A PHYSIOLOGICAL ANALYSIS OF THE QUEEN SNAKE,
REGINA SEPTEMVITTATA (SAY)

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By
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* * * * *

The Ohio State University
1978

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Approved By
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1978
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INTRODUCTION

Several physiological and behavioral parameters are employed in this study in an attempt to determine various aspects of the thermal ecology of the queen snake, Regina septemvittata, in central Ohio.

The queen snake is a semi-aquatic, temperate zone colubrid which has as its range much of the eastern United States including Ohio. Snakes included within this genus (R. septemvittata, R. grahami, R. rigida and R. alleni) all prefer a diet which consists almost exclusively of crayfish (Conant, 1938a; Raney and Roecker, 1947; Wood, 1949; Penn, 1950; Conant, 1960; Burghardt, 1968; Hall, 1969; Branson and Baker, 1974; Godley, 1976; Franz, 1977.

In central Ohio queen snakes are active from late March through early October. During extremes of their activity period, water temperatures are well below air temperatures and, more importantly, below preferred body temperatures reported for similar natricine species by Brattstrom (1965). If the queen snake possesses a temperature dependent activity pattern such as those reported for similar species, then active foraging for crayfish during periods when water is cold could be difficult.
Several studies have demonstrated that reptiles are able to physiologically thermoregulate to varying degrees through cardiovascular shunts and metabolic changes (for review see Templeton, 1970). The large Indian python, *Python molurus bivittatus*, has even been found to increase heat production over a limited range of decreasing temperatures by means of muscular contraction while brooding (Hutchison et al, 1966; Vinegar et al, 1970). The Galapagos marine iguana, *Amblyrhynchus cristatus*, presents a situation similar to that of the queen snake in that it forages for marine vegetation at water temperatures some 10-15°C cooler than its preferred temperature. Bartholomew and Laziewski (1965) and Bartholomew (1966) suggest that cardiovascular changes alter the thermal conductance of the animal in such a way that it loses body heat slowly in response to lower temperatures. Dmi'el and Borut (1972) have shown that an Israeli snake, *Spalerosophis cliffordi*, exhibits this capacity to alter heat flow.

This study attempts to answer the following questions concerning how the queen snake deals with acquiring prey in a cold environment:

1) Does the queen snake shift its feeding behavior such that terrestrial prey rather than crayfish are utilized during cold periods or is frequency of feeding changed?
2) Does the queen snake differ from other temperate zone colubrids with regard to the parameters of preferred and ecritic body temperatures?

3) Do critical thermal maximum or minimum temperatures of the queen snake thermally acclimate?

4) Does the queen snake exhibit adjustments in oxygen consumption or heart rate with room temperature acclimation (22-27C) which would assist activity at low temperatures?

5) Does the queen snake alter its thermal conductance in a cold environment when acclimated at room temperature or 10C such that heat loss is sufficiently retarded to allow time for foraging?

6) Is queen snake myosin ATPase sufficiently active at low temperatures to allow muscle contractions involved in active foraging to occur?
MATERIALS AND METHODS

Analysis of Stomach Content During Spring.

Thirty snakes (not including the thirty-eight which were studied for the other experiments) were sacrificed in the field between late March and early May of 1977. The contents of the digestive tracts of these snakes were removed and returned to the laboratory for identification.

Measurement of Body Temperature in the Field.

During the period between late March and early October of 1974, 75, and 76, thirty-eight queen snakes were collected in Franklin and Delaware counties of Ohio. Collection took place between the hours of 10:00 A.M. and 3:00 P.M. and most of the captures were of basking snakes although several were found under rocks (see Table 2). Cloacal temperatures were measured with a small animal probe in conjunction with a Yellow Springs Instrument Company telethermometer (Model 46TUC) within 30 seconds of capture. Snakes were held by the tail to prevent heat absorption from the handler (Benedict, 1932; Stewart, 1965) while cloacal temperatures were measured. Air temperature within 2 cm. of the capture site was considered to be representative of the animal's thermal
environment and water temperature was measured at the site nearest where the snake was captured. Both air and water temperatures were taken with a banjo thermister probe in conjunction with the YSI telethermometer.

Animal Maintenance within the Lab.

