Supervisor: Dr. Patrick T. Gregory

ABSTRACT

Movements of animals presumably reflect their changing needs and the changing availability of necessary resources. In cold climates, snakes often make long seasonal migrations between hibernacula and summer habitats. Finding suitably deep hibernacula with minimal delay could be critical. I hypothesized that such animals should have highly developed navigational ability. By contrast, snakes living in mild climates can hibernate in shallow sites and probably do not migrate; if so, they might be expected to show poorly developed orientation mechanisms. The objectives of this study were to determine movement patterns and navigational ability of garter snakes (*Thamnophis*) living in a mild climate and compare them with a congeneric population known to be migratory.

From 1986 - 1988 I examined, using mark-recapture, movement behaviour of two populations of garter snakes at Spectacle Lake Provincial Park (SLPP) on Vancouver Island, British Columbia, focusing on several components typically associated with migratory behaviour - distances travelled, population directionality, fidelity to seasonal sites, distinctness of seasonal habitats, and route directness. *Thamnophis sirtalis*, the common garter snake, is the most widely distributed North American snake species and high latitude populations are migratory. *Thamnophis ordinoides*, the northwestern garter snake, is restricted to the Pacific northwest and migratory behaviour has never been reported.

Both species displayed combinations of traits clearly suggesting nonmigratory behaviour. These included short-distance (< 500 m), random movements, a lack of den fidelity, and variation in the maintenance of specific home ranges between successive years. Home ranges overlapped between individuals, averaged less than 0.3 ha measured over a single active season, and were not clearly distinct from denning areas. Although some directionality of movement was evident, it was likely related to foraging strategy and unlike the typical unidirectional movements undertaken by migrating snakes. Sexual and reproductive differences in any of these traits generally were not significant.

The navigational abilities of a migratory population of *T. sirtalis* from Wood Buffalo National Park (WBNP) in northern Alberta were examined as were those of the nonmigratory populations of snakes from SLPP. Displacement studies were carried out during the active seasons of 1986 - 1988 to determine the level of orientational abilities present in each population and to examine potential orientation cues. Snakes were displaced from their home range and tested in an arena under a variety of conditions. The results demonstrated that *T. sirtalis* from both SLPP and WBNP possessed advanced navigational abilities. Advanced skills may be absent in *T. ordinoides*. *Thamnophis sirtalis* at both study sites demonstrated time-compensated solar orientation as determined by 6 hr phase-delayed tests. Pheromone trails produced by recently copulated females (but not unmated females) also provided an orientation guide for displaced WBNP males, but results from SLPP were less conclusive. *Thamnophis ordinoides* did not respond in a discernible way to either cue. Navigational skills thus vary relatively little between migrating and nonmigrating populations of the same species but may be poorly developed in completely nonmigratory species.

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ACKNOWLEDGEMENTS

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Numerous people came with me into the field on occasion, providing companionship as well as additional eyes while searching for snakes. Among them were Kari Nelson, Neville Winchester, and Margaret, Jane, and Emily Larimer, and Glen Lawson. I would especially like to thank Pat Gregory and Karl Larsen for all of their help and for introducing me to the snakes of WBNP.

My parents, Robert and Margaret Larimer, have always been supportive and I am truly greatful. My mother's help with Amy and Karen was commendable. Her help made completing my degree possible. I would not have gained such a deep appreciation for snakes had it not been for Diane Secoy. Her guidance during my Masters program at the University of Regina and her encouragement to continue will always be appreciated. Finally, special thanks go to Pat Gregory for his guidance and assistance throughout this study. His help has been constant despite time and distance.

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DEDICATION

I dedicate this dissertation to Glen, whose love, support, and encouragement were sustaining from start to finish, and to Amy and Karen who give me the opportunity to discover nature all over again.

INTRODUCTION

All facets of an organism's existence involve interactions with its biotic and abiotic environment at some level. How and why an organism responds to its environment in a particular way describe, to a large extent, its behaviour (Alcock, 1975). According to Shöne (1984), all aspects of behaviour involve movements, and all movements are oriented in some way, whether by a fish correcting for pitch or a moth showing an attraction to light. Orientational processes, therefore, demonstrate how an animal adapts its behaviour to the spatial requirements of its environment. As Jander (1975) stated, orientation ecology is "the subdiscipline at the interface between ecology and ethology."

Why do specific movement patterns occur? Explanations are varied and are not mutually exclusive. Often movements are in response to some goal or required resource. Optimal foraging theory, for example, attempts to explain and predict movements on the basis of the abundance, type, distribution, and other aspects of prey (e.g. see Krebs *et al.*, 1981; Pyke, 1984). In addition, a variety of social interactions, from interspecific competition that promotes dispersion to group living (e.g. Morse, 1980; Brown and Orians, 1970; Waser and Wiley, 1979), direct animal movements and spacing patterns. Suitable habitats must also be found. Although animals should prefer to settle in a place that maximizes survival, movements should also reflect the costs of locating such an optimal site (Orians, 1971). Whatever the directing force, animals adapt their movements to maximize their orientation fitness - their ability to "be in the right place at the right time" (Jander, 1975).

Increased orientation fitness is achieved by minimizing costs. Movement costs are perhaps most apparent in cases where long-distance migrations occur. Baker (1978) and

Morse (1980) describe some of these costs, which include exposure to a variety of environmental conditions, unpredictability of resources in the different habitats, energetic expenses, less time for other activities, and greater susceptibility to predation. Natural selection, it may be argued, should favour orientation mechanisms that improve goal-orientation for long-distance migrators, thereby reducing these costs.

Griffin (1952), in categorizing the orientation patterns of birds, suggested a useful approach to categorizing the level of orientational ability. Type I orientation (also called piloting, Schmidt-Koenig, 1965) involves either the use of familiar landmarks as guides or random wandering as the method of locating goals. Type II orientation (simple or compass orientation) refers to the ability to select a specific compass direction regardless of where it leads. Type III orientation (true navigation) is more complex. It not only requires a compass sense, but also a map component. By possessing true navigational ability, an animal is able to coordinate its present location with the location of the goal. The ability to navigate, however, does not preclude the use of other forms of orientation.

Regardless of which system is being employed, orientation requires a reference cue. Bees rely on visual and olfactory cues to orient towards objects at close range (= proximate orientation, Watson and Lashley, 1915), but use solar cues, including polarized light, when stimuli being emitted from the goal itself cannot be directly perceived (= distant orientation, Watson and Lashley, 1915; von Frisch, 1948, 1967). The reference system may be endogenously generated, allowing idiothetic orientation. Female gerbils (*Meriones*), for example, use internally generated cues to retrieve displaced young (Mittelstaedt and Mittelstaedt, 1980). Magnetic, auditory, stellar, wind, and other cues also function as reference guides. Examples are well reviewed by Able (1980), Adler (1970), Baker (1982, 1984), Emlen (1975), Ferguson (1971), and Shöne (1984). Furthermore, it appears that few, if any, organisms rely on a single orientation guide; multimodality is more likely the rule than the exception. Emlen (1975) concluded that "natural selection should favour the development of abilities to make use of all such information."

Ideally, an examination of the hypothesis that long-distance migrators have better developed navigational skills than non-migratory animals would consider studies of a variety of populations of the same or closely related species living under different conditions. Bird studies dominate vertebrate orientation research (for examples see reviews by Able, 1980; Adler, 1970; Baker, 1982, 1984; Emlen, 1975; Shöne, 1984). Perhaps because of their cryptic nature, snakes rarely have been the subject of orientation studies (Landreth, 1973; Newcomer *et al.*, 1974; Lawson, 1985). Nevertheless, snakes exhibit a wide variety of movement patterns, making them a useful group in which to make comparisons (e.g. Blanchard and Finster, 1933; Fitch and Shirer, 1971; Hirth *et al.*, 1969; Macartney, 1985; Madsen, 1984; Larsen, 1986). Extensive diversity exists within species, as exemplified by *Thamnophis sirtalis*, the common garter snake. Larsen (1987) recorded a round trip migration by one individual of 15 km during one active season in northern Alberta. These snakes presumably migrate because deep hibernating sites that permit the snakes to escape the cold are likely scarce near the summer habitat. By contrast, individuals of this same species in the milder climate of Kansas average annual movements of less than 500 m (Fitch, 1965). By examining orientational abilities in different populations of the same species, physiological and phylogenetic differences can be minimized, thus allowing a more accurate examination of the effect of ecological variation on orientational abilities. Phylogenetic differences, on the other hand, can be explored by comparing orientational behaviour of different species living in the same environment.

Investigating these questions was the basis of my research. To compare variation in orientational abilities between migratory and nonmigratory individuals of the same species living under different ecological regimes, two populations of *T. sirtalis* were studied. Migratory snakes from Wood Buffalo National Park (WBNP) in northern Alberta, previously studied by Larsen (1986, 1987), and presumed nonmigratory snakes from Spectacle Lake Provincial Park (SLPP) on Vancouver Island, British Columbia were used to assess the effects on orientation performance of annual patterns of movements. Gregory (unpubl.) has superficially examined movements of the SLPP population; a more detailed analysis was carried out during this study.

A second objective was to compare movement patterns and orientational abilities between two species inhabiting the same environment. *Thamnophis ordinoides*, the northwestern garter snake, also is common at SLPP. This species is restricted to moderate Pacific coastal climates and no migratory populations are known.

Chemosensory (Fitch, 1958, 1960; Hirth, 1966; Klauber, 1972; Brown and Parker, 1976; Lawson, 1985) and solar cues (Landreth, 1973; Newcomer *et al.*, 1974; Lawson, 1985) have been suggested as orientation guides for migratory snakes. The possible use of these reference systems was examined for the three study populations.

Finally, orientational capabilities of neonates was considered. Young snakes are often born at some distance from communal hibernacula and their ability to locate a suitable den, whether one used by the adults or a different one, has often been questioned. Scent trailing has been suggested as the primary cue used by neonates to achieve this (Brown *et al.*, 1982; King *et al.*, 1983; Duvall *et al.*, 1985), yet only a few studies have dealt specifically with this question (Brown and MacLean, 1983; Reinert and Zappalorti, 1988a). The ability of neonates to orient using solar cues alone has not been previously examined.

METHODS

Ecology and Movements

Description of Study Sites and General Snake Ecology

Wood Buffalo National Park

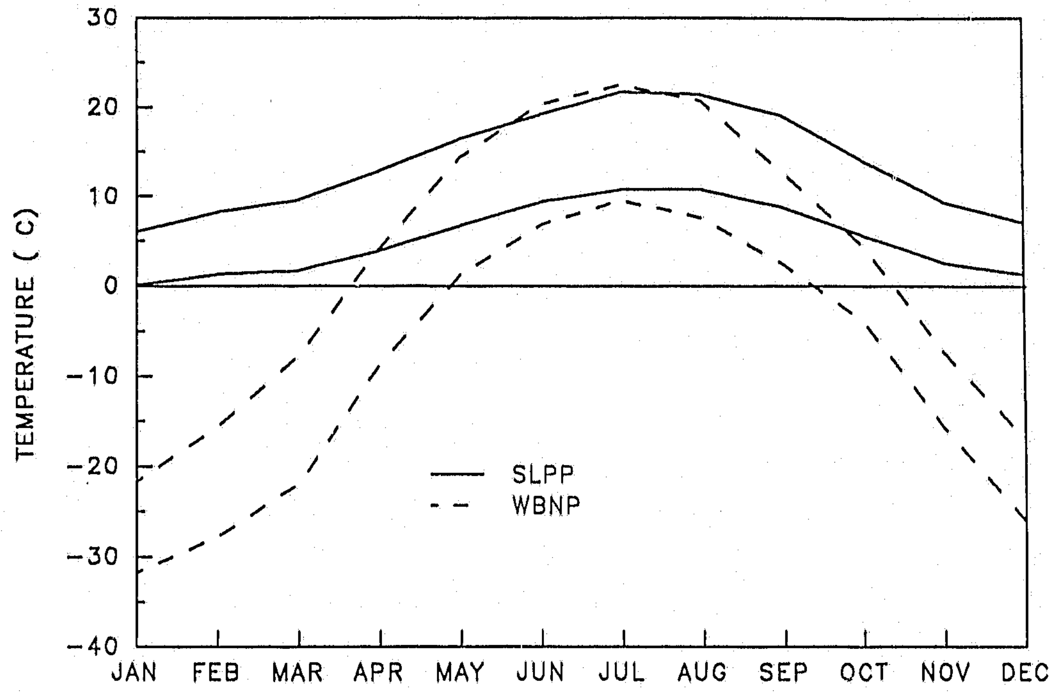
Wood Buffalo National Park (WBNP) straddles the Alberta - Northwest Territories border. It is primarily characterized as boreal forest and, as a sub-arctic environment, experiences short summers and long, cold winters. Climatic details of the region are provided in Larsen (1986) and are summarized in Figure 1 (conditions are for Fort Smith, N.W.T.; Environment Canada, 1982). Annual precipitation for Fort Smith averages 349.3 mm and mean annual snowfall is 145.9 cm.

Only one species of snake, *Thamnophis sirtalis*, is present at this latitude; populations within the park are near the northern limit of the species' range. Snakes were collected from a den near the Salt River (Salt River Den, SRD) (59°49'N, 112°W). The ecology and general movement patterns of this population have been previously studied by Larsen (1986, 1987). The population consists of between 500 and 600 individuals that hibernate communally in limestone sinks. Suitable denning sites are presumably scarce in this region, likely promoting the characteristic traits of communal denning, a high degree of den fidelity, and long migrations to the nearest suitable summer range, a marsh complex that begins approximately four km from the den. The round trip may exceed 18 km for some individuals.

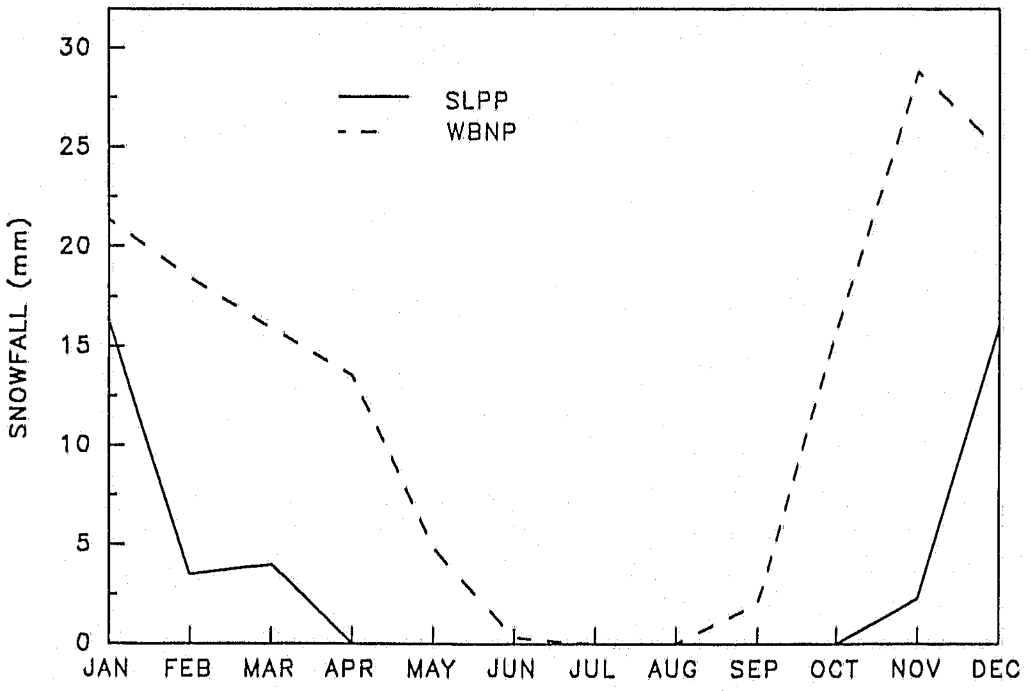
Figure 1: Climatic characteristics of WBNP and SLPP, based on 50 year averages (Environment Canada, 1982).

A. Mean temperature maxima and minima.

B. Mean monthly snowfall.



A. Temperature



B. Snowfall

Spectacle Lake Provincial Park

Spectacle Lake Provincial Park (SLPP) (48 ° 34'N, 123 ° 34'W) on southern Vancouver Island, British Columbia was the second study site. The park is largely forested and occupies approximately 83 ha. The climate is generally mild throughout the year with a winter rainy season (Figure 1. Temperatures for Vancouver Island were measured at Victoria International Airport; Spectacle Lake temperatures are likely slightly lower. Precipitation data were recorded at Bamberton Ocean Cement, located near test site B; see Figure 2, page 10). Mean annual precipitation and snowfall for Bamberton are 1131.3 mm and 42.1 cm, respectively (Environment Canada, 1982).

Gregory provided me with unpublished data from 1974 to 1986 on snakes at this site, yielding long-term records on individual movements as well as other basic ecological information. Two snake species are common at SLPP - *T. sirtalis* and *T. ordinoides*. No large communal dens have ever been noted at this site, and suitable dens appear to be abundant (see **Results**). Prey items (primarily frogs, salamanders, and worms for *T. sirtalis* and exclusively slugs and worms for *T. ordinoides*; Gregory, 1984a and pers. obs.) were common throughout the study area. Long-distance migrations apparently did not occur, although detailed analyses of movements had not been performed before my study.

Basic Data Collection

This study was conducted from 1986 to 1988. Experiments at WBNP were carried out in two-week periods during the autumns of 1986 and 1987 and during the spring of 1988. During these times most SRD snakes were near the denning area and orientation tests involved only snakes captured at the den. The work at SLPP was conducted throughout the snakes' active season (early March to late October) with the exception of the time spent at WBNP.

Snakes were captured by hand and given individual identification marks by removing unique combinations of subcaudal scutes (Blanchard and Finster, 1933). Larger snakes were sexed by probing for hemipenes (Schaefer, 1934), and small snakes were sexed by attempting to evert the hemipenes (Gregory, 1983). Snout-vent lengths (SVL) were determined to the nearest 5 mm. Unless the snakes were to be tested for their orientational ability, they were released following processing at the site of capture. Processing normally took, at most, a few minutes. The site of capture of each SLPP snake was recorded and marked with flagging tape.

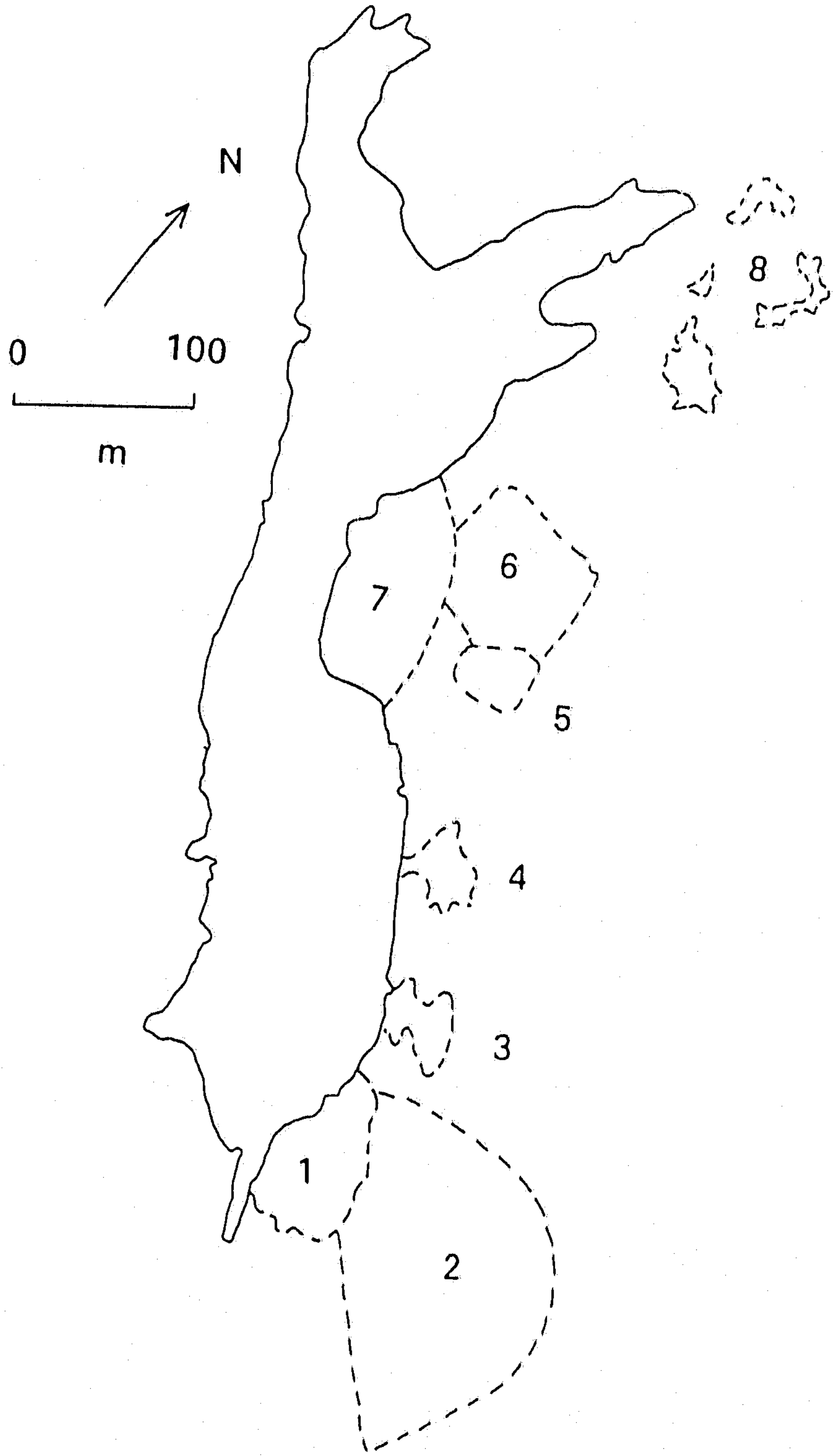
Examination of Movements of SLPP Snakes

Movement patterns of snakes at Spectacle Lake were determined from the recapture of marked snakes. Some attempts were made at using radiotelemetry, which would have provided much greater details of movement patterns and aided in locating overwintering sites. However, problems with obtaining snakes large enough to accommodate the transmitters and with the equipment precluded its use.

Reliance solely on mark-recapture methods resulted in several limitations. Snakes were difficult to locate in the forested areas of the park, and I was not able to adequately determine the extent to which snakes used these areas. During the 1987 active season searches at SLPP were concentrated in, but not limited to, seven open areas; a further zone (zone 8) was added in 1988 (Figure 2). These zones were extensively searched on a regular basis several times a week during the active seasons with the exception of the time I spent

Figure 2: Major zones searched at Spectacle Lake.

Dotted lines indicate the limits of each zone.


N
0
100
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2
3
4
5
6
7
8

conducting studies at WBNP. This resulted in a bias of snake distributions in the open regions. Also, home range areas and other measures of movements were calculated on the basis of a minimum number of sightings per individual, which undoubtedly resulted in the calculation of home range areas that are smaller than actually exist (see Rose, 1982). Nevertheless, it was possible to determine the fundamental nature of the movement patterns of the SLPP snakes.

Maps of SLPP were made using aerial photo enlargements (scale 1:33). Distances and directions were calibrated by ground survey. Consecutive capture points of snakes were mapped and directions and distances of movements were determined from the maps.

Statistical Methods - General and Movement Patterns

All results were deemed significant at $\alpha = 0.05$ and, unless otherwise indicated, are presented as the mean ± 1 standard deviation. Most analyses were performed using SAS Version 5 (1985). Sample sizes (n) used in the analyses indicate the number of records obtained, and not necessarily the number of individual snakes. Comparisons between means were analyzed by t-tests when two categories were compared and by ANOVA when three or more classes were considered.

Home range areas were calculated using the minimum convex polygon method for individuals captured at least three times over the course of one active season (Jennrich and Turner, 1969). Despite the sample size bias of this method when there is a low number of sightings, the convex polygon method is often preferred because it is based on actual sightings rather than the assumption of a theoretical normal distribution (Rose, 1982). Data used to calculate home ranges of the WBNP population were approximated from figures provided by Larsen (1986), which were based on the movements of three radiotracked females. Home range areas were calculated using McPaal (Micro-computer Programs for the Analysis of Animal Locations; Stuwe, 1987).

Directionality of movements of the SLPP populations was analyzed by circular statistics, further described in **Statistical Methods - Orientation.**

Orientation

General Considerations and Techniques

Displacements are the critical tests of determining the form of orientation (landmark orientation, simple compass orientation, or true navigation) employed by an organism (Baker, 1978). Displacement studies fall into two general categories: (1) releasing the displaced animal at a new location and allowing it unrestricted movement upon release to assess homing ability; and (2) releasing the displaced animal in an arena that prohibits possible orientation by landmarks. Both techniques are based on the assumption that "home" has been correctly identified by the researcher. This assumption is addressed in **Statistical Methods - Orientation.**

Homing studies may employ radiotelemetry or other tracking techniques (e.g. Chelazzi and Delfino, 1986; Rodda, 1984; Sinsch, 1987). This ensures that recapture success does not influence the assessment of homing ability, a problem in some studies (e.g. Fraker, 1970), and allows the directness of return movements to be monitored. Sensory deprivation (e.g. taping over the eyes, rendering the subjects anosmic, attaching magnets to the head; Chelazzi and Delfino, 1986; Sinsch, 1987) can be used to investigate the roles of various reference cues. Control tests are essential to ensure that such manipulations have a minimal effect on normal movement behaviour. Problems with homing studies include the possibility of increased predation on animals outside their home range and the possibility that the subjects may be disinclined to return to their original location if they find another suitable site. In addition, the difficulties previously mentioned regarding radiotracking of SLPP snakes, and the smaller sample sizes which would have resulted from continual monitoring, discouraged the use of this technique for this study. Instead, I relied exclusively on arena tests to examine orientation behaviour.

Test Arena

Two basic types of arenas were used for the orientation tests. During the 1986 autumn tests at WBNP, a 2 m high wire mesh screen covered with opaque plastic was formed into a 6 m diameter circle and supported by wooden stakes. This arrangement was not entirely satisfactory since its assembly was difficult and time consuming and it was easily damaged during transportation from one test site to another. Subsequent tests involved a 6 m diameter, 1 m high octagonal arena made with eight sheets of insulation board. With the exception of test site A on Vancouver Island, external visual cues, other than solar, were not visible to snakes from within the arena. At site A, trees and a large water tower were visible from within the arena. At first, there was some concern that the snakes were being attracted to these features; however, phase-shifting tests suggested that these were not influential as directional cues. The formation of shadows within the arena at all test sites caused similar concerns that were also rejected. In all cases, the arena was placed over a level sand, gravel, or dirt substrate, according to availability at the test site.

Test Procedure

Except where noted in certain tests, snakes were collected and tested on the same day. Some snakes were transported to the test site in opaque cloth bags, thus temporarily blocking potential solar cues, while others had a view of the sky between the time of capture and testing.

All snakes were tested singly to prevent the actions of any one snake influencing those of another. Each snake was placed in a release box in the centre of the arena. After a five minute adjustment period, the box was raised by a string attached to the box. The movement of the snake was monitored by an observer standing still outside the arena, and the point of contact with the arena wall was recorded as the directional choice of the snake. Unless otherwise indicated, tests involved adults and were carried out under clear skies or while the sun was not obscured by clouds.

The substrate was raked between trials to disperse any odours that might have been deposited during a trial (see **Pheromone Trails**). Wind directions both inside and outside the arena were also occasionally recorded.

Timing of and Location of Orientation Trials

Orientation trials at WBNP were carried out in the autumns of 1986 and 1987 after the snakes had begun to return to the den and in the spring of 1988 following emergence from the den. In the latter case, testing began during the period of intense mating activity at the den and continued until both sexes had commenced migrating. On Vancouver Island, tests were conducted throughout the active season in all three years.

Two test sites were selected at each study site. At WBNP (Figure 3), both sites were approximately 5 km from the den but in opposite directions. On Vancouver Island, the sites were approximately 6 km in roughly opposite directions from Spectacle Lake (Figure 4).

Age of Subjects

Testing primarily involved adults although some neonates from the SLPP populations were also tested. To obtain neonates, some gravid females were captured and kept in cages, some at SLPP and others at the laboratory (see Figure 4); no wild-born neonates were used in orientation tests. Three categories of captive-born neonates were tested: (1) born outside at SLPP; (2) born outside at the laboratory; and (3) born inside at the laboratory and kept inside until testing. In the latter category, no attempt was made to mimic natural light conditions. These categories were selected in order to test the hypothesis that neonates imprint upon solar cues present at the birth site.

Orientation Type

The testing procedure described above was the protocol for the basic orientation tests. Results of these tests were used to determine the orientation type (Type I, II, or III). In any given case. one of three general responses was possible (see **Discussion** for more detail):

(1) snakes would demonstrate random orientation at both test sites, thus indicating either that snakes required landmarks as orientation guides (Type I orientation) or that they would not orient under the given test conditions; (2) snakes would cluster around some direction,

Figure 3: Location of test sites A and B relative to the Salt River den and the summer range at WBNP.

