations, including:

1. population estimates;
2. population composition;
3. life history data; and
4. growth data (Woodbury 1951).

Several methods of estimating the population size of a species from mark and recapture data are reported in the literature. However, four critical assumptions are inherent in all methods reported:

1. equal catchability (all animals have the same chance of being caught in any sample);
2. all animals are subject to the same survival rate;
3. all animals that leave the population do so permanently; and
4. marked animals disperse completely in the population before the next sample is taken.

A common method of population estimation is the Petersen Index. A known number of marked animals are released in the study area and a second sample is taken after the appropriate time has elapsed. Only the total number of marked snakes must be known, so unique marks are not required for each individual. The population estimate is then calculated from the ratio of marked to unmarked snakes in the second sample (Krebs 1978). Confidence intervals can be calculated for the estimate. The Petersen Index involves an additional assumption that there is no recruitment between samples. Gregory (1977) calculated the number of snakes entering the den each fall by considering the fall as the marking period and the subsequent spring as the recapture period, thereby satisfying the assumption of no recruitment as the time between samples was a time of hibernation.

The Schnabel method of population estimation is a modification of the Petersen Index as captures and recaptures are accumulated (Smith 1980). The marked pool of animals becomes larger as animals are marked and released daily. Population estimates can therefore be obtained daily, or the season can be divided into a number of periods. Unique marks for each individual are not required, however confidence limits for the population cannot be calculated.

A more complicated mark and recapture method is the method of multiple recaptures, or the Jolly method (Jolly 1965). All animals caught on any particular day are marked and released, including the recaptures, so that an animal's capture history can be determined from its mark (unique marks for each individual in combination with careful record keeping will accomplish the same). Total marks recaptured each day are tabulated and related to time of initial capture. The multiple recapture Jolly method allows for both death and immigration and allows estimates of survivorship between samples. Gregory (1977) used this method throughout his studies, and Brown and Parker (1984) used the method to calculate population sizes separately for juveniles and yearling and older snakes.

Other population parameters that are often analyzed from mark and recapture data are sex ratios and size, age, and growth relationships.

The sex ratio is one of the most common and easiest parameters to derive if the animal is easy to sex. Analysis for differences in the proportion of males and females in a population usually follows the chi-square method (Clark 1974; Parker 1978; Parker and Brown 1984).

The relationship between size, age, and growth is more difficult to determine. The mark and recapture data useful in this endeavour include:

1. data on the size of the species at known ages (through multiple recaptures of young of the year);
2. records of measured growth of snakes of unknown age recaptured in successive years; and
3. multiple recaptures of adult snakes over many years (Blanchard et al 1979).

Growth data can be analyzed using Walford plots (Walford 1946), plotting length at time 1 ( $L_t$ ) versus length at time 2 ( $L_{t+1}$ ). Regressions of  $L_{t+1}$  on  $L_t$  allow tests of significance, and 95% confidence bands for the time intervals in which measurements were taken can be obtained (Gregory 1971). This method permits determination of limiting length before attainment and can be helpful in studying growth variations within and between populations.

If animals marked and released at birth are recaptured throughout their life, valuable information about growth rates and age at maturity can be obtained (Clark 1974).

Snakes of unknown age can be assigned to specific age classes based on the size and growth of recaptured individuals, as long as age class boundaries are assigned from known ages and lengths of recaptured animals (Parker 1976; Brown and Parker 1984). Several authors have attempted to assign snakes to age classes based solely on size groups present in the samples, but size groups for snakes older than juvenile tend to grade imperceptibly into one another (Carpenter 1952; Gregory 1971; Parker 1976). If one does not have any known size/age/growth data to work from, growth curves may be estimated by using hypothetical body length at birth and calculating the theoretical annual increase in length (Carpenter 1952).

### 2.3 SUMMARY

1. Literature directly related to determining the effect of harvesting on snake populations is rare.
2. The information reported in most studies on snake populations is gathered through mark and recapture methods.
3. Methods of capturing snakes reported in the literature include:
  - a) fences surrounding dens
  - b) funnel traps
  - c) a combination of funnel traps and fences
  - d) capture by hand

4. Methods of marking snakes include:
  - a) Blanchard-Finster method of clipping caudals
  - b) clipping caudals and ventral scales
  - c) clipping ventrals only
  - d) tattooing
  - e) branding
5. Population estimates can be derived from mark and recapture data through:
  - a) Petersen Index
  - b) Schnabel method
  - c) Jolly method
6. Assumptions inherent in the application of population estimates mentioned above include:
  - a) equal catchability
  - b) all animals are subject to the same survival rate
  - c) all animals leaving the population do so permanently
  - d) marked animals disperse completely in the population before the next sample is taken
7. Other population parameters which can be examined through mark and recapture data include sex ratios, growth rates, survivorship, and age/size/growth relationships.

## Chapter III

### MATERIALS AND METHODS

#### 3.1 THE STUDY AREA

The Interlake region of Manitoba is located between Lakes Winnipeg and Manitoba. The geographical characteristics of the area are described in Gregory and Stewart (1975). Generally, the Interlake region exhibits karst topography typical of an ancient ocean floor. Hibernacula are usually located in the limestone bedrock of forested ridges common throughout the region.

The harvest component of the study was conducted near Broad Valley, Manitoba, about 125 kilometers (km) north of Winnipeg (Figure 4). Den 1 (control den) and den 2 (experimental den) are located approximately 0.5 km apart and exhibit a similar topography. Den 2 has somewhat of a more southerly exposure.

The transplantation component of the study was conducted near Inwood, Manitoba, approximately 70 km north of Winnipeg. Den 4 (den 1 in Gregory 1977) was extirpated by flooding in spring, 1974. Despite subsequent clearing of surrounding woodland and the presence of some extraneous debris, it still appears suitable as a hibernaculum.

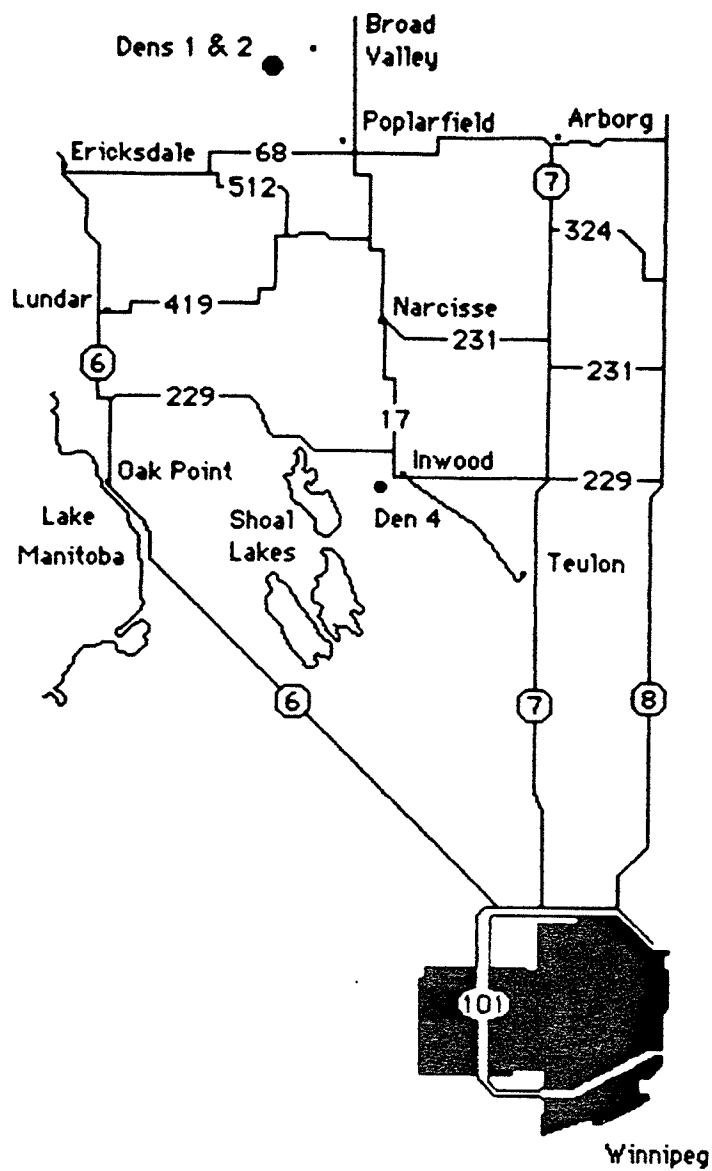


Figure 4: The Study Area

### 3.2 DATA COLLECTION

The primary research method employed was an intensive mark and recapture program. Snakes were sampled exclusively by hand. Each snake captured was marked with a ventral scute clip to ensure individual re-identification. The clipping method (Appendix A) was a modification of that described in Brown and Parker (1976). Within spring and fall sampling seasons, each marked snake had its snout-vent length (SVL) recorded to the nearest 5 mm. Additional data collection included dates of marking and recapture, location of capture, and sex.

### 3.3 TREATMENT OF OBJECTIVES

Objective One: to obtain population estimates of dens in the Broad Valley study area.

A mark and recapture program was conducted each spring and fall, 1985 and 1986, at the study dens. Snakes were captured, marked, and released on each sampling day. Population estimates were calculated in two ways.

Firstly, numbers of snakes using each den over the 1985-86 winter were calculated using the Petersen Index. The critical assumption of no recruitment between samples was satisfied by considering fall 1985 as the marking period and spring 1986 as the recapture period, with recruitment over winter being impossible. Additionally, population es-

timates for spring and fall, 1985 and 1986, were calculated using the Jolly method of multiple recaptures.

Population estimates were calculated for each sex at each study den. However, as Gregory (1974) also noted, spring estimates of female numbers were impossible to obtain due to the low proportion of females in the active above-ground population at any one time.

Objective Two: to determine the effect of harvesting on a den population.

To simulate harvesting, 50% removal of snakes was attempted at den 2 in fall 1985. Den 1 served as an unharvested control den. All previously marked snakes harvested were removed from the harvest samples and returned to the den to keep the marked pool as large as possible.

The effect of the harvest was determined by monitoring various population parameters throughout spring and fall 1986. The population parameters obtainable through mark and recapture data were sex ratio and age, size, and growth relationships. Analyses for differences in proportions of males and females in the population were provided by the chi-square method. Growth data were provided through comparisons of length at recapture after a growing season with length at previous capture. Growth variations within and between years were analyzed using Walford plots (Walford

1946). Finally, the separation of the population into age classes was attempted based on size groups present in the samples.

Objective 3: initiation of a transplant experiment.

