AN ECOLOGICAL STUDY OF SNAKES IN THE QUEBEC LAURENTIANS

BY

G. C. WEARY

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ABSTRACT

G. C. WEARY

M. Sc. Special Program in Wildlife Biology.

C/o Department of Entomology, Macdonald

College of McGill University.

This study describes several facets of the ecology of *Thamnophis sirtalis* and *Storeria occipitomaculata* near the limit of their distribution in the Quebec Laurentians. While the study was based on the mark recapture method, two new techniques were employed: (1) In order to facilitate the capture of a large number of snakes, metal shelters were distributed throughout the experimental plot, it was found that these harboured snakes during specific periods of the day and that this was due primarily to the metal's retention of heat absorbed during the day. (2) An improved method of marking snakes by branding developed during the study proved to have several advantages over techniques previously in use.

The results of the investigation suggest that temperature is the primary factor governing the observed behaviour of snakes in our area. The study has also indicated that a biannual migration between two seasonally suitable habitats, the woods and fields, occurs for approximately half the *Thamnophis* population. The remainder were found to maintain a relatively restricted sphere of activity within which stone piles, perhaps due to their thermal properties, eliminated the need of a fall migration to winter hibernacula in the woods. There was no evidence whatever to support a migration of *Storeria* in our area.

It was found that while the length at birth of *Thamnophis* young was typical (205 mm.), *Storeria* were 24 mm. longer than previously reported. Differences in growth between species and age classes were also evident. An attempt was made to estimate the size of both populations, using five standard formulae for the estimation of animal numbers from recapture data. All estimates with the exception of that obtained using a simplified derivation of the M.L.E. for the geometric distribution of capture frequency, were considered low.

ABREGE

G. C. WEARY

M. Sc. Programme spécial en "Wildlife Biology"
a/s Department of Entomology, Macdonald College
of McGill University.

Cette étude décrit plusieurs facettes de l'écologie des Thamnophis sirtalis et des Storeria occipitomaculata près de la limite de leur répartition dans les Laurentides du Québec. Tandis que l'étude était basée sur la méthode de "mark recapture", deux nouvelles techniques furent employées: (1) Afin de faciliter la "capture" d'un grand nombre de couleuvres, des abris de métal étaient répartis sur tout le terrain expérimental; on a constaté que ceux-ci avaient hébergé des couleuvres durant des périodes précises du jour et que cela était dû principalement à la rétention de la chaleur absorbée par le métal pendant la journée. (2) Une méthode améliorée pour marquer les couleuvres, au fer chaud, a été, dévelopée au cours de l'étude. Cette méthode a plusieurs avantages sur les techniques employées précédemment.

Les résultats de l'enquête suggèrent que la température est le premier facteur qui régit le comportement observé des couleuvres sur notre territoire. L'étude a aussi montré qu'un migration deux fois par année, entre deux habitats convenables pour la saison, les bois et les champs, avait lieu pour approximativement la moitié de la population des Thamnophis. On a constaté que les autres maintenaient un champ d'activité relativement restreint à l'intérieur duquel, des tas de pierres, peut-être à cause de leurs propriétés thermales, éliminent le besoin d'une migration automnale aux bois. Il n'y avait aucune donnée pour faire valoir une migration de Storeria dans notre territoire.

On a constaté que, tandis que la longueur d'un jeune Thamnophis à la naissance était typique (205 mm.), la longueur du Storeria était 24 mm. plus long que rapporté au préalable. Les différences de croissance entre les espèces et les classes d'âge étaient aussi évidentes. Une tentative a été faite pour estimer le nombre d'animaux dans les deux populations utilisant 5 formules courantes pour l'estimation du nombre d'animaux à partir de données de "recapture". Tous calculs, à l'exception de ceux obtenus en se servant d'une dérivation simplifée du "M. L. E." pour la distribution géométrique de la fréquence de "capture", étaient considérés peu élevés.

TABLE OF CONTENTS

I. INTRODUCTION

Earlier activity studies in our area had shown that at least two genera of snakes occurred in sufficient numbers to perhaps play a significant role in the community (Bider, 1968). Although the community includes populations of *Thamnophis* s. *sirtalis*, *Storeria* o. *occipitomaculata*, *Opheodrys* v. *vernalis* and *Diadophis* *punctatus* *edwarsi*, the present study was restricted to an ecological investigation of the two numerically most important species, *Thamnophis* s. *sirtalis* and *Storeria* o. *occipitomaculata*.

Similar studies on these species have been undertaken near their centers of distribution but have never been attempted at the edge of their range. While the study area is in the Quebec Laurentians, within the ranges of *Thamnophis* and *Storeria* (Conant, 1958) its climate is not dissimilar to that nearer the edge of their distribution (Thomas, 1953). In this respect the present study is unique.

A review of the literature reveals a variety of studies on colubrids, many of which deal with isolated aspects of (a) their physiology or (b) their ecology, yet provide an invaluable foundation for more complete ecological studies.

(a) The relation of size to maturity in garter snakes was studied by M. D. Burt in 1928; during the same year C. E. Burt demonstrated that dimorphism in the tail length of garter snakes may be used in sexing. While Mosauer and Lazier (1933) probed the tolerance of desert snakes to light and heat, Spealman (1933) and Tercafs (1963) were interested in the transmission of ultra-violet and infra-red radiation through the keratin layer, and in their possible harmful effects.

(b) In 1933, F. N. Blanchard and E. B. Finster, developed an efficient method of marking snakes, this opened the door to comprehensive ecological studies of snakes which require that the individual be recognized. During a study of the aggregations of *Storeria dekayi*, Nobel and Clausen (1936) found evidence of both, home range and migration but did not elaborate, it was not until 1947 that Stickel and Cope succeeded in proving the existence of home ranges for *Elaphe obsoleta* and *Coluber constrictor*. Leuth (1941), and Carpenter (1956), worked on the relationships between environmental and body temperatures, paving the way for papers such as that of Stewart (1965), on the thermal ecology of garter snakes. A study of the hibernacula of snakes in Michigan by Carpenter (1953), complimented work done by Bailey (1949) on temperature toleration during hibernation, these authors found that survival is most likely below the frost line, but Bailey has shown that garter snakes are capable of withstanding sub-freezing temperatures for a protracted period of time.

More comprehensive ecological studies have yielded information on the fecundity, growth rates, movements and numbers of both *Thamnophis* and *Storeria* populations. These include the work of Blanchard (1937), on the natural history of *Storeria occipitomaculata*, and Carpenter (1952), on the comparative ecology of three garter snake species. Fitch (1965), published the results of a complete ecological study of *Thamnophis sirtalis* in Kansas, and Stewart (1968), a similar paper on the natural history of two Oregon garter snakes.

While these papers are comprehensive, they deal with snakes near their center of distribution. Blanchard (1937) points out that since many species have significant differences in details of habits and morphology in different parts of their ranges, it is desirable that they be studied in various areas. Furthermore, an understanding of the ecology of an organism near the limits of its range is necessary to reveal the factors which limit its distribution. For these reasons an ecological study of Thamnophis and Storeria in the Quebec Laurentians can be of value.

The present study began on May 25, 1967, and was concluded on the 15 of September, 1968; no data was gathered between September 15, 1967 and April 15, 1968. In a period of approximately nine summer months, a total of 1025 captures were made of 425 individuals.

Data obtained from the recapture of marked individuals has revealed differences in behaviour between northern populations of snakes and those nearer the center of their range. An improved method of marking snakes was developed during the course of the work, and a manuscript detailing the procedure is now in press (Weary, 1969).

II. DESCRIPTION OF THE AREA

The field work was done at the Lac Carré ecology laboratory, 2 miles north of the village of Lac Carré, Terrebonne County, Quebec, (latitude 46° 09', longitude 74° 29') an area of the mid-Laurentian series, approximately 65 miles north west of Montreal. A wooded mountain side and an adjacent field were chosen as the experimental plot (fig.1.). The field measured 300 meters in length by 100 meters in width and sloped east west with a gradient of 1/33. The field was bisected by a hill running the width of the plot, 50 meters to the west a ridge cut half way across the field. Thus the area was divided into 3 sub-areas designated the upper (east), mid, and lower fields. The total area under study was approximately 3 hectares, and was bordered on the north and east sides by woods and on the south and west sides by streams.

The vegetation of the mountain side was a mixed coniferous and northern hardwood forest. The understory consisted of hobble bush (Vibernum alnifolium), hazelnut (Corylus cornuta) and a few suppressed conifers (Bider, 1961). Thick patches of moss (Lycopodium sp. and Polytrichum sp.) were common in the field, especially along the forest edge. Poverty grass (Danthonia spicata) and sheep's fescue (Festuca ovina) were ubiquitous and grass litter frequently produced thick mats close to ground level, as did the mosses. These areas of matted vegetation provided excellent cover for both snakes and field mice.

Spirea (Spiraea latifolia) and planted conifers, particularly jack pine (Pinus banksiana), were common in the mid field. There were several stone piles within the study area which provided cover for Thamnophis, as well as other small vertebrates.

III. FIELD METHODS

A. Capture - Recapture

The majority of workers studying the ecology of snakes, sampled the population by "systematic" searches of the ground cover, using walking sticks to arouse and discover any snake present (Blanchard, 1937, Carpenter, 1952, Klimstra, 1958). Tinkle (1957) painted numbers on logs and boards to insure accuracy in release and recapture data.

