REPRODUCTIVE ECOLOGY OF FEMALE GARTER SNAKES (_THAMNOPHIS_) IN SOUTHEASTERN BRITISH COLUMBIA.

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ABSTRACT

Most current theories of life history evolution are based on the presumed existence of tradeoffs between reproduction and other activities, whereby increased investment in current reproduction results in a decrease in future contributions to fitness. Often these tradeoffs are framed in terms of costs. However, directly measuring the costs of reproduction for animals in the wild is difficult. An alternative approach is to compare the ecology of reproductive and nonreproductive animals in the same population. Because these animals differ only in their reproductive state, differences in their ecology can be used to identify potential costs and suggest which selective pressures are important in determining their pattern of life history.

I compared the ecology of gravid and nongravid female garter snakes (*Thamnophis sirtalis* and *T. elegans*) from 1988-1990 at the Creston Valley Wildlife Management Area in Creston, B.C.. In particular, I focussed on three main factors that were expected to vary between females in different reproductive conditions: 1) movements, 2) habitat use, and 3) thermoregulation.

Rates of movement of gravid females were low during gestation but increased following parturition until they were similar to those of nongravid females. This pattern is presumed to reflect the fact that gravid females are burdened by the developing embryos and have impaired locomotor ability. A consequence of impaired locomotion may be an increased risk of predation, which might explain the low movement rates of gravid females. However, gravid females were found to thermoregulate with higher mean body temperatures (T_bs) and lower variances than nongravid females and it is also possible that their movements are limited by the need to stay near suitable sites for thermoregulation.

There were significant differences in the habitats used by gravid and nongravid females. Although both groups used areas characterized by high levels of cover (vegetation, rocks, or trees), there were marked differences in the habitat features of the sites selected. Gravid females remained primarily in rocky areas that were relatively rare on the study site. In contrast, nongravid females used a variety of habitats ranging from grasslands to forests. Predator avoidance may be a primary feature of habitat choice for both groups. However, gravid females appear to have an additional requirement for careful thermoregulation, and may be selecting sites that balance both needs.

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INTRODUCTION

Modern life history theory has largely attempted to interpret patterns of life history in terms of tradeoffs in which current investment in reproduction reduces the ability to invest in future reproduction (Tuomi *et al.* 1983, Reznick 1985). Organisms must balance the costs and benefits of a particular mode of reproduction, and are presumed to minimize current costs in order to maximize future contributions to fitness. This implies a compromise in which organisms ultimately may bear costs that appear to be extreme in order to reproduce (e.g. salmon swimming vast distances to reproduce in natal streams and then die). Life histories are coevolved units, and reflect compromises among all of the factors influencing reproduction in an organism (Murphy 1968, Michod 1979). Consequently, detailed study of patterns of reproduction can lead to the identification of the pressures that shape an organism's life history.

Most squamate reptiles exhibit oviparity, but approximately 20% of the extant species are viviparous (Shine 1985). The evolution of reptilian viviparity has received considerable attention over the last 25 years (Neill 1964, Tinkle and Gibbons 1977, Shine 1985) and a number of hypotheses have been put forward to explain its origin. These hypotheses have focussed on presumed differences in the costs associated with oviparity and viviparity. Currently, the leading hypothesis suggests that reptilian viviparity evolved in response to cool climates (Shine 1985). Females of viviparous species maintain their embryos *in utero* and can promote rapid development through behavioral thermoregulation, whereas the eggs of oviparous species would not experience sufficiently high temperatures in cool climates to ensure development before winter (Shine 1987a). Consequently, it has been predicted that gravid females should have higher mean body temperatures (T_b) and/or thermoregulate more precisely than do nongravid females (Charland and Gregory 1990). However, behavioral thermoregulation is presumed to have associated costs that may be either direct, if maintaining a given temperature through shuttling is energetically expensive, or indirect, if basking behavior increases the risk of predation (Huey and Slatkin 1976).

Although thermoregulation may be a central feature of reptilian viviparity, a number of additional consequences of this mode of reproduction have been identified. The physical burden of the developing embryos has been shown to decrease locomotor ability in both lizards and snakes and it has been suggested that this may lead to an increase in predation risk for gravid females (Shine 1980, Seigel *et al.* 1987). However, if viviparity necessitates basking by gravid females, then there may be a conflict between the need to thermoregulate and the risk of predation due to impaired locomotion. One way that animals may reconcile competing needs imposed by reproduction is through habitat selection (Morris 1984a), assuming that sites are available that can simultaneously accomodate these needs.

Another consequence of reptilian viviparity is that gravid females have higher metabolic rates than males and nongravid females (Birchard *et al*. 1984, Beuchat and Vleck 1990), but commonly reduce or cease feeding during gestation (Keenlyne 1972, Murphy and Campbell 1987). Therefore, they are generally emaciated following parturition. They must replenish lost fat reserves before reproducing again (Derickson 1976), which may, in turn, influence the frequency of reproduction of individual females. For northern populations of *Crotalus viridis*, this necessity may result in extended reproductive cycles that exceed four years between litters of young (Macartney and Gregory 1988). Gravid females under semi-natural conditions have been shown to feed during gestation, when food is offered (e.g. Saint Girons 1979, Charland 1987), and the low level, or absence, of feeding observed in the wild may therefore reflect a lack of opportunity imposed by reduced locomotor ability. Behavioral modification offers a mechanism for reducing costs associated with reproduction in reptiles (Brodie 1989), and gravid females may simply forgo their normal foraging behavior because it is incompatible with the needs imposed by the costs of thermoregulation and increased predation risk.

In order to study the consequences of reproduction it is important to be able to separate the effects due to reproduction from characteristics that are common to the population as a whole. This can be accomplished by comparing the ecology of reproductive and nonreproductive females, which should be otherwise similar. I undertook to study this phenomenon in the common garter snake (*Thamnophis sirtalis*) and the western terrestrial garter snake (*T. elegans*). These are suitable species because they are abundant and their ecology has been well studied (e.g. Carpenter 1952, Fitch 1965, Gregory 1977, Larsen 1986, Peterson 1987). In particular, their ecology has been studied in some detail at the Creston Valley Wildlife Management Area (CVWMA) in Creston, British Columbia (Farr 1988), providing invaluable background information.

In this study, I compared the ecology of gravid and nongravid female garter snakes (*T. sirtalis* and *T. elegans*). Specifically, I addressed the following topics:

1) Movements: What is the extent of the reduction in movements of gravid females in comparison with nongravid females? If this reduction is a function of reproduction, do gravid females show an increase in movement to levels similar to those of nongravid females following parturition?

2) Habitat Use: What are the differences in habitat use between gravid and nongravid females? Do the features of habitats used by gravid females reflect constraints imposed by the presumed costs of reproduction (predation risk, thermoregulation)? How do the patterns of habitat use by gravid and nongravid females correlate with the distribution of prey? Are sites used by gravid females located in areas of low prey availability such that foraging during gestation is not possible?

3) Thermoregulation: Do gravid females thermoregulate to higher mean T_bs, and with greater precision, than do nongravid females? If so, does this difference disappear following parturition, as would be predicted if it were simply a consequence of reproduction?

METHODS

Site Description

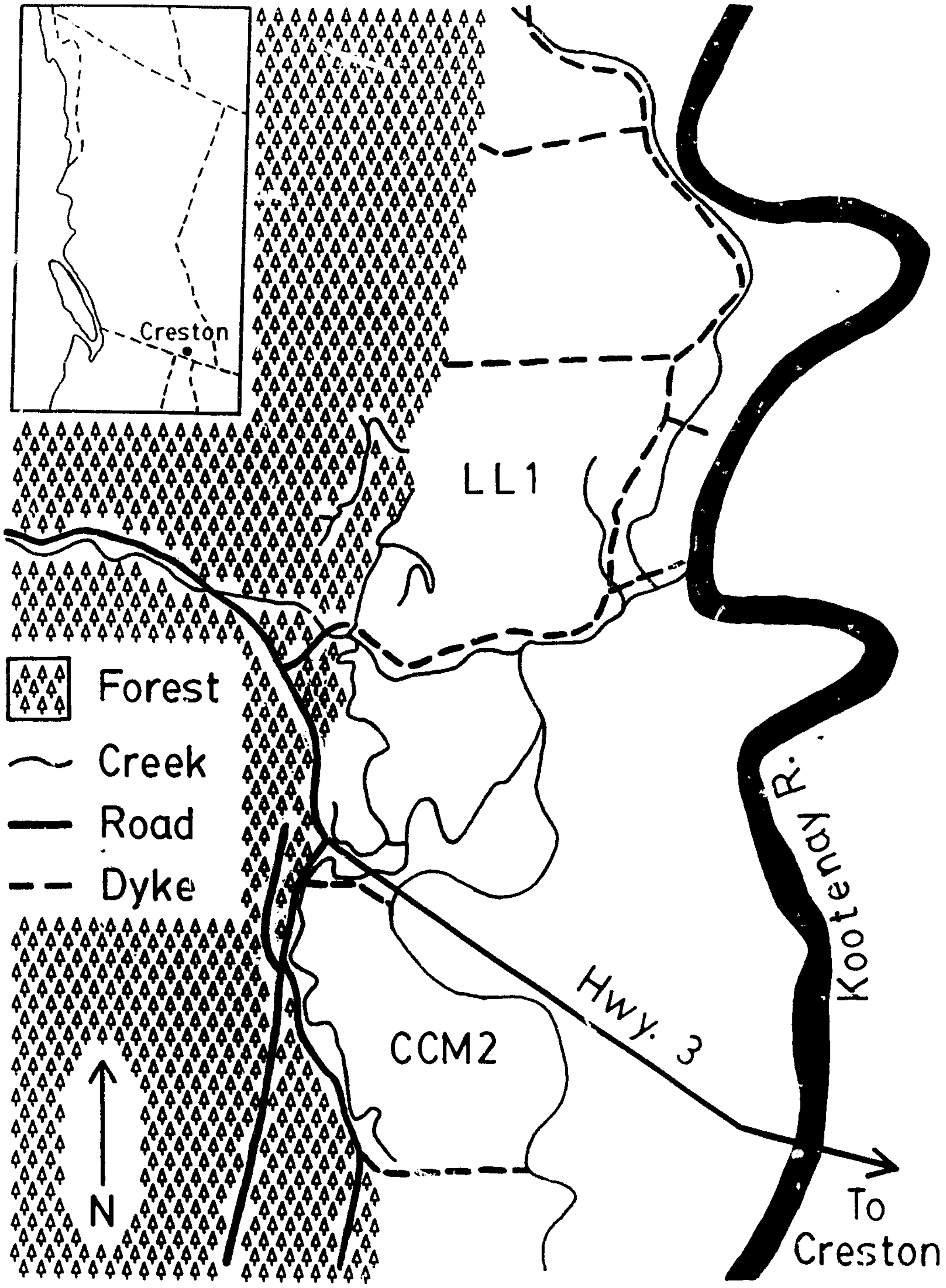
The study was conducted during May-August of 1988/89 and May-September 1990 at the Creston Valley Wildlife Management Area (CVWMA), Creston, British Columbia (49° 6′ N, 116° 31′ W, elevation 597 m). The CVWMA is a 7000 ha wetland area that is managed primarily for waterfowl and contains a variety of habitats ranging from upland forests to substantial marshes (Fig. 1). Much of the area is divided by dykes, and water levels within the ponds are controlled artificially. Details can be found in Farr (1988). Although snakes were collected from a variety of sites throughout the CVWMA, my primary study sites were Corn Creek Marsh Unit #2 (CCM2) and Leach Lake Unit #1 (LL1).

Environmental Characteristics

Habitat Structure and Species Composition

In order to determine the structure and composition of the habitat available in the study area, I mapped Corn Creek Marsh Unit #2 (CCM2) and superimposed a grid with cells 100 m X 100 m, oriented along a north-south axis. The area of CCM2 is approximately 340 ha and there were 330 grid intersections on the map. I randomly selected 110 grid

Figure 1. Map of the Creston Valley Wildlife Management Area showing primary study sites (redrawn from Farr 1988, with permission of the author). LL1 = Leach Lake Unit #1; CCM2 = Corn Creek Marsh Unit #2.

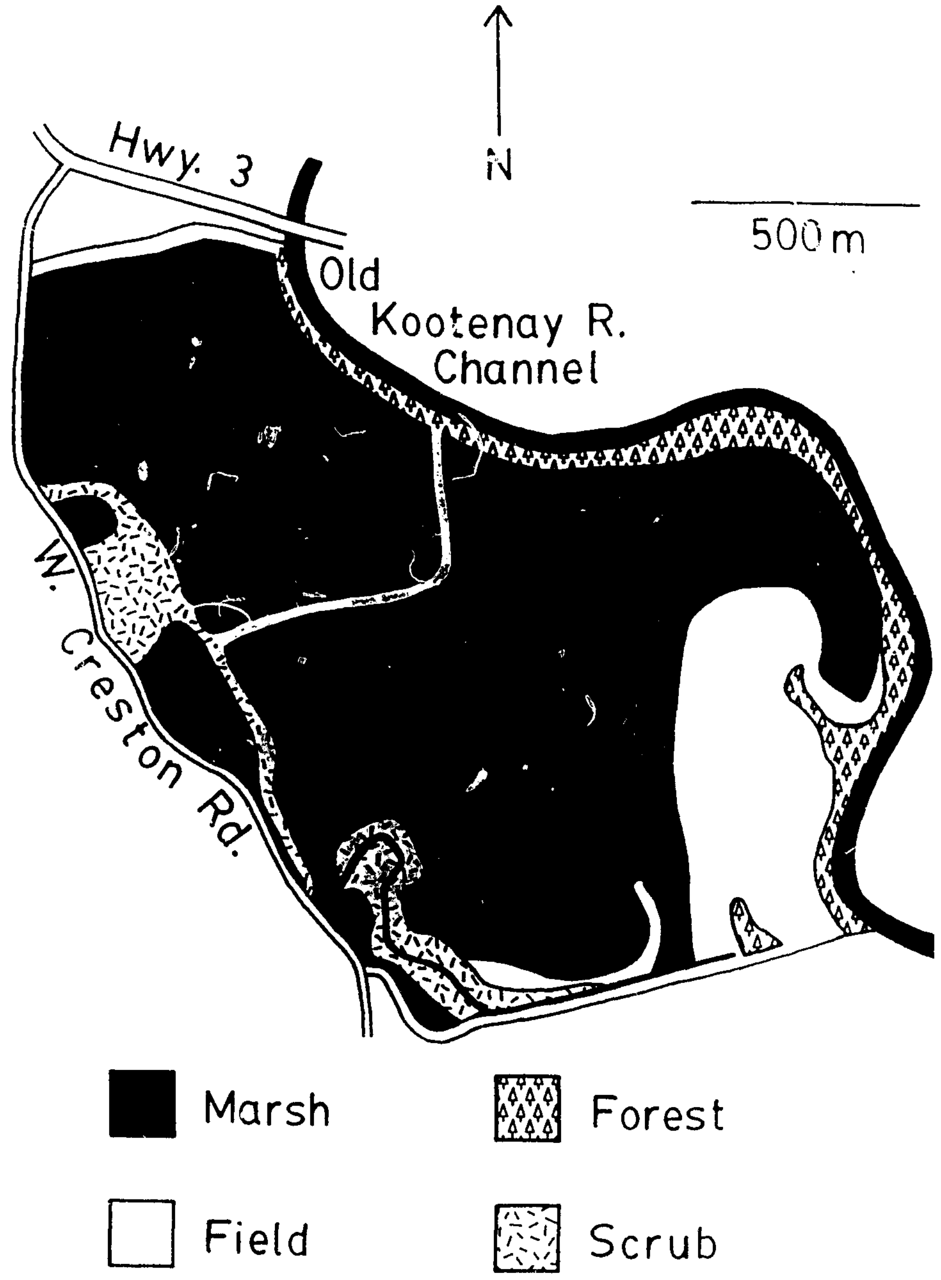

Creston
LL1
CCM2
Forest
Creek
Road
Dyke
N
Hwy. 3
Kootenay R.
To Creston

intersections in the study area to use as habitat sampling points for the duration of the study. The points were selected using the random number generator of the SMART spreadsheet package (Innovative Software, Inc.) to generate x- and y-axis coordinates independently.

Each point was assigned to one of 4 major habitat types: Marsh, Forest, Scrub, or Field. These habitat types were defined subjectively, but reflected the most noticeable differences in habitat within the study site (Fig. 2). All points located in standing water at the time of sampling were designated Marsh and no further data collected. Some points that were in standing water were exposed later in the summer by falling water levels, and data were collected for these points only when they were dry. Forest was defined as any habitat that had trees >8 m tall in an arc of at least 180° around the point. Scrub was similarly defined, but with trees 2-8 m tall. Although the tree height criteria used to define Forest and Scrub were arbitrary, they were sufficient to allow me to assign points unambiguously to one of the two categories. The absence of Forest and Scrub characteristics was used to define Field. In May 1989 I located and flagged all points in the Forest, Scrub and Field habitats.

Habitat features were classified as either fixed (values did not change with year or season) or dynamic (values expected to change with year or season). The

Figure 2. Map of Corn Creek Marsh Unit #2 (CCM2) in May 1989, showing the distribution of the four main habitat types.


N
Hwy. 3
500 m
Old Kootenay R. Channel
W. Creston Rd.
Marsh
Forest
Field
Scrub

variables measured were taken from Reinert (1984a, b) and Weatherhead and Charland (1985) and are listed in Table 1. These measures were arbitrarily selected to cover as many aspects of habitat as possible. In addition, they have been previously reported in the literature, facilitating comparisons. Fixed features were measured once for each point, but dynamic features were measured in the middle of each month of the summer.

Measures of surface cover were taken within a 1 m^2 quadrat with the sampling point located in the southwest corner. In order to measure percentage cover within any quadrat I took a color photographic slide from above using a hand-held camera with a 28 mm wide-angle lens. Slides of each quadrat were projected onto a 10 X 10 square grid and percentage cover determined by counting the number of grid intersections that overlapped the feature of interest (Reinert 1984a). Canopy closure was determined using a 3 cm diameter cross-hair sighting tube (Reagan 1974). I took 50 sightings at random within a 45° cone above the habitat point. The number of sightings in which the cross-hairs overlapped with vegetation was doubled to give a measure of percentage cover.

All distances <50 m were measured directly from each sampling point. Distances >50 m were measured from maps of CCM2 using a HIPAD digitizing board (Bausch and Lomb, Houston Instruments Division, Houston, Texas) and the

Table 1: Descriptions of the habitat features measured. In all cases, the term quadrat refers to a 1 m^2 quadrat at the sampling point.

Feature	Description
Fixed Features	
Rock Cover	Percentage cover of rocks >10 cm in length within a quadrat. Cover estimated from ground level and is irrespective of vegetation that may be growing over the rocks.
Log Cover	Percentage cover of fallen logs (>8 cm diameter) within a quadrat. Cover estimated irrespective of vegetation that may be growing above the log.
Distance to Rock	Distance to the nearest rock >10 cm in length.
Length of Rock	Length of nearest rock >10 cm in length.
Distance to Log	Distance to nearest log >8 cm in diameter.
Diameter of Log	Maximum diameter of nearest log >8 cm in diameter.
Distance to Understory Tree	Distance to nearest understory tree >2 m in height and with a DBH <8 cm.
Species of Understory Tree	Species of nearest understory tree.
Distance to Canopy Tree	Distance to the nearest tree >8 m in height.
DBH of Canopy Tree	DBH of nearest canopy tree.
Species of Canopy Tree	Species of nearest canopy tree.

Table 1: (cont'd)

Feature	Description
Dynamic Features	
Vegetation Cover	Percentage cover of living vegetation (both woody and herbaceous) within a quadrat.
Litter Cover	Percentage cover of dead plant material (includes all woody material except logs, as defined above) within a quadrat.
Herbaceous Vegetation Height	Height of the tallest herbaceous plant within a quadrat.
Dominant Herbaceous Species	Herbaceous species with the greatest percent cover within a quadrat.
Woody Stem Density	Number of woody stems <8 cm in diameter within a quadrat.
Woody Stem Height	Height of the tallest woody stem within a quadrat.
Woody Stem Species	Woody stem species with the greatest percent cover within a quadrat.
Canopy Closure	Percentage cover of vegetation above above the sampling point.
Distance to Water	Distance to the nearest standing water, including ephemeral pools of any size.

BioQuant II software package. The only rocks in the CCM2 study area were located at the roadsides. Consequently, if the distance to the nearest rock was >50 m I used the distance to the nearest roadside. The location of logs was less predictable than that of rocks, and where it was not possible to locate a log within 50 m of a point, I simply recorded it as >50 m.

Thermal Environment

In addition to characterizing the physical habitat available to snakes at the study site, I measured aspects of the thermal environment. Because *T. sirtalis* in this area eat frogs and, to a lesser extent, fish (Farr 1988), I attempted to measure the thermal characteristics of both the aquatic and terrestrial environments.

Water temperatures were taken weekly at 10 sites around CCM2, which were also used for sampling frogs (see **Prey Availability**). Temperatures at each site were recorded within 1 m of shore at a depth of 10 cm using a Yuil DT-10 Platinum Digital Thermometer (Yuil Measures Mfg. Co.). All temperatures were taken within a 1.5 h period in the morning on the day of sampling.

Measuring the potential thermal constraint imposed by water is relatively easy. Ectotherms rapidly take on the temperature of the surrounding water because of its high thermal conductance (Hailey and Davies 1987). However, measuring the appropriate thermal properties of terrestrial environments is a more complex problem because of the effect of heat exchange processes (e.g. conductance, convection, radiation) and factors associated with the animal (e.g. posture) on body temperature (T_b). One approach to measuring available temperatures in terrestrial environments is to use mathematical models that incorporate all of the relevant environmental and animal information and then calculate the T_b of an organism under those conditions (e.g. Porter *et al*. 1975). However, a far simpler method is the use of physical models with thermal properties similar to those of the animal of interest. Such models simultaneously integrate all of the factors influencing T_b in a given situation and provide an unambiguous measure of potential T_b (Bakken and Gates 1975, Walsberg and Weathers 1986).

Depending on how the models are constructed, the values that they provide can give estimates of various thermal properties of the environment. Models that match the physical properties of the animal (reflectance, conductance, *etc*.) can be used to obtain an estimate of Operative Temperature, which is a steady state value for a given set of conditions (Bakken *et al*. 1985). The temperature provided from this type of model should remain constant as long as conditions remain constant. The models that I used in this study were not of this type. By using water filled models I introduced a lag time to the temperature data collected. The temperature of the model at any given time will continue to increase (or decrease), when environmental conditions stabilize, for the duration of the lag time. Although my models did not provide a measure of Operative Temperature, they did match the heating and cooling characteristics of the snakes, which themselves have a lag time in their heating curves. Consequently, what I measured was the Maximum Attainable Temperature (MAT) for an animal remaining in a given site. Models were placed so as to receive sunlight for the maximum amount of time during the day. The only way for a snake to have the same T_b as the model would be for it to expose itself to the sun for the same period of time or to utilize a warmer retreat site; in general, it should not be possible for snake T_b to exceed model temperature during the day.

Models were constructed from 600 mm lengths of 20 mm diameter rubber bicycle inner tubes. The tubes were sealed at one end using silicon sealant and 100 ml of water was added. The open end was then sealed with a cork and coated with silicon sealant. A thermistor probe was inserted approximately 10 cm into the model through a hole drilled in the cork.

The volume of water used in the model was determined empirically by comparison with a dead snake of each species. The model and snakes were placed outside overnight so that their temperatures could equilibrate. The site chosen was an exposed location that would receive sun for the majority of the day. I then took temperature readings, using a digital thermometer attached to thermocouples in the model and snakes, every 15 min for 12-13 h starting at dawn. This technique has been used previously in the construction of snake thermal models (Charland and Gregory 1990).

Models were used to characterize the MAT in two ways. In 1988 and 1989, models were placed in exposed locations in the vicinity of snakes (either free-ranging, or in an enclosure - see **Thermal Relations**) before dawn. Model temperatures were then recorded at 15-min intervals for 24 h starting at 04:00, using a digital thermometer. In 1990, a single model was placed in an exposed location inside the enclosure used in the thermoregulation study. The temperature of the model was recorded every 3 min using an automated data logger (built at the Simon Fraser University Science Workshop) for periods of up to 30 days. In addition, in 1989, I measured differences in available temperature in different microhabitats by recording the temperatures of two models placed 1 m apart. One model was on the ground at a site exposed to sunlight for the entire day (exposed model), while the other model was placed on the ground in deep (approximately 1.5 m tall) grass (covered model).

Prey Availability

The distribution of food resources within a habitat has consequences for the movements and spatial distribution of animals (Brown and Orians 1970), and I considered prey availability to be another component of habitat. The principal difficulty associated with measuring prey availability is the same as for measuring habitat availability: is what is measured as "available" actually available to the animal? At present, there is no way to assess this and, instead, researchers rely (as with habitat availability) on knowledge of the biology of the study species in question to develop methods that provide meaningful information on prey availability. Garter snakes are active foragers (Carpenter 1952, Mushinsky 1987), and I used methods that seemed likely to provide reasonable estimates of prey availability in light of this foraging mode. None of the techniques used for prey sampling were expected to provide an absolute measure of prey abundance or availability. However, they provided an index of availability for comparisons among months and habitats.

Prey abundance was measured for the four most common prey types eaten by the two species of snakes at this site, as determined by Farr (1988): frogs (*Rana pretiosa*), worms (*Lumbricus* sp.), slugs (*Agriolimax* sp.) and voles (*Microtus pennsylvanicus*). The abundance of aquatic frogs was measured by counting the number of frogs encountered while walking ten 100 m transects along the major water courses in CCM2 (Seigel 1984, Reichenbach and Dalrymple 1986). I sampled frogs in the third week of May and then every two weeks until the end of August during both 1989 and 1990. In 1989 I arbitrarily selected transects along the periphery of CCM2, and attempted to space them evenly. However, as water levels declined during the summer, some of the transects disappeared. To eliminate this problem in 1990, I selected transects that lay along permanent water courses. This method of frog sampling is assumed to result in encounter rates correlated with those experienced by foraging garter snakes (Seigel 1984, Reichenbach and Dalrymple 1986). However, this assumption has not been tested.

Sampling for worms was conducted at mid-month of May-August 1989 and 1990, following Raw (1959). A 50 cm X 50 cm area of ground was cleared of vegetation, and 1 l of dilute formalin solution (2.5 ml of formalin in 1 l of water) was poured evenly over it. Worms crawled out of the ground to avoid the irritation of the formalin, were counted and then released nearby. After 15 min, I repeated the procedure. Worms longer than 2 cm relaxed length (i.e. neither contracted nor extended) were counted and assigned to one of 2 size classes: small (2-4 cm) or large (> 4cm). This sampling technique has been found to be an effective method of enumerating worms in the top 20 cm of soil (Raw 1959). Although garter snakes apparently capture worms only in the top few centimeters of soil (Gillingham *et al.* 1990), I assumed that the number of worms enumerated using this method would be correlated with the number of worms available to snakes.

I sampled worms at 10 arbitrarily selected sites in 1989 in order to familiarize myself with the technique. In 1990, I randomly chose 5 sampling sites in both the scrub and forest habitats. I chose 10 sampling sites in the field habitat because it was considerably larger than the other 2 habitat types. In addition, the sites were arranged in 2 intersecting transects at 90° to one another. The arrangement of the transects was such that one transect was parallel to the marsh while the other was perpendicular.

Slugs were enumerated using pit traps constructed of 15 cm diameter aluminum dishes containing 150 ml of beer (Old Style Pilsener, Molson Breweries of Canada, Ltd.) at each sampling site. The traps were filled and then left undisturbed for 3 consecutive nights, after which they were emptied and the slugs counted. I sampled slugs at the same sites as I sampled worms in both 1989 and 1990.

The arbitrary sampling scheme employed in 1989 was used as a preliminary measure of the efficacy of my prey sampling techniques. However, it was not comparable to the more rigorous sampling procedure used in 1990 and I did not attempt to make any quantitative comparisons between the two years.

Vole abundance at CCM2 was determined in 2 ways. Relative population levels for 1988-90 were obtained from researchers working on vole population dynamics at the CVWMA (M. Dehn, pers. comm.). In addition, I attempted to obtain a relative measure of vole activity and distribution in 1990 by walking a 50 m transect at each worm/slug sampling point in the Field habitat. Every 5 m along the transect I checked for fresh vole signs (grass clippings and, to a lesser extent, feces or holes). Transects ran north from the sampling point and were shifted 5 m west each month to avoid resampling along the same lines. Voles typically use grasslands and only rarely use forested areas (Morris 1984a). Consequently, I restricted use of the technique to the Field. Sampling was conducted at mid-month, in conjunction with worm/slug sampling.

I sampled frogs at the end of the the third week of May and afterwards at the end of the first and third weeks of June-August. Sampling of the other prey types was conducted at mid-month of May-August. Slug traps were placed in the same location during each sampling period. Worms were sampled in the same general area each month, but the sampling plots were separated by at least 2 m from previously sampled plots. Vole transects ran north from the sampling point and were shifted 5 m west each month to avoid resampling along the same transect.

Telemetry

Much of the data collected during the course of this study was derived from radiotelemetric monitoring of snakes, which was used to study both movements and body temperature variation. In order to avoid repetition, I will provide details of the technique here rather than in each subsequent section.

The primary assumption of radiotelemetry is that the implantation procedure and subsequent presence of the transmitter inside the body of the animal does not significantly affect the behaviors of interest (Lutterschmidt and Reinert 1990). Although telemetry has been a common technique in the study of snake ecology for the past 20 years (e.g. Fitch and Shirer 1971, Fitch 1987, Weatherhead and Hoysak 1989), and considerable mention has been made of this assumption, there has been remarkably little work done to assess its impact.

For example, it has been suggested that transmitters palpated into the gut or fed to snakes (generally while disguised as food items) affect subsequent behavior (Fitch and Shirer 1971). In particular, ingested transmitters can lead to reductions in movement (Fitch and Shirer 1971) and a thermophilic response in thermoregulation found in many snakes following feeding (Lysenko and Gillis 1980, Naulleau 1983, Lutterschmidt and Reinert 1990).

In order to avoid these effects, transmitters are now commonly implanted surgically either in or outside the body cavity. However, this requires some form of anesthesia, as well as surgery, which must heal; again, the impact of this procedure on snake behavior has been debated (Fitch 1987, Harlow and Shine 1988). Lutterschmidt and Reinert (1990) suggested that surgical implantation of transmitters that are small relative to the size of the snake does not appear to affect the behavior of snakes in long-term studies. Transmitters with masses 10% of snake mass did not have a measurable effect on locomotion in water snakes (*Nerodia*), although transmitters that were 15% of snake mass did (W.I. Lutterschmidt, personal communication). In addition, Charland (1991) presented data that suggested that the surgical implantation of transmitters with masses <10% of snake mass did not adversely affect gestation and parturition in *T. sirtalis* and *T. elegans*. When selecting animals for transmitter implantation in this study, I used only those whose mass was such that transmitters were <10% of snake mass and I feel confident that the behavior of the animals was minimally affected by the technique.

Additional difficulties associated with radiotelemetric studies have been identified. Because of the relatively high cost of individual transmitters, most studies utilize small numbers of individuals. In addition, battery life (directly related to battery size) is generally limited by the need to keep the transmitter small. Consequently, telemetric studies of snakes have generally been characterised by small numbers of animals monitored and by short duration (Shine 1987b). However, these drawbacks are counterbalanced to some extent by the detail of the information collected. For studies of secretive animals, such as snakes, radiotelemetry often offers the only way to obtain data on phenomena such as movement, habitat use, and thermoregulation.

In 1988 and 1989 I used cylindrical transmitters (Custom Telemetry and Consulting Inc., Athens, Georgia) with dimensions 25 X 10 mm (length X diameter). The units had 15 cm whip antennas and weighed approximately 6 g. These transmitters proved to be unreliable and in 1990 I switched to model CHP-2P transmitters (Telonics Canada Inc., Winnipeg, Manitoba). The Telonics transmitters had dimensions of 25 X 10 X 8 mm with 25 cm whip antennas, and weighed approximately 5 g. All transmitters had frequencies in the 150 MHz band and were monitored using either a CE-12 receiver (Custom Electronics, Urbana, Illinois) or an LA12-DS reciver (AVM Instrument Co., Livermore, California) with a hand-held, 3 element Yagi antenna.

The transmitters used in this study were temperature sensitive and I calibrated them in water baths between 12-40 C (1988 and 1989) or between 4-40 C (1990). The CTC transmitters (1988 and 1989) ceased pulsing below approximately 12 C, but would begin again as they warmed up, hence the difference in the calibration ranges between the two models of transmitters used.

Snakes were captured by hand and brought into the laboratory for surgical implantation of transmitters. The animals were anesthetized using methoxyflurane (Pitman-Moore, Inc., Washington Crossing, New Jersey), following the procedure of Aird (1986). A small volume of methoxyflurane was placed on a gauze pad by inverting the bottle once. The pad was then placed in a 750 ml jar with the snake and the jar was closed. Anesthesia was generally complete in under 5 min, as shown by the flaccid appearance of the snake and the lack of a righting reflex. Recovery usually took from 1-2 h, at which time the snakes appeared to be behaving normally.

Once anesthesia was complete, a 1.5 cm vertical incision was made in the snake's side (anterior to the mass of developing embryos in gravid females; approximately halfway along the body in nongravid females) and the transmitter inserted posteriorly. The transmitter was then massaged under the rib cage to lie extraperitoneally. Seating the whip antenna was accomplished by running a 2 mm diameter plastic tube under the skin anterior to the incision and then sliding the antenna into it, so that the flexible antenna ran lengthwise under the snake's skin. The plastic tubing was then withdrawn through a small (<0.5 cm) incision made at its anterior end, leaving the flexible antenna lying straight along the snake's side. All incisions were then closed using 3-0 chromic sutures. The entire procedure typically took 20 min, including anesthesia.

Snakes were maintained in the laboratory for 2-3 days following surgery to allow time for sutures to begin to heal and to ensure that there were no lingering effects of anesthesia or other postoperative complications. All animals were subsequently released on sunny mornings so that they would have ample time to find suitable habitat before nightfall.

Movement and Habitat Selection

Movements and habitat utilization are intimately related and information on movement patterns must be complemented with information on habitat use in order to interpret either one effectively (Macartney *et al.* 1988). To test hypotheses concerning the interaction between movement and habitat use it is necessary to demonstrate that the animals are using their environment in a nonrandom manner. This leads to a fundamental difficulty in studies of habitat use: how to define "available" habitat (Thomas and Taylor 1990). To date, studies of habitat use have relied on largely subjective selection of habitat variables, with researchers making decisions based on a knowledge of the basic biology of the animals in question (e.g. Reinert 1984a, 1984b, Weatherhead and Charland 1985, Crabtree *et al.* 1989, Unsworth *et al.* 1989).

Once habitat variables have been chosen, there remains the difficulty of making appropriate comparisons between habitat use and availability. Many habitat features are dynamic and change with season and many studies have demonstrated seasonal changes in habitat use (Shine and Lambeck 1985, Paulissen 1988, Thompson and Fritzell 1989, Castilla and Bauwens 1991). It is necessary to account for these changes in order to detect meaningful patterns of habitat use.