Snakes harvested from den 2 were relocated to den 4 after the fall 1985 harvesting season had closed. All harvested snakes were marked with a common ventral scute mark to facilitate recognition as transplanted snakes.

Samples were taken at den 4 in spring 1986 to determine if transplanted snakes utilized the den as a hibernaculum. Samples were again taken in fall 1986 to determine if any transplanted snakes returned to the den again.

Objective 4: to provide information regarding snake numbers, homing, and growth rates.

As a corollary to the previous objectives, objective 4 was satisfied from the information fulfilling objectives 1 and 2. The degree of homing exhibited by the populations was determined by calculating the percentage of snakes marked at the dens in spring which returned to the same den in fall, compared to those that returned to different dens in the immediate vicinity.

Objective 5: to make recommendations useful in the development of a red-sided garter snake management strategy.

The information collected through this study was used to formulate recommendations regarding the potential for and direction of a management strategy for den populations.

## Chapter IV

### RESULTS

#### 4.1 SAMPLING PROGRAM

Throughout spring and fall, 1985 and 1986, 1592 captures of 1398 individual snakes were made at den 1, and 1943 captures of 1413 individual snakes were made at den 2. The most intensive sampling took place during spring 1986 at den 2 with 777 captures, and at den 1 in fall 1985 with 567 captures (Appendix B).

Samples were taken entirely by hand. Drift fences and funnel traps were not used due to technical difficulties and a desire not to interfere with fall wandering of the snakes.

In the majority of cases, snakes were handled immediately after a sample was taken, and released at the den immediately after all data were collected. In cases where snakes were removed to the field station overnight, they were returned to the den at least one day prior to the next sampling to allow mixing with the rest of the population.

#### 4.2 POPULATION ESTIMATES

All recapture records obtained through sampling were not utilized in calculation of population estimates. Recapture records of snakes without a spring element to their recapture history were excluded from estimates due to uncertainty surrounding their den of origin. This uncertainty arises from the high degree of wandering exhibited in fall (see 'Homing and Wandering').

The Jolly method of population estimation was applied to all sampling seasons. However, statistically valid results were obtained only for spring 1986 at den 2. Low recapture rates in other seasons at both dens resulted in population estimates with large standard errors, often greater than 100% of the estimate. Additionally, as females were found in low numbers in both spring seasons, the Jolly method provided an estimate of above ground activity of males only (Table 2).

The Petersen method of population estimation provided an estimate of the 1985-86 overwintering populations of male snakes at both dens. However, the wandering habits of the snakes introduced some uncertainty to the estimates as the assumption of equal catchability was likely violated to some degree. The female component of the overwintering population was estimated by employing fall 1985 sex ratios and male population estimates of each den (Table 3).

Table 2: Jolly Population Estimates - Den 2 Spring 1986

| Sampling Date (d/m) | Population Estimate | Standard Error |
|---------------------|---------------------|----------------|
| 21/04               | 316                 | 212            |
| 24/04               | 824                 | 304            |
| 27/04               | 656                 | 208            |
| 29/04               | 2038                | 598            |
| 02/05               | 412                 | 98             |
| 07/05               | 816                 | 202            |
| 11/05               | 1353                | 457            |
| 13/05               | 953                 | 300            |
| 19/05               | 1169                | 832            |
| 20/05               | 433                 | -              |

Table 3: Population Estimates - Males and Females  
Fall 1985

|       | Males *    | Females** | Total |
|-------|------------|-----------|-------|
| Den 1 | 2842 (465) | 2623      | 5465  |
| Den 2 | 2495 (294) | 1174      | 3669  |

\* Petersen Index Population Estimate

\*\* Female Population Estimate Formula:

$$\text{estimate} = (p(\text{female}) \times (\text{male estimate})) / p(\text{male})$$

$$2623 = (.48 \times 2842) / .52 \quad (\text{den 1})$$

$$1174 = (.32 \times 2495) / .68 \quad (\text{den 2})$$

#### 4.3 POPULATION COMPOSITION

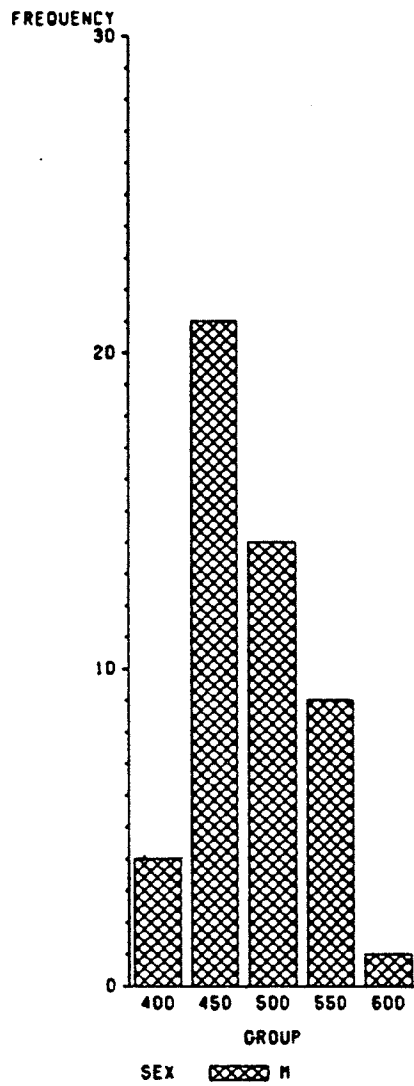
The size frequency distributions of snakes at both dens are presented in Figures 5 to 8. Snakes were grouped into intervals of 5mm SVL, except at the maximum and minimum of the size spectrum (  $\leq 350\text{mm}$ ,  $>650\text{mm}$  ).

Age classes could not be distinguished from the size frequency distributions. Age classes grade imperceptibly into one another due to the highly variable nature of growth exhibited by individuals.

Contingency table analysis ( $P < 0.05$ ) was applied to the distributions to determine differences within sexes between years. Size groups were pooled to reduce variation introduced through the effect of variable growth. For males, snakes  $\leq 450\text{mm}$  SVL were pooled as were those  $> 450\text{mm}$  SVL. Female snakes  $\leq 500\text{mm}$  SVL were pooled as were those  $> 500\text{mm}$  SVL. Thus, the population is divided into subadult and adult components. These snout-vent length ranges were based on the existing literature (see Discussion).

The size frequency distributions of males and females did not differ significantly between years at den 1. In both years, and for both sexes, the subadult component of the population was the dominant one. At den 2, however, the size frequency distributions of both sexes differ between years. In 1985, the subadult component of the population dominated for both