Previous feasability studies in our area by Drs. J. E. Mosimann and J. R. Bider in 1958 (personal communication) indicated that many snakes could be captured beneath pieces of tin. To capture large numbers of snakes with the expenditure of a minimum number of man-hours, this technique was adopted and extended. Shelters or "tins", as they are called throughout this paper, were constructed from sheets of galvanized iron one meter square some of which were framed with 1" x 1" lumber to aid in handling and to raise the tin above ground level (fig. 2a.). One meter square was an ideal size for the tins as they could be quickly turned over to expose any snakes beneath.

Initially sample tins were placed in the three sub-areas into which the plot was divided. Each of these tins was provided with Taylor thermometers to register air temperatures at one inch, and at three feet above the ground as well as the temperature beneath the tin plate. During preliminary trials the tins were employed in two ways, with the frame down and reversed. In order to observe short term temperature fluctuations beneath the tins, temperatures were recorded every five minutes over an hour on each of five days. Temperatures were recorded every two hours on all other days. Figure 3a indicates that the mean temperature difference between framed and unframed tins was 5.5° C., however as there was no significant difference in temperature fluctuation, number or species of snakes captured beneath the two tin types, the remainder of the tins were not framed.

To effectively sample the area, one hundred numbered tins were positioned approximately equidistant one from the other (fig. 1.). Twenty-seven of these were in wooded areas and do not appear in figure one.

B. Routine

Temperatures at the sample tins were taken every two hours throughout the study and were considered representative of the other tins in the same area. At the outset of the study the tins were checked for snakes several times each day, ultimately it was found that two "runs", one at 09.00 and another at 16.00 hours, yielded the most captures per unit time. Collections were subsequently confined to these times plus or minus an hour.

The traditional techniques of snake handling proved adequate for the purpose of this study and only slight modifications were found necessary. As the snakes are not venomous they were captured by hand or first pinned with a snake stick. Transporting snakes in the field was facilitated through the use of small bags, measuring 15 x 450 centimeters, sewn from white unbleached cotton. Snakes were handled only briefly while being marked, measured, sexed and sometimes relieved of their stomach content. All snakes were returned to the point of capture within the hour.

During the study two marking codes were used. The first was a simple two digit system whereby scales were counted posteriorly from the anus, marking the second left and fourth right designated the animal as number twenty-four. As it is often difficult to determine which scale is counted as first, due to the presence of a diminutive scale posterior to the anus, this code was rejected in favour of that developed by Blanchard and Finster (1933). Their system involved the marking of a maximum of three scales, the first on each side always being an even number to eliminate the problem of the diminutive scale. Marking the second and fifth left, and fourth right, designated the snake as number 254.

C. Marking

As the methods of marking snakes described in the literature proved both slow and awkward, effort was put into devising a better technique. The following is the major part of a manuscript detailing such a marking procedure (Weary, 1969, in press).

. . .

Two techniques have been developed for marking snakes, one based on tattooing and another based on scale clipping.

Woodbury (1948) used a battery operated tattooing needle to place a number under the skin. Two disadvantages to this system were that the inked numbers: (1) had a tendency to fade, and (2) were not readily visible on pigmented surfaces.

The best known, and most widely used method, was devised by Blanchard and Finster (1933). Caudal scales were clipped in combinations so that each individual was tagged with a distinctive mark. The process seemed to be painless and if care was taken, drew no blood. When there was no regeneration of the clipped scales, a scar remained, marking the snake for life. Some regeneration of clipped scales was reported by Blanchard and Finster (1933), Conant (1948), and Tinkle (1957).

At the outset of a study of snake populations in the Quebec Laurentians, both red-bellied snakes (<u>Storeria occipitomaculata</u>) and garter snakes (<u>Thamnophis sirtalis</u>) were marked using Blanchard and Finster's method. Three drawbacks to the system soon became evident: (1) several minutes were required to carefully remove a complete caudal scale, (2) despite precautions, blood was frequently drawn, allowing a possible infection, and (3) clipping proved to be very difficult on young snakes less than four inches long. These problems were circumvented by use of an electric needle with which snakes were branded.

As house current was available in the field laboratory, branding was done with a 50 watt pyrographic needle, available in hobby shops for less than five dollars (fig. 2b). The heating element of the needle was filed to form a sharp cutting edge. Brief contact with the heated needle was sufficient to burn a scale right to the base without drawing blood. More than five hundred snakes were branded, those recaptured after two years have shown no signs of regenerating burnt scales.

In the absence of a 110 V. a-c power supply, snakes may be branded with an American Beauty soldering pencil, model B2000-L, powered by a 12 volt rechargeable battery and any commercially available d-c - a-c inverter capable of producing 30 to 40 watts. The apparatus weighs about 10 pounds and costs less than fifty dollars.

The technique has proven successful and has these advantages: (1) speeds up the marking procedure, (2) is less likely to cause an open wound, which might become infected, (3) is practical for marking the smallest snakes, and (4) produces a mark which does not perceptibly change over a two year period.

IV. MICROHABITAT BENEATH TINS

A. Temperature

Leuth (1941) demonstrated that under laboratory conditions, there was a close correlation between snake and cage temperatures, and that snakes had no inherent temperature rythm. To be certain our temperature records were relevant to our study, a similar correlation was sought in the field.

A telethermometer (Yellow Springs Instrument Co. model 44TE) and thermistors were used to record the internal temperature of an adult male Thamnophis, simultaneously with temperatures of the soil surface, the air at one inch, and at three feet above the ground. Readings were taken every minute for 30 minutes, during this period the snake and all recording thermistors were periodically shaded to simulate the passing of cloud cover. Tests revealed a correlation at the one percent level ($R = +.74$) between the temperature one inch above the surface and the internal temperature of the snake, there was no correlation between the latter and either, the temperature of the soil surface or that of the air three feet above it, at the one or five percent level ($R = -.29$, $R = -.23$). This experiment revealed the importance of a particular part of the microclimate to our snakes, and that our readings would indeed reflect thermal conditions experienced by the animals themselves.

In June 1967 the tins were checked for snakes every two hours on each of five days. This revealed two daily peaks in the utilization of tin cover by our animals, one at 09:00 hours and another near 16:00 hours. Further study suggested that these periods of maximum tin utilization resulted from the varying relationship of temperatures beneath the tin and those near the ground.

Tin temperatures remain relatively constant while air temperatures near the surface fluctuate with slight changes in wind and cloud cover (fig. 3b). Beneath a tin a poikilotherm such as a snake has a slightly moderated environment with less temperature fluctuation (3-4°C.) than in exposed positions (8-10° C.). In the field snakes may regulate their temperature by alternately exposing themselves to, and seeking shelter from, the sun's rays. A tin would eliminate the necessity for such movements, permitting a snake to avoid the risk of predation while exposed.

Figure four shows the daily fluctuation of temperatures beneath the tin, at one inch, and at three feet above the soil surface. Typically the temperature beneath the tin is higher than the air at either level until 09:00 hours. On clear summer mornings snakes frequent the tins between 07:00 hours and 09:00 hours. Basking under a tin during this period allows a snake to warm rapidly and become active early in the day.

During the warmest part of the day (09:00 to 16:00 hours) surface temperatures are higher than temperatures under the tins. More important is the fact that tin temperatures are near the maximum tolerable, (Stewart, 1968) (Cowles and Bogert, 1944) and snakes abandon the tins possibly in favour of more substantial protection from the heat.

The maximum number of snakes were found beneath the tins between 16:00 hours and 19:00 hours, when surface temperatures dropped below those recorded under the tins. Figure four illustrates that while the tin itself begins to cool at 16:00 hours, the temperature beneath it remains several degrees warmer than the surface. A similar phenomenon exists in conjunction with roads and rocks which hold heat stored during the day. While these objects hold heat due to their thermal properties, a tin plate on the ground accomplishes the same result by maintaining an insulating layer of air next to the soil surface.

Should rain fall at either 09:00 or 16:00 hours, no snakes are found beneath the tins. Rain cools the tins and the temperature beneath them falls below that of the surface (table 1.). During periods of sunshine immediately following rain the tins warm rapidly to a temperature greater than that of the surface, at such times large numbers of snakes are captured beneath the tins regardless of the time of day. This warming of the tins after a rain is similar to the increase of tin temperature in the early morning of a clear day. The result in both cases is an increase in the snakes' utilization of the tin cover.

B. Other Factors

Relative humidities beneath the tins were measured three times during the study using cobalt thiocyanate papers. The mean relative humidity of those tins harbouring only Thamnophis was 64%. Those tins under which only Storeria were found had a mean relative humidity of 61% while the tins shared by both species exhibited a mean of 63%. Chi-square tests revealed no significant difference in the humidity beneath tins frequented by the two species.

Although the mean relative humidity beneath tins harbouring snakes was near 60% there was no indication this was a preferred humidity. To ascertain if a preference existed, the humidity range (0 - 100%) was divided into 19 groups each having a range of 5 percent. The number of tins in each group was compared with the number of snakes captured beneath them. Chi-square tests revealed that the number of snakes captured in any "humidity group" was a function of the number of tins in that group. This indicates that snakes utilize the tins showing no preference for a specific humidity range. The large number of snakes found beneath tins with a relative humidity of 60% is simply a reflection of the many tins having that relative humidity.