Finally, the methods used to determine habitat use may also introduce bias into the analysis. In order to determine what habitat an animal is using it is first necessary to locate it. Studies of habitat use that rely on opportunistic sightings or captures will almost certainly be biased in favor of habitats where the animals are most visible or easily caught (Weatherhead and Charland 1985, Shine 1987b, Burger and Zappalorti 1988). Radiotelemetry offers a method of obtaining unbiased information on habitat use, because the animal's location can be determined in all habitats. However, bias may still be introduced if telemetric locations systematically include particular habitat features. As an example, if animals are consistently located late in the day, the resulting pattern of habitat use may reflect features important in determining nighttime retreat sites, rather than habitat use during foraging. Clearly, it is necessary to have some knowledge of the activity patterns of the study organism (both diurnal and seasonal) before collecting data on habitat use, and to be aware of the limitations imposed by the sampling scheme.

Data on movement and habitat selection were collected in each year from free-ranging snakes, released at their sites of capture following transmitter implantation. No data were collected for 2-3 days following release in order to allow the snakes to resume their normal behavior. Snakes were then typically located between 1000-1600 every 2-3 days and their locations flagged. Once a snake had left a location I returned to the point and collected habitat data as described above (see **Habitat Structure and Species Composition**), usually within one week.

Snakes are well known for spending relatively long periods of time in single locations (e.g. Weatherhead and Charland 1985). Consequently, I defined two measures of movement rate.

Overall Movement Rate:

$$\text{OMR} = (\Sigma \text{ distances moved})/\text{No. of days in interval}$$

Actual Movement Rate:

$$\text{AMR} = (\Sigma \text{ distances moved})/\text{No. of days movement occurred in interval}$$

By definition, AMR cannot be smaller than OMR, and the two measures would be equal only if the snake moved on every day of the interval. I found it necessary to use both of these measures of movement rate because I was unable to monitor snakes daily.

I did not attempt to collect movement and habitat data from males of either species because the number of transmitters available was relatively small and males of both species were almost always too small for transmitter implantation. Furthermore, the consequences of reproduction are best studied by comparing gravid and nongravid females, which, except for reproduction, should be otherwise similar. To compare the proportion of time spent moving by gravid and nongravid females, I used the ratio of the number of days spent moving to the total number of days of monitoring (the denominators of AMR and OMR, respectively). Because snakes were typically located every 2-3 days, I have assumed that an animal whose position changed actually moved on all days between consecutive locations. Although this assumption is debatable, it should provide a rough index of the maximum proportion of time spent moving by gravid and nongravid females.

Finally, I calculated the area of the Minimum Convex Polygon enclosing the locations of gravid females using the Micro-computer Programs for the Analysis of Animal Locations (McPAAL; Stuwe 1987). I performed these calculations only for gravid females because the locations used by these animals were typically clustered and the Convex Poylgon would give a reasonable estimate of the area actually used. Locations used by nongravid females were not generally concentrated in particular areas and measurement of the Convex Polygon would not give a useful measure of the area used by these animals.

Thermal Relations

It has long been recognized that, although they derive their T_b from the heat of the surrounding environment, ectotherms are not simply passive indicators of environmental temperature. Instead, many regulate their T_b via behavioral means. However, demonstrating that an ectotherm is actually thermoregulating can be a complex problem. A given T_b may be a consequence of some other activity (e.g. foraging, mate searching) rather than an active choice. In spite of these difficulties, it is largely accepted that many ectotherms frequently thermoregulate. Studies have shown that many species of snakes select particular characteristic temperatures (the preferred temperature) under laboratory conditions. In addition, these preferred temperatures have been found to agree with the T_b's of animals measured in the field (e.g. Peterson 1987, Rosen 1991) and with the optimal temperatures for a number of physiological processes (e.g. Stevenson *et al.* 1985).

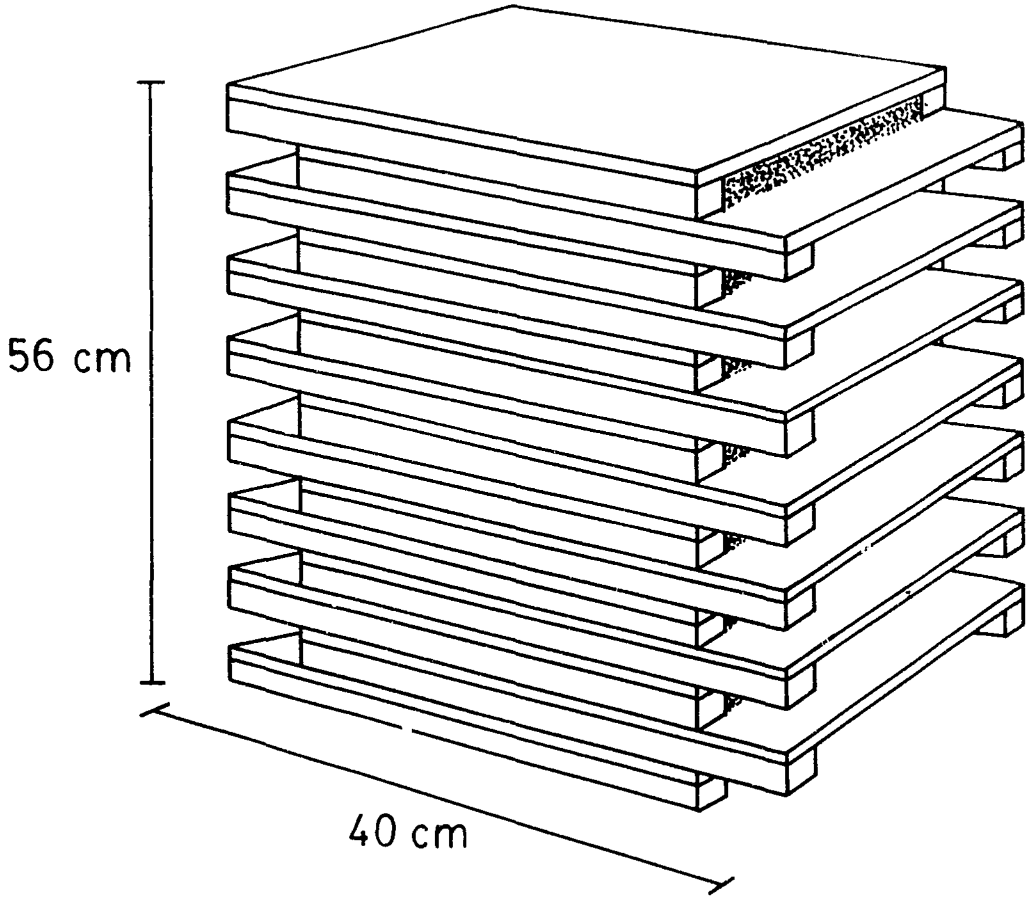
In this study, I accepted as evidence of thermoregulation the stability of T_b in the face of varying environmental temperatures, as measured by thermal models. In addition, the presence of predictable, stereotyped patterns of T_b variation in response to particular sets of environmental conditions was considered strong evidence for thermoregulation by these snakes. The most commonly reported pattern of this type is the "plateau" pattern described by Peterson (1987), in which T_b is low at night, rises rapidly after sunrise and is then maintained at a relatively stable value for the rest of the day.

In 1988 I studied thermal relations in free-ranging snakes. After transmitter implantation, the snakes were released at their sites of capture and allowed 2-3 days to resume their normal behavior. At 0330 on sampling days, I selected a site close enough to the animals to pick up their transmitter signals clearly, but not close enough to disturb them (typically 50 m). In order to measure the maximum available temperature for comparison with snake body temperatures (T_b) I placed a thermal model in an exposed location nearby. Temperatures were recorded at 15 min intervals, for the model and all snakes whose transmitters could be monitored, for 24 consecutive hours starting at 0400.

In order to maximize the number of snakes whose T_b's could be monitored simultaneously, I studied thermal relations of snakes in an enclosure in 1989 and 1990. The enclosure was located at LL1 in an open area beside a road that provided ease of access, both for construction and for subsequent data collection. Human disturbance of the site was minimal because it was situated approximately 2 km from the public portion of the CVWMA, with access controlled by locked gates.

The enclosure was 6 X 6 m and constructed of fine mesh wire screening. The screen was buried 10 cm and attached to wooden stakes placed at 2 m intervals around the perimeter of the enclosure. The habitat within the enclosure was almost exclusively tall grass and, in order to provide a more diverse selection of microhabitats, I modified the habitat available by creating rock and brush piles, and placing a log inside the enclosure. In addition, I cleared some of the grass to provide open, sandy areas. The last modification involved burying a wooden box 40 X 40 X 50 cm (L X W X HT) composed of 14 overlapping levels that would allow a snake access to cool temperatures up to 50 cm below ground (Fig. 3). A 30 X 30 X 15 cm plastic pan was buried to its rim in the enclosure and refilled as necessary to provide water *ad libitum*. Food was not provided, because I had no way of obtaining sufficient quantities of potential prey items, and because I wanted to minimize this influence.

Figure 3. Diagram of the box constructed to provide access to subterranean thermal environment in the enclosure.

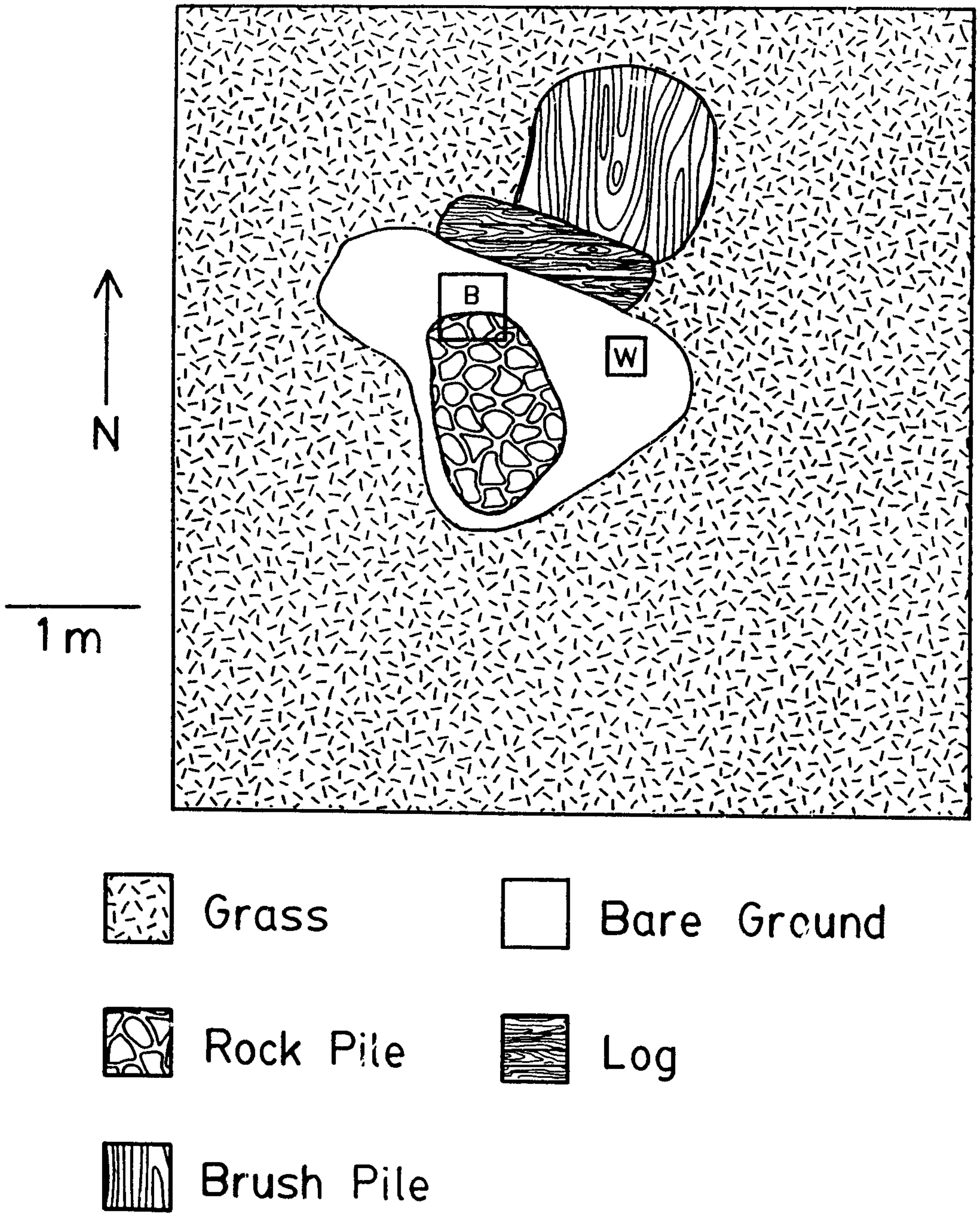

56 cm
40 cm

However, in both 1989 and 1990, snakes were found to have consumed rodents while confined in the enclosure, suggesting that at least some prey were available. The distribution of the various microhabitat types within the enclosure is shown in Fig. 4.

As with the free-ranging animals, I allowed the snakes 2-3 days to acclimatize in the enclosure before starting to collect data. In 1989, I collected data from snakes in the enclosure in the same way as for free-ranging animals in 1988. However, in 1990 I collected data using a DATACOL automated data aquisition system (AVM Instrument Co., Livermore, California). The system is composed of a Laser 128 computer (Video Technology Computers Inc., Northbrook, Illinois) and software, which control an LA12-DS receiver, with all components drawing power from a 12 V automotive battery. The equipment was housed in a waterproof box located 5 m from the enclosure. The system was set up to collect data at 15 min intervals, starting at a specified time, and write the data to disk.

In order to test for differences in thermoregulation between gravid and nongravid females (or between species), it is first necessary to define the circumstances under which such a comparison is appropriate. Clearly, all of the animals under consideration must have the opportunity to thermoregulate freely, and failing to account for this will bias the comparison towards not detecting differences. For

Figure 4. Top view of the enclosure used to study garter snake thermal relations, showing the distribution of various habitat components. B = box, W = water dish.


B
W
N
1 m
Grass
Bare Ground
Rock Pile
Log
Brush Pile

this reason, I restricted my analysis of thermoregulation in gravid and nongravid females to plateau periods on days when model temperatures were extremely high. This provided some control over environmental variation, because the days were thermally similar, and ensured that the animals were not limited by low environmental temperatures.

Statistical Methods

All mean values are shown ±1 standard deviation, unless otherwise noted. Means were compared using ANOVA and, when significant differences were detected, I used the GT2 method for unplanned comparisons (Sokal and Rohlf 1981) to determine which pairs of means were different. This method is graphical and relies on the computation of confidence limits around each mean. Pairs of means with nonoverlapping confidence limits were considered to be significantly different.

Movement data were collected from relatively small numbers of animals and for some comparisons the differences in sample variance were too large to justify a parametric test. In such cases I used the Mann-Whitney U test (Zar 1984).

Body temperature data, collected at 15 min intervals from the same animal, are obviously not independent. I therefore used repeated-measures ANOVA to account for nonindependence within days. However, individual animals dropped in and out of the study because of transmitter problems and I was unable to account for repeated measurements on the same animals among days in each summer. Consequently, I treated the data collected each day as independent, regardless of whether some, or all, of the animals had been present previously. Failure to account for this source of variation should result in a more conservative test (Keppel 1973).

Proportions were transformed, prior to analysis, using a modified arcsine transformation (equation 14.5, Zar 1984). It has been suggested that the standard arcsine transformation is not suitable for extreme values (i.e. those around 0.0 or 1.0) and that this modification provides better results under these circumstances (Zar 1984). Because my data contained numerous values in these regions I employed this transformation. Comparisons of proportions were made using a Z-test (Zar 1984) if there were only two. However, in situations in which there were more than two proportions to be compared, I used the log-likelihood ratio (G) method, followed by a Tukey test to identify pairs of proportions that were different (Zar 1984).

Data were analysed using SYSTAT 4.1 (Wilkinson 1988). For all statistical tests, a minimum significance level of $\alpha=0.05$ was used.

RESULTS

Weather Patterns

Virtually all aspects of ectotherm biology are influenced to some extent by temperature. Thus, information on the weather patterns during the study may be important in evaluating the observed patterns, particularly among years.

The mean daily maximum and minimum temperatures for May-August of 1988 (Fig. 5), 1989 (Fig. 6), and 1990 (Fig. 7) did not appear to differ appreciably from the 30 y average values (Environment Canada 1982). However, the 30 y averages have no measure of variation associated with them, so comparisons are somewhat subjective and based on the 95% Confidence Limits placed on the 1988-1990 data. A 2-way ANOVA (year by month) on mean daily maximum temperature showed no significant difference among years (F=0.900, df=2, 357, p=0.408). However, months differed significantly (F=71.388, df=3, 357, p=0.000), and there was a significant year by month interaction (F=3.588, df=6, 357, p=0.002). A similar analysis of mean daily minimum temperatures yielded the same patterns. Years were not significantly different (F=0.240, df=2, 357, p=0.786), but both the effect of month (F=92.748, df=3, 357, p=0.000) and the interaction term (F=4.277, df=6, 357, p=0.000) were significant. Therefore, the pattern of inter-month variation in temperature differed among years.

Figure 5. Daily maximum and minimum temperatures at Creston, B.C. for 1988. Means are shown ±95% confidence limits.

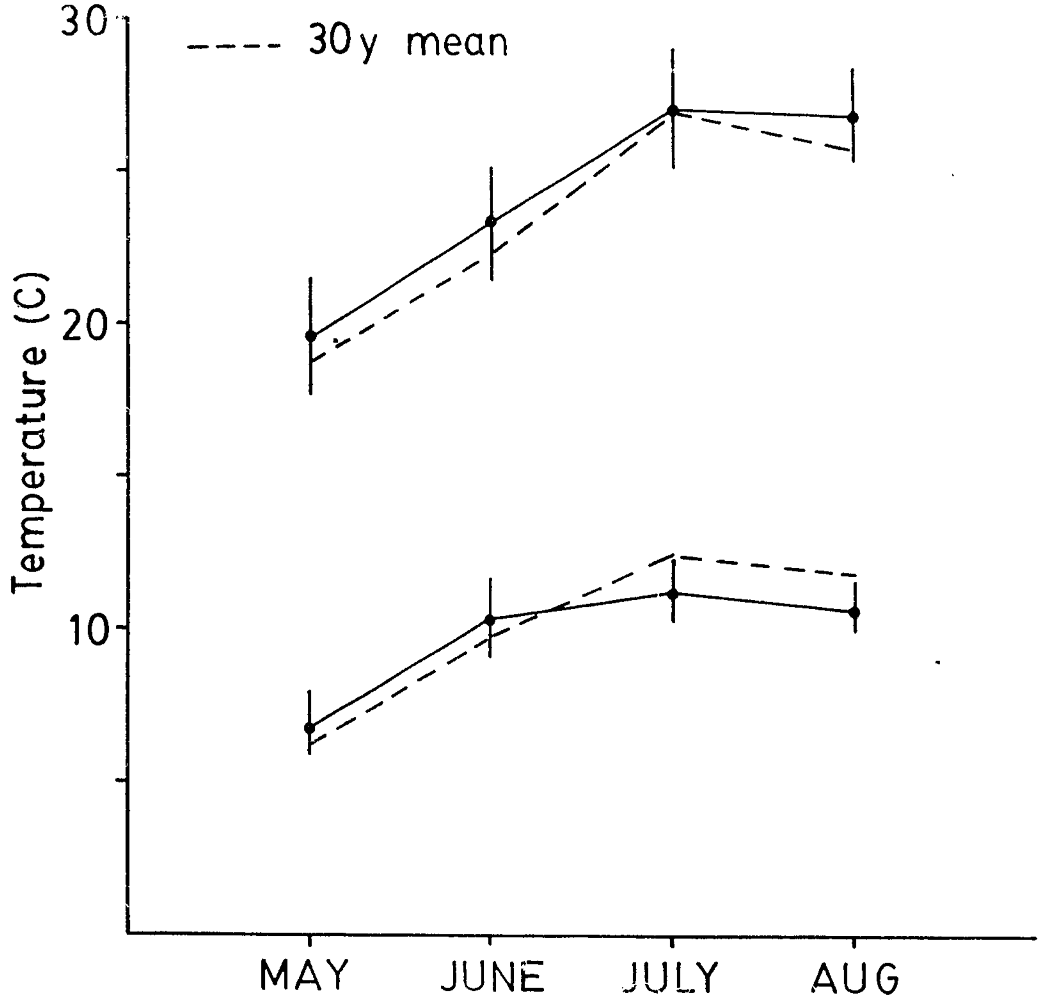

30y mean
Temperature (C)
30
20
10
MAY
JUNE
JULY
AUG

Figure 6. Daily maximum and minimum temperatures at Creston, B.C. for 1989. Means are shown ±95% confidence limits.

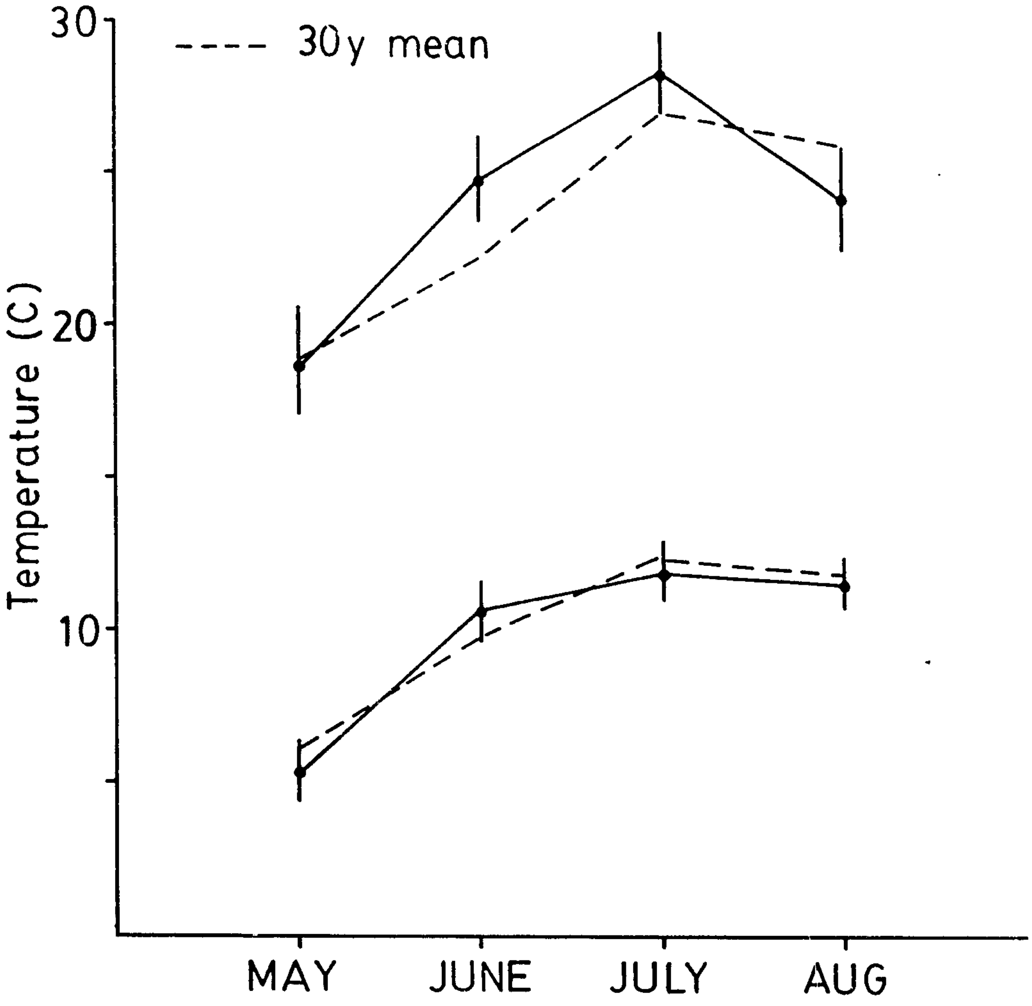
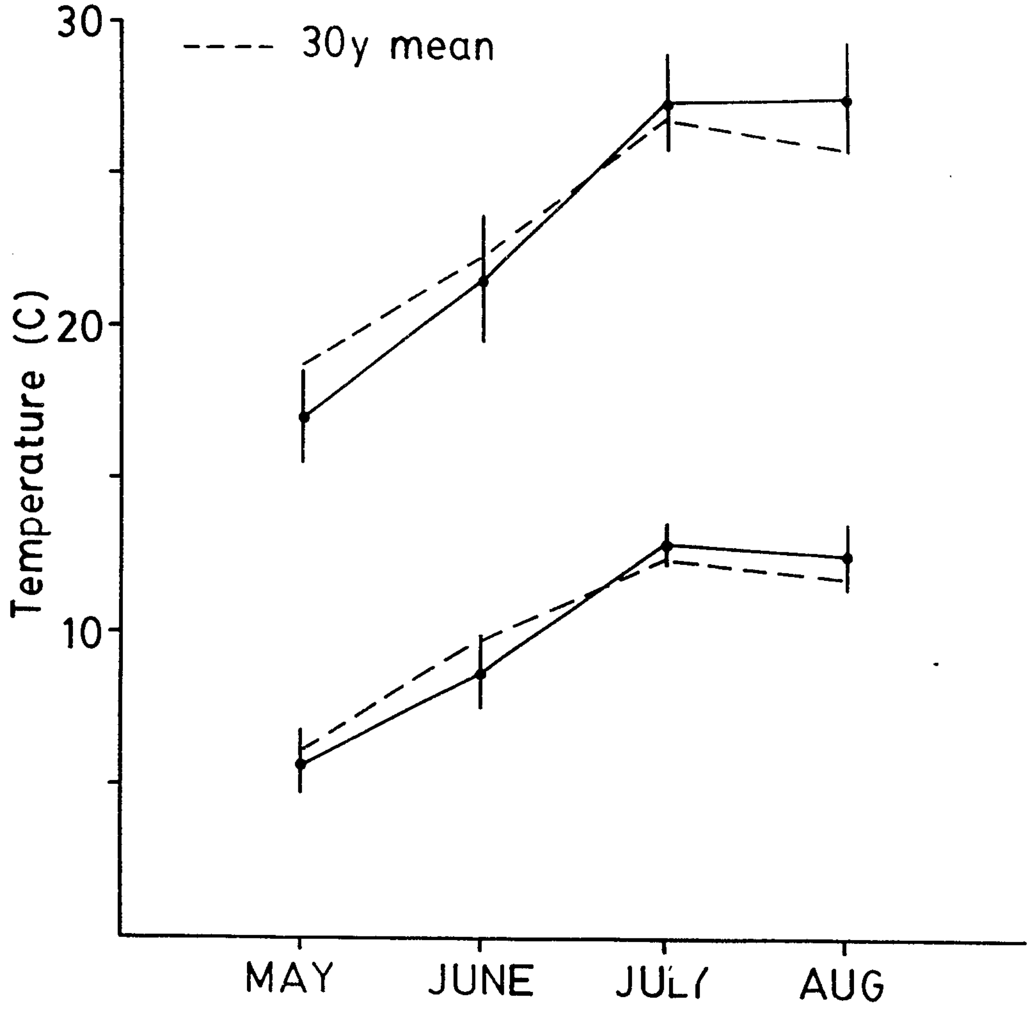

30y mean
Temperature (C)
30
20
10
MAY
JUNE
JULY
AUG

Figure 7. Daily maximum and minimum temperatures at Creston, B.C. for 1990. Means are shown ±95% confidence limits.


30y mean
Temperature (C)
30
20
10
MAY
JUNE
JULY
AUG

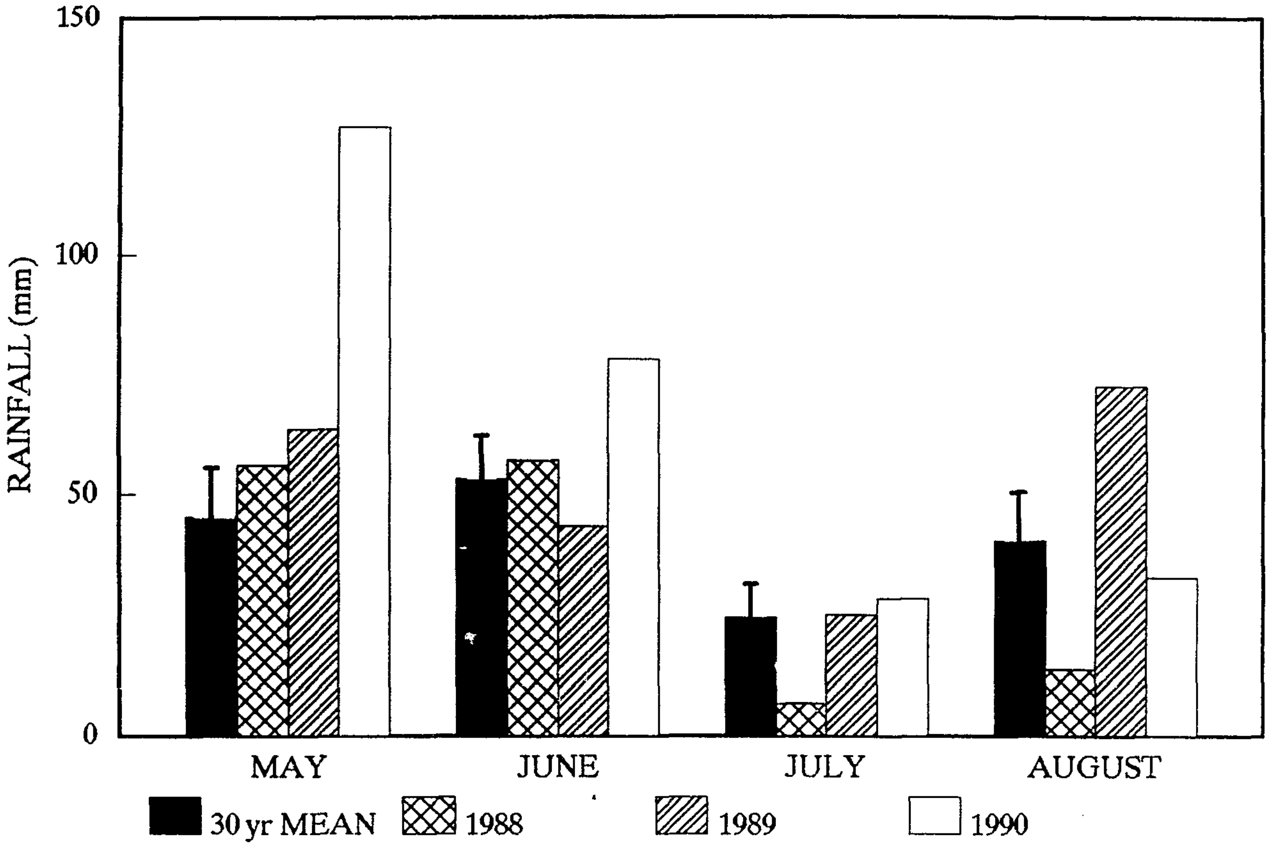
Total monthly rainfall during the summers of 1988-90 ranged from 7.0 mm (July 1988) to 126.8 mm (May 1990). Monthly rainfall patterns were quite variable from year to year (Fig. 8). May appeared to be wetter than average in all 3 summers, but particularly so in 1990. In addition, August 1989 and June 1990 had higher rainfall than average. All of the other months were similar to the 30 y mean values with the exception of July and August 1988, and June 1989, which were drier. Comparisons are again subjective, and based on the 95% confidence limits associated with the 30 y averages.

A 2-way ANOVA (year by month) on mean daily rainfall from 1988-90 revealed significant differences among years (F=3.092, df=2, 357, p=0.047) and among months (F=5.994, df=3, 357, p=0.001). However, the interaction term was not significant (F=1.657, df=6, 357, p=0.131).

Movement

I collected movement data from 15 free-ranging snakes between 1988-90. The sample consisted of 10 gravid females (5 *T. elegans*, 5 *T. sirtalis*) and 5 nongravid females (3 *T. elegans*, 2 *T. sirtalis*). However, two of the nongravid females (both *T. elegans*) provided only a single location before they were lost (one to transmitter failure and the other to predation) and so did not provide data on movement.

Figure 8. Monthly rainfall data for May-August at Creston, B.C.. Error bars are 95% confidence limits for 30 y means.

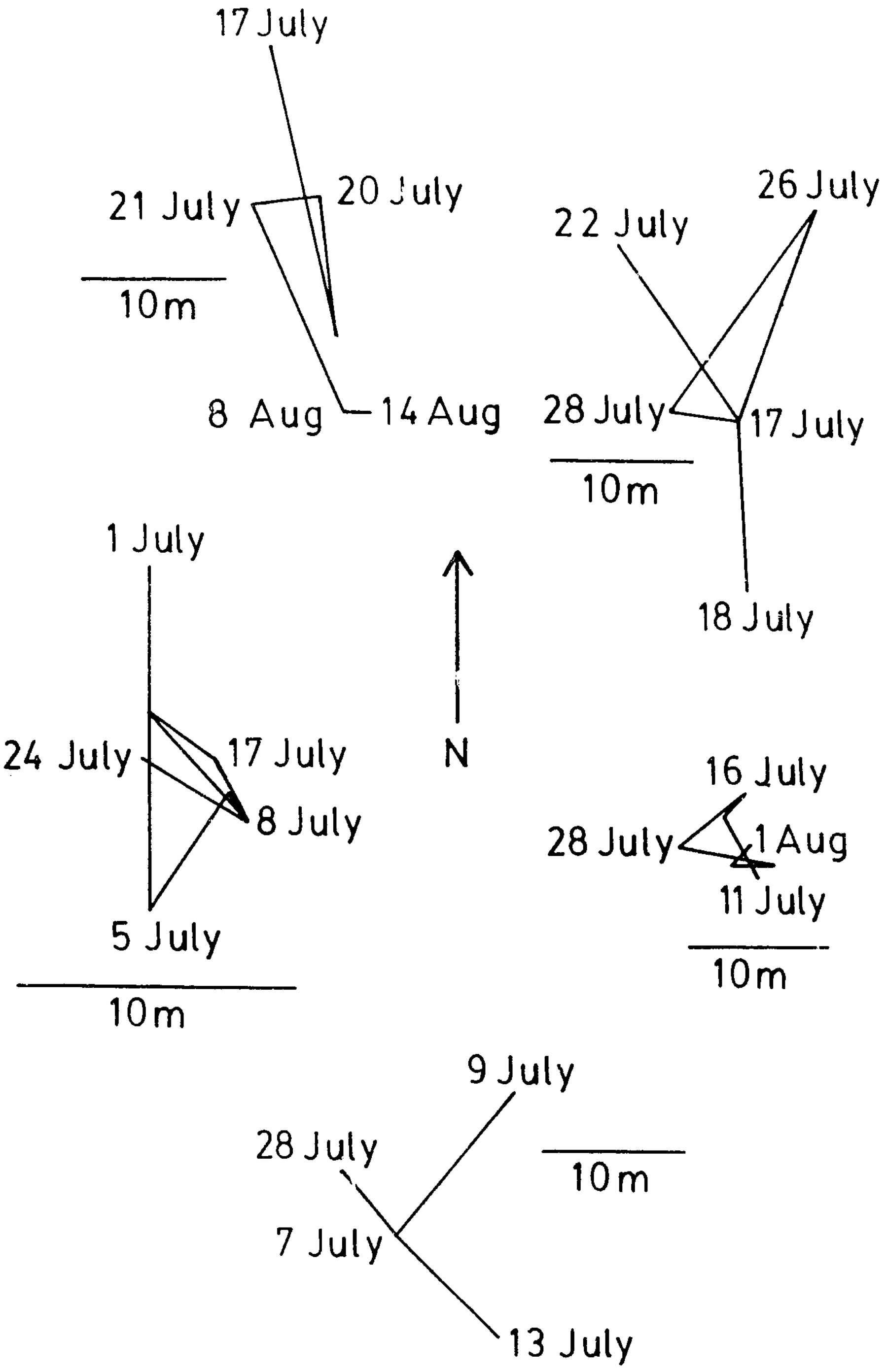

150
100
50
0
RAINFALL (mm)
MAY
JUNE
JULY
AUGUST
■ 30 yr MEAN
▩ 1988
▨ 1989
☐ 1990

Movements by gravid females following parturition were included with those of nongravid females in all analyses. I pooled the data for these snakes because both groups were "not gravid" and, thus , distinct from the animals carrying embryos. Movement rates by nongravid females (OMR: 17.4±14.8 m/day; AMR: 23.4±13.2 m/day; n=3) were lower than for post partum females (OMR: 38.7±32.5 m/day; AMR: 40.9±31.1 m/day; n=4), but the difference was not significant (OMR: Mann-Whitney U=9, p>0.05; AMR: U=8, p>0.05). Post partum females were easily identified by their emaciated condition and I included with the data from nongravid females only those movements obtained following visual confirmation of parturition. The average duration of monitoring for an individual was 32.3±15.5 days (range 9-63 days). Snakes were located a total of 222 times during the study, a success rate of 99.6%.