# DEN 1 - SPRING 1985



# DEN1 - SPRING 1986

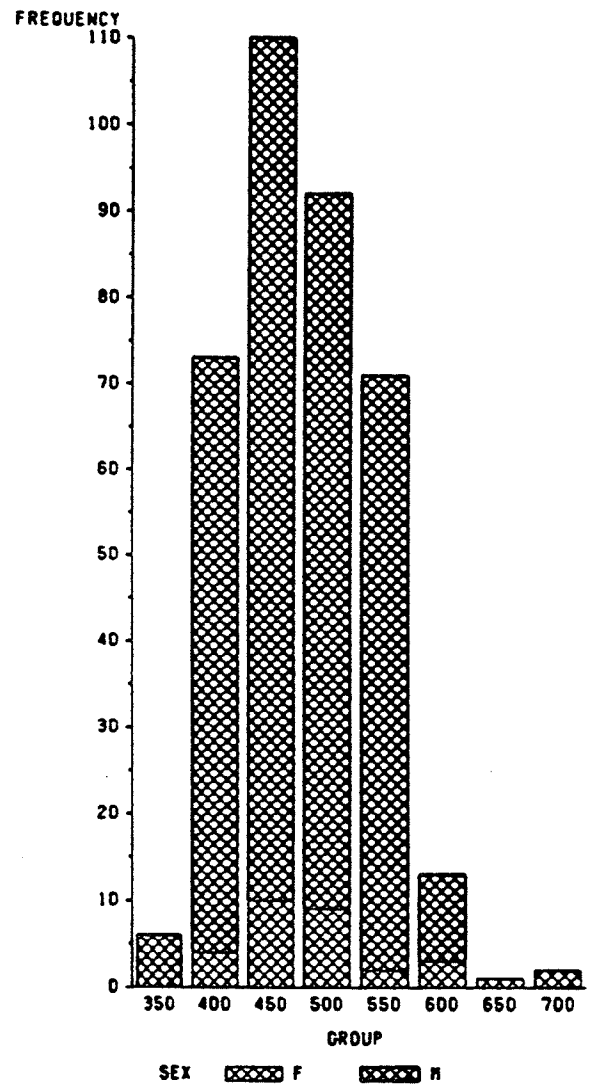


Figure 5: Population Composition - Den 1  
Spring 1985 & 1986

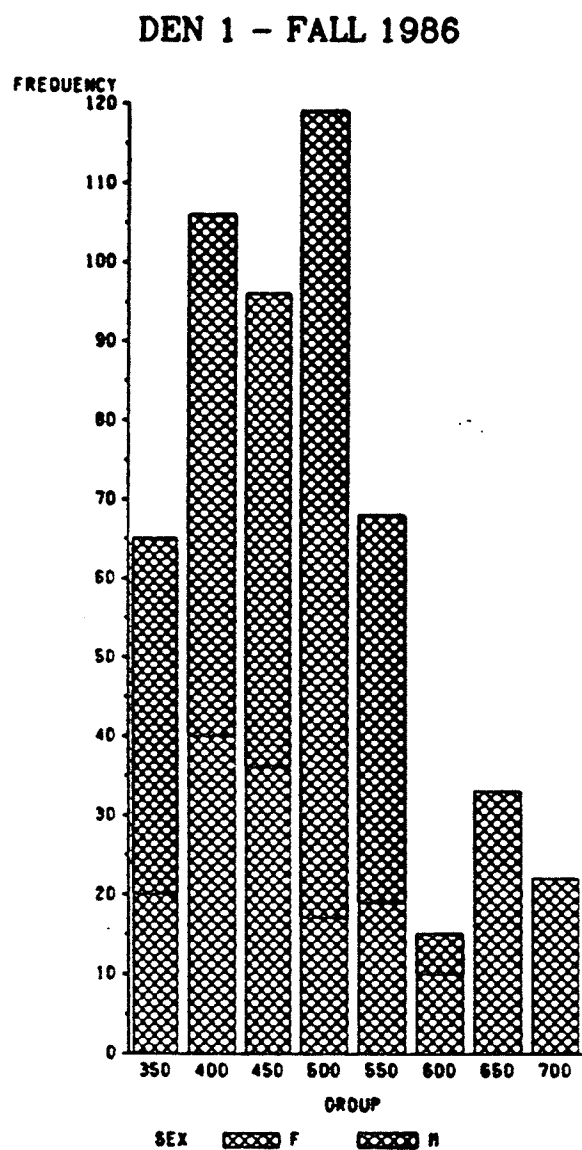
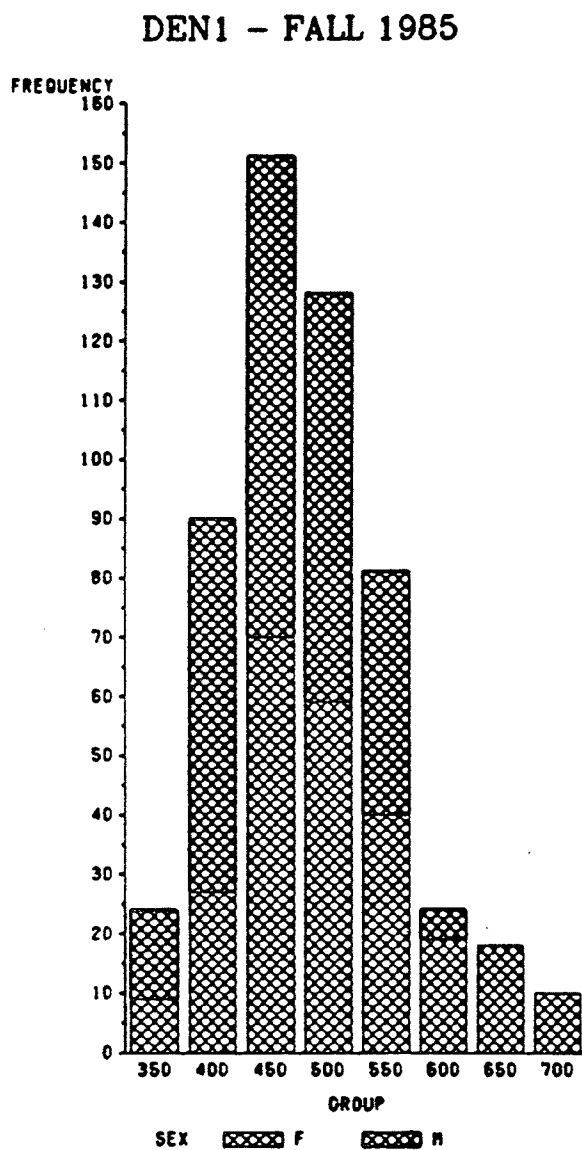
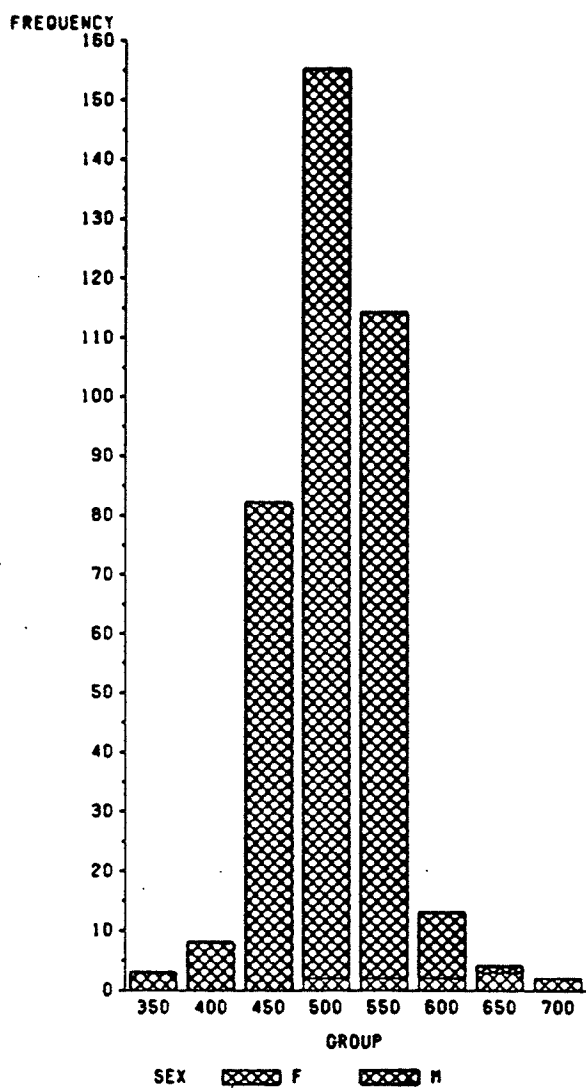


Figure 6: Population Composition - Den 1  
Fall 1985 & 1986

DEN 2 - SPRING 1985



DEN 2 - SPRING 1986

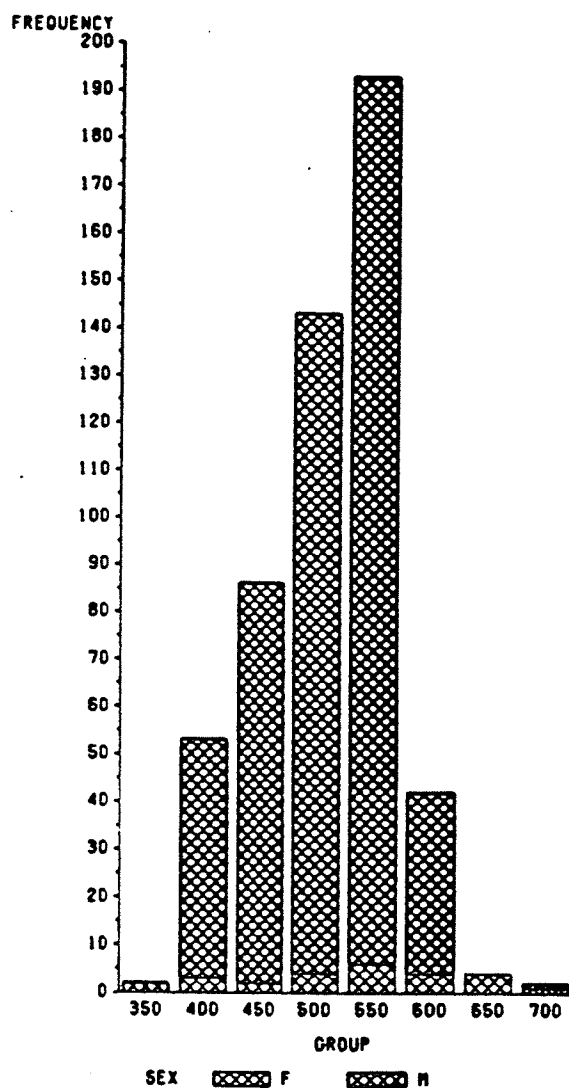
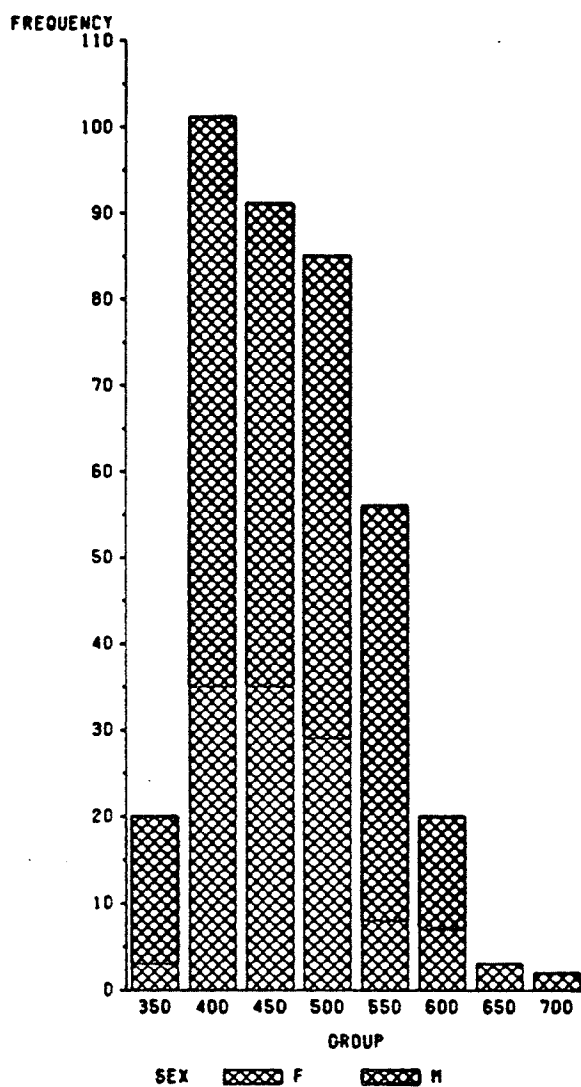


Figure 7: Population Composition - Den 2  
Spring 1985 & 1986

DEN 2 - FALL 1985



DEN 2 - FALL 1986

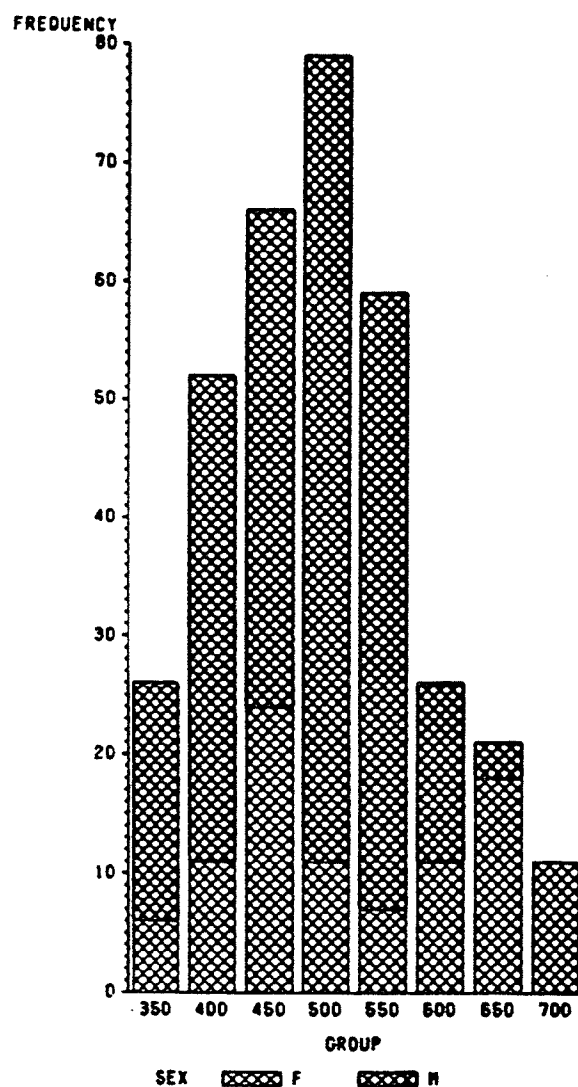


Figure 8: Population Composition - Den 2  
Fall 1985 & 1986

sexes, as at den 1. In 1986, however, subadults were under-represented and the adult component was over-represented relative to the 1985 size frequency distribution (contingency table analysis). The effect was strongest for males, as the adult component dominated in 1986.