In addition to data concerning relative humidity beneath the tins, notes were made on the tins' exposure to the sun, their elevation, the type of vegetation they covered, and the presence of other organisms beneath them. While the tins were similar in their exposure and elevation they differed in other respects. Although most tins covered a combination of grasses, plants and mosses, each had a dominant characteristic. While the data does not lend itself to statistical tests, it was found that Thamnophis were never associated with tins covering moss or sandy areas. This is perhaps due to the lack of large passages beneath these tins. One third of the tins harbouring only Thamnophis also sheltered Microtus pennsylvanicus, an important part of this snake's diet (Hamilton, 1951). More than one half of those tins beneath which only Storeria were found, covered a thick tangled mat of moss, (Polytrichum and Lycopodium species). One third of the total supported colonies of ants as evidenced by the large amounts of sand and numbers of eggs transported to the surface. Nobel and Clausen (1936) and Carpenter (1953), also found Storeria to be associated with ant colonies.

The efficiency of the tins in capturing snakes can be predicted for any period if temperature beneath the tin and surface temperature are known. Maximum utilization of tin cover occurs when the temperature beneath the tin exceeds that at the surface, both however must be within the voluntary minimum-maximum temperature range (9° C. - 35° C.) as given by Carpenter (1956). While such conditions are normally met at 09:00 hours and 16:00 hours, rain or prolonged cloud cover may cause a shift in the time of their occurrence. By referring to the temperatures taken at the tin sites, and disregarding all other factors, we were able to adjust the time of the "runs" to coincide with periods of maximum tin utilization by snakes.

In summary the tins are not used to the same extent throughout the day. This periodic use of the tins is primarily a result of the thermal conditions of the microclimate beneath them. The microclimate under a tin is perhaps more favourable to a reptile than are surface conditions as: (1) temperature fluctuation is moderate lacking extremes found on the surface and (2) the tins warm more quickly, and cool more slowly than the surface, thus providing elevated temperatures under certain circumstances.

V. MOVEMENT

Studies of the movement of snakes have produced varied results. Blanchard and Finster (1933) concluded that the wanderings of snakes may or may not be extensive and are not predictable. Seibert and Hagen (1947), and Stickel and Cope (1947), believed this conclusion was due to the fact that no attempt was made to release the snakes where originally captured and the transplanted animals scattered widely, seeking former home ranges or to restore the population density normal for the habitat. These authors suggested that home ranges do exist as the distances travelled by the snakes between captures was far less than could be expected, often only several yards per day. In fact _Elaphe obsoleta_ and _Coluber constrictor_ usually moved no farther in a year or two than they did in a few days. Nobel and Clausen (1936) presented evidence to show that _Storeria dekai_ have ranges; "The marked snakes usually remained in the region where they were released providing they were originally found there." They also observed that 40% of those released some distance from where they were captured returned to the original location within 70 days. Stickel and Cope (1947), believe that this homing tendency is one of the best tests of an animal's adherence to its home range.

Carpenter (1952), found that the movements of _Thamnophis_ were restricted, he proposed the term "activity range" which differs from home range in that it contains no home or nesting site. Fitch (1965) found that snakes held specific summer ranges in meadows and migrated to areas providing suitable hibernacula in the fall. Bider (1968), from an analysis of activity on a sand transect which runs through my experimental plot, has suggested that female _Thamnophis_ may undertake a spring and fall migration.

A. Migration

Dasmann (1966), defines migration as a two way movement... from one seasonally suitable habitat to another with a subsequent return to the first. While such a pattern has been found in the movements of Thamnophis in our area, the data does not indicate a similar migration of Storeria. Of 30 adult Storeria recaptured more than three times (some as many as twenty-five times) only 5 moved farther than the tin immediately adjacent to the one under which they were originally captured. These five individuals wandered throughout the plot. As the mean distance between adjacent tins is only 10 meters, and as Storeria generally did not occupy more than two tins during the study period, there is little data on their movement. It does seem clear however, that there is no migration for Storeria in our area.

Evidence in support of a migration of Thamnophis was obtained from the recapture of marked individuals first captured in the eastern sector (closest to the woods) and subsequently farther west. Certain individuals were recaptured frequently as they moved the 300 meters to the western edge of the plot, others however were only captured over shorter distances.

Among those animals captured more than three times, two distinctly different types of movement occurred: (1) a long swift movement of more than 90 meters in two weeks and (2) a restricted movement of less than 11 meters in a month. There was not a single individual whose movement placed him in an intermediate category.

As these two types of movement were clearly different they were treated separately, the long swift moves being considered as migratory, and the shorter movements, as moves within a home or activity range.

Figure 5 shows the migratory movements and the months in which they occurred. During the months of May and June, all movement was in a westerly direction, away from the wood into the fields. July is a transitional month with some movement in both directions. During August and September, the return migration occurs and all significant, unidirectional movement is from west to east.

If migration is in fact occurring at specific times during the season, snakes should be less sedentary, hence less likely to be captured repeatedly under the same tin at such times. Similarly areas through which snakes move should show a greater number of single captures than areas in which they are more sedentary.

On the basis of Chi-square tests the hypothesis that the number of single captures in each month were equal, was rejected. The hypothesis that the number of single captures per month in May, June, August and September was double the number during July, was acceptable. This indicates that migration occurs in the spring and fall months. A similar test confirmed that the snakes migrate through the upper and mid fields, to and from the lower field on the western edge of the plot. All migrants were mature individuals and their sex ratio was 1:1, not different from that of the entire population.

A comparison of the microhabitat of the field and woods suggests reasons for the observed migration between the two areas. In our area the woodland provides more numerous and suitable hibernacula than does the field, principally due to a more favourable fall and winter microclimate. In the spring, field soils thaw more rapidly than do those of the forest, thus when snakes emerge from hibernation, the fields are already warm and can provide a more suitable microclimate than the forest. As the trees begin to leaf and block the sun's rays from the forest floor, Thamnophis move into the open fields. In the fall forest temperature fluctuations are moderate in comparison to those in cleared areas, (Munn, 1966) and due to leaf litter, heat radiation and frost penetration are reduced considerably in the woods. Clearly a migration between the fields and the woods would permit optimum utilization of two very different microhabitats.

Because too few Thamnophis young were recaptured in their first spring, data on their movement is poor and results are inconclusive. However, it is possible that the young spend at least their first winter in the fields as only two in fourteen migrated to the wood, the remainder were found in the lower field during early May.

B. Activity Range

As data on migration was processed, it became evident that over half of the animals neither followed the migratory pattern nor wandered at random, but were extremely restricted in their sphere of activity. In addition to these, several of the migrants on completing their spring migration, confined their activity to a rather small area.

Carpenter (1952) found that the common garter snake had an average range of 2.07 acres - 600 feet long and 150 feet wide. Fitch (1965) reported a home range of 35 acres for Thamnophis males and believed the discrepancy between his conclusions and those of Carpenter arose from differences in techniques and interpretations of results, he suggested that although Carpenter did check some of the peripheral areas, "possibly many of the snakes had ranges extending beyond the limits of the study area." In order to obtain a better estimate of home range, Fitch discarded the longest and shortest moves (20% of his data) which were "unrepresentative of home ranges." When 20% of our data is discarded, it does not completely eliminate all animals which do shift their range in the spring and fall, as nearly 40% of our population underwent a biannual migration.

Our data indicates that 60% of those snakes captured more than three times, confined their activity to an area less than 30 meters in diameter for a month or longer (table 2). Such animals were considered to have an activity range, as their distance travelled per unit time was clearly different from that of migrating animals. The average migrant moved at least 90 meters, roughly 9 times that distance, in a maximum of fourteen days.

The average area of the intermigratory range was found to be .04 hectare, (radius, 11.1 meters) considerably smaller than calculated by either Carpenter or Fitch. As captures were mainly made beneath regularly spaced tins, the actual radius may be somewhat larger than I have indicated, but no more than half the distance to the surrounding tins, (Hayne, 1949) in which case the radius would average 17.1 meters and the area .09 hectare. This method of calculating range size from trapping data is commonly used in mammalogy. Periferal areas were sampled by trapping and searching, there was no indication that our population utilized these areas. The possibility exists that animals may have left this range in the late evening when searching and trapping were not in progress. Activity studies however, have indicated that nocturnal movement is most common on warm fall nights. This activity is probably related to the fall migration rather than excursions outside the activity range. Despite the possibility of nocturnal movement between captures the fact remains that in each case there was a subsequent return, often to the precise location of previous capture. Thus although this trapping technique may not reveal the total extent of a snake's wanderings, it has shown beyond question that a preferred range exists.

During the course of the study three marked individuals were inadvertently released more than 30 meters from where they had been captured, in each case the snake returned to the original locality within a month. Homing tendencies were also exhibited by two thirds of all Thamnophis that were recaptured during the second year, these were recovered beneath the same tins they had occupied the previous year. Nearly all the remaining one third were recovered in the same field as in the previous year, although not beneath the same tin.

Among these were migrants, not confined to an activity range the year round. According to Stickel and Cope (1947) this homing behaviour is a good indication that an "activity range" does exist.

To summarize, the data obtained on the movement of snakes suggest that the population may be divided into two main groups, one which undergoes a biannual migration (40%) and the other 60% which exhibits strong activity range behaviour, of the total population, 10% exhibit both types of behaviour at different times. Those snakes which do not migrate, possess activity ranges closely associated with large piles of rocks (fig. 6.). It is thought probable that these piles provide suitable hibernacula and thus eliminate the need to migrate in a portion of the population. Conversely, the data shows that migrants, after spending the winter in the woods, will occupy an inter-migratory range centering on a clump of bushes or a particular tin, rather than a stone pile.

In an attempt to verify these observations, several of the smaller piles were excavated early in the spring before the snakes emerged from hibernation. Although five of the ranges centering on one of these piles had been occupied as late as October 30, no hibernating snakes were unearthed. Beneath each pile a number of tunnel entrances lead downward, unfortunately as I was unaware of the precise nature of a hibernaculum, and as the loose soil and persistant rain made it difficult to follow the tunnels, digging was stopped.