When not under experimentation snakes were collectively housed in a metal box approximately 1 m. square and 25 cm. deep, and covered with a screen top. A 150-watt bulb illuminated the cage with a 14-hr:10-hr light-dark photo-period. Branches were provided as basking sites and wood and pieces of cardboard for retreat. A large bowl of fresh water was available constantly. Newspaper was used as a substrate and was changed periodically to avoid build-up of moisture and fecal matter which are media for several reptilian disease agents (King, 1971; Marcus, 1971; Wallace, 1971). The cage was kept in a laboratory where room temperature varied from 22-27°C and the air temperature within 2 cm. of the cage floor at the lighted end of the cage remained near 27°C during the light period.

Snakes showed no inclination to eat voluntarily so they were force-fed. Soft-shelled crayfish were not readily available on a regular basis so minnows, purchased from a local bait shop, were force-fed to the snakes at a rate of one or two fish weekly. All snakes maintained
weight on this diet and several females maintained pregnancy and gave birth.

Measurement of Preferred Temperature in a Laboratory Thermal Gradient.

Eighteen queen snakes were tested and a total of 58 body temperature measurements were recorded in a laboratory thermal gradient to establish the thermal preferendum of the species.

A thermal gradient chamber was fashioned from a metal locker which measured approximately 2 m. by 1/2 m. by 1/2 m. The locker was placed such that its long axis was parallel to the floor and the original door served as a lid to the chamber. Holes were drilled in the bottom and sides of the locker and it was elevated about 25 cm. from the floor to assure adequate ventilation. Three goose-necked lamps with incandescent bulbs of 150 watts, 75 watts, and 25 watts were placed within the chamber as heat sources. The entire apparatus was placed in an environmental room where the temperature was constantly maintained at 14°C which served as the lower temperature limit of the gradient. The distance between the three lamps, and the heights of the bulbs were adjusted to provide an even temperature gradient from 40°C to 14°C as measured with a banjo thermister (shielded by hand from above) and YSI telethermometer within 2 cm.
of the chamber floor. The photo-period within the chamber was the same as that at which the snakes had been maintained in the lab when not under experimentation.

Two snakes at a time, acclimated at room temperature (22-27°C) and starved for 48 hours, were placed in the thermal gradient chamber in late afternoon. The following day between 8:00 A.M. and 5:00 P.M. cloacal temperatures for each snake were recorded at 90 minute intervals with the use of a small animal probe and a YSI telethermometer. If the snakes were disturbed by opening the chamber door and moved from their original position before their cloacal temperatures could be recorded, no readings were taken.

Measurement of Thermal Acclimation of Critical Thermal Maximum (CTMax) and Critical Thermal Minimum (CTMin) Temperatures.

An index of the ability of an animal to thermally acclimate is exemplified by the shift in CTMax and CTMin with changing ambient temperatures (Vance, 1953).

The CTMax is the body temperature at which the snake loses muscular coordination, and becomes limp with a wide gaping mouth when subjected to increasing ambient temperatures (Cowles and Bogert, 1944). For the study of CTMax acclimation a group of seven queen snakes was acclimated at an ambient temperature of 32°C and a second
group of seven acclimated to 8C. The acclimation period was 5 days (Stewart, 1965). Water was available throughout the acclimation period though food was withheld. At the end of this period one snake at a time was placed in a waterbath approximately 25 cm. by 25 cm. by 25 cm. in which water 20 cm. in depth was circulated. Water temperature was continuously monitored with a YSI telethermometer and a banjo thermister. At the onset of this phase of the experiment water temperature was 33C. The temperature of the water was raised 1°C within each 30 minute period. When CMax was reached the individual was removed from the waterbath and its cloacal temperature measured within 10 seconds with a YSI telethermometer and small animal probe.

The CMin is the body temperature at which the snake is unable to right itself when turned on its back as it is subjected to decreasing ambient temperatures (Cowles and Bogert, 1944). For the test of CMin acclimation six snakes were acclimated at each of the two temperatures (32C and 8C) under the same conditions as described for CMax. At the end of the acclimation period one snake at a time was placed in a tin bowl 25 cm. in diameter and 5 cm. deep. The bowl was then embedded within an ice bath in a plastic container 45 cm. by 30 cm. by 10 cm. The plastic container was then covered and placed
in an incubation chamber at a temperature of 0(±2)C. The righting response was checked at 5 minute intervals and when failure to right occurred cloacal temperature was recorded with a YSI telethermometer and small animal probe.

