AN EXAMINATION OF FACTORS INFLUENCING FIRST-YEAR RECRUITMENT IN THE NORTHERN PACIFIC RATTLESNAKE, *CROTALUS VIRIDIS OREGANUS*, IN BRITISH COLUMBIA

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ABSTRACT

Survivorship of animals early in life sets the stage for, and places constraints on, the patterns of demography observed at later ages. However, a common problem in demographic studies is the difficulty of collecting information on the youngest age groups of a population, from fertilization to the end of the first year. The lack of this information can make interpretation of a species' life history very difficult, and studies of factors which act to limit first-year recruitment (*i.e.* the number of one-year-olds entering the population) are of particular interest.

In 1985 and 1986, I studied factors limiting first-year recruitment in the northern Pacific rattlesnake, *Crotalus viridis oreganus*, near the northern limit of its range, in Vernon, B.C.. In particular, I focused on the following main questions: 1) How does weight gain in the summer following parturition affect the length of the female reproductive cycle? 2) What are the thermoregulatory choices made by gravid females to ensure parturition before winter, and how do they compare to those made by males and nongravid females? 3) Does size at birth influence survivorship during hibernation? 4) Is feeding immediately following spring emergence important to summer survivorship of neonates?

Post partum females, held in individual enclosures under semi-natural conditions, were divided into high and low feeding rate groups. In spite of considerable differences in the amount of food eaten the mean weights of the two groups did not differ at any time during the study. Differences in thermoregulation by animals in the different feeding regimes may have minimized any differences due to feeding rate. In addition, there was considerable individual variation in growth among both groups. None of the females which had access to a male at the end of the study mated and the relationship between *post partum* weight gain and the length of the female reproductive cycle remains unclear.

I studied the temperature relationships of males, nongravid and gravid females under semi-natural conditions, using biotelemetry, in an outdoor enclosure. All of the snakes showed a triphasic pattern of daily body temperature variation. Temperatures rose quickly in the morning, reaching a relatively stable plateau, between 30-35°C, which was maintained until the sun began to set. At night, body temperatures fell at a slow, constant rate. Thermoconforming models in the enclosure indicated that lethal body temperatures (>40°C) occurred 60% of the time between 1200 and 2000. Gravid females, as a group, tended to have higher body temperatures than other snakes, but the difference was rarely more than 1-2 C°. There was considerable individual variation in body temperature among group members, suggesting that reproductive status may not be the most important determinant of body temperature selection. None of the gravid females gave birth during the study, and cool, wet weather during July 1986 may have resulted in longer gestation periods than in 1985, when the summer was hot and dry.

I collected 115 neonatal *C. v. oreganus* in the fall of 1985, divided the sample into two groups and released them to hibernate at two winter dens which were subsequently fenced in the spring of 1986. Recaptures suggest that minimum survivorship during the winter of 1985/86 was about 54%, and that survivorship was independent of size at birth. Prior to release in spring 1986, half of the survivors were fed. Recaptures in the fall of 1986 were few and it was not possible to determine the importance of feeding immediately after spring emergence on neonate survivorship. However, the tremendous variation in weight and length changes over the summer suggest that food for small, rodent-eating snakes may be difficult to find, and any advantage of size at birth may occur at this time.

Attributing exact causes of variation in survivorship of embryonic and juvenile rattlesnakes undoubtedly will be a difficult problem. However, the results of this preliminary investigation give reason to believe that it is tractable experimentally. The main conclusion from this study is not that any one factor is more important than others, but that apparently simple relationships may be very complex and that variation among individuals may be as important as variation between experimental groups. Considerable design improvements will be required in future studies.

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INTRODUCTION

Studies of demography provide the raw data needed to measure the scope and variation of life history parameters, necessary for the construction of a general theory of life history evolution. However, a common problem in such studies, especially among ectotherms, is the difficulty of obtaining information on the youngest age groups of the population (Bustard 1979, Plummer 1985). This may occur for a number of reasons: young animals may utilize different habitats from adults, they may exhibit different behaviors, or their smaller size simply may make them more difficult to capture (Werner and Gilliam 1984). Whatever the reason, this lack of information makes it difficult to test a variety of life history hypotheses, particularly those concerning reproductive investment, which are based on the trade-off between fecundity and survivorship of young (Pianka 1976, Boyce 1984).

In order to formulate a truly general theory of life history evolution, it is important first to collect data from as wide a taxonomic array as possible. Among reptiles, demography and life history of lizards has received considerable study, while similar information for snakes is much less common (Parker and Plummer 1987), probably due to the difficulty of collecting such data from animals which are typically solitary and secretive. Parker and Plummer (1987:281) identified the lack of quantitative information on survival, from fertilization to the end of the first year of life, as ... "the most glaring deficiency in population studies of snakes." First-year recruitment, defined here as the number of juveniles entering the population at the end of their first year of life, is a function of at least three factors: 1) the frequency with which females give birth (a combination of biological potential and environmental constraints), 2) clutch or litter size, and 3) the survivorship of young during their first year. Snakes in temperate zone environments have a relatively short period of seasonal activity sharply delimited by the cold weather of winter. Since they must compress all of their activities into a specific portion of the year, snakes in such regions should prove amenable to an examination of the factors which influence first-year recruitment.

It is thought that the length of the female reproductive cycle in many snakes is a function of the available fat reserves a female possesses following parturition (Tinkle 1962, Fitch 1970, Aldridge 1979, Blem 1981, Andrén 1982, Duvall *et al.* 1982, Diller and Wallace 1984, Seigel and Ford 1987). Gravid females may feed infrequently, or not at all (Keenlyne 1972) and subsist on stored fat during this time. Following parturition, females are emaciated and must renew their fat stores before reproducing again. The longer it takes a female to recoup these losses, the longer the time between reproductive efforts. For snakes, temperate zone regions (and high altitude areas) often are characterized by a short activity season (Neill 1964, Greer 1968, Shine and Berry 1978, Shine and Bull 1979, Shine 1981) which limits the time available to a female for renewing fat reserves. In addition, the short active season may make it impossible for female snakes to complete the entire reproductive cycle from vitellogenesis to parturition in a single year (Neill 1964, Saint Girons 1982). Thus, a common feature of the life history of many viviparous, temperate zone snakes is the extension of the female reproductive cycle over more than one season (Rahn 1942, Glissmeyer 1951, Tinkle 1962, Wharton 1966, Gibbons 1972, Keenlyne 1978, Shine 1981, Diller and Wallace 1984).

It has been suggested that viviparity in reptiles is an evolutionary response to cool climates (Neill 1964, Fitch 1970, Fitch and Fitch 1976, Shine and Berry 1978, Shine and Bull 1979, Shine 1983, Shine 1985). By maintaining the embryos internally a female should be able to control the temperature at which they develop through behavioral thermoregulation, and gravid, viviparous females are presumed to thermoregulate in order to maintain embryos at optimal temperatures and hence promote rapid, normal development (Fitch 1970, Shine 1983). At high latitude (or altitude) viviparous snakes may be able to reproduce successfully in areas where oviparous species cannot (Shine 1987).

Another consequence of the short active season of the temperate zones is that female snakes often give birth in the fall shortly before hibernation (*e.g.* Tinkle 1962, Wharton 1966, Gibbons 1972, Blem 1981). Presumably, this means that neonates have very little or no time to forage before hibernating and must survive the winter with the energy reserves with which they are born. Thus, large young, presumed to have been born with more energy reserves, may have a survival advantage. Blem (1981) suggested that the lack of foraging time before hibernation could result in high mortality among neonates during hibernation (see also Hirth 1966). In addition, appropriate sized food for newborn snakes might be difficult to obtain in some cases (Gregory 1982). Hence, size at birth may affect survivorship of young during hibernation and over the subsequent summer.

Although snakes, in general, display all of the characteristics which make studies of early life history difficult, careful selection of a study species can minimize these problems and provide opportunities to collect useful data. Snake species in which all segments of the population hibernate communally, offer a situation where it is possible to collect relatively large samples of animals in the desired age/sex groups, as well as offering opportunities for recapture in the spring and fall, to assess survivorship and reproductive characteristics. The subject of this investigation, the northern Pacific rattlesnake (*Crotalus viridis oreganus*), has a wide range extending from California in the south to British Columbia's Okanagan Valley in the north (Gregory and Campbell 1984). This species dens communally in British Columbia, and was the subject of a recent, intensive three-year study in the Okanagan Valley (Macartney 1985), which provides valuable background demographic data. In addition, there are a number of studies of this species throughout its range (*e.g.* Fitch and Glading 1947, Fitch 1949, Duvall *et al.* 1985, Diller and Wallace 1984), also providing valuable comparative data.

C. v. oreganus in British Columbia appear well suited to an investigation of factors which limit first-year recruitment and, in this study, I attempted to answer the following questions:

1. Is the length of the reproductive cycle of female *C. v. oreganus* a function of food intake following parturition and therefore limited by foraging success and/or time during the active season? In particular, does female attractivity to males depend on prior weight gain?

2. How does thermoregulation affect the length of the gestation period in this species? Is thermoregulation critical in producing young before winter?

3. What are the thermoregulatory choices made by gravid female *C. v. oreganus* and how do they compare to those made by males and nongravid females?

4. Does size at birth have an effect on neonate survivorship during hibernation and over the first active season?

5. What is the effect of obtaining food shortly after emergence from their first hibernation on survivorship of neonates during their first active season?

METHODS

Description of Study Site

The study was conducted near Vernon, British Columbia [latitude 50° 15'N, longitude 119° 12'W, elevation 425 m (Macartney 1985)]. Snakes were collected from a series of communal hibernacula on three sites: 1) Kalamalka Lake Provincial Park (site A), 2) Coldstream Ranch (site B), and 3) a British Columbia Ecological Reserve 15 km south of Vernon on Highway 97 (site C). Details of the physical characteristics of sites A,B, and C can be found in Macartney (1985). All experimental work using enclosures and fenced dens was conducted on Coldstream ranch.

General Methods

In the interest of long-term population monitoring (not reported here), all rattlesnakes encountered in the field were handled in the following manner. Snakes were captured using Pilstrom tongs and placed in a padded restraining noose which clamps the animal's neck immediately posterior to the head. Once the snake was immobilized in this way, its sex was determined by applying pressure to the base of the tail with the thumb in order to evert the hemipenes of males (Gregory 1983). Snout-vent length (SVL) was measured to the nearest 5 mm by gently stretching the snake out to its maximum length along a meter stick. The number of rattles was noted along with major scars and scale anomalies.

Snakes caught for the first time were marked by clipping ventral and subcaudal scutes in a unique combination (Blanchard and Finster 1933). In addition, a drawing of the color pattern on the posterior portion of the body was made to aid in identification during subsequent recaptures. The abdomens of females were palpated to determine the presence and number of embryos or follicles. Abdominal palpation was also used to determine the presence or absence of food in all snakes captured, although food items were never removed. Finally, the snakes were weighed by clipping a 100, 300, or 1000 g Pesola spring balance, depending on the size of the snake, to the base of the tail, releasing the animal from the noose, and suspending it off the ground. Processing was done in the field at the site of capture, and took 2-5 minutes, after which the snake was released unharmed.

Female Reproductive Cycles

If foraging success during the summer following parturition is important in determining the length of the reproductive cycle of female *C. viridis*, then *post partum* females which feed frequently during the summer and thus increase their body weight dramatically, should be receptive to mating in the fall. Females which do not feed frequently should not be receptive to mating in the fall, and should not become receptive until they have successfully replaced the fat reserves lost while gravid. In order to test this hypothesis I attempted to manipulate the feeding rates of *post partum* female *C. viridis*, under semi-natural conditions.

Post partum female *C. viridis* are easy to identify in spring because of their emaciated condition. In May and June of 1985 six *post partum* female *C. viridis* were collected on sites A and B, for use in a preliminary study of the effect of simulated foraging success under semi-natural conditions. I constructed two small outdoor enclosures, 65 cm X 60 cm X 100 cm, from lumber and 6 mm mesh hardware cloth. The enclosures were located in a quiet, tree lined clearing on Coldstream ranch, where they received direct sunlight for most of the day. In each, I dug a small pit which was covered with several layers of pine bark (*Pinus ponderosa*) to form a refuge for the captive snakes. Three *post partum* females were placed in each enclosure. The animals were fed live-trapped rodents (mostly *Mus musculus* and *Peromyscus maniculatus*). I attempted to feed the snakes in enclosure A at approximately twice the rate of the snakes in enclosure B. Meals were presented at irregular intervals, due to the difficulty of trapping rodents, and the snakes in both groups were weighed periodically until late August 1985. On 21 August, 1985 an adult male was introduced into enclosure A in order to determine whether the snakes in that enclosure were receptive to mating at this time. The male remained in the enclosure with the females until mid-September, when the study was terminated, and all animals were returned to the appropriate winter dens.

Cloacal smears (Fukada 1959), made every 1-2 days, were used to determine whether mating had taken place. Females were restrained using a padded noose and all uric acid and feces were palpated out of the cloaca, which was then cleaned using a cotton swab soaked in opthalmic saline (Lensrins, American Optical Ltd.). Mucous material was forced into the cloaca by applying pressure to the abdomen with the thumbs, approximately 20 cm anterior to the vent, and then sliding them posteriorly. The cloacal material was collected with a cotton swab soaked in opthalmic saline then smeared onto a clean glass slide bearing a drop of saline, and allowed to dry in air. Within 5 days of this procedure the slides were stained with a modified Wright's stain (Camco Quik, Cambridge Chemical Products Inc., Lauderdale, Fla.) and the slides examined for the presence of sperm. This technique was validated using an adult male during the summer of 1985. Sperm present on slides made in this way are large and easy to see at 400X magnification.

A sample of 30 *post partum* females was collected during spring 1986 from sites A, B, and C. These animals were held in the laboratory at approximately 22°C with a natural photoperiod, until the entire sample was obtained, and then moved to individual enclosures on Coldstream Ranch. The enclosures were placed in a quiet, level, well drained clearing approximately 15-20 m in diameter, surrounded on three sides by widely spaced pine trees (*Pinus ponderosa*). The fourth side of the clearing opened onto a larger grassy area bordered by pine forest. Direct sunlight fell on the clearing for most of the day, with most areas receiving short periods of shading from the surrounding trees during the course of the day.

Individual enclosures were 50 cm X 50 cm X 50 cm and constructed of 2.5 cm X 2.5 cm pine strips covered with 6 mm mesh hardware cloth. Lids were constructed of the same materials with wire hinges at the back and a latch at the front. The enclosures were placed in a rectangular block 6 cages long and 5 wide with approximately 1 m between each cage and its neighbors. A 5-10 cm deep pit was dug in each enclosure and the cage anchored in it with a tent peg. Soil was packed around the outside of the enclosure and enough of it placed within to bring the soil level with the ground outside. A 5-10 cm deep depression was made in the center of each enclosure and sheets of bark from fallen pine trees (*Pinus ponderosa*) were placed over it to provide a basking platform and refuge from the sun. Water was not provided, as daytime heat would have caused the water to evaporate rapidly from any small receptacle. However, the frequent rainfall during the summer often soaked the animals, and kept the bottom of the pits damp. None of the animals were observed to drink standing water while they were in captivity in the laboratory, prior to release in the fall, and none had difficulty in shedding their skin. Snakes were presumed to obtain water from the meals offered them (Stark 1984).

The *post partum* females were alternately assigned to either the high feeding rate (HFR) group or the low feeding rate (LFR) group according to date of capture. The snakes were placed in the outdoor enclosures between 25 May and 5 June, 1986. Members of the HFR group were offered food approximately every second day while those in the LFR group were offered food only every second week. Meals consisted of dead adult laboratory mice (obtained frozen from the University of Victoria Animal Care Facility and thawed before presentation) weighing between 25 and 30 g. A single longitudinal scalpel cut was made on the ventral surface of the mouse, to allow chemical cues from the blood and entrails to escape, before presentation. Rattlesnakes are known to accept carrion readily in captivity (Klauber 1972, Gillingham and Baker 1981, *pers. obs.*), and may do so in the wild as well (Klauber 1972, Patten and Banta 1980). Food was placed in the enclosures, usually in the afternoon, and if it was still present at the next scheduled feeding time it was removed from the enclosure and discarded. In this way only one food item was present in each enclosure at any one time, making it easier to determine if the animal had eaten or not. Snakes from both the HFR and LFR groups were weighed every week for the duration of the study, except for the period from 8 to 26 June, inclusive.

Initially, the HFR and LFR snakes were placed in separate blocks of 3 X 5 enclosures. However, to avoid any bias due to position within the clearing the cages were rearranged on 30 June 1986 so that HFR and LFR snakes alternated along both rows and columns of the rectangle. This design was maintained until the end of the study.

Between 19 and 29 August 1986, seven male *C. viridis* were introduced into the enclosures of 4 HFR and 3 LFR females. Females which had increased their body weights dramatically were presumed to be most likely to mate, and so the largest female in each group was given access to a male. The remaining 5 males were randomly assigned to females in the two groups. The males were left with the females until 7 October 1986, a period of 40-50 days.

Cloacal smears were made on 29 August and 9 September 1986, to determine whether mating had taken place. In addition, on 7 October, all females which had access to males were sampled for the presence of sperm by scraping directly the walls of the uterus using a bacteriological loop. The contents of the loop were transferred to a drop of saline on a glass slide and air dried. The slides were then stained in the same manner as cloacal smears.

All 30 captive females were palpated for the presence of enlarged follicles before their release to determine whether any of them had initiated vitellogenesis regardless of whether they had mated or not. All snakes were released at their dens of origin by 10 October 1986.

Temperature Relationships

Thermoconforming Models

The body temperature of an ectotherm is the result of a complex interaction between the animal and those aspects of its surroundings which act as heat sources and sinks, particularly the air and substrate in the immediate area, moderated by the animal's own physiological abilities. Any one of these factors alone provides a poor index of body temperature. In order to collect meaningful data on thermoregulation in snakes it is necessary to be able to sample the temperatures potentially available to the animal in its environment for comparison with the actual temperatures observed. One way of doing this is through the use of thermoconforming models (Peterson 1987), which allow for the measurement of the combined influence of all environmental factors on the animal's body temperature. Such models provide a means of determining how the snake's body temperature deviates from that of an object of similar size, shape, and heating characteristics, but which is not thermoregulating. While models provide a means of measuring the temperatures available to a snake in a particular area, there are limitations to their use in determining whether an animal is actually thermoregulating or not. If a snake's body temperature differs markedly from that of the model, then the animal is apparently controlling its body temperature to some extent, and hence thermoregulating. A lack of difference between snake and model temperatures may indicate that the animal is not thermoregulating, or it could mean that the animal chooses to regulate its body temperature at the same level as the model. In such cases there is no way to decide between the two alternatives and care must be taken in the interpretation of data.

Peterson (1987) used copper tubing, painted to match the reflectivity of his garter snakes (*Thamnophis*), as thermoconforming models, and, during the summer of 1985, I attempted to construct this type of model. The models were made from 32 mm diameter, 1 mm thick copper tubing in 800 mm lengths. The tubing was flattened on the bottom to simulate better the underside of a snake by increasing contact with the substrate, and the open ends were plugged with putty. All models were first given a coat of grey primer paint, and then painted with varying combinations of green and/or white enamel paints to raise or lower reflectivity. The white or green enamel paints were applied in an easily reproduced pattern to ensure consistency in the construction of future models. Peterson (1987) carefully matched the reflectivity of the paint on his models with that of the garter snakes with which he was working using a spectroreflectometer at a variety of wavelengths. I did not have access to this equipment, and instead, relied on direct comparison of model temperatures with those of an anesthetized, or dead snake. Thermistor probes were placed approximately 5 cm inside the snake's cloaca, and 15 cm inside one end of the model. Thermistor probes were inserted 15 cm into the models to ensure that the tip of the probe was not embedded in the putty used to seal the ends. Temperatures from the thermistors were read from digital thermometers constructed in the Biology Department Electronics Workshop.

Model trials were conducted initially by comparing model temperatures to those of a snake (male, 840 mm SVL, approx. 300 g) anesthetized with 80 mg/kg body weight of Ketamine HCL (Austin Laboratories Canada Ltd., Joliette, P.Q.). This snake died as a result of anesthesia, and all subsequent trials in 1985 were performed with the carcass. The use of a dead snake for comparison has both benefits and drawbacks associated with it, depending on what aspect(s) of thermoregulation are being studied. A dead snake can be allowed to heat to temperatures far beyond the lethal limits of the living animal, making it possible to determine the accuracy of the model over a much wider range of environmental temperatures than with a live animal. However, it is not possible to separate the physiological and behavioral aspects of thermoregulation using models of this type. Using an anesthetized snake for comparison while constructing models presumably leaves the physiological component of thermoregulation intact, and allows for the construction of models sensitive to the measurement of behavioral thermoregulation alone. The assumption that anesthesia leaves the physiological responses of the snake intact has not been demonstrated. Injectable anesthetics, such as Ketamine HCL, are typically processed by the liver and kidneys and toxicity problems are relatively common (Aird 1986); the effect on other physiological processes is unclear.

All model trials were performed between 1000 and 1600 on sunny days, using the following protocol. The snake and the various types of models being compared were placed inside on a concrete floor and allowed to equilibrate until their temperatures were constant and no more than 1-2 C° apart (30-45 min); temperatures were taken every 5 min during this period. As soon as the last equilibration temperature was taken the snake and models were moved outside and placed on a fine gravel substrate in full sun. After allowing 2 min for the move, temperatures were recorded at 1 min intervals. The snake and models were moved back inside to the concrete floor when the snake's body temperature exceeded 40°C, a value beyond the Critical Maximum for *C. viridis* (Critical

Maximum Temperature=38 °C; Brattstrom 1965). Temperatures were recorded at 1 min intervals until the cooling curves flattened out (25-35 min).

In these short-term trials, the heat load was applied and removed suddenly. To be sure that the models mimicked the thermal characteristics of the snake under natural circumstances, it was necessary to test them over a much longer period of time. To do this the snake and models were allowed to equilibrate outside overnight. Before dawn they were taken out into the field and placed side by side in an exposed location. Temperatures were then recorded every 15 min over a 12 h period to see how closely the model followed the snake under the conditions which would be in effect during the rest of the study.

A straight model represents one extreme in that it is the posture in which a snake presumably heats and cools fastest, because of its large exposed surface area. The opposite extreme is a coiled posture in which a snake minimizes its surface to volume ratio and therefore likely heats and cools more slowly. Copper tube models are difficult to bend into any type of coiled posture without breaking them, and it became necessary to seek an alternative method for the construction of coiled models. In late summer 1985 and early summer 1986 I made flexible models from bicycle inner tubes (Norco 16 X 1.75, Norco Co.) cut into 800 mm lengths. One end of the tube was sealed with glue and the structure then filled with 220 ml of water. This volume of water was determined empirically to give the best approximation of the heating and cooling characteristics of adult *C. viridis*. The open end of the tube was then plugged with a cork and a thermistor probe inserted approximately 15 cm into the model. This end (designated the posterior end) was then coated with neoprene sealant to prevent water loss.

Thermistor probes were attached to digital thermometers from which all temperatures were read. Short and long term trials were performed using the same protocol as for the copper tube models. Separate comparisons were made between the snake and this type of model in both the coiled and straight postures.

Enclosure Study

Two conditions are necessary in order to determine the patterns of body temperature variation exhibited by males, nongravid females, and gravid females. First, it is necessary to be able to obtain temperatures more or less simultaneously from all individuals and models, and second, all animals must have the same thermoregulatory opportunities. To satisfy these two criteria I conducted my study of temperature relationships in an outdoor enclosure at an undisturbed site on Coldstream Ranch.

The enclosure was on level ground in a large clearing and received unshaded sun for virtually the entire day. The vegetation of the area consisted of a continuous cover of grasses and low forbs. The enclosure itself was 6 m X 6 m and constructed of 6 mm mesh hardware cloth approximately 1 m high. Lengths of 2 cm diameter concrete reinforcing bar were driven into the ground at the corners and around the perimeter of the enclosure and the hardware cloth wired to them. The lower edge of the hardware cloth was buried to a depth of 10 cm to ensure that no gaps were available for snakes to escape through.

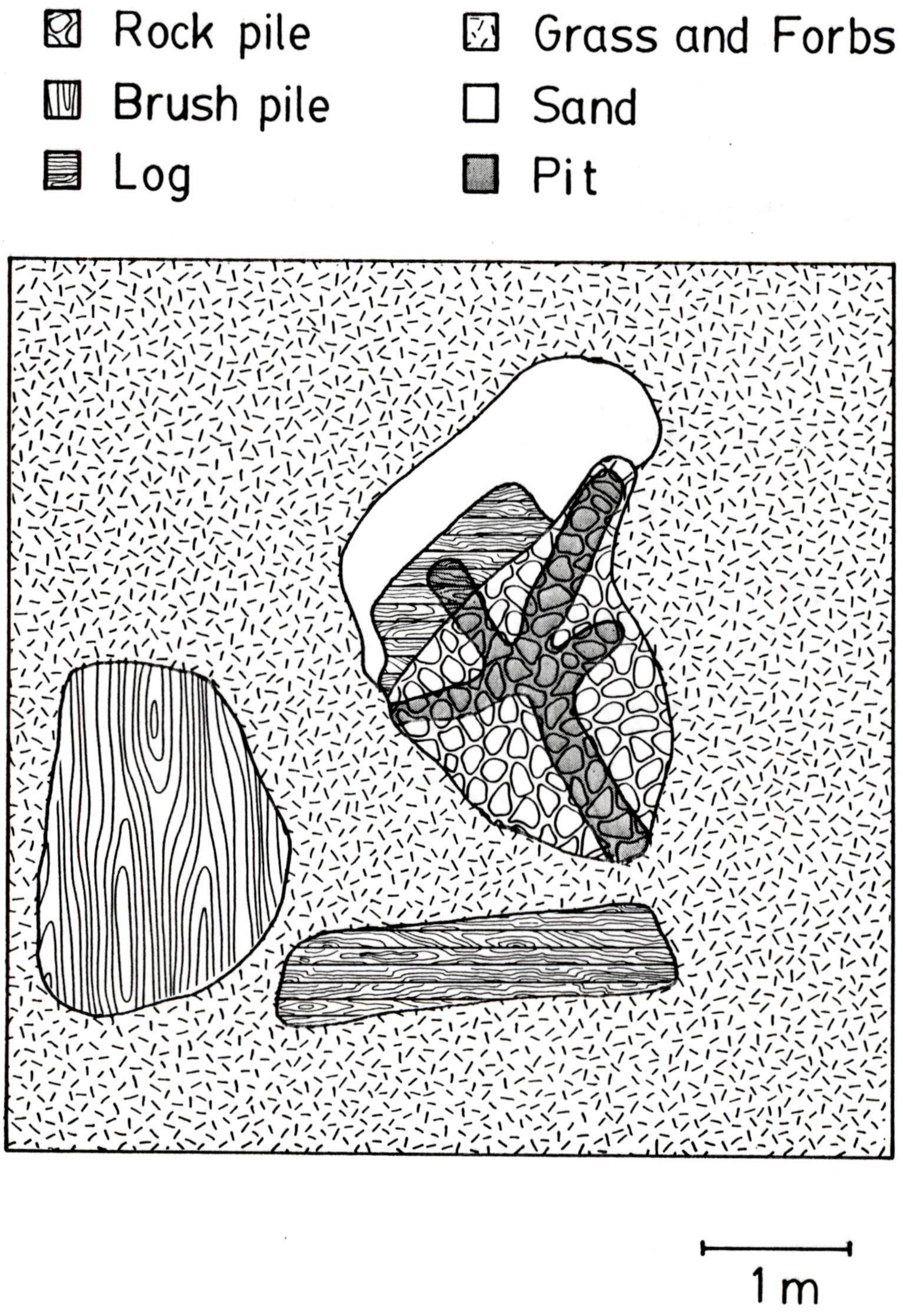
Inside the enclosure, I dug an irregular shaped pit ranging in depth from 10 cm to 60 cm. A large pile of rocks, approximately 1.5 m by 2 m and 1 m high, was then used to cover the pit. In addition, the enclosure was provided with a large dead log, a brush pile, and an area devoid of vegetation adjacent to the rock pile.