Further review of the literature revealed that although snakes can survive sub-freezing temperatures for up to 28 days (Bailey, 1949), survival is more certain below the frostline. In the open field the frostline may reach several feet in depth, while under a stone pile the depth of frost penetration is considerably reduced, due to the insulating layer of air trapped between the stones. For these reasons I feel the possibility remains, that stone piles do provide adequate hibernacula for a portion of the *Thamnophis* population.

VI. GROWTH

All snakes were marked when captured. Growth was determined from measurements of recaptured individuals. Both body length (snout to anal scale) and total length (snout to tip of tail) were recorded but total lengths were used to determine growth rates. In the few cases where part of the tail was missing, total length was estimated using the body-tail ratios given by Seibert and Hagen (1947). Error in measurement was estimated by comparing a series of measurements on a single individual. The error did not exceed 1 cm. even on the largest animals.

Stewart (1968) states that the mean length of *Thamnophis sirtalis* young is probably near 200 mm. The 45 animals born during this study averaged 205 ± 14.32 mm. Seventy-nine *Storeria* born during the same period had a mean length of 110 ± 13.00 mm., considerably larger than 86 mm. as previously noted in Michigan (Blanchard, 1937). The average length of *Thamnophis* young was six percent greater in 1968 than in 1967, this is likely due to the increased size of the breeding females. Stewart (1968) has also noted a positive correlation between the size of newborn snakes and maternal size.

The time of maximum growth in Quebec is limited to the warmer months, May through September. Three years data suggest that *Storeria* have a longer growing season than do *Thamnophis*. *Storeria* are active in late April, two weeks before *Thamnophis* have been found, and captures continue late into October after *Thamnophis* have sought out suitable hibernacula.

A difference in growth pattern between *Thamnophis* and *Storeria* is evident in the newly born snakes. During the first two weeks of September young *Storeria* grow nearly 25 mm. at a rate of 11 mm. per week, this growth continues later into the fall, as by May 1 they have reached a mean length of 156 mm. Thamnophis on the other hand, do not grow appreciably from September 1 to 14, although they add 25 mm. to their length at birth by May 14. While young Storeria show their maximum growth rate immediately after birth, Thamnophis grow most rapidly during the following spring and summer (10 mm/week). Growth rate in both species decreases yearly, becoming negligible when maximum length is attained. Maximum lengths of Thamnophis and Storeria in our area were 865 mm. and 343 mm. respectively. Growth rates, and mean lengths of snakes in different age classes are summarized in table 3.

The data of table 3 was derived from figure 7, a plot of the increase in length of individuals with time. Seibert and Hagen (1947) published a similar figure but found that it was difficult to determine the growth rate of second year individuals due to overlap in size between age groups.

Figure 7 shows three distinct size groups in the Thamnophis population. The young are born at approximately 205 mm. in the fall and begin growth the following May with an initial length of near 230 mm., growth continues to an average of 388 mm. in mid September at a rate of 10 mm/week. Some growth occurs in late fall and early spring as the mean length of individuals entering their second season of growth is 406 mm., growing nearly 9 mm. each week, they attain 549 mm. by fall. During the third year of growth Thamnophis increase in length from 559 mm. to 648 mm. at a rate of 5.5 mm./week. Growth after this stage (table 3), has been estimated from the rates of larger individuals in the population.

Interpretation of figure 7 is facilitated if it is accepted that the first four individuals captured in both 1967 and 1968 (those crossing the "winter line") have completed one season's growth and are in their second. This may be inferred from extending their growth curves downward to size at birth. Similarly the remaining 6 individuals captured in both years are in their third year of growth.

Blanchard and Finster (1933), found little evidence that growth took place in the months of April and October, the nearly vertical slope of growth curves between the last captures in 1967 and the first captures 1968 would tend to support their findings.

The mean lengths and growth rates for Storeria occipitomaculata were derived in a similar manner and are summarized in table 3.

Seibert and Hagen (1947), and Blanchard and Finster (1933), point out that growth rates vary with the season and habitat, for this reason care should be taken when comparing growth rates of snakes in various areas. Fitch (1965), found that in Kansas, first and second year Thamnophis typically grew at a rate of 1.2 mm. per day before the rate slowed with approaching maturity. It seems that Thamnophis in our area grow faster (average = 9.4 mm. per week) than this average reported by Fitch. Rates in our area are very similar to those published by Seibert and Hagen (1947) in Illinois, who report rates of 11.1 mm. and 9.3 mm. per week for first and second year individuals respectively.

The time of parturition varies from year to year with the mean temperature encountered during pregnancy (Blanchard and Blanchard, 1941). Blanchard (1937) gives August 10-23 as the range of birth dates for Storeria raised in the laboratory, but he has observed births as early as July and as late as September in the field. Similar dates are reported for Thamnophis (Seibert and Hagen, 1947).

Thamnophis in our area gave birth between August sixteenth and September tenth, young Storeria were later in arrival, first appearing on August twenty-first, no new young were found after September tenth. While Wood (1945) recorded a litter of 57 Thamnophis, Fitch (1965), in reviewing the literature, concluded that the average litter contained between 12.9 and 18.0 young. It seems unlikely that brood size for Thamnophis in our area even approached these dimensions. At the time of parturition, tins known to shelter gravid females were checked for young. It was assumed that a group of young under the same tin would be from the same litter and would give an indication of litter size. While this method may not reveal all young born, at no time did we find more than 5 newly born garter snakes beneath a tin. The average "litter" size for the 15 gravid females discovered was 3. Storeria litter size is reported to average 7.2 (Blanchard, 1937). This may well hold for our population as several "litters" examined contained as many as nine young. Eleven "litters" were discovered giving a mean brood size of 7.2.

Since young Thamnophis are active and agile soon after birth, and easily avoid capture, the estimate of 3 per litter is considered low. Young Storeria however, are more sedentary, and the estimate of their litter size is more accurate. To verify litter size under natural conditions, four visibly pregnant female snakes (two of each species) were confined in a 5 x 5 meter quadrat. The quadrat was located in the lower field and was surrounded by three foot polyethylene walls, the bottom edges of which were sealed with sand to prevent the escape of any snakes. The animals were provided with a tin, a stone pile, and free water. When the experiment was terminated, both female Thamnophis were recovered but only three young could be found. Of the two female Storeria only one remained, no young of this species were recovered. Although this attempt to verify litter size failed, I believe the method has merit as confining snakes to laboratory cages interferes with their feeding and may alter the size and success of their broods.

VII. POPULATION SIZE

Certain basic assumptions underlie all methods of capture-recapture analysis, these must be met to ensure the accuracy of the resulting estimates. (1) Marked animals are not affected by being marked and the marks will not be lost. (2) Marked animals become completely mixed in the population. (3) The population is randomly sampled. (4) Sampling time is small in relation to total time. (5) The population is a closed one. (6) No births or deaths occur in the period between sampling (Southwood, 1966).

How closely does the situation in our population approximate these conditions? It was assumed that my marking procedure was permanent and did not affect the marked animals (Weary, in press). Carpenter (1952) using a similar marking method also made this basic assumption. He also believed that marking and immediately releasing a snake where found was sufficient to allow complete remixing. This procedure was followed during our study and the mixing of marked and unmarked individuals was evident in our population. Less than 1% of the individuals recaptured demonstrated a tendency to remain precisely where released and in each instance where this occurred, the snake had been inadvertently injured. It is often difficult to verify the assumption that sampling is completely random (Delury in Southwood, 1966) however the probability of recapturing a marked animal should be the same as that of capturing any member of the population. Variation in the probability of capture due to differences in behaviour among age classes can be allowed for; bias introduced by differential trap response however, is difficult to remedy.

The population is thought to contain a number of trap-prone individuals which will result in a disproportionate number of recaptures and an underestimate of the population.

While marked snakes evidently are not attracted to any single tin and move within the population, there is evidence to show they seek out other tins and thus are trap-prone. Leslie, Chitty and Chitty (1953) developed a test for non-random sampling. Chi-square analysis is applied to the frequency distribution of recapture in a group of animals. This test when applied to our data demonstrated that being captured one or more times did increase the animal's subsequent chance of recapture. Randomness of recapture was rejected at the 5% level, thus our population does contain trap-prone individuals.

The timing and duration of sampling caused no problem in estimating the population as the influence of recruitment and reinvasion were easily eliminated. Recruitment occurs only in August, young of the year are easily recognized and eliminated from the calculation. Reinvasion is negligible as the population is almost certainly a closed one, contained by natural barriers to movement (fig. 1.). Mortality between sampling periods was considered negligible as predators were few and no instances of predation were observed in two years.

A computer program was written to apply several estimation formulae to the available data. The Lincoln Index, Schnabel, Schumacher Eschumeyer and Chapman methods were used (Lagler, 1966). A maximum likelihood estimate for the geometric distribution of capture frequency suggested by Edwards and Eberhardt (1967), was used as a check and for further comparison of population estimates (table 4.).

Of the methods used only one gave an estimate of the population which could be considered accurate. Estimates derived by the Schnabel formula are considered low as they are in each case lower than the actual number of animals marked. Similar underestimates were obtained using the Schumacher Eschmeyer method of analysis. Flyger (1959) has pointed out that the Schnabel method gives an estimate of the trappable animals in a population which is always less than the total number, it can in fact result in an estimate lower than the number of marked animals known to exist in a population. This is particularly likely to occur if a large proportion of the population is captured and animals become trap-prone as ours do. Edwards and Eberhardt (1967) as well as Nixon, Edwards and Eberhardt (1967) found that both Schnabel and Schumacher methods grossly underestimated their populations, probably due to the differential trap response among animals.

