THE ROLE OF THERMAL RELATIONS IN THE AQUATIC FORAGING ECOLOGY OF THE COMMON GARTER SNAKE, *THAMNOPHIS SIRTALIS*, AT A HATCHERY SITE ON VANCOUVER ISLAND, BRITISH COLUMBIA.

Kari Jean Nelson
B.Sc., University of Victoria, 1988

A Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

ACCEPTED
LTY OF GRADUATE STUDIES
[redacted]
DEAN
92/01/14

We accept this thesis as conforming
to the required standard

[redacted]

Dr. P.T. Gregory, Supervisor (Department of Biology)

[redacted]

Dr. V.J. Tunnicliffe (Department of Biology)

[redacted]

Dr. D.H. Mitchell (Department of Anthropology)

[redacted]

Dr. Rick Page, External Examiner (B.C. Ministry of Forests)

University of Victoria

Supervisor: Dr. Patrick T. Gregory

ABSTRACT

For ectothermic animals such as reptiles, thermal relations are an integral part of their ecology. Temperature determines activity patterns (Huey 1982) and performance levels (Greenwald 1974, Stevenson *et al*. 1985) of individuals, which in turn affect activities such as foraging and predator avoidance. The common garter snake, *Thamnophis sirtalis*, normally feeds on amphibians and earthworms, but becomes highly piscivorous at sites where fish are readily available (Fitch 1941, Carpenter 1952, White and Kolb 1974, Lagler and Salyer 1945, Gregory and Nelson 1991). At hatchery sites on Vancouver Island, British Columbia, the water in which snakes forage is extremely cold (Mundie and Traber 1983). Although fish at hatchery sites are very abundant, thermal constraints on activity patterns and/or performance may decrease actual availability of fish to snakes.

I investigated the influence of temperature on foraging behavior of common garter snakes at the Robertson Creek Hatchery near Port Alberni, British Columbia. Principally, I was interested in: (1) activity patterns of snakes at hatchery sites and nearby natural sites in different weather conditions; (2) heating and cooling rates of snakes moving between warm air and cold water; (3) the influence of temperature on swimming speeds and subsequent aquatic foraging success of snakes.

Results of both field studies and laboratory experiments suggested that snakes require warm weather conditions for foraging activity. Cooling rates of snakes and observations of foraging activity of individuals monitored by radiotelemetry, however, indicated that high body temperatures prior to foraging are not required for foraging success. Warm weather conditions may be more important in allowing snakes to achieve high body temperatures subsequent to foraging activity. Predation risks in the vicinity of the channels from other fish- and snake-eating predators are high, and movement patterns of individuals suggest that hatchery channels may not be a suitable place for snakes to remain while they are not foraging.

Thermal relations and associated predation risks impose constraints on the foraging activity of snakes that do not allow them to take full advantage of the large abundance of prey at hatchery sites. These types of constraints on foraging activity in a situation where food abundance is virtually unlimited have important implications for tests of optimal foraging models.

Examiners:

[redacted]

Dr. P.T. Gregory, Supervisor (Department of Biology)

[redacted]

Dr. V.J. Tunnicliffe (Department of Biology)

[redacted]

Dr. D.H. Mitchell (Department of Anthropology)

[redacted]

Dr. Rick Page, External Examiner (B.C. Ministry of Forests)

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

I wish to thank Don Lawseth for permission to conduct this study at the Robertson Creek Hatchery, for access to hatchery data, and for his efforts in providing me with field accomodation. I am grateful to numerous other hatchery personnel for interesting conversations and valuable observations.

Thanks to Neville Winchester for assistance in the field, and for providing me with encouragement throughout this study. I am grateful to Caroline Zek for making one of my "24 hour watches" possible. I would also like to thank Brent Charland for many interesting discussions (not always about snakes) and for his advice and expertise on many occasions.

My family has continued to provide me with support and encouragement over the years, and to Jeanne and Ivar Larsen I owe special thanks for opening their home to myself and Sherlock in the final stages of this project. I am also deeply grateful for the personal support and understanding provided by Don Lawseth.

Finally, I am indebted to Pat Gregory for introducing me to snakes, for his unfailing support and encouragement, and for providing me with invaluable guidance and advice throughout this study.

Personal financial support was provided by an N.S.E.R.C. Postgraduate Scholarship, a President's Research Scholarship, a Charles S. Humphrey Graduate Student Award, and a King-Platt Memorial Award. The research was funded by an N.S.E.R.C. operating grant to P.T. Gregory.

INTRODUCTION

Temperature regulation plays a key role in the ecology of ectothermic organisms such as reptiles. Activities such as foraging, reproduction, and predator avoidance are all dependent on temperature. Through its influence on the ability of individuals to perform activities that affect growth, survivorship and reproduction, temperature regulation in turn affects population growth and dynamics. To reach a complete understanding of these population processes we therefore require information about the influence of temperature on activities of individuals (Huey 1982).

Any analysis of the role of temperature in the ecology of an animal is necessarily complex. When more than one step is involved in an activity, temperature may affect each step in different ways and in most cases, biophysical, behavioral, ecological, and physiological data are required to reach any understanding of the interactions involved (Huey 1982). For example, a foraging animal must search for and capture prey, while at the same time avoiding predators. Temperature is important in determining activity patterns of both predator and prey, and activity patterns in turn affect encounter probabilities (Huey 1982). Body temperature of the predator will affect capture probability through its effect on performance (Greenwald 1974).

For snakes that forage aquatically, swimming speed and therefore foraging efficiency may be significantly reduced in cold water (cf. Stevenson *et al*. 1985) as body temperatures of snakes cool quickly to ambient levels in water (Hailey and Davies 1987). The common garter snake (*Thamnophis sirtalis*) is an inefficient predator on fish (Drummond 1983) and normally feeds on amphibians and earthworms. These snakes, however, become highly piscivorous when fish are readily caught (e.g. in drying pools in intermittent streams, Fitch 1941, Carpenter 1952, White and Kolb 1974, Kephart and Arnold 1982) and/or abundant (e.g. in hatcheries or rearing facilities, Lagler and Salyer 1945, Gregory and Nelson 1991).

At hatchery sites on Vancouver Island, British Columbia, the water in which snakes must forage is very cold (maximum monthly mean 12.5° C at Big Qualicum, Mundie and Traber 1983). Previous work (Nelson 1988) suggests that garter snakes at hatcheries are most active in hot, sunny weather, contrary to the usual pattern of activity in these animals (Stewart 1965). Do hot weather conditions allow snakes to achieve high body temperatures prior to foraging in cold water, and do high initial body temperatures confer any advantage to snakes foraging in cold water?

Fish in hatchery channels are extremely abundant; however, if snakes are restricted to foraging only in hot weather and if performance of snakes foraging in cold water is significantly decreased, actual availability of fish to snakes at hatchery sites may be considerably lower than apparent abundance. Evidently there may be constraints on the ability of snakes to exploit hatchery fish. Such constraints would be important influences on a snake's optimal foraging behavior (*sensu* Pyke *et al*. 1977).

The aim of this study was to investigate the influence of temperature on foraging behavior of common garter snakes at a hatchery site on Vancouver Island. Principally, I was interested in answering the following questions:

1. How does foraging activity of snakes at hatcheries vary with weather conditions, and are these patterns of activity different from those of snakes at nearby natural or reference sites?
2. How rapidly do snakes heat and cool when moving between warm air and cold water?
3. How does temperature influence swimming speeds and thus aquatic foraging success of snakes at hatchery sites?

MATERIALS AND METHODS

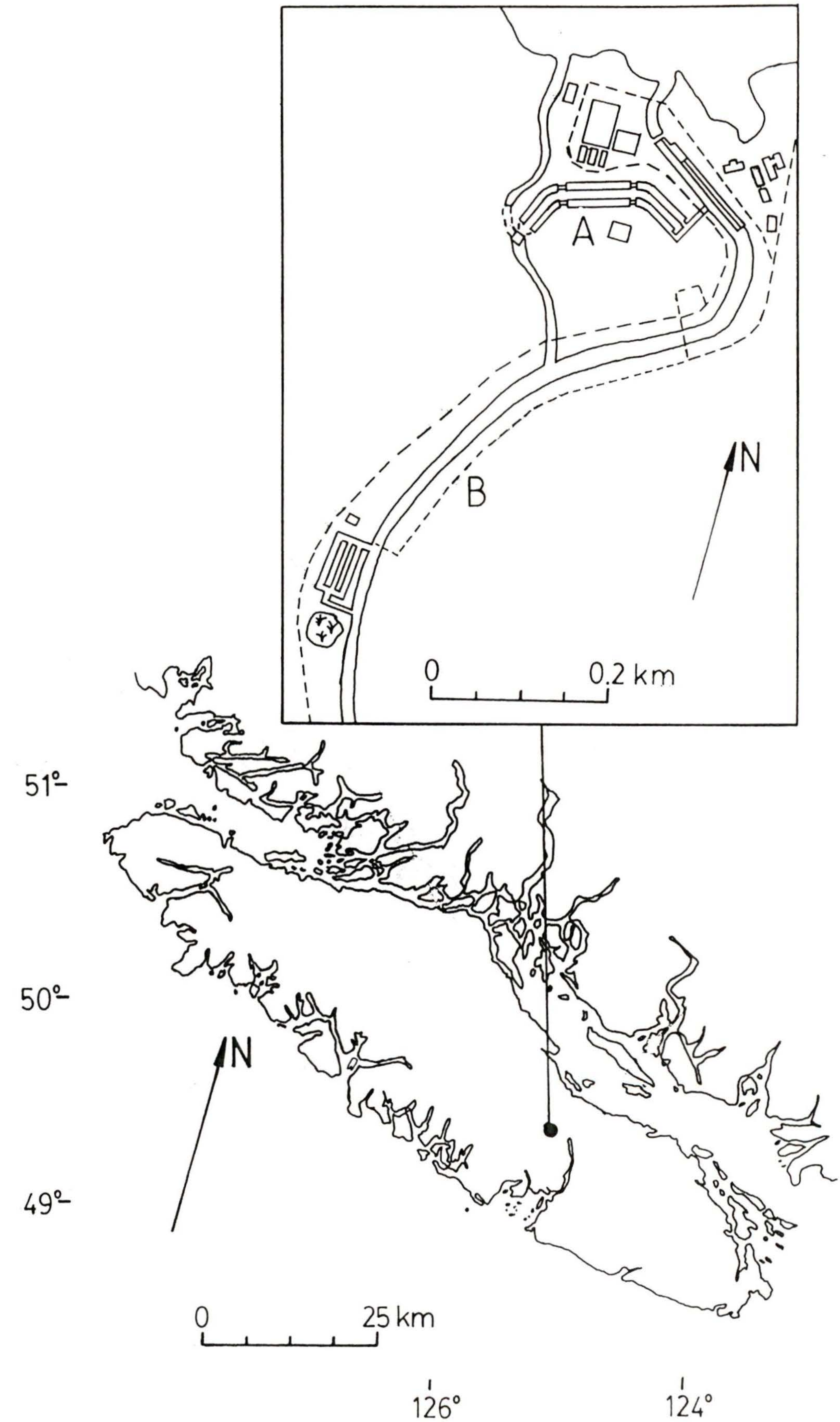
FIELD STUDY

Study Site

I conducted field studies at the Robertson Creek Hatchery, a federal government facility, located 15 km west of Port Alberni, British Columbia (Figure 1). *Thamnophis sirtalis* are abundant in the vicinity of open rearing channels at this hatchery. The six rearing channels at Robertson Creek are each approximately 20 m long and 3 m wide (Site A, Figure 1). Coho fry (*Oncorhynchus kisutch*) are present in three of these channels twelve months of the year, and chinook fry (*O. tshwawytscha*) are present in three channels for three months in the spring of each year. Natural forest vegetation in the vicinity of the channels has been cleared, and grasses, which are periodically cut by hatchery staff, line the sides of the channels. Glover Creek provides the intake for the hatchery channels, and the hatchery site borders the Stamp River.

For comparative purposes, a reference site was established about 200 m from the hatchery site (Site B, Figure 1). The reference site ran along a creek, up to some rearing channels and a small marshy pond. A variety of shrubs and mixed stands of deciduous and evergreen trees line the edges of the creek and the pond. Fish (coho fry

Figure 1. Map of Vancouver Island showing location of Robertson Creek Hatchery (inset), and hatchery site (A) and reference site (B).


A
B
N
0
0.2 km
51°
50°
49°
N
0
25 km
126°
124°

and sculpins, *Cottus*) are present in the creek and rearing channels at the reference site. In 1989 and 1990, one rearing channel at the reference site was used to rear chinook fry for three months in the spring.

General Methods

At each site, I searched for snakes on foot and captured them by hand. I gave each snake an individual mark based on a numerical system of clipping subcaudal scutes (Blanchard and Finster 1933). These marks allowed me to identify recaptured individuals and, in conjunction with notes of capture locations, to detect movement patterns of individuals. I included in the analysis of capture frequencies and movements snakes that were captured and marked in a previous study conducted in 1987 and 1988.

In addition to marking each snake and noting its capture location, I determined the sex of each snake, measured its snout-vent length (SVL, the length of the snake from the tip of the snout to the cloaca) to the nearest 5 mm, and determined its mass using a Pesola tube scale. Presence of food was detected by gentle palpation, and snakes with food were forced to regurgitate stomach contents for identification. In most cases, I then returned food items to the snake. To prevent significant disruption of regular patterns of foraging activity, I marked snakes on the head with a color of nail polish specific to each three-to-four day sampling period. This ensured that snakes were handled only once during each sampling period.

In order to compare body temperatures of active snakes between sites and weather conditions, I measured cloacal temperatures of snakes, held by the tail, within 10 sec of capture whenever possible. I also measured air temperatures (in the shade) 10 cm above the ground at the site of capture, and noted the activity of the snake at the time of capture.

Activity Patterns

In 1989, I compared activity patterns of snakes at each site during different weather conditions by counting the number of individuals seen (captured, missed, and seen but previously captured) during each search effort. Search efforts varied in length, so I divided the number of snakes seen by the amount of time spent searching, and then calculated the number of snakes observed per 60 minute search effort. To account for time spent handling snakes, I subtracted two minutes for each snake captured from the total amount of time spent searching. No attempt was made to randomize or standardize search times at each site in 1989, but I did attempt to sample each site at all times of day during different weather conditions.

In 1990, I randomly selected search times in either the morning or afternoon of alternate days and searched each site for one hour. Random selection of search times was made without replacement, so that all time intervals (from 0700 to 1800 hrs) would be represented at least twice during the summer.

To avoid biasing observations by temperature data, I subjectively categorized days by weather conditions *a priori*. Field notes and weather data (conditions-e.g. sunny, overcast, etc., from readings by hatchery personnel) were used for the classification of weather conditions. For comparisons of the number of snakes active at each site during different weather conditions, I classified weather conditions for each search effort according to whether it was predominantly cloudy or sunny at the time of the search. To examine the distribution of the number of snakes observed throughout the day, I classified weather conditions on the basis of whether the entire day was predominantly cloudy or sunny rather than just the seach interval itself. The only cases in which these two methods of classification differed was for days on which sites were searched in the cool early morning of overall hot and sunny days. I later compared my classification of weather conditions on the basis of maximum and minimum daily air temperatures recorded at the hatchery, and model temperatures (when available) (see below).

Thermoconforming models

Any investigation of body temperature regulation in reptiles must consider the complex interaction of environmental variables that determine the body temperature of an ectotherm (Tracy 1982). Measurement of just one environmental variable such as air temperature will not adequately describe the conditions (including radiation and convection) to which the animal is exposed. A more appropriate measure may be obtained through the use of thermoconforming models that heat and cool at the same rate as the animal under study (Bakken *et al.* 1985).

I constructed thermoconforming models from bicycle inner tubes as outlined by Charland (1987). Inner tubes (Arron 700 x 25 mm, and SBS 700 x 25 mm) were cut to lengths of 60 cm, and filled with 100 ml of water or to capacity (approximately 150 ml of water). One end of the tube was sealed with glue and the other was plugged with a cork. A thermocouple wire was inserted through the cork approximately 15 cm into the model and the opening in the cork was coated with silicone sealant to prevent water loss. I recorded temperatures with a digital thermometer (Omega, model HH82).

I conducted short- and long-term model trials with straight and coiled models to compare the heating and cooling characteristics of the models with those of a dead snake (575mm SVL, 65g) (cf. Charland 1987). Charland (1987) determined empirically that a model two-thirds full of water gave the best approximation of the heating and cooling characteristics of adult *Crotalus viridis*. I tested three different models (Arron with 100 ml of water, and full; SBS, full) to determine which most closely resembled the thermal characteristics of the dead snake. The two different brands of inner-tubes differed in thickness, with the Arron tubes being slightly thicker than the SBS tubes. The procedure for model trials followed that of Charland (1987).

Short-term model trials were conducted on a sunny day between 1000 h and 1600 h. The snake and models were allowed to equilibrate inside on a concrete floor until their temperatures were approximately equal (1-2^{o} C apart) and constant. During this time, I recorded temperatures every five minutes. The snake and models were then moved outside and placed in full sun on a fine sand substrate, and temperatures were recorded at one-minute intervals. When the temperature of the snake exceeded 40^{o} C (critical thermal maximum of *T. sirtalis*, 39^{o} C, Stewart 1965), I moved the models and snake back inside; temperatures then were measured at one-minute intervals until the cooling curves leveled off.

Short-term trials provide a measure of the degree to which models mimic the heating and cooling rates of the animal when the heat load is applied and removed suddenly. Long-term trials provide a better measurement of the degree to which models mimic the thermal characteristics of snakes under natural conditions because temperature changes of the snake and models will reflect previous, as well as present conditions. In the long-term trial the snake and models were allowed to equilibrate outside overnight, and, starting at 0630, temperatures were recorded every 15 minutes for 12 hours. I was unable to conduct the long-term trial for a coiled model because by the time the other trials were completed the dead snake had been in full sun for several days, and much of the body tissue of the snake had decomposed. As a result the thermocouple wire was almost exposed, and temperatures being recorded were probably more indicative of air temperatures than temperatures of a dead snake.

Because of problems with model construction and thermocouples, model trials were not completed until 21 July 1990, at which time I placed the models in the field. One straight and one coiled model were placed on the bank of the hatchery channel where they received full sun from about 0800 to 1930. Another set of straight and coiled models was placed under a tree at the bottom of one of the hatchery channels where they were shaded for most of the day, except in the early morning and late evening. While I was monitoring snake body temperatures by telemetry (below), I measured model temperatures every fifteen minutes. I also measured model temperatures prior to and following each activity pattern search interval as an index of weather conditions.

Telemetry

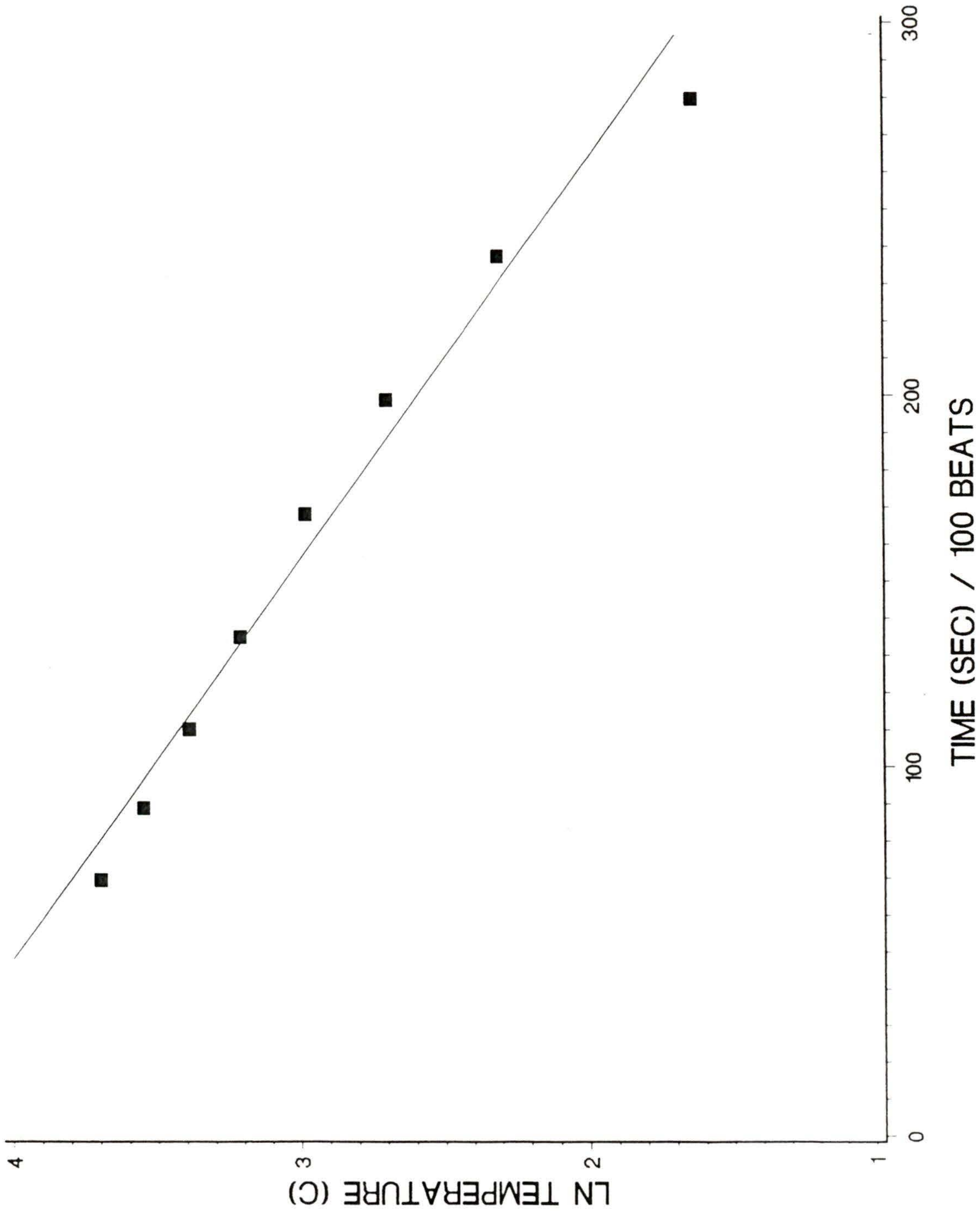
In order to monitor activity patterns, particularly the foraging activity of individual free-ranging snakes, I used temperature-sensitive radiotransmitters (Model T, Mini-Mitter Co., and Model CPH-2P, Telonics Co.). These transmitters allowed me to continuously monitor body temperatures of individuals, while observing their activity (including foraging activity). In addition, I was able to track movements of individuals.

Prior to implantation in snakes, I calibrated the transmitters using a water bath that ranged in temperature from 5 to 40°C. To ensure that there had been no shift in the calibration curve of the transmitters while they were operational, they should have been recalibrated following completion of the study. However, because of battery failure and transmitter malfunction, only two Mini-Mitter transmitters were recalibrated after they were removed from the snakes at the end of the study. The calibration curves of these transmitters did not shift during the time that they were operational, and calibration shifts have not been reported by other researchers using similar transmitters (Osgood 1970, Peterson, 1987). In addition, the transmitters were operational for at least one week prior to calibration, and should have stabilized in that time. Figure 2 shows an example of a calibration curve for a Telonics transmitter. For each transmitter implanted in snakes in the field, I recorded the amount of time for 100 pulses or the number of pulses in a one-minute time interval, and calculated snake body temperature from the equation of the regression line for the calibration curve.

To prevent the large size of the transmitters (Mini-Mitter, 2.7 x 1.0 cm, 4.0-4.5g; Telonics 3.4 x 1.7 cm, approximately 6.0 g) from impeding locomotion of snakes, I limited my selection of study animals to those that were at least 60 g as recommended by B. Luttershmidt (personal communication). Snakes were anesthetized using Metofane (Methoxyflurane, Pitman-Moore, Inc., Washington Crossing, N.J.; Aird 1986), and surgical procedure followed that of Weatherhead and Anderka (1984). Animals were held in the laboratory for at least two days to ensure recovery prior to release, and were allowed two days to acclimatize in the field before I commenced recording body temperatures.

In the summer of 1989, I implanted Mini-Mitter transmitters in three female snakes (SVL, 600 to 715 mm; weight, 64.3 to 120 g). Two snakes were captured near the hatchery channels and one snake that was captured at the reference site in the vicinity of the old hatchery channels. Chinook fry were present in one channel at this site from

Figure 2. Example calibration curve for a Telonics transmitter.The equation of the regression line is: $\ln \text{Temp.} = 4.445 - (9.268 \times 10^{-3})\text{Time}$, $r^2=0.9756$.


LN TEMPERATURE (C)
4
3
2
1
TIME (SEC) / 100 BEATS
0
100
200
300

April to June of that year, so this snake may have had some aquatic foraging experience there. The Mini-Mitter transmitters had a battery life of only ten days to two weeks, so to prevent loss of the transmitters due to my inability to locate the snakes after the batteries failed, the snakes were collected again after one week in the field.