The spatial distribution and areal coverages of these components are shown in Fig. 1.

Temperature sensitive radiotransmitters (Model L, Mini Mitter Co.) were used to record body temperatures of snakes without disturbing the animals. The need for a relatively long battery life (> 2.5 months) resulted in large transmitters (18 mm X 48 mm, 13 g) which constrained the selection of study animals to those which weighed at least 260 g. Transmitters were calibrated using a water bath ranging in temperature from 2 to 40°C. Ideally, the transmitters should have been recalibrated following the study to ensure that they had not shifted. Unfortunately, facilities for accurate recalibration were not available in the field and the batteries had died by the time facilities were available. However, the transmitters had been left running for at least a week prior to calibration and should have stabilized in that time. In addition, other workers using similar transmitters found no evidence of calibration shift (Osgood 1970, Peterson 1987).

Snakes chosen for the study were anesthetized using Halothane (Ayerst Laboratories, Montreal, P.Q.) administered through a head mask using an anesthetic machine. Anesthesia was complete after approximately 15 min, at which time the snake was flaccid and did not respond to gentle pinches with forceps. Surgical procedure was that of Weatherhead and Anderka (1984). Transmitters were implanted subcutaneously posterior to the widest part of the body and the incision closed with 3-O chromic suture (Ethicon Sutures Ltd., Peterborough, Ont.). Following surgery, the snakes were taken off the anesthetic machine and they recovered within 1 h, as indicated by a return of normal tongue flicking and rattling behavior. Animals were held in the laboratory for 2-3 days to

Figure 1: Diagram of outdoor thermoregulation enclosure, to scale.


Rock pile
Brush pile
Log
Grass and Forbs
Sand
Pit
N
1 m

ensure recovery and then released into the enclosure where they were allowed 4 days to acclimatize before temperature readings were taken.

Thermoconforming models were placed in the enclosure to provide comparative information about the temperatures actually available to the snakes in the enclosure. Initially, four models were placed in the enclosure; two coiled models (one in an exposed location, and one under cover), and two straight models (one exposed, and one under cover). On the first sample day only three of the four thermistors worked (straight, exposed; coiled, exposed; and coiled, under cover). The following sample day only two of the thermistor probes worked (coiled exposed and coiled under cover). In the time between the second and third sample days I adjusted the models so that I had a straight one in an exposed location, and a coiled one under cover. In this way I could monitor the maximum and minimum rates of heating and cooling available to the snakes in the enclosure. These two models were used for the rest of the study.

In order to obtain information on temperature change over the entire 24 h period I collected data in three 8 h shifts with an 8 h break in between each. The shifts were 0400-1200 (morning), 1200-2000 (afternoon), and 2000-0400 (night). Collecting data for a complete cycle of all 3 shifts (one sample day) took 2 days but was a necessary compromise due to available manpower. Temperature data were collected from a truck parked within 9 m of the enclosure and used as a blind. The leads from the 2 models were passed into the truck and connected to the digital thermometer. The receiver (Realistic Co., Citizens Band Transceiver) was easily capable of picking up the transmitter signals from within the truck, eliminating the necessity of approaching the enclosure. Readings were taken every 15 min for the duration of the sampling period and weather conditions were also noted at these times. It was impossible to gather information on the activities of individual snakes due to their cryptic nature and the fact that they invariably responded to a person approaching the enclosure. For these reasons I felt that it was more important to obtain accurate body temperatures than to risk biasing the data by disturbing the snakes during observations.

The snakes with transmitters were placed in the enclosure on 9 July 1986, and data were collected between 13 July and 7 September 1986, inclusive. The animals in the enclosure were fed weekly by throwing 5-10 dead mice (see Female Reproductive Cycles) into the enclosure. Most of these mice disappeared and were presumed eaten by the snakes, although snakes were rarely observed eating. It is possible that at least some of the mice were taken by small carnivores (*e.g.* weasels) which could enter the enclosure without damaging it. At the end of the study all snakes were weighed and released at their dens of origin, following removal of the transmitters on 5 October 1986, and a 2-5 day recovery period.

Effect of Thermoregulatory Opportunity on Gestation Period

The assumption has been made that thermoregulation allows females of viviparous species to complete embryonic development before the local environment becomes unsuitable (Shine 1980). A simple test of this would be to maintain two groups of gravid females, one group that is allowed to thermoregulate and another that is not, and then compare the gestation periods of the two groups. The gravid females used in the telemetry study were presumed to be able to thermoregulate at will, and, in addition to those females, three gravid females obtained from site C, for other purposes, were also placed in the enclosure. A second enclosure (2 m X 2 m), containing a rockpile covering a pit, was constructed using the same materials as for the first one. This enclosure was situated under a heavy forest canopy within 20 m of the large enclosure, and was shaded for virtually the entire day. Three gravid females were placed in it on 1 June 1986, and, presumably, their body temperatures were largely determined by ambient temperatures. Because these animals were left undisturbed, and due to the presence of the rockpile, I did not notice that one of the animals had escaped, or was eaten by a predator, until early August 1986, so information for only two snakes was available. The animals were fed at the same time, and in the same way, as those in the telemetry study, and accepted food until 14 August, at which time I ran out of frozen mice.

The gravid females in both enclosures were to be held until parturition, but since this had not occurred by 8 October 1986, reproductive status was determined by palpation, and the animals were released at their dens of origin.

First-year Survivorship

Winter Survivorship

Animals that produce large young are presumed to do so because large size offers some survival advantage for the young. Snakes of the family Viperidae produce relatively large young, compared with many other snakes, and it has been suggested that large young may be more likely to survive during their first hibernation (Blem 1981). In addition, because of their small size, appropriate sized food may be relatively scarce for young snakes, particularly those which feed primarily on rodents. Large young, presumably born with greater energy reserves, may have a survival advantage during their first active season.

To test these two hypotheses I collected neonates, in the fall of 1985, in two ways. First, near-term gravid females were collected from all areas of the study site and maintained in the laboratory until parturition. Second, wild born neonates were collected at their natal dens. Each den on the study site was visited approximately every second day from mid-August to mid-September 1985 and all neonates collected.

Once in the laboratory all individuals were marked by scale-clipping (Blanchard and Finster 1933). In addition to the subcaudal mark, each animal was marked on the twentieth left ventral scute (VL20) to identify them as members of this group. Each animal was also given another ventral mark to identify its natal den. Captive born neonates were assigned their mother's den of origin as a natal den.

Following marking, the neonates were processed in the same way as snakes encountered in the field, except that weights were determined using a top-loading Mettler analytical balance to ensure accuracy. Feces and uric acid were palpated out of all neonates before weighing to ensure measurement of body weight alone. This was done any time neonates were weighed during the course of the study. All neonates were marked and processed on the same day as they were born or captured, then held in the laboratory at 22°C with a natural photoperiod (water provided *ad libitum*) until the entire sample was obtained.

Snakes in this population, even neonates, exhibit considerable fidelity to their natal den sites (Macartney 1985) making it possible to recapture animals in the spring and fall. In order to ensure maximum recapture success in the spring and fall of 1986 I selected two winter dens (numbers 8 and 9 in Macartney 1985) that were relatively accessible and, more important, that could be fenced to restrict the snakes' access in and out. I divided the neonates between two dens to reduce the possibility of artificially increasing winter mortality due to crowding. To avoid biasing the samples at these dens with respect to sex or kinship, neonates were distributed by compiling a master list based on date of capture or birth and alternately assigning individuals to a den.

All neonates were released at the dens on 23 September 1985. By this time, the weather had cooled and very few snakes had been observed at den entrances for at least a week. The neonates were placed in the den entrance and prodded into entering until they were out of sight.

The dens were fenced on 8 March 1986, well before spring emergence, with 1 m high fine-mesh window screening held erect by wooden stakes pounded into the ground in front of the den entrance, and cemented to the rock face at either end. The bottom edge of the screen was buried approximately 10 cm deep to prevent snakes from escaping under it. The den entrances, situated on south facing slopes, were clear of snow, but temperatures were consistently below freezing at night and most of the hilltops in the study area were still snow-covered. The fenced dens were visited at least once (and frequently twice) daily, except during rain, from 17 April until the end of May 1986, after which dens were visited at irregular intervals. Again, when neonates were captured they were taken into the laboratory, identified and processed as described earlier. All neonates were then held in the laboratory at 22°C and normal photoperiod, with water provided *ad libitum*, until 20 May 1986.

Supplemental Feeding and Summer Survivorship

In order to determine the effect on neonate survivorship of feeding immediately after emergence from hibernation, the VL20 neonates collected in spring 1986 were divided into two groups by again compiling a master list according to date of recapture and alternately assigning individuals to either the feeding or non-feeding group. In addition, I alternately assigned 18 unmarked neonates (3 male and 15 female), captured at dens 8 and 9 in spring 1986, to the two groups. Initially neonates in the feeding group were to have been given a meal consisting of 1 neonatal mouse. However, mice were not available, and instead the meal consisted of 2.5 g of beef heart. The meal size of 2.5 g was an arbitrary decision and represented the largest piece of meat that it seemed possible to feed safely to these small snakes. All animals in the feeding group were force fed their meal of beef heart on either 20 or 21 May 1986, after which all snakes in both groups were reweighed. No animals regurgitated their meals during the next 24 h and the VL20 neonates were released on 22 May, 1986 at the dens in which they hibernated the previous winter. Two VL20 neonates were newly recaptured after this. One was assigned to the feeding group and one to the non-feeding group. Both animals were processed accordingly and released the next day. On the last regular visit to the fenced dens (6 June 1986) holes were cut in the fences at ground level to provide snakes with free access to and from the dens during the summer.

Regular checks of the dens resumed in late August 1986 and funnel traps (Fitch 1951) were installed at the fenced dens on 4 September 1986, when snakes were just starting to return. Following the installation of traps the fenced dens were again checked daily to recapture VL20 neonates which had survived the summer. In addition to the funnel traps, I searched the area around the den entrance, and other dens in the area, in case any of the VL20 neonates had switched dens. Daily checking continued until 11 October 1986, by which time no new snakes were appearing at the dens. The fences were dismantled and all evidence of disturbance removed from the den sites.

Statistical Analyses

To avoid unnecessary clutter in the text of the Results, the sources and assumptions of all statistical procedures are presented here.

Unless otherwise noted, means are shown ± 1 standard deviation. Comparisons of means were preceded by an F-test (Zar 1984) to determine whether there was equality of variance between the two samples. If this was so, then means were compared using a standard t-test (Zar 1984). In cases where variances were unequal, a modified t-test (Walpole 1982:311, test statistic=t') was used. This test is extremely conservative and results in fewer degrees of freedom than the unmodified version, depending on how different the variances are. Both types of t-test assume that the underlying distribution is normal. This may not be the case for some of the body temperatures collected in the thermoregulation study, as body temperatures of snakes are frequently negatively skewed (Gibson and Falls 1979). Therefore, caution is required in the interpretation of such tests.

In the study of body temperature variation the animals were grouped according to reproductive status, and the data analyzed by 8 h sampling period. The male and nongravid females were grouped together as nonreproductive (NR), and the gravid females comprised the reproductive (R) group. In order to compare the body temperatures of animals within each of these two groups, I performed one-way analyses of variance (ANOVA) using the ISTAT statistical package resident on the University of Victoria's mainframe computer. Degrees of freedom for such tests were few, and entries in each cell were not independent. However, the analysis is exploratory only, and limitations on the generalization of these results are understood. Comparisons between the two groups were made by pooling all of the values for the animals in a group, and calculating the grand mean and variance. The grand means were then compared using t-tests, as described earlier, and the associated variances were compared using F-tests.

To determine whether significant differences in mean body temperature among group members in the NR and R groups occurred at high environmental temperatures, I used contingency table analysis (Walpole 1982). Comparisons of frequency distributions were made using the Kolmogorov-Smirnov 2-sample test (Sokal and Rohlf 1981). The test statistic, D, is the maximum difference between the cumulative frequencies of the two samples, and is compared with a critical value calculated from the sample sizes involved. Correlation coefficients were calculated according to Zar (1984), and their significance determined using tables provided in Zar (1984).

For all statistical procedures a minimum significance level of $\alpha=0.05$ was employed.

RESULTS

Weather Patterns

All aspects of this study were affected in some way by the weather conditions during the summer. To avoid unnecessary repetition in subsequent sections, all data concerning weather patterns are collected here. The 30 yr mean values (Environment Canada, Atmospheric Environment Service 1982) did not have any measure of variation provided so comparisons with data from 1985 and 1986 are somewhat subjective, and based on the 95% confidence limits for these two summers.

Fig. 2 shows the 30 yr means of daily maximum temperature, daily minimum temperature, and rainfall for April to September at Coldstream ranch. This same information, for the years 1985 and 1986, is shown in Figs. 3 and 4 respectively. In 1985 the mean daily maximum temperature followed the 30 yr mean with the exception of July which had a considerably higher mean, and September, which was cooler than average. July also showed a higher mean daily minimum temperature than the 30 yr mean. The pattern of rainfall in 1985 did not appear to differ from that of the 30 yr mean with the exception of September, which received almost twice as much rain, and July, which received less than half. The total rainfall for 1985 was similar to that of the 30 yr mean.

The summer of 1986 differed from the 30 yr mean in a number of respects. First, the mean daily maximum temperature for July 1986 was much lower than

Figure 2: Mean daily maximum and minimum temperatures and total rainfall, April to September inclusive, for the years 1951 to 1980 at Coldstream Ranch, Vernon, B.C..

(source: Environment Canada, Atmospheric Environment Service 1982)

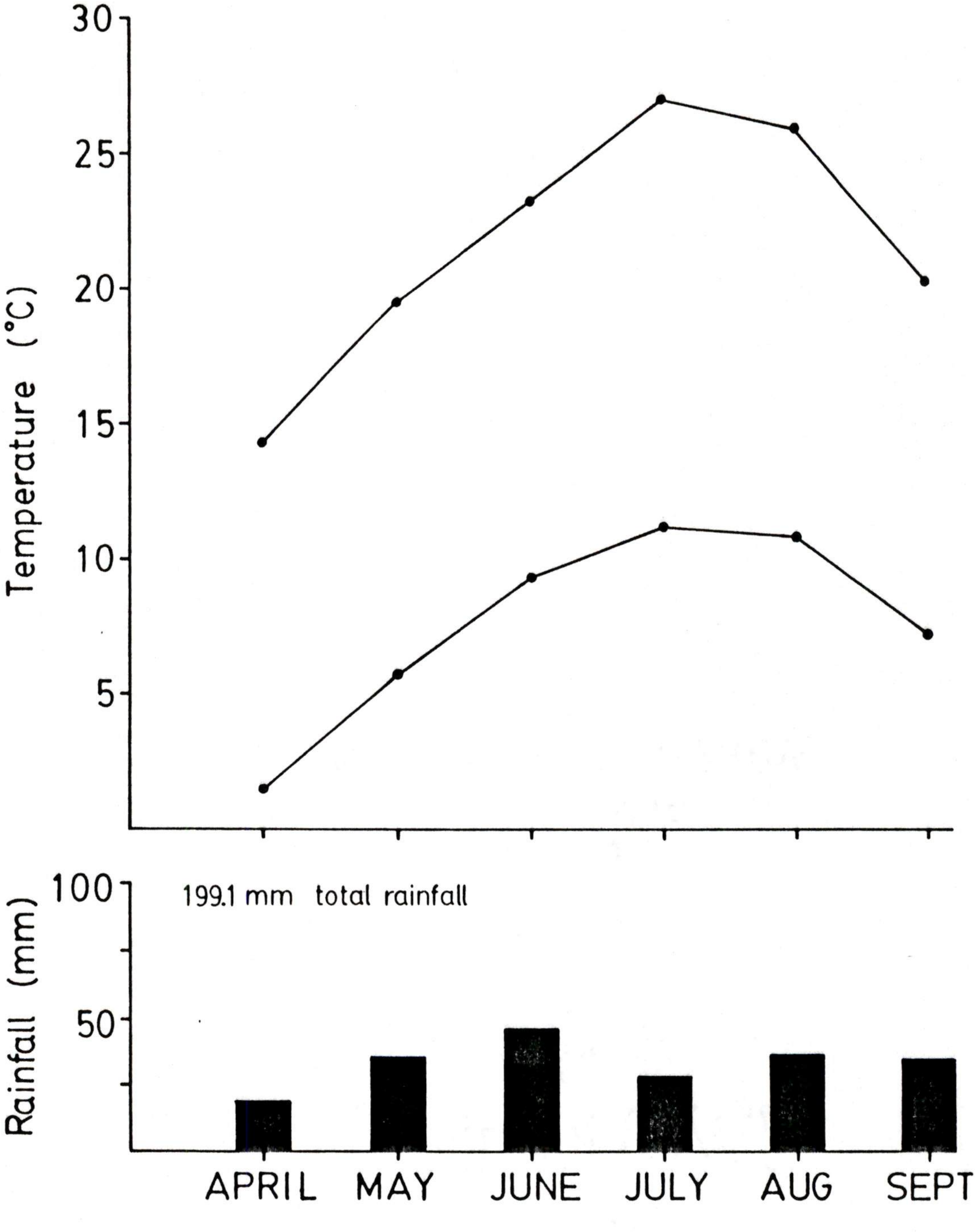

Temperature (°C)
30
25
20
15
10
5
Rainfall (mm)
100
50
199.1 mm total rainfall
APRIL
MAY
JUNE
JULY
AUG
SEPT

Figure 3: Weather patterns for the summer of 1985 on Coldstream Ranch.

Mean daily maximum and minimum temperatures for each month are shown with 95% confidence intervals to facilitate comparison with the summer of 1986. Numbers above the monthly rainfall bars are the number of days in the month with measurable rainfall. (source: Environment Canada Climatological Station, Coldstream ranch, Vernon, B.C.)

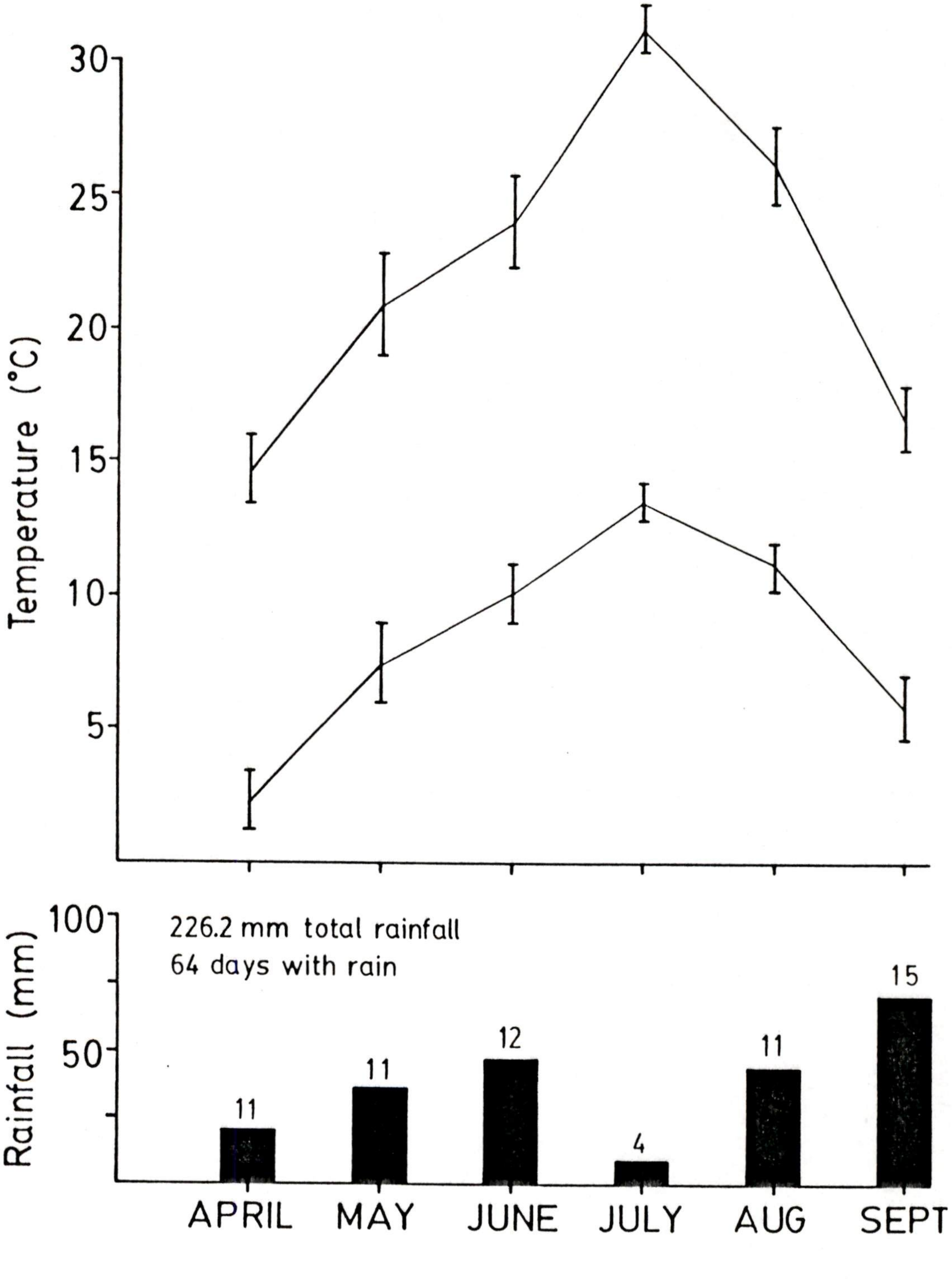
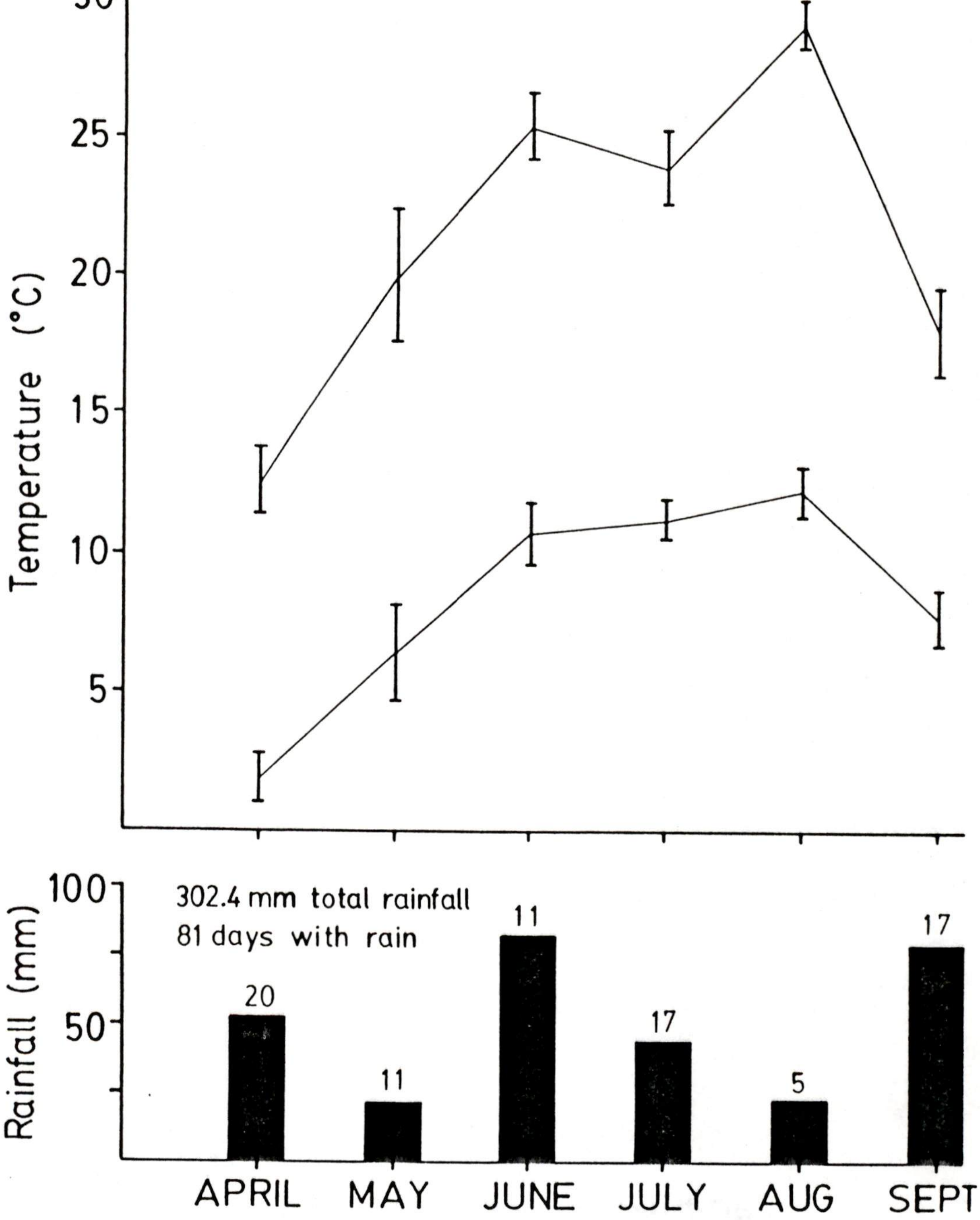

Temperature (°C)
30
25
20
15
10
5
Rainfall (mm)
100
50
226.2 mm total rainfall
64 days with rain
11
11
12
4
11
15
APRIL
MAY
JUNE
JULY
AUG
SEPT

Figure 4: Weather patterns for the summer of 1986 on Coldstream Ranch.

Mean daily maximum and minimum temperatures for each month are shown with 95% confidence intervals to facilitate comparison with the summer of 1985. Numbers above rainfall bars are the number of days in the month with measurable rainfall. (source: Environment Canada Climatological Station, Coldstream ranch, Vernon, B.C.)