All snakes which underwent these procedures (for both CTMax and CTMin) recovered quickly at room temperature.

Measurement of Oxygen Consumption during Rest and Activity at Several Temperatures.

Oxygen consumption of queen snakes during rest and electrically induced activity was recorded for 7-10 snakes ranging in weight from 36.7 g - 108.1 g at each of the following body temperatures: 10, 15, 20, 25, 30, 35C. Snakes had been acclimated at room temperature for several weeks and starved for 72 hours (Regal, 1966; Roberts, 1968) prior to experimentation.

During measurement of oxygen consumption body temperature of the snake was monitored with the use of a YSI telethermometer and a small animal probe secured cloacally with adhesive tape. Gold plated safety pins were soldered to 24 gauge electrical wires and attached subcutaneously to the snake on each side of the heart (the position of which was determined by palpation and in several cases dissection) and on the back about 4 cm.
cranial to the cloaca. A band of adhesive tape was wrapped around the two wires which were adjacent to the heart at a point about 3 or 4 cm. posterior to the pin attachments. The tape was then wrapped around the body of the snake so that if the wires became tangled pressure would be exerted on this tape rather than the pin attachments. These wires served a dual role by which heart rate could be monitored and electrical stimulation could be administered. With lead wires and thermocouple in place, a loop of tygon tubing was placed around the snake's neck with which the animal was pulled into a glass tube 60 cm. long with an inside diameter of 2.5 cm. The tube was then sealed with rubber stoppers with airtight entry ports for lead wires, thermocouple, and passage of air. This tube served as a metabolic chamber and will henceforth be referred to as such. During analysis of resting $O_2$ consumption the chamber was darkened by wrapping black electrical tape around the outside surface. During measurement of active oxygen consumption this tape was removed. The entire apparatus was submerged in a circulating waterbath (American Instrument Co. ±5%) immediately prior to entry to the chamber. All oxygen consumption data reported in this study were collected between 0700 and 1200 hours (EST).
Measurement of $O_2$ consumption of the queen snake was accomplished through the use of a flow-through system in conjunction with a paramagnetic Beckman Oxygen Analyzer (Model F3M3-1AA, ACC. ± 1% of full scale) in all cases except resting oxygen consumption at 10, 15, and 20°C.

The analyzer was calibrated with known gases and connected to the metabolic chamber. Air which had been dried by passage through two drierite columns flowed at a rate of 100 cc/min as measured in a flowmeter immediately prior to entry into the chamber. Upon leaving the chamber the air was again passed through two drierite columns, then into the oxygen analyzer. The percent of oxygen in the air passing through the analyzer was continuously recorded on a Heath Servo Recorder (Model EVW 20P). The lowest oxygen percent recorded for 20 minutes or more at each temperature was considered to be representative of the resting state of the animal. Oxygen consumption during activity (all temperatures) and at rest (25, 30, 35°C) was calculated using the equation given by Depocas and Hart (1957) for the open-circuit system when $CO_2$ is not absorbed.

At those temperatures below 25°C at which resting oxygen consumption was recorded, the Beckman Oxygen Analyzer in conjunction with the flow-through system described above was not sensitive enough to record small
changes in percent oxygen. Thus, a closed system was designed. The volumes of the chamber, associated tubing, and each snake were determined. The snakes were set up and allowed to equilibrate overnight in the chamber as before. The oxygen analyzer was calibrated as before. Air was passed into the chamber after passing through the two drierite columns for a time period exceeding sufficient length for air from the previous night to reach 99% equilibrium with the fresh air. This time period was calculated by applying the equation:

\[ t = 4.6 \frac{V}{D} \]