In 1990, I implanted Telonics transmitters (which had a battery life of approximately 90 days) in four female snake (SVL, 610 - 660 mm; weight, 78.4 - 86.4 g), which were subsequently released at the hatchery channels. One of these snakes was found dead two weeks after release, so this transmitter was subsequently implanted in another snake (male, 580 mm SVL, 76 g). All of these snakes were collected in the vicinity of the hatchery channels. In order to record body temperature changes of snakes foraging in hatchery channel water, I monitored body temperatures of as many snakes as possible every fifteen minutes for 6 hours in either the morning (0700 to 1300) or afternoon (1300 to 1900) of alternate days, although readings were sometimes taken at mid-day (0930 to 1330, 1000 to 1400, or 1030 to 1430). To compare normal temporal patterns of body temperature variation of these snakes with those from other studies, I monitored snakes for a 24-hour period on two occasions, once in 1989 and once in 1990. I also monitored patterns of body temperature variation of snakes during the night (1900 to 0700) on three occasions in 1990. All of the times reported are Pacific Daylight Savings Time.

LABORATORY EXPERIMENTS

Feeding Experiments

I examined the effect of variable land and water temperatures on the foraging activity of *T. sirtalis* by conducting controlled laboratory experiments in which the activity of snakes foraging for goldfish (*Carassius auratus*) was monitored under conditions of cold water with both warm and cold land conditions, and warm water with both warm and cold land conditions. I collected snakes for these experiments from a variety of locations on Vancouver Island, including the Robertson Creek Hatchery. To ensure that goldfish would be recognized as prey items and that all snakes used in the experiments were actively feeding, snakes were housed in individual plastic boxes, and regularly offered goldfish in a small water dish.

In 1990, snakes were offered one goldfish once a week for the seven months prior to testing. Most of the snakes on this feeding regimen lost weight during the time interval prior to experimentation. In 1991, therefore, I repeated the experiments, and fed snakes one to three goldfish three times per week for the seven months prior to testing. Most snakes used in the 1991 experiments gained weight during the period prior to testing. Only those snakes that were healthy and feeding regularly were used in experimental trials, and individuals were forced to fast for two weeks prior to experimentation.

The experimental apparatus consisted of two identical aquaria (90 x 45 x 45 cm), divided by a glass partition into a land area and a water area (30 x 45 x 15 cm deep). The aquaria were set up in an environmental chamber maintained at 13° C (the mean temperature of hatchery channel water in the summer). The water in one aquarium was allowed to equilibrate to this temperature, whereas the water in the second aquarium was heated to 23° C with a submersible water heater. Twenty-three degrees C was chosen for the warm land and water temperature because goldfish can be acclimated to this temperature (Fry and Hart 1948), and garter snakes should be able to swim at approximatly 80% of their maximal speeds at this temperature (Stevenson *et al*. 1985). The land area of each aquarium was heated to 23° C by heating lamps located at the appropriate height above the aquaria, or allowed to equilibrate to ambient temperature (13° C). I constructed cardboard blinds around the aquaria, and made observations through slits in these blinds.

I conducted experimental trials two at a time, one in the aquarium with warm water, and one in the aquarium with cold water. Snakes were randomly assigned to experimental conditions and the order of experimental conditions was randomized. Each snake was used in only one experimental trial. For each trial, I placed snakes in the appropriate aquarium for a 36-40 hour acclimation period prior to introduction of goldfish into the water portion of the aquarium. I then made detailed, continuous observations of the behavior of the snakes (including foraging behavior) for the eight-hour (1990) or four-hour (1991) experimental period subsequent to introduction of the goldfish. I classified foraging behavior *a priori* on the basis of observations made in previous experiments (Nelson 1988). Foraging behavior consisted of (1) the snake lying on land with its head out over the edge, looking into the water, (2) the snake lying on land, moving its head around in the water with its mouth open, and (3) the snake swimming around in the water with its head under the water and its mouth open (open-mouth searching behavior, Drummond 1983).

After the feeding trials were completed, I recorded the effect of these experimental conditions on heating and cooling rates of snakes. I inserted a thermocouple wire in the cloaca of one of the largest snakes (595 mm SVL, 76 g) and one of the smallest snakes (480 mm SVL, 28.7 g) used in the experiments. Using a cardboard partition to separate the land and water areas of the aquarium, I isolated each snake on either cold or warm land until its body temperature stabilized, and then I moved the snake into warm or cold water respectively. The snakes were isolated in the water area of the aquarium for 9.5 minutes, and then returned to cold or warm land. Body temperatures were measured every ten seconds throughout these trials.

Swimming Speeds

To determine the effect of variable water temperatures on swimming speeds of cold- and warm-acclimated snakes, I measured maximum swimming speeds of 20 snakes at 5°C intervals between 5°C and 35°C. Snakes for these experiments included snakes used in the feeding trials, two snakes from the Okanagan Valley, and one snake from Alberta. Cold-acclimated snakes were held at 5°C for 2 weeks prior to testing and throughout the experimental period. Warm-acclimated snakes were maintained at room temperature (approximately 23°C) prior to and during the experiments. Snakes were tested in a Plexiglas ™ trough (1.7 m long, 0.3 m wide and 0.3 m deep) filled with water of the appropriate experimental temperature to a depth of 0.1 m. Low water temperatures (5 to 15°C) were achieved by placing the trough in an environmental chamber maintained at the experimental temperature. High water temperatures (20 to 35°C) were achieved by filling the trough with tap water of the appropriate temperature.

Because several days were required to change the temperature of the environmental chamber, and I had limited time in which to complete the trials, I conducted a cold water trial first, followed by two warm water trials, another cold water trial, the remaining two warm water trials, and the final cold water trial. Within these constraints, the order of the experimental temperatures was randomized. Each snake was tested at all of the experimental temperatures, and the order in which different snakes were tested at each experimental temperature was randomized.

Before each swimming trial, snakes were placed in the water in an inverted glass container, with an air space at the top, for 2 to 3 minutes. I measured the body temperature (with a cloacal thermometer) of each snake prior to the first trial at each experimental temperature to ensure that this was long enough to allow equilibration of the snake's body temperature with the water temperature. Each trial consisted of forcing the snakes to swim the length of the trough (by tail prodding if necessary), and recording the time required for snakes to swim 1.5 m. Three trials were conducted for each snake at each temperature, and the minimum time recorded for the snake to swim 1.5 m was taken as an indication of maximum swimming speed. Snakes rested for at least 60 minutes between each trial.

STATISTICAL ANALYSIS

Statistical analysis followed methods described in Zar (1984) and the data were analyzed using SAS P\C Version 6.04. Significance of regressions was determined by using either t-tests or F-tests. I used analysis of variance

(ANOVA) to compare mean maximum and minimum air temperatures of weather conditions in both years (year*weather condition), and a t-test to compare mean model temperatures between weather conditions in 1990. ANOVA was also used to compare mean numbers of snakes active at each site during each weather condition, mean body temperatures of captured snakes (year, sex, site*weather condition), and mean number of fish consumed and amount of time spent foraging by snakes in the feeding experiments. In all cases in which two way ANOVA's involved unequal replication, significance of the type III sum of squares (Proc GLM) was reported (SAS 1985). For the analysis of swimming speeds of snakes, individual snakes (repeated measures) were nested within acclimation group in the two way analysis of variance (test temperature*acclimation temperature). The curves for the plot of swimming speeds of snakes at different temperatures were fitted using a spline technique (SAS 1988).

Statistical tests were considered significant at $\alpha=0.05$.

RESULTS

FIELD STUDY

Activity Patterns

Maximum and minimum air temperatures (recorded by hatchery staff) and model temperatures for different weather conditions in 1989 and 1990 are shown in Table 1. There was a significant difference in both mean maximum (ATMax) and minimum (ATMin) air temperatures between years [ATMax, $P(F_{1,49} \geq 39.77)=0.0001$; ATMin, $P(F_{1,49} \geq 11.25)=0.0015$]. In 1990, maximum and minimum air temperatures were higher for both sunny and cloudy conditions than in 1989. Cloudy conditions in 1990 were almost as hot as sunny conditions in 1989. This inconsistency was due primarily to the fact that 1990 was much hotter than 1989, so both sunny and cloudy days in 1990 were hotter than in 1989. Because these weather categories represent relative measures, only comparisons within years are meaningful.

Mean maximum air temperatures were significantly higher for sunny conditions than for cloudy conditions [$P(F_{1,49} \geq 87.79)=0.0001$], and this effect was the same for both years [$P(F_{1,49} \geq 0.24)=0.6245$]. Mean minimum air temperatures did not differ significantly between conditions [$P(F_{1,49} \geq 1.15)=0.2881$], and the effect of condition was similar in both years [$P(F_{1,49} \geq 0.00)=0.9493$]. In 1990, I measured model temperatures prior to each search interval.

Table 1. Maximum (ATMax) and minimum (ATMin) air temperatures (recorded by hatchery personnel) and model temperatures for sunny and cloudy weather conditions in 1989 and 1990.

		ATMax			ATMin			Model	
	n	$\bar{x}$±S.D.	Range	n	$\bar{x}$±S.D.	Range	n	$\bar{x}$±S.D.	Range
Year*Condition									
1989									
Sunny	12	24.67±2.99	19.5-30.0	12	9.13±2.59	6.0-13.5			
Cloudy	10	16.50±3.16	12.0-21.5	10	8.25±3.01	3.5-12.0			
1990									
Sunny	21	29.48±3.16	23.5-35.0	21	12.09±3.13	5.0-18.5	10	30.7±5.54	23.9-42.6
Cloudy	10	22.13±1.39	20.0-24.0	10	11.10±3.22	6.5-15.5	8	20.6±5.54	12.4-27.2

These temperatures provide a better indication of temperatures potentially available to snakes. There was some overlap in the ranges of model temperatures between conditions, but the difference between means was significant [$P(t_{0.05(2)16} \geq 3.8435) < 0.0014$].

The mean number of snakes observed per 60 minute search effort during 1989 was higher during sunny weather conditions than during cloudy weather conditions (Figure 3) [$P(F_{1,80} \geq 4.24) = 0.0428$]. The effect of weather condition on the mean number of snakes observed was the same for both sites [$P(F_{1,79} \geq 2.02) = 0.1589$], although lower numbers of snakes were observed at the reference site than at the hatchery site during sunny weather conditions, whereas higher numbers of snakes were observed at the reference site than at the hatchery site during cloudy weather conditions. The mean number of snakes observed at each site during both weather conditions combined was similar [$P(F_{1,79} \geq 0.54) = 0.4658$].

In 1990, the mean number of snakes observed during each one-hour sampling period at the hatchery site was higher during sunny weather conditions than during cloudy weather conditions, whereas the reverse trend was observed at the reference site (Figure 4). The mean number of snakes observed at each site and in each weather condition was not significantly different [site, $P(F_{1,58} \geq 2.07) = 0.1556$; weather, $P(F_{1,58} \geq 0.89) = 0.3490$], but there was a

Figure 3. Means (circles), 95% confidence intervals (open bars), and ranges (lines) for the number of snakes observed during each 60 minute search effort in 1989 at the hatchery site in sunny (HS) and cloudy (HC) weather, and the reference site in sunny (RS) and cloudy (RC) weather. Numbers beside means represent the number of sampling intervals.

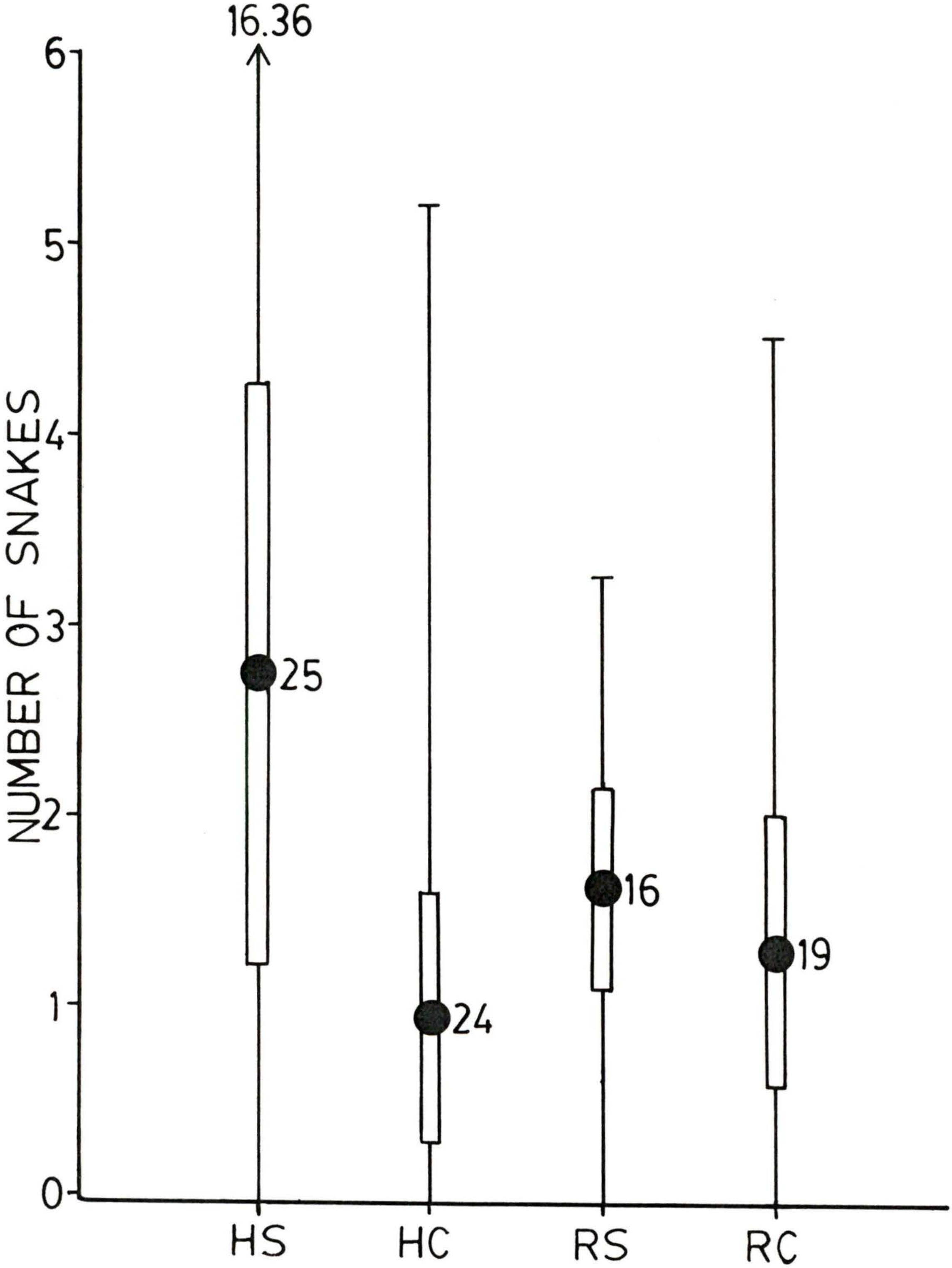
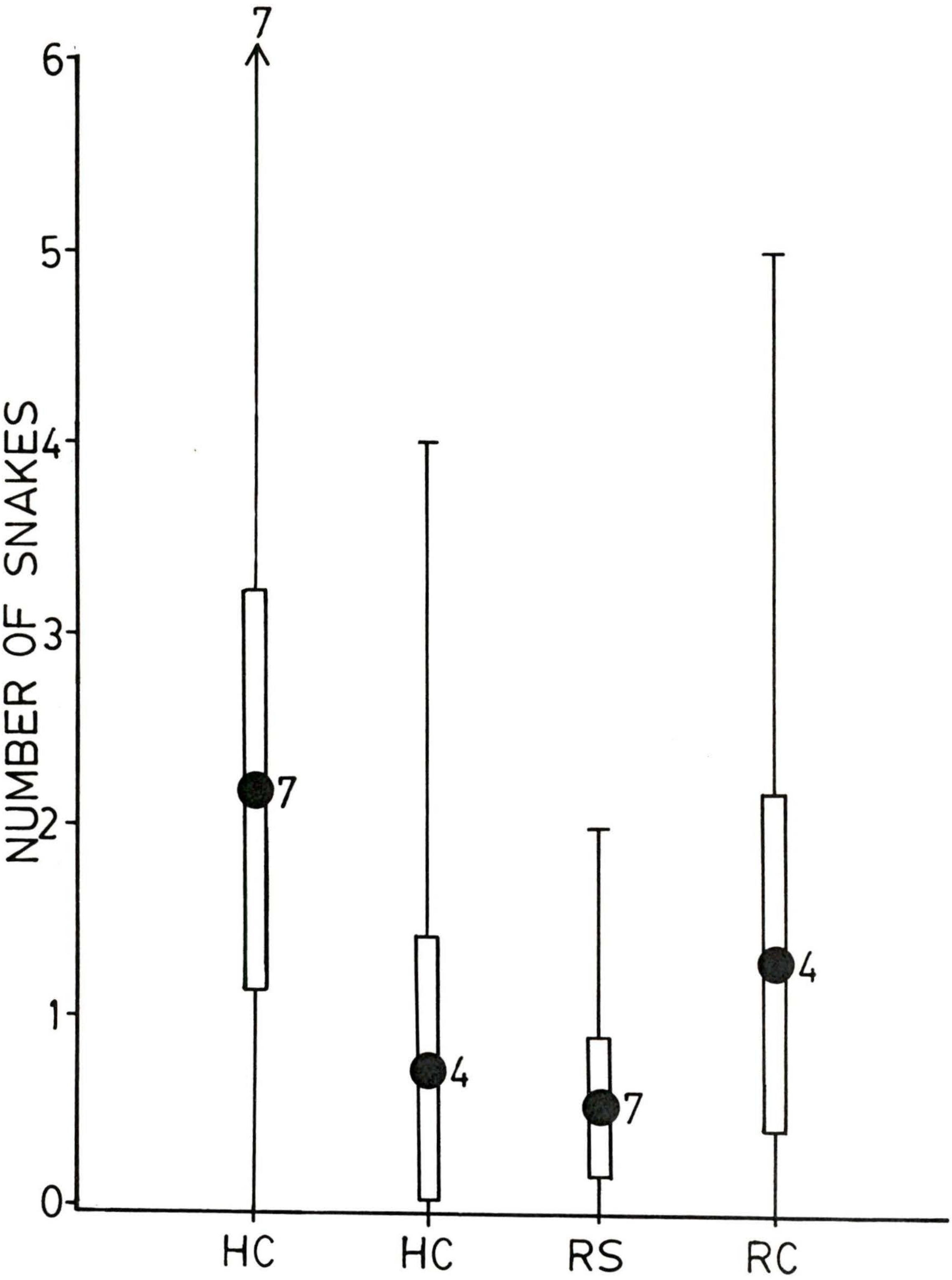

16.36
6
5
4
3
2
1
0
NUMBER OF SNAKES
25
24
16
19
HS
HC
RS
RC

Figure 4. Means (circles), 95% confidence intervals (open bars), and ranges (lines) for the number of snakes observed during each 60 minute search interval in 1990 at the hatchery site in sunny (HS) and cloudy (HC) weather, and the reference site in sunny (RS) and cloudy (RC) weather. Numbers beside means represent the number of sampling intervals.


NUMBER OF SNAKES
0
1
2
3
4
5
6
7
7
4
7
4
HC
HC
RS
RC

significant interaction of site and weather on the mean number of snakes observed [$P(F_{1,58} \geq 8.81) = 0.0044$].

In 1990, snakes at both sites were active primarily in the morning (0900 to 1300) and in the late afternoon (1500 to 1900) of sunny days, whereas they were active in the early afternoon (1300 to 1500) on cloudy days (Figure 5).

Because of extreme nonorthogonality of the data, I could not do a complete factorial analysis of the effects of year, sex, site and weather condition on mean body temperatures of snakes captured in the field (Table 2). However, one-way ANOVAs revealed no significant effect of year (1989 and 1990) [$P(F_{1,119} \geq 1.93) = 0.1671$] or sex/reproductive condition (males, non-gravid females and gravid females) on mean body temperatures of snakes [$P(F_{2,118} \geq 0.55) = 0.5799$]. There was also no significant effect of site on body temperatures of snakes captured in the field [$P(F_{1,117} \geq 0.00) = 0.9461$]. Body temperatures of snakes captured in sunny weather were slightly higher than those of snakes captured in cloudy weather [$P(F_{1,117} \geq 4.48) = 0.0364$], and there was a significant interaction of site and weather condition on the mean body temperature of snakes captured [$P(F_{1,117} \geq 4.51) = 0.0359$]. There was a significant correlation between air temperature at the time of capture and body temperatures of snakes [$P(r_{121} \geq 0.42888) < 0.0001$.] (Figure 6).

There was no significant difference in mean body

Figure 5. Total number of snakes observed at hatchery and reference sites in sunny (open bars) and cloudy (closed bars) weather conditions in 1990. The hatched bar represents foggy conditions on an otherwise sunny day. Numbers above the bars indicate the number of 1 hour search intervals during each time period.

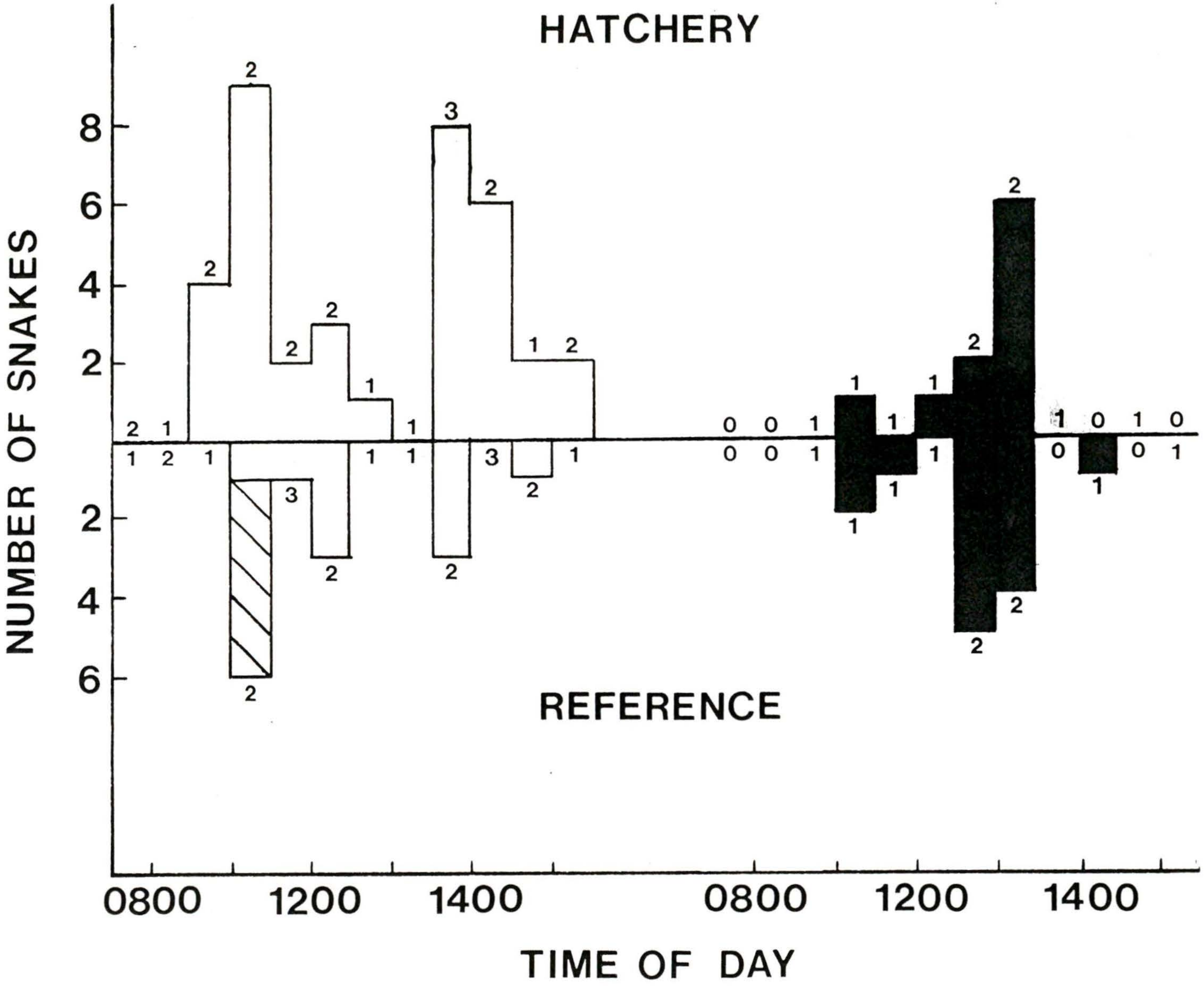
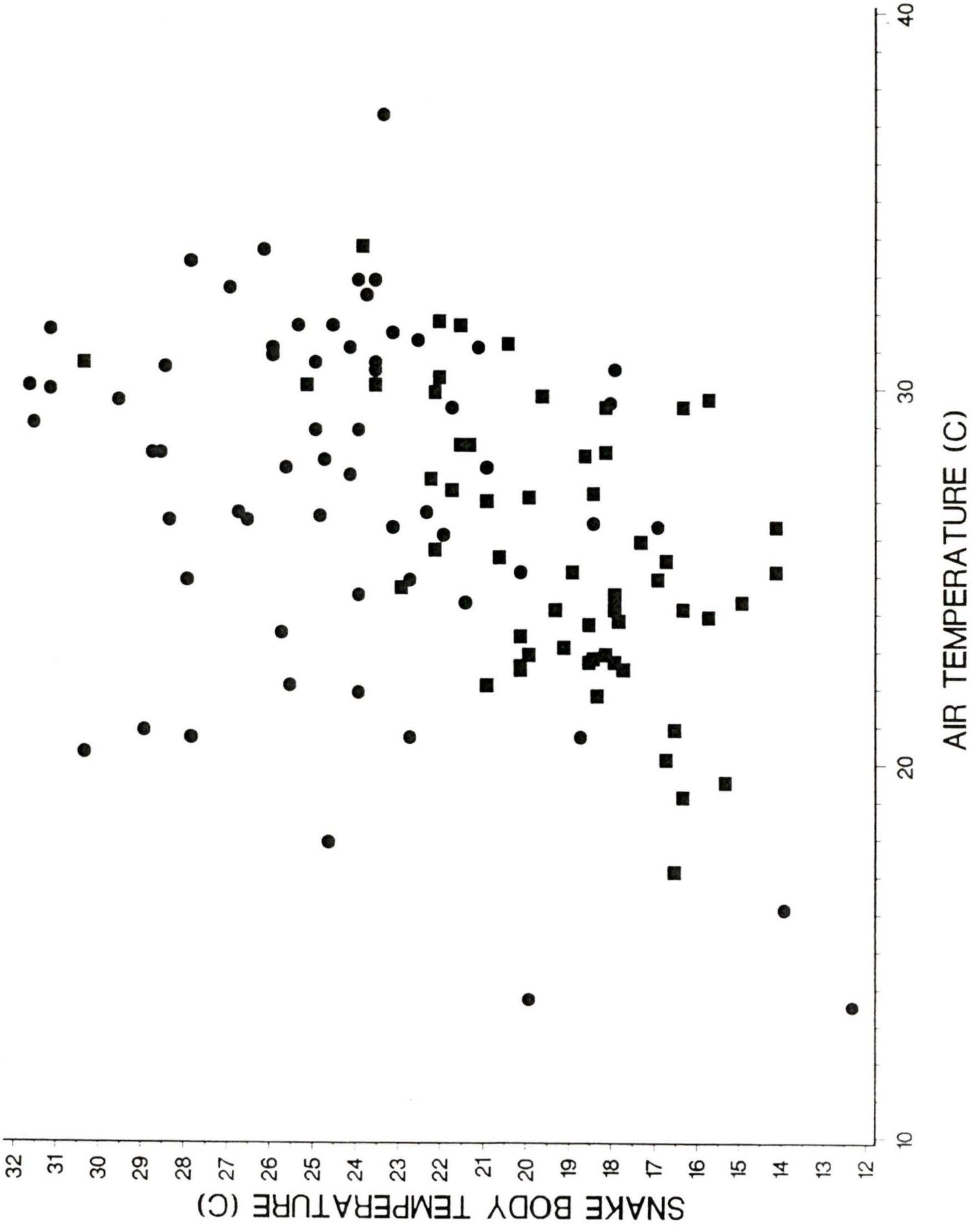