30
25
20
15
10
5
Temperature (°C)
100
50
Rainfall (mm)
302.4 mm total rainfall
81 days with rain
20
11
11
17
5
17
APRIL
MAY
JUNE
JULY
AUG
SEPT

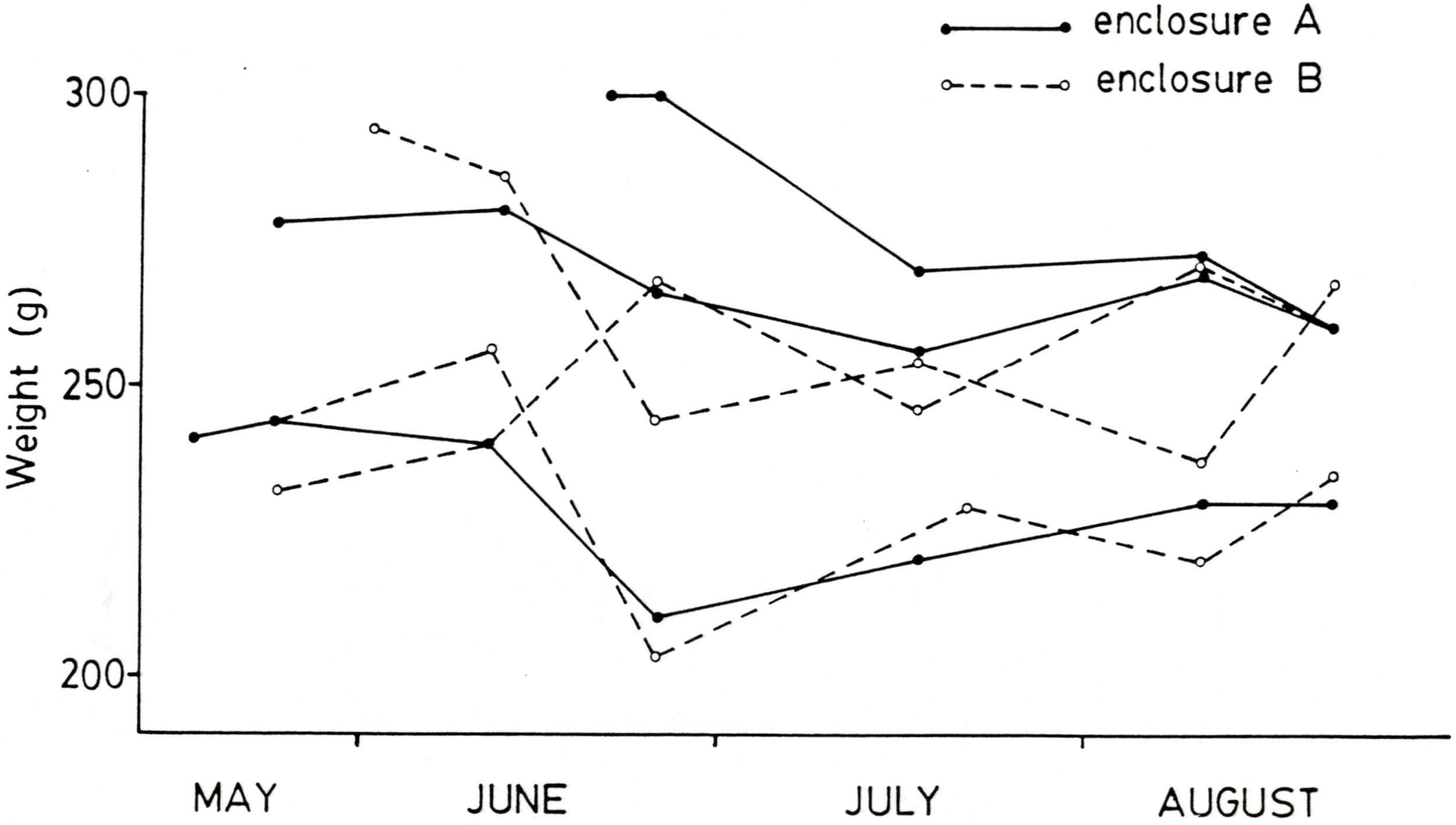
the 30 yr mean, while in August it was somewhat higher. The mean daily minimum did not differ from the 30 yr mean for either month. The summer of 1986 was considerably wetter than 1985 in terms of both total rainfall and the number of days of rainfall. I include the number of days with rainfall because many such days would have been at least partially cloudy, even when not raining, restricting thermoregulatory opportunities, and thus affecting temperature dependent processes.

Female Reproductive Cycles

During the summer of 1985, rodent trapping was initially successful, but became very difficult after mid-June. As a result, it was impossible to feed the snakes on any sort of schedule. Feeding was so erratic that the snakes in enclosure A (high feeding rate) probably did not receive a great deal more food than the snakes in enclosure B (low feeding rate), and neither group received a feeding rate appropriate to the study. Feeding records show that during the second half of July 1985, only 4 mice were caught (2 for each group of snakes). Trapping in August resulted in only 7 rodents being caught, 6 of which were fed to the snakes in enclosure A, in order to increase their weights. However, most of the snakes (5 of 6) had lower weights at the end of the study than at the beginning, although all showed periods of weight gain (Fig. 5).

No mating behavior was observed following the introduction of the male into enclosure A. However, immediately following introduction, the male showed signs of beginning ecdysis (clouded eyes), and was so engaged until 8 September 1985. None of the cloacal smears from the females in enclosure A showed sperm, and it is almost certain that no mating took place.

Figure 5: Weight changes of individual post partum females in enclosures A and B during summer 1985.


enclosure A
enclosure B
Weight (g)
300
250
200
MAY
JUNE
JULY
AUGUST

Because of sub-zero night-time temperatures on the study site throughout the spring of 1986, I did not release snakes into the individual outdoor enclosures until 25 May 1986. The snakes were kept indoors at Okanagan College from the time of capture until release into the enclosures ($\bar{x}$=24.2 ± 8.8 days, range 0-37 days) and did not feed, presumably because of the unusual surroundings. As a result the snakes lost an average of 15.12 ± 6.76% (range 0-29.1%) of their body weight before release into the outdoor enclosures. The mean weights of the two groups were not significantly different either at the time of capture or at the time of release (Table 1).

Snakes in the HFR group ate an average of 9.13 ± 2.83 meals during the 12 weeks of the study, while those in the LFR group ate only 3.73 ± 1.16 meals on average during the same time, a difference which was highly significant (t'=6.84, df=8, $p<0.001$). The distribution of the number of meals eaten by each snake is shown in Fig. 6. In addition to a difference in the mean number of meals eaten by individuals in the two groups there were also differences in terms of consumption on a weekly basis (Fig. 7). HFR snakes ate at a high, constant rate while LFR snakes ate at rates lower than food was available. LFR snakes were offered food once a week in both the first and second weeks of the study to try and make up for the weight loss incurred prior to release into the enclosures, after which they were maintained on the bi-weekly schedule.

Despite considerable differences in both the timing and quantity of food consumed the mean weights of the two groups remained virtually identical during the entire period of the study (Fig. 8). Both groups showed a steady decline following week 7, which corresponded with the extremely cool, wet weather of

Table 1: Mean weights for LFR and HFR snakes at the time of their capture and at the time of their release into the enclosures on Coldstream ranch.

		n	MEAN	S.D.	RANGE	t	p
At Capture	HFR	15	184.3	35.77	142-299	0.408	>0.05
	LFR	15	189.5	33.18	144-264		
At Release	HFR	15	156.6	40.78	120-285	0.422	>0.05
	LFR	15	162.5	35.58	110-250		

Figure 6: Distribution of the number of meals eaten by LFR and HFR snakes, during the 12 weeks of the study.

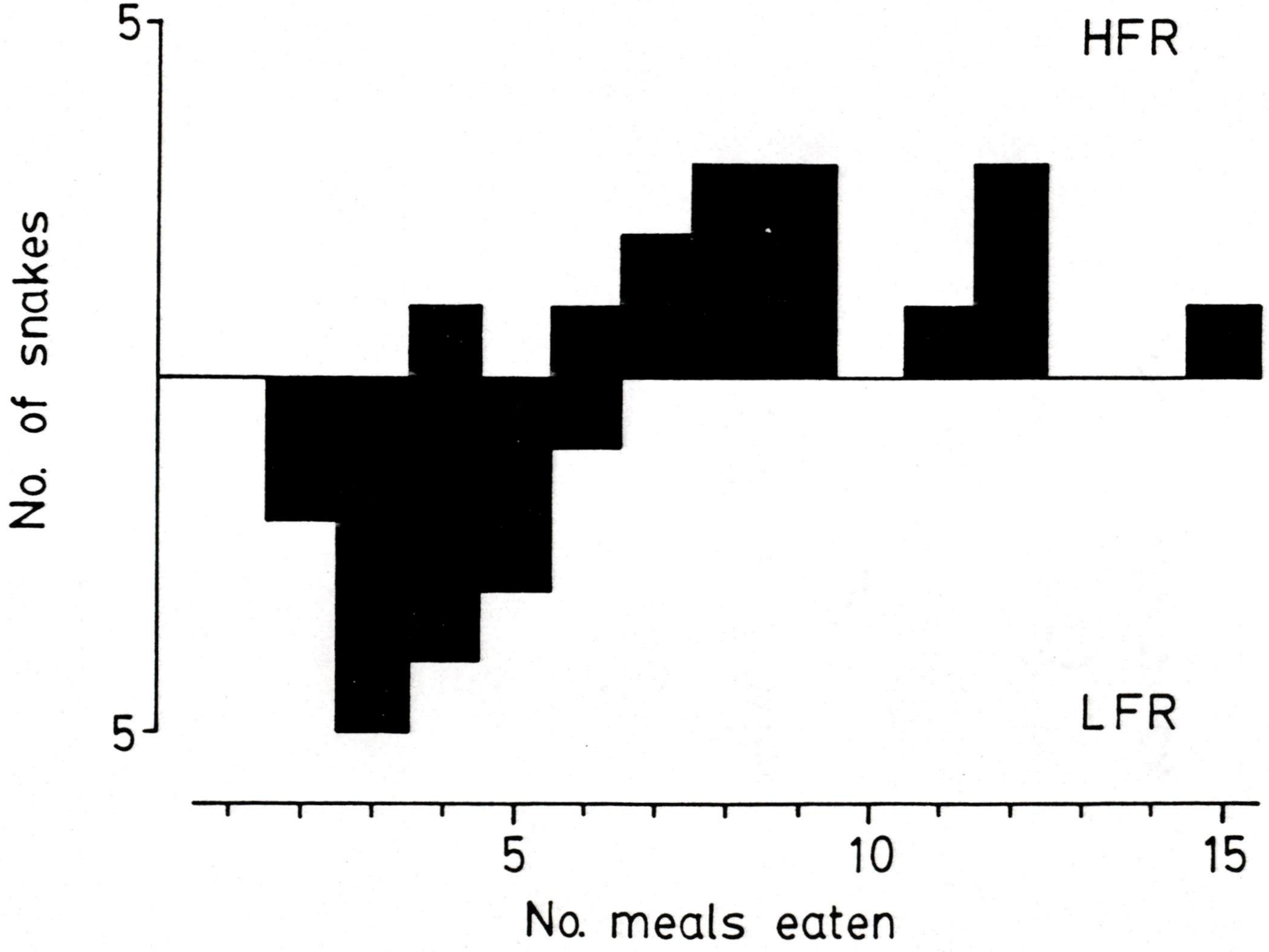

5
HFR
No. of snakes
5
LFR
5
10
15
No. meals eaten

Figure 7: Weekly food consumption by LFR and HFR snakes.

Number of meals eaten, on a weekly basis, for all 15 animals in each group. Each meal represents one adult mouse and all meals eaten (including multiple meals/individual/week) are shown.

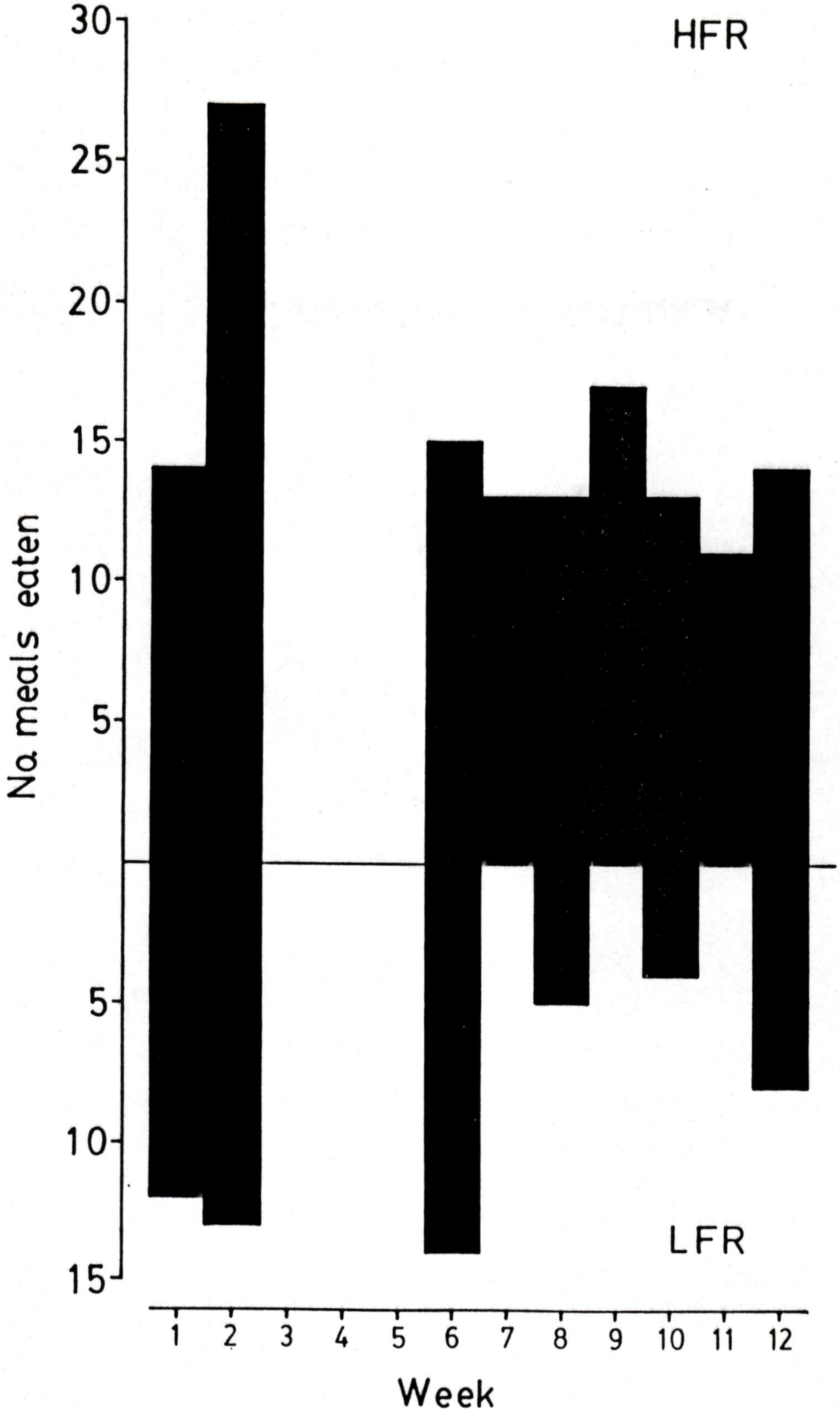
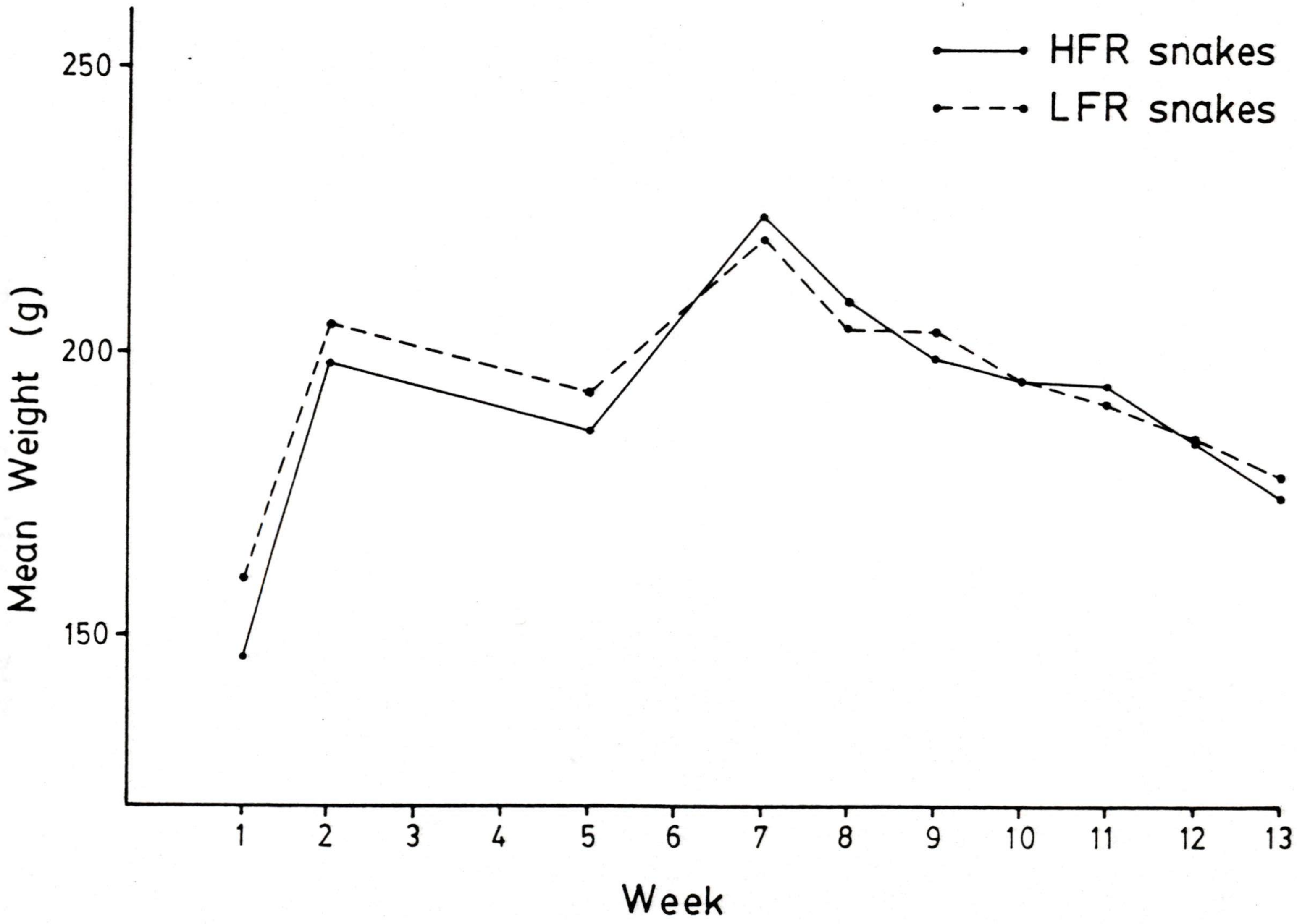

HFR
LFR
No. meals eaten
30
25
20
15
10
5
5
10
15
1
2
3
4
5
6
7
8
9
10
11
12
Week

Figure 8: Weight changes by LFR and HFR snakes during summer 1986.

The mean weight (n=15) for each group is plotted for each week of the summer. Error bars are not included, but in no cases are the pairs of means significantly different.


HFR snakes
LFR snakes
Mean Weight (g)
250
200
150
1
2
3
4
5
6
7
8
9
10
11
12
13
Week

July. This decline occurred even in individuals which continued to feed at a high rate (Fig 9).

Absolute growth, from time of capture in spring to time of release in the fall, for snakes in the two groups was highly variable and there was no significant difference between the means (LFR: $\bar{x}=10.67 \pm 12.51$ mm, n=15; HFR: $\bar{x}=10.33 \pm 10.77$ mm, n=15; $t=0.08$, df=28, $p>0.05$). In addition, while there was no correlation between growth and initial SVL for HFR snakes ($r=-0.314$, n=15, $p>0.05$), there was a significant positive correlation among the LFR snakes ($r=0.599$, n=15, $p<0.05$). There was no relationship when the two groups were combined ($r=0.060$, n=30, $p>0.05$; Fig 10). Growth in length was not at the expense of weight gain as there was no correlation between change in length and change in weight for either the LFR snakes ($r=0.051$, n=15, $p>0.05$) or the HFR snakes ($r=-0.045$, n=15, $p>0.05$). In order to account for possible effects due to the differences in initial SVL I calculated relative growth $[(SVL_{t+1}-SVL_t)/SVL_t]$. The number of meals eaten by each snake was not correlated with relative growth (LFR: $r=0.358$, n=15, $p>0.05$; HFR: $r=0.032$, n=15, $p>0.05$; both groups combined: $r=0.019$, n=30, $p>0.05$), and although there was no significant relationship between relative growth and initial SVL in the HFR group ($r=-0.342$, n=15, $p>0.05$) there was a significant positive relationship in the LFR group ($r=0.585$, n=15, $p<0.05$). Again, there was no correlation when the two groups were combined ($r=0.030$, n=30, $p>0.05$). The number of meals eaten was not correlated with initial SVL for HFR snakes ($r=0.204$, n=15, $p>0.05$), but was for LFR snakes ($r=0.507$, n=15, $p<0.05$). There was no correlation for the two groups combined ($r=0.224$, n=30, $p>0.05$).

Figure 9: Weight change for one HFR snake during summer 1986.

Weight change for the snake which ate the most during the study (15 mice). Note the decline in weight, despite continued feeding, starting in early July. Arrows indicate meals eaten.

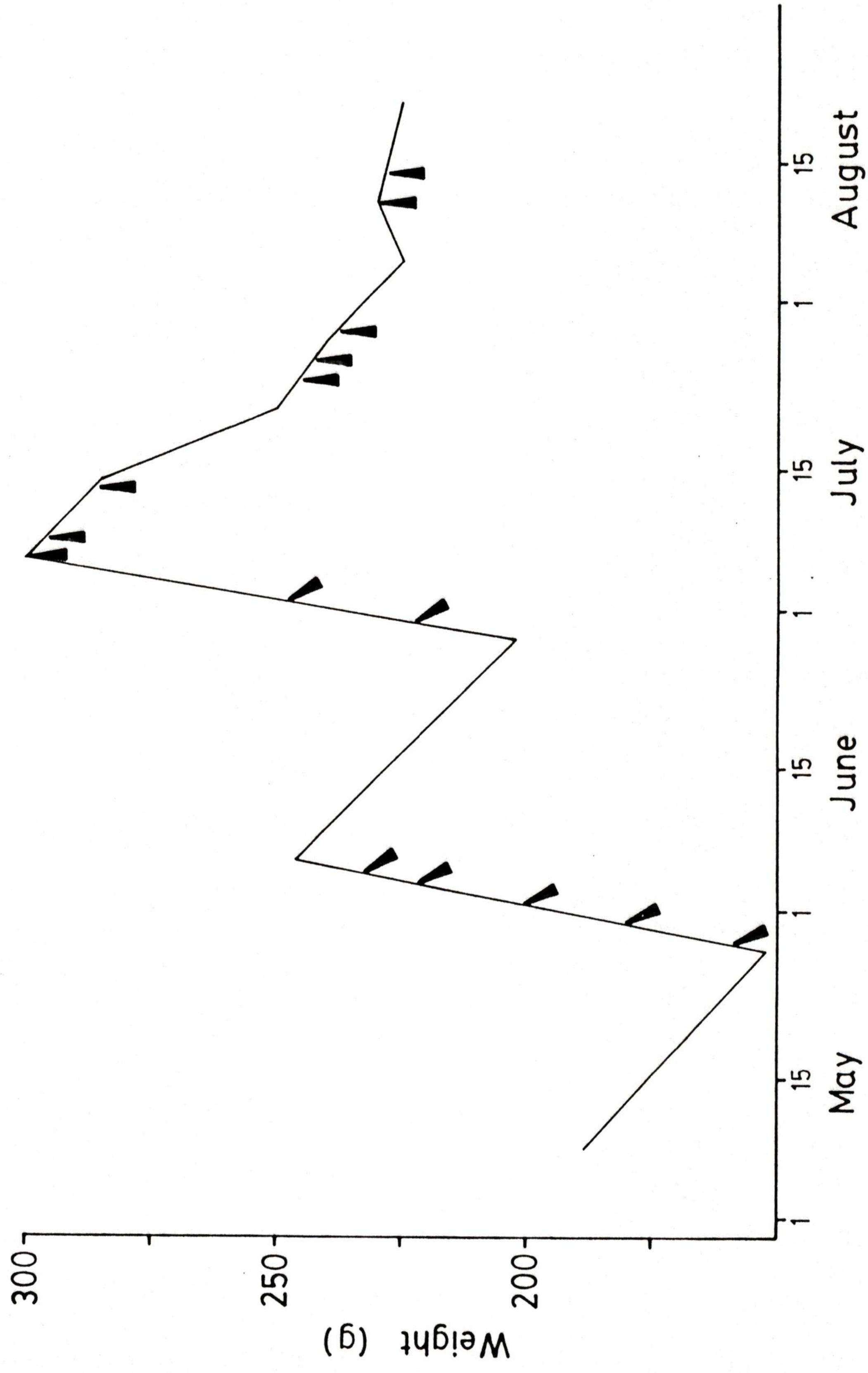
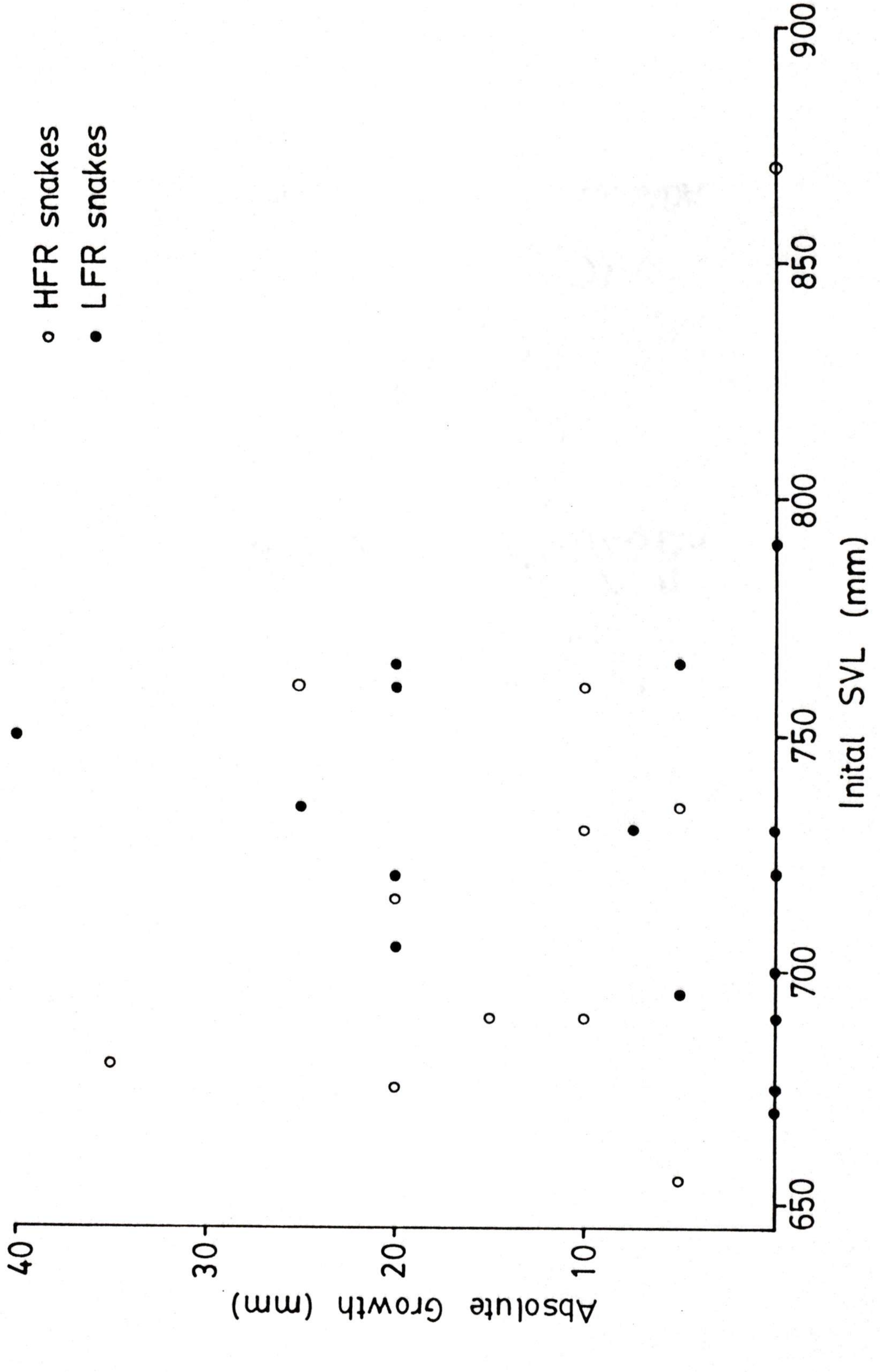

Weight (g)
300
250
200
1
15
May
1
15
June
1
15
July
1
15
August

Figure 10: Absolute growth by LFR and HFR snakes measured from time of capture to time of release in 1986.