where \( V \) equals the volume of the chamber, and \( D \) is the air flow rate (Lasiewski et al., 1966). At this point the inlet and outlet portals of the chamber were connected with tygon tubing, thus closing the system. A Manostat Varistaltic Pump (advanced model) was adjusted to circulate the air within the system in one direction through the tygon tubing at 100 cc/min. Circulation continued for 40 minutes, at which time 10 cc of air were drawn from the tube through a 5 cc drierite column with a 50 cc hypodermic syringe and discarded to displace the unused air in the drierite container. Then 50 cc of air were withdrawn from the tube in the same manner. These 50 cc were then injected into the entry port of the Beckman Oxygen Analyzer through a small plastic tube over the
period of one minute. The percent of oxygen of the sample was then read directly from the dial of the analyzer. Oxygen consumption in this closed system was calculated as follows:

\[
\frac{\text{vol of system} - \text{vol of snake}}{\text{weight (g)}} \times \left(21\%-\text{dial reading}\right) \times \frac{60 \text{ min}}{\text{hr}} \times \left(\frac{1 \times 40 \text{ min}}{\text{STP}}\right)
\]

This method was validated by testing three snakes at 25, 30, and 35°C using this method and comparing the results to those acquired by the flow-through system.

All active oxygen consumption rates were collected with the use of the flow-through system described above. Snakes were electrically stimulated to activity through the lead wires with a Grass Electrical Stimulator (Model SD 9). A continuous stimulus was administered at 5-20 volts and a frequency of 1-100 pulses per second for whatever pulse duration was adequate to maintain activity. Upon stimulation snakes were observed to writhe violently though restrained by the lead wires, turn over, and in some cases attempt to turn around within the chamber in an apparent effort to attack the lead wires pinned to their backs. Intermittent periods of rest were observed and oxygen consumption readings were erratic. The three highest readings at each temperature for each snake were averaged as the oxygen consumption during activity for the individual.
Measurement of Heart Rate during Rest and Activity at Several Temperatures.

In conjunction with the oxygen consumption study, resting and active heart rates of 7-10 snakes were recorded at each of the six temperatures (10, 15, 20, 25, 30, 35°C). At 25, 30, and 35°C when oxygen consumption remained at a resting level (as interpreted from the chart of the Heath Servo Recorder) for 20 minutes, heart rate was recorded for 10 minutes with the use of a Harvard Biograph (Model 2120). The lowest one minute heart rate reading to be repeated three or more times during this period was considered the resting heart rate at these temperatures. At 20, 15, and 10°C, when the closed system was used to determine resting oxygen consumption, heart rate was monitored for 3 minute periods with alternating 3 minute intervals in which no readings were collected. The lowest one minute heart rate reading to be repeated three or more times was considered to be the resting heart rate at these temperatures.

Since the lead wires were used both to monitor heart rate and to administer stimuli at all temperatures, stimulation to maximum activity had to be ceased in order that heart rate data could be collected. As active oxygen consumption approached maximum levels (as interpreted from the chart of the Heath Servo Recorder) stimulation
was stopped for three minute intervals and heart rates were monitored. If oxygen consumption continued to increase upon further stimulation the previous heart rates were discarded. The highest one minute heart rate which was repeated three times or more, and was not followed by an increase in oxygen consumption, was considered the active heart rate at each temperature.

**Measurement of Heating and Cooling Rates in Air and Water.**

A group of six snakes, acclimated at room temperature for six weeks or more and ranging in weight from 56-101 gms, was tested to determine the rates of heat loss and gain in air. A second group of eight snakes captured within 2 weeks of spring emergence and acclimated at 10C (14L; 10D) for an additional 3 weeks was also tested for rate of change of body temperature in air. Snakes were equipped with lead wires, cloacal probe, and placed in the tubes as described in the oxygen consumption section of this paper.

Snakes within the tubes were then submerged in a waterbath at 30C. When the body temperature of the snake reached 29C the tube was moved to a second bath at 10C and body temperature and heart rate changes were continuously monitored until the snake's body temperature reached 11C. At this point the tube was returned to the
30C bath and body temperature and heart rate changes monitored during heating to a body temperature of 29C.

It was determined in a preliminary test that air temperature inside the tube reached that of each waterbath within 40 seconds after the tube was placed in the water.