HATCHERY
REFERENCE
NUMBER OF SNAKES
8
6
4
2
2
4
6
TIME OF DAY
0800
1200
1400
0800
1200
1400
2 1 2 2 2 2 1 1 3 2 1 2
1 2 1 3 2 1 1 2 3 2 1
2 2
0 0 1 1 1 1 2 2 1 0 1 0
0 0 1 1 1 1 2 0 1 0 1
1 2 2

Table 2. Body temperatures of snakes captured in the field (including original captures and snakes captured more than once) compared by year, sex and reproductive condition, site*condition, and presence or absence of food in the stomach.

		n	Body Temperature $\bar{x}$±S.D.	Range
Year				
1989		80	26.23±4.56	13.6-36.0
1990		41	27.43±4.47	17.2-37.4
Sex and Reproductive Condition				
Male		69	26.61±4.26	16.2-37.4
Non-gravid Female		42	26.34±5.23	13.6-33.9
Gravid Female		10	28.02±3.34	24.0-33.0
Site*Condition				
Hatchery	Sunny	40	26.90±5.00	13.6-33.8
	Cloudy	23	26.90±3.43	20.2-33.9
Reference	Sunny	21	28.62±4.90	16.2-37.4
	Cloudy	37	25.06±4.04	17.2-36.0
Presence or Absence of Food				
With Food		78	26.40±4.74	13.6-37.4
Without Food		43	27.06±4.20	13.8-33.9

Figure 6. Snake body temperatures plotted against air temperatures at the time of capture for snakes captured at the hatchery site (circles) and the reference site (squares).


SNAKE BODY TEMPERATURE (C)
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
AIR TEMPERATURE (C)
10
20
30
40

temperatures of snakes that had food in their stomachs and those without food at the time of capture (Table 2) [$P(t_{119} \geq 0.7551) = 0.4517$].

Model Trials

In short-term model trials, the dead snake heated and cooled more rapidly, and reached higher temperatures overall, than both the straight (Figure 7) and coiled models (Figure 8). In the long-term trial of the straight model, however, the temperature of the dead snake resembled that of the model quite closely (Figure 9). The model that most closely resembled a snake in this trial was the Arron tube filled with 100 ml of water. There was a 1:1 relationship between snake temperature and the temperature of this model (Figure 10). The slope of the regression line did not differ significantly from one [$0.20 < P(t_{0.05(2)1} \geq 3.038) < 0.50$], and the intercept did not differ significantly from zero [$P(t_{0.05(2)1} \geq 0.980) = 0.3322$].

Models constructed in 1989 were slightly smaller in diameter than 1990 models, but model trials were not conducted in 1989. The extremely high temperatures reached by models in 1989 (see Figure 15) suggest that they overestimated temperatures potentially available to snakes.

Figure 7. Snake temperatures (open triangles) and model temperatures (closed circle=SBS, full; open square=Arron, full; closed square=Arron, 100 ml) for the short-term trial of the straight models.

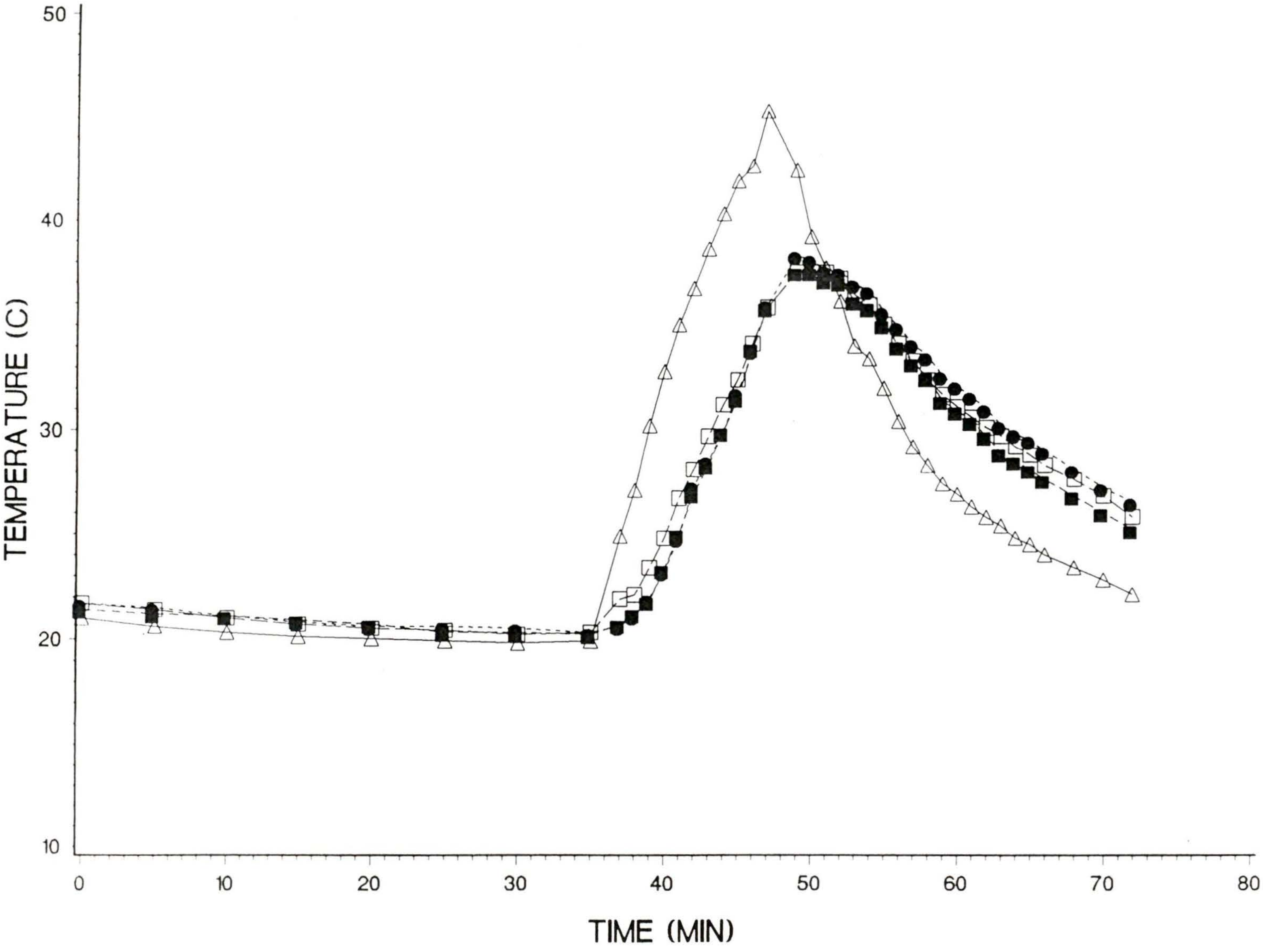

TEMPERATURE (C)
50
40
30
20
10
TIME (MIN)
0
10
20
30
40
50
60
70
80

Figure 8. Snake and model temperatures for the short-term trial of the coiled models (symbols as in Figure 7).

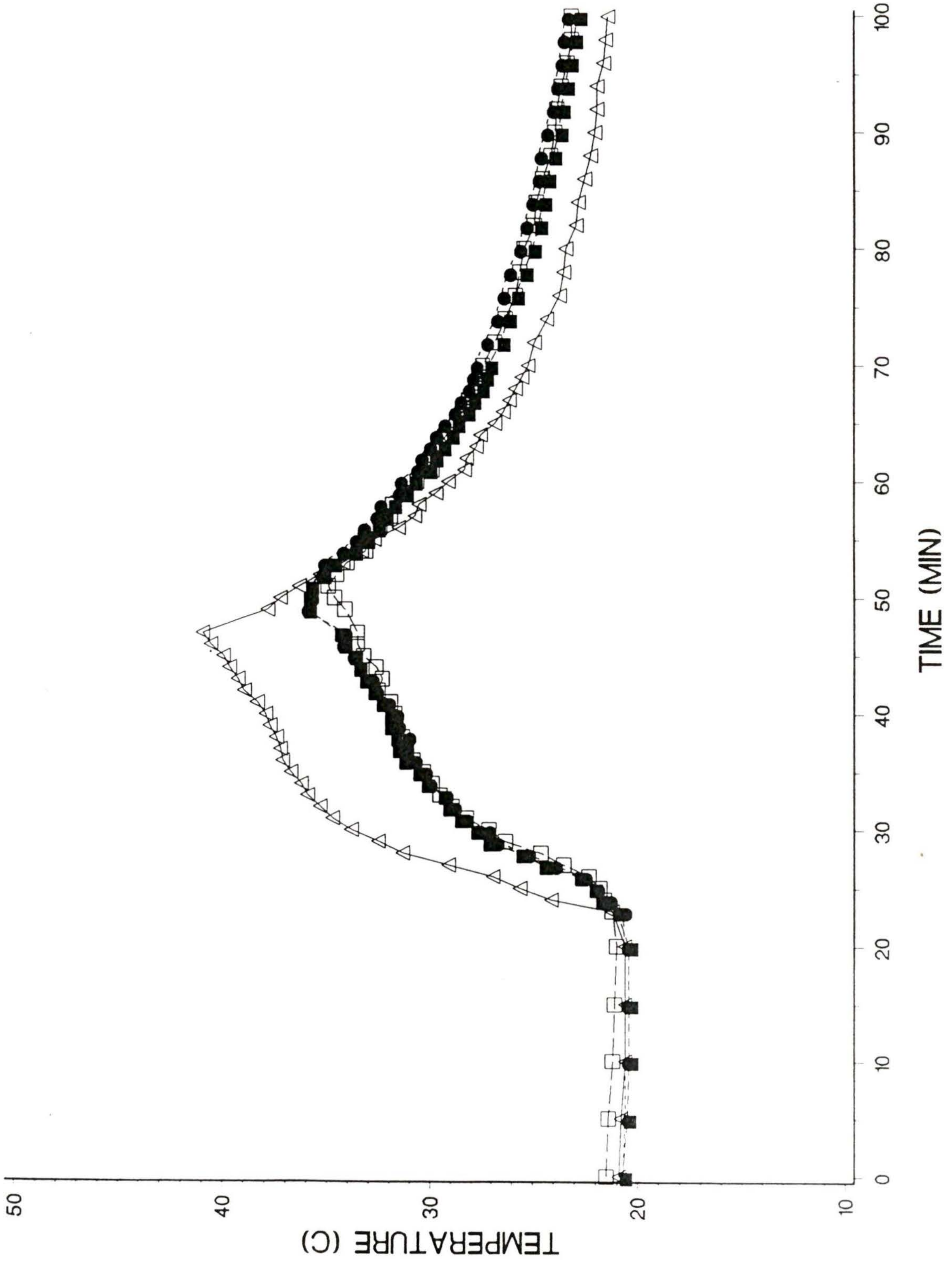

TEMPERATURE (C)
10
20
30
40
50
TIME (MIN)
0
10
20
30
40
50
60
70
80
90
100

Figure 9. Snake and model temperatures for the long term trial of the straight models (symbols as in Figure 7).

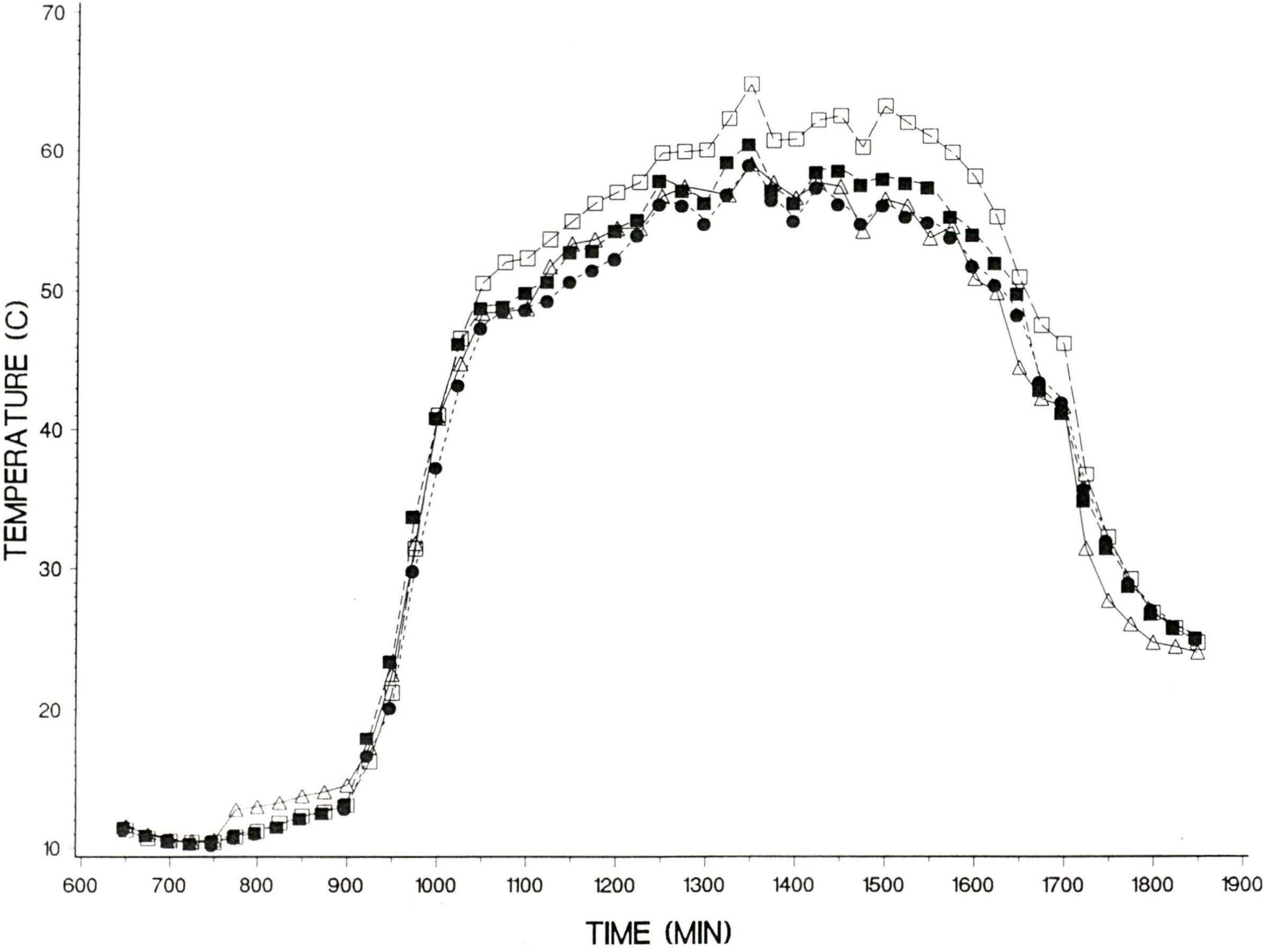
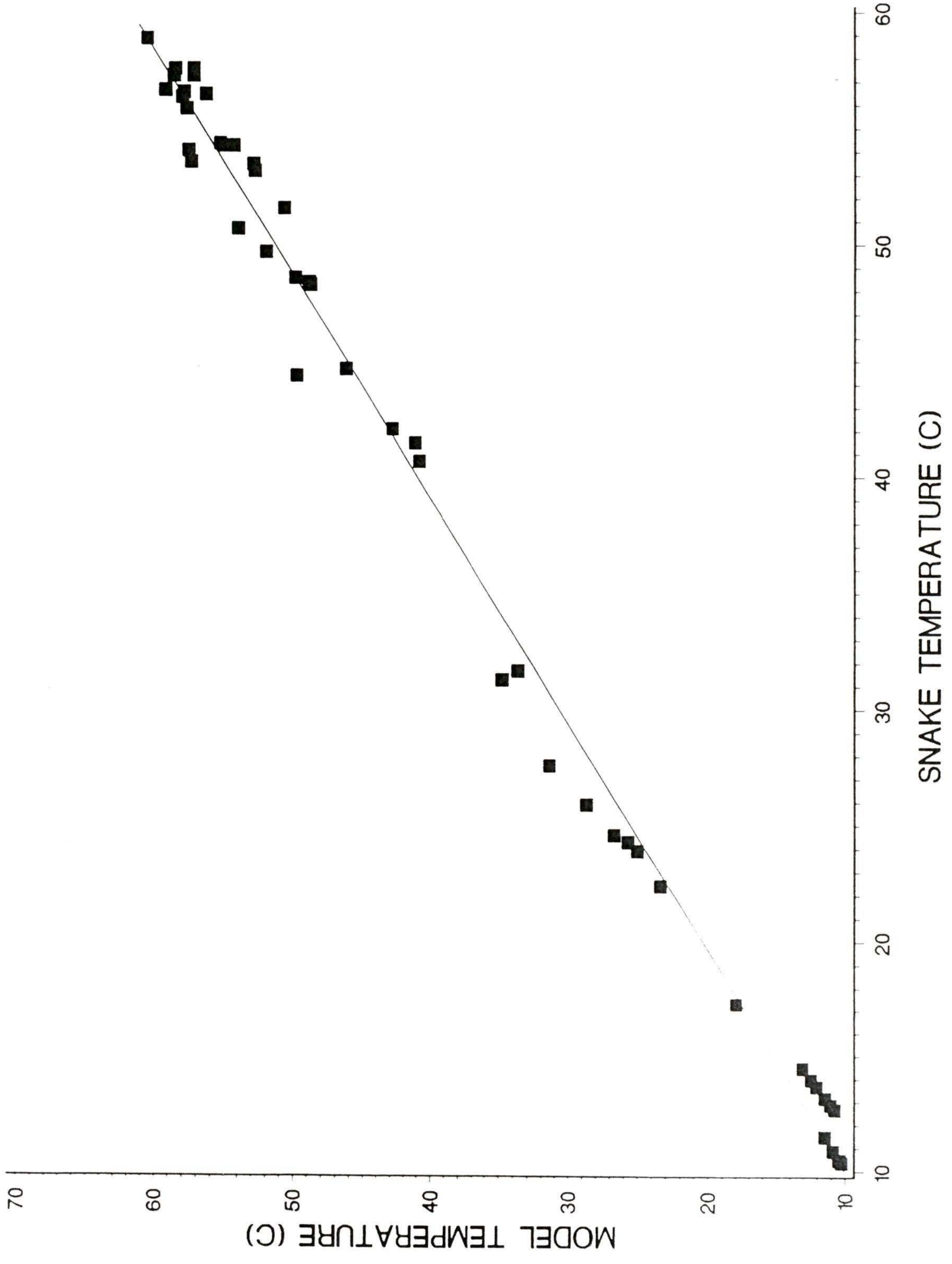

TEMPERATURE (C)
10
20
30
40
50
60
70
TIME (MIN)
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
1700
1800
1900

Figure 10. Relationship between snake and model temperatures (Arron, 100 ml) for the long-term trial of a straight model. The equation of the regression line is:
Model temperature = 0.500 + (0.984)(Snake temperature), r^2=0.98.

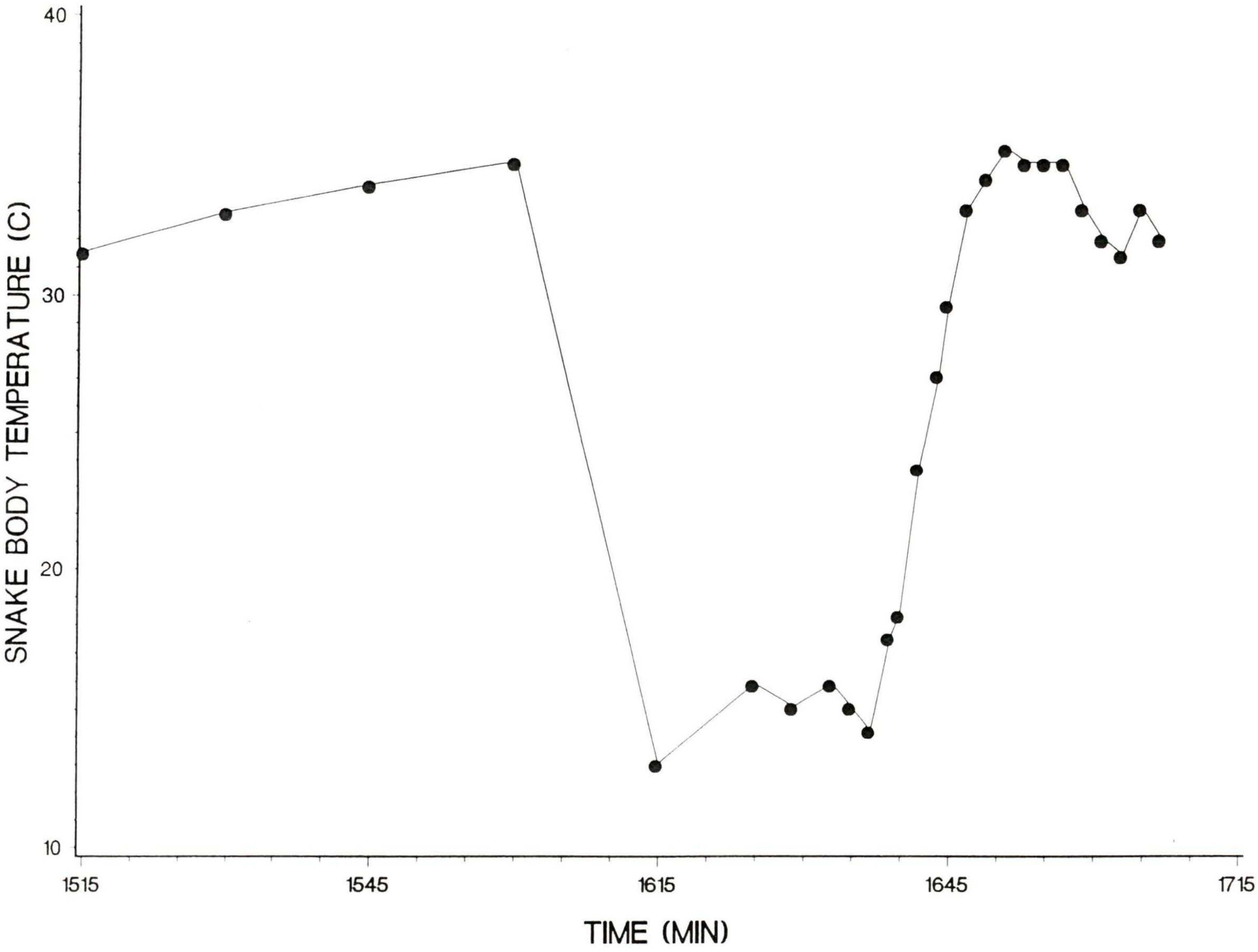

MODEL TEMPERATURE (C)
70
60
50
40
30
20
10
SNAKE TEMPERATURE (C)
10
20
30
40
50
60

Aquatic Foraging Behavior

In 1989 and 1990, forty snakes were captured at hatchery channels with fish in their stomachs. The fish in seventeen of these snakes was fresh, and probably captured the day the snake was captured. In all cases, the snakes with fresh fish were captured on sunny days, or on sunny days with some cloudy periods. Maximum air temperatures on these days ranged from 16^{o} to 32^{o} (mean ± s.d.=26.65 ± 3.91, n=17).