The application of Chapman's formula to the data gives estimates which are slightly greater than the total number of animals captured, but as unmarked snakes were being captured even after the last sampling period, it is certain that any population estimate approximating the number of snakes marked is low.

Seibert and Hagen (1947), Seibert (1950), and Carpenter (1952) have used the Lincoln Index to estimate snake populations with some success. Our population was estimated at 150, 75 of each species. It is important to realize that this is most certainly an underestimate due to the failure of assumption three.

Edwards and Eberhardt (1967), and Nixon et al. (1967) working with known populations and unbiased sampling methods, compared various population estimation formulae. They concluded, that in spite of trap-prone tendencies in their population, the simplified derivation of the M.L.E. for the geometric distribution of capture frequency, produced the best population estimates from livetrapping data. This method applied to our data gives estimates of approximately twice the number of animals marked, and is considered to best represent the actual number of animals in our population.

VIII. SUMMARY AND CONCLUSION

The object of this study was to obtain information on the ecology of *Thamnophis sirtalis* and *Storeria occipitomaculata* near the limit of their distribution. The project was carried out sixty-five miles north west of Montreal in the Quebec Laurentians during the summer months of 1967 and 1968.

While the "mark-recapture" method was the basis of this study a departure from the usual practice was made in that the area was not systematically searched for snakes. As earlier studies had suggested that many snakes could be found beneath pieces of metal, sheets of galvanized iron ("tins") were scattered throughout the plot in an effort to capture a maximum number of snakes with the expenditure of a minimum number of man-hours.

Tests on two types of "tins", framed and unframed, revealed no significant difference in temperature fluctuation, number or species of snakes captured beneath them, and resulted in the majority of the shelters being constructed without a frame. To effectively sample an area of approximately 3 hectars, one hundred numbered tins were positioned equidistant one from the other throughout the area.

Through trial and error, a sampling routine was established, two "runs" per day one at 09.00 and another at 16.00 hours yielded the greatest number of captures per man-hour. During the study 1025 captures were made of 425 individuals. Details on the location movement and size of each individual were recorded at each capture.

An important by-product of this study was the development of an improved method of marking snakes by branding. This technique has several advantages over those previously employed: (1) it speeds up the marking procedure, (2) is less likely to cause an open wound which might become infected, (3) is practical for marking the smallest snakes, and (4) produces a mark which does not perceptibly change over a two year period.

Experiments in the field revealed that the internal temperature of snakes was most closely correlated with the temperature near the ground, temperature readings taken at this level were used throughout the study as they reflected thermal conditions experienced by the snakes themselves.

Frequent sampling revealed two daily peaks in the utilization of tin cover by snakes. These peaks were found to coincide with periods during which the temperature beneath the tin was higher than temperature at the surface. Such conditions normally occurred at 09.00 hours and 16.00 hours but rain or prolonged cloud cover shifted the time of their occurrence. By referring to the temperatures taken at the tin sites we were able to adjust the time of the sampling "runs" to coincide with the periods of maximum tin utilization by snakes.

Study of the movement of snakes indicated that approximately half the _Thamnophis_ population undergo a biannual migration. Chi-square tests supported the hypothesis that migration between the woods and lowest areas of the field, occurred in the spring and fall months. It was thought that such a migration allowed optimum use of the seasonally suitable microclimates found in the woods and field.

Over half the _Thamnophis_ captured more than three times confined their activity to an area less than 30 meters in diameter for a month or longer, the activity range of these individuals was calculated as .09 hectar, smaller than previously suggested. Further evidence of the existence of an activity range was found in the homing behaviour of displaced individuals.

As it seemed, from the results of other workers that the size of activity ranges varied with the type of habitat, the evidence that both activity range and migration behaviour existed in our population was considered more important than their absolute size. Among those animals captured more than three times two distinctly different types of movement occurred: (1) a long swift move of more than 90 meters in two weeks and (2) a restricted movement of less than 11 meters in a month. There was not a single individual whose movement placed him in an intermediate category. Those individuals having a restricted sphere of activity (non-migrants) occupied ranges which typically centered on a large stone pile, migrants on the other hand were seldom associated with these structures. It seemed probable that these piles provided suitable hibernacula for a portion of the population and thus eliminated the need to migrate.

Data obtained on the movement of Storeria was inconclusive. Although this species was active, their sphere of activity was extremely small and difficult to measure using our fixed tin technique.

Growth statistics have been obtained for both Thamnophis and Storeria in our area. The mean length of Thamnophis at birth was near 205 mm., close to that reported in other areas. Storeria on the other hand had a mean length of 110 mm. at birth, considerably greater than previously suggested. Both species give birth in early September, somewhat later than reported in Michigan and Illinois.

Differences in the pattern of growth between the two species have become evident, while Storeria young grow at a rate of 11 mm. per week immediately after birth, Thamnophis grow only slightly until the following spring when their maximum growth rate of 10 mm. per week is attained.

Growth rates of Thamnophis in different age classes correspond closely only with those found in Illinois, but may not be significantly different from those rates found in other areas unless the habitat and season are similar.

Data on litter size were inconclusive but suggest that while Storeria bear litters of a size equal to those farther south, Thamnophis may produce fewer young in our area than elsewhere.

An attempt was made to estimate the numbers of both Thamnophis and Storeria. Bearing in mind that our populations contained a number of trap-prone individuals, five standard formulae for the estimation of animal numbers were applied to the data. Due to the failure of the assumption that the population is randomly sampled, i.e., that each individual has an equal chance of capture, estimates derived by four of the methods were low. The simplified derivation of the M.L.E. for the geometric distribution of capture frequency, as it seems less affected by trap-prone tendencies in a population, gave what are considered to be the most reasonable estimates of the number of animals in our population.

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XI. LIST OF FIGURES

Figure 1.

Map of the study area showing the distribution of tins, the orientation of fields one, two and three, and the location of rock piles.

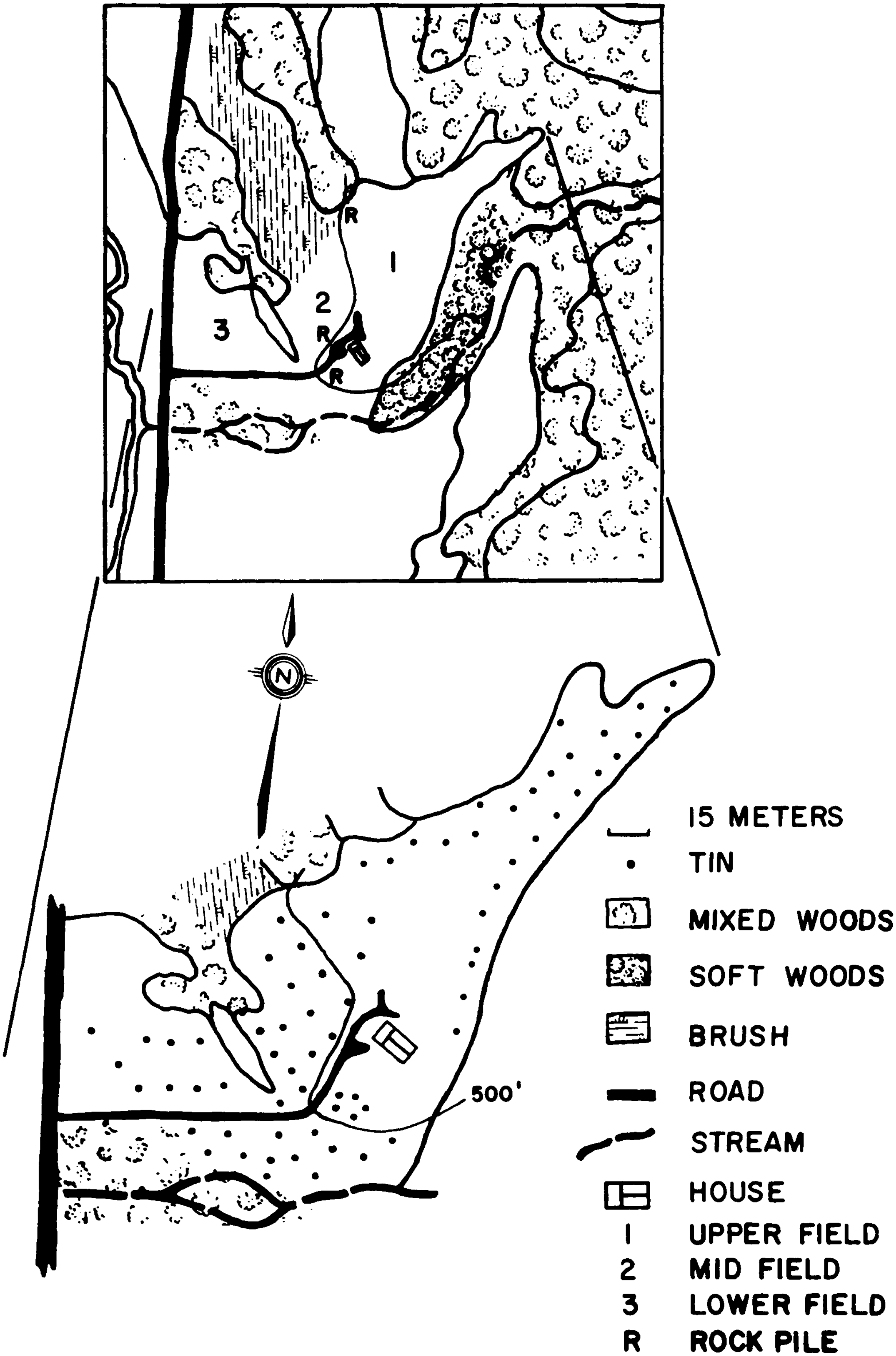
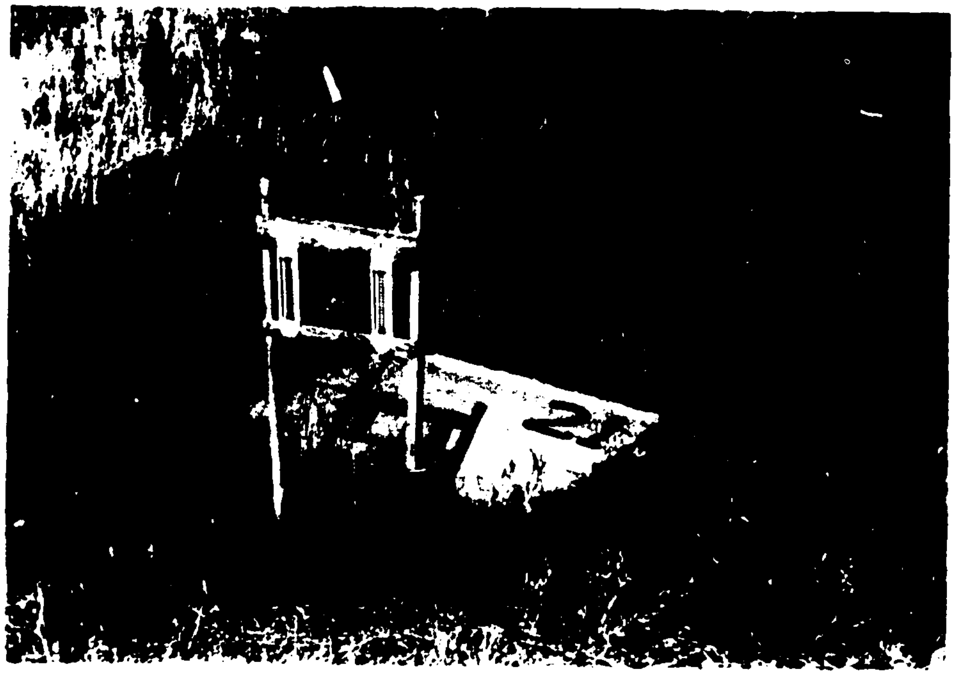