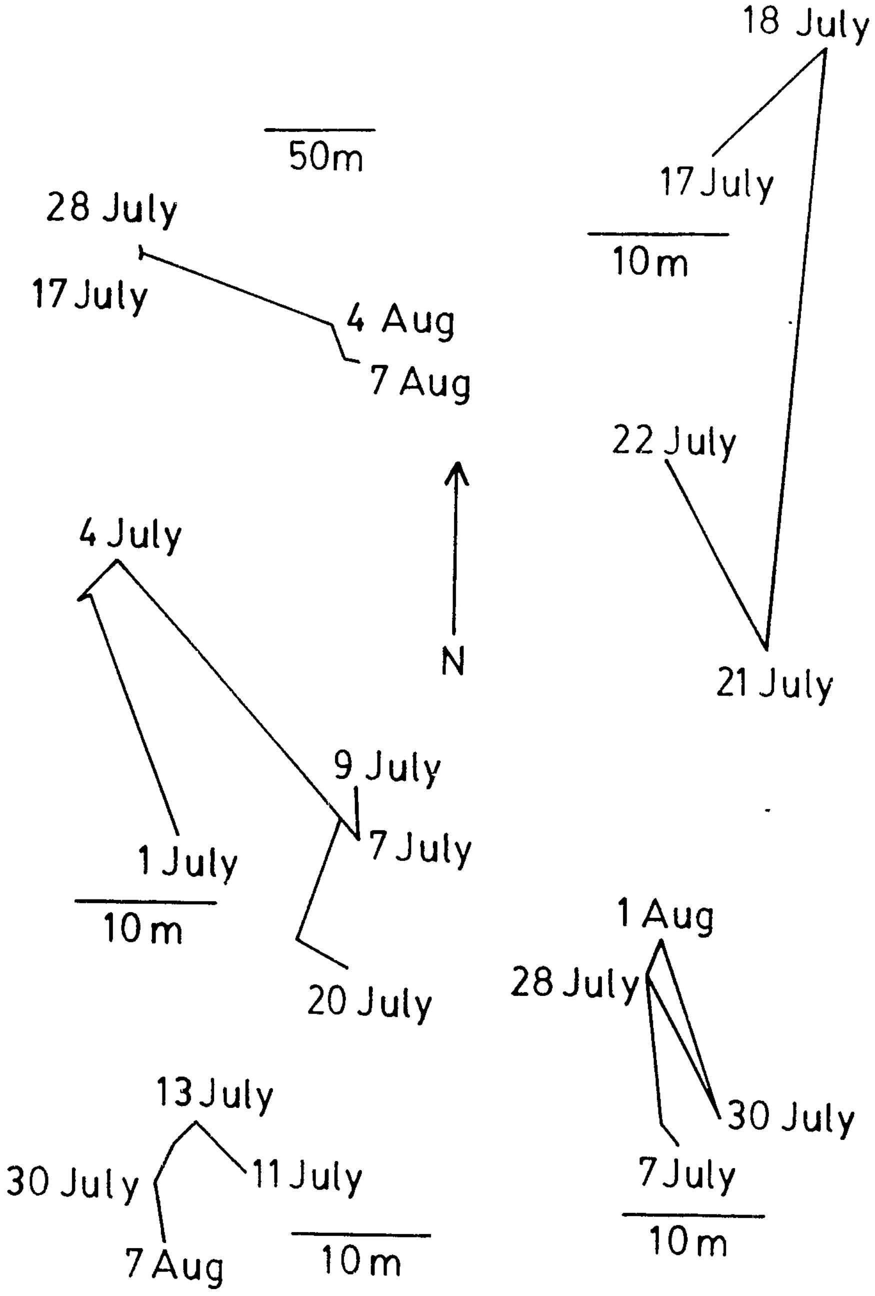
Gravid females of both species moved very little during gestation (Fig. 9) and occupied relatively small areas for the majority of that time. The average area (Minimum Convex Polygon) occupied by a gravid female was 95.5±95.2 m^2. Because all gravid females were monitored for approximately one month, I felt justified in pooling the area measures and presenting the mean value. There was considerable variation in these areas, with some snakes spending as much as one month in an area 0.25 m^2 (a 3 m section of roadside), while others used areas as large as 243.0 m^2. In contrast, the

Figure 9. Movement patterns of gravid *T. elegans* (A) and *T. sirtalis* (B). The dates on the figure include the first and last date the animal was located and 2-3 additional dates to provide temporal scale.

A. *T. elegans*


17 July
21 July
20 July
10m
8 Aug
14 Aug
22 July
26 July
28 July
17 July
10m
18 July
1 July
24 July
17 July
8 July
5 July
10m
N
16 July
28 July
1 Aug
11 July
10m
9 July
28 July
10m
7 July
13 July

B. *T. sirtalis*

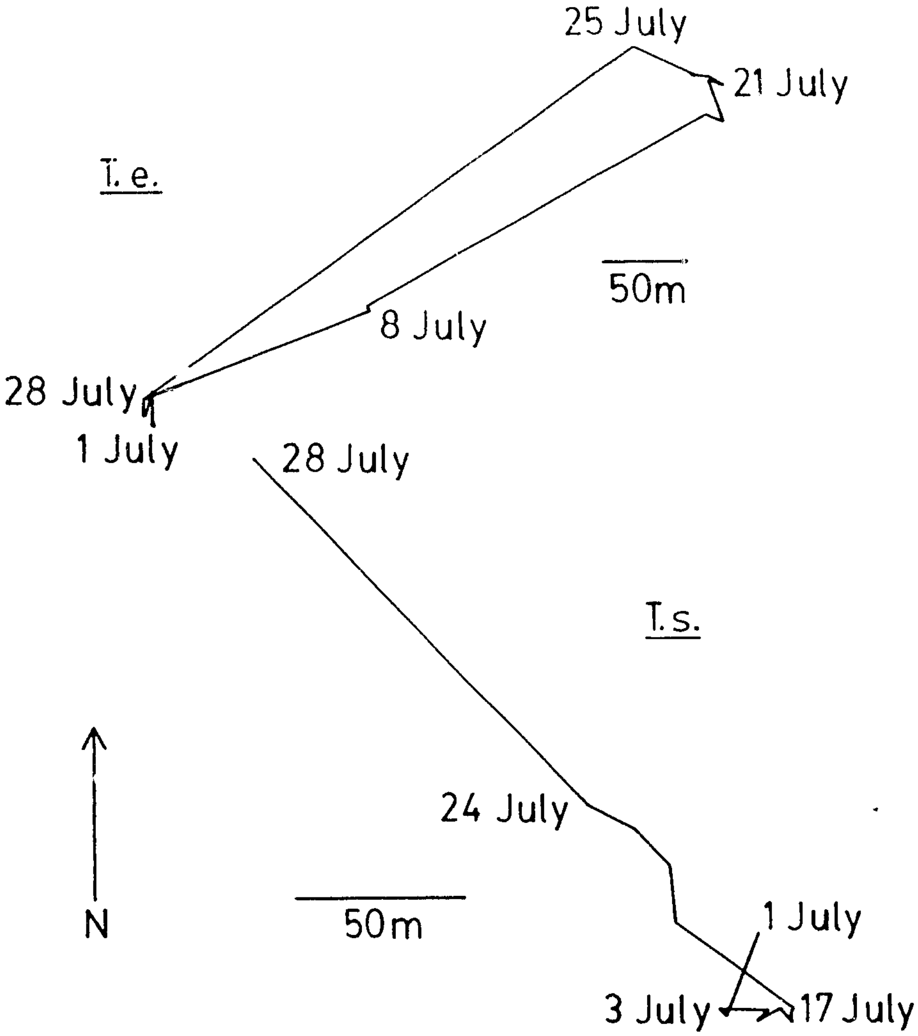

18 July
17 July
10 m
21 July
22 July
50m
28 July
17 July
4 Aug
7 Aug
N
4 July
1 July
9 July
7 July
10 m
20 July
1 Aug
28 July
30 July
7 July
10 m
13 July
30 July
11 July
7 Aug
10 m

movement patterns observed among nongravid females were characterized by relatively long movements followed by intervals of shorter movements (Fig. 10). Following parturition, the pattern of movement among gravid females was very similar to that of nongravid females (Fig. 11).

Movement rates of gravid females were low, whether they were expressed as OMR (2.5±1.7 m/d) or AMR (6.4±6.7 m/d), and the difference between OMR and AMR, although large, was not significant (t=1.791, df=18, p=0.090). In addition, movement rates of gravid *T. sirtalis* (OMR: 2.7±2.1 m/day; AMR: 8.3±8.9 m/day; n=5) and *T. elegans* (OMR: 2.2±1.4 m/day; AMR: 4.4±3.3 m/day; n=5) did not differ significantly (OMR: Mann-Whitney U=12, p>0.05; AMR: U=10, p>0.05). Nongravid females had much higher movement rates (OMR: 29.5±27.0 m/d; AMR: 33.4±25.1 m/d; n=7) and, again, there was no significant difference between OMR and AMR (t=0.278, df=12, p=0.786). There were too few nongravid *T. elegans* to make an interspecific comparison. However, there were no obvious differences between nongravid females of the two species. Although OMR and AMR were not significantly different for gravid females, the difference was large enough that I felt it advisable to keep the two measures separate in subsequent analyses for both gravid and nongravid females.

The longest distance moved by a gravid female was 93 m over 2 days (*T. sirtalis*, 1988), whereas the longest

Figure 10. Movement patterns of nongravid garter snakes. Dates on the figure include the first and last date the animal was located. Additional dates are provided for temporal scale.


25 July
21 July
T. e.
50m
8 July
28 July
1 July
28 July
T.s.
24 July
N
50m
1 July
3 July
17 July

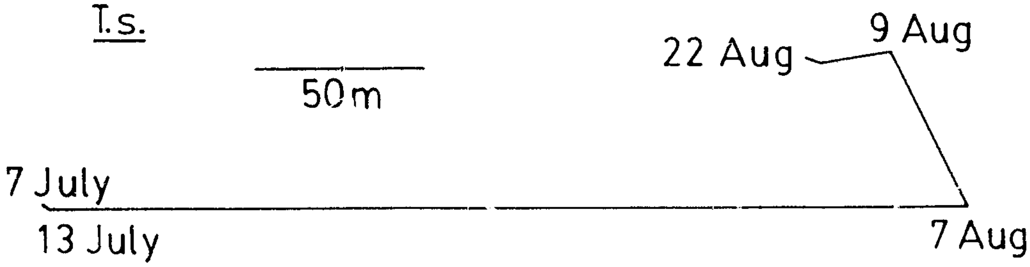
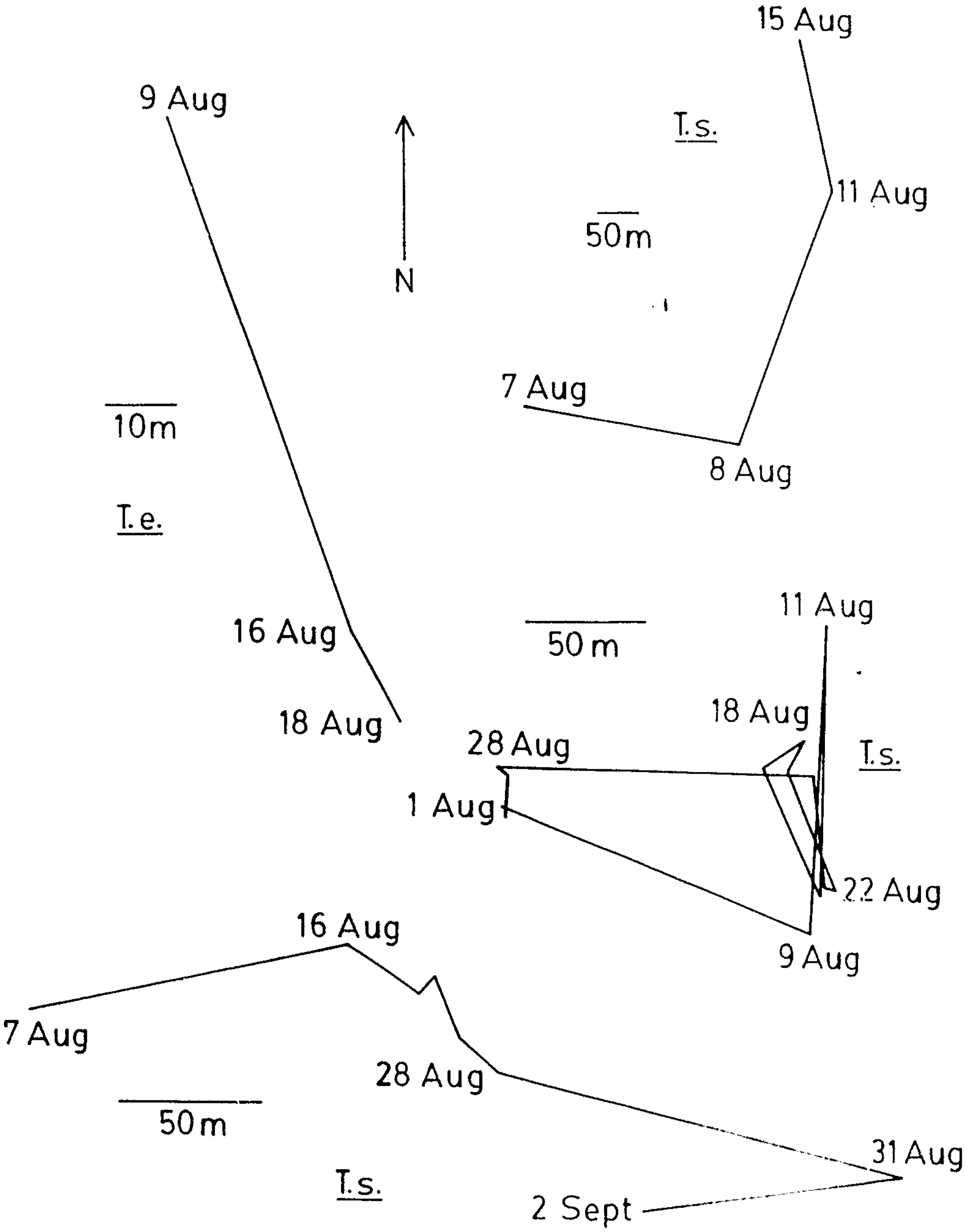

T.s.
9 Aug
22 Aug
50m
7 July
13 July
7 Aug

Figure 11. Movement patterns of post partum garter snakes. Dates on the figure include the first and last date the animal was located. Additional dates are provided for temporal scale.


15 Aug
9 Aug
T.s.
11 Aug
50m
N
7 Aug
10m
8 Aug
T.e.
11 Aug
16 Aug
50 m
18 Aug
18 Aug
T.s.
28 Aug
1 Aug
22 Aug
16 Aug
9 Aug
7 Aug
28 Aug
50 m
31 Aug
T.s.
2 Sept

distance moved by a nongravid female was 236 m in a single day (*T. sirtalis*, 1988). Because nongravid females moved long distances followed by periods of short movements, the variances associated with both OMR and AMR were very high and condiderably different from those of gravid females. Consequently, I compared movement rates between gravid and nongravid females using Mann-Whitney U tests. Nongravid females moved at higher rates than gravid females, whether measured as OMR (U=0, p=0.001) or AMR (U=4, p=0.002).

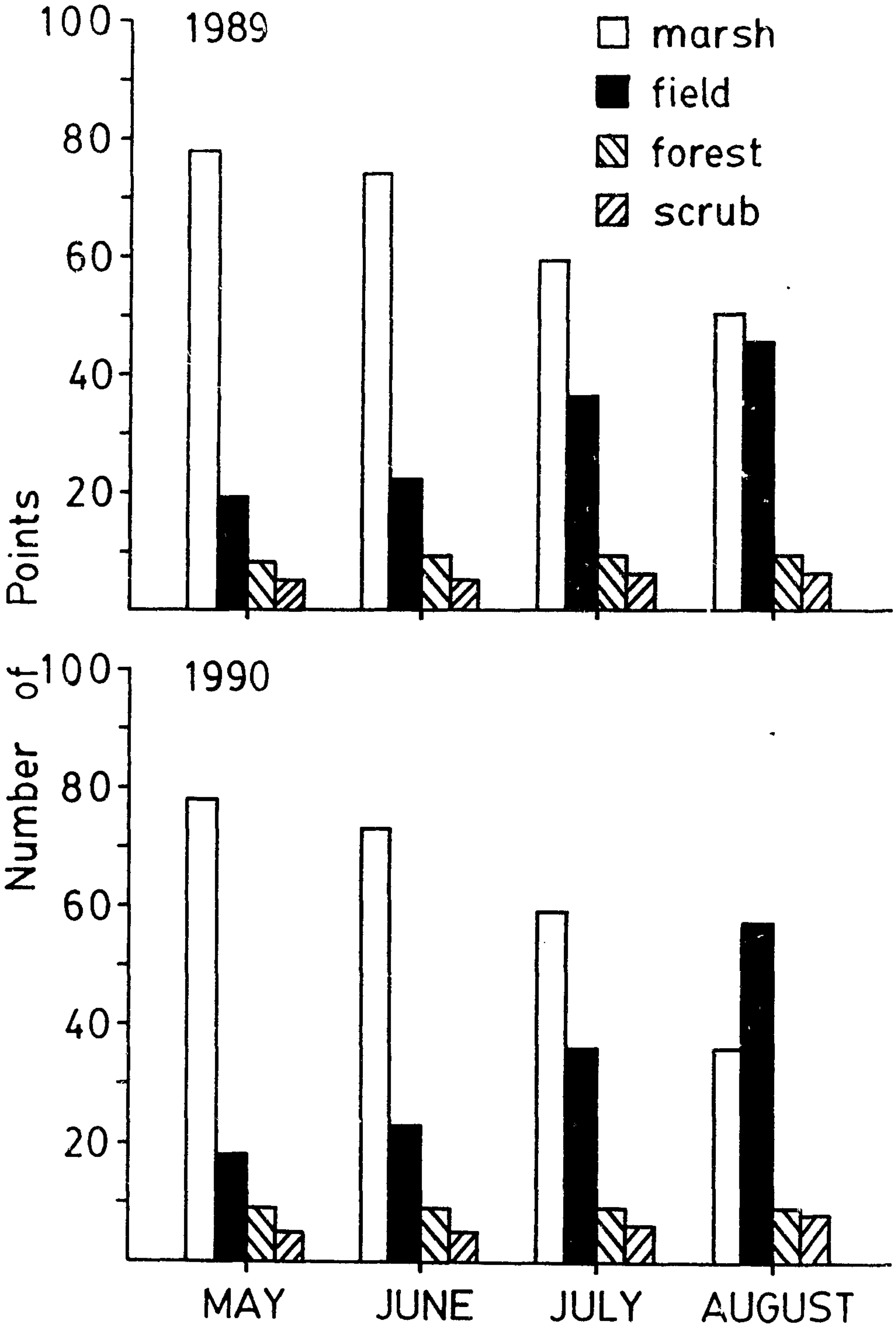
In addition to movement rates, I compared the proportion of time spent moving by gravid and nongravid females. Gravid females moved on 55.6±25.3% (n=10) of days monitored while nongravid females moved on 84.6±25.1% (n=7) of days monitored. A comparison of the mean proportion of time spent moving indicated that nongravid females spent a significantly higher proportion of their time moving than did gravid females (t=2.521, df=15, p=0.024).

Environmental Characteristics

Available Habitat

The monthly distributions of the four major habitat types are shown in Fig. 12. Forest and Scrub remained constant throughout the year and each accounted for <10% of the area of CCM2 in a given month. In May of both years,

Figure 12. Changes in the distribution of the four main habitat types at CCM2 in 1989 and 1990.


Number of Points
100
80
60
40
20
1989
□ marsh
■ field
▧ forest
▨ scrub
100
80
60
40
20
1990
MAY
JUNE
JULY
AUGUST

the most abundant habitat type was Marsh. However, as the summer progressed and water levels fell, the amount of Marsh decreased while the amount of Field increased. In 1990, CCM2 was drawn down as part of the continuing management scheme for the CVWMA, and by August the amount of Field exceeded that of Marsh.

In total, there were 75 sampling points that were not characterized as Marsh during at least one month of either 1989 or 1990, and I measured fixed habitat features at these points. Rocks were not found at any of the sampling points and there were only 3 points where fallen logs were located within the quadrat. The mean distance to the nearest rock was 784±4[illegible]4 m (n=75) and reflected the relative scarcity of rocks at CCM2. Logs also were relatively rare and were located within 50 m at only 16 of the 75 points (21.3%). The average diameter of these logs was 16.3±7.2 cm (n=16).

The mean distance to the nearest understory tree was 133±151 m (n=74, one data point lost), and to the nearest canopy tree 212±192 m (n=75). Understory trees were primarily Bebb Willow (*Salix bebbiana*) and Red-Osier Dogwood (*Cornus stolonifera*), along with small numbers of other species (Table 2). Black Cottonwood (*Populus trichocarpa*) was the most common canopy tree (Table 3) and the average DBH of canopy trees was 36.1±25.7 cm (n=22).

Dynamic habitat features were measured in the middle of the month for all sampling points not characterized as

Table 2: Species composition of understory trees in the available habitat. Identifications were made only for trees that were ≤50 m from sampling points.

Species	**Frequency**
Bebb Willow (*Salix bebbiana*)	21
Red-Osier Dogwood (*Cornus stolonifera*)	10
Black Cottonwood (*Populus trichocarpa*)	4
Black Hawthorn (*Crataegus douglasii*)	2

Table 3: Species composition of canopy trees in the available habitat. Identifications were made only for trees ≤50 m from sampling points.

Species	**Frequency**
Black Cottonwood (*Populus trichocarpa*)	12
White Birch (*Betula papyrifera*)	4
Bebb Willow (*Salix bebbiana*)	4
Mountain Alder (*Alnus tenuifolia*)	2

Marsh. Consequently, the number of sampling points varied among months.

Vegetation cover was high throughout the summer of 1989, ranging from 78.4-79.2%, and there was no significant difference among months (F=0.016, df=2, 145, p=0.984). In 1990, vegetation cover was low at the beginning of the summer (27.4%) and increased until August (81.2%), and there was a significant difference among the months (F=28.510, df=3, 190, p=0.000). I performed a 2-way ANOVA using data from June-August to test for differences between different years and months. There were significant differences between years (F=4.476, df=1, 304, p=0.035) and between months (F=4.496, df=2, 304, p=0.012), and there was a significant interaction term (F=4.113, df=2, 304, p=0.017). These differences appeared to be largely the result of low vegetation cover early in the summer of 1990 (Fig. 13), because there appears to be little difference in the July/August values of the two years.

The dominant herbaceous species reflected both the abundance of Field habitat and the decline in water levels during the summer (Table 4). By far the most common herbaceous species encountered, in all months and both years, were grasses. However, as the summer progressed, species that were characteristic of moist and wet areas began to appear as the dominant species in some quadrats. Most noticeably, sedges became a relatively common dominant

Figure 13. Mean vegetation cover during the summers of 1989 and 1990. Means are shown with 95% confidence limits.

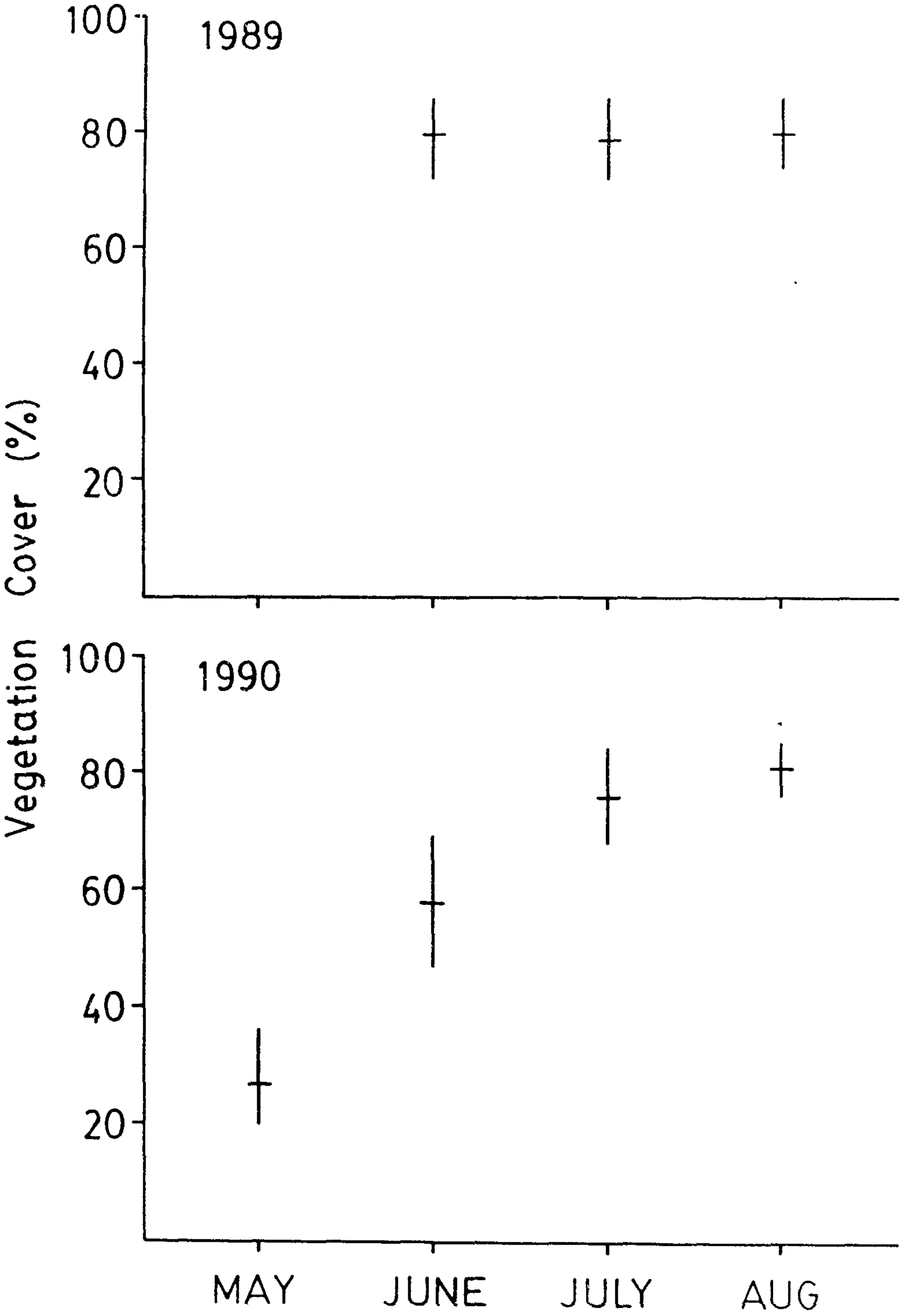

100
80
60
40
20
1989
Vegetation Cover (%)
100
80
60
40
20
1990
MAY
JUNE
JULY
AUG

Table 4. Species composition of dominant herbaceous plants in the available habitat. The dominant species at any sampling point was defined as the species with the greatest percentage cover within the 1 m^2 quadrat. Data tabulated are the number of quadrats in which the given species was dominant

		Month			
	Species	**May**	**June**	**July**	**August**
1989					
	Grasses	-	30	32	38
	Thistle (*Cirsium* spp.)	-	2	3	3
	Dandelion (*Taraxacum officinale*)	-	1	0	0
	Sedge	-	1	7	8
	Horsetail (*Equisetum* spp.)	-	1	3	5
	Mountain Dandelion (*Agoseris* spp.)	-	0	2	2
	Canada Mint (*Mentha arvensis*)	-	0	1	2
	Water Plantain (*Alisma plantago-aquatica*)	-	0	1	0
	Cattail (*Typha* spp.)	-	0	1	2
1990					
	Grasses	27	25	32	43
	Thistle (*Cirsium* spp.)	3	8	8	7
	Star-flowered Solomon's Seal (*Smilacina stellata*)	1	0	0	0

Table 4: (cont'd)

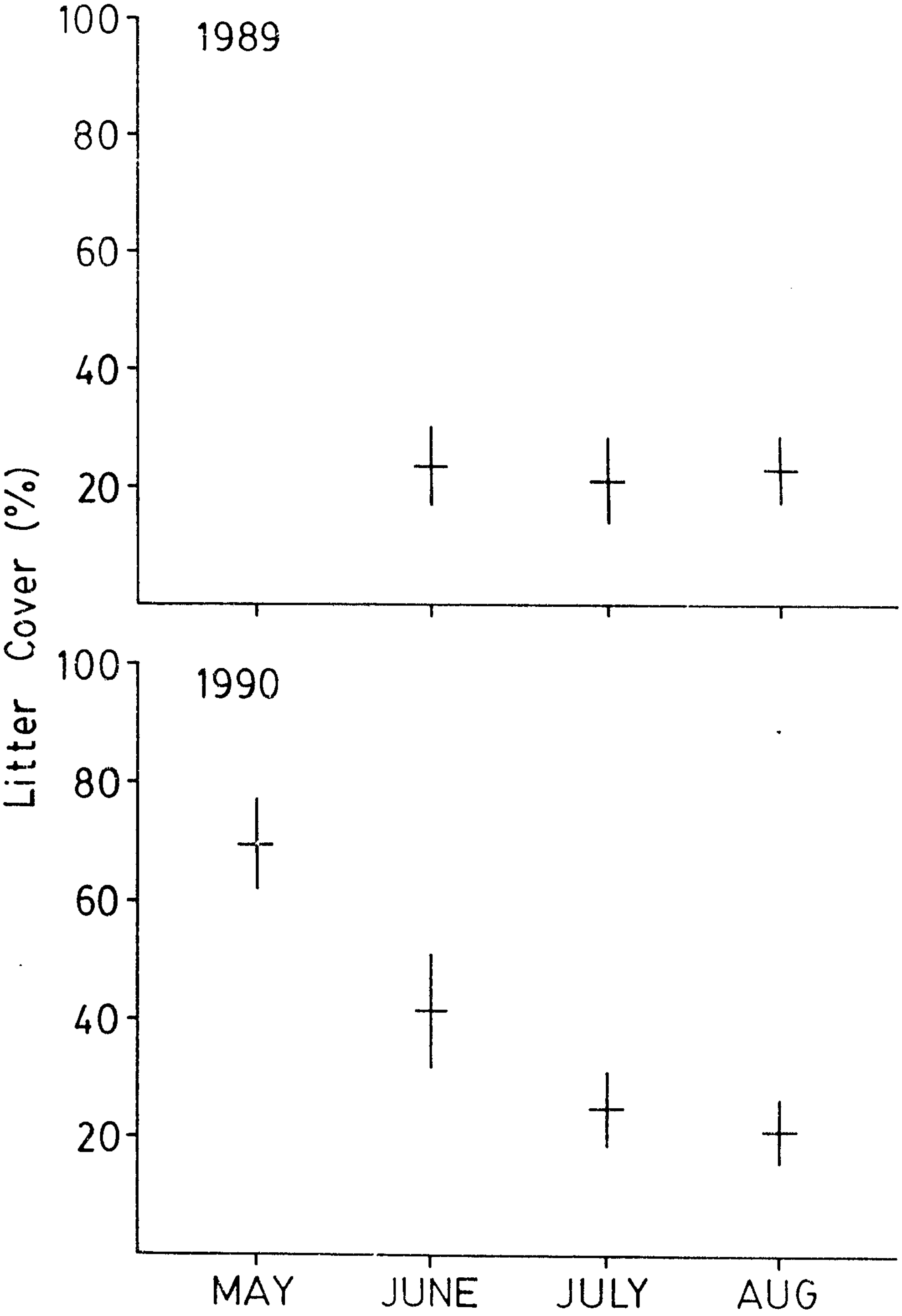
	Month			
Species	**May**	**June**	**July**	**August**
Sedge	0	3	5	10
Horsetail (*Equisetum* spp.)	0	0	2	4
Cattail (*Typha* spp.)	0	0	1	3
Water Plantain (*Alisma plantago-aquatica*)	0	0	1	0
Canada Mint (*Mentha arvensis*)	0	0	1	4
Northern Bedstraw (*Galium boreale*)	0	0	0	2

species in the second half of both summers. In addition, by the end of the summer there were a few quadrats dominated by primarily aquatic species such as Cattails (*Typha* spp.).

Litter cover was relatively low and stable in 1989, but decreased markedly during the summer of 1990 (Fig. 14). There was no significant difference in mean litter cover among months in 1989 (F=0.345, df=2, 145, 145, p=0.709), but there was a significant difference in 1990 (F=34.113, df=3, 190, 190, p=0.000). A 2-way ANOVA (Year X Month) for June-August of 1989 and 1990 revealed significant main effects (Year: F=5.651, df=1, 304, p=0.018; Month: F=6.487, df=2, 304, p=0.002) and a significant interaction term (F=3.954, df=2, 304, p=0.020).