Body temperature records during foraging activity were obtained for radiotracked snakes on only four occasions in 1990. The first record was on 1 August (Figure 11). This snake was in the forest by Glover Creek in the morning, and the signal could periodically be picked up at my monitoring location at the hatchery channels. At 1615, the body temperature of this snake (as determined by transmitter pulse rate) decreased rapidly, presumably because it entered the cold channel water. By the time the snake was located, it was on the bank of one of the channels. Its body temperature remained low, decreasing slightly when it was observed moving into the water 14 minutes later. The snake remained at the edge of the bank on top of the grass mat in the water until 1639 when it was observed back on the bank in the sun. Its body temperature increased rapidly to a maximum of 35^{o} C at 1651. The snake later disappeared into a pile of rocks at the end of Glover creek at the edge of

Figure 11. Body temperatures of snake R8L7 during foraging activity on August 1, 1990.


40
30
20
10
SNAKE BODY TEMPERATURE (C)
1515
1545
1615
1645
1715
TIME (MIN)

the forest. Model temperatures recorded just prior to this period of foraging were approximately 30^{o} C.

The remainder of the foraging records were all obtained from one snake that remained in the vicinity of the hatchery channels for the entire summer. On 2 August, I observed this snake on the bank of the hatchery channel at 1000. It was observed moving around on the bank of the channel until 1210, when its body temperature dropped (Figure 12), and it moved out of sight. The body temperature of the snake continued to drop to 12.7^{o} C at 1215, and then the snake was observed back on the bank, corresponding with a rapid increase in body temperature. This pattern continued, with the snake moving in and out of the water, and its body temperature decreasing and increasing rapidly as a result. While the snake was in the water, it was most frequently observed lying on the grass mat at the edge of the channel. Model temperatures during this period of activity ranged from 26 to 33^{o} C.

The second record for this snake was on 5 August (Figure 13). The body temperature of the snake dropped dramatically while it was being monitored from another location. On this occasion, the snake remained at the edge of the channel on the grass mat, in and out of sight from 1355 to 1508. During this time, its body temperature remained low, at approximately 12^{o} C. Within 22 minutes after emerging from the water, the snake's body temperature

Figure 12. Body temperatures of snake R5L10 during foraging activity on August 2, 1990.

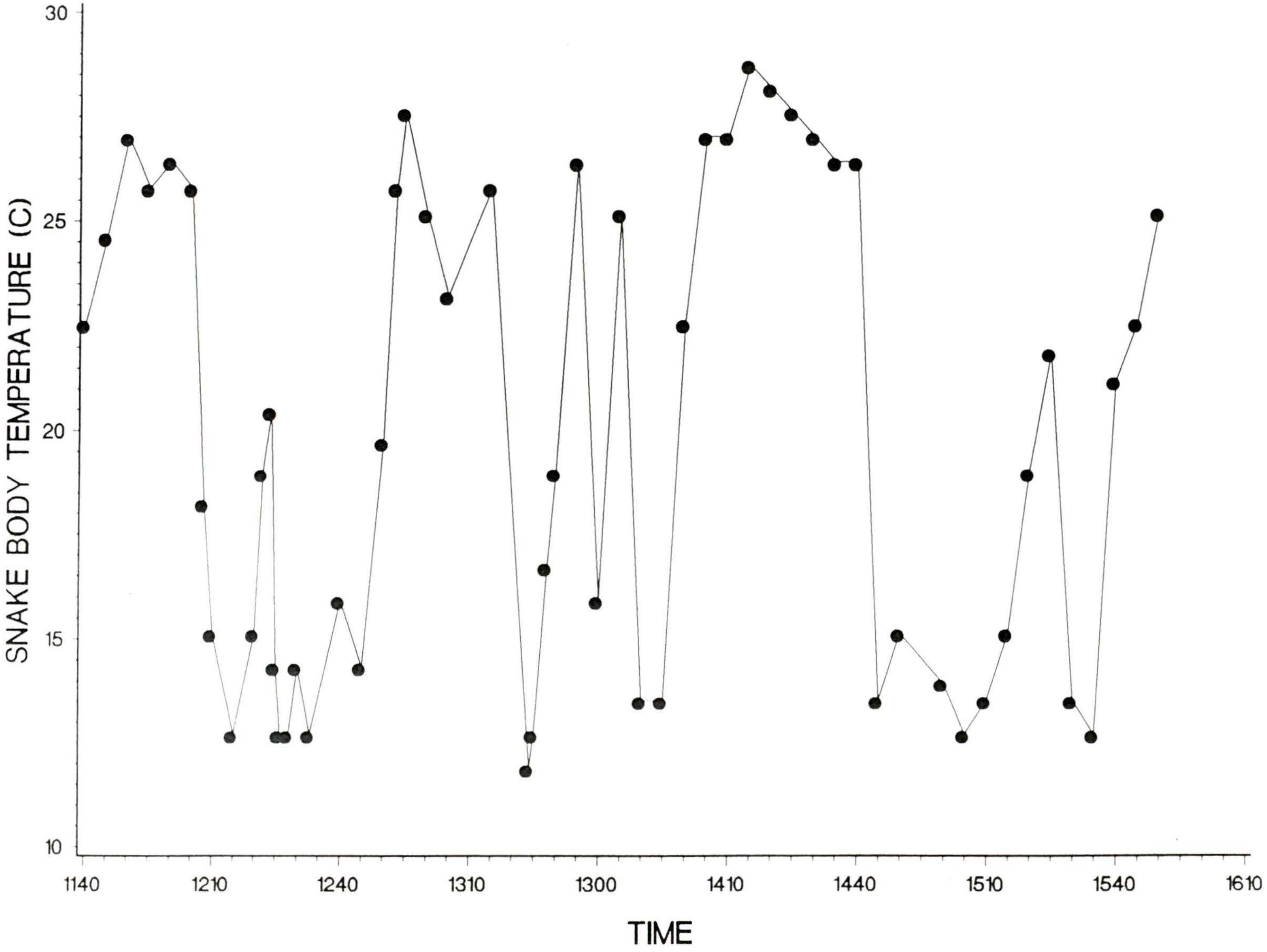
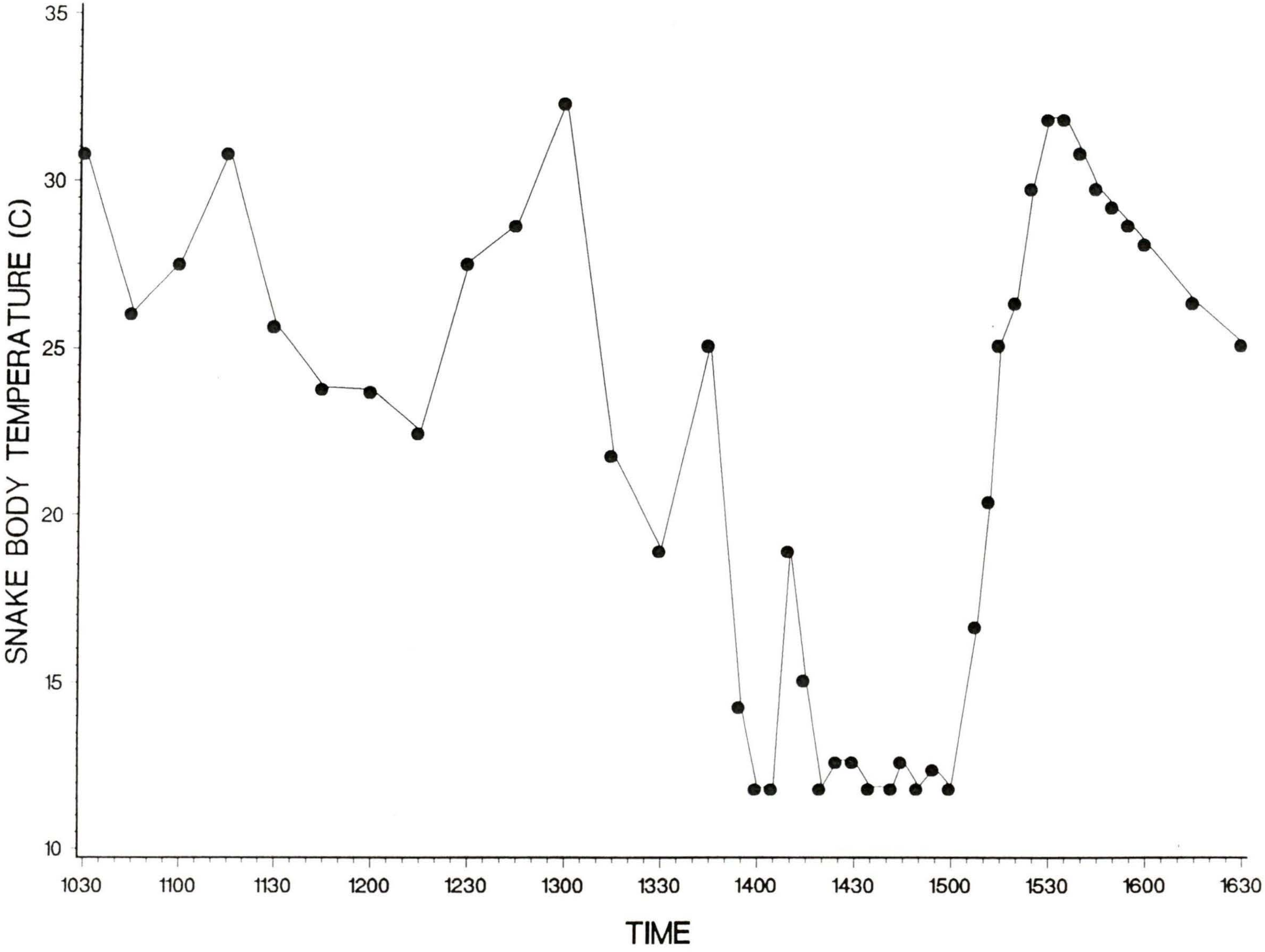

SNAKE BODY TEMPERATURE (C)
30
25
20
15
10
1140
1210
1240
1310
1300
1410
1440
1510
1540
1610
TIME

Figure 13. Body temperatures of snake R5L10 during foraging activity on August 5, 1990.


SNAKE BODY TEMPERATURE (C)
35
30
25
20
15
10
1030
1100
1130
1200
1230
1300
1330
1400
1430
1500
1530
1600
1630
TIME

had increased to 32° C. Model temperatures ranged from 32 to 35° C during this period of time.

Similar behavior was displayed by this snake again on 12 August (Figure 14). The snake, after entering the water, remained at the edge of the channel on the grass mat. Body temperatures were slightly higher than while it was in the water on 5 August, ranging from 13.5 to 16° C. The snake entered the water initially at 1500. At 1548 it was observed swimming out from shore, disappearing under the water for about a second, and returning to shore with a fish in its mouth. The snake's body temperature rose slightly while it consumed the fish on the bank, and then the snake returned to the grass mat in the water at the edge of the channel. At 1720, it moved up onto the bank and, within 25 minutes, its body temperature had reached 33° C. Model temperatures ranged from 32 to 39° while the snake was engaged in this activity.

Daily Patterns of Body Temperature Variation

Continuous records of body temperature over six to 24-hour periods for one to four snakes at a time were obtained on four days between 2 July and 23 July, 1989 and on 39 days between 3 July and 24 September 1990.

On two days, once in 1989 and once in 1990, snake body temperatures were monitored for a continuous 24-hour period. Figure 15 shows temperatures of one snake and models on 23

Figure 14. Body temperatures of snake R5L10 during foraging activity on August 12, 1990. The arrow represents the point where the snake was observed capturing a fish.

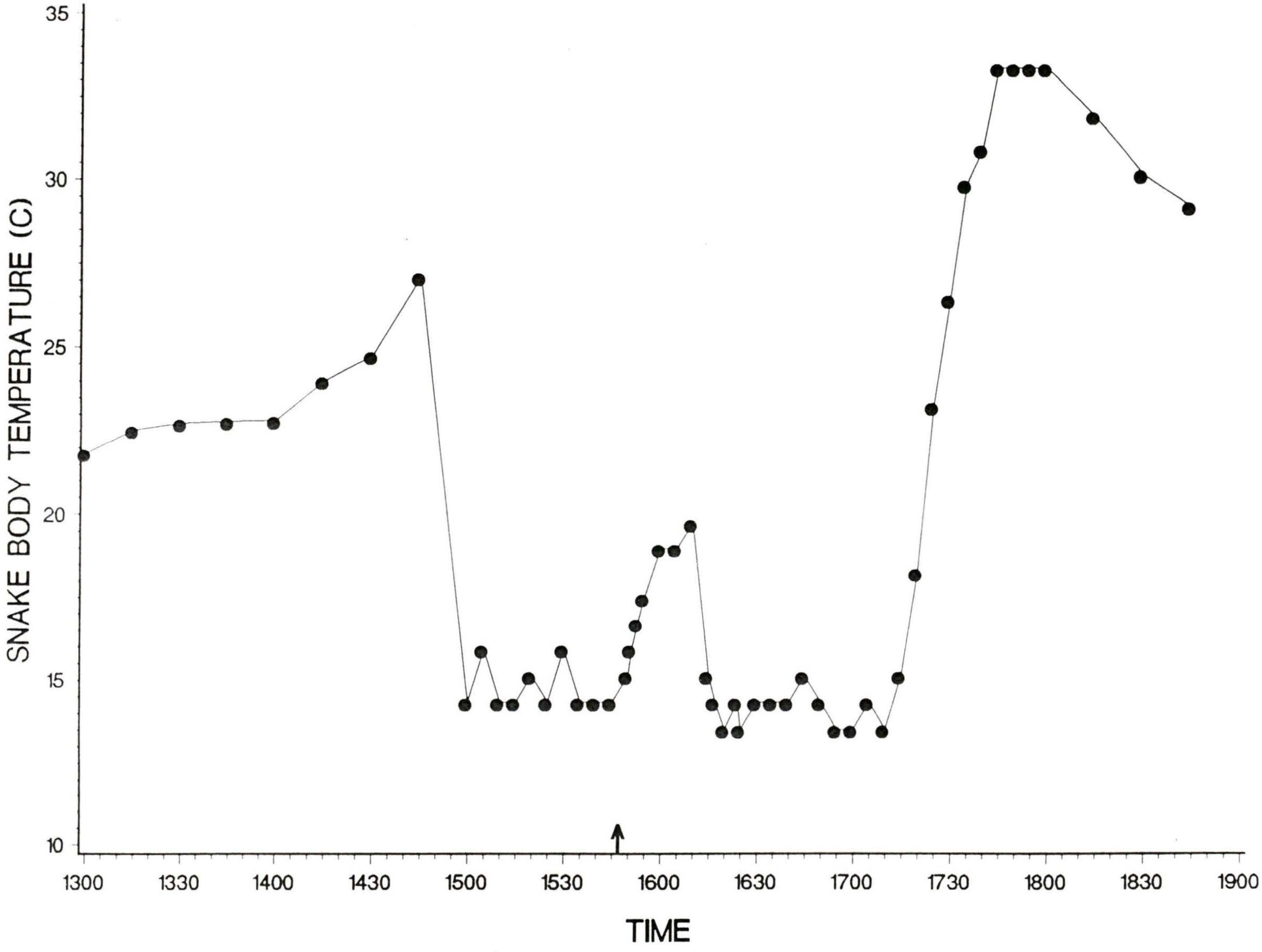
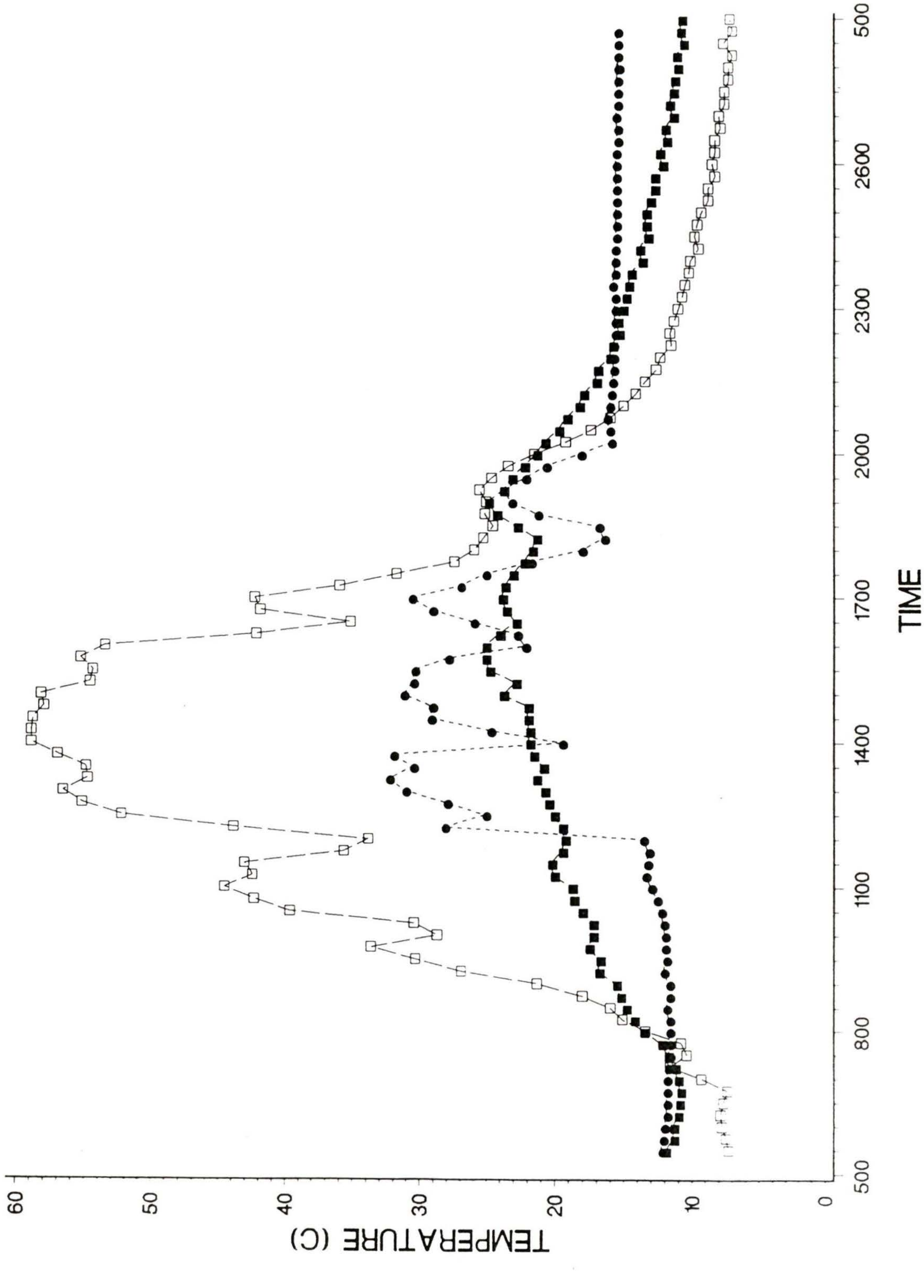

35
30
25
20
15
10
SNAKE BODY TEMPERATURE (C)
1300
1330
1400
1430
1500
1530
1600
1630
1700
1730
1800
1830
1900
TIME

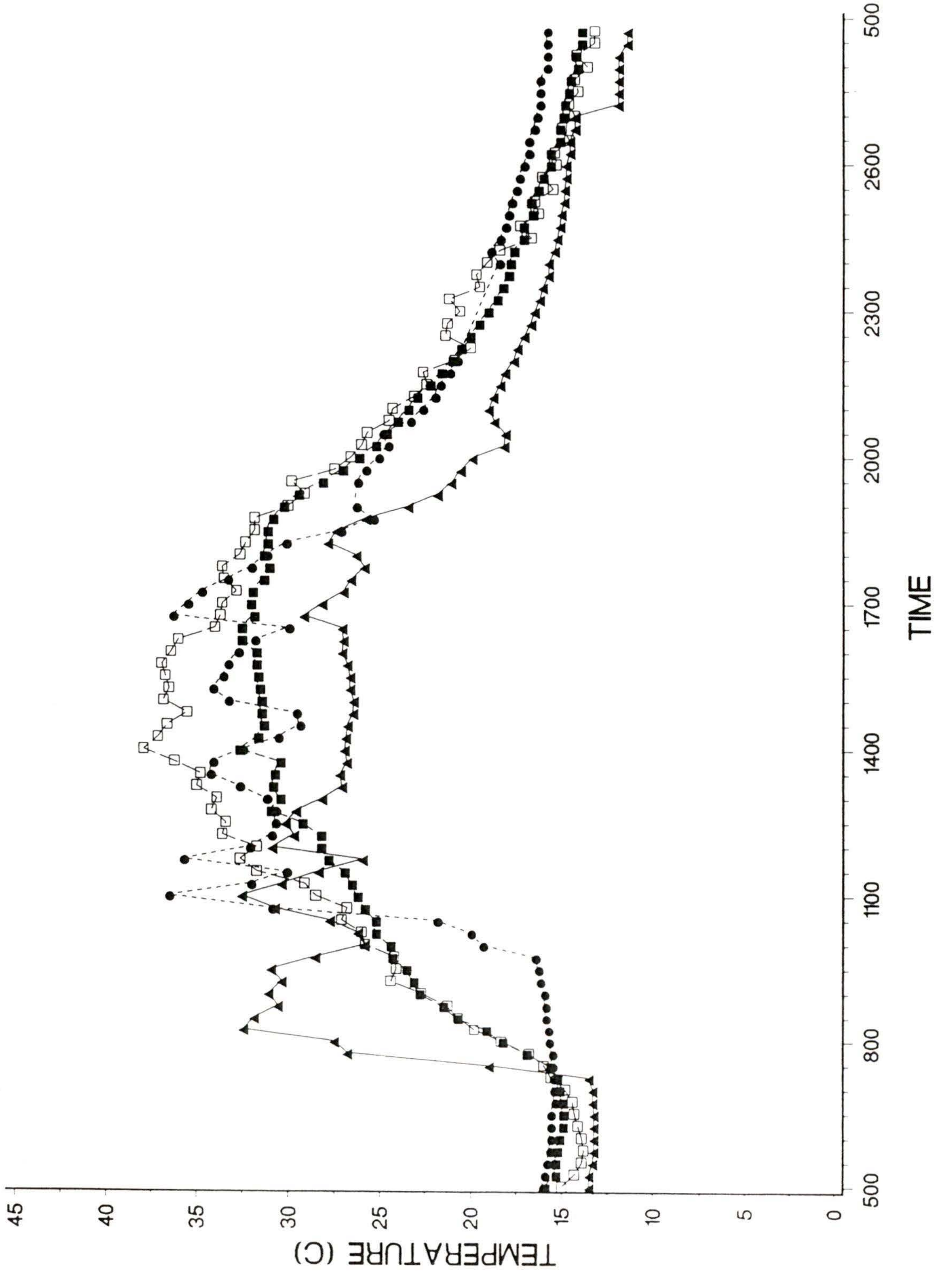
Figure 15. Temperatures of snake and models monitored over a 24-hour period on July 23 to July 24, 1989. Snake R7 (circles), straight model in the sun (open squares), coiled model in the shade (closed squares).


TEMPERATURE (C)
0
10
20
30
40
50
60
TIME
500
800
1100
1400
1700
2000
2300
2600
500

July, 1989. For clarity, only temperatures of the straight model in the sun and the coiled model in the shade are plotted, as these temperatures should define the range of temperatures potentially available to snakes. Weather conditions on this day were clear in the early morning, becoming foggy at 0800, then sunny with cloudy periods for the remainder of the day starting at 1000. Body temperature of the snake was low, but slightly higher than model temperatures from 530 hrs to 800 hrs, at which point model temperatures rose above snake temperature. The temperature of the model in the sun increased rapidly, with some fluctuations reflecting cloudy periods, to a high of 58.8^{o} at 1400 hrs. Temperatures of the shaded model rose gradually to reach a high of 26^{o} at 1430 hrs. The body temperature of the snake did not increase until 1215, when the snake was observed on the bank in the sun. At 1345 the snake moved into the rocks at the end of one of the channels, and its body temperature decreased to 19.5^{o}. The snake reemerged at 1415, and its body temperature increased again. From this time until 1745 the snake was observed moving around on the bank of the hatchery channel, with body temperatures fluctuating between 22.2^{o} and 32.7^{o}. At 1745, the snake moved away from the immediate vicinity of the channels into the forest adjacent to them. Its body temperature dropped slightly at this point, then rose again before the sun went down behind the trees. At 1945 the snake went under a log, and its body temperature began to decrease gradually to 15.9° at 2030. Between 2045 and 0515 snake temperature remained very constant, between 15.3° and 15.8°, while temperatures of both exposed and shaded models continued to decrease throughout the night. The temperature of the exposed model decreased more rapidly than that of the shaded model, and reached a lower temperature by the end of the monitoring period.