Heating and cooling rates and changes in heart rate were collected for 10 snakes acclimatized at room temperature and tested in water. The small animal probe was secured cloacally as before but single strand wire electrodes instead of gold plated safety pins were inserted subcutaneously for measurement of heart rate. Nail polish was applied to the skin-electrode junctions to assure that the connections were waterproof. After the snake was wired, it and the wires were wrapped in a thin mesh hardware cloth to limit movement during experimentation.

Heating and cooling of the snake were again completed in two separate waterbaths set at 30 and 10C. Data were collected as before except the snakes were not placed in the glass tubes so they were in direct contact with the water.

Measurement of the Optimum Temperature for Myosin ATPase Activity.

Myosin ATPase homogenates of 4 queen snakes were tested at each of 10 temperatures between 15 and 45C.
The extraction and purification of queen snake myosin ATPase followed the procedures of Perry (1955) with slight modification.

Individual snakes acclimated at room temperature for several weeks were cooled, decapitated, and rapidly skinned and eviscerated. The carcass was then further cooled in ice water for several minutes. Since myosin is quite sensitive to heavy metal contamination, distilled water, and ice made from distilled water, were used throughout the experiment (Szent-Gyorgyi, 1951). Approximately 10-20 g of muscle could be obtained by removing trunk musculature. Muscles were chopped and torn with forceps and a scalpel first, then for several minutes in a Waring blender with three volumes of cold KCl-potassium phosphate buffer (Gubba and Straub, 1943) containing 0.015 M ethylenediamine-tetraacetate for removal of endogenous calcium (Licht, 1964). Upon removal from the blender the muscle-buffer mixture was gently stirred with a glass rod for 15 minutes for extraction of myosin. All procedures to this point were completed in an environmental room at 0°C. The mixture was then filtered through a buffer-soaked paper pulp pad. The extract was then diluted with 14 volumes of distilled water (0°C) and the enzyme allowed to precipitate overnight (12-16 hrs) in the cold room.
Since extreme levels of myosin purity were not necessary, actomyosin was not removed. The mixture was centrifuged (25000 g) at 0°C for 10 minutes. The supernatant was discarded while the myosin-containing sediment was dissolved in 0.6 M KCl. The myosin was then reprecipitated by dilution with 14 volumes of distilled water.

The procedures for measurement of myosin ATPase activity were similar to those of Licht (1964) and were completed within 36 hours after the snake was sacrificed. The precipitated myosin was dissolved in 0.6 M KCl. Dilution ratios of 1:1, 2:1, and 3:1 were tested at several temperatures and results indicated that these concentration differences did not affect the temperature dependence of the enzyme. To measure temperature dependence of myosin ATPase, each of five test tubes containing 0.2 ml of dilute myosin was mixed with 0.9 ml of sodium adenosine-5'-triphosphate (5 mM) and adjusted to a pH of 8. The tubes were allowed to equilibrate to the experimental temperature for 7 minutes. At this point all tubes received 0.1 ml of 1 mM CaCl₂ to start the reaction and one tube also received 0.4 ml of 30% trichloroacetic acid which stopped any possible activity. This tube would be the blank (i.e. 100% transmission of
light). The reactions in two tubes were then stopped by addition of trichloroacetic acid after an additional 7 minutes and the final 2 tubes were stopped after 15 more minutes. Thus the blank was stopped at 0 minutes, the first 2 tubes after 7 minutes and the last 2 tubes after 22 minutes.

The amount of inorganic phosphate liberated during the last 15 minutes of incubation was considered indicative of the extent of ATPase activity (Licht, 1964). This was measured colorimetrically in a (Coleman Model 6C, 0.5% absolute instrument error) spectrophotometer at a wavelength of 700 μm using Licht's (1964) modification of the method of Fiske and Subba Row (1925). A 1.0 ml aliquot of the reaction mixture was added to 0.1 ml of 4% ammonium molybdate (dissolved in 8N H₂SO₄) and 1.0 ml of 0.05% N-phenyl-p-phenylene-diamine (dissolved in 1% NaHSO₃). The ammonium molybdate reacts slowly over time with N-phenyl-p-phenylene-diamine to turn blue. Inorganic phosphate serves to speed this reaction with increasing phosphate concentrations accounting for a deepening of the color. The spectrophotometer was calibrated to 100% transmission with the blank tube. All mixtures were allowed to react for 20 minutes at room temperature before optical densities were recorded.
The average difference between the optical densities of the tubes that reacted for 7 minutes and those that reacted for 22 minutes at each temperature was used as a measure of ATPase activity at that temperature.
RESULTS

Analysis of Stomach Content During Spring.