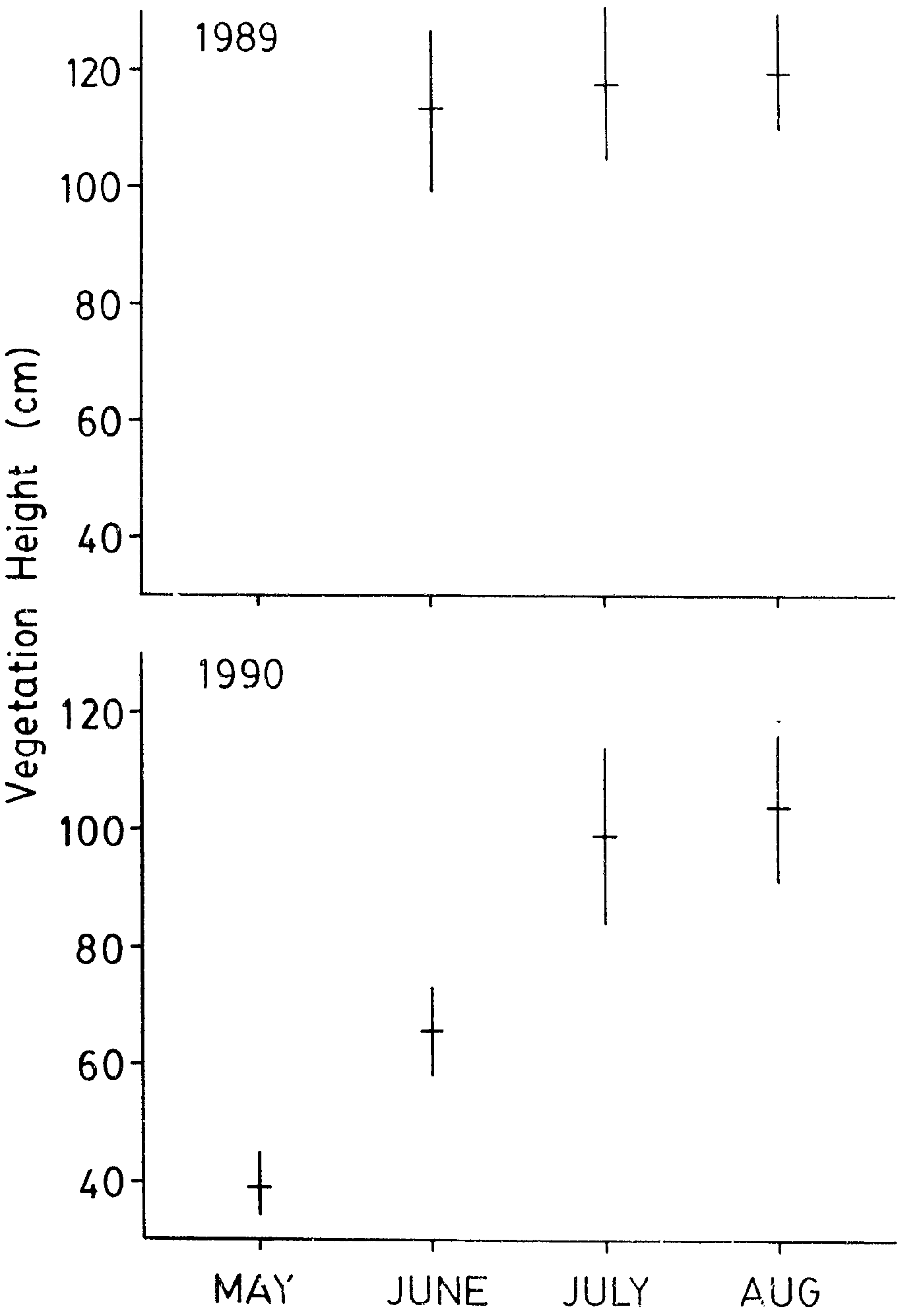
The changes in herbaceous vegetation height during the summers of 1989 and 1990 (Fig. 15) also show patterns similar to that of vegetation cover. In 1989, vegetation height was high and constant all summer (F=0.264, df=2, 139, p=0.768). However, in the summer of 1990, herbaceous vegetation increased in height throughout the summer and there was a significant difference among the months (F=19.421, df=3, 186, p=0.000). These differences are reflected in the comparison between years, using data from June-August, which indicated significant differences for both main effects (Year: F=25.252, df=1, 295, p=0.000; Month: F=6.012, df=2, 295, p=0.003) and a significant interaction term (F=3.161, df=2, 295, p=0.044).

Figure 14. Mean litter cover during the summers of 1989 and 1990. Means are shown with 95% confidence limits.



Litter Cover (%)
100
80
60
40
20
1989
100
80
60
40
20
1990
MAY
JUNE
JULY
AUG

Figure 15. Mean vegetation height during the summers of 1989 and 1990. Means are shown with 95% confidence limits.


1989
1990
Vegetation Height (cm)
120
100
80
60
40
MAY
JUNE
JULY
AUG

Woody stemmed plants were rarely encountered on the study site, leading to low, and relatively constant, estimates of woody stem density (Table 5). In addition, the height of woody stemmed vegetation remained constant among months and between years (Table 5). The most commonly encountered woody stemmed species were Waxberry (*Symphoricarpos albus*) and Bebb Willow (*Salix bebbiana*), along with smaller numbers of other species (Table 6).

Canopy cover at CCM2 was generally sparse, and restricted to the same 12 sampling points in both years, with one additional point, initially flooded, being included later in each summer as water levels declined. Although canopy cover could be as high as 98% at a given point, the abundance of Field habitat (where canopy cover=0% by definition) led to low average values for canopy cover, ranging from 3.9% (August 1990) to 10.8% (May 1990). The average canopy cover tended to decrease during the summer. However, the trend was not significant for either 1989 (F=0.416, df=2, 145, p=0.661) or 1990 (F=1.145, df=3, 190, p=0.332). A 2-way ANOVA on data from June-August also indicated that there was no significant difference between years (F=0.121, df=1, 304, p=0.728), or among months (F=1.378, df=2, 304, p=0.253), and that the year X month interaction was not significant (F=0.053, df=2, 304, p=0.949).

The average distance to standing water at CCM2 ranged

Table 5. Woody stem density and woody able habitat for each month. Means are shown ± 1 s .. Sample sizes are in parentheses.

Woody Stem Density (stems/m^2)

Year	May	June	July	August
1989	–	1.4±3.6 (36)	1.1±3.2 (51)	1.4±3.9 (61)
1990	1.7±4.8 (32)	1.5±4.5 (37)	1.1±3.9 (51)	1.0±3.7 (74)

Woody Stem Height (cm)

Year	May	June	July	August
1989	–	82.4±37.1 (8)	83.5±54.4 (10)	84.9±48.1 (12)
1990	73.0±27.6 (7)	72.4±26.4 (7)	79.6±36.8 (7)	103.4±60.4 (9)

Table 6. Woody stem species encountered each month in available habitat. The values tabulated are the frequencies of occurrence of each species in the total number of sampling points for that month.

		Month			
	Species	**May**	**June**	**July**	**August**
1989					
	Waxberry (*Symphoricarpos albus*)	-	3	3	3
	Bebb Willow (*Salix bebbiana*)	-	3	3	4
	Black Cottonwood (*Populus trichocarpa*)	-	1	2	2
	Red-Osier Dogwood (*Cornus stolonifera*)	-	1	1	2
	Black Hawthorn (*Crataegus douglasii*)	-	0	1	1
1990					
	Waxberry (*Symphoricarpos albus*)	3	3	3	3
	Bebb Willow (*Salix bebbiana*)	0	0	1	2
	Black Cottonwood (*Populus trichocarpa*)	1	1	1	2
	Red-Osier Dogwood (*Cornus stolonifera*)	1	1	1	1
	Black Hawthorn (*Crataegus douglasii*)	2	2	1	1

from 38.8±68.4 m to 86.1±96.1 m, with the distance increasing over the summer(Fig. 16). This difference was significant in 1990 (F=3.763, df=3, 190, p=0.012), but not in 1989 (F=1.053, df=2, 145, p=0.352). A comparison of the two years using data from June-August indicated that there was no difference between years (F=0.088, df=1, 304, p=0.767), although the months were significantly different (F=4.321, df=2, 304, p=0.014). The interaction term was not significant (F=0.325, df=2, 304, p=0.723).

Habitat Utilization

The small number of animals from which habitat data were collected in 1989 and 1990 (see **Movements**) precluded an interspecific analysis of habitat utilization. Instead, I have restricted the analysis to a comparison of gravid and nongravid females. This pooling of species appeared to be reasonable, because both species were found at the same sites. Habitat use by gravid and nongravid females is shown along with the available habitat in Fig. 17. The values for available habitat are the means of the July and August 1989/90 values (n=4). Gravid females used Field habitat almost exclusively and both species were often observed using the same sites. Nongravid females used Field, Scrub and, to a lesser extent, Forest (largely a single individual). Neither group of snakes used Marsh, except for

Figure 16. Distance to standing water in 1989 and 1990. Means are shown with 95% confidence limits.

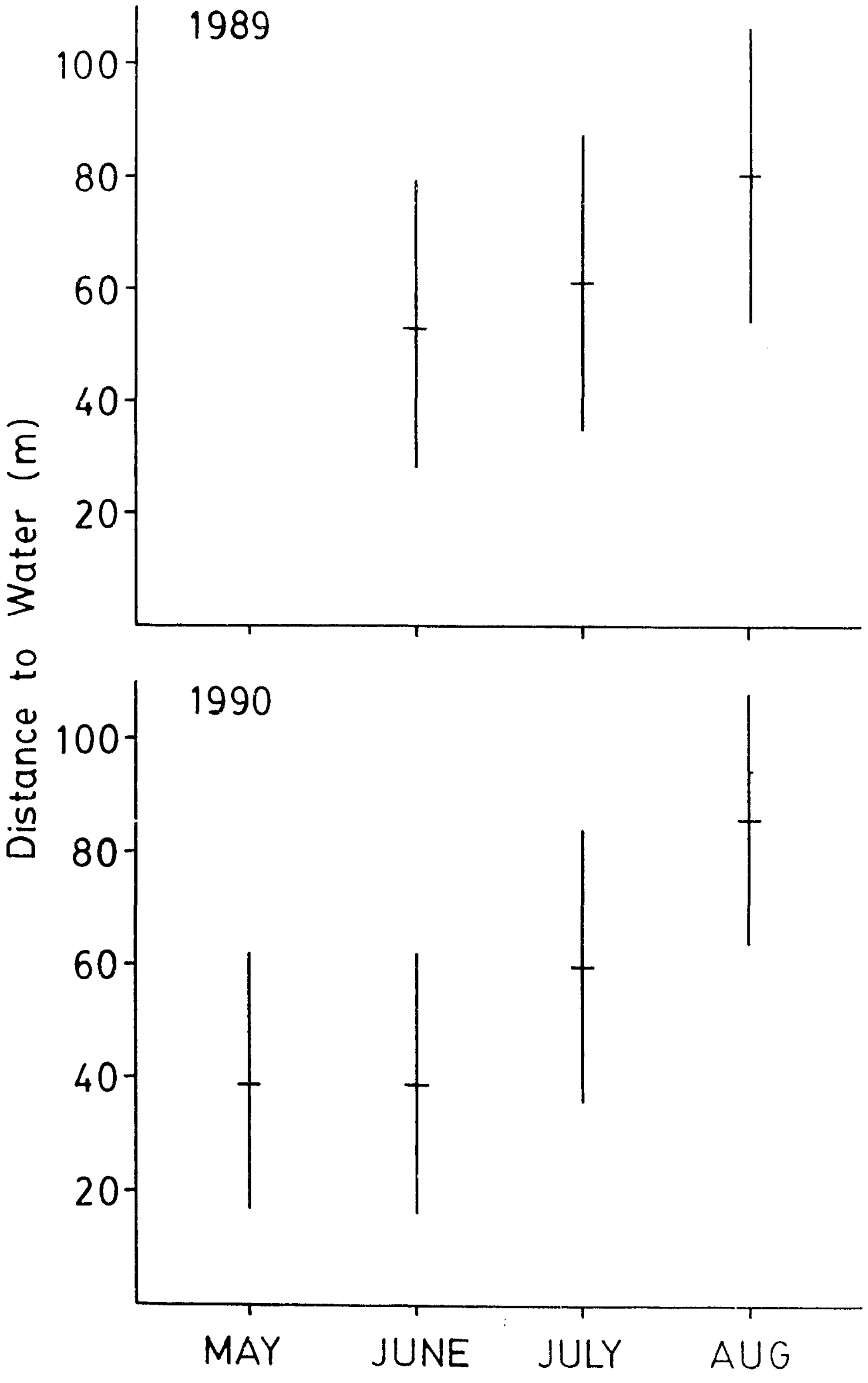
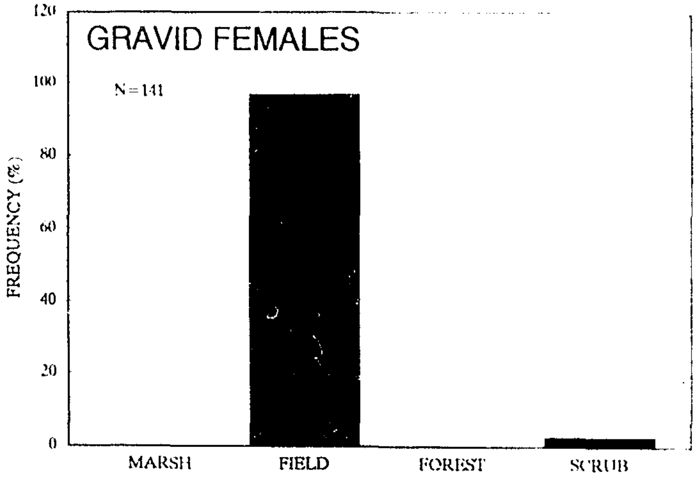
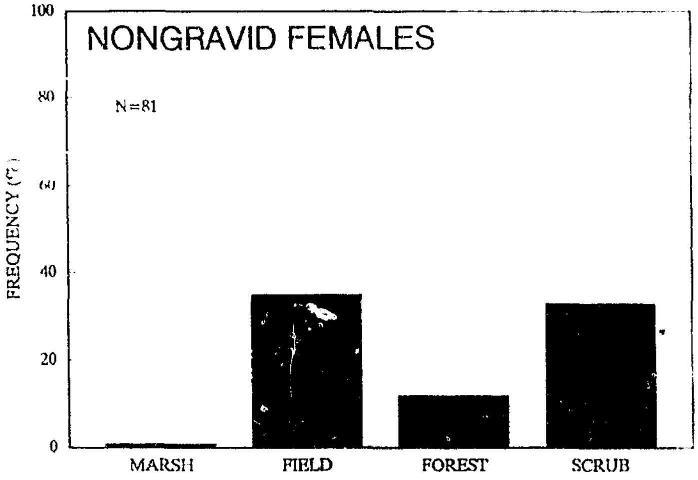
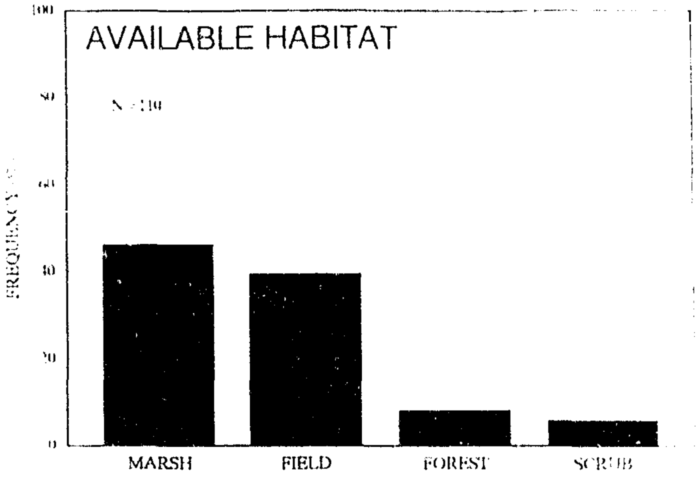

1989
100
80
60
40
20
Distance to Water (m)
1990
100
80
60
40
20
MAY
JUNE
JULY
AUG

Figure 17. Use of the major habitat types by gravid and nongravid females. The reproductive categories are pooled values for both species over both years. Available habitat is the average for July and August of both years.


GRAVID FEMALES
N=141
FREQUENCY (%)
120
100
80
60
40
20
0
MARSH
FIELD
FOREST
SCRUB


NONGRAVID FEMALES
N=81
FREQUENCY (%)
100
80
60
40
20
0
MARSH
FIELD
FOREST
SCRUB


AVAILABLE HABITAT
N=110
FREQUENCY (%)
100
80
60
40
20
0
MARSH
FIELD
FOREST
SCRUB

a single record of a nongravid female. Consequently, I compared the use of just the terrestrial habitats by gravid and nongravid females with the available habitat using log-likelihood ratio goodness-of-fit-tests. Habitat use differed significantly from available for both gravid (G=64.764, df=2, p<0.001) and nongravid (G=50.236, df=2, p<0.001) females. In addition, contingency table analysis indicated that gravid and nongravid females used the terrestrial habitat types differently (G=126.614, df=2, p<0.001).

Table 7 shows the availability and utilization of fixed habitat features by gravid and nongravid females. In all cases if the differences among means for a given habitat feature were significant, I then compared pairs of means using the GT2 method for unplanned comparisons. In cases where either no data were collected for a given habitat feature (e.g. Length of Rock for available habitat) or where the value of the habitat feature was 0 for all sampling points (e.g. Rock Cover for available habitat) the ANOVA was done using just the remaining two groups.

Rock cover was 0 for all sampling points in the available habitat. However, snakes used sites that had rocks. Gravid females utilized sites with much higher average rock cover than did nongravid females. Log cover was sparse at CCM2 and there was no significant difference between usage of sites with log cover by nongravid females

Table 7. Availability and utilization of fixed habitat features. Mean values for each feature are shown ± 1 standard deviation, with sample sizes in parentheses. F-values are tabulated for 1-way ANOVAs comparing the means for a given habitat feature.

Habitat Feature	**Available**	**Gravid**	**Nongravid**	**F**	**p**
Rock Cover (%)	0 (75)	45.4±44.0 (37)	3.7±14.3 (56)	43.891	<0.001
Log Cover (%)	0.3±1.6 (75)	0 (37)	0.3±1.3 (56)	0.031	NS
Distance to Rock (m)	784.4±454.0 (75)	3.8±13.5 (37)	358.2±389.8 (56)	56.430	<0.001
Length of Rock (cm)	-	47.1±20.0 (37)	50.7±18.7 (12)	0.303	NS
Diameter of Log (cm)	16.3±7.2 (16)	12.1±5.8 (27)	20.6±9.5 (25)	7.954	<0.001
Distance to Understory Tree (m)	133.0±151.6 (74)	5.0±2.6 (37)	5.7±6.7 (56)	33.164	<0.001
Distance to Canopy Tree (m)	212.4±192.1 (75)	46.4±14.2 (37)	105.6±115.9 (56)	18.580	<0.001
DBH of Canopy Tree (cm)	36.1±25.7 (22)	-	44.9±25.6 (23)	1.323	NS

and what was available. Sites used by gravid females never included log cover.

Gravid females were found significantly closer to rocks than were nongravid females, and both groups were found closer to rocks than expected from general availability. Sampling points in the available habitat were always >50 m from rocks, so no data were collected on the lengths of rocks available at CCM2. However, there was no significant difference in rock length between sites used by gravid and nongravid females.

The average diameters of logs within 50 m of sampling points were significantly different among the three samples, with gravid females having the smallest mean and nongravid females the largest. However, the only pairwise significant difference was between the mean diameter of logs at sites used by gravid females and nongravid females.

The average distance to the nearest understory tree was not significantly different between gravid and nongravid females. However, both were significantly less than the average distance available at CCM2. In addition, both gravid and nongravid females were found closer to canopy trees than would be expected by chance, although gravid females were significantly closer than nongravid females. I did not measure DBH for canopy trees associated with the locations of gravid females because they were always >50 m from the sampling point. However, 23 of the 57 sampling points for nongravid females were within 50 m of canopy trees and the mean DBH of these trees did not differ from what was available at CCM2.

Because logs were relatively rare at CCM2, and I did not measure the distance to the nearest log if it was >50 m, I expressed proximity to logs as the proportion of sampling points <50 m from a log. In the available habitat the proportion was 0.213 (n=75), whereas for gravid females it was 0.730 (n=37) and 0.446 (n=56) for nongravid females. A log-likelihood contingency table analysis indicated that the three proportions were significantly different (G=28.844, df=2, p<0.001). I then used a Tukey test to determine which pairs of proportions differed. A significantly smaller proportion of sampling points were within 50 m of a log in the available habitat than for either gravid or nongravid females. In addition, gravid females had a significantly higher proportion of points within 50 m of logs than did nongravid females.

The species of understory and canopy trees within 50 m of sampling points for gravid and nongravid females are shown in Table 8. The two most frequently encountered species of understory trees were Red-Osier Dogwood (*Cornus stolonifera*) and Bebb Willow (*Salix bebbiana*). However, the frequency of occurrence of the three species common to both groups differed between gravid and nongravid females (G=21.4, df=2, p<0.05). These understory species were also

Table 8. Species composition of understory and canopy trees associated with gravid and nongravid females. Identifications were made only for trees that were ≤50 m from sampling points.

Species	**Gravid**		**Nongravid**	
	Frequency	**Percent**	**Frequency**	**Percent**
Understory Trees				
Red-Osier Dogwood (*Cornus stolonifera*)	21	56.8	5	9.6
Bebb Willow (*Salix bebbiana*)	13	35.1	32	61.5
Black Cottonwood (*Populus trichocarpa*)	3	8.1	10	19.2
Black Hawthorn (*Crataegus douglasii*)	0	0.0	5	9.6
Canopy Trees				
Black Cottonwood (*Populus trichocarpa*)	4	100.0	18	78.3
White Birch (*Betula papyrifera*)	0	0.0	5	21.7

the most abundant in the available habitat. The most abundant canopy species in the samples from gravid and nongravid females was Black Cottonwood (*Populus trichocarpa*), which was also the most common canopy species available at CCM2.

Dynamic habitat features used by gravid and nongravid females are presented in Table 9. Because all habitat points from snakes were collected in July and August, I performed 2-way ANOVAs (year X month) on the data from the available habitat for these two months. There were no significant differences between years or between months for any of the habitat features, and there were no significant interaction terms (Table 10). The sole exception was Herbaceous Vegetation Height, which differed between years but not months, and, again, the interaction term was not significant. Consequently, I used the average value for July and August 1989/90 (n=4) as the measure of available habitat. In the case of Herbaceous Vegetation Height I kept the years separate and used the July/August average. Statistical comparisons were made as described for the fixed habitat features.

The amount of litter cover at sites used by nongravid females was considerably less than what was available; however, the difference was not quite significant. Gravid females utilized sites with significantly less litter cover than was generally available, but the figure for gravid

Table 9. Availability and utilization of dynamic habitat features. Unless otherwise noted, the available habitat is the average for July and August 1989 and 1990. Mean values for each feature are shown ±1 standard deviation with sample sizes in parentheses. F-values are tabulated for 1-way ANOVAs comparing the means for a given habitat feature.

Habitat Feature	**Available**	**Gravid**	**Nongravid**	**F**	**p**
Litter Cover (%)	21.2±17.1 (75)	14.2±15.2 (37)	15.1±14.0 (56)	4.176	<0.05
Vegetation Cover (%)	75.9±18.0 (75)	49.6±29.5 (37)	78.4±21.8 (56)	19.673	<0.001
Vegetation Height (cm)					
1989	118.5±40.1 (60)	85.8±39.8 (14)	110.4±36.3 (28)	4.012	<0.05
1990	107.0±48.1 (73)	81.7±40.8 (19)	86.5±38.0 (28)	3.565	<0.05
Canopy Closure (%)	10.7±26.6 (75)	0.5±3.3 (37)	36.9±36.7 (56)	24.827	<0.001
Distance to Water (m)	74.8±87.9 (75)	4.2±3.1 (37)	16.2±12.8 (56)	24.097	<0.001

Table 10 Two-way ANOVA results for comparisons of dynamic features of the available habitat in July and August.

Source	**SS**	**DF**	**MS**	**F**	**p**
Litter Cover					
Year	44.582	1	44.582	0.151	0.698
Month	44.055	1	44.005	0.149	0.700
Year X Month	310.968	1	310.968	1.052	0.306
Error	68883.583	233	295.638		
Vegetation Cover					
Year	0.153	1	0.153	0.000	0.982
Month	249.903	1	249.903	0.798	0.372
Year X Month	134.223	1	134.223	0.429	0.513
Error	72929.631	233	313.003		
Vegetation Height					
Year	15828.993	1	15828.993	6.830	0.010
Month	637.483	1	637.483	0.275	0.600
Year X Month	164.838	1	164.838	0.071	0.790
Error	523800.560	226	2317.702		

Table 10. (cont'd)

Source	**SS**	**DF**	**MS**	**F**	**p**
Canopy Closure					
Year	122.227	1	122.227	0.244	0.622
Month	391.421	1	391.421	0.781	0.378
Year X Month	18.339	1	18.339	0.037	0.848
Error	116801.086	233	501.292		
Distance to Water					
Year	382.234	1	382.234	0.043	0.837
Month	28919.990	1	28919.990	3.227	0.074
Year X Month	922.930	1	922.930	0.103	0.749
Error	2088369.211	233	8962.958		

females did not differ significantly from that for nongravid females. There was no difference in vegetation cover between sites selected by nongravid females and what was available. However, gravid females used sites with significantly less vegetation cover than did nongravid females.

In 1989, the Herbaceous Vegetation Height in the available habitat appeared to be considerably greater than that at sites used by either group of snakes. However, only the difference between sites used by gravid females and the available habitat was significant. The situation in 1990 was similar in that the overall ANOVA revealed significant differences among the means. However, I was unable to detect differences between any pair of means.

Mean Canopy Closure differed significantly overall, as well as in all pairwise comparisons. Gravid females utilized sites with almost no canopy cover, whereas nongravid females used sites with much higher canopy cover than was generally available.

The analysis of Distance to Water also revealed a significant difference among the means, with both gravid and nongravid females being found significantly closer to water than expected from the available habitat. In addition, gravid females were found significantly closer to water than nongravid females.

The proportion of sampling points that contained woody stemmed plants was 0.160 (n=75) in the available habitat, but was 0.378 (n=37) for gravid females and 0.396 (n=56) for nongravid females. The difference among the proportions was significant (log-likelihood contingency table analysis: G=10.942, df=2, p<0.005), and a Tukey test of multiple proportions indicated that sites used by gravid and nongravid females did not differ from each other. In addition, sites used by gravid and nongravid females had a higher proportion containing woody stems than found in the available habitat.

There appeared to be a difference in the woody stemmed species encountered at sites used by gravid and nongravid females (Table 11). Penstemon (*Penstemon* spp.) and Red-Osier Dogwood (*Cornus stolonifera*) were the most common species associated with gravid females, whereas nongravid females were most frequently found in association with Black Cottonwood (*Populus trichocarpa*), Bebb Willow (*Salix bebbiana*) and Waxberry (*Symphoricarpos albus*). I compared the numerical importance of the woody stemmed species encountered using a Spearman rank correlation. The correlation was not significant (r_s=-0.414, n=8, p>0.05), indicating that sites used by gravid and nongravid females were different with respect to woody stemmed species. The most common woody stemmed species at sites used by nongravid females were also the most common in the available habitat. However, gravid females differed from what was generally

Table 11. Woody stemmed species associated with gravid and nongravid females.

Species	**Gravid**		**Nongravid**	
	Frequency	**Percent**	**Frequency**	**Percent**
Penstemon (*Penstemon* spp.)	11	78.6	0	0.0
Red-Osier Dogwood (*Cornus stolonifera*)	2	14.3	1	4.5
Black Cottonwood (*Populus trichocarpa*)	1	7.1	7	31.8
Bebb Willow (*Salix bebbiana*)	0	0.0	5	22.7
Waxberry (*Symphoricarpos albus*)	0	0.0	4	18.2
Wild Rose (*Rosa* spp.)	0	0.0	2	9.1
Blueleaf Strawberry (*Fragaria glauca*)	0	0.0	2	9.1
Black Hawthorn (*Crataegus douglasii*)	0	0.0	1	4.5

available because of the abundance of *Penstemon*, a species not encountered in the sample of the available habitat.

The most common herbaceous species at sites used by both gravid and nongravid females were grasses (Table 12), which were also the most common herbaceous species available at CCM2. A major difference in the herbaceous species associated with gravid and nongravid females is the abundance of sedge in the sample of sites used by nongravid females. In addition, there was one record of a site used by a nongravid female being dominated by Cattail (*Typha* spp.), as occasionally happened in the late summer samples of the available habitat. The numerical importance of herbaceous species was not the same between sites used by gravid and nongravid females, as indicated by a nonsignificant Spearman rank correlation (r_S=0.251, n=12, p>0.05).

Prey Availability

I sampled aquatic frogs (*Rana pretiosa*) from ten 100 m transects in 1989 and 1990. The total number of frogs seen during each sampling period showed a similar pattern in both years. The number of frogs was relatively low for most of the summer, but increased dramatically in August. The mean number of frogs seen ranged from 0/100 m to 4.9/100 m (Fig. 18), and there was a significant change in the mean number

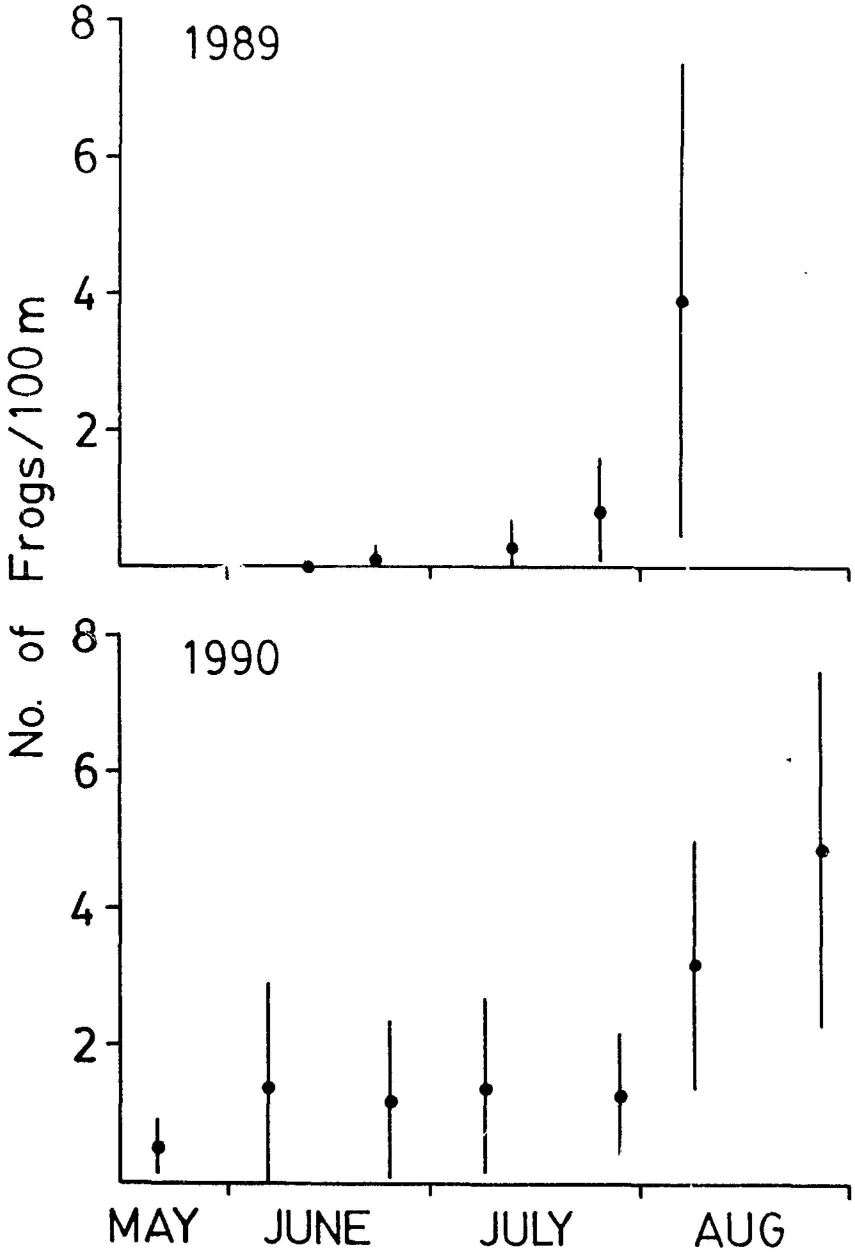
Table 12. Herbaceous vegetation species associated with gravid and nongravid females.

Species	**Gravid**		**Nongravid**	
	Frequency	**Percent**	**Frequency**	**Percent**
Grass	16	53.3	25	46.3
Knapweed (*Centaurea* spp.)	4	13.3	0	0.0
Aster (*Aster* spp.)	3	10.0	3	5.6
Horsetail (*Equisetum*)	2	6.7	2	3.7
Great Mullein (*Verbascum thapsus*)	1	3.3	0	0.0
Common Plantain (*Plantago major*)	1	3.3	0	0.0
Sedge	1	3.3	15	27.8
Skunk Cabbage (*Lysichiton kamtschatcense*)	1	3.3	0	0.0
Thistle (*Cirsium* spp.)	1	3.3	6	11.1

Table 12. (contd)

Species	Gravid		Nongravid	
	Frequency	**Percent**	**Frequency**	**Percent**
Canada Mint (*Mentha arvensis*)	0	0.0	1	1.9
Dandelion (*Taraxacum officinale*)	0	0.0	1	1.9
Cattail (*Typha* spp.)	0	0.0	1	1.9

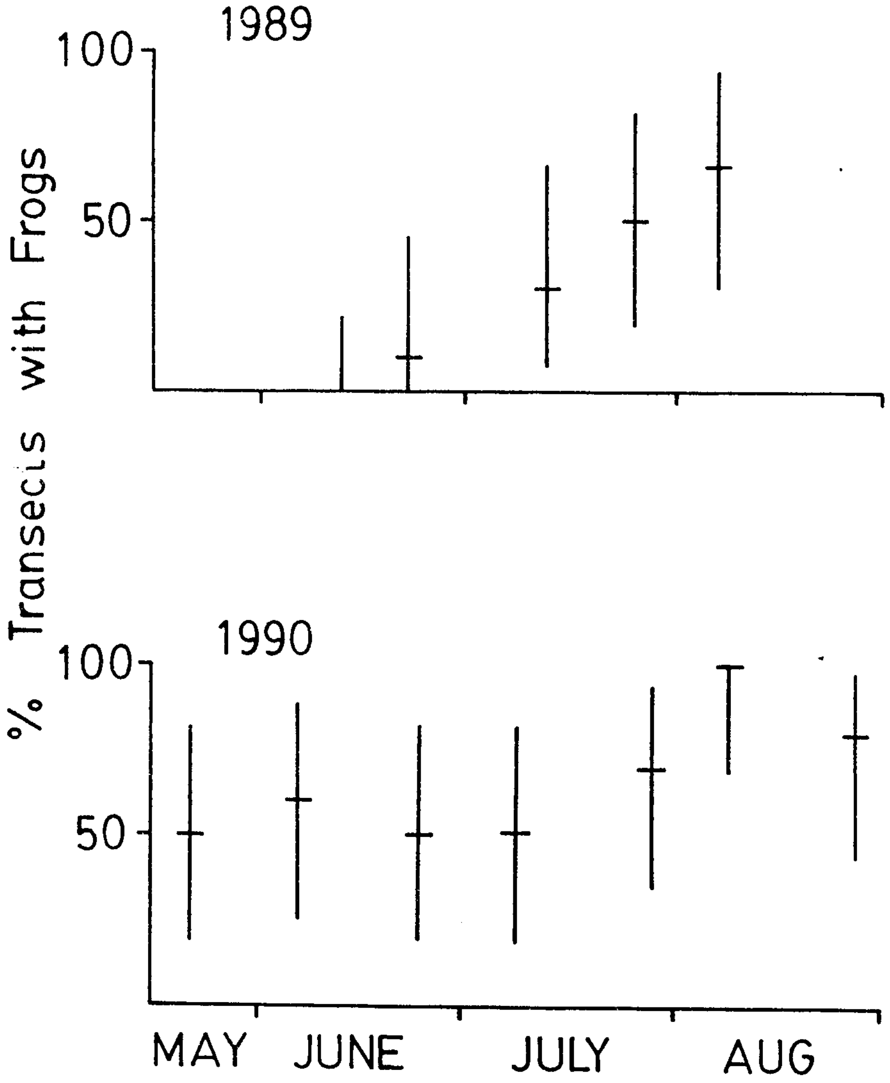
Figure 18. Mean number of frogs/100 m transect at each sampling period. Means are shown with 95% confidence limits.