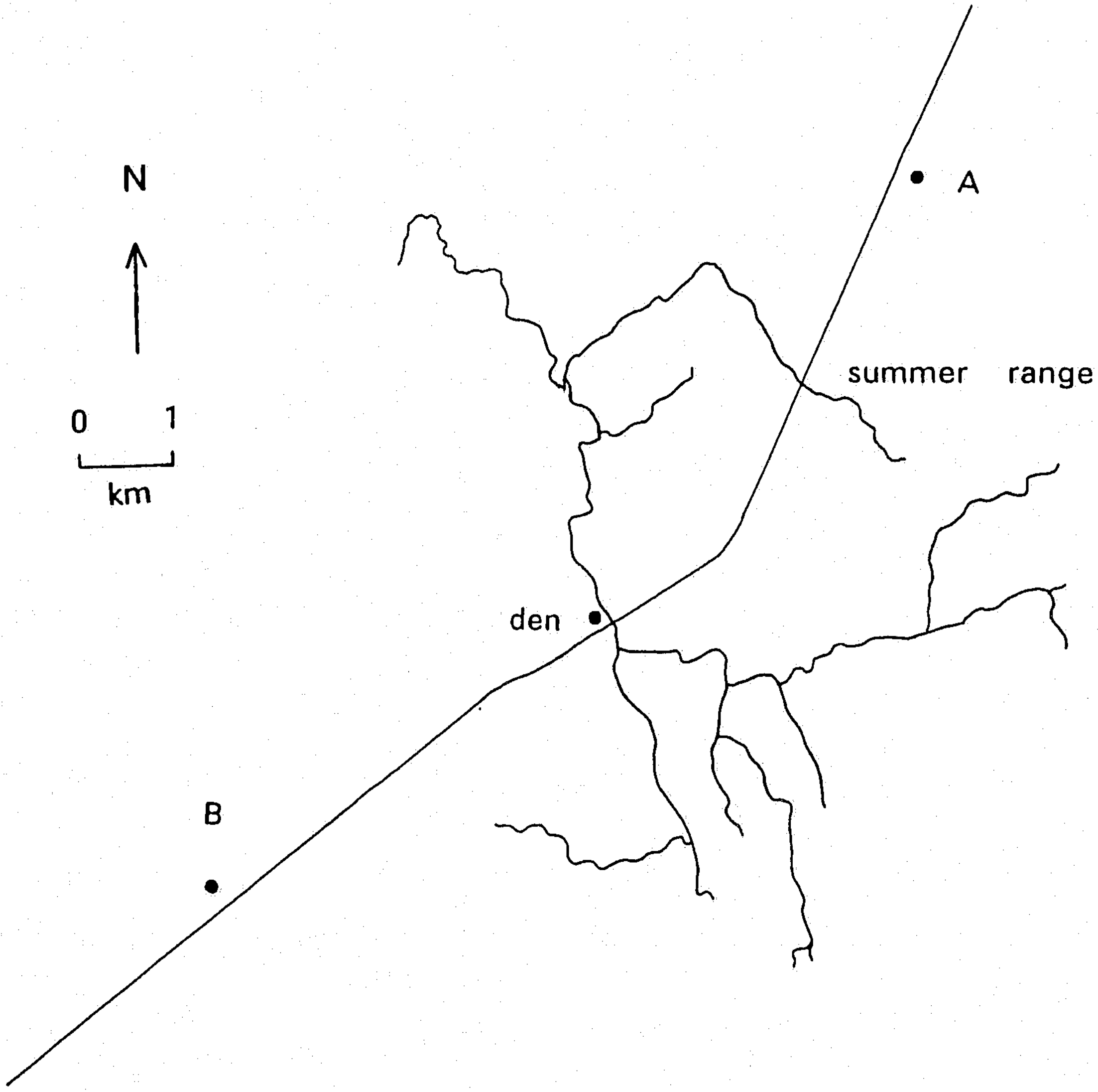
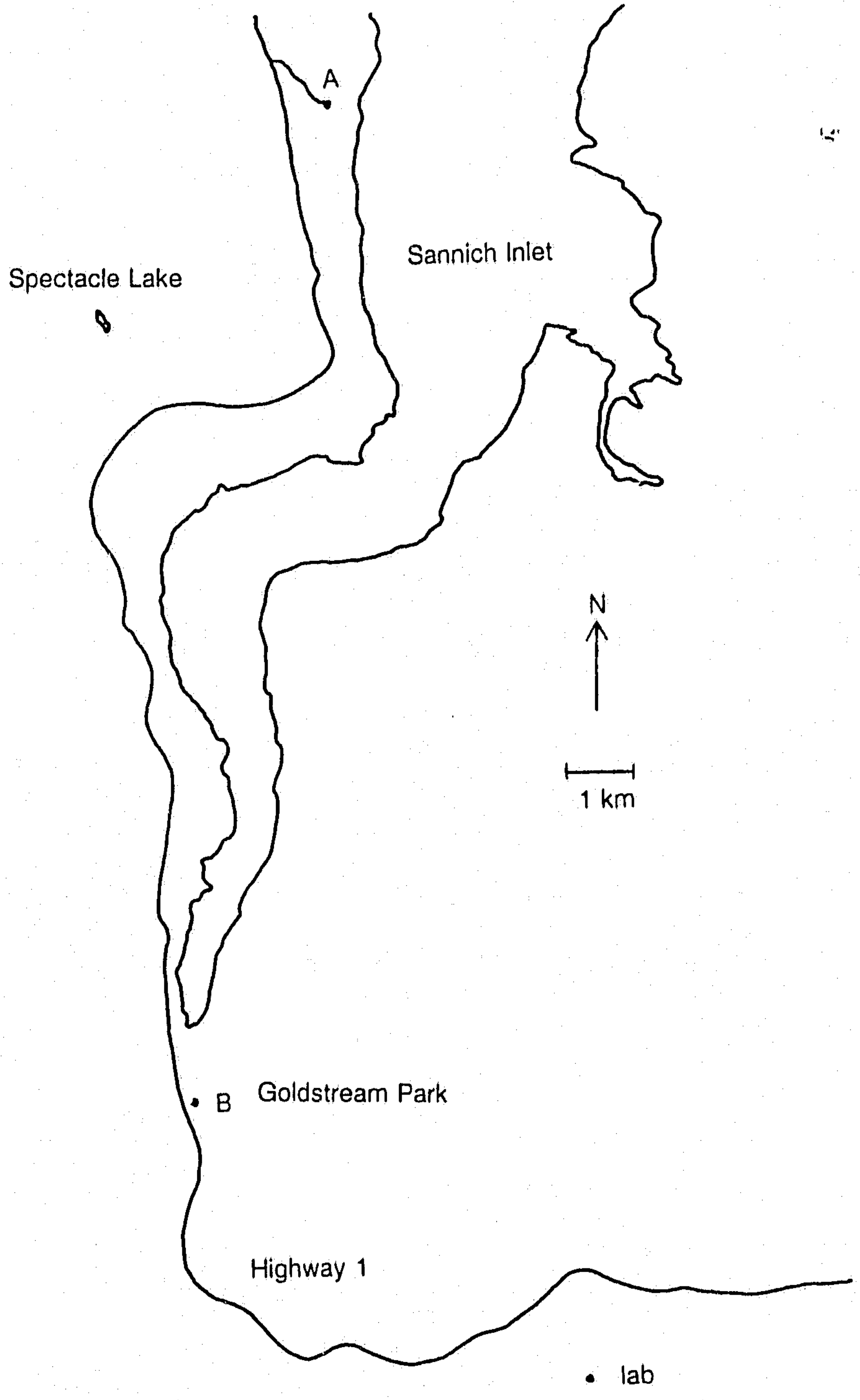

N
0
1
km
A
summer range
den
B

Figure 4: Location of test sites A and B and laboratory relative to SLPP.


A
Sannich Inlet
Spectacle Lake
N
1 km
B
Goldstream Park
Highway 1
lab

but not as predicted (see **Statistical Methods - Orientation**), indicating Type II orientation; or (3) snakes would select the predicted direction, demonstrating Type III orientation.

Orientation Cues

Solar Azimuth Position

Phase-shifting was used to identify the use of time-compensated azimuth position as an orientation guide. In all but one phase-shift test, snakes were removed from the field and subjected to a 6 hr delayed LD shift by keeping the snakes in indoor tanks under an artificial photoperiod (1 60 W incandescent bulb). "Sunrise" was delayed 2 hr/day from true sunrise for the first 3 days of captivity, and the snakes were maintained under the 6 hr delay for an additional day. No attempts were made to mimic ambient temperatures, and room temperatures were approximately 20° over the course of the phase-shifts. One group of SLPP *T. sirtalis* was subjected to a 6 hr phase-advance. A control test, in which the animals were removed from the field but kept under natural light conditions for four days prior to testing was also performed for SLPP *T. sirtalis*. Males and females were housed together during the phase-shift. Snakes from WBNP mated during captivity.

Pheromone Trails

Pheromone trails were produced by directing a conspecific along a narrow corridor inside the arena prior to a test. The direction at which the trail was laid down differed from that demonstrated in the general displacement tests. Occasionally a stimulus snake was allowed to select its own direction. This trail was used as a stimulus only if it was outside the 95% confidence interval of the mean direction from the basic tests. Trail tests were performed on both clear and cloudy days.

Pheromone trailing tests of WBNP snakes were performed in the spring of 1988. Because of difficulties in obtaining enough females for use in these tests, I focused on examining trailing responses of adult males. Tests involved trails produced by males, unmated but sexually attractive females (evidenced by involvement in courtship behaviour), and recently mated females (evidenced by copulatory plugs). During the mating period, males use pheromonal cues to distinguish between sexually receptive females and recently copulated females (e.g. Crews, 1976; Devine, 1976, 1977; Gartska and Crews, 1981; Ross and Crews, 1977, 1978). Typically, males will follow trails of only unmated females.

SLPP trailing tests involved males and females as both stimulus and subject snakes. Because mating activities were never observed at SLPP, females were not categorized as mated or unmated; instead, only gravid females were used as stimulus snakes. Tests involving stimulus trails produced by males preceded female-produced trail tests.

As a means of accurately examining trailing response, this methodology left much to be desired, for it was not possible to quantify accurately various trailing measures such as tongue flick rates and the degree of fidelity by the subject to the trail. However, I selected this methodology for two reasons: (1) to provide consistency with the other orientation tests; and (2) to allow a snake to make its own directional choice rather than be restricted to choice arms (as in standard Y-maze trailing experiments). Under natural field conditions, a snake that trails conspecifics must make similar choices. Therefore, despite the limitations of the arena tests, I felt this technique more accurately represented what occurs in the field.

Statistical Methods - Orientation

The results of the orientation tests were analyzed by circular statistics described by Batschelet (1981). A significance level of $\alpha = 0.05$ was selected for all tests. Individual scores were first plotted on polar diagrams. The centre of the diagram represents the release point within the arena, and the outer margin represents the arena walls. Individual test scores, measured as angles, are represented by dots along the circumference of the circle. For basic and phase-shift tests, north, 0°, is located at the top of the diagram. For pheromone trail tests, the trail direction is at the top of the diagram. The predicted direction (θ) is indicated by a triangle outside the circle.

The mean angle, ϕ, of each test series was calculated as[†]:

$$\begin{aligned} \phi &= \arctan(\bar{y}/\bar{x}) && \text{if } \bar{x} > 0 \\ &= 180^\circ + \arctan(\bar{y}/\bar{x}) && \text{if } \bar{x} < 0 \end{aligned}$$

where:

$$\bar{x} = \frac{1}{n}\sum \cos\phi_i$$
$$\bar{y} = \frac{1}{n}\sum \sin\phi_i$$

where ϕ_i is one of n observed angles.

The length, r, of this vector is calculated as:

$$r = (\bar{x}^2 + \bar{y}^2)^{1/2}$$

[†] Exceptional cases: $\phi = 90°$ if $\bar{x} = 0$ and $\bar{y} > 0$; $\phi = 270°$ if $\bar{x} = 0$ and $\bar{y} < 0$; and ϕ is undetermined if $\bar{x} = 0$ and $\bar{y} = 0$.

This value serves as a measure of the concentration of the sample points about the median direction, and has a maximum value of 1.0 when all sample points lie at the same position. If the sample is not randomly oriented (see below) the direction and length of the mean vector are represented in the polar diagrams as an arrow of appropriate length inside the circle.

Mean angular deviations, s, were calculated as:

$$s = \frac{180^\circ}{\pi}[2(1-r)]^{1/2}$$

and mean vectors are presented as $\phi \pm 1$ s. Mean angular deviations are equivalent to standard deviations in linear statistics. Confidence intervals at the 95% level were determined from published charts (Batschelet, 1981) and are shown on the polar diagrams as dotted lines.

In all tests an *a priori* predicted, or "homeward", direction was selected. For basic tests of WBNP snakes, this direction was denward for autumn tests and towards the mid-point of the summer range for spring tests. Both dens and summer ranges are distinct at WBNP; thus I felt that these sites accurately represented "home". For SLPP snakes, Spectacle Lake was the predicted direction in basic tests with the exception of neonates born at the laboratory. On the basis of the analysis of movements of SLPP snakes, it was not possible to make more accurate predictions regarding specific home sites; in any case, the orientation tests would have been unable to differentiate between sites given the small distances between them (see **Results**). In the case of laboratory-born neonates, the direction towards the laboratory served as the predicted direction.

With the sun moving across the sky at a rate of 15°/hr over a 24 hr period, phase-shift tests altered the predicted direction by 90° clockwise (for phase-delayed tests) or counterclockwise (for phase-advanced tests). Pheromone trailing test results were analyzed by considering two predicted directions - the homeward direction as described above and the direction of the trail.

In circular statistics, when a predicted direction is selected, both the concentration of points around the mean and the extent of the deviation from the predicted direction are important (Batschelet, 1981). The relationship between them is defined as:

$$\upsilon = r \cos(\phi - \theta)$$

where υ is called the "homeward component" and is a measure of the deviation of the mean vector from the predicted direction. Its value ranges from -1.0 to a maximum of 1.0 when all animals move exactly homeward. Significant directionality, versus a null hypothesis of randomness, can be tested by the V-test:

$$u = \upsilon\sqrt{2n}$$

where n = sample size. The V-test was used to detect clustering around a predicted direction; however, it cannot be used to detect significant deviations from this direction (Aneshansley and Larkin, 1981). For this purpose, 95% confidence intervals were used (Batschelet, 1981). A significant deviation of the mean vector from the predicted direction was concluded when the predicted direction was outside the confidence interval.

In some cases the polar diagrams suggested strong directionality but not towards the predicted direction. In these instances, significant directionality was tested by Rayleigh's test, which is based on the value of r and the sample size. Critical levels are given in charts in Batschelet (1981). For a unimodal sample, significance by this test indicates a concentration of the sample points about the mean. This test also was used to test the significance of axial data; that is, when it appeared that snakes selected two directions that differed by

180°. To examine this response, angles were first doubled (Krumbein, 1939) and reduced *modulo* 360° to obtain r_2, ϕ_2, and s_2. A significant value of r established that the snakes were oriented along an axis. The mean angle and its deviation were converted to axial measures by:

$$\begin{aligned} \phi &= \frac{\phi_2}{2} \quad \textit{or} \\ &= \frac{\phi_2}{2} + 180^\circ \end{aligned}$$

and

$$s = \frac{s_2}{2}$$

I found no precedent for analyzing trailing responses; therefore I examined this response by determining the significance of the homeward component both to the trail and to the homeward direction. In cases where stimulus snakes were allowed to select their own direction, angles were rotated by an appropriate amount so that the trail was standardized at 0°.

RESULTS

General Ecology and Movements

WBNP

Spring Behaviour

Spring emergence for the WBNP population occurred during the latter part of April and early May (Larsen, 1986, and pers. obs.). Males emerged from the den one to two weeks before the females and remained near the den until the majority of the females had appeared and begun their migration. Males did not begin to migrate until the majority of the females had left (but see below).

As the females emerged, most were courted *en masse*, forming characteristic mating balls with approximately 20 males courting a single female. Sexually attractive females that were not involved in a mating ball near the den entrance were actively trailed by males. On one occasion, I picked up a large female as she was travelling away from the den and placed her in an opaque snake bag. Within two minutes, a male headed towards me, apparently along the same path taken by the female. When he reached the point at which I had lifted the female off the ground, his movements ceased being rapid and direct and he began to search the immediate area. At one point he raised his head towards the snake bag. Within six minutes, an additional five males came along the same path and also began searching movements once they reached the point of pick-up. This behaviour continued for approximately ten minutes before the males moved away.

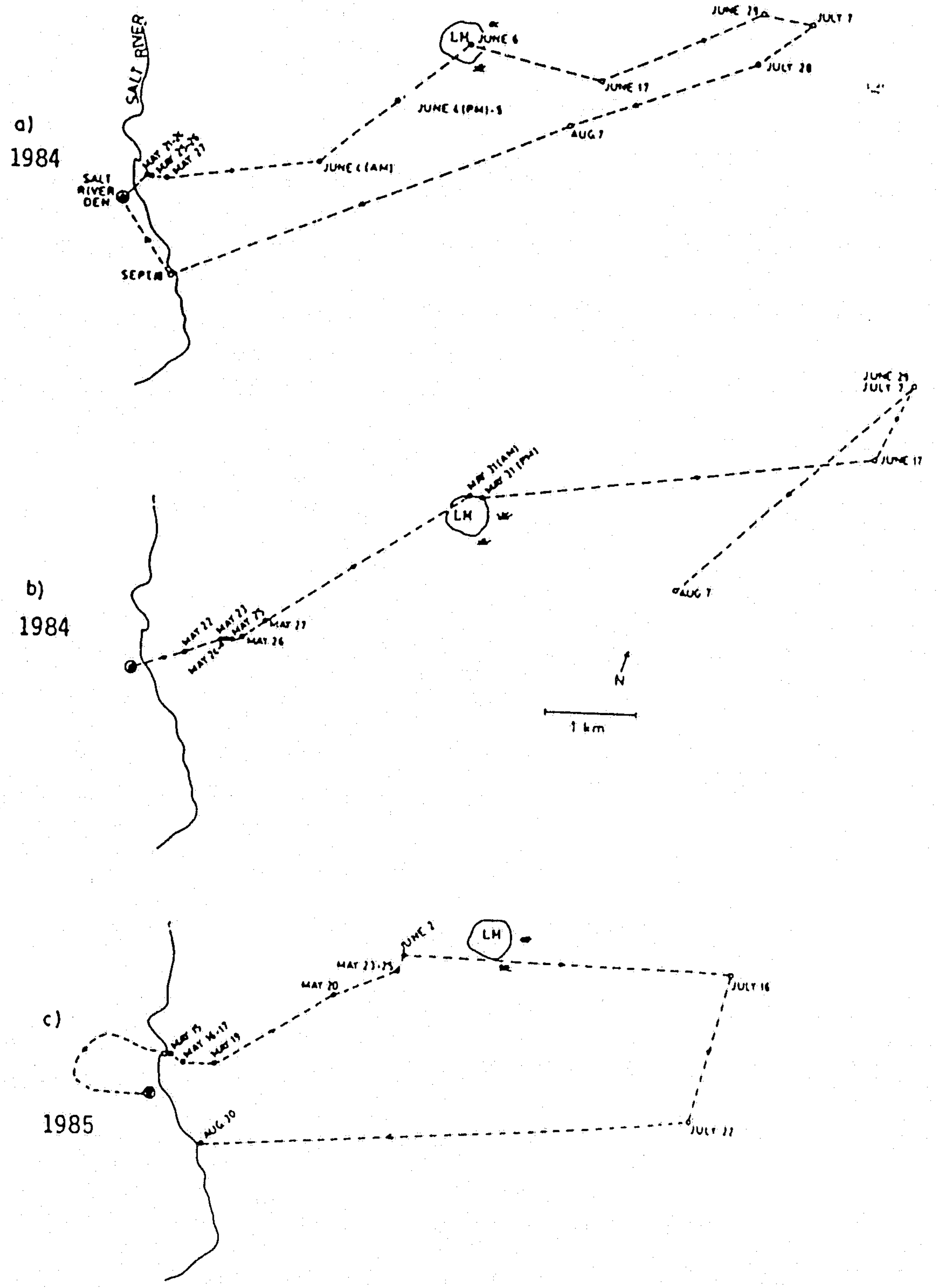
I also noted that some males moved approximately 10 to 15 m away from the immediate den openings during the period of female emergence. These males were not observed to mate during the first few days of emergence by the females, but they were involved in mating balls later. The direction of these outlying groups of males from the den, along an arc from 10° to 105°, was in the same direction as the early migratory route of the population.

Movements

Movements of three female *T. sirtalis* from WBNP are shown in Figure 5 (taken from Larsen, 1986). Although actual movement patterns were detailed for only these individuals, Larsen argued that most individuals displayed similar movements. Fidelity to the communal den was high between years. Movements were extensive, with some individuals travelling at least nine km away from the den, although the closest point of the summer range (Lost Marsh, indicated as LM on Figure 5) was less than four km from the den. These two seasonal habitats were clearly distinct and separate. Larsen noted that the majority of the population left the den in a common direction, and all three radiotracked snakes followed a loop pattern - that is, snakes did not retrace the outward path upon returning to the den in the fall. One female apparently began migrating in the wrong direction before making corrections (Figure 5C). Radiotracked females continued to show apparently directional movements rather thanswitching to a more random pattern (wandering), although it was not known how much wandering actually occurred between sampling dates.

Figure 5: Movements of three radiotracked female *T. sirtalis* at WBNP (from Larsen, 1986).

LM = Lost Marsh


a)
1984
SALT RIVER
SALT RIVER DEN
MAY 21-22
MAY 23-26
MAY 27
JUNE 4 (AM)
JUNE 4 (PM)-5
LH
JUNE 6
JUNE 17
JUNE 29
JULY 7
JULY 28
AUG 7
SEPT 18
b)
1984
MAY 22
MAY 23
MAY 25
MAY 24
MAY 26
MAY 27
MAY 31 (AM)
MAY 31 (PM)
LH
JUNE 17
JUNE 29
JULY 7
AUG 7
N
1 km
c)
1985
MAY 15
MAY 16-17
MAY 19
MAY 20
MAY 23-25
JUNE 2
LH
JULY 16
JULY 22
AUG 20

Larsen (1986) also noted that:

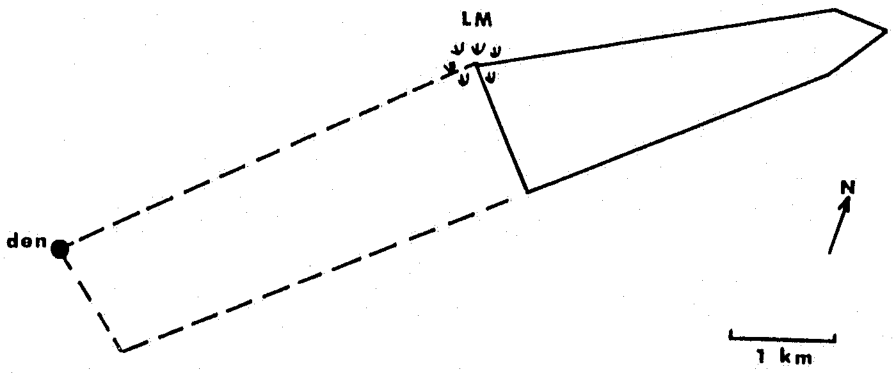
> "... it was not uncommon in the morning to find one or more males near a female during the early part of its migration. For example, on May 22, 1983, three males were near a transmitter-equipped female. Interestingly, on May 24, one of these males was recaptured within 10 m of the female, which had moved approximately 360 m during the two-day interval."

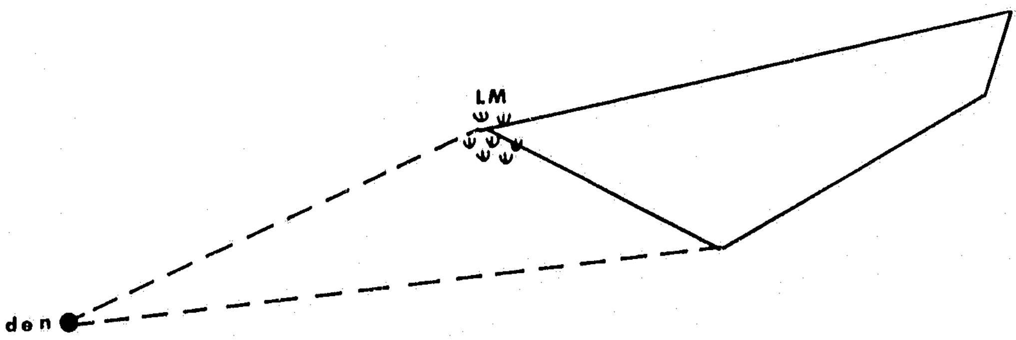
Home Range Areas

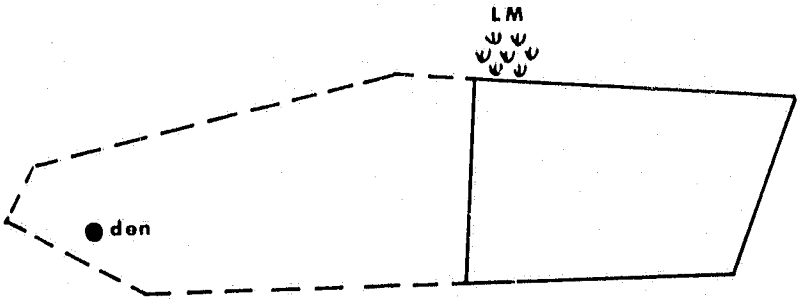
Home range areas for the WBNP population were calculated from movement diagrams provided in Larsen (1986). For the three radiotracked females, a mean home range area of 852 ± 160 ha was calculated on the basis of the movements made during the entire active season. If only the areas that included what was presumably the summer range (beginning at Lost Marsh) were considered, the mean home range estimate was sharply reduced to 340 ± 160 ha. The extent of movements within the outer edges of the polygons is not known, but it may be minimal. Assuming restricted movements within a corridor along the margins of the polygon, summer home range areas were further calculated based on a corridor width of 600 m, resulting in a mean home range area of 247 ± 54 ha. Home ranges for these individuals are shown in Figure 6.

Figure 6: Home range areas for three female *T. sirtalis* at WBNP, determined as minimum convex polygons.

LM = Lost Marsh


LM
den
N
1 km


LM
den


LM
den

SLPP

Sample Sizes and Recapture Success

Between 1974 and 1988 (1974 - 1985 data provided by Gregory, unpub.), 234 *T. sirtalis* and 270 *T. ordinoides* were captured at least once and marked at SLPP. Of these, 87 *T. sirtalis* and 83 *T. ordinoides* were recaptured at least once with maximum numbers of recaptures per individual of eight for *T. sirtalis* and seven for *T. ordinoides*. The maximum period (years) between first and last recapture was 10 years for a female *T. sirtalis* and eight years for two female *T. ordinoides*.

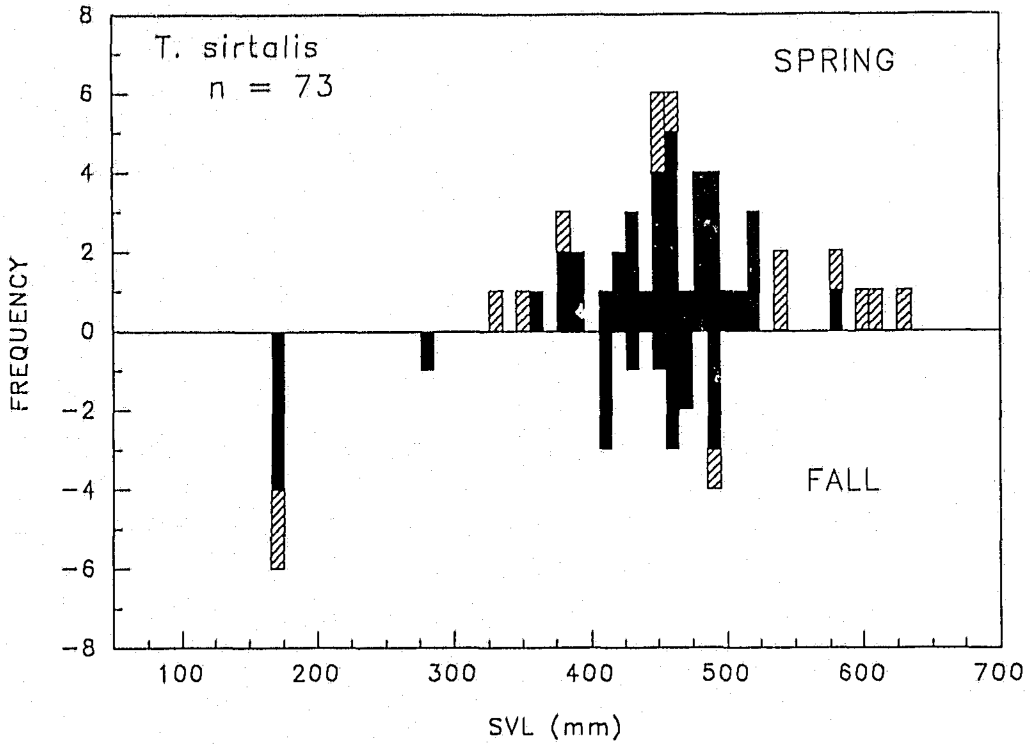
During this study, 95 *T. sirtalis* and 167 *T. ordinoides* were captured at SLPP for the first time and marked, with 52% and 39% of these individuals for the two species, respectively, being recaptured at least once. I obtained 128 and 134 recapture records for the two respective species, giving average recaptures per individual of 1.35 for *T. sirtalis* and 0.80 for *T. ordinoides*.

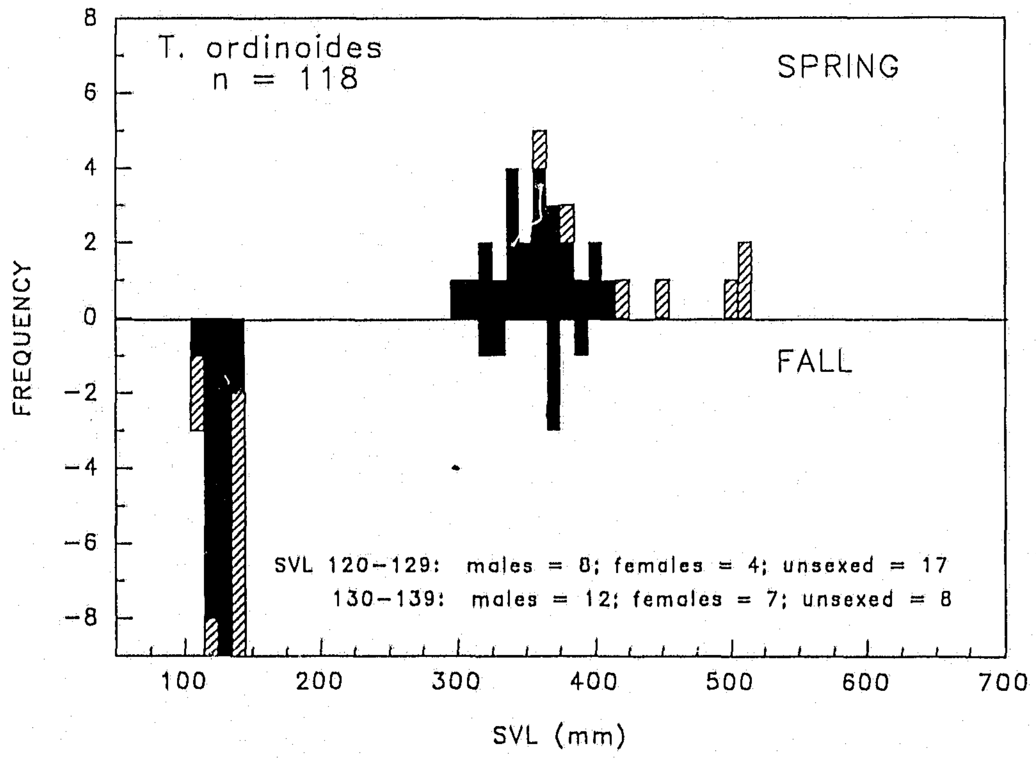
Size

Size frequency distributions for the two species (Figure 7) were based on original captures and determined for 1986 - 1988 spring (mid-March to May 31) and fall (September 1 - October 15). Neonate records, which included captive born individuals, provided the only distinct age class. Neonate *T. sirtalis* SVLs were less than 200 mm; *T. ordinoides* neonates were considerably smaller with maximum SVLs of 150 mm. An intermediate or juvenile age class is suggested for both species, although with few captures of individuals in this size range (280 - 360 mm for *T. sirtalis*; 220 - 230 mm for *T. ordinoides*), it is not clear whether this represents a real age group.

Figure 7: Spring and fall size-frequency distributions of SLPP snakes (1986 - 1988).

▨ = females ■ = males





SVL 120–129: males = 8; females = 4; unsexed = 17
130–139: males = 12; females = 7; unsexed = 8

The smallest gravid females recorded since 1974 had SVLs of 455 mm (*T. sirtalis*) and 350 mm (*T. ordinoides*), which reflects the smaller size of the latter species. This size discrepancy is not reflected in the largest individuals captured of each species. Females had maximum SVLs of 655 mm (*T. sirtalis*) and 645 mm (*T. ordinoides*) (Gregory, unpub. data).