Of 30 snakes examined for stomach contents 17 (56.6%) contained food in various stages of digestion. Of the 17 food samples 16 (94.1%) were crayfish, *Orconectes rusticus* [?], identified by Dr. D. Stansbery and Mr. R. Thoma of the Museum of Zoology, The Ohio State University, and one was unidentifiable (see Table 1). Each water temperature reported in Table 1 represents the average of all temperatures for each capture date. The mean of all the water temperatures is 11°C.

Eccritic and Preferred Body Temperatures.

The mean (eccritic $T_B$) body temperature ($T_B$) of 38 *R. septemvittata* captured in the field was 27.2°C (S.E. = 0.49; Range = 19.9-34.8°C). The mean ambient air temperature ($T_A$) at which these snakes were found was 22.8°C (S.E. = 0.61; Range = 15-31.6°C). Table 2 lists some information pertinent to each capture and it should be noted that 71% of the captures took place while snakes were basking. The fact that these snakes are more easily found while basking probably influences this statistic.
Table 1. Capture data and water temperatures of 30 queen snakes studied for gut content in 1977.

<table>
<thead>
<tr>
<th>Date of capture</th>
<th>Collecting site</th>
<th>Water temperature °C</th>
<th>Number of snakes captured</th>
<th>Number of snakes containing food</th>
</tr>
</thead>
<tbody>
<tr>
<td>March 27</td>
<td>Olentangy</td>
<td>5</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>March 29</td>
<td>Olentangy</td>
<td>13</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>April 7</td>
<td>Scioto</td>
<td>6</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>April 12</td>
<td>Olentangy</td>
<td>9</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>April 15</td>
<td>Scioto</td>
<td>10</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>April 18</td>
<td>Scioto</td>
<td>18</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>April 24</td>
<td>Olentangy</td>
<td>12</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>May 13</td>
<td>Olentangy</td>
<td>15</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Capture</td>
<td>$T_B$</td>
<td>$T_A$</td>
<td>$T_W$</td>
<td>Comments</td>
</tr>
<tr>
<td>---------</td>
<td>------</td>
<td>------</td>
<td>------</td>
<td>----------</td>
</tr>
<tr>
<td>1</td>
<td>22.7</td>
<td>18.7</td>
<td>-</td>
<td>B</td>
</tr>
<tr>
<td>2</td>
<td>19.9</td>
<td>18.3</td>
<td>-</td>
<td>B</td>
</tr>
<tr>
<td>3</td>
<td>28.2</td>
<td>27.8</td>
<td>-</td>
<td>B,OC</td>
</tr>
<tr>
<td>4</td>
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<td>24.2</td>
<td>-</td>
<td>B,OC</td>
</tr>
<tr>
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<td>27.0</td>
<td>24.8</td>
<td>-</td>
<td>B,OC</td>
</tr>
<tr>
<td>6</td>
<td>21.4</td>
<td>24.2</td>
<td>17.1</td>
<td>B,OC</td>
</tr>
<tr>
<td>7</td>
<td>28.3</td>
<td>24.4</td>
<td>16.4</td>
<td>B,LSM</td>
</tr>
<tr>
<td>8</td>
<td>34.8</td>
<td>29.5</td>
<td>-</td>
<td>B,LSM</td>
</tr>
<tr>
<td>9</td>
<td>27.1</td>
<td>31.6</td>
<td>-</td>
<td>B,DS</td>
</tr>
<tr>
<td>10</td>
<td>27.0</td>
<td>27.2</td>
<td>-</td>
<td>B,LSM</td>
</tr>
<tr>
<td>11</td>
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<td>25.7</td>
<td>-</td>
<td>B,LSM</td>
</tr>
<tr>
<td>12</td>
<td>27.0</td>
<td>20.4</td>
<td>18.3</td>
<td>B,DS</td>
</tr>
<tr>
<td>13</td>
<td>28.4</td>
<td>20.4</td>
<td>18.3</td>
<td>B,DS</td>
</tr>
<tr>
<td>14</td>
<td>27.0</td>
<td>21.4</td>
<td>16.5</td>
<td>B,SH</td>
</tr>
<tr>
<td>15</td>
<td>28.1</td>
<td>24.2</td>
<td>-</td>
<td>B,DS</td>
</tr>
<tr>
<td>16</td>
<td>25.5</td>
<td>19.0</td>
<td>-</td>
<td>B,OC</td>
</tr>
<tr>
<td>17</td>
<td>25.6</td>
<td>22.3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>18</td>
<td>27.0</td>
<td>18</td>
<td>15</td>
<td>UR</td>
</tr>
<tr>
<td>19</td>
<td>29.0</td>
<td>24</td>
<td>20</td>
<td>B,DS</td>
</tr>
<tr>
<td>20</td>
<td>32.0</td>
<td>19</td>
<td>12</td>
<td>B,DS</td>
</tr>
<tr>
<td>21</td>
<td>24</td>
<td>17</td>
<td>12</td>
<td>B,LSM</td>
</tr>
<tr>
<td>22</td>
<td>29</td>
<td>24</td>
<td>15</td>
<td>B,DS</td>
</tr>
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</table>
Table 2. (continued)