1
2
3
R
R
R
N
500'
15 METERS
TIN
MIXED WOODS
SOFT WOODS
BRUSH
ROAD
STREAM
HOUSE
1 UPPER FIELD
2 MID FIELD
3 LOWER FIELD
R ROCK PILE

Figure 2.

(a) Photograph of a tin with Taylor indoor-outdoor thermometers to register air temperature at three feet and at one inch above the ground as well as the temperature beneath the tin.

(b) Photograph showing a snake being marked by branding.



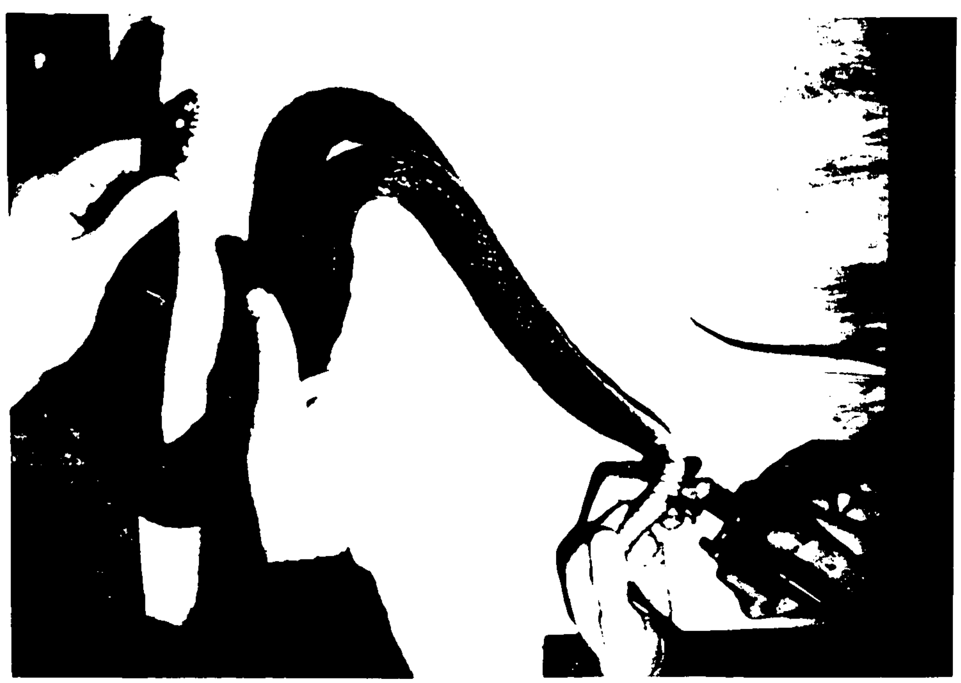
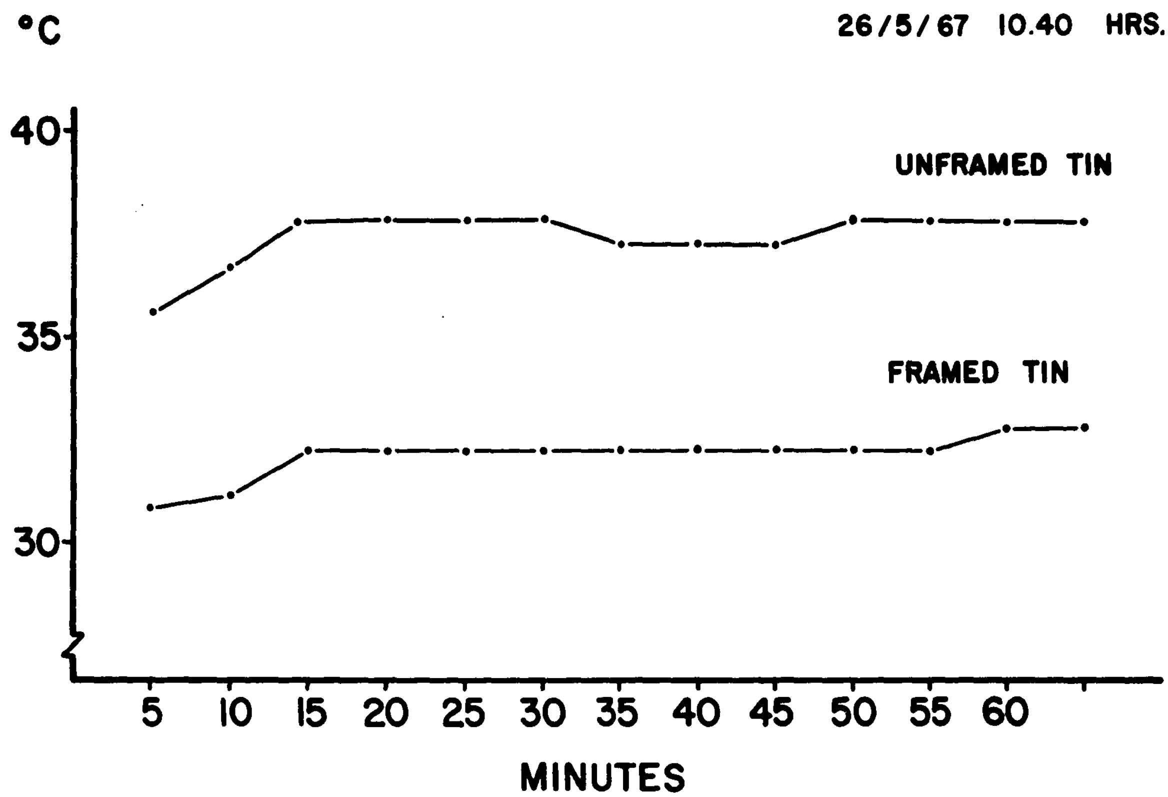


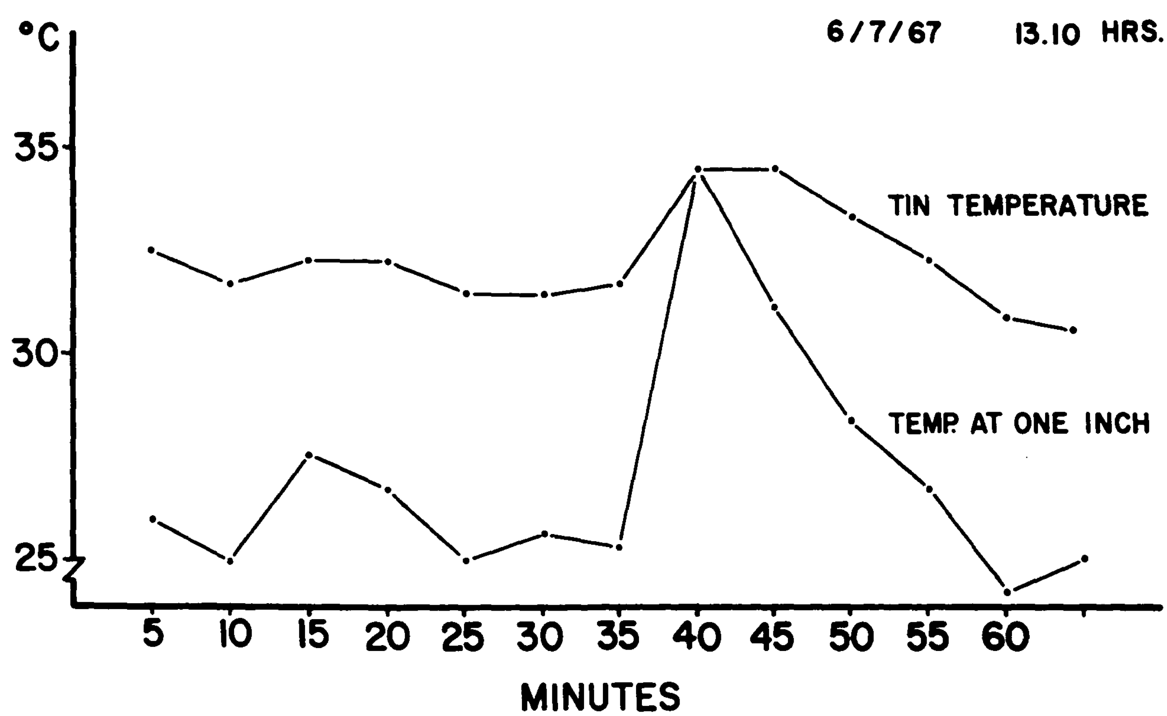
Figure 3.