The mean size of the ten largest female *T. sirtalis* captured since 1974 was 625 mm (range 600 - 655 mm) versus a mean SVL of 575 mm for the ten largest *T. ordinoides* (range 545 - 645 mm). Males were smaller for both species. For *T. sirtalis* the mean SVL of the ten largest individual males was 562 mm (range 525 - 585 mm). The mean SVL of the ten largest male *T. ordinoides* was 403 mm (range 390 - 425 mm).

Dens, Spring Activity, and Aggregations

The earliest appearance of snakes during my study was on March 12, 1988, when five males (four *T. sirtalis* and one *T. ordinoides*) were captured together in zone 8. Patches of snow were still present in the area. Gregory captured two males in zone 7 on February 27, 1983. The earliest spring appearances of females occurred on March 29, 1986 (*T. sirtalis*) and on April 1, 1987 (*T. ordinoides*).

It was difficult to confirm any site as a den, although these early sightings most likely occurred in the immediate vicinity of dens. Snakes captured near the end of the active season in October were also presumably at or near dens. Additional evidence that these were denning sites came from the observation that snakes remained stationary between recaptures during the early spring. One male, for example, was recaptured at a presumed den in zone 8 on March 12, 1988 and again on April 7, 1988. On April 10 he was captured 230 m away in zone 6. Only males were observed during this period in zone 8 but both males and females were present in zone 6, beginning on April 8. Males appeared to remain in suspected denning areas later if both sexes were present. One male showed no movement after 13 days (first capture: April 7, 1987; second capture: April 20, 1987) at a presumed den in zone 1 where both males and females were collected. The relative immobility of snakes during early spring is further examined in **Seasonal Movement Patterns.**

Suspected dens consisted of tree root systems, rock piles, and small holes in the ground. I made no temperature or other measurements of these dens, but there were no obvious differences between sites apparently used as dens in any year and numerous other sites that were not identified as dens.

I never observed courtship or mating activities in the field for either species. Courtship behaviour, involving chin rubbing by the male along the back of the female, was seen twice by captive SLPP *T. sirtalis*, on April 23, 1987 and on October 10, 1988. The latter observation suggested the possibility of fall mating.

Aggregations of snakes (defined here as two or more snakes within a one meter radius) were found occasionally. This often involved contact between the snakes. Male-only aggregations of *T. sirtalis* consisting of two to five males were noted on nine occasions. All but two occurred prior to May 5 at suspected den sites, with the exceptions occurring in August and, in both cases, involving one adult male and one juvenile male (< 400 mm SVL). Male *T. ordinoides* also were present in addition to *T. sirtalis* in some of these aggregations. Aggregations of males and nongravid females consisted of combinations of up to two individuals of each sex. These groups occurred throughout the active season. On one occasion a male was found next to a gravid female, and one pair of nongravid females was found. No other aggregations of gravid females were observed.

There was one occasion in which two snakes appeared to travel together. This involved a male and a nongravid female that were first found near one another on July 29, 1988. They were again captured together 14 days later, 145 m from the original capture site.

Thamnophis ordinoides displayed similar patterns. Three out of four male-only aggregations occurred during early spring at suspected dens, with the exception again occurring in August. Male - nongravid females groups were found on three occasions, once each in April, June and July in groups of two males and one or two females. Twice, both in June, a male was found next to a gravid female. Aggregations of up to three gravid females were found on four occasions, twice each in May and August. There was no evidence that any pairs of snakes travelled together.

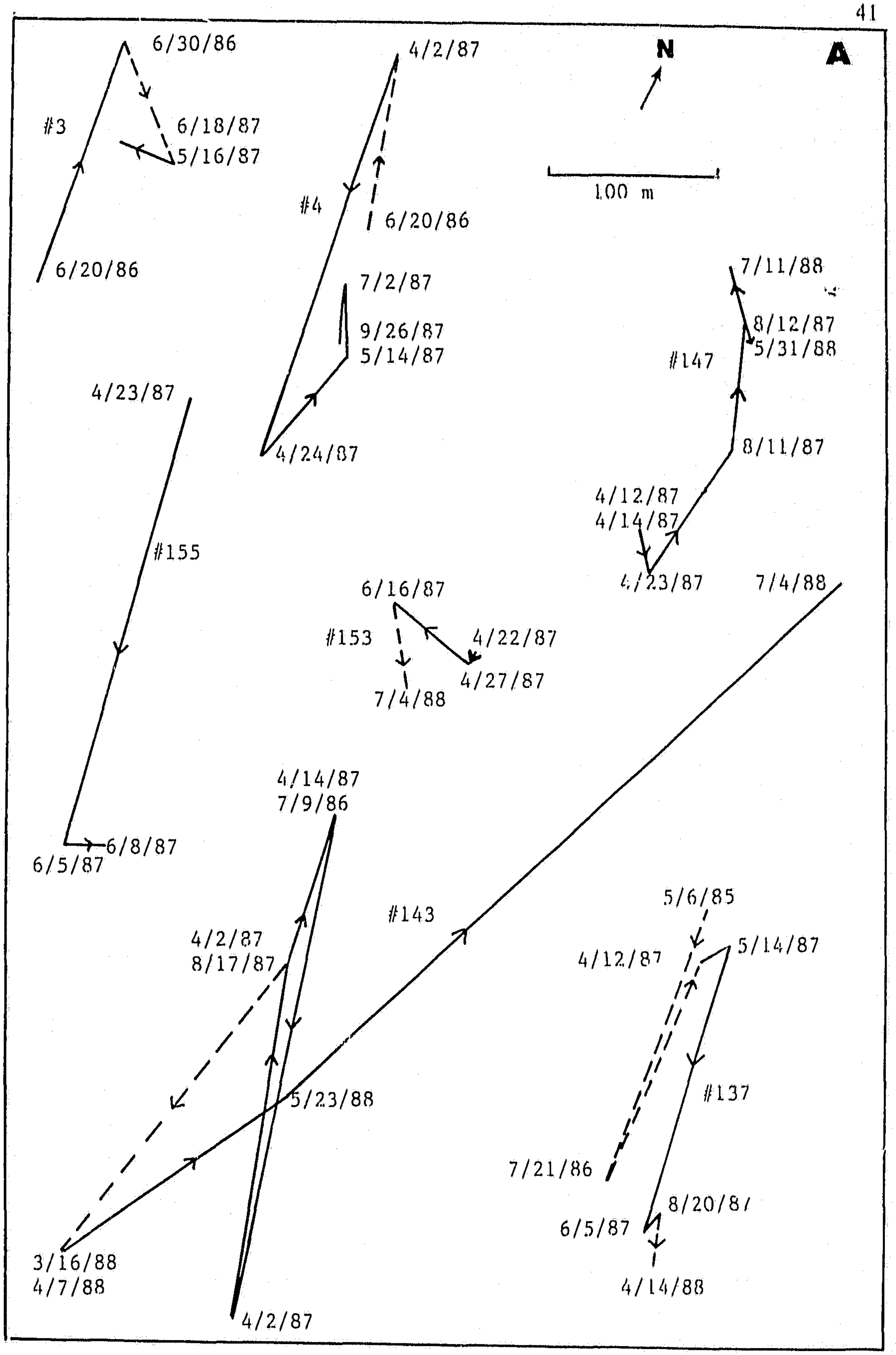
In addition to these aggregations, it was not uncommon to find snakes concentrated in a restricted area. For example, in zone 3 on April 14, 1988, four *T. sirtalis* (three males, one female) and five *T. ordinoides* (three males, two females) were captured within a 2.5 hr period in the same localized area of the zone. Snakes were not again observed in zone 3 until May 23. This apparently discontinuous use of a zone was fairly common.

Movements

Figure 8 illustrates a representative sampling of movements made by *T. sirtalis* at Spectacle Lake. To aid in clarity, they are shown without the actual spatial overlap that existed. Unlike WBNP, there was no large communal den from which all movements originated. Distances travelled between recaptures were short overall, with 435 m being the longest straight-line movement recorded during a single active season (May 23 - July 4, 1988; snake #143). Without continual monitoring, the actual routes taken by snakes

Figure 8: Representative movements of SLPP *T. sirtalis*.

Solid lines represent movements occurring within a year; dashed lines represent movements between years. Dates are given as Month/Day/Year.


A
N
100 m
#3
6/30/86
6/18/87
5/16/87
6/20/86
#4
4/2/87
6/20/86
7/2/87
9/26/87
5/14/87
4/24/87
#155
4/23/87
6/5/87
6/8/87
#147
7/11/88
8/12/87
5/31/88
8/11/87
4/12/87
4/14/87
4/23/87
#153
6/16/87
4/22/87
4/27/87
7/4/88
#143
7/4/88
4/14/87
7/9/86
4/2/87
8/17/87
5/23/88
3/16/88
4/7/88
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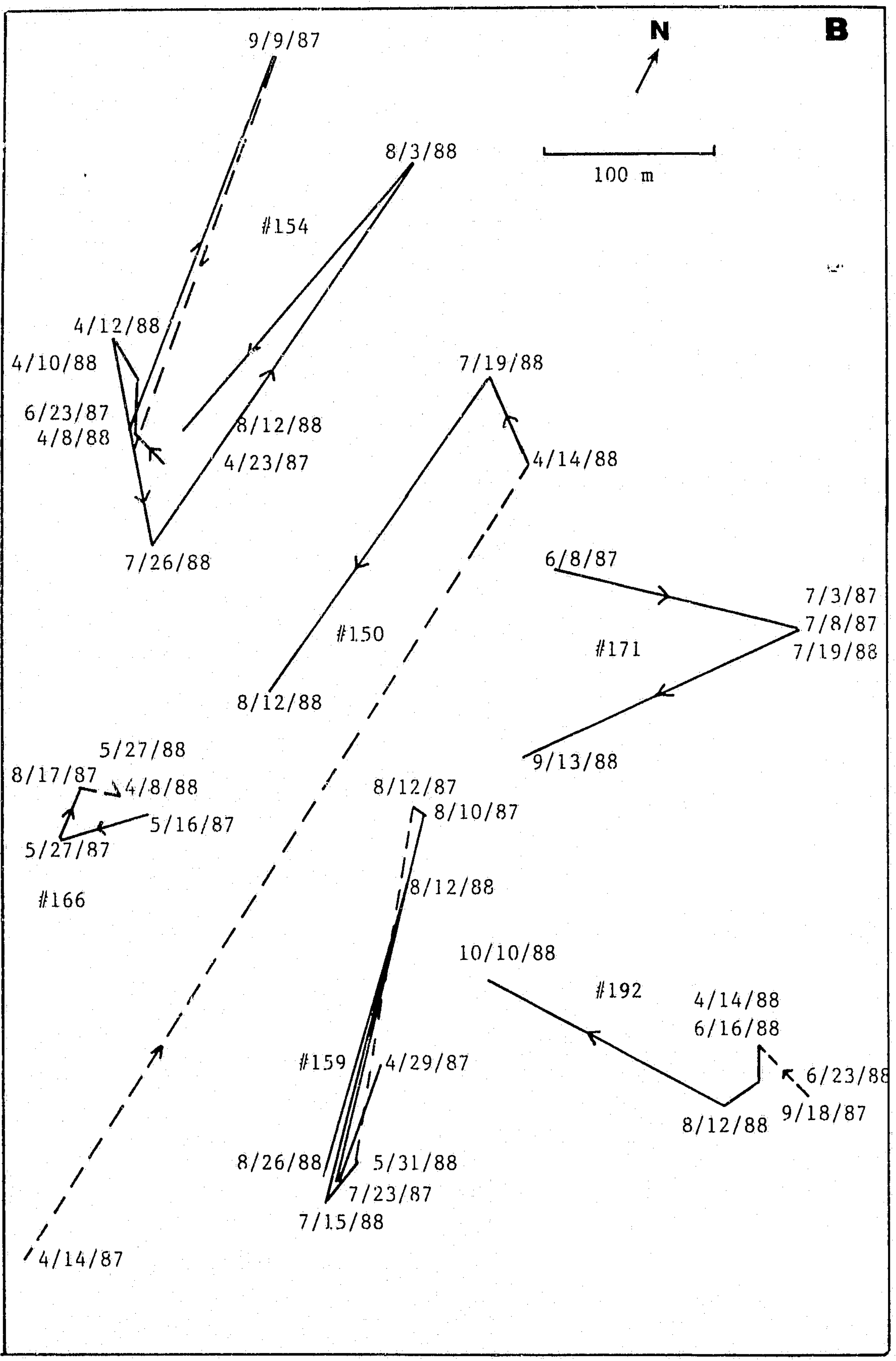
8/20/87
6/5/87
4/14/88


B
N
100 m
9/9/87
8/3/88
#154
4/12/88
4/10/88
6/23/87
4/8/88
8/12/88
4/23/87
7/26/88
7/19/88
4/14/88
#150
8/12/88
6/8/87
7/3/87
7/8/87
7/19/88
#171
9/13/88
5/27/88
8/17/87
4/8/88
5/16/87
5/27/87
#166
8/12/87
8/10/87
8/12/88
10/10/88
#192
4/14/88
6/16/88
6/23/88
9/18/87
8/12/88
#159
4/29/87
8/26/88
5/31/88
7/23/87
7/15/88
4/14/87

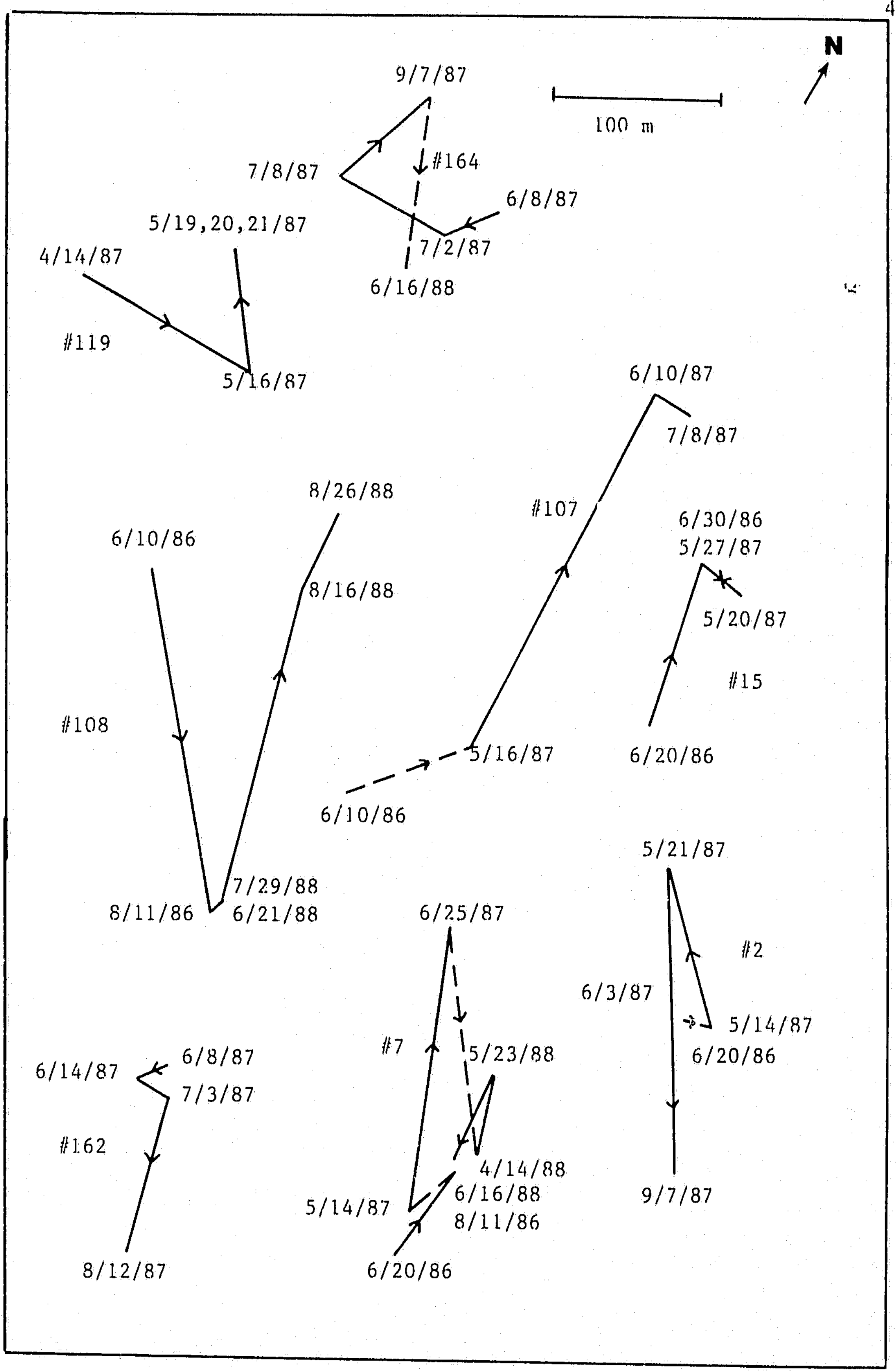
between recaptures could not be determined, but such extensive straight-line movements appeared to be the exception; rather, wandering appeared to be the predominant pattern.

The tendency of snakes to return to specific locations, either within an active season or between years, varied among individuals. One female (not shown in Figure 8) was captured seven times in the same zone over a period of eight years. Snake #143 (Figure 8A) was captured at a specific site on July 9, 1986, and again on April 14, 1987. He was also captured twice at a different location on April 2, 1987 and August 17, 1987. The early sighting of this male at the second location suggests that he overwintered near that site. This male remained stationary at a different presumed den from March 16, 1988 to April 7, 1988. Additional examples are shown in Figure 8B. Snake #154 was captured at a specific location on June 23, 1987, and again on April 8, 1988. Snake #171 was found at a specific site in July of 1987 and 1988. By contrast, snake #150 was captured on April 14 of both 1987 and 1988 at locations 530 m apart.

Representative movements of *T. ordinoides* are shown in Figure 9. Movement patterns were similar to those of *T. sirtalis*. The longest straight-line movement between successive captures was by a gravid female that travelled 230 m in 25 days. As with *T. sirtalis*, the tendency to return to specific sites appeared to vary among individuals. Snake #107 was captured on June 10, 1986 and 1987 at sites 295 m apart. Snake #7 was captured on June 20, 1986, June 25, 1987, and June 16, 1988, at three different locations - 190 m apart between 1986 and 1987 but less than 60 m apart between the 1986 and 1988 dates. Capture locations for snake #2 on June 20, 1986 and June 3, 1987 were only 12 m apart.

Figure 9: Representative movements of SLPP *T. ordinoides*.

Solid lines represent movements occurring within a year; dashed lines represent movements between years. Dates are given as Month/Day/Year.


N
100 m
9/7/87
7/8/87
#164
6/8/87
7/2/87
6/16/88
5/19,20,21/87
4/14/87
#119
5/16/87
6/10/87
7/8/87
8/26/88
#107
6/30/86
5/27/87
6/10/86
8/16/88
5/20/87
#15
#108
5/16/87
6/20/86
6/10/86
5/21/87
7/29/88
8/11/86
6/21/88
6/25/87
#2
6/3/87
5/14/87
#7
6/20/86
6/8/87
5/23/88
6/14/87
7/3/87
#162
4/14/88
6/16/88
9/7/87
5/14/87
8/11/86
8/12/87
6/20/86

Fidelity

Few recaptures of snakes occurred in early spring and/or late autumn; therefore conclusions regarding population fidelity to apparent dens are tenuous. Of the six *T. sirtalis* captured during early spring and/or late autumn of consecutive seasons, none showed evidence of returning to a specific den site (Table 1). Given the short distances between recaptures for some of these males (mean 230 m) and the range of daily movement rates for this population (see **Distances Travelled during Various Time Periods**), it is possible that some of these males were captured while en route to a den. Yet, snakes typically were observed near a suspected den in early spring of one year while none were seen at that site the following autumn or spring. This suggested that at least some overwintering sites were not used in consecutive years.

Seasonal site fidelity was also examined using the following approach. Under the assumption that snakes demonstrating fidelity will be closest to a specific site one year after they last used it, I examined distances between recaptures occurring in successive years for two general categories - one year apart (365 ± 15 days) and 'other' (outside the one year range). In the former case, all records of recaptures occurring one year apart were included in the analysis. In the latter category, only consecutive data points were used (e.g. the last capture of 1987 and the first of 1988). To ensure that no relationship existed between intercapture interval and distance travelled, scatter plots were drawn and correlations were calculated (Figure 10). The one year period was divided into two groups: 350 - 365 days and 365 - 380 days to ensure that distance did not decrease as the 365 day mark was approached from either direction. In no case for either species were any relationships noted [*T. sirtalis*: 350-365 days, $r = 0.36$, $p > .05$, $n = 7$ (6 snakes); 365-380 days, $r = -0.45$, $p > .05$, $n = 11$ (10 snakes); Other, $r = -0.11$, $p > .05$, $n = 24$ (23 snakes). *T. ordinoides*:

Table 1: Distance (m) between recaptures in consecutive denning seasons of male *T. sirtalis* captured near suspected dens.

Snake Number	1st Capture Date	2nd Capture Date	Distance between recaptures
135	Apr 12, 1987	Apr 7, 1988	65
137	Apr 12, 1987	Apr 14, 1988	170
143	Apr 2, 1987	Mar 16, 1988	220
150	Apr 14, 1987	Apr 14, 1988	530
151	Apr 14, 1987	Oct 10, 1988	80
198	Mar 12, 1988	Oct 10, 1988	450

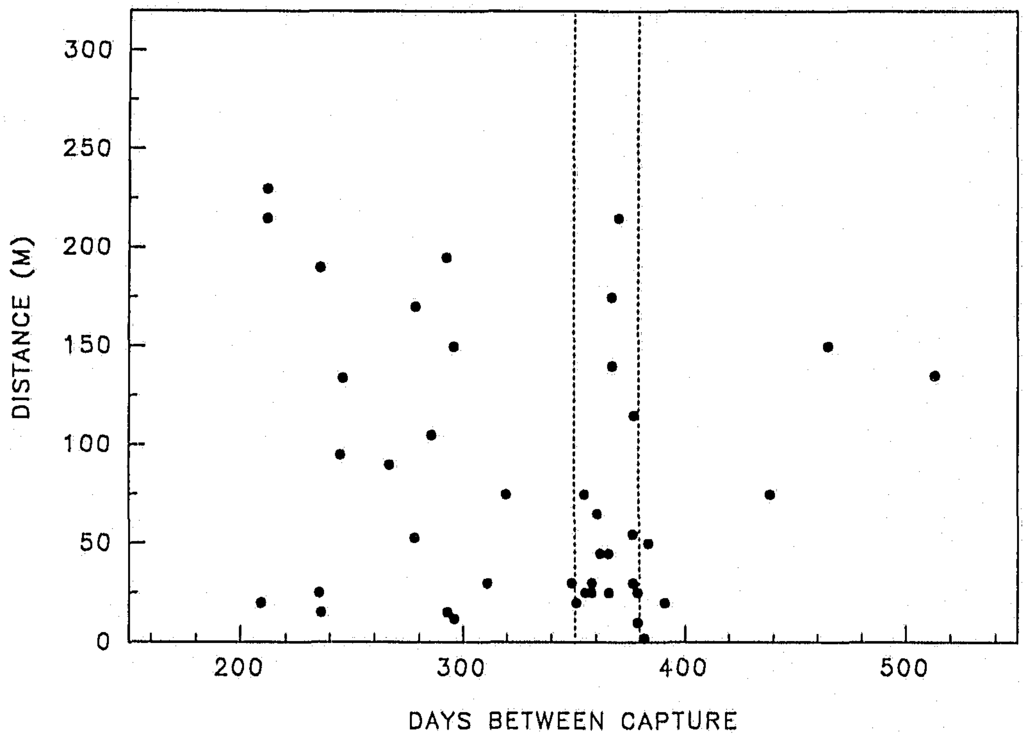
Figure 10: Relationship between distance travelled between captures occurring in successive years and inter-capture interval for SLPP snakes.

Dashed lines indicate the one year range (365 ± 15 days).

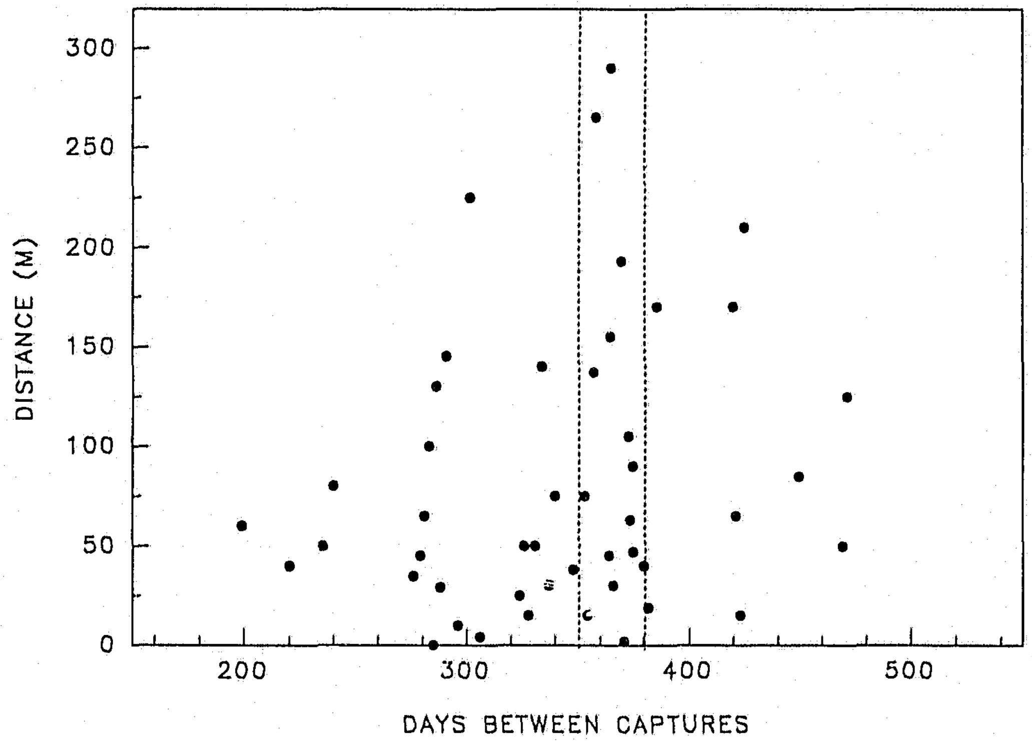
A. *T. sirtalis*
Inside one year range: n = 18 (15 snakes)
Outside one year range: n = 24 (23)

B. *T. ordinoides*
Inside one year range: n = 15 (13)
Outside one year range: n = 32 (28)

A. T. sirtalis



B. T. ordinoides



350-365 days, r = -0.22, p > .05, n = 6 (6 snakes); 365-380 days, r = -0.33, p > .05, n = 9 (8 snakes); other, r = 0.24, p > .05, n = 32 (29 snakes)].

I then compared mean intercapture distances between groups (Table 2). For the one year period, I first compared spring and summer recaptures because snakes may have shown seasonal differences in fidelity. Seasonal patterns were not significantly different for either species [*T. sirtalis*: t = 1.80, p > .05, n = 18 (15 snakes). *T. ordinoides*: t = 0.10, p > 0.05, n = 15 (14 snakes)]; therefore data for the two seasons were pooled.

Finally I compared mean distance between capture points for the one year period versus other. In neither species, were individuals found to be closer, on average, to their original capture point following recaptures occurring one year apart versus other times between successive active seasons [*T. sirtalis*: t = 1.57, p > .05, n = 42 (38 snakes). *T. ordinoides*: t = 0.34, p > .05, n = 47 (43 snakes)]. In other words, snakes were no closer to any specific site following a period of one year than after any other period between two active seasons.

Distances Travelled during Various Time Periods

Recapture data were divided into three periods - recaptures occurring within 1 month (30 days or less), from 2 - 5 months, and from 6 - 12 months. For each category for both species, scatter plots revealed no relationships between distance moved and days between capture [*T. sirtalis*: 1 month, r = 0.24, p > .05, n = 61 (38 snakes); 2 - 5 months, r = -0.05, p > .05, n = 52 (32 snakes); 6 - 12 months, r = -0.31, p > .05, n = 22 (20 snakes). *T. ordinoides*: 1 month, r = 0.24, p > .05, n = 50 (34 snakes); 2 - 5 months, r = 0.28, p > .05, n = 32 (30 snakes); 6 - 12 months, r = 0.18, p > .05, n = 27 (27 snakes)] (examples are shown in Figure 11).

Table 2: Examination of seasonal and yearly fidelity for SLPP snakes.

Values given are mean distances (m) between recaptures ± 1 S.D. occurring between successive springs, summers, pooled data for spring or summer recaptures (= 1 year), or during other periods between two years but not within the one year period (365 ± 15 days).

Spring = March 1 - May 31 Summer = June 1 - August 31

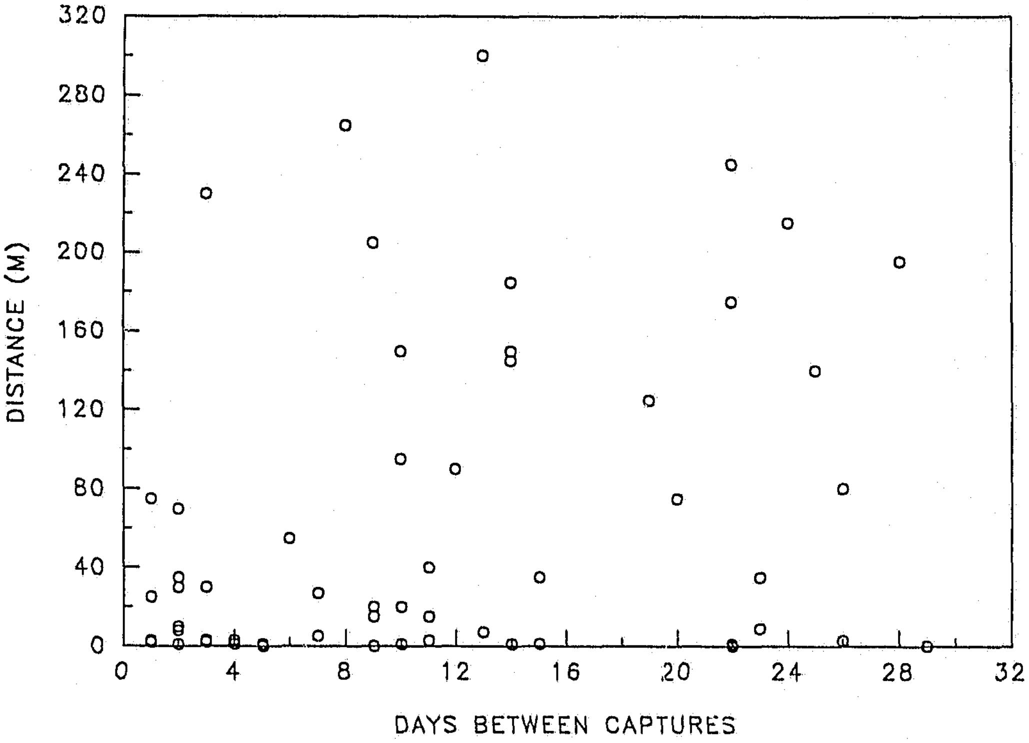
Species	Time Period	n	No. Snakes	Mean Distance ± 1 S.D.
T. sirtalis	Spring	6	5	99 ± 70.9
	Summer	12	10	44 ± 39.9
	1 year	18	15	62 ± 58.4
	Other	24	23	95 ± 69.4
T. ordinoides	Spring	5	5	100 ± 85.3
	Summer	10	9	105 ± 85.4
	1 year	15	14	103 ± 88.1
	Other	32	29	73 ± 60.6

Figure 11: Examples of the relationships between distance travelled during various time periods and inter-capture interval for SLPP snakes.