○ HFR snakes
● LFR snakes
Absolute Growth (mm)
40
30
20
10
Inital SVL (mm)
650
700
750
800
850
900

Condition factors are a way of combining the weight and length of an animal into a single value. The most common condition factor is Wt/Length^3 (Ricker 1975) and assumes that weight is proportional to the cube of length. This assumption is met among adult rattlesnakes in this population (Macartney 1985) and I calculated condition factor as Wt/SVL^3. To see how condition factor changed over the summer I calculated condition factors from the first weight and SVL for each animal during the study, and from the weight in week 12 (the last week for which there was abundant food) and the final SVL of each animal. The mean condition factors for LFR snakes ($\bar{x}=4.3 \times 10^{-4} \pm 7 \times 10^{-5}$ g/cm^3), and HFR snakes ($\bar{x}=4.1 \times 10^{-4} \pm 7 \times 10^{-5}$ g/cm^3) were not significantly different at the beginning of the study ($t=0.782$, df=28, $p>0.05$), nor was the mean change in condition factor over the summer (LFR: $\bar{x}=4.2 \times 10^{-5} \pm 7 \times 10^{-5}$ g/cm^3; HFR: $\bar{x}=4.7 \times 10^{-5} \pm 7 \times 10^{-5}$ g/cm^3; $t=-0.188$, df=28, $p>0.05$). Although mean change in condition factor did not differ between the two groups there was a significant correlation between change in condition factor and number of meals eaten among the HFR snakes (Fig. 11), but not among the LFR snakes ($r=0.317$, n=15, $p>0.05$)

During the summer, 22 of the 30 snakes underwent ecdysis (12 of 15 LFR snakes, and 10 of 15 HFR snakes). The timing of ecdysis for the captive snakes is shown in Fig. 12.

Table 2 summarizes the information on the male rattlesnakes which were used in the mating trials. Information on the females with which they were paired is found in Table 3. None of the females with access to males were observed in copulation, although in one instance the male (with female 14, the largest female) showed considerable tongue-flicking and apparent interest, shortly after

Figure 11: Net change in condition factor over the 12 weeks of the study as a function of food intake for the HFR snakes.

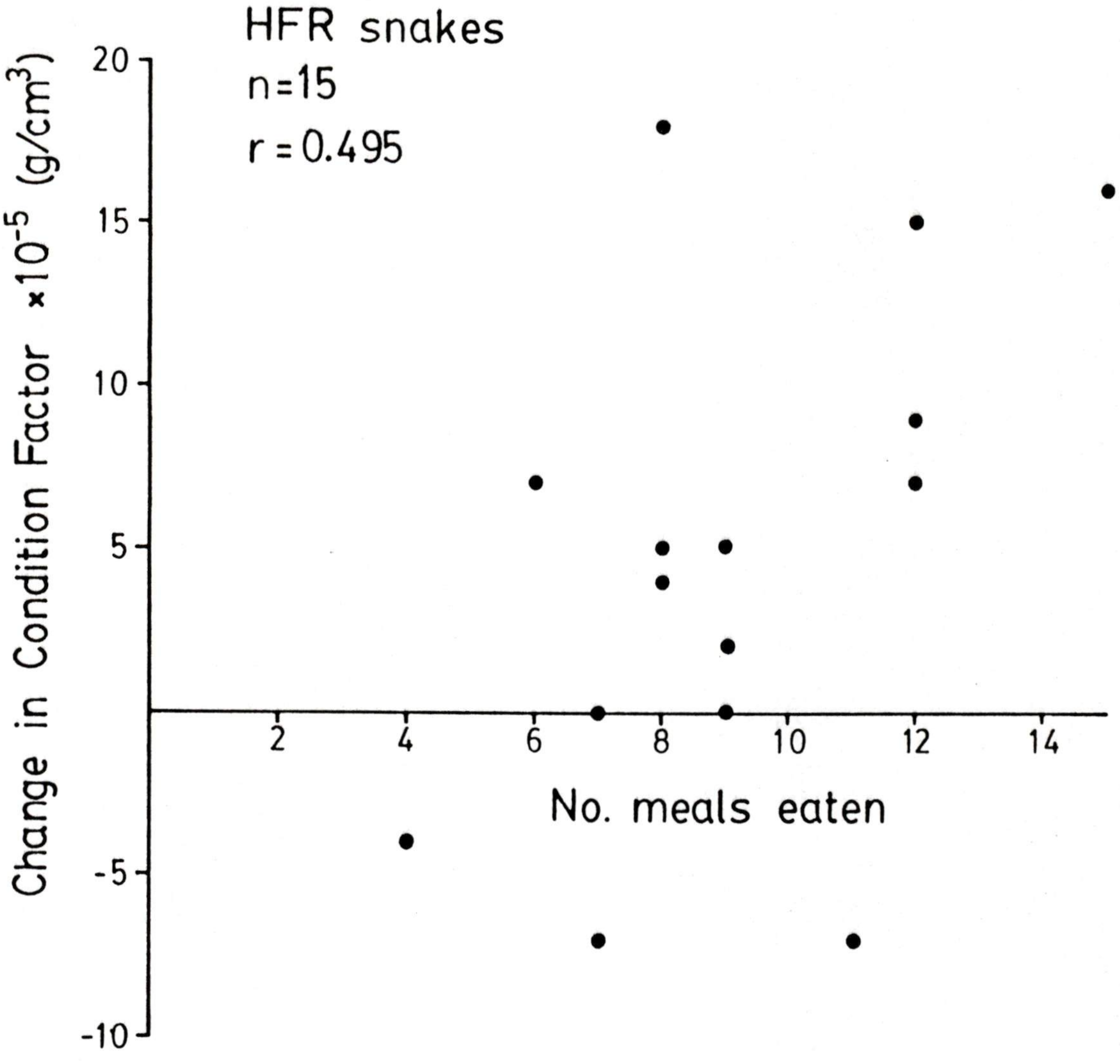

HFR snakes
n=15
r = 0.495
Change in Condition Factor ×10^{-5} (g/cm^3)
20
15
10
5
-5
-10
2
4
6
8
10
12
14
No. meals eaten

Figure 12: Timing of ecdysis for LFR and HFR snakes during summer 1986..

Bars for the two groups are not overlain, but stand one on top of the other.

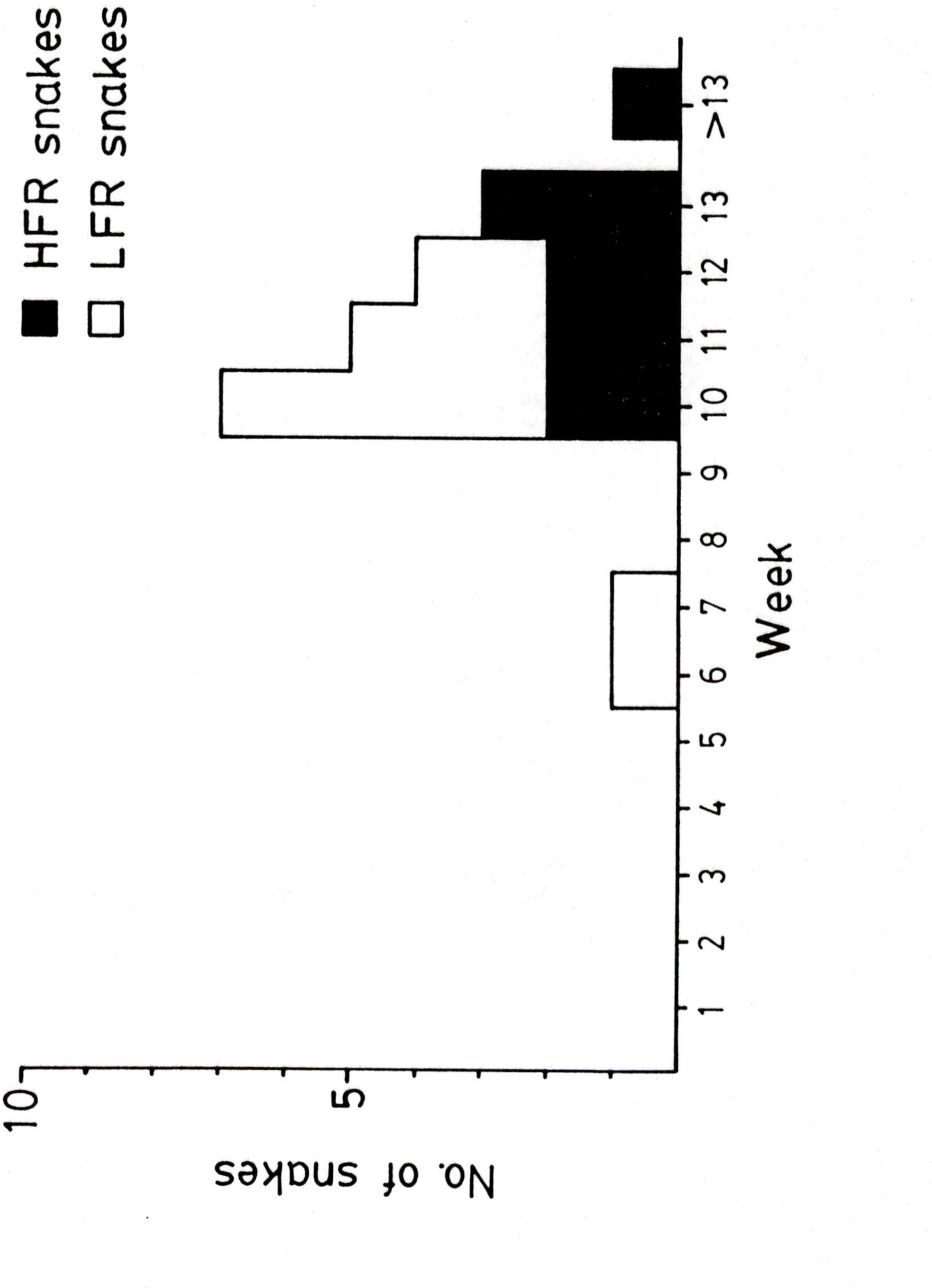

■ HFR snakes
□ LFR snakes
No. of snakes
10
5
Week
1
2
3
4
5
6
7
8
9
10
11
12
13
>13

Table 2: Weights and lengths of males used in mating trials.

MALE	SVL mm	WEIGHT g	FEMALE PAIRED WITH	FEEDING GROUP
1	910	455	5	LFR
2	830	350	9	LFR
3	1000	810	11	LFR
4	670	140	6	HFR
5	930	640	14	HFR
6	780	280	16	HFR
7*	880	370	26	HFR
8	860	500	26	HFR

* died on 21 August 1986, presumably from overheating, and was replaced with male number 8.

Table 3: Summary of information for females with access to males.

SVL and weight changes are calculated over the period that the females were in the enclosures, not from their time of capture.

	I.D. NO.	INIT. SVL mm	FINAL SVL mm	INIT. WT. g	FINAL WT. g	SVL CHANGE %	WT. CHANGE %	MALE INTRO. DATE
LFR	5	750	790	250	260	5.33	4.00	19 AUG.
	9	670	670	110	140	0.00	27.27	23 AUG.
	11	720	740	132	180	2.78	36.36	29 AUG.
HFR	6	760	770	140	170	1.32	21.43	19 AUG.
	14	870	870	285	365	0.00	28.07	23 AUG.
	16	680	715	150	140	5.15	-6.67	29 AUG.
	26	675	695	120	150	2.96	25.00	19 AUG.

introduction to the enclosure. Cloacal smears done on 29 August and 9 September 1986 showed no evidence of sperm and the same results were obtained from slides made by scraping the uterine walls directly on 7 October. In addition, none of the 30 females had enlarged follicles at the time of their release on 8 October 1986.

Temperature Relationships

Model Trials

The copper tube models, constructed during summer 1985, performed well in both the short (Fig. 13) and long-term (Fig. 14) trials, suggesting that it is possible to construct simple thermal models with relative ease. However, these models were limited to a single posture. The inner tube models appeared to be much more versatile, and less difficult to construct, as well as being considerably cheaper than copper tubing. The results of the short-term heating/cooling trials using the inner tube models are shown in Fig. 15 (straight models) and Fig. 16 (coiled models). I varied the amount of water in the three models (220, 300, and 400 ml) to determine what volume provided the closest match with the snake. In both postures the model with the least water heated more quickly than the snake, but then cooled in a similar fashion. Under the more natural conditions of the long-term trials the model containing 220 ml of water was the most accurate overall, whether it was straight (Fig. 17) or coiled (Fig. 18). The model tended to underestimate the snake's temperature when coiled, but overestimate it when straight. However, since models in both postures appeared to be relatively accurate at temperatures below 40°C, and hence at temperatures at which *C. viridis* is active (Brattstrom 1965), models containing 220 ml of water were used in the enclosure study.

Figure 13: Temperature changes during short-term model trial, using copper tube model, 21 June 1985.

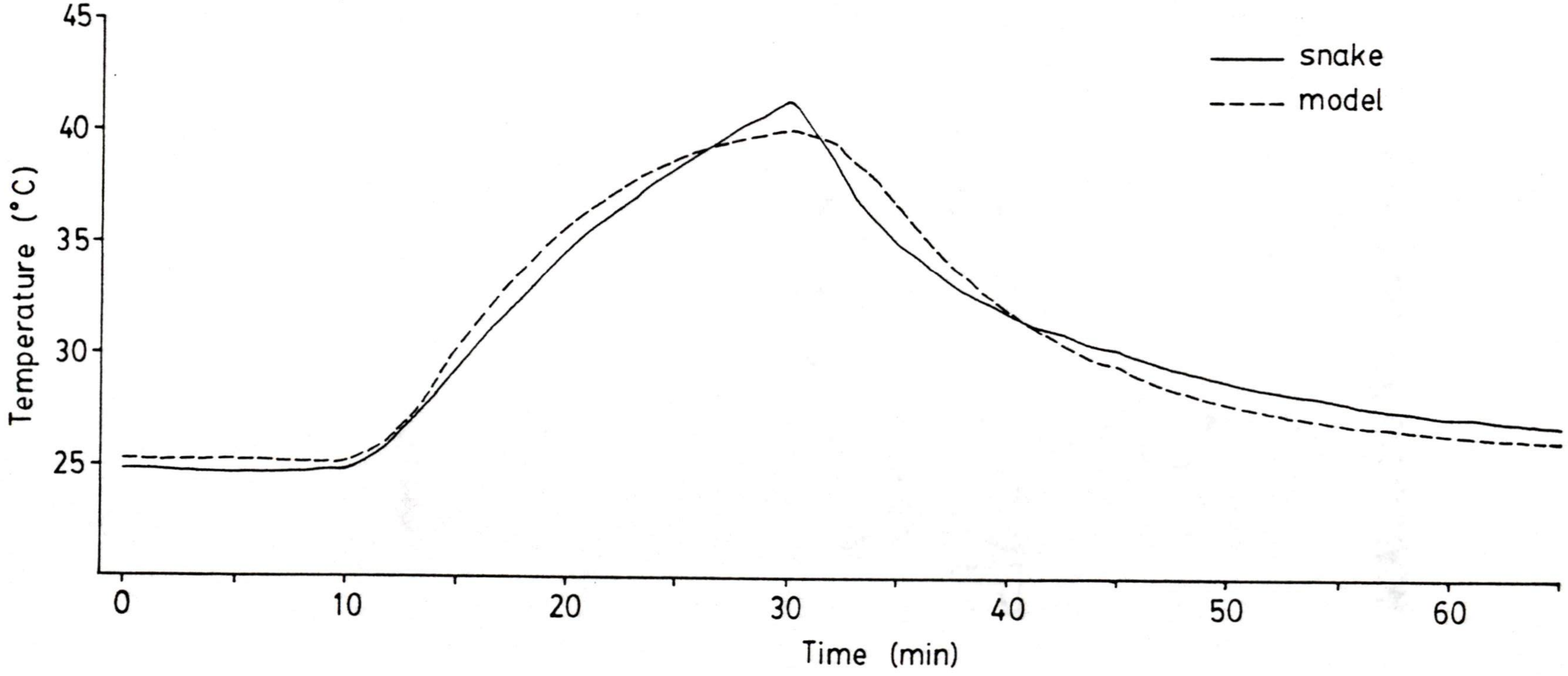

45
40
35
30
25
Temperature (°C)
0
10
20
30
40
50
60
Time (min)
snake
model

Figure 14: Temperature changes during long-term model trial, using copper tube model, 24 July 1985.

Models 1, 2 and 3 are light-colored, intermediate and dark-colored, repectively.

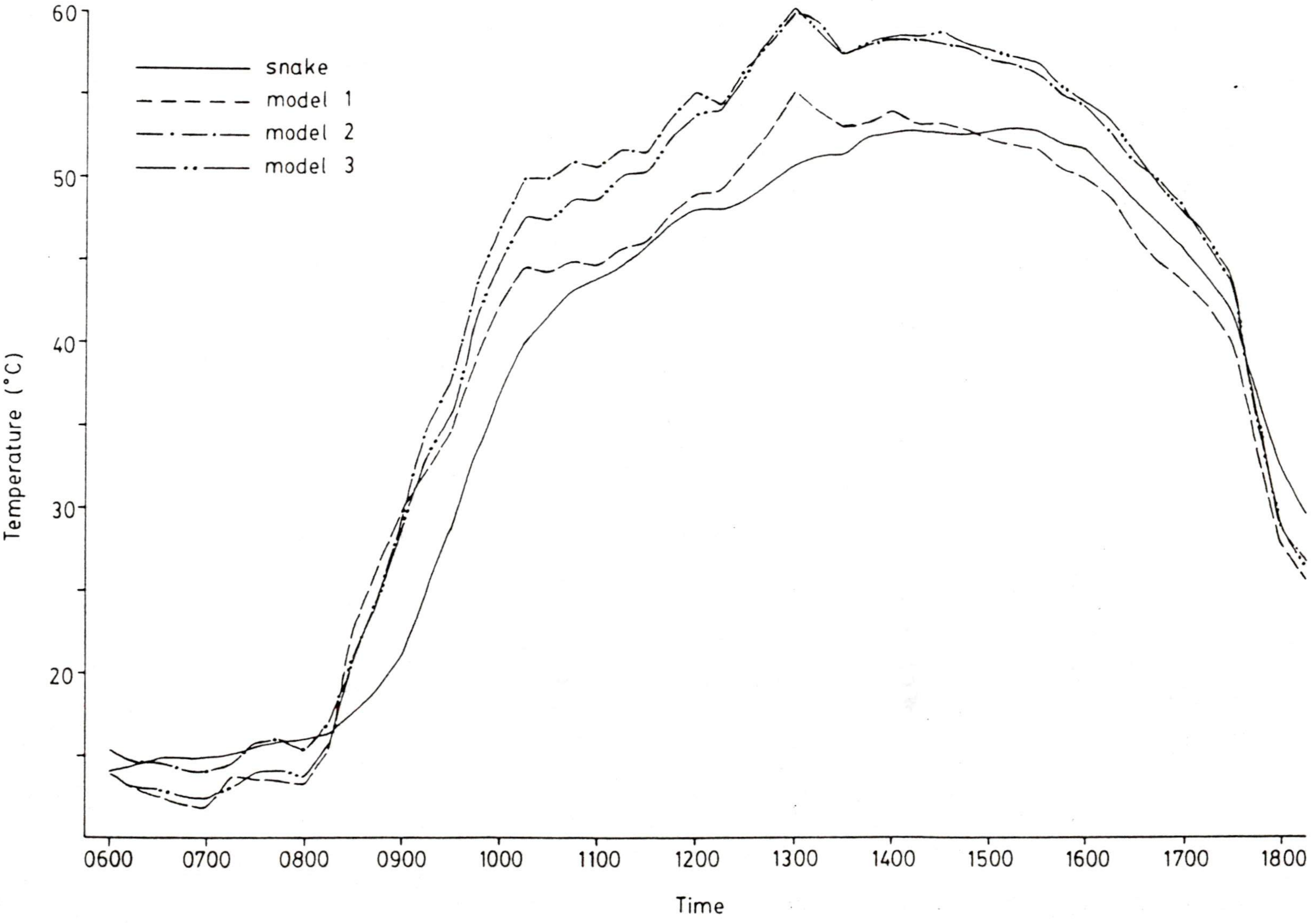
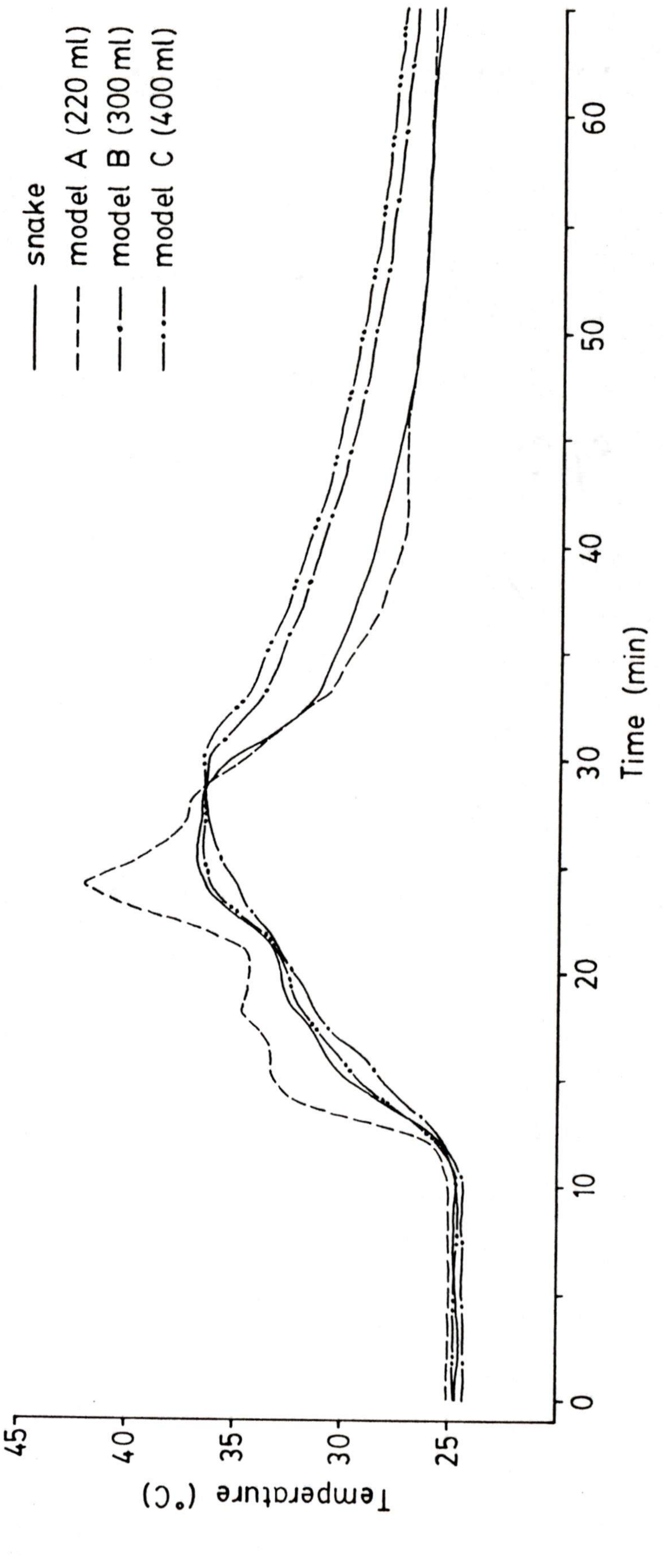

snake
model 1
model 2
model 3
Temperature (°C)
20
30
40
50
60
Time
0600
0700
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700
1800

Figure 15: Temperature changes during short-term heating trial, using straight inner tube models, conducted on 6 July 1986.



Temperature (°C)
25
30
35
40
45
Time (min)
0
10
20
30
40
50
60
snake
model A (220 ml)
model B (300 ml)
model C (400 ml)

Figure 16: Temperature changes during short-term heating trial, using coiled inner tube models, conducted on 7 July 1986.

Models A, B and C are the same as in Fig. 15.