(a) A graph of the temperatures beneath framed and unframed tins showing a mean difference of 5.5° C. between the two and no significant difference in temperature fluctuation over an hour.

(b) A graph comparing the temperature beneath a tin with that one inch above the ground in an exposed position, indicating that the former remains relatively constant while the latter fluctuates rapidly with changes in wind and cloud cover.



°C
26/5/67 10.40 HRS.
40
35
30
UNFRAMED TIN
FRAMED TIN
5 10 15 20 25 30 35 40 45 50 55 60
MINUTES



°C
6/7/67 13.10 HRS.
35
30
25
TIN TEMPERATURE
TEMP. AT ONE INCH
5 10 15 20 25 30 35 40 45 50 55 60
MINUTES

Figure 4.

A comparison of air, tin and surface temperatures, illustrating the inversion of tin and surface temperatures at 08.30 and 15.30 hours.

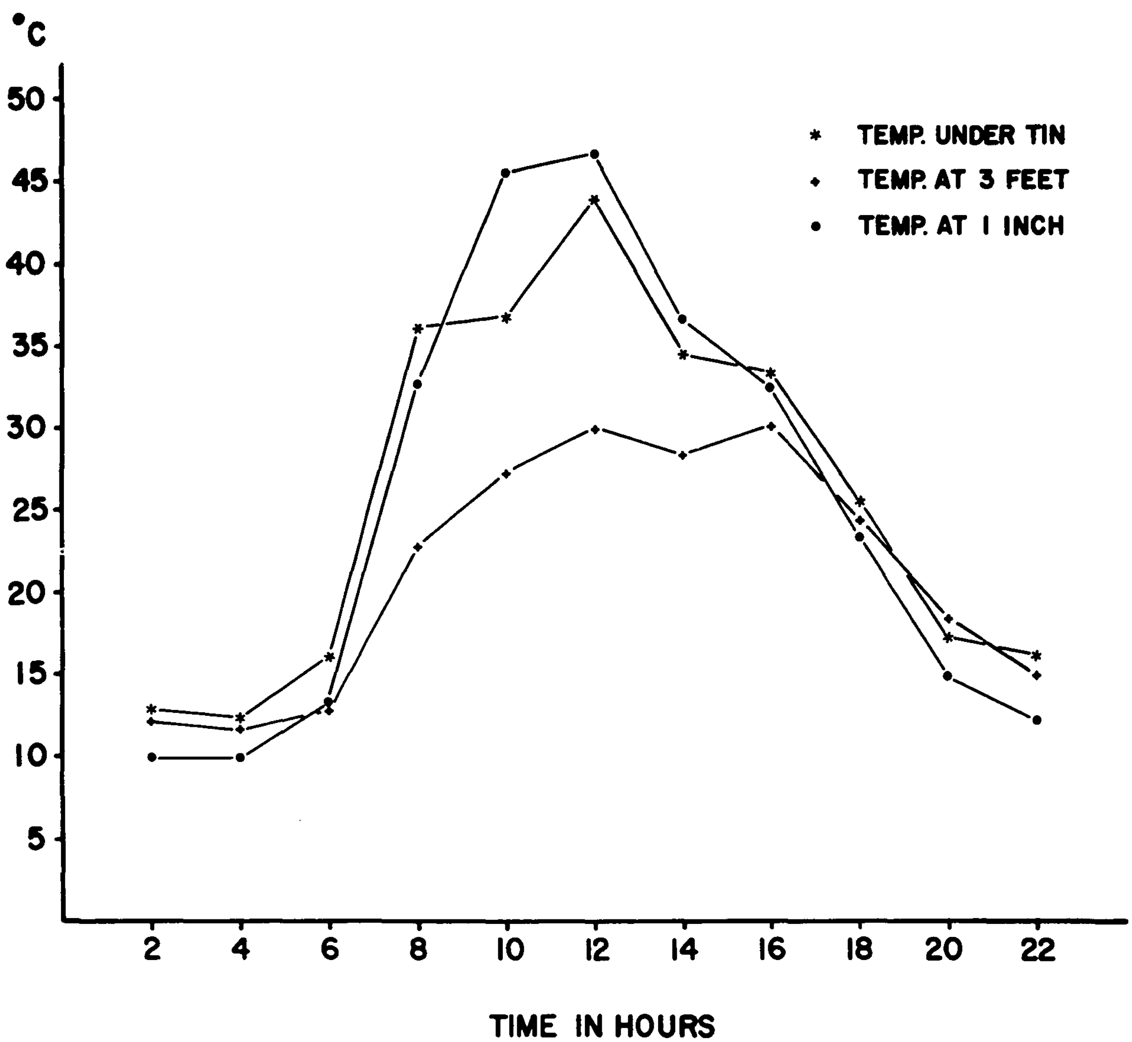

°C
50
45
40
35
30
25
20
15
10
5
TEMP. UNDER TIN
TEMP. AT 3 FEET
TEMP. AT 1 INCH
2
4
6
8
10
12
14
16
18
20
22
TIME IN HOURS

Figure 5.

Showing migratory movements and the month in which they occurred. (T. sirtalis)

⬇ A movement of more than 90 meters within a two week period in a westerly direction.

⇧ A movement of more than 90 meters within a two week period in an easterly direction.

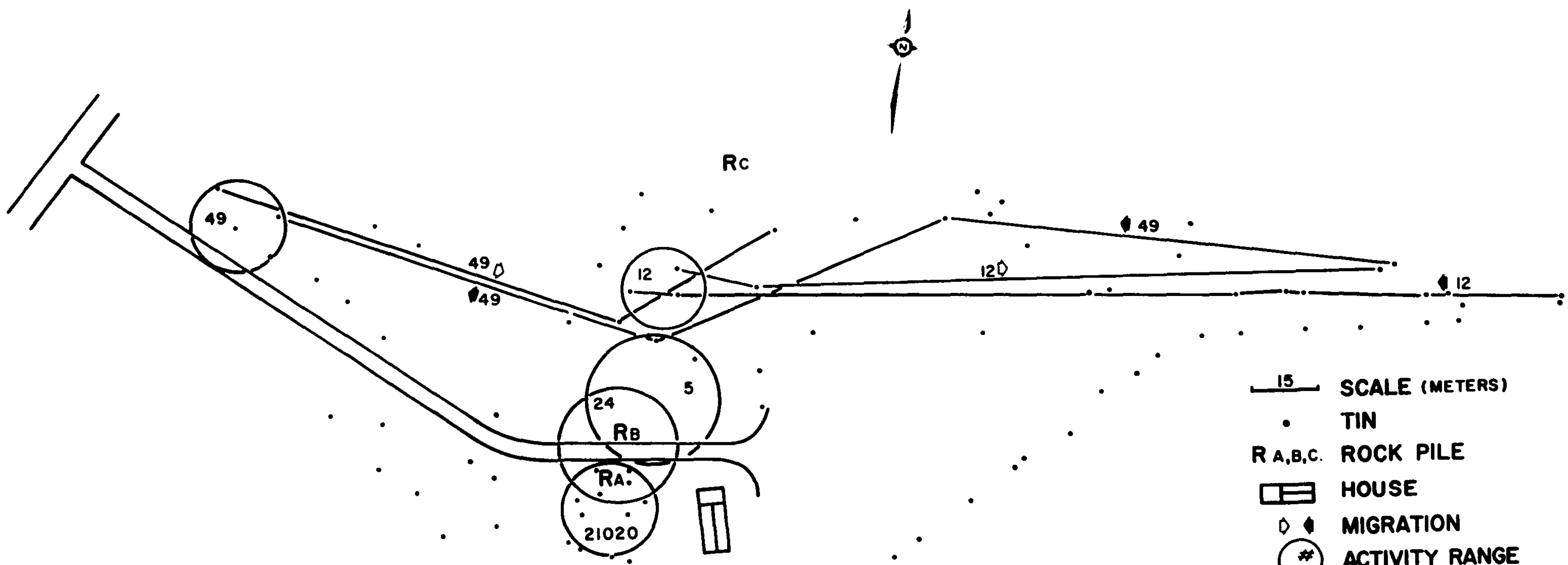
— No captures made.

O A single capture only, thus no data on movement.