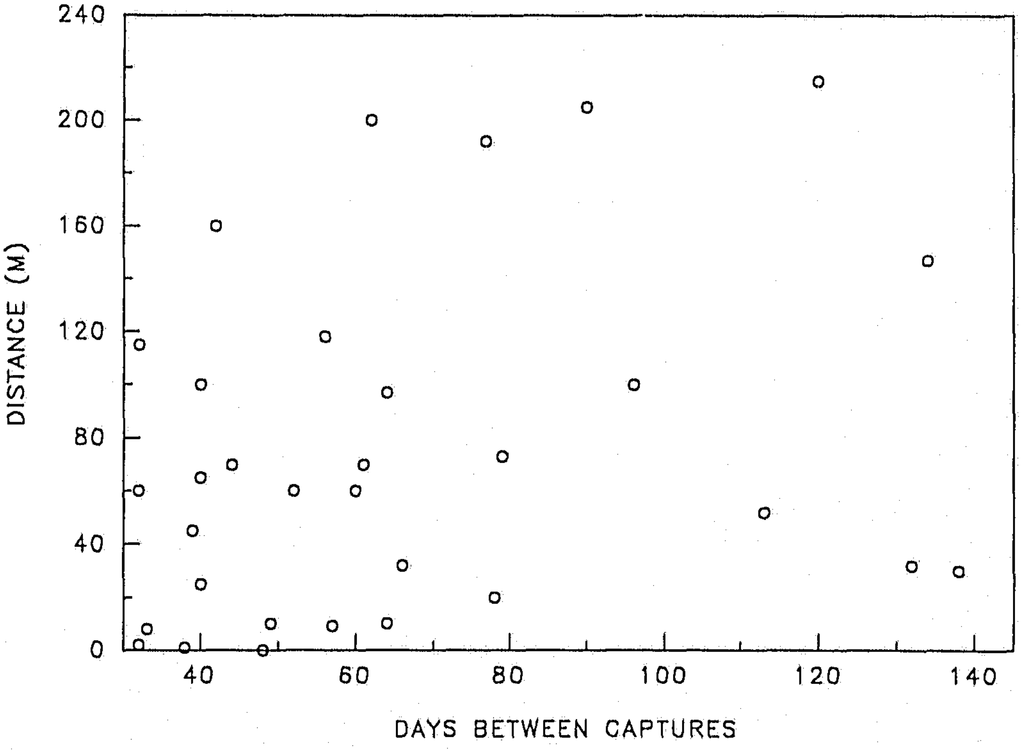
A. *T. sirtalis*, 1 month or less. n = 61 (39 snakes).

B. *T. ordinoides*, 2 - 5 months. n = 32 (30 snakes).

A. T. sirtalis, 1 month or less



B. T. ordinoides, 2 – 5 months



Mean distances between capture points of adult snakes over various time periods were determined for both *T. sirtalis* and *T. ordinoides* (Table 3). I first examined possible differences due to sex and reproductive condition. Among *T. sirtalis*, gravid females tended to travel farther between captures for the 1 month and 2 - 5 month periods. Only one female record was obtained for the 6 - 12 month period. Males travelled farther than did nongravid females. None of these differences were significant (1 month: $F_{2,58} = 0.81$, $p > .05$; 2 - 5 months: $F_{2,49} = 0.41$, $p > .05$; 6 - 12 months: $F_{2,19} = 0.15$, $p > .05$).

Somewhat different trends were noted in *T. ordinoides*, although again the differences were not significant (1 month: $F_{2,47} = 0.97$, $p > .05$; 2 - 5 months: $F_{2,29} = 0.02$, $p > .05$; 6 - 12 months: $F_{2,24} = 0.72$, $p > .05$). During movements of 1 month or less, gravid females apparently travelled the farthest and nongravid females travelled the least. For the 2 - 5 month period, snakes from all groups travelled approximately the same distance between recaptures. Gravid females moved the shortest distances and nongravid females covered the greatest distances in the longest time period.

Next I examined differences in distance travelled between the time periods. The same result was obtained for both species - significant differences were noted between the three time periods (*T. sirtalis*: $F_{2,132} = 6.67$, $p < .0025$. *T. ordinoides*: $F_{2,106} = 3.98$, $p < .025$).

Comparisons between the two species were made for each time period. Mean distances travelled by each species did not differ significantly for either the 1 month period [$t = 1.42$, $p > .05$, $n = 111$ (72 snakes)] or for the 6 - 12 month period [$t = 0.88$, $p > .05$,

Table 3: Distances travelled (m) by adult SLPP snakes between captures for various time periods.

FNG = nongravid females FG = gravid females M = males

	Time between captures	Sex	n	No. Snakes	Mean ± 1 S.D.	Range
T. sirtalis	≤ 1 month	FNG	12	8	44 ± 39.0	1 - 500
		FG	10	7	87 ± 86.4	2 - 265
		M	39	24	59 ± 82.5	0 - 300
		TOTAL	61	39	60 ± 80.7	
	2 - 5 months	FNG	9	7	107 ± 91.4	8 - 265
		FG	7	6	162 ± 165.8	5 - 435
		M	36	22	126 ± 114.4	1 - 435
		TOTAL	52	35	107 ± 120.1	
	6 - 12 months	FNG	6	6	84 ± 79.4	15 - 230
		FG	1	1	75	
		M	15	13	101 ± 67.2	12 - 215
		TOTAL	22	20	95 ± 69.8	
T. ordinoides	≤ 1 month	FNG	5	4	18 ± 17.8	0 - 50
		FG	29	18	50 ± 63.6	0 - 230
		M	16	12	32 ± 39.8	0 - 140
		TOTAL	50	34	41 ± 54.8	
	2 - 5 months	FNG	5	5	79 ± 62.5	30 - 200
		FG	16	14	72 ± 65.9	0 - 205
		M	11	11	75 ± 61.3	8 - 215
		TOTAL	32	30	75 ± 63.9	
	6 - 12 months	FNG	9	9	88 ± 70.2	0 - 225
		FG	6	6	47 ± 33.2	4 - 100
		M	12	12	76 ± 66.9	10 - 265
		TOTAL	27	27	73 ± 64.1	

n = 49 (47 snakes)], but *T. sirtalis* travelled significantly farther than did *T. ordinoides* during the 2 - 5 month recapture interval [t = 2.11, p < .05, n = 84 (62 snakes)].

Daily movement rates also were calculated for snakes recaptured within a 1 month period (Table 4). Rates were not significantly different among sex/reproductive categories for either species (*T. sirtalis*: $F_{2,58} = 2.01$, $p > .05$; *T. ordinoides*: $F_{2,47} = 1.61$, $p > .05$). Pooling scores for sex and reproductive condition showed no significant differences in rates between the two species [t = 1.34, p > .05, n = 111 (72 snakes)].

Seasonal Movement Patterns

To examine possible seasonal differences in activity patterns, distances travelled and rates of movement, determined for a one month or less recapture period, were plotted against the middate between successive captures. *T. sirtalis* males (Figure 12) appeared to be most active during early April, especially in terms of distance moved, following a period during which they remained stationary (at presumed dens). Females did not display a similar spring activity peak, but otherwise seemed to be as active as males in their movements. A slight increase in movements occurred in mid-August. These patterns were also evident when rates of movement were used as an indicator of activity (Figure 12B).

Both male and female *T. ordinoides* appeared to be most active from mid-May to mid-June (Figure 13A and 13B). There was no obvious spring peak of activity by males. Considerable individual variation existed for both species throughout most of the active season regardless of the measure of activity.

Individual variations in movement were not related to differences in size, at least among adults. Figure 14 shows a plot of the relationship between distance between recaptures of one month or less and SVL for the two species (duplicate records for the

Table 4: Minimum rates of movement (m/day) determined for recaptures of one month or less for SLPP snakes.

Days = mean ± 1 S.D. number of days between captures.

FNG = nongravid female FG = gravid female M = male

	Sex	n	No. Snakes	Rate Mean ± 1 S.D.	Rate Range	Days Mean ± 1 S.D.
T. sirtalis	FNG	12	8	14 ± 19.8	0.4 - 75.0	8 ± 8.3
	FG	10	7	12 ± 12.8	1.5 - 35.0	9 ± 5.6
	M	39	24	5 ± 12.6	0 - 76.7	13 ± 8.5
	Total	61	39	8 ± 14.8		11 ± 8.3
T. ordinoides	FNG	5	4	2 ± 2.0	0 - 5.6	17 ± 9.1
	FG	29	8	5 ± 4.2	0 - 13.6	12 ± 8.5
	M	16	12	7 ± 9.9	0 - 35.0	7 ± 7.7
	Total	50	24	5 ± 6.7		11 ± 8.9

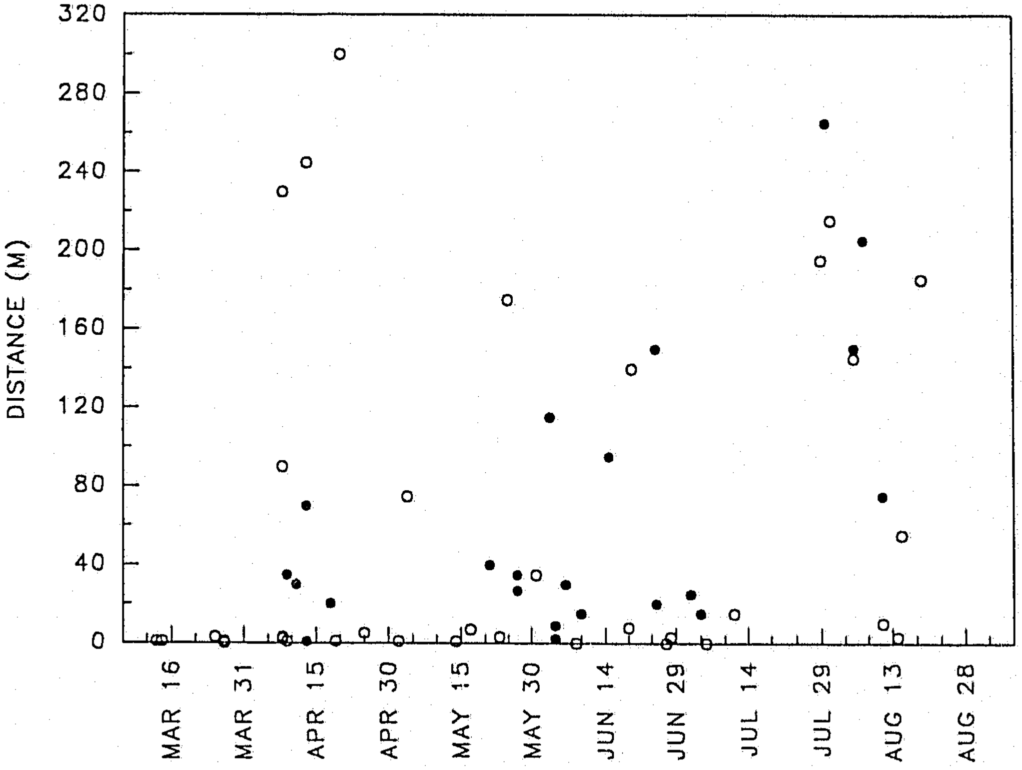
Figure 12: Seasonal activity patterns of SLPP *T. sirtalis*.

A. Distance travelled between captures of 1 month or less.

B. Movement rates determined for captures of 1 month or less.

○ = males n = 38 (27 snakes)
• = females n = 22 (15 snakes)

A. Distance



B. Rate of Movement

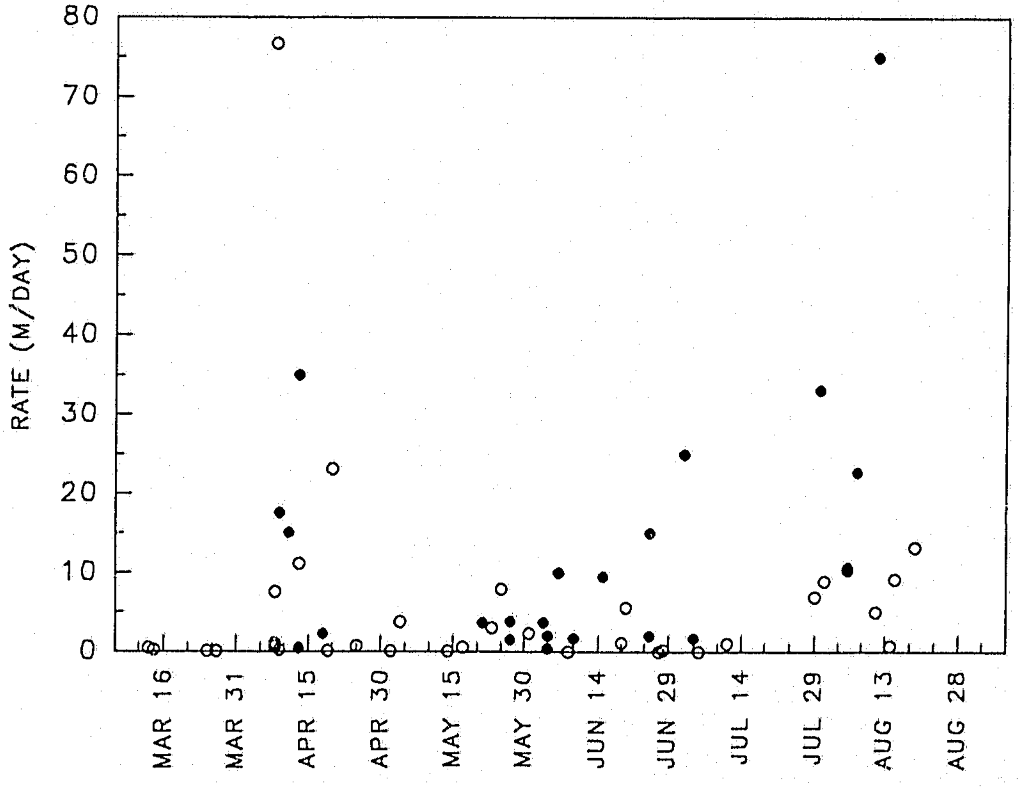


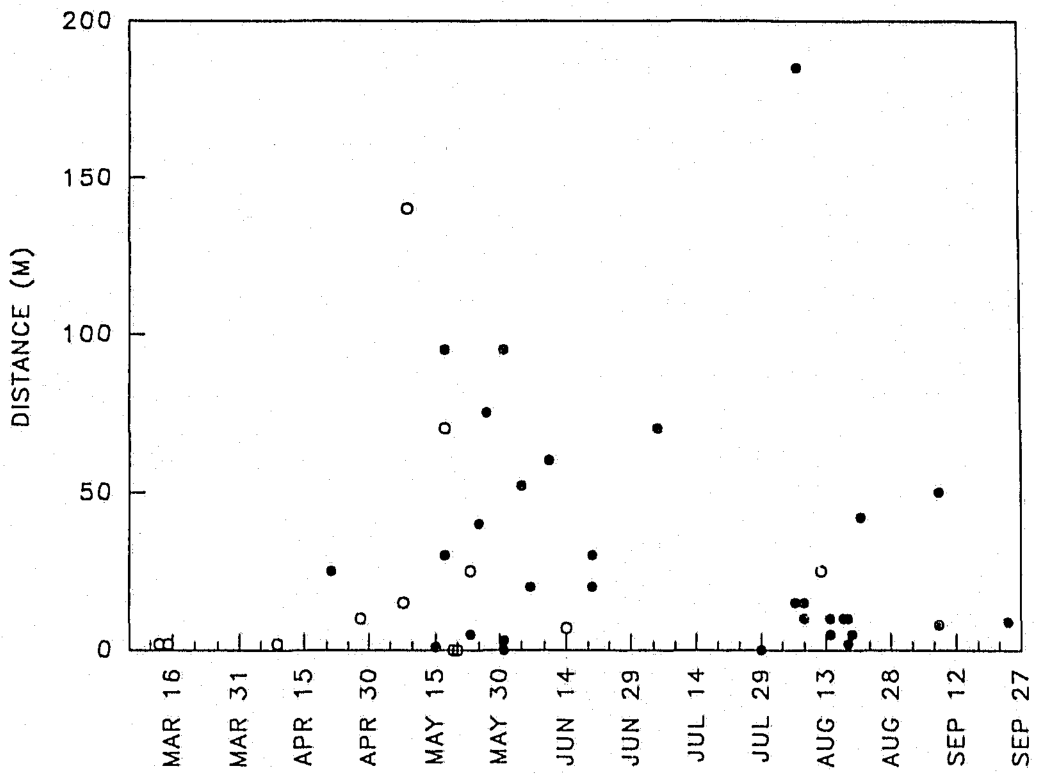
Figure 13: Seasonal activity patterns of SLPP *T. ordinoides*.

A. Distance travelled between captures of 1 month or less.

B. Movement rates determined for captures of 1 month or less.

○ = males n = 13 (10 snakes)
• = females n = 31 (19 snakes)

A. Distance



B. Rate of Movement

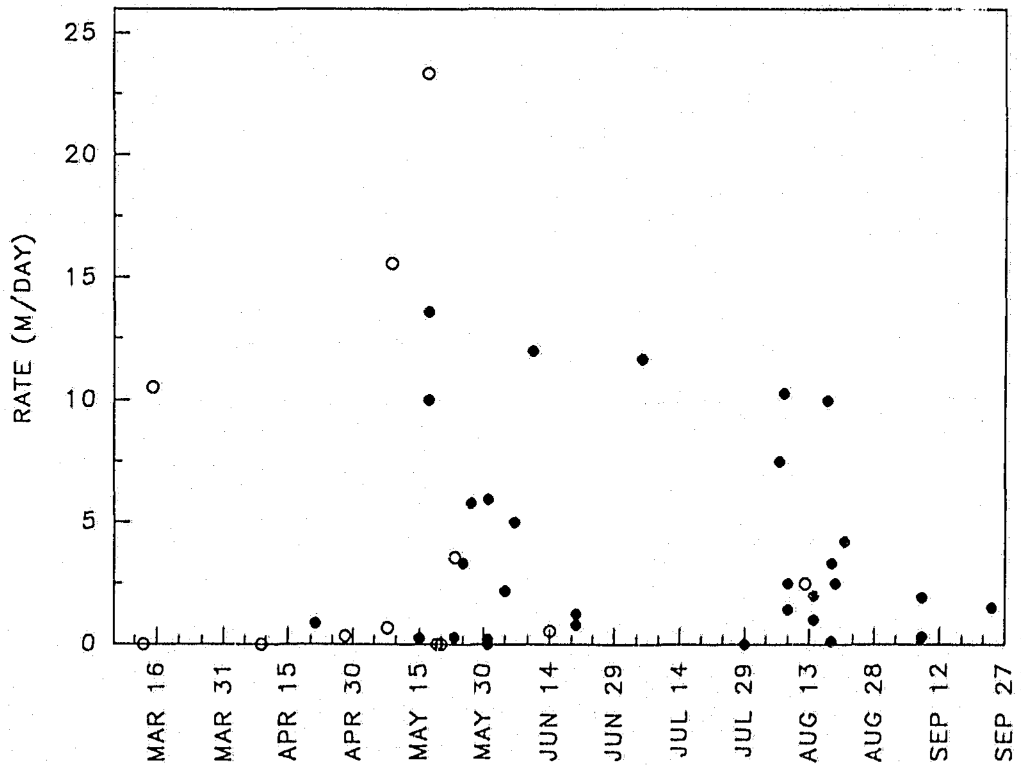
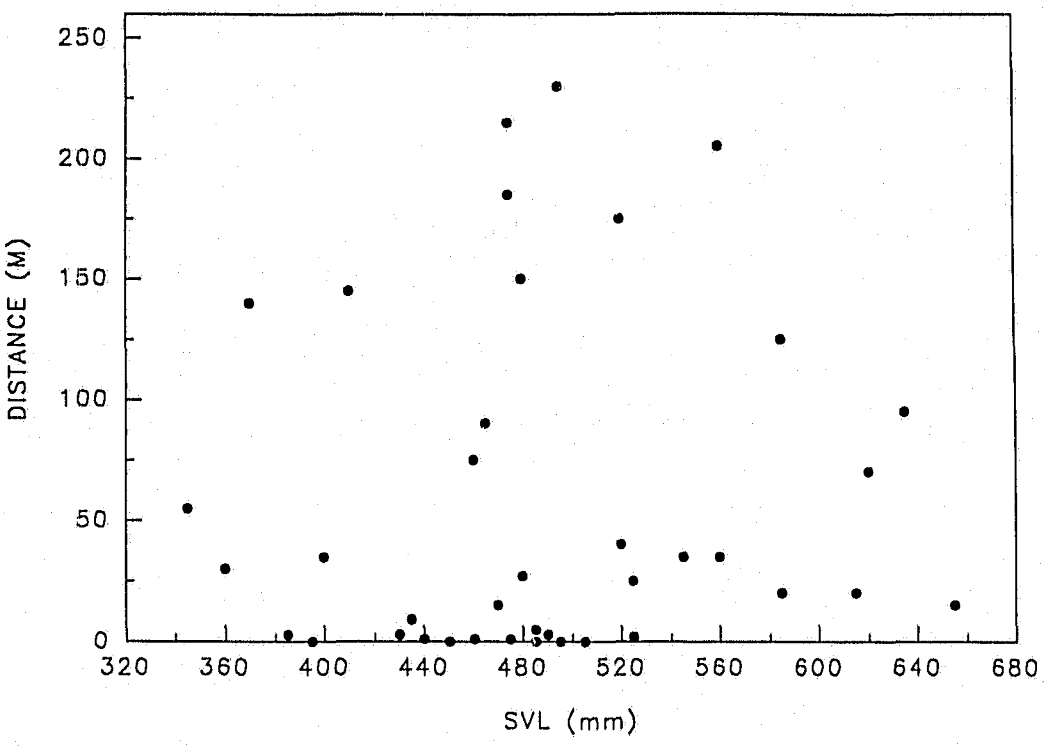


Figure 14: Relationship between distance between recaptures of one month or less and SVL for SLPP snakes.

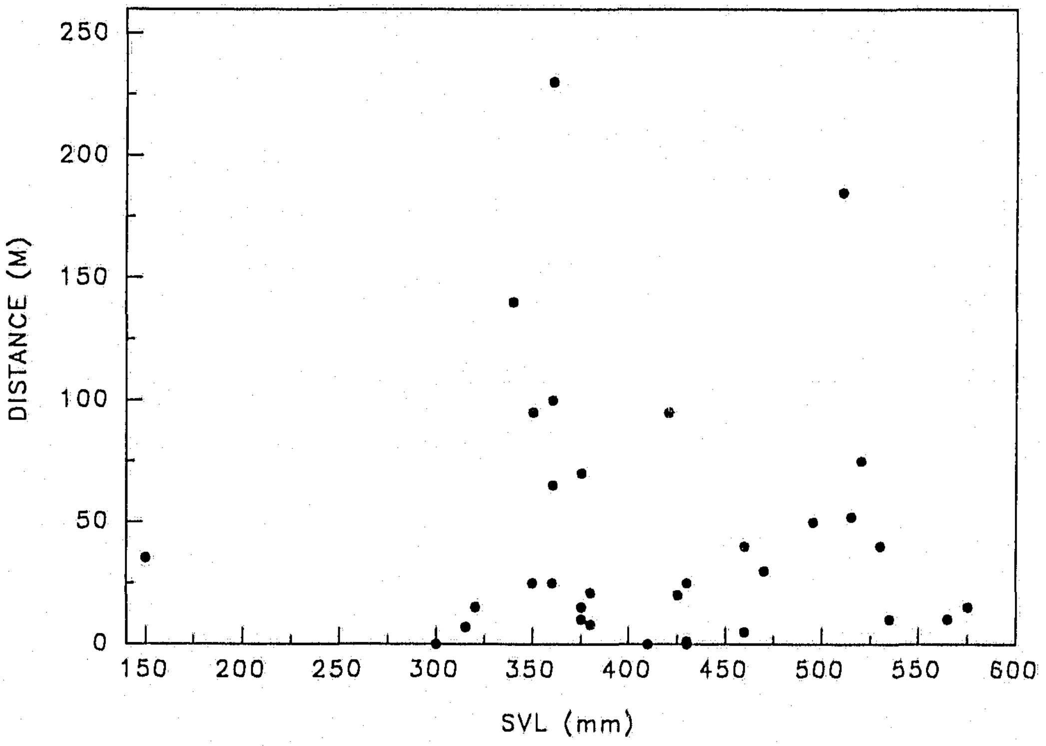
A. *T. sirtalis*. n = 40

B. *T. ordinoides*. n = 33

A. *T. sirtalis*



B. *T. ordinoides*



same individual occurring within the same year have been omitted). In neither case did a significant relationship exist (*T. sirtalis*: $r = 0.08$, $p > .05$, $n = 40$. *T. ordinoides*: $r = -0.04$, $p > .05$, $n = 33$).

Home Range Areas

Home range areas for a single active season were determined for 26 individual *T. sirtalis*. The analyses of distances between recaptures for various time periods indicated that snakes moved the maximum distances in the 2 - 5 month time period and that these distances were significantly greater than those covered in a 1 month recapture period. Thus, home range calculations based on movements of 30 days or less (two individuals) were excluded in the calculation of home range areas. A significant correlation between home range area vs days between captures (Figure 15) was found to exist for *T. sirtalis* ($r = 0.48$, $p < .05$, $n = 24$), with home range size increasing over sampling period. This significance did not persist when the two largest home ranges were omitted from the data set ($r = 0.13$, $p > .05$, $n = 22$). The special case of these two individuals will be further examined. The results in Table 5 exclude these two cases. Home ranges for *T. sirtalis* are shown in Figure 16.

Mean home range areas did not differ significantly between sexes for either year (1987: $t = -0.41$, $p > .05$, $n = 10$. 1988: $t = 0.78$, $p > .05$, $n = 12$), or between years for either sex (males: $t = 0.81$, $p > .05$, $n = 13$. females: $t = 0.69$, $p > .05$, $n = 9$). Gravid females had the largest home ranges, with a mean of 0.658 ± 0.555 ha ($n = 3$), while home ranges of nongravid females were the smallest at 0.145 ± 0.134 ha ($n = 6$). This difference was not significant ($t = 2.29$, $p > .05$), although larger sample sizes may have detected a

Figure 15: Relationship between length of the sampling period and home range area in SLPP *T. sirtalis*.

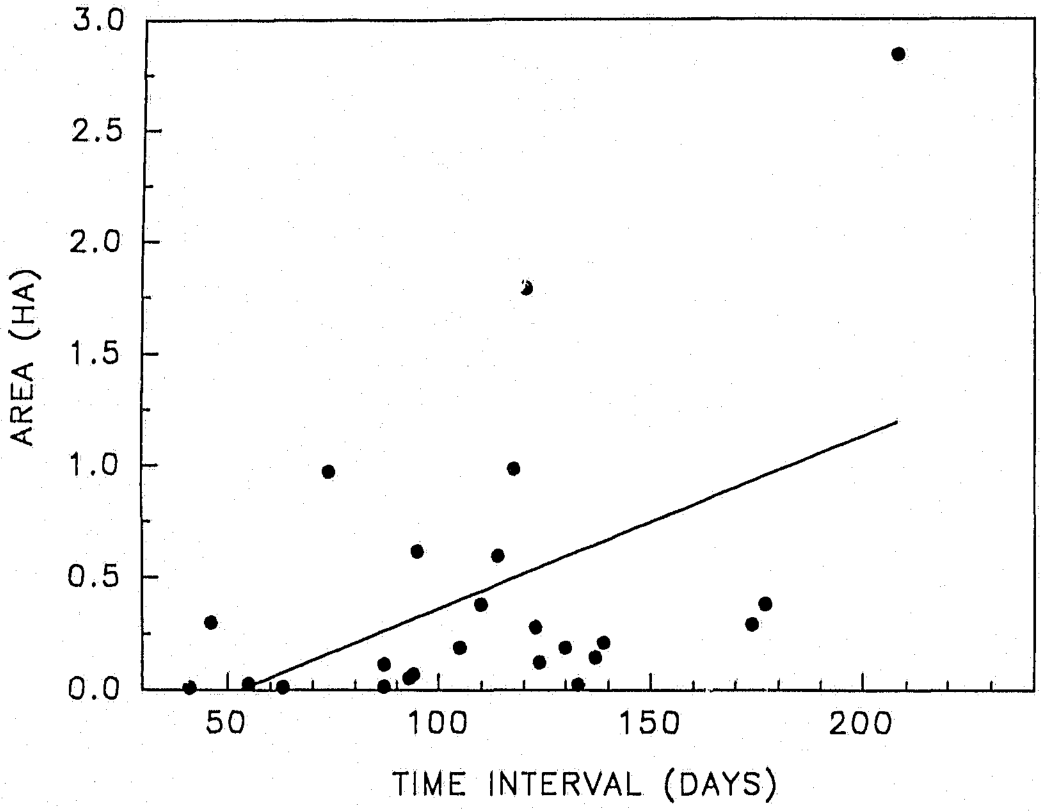
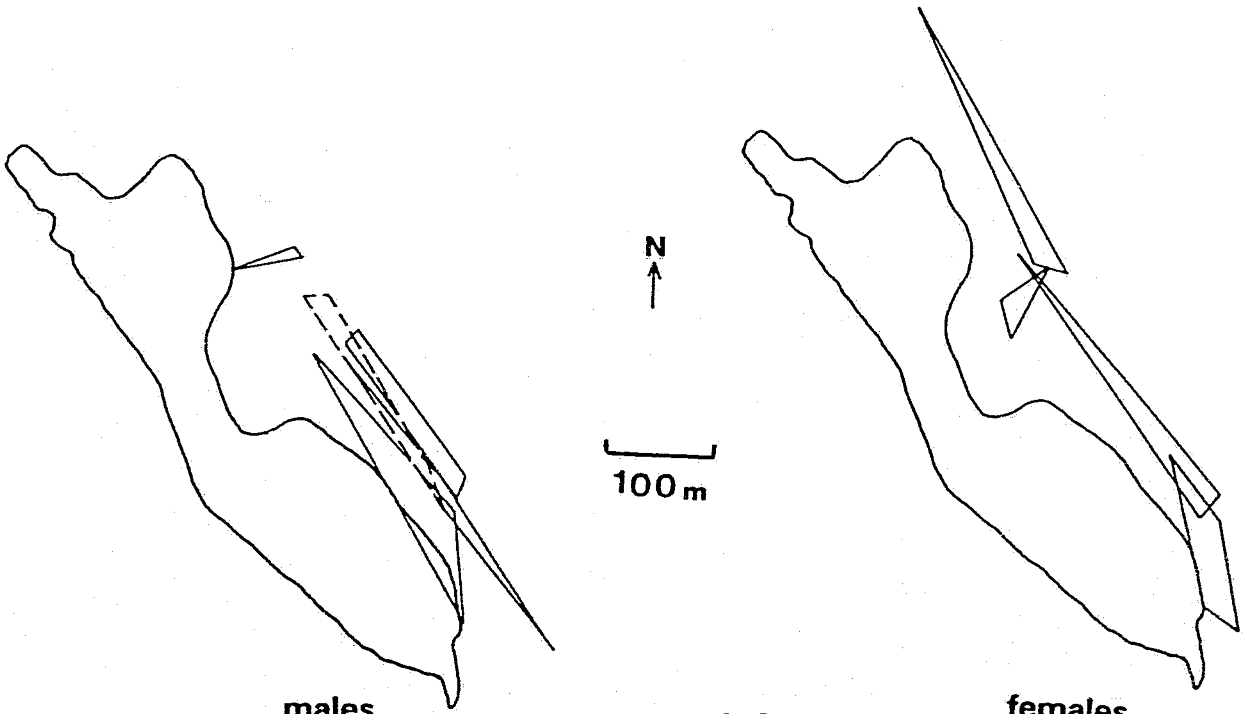

3.0
2.5
2.0
1.5
1.0
0.5
0.0
AREA (HA)
50
100
150
200
TIME INTERVAL (DAYS)

Table 5: Home range areas (ha) for SLPP snakes.