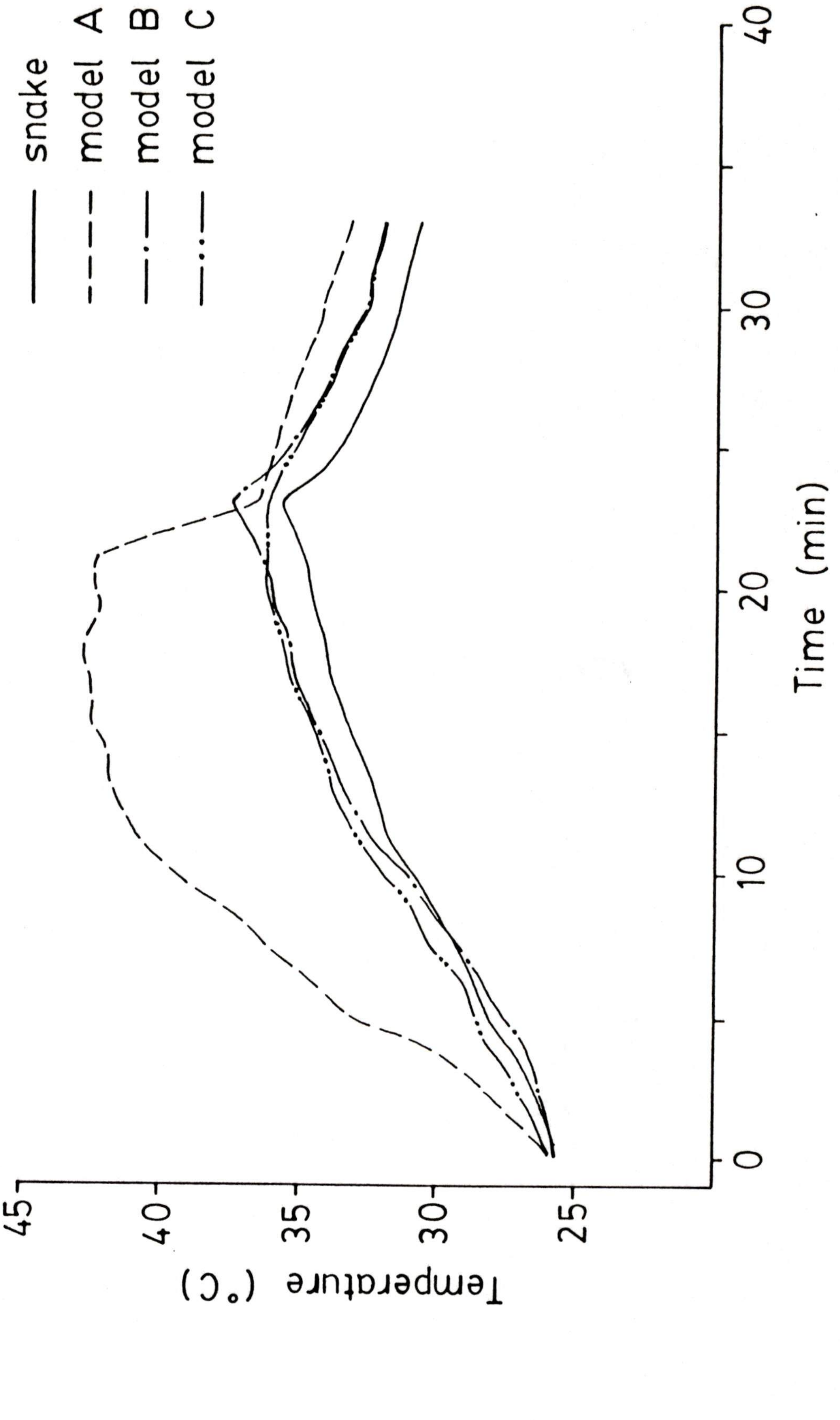

Temperature (°C)
45
40
35
30
25
0
10
20
30
40
Time (min)
snake
model A
model B
model C

Figure 17: Temperature changes during long-term heating trial, using straight inner tube models, conducted on 8 July 1986.

Models A, B and C are the same as in Fig. 15. The horizontal bar at the base of graph indicates the weather conditions at the time of the reading.

■ cloudy

□ sunny

⬚ rain

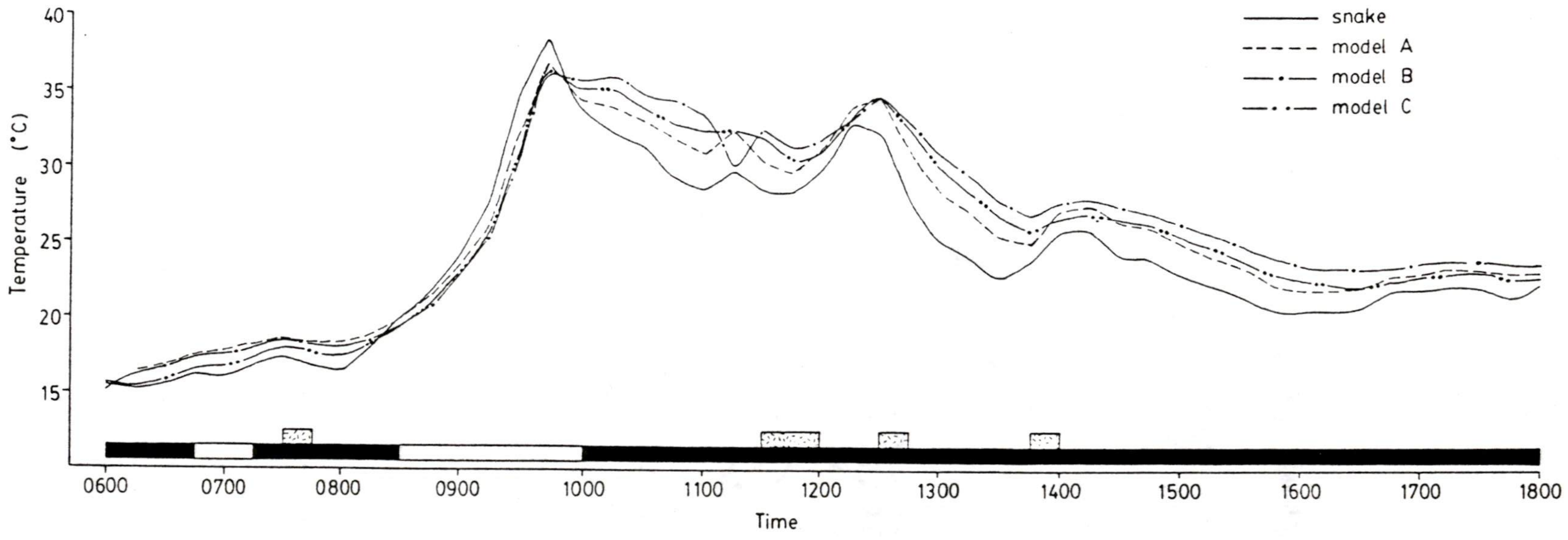

40
35
30
25
20
15
Temperature (°C)
0600
0700
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700
1800
Time
snake
model A
model B
model C

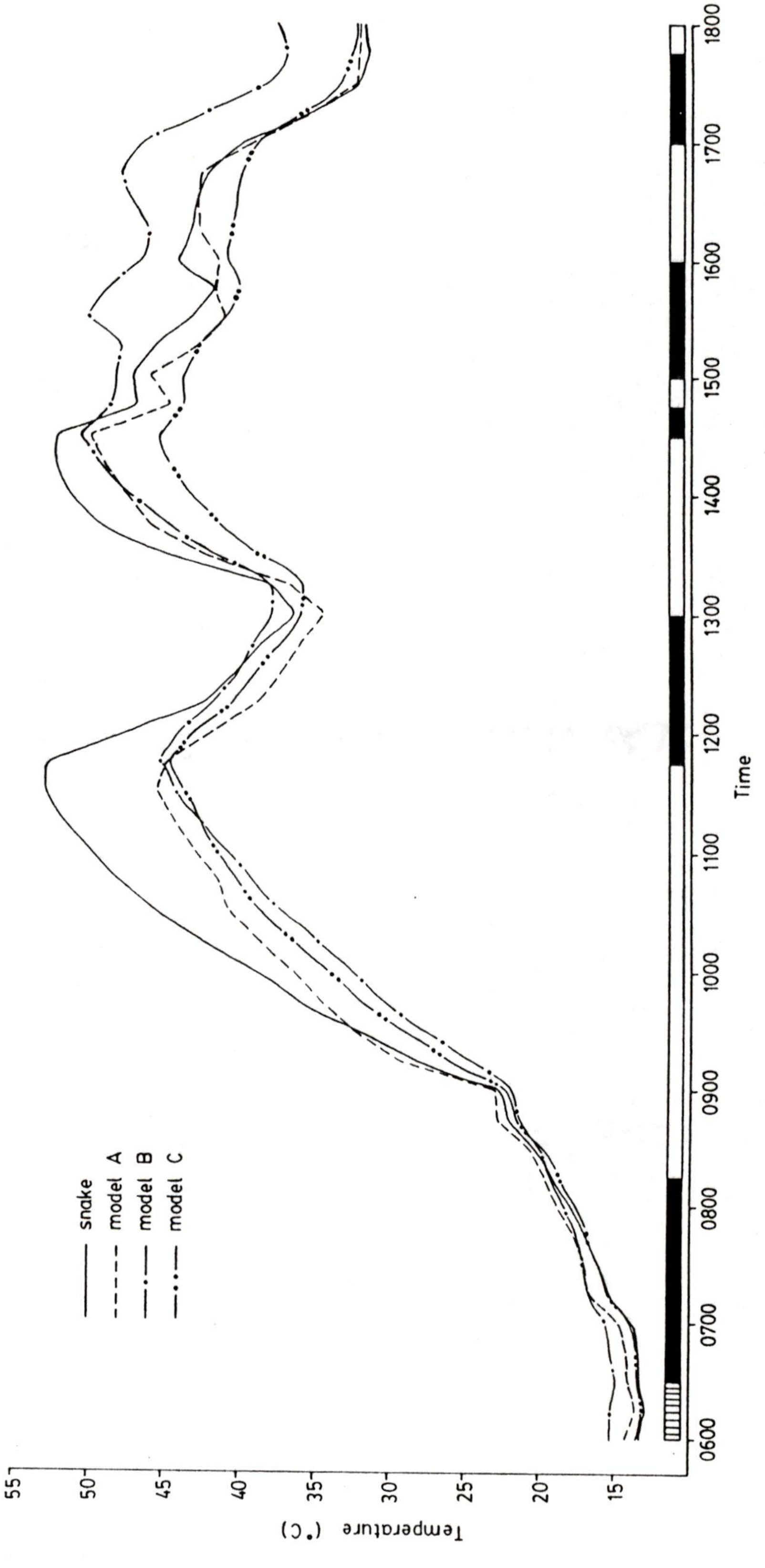
Figure 18: Temperature changes during long-term heating trial, using coiled inner tube models, conducted on 9 July 1986.

Models A, B and C are the same as in Fig. 15. The horizontal bar at the base of the graph indicates the weather conditions at the time of the reading.

▥ shade

■ cloudy

□ sunny


snake
model A
model B
model C
Temperature (°C)
55
50
45
40
35
30
25
20
15
Time
0600
0700
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700
1800

Daily Pattern of Body Temperature Variation

Between 13 July and 7 September 1986, snake and model temperatures were monitored for a total of 240 hours, representing 30 eight-hour shifts evenly divided among morning (0400-1200), afternoon (1200-2000), and night (2000-0400). A total of 1980 environmental temperatures (990 from each model) and 5643 individual body temperature measurements (from 1 male, 4 nongravid females, and 3 gravid females) were obtained during the study. The snakes commonly showed a pattern of body temperature change which corresponded with the "plateau" pattern of Peterson (1987). In the morning (Fig. 19a) body temperatures initially declined slowly until shortly after the temperature of the straight model started to rise. At this time the snakes underwent a rapid heating phase followed by a "plateau" of relatively stable body temperatures,typically between 30-35 °C, with variances as low as 0.61 ($\bar{x}$=31.7 °C, between 1200 and 2000) for a given individual over the entire 8 h period. This plateau persisted through most of the afternoon (Fig. 19b), and temperatures eventually started a slow decline as the sun set. Night-time temperatures (Fig. 19c) were characterized by slow and constant cooling over the entire period. Body temperatures of individual snakes rarely fell below 14 °C, although the straight, exposed model experienced temperatures as low as 6.5 °C.

The lowest body temperature measured during the study was 11.9 °C (nongravid female, 0400 29 July), and the highest was 37.8 °C (gravid female, 1330 5 Sept.). On only one sample day (16-17 July 1986) did the snakes vary to any degree from the plateau pattern described above. The weather was cloudy and cool, with scattered rain, for the entire time and the only models in the enclosure were two

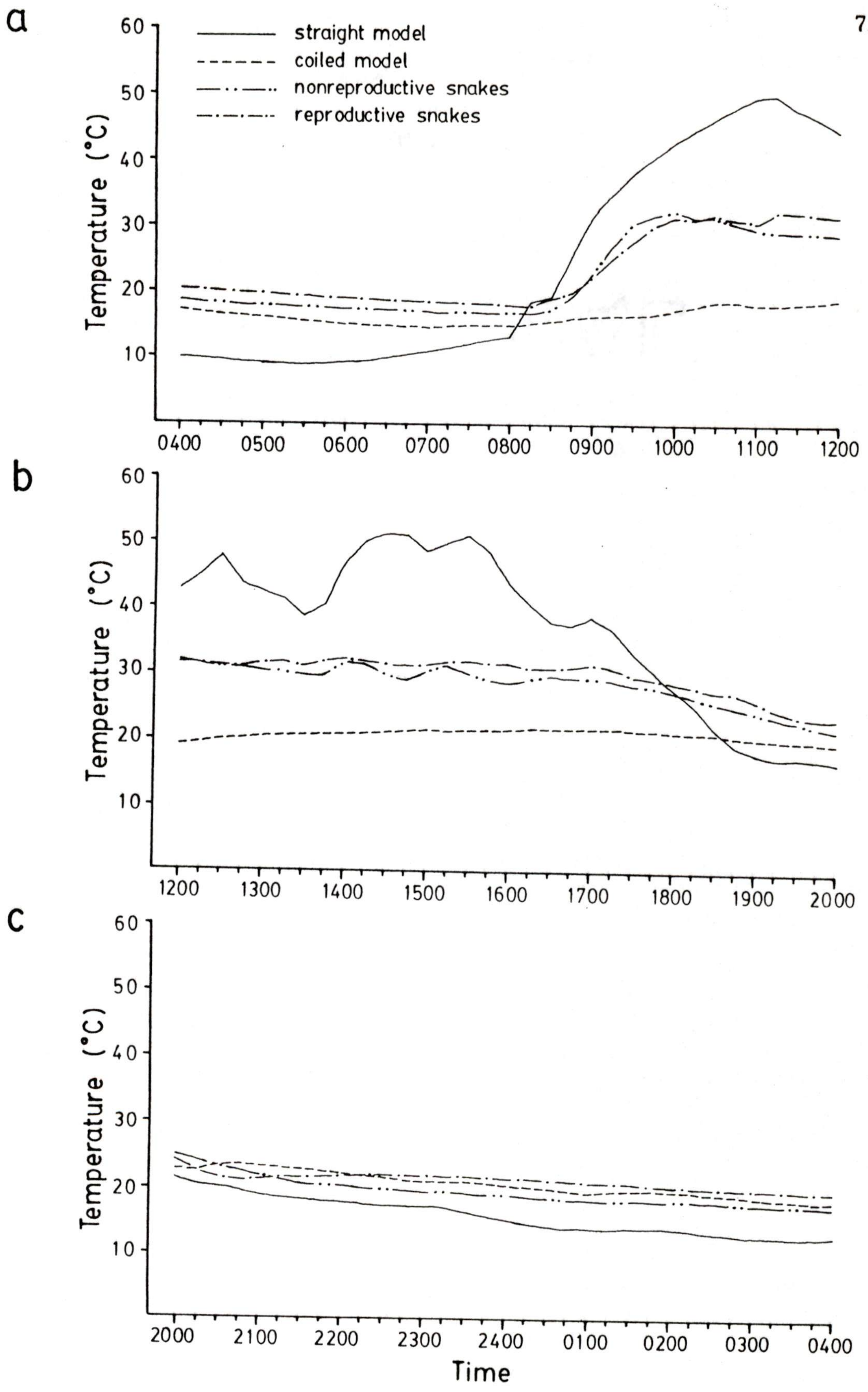
Figure 19: Representative example of the daily pattern of temperature change.

Model and pooled mean body temperatures for snakes in the reproductive and nonreproductive groups taken during 8 h periods on 24 and 25 July 1986.

a) The pattern between 0400 and 1200 shows a rapid increase in body temperature followed by a relatively stable plateau.

b) Body temperatures remain relatively low and stable between 1200 and 2000 in spite of extremely high environmental temperatures. In the early evening body temperatures slowly begin to decrease.

c) Body temperatures at night (2000-0400) cool slowly and are similar to those of the coiled model under cover.


a
straight model
coiled model
nonreproductive snakes
reproductive snakes
Temperature (°C)
60
50
40
30
20
10
0400
0500
0600
0700
0800
0900
1000
1100
1200
b
Temperature (°C)
60
50
40
30
20
10
1200
1300
1400
1500
1600
1700
1800
1900
2000
c
Temperature (°C)
60
50
40
30
20
10
2000
2100
2200
2300
2400
0100
0200
0300
0400
Time

coiled ones (one exposed, and one under cover), due to equipment malfunction. The temperature of the exposed model remained low (max.=25 °C) during the entire day, and body temperatures of snakes followed those of that model throughout the sampling period.

The temperature of the straight model typically rose rapidly following sunrise and reached high temperatures (max.=65.5 °C) before cooling during the night. In contrast, the coiled model, under the cover of rocks, maintained a remarkably constant temperature during all periods. Body temperatures of snakes rarely fell below those of the coiled model.

In 9 sample days (three 8 h trials separated by 8 h each) during which a straight model was present in the enclosure, it was possible to calculate the amount of time the model spent above 40 °C. Between 0400 and 1200 the model spent a mean of 71.7 ± 60.8 min above 40 °C (14.9% of the time), always at the end of the period. For the period 1200-2000 the model spent a average of 293.3 ± 110.8 min above 40 °C (61.1% of the time), usually at the beginning of the period. Night-time temperatures (2000-0400) never exceeded 40 °C.

Body Temperature Variation and Reproductive Condition

In viviparous reptiles, thermoregulation is presumed to be used by gravid females to speed embryonic development. Thus, differences in the degree of body temperature variation between animals in reproductive condition (gravid females) and those in nonreproductive condition (males and nongravid females) should be expected. However, implicit in this hypothesis is the important, but untested, assumption that thermoregulation is somehow less important to nonreproductive animals.

I calculated the mean body temperature and variance for each individual over each 8 h period and Table 4 shows the average mean body temperature and variance for individual snakes in the NR and R groups. In order to look for differences between the two groups I pooled the body temperature measurements for the animals in each of the groups, for each 8 h period. The means and variances discussed subsequently in this section refer to these "grand means" and their associated variances.

Whether in the morning, afternoon, or night the nonreproductive group never had a higher mean body temperature than the reproductive group (Table 5) and only rarely was there no difference. The difference between the mean body temperatures of the two groups rarely exceeded 2°C, at any time. Mean body temperatures of the two groups were more likely to be the same as the day wore on, but the tendency is slight.

The variances associated with these means give an index of the precision of body temperature variation, and show no obvious pattern (Table 5). In most cases the variances were not significantly different. However, in the morning the nonreproductive group was always less variable than the reproductive group when there was a difference. The reverse was true in the afternoon when the reproductive group was always less variable when differences occurred. At night neither group appeared to be consistently more or less variable.

The 8 h periods can be further divided into 2 h blocks in order to examine how body temperature in the two groups of snakes changed on a finer time scale. Again, the reproductive group always had a higher mean body temperature than the nonreproductive group at all times during the morning, and only rarely was

Table 4: Average mean body temperatures and variances, for R and NR snakes during the morning, afternoon and night.

The mean body temperature for an individual is composed of 33 body temperature measurements taken during the 8 h period and n indicates the number of individuals included. The variance of mean body temperature represents the average variance associated with the mean body temperature of an individual.

		n	Mean Body Temperature		Variance of Mean Body Temperature	
			$\bar{x}$ ± s.d.	(range)	$\bar{x}$ ± s.d.	(range)
0400-1200	NR	34	22.4 ± 3.0	(15.2-26.5)	18.21 ± 15.22	(0.04-50.68)
	R	23	22.2 ± 3.6	(17.3-29.2)	23.44 ± 13.35	(0.29-47.66)
1200-2000	NR	34	28.8 ± 2.9	(17.5-32.3)	7.45 ± 5.57	(1.19-19.59)
	R	23	29.9 ± 3.0	(23.9-34.6)	5.55 ± 5.12	(0.61-22.34)
2000-0400	NR	34	21.1 ± 3.7	(15.2-28.5)	4.76 ± 3.65	(0.04-15.12)
	R	23	21.9 ± 4.3	(15.5-29.7)	3.75 ± 3.25	(0.57-11.48)

Table 5: Comparison of the means and variances of the pooled samples of body temperatures of reproductive (R) and nonreproductive (NR) snakes over 8 h periods.

Values tabulated are the frequency of occurrence of the specified outcome for the 8 sample days for which there were at least 2 animals in each group.

		0400-1200	1200-2000	2000-0400
MEANS	R>NR	7	6	5
	NR>R	0	0	0
	R=NR	1	2	3
VAR.	R>NR	3	0	2
	NR>R	0	3	4
	R=NR	5	5	2

there no significant difference (Table 6). Approximately 50% of the time the variances associated with these means were not significantly different. When there was a difference, the reproductive group tended to have a lower variance until 0745, at which point the variance for the group became higher than for the nonreproductive group (Table 6).

Between 1200 and 2000 the reproductive group maintained a significantly higher mean body temperature in almost all cases. However, later in the afternoon and early evening mean body temperatures for the two groups were more likely to be the same (Table 7). In only one instance did the nonreproductive group have a higher mean body temperature than the reproductive group, and this occurred between 1400-1545, the hottest time of day. Variances were not significantly different between the two groups at least half of the time during any 2 h block (Table 7), and there is no evidence that either group was more precise.

At night, the mean body temperature of the reproductive group was always higher than that of the nonreproductive group, when there was a difference (Table 8). At the beginning of the evening the two groups did not differ half of the time. However, by the end of the night the reproductive group almost always had a higher mean body temperature. The reproductive group rarely had a higher variance than the nonreproductive group during the first half of the night, and never during the second half (Table 8). However, the high frequency of cases where the two groups did not differ in variance of body temperature suggests that this pattern be interpreted cautiously.

Table 6: Comparisons of the mean and variance of the pooled sample of body temperatures for the reproductive (R) and nonreproductive (NR) groups between 0400 and 1200.

The period has been divided into 2 h intervals, and the values tabulated are the frequencies of the specified outcomes for the 8 sample days for which there were at least 2 animals in each group.

		0400-0545	0600-0745	0800-0945	1000-1200
	R>NR	6	6	5	6
MEANS	NR>R	0	0	0	0
	R=NR	2	2	3	2
	R>NR	1	1	4	2
VAR.	NR>R	4	3	1	2
	R=NR	3	4	3	4

Table 7: Comparisons of the mean and variance of the pooled sample of body temperatures for the reproductive (R) and nonreproductive (NR) groups between 1200 and 2000.

The period has been divided into 2 h intervals, and the values tabulated are the frequencies of the specified outcomes for the 8 sample days for which there were at least 2 animals in each group.

		1200-1345	1400-1545	1600-1745	1800-2000
MEANS	R>NR	6	5	5	4
	NR>R	0	1	0	0
	R=NR	2	2	3	4
VAR.	R>NR	2	1	0	1
	NR>R	2	3	3	3
	R=NR	4	4	5	4

Table 8: Comparisons of the mean and variance of the pooled sample of body temperatures for the reproductive (R) and nonreproductive (NR) groups between 2000 and 0400.

The period has been divided into 2 h intervals, and the values tabulated are the frequencies of the specified outcomes for the 8 sample days for which there were at least 2 animals in each group.

		2000-2145	2200-2345	0000-0145	0200-0400
MEANS	R>NR	4	5	5	6
	NR>R	0	0	0	0
	R=NR	4	3	3	2
VAR.	R>NR	1	1	0	0
	NR>R	3	4	3	5
	R=NR	4	3	5	3

Individual Variation in Body Temperature

Although the snakes can be assigned unambiguously to either the reproductive or nonreproductive group, there are still observable differences between group members, suggesting that reproductive condition is not the sole determinant of body temperature. To determine whether the observed variability was significant, I performed one-way ANOVA's on each group (reproductive and nonreproductive) separately for each 8 h period where there were at least 2 animals in each group.

From the 8 sample days (three 8 h trials for each sample day) with enough animals, there were only 14 cases where there were no significant differences between the members of a group. Among the nonreproductive snakes there were only 6 cases out of 24 where the group members did not differ, and only 8 cases out of 24 among the reproductive snakes.

A lack of difference among animals in the same group, or between animals of different groups, may be the result of reduced opportunities to thermoregulate, such as during the night or on cloudy days. If this is the case, then body temperatures should be uniformly low in cases where there is no significant difference among group members. To test this I constructed a frequency distribution, in 5 C° intervals, of the mean body temperatures of animals from the 14 groups within which the members did not differ from one another. I then compared this distribution to that of the mean body temperatures of all other animals (Table 9). There was no significant difference ($\chi^2=2.101$, df=3, $p>0.05$), suggesting that a lack of difference between members of a group is not a function of temperature.

Table 9: The frequency distribution of the mean body temperatures of all snakes in groups where members did not differ significantly from each other compared with that for all other animals.

Mean body temperatures are placed in 5 C° intervals and only sample days for which there were at least 2 animals in each group are included.

	15.0-19.9°C	20.0-24.9°C	25.0-29.9°C	>30.0°C
Members of groups with N.S. differences	14	13	5	6
All others	34	29	25	15

Effect of Thermoregulatory Opportunity on Gestation Period

None of the gravid females in either enclosure gave birth before the end of the study (8 October 1986). However, one of the gravid females from the large thermoregulation enclosure appeared to be *post partum* when caught in the spring of 1987 (P.T. Gregory *pers. comm.*). This individual was noted to have the largest, and most developed, embryos of any of the gravid females at the time of release, at least as determined by external examination.

Abdominal palpation revealed that the gravid females in the shaded enclosure had exhibited little or no embryonic development during the summer. Both had only small, hard masses in their uteri by the end of the season. Females in the large thermoregulation enclosure seemed to fare somewhat better and had slightly more advanced embryos by the end of the season. However, one of these females aborted her embryos on 27 August 1986, suggesting that even among females presumed to be thermoregulating freely, conditions for development were poor. In addition, one female, captured at the winter den in fall 1986, contained apparently underveloped embryos, as determined by palpation, similar to those in gravid females in the thermoregulation enclosure, suggesting that conditions in the enclosure may have reflected those in the wild. If the effect of the July weather was as severe as suggested it is not surprising that none of the gravid females in captivity gave birth.

Parturition in the wild, as measured by the presence of neonates at the winter dens, may have been later in 1986 than in 1985. During the summer of 1986 I saw one neonate on 29 August and then another litter of five on 11 September. A single gravid female captured in mid-September did not give birth until 29

September. In contrast, parturition in late August, and early September, were common in 1985, and large numbers of neonates were present at the dens during the first week of September.