Two snakes were monitored for a 24-hour period on 12 July 1990 (Figure 16). The weather on this day was clear and very hot. At 0500 R4L2 was slightly warmer than the models at 16.1°, and R5L10 was slightly cooler at 13.5°. At 0715, model temperatures began to rise gradually, and at this time R5L10 emerged to bask, resulting in a rapid increase in its body temperature. The other snake (R4L2) remained under cover, maintaining a stable body temperature until 1000, when it was observed emerging to bask, and its body temperature increased rapidly to a high of 36.6°. The body temperature of this snake fluctuated somewhat, but generally remained just below the temperature of the exposed model (approx. 36°) throughout the afternoon. The body temperature of R5L10 also fluctuated considerably in the morning, but remained fairly stable at approximately 27° throughout the afternoon. This temperature was lower than that of the shaded model. At 1815 the temperature of R4L2 had also dropped below the level of both models, which at

Figure 16. Temperatures of snake and models monitored over a 24-hour period on July 12 to July 13, 1990. Snake R4L2 (circles), snake R5L10 (triangles), models as in Figure 15.


TEMPERATURE (C)
0
5
10
15
20
25
30
35
40
45
TIME
500
800
1100
1400
1700
2000
2300
2600
500

this point were approximately equal and decreasing steadily. The body temperatures of both snakes declined steadily throughout the night, with R4L2 maintaining slightly higher temperatures that exceeded model temperatures by 2400. The body temperature of R5L10 remained below model temperatures, reaching a low of 11.4° by 0445.

Similar gradual decreases in body temperatures during the night were shown by snakes monitored on 3 occasions in 1990 for a 12-hour period from 1900 to 0700 hrs. On the warmest night (low of 17°, cloud cover after a hot day), the body temperature of the snake remained above 27° from 1900 until 100 hrs, at which point it declined suddenly to 24.5° (Figure 17). The body temperature of this snake remained above 23° for the entire night, whereas model temperatures fell gradually to a low of 21°. The snake remained in the rocks at the end of one of the hatchery channels throughout the night.

The evenings of 16 August and 30 August were cooler, with clearing in the evening after cool, cloudy days (lows of 12° and 10.5° respectively). The body temperature of one snake monitored on 16 August dropped rapidly in the early part of the night, reaching 14.2° by 2015 (Figure 18). The snake then experienced more gradual declines to reach a low of 12.5° by 0645. This snake was under cover in an exposed location (a cleared area under power lines) some distance from the monitoring location, so model temperatures may not

Figure 17. Temperatures of snake and models monitored from 7 PM to 7 AM on August 10, 1990. Snake R5L10 (circles), models as in Figure 15.

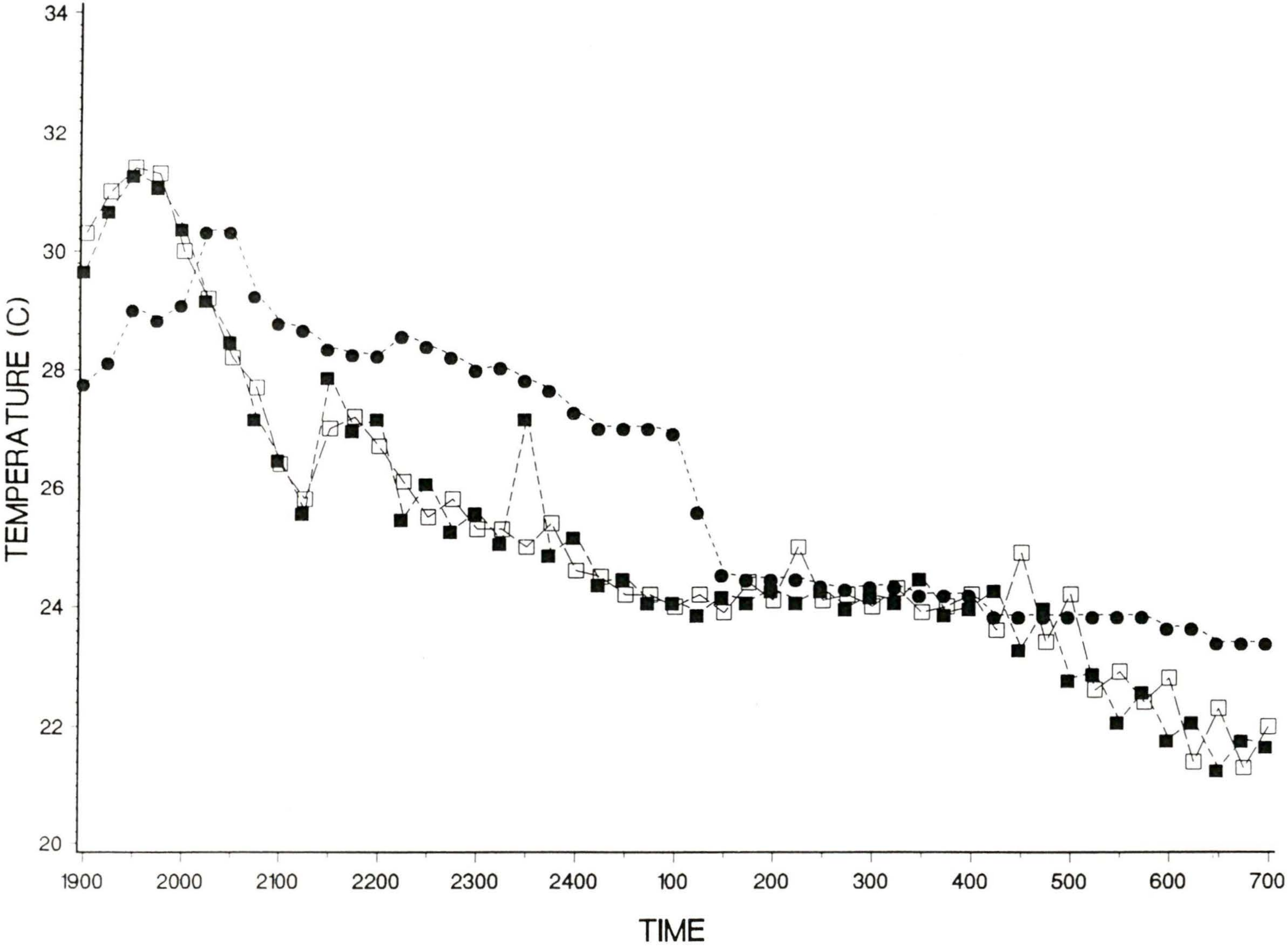
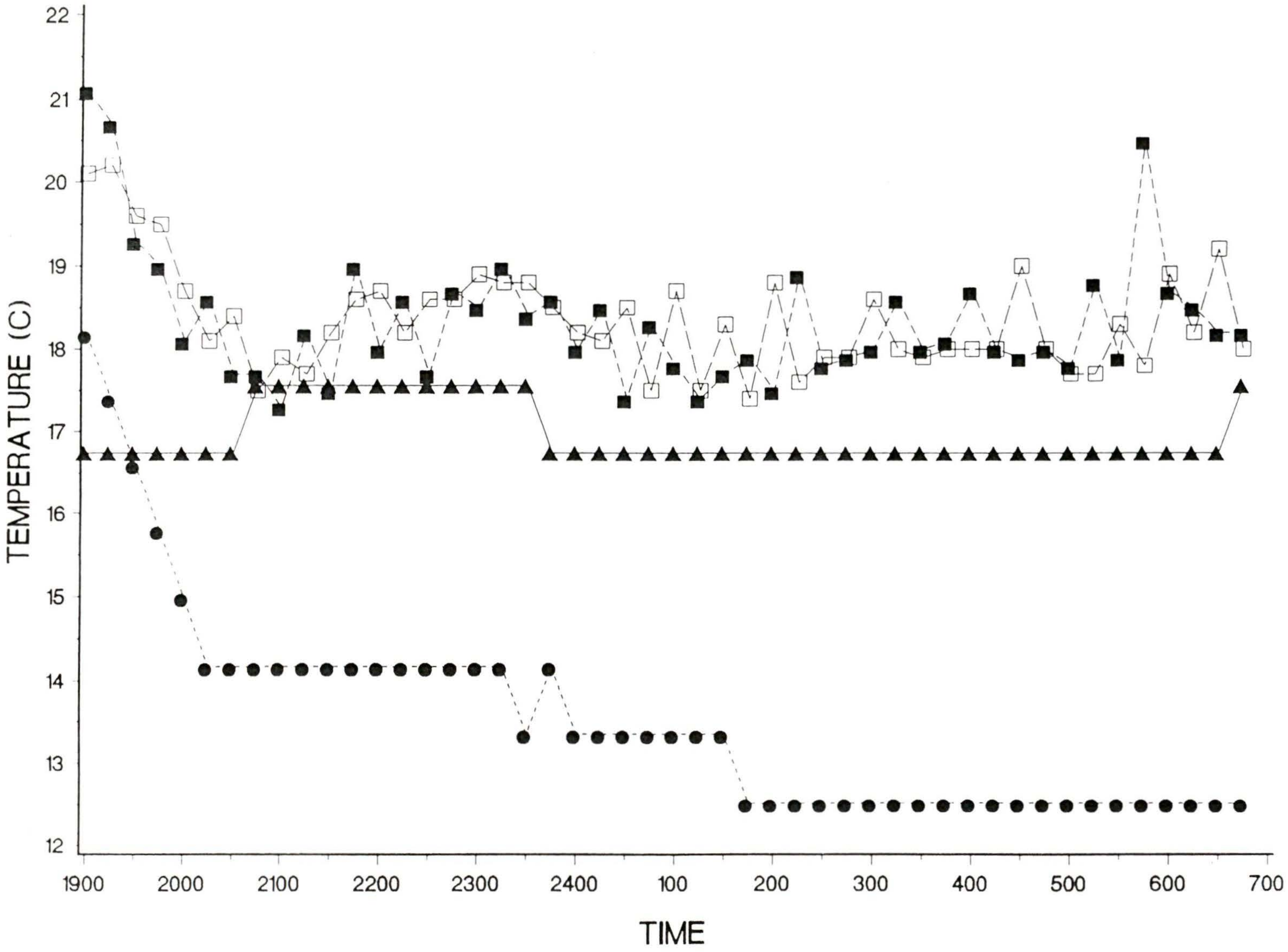

34
32
30
28
26
24
22
20
TEMPERATURE (C)
1900
2000
2100
2200
2300
2400
100
200
300
400
500
600
700
TIME

Figure 18. Temperatures of snakes and models monitored from 7 PM to 7 AM on August 16, 1990. Snake R7L6 (circle), snake R8L7 (triangle), models as in Figure 15.


TEMPERATURE (C)
22
21
20
19
18
17
16
15
14
13
12
1900
2000
2100
2200
2300
2400
100
200
300
400
500
600
700
TIME

have reflected temperatures in this area. The other snake (R8L7) maintained a higher, and more stable, body temperature throughout the night, only slightly lower than model temperatures. This snake was in a bank at the edge of the forest. A very stable body temperature throughout the night was also maintained by a snake monitored on 30 August (Figure 19). Model temperatures fluctuated a great deal during the night, but for the most part, snake temperature remained slightly higher than model temperatures.

On cloudy mornings, snakes exhibited two patterns of body temperature variation (Figure 20). Body temperatures were either initially low, and increased gradually, or remained relatively stable throughout the morning. Gradual increases in body temperature may have corresponded with emergence of the snake from cover, whereas stable body temperatures resulted from the snake remaining under cover. One snake maintained a stable body temperature of approximately 23^{o} C on a cloudy morning. Model temperatures on cloudy mornings generally increased gradually. Similar patterns occured on cloudy afternoons, with snakes that remained under cover maintaining stable body temperatures, and snakes that had emerged and warmed up cooling gradually when they took cover again (Figure 21).

On warm sunny mornings, snakes that emerged to bask achieved high body temperatures very quickly (Figure 22). On most sunny mornings, however, the snakes that were

Figure 19. Temperatures of snake and models monitored from 7 PM to 7 AM on August 30, 1990. Snake R5L10 (circles), models as in Figure 15.

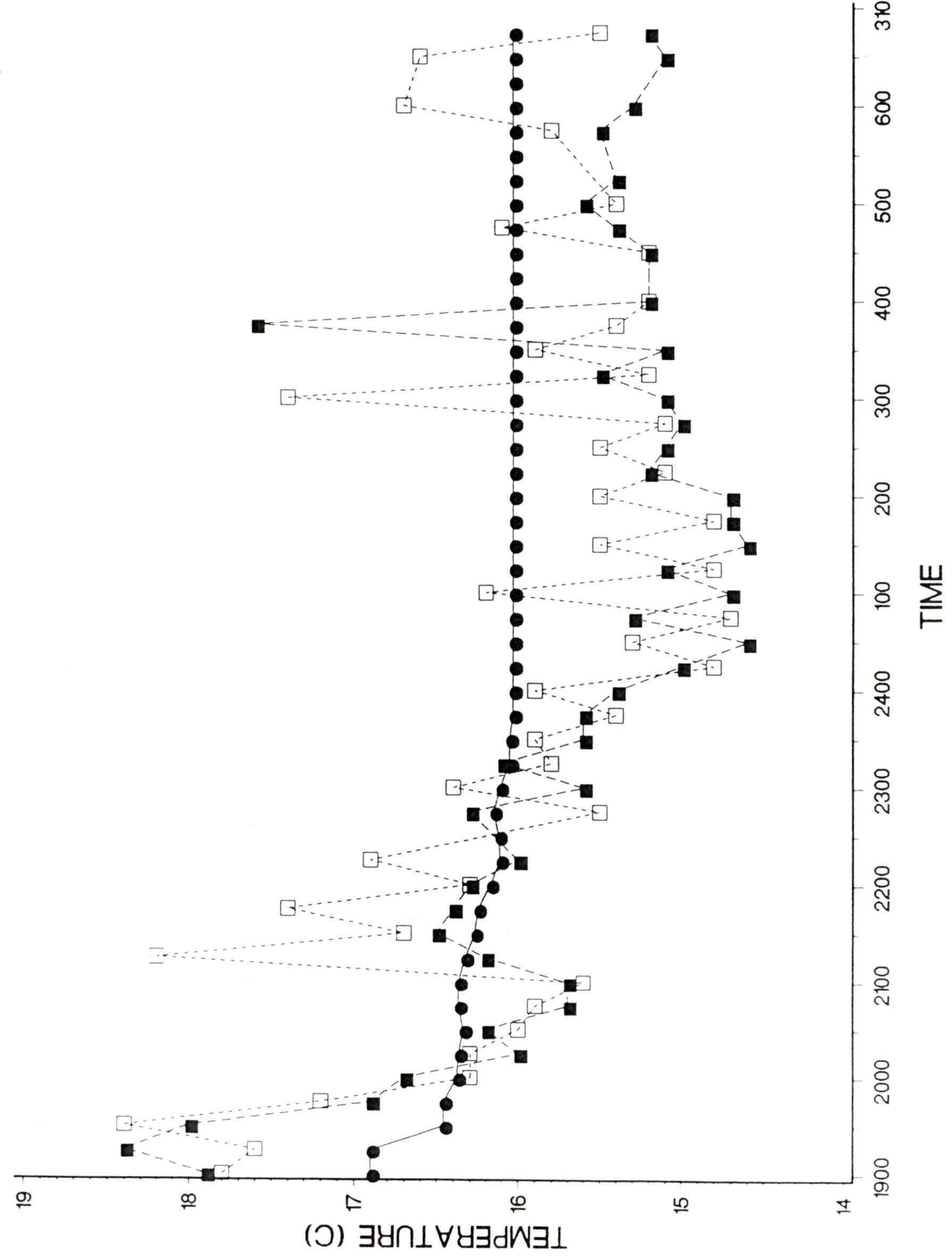

TEMPERATURE (C)
19
18
17
16
15
14
TIME
1900
2000
2100
2200
2300
2400
100
200
300
400
500
600
3100

Figure 20. Representative patterns of body temperature variation for two snakes monitored on a cloudy morning (August 15, 1990). Snake R7L6 (circles), snake R8L7 (triangles), models as in Figure 15.

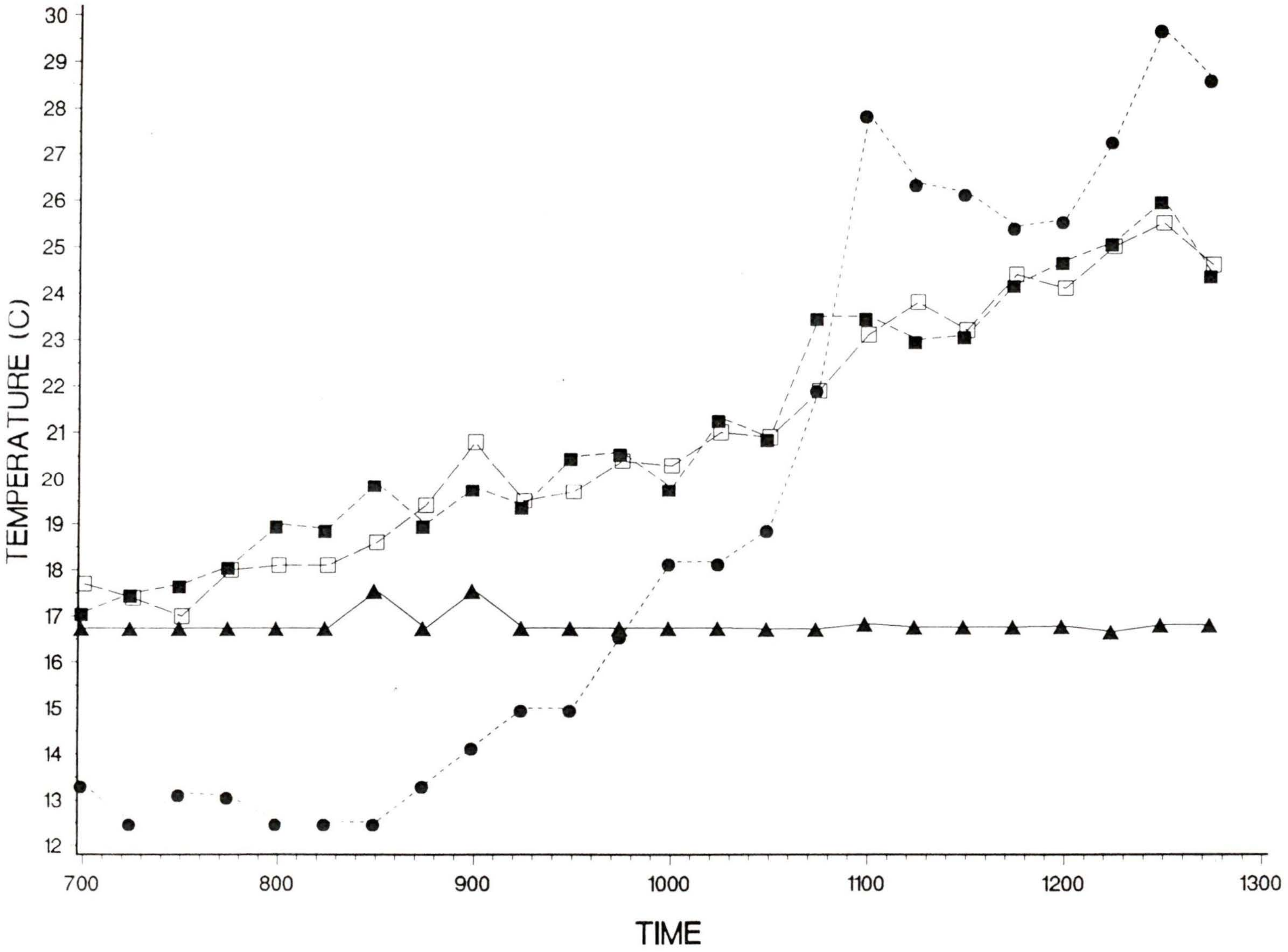

TEMPERATURE (C)
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
TIME
700
800
900
1000
1100
1200
1300

Figure 21. Representative patterns of body temperature variation for two snakes monitored on a cloudy afternoon (September 1, 1990). Snake R5L10 (circles), snake R8L7 (triangles), models as in Figure 15.

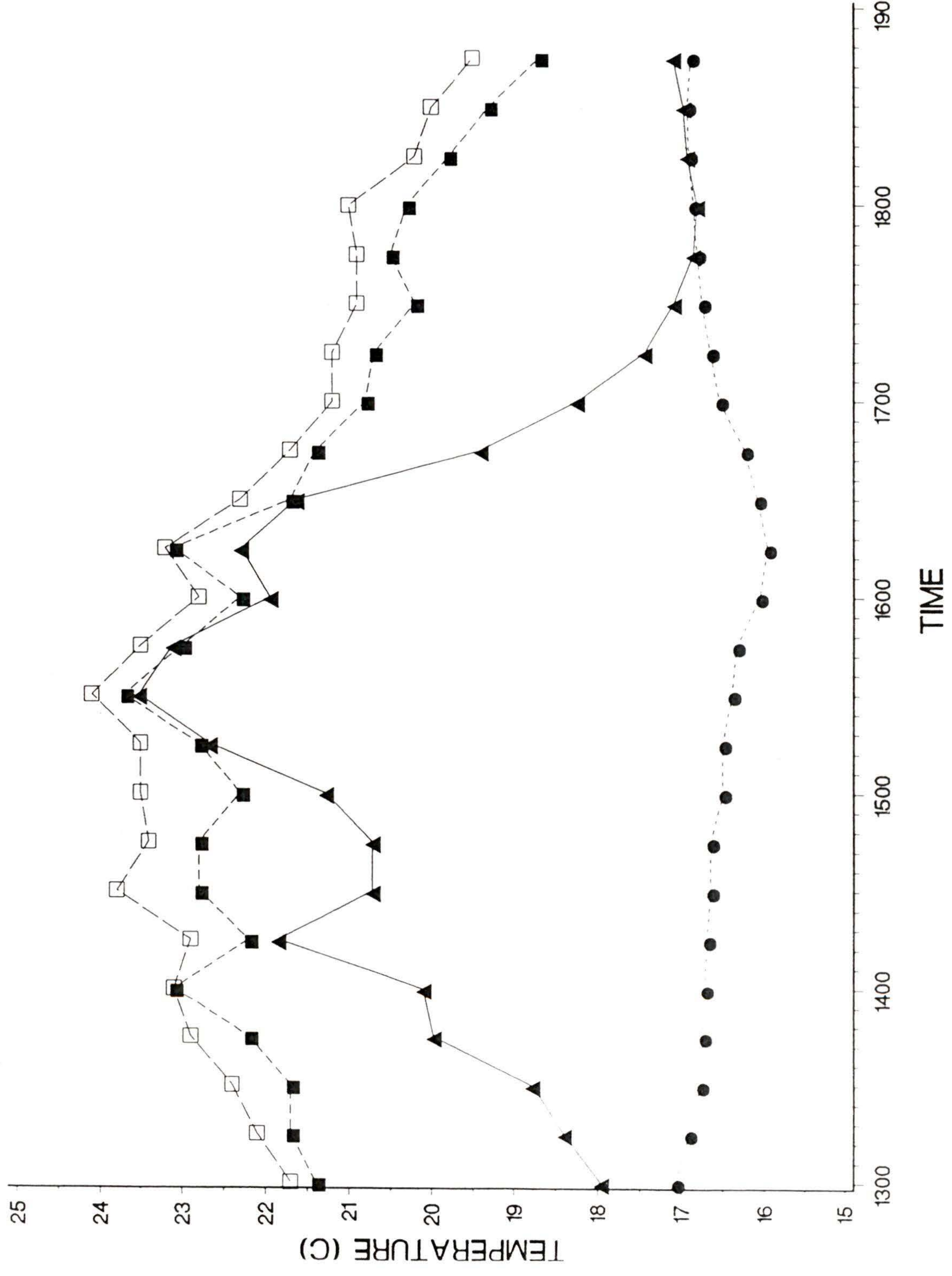
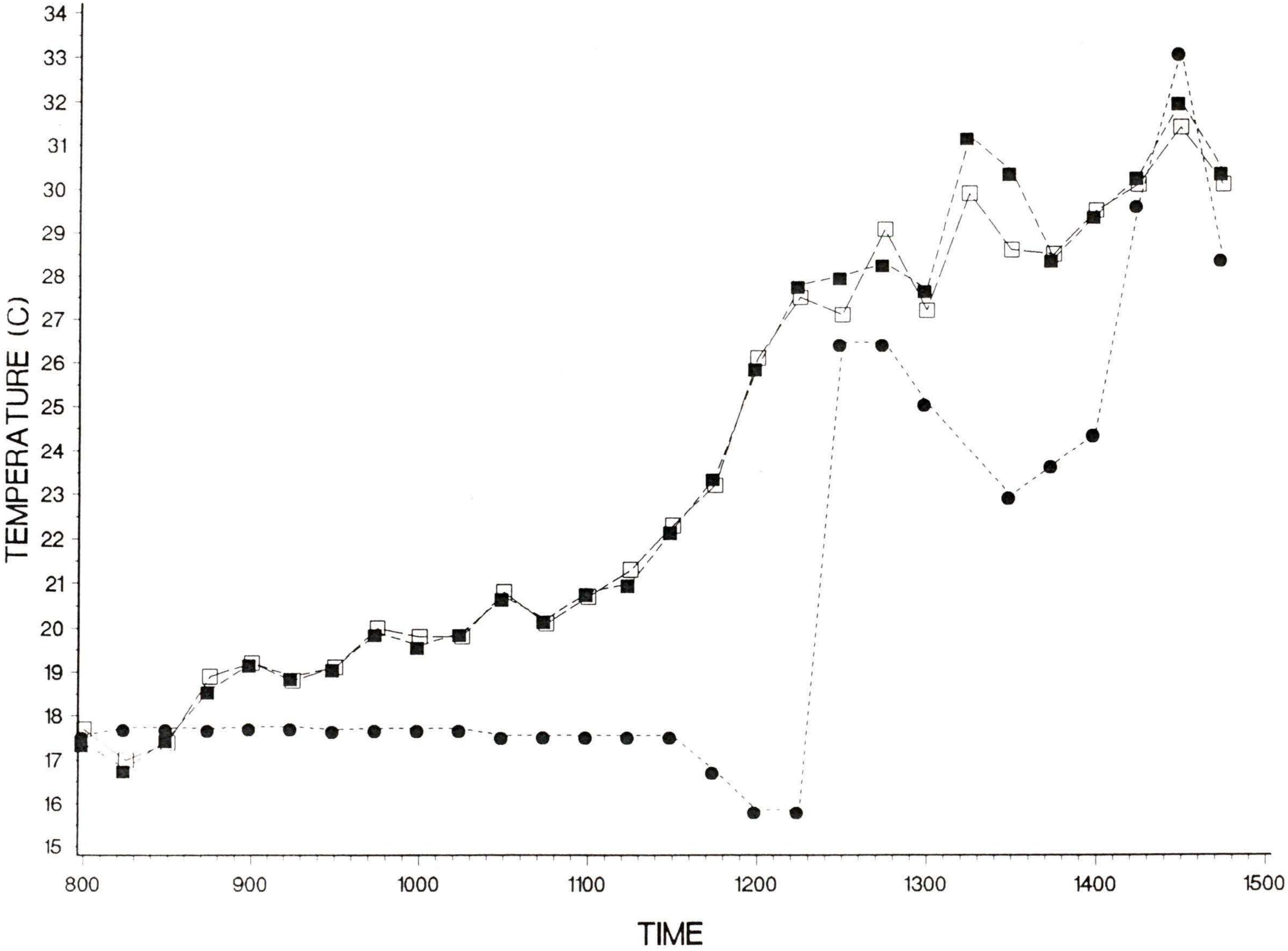

TEMPERATURE (C)
25
24
23
22
21
20
19
18
17
16
15
TIME
1300
1400
1500
1600
1700
1800
1900

Figure 22. Representative pattern of body temperature variation for a snake monitored on a sunny morning (August 2, 1990). Snake R8L7 (circles), models as in Figure 15.