	Note	Sex	n	Mean ± 1 S.D.	Range
*T. sirtalis**	1987	M	6	0.258 ± 0.210	0.028 - 0.618
		F	4	0.211 ± 0.112	0.052 - 0.298
		all	10	0.239 ± 0.171	
	1988	M	7	0.229 ± 0.206	0.024 - 0.597
		F	5	0.400 ± 0.528	0.010 - 0.985
		all	2	0.300 ± 0.363	
	1 season	all	22	0.272 ± 0.288	0.010 - 0.985
	2 seasons	all	8	1.285 ± 1.602	0.090 - 4.760
*T. ordinoides**	1 season	all	9	0.178 ± 0.133	0.014 - 0.333

* Excludes home ranges calculated on the basis of movements of less than 31 days as well as the two largest home ranges calculated for *T. sirtalis*. See text for explanation.

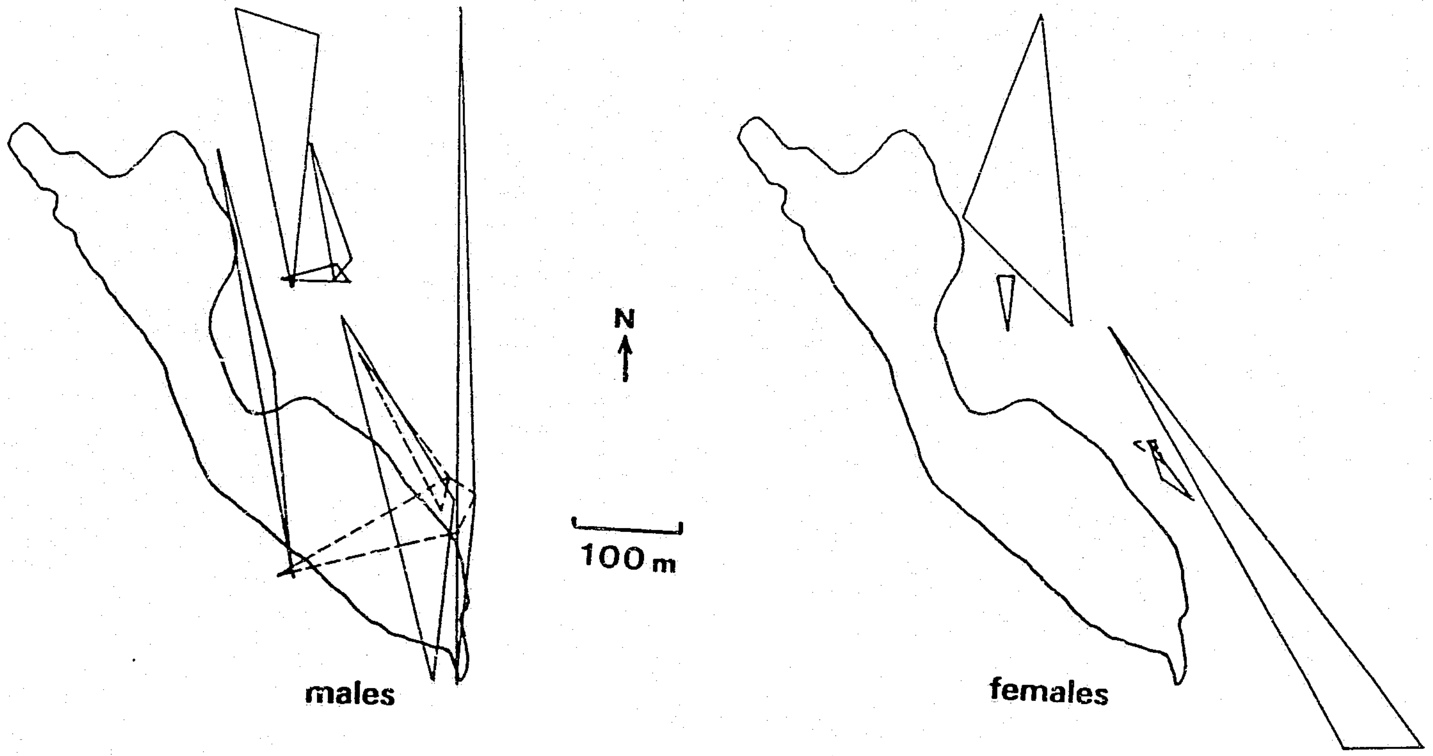
Figure 16: Home ranges of SLPP *T. sirtalis*, determined as minimum convex polygons.



males

females

1987



males

females

1988

significant difference. As is evident from Figure 16, there was considerable overlap between home ranges as well as extensive variation in areas.

Figure 17 illustrates the two largest home ranges for *T. sirtalis*, both calculated for males during 1988. Inclusion of these areas increased the 1988 mean home range area of males to 0.693 ha from 0.229 ha, and the mean of both sexes combined for that year from 0.300 ha to 0.588 ha. This did not affect the lack of significant differences between male and female home range areas for 1988 ($t = 0.64$, $p > .05$, $n = 14$), between males for the two years ($t = 1.19$, $p > .05$, $n = 15$), or between the pooled scores of the two sexes for the two years ($t = 1.45$, $p > .05$, $n = 24$). Also shown on Figure 17 are the dates of capture for these two males. The largest single season home range (2.84 ha) belonged to the individual (#198) with the longest period between captures (208 days, versus a mean of 107 days between first and last capture). The second largest home range (1.79 ha, snake #199) also involved a longer-than-average capture period (121 days), but eight individuals had longer capture periods but much smaller home ranges, with a mean of 0.206 ha. Thus, while the time period may be involved in the discrepancy in estimates of home range areas of these two males relative to other individuals, other factors were likely involved. One important factor was likely the paucity of captures occurring at presumed dens. Figure 18 shows the home ranges calculated for male #143 using 1987 capture data only, 1988 capture data only, and 1987 data plus the first sighting of this snake in early spring, 1988. Using only the 1987 data, his home range area for that year was 0.146 ha. Assuming that he reached the spring 1988 location in the fall of 1987, his home range for 1987 increases to 1.51 ha. In 1988 his calculated home range area was 0.382 ha.

Snakes #198 and #143 demonstrated other problems, namely that some snakes evidently did not show den fidelity (#198) and/or shifted their home range (#143) while other

Figure 17: The two largest home ranges for SLPP *T. sirtalis*.

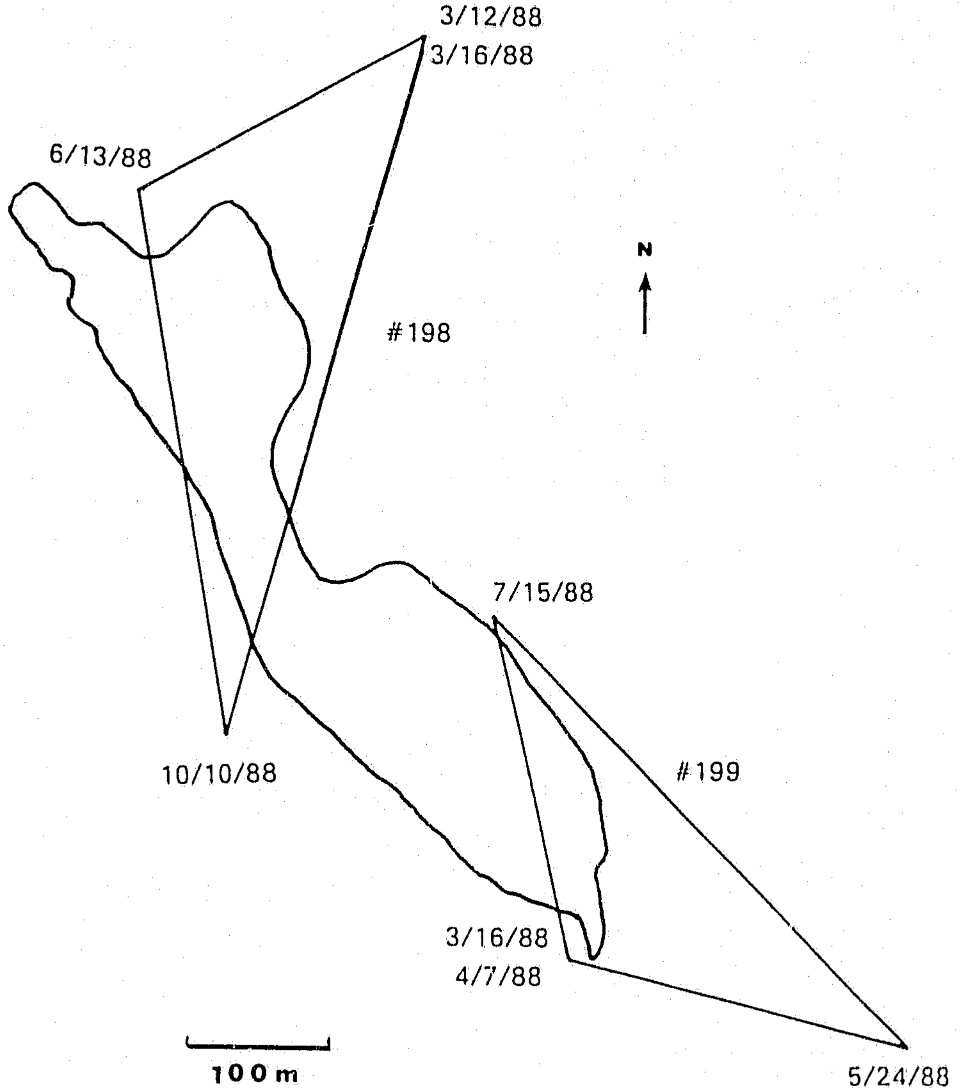
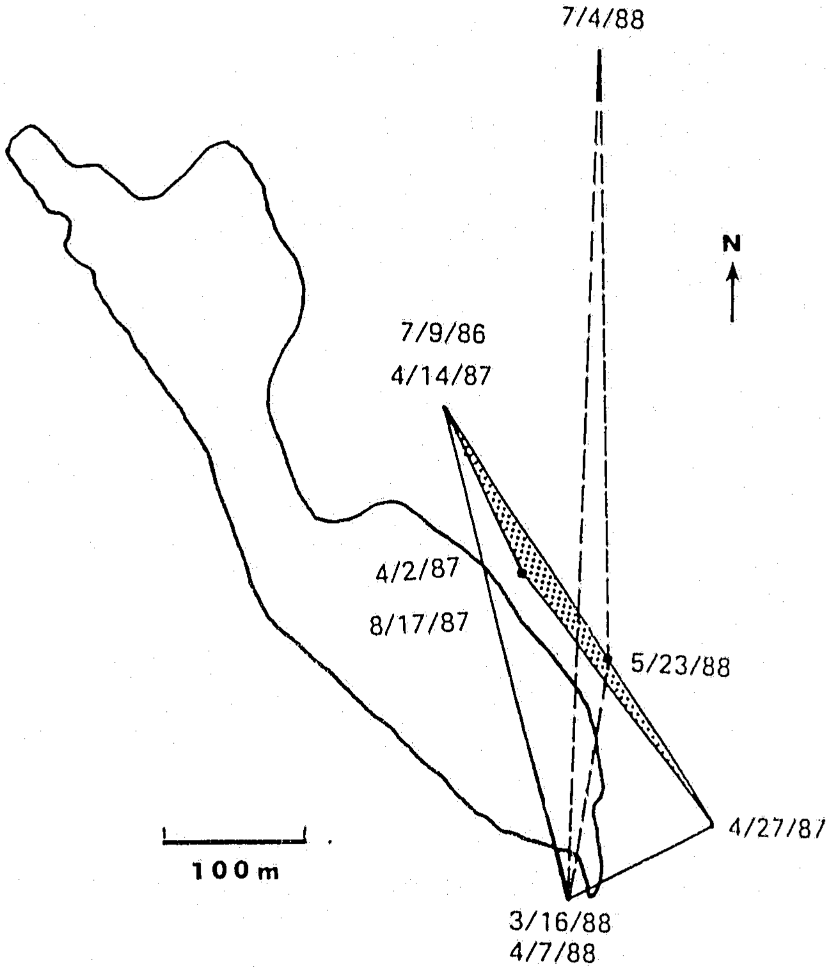

3/12/88
3/16/88
6/13/88
N
#198
7/15/88
10/10/88
#199
3/16/88
4/7/88
100 m
5/24/88

Figure 18: Home range of SLPP *T. sirtalis* #143.

Shaded area = 1987 data only.

Dashed line = 1988 data only.

Solid lines = 1987 data + first sighting of 1988.


7/4/88
N
7/9/86
4/14/87
4/2/87
8/17/87
5/23/88
4/27/87
100 m
3/16/88
4/7/88

individuals remained in the same area between successive years. Figure 19 shows the 1987 and 1988 home ranges of the other *T. sirtalis* caught a minimum of three times during both 1987 and 1988. Snakes #166 (female) and #159 (male) maintained the same home ranges both years, but #154 (female) may have shifted her range between years. Her shift, however, was less apparent than that demonstrated by #143.

Shift in home ranges between successive years was also examined by comparing mean home range size measured during a single active season and the area covered by individuals over two consecutive years. If individuals maintained the same range, then the area covered by a two year period should not differ from that covered in a single active season; conversely, a larger area over the two year period would suggest a home range shift. Snake #143 demonstrated this, with home range areas for 1987 and 1988 of 0.147 ha and 0.382 ha respectively. When his movements for the two years were combined, his two year home range area increased to 4.76 ha. The mean area covered over a two year period based on eight individuals (Table 5) was 1.29 ha, which was significantly larger than the mean home range area calculated for a single season of 0.272 ha ($t = 2.93$, $p < .01$, $n = 30$). Because home range areas measured over a single active season did not vary between 1987 and 1988, the increase must be due to some individuals undergoing a home range shift between these years.

Fewer records were available for *T. ordinoides* and the mean home range area (Table 5) was based on the movements of nine individuals (two males, seven females). No relationship existed between area and length of the sampling period ($r = -0.14$, $p > .05$, $n = 9$). Home range areas in a single season did not differ between the two SLPP species ($t = 0.94$, $p > .05$, $n = 31$).

Figure 19: Home range areas for SLPP *T. sirtalis* determined for both 1987 and 1988.

Solid lines = 1987 Dashed lines = 1988

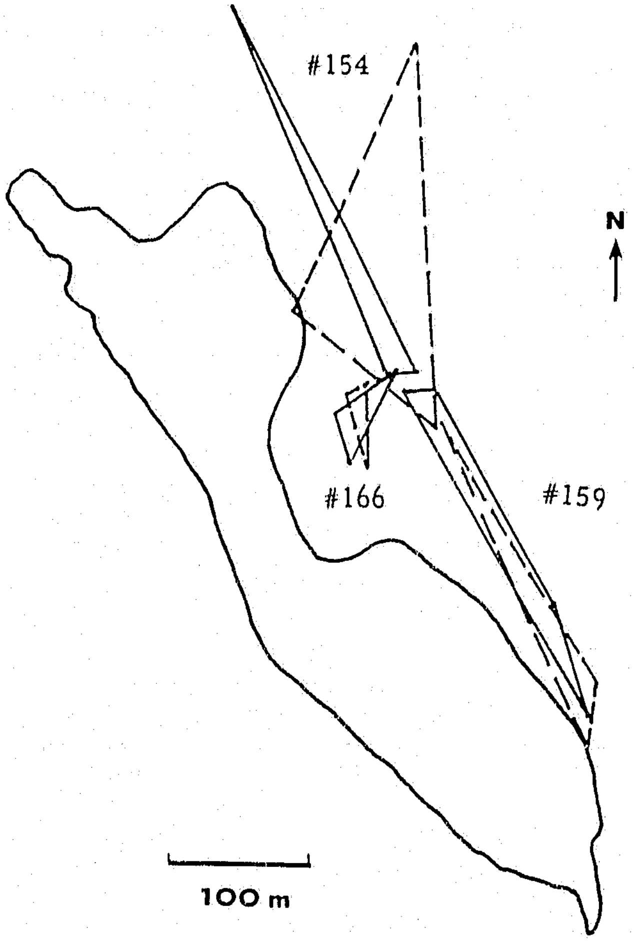

#154
N
#166
#159
100 m

Figure 20, which illustrates *T. ordinoides* home ranges, suggests three largely distinct (i.e. nonoverlapping) regions along the north/south axis during 1987. The three home ranges determined for 1988 were all located in the middle region. Within any single year, other than the slight overlap illustrated, I obtained no movement records that violated this regional distinction, although several movements were recorded between the southernmost region and a hilly area southeast of this region. Some between-year movements of individuals among these three major regions did occur, perhaps indicating shifts in home range. However, this conclusion is very tenuous given the small sample sizes.

Directionality of Movements

Figure 21 and Table 6 present the analysis of seasonal directionality in *T. sirtalis*. To consider population directionality, the first capture location of an individual was standardized to a common point, indicated by the closed circle in Figure 21. The direction and distance moved by the snake between its first and second capture are indicated by open circles. Only movements of 10 m or more were considered for directional analysis. I examined directionality for three periods: (a) movements occurring during spring (March 1 - May 31) , (b) movements occurring during summer (June 1 - August 31), and (c) movements in which the snake was first captured in the spring and captured for the second time in the summer. Autumn movements were not examined due to insufficient sample sizes. Data were examined for both unimodal and bimodal tendencies with the latter case indicating an axis of travel rather than a single direction.

In no case were *T. sirtalis* oriented in a single common direction, but in three time periods (spring 1987, spring to summer 1987, and summer 1988) significant movement along an axis occurred. In all of these cases snakes oriented along a northwest - southeast axis.

Figure 20: Home ranges of SLPP *T. ordinoides*, determined as minimum convex polygons.

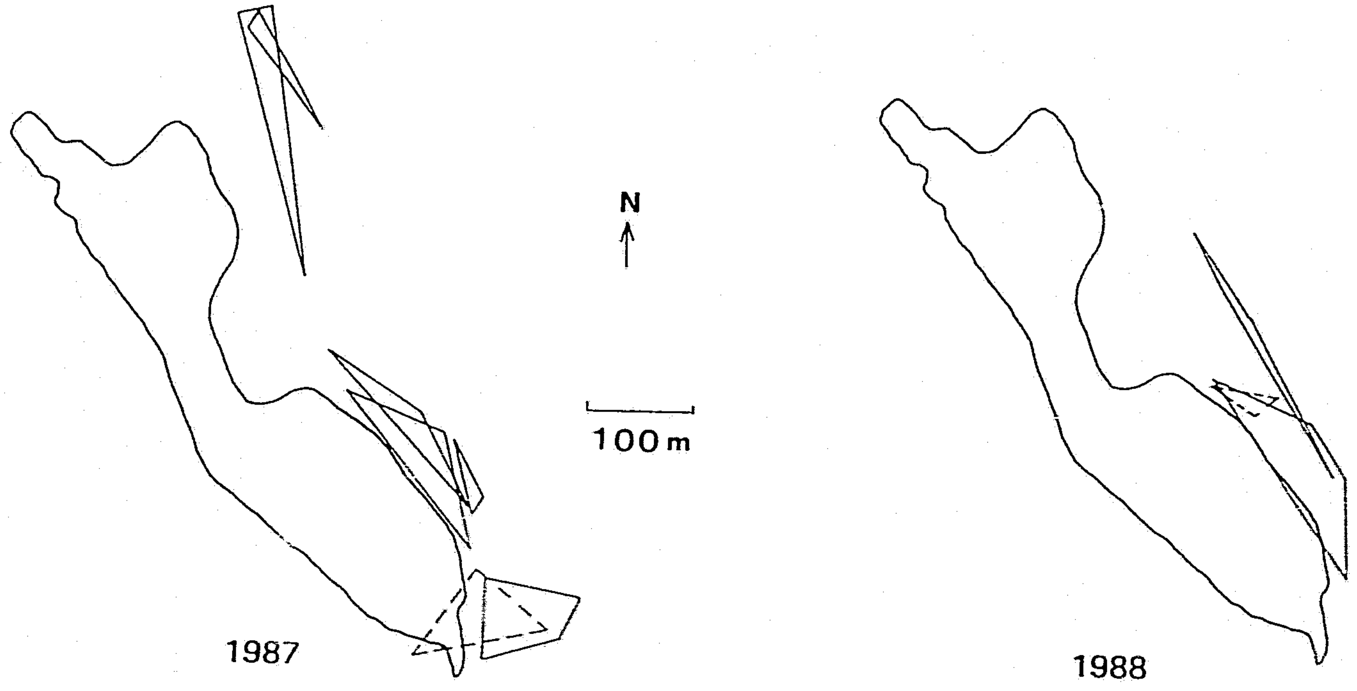

N
100 m
1987
1988

Figure 21: Seasonal directionality exhibited by SLPP *T. sirtalis*.

A. Movements occurring during spring.

B. Movements occurring from spring to summer.

C. Movements occurring during summer.

Open circles represent the distance and direction moved by an individual between successive captures. First captures of each snake within each time category have been standardized to a common starting point (closed circle). Solid lines indicate significant directionality in the indicated direction. Dashed lines represent the 95% confidence interval around that direction.

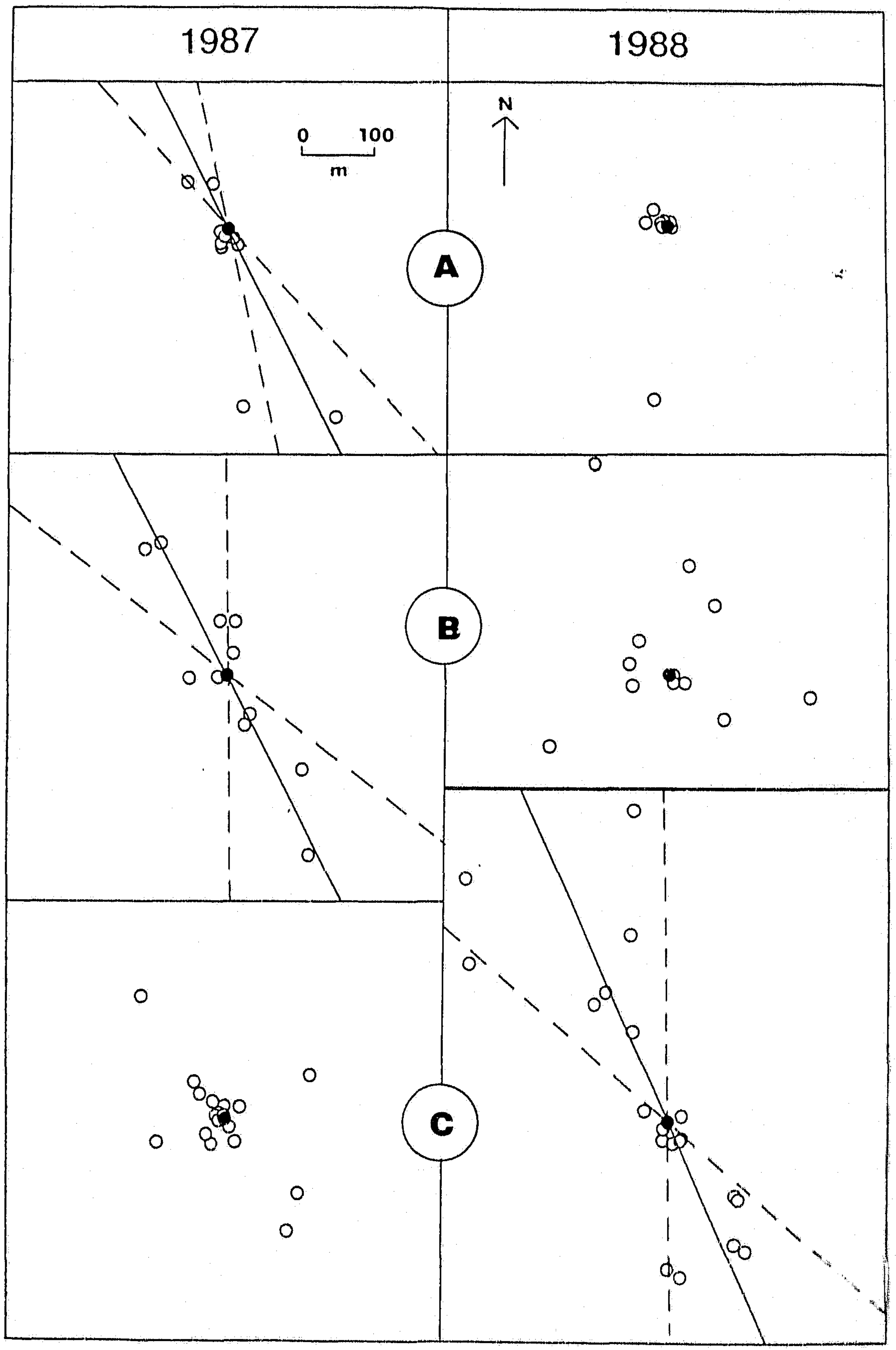

1987
1988
N
0
100
m
A
B
C

Table 6: Seasonal directionality in SLPP snakes.

* indicates bimodal rather than unimodal directionality. The largest r value of the two is given below. Mean angle (ϕ) given only if significant directionality was evident.

ϕ = mean vector; s = 1 angular deviation; r = length of mean vector

Sp = spring Su = summer

	Season of 1st/2nd Capture	Year	n	No. Snakes	$\phi \pm s$	r	p	95% C.I.
T. sirtalis	Sp - Sp	1987	5	4	333 ± 30	0.89*	< .05	315 - 345
		1988	3	3	sample size too small			
	Sp - Su	1987	11	11	333 ± 27	0.56*	< .05	306 - 360
		1988	12	12	---	0.33*	> .05	---
	Su - Su	1987	18	15	---	0.26	> .05	---
		1988	20	16	336 ± 24	0.66*	< .001	312 - 360
T. ordinoides	Sp - Sp	1987	11	9	---	0.32*	> .05	---
		1988	3	3	sample size too small			
	Sp - Su	1987	7	7	333 ± 21	0.74*	< .05	312 - 354
		1988	11	11	---	0.39*	> .05	---
	Su - Su	1987	22	16	---	0.09	> .05	---
		1988	7	6	323 ± 37	0.79	< .01	286 - 360

Figure 22 illustrates the 1988 summer movements, in a simplified manner, in relation to the lake. It is readily apparent that the axis of travel ran parallel to the shore. As can be seen in this figure, the lake did not act as a barrier to movements, and it was not uncommon to see snakes in the water.

Seasonal directional patterns in *T. ordinoides* were examined in the same manner and are presented in Table 6 and Figure 23. Significant orientation along the northwest - southeast axis during movements occurred between the spring and summer of 1987 and in a northwest direction in the summer of 1988.

Figure 22: Generalized seasonal movements of *T. sirtalis* at SLPP during summer, 1988.

Lines indicate movements made by individual snakes between consecutive captures. Movements have been generalized as movements between zones rather than representing the actual points of capture. Numbers indicate the number of snakes showing movement between zones if greater than one. Partial circles represent movements occurring within a zone.