First-year Survivorship

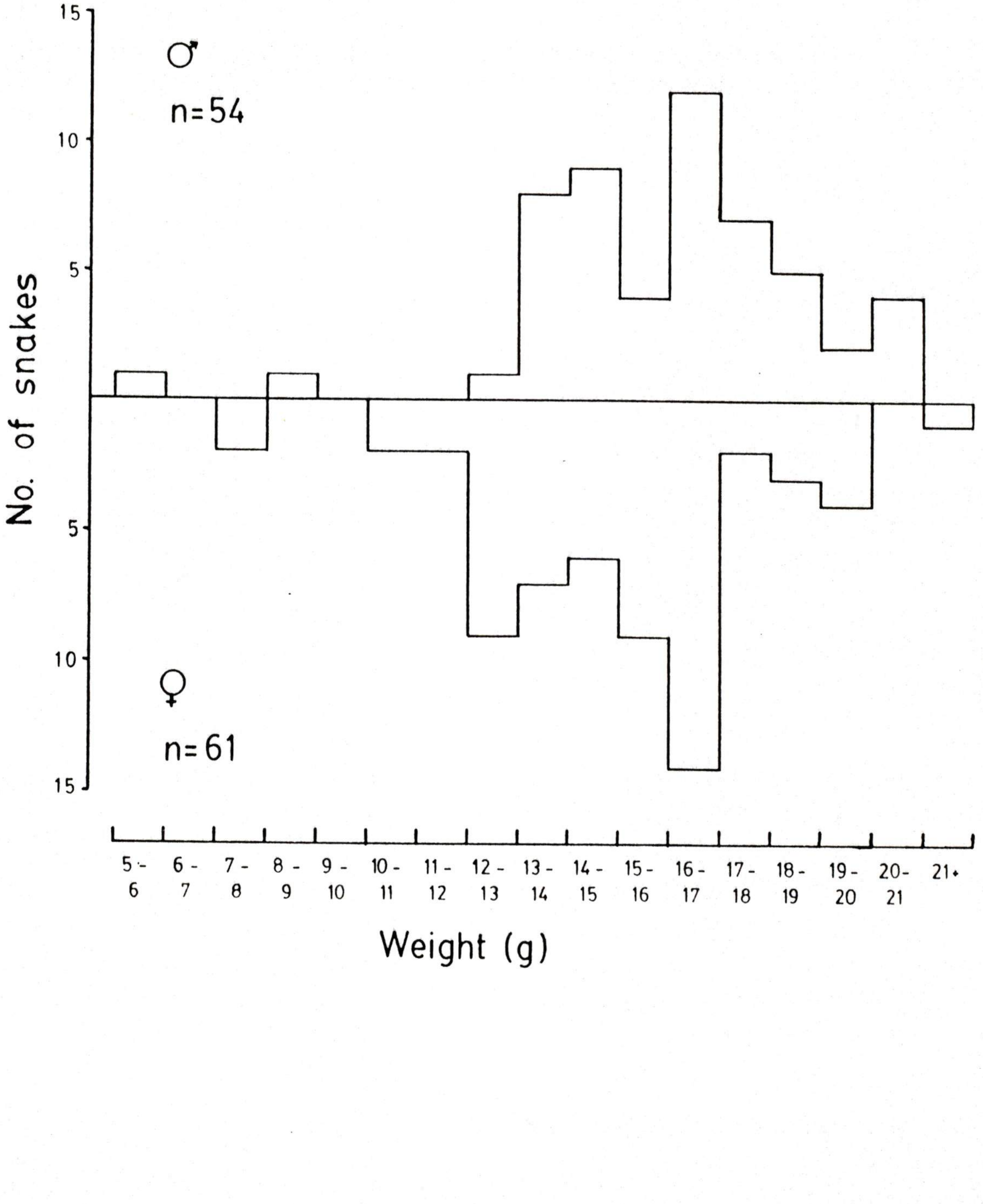
Original Sample

A total of 115 neonate *C. viridis* (54 males and 61 females) were collected between late August and late September 1985. Sixty-nine of these snakes (33 males and 36 females) were collected in the field at winter den sites. The remaining 46 (21 males and 25 females) were the offspring of nine gravid females which were held in the laboratory until parturition. Neonates were individually marked and maintained in the laboratory until the entire sample was collected. All were weighed on an analytical balance the day before their release.

Mean SVL of neonates was 284.1 ± 24.0 mm (range 195-325 mm) for males and 285.1 ± 21.3 mm (range 235-345 mm) for females. Mean SVL's at birth were not significantly different between sexes (t=0.254, df=113, $p>0.05$). The mean weight of newborn males was 15.98 ± 2.85 g (range 5.01-20.74 g) and was 14.92 ± 2.71 g (range 7.43-21.02 g) for females. There was a significant difference between the mean weights of the sexes (t=2.043, df=113, $p<0.05$). The distribution of the weights of the two sexes are shown in Fig 20.

A total of 59 neonates (24 male, 35 female)were released at den 8, while 56 neonates (30 male, 26 female) were released at den 9. The mean weight of males released at den 8 ($\bar{x}$=16.27 ± 2.06 g) and den 9 ($\bar{x}$=15.75 ± 3.40 g) were not significantly different (t'=0.698, df=48, $p>0.05$). The mean weight of females

Figure 20: Frequency distribution of the weights of male and female neonates at birth in fall 1985.


15
10
5
5
10
15
♂
n=54
♀
n=61
No. of snakes
5 - 6
6 - 7
7 - 8
8 - 9
9 - 10
10 - 11
11 - 12
12 - 13
13 - 14
14 - 15
15 - 16
16 - 17
17 - 18
18 - 19
19 - 20
20 - 21
21+
Weight (g)

released at den 8 ($\bar{x}=15.12 \pm 2.66$ g) and den 9 ($\bar{x}=14.64 \pm 2.80$ g) were not significantly different either ($t=0.68$, df=59, $p>0.05$).

Winter Survivorship

Neonates which survived the winter of 1985/1986 were captured between 17 April and 3 June 1986. These small snakes tended to emerge from small secondary entrances to the dens and avoided being trapped behind the fence. Although recapture success was almost certainly less than 100%, I recaptured a total of 59 neonates (29 male and 30 female) during this period. A further 3 females that survived the winter, but which were not seen in spring, were recaptured in the fall of 1986, bringing the total number of known survivors of winter 1985/86 to 62 or 53.91% of the original sample. Winter survivorship of males (53.70%) and females (54.10%) did not differ ($\chi^2=0.002$, df=1, $p>0.05$).

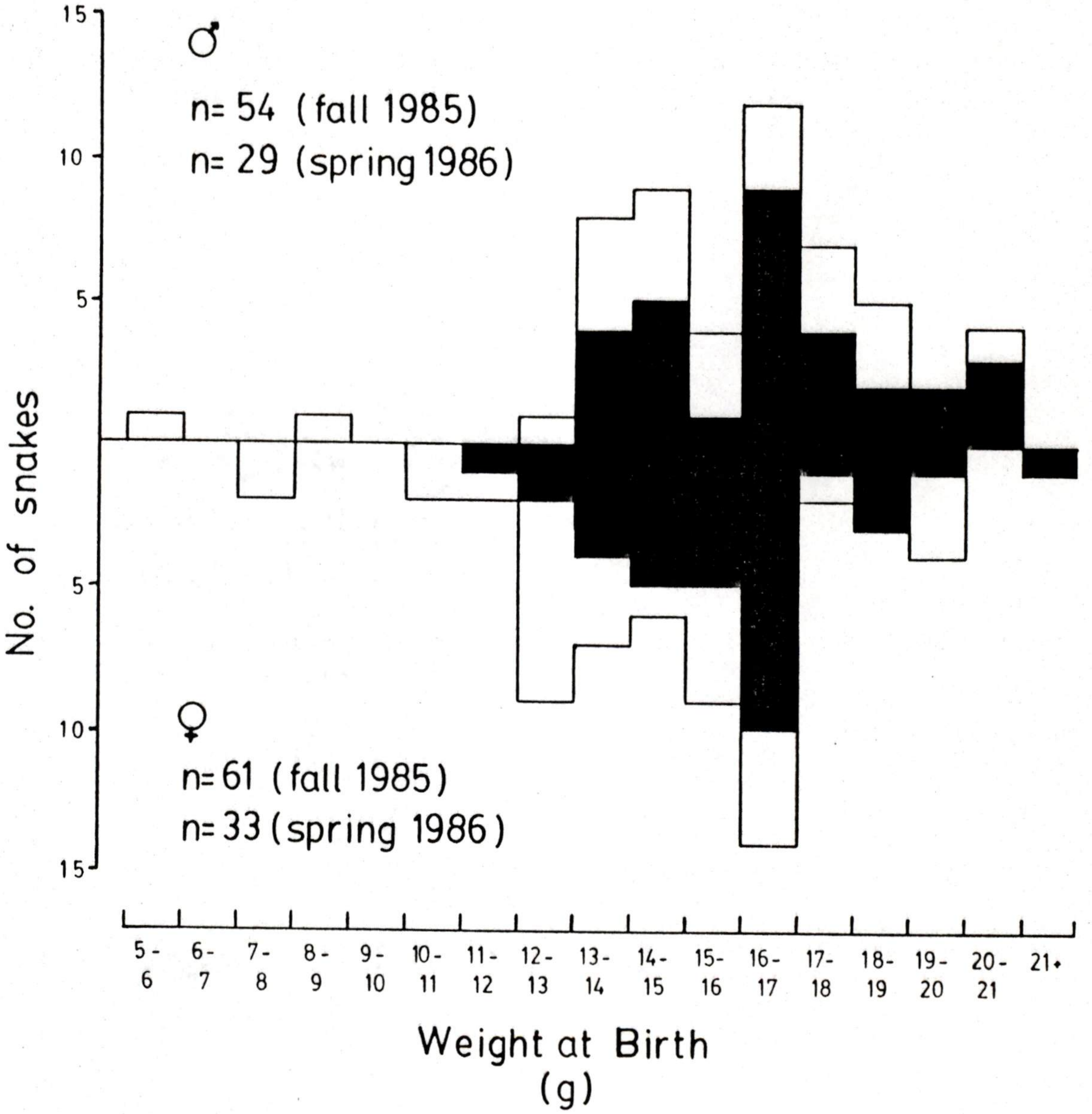
Effect of Size at Birth on Winter Survivorship

In order to determine whether or not size at birth had any influence on winter survivorship the weight at birth of each survivor was replotted on the original distribution of weight at birth (Fig. 21). The distributions were not significantly different for either males ($D=0.099$, $D_{0.05}=0.313$, $p>0.05$) or females ($D=0.155$, $D_{0.05}=0.293$, $p>0.05$), indicating that size at birth did not affect neonate survivorship during the winter of 1985/86, although extremely small individuals were never recaptured.

To this point I have used weight at birth as the sole measure of size at birth. However, body form may be of greater importance: a heavy neonate which is very long is actually thin, whereas a lighter neonate which is very short will be fat, and

Figure 21: Effect of size at birth on neonate survivorship during the winter of 1985/86.

The distribution of the weights at birth of survivors to spring 1986 (dark bars) is superimposed on the original distribution of weights at birth. The distribution of survivors includes 3 individuals recaptured in fall, but not spring, 1986.


15
10
5
5
10
15
No. of snakes
♂
n= 54 (fall 1985)
n= 29 (spring 1986)
♀
n= 61 (fall 1985)
n= 33 (spring 1986)
5-6
6-7
7-8
8-9
9-10
10-11
11-12
12-13
13-14
14-15
15-16
16-17
17-18
18-19
19-20
20-21
21+
Weight at Birth
(g)

perhaps have a survival advantage. Condition factors, which incorporate weight and length in a single measure, have long been used in fisheries research to assess the "condition" of animals of different sizes with respect to one another (Ricker 1975). The relationship between weight and length is usually best described by the power function $\mathrm{WEIGHT}=a(\mathrm{LENGTH})^b$. Condition factor can then be calculated as $\mathrm{WEIGHT}/\mathrm{LENGTH}^b$ (Ricker 1975).

The weight-length relationships for males and females at birth are shown in Fig. 22. In both cases simple linear correlations are significant (r=0.593, n=54, $p<0.001$ for males; r=0.648, n=61, $p<0.001$ for females). However, log-transformation of the data produced even stronger correlations (r=0.693, n=54, $p<0.001$ for males; r=0.658, n=61, $p<0.001$ for females), indicating that the relationship between weight and length is better described by a power function in this case.

Linear regression of the log-transformed data yielded b-values of 1.729 for males and 1.753 for females. These values were significantly different (t=-2.84, df=111, $p<0.01$) and so condition factors for each sex were calculated as $\mathrm{WEIGHT}/\mathrm{SVL}^{1.729}$ for males and $\mathrm{WEIGHT}/\mathrm{SVL}^{1.753}$ for females.

The distribution of condition factors at birth for survivors in spring 1986 was superimposed on the original distribution of condition factor at birth for the entire sample of neonates (Fig. 23). There was no significant difference between the original and survivor distributions for either males (D=0.073, $D_{0.05}$=0.313, $p>0.05$) or females (D=0.085, $D_{0.05}$=0.293, $p>0.05$), again indicating no effect of size at birth on survivorship during the winter of 1985/1986. It is interesting to note, however, that the original distributions of condition factors at birth of males and

Figure 22: Weight-length relationships for male and female neonates born in fall 1985.

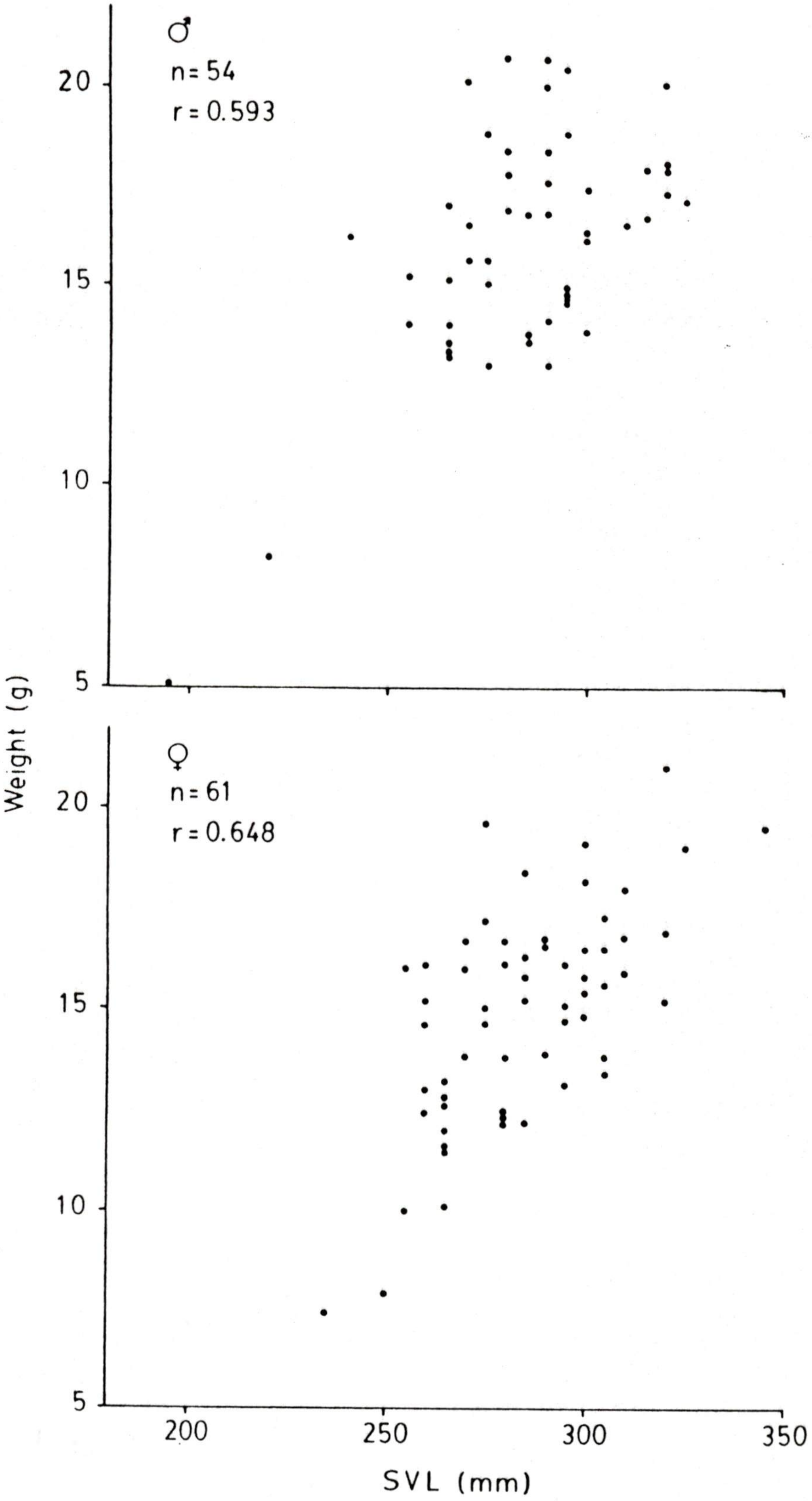
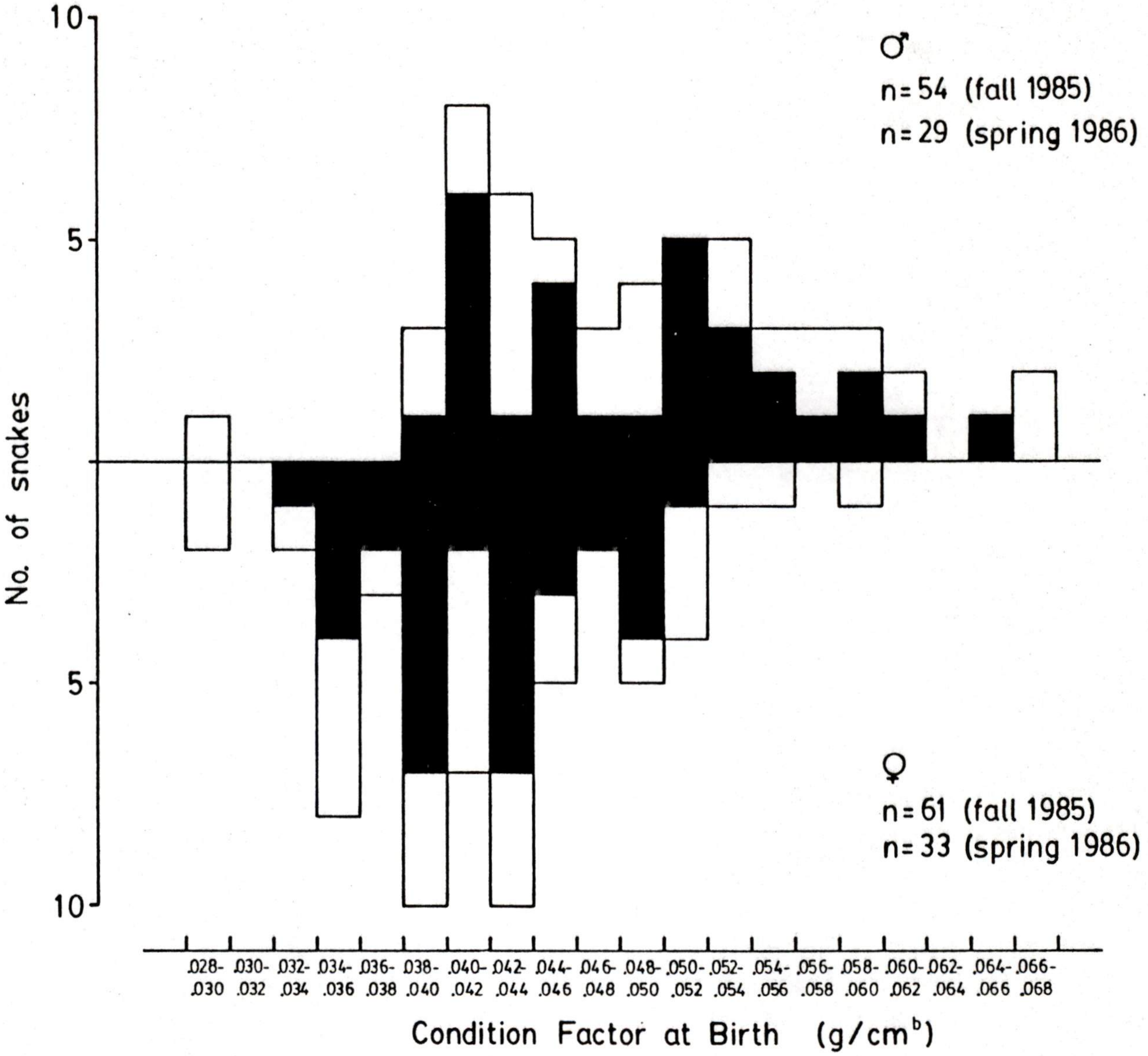

♂
n = 54
r = 0.593
♀
n = 61
r = 0.648
Weight (g)
5
10
15
20
200
250
300
350
SVL (mm)

Figure 23: Effect of condition factor on winter survivorship.

The distribution of condition factors at birth of the survivors to spring 1986 (dark bars) is superimposed on the distribution for the entire sample collected in the fall of 1985. Note that the b-values for males and females are different (b=1.729 for males, b=1.753 for females).


10
5
5
10
No. of snakes
♂
n= 54 (fall 1985)
n= 29 (spring 1986)
♀
n= 61 (fall 1985)
n= 33 (spring 1986)
.028-.030
.030-.032
.032-.034
.034-.036
.036-.038
.038-.040
.040-.042
.042-.044
.044-.046
.046-.048
.048-.050
.050-.052
.052-.054
.054-.056
.056-.058
.058-.060
.060-.062
.062-.064
.064-.066
.066-.068
Condition Factor at Birth (g/cm^b)

females were significantly different ($D=0.356$, $D_{0.01}=0.304$, $p<0.01$) with the females having lower condition factors than the males.

Whether size was defined as weight at birth or condition factor at birth there did not appear to be any effect on survivorship during hibernation. Since condition factor was highly correlated with weight in both males ($r=0.720$, $n=54$, $p=0.0001$) and females ($r=0.716$, $n=61$, $p=0.0001$), but not with either SVL (males: $r=-0.110$, $n=54$, $p>0.05$; females: $r=-0.060$, $n=61$, $p>0.05$) or SVL^b (males: $r=-0.140$, $n=54$, $p>0.05$; females: $r=-0.060$, $n=61$, $p>0.05$), I felt justified in using weight as the measure of size in the subsequent analyses.

Although size at birth did not seem to affect survivorship over the winter of 1985/1986, it is possible that the winter was in some way benign and not representative of the general pattern of survivorship among neonates. To look for nonlethal size effects I plotted winter weight loss against weight at birth for both sexes combined (Fig. 24) to see if larger individuals were less likely to lose weight and hence potentially able to stay in hibernation longer than small individuals. The relationship was significant ($r=-0.310$, $n=59$, $p<0.05$), but negative, indicating that larger neonates lost proportionally more weight than smaller ones. Mean weight loss was 6.75 ± 5.52% for the entire sample of survivors. Weight loss of males averaged 6.36 ± 5.71% while females lost 7.12 ± 5.40% on average, a difference which was not significant ($t=0.526$, $df=57$, $p>0.05$).

Since weight loss was correlated with size at birth, it is possible that the lack of size dependent survivorship may have been the result of a physical response by the neonates. Perhaps individuals that had lost a lot of weight emerged from the den earlier and hence avoided lethal weight loss in the den. A plot of weight loss against date of emergence (Fig. 25) shows no such pattern ($r=0.049$, $n=59$, $p>0.05$).

Figure 24: The effect of size at birth on winter weight loss for both dens combined. Change in body weight is the per cent of weight at birth.

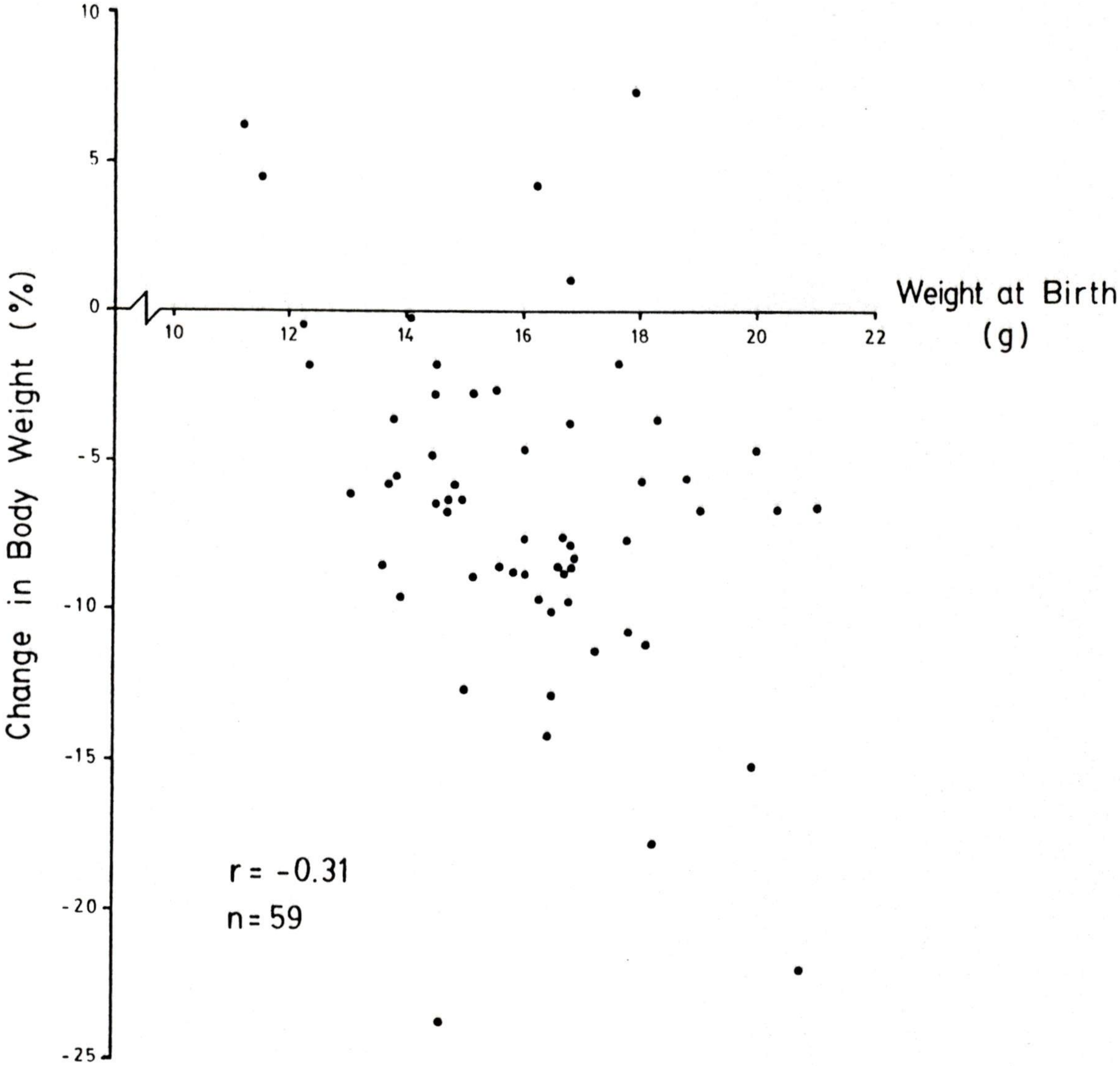
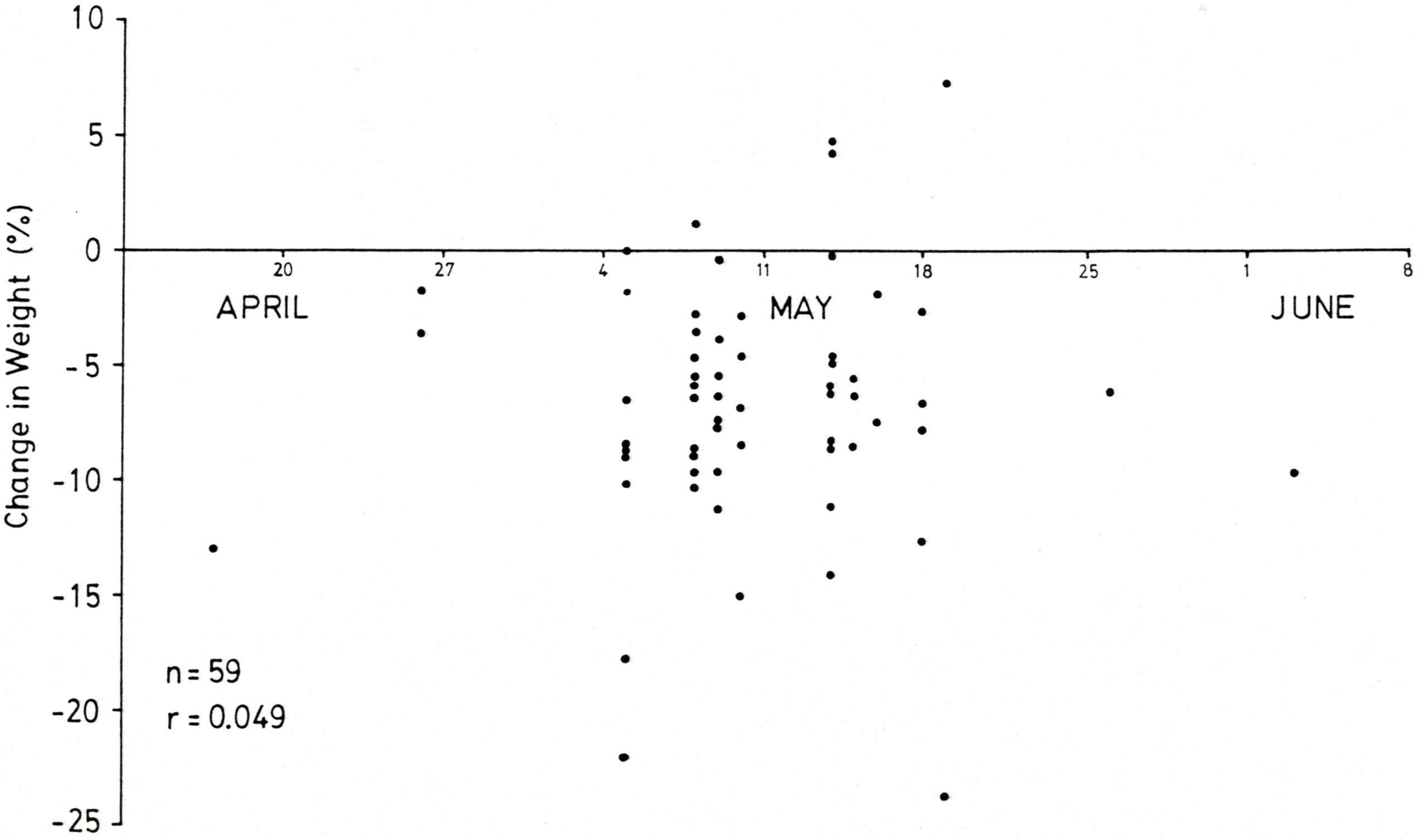

10
5
0
-5
-10
-15
-20
-25
Change in Body Weight (%)
10
12
14
16
18
20
22
Weight at Birth (g)
r = -0.31
n = 59

Figure 25: Relationship between weight loss and date of emergence for both dens combined.