The size frequency distributions of males at both dens were compared between fall 1985 and spring 1986 to check for changes in size frequency distribution which may have taken place over winter. Again, the distribution of males at den 1 did not differ between seasons. However, at den 2 the subadult component was again under-represented and the adult component was dominant in spring 1986 on comparison with fall 1985.

#### 4.4 SEX RATIOS

Sex ratios for both dens in fall sampling periods were analysed using the chi-square method. Equal proportions of sexes only occurred at den 1 in fall 1985 (Table 4). Otherwise, males significantly outnumbered females. This relationship was always more pronounced at den 2. At both dens, the proportion of male snakes increased in 1986, the increase being significant at den 1.

The subadult and adult segments of the population were analysed separately. Again, in both components, the sex ratio was biased significantly in favour of males, the exception being den 1 in fall 1985.

Table 4: Proportion of Population Male: 1985-1986

| Fall 1985 |                     |                        |                     |
|-----------|---------------------|------------------------|---------------------|
| Den       | Total<br>Pop'n (se) | Subadult<br>Pop'n (se) | Adult<br>Pop'n (se) |
| 1         | .52 (.02)           | .60 (.03)              | .44 (.03)           |
| 2         | .68 (.02)           | .68 (.03)              | .70 (.04)           |
| Fall 1986 |                     |                        |                     |
| Den       | Total<br>Pop'n (se) | Subadult<br>Pop'n (se) | Adult<br>Pop'n (se) |
| 1         | .62 (.02)           | .64 (.03)              | .60 (.03)           |
| 2         | .71 (.03)           | .69 (.04)              | .72 (.03)           |

The overall balanced sex ratio at den 1 in fall 1985 apparently resulted from an excess of subadult males and an excess of adult females.

Sex ratios were also calculated and analysed for the 1985 harvest data. Although males were still dominant, females showed a significantly larger representation in comparison with the regular fall 1985 sampling data.

Sex ratios were not calculated for the spring seasons as females were characteristically under-represented as a result of well documented behavioural differences related to emergence (Gregory 1974).

#### 4.5 HOMING AND WANDERING

Two methods were employed to examine the degree of homing exhibited by each den population.

Initially, homing was assessed by calculating the percentage of spring-marked snakes which returned to the den of initial capture the following fall (Table 5). Homing was highest for den 2 in fall 1985. Homing was not calculated for den 1 in fall 1985 as no spring marked snakes were recaptured due to low intensity spring marking.

Records of individual snakes travelling between dens within fall seasons prompted consideration of the extent of fall wanderings in the study area (Tables 6 and 7).

**Table 5: Degree of Homing Exhibited in Study Area  
(dens 1 and 2 combined - method 1)**

| Den | % Homing Exhibited |           |
|-----|--------------------|-----------|
|     | Fall 1985          | Fall 1986 |
| 1   | -                  | 75        |
| 2   | 89                 | 70        |

**Table 6: Degree of Wandering Exhibited by  
Populations in Fall - 1985 and 1986**

| Den | (1) # Captured<br>≥ 2x |      | # of (1) Captured<br>at Both Dens |      | % Wandering<br>Exhibited |      |
|-----|------------------------|------|-----------------------------------|------|--------------------------|------|
|     | 1985                   | 1986 | 1985                              | 1986 | 1985                     | 1986 |
| 1   | 30                     | 32   | 14                                | 4    | 46                       | 13   |
| 2   | 66                     | 32   | 11                                | 7    | 16                       | 22   |

**Table 7: Size Frequency Distribution of Wandering  
Snakes in the Study Area - Males Only  
(1985-1986)**

| Den   | Snout-Vent Length Group (mm) |         |         |         |         |
|-------|------------------------------|---------|---------|---------|---------|
|       | ≤350                         | 351-400 | 401-450 | 451-500 | 501-550 |
| 1     | 2                            | 4       | 1       | 7       | 2       |
| 2     | -                            | 4       | 2       | 4       | 3       |
| Total | 2                            | 8       | 3       | 11      | 5       |

The degree of wandering exhibited was calculated as the percentage of snakes captured at least twice in one fall which were captured at both dens.

The degree of wandering appeared to drop off significantly after September 15 in both years, but this may be an artifact of reduced sampling effort later in the fall. Wandering is exhibited by snakes of all ages (male data only) but males seem to have a greater tendency to wander.

As wandering appeared to be extensive, a second method of calculating the degree of homing was developed to minimize the effect of wandering. Homing was calculated as the percentage of spring 1985 snakes recaptured at the same den in spring 1986 (there was no evidence of spring wandering before May 10, after which snakes began to disperse). Calculations could only be made for den 2 as marking intensity in spring 1985 and recapture rates in spring 1986 at den 1 were too low for meaningful results. Based on 68 recaptures, 100% of snakes recaptured from spring 1985 were again found at den 2 in spring 1986. Thus homing in 1985 is assumed to be about 100%.

#### 4.6 GROWTH

Growth measurements were obtained for individual snakes whose recapture history encompassed a growth period. Growth data were combined whether the measurements refer to fall-fall, spring-spring, or spring-fall capture-recapture periods. When available, fall-fall growth measurements are probably more accurate as there is an apparent growth spurt in early spring as snakes emerge (Gregory 1977). Sufficient data for analysis were available only for males, as females were recaptured infrequently.

A total of 165 growth measurements were obtained for both dens (105-1985; 60-1986). Great individual variation in growth is apparent. Mean growth by size group in each year indicates that younger snakes display a greater growth rate than older snakes (Table 8).

The relationship between size and growth is shown in the Walford plot of SVL at initial capture ( $t$ ) against SVL at recapture ( $t+1$ ). The regression lines, with equations and confidence intervals, are plotted in Figure 9. Apparently, conditions for growth were better for older snakes than for younger snakes in 1985 on comparison with 1986.

**Table 8: Mean Growth by Snout-Vent Length Group  
Dens 1 and 2 Combined (Males Only)**

| Year | Snout-Vent Length Group (mm) |         |         |         |         |         |
|------|------------------------------|---------|---------|---------|---------|---------|
|      | <=350                        | 351-400 | 401-450 | 451-501 | 501-551 | 551-600 |
| 1985 | -                            | 70 (3)  | 51 (20) | 35 (51) | 30 (34) | 20 (1)  |
| 1986 | -                            | 76 (10) | 73 (9)  | 28 (21) | 19 (16) | 8 (5)   |

( ) = number of observations

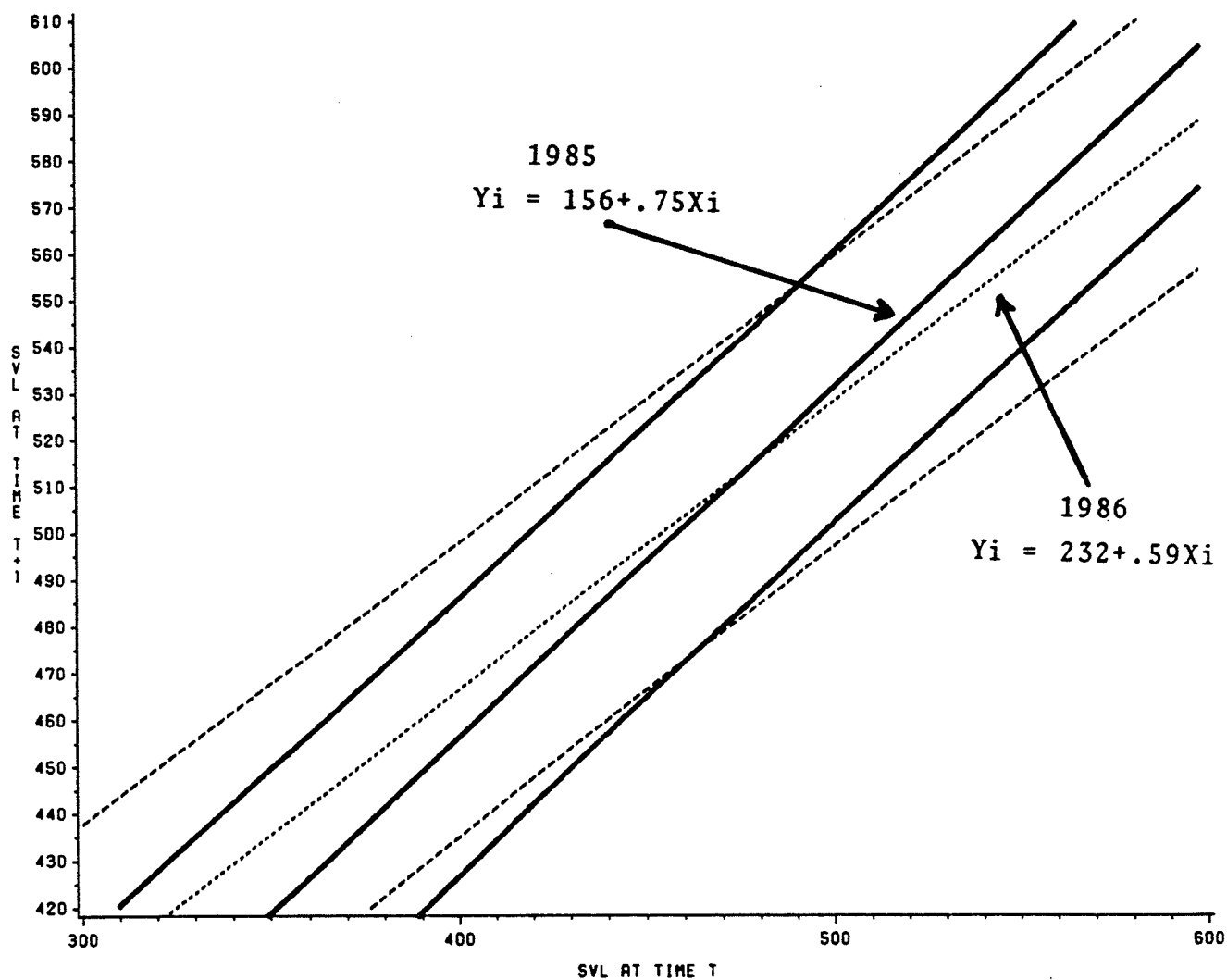


Figure 9: Walford Plot of Growth (1985 & 1986)  
 (male data only)  
 (— = 1985 growth plot and confidence limits)  
 (--- = 1986 growth plot and confidence limits)

#### 4.7 HARVEST

Snakes were harvested at den 2 from 11 September to 20 October 1985 (Table 9). Initially, it was hoped that 50% of the population would be removed from the den. However, delaying the start of harvesting and subsequent inclement weather combined to make harvesting difficult. It would have been optimal to harvest throughout the legal harvest season, but mark-recapture data were required for part of the fall season. In total, 720 snakes (451 males, 269 females) were harvested, representing an estimated 16% of the overwintering population.