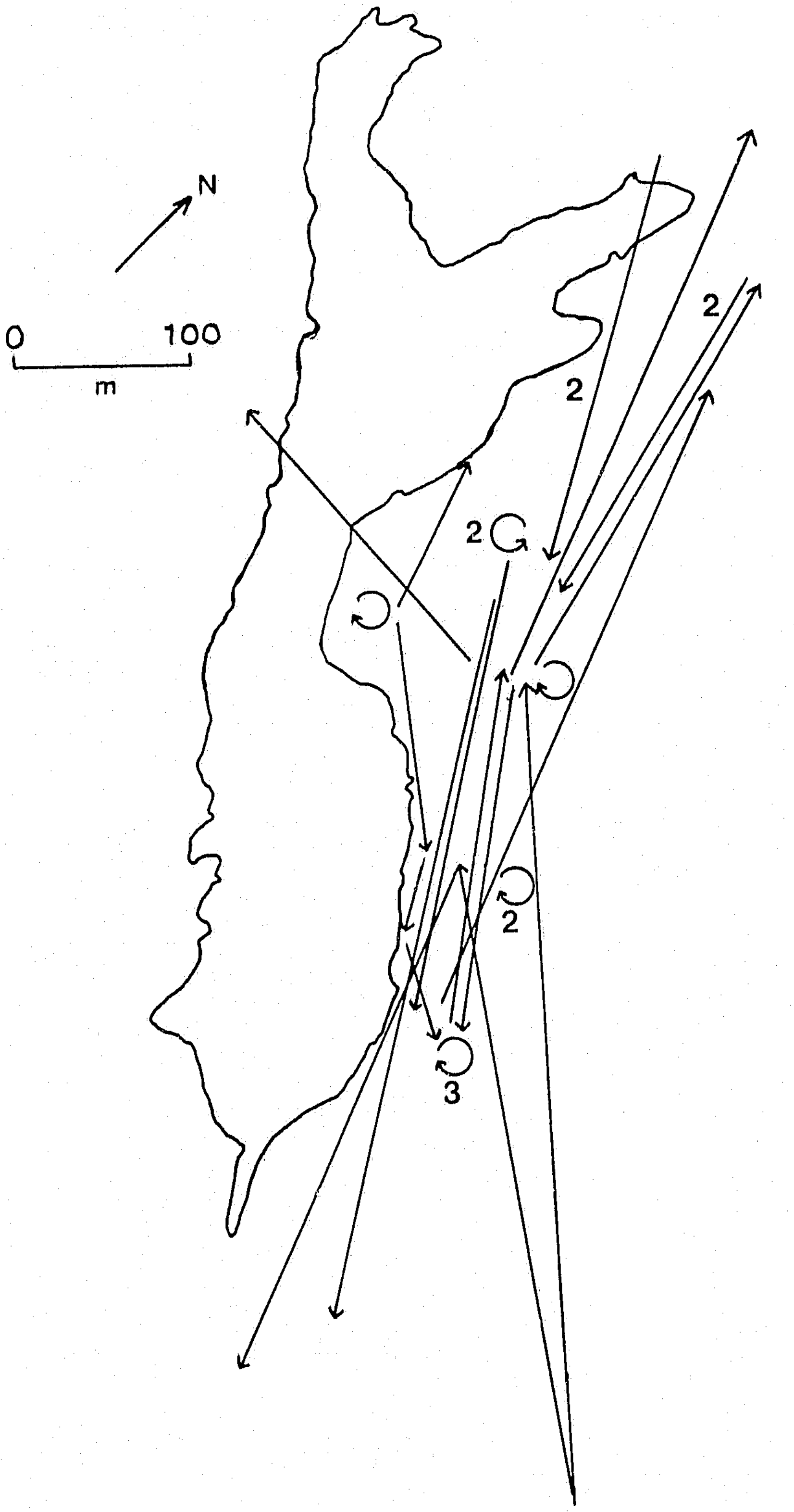

N
0
100
m
2
2
2
2
2
3

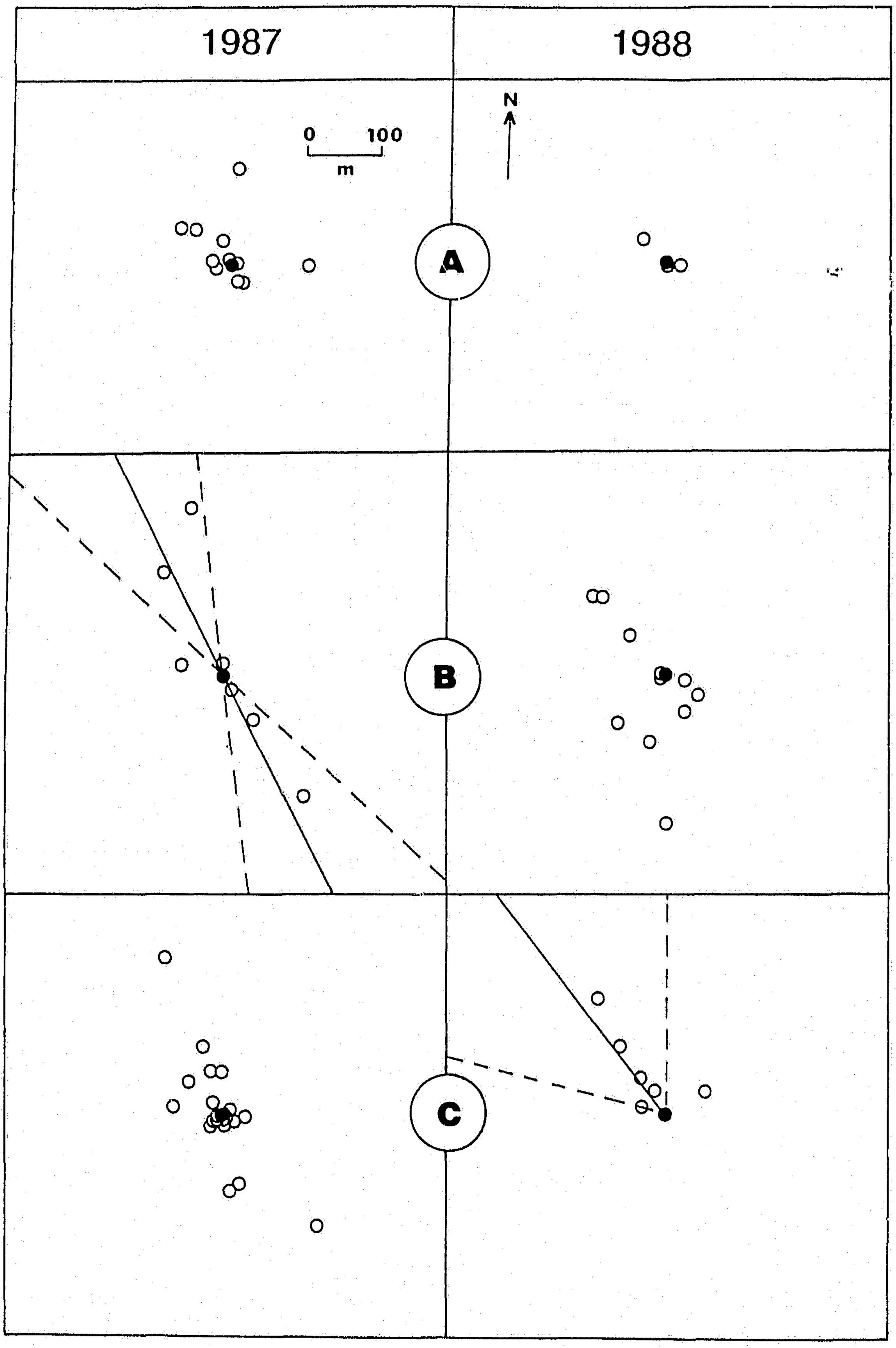
Figure 23: Seasonal directionality exhibited by SLPP *T. ordinoides*.

A. Movements occurring during spring.

B. Movements occurring from spring to summer.

C. Movements occurring during summer.

Open circles represent the distance and direction moved by an individual between successive captures. First captures of each snake within each time category have been standardized to a common starting point (closed circle). Solid lines indicate significant directionality in the indicated direction. Dashed lines represent the 95% confidence interval around that direction.


1987
1988
N
0
100
m
A
B
C

Orientation Tests

WBNP

Orientation Type

Most autumn orientation tests carried out at WBNP were performed during 1986. Poor weather conditions during 1987 precluded many of the planned tests. Spring tests were performed in 1988 and began one week following the start of emergence from the den and continued until migration by males had begun. Results are summarized in Table 7. Snakes were transported between the collection site and the testing sites in opaque cloth bags during 1986 tests; subsequent testing involved transport in wire cages that permitted the snakes a continual view of the sky.

Snakes collected at the Salt River den and tested at site A during autumn 1986 were oriented (Figure 24A) but not towards the den. Similar results were obtained at test site B (Figure 24B) - a preferred direction was selected that was not directed towards the den.

Various explanations for these deviations were considered. For example, Larsen (pers. comm.) suspected that a hibernaculum existed somewhere in the vicinity of test site A. If so, some cue, possibly olfactory, might have caused the observed deviation in directional selection from the predicted direction. However, wind conditions within the arena at the time of testing and substrate mixing were felt to be adequate to remove any potential olfactory cues. Furthermore, a similar situation was not known to exist at test site B. Sexual differences also were not apparent. A more parsimonious explanation was sought.

Table 7: Components of the mean vectors of orientation tests for WBNP *T. sirtalis* and degree of homeward orientation.

ϕ = mean vector; s = 1 angular deviation; r = length of mean vector;
v = homeward component; u = V test statistic; θ = predicted direction
R = males tested during peak of reproductive activity at the den;
M = males tested once most females had been mated and begun their migration.
Corrected = predicted direction modified to account for shift in azimuth position during transport.
All tests performed under clear skies unless otherwise indicated.
*** Confidence limits outside the range of published charts.

Condition	Site	n	$\phi \pm s$	r	v	u	p	θ	95% C.I.
A. BASIC									
Autumn	A	22	296 ± 56.1	0.52	0.17	1.12	> .05	225	261 - 331
Corrected	A	22	296 ± 56.1	0.52	0.49	3.22	< .001	313	261 - 331
Autumn	B	19	118 ± 61.7	0.42	0.17	1.05	> .05	52	69 - 167
Group 1 corrected	B	8	47 ± 53.1	0.57	0.49	1.98	< .05	77	352 - 102
Group 2 corrected	B	11	151 ± 43.6	0.71	0.54	2.51	< .01	110	104 - 198
Spring									
females	A	15	189 ± 47.9	0.65	0.64	3.52	< .001	180	159 - 219
males R	A	22	109 ± 56.1	0.52	0.17	1.12	> .05	180	74 - 144
males M	A	14	191 ± 45.1	0.69	0.68	3.58	< .001	180	162 - 220
Spring									
females	B	18	51 ± 44.4	0.70	0.69	4.14	< .0001	60	27 - 75
males R	B	22	107 ± 46.6	0.67	0.46	3.03	< .001	60	82 - 132
Spring Cloud									
females	A	12	180 ± 47.9	0.65	0.65	3.18	< .001	180	130 - 230
males E	A	11	123 ± 40.5	0.75	0.41	1.92	> .05	180	94 - 152

Condition	Site	n	$\phi \pm s$	r	v	u	p	θ	95% C.I.
B. PHASE-DELAY									
Autumn both	B	12	173 ± 56.7	0.51	0.44	2.14	< .05	142	116 - 232
Spring									
females	A	8	247 ± 49.3	0.63	0.58	2.32	< .01	270	197 - 297
males	A	15	273 ± 45.8	0.68	0.68	3.72	< .001	270	245 - 310
both	A	23	265 ± 47.9	0.65	0.65	4.39	< .0001	270	240 - 290
Spring									
females	B	7	157 ± 38.0	0.78	0.77	2.90	< .001	150	***
males	B	14	140 ± 48.6	0.64	0.63	3.34	< .001	150	103 - 177
both	B	21	147 ± 45.8	0.68	0.68	4.40	< .0001	150	120 - 172
C. PHEROMONE TRAILING									
Male Trail									
To home	A	10	120 ± 58.4	0.48	0.24	1.07	> .05	180	56 - 184
To trail	A	10	120 ± 58.4	0.48	-0.45	-2.02	> .05	320	56 - 184
Female Trail, Sexually attractive									
To home	A	17	119 ± 72.0	0.21	0.10	0.60	> .05	180	***
To trail	A	17	233 ± 69.2	0.27	-0.16	-0.93	> .05	0	***
Female Trail, Copulatory plug									
To home	A	13	114 ± 56.1	0.52	0.21	1.08	> .05	180	66 - 162
To trail	A	13	351 ± 46.6	0.67	0.67	3.39	< .001	0	315 - 27

Note: Female trail angles have been rotated so that the trail direction is standardized at 0°.

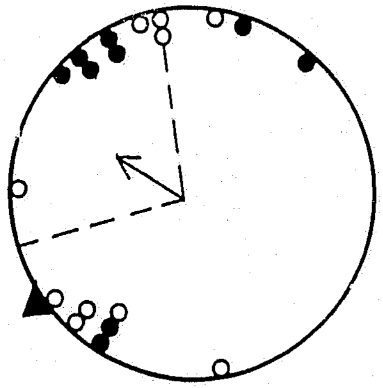
Figure 24: Autumn basic orientation tests of WBNP *T. sirtalis*.

A. Site A.

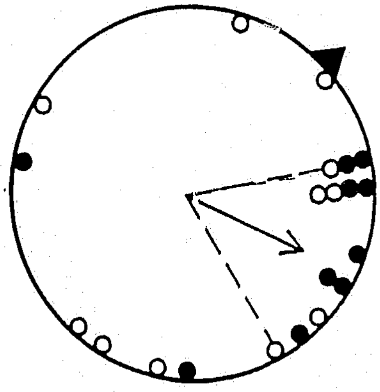
B. Site B.

closed circles = males open circles = females

Arrows inside the circles represent the mean direction; the length of the arrow indicates the degree of clustering around the mean. Dashed lines represent the 95% confidence interval of the mean vector. No arrow is drawn if both Rayleigh's test and the V-test found orientation to be random. The triangle outside the circle represents the predicted direction.



A



B

During the testing of snakes at site B, a definite change in the directional selection of individual snakes occurred following a break in testing. Whereas the first snakes tested tended to select a homeward direction, later snakes showed a definite shift away from the predicted direction. The directional selections of the test group were then reanalysed by dividing the data into two groups according to testing sequence. The first eight snakes selected a direction of 47° which was strongly homeward oriented. The second group of 11 snakes selected a direction of 151°. The homeward direction was outside the 95% confidence interval of the second group; therefore the direction selected deviated significantly from the homeward direction.

This suggested that some factor was influencing the directional choice of the last snakes tested but not the first group of snakes. The time spent in the opaque bag between capture and testing was considered. Although the rate of azimuthal shift averages 15°/hr over a 24 hr period, this rate is not constant throughout the day. Furthermore, the rate varies with latitude and with the date. Dr. J. Tatum of the University of Victoria Physics and Astronomy department provided me with a computer program that calculated the actual azimuth position at various times of the day for various dates and latitudes. Using this information, the true shift in azimuth position during the period when the snakes were kept in the bag could be determined. If, as I suspected, the time spent in the cloth bag acted as a brief phase-shift, then the directions selected by the snakes should show deviations corresponding with the true shift in azimuth position. This was found to be the case. For the first group of eight snakes, the azimuth shifted an average of 25° during the time the snakes were kept in the dark. This would result in a new predicted direction of 77° (as opposed to 52°) (Figure 25B). While this apparently suggests less accurate homeward orientation by this group, the correction still allows for homeward orientation to be concluded on the

Figure 25· Orientation test results of WBNP *T. sirtalis* corrected for the shift in solar azimuth position during transport.

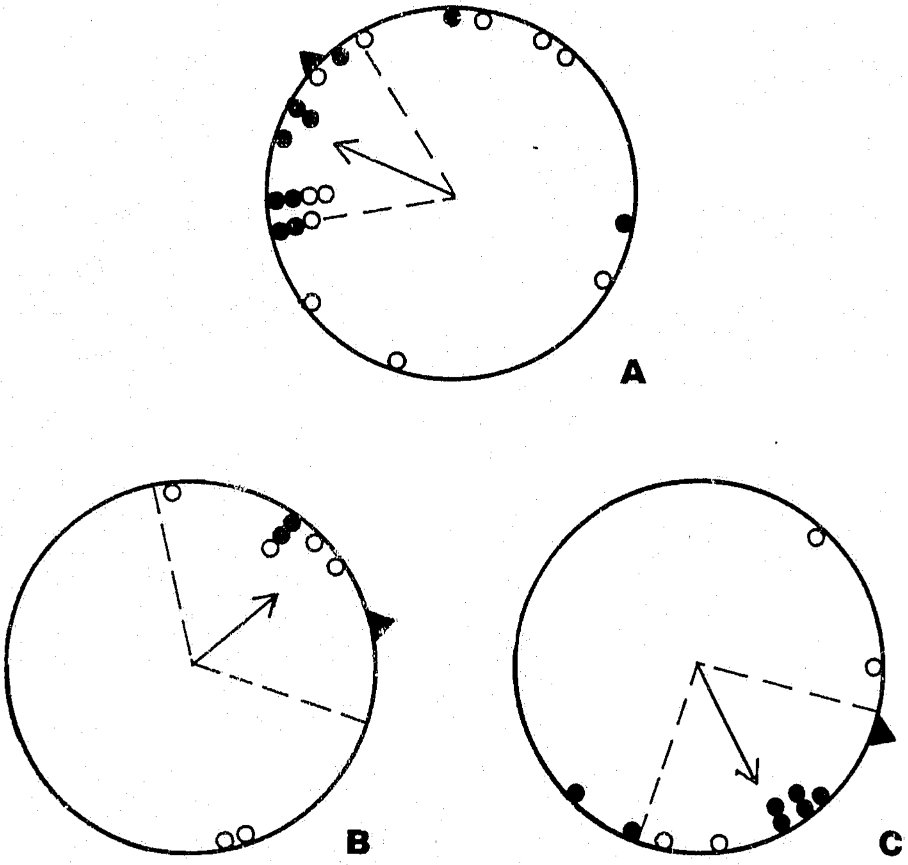
A. Site A

B. Site B, 1st group

C. Site B, 2nd group

closed circles = males; open circles = females

See Figure 24 for explanation of additional figure symbols.


A
B
C

basis of the V-test (Table 7), and the predicted direction lies within the 95% confidence interval. For the second set of snakes, the azimuth shifted an average of 58°, yielding a new predicted direction of 110° (Figure 25C). Orientation was directed towards this point.

This explanation can also account for the deviation noted at site A. During the period that the snakes were kept in the dark bag, the solar azimuth position shifted an average of 88°, producing a new predicted direction of 313° (Figure 25A). Snakes did show significant clustering around this direction. Thus, the evidence suggests that this factor was responsible for the observed deviations in directional choice from the predicted homeward direction. For this reason, further tests involved transporting snakes in clear containers rather than in opaque bags.

Females transported in cages that permitted a continuous view of the sky during spring tests oriented towards the summer range as predicted at both test sites (Figure 26A and D). Males tested during the peak of the mating period were oriented but not in the predicted direction (Figure 26C and E). However, males tested at site A once mating activity at the den had decreased in intensity did orient towards the summer range (Figure 26B).

Spring tests at site A performed under partial cloud cover produced similar results (Figure 27). Females oriented towards the summer range; males tested during the mating period also were oriented, but not towards the summer range.

Figure 26: Spring basic orientation tests of WBNP *T. sirtalis*.

A. Site A, females

B. Site A, males tested once migration by males had begun

C. Site A, males tested during the mating period

D. Site B, females

E. Site B, males tested during the mating period

closed circles = males; open circles = females

See Figure 24 for explanation of additional figure symbols.

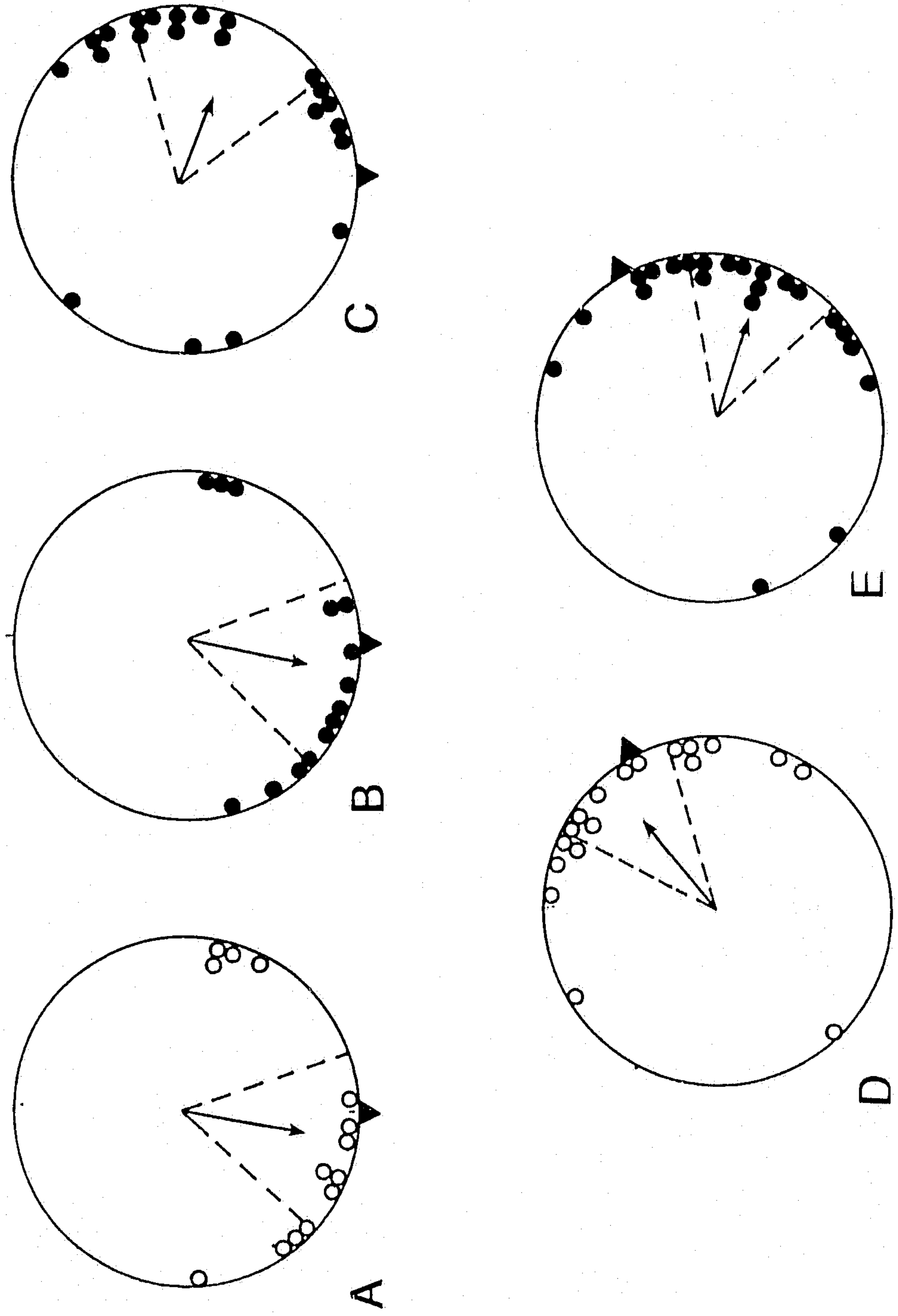

A
B
C
D
E

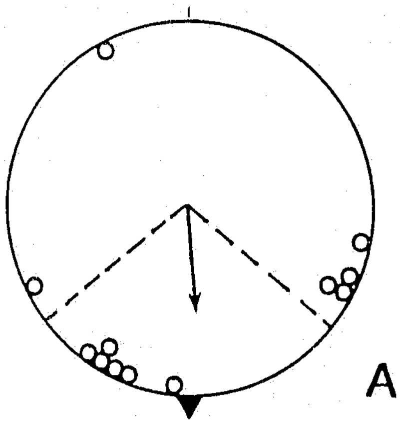
Figure 27: Spring basic orientation tests of WBNP *T. sirtalis* performed under cloudy skies.

A. Females

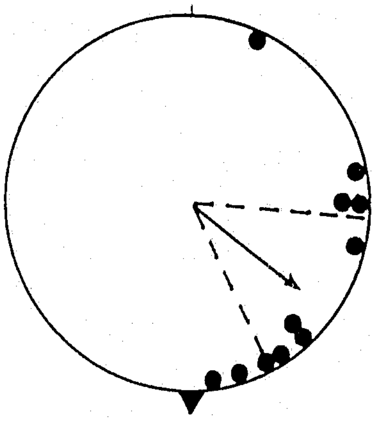
B. Males tested during the mating period

closed circles = males; open circles = females

See Figure 24 for explanation of additional figure symbols.



A



B

Solar Orientation

Phase-shift (6-hr delay) tests were performed in the autumn of 1987 and in the spring of 1988 (Table 7 and Figure 28). Snakes oriented around the predicted direction in all tests. No differences were noted between male and female responses in spring tests.

Pheromone Trailing

Pheromone trailing tests were performed in the spring of 1988 (Table 7). Males displayed no tendency to trail other males (Figure 29A); instead they continued to orient in the same direction as they had in the basic tests. Males also did not trail females lacking copulatory plugs (Figure 29B), even though males clearly trailed unmated females at the den. Females used to produce these trails mated once they were reintroduced to the males following testing. Males did trail females that had fresh copulatory plugs (Figure 29C).

SLPP

Orientation Type

The results of orientation tests performed on Vancouver Island are summarized in Tables 8 (*T. sirtalis*) and 9 (*T.ordinoides*). Adult tests were performed in the spring and summer of 1987 and 1988. Unless otherwise indicated, tests were performed on either clear days or on partially cloudy days while the sun was visible. Snakes were transported in clear containers. Neonate tests are described in a separate section.

SLPP *T. sirtalis* demonstrated homeward orientation (towards SLPP) at both test sites (Figure 30A and B) under clear skies. One group of nine *T. sirtalis* from Goldstream

Figure 28: Phase-delayed orientation tests of WBNP *T. sirtalis*.

A. Autumn tests, site B

B. Spring tests, site A

C. Spring tests, site A

closed circles = males; open circles = females

See Figure 24 for explanation of additional figure symbols.

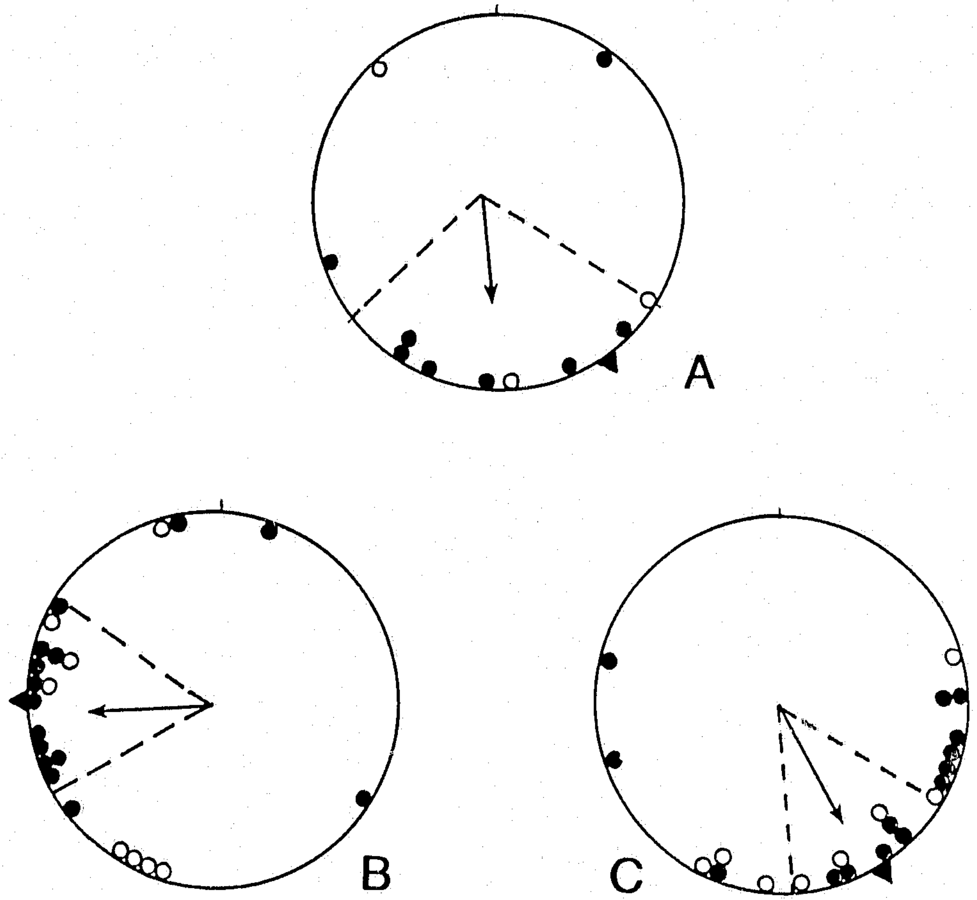

A
B
C

Figure 29: Pheromone trailing tests of WBNP male *T. sirtalis*.

A. Trails produced by males

B. Trails produced by sexually attractive females

C. Trails produced by females containing copulatory plugs

Outer triangle represents the direction of the trail.

See Figure 24 for explanation of additional figure symbols.

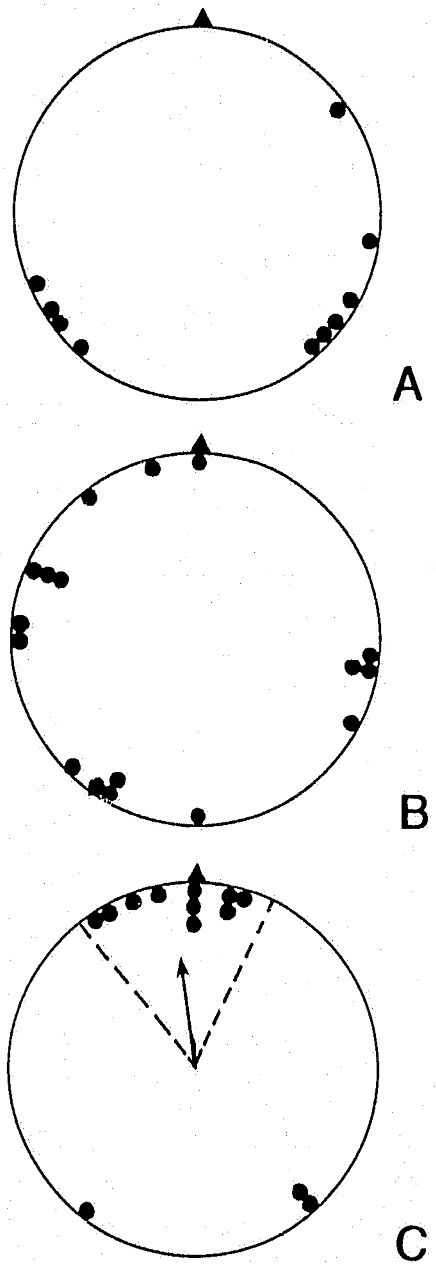

A
B
C

Table 8: Components of the mean vectors of orientation tests for SLPP *T. sirtalis* and degree of homeward orientation.

ϕ = mean vector; s = 1 angular deviation; r = length of mean vector;
v = homeward component; u = V test statistic; θ = predicted direction
All tests performed under clear skies unless otherwise indicated.
*** Confidence limits outside the range of published charts.

Condition	Site	n	$\phi \pm s$	r	v	u	p	θ	95% C.I.
A. BASIC									
Spring	A	14	263 ± 52.5	0.58	0.46	2.42	< .01	225	223 - 303
Summer	B	11	17 ± 36.2	0.80	0.74	3.48	< .0001	355	351 - 43
Summer Cloud	A	9	211 ± 44.4	0.70	0.63	2.67	< .005	185	173 - 249
B. PHASE-SHIFT									
Spring phase-advanced	A	12	125 ± 38.9	0.77	0.76	3.71	< .0001	135	98 - 152
Spring phase-delay	A	11	323 ± 40.5	0.75	0.74	3.48	< .0001	315	293 - 353
Spring phase-delay	B	9	101 ± 53.1	0.57	0.55	2.32	< .01	85	47 - 153
C. NEONATES - BASIC									
Autumn Clear									
Born lab indoors	B	10	67 ± 78.6	0.06	0.03	0.12	> .05	130	***
D. PHEROMONE TRAILING									
Male Trail									
Summer Cloud									
To home	B	8	109 ± 66.8	0.32	-0.13	-0.52	> .05	355	***
To trail	B	8	109 ± 66.8	0.32	-0.21	-0.84	> .05	240	***
Gravid Female Trail									
Summer Clear & Cloud									
To home	B	18	229 ± 63.3	0.39	-0.23	-1.37	> .05	55	***
To trail	B	18	229 ± 63.3	0.39	0.38	2.34	< .01	240	***

Condition	Site	n	$\phi \pm s$	r	v	u	p	θ	95% C.I.
D. PHEROMONE TRAILING (cont)									
Clear skies									
To home	B	8	190 ± 69.2	0.27	-0.26	-1.04	> .05	355	***
To trail	B	8	190 ± 69.2	0.27	0.17	0.69	> .05	240	***
Cloudy skies									
To home	B	10	243 ± 54.4	0.55	-0.21	-0.92	> .05	355	193 - 293
To trail	B	10	243 ± 54.4	0.55	0.55	2.46	< .01	240	193 - 293

Table 9: Components of the mean vectors of orientation tests for SLPP *T. ordinoides* and degree of homeward orientation.