1989
1990
No. of Frogs/100 m
8
6
4
2
MAY
JUNE
JULY
AUG

of frogs seen during the summer in both 1989 (ANOVA: F=6.314, df=4, 44, $p<0.001$) and 1990 (ANOVA: F=5.130, df=6, 63, $p<0.001$). The proportion of transects that contained frogs is shown in Fig. 19. In 1989, the proportion increased with time over the season (r_s=1.0, df=4, $p<0.05$). This pattern was not evident in 1990 (r_s=0.784, df=6, $p>0.05$). Although I did not quantify it, there was a noticeable change in frog size during both summers. Early in the season, all of the frogs seen were adults. As the number of frogs observed increased in August, I noticed that there were increasingly large numbers of small, newly metamorphosed frogs in each transect.

I sampled slugs (*Agriolimax* sp.) monthly at 10 sites during June-August 1989. The number of slugs captured in a single trap ranged from 0-9 with a grand mean of 2.9±3.1 slugs/trap (n=29). However, the mean number of slugs (Fig. 20) did not vary significantly among months (ANOVA; F=0.713, df=2, 26, p=0.499). In 1990, sampling effort was increased to include the 3 major habitat types and the number of slugs captured in that year ranged from 0-43 in a single trap with a grand mean of 5.6±8.8 slugs/trap (n=72). A 2-way ANOVA of month by habitat indicated that there were significant differences among months (F=9.647, df=3, 60, p=0.000) and habitats (F=5.513, df=2, 60, p=0.006), but no significant interaction term (F=1.780, df=6, 60, p=0.118). The differences among months appeared to be due to a decline

Figure 19. Proportion of transects containing frogs, as a function of season. Proportions are shown with 95% confidence limits.


1989
1990
100
50
100
50
% Transects with Frogs
MAY
JUNE
JULY
AUG

in slug numbers in July and August (Fig. 20). Differences among habitats appeared to stem from relatively high abundance in the scrub and relatively low abundance in the forest (Fig. 21).

Worms (*Lumbricus* sp.) were sampled at the same sites as slugs in both 1989 and 1990. The total number of worms counted/site in 1989 ranged from 1-42 with a grand mean of 14.9±11.8 worms/site. The mean number of worms counted/site (Fig. 22) did not differ significantly among months (ANOVA: F=2.118, df=2, 27, p=0.140). In order to determine whether there were differences in the availability of different sized worms, I compared the average number of small (7.6±6.5) and large (7.3±8.0) worms/site and found no significant difference (paired-sample t=0.145, df=29, p=0.886). In addition, I performed 1-way ANOVA's, keeping small and large worms separate, to test for temporal changes in worm numbers with respect to size. There was no significant difference among months for either small (F=0.742, df=2, 27, p=0.486) or large worms (F=2.465, df=2, 27, p=0.104) in 1989.

During 1990, the total number of worms counted/site ranged from 1-75 with a grand mean of 24.0±15.4 worms/site. I performed a 2-way ANOVA (month, habitat) on the mean number of worms/site in order to examine patterns of worm abundance. There was a significant difference among months (F=4.209, df=3, 68, p=0.009), which appeared to be due to a

Figure 20. Monthly distribution of slug captures. Means are shown with 95% confidence limits. The sample sizes (n) are the number of points sampled each month.

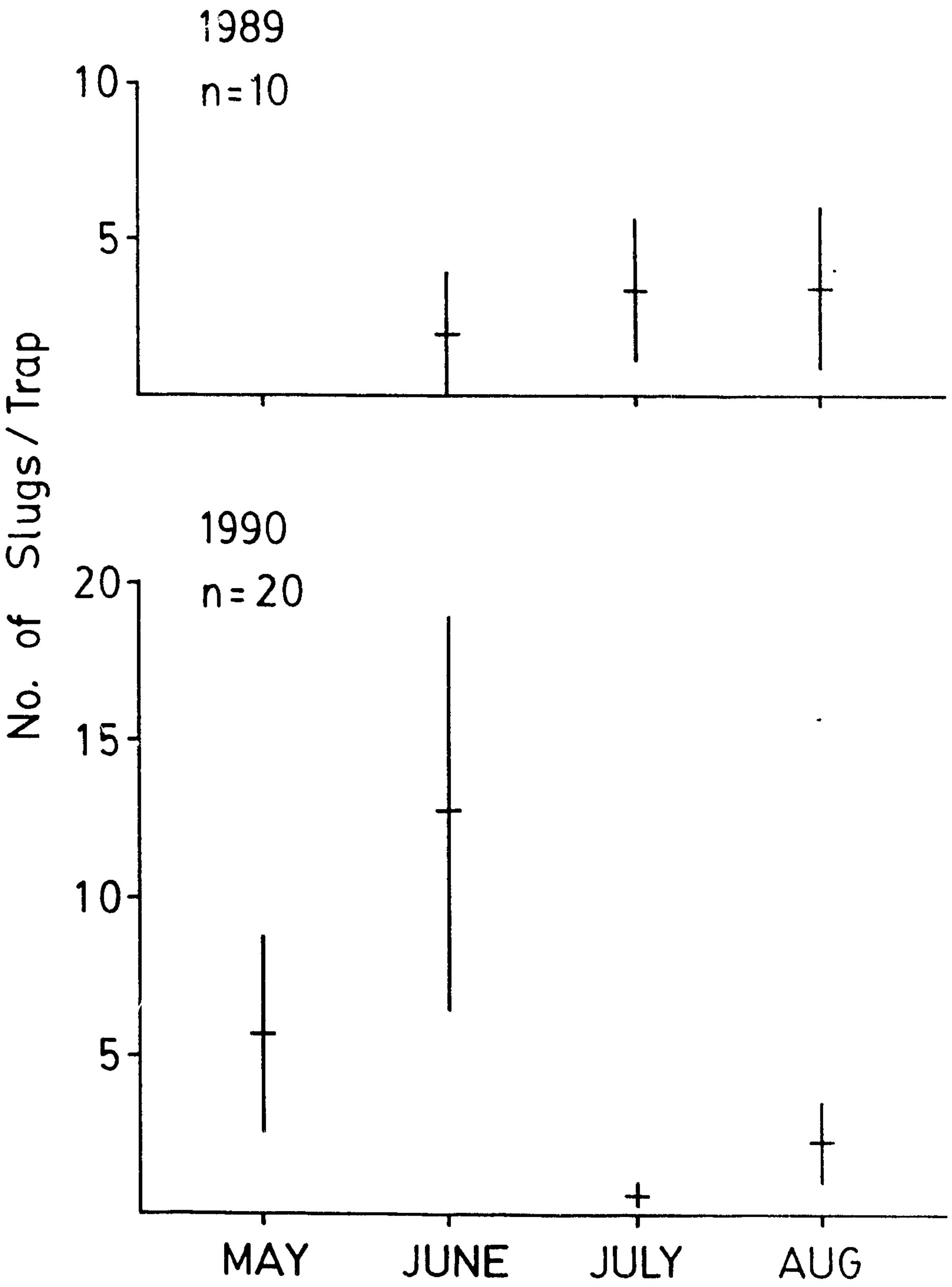
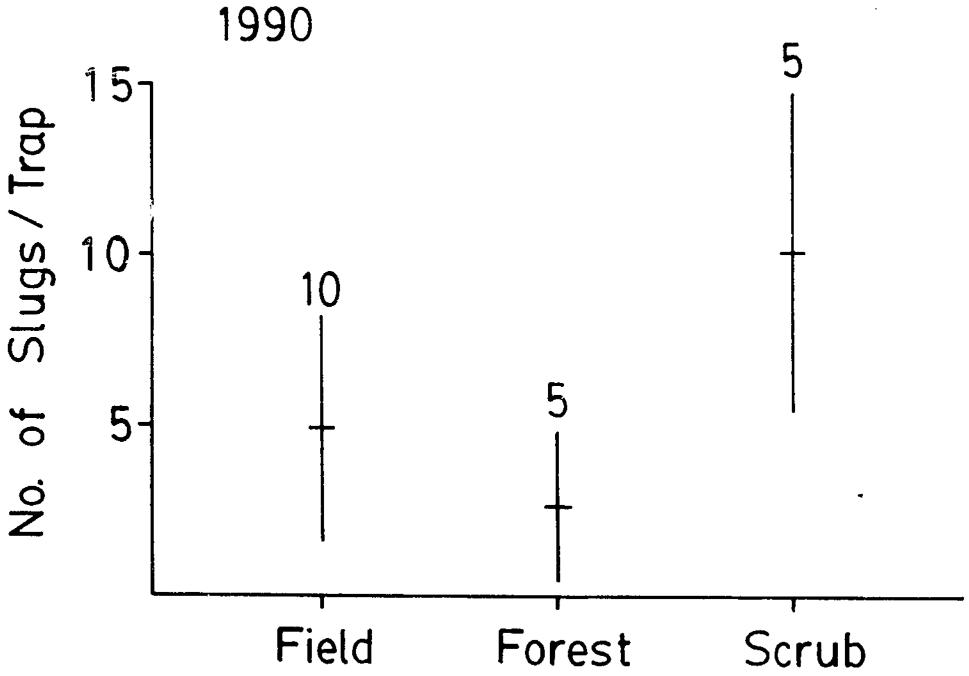

1989
n=10
10
5
1990
n=20
20
15
10
5
No. of Slugs / Trap
MAY
JUNE
JULY
AUG

Figure 21. Distribution of slugs captured in each habitat type. Means are shown with 95% confidence limits and the sample sizes are the number of points sampled in each habitat.


1990
No. of Slugs / Trap
15
10
5
10
5
5
Field
Forest
Scrub

decline in the number of worms in July (Fig. 22). However, there was no significant difference among habitats (F=1.489, df=2, 68, p=0.233), nor was the interaction term significant (F=0.481, df=6, 68, p=0.820).

There was a significant difference in the mean number of small (13.8±11.1) and large (10.2±7.0) worms sampled in 1990 (paired-sample t=2.384, df=79, p=0.020). In order to examine further the patterns of worm abundance related to size I performed 2-way ANOVA's (month, habitat) keeping small and large worms separate. The average number of small worms sampled differed among months (F=3.607, df=3, 68, p=0.018) but not among habitats (F=1.847, df=2, 68, p=0.166), and the interaction term was not significant (F=0.840, df=6, 68, p=0.543). In contrast, there was no significant variation in the mean number of large worms sampled either by month (F=2.211, df=3, 68, p=0.095), or by habitat (F=0.955, df=2, 68, p=0.390), and the interaction term was not significant (F=0.235, df=6, 68, p=0.963). Fig. 23 shows a comparison of the numbers of small and large worms as a function of month. The significant difference found among months for the small worms appeared to be due to a decline in abundance in July, which is much less apparent in the large worms. Although there were no significant differences in worm abundance in the different habitats for either small or large worms (Fig. 24), there appeared to be fewer small worms in the forest than in the other two

Figure 22. Monthly distribution of worm captures. Means are shown with 95% confidence limits. Sample sizes (n) are the number of points sampled each month.

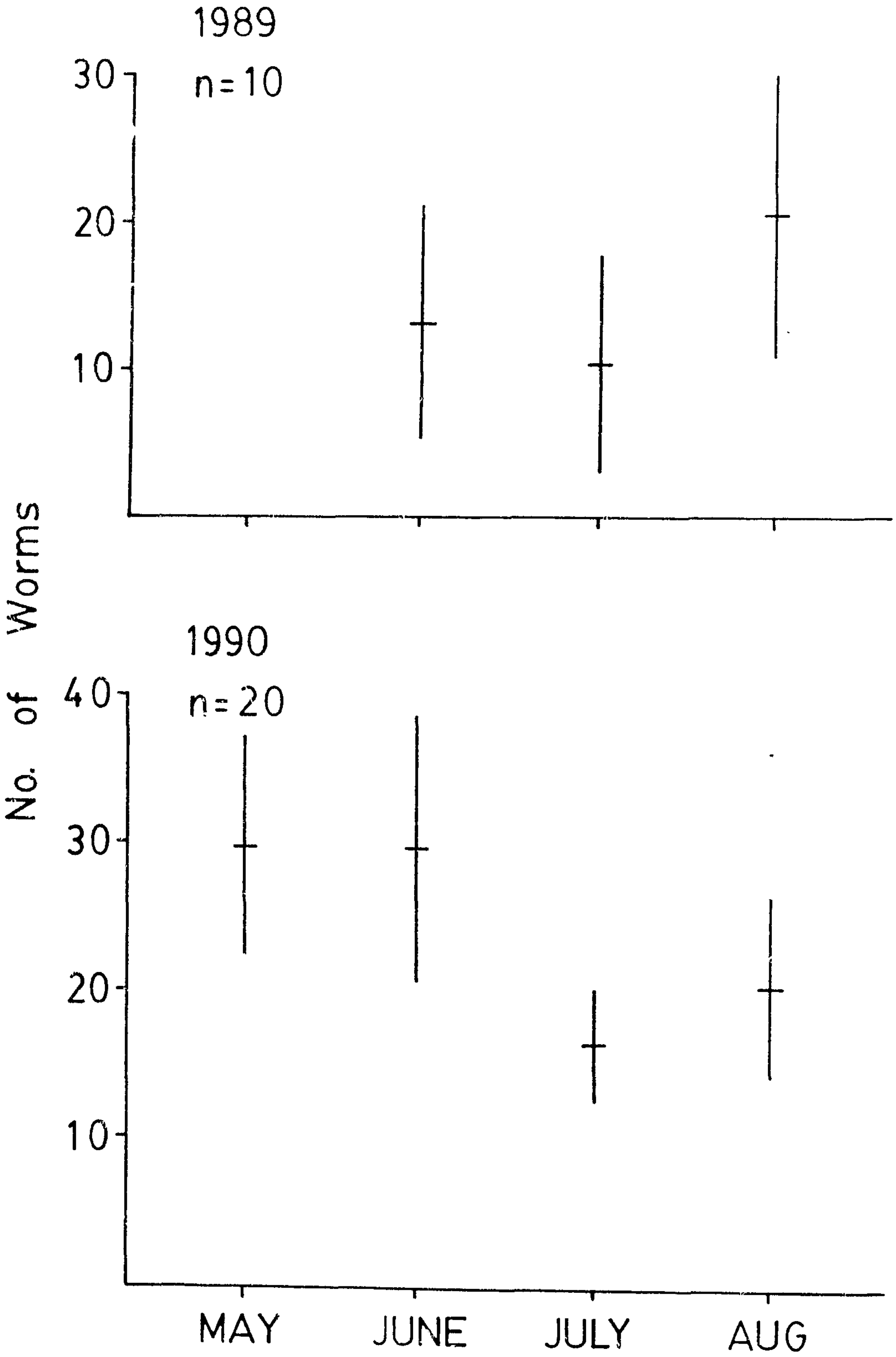

1989
n=10
30
20
10
1990
n=20
40
30
20
10
No. of Worms
MAY
JUNE
JULY
AUG

Figure 23. Distribution of small and large worms captured each month in 1990. Means are shown with 95% confidence limits and sample sizes (n) are the number of points sampled each month.

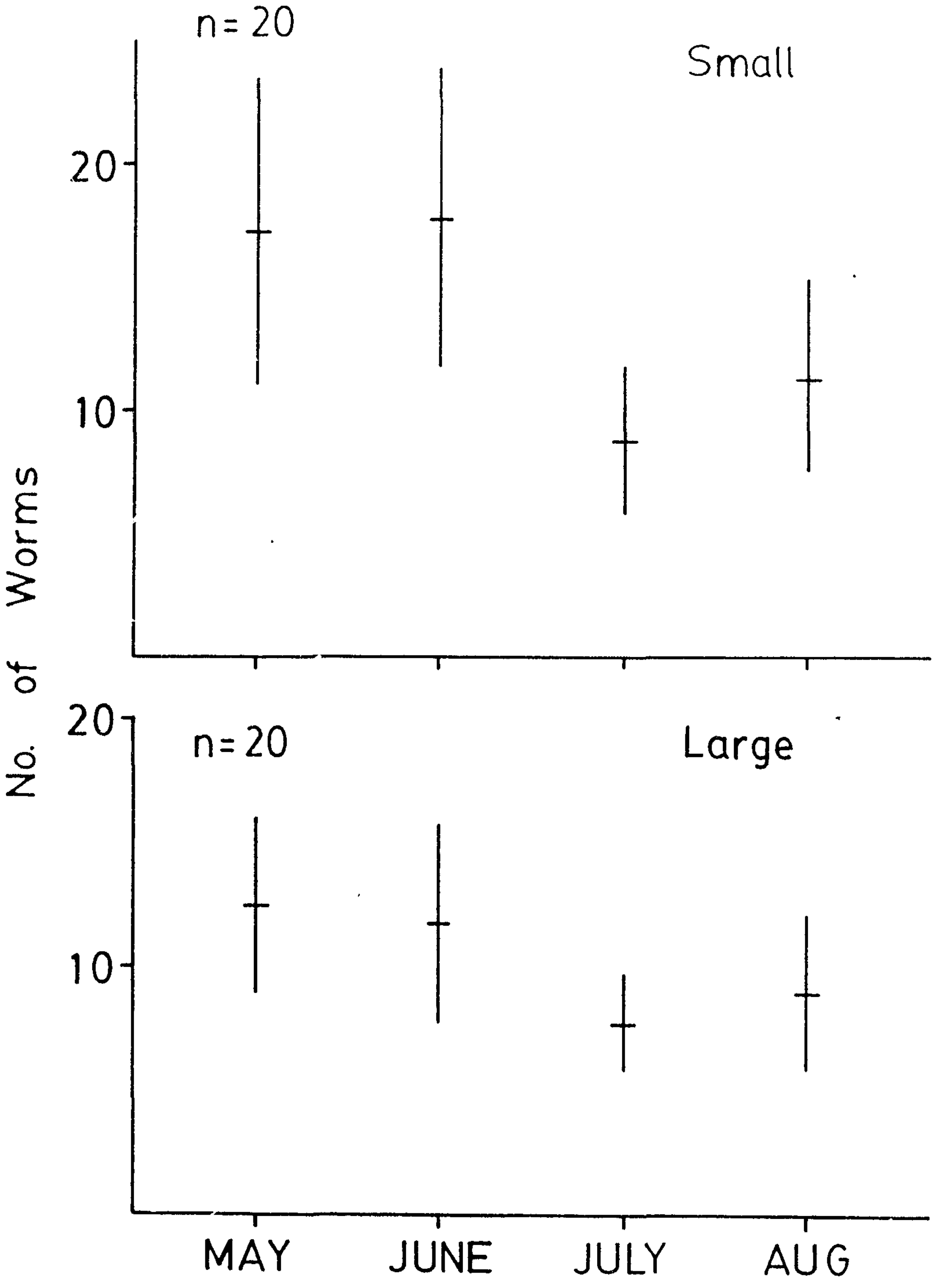
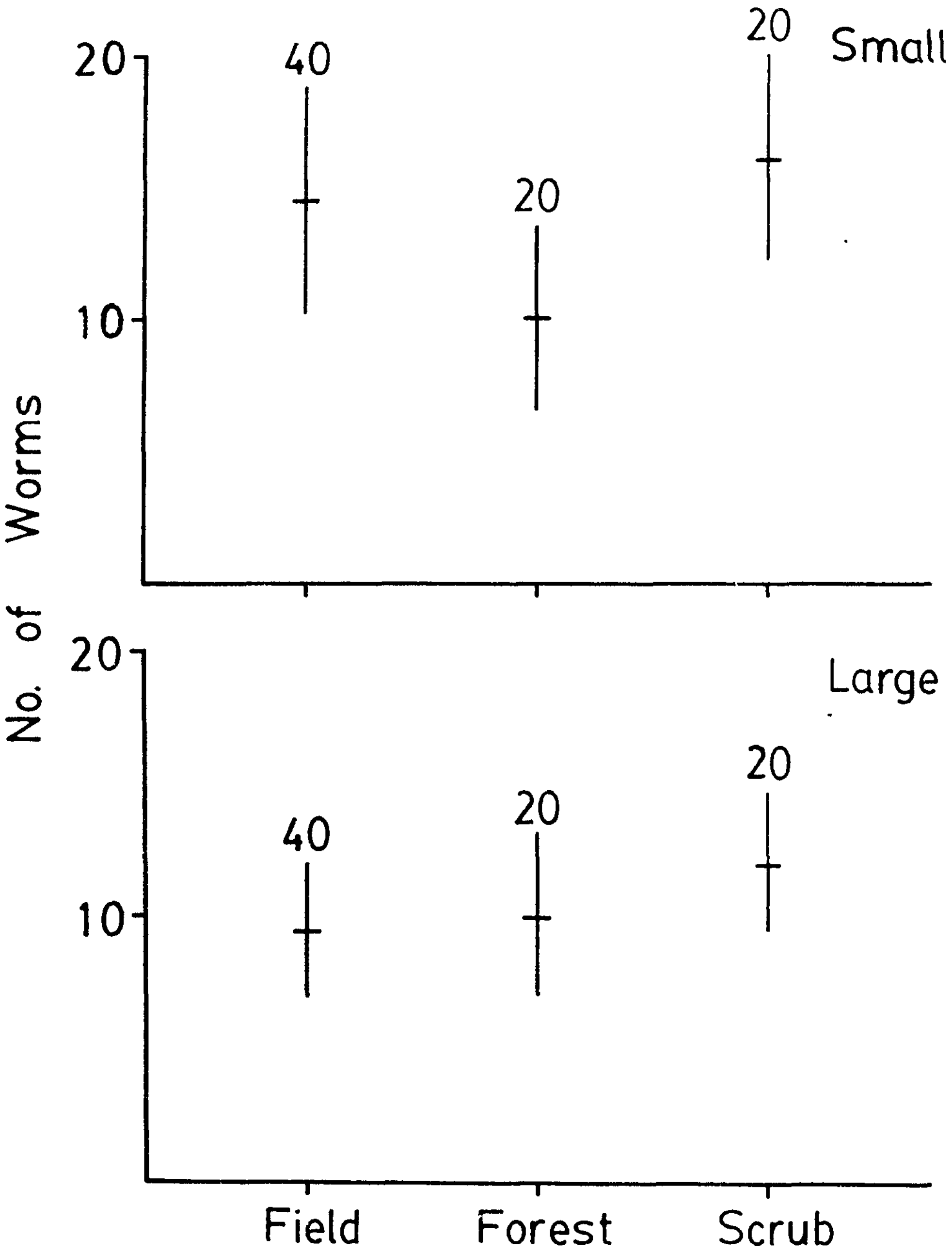

n= 20
Small
20
10
No. of Worms
20
n= 20
Large
10
MAY
JUNE
JULY
AUG

Figure 24. Distribution of small and large worms captured in each habitat type. Means are shown with 95% confidence limits. Sample sizes are the number of points sampled in each habitat type over the entire summer.


20
10
20
10
No. of Worms
40
20
20
Small
Large
40
20
20
Field
Forest
Scrub

habitat types.

Vole populations at Creston appear to follow a peak-to-trough cycle of 4-5 years (M. Dehn, personal communication). The summer of 1988 was a trough year in which voles were rare (M. Dehn, personal communication). However, population levels rose to near peak levels by the summer of 1990 (M. Dehn, personal communication) and voles were commonly seen crossing dykes on the CVWMA (personal observation). I sampled for evidence of vole activity only in 1990. Vole activity was highest in May, when 83% of the sampling points along the transects showed evidence of recent use (Fig. 25), usually fresh grass clippings along runways. This index of activity declined significantly during the summer to a low in July and August ($G=164.64$, $df=3$, $p<0.05$).

Thermal Environment

I measured water temperatures weekly at 10 sites around CCM2 from 6 June to 5 September 1990. Temperatures ranged from a low of 11.1 C (6 June) to a high of 28.8 C (18 July). A 1-way ANOVA indicated that mean water temperature varied significantly among days ($F=40.197$, $df=13, 126$, $p<<0.05$). In general, temperatures rose until mid-July and then fell (Fig. 26). However, there was a sharp decline in temperature between 18 and 25 July followed by a modest peak at 8 August.

Figure 25. Monthly proportion of sampling sites at which there were signs of recent vole activity. Proportions are shown ±95% confidence limits.

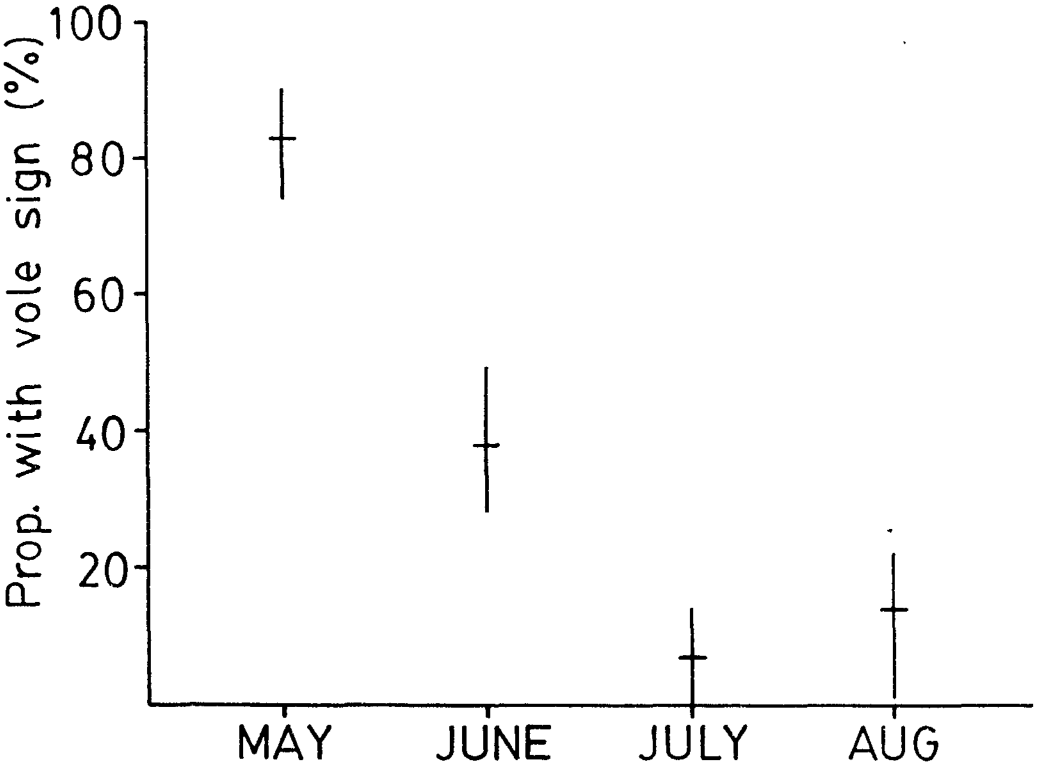
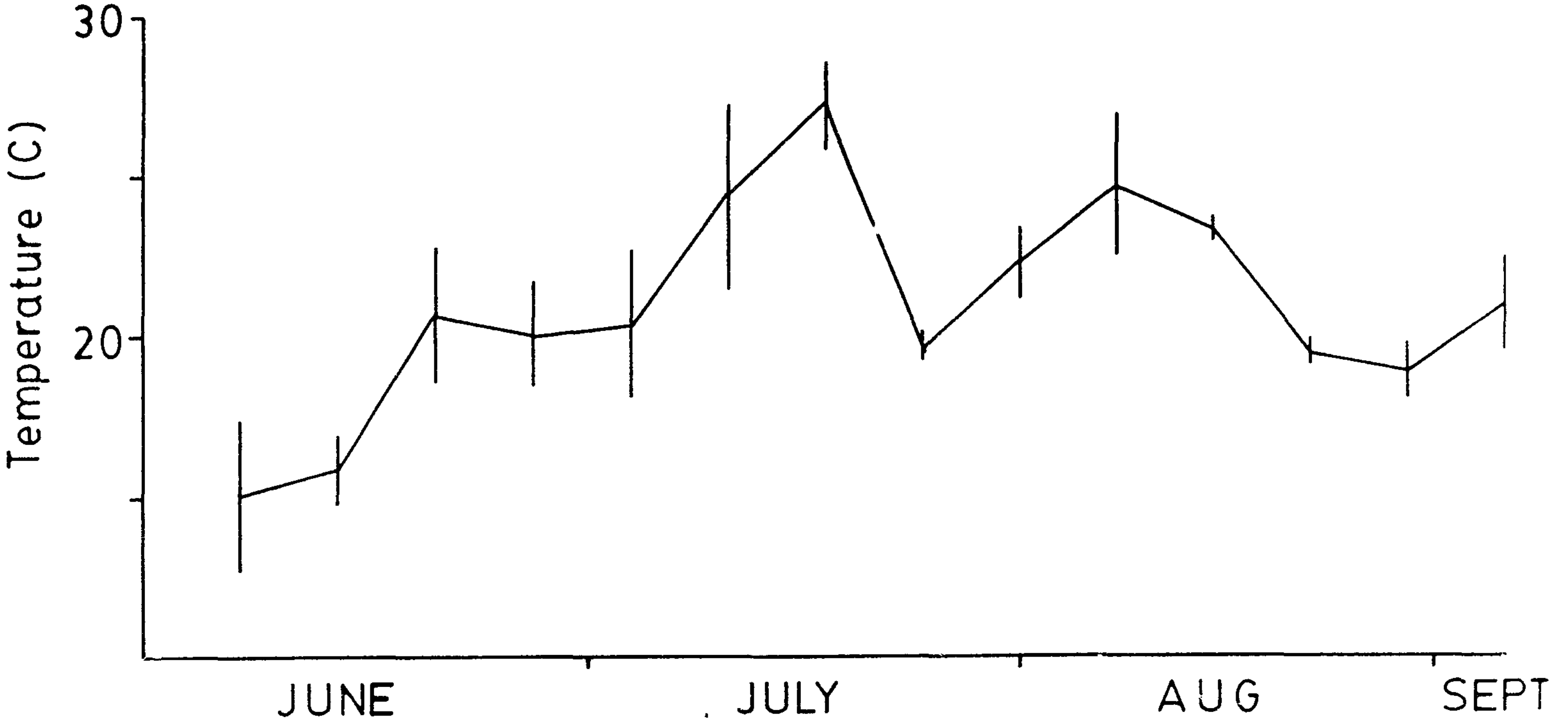

Prop. with vole sign (%)
100
80
60
40
20
MAY
JUNE
JULY
AUG

Figure 26. Average weekly water temperatures during 1990. Means are shown ±1 standard deviation, and n=10 for each mean.


30
20
Temperature (C)
JUNE
JULY
AUG
SEPT

Maximum terrestrial temperatures were measured using thermal models. However, I first determined that a single model type was suitable for comparisons with both *T. sirtalis* and *T. elegans*. Fig. 27 shows the results of paired comparisons in which I monitored the T_b of dead snakes of both species over a 12 h period. The slope of the least squares regression line was not significantly different from 1 ($F=0.318$, $df=1, 47$, $p>0.05$) and the intercept was not significantly different from 0 ($t=1.086$, $df=48$, $p>0.05$), indicating equality of T_b's. Thermal models containing 100 ml of water were reasonable predictors of snake T_b (Fig. 28), although the slope of the least squares regression line differed significantly from 1 ($F=154.561$, $df=1, 96$, $p<0.001$), and the model tended to slightly overestimate snake temperature. However, the Critical Maximum Temperature at which *Thamnophis* lose the ability to right themselves if turned over is approximately 40 C (Brattstrom 1965), so models clearly identified conditions too hot for snakes.

All models were placed in sites that received sunlight for the entire day. The highest temperature recorded was 72.9 C (July 1989) and the lowest 1.8 C (July 1989). The distribution of model temperatures collected shows largely the same pattern each year (Fig. 29). In 1988 and 1989, temperatures were below 20 C approximately 50% of the time and ≥40 C a further 25% of the time in both July and August.

Figure 27. Comparison of the T_b of *T. sirtalis* and *T. elegans* during 12 h trial. The trial took place from 0530-1730 on 10 July 1988. The line shown is the diagonal, where the temperatures of the two snakes are equal.

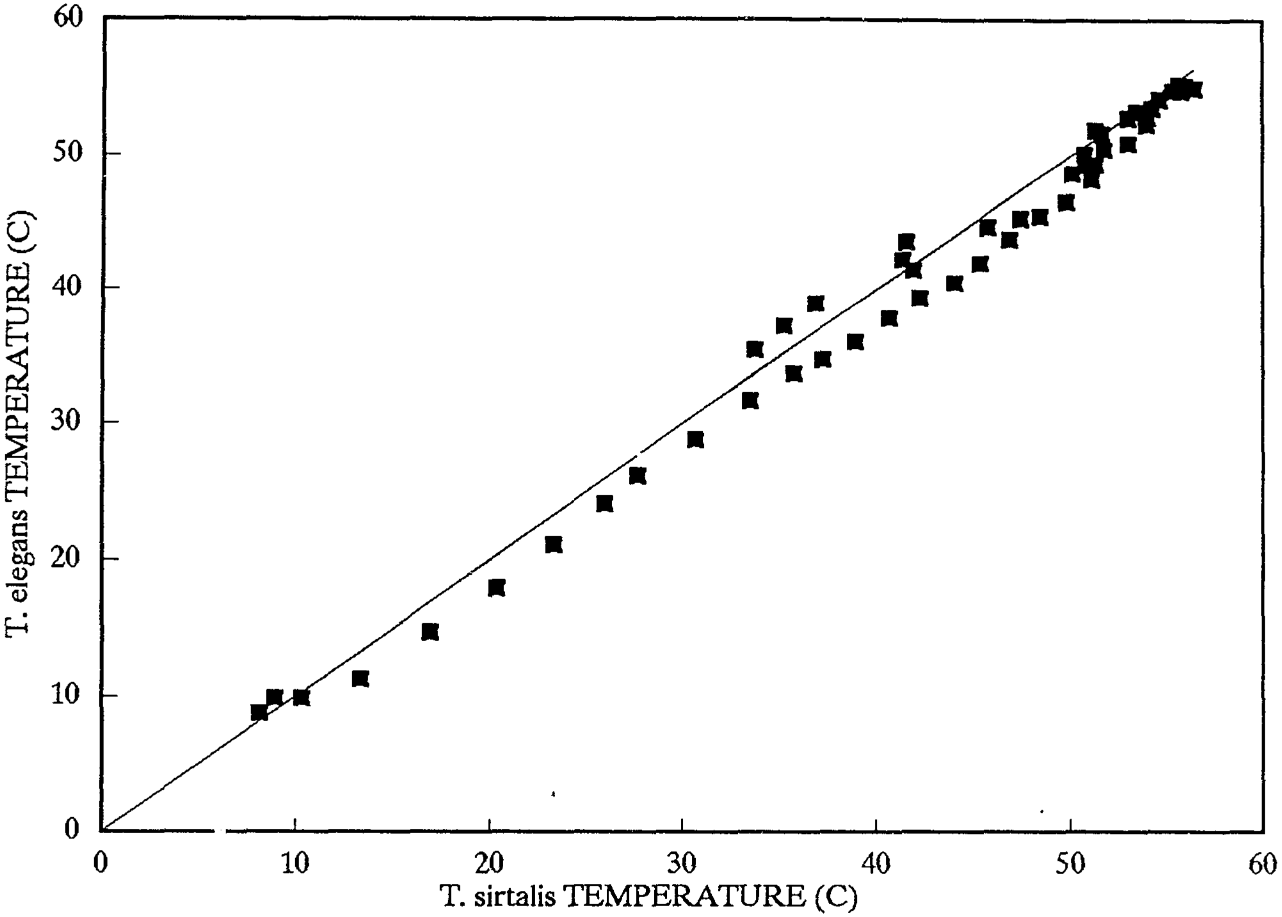

60
50
40
30
20
10
0
T. elegans TEMPERATURE (C)
0
10
20
30
40
50
60
T. sirtalis TEMPERATURE (C)

Figure 28. Comparison of snake and model temperatures during 12 h trials. Snake temperatures were taken simultaneously from one *T. sirtalis* and one *T. elegans*. The trials took place from on 10 July 1988 and 30 August 1990. The line extending through the origin is the diagonal where model and snake temperatures are equal. The other line is the least -squares regression line.