<table>
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<tr>
<th>Capture</th>
<th>$T_B$</th>
<th>$T_A$</th>
<th>$T_W$</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>23</td>
<td>32</td>
<td>16</td>
<td>15</td>
<td>B, LSM</td>
</tr>
<tr>
<td>24</td>
<td>31</td>
<td>15</td>
<td>15</td>
<td>B, DS</td>
</tr>
<tr>
<td>25</td>
<td>25</td>
<td>22</td>
<td>15</td>
<td>B, DS</td>
</tr>
<tr>
<td>26</td>
<td>23</td>
<td>19</td>
<td>14</td>
<td>Partially hidden in leaves and roots</td>
</tr>
<tr>
<td>27</td>
<td>30</td>
<td>26</td>
<td>16</td>
<td>B, DS</td>
</tr>
<tr>
<td>28</td>
<td>29</td>
<td>25</td>
<td>17</td>
<td>B, DS</td>
</tr>
<tr>
<td>29</td>
<td>23</td>
<td>19</td>
<td>16</td>
<td>UR (w/ N. sipedon)</td>
</tr>
<tr>
<td>30</td>
<td>29</td>
<td>30</td>
<td>16</td>
<td>M, DS</td>
</tr>
<tr>
<td>31</td>
<td>29</td>
<td>24</td>
<td>16</td>
<td>UR</td>
</tr>
<tr>
<td>32</td>
<td>27</td>
<td>24</td>
<td>16</td>
<td>UR</td>
</tr>
<tr>
<td>33</td>
<td>25</td>
<td>24</td>
<td>16</td>
<td>UR</td>
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<td>16</td>
<td>UR</td>
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<td>25</td>
<td>16</td>
<td>B, DS</td>
</tr>
<tr>
<td>37</td>
<td>29</td>
<td>23</td>
<td>11</td>
<td>B, DS</td>
</tr>
<tr>
<td>38</td>
<td>27</td>
<td>22</td>
<td>21</td>
<td>UR</td>
</tr>
</tbody>
</table>

Legend: $T_B$ = body temperature, $T_A$ = ambient temperature, $T_W$ = water temperature, $B$ = basking, $UR$ = under rock, $M$ = moving, $DS$ = direct sun, $LSM$ = light-shade mosaic, $OC$ = overcast, $SH$ = shade.
The temperature data from Table 2 are plotted in Figure 1. The relationship between \( T_B \) and \( T_A \) is best described linearly by the equation

\[
T_B = (0.202) T_A + 22.6
\]

\((N = 38; r = 0.296; 95\% \text{ c.l. for } b = 0.16-0.24)\)

The slope of this line is significantly different from zero \((t_s = 10.4, P < .05)\). This line crosses the theoretical line \( T_B = T_A \) at 28.3C. In only 4 cases (10.5\%) did \( T_A \) exceed \( T_B \).