ϕ = mean vector; s = 1 angular deviation; r = length of mean vector;
v =homeward component; u = V test statistic; θ = predicted direction
All tests performed under clear skies unless otherwise indicated.
*** Confidence limits outside the range of published charts.

Condition	Site	n	$\phi \pm s$	r	v	u	p	θ	95% C.I.
A. BASIC									
Spring	A	14	294 ± 56.7	0.51	0.18	0.97	> .05	225	248 - 340
Summer	B	10	21 ± 30.3	0.86	0.77	3.46	< .0001	355	4 - 38
B. PHASE-SHIFT									
Spring phase-delay	B	11	157 ± 30.3	0.86	0.27	1.25	> .05	85	136 - 178
C. NEONATES - BASIC									
Autumn Clear									
Born lab outdoors	B	10	131 ± 54.4	0.55	0.55	2.46	< .01	130	81 - 181
Autumn Cloud									
Born SLPP outdoors	B	7	256 ± 60.6	0.44	-0.07	-0.23	> .05	355	***
D. PHEROMONE TRAILING									
Male Trail									
Summer Clear									
To home	B	10	37 ± 67.8	0.30	0.23	1.01	> .05	355	***
To Trail	B	10	37 ± 67.8	0.30	-0.28	-1.23	> .05	240	***

Condition	Site	n	$\phi \pm s$	r	v	u	p	θ	95% C.I.
Gravid Female Trail									
Summer Clear & Cloud									
To home	B	12	59 ± 72.0	0.21	0.09	0.45	> .05	355	***
To trail	B	12	59 ± 72.0	0.21	-0.21	-1.02	> .05	240	***
Summer Clear									
To home	B	6	95 ± 64.8	0.37	-0.06	-0.22	> .05	355	***
To trail	B	6	95 ± 64.8	0.37	-0.30	-1.05	> .05	240	***
Summer Cloud*									
To home	B	6	36 ± 16.7	0.83	**	**	= .009	355	***
E. NEONATE TRAILING									
Mother Trail/Autumn Cloud									
Born SLPP outdoors									
To home (SLPP)	B	7	339 ± 32.4	0.84	0.81	3.01	< .001	355	***
To trail	B	7	339 ± 32.4	0.84	0.84	3.13	< .001	340	***
Mother Trail/Autumn Clear									
Born lab outdoors									
To home (lab)	B	7	172 ± 55.0	0.54	0.40	1.50	> .05	130	***
To trail	B	7	172 ± 55.0	0.54	0.20	0.76	> .05	240	***

* Examined for bimodality. Results are for axial rather than unimodal directionality. Level of p for Rayleigh's test.

Figure 30: Basic orientation tests of *T. sirtalis* on Vancouver Island.

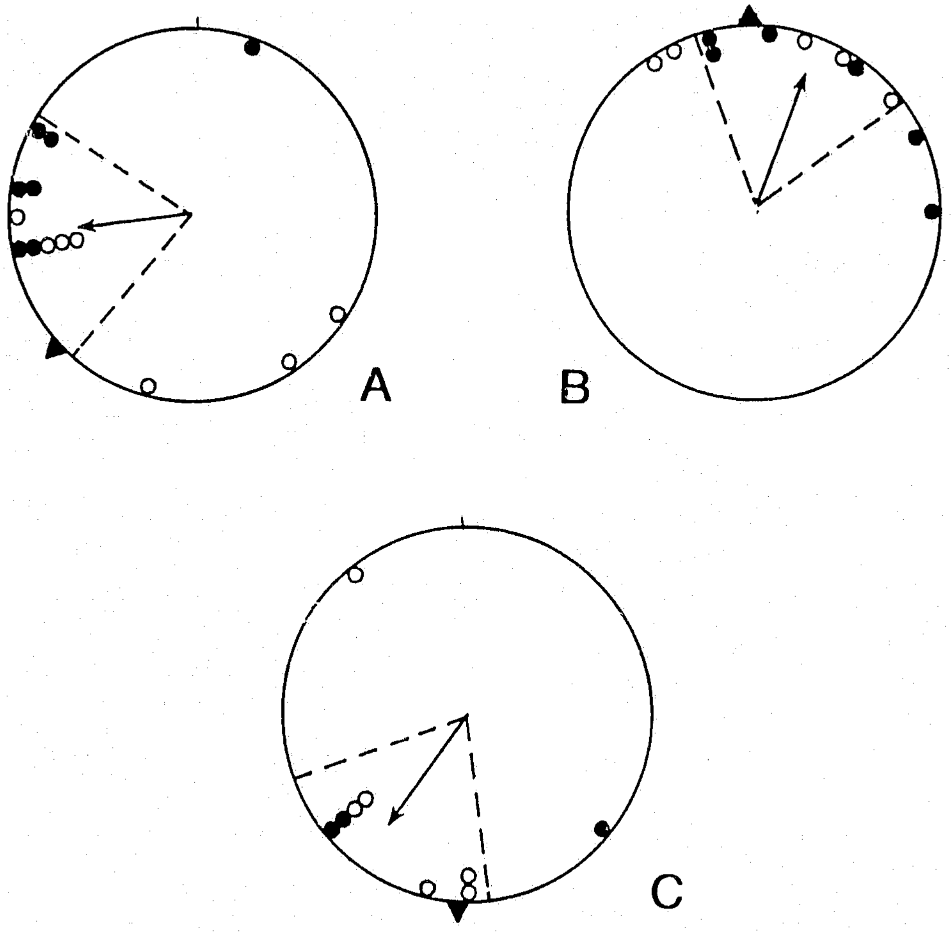
A. SLPP snakes tested at Site A

B. SLPP snakes tested at Site B

C. Snakes from Site B tested under cloudy skies at site A

closed circles = males; open circles = females

See Figure 24 for explanation of additional figure symbols.


A
B
C

Park (test site B) was also tested at site A while the sun was obscured on a day with 95% cloud cover (Figure 30C). Orientation was directed towards Goldstream Park.

Thamnophis ordinoides were homeward oriented at site B but showed random orientation at site A (Figure 31).

Solar Orientation

Phase-shift tests were carried out for *T. sirtalis* at both test sites but only at test site B for *T. ordinoides*. One *T. sirtalis* test involved a 6 hr phase-advance; all others involved a 6 hr phase-delay. Directions selected by phase-delayed *T. sirtalis* were oriented in the predicted direction (direction to SLPP + 90°) at both sites (Figure 32A and B) as were those selected by the phase-advanced group (direction to SLPP - 90°; Figure 32C).

Thamnophis ordinoides displayed oriented behaviour but not in the predicted direction (SLPP + 90°) nor towards Spectacle Lake (Figure 32D).

Pheromone Trailing

All trailing tests were performed at test site B. *Thamnophis sirtalis* did not trail conspecific males under cloudy skies (Figure 33A). Orientation in this group was random. Some trailing of gravid females did occur although there was considerable variation in response (Figure 33B), with results on clear and cloudy days combined. When distinguished by sky condition, significant trailing was noted only under cloudy skies (Figure 33C). Females appeared to demonstrate a stronger trailing response. Under clear skies, orientation was random (Figure 33D). In no case did snakes orient towards SLPP.

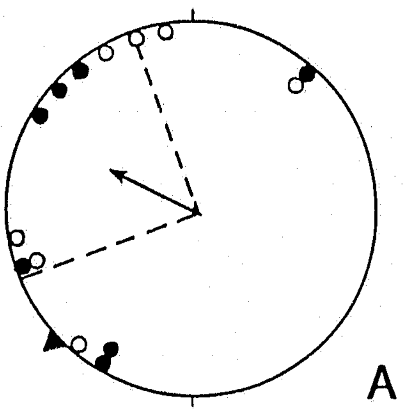
Figure 31: Basic orientation tests of SLPP *T. ordinoides*.

A. Site A

B. Site B

closed circles = males; open circles = females

See Figure 24 for explanation of additional figure symbols.


A

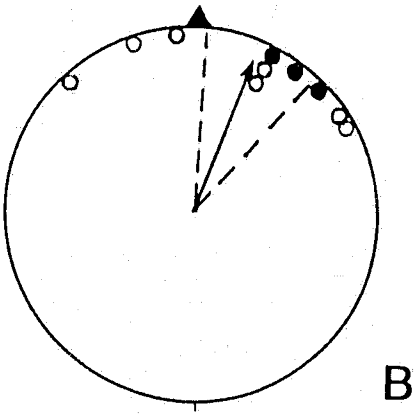

B

Figure 32: Phase-shift orientation tests of snakes on Vancouver Island.

A. *T. sirtalis* site A phase-delayed

B. *T. sirtalis* site B phase-delayed

C. *T. sirtalis* site A phase-advanced

D. *T. ordinoides* site A phase-delayed

closed circles = males; open circles = females

See Figure 24 for explanation of additional figure symbols.

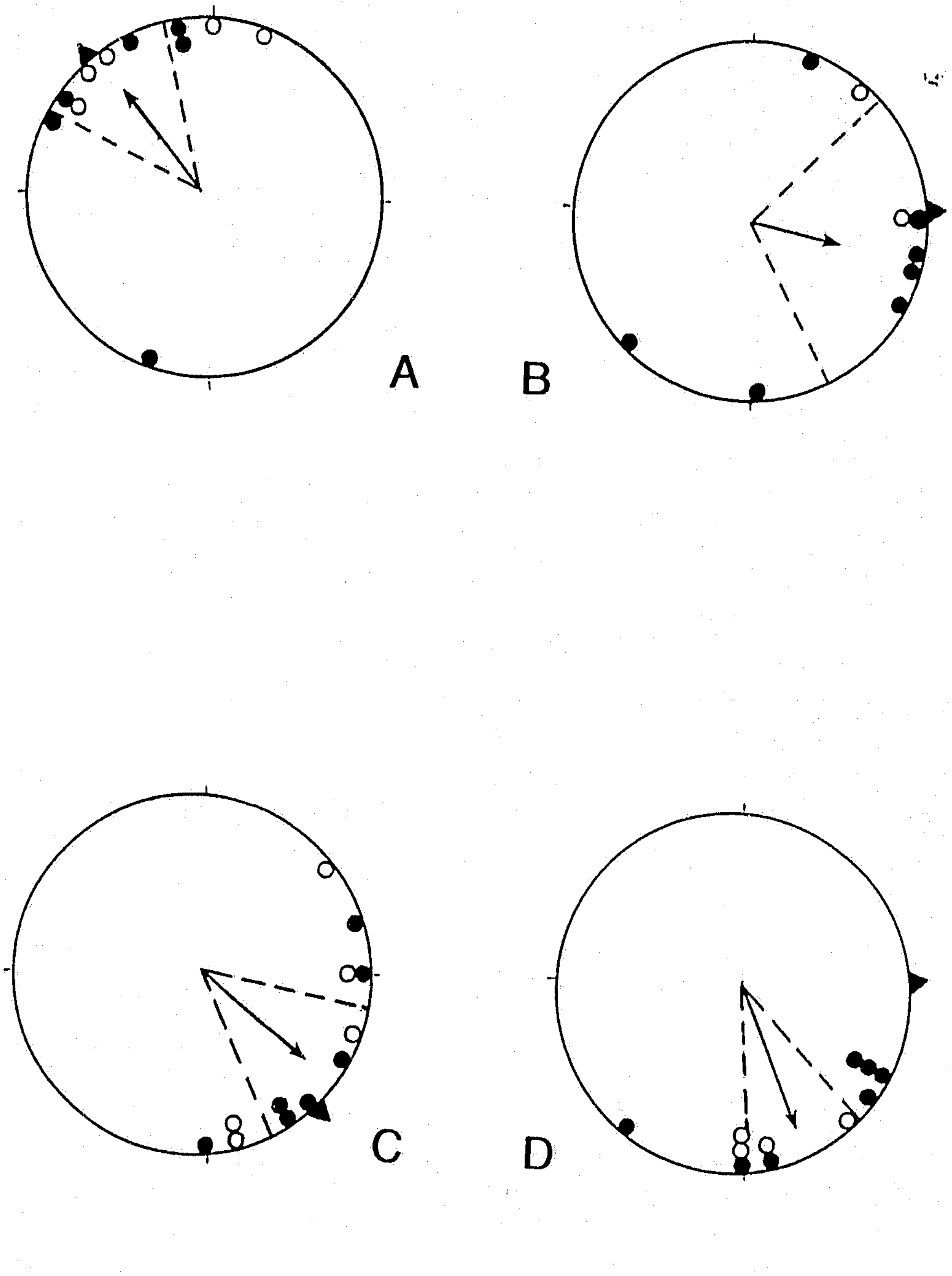

A
B
C
D

Figure 33: Pheromone trailing tests of SLPP *T. sirtalis.*

A. Trails produced by males

B. Trails produced by gravid females

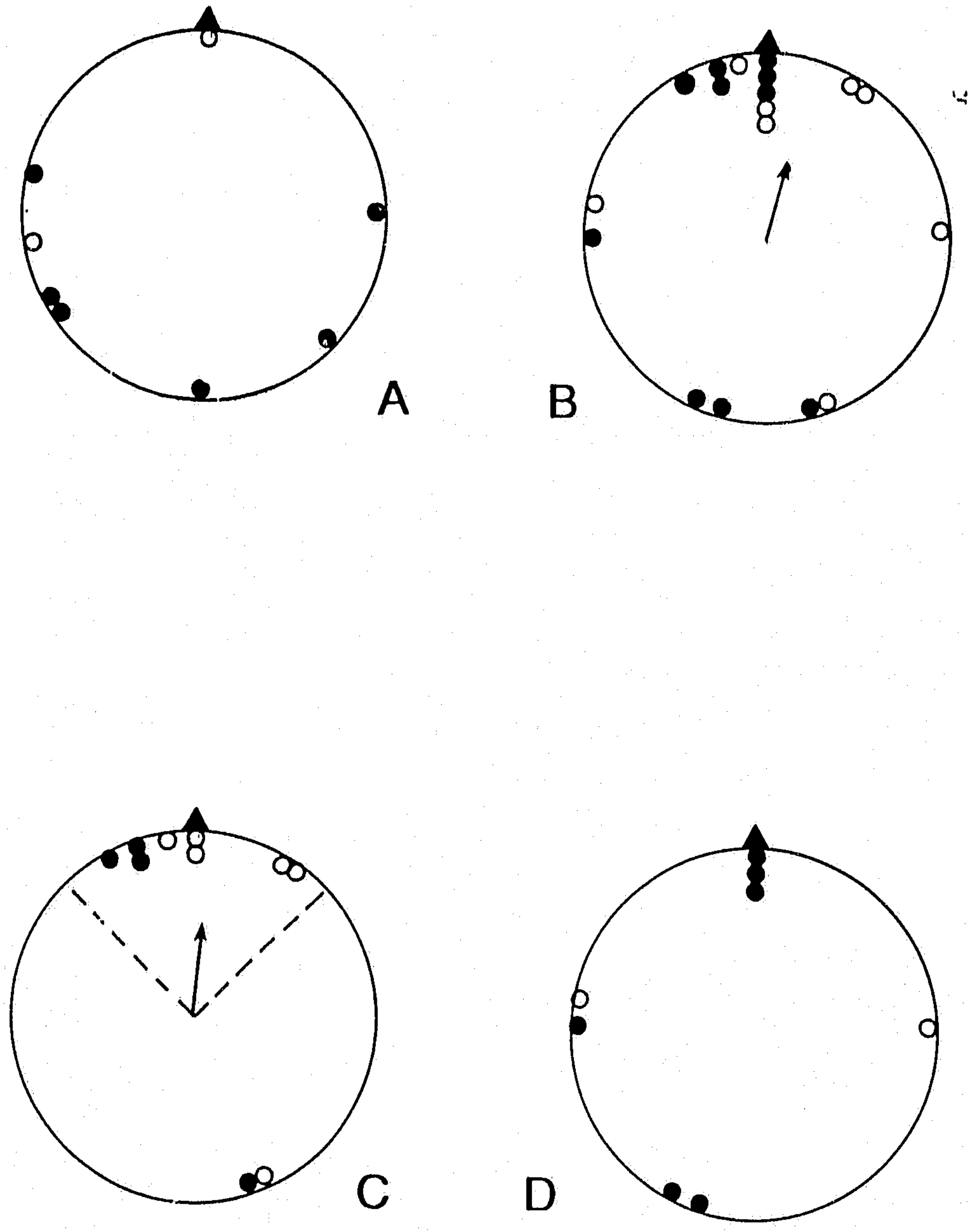
C. Trails produced by gravid females, cloudy skies

D. Trails produced by gravid females, clear skies

Closed circles = males; open circles = females

Triangle outside the circle represents the trail direction.

See Figure 24 for explanation of additional figure symbols.


A
B
C
D

Results for *T. ordinoides* trailing tests are shown in Figure 34. Snakes showed no tendency to cluster around either the trail or the homeward direction when either male or female trails were present.

Neonate Tests

Neonates were tested during autumn, 1988. Unfortunately I had poor success obtaining neonates for testing, either from the field or captive litters, especially for *T. sirtalis*. Nevertheless, preliminary tests were run and their results are presented in Tables 8 and 9.

I performed one set of tests of *T. sirtalis* neonates involving seven snakes born in captivity at the laboratory and kept indoors until the day of testing. When tested at site B in the autumn of 1987, these snakes were randomly oriented (Figure 35A) under clear skies.

Basic tests of neonate *T. ordinoides* resulted in an oriented response on one occasion but not on another. Snakes born outdoors at the laboratory and kept under natural light conditions did orient towards the laboratory, their birth site, (Figure 35B) when tested under clear skies. Snakes from a captive-born litter from Spectacle Lake tested under full cloud were randomly oriented (Figure 35C). However, littermates of this last group tested on the same day did show clustering around the trail produced by the mother (Figure 36A). An outdoor, laboratory-born group showed no evidence of orienting either towards their mother's trail (Figure 36B) or towards the laboratory when tested under clear skies.

Figure 34: Pheromone trailing tests of SLPP *T. ordinoides*.

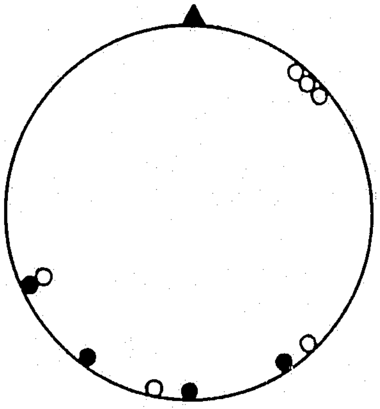
A. Trails produced by males

B. Trails produced by gravid females

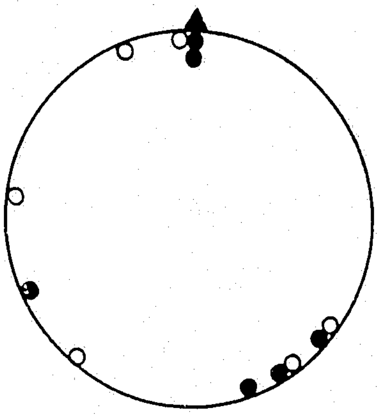
Closed circles = males; open circles = females

Triangle outside the circle represents the trail direction.

See Figure 24 for explanation of additional figure symbols.



A



B

Figure 35: Basic orientation tests of SLPP neonates.

A. *T. sirtalis* born and kept indoors at laboratory and tested under clear skies.

B. *T. ordinoides* born outside at laboratory and tested under clear skies.

C. *T. ordinoides* born outdoors in captivity at SLPP and tested under cloudy skies.

Scores not distinguished by sex.

See Figure 24 for explanation of additional figure symbols.

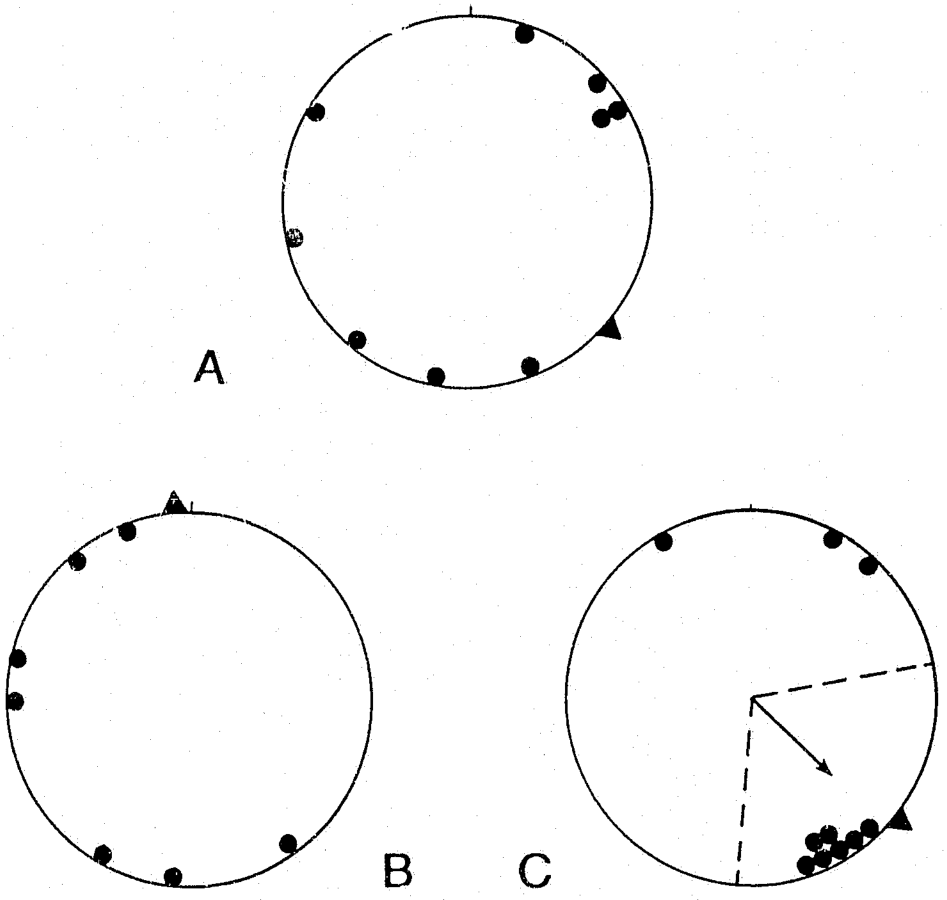

A
B
C

Figure 36: Trailing tests of SLPP *T. ordinoides* neonates.

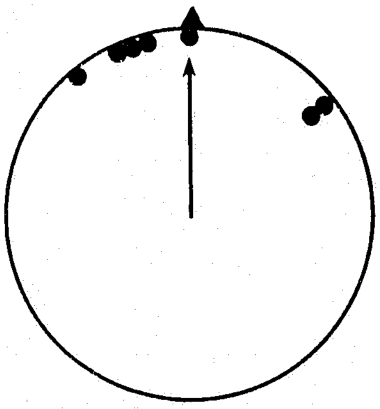
A. Born outdoors in captivity at SLPP and tested under cloudy skies.

B. Born outdoors at laboratory and tested under clear skies.

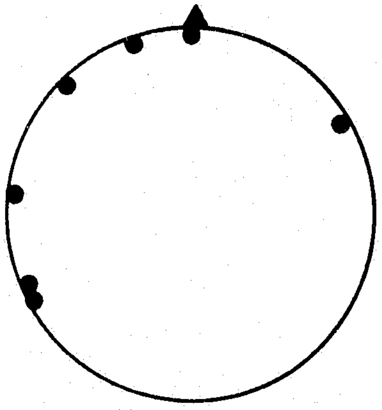
Outer triangle represents the direction of the trail produced by the mother. Scores not distinguished by sex.

See Figure 24 for explanation of additional figure symbols.

A



B



Behavioral Actions of Orientation-tested Snakes

A typical behavioral pattern was seen in all test categories. In slightly over 50% of all tests for all three populations, once the box was raised the snake would remain stationary with the head and upper body raised above the substrate. Usually within a few seconds, the snake would begin to flick its tongue as it lowered its head to the substrate and would slowly sway its head from side to side. This head-swaying action would typically cease as the animal began to crawl away from the release point, but tongue-flicking would usually continue, albeit at a slower rate. I did not record the rate of tongue-flicking, which is often used as a measure of vomeronasal stimulation (see Ford, 1986). In most cases, any shifts in direction by the snake would occur as the snake lowered its head to the substrate; movements following this usually continued in the same direction and the snake would move to the arena edge without stopping. Rarely did major changes in direction occur once movement away from the release point had begun.

Trailing tests elicited some different distinctive behaviours. The sand substrate at WBNP test site A clearly showed the path taken by the stimulus snake and the relation of the trailing snake to this path. When following a trail, the male would often deviate slightly from the trail, travelling back and forth across the trail rather than following it exactly. Other trailing behaviours were more unusual, and were never seen under natural conditions. During trailing tests of WBNP snakes, I observed a mouth-gaping, head-jerking action. The trailing snake would hold its head in contact with the substrate, depressing it to the ground rather than just resting it on the surface, open its mouth widely, rapidly move its head from side to side in an exaggerated manner (more so than as described above) and flick its tongue at a rapid rate (again, more so than as described above). This action was demonstrated by WBNP *T. sirtalis* in five of thirteen (31.8%) of the trials involving a trail produced by a female containing a copulatory plug and once in 17 (5.8%) trials of trails produced by unmated females. As these tests involved only males as trailing subjects, I never observed this behaviour by a female. This action was not seen in any of the tests involving a male as a stimulus snake.

I also observed a similar mouth-gaping, but without the exaggerated head-swaying and other actions, twice in tests involving SLPP snakes. One involved a male *T. sirtalis* during a basic orientation test and the second involved a female neonate of the same species, also during a basic test. The lowered head action was observed once in a male during a trailing test of a SLPP gravid female.

Two other interesting actions were also observed occasionally - a "cloacal press", in which a snake appeared to depress its cloacal region to the substrate, and a "tail raise", in which the tail portion of the body would be briefly (< 30 sec) lifted off the substrate at approximately a 90° degree angle. Both occurred while the snake was stationary. I observed cloacal presses on two occasions, once by a gravid female *T. ordinoides* during a male-produced trail test and once by a male *T. sirtalis* during a female-produced trail test. Tail raises were seen on six occasions. In SLPP snakes, I observed this twice by female and once by a male *T. sirtalis*, all while following female-produced trails, once by a neonate *T. ordinoides* during a basic test, and once by a male *T. sirtalis* during a phase-shift test. A WBNP male performed a tail-raise once during a basic test.

DISCUSSION

Movement Patterns of Snakes

Snake movements range from irregular, erratic wanderings (e.g. Blanchard and Finster, 1933; Fitch and Shirer, 1971; Hirth *et al.*, 1969) to unidirectional migrations (Macartney, 1985; Madsen, 1984; Larsen, 1986). Although the analyses of movements of SLPP snakes are rudimentary, the results clearly indicate that *T. sirtalis* at this site represent one end of the spectrum; WBNP snakes lie at the opposite end. This provided a suitable basis for examining the hypothesis that snakes from migrating and nonmigrating populations of the same species may possess differences in their orientational abilities.

Of potential factors governing snake movements, den availability may be of primary importance in determining whether or not individuals of any particular population undergo long-distance migrations (Gregory, 1984b). Hibernating sites may be scarce in some environments, particularly in colder climates where snakes must go deep underground to escape the cold (Macartney *et al.*, 1989). Communal denning is an additional correlate of low den availability (Gregory, 1984b). Larsen's (1986) finding that SRD snakes from WBNP are communal denners that undergo long migrations are thus expected. By contrast, in mild climates, snakes can hibernate at shallow depths (Gregory, 1987). Generally, shallow sites will be more abundant than deep sites in an area and neither long movements to feeding areas or denning in large numbers are likely to occur. Despite the difficulties in confirming any site as a den at SLPP, it is likely that dens are plentiful there. Therefore, shorter movements and small denning numbers are reasonable assumptions.

Certain advantages have been ascribed to communal denning. The predominance of spring and, to a lesser extent, autumn mating in temperate zone colubrid snakes (see Seigel and Ford, 1987) presumably take advantage of the availability of potential mates at communal dens. At sites like SLPP, snakes may trade off this advantage in favour of selecting the first suitable hibernating site that they find in the fall, thereby avoiding the risks inherent in movement or in getting caught out in an early fall cold spell. This would explain the apparent lack of fidelity of SLPP snakes for overwintering sites. At WBNP, high fidelity is probably a natural result of the scarcity of suitable hibernacula, but, in such a harsh climate, there may be additional pressure to hibernate at a den where the snake has been successful before (Gregory, 1984b). Furthermore, because dispersal distances are not large for the SLPP population, compared to WBNP snakes, it may not be as difficult for SLPP males to locate females once they have left the denning area.

Other determinants of snake movements, not fully explored in this study, are presumably of lesser importance in predicting whether or not individuals will undergo long migrations. Foraging strategies and other dietary considerations, reviewed by Mushinsky (1987), are significant. In general, prey for both SLPP species appeared to be abundant and widely distributed throughout the SLPP study site, correlating with the generally erratic nature of movements. Certain prey items, particularly amphibians, which comprise the majority of the SLPP *T. sirtalis* diet, may be more abundant along the shore, which would account for the directionality (along the long axis of the lake) occasionally recorded. Madsen (1984) noted that *Natrix natrix* displayed unidirectional movements resulting from foraging along stone fences. Both ontogenetic and sexual differences may influence feeding habits and, through this, can produce variation in movement patterns. Gravid females, for example, may not migrate to summer feeding ranges and/or may show more restrictive movements than males and nongravid females (Brown *et al.*, 1982; Macartney, 1985; Reinert and Zappalorti, 1988b; Shine, 1979; Viitanen, 1967). This is likely a result of trade-offs between various reproductive costs and benefits (e.g. see Seigel *et al.*, 1987; Shine, 1980). Gravid reptiles are often slower and hence perhaps subject to greater predation. Survival may therefore be enhanced by undergoing fewer and shorter movements. At SLPP, however, there were no strong indications of sexual variation in movement patterns with the exception of early spring movements by male *T. sirtalis*. Larger sample sizes are needed to fully explore any differences.

Sexual differences in movement behaviour may also be attributed to reproductive behaviour. Males may make more extensive movements while they search for females (King and Duvall, 1990; Madsen, 1984; Reinert and Zappalorti, 1988b; Shine, 1987), and this may have been the case for early spring movements made by male SLPP *T. sirtalis*. Longer movements by males during this time may be particularly necessary in the absence of communal dens that contain both sexes, as apparently existed in some cases at SLPP. There was some evidence to suggest that males that did not den with females made longer and earlier movements than did males that were found near females at presumed dens.

Some studies have suggested a correlation between body size and movement distances, but a review by Macartney *et al.* (1988) showed no consistent trends. Body size and movements were not related in adult SLPP snakes. Microhabitat features also influence movements (Madsen, 1984; Reinert and Zappalorti, 1988b; Shine, 1987; Weatherhead and Charland, 1985), but I did not examine this factor in this study.