TEMPERATURE (C)
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
800
900
1000
1100
1200
1300
1400
1500
TIME

monitored remained under cover, and their body temperatures rose gradually to high levels (Figure 23). Model temperatures on hot, sunny mornings increased steadily from fairly low temperatures (approx. 13 to 17° C) to high temperatures (generally above 30° C) by 1300. With the exception of snakes that were observed foraging, most of the snakes remained under cover on hot, sunny afternoons, and maintained body temperatures between 25 and 35° C (Figure 24). Body temperatures declined gradually in the late afternoon, but in general were still above 20° C at 1845. Model temperatures on hot, sunny afternoons ranged from 30° C to 50° C in the early afternoon, and declined gradually in the late afternoon. Snake body temperatures were almost always lower than model temperatures in the early afternoon, although they often approached model temperatures in the late afternoon as model temperatures decreased more quickly than snake temperatures.

Capture Frequencies and Movements

Between June 1987 and September 1990, I captured 106 new snakes and made 63 captures of previously marked snakes at the hatchery channels. One of these snakes was recaptured five times, one four times, one three times, and nine twice during the study. Thirty-six snakes were recaptured only once. The time interval between recaptures ranged from seven days to three years. I also captured 23

Figure 23. Representative pattern of body temperature variation for a snake monitored on a sunny morning (August 8, 1990). Snake R8L7 (circles), models as in Figure 15.

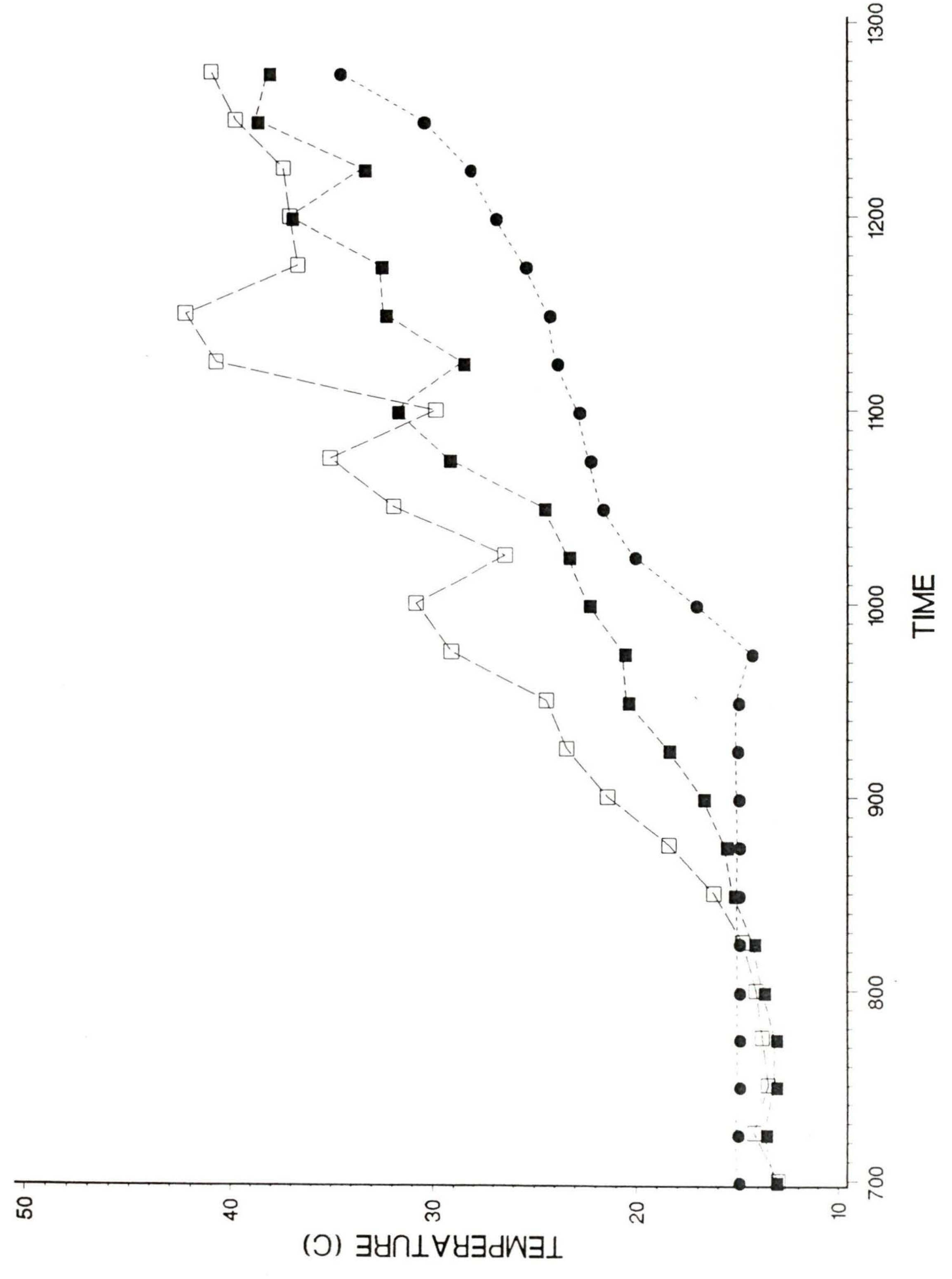
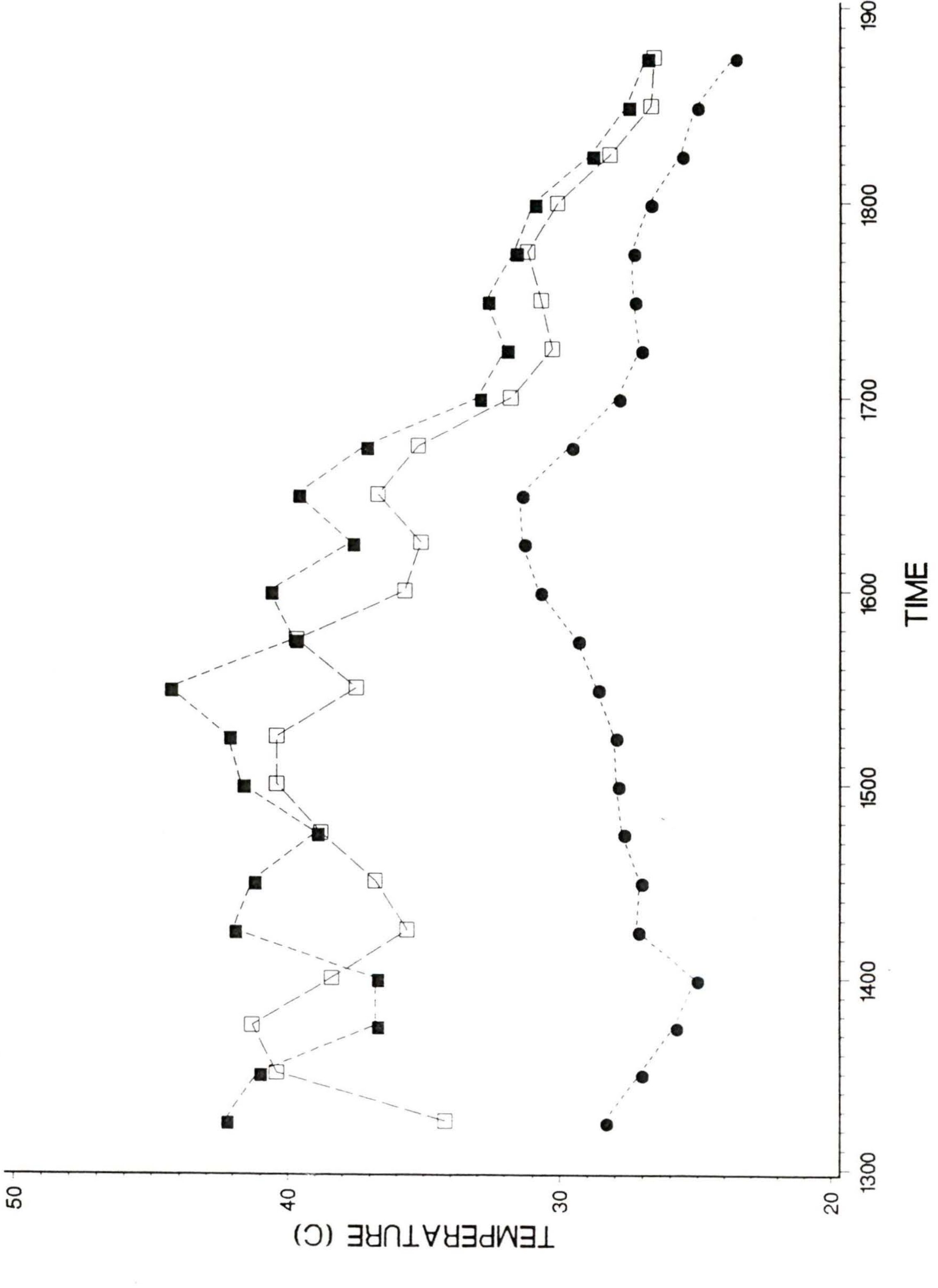

TEMPERATURE (C)
50
40
30
20
10
TIME
700
800
900
1000
1100
1200
1300

Figure 24. Representative pattern of body temperature variation for a snake monitored on a sunny afternoon (August 21, 1990). Snake R8L7 (circles), models as in Figure 15.

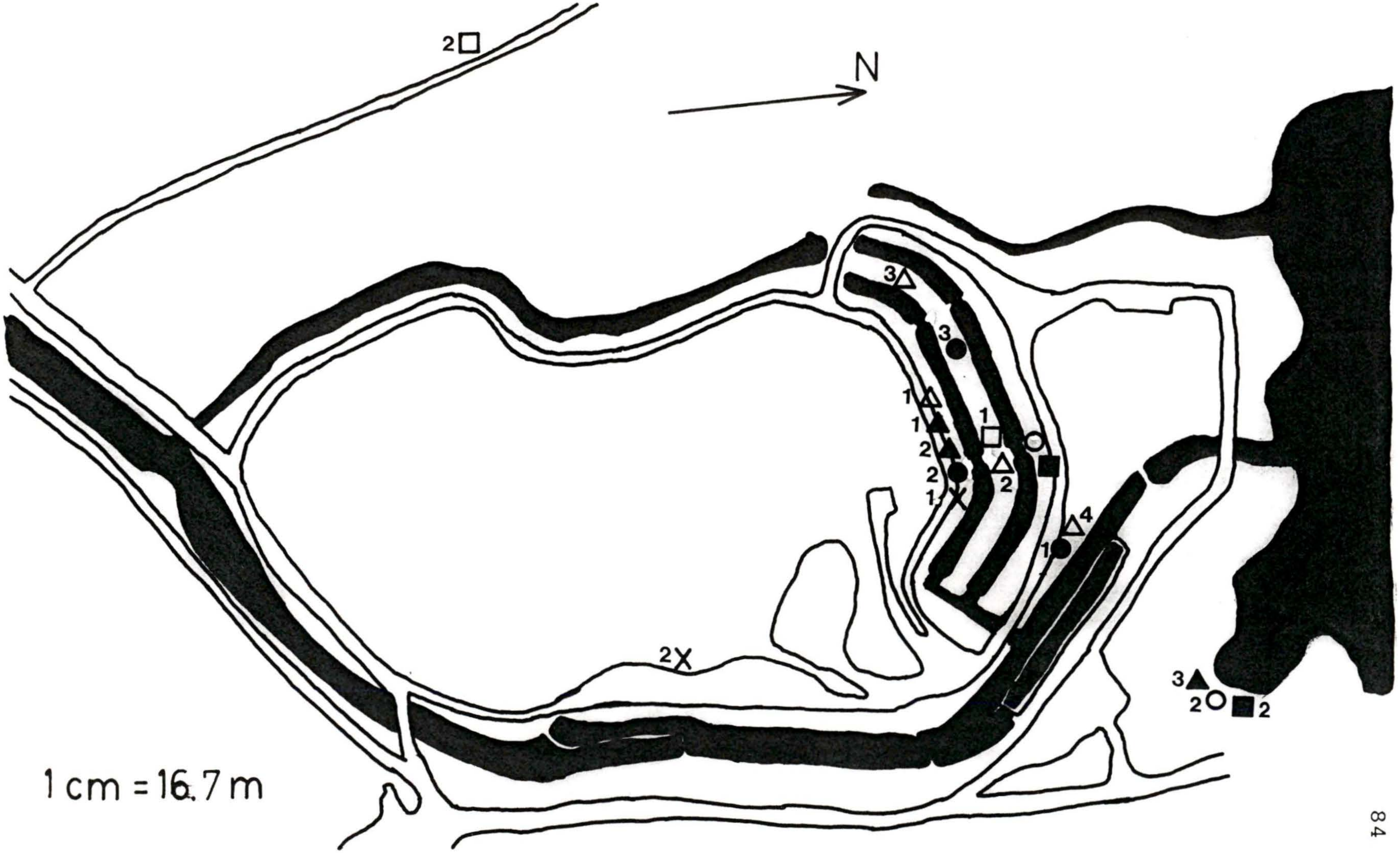

TEMPERATURE (C)
50
40
30
20
TIME
1300
1400
1500
1600
1700
1800
1900

new snakes and recaptured 11 marked snakes at the hatchery site away from the immediate vicinity of the channels. Two snakes (R5L7, R8L6) originally caught at the channels were recaptured for the first time away from the channels, two snakes (L10, R7L11) from the channels were recaptured there after being recaptured once at the channels, and one snake (R4L8) from the channels was recaptured twice there before being recaptured on the bank of Robertson Creek (Figure 25). One snake (R4L3) originally captured at the channels was recaptured three years later 240 m away (Figure 25). Two snakes (VL4L3, VR4R9L4) originally captured at the hatchery site away from the channels were recaptured 56 days and over one year later, respectively, at the hatchery channels.

At the reference site, I captured 66 new snakes and recaptured 32 marked snakes from June 1987 to September 1990. Twelve of the recaptured individuals were recaptured only once, four twice, one three times, one four times and one five times. All of these snakes were recaptured at the reference site, and no movements were recorded between the reference and hatchery sites.

Of the five snakes studied by telemetry, only one snake remained in the vicinity of the hatchery channels for the entire summer. This snake was observed around the channels and located in the rocks at the bottom of the channels from the time it was released on 30 June 1990 until 2 August, when it was observed foraging. On 3 August it moved to the

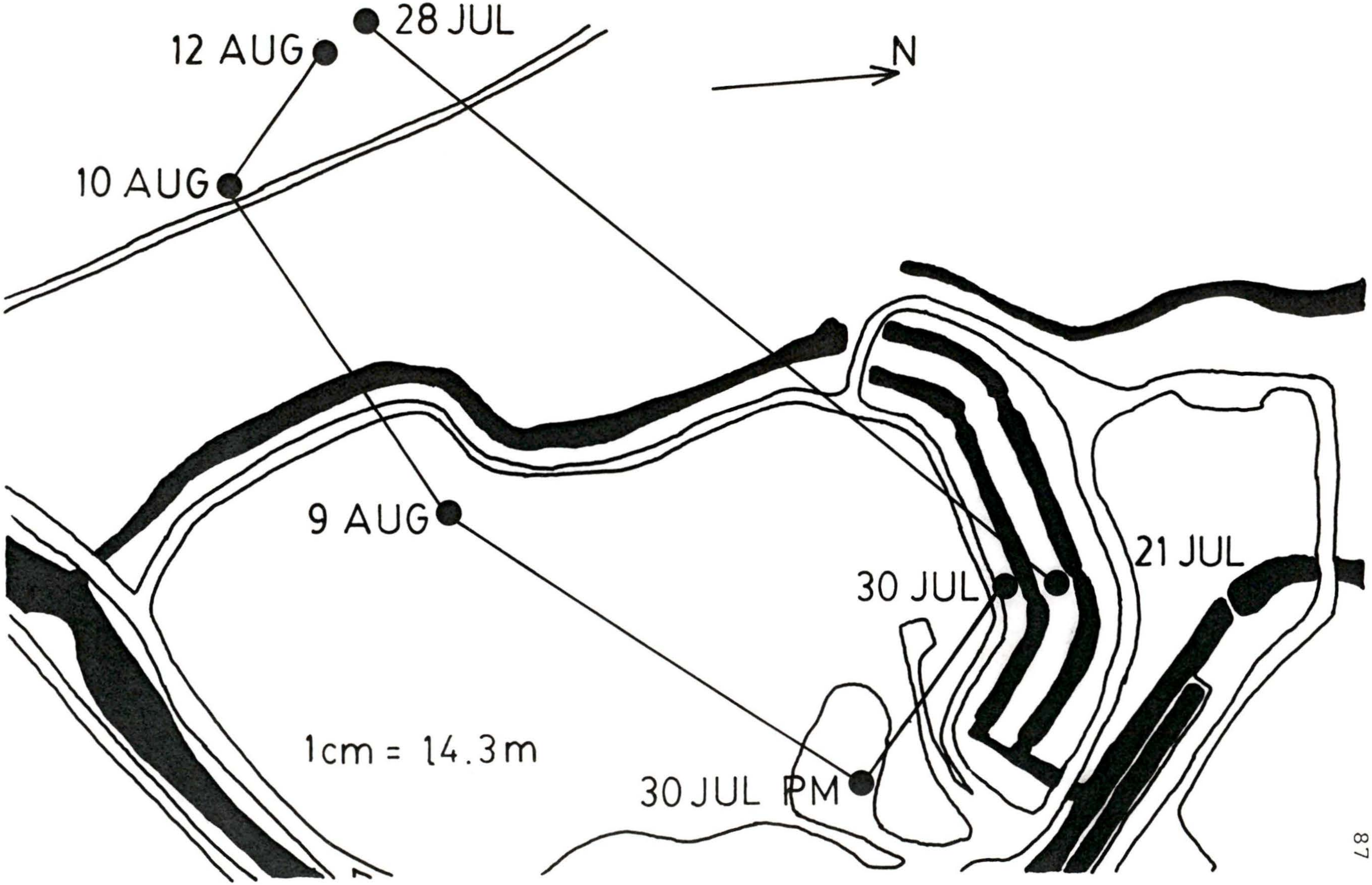
Figure 25. Map of the hatchery site showing known movements of individual snakes between hatchery channels and surrounding areas.
Symbols and capture dates: R5L7 (X) 1=23 JUL 1987, 2=2 SEP 1990; R8L6 (open circle) 1=14 JUN 1989, 2=11 MAY 1990; L10 (closed triangle) 1=14 JUN 1989, 2=15 JUL 1987, 3=14 AUG 1987; R4L8 (open triangle) 1=7 JUL 1987, 2=24 MAY 1989, 3=2 SEP 1990, 4=10 SEP 1990; R4L3 (open square) 1=30 JUN 1987, 2=30 JUN 1990; VL4L3 (closed circle) 1=1 JUL 1987, 2=26 AUG 1987, 3=24 AUG 1988; VR4R9L4 (closed square) 1=11 MAY 1989, 2=23 AUG 1990.


2□
N
3△
3●
1△
1▲
2▲
2●
1X
1□
○
△2
■
△4
1●
2X
3▲
2○
■2
1 cm = 16.7 m

bank of Robertson Creek (Figure 25, closed circle-1) and remained there until 5 August, when it again was observed foraging in the channels. It remained in the vicinity of the channels until 18 August, when it was collected because of transmitter malfunction. I released it with a new transmitter on 22 August, and it moved to the base of a cedar tree near Robertson Creek. It remained in this location until 3 September, when it was observed along the bank of the creek engaged in mating activity with three males. It remained in this area and was observed mating with the same individuals on several occasions until it was collected on 27 September.

All of the other snakes moved away from the vicinity of the channels within several days of their release. One individual moved away by 1 July, and was found dead at the edge of the Stamp River on 13 July. The transmitter from this individual was implanted in another snake that was released at the channels on 21 July. This snake moved away from the channels immediately, and was not located until 28 July, near the road under the power lines approx 240 m away from the channels (Figure 26). I captured this snake on 30 July, and re-released it at the channels. It moved from there to the equipment dump, and remained there until 9 August, when it began to move back toward the power lines. By 12 August it was located in the same area under the power lines. I collected this snake on August 19 to implant the

Figure 26. Map of hatchery sites showing movements of one of the snakes monitored by telemetry in 1990.

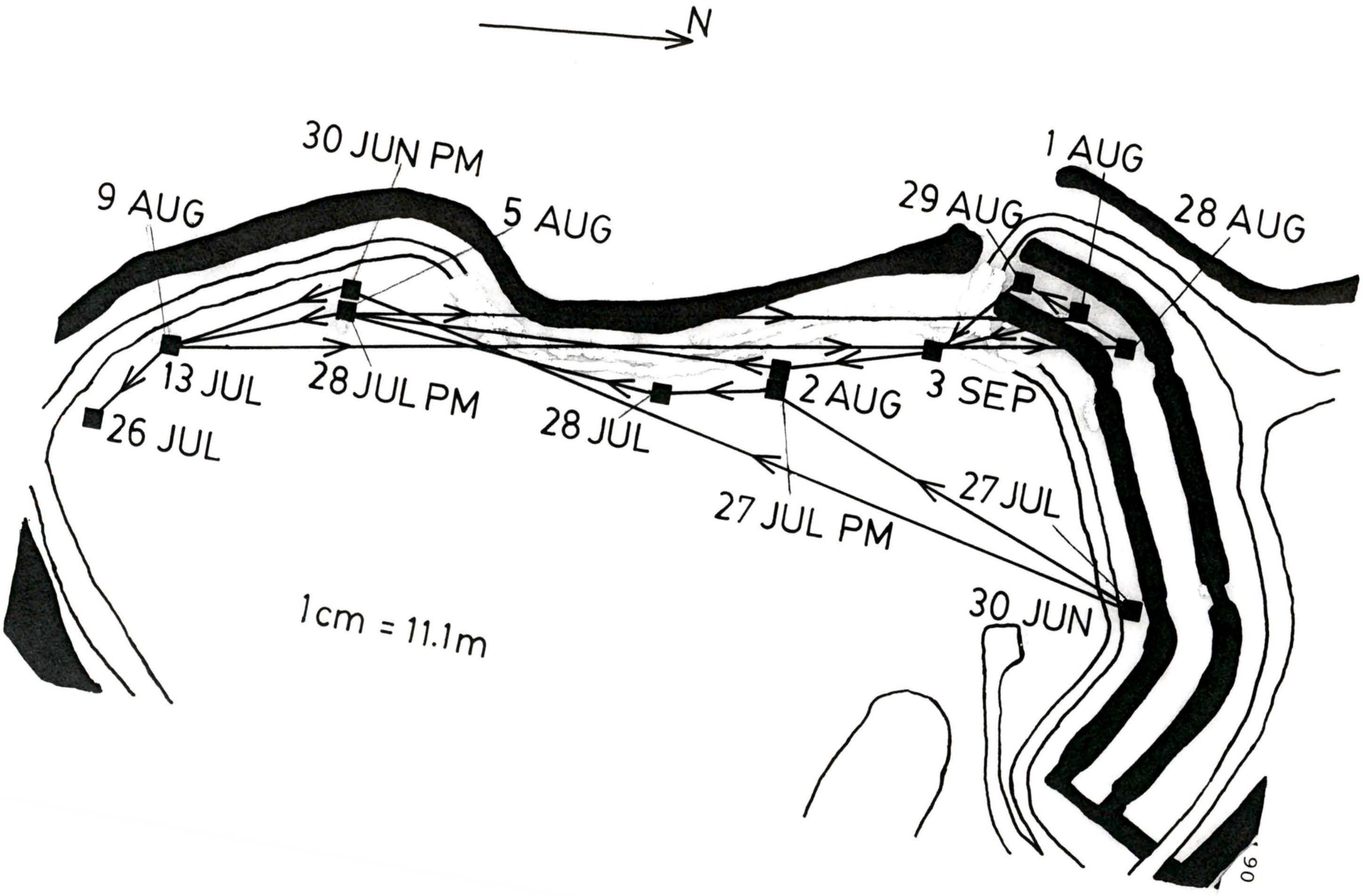

28 JUL
12 AUG
N
10 AUG
9 AUG
21 JUL
30 JUL
1cm = 14.3m
30 JUL PM

transmitter in R5L10.