It is possible that, due to fall wandering, some of the harvested snakes were not den 2 snakes. Therefore, the proportion of the population harvested may be somewhat less than 16%.

#### 4.8 TRANSPLANTATION

Snakes harvested from den 2 in fall 1985 (451 males, 269 females) were transplanted to den 4 from 15 September to 20 October 1985. Data collected from the first day of harvesting indicated that the size frequency distribution of harvested animals did not differ from that of the previous fall sampling (contingency table analysis,  $P < .05$ ). Additional snakes were transplanted from dens near Narcisse, Manitoba, to den 4 in spring 1985 (94 males, 28 females) and spring

Table 9: Sample Record - Den 2 (Fall 1985 - Harvest)

| Harvest Date | Males Harvested | Spring * Recaptures | Total Male Harvest | Females Harvested | Total # Harvested |
|--------------|-----------------|---------------------|--------------------|-------------------|-------------------|
| 11/09/85     | 70              | 7                   | 63                 | 40                | 103               |
| 12           | 106             | 10                  | 96                 | 37                | 133               |
| 14           | 109             | 7                   | 102                | 48                | 150               |
| 15           | 53              | 0                   | 53                 | 37                | 90                |
| 21           | 100             | 6                   | 94                 | 74                | 168               |
| 22           | 23              | 2                   | 21                 | 10                | 31                |
| 28           | 19              | 0                   | 19                 | 12                | 31                |
| 04/10/85     | 3               | 0                   | 3                  | 6                 | 9                 |
| 20           | 0               | 0                   | 0                  | 5                 | 5                 |
| TOTALS       |                 |                     | 451                | 269               | 720               |

\* = spring recaptures (all male) not harvested.

1986 (151 males, 129 females). However, these snakes had been kept under laboratory conditions in Texas over at least one winter and may not have behaved normally.

Den 4 was sampled on eight occasions in spring 1986 to determine if transplanted snakes utilized the den as a hibernaculum. A total of 84 transplanted snakes were found (77 males, 7 females) as were 65 unmarked snakes (64 males, 1 female), indicating use of the den overwinter (Table 10). No spring 1985 Narcisse snakes were found at den 4.

Sampling continued in fall 1986 to determine if any transplanted snakes developed a loyalty to the den. Through six sampling days, only one male transplanted snake and seven (6 male, 1 female) of the new spring 1986 snakes (marked in the spring for future identification) were found. A total of 107 new (unmarked) snakes were found in the same period (Table 10).

Unfortunately, sampling in fall 1986 was interrupted by the presence of commercial snake pickers. Thus, marked snakes returning to the den may have been picked and, therefore, not available for recapture. Additionally, at the beginning of September (typically a time of great activity), recapture effort had to be postponed. As a result of this interference with sampling effort, an element of uncertainty was introduced to the results of this aspect of the study.

Table 10: Transplantation Sampling Data  
Den 4 - 1986

| Season     | Recaptures<br>of Transplants |         | New<br>Animals (1) |         | Fall 1986<br>Recaptures of (1) |         |
|------------|------------------------------|---------|--------------------|---------|--------------------------------|---------|
|            | Males                        | Females | Males              | Females | Males                          | Females |
| Spring '86 | 77                           | 7       | 64                 | 1       | -                              | -       |
| Fall 1986  | 1                            | -       | 62                 | 45      | 6                              | 1       |

## Chapter V

### DISCUSSION

#### 5.1 POPULATION ESTIMATES

##### 5.1.1 Fall

Jolly population estimates of snake numbers above ground in fall are meaningless due to low recapture rates and resultant large standard errors. King (1986) calculated Jolly estimates for watersnakes (Nerodia sipedon insularum) with standard errors sometimes exceeding 100% of the estimate. Estimates of greater reliability can be achieved by completely fencing dens, thus increasing recapture rates (Brown and Parker 1984). However, greater reliability introduced through increased sampling intensity in the present study would probably have been offset by the high degree of wandering exhibited by the snakes in fall. Wandering not only lowers recapture rates, but violates the assumption of equal catchability so necessary in obtaining reliable estimates (Jolly 1965). Due to the nature of the populations under study, then, the Jolly method of population estimation is inappropriate in fall seasons.

### 5.1.2 Spring

The Jolly estimates for spring 1986 at den 2 are acceptable. There is no evidence of wandering between dens in spring, and recapture rates are high enough to lower the standard errors of estimation significantly. The close correlation between the peak of male activity in spring and the Petersen estimate of the overwintering population imparts additional confidence in both estimates. Peak activity occurred on 29 April 1986, quite early in the season, and there was much daily variation depending on the weather.

### 5.2 GROWTH, REPRODUCTION, AND MATURITY

Growth data for 1985-86 parallel that presented by Gregory (1977), also indicating great individual variation in growth, and growth rates differing between years.

Although neither study collected information on growth immediately after birth, growth for most snakes is most rapid in the first year of life (Carpenter 1952; Fitch 1963; Fitch and Fleet 1970; Shine 1978b). Female red-sided garter snakes grow at a faster rate and achieve a larger size than do males. After the first complete summer of growth, males can achieve 400-500 mm SVL while the largest females range from 500-550mm SVL (Gregory 1977). In Michigan, Carpenter (1952) found female garter snakes (T.s. sirtalis) to grow to larger sizes than males, and found growth rates of males to

decrease faster than females. The literature indicates that females achieve larger sizes than males in most snakes, except those species which show male-male combat in their behavioural repertoire (Shine 1978b; Diller and Wallace 1984). The typically smaller maximum size of males may have evolved in response to higher predation pressure on the more active sex (Jackson and Franz 1981).

Male and female garter snakes may attain sexual maturity after their first full season of growth (Carpenter 1952; Clark 1974; Gregory 1977). In the Interlake region, females less than 400mm SVL do not reproduce, but the percentage of reproductive females increases with size until almost all females greater than 500mm SVL are potentially reproductive (Gregory 1977). In Michigan, female garter snakes can mature by their second spring at snout-vent lengths between 450 and 500mm (Carpenter 1952), however many individuals of both sexes may not mature until their third year. Burt (1928) did not find female garter snakes to mature until 550mm SVL. Clark (1974) found male ribbon snakes (Thamnophis proximus) in Texas attaining sexual maturity at 400mm SVL, thus being capable of mating (at least in some instances) in their first spring. Females, though, do not mature until after their first full season of growth, indicating sexual bimaturism. Interlake garter snakes may also exhibit bimaturism since, although attractive, smaller females (most <450mm SVL) are not sexually receptive and therefore may not be mated until their third year (Hawley and Aleksiuik 1976).

Selection pressures may favour bimaturism in most species of snakes. In a study of Australian coral snakes (Elapidae), Shine (1978b) found females to mature slightly later than males, and concluded that selection pressures favoured bimaturism. Since female fecundity is positively related to body size, delayed maturity may convey a reproductive advantage as lifetime reproductive fecundity could be increased (Bull and Shine 1979). Other studies have also found a significant correlation between female size and clutch size (Fitch 1963; Diller and Wallace 1984). Of 14 intact Interlake broods, the mean number of young/brood was 16 (range 7-26), with larger litters produced by larger females (Gregory 1977). Theoretically, then, bimaturism may be selected for in the Interlake.

Sexually mature female red-sided garter snakes in the Interlake region may not breed annually due to the high costs of reproduction. These costs involve the opportunity cost of the inability to feed while gravid and the increased risk of mortality while basking. These costs become more acute as the growing season becomes shorter and the percentage of the season consumed by reproductive activities increases. In the Interlake region, the energy costs associated with reproduction may be too high to permit annual reproduction. Gregory (1977) suggests biennial reproduction might be expected, with the frequency of reproduction depending on the date of parturition and the subsequent availability of food.

Aldridge (1979) believes a true biennial cycle probably does not exist, but that the availability of energy, either as stored fat from a favorable growing season the year before or resulting from spring foraging success, determines the proportion of females reproducing in a given year. Weather ultimately determines the availability of energy as weather influences both the date of parturition and subsequent foraging success. If young are born late because a cold summer prolonged gestation, reproducing females may have little or no time to feed before they begin the migration from the summer feeding area. Female garter snakes in the Interlake region can potentially breed annually, as animals removed to the laboratory and sufficiently fed produce litters in most years (Mason, pers.comm.).

In summary, female red-sided garter snakes in the Interlake region grow at a faster (though decreasing) rate than males. Males may mature earlier than females, with most males maturing in their second year and almost all females being mature in their third year. Fecundity in females increases with size. Females have the potential to reproduce annually but may not if the costs of reproduction in the previous year were too high and the availability of energy too low.

### 5.3 POPULATION COMPOSITION

It is impossible to assign snakes to age classes at dens 1 and 2 based on the size frequency distributions. Gregory (1977) attempted unsuccessfully to separate age classes by employing Cassies' (1954) method, differentiating only the smallest age class of males. Gregory assumed at least four age groups were present at his dens, as marked individuals were recaptured over four years.

Other studies have had similar difficulty in identifying age classes from size frequency distributions (Carpenter 1952; Parker 1976; Semlitsch et al. 1981; Diller and Wallace 1984). Most success has come using size frequency distributions in combination with records of actual growth over several years when body size is well correlated with age. Prestt (1971) distinguished four age groups for vipers (Vipera berus) and Brown and Parker (1984) separated juvenile, immature, and adult racers (Coluber constrictor mormon) based on the size and growth of marked individuals.