Date of emergence was converted to Julian date in order to calculate the correlation coefficient.


Change in Weight (%)
10
5
0
-5
-10
-15
-20
-25
20
27
4
11
18
25
1
8
APRIL
MAY
JUNE
n = 59
r = 0.049

Inter-den Comparisons

Survivorship at dens 8 (54.24%) and 9 (53.57%) did not differ significantly ($\chi^2=0.005$, df=1, $p>0.05$), and neither appeared to differ from the overall survivorship value of 53.91%. Mean weight loss in den 8 was 8.52 ± 4.67%, whereas neonates in den 9 lost an average of only 4.92 ± 5.80%, a difference which was highly significant ($t=-2.631$, df=57, $p<0.005$).

In addition to the difference in mean weight loss the two dens exhibited a difference in the pattern of weight loss. The slight but significant negative correlation between weight loss and weight at birth seen in the total sample of survivors is actually the result of a strong negative correlation for neonates at den 8 ($r=-0.636$, n=30, $p<0.05$; Fig 26). There was no significant correlation at den 9 ($r=-0.100$, n=29, $p>0.05$; Fig 27) and, in fact, four individuals at this den gained weight over the winter, presumably due to water uptake. This assumption receives some support from the observation that more than half of the surviving neonates gained weight from the time of emergence and capture in spring to the their release on 22 May, 1986. These animals were held without food (except as noted in the next section), but were provided with water *ad libitum*.

Given the difference in weight loss between the two dens there is the possibility that a lack of difference in survivorship might have been due to earlier emergence of neonates from den 8, allowing them to avoid lethal weight losses in the den. The patterns of neonate emergence from the two dens (Fig. 28) were not different (Kolmogorov-Smirnov 2-Sample test; $D=0.264$, $D_{0.05}=0.354$, $p>0.05$), suggesting that timing of emergence was not reflected in differences in weight loss between the two dens.

Figure 26: Winter weight loss as a function of size at birth for neonates hibernating at den 8.

Per cent weight change is calculated as per cent of weight at birth.

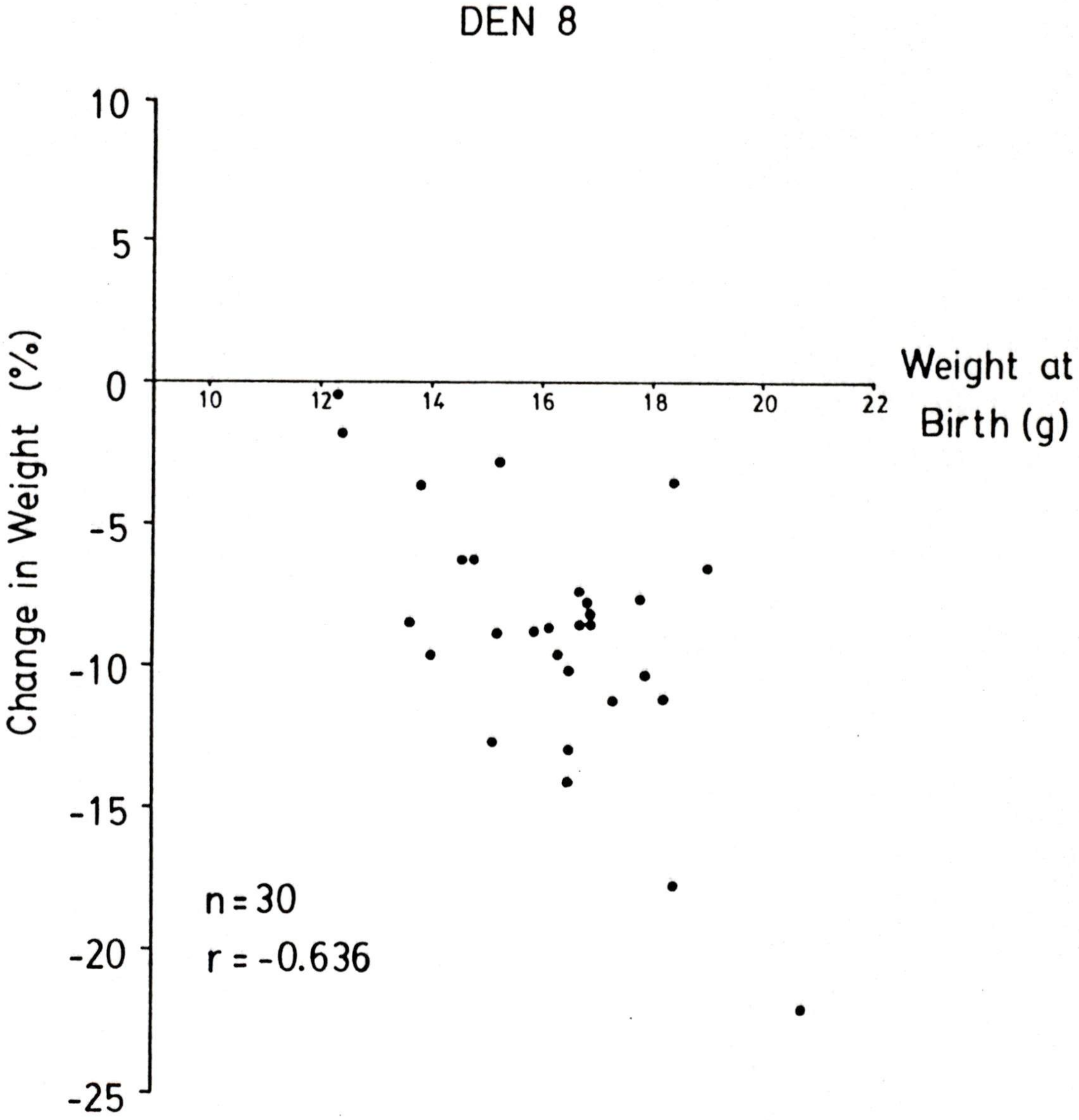

DEN 8
Change in Weight (%)
10
5
0
-5
-10
-15
-20
-25
10
12
14
16
18
20
22
Weight at Birth (g)
n = 30
r = -0.636

Figure 27: Winter weight loss as a function of size at birth for neonates hibernating at den 9.

Per cent weight change is calculated as per cent of weight at birth.

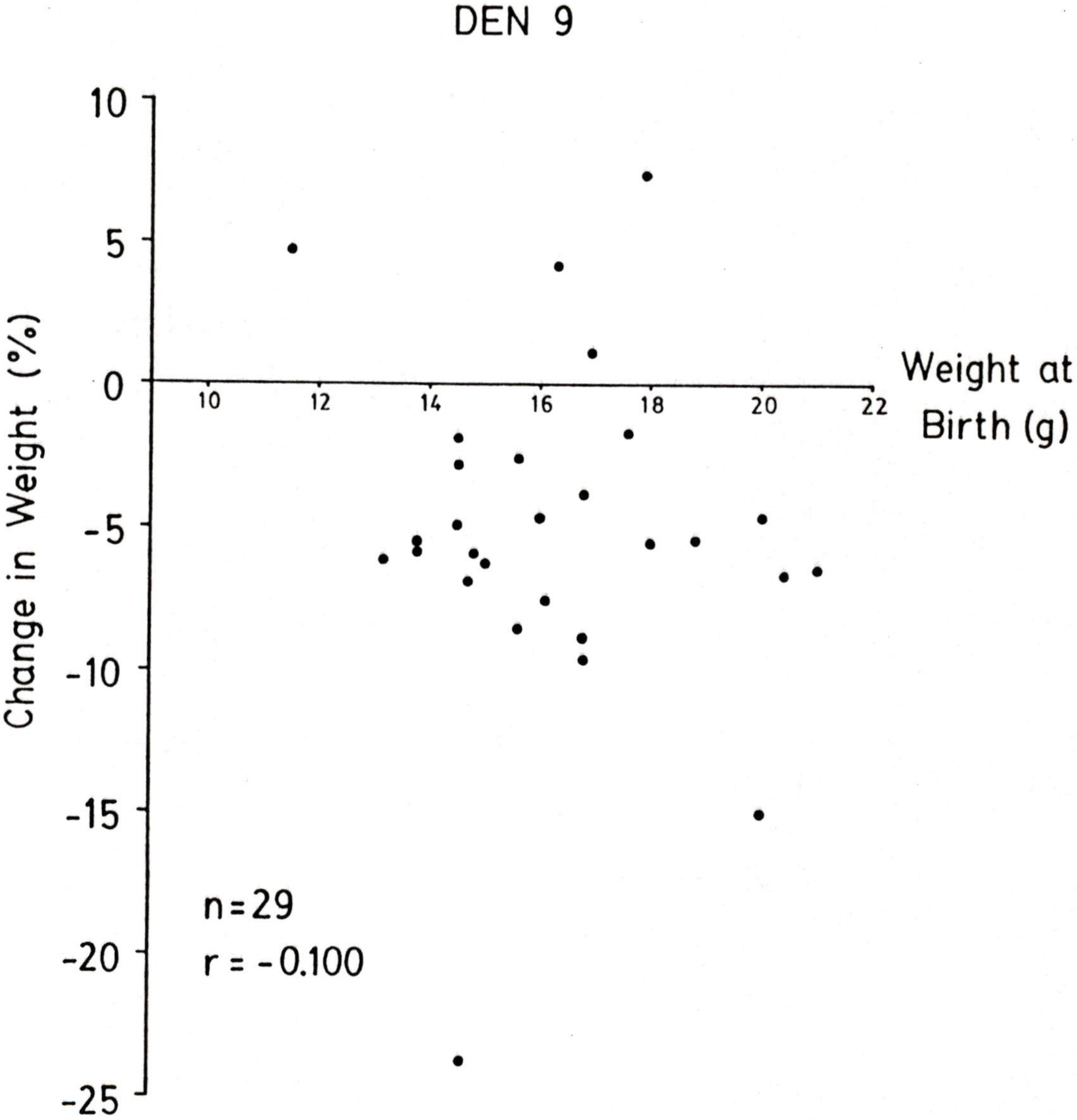
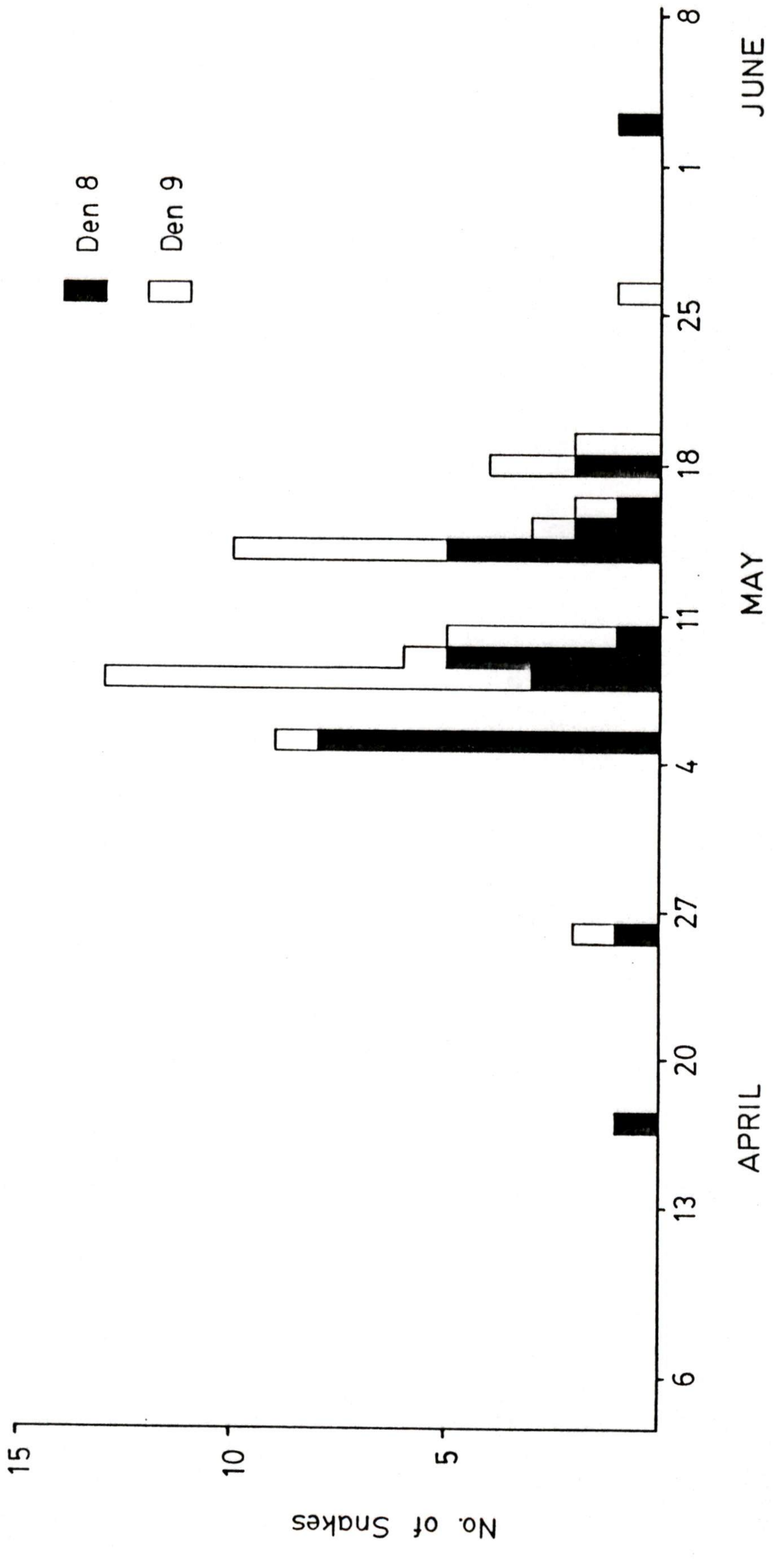

DEN 9
Change in Weight (%)
10
5
0
-5
-10
-15
-20
-25
Weight at Birth (g)
10
12
14
16
18
20
22
n=29
r = -0.100

Figure 28: Patterns of emergence of neonates from dens 8 and 9.

Frequency distribution of the timing of emergence of neonates from dens 8 and 9. The bars for the two dens are not overlain, but stand one on top of the other.


No. of Snakes
15
10
5
6
13
20
27
4
11
18
25
1
8
APRIL
MAY
JUNE
■ Den 8
□ Den 9

Supplemental Feeding and Summer Survivorship

The mean weight at capture of all neonates that were fed was 14.68 ± 1.85 g, while the mean weight for all neonates not fed was 15.19 ± 2.03 g. This difference was not significant (t=-1.12, df=71, p>0.05). The numbers of neonates in each treatment and from each den are shown in Table 10. Of the 59 VL20 neonates recaptured during spring 1986 three died in captivity before being included in the feeding experiment and one that was fed died before release. None of these animals are included in the totals used in this section.

Recapture success in fall 1986 was very low, with only 3 of the original 73 neonates from spring 1986 being found. An additional 3 VL20 individuals which survived the previous winter but were missed during the spring emergence were recaptured at this time. These animals can be considered members of the group which did not receive supplemental food, and minimum summer survivorship can be estimated as 6 out of 76, or 7.89%. This is almost certainly an underestimate. One of the neonates was initially released at den 9 and was recaptured at den 8 at the end of the summer. In addition, the number of unmarked 1-year old snakes seen at dens 8 and 9 (11) during fall 1986 suggests that den switching may have been occurring. Snakes of all sizes were frequently found inside the fences in the fall and it appeared that they had little trouble entering the dens, suggesting that some snakes may have entered before I could capture them, again leading to an underestimate of summer survivorship.

A summary of the information obtained from the neonates recaptured in fall 1986 is shown in Table 11. These data clearly show the tremendous variablity in length and weight changes that neonates may experience during their first

Table 10: Distribution of individuals by sex and by treatment for the supplemental feeding experiment.

Neonates caught for the first time at dens 8 and 9 during spring 1986 are included here.

	DEN 8			DEN9		
	FED	NOT FED	TOTAL	FED	NOT FED	TOTAL
MALE	7	6	13	9	7	16
FEMALE	12	16	28	10	6	16
TOTAL	19	22	41	19	13	32

TOTAL FED = 38
TOTAL NOT FED = 35

Table 11: Summary of weight and SVL changes for neonates recaptured in the fall of 1986.

MARK	SEX	DEN	SVL AT BIRTH (mm)	WEIGHT AT BIRTH (g)	WEIGHT AT EMERGENCE (g)	SUPPL. FEEDING	SUMMER SVL CHANGE (%)	SUMMER WEIGHT CHANGE (%)	TOTAL WEIGHT CHANGE (%)
VL20VL2R3L10	F	9	320	21.02	19.68	YES	4.69	-4.47	-10.56
VL20VL11R3L9	M	9	295	20.38	19.04	NO	13.56	8.40	1.28
VL9R4L11 *	F	9			13.38	YES	8.33	29.67	
VL20VL8R5L7 **	F	8	280	16.56			5.36		-18.66
VL20VL15R4L3 **	F	8	290	13.88			24.14		101.15
VL20VL15R4L5 **	F	9	305	13.36			11.48		34.96

* Individual caught during spring emergence 1986, and used in feeding study. Growth during hibernation is assumed to be 0, therefore change in SVL during summer represents growth from birth.

** These three individuals were recaptured in fall 1986, but not at the spring emergence of 1986.

summer, although the small number of animals makes it impossible to determine the effect of early feeding on summer survivorship.

In the fall of 1986 I captured two first-year snakes which had fed recently. Both animals had consumed near-adult mice. In one animal, ingestion had occurred so recently, and the mouse was so large, that it was possible to see the outline of the mouse's front legs through the snake's skin. The mouse measured 9 cm from nose to base of tail, as measured while still inside the snake. Neither snake was exceptionally large for a one-year old (SVL's were 350 and 375 mm), and it is obvious that juvenile *C. viridis* may take immense prey if given the opportunity.

DISCUSSION

The term "life history" is a rather general one used to refer to numerous aspects of an organism's life cycle, including the breeding system, timing and frequency of reproductive events, reproductive behavior, mortality, *etc.* (Allen and Canning 1985). Life history has been traditionally the domain of natural history, and much of the older literature is descriptive in nature (Allen and Canning 1985). This descriptive work provides the necessary material for the formulation of hypotheses concerning life history evolution (Greene 1986). However, experimental tests of these hypotheses have lagged behind their construction. Laboratory experiments concerning life history evolution have a number of drawbacks associated with them. It is difficult to assess how similar (or different) conditions in the laboratory are from those in the field, and how suitable the controls imposed. In field experiments, conducted under natural or semi-natural conditions, the main difficulty is implementing any type of control at all. However, an approach which combines laboratory and field experiments is proving both useful and powerful (Arnold 1986).

I consider my work to be a hybrid between experimental tests of hypotheses in the field and descriptive studies which provide data for the refining of such hypotheses. In many areas of snake ecology descriptive data needed to frame explicit hypotheses are sorely lacking. The work presented here represents a first attempt to address some of these hypotheses. Unfortunately, I have been unable to obtain clear answers to the questions posed, and the data set, in retrospect, is more limited, in kind if not size, than I had hoped it would be. Nonetheless, I feel that this study has been very successful in exposing weaknesses in either the techniques used or in the underlying assumptions that will be of immense value in designing future studies of this type.

Female Reproductive Cycles

The preliminary study of the effect of feeding rate on weight gain in *post partum* females, in 1985, was unsatisfactory for a number of reasons. Live trapping rodents proved to be particularly difficult, and success was sporadic. For this reason, the animals in the two enclosures probably did not receive substantially different amounts of food during the study. In addition, housing all of the animals at a particular feeding level in the same enclosure made it impossible to determine the feeding rates of individuals. The weight changes recorded over the summer of 1985 show that one animal in an enclosure typically gained weight while the others declined. Presumably, one animal during any feeding period ate most of the available food, while the others went without.

Because none of the females in either enclosure showed any substantial weight gain, it is not surprising that the females in enclosure A did not mate when they had access to a male. In B.C., *C. viridis* mate in August and early September (Macartney 1985); however, the male used was not captured until late August, near the end of the mating period, and may not have been inclined to mate. In addition, the male started ecdysis almost immediately after being placed in enclosure A, and, again, may not have been inclined to mate at that time.

During the summer of 1986, snakes in the HFR group had access to food at high rates and yet failed to gain weight at a rate different from LFR snakes. In a 5 yr study of *Vipera* living in a large outdoor enclosure, Saint Girons (1979) found that *post partum* females ate prey totalling 276% of their body weight during the summer. The mice that were fed to the snakes in this study weighed approximately 30 g, so snakes in the HFR group appeared to be feeding at a rate similar to that reported for *Vipera*. The lack of a difference in mean weight between the two groups may have been due to the conditions of captivity. Brett (1971) found that when food is abundant salmon grow fastest at high body temperatures; however, if food is scarce optimal growth is achieved by maintaining a low body temperature. When food is abundant the fish maintain a high metabolic rate (by means of a high body temperature) and thus grow quickly. A high metabolic rate, while speeding growth, requires more energy for body maintenance than a low metabolic rate and, if food is scarce, may leave little energy for somatic growth. However, maintenance of a lower body temperature, which minimizes metabolic expenditure, will allow for maximum growth when food availability is low. Whether optimal growth under both conditions results in similar absolute growth (either weight or length) has not been demonstrated.

If this relationship is also true in reptiles, as suggested by Huey (1982), then restricting thermoregulation of animals in enclosures could have a profound effect. All of the enclosures received sunlight for most of the day, but because of the limited amount of cover in each enclosure night-time body temperatures may well have been lower than those selected by free-ranging snakes. However, if the snakes in the two groups were able to thermoregulate at different levels appropriate to their food intake, then differences in weight gain would be minimized. The importance of thermoregulation to feeding snakes is supported by Saint Girons (1975) who found elevated body temperatures, immediately following feeding, in four species of *Vipera* studied in large outdoor enclosures. Clearly, a comparison of the body temperatures of LFR and HFR snakes during the day and night, would be necessary to address this question properly.

There was a considerable period of time between capture and placement in the outdoor enclosures for many of the snakes, and virtually all animals lost weight during this time. In the wild, most feeding takes place from June to mid-August (Macartney 1985) and the delay in starting the study may not have been critical. However, there is no information on normal weight changes of *post partum* females immediately after emergence from hibernation and before the onset of summer feeding for comparison. In addition, not all of the animals had access to standing water while they were in the laboratory, and much of the weight loss was likely due to loss of body water. However, rattlesnakes are known to drink standing water rarely, and instead gain much, or all, of the water they require from the prey that they eat (Klauber 1972, Stark 1984).

During the summer, animals in the enclosures did not have access to standing water, allowing me to measure weight gain due to feeding without the confounding influence of weight gain as a result of drinking. However, the snakes received water, in the form of rainfall, on 40% of the days of the study, and patterns of weight change probably do not reflect a lack of available water. When dehydrated, snakes frequently have difficulty in ecdysis (Klauber 1972). The snakes in the enclosures displayed the same pattern of shedding as for nongravid females in the wild, with a peak in early August (Macartney 1985), and showed no apparent difficulty during this process.

Another curious result of this study was that LFR snakes clearly passed up opportunities to feed later in the summer when only about one-third of the animals accepted food any time it was offered. Willingness to feed in snakes is also temperature dependent in that they are less likely to feed at lower temperatures (*e.g.*Greenwald 1974). However, the HFR and LFR snakes were under apparently identical conditions and HFR snakes were eating once a week on average. Thus, LFR snakes would be expected to eat when offered food every second week. It is possible that, as a consequence of low food availability, LFR snakes actively selected lower body temperatures than HFR snakes, in order to lower their metabolic rates and conserve energy, until such time as access to food was increased. This tactic has been shown for the toad, *Bufo boreas* (Lillywhite *et al.* 1973), and probably functions to limit energy losses during times of low food availability. Davies *et al.* (1980) suggest a similar phenomenon in snakes, and selection of lower body temperatures could reduce the willingness to feed. Again, comparisons of the body temperatures of LFR and HFR snakes are required to address this question properly.