Another individual also moved away from the vicinity of the channels after it was released on 30 June, and was subsequently located at the edge of the forest by Glover Creek (Figure 27). The snake remained in this area until 26 July, when I captured it and attempted to re-release it at the channels. It moved back up the creek to the same location after release. On 1 August, however, the snake was observed foraging in the hatchery channels. It then slowly made its way back up the creek, to the same location, and remained here until 28 August, when it was again located at the hatchery channels. It remained in the vicinity of the channels until 3 September, when it began moving back up Glover Creek. On 4 September, the transmitter malfunctioned and the snake was collected.

One snake remained in the vicinity of the channels from the time it was released on 30 June until 17 July, but on 21 July the signal from this transmitter was very weak in the vicinity of the channels, fading in and out, and the snake could not be located after this date. The snake may have moved away from the channels to an area where it could not be located by my search efforts, it may have been killed by a predator, or the transmitter may have malfunctioned.

Figure 27. Map of hatchery sites showing movements of one of the snakes monitored by telemetry in 1990.


N
30 JUN PM
9 AUG
5 AUG
1 AUG
29 AUG
28 AUG
13 JUL
28 JUL PM
26 JUL
28 JUL
2 AUG
3 SEP
27 JUL
27 JUL PM
30 JUN
1cm = 11.1m

LABORATORY EXPERIMENTS

Feeding Experiments

1990 Trials

In the 1990 feeding experiments, the greatest number of fish was eaten by snakes exposed to both warm air and warm water, whereas no fish were consumed by snakes in the cold land and cold water condition (Table 3). There was a significant effect of both land and water temperatures on the mean number of fish eaten in each condition [Land, $P(F_{1,12} \geq 8.117)=0.015$; Water, $P(F_{1,12} \geq 8.117)=0.015$]. There was no significant interaction of land and water temperature on mean number of fish eaten [$P(F_{1,12} \geq 3.110)=0.103$].

Snakes in both warm land conditions spent significantly more time engaged in foraging activity than snakes in the cold land conditions (Table 4) [$P(F_{1,12} \geq 5.34)=0.0395$]. Two snakes in both of the cold land conditions spent little (1 minute) or no time foraging. The mean amount of time spent foraging by snakes in the warm or cold water conditions was not significantly different [$P(F_{1,12} \geq 0.66)=0.4311$], and there was no significant interaction between land and water temperature on the mean amount of time spent foraging [$P(F_{1,12} \geq 0.19)=0.6739$]. There was no relationship between the amount of time spent foraging and the number of fish eaten in 1990 [$P(r_{16} \geq 0.255)=0.341$] (Figure 28).

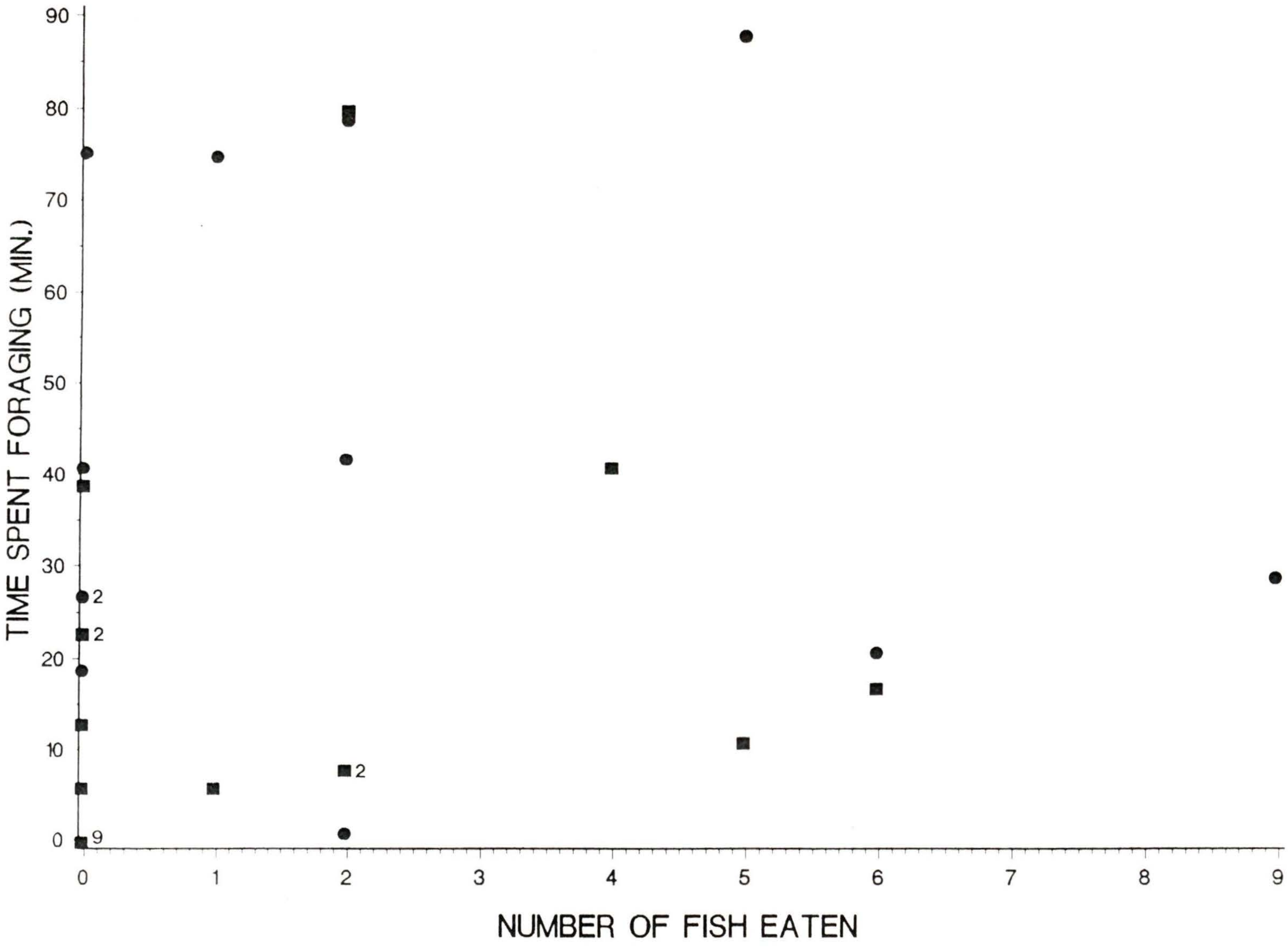
Table 3. Number of fish eaten by snakes in each experimental condition in 1990 and 1991. Numbers in brackets represent the number of fish eaten in each experiment, and correspond directly to the amount of time spent foraging in each experiment (Table 4).

	Land Temperature	
	Warm $\bar{x}$±S.D.	Cold $\bar{x}$±S.D.
Water Temperature		
1990		
Warm	5.25±1.65 (9,6,1,5)	1.00±0.58 (2,0,2,0)
Cold	1.00±0.58 (2,2,0,0)	0 (0,0,0,0)
1991		
Warm	2.25±1.31 (4,0,0,5)	2.00±1.41 (0,2,6,0)
Cold	0.50±0.50 (0,0,2,0)	0.25±0.25 (0,0,0,1)

Table 4. Amount of time spent foraging in each experimental condition in 1990 and 1991. Numbers in brackets represent times for each experiment, and correspond to number of fish eaten in each experiment (Table 3).

	Land Temperature	
	Warm $\overline{x}$±S.D.	Cold $\overline{x}$±S.D.
Water Temperature		
1990		
Warm	53.25±16.61 (29,21,75,88)	17.50±10.28 (42,27,1,0)
Cold	37.00±15.69 (8,79,19,41)	12.50± 7.26 (0,23,0,27)
1991		
Warm	14.50± 9.12 (41,0,6,11)	6.25± 4.05 (0,8,17,0)
Cold	29.00±17.64 (0,23,80,13)	11.25± 9.36 (39,0,0,6)

Figure 28. Amount of time spent foraging plotted against the number of fish eaten in 1990 (circles) and 1991 (squares) feeding experiments.


TIME SPENT FORAGING (MIN.)
90
80
70
60
50
40
30
20
10
0
NUMBER OF FISH EATEN
0
1
2
3
4
5
6
7
8
9
2
2
2
9

1991 Trials

Only six snakes in the 1991 trials consumed fish. The highest number of fish was consumed by a snake in the cold land, warm water condition, followed by two snakes in the warm land warm water condition (Table 3). There were no significant effects of land or water temperature on the mean number of fish eaten by snakes in each condition [land, $P(F_{1,12} \geq 0.06)=0.8078$; water, $P(F_{1,12} \geq 3.03)=0.1072$], and there was no significant interaction of land and water temperature on mean number of fish eaten [$P(F_{1,12} \geq 0.00)=1.00$].

There were also no significant effects of land or water temperature on the mean amount of time spent foraging by snakes in each condition (Table 4) [land, $P(F_{1,12} \geq 1.36)=0.2667$; water, $P(F_{1,12} \geq 0.76)=0.3995$], and the interaction between land and water temperature was not significant [$P(F_{1,12} \geq 0.18)=0.6779$]. Foraging success of snakes in 1991 was also variable, and there was no significant correlation between amount of time spent foraging and number of fish eaten in 1991 [$P(r_{16} \geq 0.168)=0.534$] (Figure 28).

Heating and cooling rates

Both the large and small snake cooled very rapidly (within 1 minute) from moderate body temperatures (approx. 19° C) when taken from the warm land condition and placed in the cold water condition (Figures 29 and 30 respectively). The body temperature of the small snake rose much more rapidly than that of the large snake when they were placed back on warm land after being in cold water. The body temperature of the small snake was also much lower initially than that of the large snake isolated in cold land. The body temperature of this snake rose from 11.7° to 22° within one minute of being place in warm water, whereas it took 2.5 minutes for the body temperature of the large snake to rise from 15.7° on cold land to 22.1° in warm water. When the small snake was placed back on cold land, its body temperature again decreased quite rapidly (from 21.8° to 13.2° in 4.5 minutes). The body temperature of the large snake taken from warm water and placed back on cold land decreased relatively slowly (from 23.0° to 16.9° in 7.5 minutes), and did not reach a level as low as that of the small snake under similar conditions.

Swimming Speeds

To determine whether size of snake had an effect on swimming speed, I regressed swimming speed on SVL at each of the experimental temperatures. There was a significant relationship between swimming speed and SVL only at 15° C [$P(F_{1,18} \geq 6.264) = 0.0222$]. However, only 22% of the total variation in swimming speed was accounted for by SVL in that regression, and as there was no relationship between SVL and

Figure 29. Cooling and heating curves for a large snake exposed to experimental temperatures. Dashed line represents snake moved from cold land to warm water and back, solid line represents snake moved from warm land to cold water and back. Hatched area on horizontal axis represents time that the snake was in the water, open area represents time that the snake was on land.

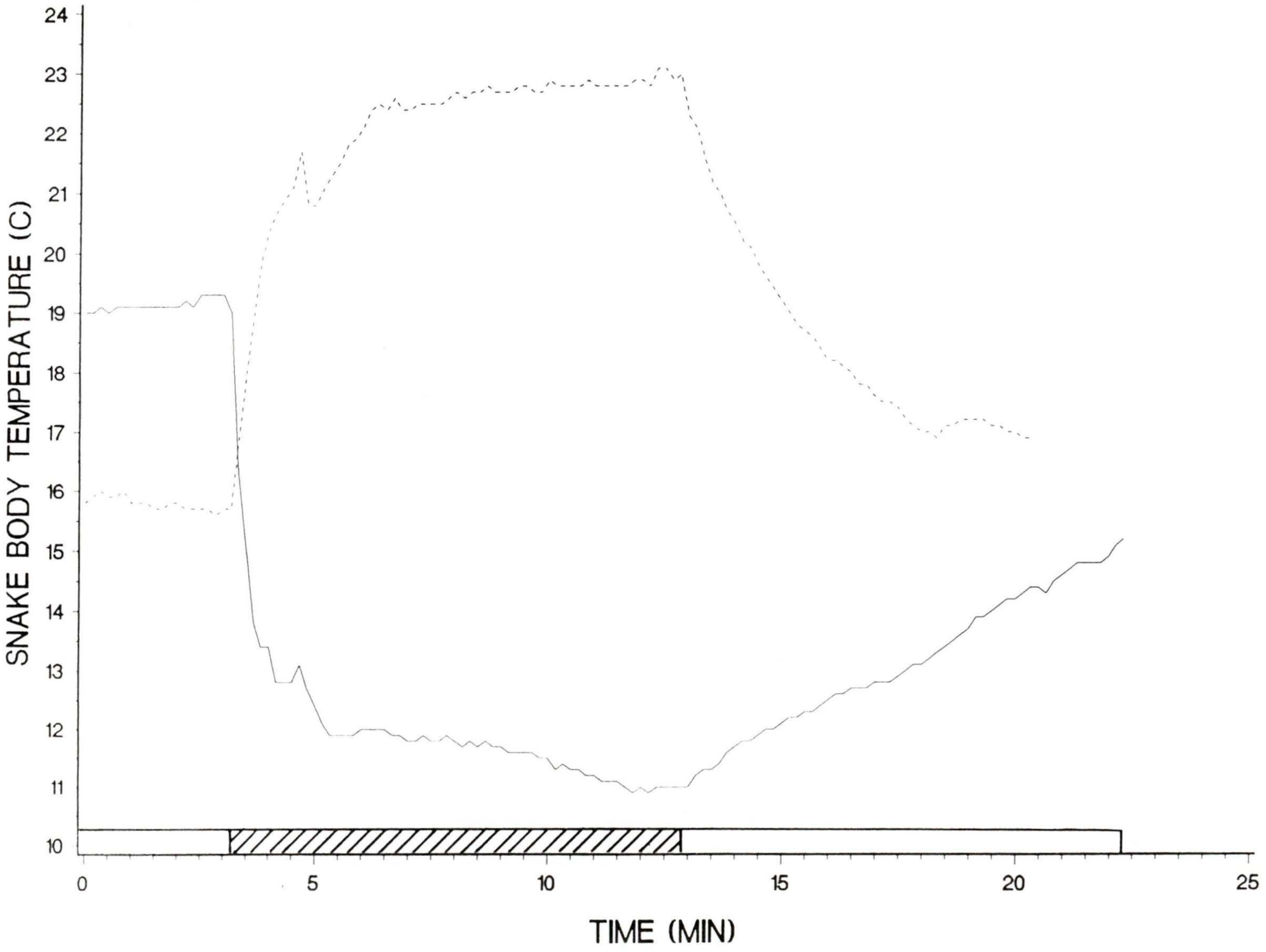
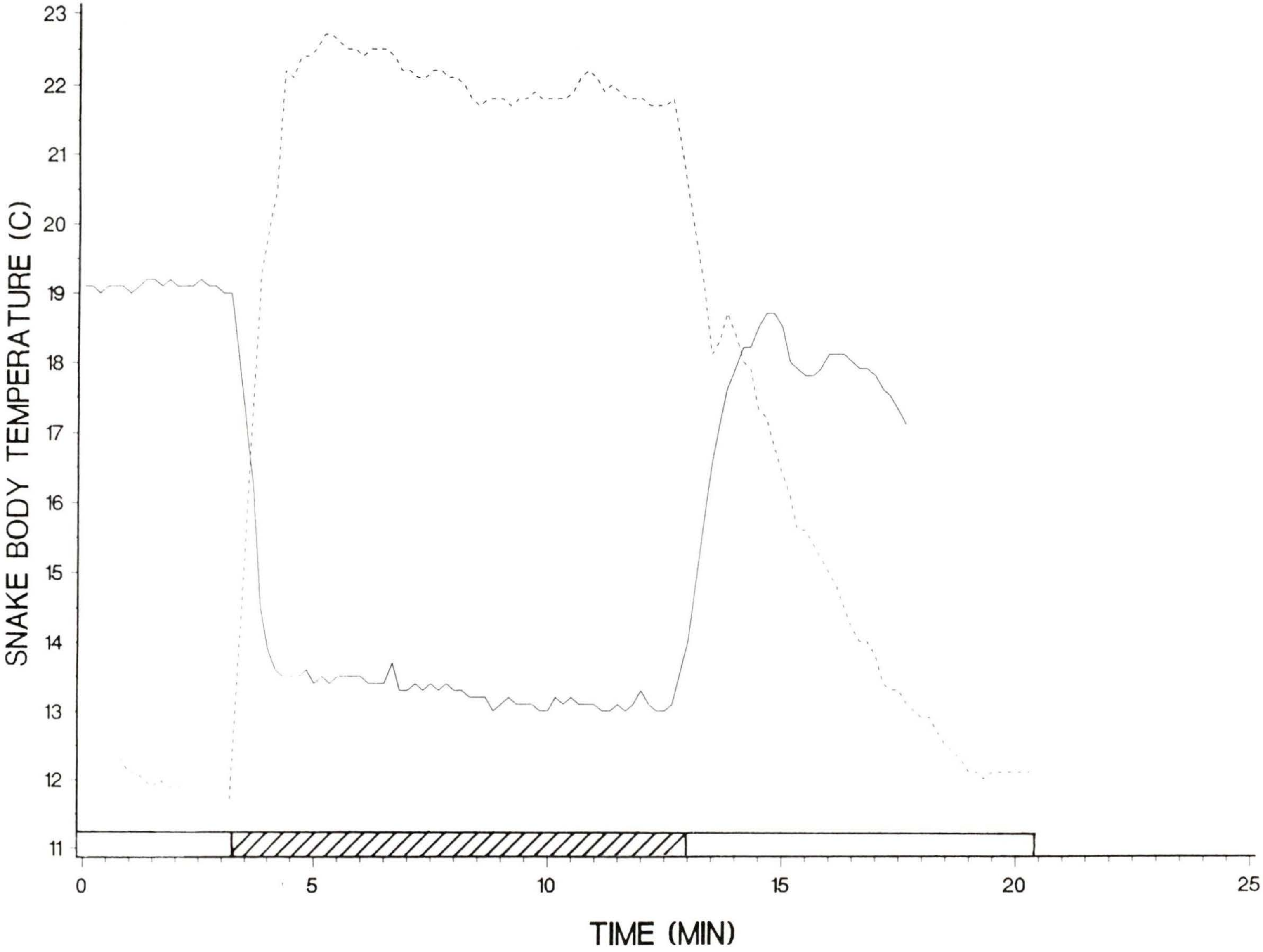

SNAKE BODY TEMPERATURE (C)
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
0
5
10
15
20
25
TIME (MIN)

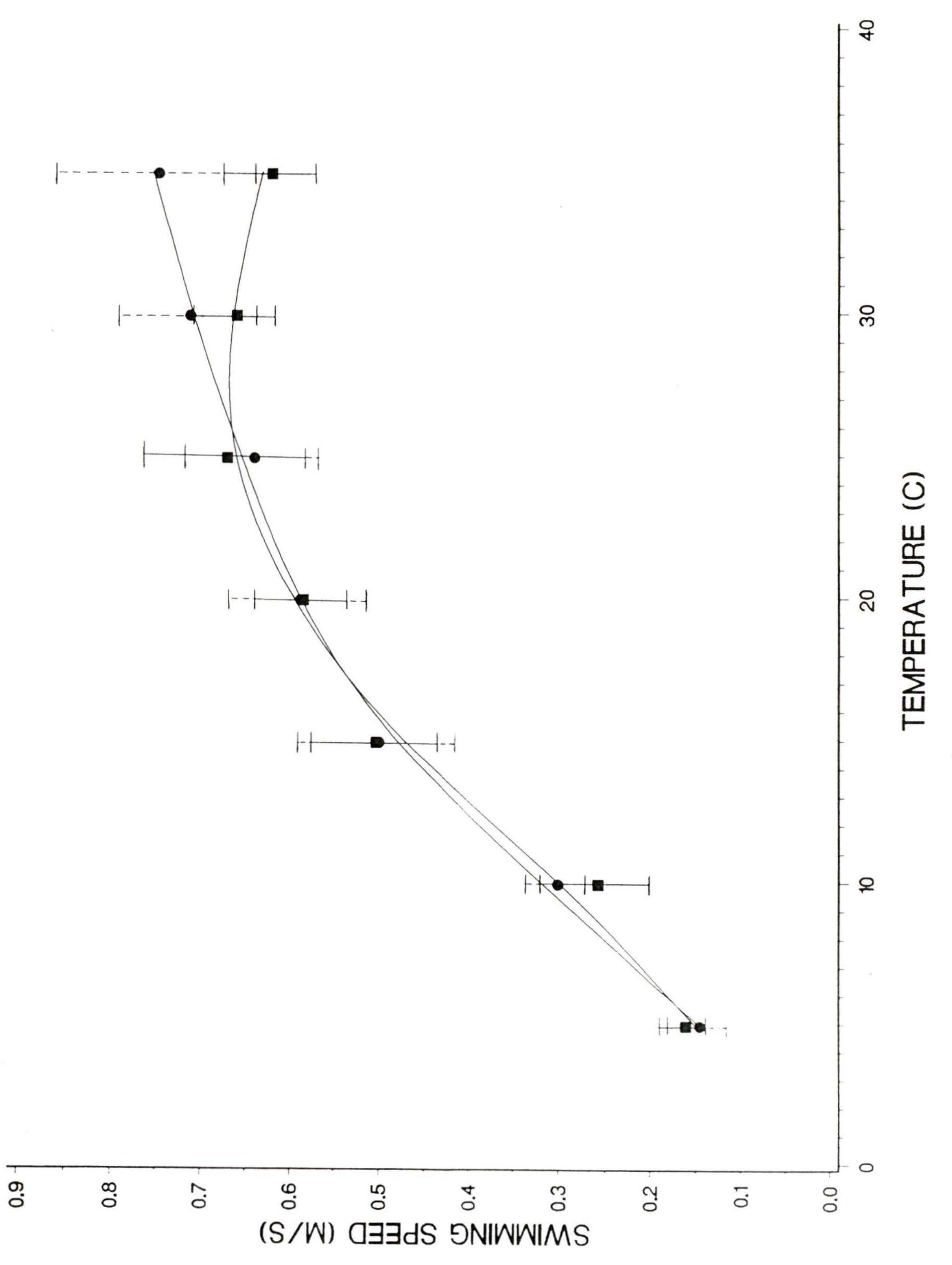
Figure 30. Cooling and heating curves for a small snake exposed to experimental temperatures. Dashed line represents snake moved from cold land to warm water and back, solid line represents snake moved from warm land to cold water and back. Hatched area on horizontal axis represents time that the snake was in the water, open area represents time that the snake was on land.


SNAKE BODY TEMPERATURE (C)
23
22
21
20
19
18
17
16
15
14
13
12
11
0
5
10
15
20
25
TIME (MIN)

speed at other temperatures, SVL was not considered an important covariable in the following analysis of variance.

Mean swimming speeds of snakes increased gradually from their lowest rates at 5 and 10° C to approximately 80% of maximum rates at 15° C (Figure 31). Swimming speeds of cold acclimated snakes reached a maximum at 25° C, after which they declined slightly. Speeds of warm-acclimated snakes continued to increase gradually up to the highest test temperature of 35° C (Figure 31). Results of a two way anova with individuals nested within acclimation group showed that temperature, acclimation and the interaction of temperature and acclimation all had a significant effect on the mean swimming speed of snakes [temperature, $P(F_{6,108} \geq 161.33)=0.0001$; acclimation (snake), $P(F_{18,108} \geq 5.35)=0.0001$; temperature*acclimation, $P(F_{6,108} \geq 2.61)=0.0213$]. The significant effect of acclimation was due mainly to the difference in swimming speeds of warm- and cold-acclimated snakes at 35° C.

Figure 31. Mean swimming speeds with 95% confidence intervals of warm- (circle) and cold- (square) acclimated snakes at different experimental temperatures.


SWIMMING SPEED (M/S)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
TEMPERATURE (C)
0
10
20
30
40

DISCUSSION

Many species of snakes exhibit seasonal shifts in their daily patterns of activity in response to differing environmental temperatures (Heckrotte 1962, Landreth 1973, Moore 1978, Mushinsky *et al*. 1980, Patterson and Davies 1982, Saunders and Jacob 1980). These changes often represent a shift from diurnal activity in cooler seasons to nocturnal activity in summer (Landreth 1973, Saunders and Jacob 1980, Moore 1978, Mushinsky *et al*. 1980). Other snakes remain active diurnally throughout the season, but shift their activity patterns in response to daily temperatures (Platt 1969, Stewart 1965). For example, on hot days during the summer, Stewart (1965) found that *T. sirtalis* and *T. ordinoides* were active primarily in the mid-morning and late afternoon, whereas on cloudy days, snakes were observed throughout the day. Other researchers have also reported that snakes are rarely observed in the open during the hottest part of the day in summer (Hammerson 1987, Scott *et al*. 1982).