For the purposes of this study, I considered 450mm SVL for males and 500mm SVL for females to form the upper boundary of the subadult component of the population. I based these boundaries on information in the literature indicating that some males 400-500mm SVL and some females 450-550mm SVL will be immature while others will be mature (Burt 1928; Carpenter 1952; Gregory 1977). Above these limits, the vast majority of both sexes will be mature.

Applying these boundaries, there were more subadults than adults in the population at both dens in fall 1985 and at den 1 in fall 1986. Gregory (1977) found the smallest separable age class (averaging 440-450mm SVL for males and 520-530 for females) to dominate as well. Brown and Parker (1984) found many immature and young adult racers in all years in Utah. However, older snakes represented at least as large a component of the population (24-38%). Second year racers, in very good seasons, can make up half the population (Hirth and King 1968).

The size frequency distribution at den 2 changed between fall 1985 and spring 1986 such that the subadult component of the population was under-represented and, in the case of males, no longer dominated. The reason for this change is unclear. One might suspect over-winter mortality, for it is known to be significant in the Interlake (Gregory 1977). However, there is no evidence to indicate differential mortality between adult and subadult components of the population. Differential behaviour in the spring, related to mating activities and resulting in differential susceptibility to capture, may bias spring representation in sample records, but this effect is expected to be equal between dens. In the absence of other explanations, the harvest at den 2 was the only factor not common between dens.

#### 5.4 SEX RATIOS

Males outnumbered females at both dens in fall in both the subadult and adult components of the population. The exception was den 1 in fall 1985, where males were dominant only in the subadult component.

Sex ratios heavily biased towards males in autumn are not reported extensively for garter snakes or other colubrids. Gregory (1974, 1977) found both the primary and the population sex ratios of red-sided garter snakes to be close to 1:1, with only a slight surplus of males in one fall season. Clark (1974) assumed an overall sex ratio of 1:1 for ribbon snakes (Thamnophis proximus). Racers (Coluber constrictor mormon) and whipsnakes (Masticophis) also exhibit equal primary and population sex ratios (Parker and Brown 1973; Parker 1976; Brown and Parker 1984). Sex ratios biased towards males have been reported for bullsnares (Pituophis) (Gutzke et al. 1985), rattlesnakes (Crotalus) (Galligan and Dunson 1979), and crowned snakes (Tantilla coronata) (Semlitsch et al. 1981), but these studies temper their results by attributing any imbalance in favour of males to potential sampling bias related to differential susceptibility to capture of the more vagile males.

Based on the literature, one might conclude the sex ratios reported here to be artificially biased. However, samples were collected by hand and bias introduced through the

higher vagility of males should be less than if samples were trap collected, since females could be sampled whether moving or sedentary. For this reason, I feel the sex ratio reported here to be unbiased enough to be considered as real. However, the increased female representation in harvest samples suggests that females may travel to hibernacula in greater numbers later in the fall. Therefore, the overall male bias may not be as great as samples taken earlier in fall indicate.

The sex ratio of any population reflects the effect of natural selection on the primary sex ratio (Shine and Bull 1977). If the primary sex ratio of red-sided garter snakes in the Interlake region is 1:1 (Gregory 1977), the female component of the population must suffer higher mortality if the population sex ratio is truly biased in favour of males. Older reproductive females might be expected to be at greater risk of predation when gravid and basking. However, subadult snakes may also be predominantly male, suggesting that females are selected against early in life. Inclement weather may play a role in such selection if younger, non-reproductive females disperse earlier in spring than older females and are subsequently caught afield by a late frost or snowfall. Alternatively, further investigation of the primary sex ratios of the populations may reveal an unbalanced primary sex ratio.

## 5.5 DEN FIDELITY AND WANDERING

The populations of snakes in the study area exhibit a very strong tendency to home. These results agree with Gregory (1971, 1974), indicating a high degree of den fidelity and little spring wandering. Other studies have shown that snakes which den communally tend to use the same den each year (Prestt 1971; Landreth 1973; Parker and Brown 1973; Brown and Parker 1976, 1984). The adaptive significance of homing is clear, as it ensures snakes will den communally, and communal denning offers several advantages to north temperate snakes in terms of reproductive efficiency on emergence and metabolic stress reduction during hibernation (Parker and Brown 1973; Gregory 1974).

The ability to home demonstrates an orientation capability. In short migrations ( $< 1$  km) snakes may orient to known landmarks and odours, employ random searching, or combine mechanisms (Fraker 1970; Brown and Parker 1976). In longer migrations, as in the Interlake (Gregory and Stewart 1975), sun compass orientation may operate to guide the snakes (Landreth 1973).

A high degree of wandering in fall before hibernation appears to be an important aspect of behaviour in the study area. Wandering snakes, by definition, may have been travelling to their home den when captured at a different den along the way, or may have previously reached their home den

and were wandering within a short distance of the den before low temperatures prompted hibernation. Gregory (1974) did not report wandering or intermingling between dens in any one season. However, the minimum distance between dens in his study (0.8 km) was greater than the distance between dens 1 and 2 in this study (0.5 km). Other studies have shown that movements in late fall, winter, and early spring are usually short treks easily identified as movements associated with the den (Landreth 1973). Dens 1 and 2 are apparently close enough to each other that movements associated with one den may bring snakes into the vicinity of the other.

Wandering snakes do not appear to be characterized by age, but males seem to wander more than females. Fitch (1963) found some black rat snakes (Elaphe o. obsoleta) of all ages to wander, but suggested that young may be more inclined to wander than adults. Fitch also found males more inclined to wander than females. Male rattlesnakes (Crotalus viridis oreganus) and watersnakes (Nerodia) also seem to wander more than females (Preston, pers. comm. 1987). The adaptive significance of such differences is not clear. Perhaps fall wanderings, by familiarizing male snakes with the local environment, confer a reproductive advantage the next spring. As competition at the den surface itself is intense during the spring mating period, familiarity with the surrounding area may aid males occupying these areas in securing copulations with dispersing females.

Intraspecific competition and weather may play a role in determining the degree of wandering (Hirth et al 1969). Competition for denning space may necessitate wandering if the proportion of snakes relative to available denning space is high and new hibernacula must be found. Interspecifically, Parker and Brown (1973) suggest the abundance of bullsnakes (Pituophis) and racers (Coluber) at den sites in Utah may have been restricted by the presence of whipsnakes (Masticophis) and rattlesnakes (Crotalus), if the latter were first to colonize. Wandering decreases after the middle of September, suggesting snakes respond to cooler temperatures by remaining closer to their home den. Snakes of both sexes may wander in the fall while weather permits in search of small scattered sources of food.

#### 5.6 TRANSPLANTATION

It is not clear whether transplanting snakes as a mechanism of repopulating uninhabited dens is feasible. Interruption of sampling in fall 1986 by commercial harvesters introduced an element of uncertainty to this aspect of the study.

Other studies have had difficulty in changing den loyalty by transplanting snakes. Galligan and Dunson (1979) attempted to transplant adult and newborn timber rattlesnakes (Crotalus h. horridus) to new dens in Pennsylvania. Of 49 adults transplanted in fall, only 3 were found the next

spring and none were found the following fall. Only one of 48 newborns (released within 48 hours of birth) was found the next spring. Racers (Coluber constrictor mormon) displaced 300 m from their den behaved opportunistically toward a strange den (Brown and Parker 1976). Theoretically, racers used the strange den as the 'stimulus of another dens presence temporarily suppressed any motivation to seek the home den when failure could result in winter mortality'. Half of the displaced racers found their way back to the home den the next year. Perhaps the transplanted garter snakes of this study behaved opportunistically as well.

The presence of unmarked snakes at den 4 warrants discussion. Presumably, most of these snakes were not present upon transplantation, as Gregory (1977) reported the population at den 4 to be completely exterminated in 1974 and few snakes have been found frequenting the den since (K.W. Stewart pers. comm.). The presence of the transplanted snakes may have attracted wandering snakes looking for a hibernaculum if other suitable dens were saturated with snakes. As there is evidence that snakes follow the trails of conspecifics to facilitate aggregation (Ford 1978; Heller and Halpern 1981; Ford and Schofield 1984), wandering snakes may have detected the scent trails of the transplanted snakes conducting localized movements around den 4 in fall 1985. However, as the den is well known to local residents, the unmarked snakes may well be surplus snakes from the fall

1985 harvest season that were dumped there as they were not marketable. Snake pickers may have chosen the site in hope of recapturing the snakes at the den in fall 1986.

Both transplanted snakes and unmarked snakes from fall 1985 were found in low numbers at den 4 in fall 1986. It is not clear whether these snakes suffered high mortality, emigrated, or were captured by commercial pickers. Mortality could be a factor in transplant success, as home range familiarity could play a major role in survival. Madsen (1984) suggests that familiarity with the immediate surroundings is probably of great importance upon attack, as grass snakes (Natrix natrix) often escape to a location where they were found earlier. Familiarity with the environment may also provide thermal benefits and facilitate food procurement (Fraker 1970; Chelazzi and Calzolari 1986).

More research is needed to determine the potential for re-establishing populations of snakes at abandoned dens. The literature indicates that transplanted snakes will not recolonize a den. The results of this study are inconclusive as harvesters introduced an element of uncertainty through interference with sampling.

## 5.7 EFFECT OF HARVEST

Approximately 16% of the population at den 2 was removed in fall 1985. Harvesting effort was much less than that of a commercial harvest in terms of man hours, and was not concentrated within the time of greatest activity at the dens. Still, some effects of the harvest are apparent.

The subadult component of the population appeared to suffer most, although the size frequency distribution of the harvest reflected that of the population. Stewart (pers. comm.) hypothesized that the increased human activity associated with harvesting at den 2 may have been responsible for the decline in subadult representation in 1986. Subadult snakes are typically in poor physical condition in fall (Aleksiuk and Stewart 1971) and harassment during harvesting may be severe enough to cause significant mortality in this segment of the population. Subsequently, as the harvest had its greatest impact on snakes which represent the future reproductive potential of the population, the potential for the population to maintain itself will decline rapidly as the numbers of snakes attaining reproductive age falls and older reproductive snakes are harvested or die off.