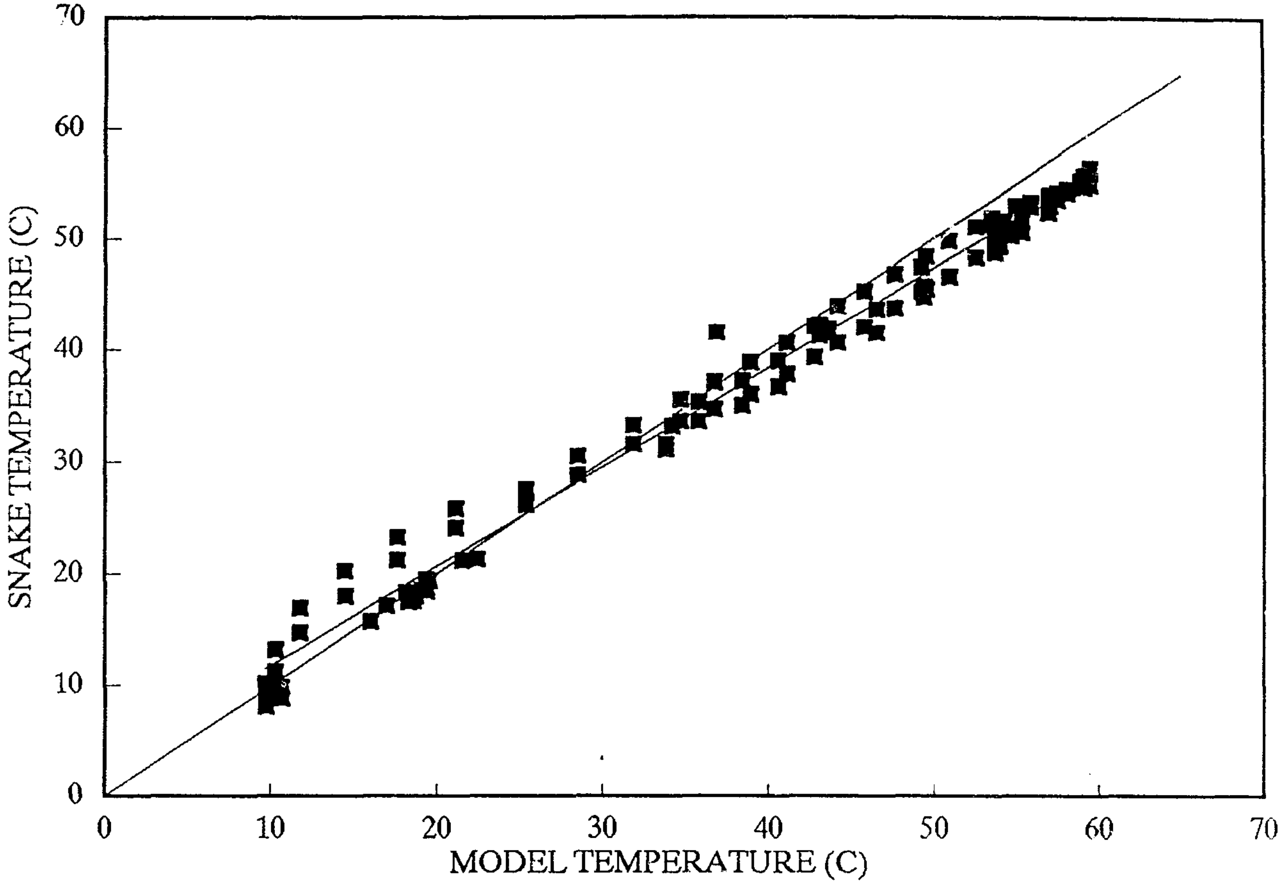
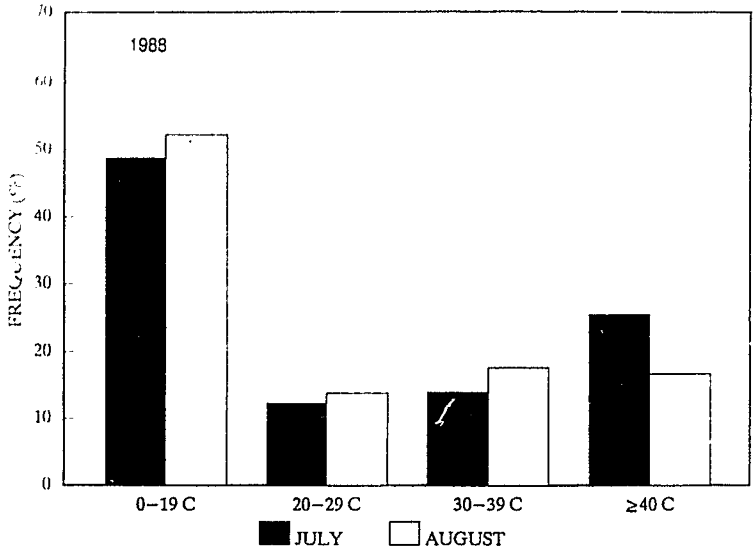
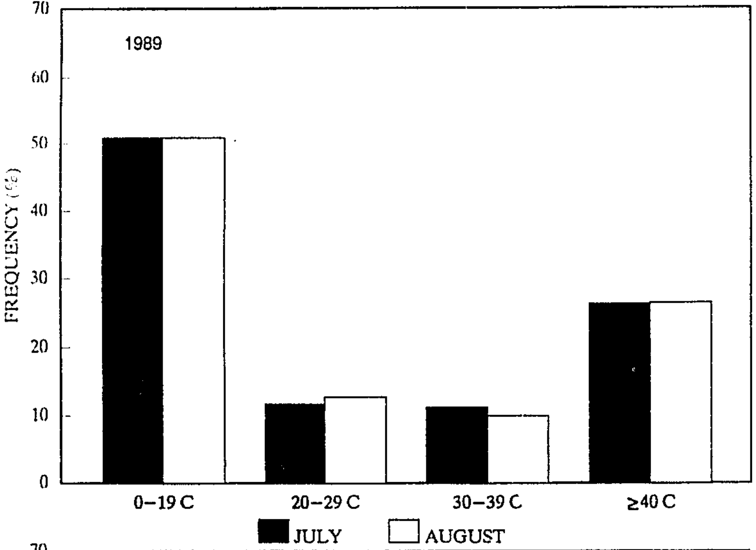
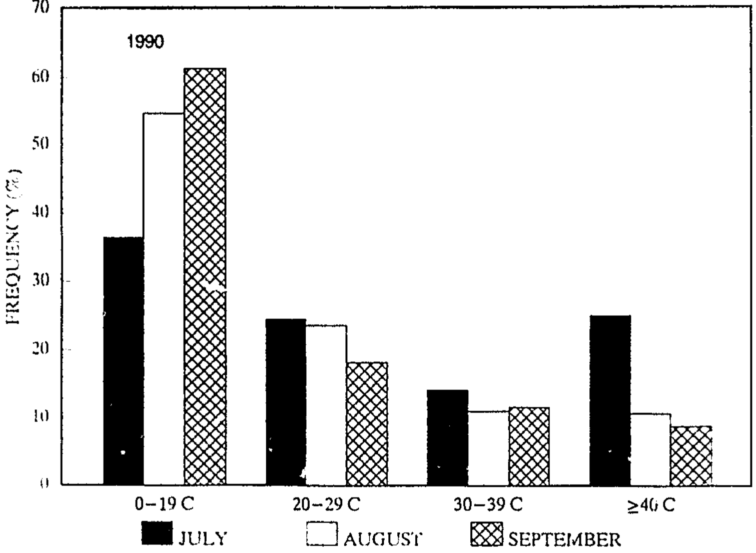

SNAKE TEMPERATURE (C)
0
10
20
30
40
50
60
70
MODEL TEMPERATURE (C)
0
10
20
30
40
50
60
70

Figure 29. Frequency distribution of exposed model temperatures.


1988
FREQUENCY (%)
0
10
20
30
40
50
60
70
0–19 C
20–29 C
30–39 C
≥40 C
JULY
AUGUST


1989
FREQUENCY (%)
0
10
20
30
40
50
60
70
0–19 C
20–29 C
30–39 C
≥40 C
JULY
AUGUST


1990
FREQUENCY (%)
0
10
20
30
40
50
60
70
0–19 C
20–29 C
30–39 C
≥40 C
JULY
AUGUST
SEPTEMBER

In 1990, I used a data logger to collect model temperatures every 3 min from 3-17 July and again from 7 August-7 September. Consequently, these data represent a less biased sample than for 1988/89, because I collected data for all days (24 h) and not just those on which I was also monitoring snake temperatures. A contingency table analysis indicated that the distribution of model temperautures was not independent of month (G=1082.16, df=6, p<0.05). This appeared to be due to a pronounced increase in the proportion of temperatures below 20 C between July and September, while the proportion of temperatures ≥40 C decreased over the same period. The proportion of temperatures between 20 and 39 C remained relatively constant each month.

During 1989, I measured differences in available temperature in different microhabitats by recording the temperatures of two models placed 1 m apart. One model was on the ground at a site exposed to sunlight for the entire day (exposed model), and the other model was placed on the ground in deep (approximately 1.5 m tall) grass (covered model). A comparison of the distribution of model temperatures at the two sites indicated that there were considerable differences in the temperatures available (Fig. 30). The covered model never exceeded 40 C, and had a maximum temperature of 33.6 C. The difference in temperature between the two models is shown in Fig. 31. For

Figure 30. Comparison of the frequency distributions of exposed and covered model temperatures.

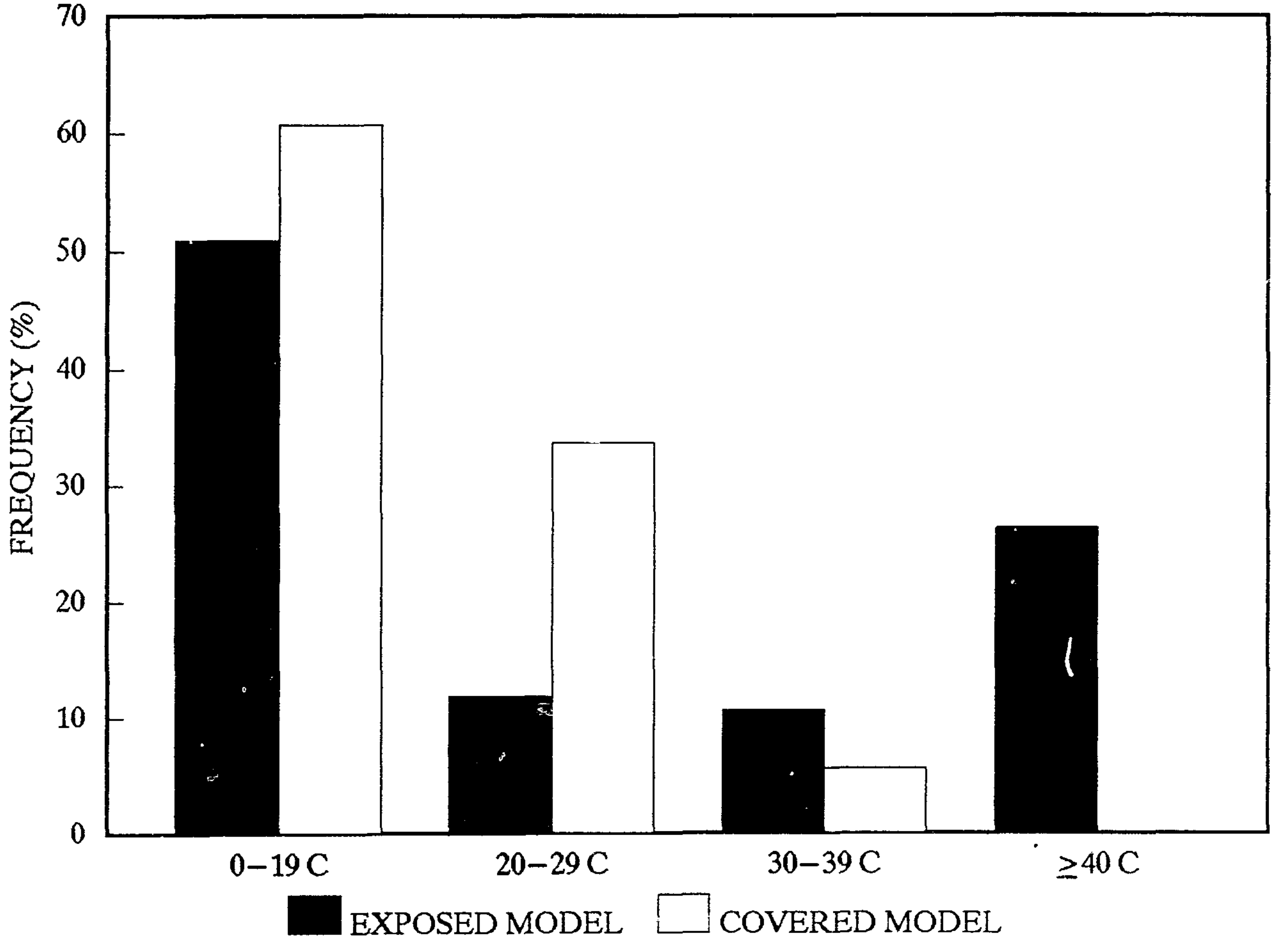
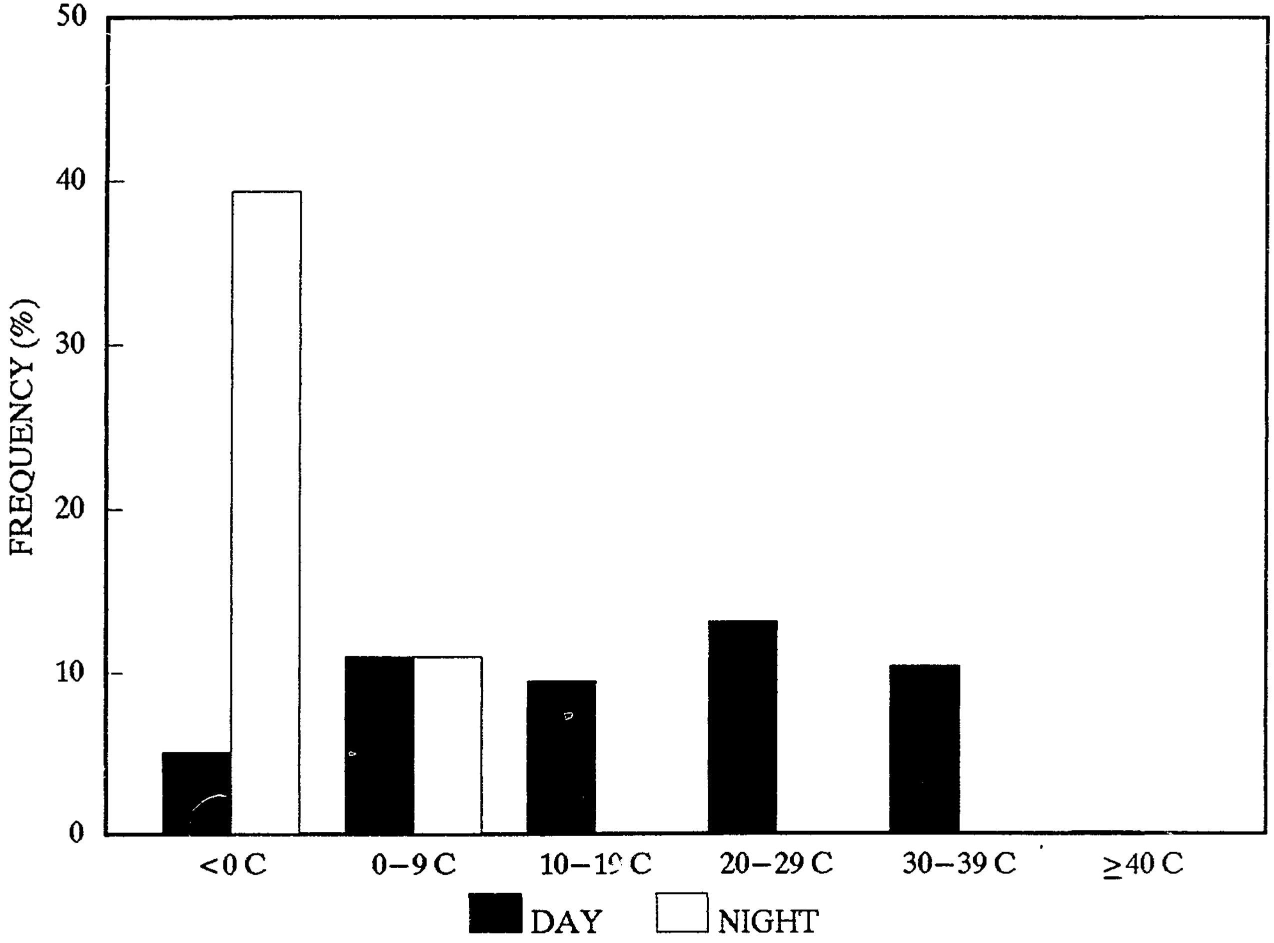

70
60
50
40
30
20
10
0
FREQUENCY (%)
0–19 C
20–29 C
30–39 C
≥40 C
EXPOSED MODEL
COVERED MODEL

Figure 31. Frequency distribution of the temperature difference between exposed and covered models. Temperature difference was calculated as $(T_{exp} - T_{cov})$. Day and night were arbitrarily defined as being 0600-1745 (day) and 1800-0545 (night).


50
40
30
20
10
0
FREQUENCY (%)
<0 C
0–9 C
10–19 C
20–29 C
30–39 C
≥40 C
DAY
NIGHT

almost 50% of the time (almost always at night) the covered model was warmer than the exposed model. However, during the day, the situation was reversed and the temperature of the exposed model exceeded that of the covered model by as much as 40 C.

Thermal Relations

I collected data on thermoregulation during the summers of 1988-90, from a total of 21 snakes (9 *T. elegans*, 12 *T. sirtalis*). The sample consisted of 15 gravid females (7 *T. elegans*, 8 *T. sirtalis*) and 6 nongravid females (2 *T. elegans*, 4 *T. sirtalis*). In 1988 I collected data from free-ranging animals exclusively, whereas the data from 1989 and 1990 were obtained from snakes in an outdoor enclosure. Overall, I was able to collect data on 36 complete days during the 3 summers (5 in 1988, 10 in 1989, and 21 in 1990), for a total of 177 snake-days (monitoring of 1 snake for 1 day = 1 snake-day) and more than 17,000 individual T_b measurements.

Plateau Thermoregulation

In order to make valid comparisons among groups it is necessary to restrict the analysis to periods when the snakes are able to thermoregulate freely. When temperatures available in the environment are low, a lack of difference between the two groups would occur simply as a result of this constraint. Consequently, I have used only data for the period 1200-1600 from days on which the temperature of exposed thermal models exceeded 38 C at least 80% of the time, and never went below 30 C at any time. These criteria were chosen so that comparisons between groups could be made when environmental temperatures exceeded the Critical Maximum Temperature of *Thamnophis* for the majority of the period. Under these circumstances, garter snakes exhibit stable body temperatures (Fig. 32) in what has been referred to as the plateau phase of thermoregulation (Peterson 1987). When model temperatures did not meet these criteria, the T_b of snakes was much more variable and reflected changes in MAT, as measured by the models (Fig. 33). In addition, I used only data collected before the birth of neonates so that any comparisons were made when I was certain that females were still carrying embryos. In 1988 and 1989, data collection ended before the birth of neonates. However, in 1990 the first neonates were observed in the enclosure on 7 August and I used only data collected prior to that date.

Mean T_b's for gravid females of both species are shown in Fig. 34. I performed repeated-measures ANOVAs (Day by Species), keeping each year separate, to determine whether restricting the data as I have done eliminated differences among days, and to test for differences between the species

Figure 32. Representative 24 h record of garter snake T_b showing plateau thermoregulation. Data were collected on 14-15 July, 1989.

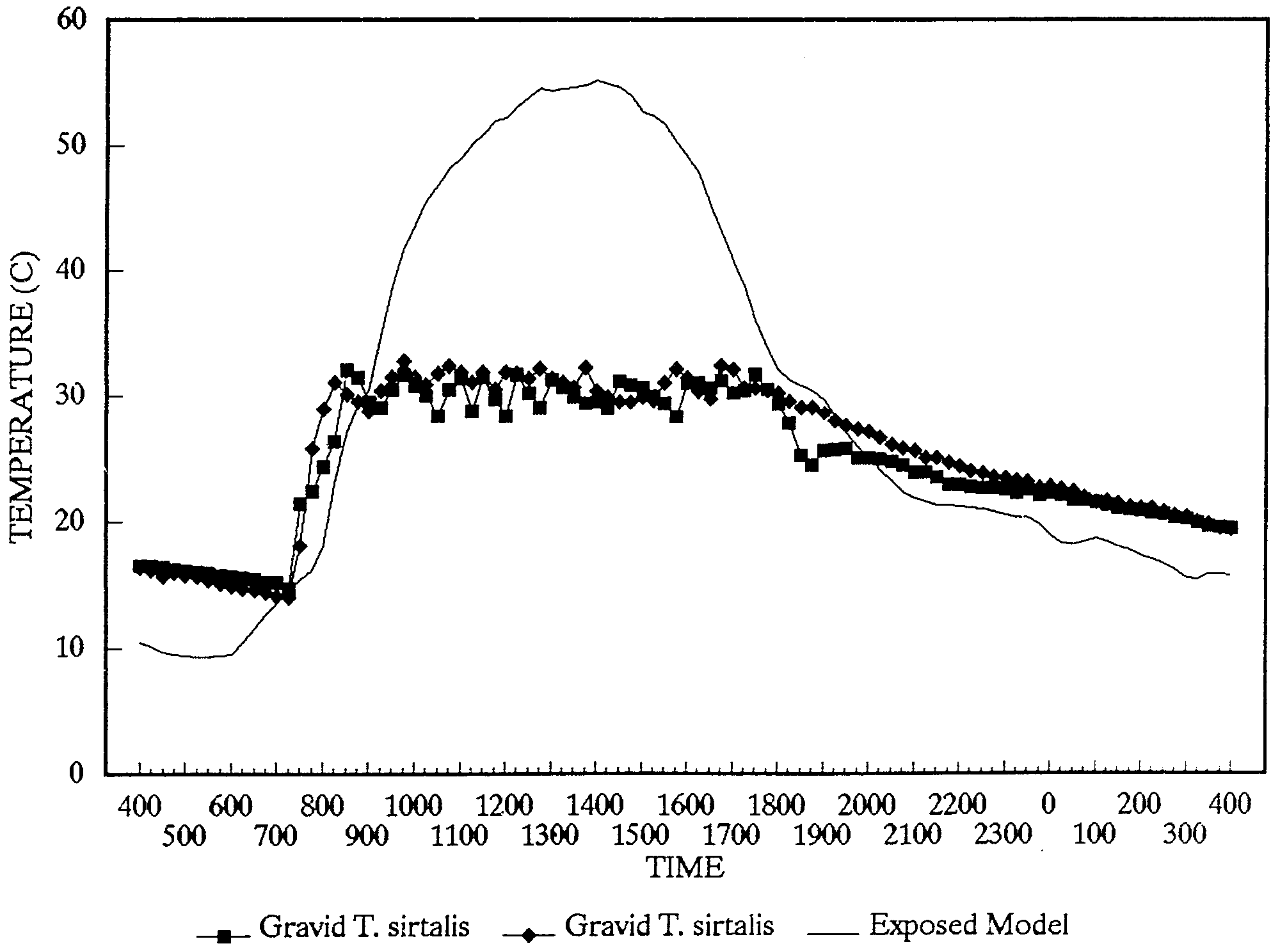
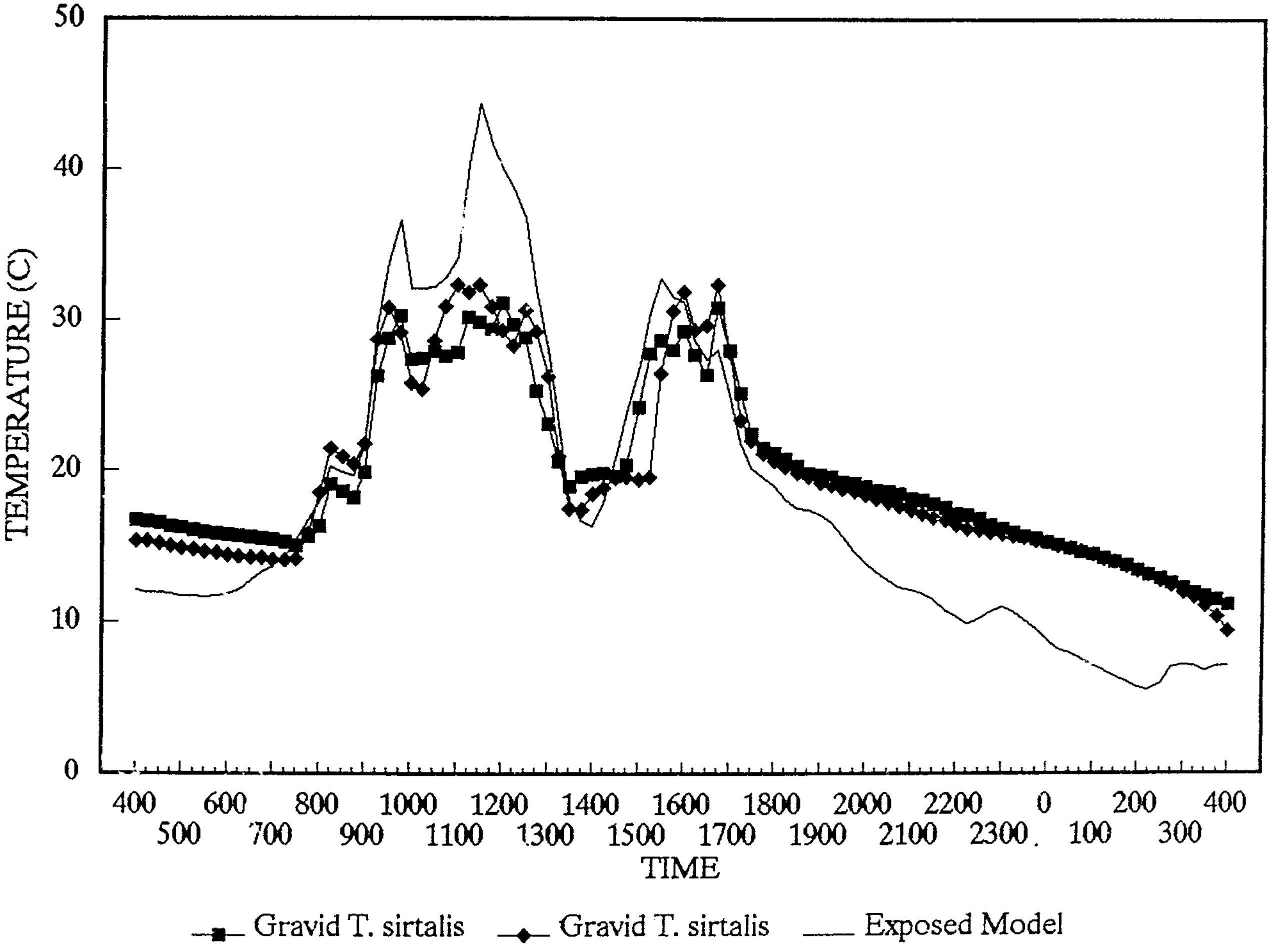
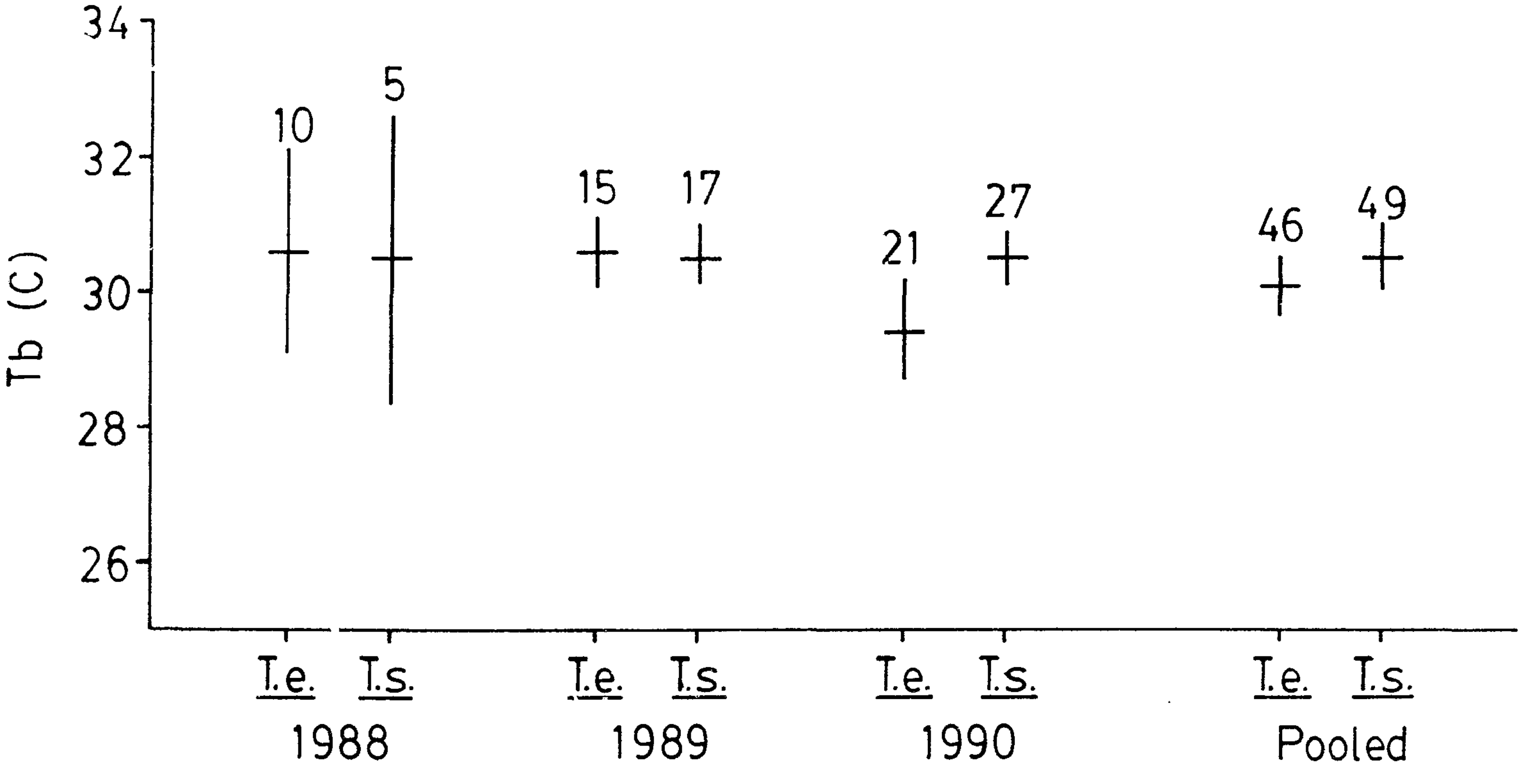

60
50
40
30
20
10
0
TEMPERATURE (C)
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
1700
1800
1900
2000
2100
2200
2300
0
100
200
300
400
TIME
Gravid T. sirtalis
Gravid T. sirtalis
Exposed Model

Figure 33. Representative 24 h record of garter snake T_b when model temperatures were not high for long enough to produce plateau thermoregulation. Data were collected on 10-11 July, 1989.



50
40
30
20
10
0
TEMPERATURE (C)
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
1700
1800
1900
2000
2100
2200
2300
0
100
200
300
400
TIME
Gravid T. sirtalis
Gravid T. sirtalis
Exposed Model

Figure 34. Mean T_b of gravid females during plateau phase thermoregulation. Each value plotted is the grand mean for that year and is shown with 95% confidence limits. Sample sizes are the number of means from which the grand mean was calculated and are the sample sizes used to calculate confidence limits.


34
32
30
28
26
Tb (C)
10
5
15
17
21
27
46
49
T.e.
T.s.
1988
T.e.
T.s.
1989
T.e.
T.s.
1990
T.e.
T.s.
Pooled

(Table 13). Temperatures were not significantly different among days in any of the three years, and there was no difference between the species in either 1988 or 1989. However, there was a significant difference in mean T_b between the two species in 1990, with the mean T_b of *T. elegans* being lower than that of *T. sirtalis*. This difference appeared to be largely due to consistently low T_bs from a single female (Fig. 35). There was no evidence to suggest that this individual was otherwise unusual. She was the first noted to have given birth in the enclosure that year, and subsequently captured and ate a large rodent.

The number of individual snakes monitored in a given year was small and I therefore performed a repeated-measures ANOVA to test for differences among years and species using the entire data set (Table 13). There was no difference among years or species and the interaction term was not significant.

The number of nongravid females was too small to allow me to compare their T_b's among years. Consequently, I pooled all data and simply tested for a difference between the two species (Table 14). Although the mean T_b of nongravid *T. elegans* was lower than that of *T. sirtalis* (Fig. 36), the difference was not significant. Because there were no species-specific differences in either gravid and nongravid females, I pooled the data for both species and tested for a difference between the two reproductive

Table 13. Repeated-measures ANOVA results for comparisons of mean T_b of gravid females within and among years.

Source	**SS**	**DF**	**MS**	**F**	**p**
1988					
Day	312.128	4	78.032	0.817	0.565
Species	1.136	1	1.136	0.012	0.917
Day X Species	104.521	4	26.130	0.274	0.883
Error	477.499	5	95.500		
1989					
Day	131.001	8	16.375	1.290	0.323
Species	0.383	1	0.383	0.030	0.865
Day X Species	82.143	8	10.268	0.809	0.606
Error	177.737	14	12.695		
1990					
Day	151.822	6	25.304	0.704	0.648
Species	241.211	1	241.211	6.712	0.014
Day X Species	92.406	6	15.401	0.429	0.855
Error	1221.777	34	35.935		
All Years					
Year	140.811	2	70.441	2.276	0.109
Species	26.976	1	26.976	0.872	0.353
Year X Species	135.045	2	67.522	2.182	0.119
Error	2754.682	89	30.951		

Figure 35. Plateau T_b of gravid females on 12 July 1990. Note the low, but stable, T_b of T.e. #3 compared with all of the other snakes.