SNAKE NUMBER	MONTH 5	6	7	8	9
12	–	⬇	⬇	⇧	–
248	⬇	–	–	–	–
2412	⬇	⬇	⇧	⇧	–
2420	⬇	⬇	⬇	–	–
2610	–	⬇	0	⇧	–
2814	–	⬇	⇧	–	–
21014	–	–	–	⇧	–
21214	–	0	⇧	⇧	–
21216	–	–	⬇	–	⇧
21416	–	0	0	0	⇧
33	–	0	⬇	0	⇧
468	–	–	–	⇧	–
47	–	⬇	0	0	⇧
49	–	0	⬇	0	⇧
53	–	–	–	–	⇧
61	⬇	⬇	–	–	–
79	⬇	–	–	–	⇧

Figure 6.

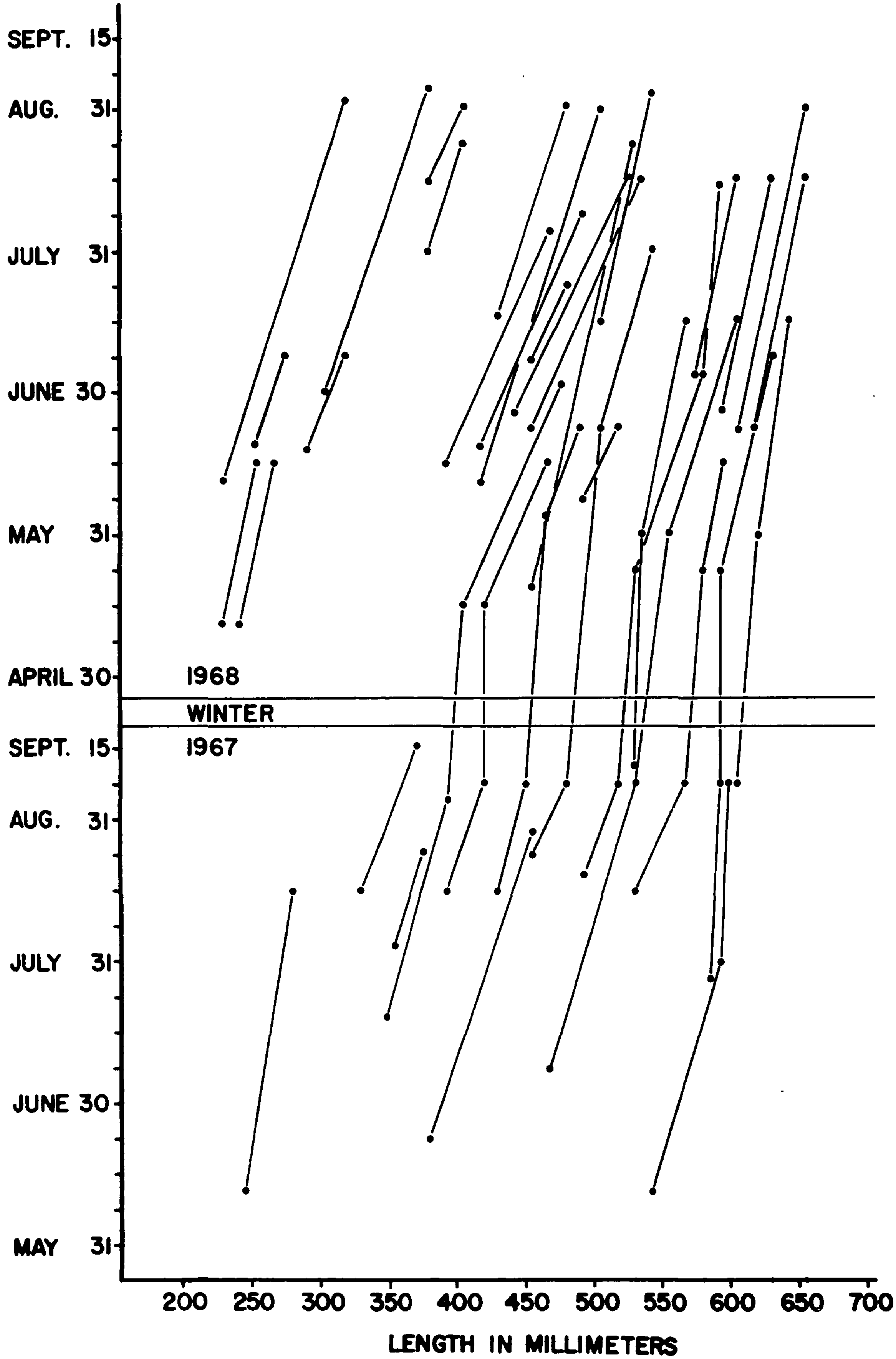
An extract from figure one combined with data from table two and figure five, showing the movements of two typical migrants, numbers 12 and 49, which move from east to west in the spring, (black arrows) set up a home range, then return to the wooded eastern edge of the plot in the fall (clear arrows).
The restricted activity spheres of 3 non-migrants are shown (circles 5, 24, 21020). Typically these center on rock piles (RA and RB).
Other data when added to this figure is merely superimposed on that shown, and has been omitted for clarity.



RC
49
12
5
24
RB
RA
21020
49
49
49
12
49
12
15 SCALE (METERS)
TIN
R A,B,C. ROCK PILE
HOUSE
MIGRATION
ACTIVITY RANGE

Figure 7.

A graph of the increase in the length of *Thamnophis* with time, showing three distinct size groups. Young born in the fall at 205 mm. grow to mean length of 388 mm. in September of the first growing season. Second and third year individuals reach 549 mm. and 648 mm. respectively by fall.


SEPT. 15
AUG. 31
JULY 31
JUNE 30
MAY 31
APRIL 30
1968
WINTER
1967
SEPT. 15
AUG. 31
JULY 31
JUNE 30
MAY 31
200
250
300
350
400
450
500
550
600
650
700
LENGTH IN MILLIMETERS

XII. LIST OF TABLES

Table 1.

A comparison of "tin" and "surface" temperatures ($^{o}F.$) during the period of maximum snake captures, illustrating the inversion of their relationship during periods of rain.

CONDITIONS - RAIN			CONDITIONS - CLEAR		
Date	Temperature Under Tin	Temp. at 1"	Date	Temperature Under Tin	Temp.at 1"
12-6-67 1730	62	68	10-6-67 1800	74	68
26-7-67 1730	82	86	21-7-67 1700	94	84
18-8-67 1200	55	62	17-8-67 1800	77	72
9-7-68 1600	59	64	6-7-68 1700	86	79
7-8-68 1600	60	68	5-8-68 1800	82	69
6-9-68 1630	58	61	9-9-68 1700	80	72

Table 2.

The activity ranges of *Thamnophis*; their size, center, and length of occupancy. Range centers refer to fields and stone piles (figs. 1 and 6).

Snake Number	Range		Time		Recaptures	Migration
	Center	Radius Meters	1967	1968		
5	RB	15	2.0	2.0	6	-
12	Field 2	10	1 mo.	-	6	+
24	RB	14	1 capt.	1.5 mo.	9	-
2410	RC	9	-	1 mo.	3	-
2414	RB	12	-	2 mo.	15	-
2610	Field 2	15	-	1 mo.	3	+
2618	RB	6	-	1 mo.	5	-
2810	RB	9	-	1.5 mo.	5	-
2816	Field 3	11	-	2 mo.	4	-
21016	RA	14	-	1.5 mo.	4	-
21020	RA	11	-	2 mo.	15	-
21420	RA	12	-	2 mo.	3	-
21618	RA	8	-	1.5 mo.	6	-
33	RA	10	-	2 mo.	16	+
38	RA	10	-	2 mo.	11	-
40	RA	15	1 mo.	-	3	-
45	RB	12	1 mo.	1.5 mo.	5	-
4614	Field 3	13	-	1 mo.	4	-
47	RA	14	2 mo.	-	18	+
49	Field 3	15	1 mo.	1 mo.	7	+
51	RB	11	1 mo.	1 mo.	10	-
68	RA	9	1 capt.	1 mo.	4	-
73	RC	10	1 capt.	1 mo.	4	-
89	RA	7	-	1 mo.	6	-
99	RB	5	1 mo.	1 capt.	4	-

Table 3.

Growth statistics for both Thamnophis and Storeria. Figures given for third and fourth years are estimates, as overlap of lengths between successive age classes may cause confusion between three and four year old individuals.

THAMNOPHIS

Age	Date	Original Length mm.	Growth/Wk. mm.	Length Sept. 14 mm.	Length May 14 mm.
Birth	Sept. 1	205	-	205	229
1	M14-S14	229	10	388	406
2	M14-S14	406	8.8	549	559
3	M14-S14	559	5.5	648	660
4	M14-S14	660	2.7	703	

STORERIA

Age	Date	Original Length mm.	Growth/Wk. mm.	Length Sept. 14 mm.	Length May 14 mm.
Birth	Sept. 1	110	11.0	132	156
1	M1-S14	156	4.5	238	251
2	M1-S14	251	3.5	305	305
3	M1-S14	305	2.3	343	

Table 4.

The number of animals marked during each of two years, (excluding juveniles) and the population estimates derived using five standard formulae for the estimation of animal numbers from recapture data.

Estimation Formulae		Lincoln Index	Eberhardt	Schnabel	Schumacher Eschumeyer	Chapman
	Thamnophis # Marked					
1967	45	55	75	42	48	50
1968	65	75	95	57	63	64

Estimation Formulae		Lincoln Index	Eberhardt	Schnabel	Schumacher Eschumeyer	Chapman
	Storeria # Marked					
1967	36	67	75	32	47	49
1968	52	75	88	38	45	51