The harvest also exerts a negative effect on the population through degradation of den structure. Harvested dens typically show signs of trampling (evident in the study area despite low harvest effort), digging, and general disruption.

tion. Koonz (pers. comm. 1986) believes some commercial harvesters block entrances to dens with debris, thus forcing snakes to remain above ground and available for capture. Such disruption may reduce available hibernation space and contribute to a reduction in denning populations (Parker and Brown 1973). The Pennsylvania Fish Commission, charged with protecting all amphibians and reptiles in the state, recognizes this as fact. The only protective regulation regarding timber rattlesnakes in Pennsylvania makes it illegal to damage a den while trying to catch the snakes (Galligan and Dunson 1979). As hibernation space is reduced, snakes may be forced to wander in search of new hibernacula. These snakes will die if active above ground at the first heavy frost, and may suffer increased mortality due to home range unfamiliarity even if a den is found.

Other effects of long term harvesting pressure may not be apparent due to the short duration of this study. In fairness, one must also stress the danger of interpreting observations from a short term study as being unique to the time frame involved, when such occurrences may be normal aspects of the life history of the population. I feel confident, however, in attributing the change in population composition at den 2 to the harvest. No other explanation is immediately apparent, and dens 1 and 2 are sufficiently close together that environmental factors acting on the populations can be considered equal.

## Chapter VI

### CONCLUSIONS AND RECOMMENDATIONS

#### 6.1 CONCLUSIONS

Although the red-sided garter snake is not endangered as a species, the phenomena of large denning aggregations may be. Intensive harvesting over a period of years leads to a severe reduction in numbers. Exterminated dens show little sign of repopulation decades after disturbance, and transplantation as a means of re-establishing populations may not be feasible. As a result, the remaining unexploited dens have come under increasing harvest pressure over time.

Current management practices are inappropriate as the character of the harvesting industry has changed in the last decade. Despite a two week season, pickers may exploit populations before and after the season with little fear of detection, functionally extending the season to four weeks or more. Dens are subjected to indiscriminate harvesting pressure, regardless of population composition or den condition. The magnitude of the harvest is not precisely known, as mortality suffered through handling and release if not marketable is not known. No rigorous survey of remaining large denning populations, enabling evaluation of the status of

the resource, has been conducted. Normally, awareness of the status of a resource is a pre-requisite for successful management.

Ignorance of the status of dens in Manitoba and of the biological needs of the species is a major hindrance to effective management of the denning populations. An attitude, symptomatic of this problem, accepts the notion that, since harvest figures remain high, denning populations must be maintaining themselves. The yearly harvest is remaining high, but due only to increased harvest effort and the exploitation of a declining number of unexploited dens. As this trend continues, the harvest may be expected to decline, for exploited dens do not repopulate (in a practical time frame) and large denning populations are scarce. With time, few major denning populations will remain.

There must be a change in current management practices if some large denning aggregations are to remain. However, the nature of the denning populations themselves makes it impossible to propose general commercial harvest guidelines appropriate for all denning populations. The results of this study indicate that population parameters may be den-specific. Numbers, sex ratios, and the population composition of dens in one area are probably different from those of dens in another area. Therefore, the impact of management guidelines on different dens will not be the same. The wandering tendencies of snakes in fall tends to complicate the issue

further, as pickers at one den could effectively harvest two or more dens at the same time. Additionally, much of the information necessary to evaluate population parameters must be collected annually in fall without interference from commercial harvesters.

Effective den population management in the face of continued commercial exploitation necessitates a den-specific management scheme. However, the cost of such a scheme, if theoretically possible, would likely exceed revenues generated by the harvest. While the value of the industry to Manitobans in 1985 fell between \$60-90,000 (average earnings/picker of \$340; average earnings/buyer of \$20-45,000), the cost of enforcing regulations restricting harvesting was estimated at \$22,500 (Regional Services 1986). The cost of enforcing additional regulations respecting specific dens would likely be prohibitive. The effective enforcement of a ban on harvesting at 3 neighboring dens in the Narcisse Wildlife Management Area alone would require at least 504 man hours of departmental time and an estimated cost exceeding \$5,000 (R. Cameron pers. comm.). The red-sided garter snakes of Manitoba's Interlake region, then, should be viewed as not economically exploitable.

Manitoba's concentrations of red-sided garter snakes represent a unique wildlife heritage whose intrinsic value, through adding to the diversity of the wildlife landscape and fostering an understanding of nature's complexity, far

exceeds that accruing from commercial exploitation. If we want to ensure the future of this unique aspect of our wildlife heritage, the annual commercial harvest must be terminated immediately.

## 6.2 RECOMMENDATIONS

1. Terminate the annual commercial harvest of red-sided garter snakes in Manitoba.
2. Assign threatened status to the remaining denning aggregations of red-sided garter snakes in Manitoba.
3. Initiate further research to evaluate the status of the remaining large denning aggregations.

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Appendix A  
MARKING METHOD

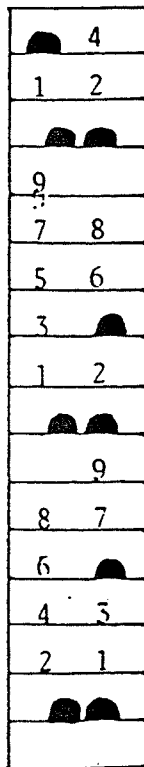
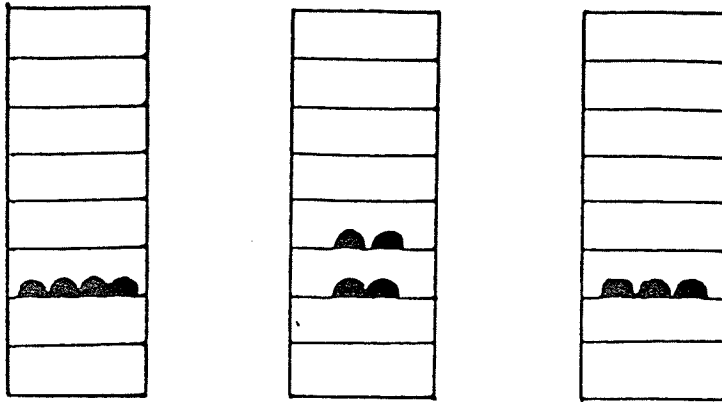
Marking is facilitated by clipping the ventral scutes of the snake. The information coded for in each mark includes sex, capture site, and individual identification number.

The method is illustrated in figure A1. Proceeding anteriorly, the first ventral scute(s) clipped indicate the site of capture. This scute always bears multiple clips: 4 clips indicates den 1 ( < 1000), 2-2 indicates den 1 ( > 1000), 3 indicates den 2 ( < 1000), and 2 indicates den 2 ( > 1000). The multiple clips on a single ventral scute also serve as a base mark, indicating the start of the numbering sequence.

The numbering sequence begins immediately following the base clip. The first five scutes are the 'unit' scutes. The sixth scute following the unit scutes is clipped twice to separate the unit scutes from the 'tens' scutes (the next five scutes). The twelfth scute is clipped twice to separate the tens scutes from the 'hundreds' scutes. The base clip is changed to indicate numbers above one thousand to minimize the area occupied by the mark on the belly of the snake.

Individual number designations are facilitated by clipping the appropriate side of the appropriate scute to give the snake a number. Female snakes are given even numbers and male snakes are given odd numbers.

This marking method allows large numbers of snakes to be marked quickly and to be recognized individually upon recapture.



Above (L-R): Den 1 - 1-1000  
 Den 1 - over 1000  
 Den 2 - 1-1000

At Left: #1345 - Den 2 (male)

Figure A-1: The Marking Method

Appendix B  
SAMPLE RECORDS

Table B-1: Sample Record - Den One (Spring 1985)

| Capture Date | Release Date | Both Sexes |         |    | Males |         |    | Females |         |    |
|--------------|--------------|------------|---------|----|-------|---------|----|---------|---------|----|
|              |              | ni         | (ni-mi) | mi | ni    | (ni-mi) | mi | ni      | (ni-mi) | mi |
| 15/05        | 15/05        | 14         | 14      | 0  | 14    | 14      | 0  | 0       | 0       | 0  |
| 17/05        | 17/05        | 32         | 27      | 5  | 32    | 27      | 5  | 0       | 0       | 0  |
| 21/05        | 21/05        | 10         | 8       | 2  | 10    | 8       | 2  | 0       | 0       | 0  |
|              | Total        | 56         | 49      | 7  | 56    | 49      | 7  | 0       | 0       | 0  |

ni=total sample size

mi=numbers of recaptures in sample

(ni-mi)=number of new animals in sample

Table B-2: Sample Record - Den Two (Spring 1985).

| Capture Date | Release Date | Both Sexes |         |    | Males |         |    | Females |         |    |
|--------------|--------------|------------|---------|----|-------|---------|----|---------|---------|----|
|              |              | ni         | (ni-mi) | mi | ni    | (ni-mi) | mi | ni      | (ni-mi) | ni |
| 10/05        | 10/05        | 20         | 20      | 0  | 18    | 18      | 0  | 2       | 2       | 0  |
| 14/05        | 14/05        | 30         | 30      | 0  | 27    | 27      | 0  | 3       | 3       | 0  |
| 15/05        | 17/05        | 88         | 85      | 3  | 88    | 85      | 3  | 0       | 0       | 0  |
| 17/05        | 19/05        | 80         | 69      | 11 | 80    | 69      | 11 | 0       | 0       | 0  |
| 20/05        | 20/05        | 76         | 63      | 13 | 71    | 58      | 13 | 5       | 5       | 0  |
| 21/05        | 21/05        | 93         | 70      | 23 | 92    | 69      | 23 | 1       | 1       | 0  |
| 22/05        | 22/05        | 64         | 45      | 19 | 64    | 45      | 19 | 0       | 0       | 0  |
|              | Total        | 451        | 382     | 62 | 440   | 371     | 69 | 11      | 11      | 0  |

ni=total sample size

mi=number of recaptures

(ni-mi)=number of new animals in sample

Table B-3: Sample Record - Den 1 (Fall 1985)