Similar patterns of activity were observed at both reference and hatchery sites in this study. On sunny days, most snakes were observed in the morning or late afternoon, whereas on cloudy days most snakes were observed in the early afternoon. There were significantly different patterns, however, in the mean number of snakes observed at each site during different weather conditions. At hatchery sites, higher numbers of snakes were observed on sunny days than on cloudy days in both years, whereas at reference sites, similar numbers of snakes were observed under both weather conditions, or fewer snakes were observed in sunny conditions. These findings are consistent with results of a previous study at this hatchery (Nelson 1988).

This increase in the number of snakes observed at hatchery sites in sunny weather appears to be correlated with foraging activity by snakes in cold hatchery channel water. All snakes captured at the hatchery site with fresh fish in their stomachs were caught on warm days that were either clear, or clear with cloudy periods. In addition, all records of foraging activity for radiotagged snakes were obtained on hot, sunny days when model temperatures ranged from 26 to 39^{o} C.

Several hypotheses might explain why higher numbers of snakes are active at hatchery sites in hot weather. I hypothesized that hot weather conditions allow snakes at hatchery sites to raise their body temperatures above some threshold level for efficient foraging activity. This temperature must be high enough to allow sufficient time for foraging activity before the rapid cooling rates experienced by snakes in cold water reduce body temperatures to levels at which foraging is no longer possible. Patterson and Davies (1982) suggested that low water temperatures in spring were responsible for different foraging modes in *Natrix maura*. In the summer, snakes engaged in "sentinel" predation and rarely emerged from the water to bask, whereas in the spring, snakes engaged in "predatory foraging behavior" and were often observed basking near the water. They suggested that, with predatory foraging behavior, snakes could forage until body temperatures became too low and then emerge to bask, whereas sentinel predation would not be efficient in the spring because the low body temperatures caused by the cold water would not allow them to lunge quickly enough (Patterson and Davies 1982).

If snakes were active in sunny weather to increase body temperatures prior to foraging then snakes captured in sunny weather would be expected to have higher body temperatures than snakes captured in cloudy weather. I did find a significant relationship between air temperature and body temperature of snakes captured at both sites. Air temperature, however, accounts for only 18.5% of the variation in observed body temperature. Other researchers have also found that little variation in body temperature is explained by this relationship (Gregory and McIntosh 1980, Gibson and Falls 1979). In my study, as in other studies (Slip and Shine 1988, Gibson and Falls 1979), snakes captured in sunny weather had higher mean body temperatures than snakes captured in cloudy weather. However, body temperatures of snakes captured at hatchery sites were lower on sunny days than on cloudy days, whereas the reverse trend was observed at the reference site. The lower mean body temperatures of snakes at hatchery sites may have resulted from cooling of snakes exposed to cold hatchery channel water during foraging activity, but I could not distinguish between snakes that were about to forage and those that had just finished foraging.

Even if snakes at hatchery sites did achieve high body temperatures prior to foraging activity, cooling rates of snakes taken from warm land and isolated in cold water in the laboratory suggest that there would be no advantage of these high temperatures in terms of increasing foraging time and efficiency. Both small and large snakes cooled very rapidly from initial body temperatures of 19^{o} C to 12.8 and 13.5^{o} C respectively. Snakes monitored by telemetry in the field also experienced extremely rapid cooling rates when they entered the water. Hailey and Davies (1987) found that heating and cooling rates of *Natrix maura* were both related to body mass, but all sizes of snakes cooled from initial body temperatures of 30^{o} C to water temperature (15^{o} C) within 5 minutes. These rapid rates of cooling experienced by snakes in cold water led Hailey and Davies (1987) to conclude that basking by *Natrix maura* in the spring would confer no advantage in terms of increasing available foraging time, as suggested by Patterson and Davies (1982).

Snakes monitored by telemetry all maintained low body temperatures (approximately 13° C) during foraging activity. On the one occasion when a snake was observed catching a fish, its body temperature was just over 14° C, and had been at this level for 60 minutes. Thus, high body temperatures do not appear to be required for foraging activity. Swimming speeds of snakes decline rapidly below 15° C, and results of my swimming speed trials suggest that at 14° C, snakes would be swimming at approximately 62% of the maximal levels shown by warm-acclimated snakes at 35° C. Stevenson *et al.* (1985) constructed performance curves for swimming speeds of *Thamnophis elegans* and found that with body temperatures between 18° and 35° C snakes could perform at 80% of maximal levels. They calculated that a snake with a body temperature of 13° would be performing at only 36% of maximal levels (Stevenson *et al.* 1985).

Although foraging efficiencies of snakes may be affected by this decrease in swimming speeds at low body temperatures, the extremely high densities of fish in hatchery channels probably compensate to a large degree. *Thamnophis sirtalis* engages in open-mouth searching behavior while foraging aquatically (Drummond 1983, and personal observation). Because *T. sirtalis* rarely chases prey, swimming speeds may not be an important measure of foraging efficiency, especially at hatchery channels where prey densities are extremely high.

Although low body temperatures do not appear to inhibit foraging activity, results of laboratory experiments suggest that snakes exposed to both cold air and cold water conditions do not engage in foraging activity. Warm water conditions, warm land conditions or both appeared to be required for successful foraging activity. While differences in mean number of fish caught between conditions were not significant in the 1991 experiments, the trends were generally similar to those observed in the 1990 experiments, which were significant. Similar results were also obtained in a previous study (Nelson 1988). Fewer snakes consumed fish in the 1991 experiments than in 1990, perhaps as a result of being fed at higher levels prior to experimentation, or because of the shorter length of the experimental period. This is reflected in the high number of snakes in 1991 that spent no time engaged in foraging activity. In both years, there was no relationship between the amount of time spent foraging and the number of fish eaten, suggesting that there is a large amount of variation in individual foraging success.

If hot weather conditions confer no advantage on snakes during foraging activity itself, perhaps they are important in allowing snakes to achieve high body temperatures subsequent to foraging activity. All snakes monitored by telemetry engaged in basking behavior after foraging and, as a result, raised their body temperatures to high levels.

Snakes may engage in basking behavior to raise body temperatures so that digestion rates may be increased (Skoczylas 1970, Naulleau 1983). Although several researchers have demonstrated a thermophilic response to feeding in snakes (Lysenko and Gillis 1980, Marcellini and Peters 1982, Regal 1966), other researchers have not found such a response (Hammerson 1987, 1989, Kitchell 1969). If snakes in my study were merely demonstrating a thermophilic response to feeding, then high numbers of snakes also should have been observed at reference sites in sunny weather, which was not the case. Furthermore, I found no differences in mean body temperatures between snakes with food and snakes without food. If snakes were attempting to increase digestive efficiency through attaining higher body temperatures, then snakes with food should have had higher body temperatures than those without food. Gregory and McIntosh (1980) also found no significant difference in body temperatures of garter snakes with and without food.

An alternative hypothesis is that predation pressure in the vicinity of hatchery channels from other fish- and snake-eating predators such as mink (*Mustela vison*) and heron (*Ardea herodias*) is high, and achieving high body temperatures subsequent to foraging activity might be important to snakes in the vicinity of channels in reducing the risk of predation, especially given that vegetation and other cover is sparse. In fact, movement patterns of radiotagged snakes away from channels suggest that these areas may not be suitable sites for snakes when they are not foraging. Recaptures of snakes away from channels also indicate that snakes may not remain in the area for extended periods, but may move there just to forage, and then move away to other areas with more protective cover. This behavior was demonstrated by one of the radiotagged snakes on two occasions during 1990. These considerations strongly suggest that the actual availability of fish to snakes at hatcheries is much less than the apparent superabundance of such prey.

When snakes monitored by telemetry were not engaged in foraging behavior, their patterns of body temperature regulation were similar to the plateau, oscillating, and smooth patterns observed by Peterson (1987) for *T. elegans*, and the body temperatures that I recorded were similar to those reported by other researchers for garter snakes (Lillywhite 1987). Radiotagged snakes also remained under cover for extensive periods, in both cloudy and sunny weather conditions.

Remaining under cover will reduce risk of predation through decreased conspicuousness (Huey 1982), but by doing this even when conditions are suitable for foraging activity, snakes do not take full advantage of the high abundance of prey at hatchery sites. By not maximizing their food intake, snakes are failing to realize their maximum potential growth rates and reproductive rates, therefore reducing their ultimate fitness. Thermal relations and associated risks of predation are clearly important factors in this trade-off, and must be balanced against the potential benefits of increasing food intake.

The results of this study illustrate the complex nature of the relationship between temperature regulation and foraging ecology of snakes at hatchery sites. Although food at hatchery sites is extremely abundant and results in an almost complete switch to piscivory in snakes, at least while they are in the vicinity of channels (Gregory and Nelson 1991), actual food availability to snakes appears to be much lower. Snakes at hatchery sites are limited to foraging in sunny weather presumably so that they thereby minimize associated predation risks. In addition, snakes do not forage as frequently as might be expected, even when conditions appear to be suitable. I hypothesize that risk of predation in the vicinity of channels is high enough to outweigh the increase in fitness that may result from increasing food intake.

This type of constraint on foraging activity in a situation where food abundance is virtually unlimited has important implications for tests of optimal foraging models. Optimal foraging models are based on the premise that individuals have heritable characteristics that allow them to forage in a manner that maximizes their fitness (Pyke *et al.* 1977). These models involve determining: (1) the type of choice that the animal must make (decision assumptions), such as the type of prey item to consume, or the amount of time to spend foraging in an area (or patch); (2) the currency involved (currency assumptions), which in most cases is the net rate of energy gain; (3) the relationship between the decision and currency variables (constraint assumptions, Stephens and Krebs 1986). The constraint assumptions made by most optimal foraging models are that the predator cannot search for new prey items or patches while another is being exploited, that encounters with prey items or patches are random, independent events, and that the predator has complete information about its environment and its own foraging limitations (Stephens and Krebs 1986).

Many optimal foraging models have focused on determination of the optimal diet of an animal. In an optimal diet, food types are ranked in terms of their ratio of energy content to handling time (including search time). Food types are included in the optimal diet in their rank order, until the net rate of food intake is no longer increased by the addition of subsequent food types of lower rank (Pyke *et al.* 1977). Three predictions follow from this theory: (1) the inclusion of a less preferred food type in the diet should be influenced only by the absolute abundance of food types of higher rank, and not by the abundance of less preferred food types; (2) the number of less preferred food types in the diet should decrease with an increase in the abundance of a more preferred food type; (3) food types, if included in the optimal diet, should be eaten whenever they are encountered (Pyke *et al.* 1977). Although the validity of optimal foraging models has been questioned (Pierce and Ollason 1987), these models may be useful predictive tools for generating hypotheses about foraging behavior (Stephens and Krebs 1986). For example, situations in which the availability of a preferred food type is unlimited should theoretically lead to complete specialization on this food type.

The abundance of food at fish hatcheries has in many instances led to a shift in the diet of snakes in the area. Lagler and Salyer (1945) found an increased percentage of fish in the diet of *T. sirtalis* from hatchery sites in Michigan compared with snakes from a nearby natural site. At a hatchery in Arkansas, Baumann and Metter (1975) found an increased percentage of goldfish in the diet of *Nerodia sipedon*, and at two hatchery sites on Vancouver Island, *T. sirtalis* feeds almost exclusively on fish (Gregory and Nelson 1991).

These findings may be considered consistent with the predictions of optimal foraging theory only if fish are preferred prey items in the diet of snakes. Fish are higher in terms of calories per gram dry mass (Cummins and Wuycheck 1971) when compared with other food items consumed at hatchery and reference sites on Vancouver Island. It is evident from this study, however, that when the relative profitability of different prey types is assessed, foraging constraints imposed on the predator must also be considered. I hypothesize that aquatic foraging behavior of snakes at hatchery sites is constrained by thermal relations and associated risks of predation. One of the main criticisms of optimal foraging models in the past is that foraging activity must be considered independent of all other activities if the rate of energy intake is to be maximized (Pierce and Ollason 1987). Foragers can be constrained to feeding at less than maximal rates by conflicting demands such as the need to avoid predators (Pierce and Ollason 1987). Dynamic optimal foraging models take into account constraints such as these on foraging behavior, and can be used to analyse trade-offs involved in choices between different behaviors (Houston *et al*. 1988).

If animals do attempt to optimize their net rate of energy intake (Pierce and Ollason 1987), there must be a balance between the costs and benefits associated with achieving that optimum. In the case of ectotherms, temperature clearly plays an important role in determining the costs associated with obtaining a resource, and must be incorporated into tests of optimal foraging theory using these animals.

CONCLUSIONS

Thermal relations are clearly an important aspect of the aquatic foraging behavior of *T. sirtalis* at the Robertson Creek Hatchery. Snakes at the hatchery site were active primarily in sunny weather and foraging activity of snakes studied by telemetry took place on hot, sunny days. At reference sites more snakes or similar numbers of snakes were active in cool, cloudy weather compared with hot, sunny weather. In laboratory experiments, snakes required warm air or land conditions or both for foraging activity. Snakes at hatchery sites thus appear to be constrained to foraging on warm, sunny days.

I hypothesized that warm weather conditions allow snakes to raise their body temperatures above some threshold level that is required for efficient foraging activity. Cooling rates experienced by snakes, both in the laboratory and in the field, however, suggest that high body temperatures cannot be maintained for a sufficient length of time to confer any advantage for foraging activity. Although swimming speeds of snakes were significantly reduced at body temperatures below 15° C, observations of foraging activity of radiotagged individuals indicated that high body temperatures are not required for foraging success. The density of fish in hatchery channels is so high that swimming speed is probably not an important component of foraging success for snakes at hatchery sites.

Warm weather conditions may be important in allowing snakes to achieve high body temperatures subsequent to foraging activity. Snakes could be demonstrating a thermophilic response to feeding, but if this were the case, then high numbers of snakes should also be observed at reference sites in sunny weather. In addition, if snakes were attempting to increase digestive efficiency through attaining higher body temperatures, then snakes with food should have had higher body temperatures than those without food, which was not the case.

An alternative hypothesis is that achieving high body temperatures subsequent to foraging activity may be important to snakes in the vicinity of the hatchery channels in reducing the risk of predation from other fish- and snake-eating predators, which are abundant near hatchery channels. Recaptures of marked snakes and movement patterns of radiotagged snakes away from the hatchery channels suggest that channels may not be suitable sites for snakes to remain when they are not foraging. Snakes monitored by telemetry also remained under cover for extensive periods of time, in both cloudy and sunny weather.

Thermal relations and associated predation risks impose constraints on the foraging activity of snakes that do not allow them to take full advantage of the abundance of prey at hatchery sites. This study illustrates the importance of obtaining a detailed understanding of the types of trade-offs involved in foraging activity so that such factors may be included in models of foraging behavior.

LITERATURE CITED

Aird, S.D. 1986 Methoxyflurane anesthesia in *Crotalus*: comparisons with other gas anesthetics. Herpetolological Review 17:82-84.

Bakken, G.S., W.R. Santee and D.J. Erskine 1985. Operative and standard operative temperature: tools for thermal energetic studies. American Zoologist 25:933-943.

Baumann, M.A., and D.E. Metter 1975. Economics, feeding, and population structure of *Natrix s. sipedon* in a goldfish hatchery. Progressive Fish-Culturalist 37:197-201.

Blanchard, F.N. and E. B. Finster 1933. A method of marking living snakes for future recognition, with a discussion of some problems and results. Ecology 14:334-347.

Carpenter,C.C. 1952. Comparative ecology of the common garter snake (*Thamnophis s. sirtalis*), the ribbon snake (*Thamnophis sauritis*), and the Butler's garter snake (*Thamnophis butleri*). Ecological Monographs 22:235-258.

Charland, M.B. 1987. An examination of factors influencing first-year recuritment in the Northern Pacific Rattlesnake, *Crotalus viridis oreganus*, in British Columbia. Unpubl. M.Sc. Thesis, University of Victoria, Victoria, British Columbia. 143 pp.

Cummins, K.W. and J.C. Wuycheck 1971. Caloric equivalents for investigations in ecological energetics. International Association of Theoretical and Applied Limnology 18:1-158.

Drummond, H. 1983. Aquatic foraging in garter snakes: A comparison of specialists and generalists. Behavior 86:1-30.

Fitch, H.S. 1941. The feeding habits of California garter snakes. California Fish and Game 27:2-32.

Fry, E.E.and J.S. Hart 1948. Cruising speed of goldfish in relation to water temperature. Journal of the Fisheries Research Board of Canada 7:169-175.

Gibson, A.R. and J.B. Falls 1979. Thermal biology of the common garter snake, *Thamnophis sirtalis* (L.) I. Temporal variation, environmental effects and sex differences. Oecologia 43:79-97.

Greenwald, O.E. 1974. Thermal dependence of striking and prey capture in Gopher snakes. Copeia 1974:141-148.

Gregory, P.T. and K.J. Nelson 1991. Predation on fish and intersite variation in the diet of common garter snakes, *Thamnophis sirtalis*, on Vancouver Island. Canadian Journal of Zoology 69:988-994.

Gregory, P.T. and A.D.G. McIntosh 1980. Thermal niche overlap in garter snakes (*Thamnophis*) on Vancouver Island. Canadian Journal of Zoology 59:351-355.

Hailey, A. and P.M.C. Davies 1987. Activity and thermoregulation of the snake *Natrix maura*. 1. r and K thermoregulation. Journal of Zoology 213:71-81.

Hammerson, G.A. 1987. Thermal behavior of the snake *Coluber constrictor* in west-central California. Journal of Thermal Biology 12:195-197.

Hammerson, G.A. 1989. Effects of weather and feeding on body temperature and activity in the snake *Masticophis flagellum*. Journal of Thermal Biology 14:219-224.

Heckrotte, C. 1962. The effect of environmental factors in the locomotory activity of the plains garter snake (*Thamnophis radix radix*). Animal Behavior 10:193-207.

Houston, A., C. Clark, J. McNamara and M. Mangel 1988. Dynamic models in behavioral and evolutionary ecology. Nature 332:29-34.

Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles. *In* Biology of the Reptilia. Vol. 12. (C. Gans and F.H. Pough, eds.) Academic Press, London pp. 25-91.

Kephart, D.G. and S.J. Arnold 1982. Garter snake diets in a fluctuating environment: a seven-year study. Ecology 63:1232-1236.

Kitchell, J.F. 1969. Thermophilic and thermophobic responses of snakes in a thermal gradient. Copeia 1969:189-191.

Krebs, J.R., A.I. Houston and E.L. Charnov 1981. Some recent developments in optimal foraging. *In* Foraging

Behavior: Ecological, Ethological, and Psychological Approaches (A.C. Kamil and T.D. Sargent, eds.). Garland Press, New York.

Lagler, K.F. and J.C. Salyer III 1945. Influence of availability on the feeding habits of the common garter snake. Copeia 1945:159-162.

Landreth, H.F. 1973. Orientation and behavior of the rattlesnake *Crotalus atrox*. Copeia 1973:26-31.

Lillywhite, H.B. 1987. Temperature, energetics, and physiological ecology. *In* Snakes: Ecology and evolutionary biology. (R.A. Seigel, J.T. Collins and S.S. Novak, eds.) MacMillan Publishing Co., New York. pp. 422 -477.

Lysenko, S. and J.E. Gillis 1980. The effect of ingestive status on the thermoregulatory behavior of *Thamnophis sirtalis sirtalis* and *Thamnophis sirtalis parietalis*. Journal of Herpetology 14:155-159.

Marcellini, D.L. and A Peters 1982. Preliminary observations on endogenous heat production after feeding in *Python molurus*. Journal of Herpetology 16:92-94.

Moore, R.G. 1978. Seasonal and daily activity patterns and thermoregulation in the southwestern speckled rattlesnake (*Crotalus mitchelli pyrrhus*) and the Colorado desert sidewinder (*Crotalus cerastes laterorepens*). Copeia 1978:439-442.

Mundie, J.H. and R.E. Traber 1983. Carrying capacity of an enhanced side-channel for rearing salmonids. Canadian Journal of Fisheries and Aquatic Science 40:1320-1322.

Mushinsky, H.R., J.J. Hebrard and M.G. Walley 1980. The role of temperature on the behavioral and ecological associations of sympatric water snakes. Copeia 1980:744-754.

Naulleau, G. 1983. The effects of temperature on digestion in *Vipera aspis*. Journal of Herpetology 17:166-170.

Nelson, K.J. 1988. Changes in the foraging ecology of *Thamnophis sirtalis* in response to enhanced prey availability at a hatchery site on Vancouver Island. Unpubl. Honors Thesis, University of Victoria, Victoria, British Columbia.

Osgood, D.W. 1970. Thermoregulation in water snakes studied by telemetry. Copeia 1970:568-571.

Patterson, J.W. and P.M.C. Davies 1982. Predatory behavior and temperature relations in the snake *Natrix maura*. Copeia 1982:472-474.

Peterson, C.R. 1987. Daily variation in the body temperatures of free-ranging garter snakes. Ecology 68:160-169.

Pierce, G.J. and J.G. Ollason 1987. Eight reasons why optimal foraging theory is a complete waste of time. Oikos 49:111-118.

Platt, D.R. 1969. Natural history of hognose snakes *Heterodon platyrhinos* and *Heterodon nasicus*. University of Kansas Publications of the Museum of Natural History 18:253-420.

Pyke, G.H., H.R. Pulliam and E.L. Charnov 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52:137-154.

Regal, P.J. 1966. Thermophilic response following feeding in certain reptiles. Copeia 1966:588-590.

SAS 1985. SAS User's Guide: Statistics. Version 5 edition. Statistical Analysis Systems Institute Inc., Carey, N.C. 956 pp.

SAS 1988. SAS Graph User's Guide, Release 6.03 edition. Statistical Analysis System Institute Inc., Cary, N.C. 549 pp.

Saunders, J.S. and J.S. Jacob 1980. Thermal ecology of the copperhead (*Agkistrodon contortrix*). Herpetologica 37:264-270.

Scott, J.R., C.R. Tracy and D. Pettus 1982. A biophysical analysis of daily and seasonal utilization of climate space by a montane snake. Ecology 63:482-493.

Skoczylas, R. 1970 Influence of themperature on gastric digestion in the grass snake, *Natrix natrix* L. Comparative Biochemistry and Physiology 33:793-804.

Slip, D.J. and R. Shine 1988. Reptilian endothermy: a field study of thermoregulation by brooding diamond pythons. Journal of Zoology (London) 216:367-378.

Stephens, D.W. and J.R. Krebs 1986. Foraging Theory. Princton University Press, Princeton, N.J. 247 pp.

Stevenson, R.D., C.R. Peterson and J.S. Tsuji 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. Physiological Zoology 58:46-57.

Stewart, G.R. 1965. Thermal ecology of the garter snakes *Thamnophis sirtalis concinnus* (Hallowell) and *Thamnophis ordinoides* (Baird and Girard). Herpetologica 21:81-102.

Tracy, C.R. 1982. Biophysical Modeling in Reptilian Physiology and Ecology *In* Biology of the Reptila Vol. 12 (C. Gans, ed.). Academic Press, New York. pp. 275-321.

Weatherhead, P.J. and F.W. Anderka 1984. An improved radio transmitter and implantation technique for snakes. Journal of Herpetology 18:264-269.

White, M. and J.A. Kolb 1974. A preliminary study of *Thamnophis* near Sagehen Creek, California. Copeia 1974:126-136.

Zar, J.H. 1984. Biostatistical Analysis 2nd. ed., Prentice Hall, Englewood Cliffs, N.J.

VITA

Surname: Nelson
Given Names: Kari Jean
Place of Birth: Vancouver, British Columbia
Date of Birth: 25 October 1963

Educational Institutions Attended:

University of Victoria	1984 to 1991
Camosun College	1982 to 1984

Degrees, Diplomas, Etc., Awarded:

B.Sc. (honors, Co-op)	1988	University of Victoria

Honors and Awards:

1990-91	Graduate Student Teaching Award
1990-91	King-Platt Memorial Award
1989-90	Charles S. Humphrey Graduate Student Award
1989-90	President's Research Scholarship
1988-89	President's Research Scholarship
1988-90	NSERC Postgraduate Scholarship
1988	NSERC Undergraduate Student Research Award
1987-88	B.C. Post Secondary Scholarship
1987-88	B.W. Pearse Science Scholarship
1987	NSERC Undergraduate Student Research Award
1986-87	Samuel Simco Bursary
1986-87	Victoria Natural History Society Scholarship
1985-86	B.C. Post Secondary Scholarship
1994-85	President's Regional Entrance Scholarship
1984-85	C.U.P.E. Entrance Scholarship

Publications:

Gregory, P.T. and K.J. Nelson. 1991. Predation on fish and intersite variation in the diet of common garter snakes, *Thamnophis sirtalis*, on Vancouver Island. Canadian Journal of Zoology 69: 988-994.

PARTIAL COPYRIGHT LICENSE

Title of Thesis:

The role of thermal relations in the aquatic foraging ecology of the common garter snake, *Thamnophis sirtalis*, at a hatchery site on Vancouver Island, British Columbia.

Author: [redacted]

Kari J. Nelson

Dec. 27/91

Date