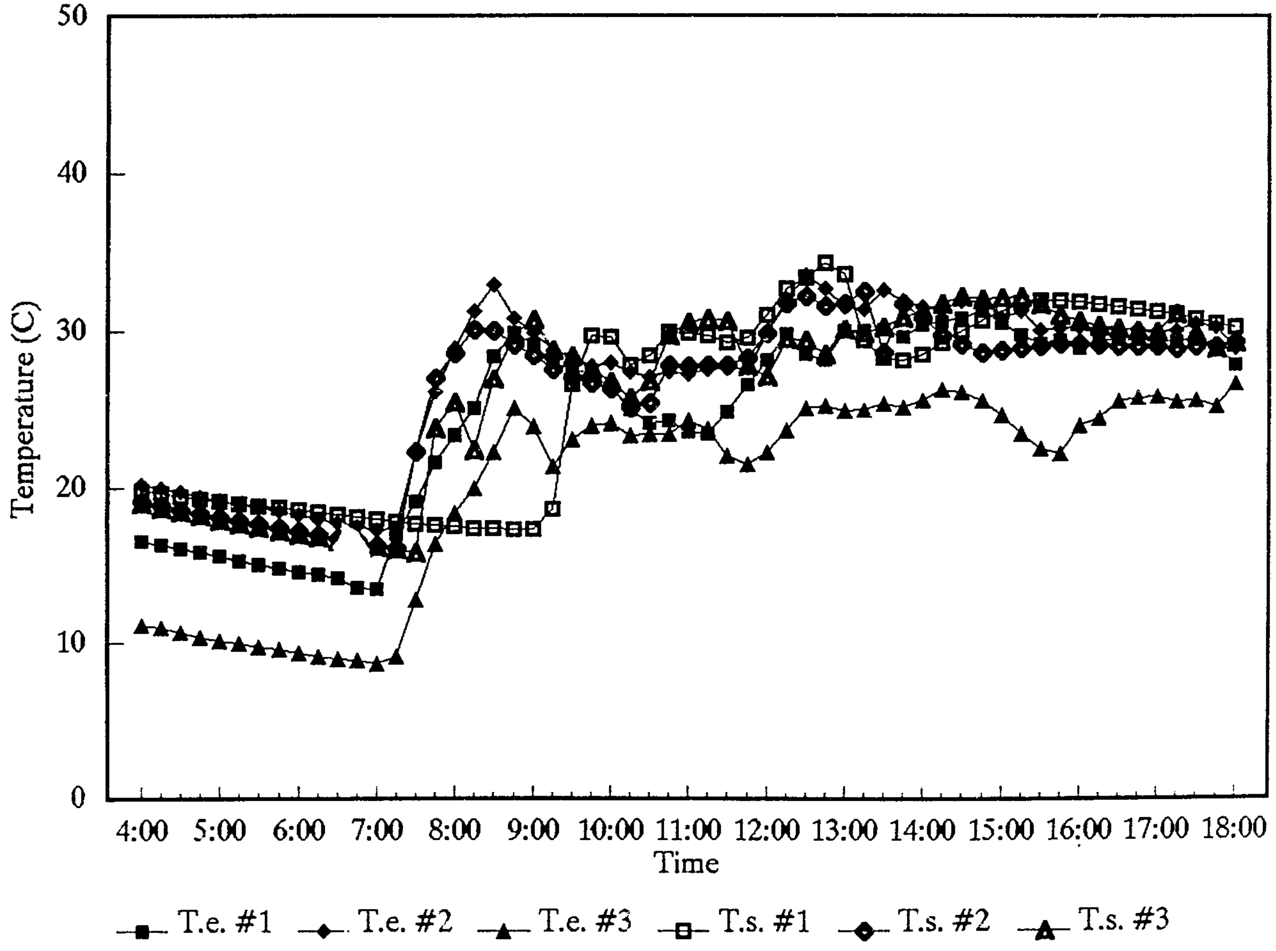
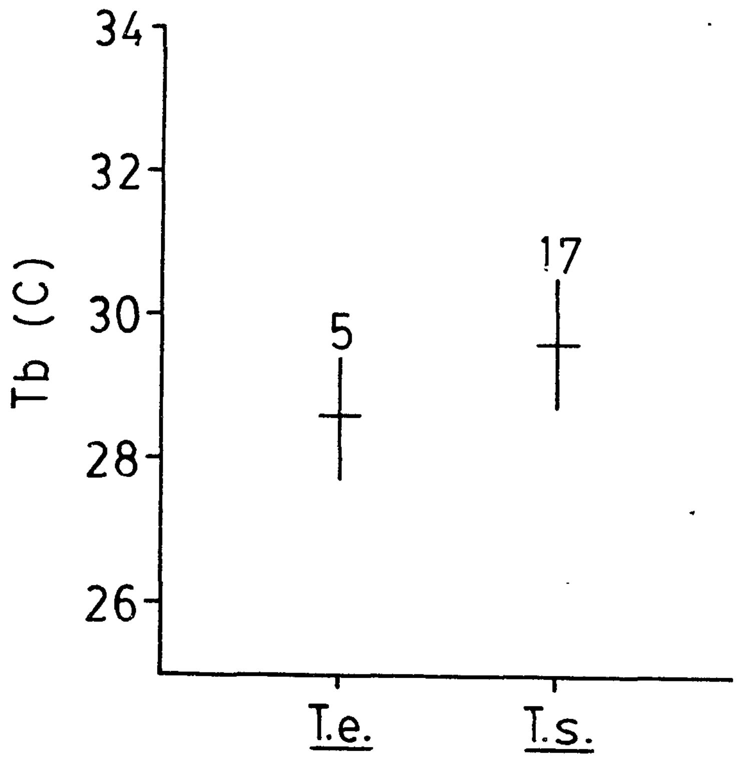

50
40
30
20
10
0
Temperature (C)
4:00
5:00
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
Time
T.e. #1
T.e. #2
T.e. #3
T.s. #1
T.s. #2
T.s. #3

Table 14 Repeated-measures ANOVA results for interspecific comparison of mean T_b of nongravid females, all years combined.

Source	**SS**	**DF**	**MS**	**F**	**p**
Species	72.610	1	72.610	1.609	0.219
Error	902.457	20	45.123		

Figure 36. Mean T_b of nongravid females during plateau phase thermoregulation. The values plotted are the grand means for each species and are shown with 95% confidence limits. Sample sizes are the number of means from which the grand mean was calculated and are the sample sizes used to calculate the confidence limits.


34
32
30
28
26
Tb (C)
5
17
T.e.
T.s.

conditions (Table 15). Gravid females had a significantly higher mean T_b than did nongravid females (Fig. 37).

In addition to examining mean T_b, I examined the precision of thermoregulation. I used the variance of mean T_b as my measure of precision, following the recommendation of Sievert and Hutchison (1988), with a low variance around mean T_b indicating high precision of thermoregulation. I calculated the variance for each individual in each 4 h plateau phase during the study, so that I could examine the average precision of thermoregulation by animals in the different groups.

The precision of thermoregulation by gravid females of the two species is shown in Fig. 38. The mean precision for gravid *T. elegans* in 1988 was much lower than for any other group. However, this appeared to be due to a single low temperature from one female. This animal was free-ranging and had a T_b above 30 C between 1200 and 1430. At 1445 her T_b dropped to 19.6 C and then rose again to 30 C over the following half-hour. The proximity of this animal to a pond suggests that she entered the water for a brief period. If this single low temperature is ignored, the mean precision increases substantially and the size of the 95% confidence limit is reduced by more than half. Because the snake was free-ranging and entered the water of her own accord, I have left this reading in all subsequent analyses. In spite of this, there were no significant differences in precision

Table 15. Repeated-measures ANOVA results for comparison of mean T_b between gravid and nongravid females, all years and both species combined.

Source	**SS**	**DF**	**MS**	**F**	**p**
Reproductive Condition	256.166	1	256.166	7.208	0.008
Error	4086.884	115	35.538		

Figure 37. Comparison of mean T_b of gravid and nongravid females during plateau phase. The values plotted are the grand means for each reproductive group and are shown with 95% confidence limits. Sample sizes are the number of means from which the grand mean was calculated and are the sample sizes used to calculate confidence limits.

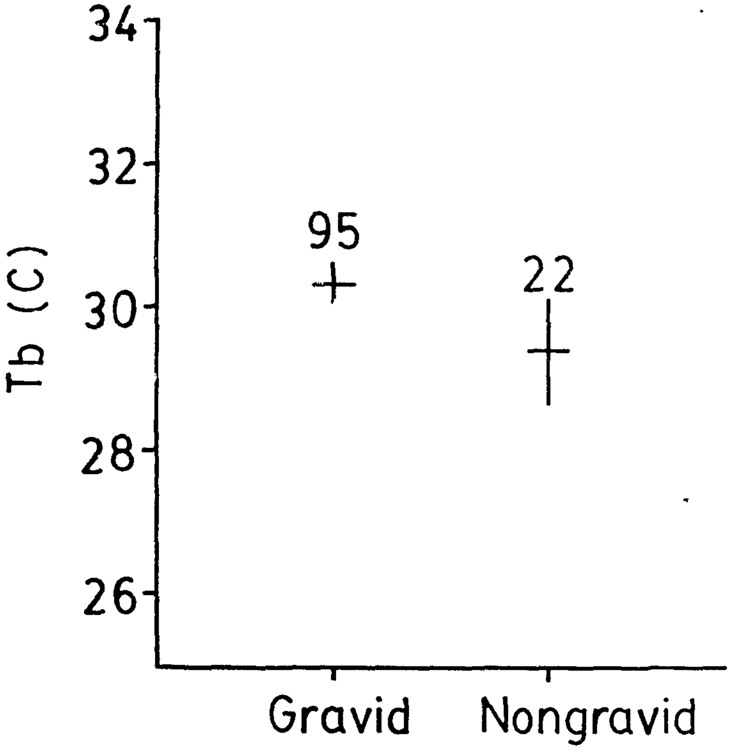
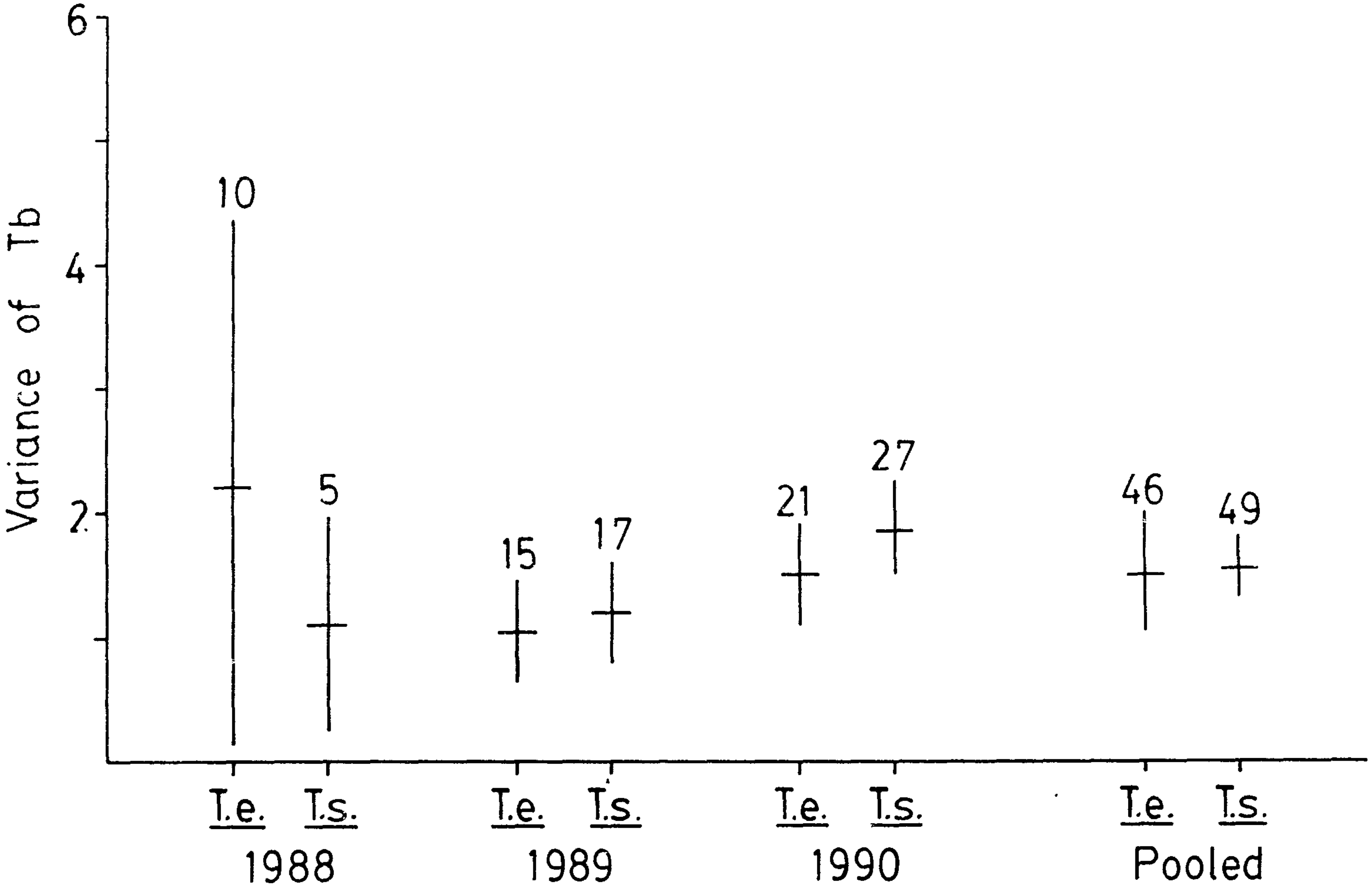

34
32
30
28
26
Tb (C)
95
22
Gravid
Nongravid

Figure 38. Precision of thermoregulation by gravid females during plateau phase. Means are shown with 95% confidence limits and sample sizes.


6
4
2
Variance of Tb
10
5
15
17
21
27
46
49
T.e.
T.s.
T.e.
T.s.
T.e.
T.s.
T.e.
T.s.
1988
1989
1990
Pooled

among days or between species for any of the three years and there were no significant interactions (Table 16). In addition, I found no differences among years or between species when the data for all three years were pooled (Table 16).

There was no significant difference in precision of thermoregulation between nongravid females of the two species (Table 17), although *T. elegans* tended to show higher precision than did *T. sirtalis* (Fig. 39). Because there were no differences between species for either gravid or nongravid females, I pooled the data by species and tested for a difference between the two reproductive conditions (Table 18). There was a significant difference, with gravid females showing much higher precision of thermoregulation than nongravid females (Fig. 40).

It has been suggested that poikilotherms thermoregulate between an upper and lower set point, rather than around a single preferred temperature (Heath 1970). If this is the case, then differences in patterns of T_b variation between gravid and nongravid females may also be reflected in the maximum (T_{max}) and minimum (T_{min}) temperatures during plateau thermoregulation. Plots of T_{max} and T_{min} against mean T_b for gravid and nongravid females (Fig. 41) revealed such differences. Gravid females showed largely the same difference between T_{max} and T_{min} regardless of mean T_b, although the the slopes of the two lines differed

Table 16. One-way ANOVA results for within and among years comparisons of precision of thermoregulation by gravid females.

Source	**SS**	**DF**	**MS**	**F**	**p**
1988					
Day	11.732	4	2.933	0.279	0.880
Species	4.401	1	4.401	0.418	0.546
Day X Species	7.309	4	1.827	0.174	0.943
Error	52.633	5	10.527		
1989					
Day	7.180	8	0.898	1.999	0.123
Species	0.298	1	0.298	0.663	0.429
Day X Species	2.874	8	0.359	0.800	0.613
Error	6.287	14	0.449		
1990					
Day	3.707	6	0.618	0.774	0.596
Species	1.781	1	1.781	2.231	0.144
Day X Species	7.144	6	1.191	1.492	0.211
Error	27.141	34	0.798		
All Years					
Year	6.502	2	3.251	2.169	0.120
Species	0.837	1	0.837	0.558	0.457
Year X Species	5.988	2	2.994	1.998	0.142
Error	133.368	89	1.499		

Table 17. One-way ANOVA results for between species comparison of precision of thermoregulation by nongravid females, all years combined.

Source	**SS**	**DF**	**MS**	**F**	**p**
Species	57.139	1	57.139	1.257	0.276
Error	909.405	20	45.470		

Figure 39. Precision of thermoregulation by nongravid females during plateau phase. Means are shown with 95% confidence limits and sample sizes.

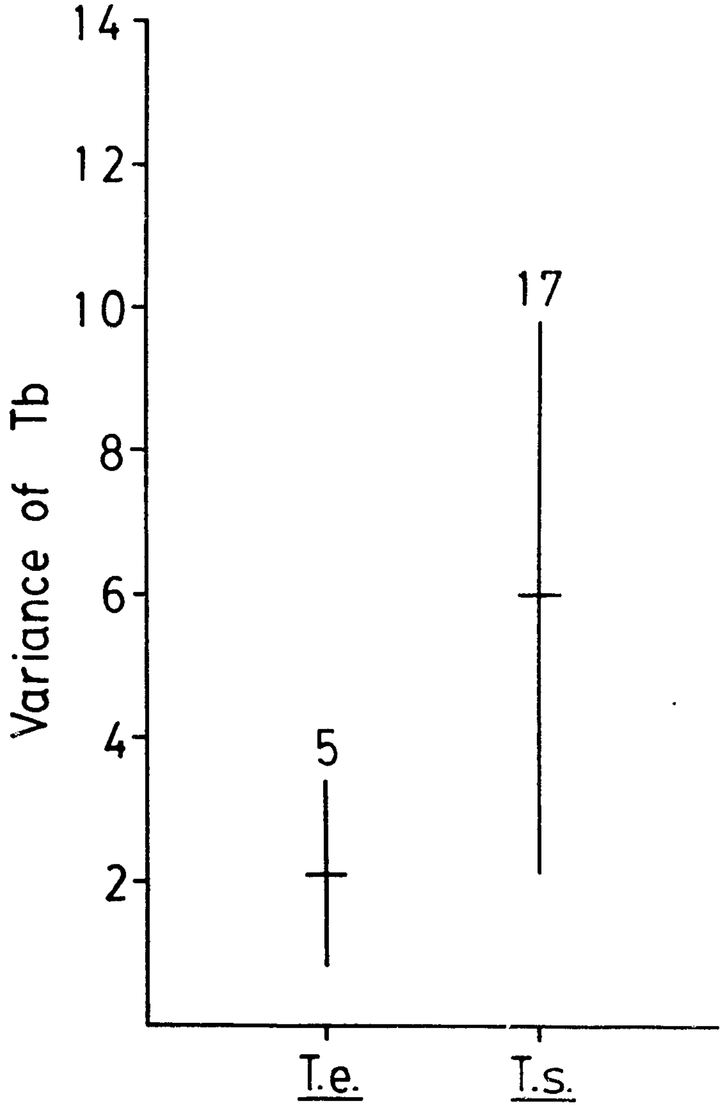

Variance of Tb
14
12
10
8
6
4
2
5
17
T.e.
T.s.

Table 18. Comparison of precison of thermoregulation between gravid and nongravid females, all years and both species combined, using one-way ANOVA.

Source	**SS**	**DF**	**MS**	**F**	**p**
Reproductive Condition	225.289	1	225.289	23.249	0.000
Error	1114.398	115	9.690		

Figure 40. Comparison of precision of thermoregulation by gravid and nongravid females during plateau phase. Means are shown with 95% confidence limits and sample sizes.

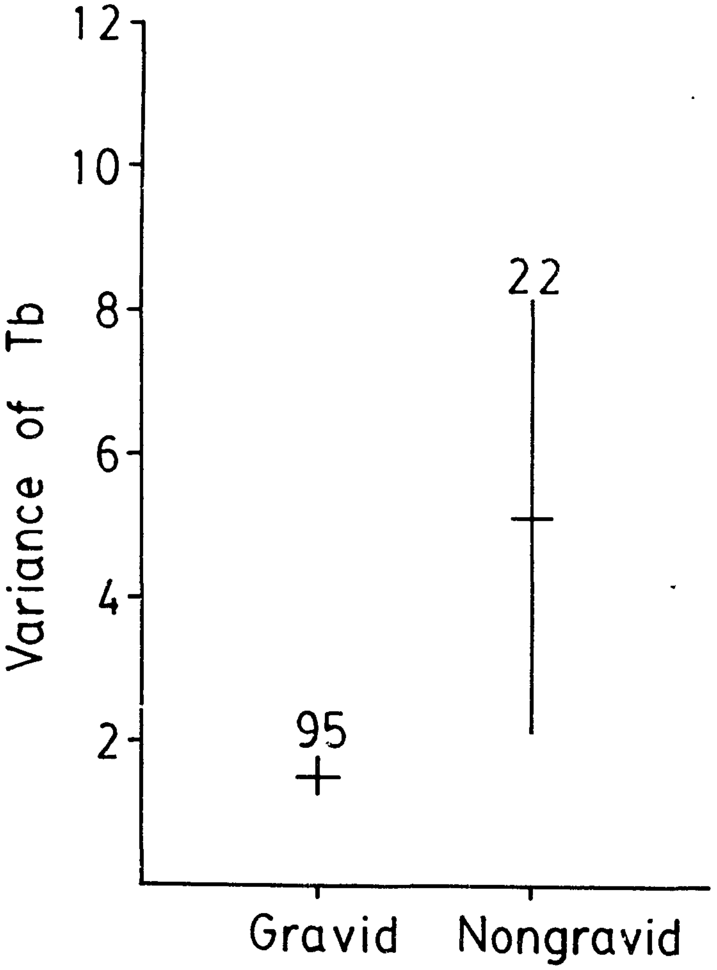

12
10
8
6
4
2
Variance of Tb
22
95
Gravid
Nongravid

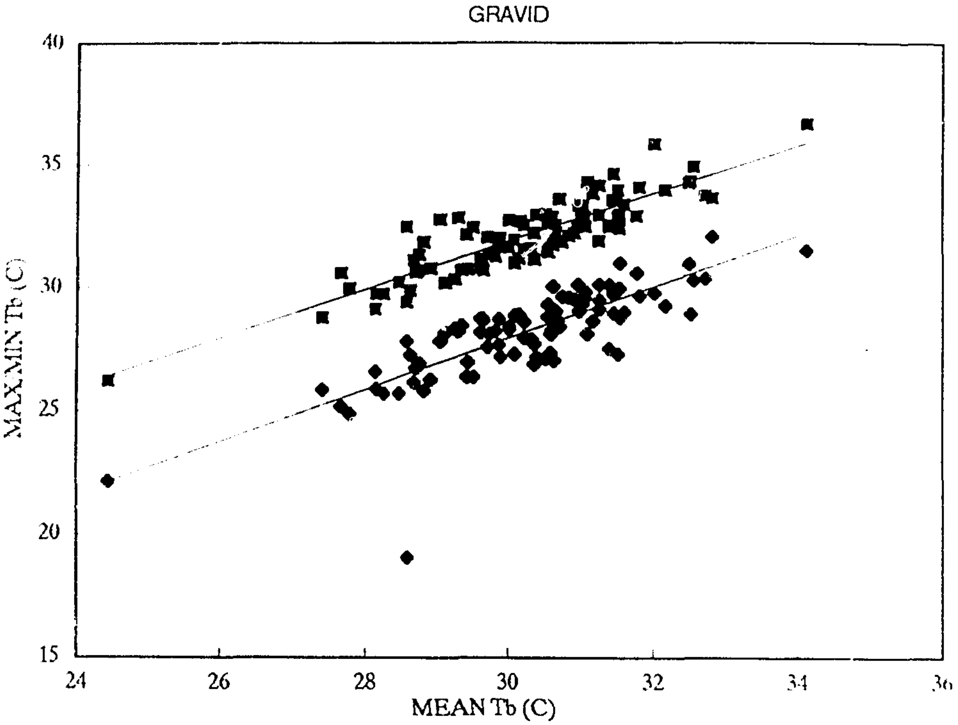
Figure 41. Maximum and minimum T_b during plateau thermoregulation plotted against mean T_b for gravid and nongravid females. The equations of the lines are:

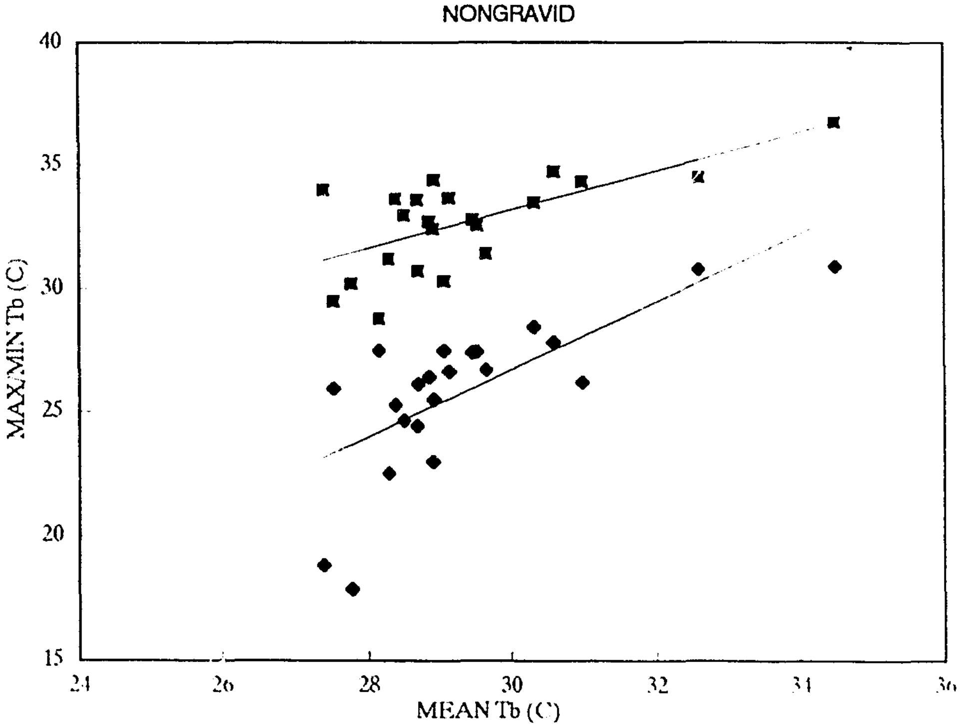
Gravid (n=95):

$$\text{Max} = 2.294 + 0.985(\text{Mean})$$
$$\text{Min} = -3.379 + 1.043(\text{Mean})$$

Nongravid (n=22):

$$\text{Max} = 9.898 + 0.775(\text{Mean})$$
$$\text{Min} = -14.089 + 1.360(\text{Mean})$$


GRAVID
MAX/MIN Tb (C)
MEAN Tb (C)
15
20
25
30
35
40
24
26
28
30
32
34
36

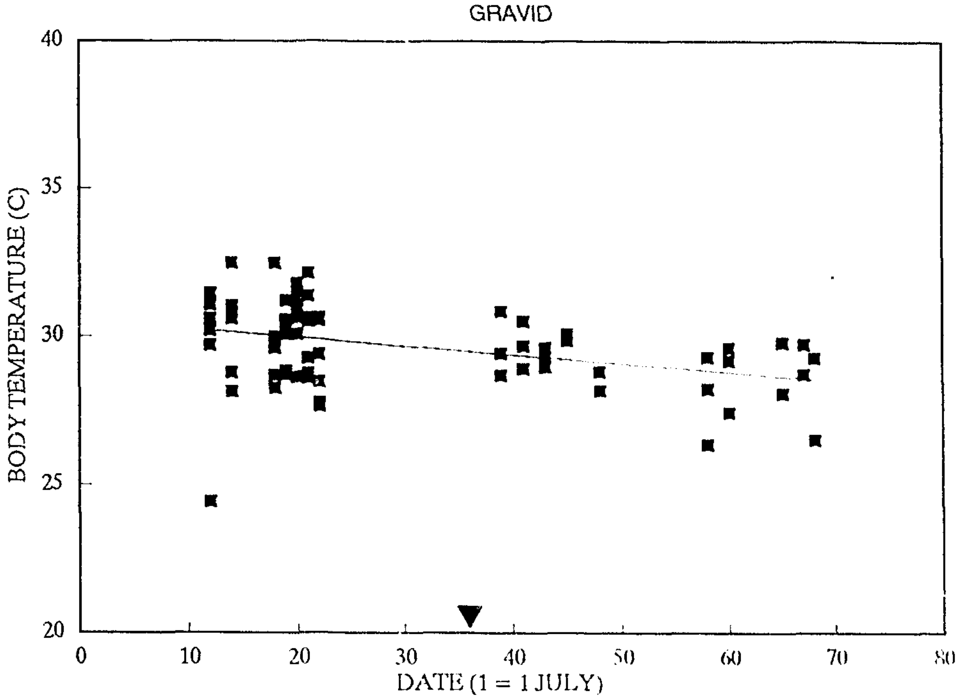

NONGRAVID
MAX/MIN Tb (C)
MEAN Tb (C)
15
20
25
30
35
40
24
26
28
30
32
34
36

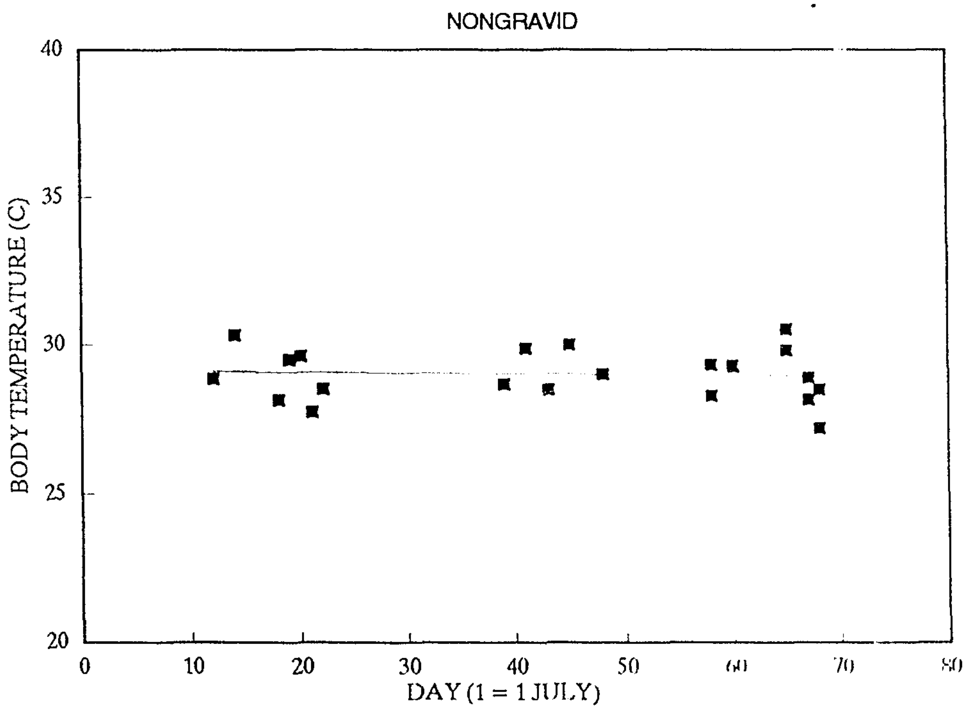
significantly ($t=12.775$, df= 186, $p<0.05$). Nongravid females showed a much wider difference at low mean T_b than at high mean T_b, and, again, the slopes of the two lines differed significantly ($t=29.817$, df=40, $p<0.05$). A comparison of the slopes of the lines between reproductive groups indicated significant differences in both the T_{max} ($t=28.417$, df=113, $p<0.05$) and T_{min} ($t=28.559$, df=113, $p<0.05$) lines.

If the differences in the pattern of T_b variation between gravid and nongravid females are simply a function of reproductive condition then they should disappear following parturition. I collected data following parturition only in 1990 and the weather was not warm enough to meet the requirements set initially in the analysis of plateau thermoregulation. However, by relaxing the criteria slightly and including days on which thermal model temperatures exceeded 32 C (above the mean T_b of both gravid and nongravid females) at least 80% of the time, I was able to use data collected between 12 July and 6 September.

Gravid females showed a significant decline in mean T_b following the observation of the first neonates in the enclosure ($r=-0.371$, $n=74$, $p<0.05$), whereas the mean T_b of nongravid females showed no change ($r=0.073$, $n=22$, $p>0.05$). By the end of August, the mean T_bs of gravid females (now post partum) appeared to be the same as those of nongravid females (Fig. 42). Similarly, gravid females showed a

Figure 42. Seasonal patterns of mean Tb during plateau phase for gravid and nongravid females in 1990. The triangle indicates the date on which the first neonates were observed in the enclosure.


GRAVID
BODY TEMPERATURE (C)
40
35
30
25
20
0
10
20
30
40
50
60
70
80
DATE (1 = 1 JULY)

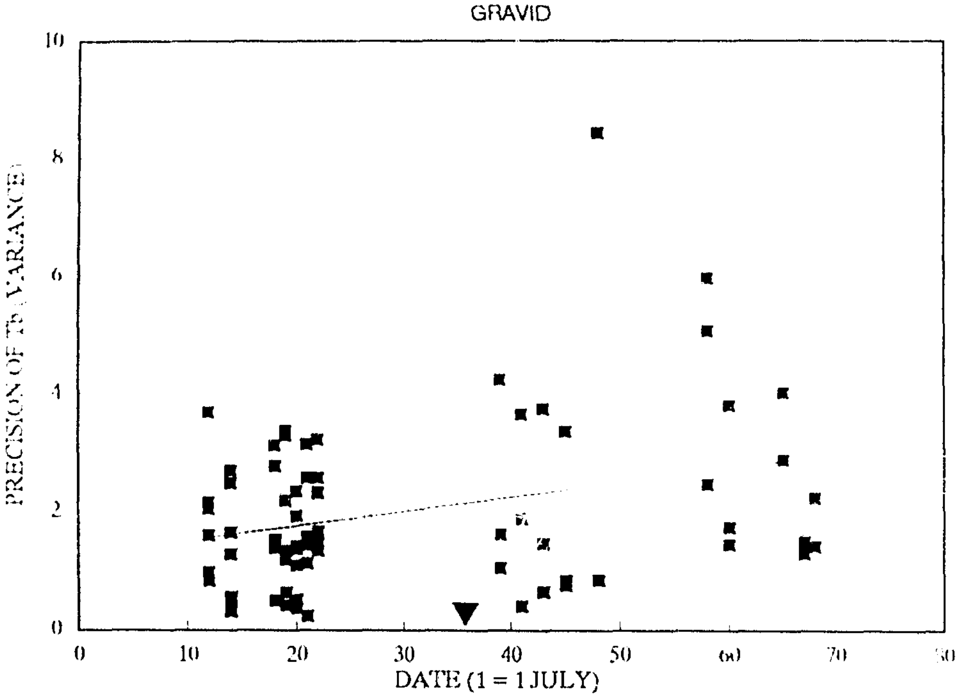

NONGRAVID
BODY TEMPERATURE (C)
40
35
30
25
20
0
10
20
30
40
50
60
70
80
DAY (1 = 1 JULY)

decrease in the precision of thermoregulation (=increased variance) following the first sighting of neonates in the enclosure ($r=0.307$, $n=74$, $p<0.05$), whereas nongravid females showed no change ($r=0.029$, $n=22$, $p>0.05$) during the same period. Once again, the formerly gravid females appeared to be similar to the nongravid females by late August (Fig. 43).