When migrations between winter and summer ranges do occur, they occasionally involve distances of several kilometres (Duvall *et al.*, 1985; Gregory and Stewart, 1975; Klauber, 1972; Larsen, 1987). The differences in distances travelled by the SLPP and

WBNP *T. sirtalis* clearly distinguish them as nonmigratory and migratory populations. Distance is not always a reliable indicator of migration, however. Shorter movements have also been described as migratory (e.g. approximately 500 m, *Nerodia sipedon*, Tiebout and Carey, 1987; 420 m, *Elaphe obsoleta*, Weatherhead and Hoysak, 1988; approximately 200 m, *T. sirtalis*, Fitch and Shirer, 1971). Other characteristics may be used instead to indicate migration.

For a migratory population demonstrating fidelity, two activity or movement peaks should be seen, corresponding to vernal and autumnal migrations. Bimodal peaks of activity have been reported in several North American snake populations (see review by Gibbons and Semlitsch, 1987). Brown and Parker (1976; Parker and Brown, 1980) found that movement rates recorded during migratory movements were much greater than those occurring in the summer range for *Coluber constrictor*, *Masticophis taeniatus* and *Pituophis melanoleucus*.

Because I was unable to capture many snakes in late summer and fall at SLPP, I was unable to fully examine whether similar bimodal peaks were evident at that site. The spring movement "peak" by male *T. sirtalis* was more likely related to locating mates than any other factor. Movement rates for this species seemed to increase in late summer, but movement distances did not clearly reflect a similar trend.

When movement distances are short, migration may be considered to occur when snakes move between discrete habitats. This appeared to be the criterion used by Fitch and Shirer (1971) in describing the migration of gravid females to rocky outcrops, which were distinct from the tall grass habitat of the summer range. At WBNP, denning areas and summer feeding ranges were clearly distinct; this was not the case at SLPP.

Habitat distinctness may also be considered when the summer range does not include the den. Weatherhead and Hoysak (1988) incorporated this aspect in deciding which individual rat snakes migrated to a summer range. Other snakes in their population did not migrate but rather included the hibernaculum within the home range. Because it is often difficult to accurately define the limits of snake home ranges, distinguishing between discrete summer and winter ranges is often untenable. This is especially the case when movements are erratic or unidirectional throughout the active season. Various authors have thus favoured the use of either the "total range" (Hirth *et al.*, 1969; Macartney, 1985) or "activity range" (Reinert and Zappalorti, 1988b; Shine, 1987). Other problems in defining home ranges are discussed by Gregory *et al.* (1987) and Rose (1982).

Although estimates of home range areas of WBNP snakes varied considerably, based on which portion of the entire migratory route was used in the calculations, "winter" and "summer" home ranges are clearly distinct for this population. A similar assessment was difficult for the SLPP snakes. Because den sites could not be positively identified, their location relative to summer home ranges and the size of the home ranges could not be definitely determined. However, there was little indication that denning areas and summer ranges were distinct, suggesting that migration between distinct habitats did not occur. Also, the large disparity in home range areas between the two populations further differentiated their movement patterns.

Orientation and Navigation in Snakes

Types of Orientation

General

Animals that migrate long distances presumably have well-developed orientational abilities that allow them to locate widely separated goals rapidly and accurately. Migrating snakes commonly do not seem to disperse in all directions but rather demonstrate strong directionality, radiating into one or two adjacent quadrants (*T. sirtalis*, Gregory and Stewart, 1975; Larsen, 1986; *Coluber constrictor*, Hirth *et al.*, 1969; *Masticophis taeniatus*, Hirth *et al.*, 1969; *Vipera berus*, Prestt, 1971; Viitanen, 1969; *Crotalus horridus*, Brown *et al.*, 1982; *Crotalus viridis*, Duvall *et al.*, 1985; Hirth *et al.*, 1969; Macartney, 1985), although exceptions exist (King and Duvall, 1990; Parker, 1976). In most cases, this strong directionality undoubtedly exists because of the distribution pattern of suitable summer habitats. However, strong directionality may still occur despite the presence of other suitable summer ranges in other directions, but which would seem to be more easily reached (Gregory and Stewart, 1975; Macartney, 1985; Viitanen, 1967). Whatever the cause, this directionality suggests that random wandering, a form of Type I orientation (Griffin, 1952), is not the means by which dens or summer ranges are located over great distances.

It is more difficult to evaluate under natural conditions the importance of piloting by use of familiar landmarks (the other form of Type I orientation), and it was for this reason that arena displacement tests were performed as has been previously discussed in the **Methods**. Type I orientation is suspected during arena tests when subjects display random orientation. Random orientation, however, may not be a result of a loss of reference guides. It may also occur because the subjects are too disturbed by the test conditions and are, perhaps, demonstrating an escape reaction, or because they lack the motivation to select a specific direction. Thus, a random response cannot be used to confirm a lack of orientational ability. However, this is true only if all orientation tests, including those done at different seasons, show random responses. For example, if the subjects demonstrate a directional choice during autumn tests but not during mid-summer tests, it suggests that either the orientation cues have somehow been removed, which seems unlikely, or that the motivation to select a specific direction is not present.

Type III orientation is indicated when subjects select the predicted direction. In this case, true navigation must be in operation. The test subjects are able to correct for their shift in location and orient towards the goal despite displacement. Navigation is also suggested if the directions selected at each of the two test sites are different but both point towards the same location. In this case the animals may be oriented towards a goal unrecognized by the experimenter. To ensure that orientation towards the predicted goal is not a result of the location of the arena relative to the goal (see below), at least two test sites, located in opposite directions, should be selected.

Type II orientation is suspected when the subjects select a direction but not in the predicted direction. Possible explanations for this directional selection must first be evaluated:

1) If the directions selected at each of the two displacement sites are the same and oriented along the line which would take the animal to its goal had it not been displaced, then Type II orientation may be in operation.

2) If the directions selected at each of the two test sites are different (i.e. "release-site bias"; Keeton, 1973), then the subjects are likely being directed by some local cue unknown to the experimenter.

3) If the directions selected at each of the two test sites are the same but (a) not oriented along the predicted path, (b) nor along the line which would take the animal to its goal had it not been displaced, (c) nor directed towards a common point (perhaps an unidentified goal), then they are likely exhibiting a "preferred compass direction", or PCD (Wallraff, 1978), analogous to that often demonstrated in bird studies. There is as yet no adequate explanation, other than experimental effect, as to why animals should select a direction that has no known relationship to the homeward direction.

WBNP

The results of the basic orientation tests of WBNP *T. sirtalis* did not always indicate Type III orientation. During autumn tests, snakes did make significant directional choices at both sites, but these directions were not in the predicted direction and were different at the two sites ("release-site bias"). However, these results are most easily explained by a "phase-shift" argument previously offered - that the snakes were not correcting for the shift in solar azimuth position during the time spent in the opaque bag. Other alternatives could not account for the deviations seen at both sites.

To further support this conclusion it is necessary to consider the placement of the test sites, the summer range, and the den. Based on the findings of Larsen (1986 and pers. comm.), snakes travel in a direction of approximately 190° - 270° in order to reach the den from the summer range. The direction selected by snakes tested at site A (296°) did not differ greatly from this range. Thus, the possibility of Type II orientation could not be rejected. However, if this form of orientation was in effect, snakes tested at site B would have shown a similar directional selection. This was not the case. Instead, snakes demonstrated denward orientation once the corrections had been applied to the data. Additionally, with the exception of early spring tests of males, transportation in the light did not produce similar "misdirected" results.

Sexual differences were apparent in spring orientation tests. Whereas females demonstrated true navigation by orienting in the predicted direction at both test sites, males tested during the peak of the mating period selected a different preferred direction. Perhaps coincidentally, males at both test sites selected the same direction (approximately 108 °). This direction, however, was similar to the position of outlying males at the den site. This suggests that during this time period the males were demonstrating a Type II response. Other evidence of motivational differences were evident in the trailing tests and are examined later. Once most females had departed the den area and migration by males had begun, males oriented towards the summer range, thus displaying true navigation.

SLPP

Thamnophis sirtalis from Spectacle Lake selected directions that led to the lake from both test sites, suggesting Type III navigation. However, it is necessary to view these directional selections in relation to the normal movement patterns of snakes in this population. Movements at Spectacle Lake by this species were usually irregular, although significant directionality running parallel to the lake did occur. Comparative statistical techniques for circular measures require several restrictive assumptions which were not met; therefore as an approximate indicator of differences I examined overlap between the 95%

confidence intervals of angles selected during arena test and angles of movements occurring at Spectacle Lake (values are given in Tables 6 and 8, pages 84 and 108, respectively). For both test sites, there was some overlap; thus, the possibility existed that snakes were exhibiting Type II orientation. That is, the snakes may not have been correcting for displacement and were continuing to orient as if they had not been displaced. Yet, orientation by snakes at SLPP was always directed along an axis rather than in a single direction, whereas the arena tests never suggested bimodality. The results of the phase-shift tests gave further evidence that these snakes displayed Type III navigation.

Several differences between the Vancouver Island tests and the WBNP tests should be noted. Movements by Spectacle Lake snakes are short and it was not possible to identify specific goals such as dens and summer ranges. Although tests were performed throughout the active season, seasonal differences in preferred directions, if any existed, could not be detected. Also, reproductive activities were never observed in snakes being tested so it was not possible to examine seasonal sexual differences such as those that were noted for the WBNP snakes. Because of the relatively small sample sizes, it was not possible to statistically examine orientation responses with regard to sex. No differences were apparent, however.

Mixed results were obtained for *T. ordinoides*. Although homeward orientation was observed at one test site, snakes were randomly oriented at the second. It is possible that snakes were attracted to some cue outside the arena at this second site and were thus not motivated to home, but I was not able to determine this. At the first test site, overlap between the 95% C.I. of the selected direction and the spring-to-summer directionality noted in 1987 did exist, again raising the possibility that snakes were orienting in accordance with normal movement patterns rather than towards home. Definite conclusions regarding their level of orientational ability could not be reached from these data.

Orientation Cues

General

With the possible exception of random wandering, some cue or cues are required to guide migrating animals towards their goal. Extensive reviews of orientation mechanisms used by a wide variety of animals are given by Able (1980) and Shöne (1984).

The extensive variability in known snake movements does not suggest any clear cut-off point at which proximate orientation must be replaced by distant orientation. It is therefore useful to review relevant aspects of goal-directed behaviour in snakes.

Snake aggregations have been commonly reported in the literature and are reviewed by Ford (1986) and Gregory *et al.* (1987). In addition to denning and mating aggregations, concentrations of snakes have been noted under cover objects, at feeding sites, and, for gravid females, at oviposition sites and preferred basking locations. It was not uncommon to see loose aggregations of snakes at SLPP. Aggregations seen during the early spring suggested small denning and/or mating groups. It was not clear why aggregations formed at other times of the active season.

Gregory *et al.* (1987) suggested two alternative, but not mutually exclusive, explanations for the formation of snake aggregations: independent habitat selection and social attraction. Although they considered the former to be a more parsimonious explanation, numerous studies, principally in laboratories, have demonstrated that under certain conditions snakes are attracted to some conspecific cue or cues, most likely pheromones (Burghardt, 1970, 1980, 1983; Brown and MacLean, 1983; Dundee and Miller, 1968; Ford, 1979, 1981, 1986; Ford and Low, 1982, 1984; Ford and O'Bleness, 1986; Graves *et al.*, 1986; Heller and Halpern, 1981, 1982a, b; Noble and Clausen, 1936; Porter and Czaplicki, 1974; Scudder *et al.*, 1980). It may also be speculated that snakes "condition" (Dundee and Miller, 1968) the substrate at preferential sites by depositing some chemical cue. Ford and O'Bleness (1986) found that while female *T. marcianus* would not trail one another in laboratory tests, aggregation sites were attractive to other gravid females when snakes were tested singly. Thus Ford and O'Bleness concluded that while trailing may not lead individuals to a specific area, the suitability of a refuge may be identified by chemical cues. Gregory *et al.* (1987) also speculated that habitat conditioning plays a role in site fidelity. It may be that once a snake has identified an ideal location, it "marks" it by depositing a chemical cue which would assist the animal in later returning to that site. Other individuals passing through the area may respond to these odours, resulting in several individuals selecting the same spot. Further field work is essential in assessing this hypothesis. Field evidence also strongly suggests that snakes can and do follow conspecific trails. In most cases these observations have involved a male following the pheromone trail of a sexually attractive female (e.g. Aleksiuk, 1976; Aleksiuk and Gregory, 1974; Carpenter, 1952; Finneran, 1949; Lillywhite, 1985; Munro, 1948; Noble and Clausen, 1936; Truitt, 1927). Sexual trailing was clearly evident during the spring mating period at WBNP, and its absence during pheromone trailing tests was unexpected (see **WBNP** below).

Sex pheromones in garter snakes are relatively well understood and have recently been isolated (Mason *et al.*, 1989). Noble (1937) was perhaps the first to suggest that the female attractant pheromone was released through the dorsal integument rather than from the cloaca, and this has been proven by more recent studies (Crews, 1976; Devine, 1976;

Gartska and Crews, 1981). This attractant pheromone is likely the same as the trailing pheromone (Ford, 1986) and is nonvolatile (Ford and Low, 1984). It is also relevant to note that the female attractant pheromone is easily transferred to other snakes or objects. Thus, as a female travels along the ground a pheromone trail can be produced. Occasionally this may produce unusual results. Aleksiuk and Gregory (1974) reported that male *T. sirtalis* that had recently mated were pursued and courted by other males. Crews and Kubie *et al.* (1978) have also reported on this apparent transference. However, the inappropriate courting of males by other males may be due to the "she-male" phenomenon (Mason, 1987; Mason and Crews, 1985), in which some male *T. sirtalis* produce their own attractant pheromone.

A second pheromonal system is also involved in garter snake mating behaviour. During intromission, males deposit a gelatinous plug in the cloaca of the female. These plugs were obvious in mated WBNP females, giving a clear indication of whether or not a female had recently mated. This plug may remain in place for several days before being expelled by the female (Devine, 1975). In addition to its possible function as a means of sperm retention, copulatory plugs also inhibit mating by other males both mechanically and through pheromonal mediation. Several studies have reported that sexually active males immediately ignore recently mated females (Devine, 1977; Fitch, 1965; Noble, 1937; Ross and Crews, 1977, 1978; Whittier *et al.*, 1985). Ross and Crews (1978) found that female *T. radix* were unattractive to sexually active males for at least 48 hours. Other evidence, however, suggests that the change in female status is not always immediately apparent to males. Mason (1987) reported that Whittier occasionally observed intromission by males of plug-containing females. The functions of these two sex pheromonal systems became particularly evident during the WBNP trailing studies.

Field evidence of trailing by adults in a nonsexual context is rare, although I suspect that difficulties in observing snakes under natural conditions may be largely to blame. Larsen (1986) reported a case where a male was recaptured twice near the same transmitted-equipped female, the second occasion occurring two days after the first following movement of approximately 360 m. I noted a similar event at Spectacle Lake; a male and female *T. sirtalis* were captured together for a second time two weeks after moving a minimum distance of 145 m. Unfortunately, movements occurring between the first and second capture for both cases were not known. Coincidence, therefore, must be considered a valid explanation for these apparent trailing events.

Evidence that neonates are capable of trailing adults of both sexes in the field is slightly stronger. The ecology and movement behaviours of young snakes are still largely unknown although some progress is being made. In many snake populations, gravid females congregate at oviposition sites or nesting sites prior to parturition (see examples in Graves *et al.*, 1986; Swain and Smith, 1978), resulting in neonatal aggregations, sometimes at dens. Parturition also may occur at considerable distances from communal dens, which may either force the young to overwinter in areas other than those used by adults or result in their later arrival at the den (e.g. see Gregory, 1982, 1984b; Reinert and Zappalorti, 1988a). In cases where neonates do appear at the communal den but were not born there, pheromone trailing of adults has been commonly suggested as the means by which the young locate the den (Brown and Parker, 1976; Graves *et al.*, 1986; Hirth, 1966; Klauber, 1972). Several laboratory studies have demonstrated that neonates are attracted to other neonates via chemical cues (Burghardt, 1977; Scudder *et al.*, 1980) and will follow adult-produced pheromone trails (Brown and MacLean, 1983; Brown and Parker, 1976; Graves *et al.*, 1986). Reinert and Zappalorti (1988a) provided field evidence of trailing of adults, both males and females, by neonatal *Crotalus horridus*. The positive response by neonates to adult odours cannot necessarily be extended to adults, however. Neonatal *Nerodia sipedon* aggregate in response to conspecific odours (Scudder *et al.*, 1980), whereas adults avoid areas soiled by conspecifics (Porter and Czapliki, 1974).

Visual cues may also mediate snake aggregations. Noble (1937) and Noble and Clausen (1936) concluded that vision plays the most important role in promoting sexual and other aggregations, and other studies have suggested that vision plays at least some role in creating spacing patterns in snakes (Dundee and Miller, 1968; Heller and Halpern, 1982b; Lawson, 1985). Certain aspects of Noble and Clausen's studies have been criticized, however (Burghardt, 1970; Kubie *et al.*, 1978), and more recent studies have demonstrated that the vomeronasal system is the key sensory system mediating the formation of aggregations (Heller and Halpern, 1982a,b; Kubie *et al.*, 1978). Visual cues appear to have limited value in the social behaviour of snakes considering their habitats and cryptic coloration.

The use of pheromones as the primary natural orientation guide, especially for longer movements, is questionable, however, for a variety of reasons: (1) odour trails and/or deposited cues may not last long enough for them to be effective over any length of time (Brown and Parker, 1976; Stoddart, 1980); (2) trails are nonvolatile (Ford and Low, 1984) and thus snakes may not be able to perceive them over long distances; (3) this hypothesis requires snakes to discriminate between trails leading to the home den versus other sites (Gregory, 1982), and (4) the use of pheromone trails as migratory cues is insufficient because it cannot account for the orientational abilities of the "leaders" (Viitanen, 1967).

For the most part, these difficulties are based on speculation rather than direct evidence but there is also little evidence to refute them. Preferably, studies should examine how pheromone trails and odour deposition function in the natural environment. Beyond anecdotal accounts, little progress has been made. In a laboratory study, Heller and Halpern (1982a) found that snakes returned to a preferred shelter after being removed from the apparatus for up to one week. Longer time periods were not examined. Gregory *et al.* (1987) considered this question with respect to long-distance migration and wondered whether "well worn" trails could persist over the course of a season. The fact that some snakes in some populations cross water during their migrations, such as the WBNP *T. sirtalis* (Larsen, 1986), and/or return via a different path (Larsen, 1986; Macartney, 1985; Madsen, 1984; Reinert and Zappalorti, 1988b) diminishes the likely importance of pheromone trails in long-distance orientation.

The nonvolatility of odour trails renders them unsuitable as aggregation cues when snakes are widely dispersed. Within limited home ranges, random wandering may bring a snake into contact with a trail that may then be followed, but this seems a chancy mechanism if trailing is an essential goal-directing cue. Such trails, however, are likely distinct from deliberate discharges presumably involved in marking substrate and it is conceivable that these other odours are more volatile and thus can be perceived over greater distances. When snakes disperse from a communal den prior to vernal migrations, or once the group begins to coalesce upon return to the den, pheromone trails *per se* may be more useful.

Several studies have demonstrated that snakes can discriminate between male and female trails (Gehlbach *et al.*, 1971; Ford, 1986), between conspecifics and heterospecifics (Devine, 1976; Ford, 1982, 1986; Ford and Shofield, 1984), and between their own odours versus those of others (Heller and Halpern, 1982a). The discriminatory abilities demonstrated in these studies suggest that a variety of kinds of information is present in pheromone trails. Perhaps snakes from different dens possess distinct differences in odours, as suggested by Galligan and Dunson (1979). This possibility, however, remains speculative.

It is insufficient to reject the role of pheromone trails as migratory orientation guides because they do not address the orientational abilities of the leaders for two reasons. First, as with all other aspects of snake movements, considerable individual variation exists and it does not seem unreasonable to expect individual differences in orientational ability. Unfortunately, most studies examining such differences in snakes concentrate on sexual rather than individual differences in trailing ability. Heller and Halpern (1982a), nevertheless, did find that some *T. sirtalis* preferred, on the basis of chemical cues, their own shelters rather than those of the group. Individual variation has been more strongly documented in other animals. Herrnkind (1972) found differences in the use of solar and landmark guides among orienting crabs. His results suggested that crabs with weak directional preferences were following more well-oriented individuals. Emlen (1967) found that individual migrating indigo buntings relied on different stellar cues. Ontogeny also has an important influence on orientational abilities (e.g. see Ferguson, 1971, for ontogenetic differences in orientation in amphibians, and Emlen, 1969, 1972, for birds).

Second, multimodality of orientation mechanisms appears to be the rule rather than the exception for all other animals studied (see Able, 1980; Ferguson, 1971; Keeton, 1974), and it undoubtedly exists for snakes as well. Multimodality provides numerous benefits for the organism, not least of which is the ability to switch cues as one becomes unavailable (for example, loss of solar cues because of cloud cover) or less precise.

The results of the WBNP tests suggested an important role for pheromone trails for migrating snakes, particularly during the vernal dispersal phase. As will be discussed, a hypothesis was developed expanding the role of sexual pheromones to include an additional orientation function. It is doubtful, however, that pheromone trails provide the only orientation cue.

When migrations or exploratory movements involve long distances, it is likely that significant changes occur in the means by which goal-directed behaviour is accomplished. Local visual landmarks and/or odour gradients that are used by the animal to orient within a localized region may not be available for a long-distance migrator. Route memorization may be inadequate over great distances and is a mechanism not available to neonates.

Orientation by visual landmarks doubtless is important, especially considering objects present within the "familiar" range but outside the home range. Larsen (1986) and Lillywhite (1985) reported similar behavioral observations of undisturbed snakes that suggested visual orientation. In both studies, snakes were observed to stop and raise their heads above the ground for a short period. Larsen reported that tongue flicking was absent, suggesting that chemical cues were not being sampled.

In addition to landmarks and route memorization, celestial guides (solar azimuth position predominantly, but also polarized light patterns) have been identified as the most commonly used guides in diurnal migrants (Able, 1980; Shöne, 1984). Because of the consistent nature of solar cues and presumably their ease of perception, this hypothesis has much merit. Only a few studies, however, have specifically examined whether snakes are capable of using solar cues. Aside from this study, solar orientation has been examined and demonstrated in snakes by Landreth (1973) for *Crotalus atrox*, Lawson (1985) for *Thamnophis radix*, and Newcomer *et al.* (1974) for *Nerodia sipedon* and *Regina septemvittata*.

Phase-shifting tests, which are required to validate the use of the sun as an effective compass because animals must be able to compensate for the sun's movement across the sky, have previously been performed only in Newcomer *et al.*'s study.

WBNP

The use of solar azimuth position as an orientation guide was confirmed for the WBNP population through the phase-shifting tests. Of special interest was the absence of sexual differences in the spring tests of phase-shifted snakes. This may have been due to the absence of a fresh supply of emerging, sexually attractive females. Krohmer and Crews (1989) reached a similar conclusion, noting that the length of the courtship season in *T. sirtalis* was controlled by the presence of attractive females.

Snakes continued to orient towards home when the sky was partially cloudy and the sun was not visible. This suggests that polarized light, which can provide directional information in the absence of the sun as long as some blue sky is present (see Waterman, 1955, for more details), may also function as a directional guide. A variety of animals are known to be able to respond to polarized light patterns, including tiger salamanders (Adler and Taylor, 1973; Taylor and Adler, 1973), bullfrogs (Auburn and Taylor, 1979), and fringe-toed desert lizards (Adler and Phillips, 1985). Although orientation by polarized light has also been suggested as an orientation guide for snakes (Lawson, 1985, for *T. radix*), further studies specifically examining its use need to be done. It is important to note, however, that other cues may be relied upon in the sun's absence. In addition to pheromonal cues, magnetic cues, airborne olfactory gradients, inertial navigation, and other mechanisms could be involved and are worthy of investigation. Rodda (1984), for example, found that alligators may use magnetic cues to orient. Thus, the absence of a cue at a particular time for one individual does not preclude its use when available.

Some of the most interesting and unexpected results of this study were obtained during the spring WBNP trailing tests. Because these tests were performed during the mating period, I had suspected that males would show a strong response towards sexually attractive females but not towards males or recently copulated females. Although males showed no attraction to trails of other males as predicted, the positive response to trails of copulated females, but generally not to sexually attractive females, was unforeseen.

There are at least three possible explanations of the tendency of males to trail recently copulated females:

(1) The pheromone was transferred during transport from the sexually attractive females to the females containing copulatory plugs;

(2) The inhibitory effect of the copulatory plug is not immediate, and the males were still exhibiting sexual trailing.

(3) Males were using the trails of copulated females as migratory orientation guides.

The first two interpretations cannot account for the absence of trailing by males of sexually attractive females. The third, however, suggests the following hypothesis: Upon spring emergence, mating is of primary importance for males, and females are located primarily via pheromone trails. Once the majority of the females have mated and left the den area, producing trails, migration then becomes the central motivating factor for males. Males, although capable of solar orientation, may then use trails produced by copulated females as initial orientation guides. Artificial displacements during the mating period, however, produced a conflict for males - whether to locate sexually attractive females or begin migrating. This, I believe, resulted in the random responses of males during tests involving sexually attractive females. No conflict apparently existed when non-sexually attractive females laid the trails, and males used these trails as orientation guides. Furthermore, this suggests that trails overrode the use of available solar cues because the female trails were not directed towards the summer range, leading to the speculation that it is somehow easier to follow trails than to read solar cues.

Unfortunately I was not able to perform fall trailing tests and it is unknown whether males also use female trails as an orientation guide in the fall. It is also not known whether females use pheromone trails as orientation guides. Considerable variation exists in which sex is the first to return to communal hibernacula in the fall, although females are more often the first to return (see Gregory, 1982); thus if trailing is indeed important during fall migrations it may not be sex-specific. The greater dispersion of snakes within their summer habitat as compared to following spring emergence makes it likely that pheromone trails would be more difficult for snakes to locate. However, as snakes begin to coalesce upon their return to the den, trails may become more available. For snakes from populations that exhibit a high degree of directionality, pheromone trails may begin to be useful at considerable distances from the den.

Behavioral actions of trailing snakes gave further evidence that pheromone trails were being followed. The back and forth movements across the trail by males were similar to trailing behaviours described by others (Ford, 1986; Ford and O'Bleness, 1986; Gehlbach *et al.*, 1971; Lillywhite, 1985).

The mouth-gaping, head-jerking actions with the head depressed to the substrate were especially distinctive behaviours. Depression of the head to the substrate during trailing tests, also noted once during a test involving a SLPP male *T. sirtalis* following a gravid female trail, has been noted by Brown and MacLean (1983), Dundee and Miller (1968), Gehlbach *et al.*, and Scudder *et al.* (1980). Scudder *et al.* and Dundee and Miller suggested that this action enhances chemoreception, a conclusion with which I concur. This behaviour appeared to be very similar to the chin-pressing behaviour by males during courtship. It is interesting to speculate that the chin-pressing behaviour of males during courtship may enhance the reception of the female attractiveness pheromone as well as physically stimulate the female (Carpenter, 1977; Noble, 1937; Schuett and Gillingham, 1988).

Mouth-gaping (Duvall *et al.*, 1985; Graves *et al.*, 1986; Graves and Duvall, 1983) and head-jerking (Lillywhite, 1985) are also suggestive of enhancing chemoreception. Although not reliable indicators of trailing, since they were not always observed, the frequency of these actions was much greater during tests involving trails of copulated females; only once were they observed when a male was following a sexually attractive female.

I am less sure of the function of other behaviours noted during the course of orientation tests performed during this study. Mouth-gaping was observed twice in basic tests involving SLPP snakes, but without the other associated actions. It is quite possible that aerial chemical cues were being sampled in these instances. The tail-raising and cloacal press actions, performed by *T. ordinoides* and by snakes from both populations of *T. sirtalis*, and seen under all test conditions, are more difficult to assess. Although they were suggestive of some form of scent-marking, I never noted any special response by other snakes to the sites where this action was performed.

SLPP

Nonmigratory *T. sirtalis* from Spectacle Lake are capable of orienting with respect to solar azimuth position as demonstrated by the phase-shifting tests, and, as with the WBNP results, there is evidence to suggest that solar cues are available in the absence of the sun itself.

Trails laid by gravid females, but not by males, also appeared to be effective orientation cues, but the response did not seem as strong as that exhibited during the WBNP tests. Trailing abilities appeared to be slightly enhanced under cloudy conditions, suggesting that solar cues are more important orientation guides.

Neither solar cues nor pheromone trails were effective as orientation guides for adult *T. ordinoides*.

Unfortunately I had poor success in acquiring neonates for testing so I am unable to draw conclusions about the ontogeny of orientation behaviour in these animals. Not unexpectedly, neonate *T. sirtalis* that had no prior exposure to the sun demonstrated random orientation. Tests of neonate *T. ordinoides* suggested that they might imprint on solar cues at the birth site, similar to Galligan and Dunson's (1979) suggestion that neonate *Crotalus* imprint on den odours and Carr's (1967, 1972) hypothesis that turtle hatchlings imprint on cues characteristic of their natal beach. In the absence of solar cues, *T. ordinoides* apparently will follow pheromone trails produced by the mother. This supports the hypothesis proposed by Brown and Parker (1976) and Brown and MacLean (1983) that neonates that hibernate in the communal den during their first winter use adult pheromone trails as orientation guides.

Conclusions

Snakes have critical resources that they must locate - food, mates, and overwintering sites being among the most important - and the distribution of these resources relative to one another determines overall movement patterns of snakes. When geographic and environmental conditions exist that limit the availability of these resources and shortens the time available to search for these resources, as exemplified in WBNP, an effective means of locating them presumably becomes critical. Advanced navigational skills for WBNP *T. sirtalis* are therefore expected. However, the wide range of migratory behaviours exhibited by snakes suggests that there is no identifiable cut-off point at which navigational abilities would become superfluous, at least within a species.

The same may not be true between species, however. *Thamnophis ordinoides* has received very little attention in terms of ecological studies, and I am not aware of any other research that has specifically examined its movement patterns. As it appears to forage almost exclusively on slugs and earthworms throughout its restricted range in relatively mild climates (thus dens near or within feeding ranges are likely abundant), it would not be surprising if no long-distance migratory populations existed. Because migrations do not appear to be important in their history, sufficient evolutionary time and the lack of requirement for longer movements may have either resulted in the loss of advanced navigational skills, assuming that these skills were present in the ancestral form, or that pressures to promote their development were never strong enough to do so. Thus a case may be made for differences in orientational abilities between nonmigrating and non-migrating species, but not between migratory and nonmigratory populations of a species.

The presence of redundant cues and of navigational abilities does not imply that these systems are used extensively during the normal movements of individuals. Route memorization and the use of visual or olfactory landmarks, both within a limited home range and during longer migrations, probably play dominant roles under normal conditions. According to Baker's (1978) least-navigation hypothesis, when an animal possesses a navigational repertoire, cues that permit movements with a minimum time investment in locating goals will be used, but the most effective cue may vary according to circumstances.

I was able to add little to the understanding of ontogenetic development of orientation in snakes, but the results lend support to the hypothesis that neonates locate hibernacula by trailing adults. It is also possible that newborn snakes imprint on solar cues available at the birth site. Further research in this area is essential in order to accurately explore this possibility.

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