Both the LFR and HFR groups showed weight losses beginning in July, which continued to the end of the study. This decline corresponded with the onset of an exceptionally cool, wet July, and continued through August which was, in contrast, hot and dry. Digestion and assimilation of food are temperature dependent processes in ectotherms, and the low temperatures and generally poor weather during July may have had a marked effect, although feeding rates remained constant.

Growth in length showed a high degree of variability among individuals which must, at least in part, account for the lack of correlation between any measure of growth in length, initial size, and number of meals eaten. The lone exception was a significant positive correlation between change in condition factor and number of meals eaten among HFR snakes. However, this should be interpreted cautiously. Maximum weights, and hence probably condition factors, occurred at the beginning of July, while the changes in condition factor reported are net changes over the entire summer, and do not reflect weekly variations in condition factor during the summer. In addition, sample sizes are small, and the changes in condition factor are tiny and of uncertain biological importance.

Macartney (1985) stated that *post partum* females in this population must double their body weight during the summer following parturition in order to mate in the fall and produce young the following year. Clearly, none of the animals in either the LFR or HFR groups achieved this, and it is not surprising that there was no evidence of mating once males were introduced into the enclosures. Female garter snakes (*Thamnophis*) appear to be particularly attractive to males immediately after shedding (Kubie *et al.* 1978) and the situation may be similar for rattlesnakes (Macartney 1985). The probability of mating (particularly for the largest females) might have been greater if the male could have been presented while the female was undergoing ecdysis. Unfortunately, it proved difficult to acquire males from their summer range at the end of July because of the amount of time required by the thermoregulation study. Hence, all males were introduced into the enclosures in late August after the females had shed their skins.

A fundamental weakness of this study was the lack of replication in more than one year. The apparent relationship between poor summer weather and its effect on feeding and weight gain would be strengthened if it could be demonstrated that significant growth occurs at high feeding rate in years with good summer weather, but not in years with poor summers. Conditions in the enclosures may be sufficiently artificial that the snakes would not mate regardless of physiological condition. It may be necessary to uncouple the questions of foraging success and mating, and approach them in separate ways. The effects of feeding and environment, on weight gain can be addressed as discussed above, while the relationship between weight gain and mating would require a different method. *Post partum* females collected in the field in spring could be maintained under rigorously controlled conditions in the laboratory, and divided into a high and low feeding group. The animals in the high feeding group could be carefully force fed to ensure that they increased their weights to the desired level. In early or mid-July, before the beginning of the mating season, the females could be released at their winter dens and allowed to disperse naturally over the summer range. In this way mating would be allowed to occur under natural conditions, and success in mating could be determined through recaptures at the winter dens over the next two years. Females with enlarged follicles, either in fall or the next spring, would be presumed to have mated. Females recaptured gravid during the summer and fall, one year after the start of the experiment, clearly would have mated, and females which were *post partum* in the fall or spring (1.5 to 2 years after the start of the study) must also have mated immediately following their initial release. Recaptures are unlikely to provide complete recovery of all snakes used in the study, but this design, used in a number of years, and with large enough samples, probably offers the best method of examining, in detail, the link between female reproductive cycles and weight gain following parturition.

Although I failed to demonstrate a correlation between increased food availability and reproduction in *C. viridis* in this study, the results did provide circumstantial evidence for the complex interaction among food availability, intake, and weight gain. Considerable annual variation occurs in a number of aspects of reproduction in snakes, such as clutch or litter size, suggesting that studies of reproduction based only on a few years' data be interpreted with great caution (Andrén and Nilson 1982, Seigel and Fitch 1985, Seigel *et al.* 1986). The amount of variation in clutch size observed among years for four species of snakes was greater than that observed among sites, suggesting either that there is tremendous variation in reproduction inherent among individuals of the same population, or that environmental influences on snakes in the same population are far from homogeneous (Seigel and Fitch 1985). Studies of individual variation in reproductive parameters among snakes in the same population, along with careful study of the extent to which these same animals are able to respond to changes in their environment, are required to determine whether the observed patterns of reproduction themselves represent adaptations to the local environment, or whether the adaptation is the phenotypic plasticity required to respond to an unpredictable environment.

Temperature Relationships

Reptiles regulate their body temperature by a number of behavioral and physiological means, and many studies have attempted to assess the limits and ecological significance of reptilian thermoregulation (see reviews by Avery 1982, Huey 1982, Lillywhite 1987). However, Heath (1964), in an experiment in which the temperature of beer cans full of water varied over a day in a manner similar to that reported for many putatively thermoregulating heliothermic lizards, showed that accurate determination of the temperatures actually available to an animal was vital to any demonstration of thermoregulation. In response to this, body temperature measurements for reptiles are commonly accompanied by a variety of air and substrate temperatures (*e.g.* Huey 1974, Gibson and Falls 1979, Gregory 1984) in an attempt to provide some measure of available environmental temperatures. Despite this, a problem remains in that an ectotherm's body temperature must be a function of the interaction of a variety of environmental factors. Air temperature, solar radiation, convective heating, substrate composition and temperature, and wind all contribute simultaneously to an animal's body temperature, but vary temporally and/or spatially. In addition, the physical characteristics of the animal (reflectance/absorptivity, body composition) also contribute to its body temperature. Measurement of one, or a few, of these variables is insufficient to assess accurately the body temperatures available to a snake in a particular time and place. Bakken *et al.*(1985) suggest that a resolution is provided by the use of taxidermic mounts or models which heat and cool at the same rate as the organism under study. Such models can provide a single value that expresses the complex interaction of all environmental variables influencing body temperature at a given time. Differences between snake and model temperatures should demonstrate the degree to which the snake is controlling its own body temperature independently of environmental temperatures, through either behavior or physiology. If snake and model temperatures do not differ, then the animal's body temperature may simply reflect the combined effect of all environmental heat sources and sinks. It is possible, however, that the snake is thermoregulating to maintain its body temperature at that level and, in such cases, models would be of no value in determining whether thermoregulation is actually occurring. Although limited in some respects, the use of thermal models appears to be a promising avenue of research and the application of this approach to studies of thermoregulation in snakes is just beginning (Peterson 1987).

In order to be effective any proposed model must, in some sense, be a thermoconformer and provide a measure of the body temperatures available to a snake in the local environment. However, thermoconformity can be defined on a number of levels, each of which may be suitable to studying a particular facet of thermoregulation, and each of which has its own advantages and disadvantages. For studies of physiological thermoregulation, an ideal model would eliminate the influence of behavior on body temperature. If behavioral thermoregulation is of interest then models can be matched to the body temperature of a live, anesthetized snake, which is not thermoregulating behaviorally, but which presumably has its physiological responses intact. Because of the difficulty of obtaining information on how the snakes were behaving in the enclosure, my study did not differentiate between behavioral and physiological thermoregulation, and my models were constructed to match the heating and cooling characteristics of a dead snake. Models of this type possess the important physical characteristics of heat transfer of rattlesnakes, without the biological ones.

Peterson (1987) used straight, hollow models made of copper tubing and tested them against anesthetized garter snakes in a fashion similar to my short-term trials. In the construction of the models, Peterson (1987) carefully matched the reflectance of the paint he used on the models with that of the skin of his garter snakes. Although my technique of direct comparison between model and snake was simpler, the results of the short-term trials show agreement between the temperature of the snake and model similar to those presented by Peterson (1987). The inner tube models did not appear to be any less accurate than the copper tube models, but were both simpler and cheaper to construct, resulting in models which were more flexible, both physically and experimentally.

A comparison of the results of the short and long-term model trials suggests drawbacks associated with using the former method exclusively, as Peterson (1987) did. The model which was least like the snake in both short-term trials was the most similar under the more natural conditions of the long-term trials. Thus, Peterson's (1987) models might have been less accurate than suggested. The models I constructed were quite accurate below 40°C, but less so above, either underestimating (coiled model) or overestimating (straight model) the snake's body temperature. In spite of this, the models were accurate enough to indicate times when the environmental temperatures were high enough to restrict activity by the snakes as well as provide useful comparative data when environmental temperatures were in the snakes' normal activity range.

The common pattern of thermoregulation for individuals in this study was the same as the "plateau" pattern described by Peterson (1987). In the morning, body temperatures were low until direct sunshine struck the enclosure, at which time body temperatures increased rapidly until they levelled off and became relatively stable, between 30-35°C. Precision of thermoregulation during the plateau phase was relatively high, and was similar to that reported for free ranging garter snakes (Peterson 1987), and for 12 species of African lizards studied in enclosures (Bowker 1984). The stable plateau lasted throughout the afternoon until the sun began to set and body temperatures slowly began to drop. This slow cooling continued through the night and early morning until sunrise. This general pattern of thermoregulation is common among heliothermic species of both snakes and lizards (*e.g.* DeWitt 1967, Osgood 1970, Huey 1974, Hammerson 1977, 1979). However, some snakes are not heliothermic or do not show such a pronounced daily pattern (*e.g. Boa constrictor*, McGinnis and Moore 1969; *Agkistrodon contortrix*, Sanders and Jacob 1981).

Peterson (1987) observed the plateau pattern whenever environmental temperatures (as measured by thermoconforming models) exceeded 30°C. If the model temperature remained between 15 and 30°C he observed what he termed an oscillating pattern in which snakes were unable to maintain a constant, high body temperature and instead experienced variable daytime body temperatures. On the one day of this study during which the available environmental temperatures in the daytime were lower than 30°C (See Results: Daily Pattern of Body Temperature Variation), the body temperatures of the snakes closely followed the temperature of a coiled model in an exposed location within the enclosure. Body temperatures were approximately 25 °C at their highest and were not subject to extreme variation as were the body temperatures of garter snakes in the "oscillating" pattern. Rather, they rose to a peak and then fell again slowly, creating a smooth arc. In B.C., *C. viridis* is apparently heliothermic throughout the active season and displays a typical triphasic pattern of body temperature variation when environmental temperatures are high. Rattlesnakes are large bodied snakes, and the animals used in my study were relatively large individuals. It is possible that their large size buffers them to some extent from changes in body temperature, and studies of small animals are needed to determine whether the patterns observed here are typical of the species or simply a function of size.

The most commonly cited proximate benefit of viviparity in reptiles is that gravid females can speed embryonic development through thermoregulation, and partially counteract the effects of a shortened active season (Shine 1983, 1985). From this hypothesis it has been predicted that gravid females should prefer higher and/or less variable body temperatures than nongravid females and males. However, field studies have produced a variety of often contradictory evidence. Gibson and Falls (1979) found that female *Thamnophis sirtalis* in general had a higher mean body temperature than males, but that there was no difference between gravid and nongravid females. However, in a study of *Nerodia fasciata* and *N. taxispilota*, gravid females had the same mean body temperature as males and nongravid females, but had significantly lower variances (Osgood 1970). Still other studies have shown that gravid females maintain lower body temperatures than nonreproductive individuals (*e.g. Agkistrodon contortrix*, Sanders and Jacob 1981).

In this study, when animals of the same reproductive class were pooled, comparisons revealed that gravid females, as a group, often had higher mean body temperatures than nonreproductive animals, although the differences were small. Comparisons of the variances associated with these means indicated that there was likely little difference in the precision of thermoregulation of the two groups. In the morning, gravid females frequently appeared to be less precise thermoregulators than the nonreproductive snakes, but consistent differences in precision between the two groups appeared to be a function of timing, rather than true precision. Gravid females appeared to begin heating earlier in the morning than the other snakes and, hence, had more variable body temperatures at that time. By early afternoon, all snakes had achieved the plateau phase and there were no consistent differences in precision.

It has been suggested that the prediction of higher body temperatures for gravid viviparous females, in order to speed the development of embryos, may be based on assumptions which are too simplistic (Beuchat and Ellner 1987). By definition, the rate of embryonic development is lowered, both above and below the optimum temperature. Reduced thermal energy results in slower development below the optimum temperature. However, above the optimum, development is slowed, and eventually stopped, as a result of damage to the embryos. If a gravid female is maintaining a body temperature at the optimum for embryonic development, then deviations above and below this set point are required to stimulate her to adjust her body temperature. Thus, even very precise thermoregulation will result in the embryos being exposed to potentially harmful temperatures above the optimum. Only in an environment where there is no variation in body temperature can a gravid female choose the optimum for embryonic development. Any variance must necessarily decrease the female's mean body temperature to avoid fluctuations above the optimum which could damage the embryos (Gibson and Falls 1979, Beuchat and Ellner 1987). The term "rookeries" has been applied to areas where gravid female rattlesnakes spend extended periods of time (Klauber 1972). On my study sites rookeries are either areas on the winter den outcrop itself, or flat table rocks in the general vicinity (Macartney 1985). A potential function for rattlesnake rookeries might be to provide sites with reduced variance in environmental temperature, allowing gravid females to maximize thermoregulatory precision, and select temperatures closer to the optimum for embryonic development alone. Aggregations of females at these rookeries would simply be the result of the scarcity of suitable sites.

The relation between thermoregulation and reproduction in viviparous reptiles is apparently strong (Shine 1985); however, within both the reproductive and nonreproductive groups, individuals were found to differ significantly from other members of the same group almost 70% of the time. Few studies of snake thermoregulation have examined individual variation. Hammerson (1979) found generally similar mean body temperatures in *Masticophis* studied in a semi-natural enclosure, but a significant variability in variance among individuals. Peterson and Arnold (1986) found tremendous variation in the thermoregulatory behavior of 15 gravid female *Thamnophis elegans* monitored simultaneously in the wild using telemetry. Mean time of emergence in the morning varied by almost 2 h among individuals, and, in addition, individuals varied their own behavior from day to day.

Recently, the concept of multiple thermal optima, which suggests that various processes have different thermal optima which an organism must balance, has begun to supplant the traditional view that an animal thermoregulates to a single temperature which optimizes all of its physiological processes (Huey 1982). Beuchat and Ellner (1987) developed a model, incorporating multiple thermal optima, of thermoregulation for the viviparous lizard, *Sceloporus jarrovi*. They suggest that, at the very least, a gravid female must balance two major factors. First, gravid females which feed little or not at all must minimize energy loss during gestation, and hence should prefer lower body temperatures. Second, gravid females should maximize the developmental rate of their embryos by selecting high body temperatures to ensure parturition before winter (or, in some lizards, to allow for a second clutch). The resolution of the conflict between these two thermal optima is expected to vary between individuals depending on a number of factors (Beuchat and Ellner 1987). For example, a well nourished female may be able to speed embryonic development through higher body temperatures despite the higher energy cost, while a less well nourished female must choose lower temperatures to save energy, even though it results in a longer gestation period. Hence, one would expect to see variability in thermoregulation among animals in the same reproductive group, as well as in the population as a whole. It is interesting to note that the model of Beuchat and Ellner (1987) predicted lower body temperatures for gravid females than for other lizards in the population, and this prediction was verified in the field. For gravid females, maintenance of a mean body temperature similar to that of males and nongravid females would result in a 13% reduction in fitness compared with the optimal temperature. This reduction in fitness is primarily the result of increased embryo mortality, but increased mortality and reduced growth of the female also contribute.

There is no doubt that thermoregulation helps to ensure rapid and complete development of embryos (Shine 1983). Shine (1987) has shown that the distribution of viviparous and oviparous species of the genus *Pseudechis* can be predicted from environmental data. Specifically, viviparous species are found in areas where substrate temperatures do not allow time for the hatching of eggs. Presumably, maternal thermoregulation allows viviparous forms to reproduce successfully in such areas. Fox (1948) reported that holding gravid female *Thamnophis elegans atratus* between 18 and 29°C resulted in considerable embryo mortality and abnormal development compared with those kept between 24 and 35°C. In addition, Vinegar (1974) reported similar abnormalities in hatchlings of the oviparous species, *Python molurus*, incubated at low temperatures.

None of the gravid females used in this study, either in the large thermoregulation enclosure or in the smaller, shaded enclosure, gave birth before 8 October 1986. Embryonic development was very slow and only one female may have given birth (see Results: Effect of Thermoregulatory Opportunity on Gestation Period). Female rattlesnakes in this population are presumed to fertilize their eggs in June, from a copulation the previous August, and usually give birth in late September or October (Macartney 1985). Starting in late June and continuing through July 1986 the weather at the study site was unseasonably cool and wet. Osgood (1970) states that in *Nerodia fasciata* embryos cannot tolerate temperatures outside the range of 21-30°C for long, and that they are particularly vulnerable early in development. Embryonic development in many, if not all, animals is characterized by high respiration rates during early development which decline as development progresses (Zotin 1972). Presumably it is this high metabolic rate which makes the early stages of embryonic development so susceptible to disturbance by variations in temperature. Small changes early in development may be amplified and lead to large-scale disruptions later on. Thus, the cool weather of summer 1986 may have occured at a particularly poor time for gravid female *C. viridis*. The summers of 1985 and 1986 were virtually identical in terms of temperature for all months except July. In 1985 the mean daily maximum and minimum temperatures were higher than the 30 yr mean and were far higher than in 1986. There was also a considerable difference in the dates of parturition, as measured in the lab and through observations of neonates at the dens, between the two years, with the gestation period apparently being much shorter in 1985.

If the concept of multiple thermal optima is important in determining the patterns of thermoregulation in snakes, then variation in preferred body temperature should occur as an individual's reproductive and nutritional status change. Detailed studies of these aspects of thermoregulation are needed. I was unable to address these questions in my study, beyond demonstrating the large amount of individual variation in body temperature selection during the summer. Ideally, future studies should attempt to follow the same individuals over more than one year, in order to determine whether thermoregulation varies from year to year in the same individual, or whether consistent differences between individuals are maintained. Some animals may prefer higher or lower temperatures for all activities, while still following the general patterns predicted by the balancing of multiple thermal optima. Performing thermoregulation studies in enclosures must, to some extent, affect the animals' responses. Although every effort was made to provide a sufficient diversity of microsites within the enclosure, it is not known whether the snakes were thermoregulating to the same degree as in the wild. The data collected generally agree with the limited information reported for this population, although a single 24 h record for a gravid female shows the maintenance of very high (near 30°C) night-time temperatures (Macartney 1985). I rarely observed gravid females in my study maintaining such high night-time temperatures, and it is possible that the enclosure lacked sites suitable for this. Enclosures provide the best method of obtaining comparative data on thermoregulation among individuals since they provide all of the animals with the same thermoregulatory opportunities. However, technology already exists for simultaneous monitoring of free-living snakes in favorable environments, and it may soon be possible under a much wider variety of circumstances.

First-year Survivorship

Parker and Plummer (1987) state that the lack of quantitative data on first-year survivorship is probably the single biggest problem in population studies of snakes. A number of features made this population of *C. viridis* seem particularly amenable to an investigation of first-year survivorship. Knowledge of their communal denning behavior and high den site fidelity, as well as detailed knowledge of the location of winter den sites allowed me to collect relatively large numbers of young, and to choose dens that would provide the greatest opportunity for the recapture of neonates.

Winter survivorship of hibernating snakes has been found to be variable, but, in general, adults have higher survivorship than young (Gregory 1982). Parker and Brown (1980) found that in *Masticophis taeniatus*, adult survivorship in hibernation was about 95%, while for juveniles it was only 25%. They also found a similar pattern in *Pituophis melanoleucas* (adults 88-89%, juveniles 29%). However, Viitanen (1967) found a less pronounced difference (85% for adults, and 60-70% for juveniles) in *Vipera berus*. Overwinter survivorship in this population of *C. viridis* was shown, in an earlier study, to vary between 0 and 76.5% for neonates, and was virtually 100% for adults (Macartney 1985). The results of my study show that overwinter survivorship in juvenile *C. viridis* is quite high and is similar to that in *Vipera berus*. The estimate of winter survivorship (53.91%) was remarkably consistent between the sexes and between neonates from the two dens.

C. viridis in this population give birth in the fall and neonates enter hibernation without having an opportunity to forage (Macartney 1985). Thus, they must survive hibernation with whatever energy reserves they are born with. It has been suggested that this might lead to high mortality among neonates during their first hibernation (Blem 1981). If this is so then large neonates, born with greater energy reserves, should be at an advantage. Goulden *et al.* (1987) suggest that the relationship between neonate size and energy reserves is a general phenomenon, and holds for a number of taxa, both vertebrate and invertebrate. The internalized remnants of the yolk, referred to as the posthatching yolk, are used to provide the offspring with an energy source early in life in many reptiles

(Troyer 1987). Bellairs *et al.* (1955), in a study of placentation in *Vipera berus*, suggested that the posthatching yolk of neonates provides enough energy for several months of continuous activity, and should provide adequate energy for survival over winter. However, a similar study of *Agkistrodon contortrix* showed that neonates had fully utilized their internal yolks 15 days after birth (Gloyd 1934). Information is needed on the relative provisioning of neonates with posthatching yolk and body fat at birth, and the rates at which these resources are used. My results do not indicate any difference in survivorship, related to size at birth, during hibernation. The low temperatures experienced by hibernating snakes result in low metabolic rates, and so hibernation may not be energetically costly. Water loss may be an important factor in winter weight loss (Gregory 1982) and a survival advantage for large young during this time may be their lower surface area to volume ratio. Although survivorship was independent of size at birth during the winter of 1985/86, annual variation in winter survivorship of snakes has been noted (*e.g.* Parker and Brown 1980, Macartney 1985). The relatively high survivorship of this particular winter may have reduced any potential size effects. In years where there is generally low survivorship, size at birth well may be important.

Macartney (1985) found that winter survivorship of neonate *C. viridis* varied from 0 to 76.5%, depending on the den and the year. There were no differences in survivorship between the two dens in this study, but they did differ considerably in other ways. The mean weight loss at den 8 was twice that seen at den 9. Some individuals at den 9 increased their weight during hibernation, probably through water uptake. In addition, the pattern of weight loss differed between the dens.

At den 9 there was no relationship between weight at birth and winter weight change, while at den 8 large young experienced greater weight losses than small young. In general, winter weight loss should be greatest in smaller animals (Gregory 1982) and the pattern of weight loss in den 8 is difficult to understand.

Young snakes, by virtue of their size, often may have less suitable prey available to them than adults, but at the same time experience high energy demands associated with growth (Mushinsky 1987). Thus, it seems likely that it is during their first summer that larger size is advantageous. Saint Girons and Naulleau (1981) found that during the first 10 months of life larger neonates of a variety of species of *Vipera* showed higher survivorship than smaller neonates in outdoor enclosures. However, in lizards, survival advantage for large young has been shown to vary seasonally (Ferguson *et al.* 1982) and annually (Ferguson and Fox 1984), depending on food availability and predation pressure. In California, young *C. viridis* feed mainly on small rodents, lizards, and toads (Fitch and Twining 1946, Fitch 1949). However, in British Columbia neonates feed exclusively on rodents (Macartney 1985). The rarity of small lizards in the north may mean that suitable prey for neonates in this population is more difficult to find than further south. Unfortunately, recapture success during fall 1986 was low and it was impossible to assess the effect of size at birth on summer survivorship. However, examination of the data reveals a tremendous amount of variation in length and weight changes during the first year of life. Changes in length ranged from 4.69 to 24.14%, while changes in weight varied from a loss of 18.66% of the weight at birth to an increase of 101.15%. These dramatic changes in weight described represent true growth as none of the animals had either food in their stomach, or feces in their intestines when weighed. The amount of variation shown by these individuals clearly suggests that food may indeed be difficult to obtain for first-year *C. viridis*, as suggested by Fitch and Glading (1947).

Low recapture success also made it impossible to assess the effect on summer survivorship of feeding soon after emergence from hibernation. However, anecdotal observations of the large prey items that juvenile *C. viridis* will take suggest that the 2.5 g meal of beef heart was insufficiently large to have an appreciable effect. A better way to conduct this phase of the study would have been to offer the neonates live food of a variety of sizes for some period after emergence, and allow them to select their own meals. However, until information on normal feeding rates and prey size of neonates is available, it will be difficult to determine the effect of supplemental feeding.

The difficulty of recapturing neonates in large numbers is the greatest problem in collecting survivorship data. Although I selected winter dens which appeared to have only one entrance, the steep topography of the area made fencing difficult. Smaller snakes appeared to use these secondary entrances, and avoided being trapped either by the fences in spring, or the funnel traps in fall. No real alternatives to the mark-recapture methods used here are currently available, and the best that can be done is to continue marking as many neonates as possible. Recaptures of these individuals, even when they are 2, 3, or more years old, can be used to estimate the minimum number alive at the end of year one. Unfortunately, it will be very difficult to address the questions of seasonal and annual variation in survivorship using this approach.

Conclusions

Although the results of this study do not provide unequivocal evidence of the effect of any one factor on first-year recruitment, they do provide some insight into the complexity of interactions which underly them. Foraging success undoubtedly imposes limits on the speed with which a *post partum* female replaces the fat reserves depleted while gravid. However, there appears to be considerable variation among individuals in feeding rate, as well as growth in length and weight, at least under the conditions of this study. In addition, reproductive cycles may also be constrained by environmental factors, particularly temperature. These same factors may be of crucial importance to gravid females in July when embryonic development is in its early stages, and is most vulnerable.

Thermoregulation, which is presumed to be used by gravid females to optimize embryonic developmental rate, appears to have a large component of individual variation. Gravid females, as a group, tend to maintain higher body temperatures than nonreproductive snakes, but animals within either group frequently differ significantly from one another. Conflicting multiple thermal optima may vary among individuals depending, for example, on nutritional status, foraging history, and reproductive state, resulting in different optimal body temperatures for different individuals. In addition, the effect of the local environment on the variance of a gravid female's body temperature may act to reduce the mean below the optimal temperature for embryonic development alone. The result of these conflicting pressures on body temperature may be that embryonic development is slowed, and a gravid female may be unable to complete gestation before winter, under some conditions.

Rattlesnakes have relatively large offspring which show considerable variation in size at birth. Although they have no opportunity to feed before hibernation, size at birth does not appear to affect survivorship during the winter. Instead, large young may be at an advantage the following summer when the tremendous variability in growth indicates that suitable prey for small, rodent-eating snakes is difficult to find. Survivorship during hibernation, and the first summer, likely varies annually and any survivorship advantage for large young is expected to vary as well.

A comprehensive theory of life history evolution will require a broad data base from a wide array of taxa. Snakes are one of the most successful of modern reptile groups (Goin *et al.* 1978), but information on life history and experimental tests of life history theory are lacking, especially compared to lizards (Parker and Plummer 1987). In this study I attempted to address, through field experiments, some of the main questions concerning the factors which limit first-year recruitment in *C. viridis*, and, in a broader context, to increase our knowledge of the selective forces which may have shaped some of the life history traits of this species. Although the results here demonstrate some of the weaknesses of this approach, I believe that they provide a valuable starting point for the refinement of hypotheses concerning life history evolution in snakes, and the techniques needed to test them in the field.

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Title of Thesis

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