Nighttime Body Temperatures

Differences in the pattern of T_b variation between gravid and nongravid females may also be manifested in the selection of warmer nighttime retreat sites by gravid females. However, it is difficult to standardize conditions for a comparison of nighttime T_bs. Consequently, I used the average T_b for the period between 0000 and 0400 as a measure of nighttime T_b, and plotted it against the mean temperature of the exposed model during the same period, for all nights for which I had complete data for both snakes and models (Fig. 44). There was no correlation between snake and model temperatures for either gravid ($r=0.204$, $n=47$, $p>0.05$) or nongravid females ($r=0.147$, $n=12$, $p>0.05$). Furthermore, snakes in both groups were substantially warmer than the model at all times. The mean model temperature was 10.7±2.7 C ($n=59$) whereas gravid females had a mean T_b of 21.2±3.7 C ($n=47$) and nongravid females had a mean T_b of

Figure 43. Seasonal patterns of precision of thermoregulation during plateau phase for gravid and nongravid females in 1990. The triangle indicates the date on which the first neonates were observed in the enclosure.


GRAVID
PRECISION OF Tb (VARIANCE)
10
8
6
4
2
0
0
10
20
30
40
50
60
70
80
DATE (1 = 1 JULY)

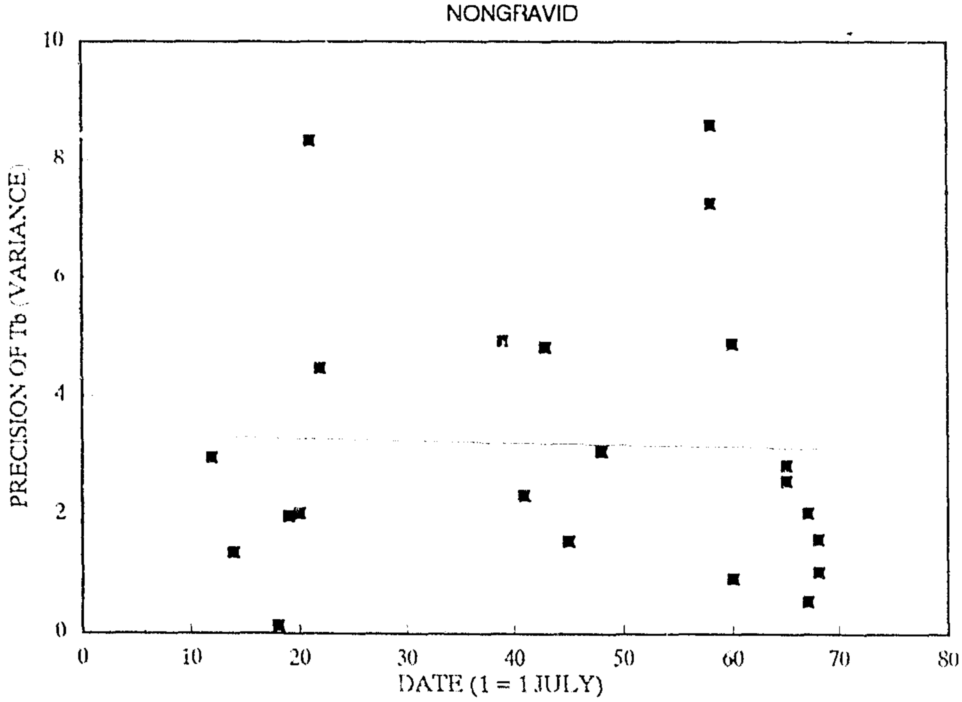
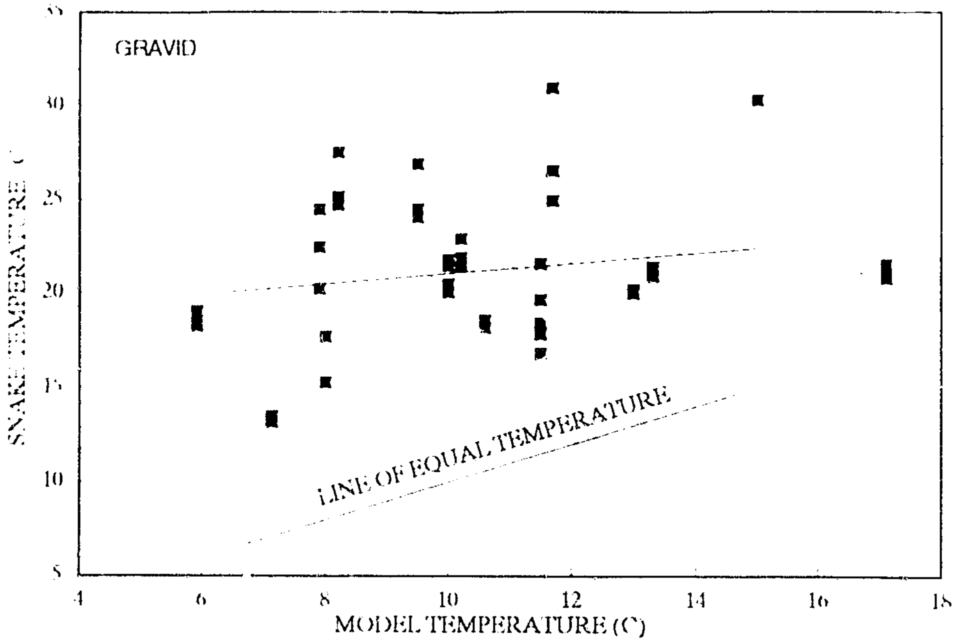
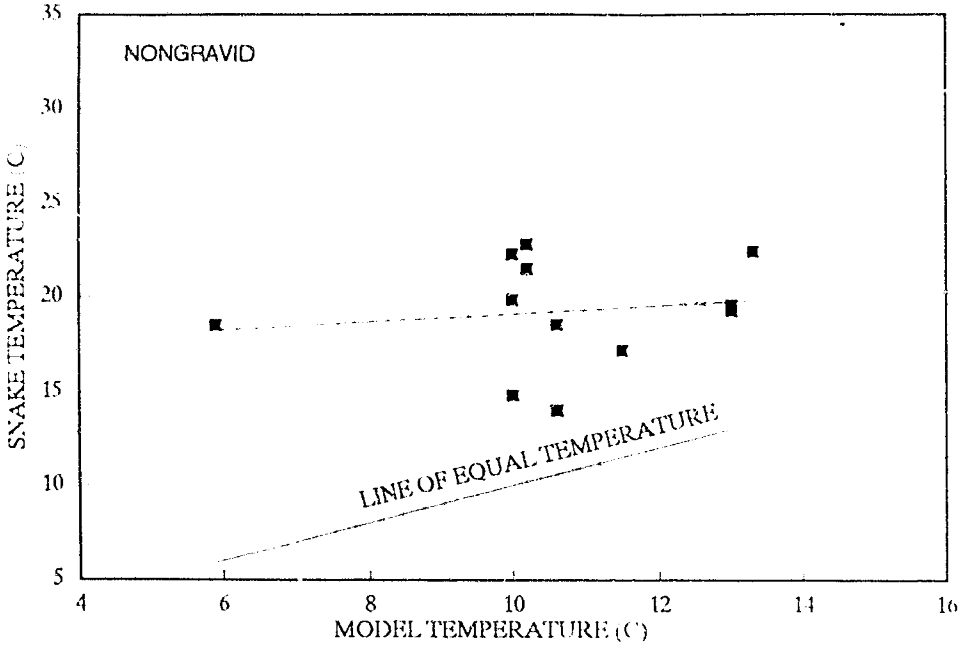

NONGRAVID
PRECISION OF Tb (VARIANCE)
10
8
6
4
2
0
0
10
20
30
40
50
60
70
80
DATE (1 = 1 JULY)

Figure 44. Comparison of nighttime T_bs of gravid and nongravid females with exposed model temperatures.


GRAVID
SNAKE TEMPERATURE (C)
35
30
25
20
15
10
5
4
6
8
10
12
14
16
18
MODEL TEMPERATURE (C)
LINE OF EQUAL TEMPERATURE


NONGRAVID
SNAKE TEMPERATURE (C)
35
30
25
20
15
10
5
4
6
8
10
12
14
16
MODEL TEMPERATURE (C)
LINE OF EQUAL TEMPERATURE

19.3±2.95 C (n=12). The difference in mean T_b between gravid and nongravid females was approximately 2 C, and was not significant ($F=2.953$, $df=1, 57$, $p>0.05$).

DISCUSSION

Movement

Animal movements are presumed to have associated costs (either energetic or in terms of risks such as predation) and should reflect a balance between the costs and benefits of acquiring necessary resources (Waser and Wiley 1979, Macartney *et al.* 1988). Gravid females of many viviparous snakes are well known for being sedentary in comparison with other members of the population (Gibbons and Semlitsch 1987, Gregory *et al.* 1987, Reinert and Zappalorti 1988). However, gravid females of some species or populations have been shown to be more active than nongravid females (Gannon and Secoy 1985), although the definition of activity in this study apparently included any animal above ground, and these results should be interpreted cautiously (Gibbons and Semlitsch 1987).

The reduction in movements by gravid females of viviparous reptiles has been found to be associated with a decrease in locomotor performance due to the burden of developing embryos (Bauwens and Thoen 1981, Garland and Else 1987). Following parturition, locomotor performance of *Scelcporus occidentalis* increases by 20-45% over levels during gestation (Sinervo *et al.* 1991). In addition, gravid females have been shown to experience higher mortality than other members of the population in both laboratory (Shine 1980) and field (Andren 1982, Madsen 1987) studies, although gravid females have had low mortality in other studies (Bauwens and Thoen 1981). Presumably, high mortality of gravid females is a result of increased predation risk as a consequence of reduced locomotor performance (Shine 1980, Seigel *et al.* 1987), and may act as a major constraint on the evolution of life history traits in viviparous snakes (Seigel *et al.* 1987)

Gravid females in this study were clearly very entary, showing movement rates (m/day) that were only 10- f those found for nongravid females. This is a minimum e of the difference, because my measures of movement IR or AMR) were relatively crude and a consequence of unable to locate snakes daily. The movement pattern f a snake that moves 100 m on one day and then remains stationary for the following four is different from that of a snake that moves 20 m/day for five consecutive days, even though they may appear equal by my measurement criteria. The fact that I was able to detect clear differences between gravid and nongravid females using my measures of movement suggests that these general patterns are real. However, studies of movement in which animals are located much more frequently are needed to quantify these differences in detail.

Although nongravid females moved longer distances (on average) than did gravid females, they appeared to move in bursts of long movements followed by periods of short movements. A similar pattern of movement has been observed in *Crotalus viridis* (Duvall *et al.* 1985, King and Duvall 1990). This pattern has been interpreted as representing long movements through areas where prey are either absent or present only at very low densities, followed by periods of foraging (short movements) once the animals reach areas of high prey abundance (King and Duvall 1990). This situation may have been occurring with the nongravid garter snakes in my study. However, in order to test this it would be necessary to sample prey availability along the routes taken by individual snakes (King and Duvall 1990). Alternatively, nongravid females may be foraging during the long movements and the relatively sedentary periods may represent a reduction in movement associated with digestion or ecdysis (Fitch and Shirer 1971).

The sedentary movement patterns of gravid females are presumed to result, at least in part, from a reduction in locomotor ability that accompanies the mass of the developing embryos (Shine 1980, Seigel *et al.* 1987). Consequently, gravid females should be freed from this constraint following parturition and begin to move in a pattern similar to that of nongravid females. This appeared to be the case in this study. Gravid females, in addition to moving little, spent much of gestation (in July and August) in very restricted areas (sometimes as little as 0.25 m^2 over a 30 day period). Following parturition, the previously gravid females displayed the same movement patterns as did nongravid females. Because gravid females of both species feed very little, or not at all, during gestation (Farr 1988) they are extremely emaciated following parturition. Therefore, the increase in movements at this time likely reflects foraging by post partum females as they attempt to replenish fat reserves depleted during gestation.

Although the effect of pregnancy on locomotion has been well documented for snakes (e.g. Seigel *et al*. 1987, Brodie 1989), alternative explanations for the patterns observed in this study remain. In particular, it was not possible to separate reductions in movement due to decreased locomotor ability from those that might be imposed by the need to thermoregulate. If adequate thermoregulation requires gravid females to remain in a single location then the same patterns of movement could result even if there were no difference in locomotor ability between gravid and nongravid females.

Habitat Utilization

Habitat selection has been proposed as a mechanism for reducing costs associated with reproduction (Morris 1984a). If reduced locomotor ability of gravid female *Thamnophis* leads to an increased risk of predation, or if thermoregulation imposes particular requirements, then utilization of habitats that reduce these associated costs may be critical. However, an assessment of the significance of patterns of habitat utilization requires first an understanding of the available habitat.

Seasonal changes in the available habitat at CCM2 were pronounced. The distribution of the four main habitat types (Marsh, Field, Forest, and Scrub) reflected the reduction in water levels as the season progressed. At the least, these changes suggested that there are substantial differences in the available habitat between the time that gravid females become sedentary in the spring and the time that they begin moving again following parturition.

The two years for which I collected habitat data differed significantly in most of the dynamic habitat features measured. In 1989, many of these features appeared to remain constant from June-August, whereas the same features varied appreciably over the same period in 1990. However, it appeared that the differences between years were almost exclusively due to differences early in the summer. July and August did not differ within or between years. This suggests that the habitat at CCM2 may be more variable at the beginning of the summer, but more predictable at the end. Predictability of the environment following parturition may be of some importance to gravid females. Kushlan and Jacobsen (1990) showed that the reproductive success of female alligators (*Alligator mississippiensis*) in the Florida Everglades depended in part on the female's ability to predict environmental conditions at the time of egg hatching from cues at the start of the nesting season. Although there are limits to the ability of reproductive females to deal with environmental variation, some level of predictability may be important in successful reproduction.

Habitat use was definitely nonrandom with respect to the major habitat types. Both gravid and nongravid females avoided Marsh in favor of the three terrestrial habitats. On only one occasion was a snake found in Marsh habitat (nongravid *T. elegans*). However, the locations used by a number of nongravid females suggested that they must have crossed Marsh habitat at some point. It appears likely that nongravid females do not spend very much time in Marsh habitat, but that it does not constitute a barrier to movement or foraging. Nongravid females showed a preference for Scrub habitat, whereas gravid females used Field almost exclusively. However, the use of habitats designated as Field is largely a function of the definition employed (the absence of Marsh, Forest or Scrub characteristics).

Among the habitat features measured (fixed and dynamic), the most striking aspect of habitat use by both gravid and nongravid females was the importance of cover. Gravid females used sites that were characterised by high rock cover or by close proximity to rocks. Nongravid females used sites that had high vegetation cover and higher than expected (from the available habitat) canopy cover. Snakes in both groups were found in close proximity to understory trees, which should also provide cover. In addition, gravid and nongravid females used sites that were close to standing water. However, the association with standing water may be artifactual. The Scrub habitat used by nongravid females was generally located along water courses, and high use of this habitat type would necessarily place snakes in proximity to water. Gravid females used sites along the roadside, and because the roads always ran beside water, their association with water simply may reflect this.

The importance of cover to both gravid and nongravid females suggests that risk of predation is a major factor in determining habitat use. Birds (especially raptors) are often major predators on snakes (Greene 1988, Brugger 1989), and sites with high cover seem likely to provide protection. Greene (1988) suggested that the choice of retreat sites (and, by extension, habitat choice) might be an important antipredator mechanism among snakes, and that this might be subject to selection. Some studies, particularly of fish, have shown that habitat choice can be strongly influenced by the presence of predators (e.g. Gotceitas and Colgan 1990). However, many studies of the effect of predation on habitat use have been conducted in the laboratory and it has been suggested that these artificial conditions magnify the importance of predation above what it is in the wild (Butler 1988). Among reptiles, Chandler and Tolson (1990) have shown that free-ranging lizards (*Anolis*) apparently select habitat in order to minimize risk of predation by boas (*Epicrates*), thereby demonstrating that predation can be an important influence on habitat selection in the wild.

Factors other than predation are probably also important. In particular, thermoregulatory requirements have been shown to have a strong influence on habitat selection in a number of reptiles (Huey *et al.* 1989, Adolph 1990a, 1990b, Law and Bradley 1990). Although gravid and nongravid females in this study both selected cover, they did so in different ways. Gravid females used rocky areas, and nongravid females used areas with high vegetative cover (both ground vegetation and understory trees). This may reflect differences in thermoregulation between the reproductive groups. If behavioral thermoregulation requires sites particularly suited for basking, then rocky sites that provide both cover and access to warm microhabitats may be important. It is also possible that sites that provide appropriate temperatures at night are critical (Huey *et al.* 1989) and this requirement may further constrain the selection of daytime sites. Even if thermoregulation does not impose particular habitat choices directly, it may do so indirectly through increased predation risk. If this is the case, it will be difficult to separate the influences of reduced locomotor ability and thermoregulation on habitat choice.

Gravid females in this study were very consistent in their choice of habitat, with virtually all individuals showing the same preference. However, all of my snakes (both gravid and nongravid) came from the west side of CCM2, along the roadside. I also observed gravid females of both species on the east side of CCM2 where conditions were different. Particularly notable was the absence of rocks. These females were found in association with large fallen logs and brush piles, both of which would provide cover. However, in most instances, females on the east side of CCM2 were in sites that did not receive sun until relatively late in the morning, compared with the roadsides. Whether this leads to differences in thermoregulation among females at the two sites might provide valuable insight into the determinants of habitat choice during gestation.

In contrast, nongravid females showed evidence of individual preferences for particular habitats. For example, a single individual was responsible for almost all of the use of Forest habitat. Shine (1987b) found similar evidence of individual variation in habitat use among *Pseudechis* and suggested that studies of habitat use be interpreted cautiously when based on few individuals or short durations. However, the preferences shown by individual nongravid females in this study were noticeable primarily at the coarse level of the major habitat types, and patterns of fine-scale habitat use were largely the same among individuals.

Habitat use should reflect the distribution of resources required by an animal. Clearly, food is a fundamental resource and should have considerable influence on patterns of habitat use. Studies of feeding ecology and diets of snakes are common in the literature but, until recently, have primarily been anecdotal in nature (Mushinsky 1987). Typically, studies report on prey use by examining gut contents of living or preserved snakes (e.g. Macartney 1989, Shine 1939, Wallace and Diller 1990). However, these are rarely accompanied by measures of prey availability (but see Reichenbach and Dalrymple 1986, Diller and Johnson 1988) and there has been considerable debate over whether snakes are prey-limited (Toft 1985, Drummond and Macias Garcia 1989, Gregory and Nelson 1991).

Changes in the measured abundance of invertebrate prey seemed to reflect the patterns of rainfall at Creston in that July and August are the driest months. However, there were no significant differences in abundance of prey among the three terrestrial habitat types. This suggests that the use of areas with high tree cover (Forest or Scrub) should not radically reduce feeding opportunities, assuming that prey are equally accessible in all habitats. This assumption is likely unrealistic. Garter snakes find prey through the use of the vomeronasal organ (Kubie and Halpern 1979, Gillingham *et al*. 1990) and invertebrates living in leaf litter on the ground in Forest or Scrub may well be more detectable (and hence accessible) than those living just below ground in the Field. Consequently, the habitats with the greatest tree cover may be the ones in which invertebrate prey are most available. An important consequence of the apparent correlation of invertebrate numbers with rainfall is that there may be fewer such prey available to gravid females following parturition because average rainfall patterns indicate that August is a relatively dry month at Creston.

Although seasonal decreases in invertebrate abundance may have implications for feeding following parturition, the apparent lack of differences among habitats poses an interesting question. If invertebrate prey are available in habitats characterized by high cover, why do gravid females not use these areas so that they can feed during gestation? The answer probably rests in the thermoregulatory requirements of gravid females. Although both the Scrub and Forest habitats appear to provide food and cover against predators, they are shaded by trees and may not be suitable for thermoregulation. Consequently, gravid females may be forced to chose habitats that provide cover and theromregulation over those that offer cover and food.

The distribution and abundance of vertebrate prey differed from that of invertebrate prey. Vole numbers in Creston appear to vary annually over a 4-5 year cycle (M. Dehn, personal communication). In addition, vole populations that show a multiannual cycle also show seasonal population changes (Morris 1984b). In particular, population levels increase during the active season, regardless of their spring starting point (Morris 1984b). Although my index of vole activity showed a decrease over the summer, I believe that this result is artifactual. The major sign of vole activity in my study was the presence of fresh grass clippings. Old, dried clippings were found virtually everywhere in the Field habitat and the designation "fresh" was a subjective one that depended primarily on the bright green color of the clippings. Consequently, the length of time that clippings remained in a condition that would be considered fresh likely varied with season. In May, when I found the highest level of vole activity, clippings would appear to be fresh for a longer period due to the high rainfall and generally moist conditions. Later in the summer, when conditions were dry and the grass was turning brown, it was much more difficult to assess whether clippings were fresh or not. Consequently, I feel that the seasonal decline in vole activity reflected the limitations of the technique and that vole abundance was actually high throughout the summer.

Voles are particularly known for their use of grassland areas, and are not commonly found in forests (Morris 1984a). Although gravid females used the Field habitat as defined in this study, they were not using grasslands and, thus, were likely not in areas of high vole abundance. As with the invertebrate prey, the habitat used by gravid females was incompatible with feeding during gestation. However, if vole abundance increases during the summer, then post partum females (particularly *T. elegans*) may find higher levels of mammalian prey following parturition than they would during gestation. This may be a particularly important, because large females (>400 mm SVL, and hence sexually mature) of both species take high proportions of mammalian prey in this area (Farr 1988).

Frogs became more abundant as the season progressed. This increase appeared to be due to two factors. First, declining water levels during the summer concentrated the frogs in smaller areas, so that I was more likely to encounter them. Second, metamorphosing tadpoles entered the population at this time, and drastically increased the number of frogs available to snakes. Presumably, tadpoles are also available to snakes, but there is little evidence that they are taken as prey at my study site (Farr 1988). Arnold and Wassersug (1978) found that metamorphosing tadpoles were particularly susceptible to snake predation because of their intermediate morphology that was not well suited to either an aquatic or a terrestrial existence. Both of these factors are likely to have had a positive effect on frog availability, such that gravid *T. sirtalis* entering the foraging population following parturition do so at a time when such food is more abundant than during gestation. Another implication of this pattern is that, although gravid females were using sites that were close to standing water, there were relatively few frogs available to them until late in gestation.

Differences in the patterns of availability of prey types may mean that the cost of not feeding among gravid females differs between species (e.g. the "bloom" of frogs at the time of parturition may make it easier for *T.*

sirtalis to replenish energy lost during gestation). However, data are needed on feeding rates and prey selection by gravid and nongravid females of both species in order to test this. Such data are likely to be very difficult, but not impossible, to obtain. In any event, if the cost of not feeding is relatively low, because of high prey availability following parturition, then other factors (such as predation or thermoregulation) could be strong enough to select for animals that forgo feeding during gestation (Mrosovsky and Sherry 1980).

Thermal Relations

Considerable attention has been focussed on thermal constraints to activity in reptiles (Porter and Gates 1969, Grant 1990, Grant and Dunham 1990). In many instances, activity patterns of ectothermic organisms have been shown to reflect these limits (e.g. Grant and Dunham 1988, Gillis 1991) and failure to identify them makes it difficult to interpret the significance of observed patterns. The snakes in this study appeared to thermoregulate, based on my previously defined criteria. All of the animals maintained T_b within a narrow subset of the environmental temperatures, at least in hot weather, as measured using thermal models. In addition, they showed the same pattern of T_b variation whenever environmental temperatures were high. Clearly, these snakes excercised considerable control over their patterns of T_b variation in such a way as to suggest that they were thermoregulating.

Water temperatures measured at CCM2 during the summer of 1990 were consistent with those necessary for good to optimal swimming performance in *T. elegans* (Stevenson *et al.* 1985). Consequently, water temperatures should not limit foraging in Marsh habitat (*T. sirtalis*) or provide a barrier to movement (*T. elegans*).

Model temperatures over the three years of this study suggest that extremely high (≥40 C) temperatures are common in July and August, but decrease over the summer. This decrease is largely accompanied by an increase in low (<20 C) temperatures, with temperatures between 20-39 C remaining remarkably constant in occurrence among months and years. Garter snakes have been found to have a preferred T_b between 25-31 C (Lillywhite 1987), so temperatures at the study site should have been adequate for snakes to achieve preferred T_b throughout the summer. In addition, a comparison of exposed and covered model temperatures within the thermoregulation enclosure is instructive. Although the two models were only 1 m apart, they commonly differed by more than 20 C during the day, and the covered model was always warmer than the exposed model at night. The high diversity of potential T_bs available to snakes in this restricted and arbitrarily selected area suggests that the thermal environment, in general, is extremely diverse. Consequently, thermoregulation *per se* may not be energetically expensive if snakes can achieve desired T_bs with little effort in a wide range of environments (Huey *et al.* 1989). If this diversity is a general feature of thermal environments inhabited by snakes, it suggests that hypotheses based on the high energetic cost of behavioral thermoregulation (see review by Huey 1982, Peterson 1987) may need to be rethought.

Because T_b in ectotherms is, at least in part, a function of environmental temperature, comparisons of thermoregulation between groups of animals must be made carefully. Differences due to variation in environment must be accounted for so that differences in thermoregulation can be examined. Peterson (1987) found that *T. elegans* followed three basic patterns of T_b variation, depending on environmental temperature (as measured using thermal models). When model temperatures were high, snakes usually showed a plateau pattern in which T_b rose rapidly in the morning and was then maintained at a relatively stable level for the rest of the day. At intermediate model temperatures (15-30 C), snake T_b oscillated widely with environmental temperatures. Finally, T_b was low and stable on days when model temperatures were also low. Such patterns have also been noted for other species (Charland and Gregory 1990). The existence of multiple patterns of T_b variation immediately suggests the potential difficulties of comparing thermoregulation among groups, even intraspecifically.

Previous studies of thermoregulation by gravid and nongravid females have largely failed to account for environmental variation when making comparisons and few general patterns have emerged (Charland and Gregory 1990). Some studies have revealed that gravid females had higher mean T_bs than nongravid females (Charland and Gregory 1990), while other studies have found the opposite (Sanders and Jacob 1981). In some cases gravid females had the same mean T_b but thermoregulated more precisely than nongravid females (Osgood 1970), but other studies have found no difference in either mean T_b or precision of thermoregulation between gravid and nongravid females (Gibson and Falls 1979, Gier *et al.* 1989). However, it is impossible to determine the reliability of these studies in the absence of specific information on the environmental conditions to which the animals were exposed.

In this study, gravid females of the two species did not differ in mean plateau T_b overall, and there were no significant differences among years when the species were pooled. Although I had fewer data for nongravid females, there was no evidence of interspecific differences in mean plateau T_b for them either. The final comparison of mean plateau T_b of gravid and nongravid females supported the initial predictions based on the Cold Climate Hypothesis: gravid females maintained higher mean T_bs than nongravid females. However, the difference was barely 1 C and the biological significance of such a small difference is uncertain. Stevenson *et al.* (1985) provide performance curves for a number of physiological and behavioral processes in *T. elegans*. All of the curves show relatively broad peaks and it appears that performance is not significantly lowered over a range of T_b of as much as 5 C. An important question then is whether development shows a sharper peak than these other processes, making small differences in mean T_b important for successful development.

A number of studies have addressed the effects of incubation temperature on offspring traits of reptiles and have found that relatively small differences in temperature can manifest themselves in measurable changes in those traits (e.g. Choo and Chou 1987, Beuchat 1988, Burger 1990). In particular, length of development can be altered considerably by small changes in developmental temperature (e.g. Choo and Chou 1987, Beal and Webb 1989). However, studies of this type are typically conducted under conditions of constant temperature, and Beuchat (1988) has shown that constant incubation temperature can result in poor development in comparison with variable thermal regimes in which lower nighttime temperatures occur.

Although the difference in mean T_b between gravid and nongravid females was small, its importance is likely to be magnified by the higher temperature-specific metabolic rates of gravid females. It has been shown that gravid females of viviparous lizards (Beuchat and Vleck 1990) and snakes (Birchard *et al.* 1984) have much higher metabolic rates (as much as 40 %) at a given temperature than nonreproductive animals. The difference is higher than can be accounted for by scaling for the increased mass of gravid females, or by factoring in the metabolic rate of the developing embryos, and may constitute an important cost of viviparous reproduction (Beuchat and Vleck 1990). Consequently, the small increase in mean T_b by gravid females observed in this study may result in a considerable difference in metabolic rate between the two reproductive conditions.

The initial prediction of higher mean T_bs for gravid females assumes that high T_b has a lower priority for nongravid females. However, numerous factors could influence nongravid females to select high T_bs, most notably the thermophilic response following feeding (Lillywhite 1987). The confounding effect of such factors would reduce the difference in mean T_b between gravid and nongravid females. Although I did not supplement food resources in the enclosure, gut palpation at the end of the season indicated that several snakes had eaten during the summer of 1990. If nongravid females were feeding regularly in the enclosure it might account in part for the small difference in mean T_b, but I am unable to assess this. Clearly, studies examining the different thermoregulatory priorities of gravid and nongravid females under varying conditions are needed.

Precision of thermoregulation was a consistent feature of thermoregulation by gravid females in this study and the magnitude of the difference between gravid and nongravid females suggests that it may be as important a consideration as mean T_b. Charland and Gregory (1990) found that gravid *Crotalus* also showed very high precision of thermoregulation in comparison with nongravid females. However, it could be argued that high precision is merely a function of the high mean T_b of gravid females. At some point, there is a maximum temperature above which snakes will not allow their T_b to go (voluntary maximum temperature, Pough and Gans 1982) and the higher the mean T_b, the closer the animal is to the maximum. Consequently, high mean T_b must be accompanied by high precision if the animal is to avoid exceeding the critical temperature. At lower mean T_bs the animal can allow its temperature to vary more widely (lower precision of thermoregulation) without exceeding the critical temperature. This appeared to be the case for nongravid females. At high mean T_b they maintained a much narrower range of temperatures than they did at low mean T_b. However, the situation was different for gravid females, which exhibited more precise thermoregulation over a wide range of mean T_bs. This same pattern has been shown for gravid and nongravid *Crotalus* (Charland and Gregory 1990) and suggests that high precision is an important facet of thermoregulation by gravid females and not simply a correlate of high mean T_b.

Implicit in the predictions of differences in thermoregulation between gravid and nongravid females is the assumption that, following parturition, the previously gravid females will show a different pattern of thermoregulation from the one they showed while carrying developing embryos. Such changes have rarely been documented (but see Gier *et al.* 1989), but my data suggest that they do happen. The mean T_b of gravid females dropped to that of the nongravid females following the appearance of the first neonates in the enclosure. Although the decrease was relatively small, there was only a 1 C difference in mean T_b between gravid and nongravid females earlier in the season and a large decline would not be expected. Gier *et al.* (1989) found a 2 C decrease in T_b following parturition in *Crotalus viridis oreganus*, but this was in the laboratory and such a pattern has not been shown in the field. During this same period, gravid females showed a decrease in the precision of thermoregulation and, again, appeared to be similar to the nongravid females. That these changes are real is suggested by the observation that mean T_b and precision of thermoregulation in nongravid females remained unchanged over the same period that changes were observed in gravid females.

The diurnal component of thermoregulation has received considerable study, especially for heliothermic reptiles (Hammerson 1979, Van Damme *et al.* 1987, Slip and Shine 1988, Schwaner 1989, Bauwens *et al.* 1990). However, many reptiles spend a considerable portion of their lives in retreat sites (during the night, or during periods of unfavorable environmental conditions) and thermal relations during these periods has received scant attention (Peterson 1987, Huey *et al.* 1989). In this study, I found that both gravid and nongravid females maintained nighttime T_b at levels much higher than those of an exposed model in the same area. The difference in mean nighttime T_b between gravid and nongravid females was more than 2 C, but the difference was not significant. Two main problems attend any attempt to make comparisons of nighttime T_b in this study. First, I am unable to determine whether my enclosure provided suitable nighttime retreat sites. Huey *et al.* (1989) were able to identify a number of important characteristics of nocturnal retreat sites used by *T. elegans* (particularly the use of large rocks with particular dimensions), which were likely absent from my enclosure. A second problem is in determining the circumstances under which to make comparisons between gravid and nongravid females. Presumably, weather conditions on the previous day (or few days) will have an effect on the range of thermal microhabitats available during the night. I was unable to account for this in my analysis and a lack of difference between gravid and nongravid females (despite a trend in that direction) may have been a consequence. Clearly, studies of nighttime thermal relations are required in order to obtain a complete picture of thermoregulatory differences between gravid and nongravid females.

Conclusions

According to current theory, the life history of an organism reflects a compromise between the costs and benefits of reproduction, such that current costs are minimized and future benefits are maximized. For viviparous reptiles, the costs have typically been expressed in terms of an increased risk of predation, a loss of feeding opportunities while gravid, and an energetic expense associated with behavioral thermoregulation. Clearly, these costs must be balanced by countervailing benefits in order for this mode of reproduction to persist.

Gravid female *Thamnophis* in this study showed lower movement rates than nongravid females. Presumably, this reflected a reduction in locomotor ability due to the burden of developing embryos. However, gravid females were also shown to thermoregulate with higher mean T_bs and precision than nongravid females, and the low movement rates may have reflected the need to stay near sites suited for such thermoregulation.

Habitat selection offers a means of reducing the costs associated with reproduction and I found significant differences between gravid and nongravid females. Gravid females utilized rocky sites that were rare on the study area, while nongravid females tended to use habitats characterized by high cover (Scrub and Forest). The importance of cover in the habitats used by both gravid and nongravid females suggested that predator avoidance might have been a major factor in habitat choice. However, snakes in the two reproductive categories chose different habitats, and gravid females may have been selecting sites that offered both protection from predators and suitable opportunities for thermoregulation.

Although there were seasonal declines in the abundance of invertebrate prey, there were no differences among the major habitats. Vertebrate prey were concentrated in particular habitats (frogs in the marsh, and voles in grasslands), but apparently increased in availability during the summer. Consequently, habitats used by nongravid females appeared to provide access to both cover and food. In contrast, actual sites used by gravid females were not located in areas where prey were available. Presumably, the need to avoid predators when locomotion was impaired, and to thermoregulate while gravid, were sufficiently strong to cause gravid females to forgo feeding. The increase in the abundance of vertebrate prey following parturition may facilitate the replenishment of fat reserves, depleted during gestation.

Life history theory predicts that there should be differences in the ecology of reproductive and nonreproductive animals, and that these differences should reflect the costs associated with reproduction. In order to frame explicit hypotheses concerning the evolution of life histories, it is necessary to identify these costs and their relative importance. Although I did not measure the costs of reproduction directly in this study, I did measure the consequences of reproduction by comparing gravid and nongravid females. Presumably, these consequences reflect the interaction of all of the factors influencing reproduction in female *Thamnophis* at Creston, and should provide a basis for detailed studies of the specific costs.

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