| Capture<br>Date | Release<br>Date | Both Sexes |    |         | Males |    |         | Females |    |         |
|-----------------|-----------------|------------|----|---------|-------|----|---------|---------|----|---------|
|                 |                 | ni         | mi | (ni-mi) | ni    | mi | (ni-mi) | ni      | mi | (ni-mi) |
| 27/08           | 27/08           | 5          | 0  | 5       | 5     | 0  | 5       | 0       | 0  | 0       |
| 29              | 29              | 7          | 1  | 6       | 7     | 1  | 6       | 0       | 0  | 0       |
| 30              | 30              | 7          | 0  | 7       | 6     | 0  | 6       | 1       | 0  | 1       |
| 31              | 31              | 25         | 0  | 25      | 5     | 0  | 5       | 20      | 0  | 20      |
| 01/09           | 01/09           | 30         | 0  | 30      | 18    | 0  | 18      | 12      | 0  | 12      |
| 03              | 03              | 28         | 0  | 28      | 17    | 0  | 17      | 11      | 0  | 11      |
| 06              | 06              | 38         | 5  | 33      | 22    | 3  | 19      | 16      | 2  | 14      |
| 09              | 10              | 137        | 3  | 134     | 80    | 3  | 77      | 57      | 0  | 57      |
| 11              | 11              | 95         | 4  | 91      | 46    | 1  | 45      | 49      | 3  | 46      |
| 12              | 13              | 66         | 3  | 63      | 30    | 1  | 29      | 36      | 2  | 34      |
| 21              | 22              | 57         | 1  | 56      | 28    | 1  | 27      | 29      | 0  | 29      |
| 28              | 28              | 22         | 1  | 21      | 8     | 0  | 8       | 14      | 1  | 13      |
| 04/10           | 06/10           | 28         | 0  | 28      | 11    | 0  | 11      | 17      | 0  | 17      |
| TOTAL           |                 | 545        | 18 | 527     | 283   | 10 | 273     | 262     | 8  | 254     |

ni=total sample size

mi=number of recaptures in sample

(ni-mi)=number of new animals

Table B-4: Sample Record - Den 2 (Fall 1985 - Pre-Harvest)

| Capture Date | Release Date | Both Sexes |    |         | Males |    |         | Females |    |         |
|--------------|--------------|------------|----|---------|-------|----|---------|---------|----|---------|
|              |              | ni         | mi | (ni-mi) | ni    | mi | (ni-mi) | ni      | mi | (ni-mi) |
| 27/08        | 27/08        | 11         | 0  | 11      | 11    | 0  | 11      | 0       | 0  | 0       |
| 29           | 29           | 15         | 0  | 15      | 15    | 0  | 15      | 0       | 0  | 0       |
| 30           | 30           | 22         | 2  | 20      | 22    | 2  | 20      | 0       | 0  | 0       |
| 31           | 31           | 40         | 1  | 39      | 12    | 0  | 12      | 28      | 1  | 27      |
| 01/09        | 01/09        | 10         | 0  | 10      | 4     | 0  | 4       | 6       | 0  | 6       |
| 03           | 05           | 107        | 4  | 103     | 64    | 2  | 62      | 43      | 2  | 41      |
| 06           | 07           | 69         | 7  | 62      | 49    | 4  | 45      | 20      | 3  | 17      |
| 09           | 10           | 76         | 3  | 73      | 42    | 2  | 40      | 34      | 1  | 35      |
| TOTAL        |              | 350        | 17 | 333     | 219   | 10 | 209     | 131     | 7  | 124     |

ni=total sample size  
mi=number of recaptures  
(ni-mi)=number of new animals in sample

Table B-5: Sample Record - Den 2 (Fall 1985 - Harvest)

| Harvest Date | Males Harvested | Spring * Recaptures | Total Male Harvest | Females Harvested | Total # Harvested |
|--------------|-----------------|---------------------|--------------------|-------------------|-------------------|
| 11/09/85     | 70              | 7                   | 63                 | 40                | 103               |
| 12           | 106             | 10                  | 96                 | 37                | 133               |
| 14           | 109             | 7                   | 102                | 48                | 150               |
| 15           | 53              | 0                   | 53                 | 37                | 90                |
| 21           | 100             | 6                   | 94                 | 74                | 168               |
| 22           | 23              | 2                   | 21                 | 10                | 31                |
| 28           | 19              | 0                   | 19                 | 12                | 31                |
| 04/10/85     | 3               | 0                   | 3                  | 6                 | 9                 |
| 20           | 0               | 0                   | 0                  | 5                 | 5                 |
| TOTALS       |                 |                     | 451                | 269               | 720               |

\* = spring recaptures (all male) not harvested.

Table B-6: Sample Records - Den 1 (Spring 1986)

| Capture Date | Release Date | Both Sexes |     |         | Males |     |         | Females |    |         |
|--------------|--------------|------------|-----|---------|-------|-----|---------|---------|----|---------|
|              |              | ni         | mi  | (ni-mi) | ni    | mi  | (ni-mi) | ni      | mi | (ni-mi) |
| 21/04        | 21/04        | 23         | 0   | 23      | 23    | 0   | 23      | -       | -  | -       |
| 27/04        | 27/04        | 22         | 4   | 18      | 17    | 3   | 14      | 5       | 1  | 4       |
| 29/04        | 29/04        | 73         | 14  | 59      | 57    | 12  | 45      | 16      | 2  | 14      |
| 04/05        | 04/05        | 80         | 11  | 69      | 75    | 10  | 65      | 5       | 1  | 4       |
| 11/05        | 11/05        | 80         | 16  | 64      | 77    | 14  | 63      | 3       | 2  | 1       |
| 13/05        | 13/05        | 95         | 25  | 70      | 95    | 25  | 70      | -       | -  | -       |
| 19/05        | 19/05        | 49         | 29  | 20      | 49    | 29  | 20      | -       | -  | -       |
| 23/05        | 23/05        | 13         | 10  | 3       | 13    | 10  | 3       | -       | -  | -       |
| TOTAL        |              | 435        | 109 | 326     | 406   | 103 | 303     | 29      | 6  | 23      |

ni=sample size

mi=recaptures in sample

(ni-mi)=number of recaptures in sample

Table B-7: Sample Record - Den 2 (Spring 1986)

| Capture Date | Release Date | Both Sexes |     |         | Males |     |         | Females |    |         |
|--------------|--------------|------------|-----|---------|-------|-----|---------|---------|----|---------|
|              |              | ni         | mi  | (ni-mi) | ni    | mi  | (ni-mi) | ni      | mi | (ni-mi) |
| 17/04        | 17/04        | 31         | 7   | 24      | 31    | 7   | 24      | -       | -  | -       |
| 21/04        | 21/04        | 64         | 17  | 47      | 60    | 17  | 53      | 4       | -  | 4       |
| 24/04        | 24/04        | 85         | 28  | 57      | 85    | 28  | 57      | -       | -  | -       |
| 27/04        | 27/04        | 44         | 16  | 28      | 44    | 16  | 28      | -       | -  | -       |
| 29/04        | 29/04        | 109        | 32  | 77      | 101   | 32  | 69      | 8       | -  | 8       |
| 02/05        | 04/05        | 42         | 29  | 13      | 42    | 29  | 13      | -       | -  | -       |
| 07/05        | 09/05        | 76         | 37  | 39      | 75    | 37  | 38      | 1       | -  | 1       |
| 11/05        | 12/05        | 78         | 42  | 36      | 76    | 42  | 34      | 2       | -  | 2       |
| 13/05        | 13/05        | 102        | 51  | 51      | 99    | 50  | 49      | 3       | 1  | 2       |
| 19/05        | 19/05        | 31         | 19  | 12      | 31    | 19  | 12      | -       | -  | -       |
| 20/05        | 20/05        | 57         | 41  | 16      | 57    | 41  | 16      | -       | -  | -       |
| 23/05        | 23/05        | 17         | 14  | 3       | 17    | 14  | 3       | -       | -  | -       |
| TOTAL        |              | 736        | 333 | 403     | 718   | 332 | 396     | 18      | 1  | 17      |

ni=total sample size

mi=recaptures

(ni-mi)=number of new animals in sample

Table B-8: Sample Record - Den 1 (Fall 1986)

| Capture<br>Date | Release<br>Date | Both Sexes |    |         | Males |    |         | Females |    |         |
|-----------------|-----------------|------------|----|---------|-------|----|---------|---------|----|---------|
|                 |                 | ni         | mi | (ni-mi) | ni    | mi | (ni-mi) | ni      | mi | (ni-mi) |
| 26/08           | 26/08           | 21         | 1  | 20      | 8     | -  | 8       | 13      | 1  | 12      |
| 30/08           | 30/08           | 46         | 1  | 45      | 30    | 1  | 29      | 16      | -  | 16      |
| 01/09           | 01/09           | 46         | 2  | 44      | 27    | 2  | 25      | 19      | -  | 19      |
| 03/09           | 03/09           | 30         | 1  | 29      | 23    | 1  | 22      | 7       | -  | 7       |
| 05/09           | 05/09           | 73         | 10 | 63      | 42    | 5  | 37      | 36      | -  | 36      |
| 07/09           | 09/09           | 159        | 20 | 139     | 110   | 17 | 93      | 49      | -  | 46      |
| 11/09           | 11/09           | 92         | 11 | 81      | 51    | 7  | 44      | 41      | 4  | 37      |
| 13/09           | 13/09           | 52         | 7  | 45      | 30    | 4  | 26      | 22      | 3  | 19      |
| 18/09           | 18/09           | 37         | 7  | 30      | 30    | 5  | 25      | 7       | 2  | 5       |
| TOTAL           |                 | 556        | 60 | 496     | 351   | 42 | 309     | 210     | 18 | 192     |

ni=total sample size

mi=number of recaptures in sample

(ni-mi)=number of new animals

Table B-9: Sample Record - Den 2 (Fall 1986)

| Capture Date | Release Date | Both Sexes |    |         | Males |    |         | Females |    |         |
|--------------|--------------|------------|----|---------|-------|----|---------|---------|----|---------|
|              |              | ni         | mi | (ni-mi) | ni    | mi | (ni-mi) | ni      | mi | (ni-mi) |
| 26/08        | 26/08        | 28         | 9  | 19      | 23    | 9  | 14      | 5       | -  | -       |
| 30/08        | 30/08        | 55         | 13 | 42      | 37    | 13 | 24      | 18      | -  | 18      |
| 01/09        | 01/09        | 44         | 5  | 39      | 25    | 4  | 21      | 19      | 1  | 18      |
| 03/09        | 03/09        | 77         | 15 | 62      | 55    | 13 | 42      | 22      | 2  | 20      |
| 05/09        | 05/09        | 40         | 10 | 30      | 25    | 8  | 17      | 15      | 2  | 13      |
| 07/09        | 09/09        | 84         | 16 | 68      | 60    | 14 | 46      | 24      | 2  | 22      |
| 11/09        | 11/09        | 22         | 8  | 14      | 17    | 6  | 11      | 5       | 2  | 3       |
| 18/09        | 18/09        | 243        | 3  | 21      | 16    | 3  | 13      | 8       | -  | 8       |
| TOTAL        |              | 374        | 79 | 295     | 258   | 70 | 188     | 116     | 9  | 107     |

ni=total sample size  
mi=number of recaptures in sample  
(ni-mi)=nuber of new animals