The mean body temperature of 58 temperature readings recorded for 18 snakes in a laboratory thermal gradient between 8:00 A.M. and 5:00 P.M. is 23.6C \((S.E. = 0.49; \text{Range} = 14.9-30.4C)\). The mean \( T_B \) readings at various times of day are plotted in Figure 2 thus allowing for discussion of the daily activity pattern of this snake.

**Thermal Acclimation of CTMin and CTMax.**

Data for critical thermal maximum and minimum body temperatures of queen snakes acclimated to temperatures of 32C and 8C are presented in Table 3. At 32C acclimation mean CTMax is 37.9C \((N = 7; S.E. = 0.43)\) and mean CTMin is 9.7C \((N = 6; S.E. = 0.96)\). When acclimated to 8C mean CTMax is 36.4C \((N = 7; S.E. = 0.39)\) and mean CTMin is 4.2C \((N = 6; S.E. = 0.27)\). The means of CTMax are not significantly different but the means of the CTMin differ at the 0.005 level \((\text{Student's } t)\).
Figure 1. Relation of cloacal temperatures ($T_c$) to air temperature ($T_a$) of 38 R. septemvittata recorded in the field. Circle indicates one data point at the temperature; square indicates two data points, and a triangle indicates three data points. (Data from Table 2)
Figure 2. Relation of body temperature in a thermal gradient to time of day for room temperature acclimated R. septemvittata. Data points represent means and adjacent numbers indicate number of temperature readings at each time. Vertical lines are ±2 S.E.
Figure 2

TIME OF DAY

1600
1400
1200
1000
800

BODY TEMPERATURE °C

28 27 26 25 24 23 22 21 20 19
Table 3. Critical thermal maximum and critical thermal minimum temperatures of R. septemvittata at acclimation temperatures of $32^\circ$ and $8^\circ$C.

<table>
<thead>
<tr>
<th>Critical thermal maximum ($^\circ$C)</th>
<th>Critical thermal minimum ($^\circ$C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$32^\circ$C</td>
<td>$8^\circ$C</td>
</tr>
<tr>
<td>38.9</td>
<td>36.4</td>
</tr>
<tr>
<td>38.6</td>
<td>36.5</td>
</tr>
<tr>
<td>37.0</td>
<td>34.5</td>
</tr>
<tr>
<td>37.0</td>
<td>37.4</td>
</tr>
<tr>
<td>37.5</td>
<td>36.2</td>
</tr>
<tr>
<td>36.7</td>
<td>37.6</td>
</tr>
<tr>
<td>39.6</td>
<td>36.0</td>
</tr>
</tbody>
</table>

MEAN = 37.9       MEAN = 36.4       MEAN = 9.7       MEAN = 4.2
S.E. = 0.43       S.E. = 0.39       S.E. = 0.96       S.E. = 0.27
Oxygen Consumption during Rest and Activity.

In both resting and active snakes oxygen consumption increases with increasing body temperatures. The relationships between resting and active metabolism expressed in units of watts per kilogram \( (W \cdot kg^{-1}) \) and \( T_B (C) \) are presented in Figure 3. The lowest mean squared error value calculated by piecewise linear regression was used to determine the appropriate breaking point for each line (Neter & Wasserman, 1974).

Resting oxygen consumption where \( T_B = 10-20C \) varies with \( T_B \) according to the equation:

\[
\log W \cdot kg^{-1} = -1.42 + 0.028 T_B
\]

\((N = 23; r = 0.90; 95\% c.l. for b = 0.020-0.036)\)

with a slope corresponding to a \( Q_{10} \) of 1.96. Where \( T_B = 20-35C \) the equation for resting metabolism is:

\[
\log W \cdot kg^{-1} = -1.96 + 0.055 T_B
\]

\((N = 31; r = 0.96; 95\% c.l. for b = 0.039-0.070)\)

with a \( Q_{10} \) value of 3.38.

Active oxygen consumption where \( T_B = 10-25C \) varies linearly with \( T_B \) according to the equation:

\[
\log W \cdot kg^{-1} = -0.59 + 0.035 T_B
\]

\((N = 28; r = 0.96; 95\% c.l. for b = 0.030-0.039)\)

and its slope has a \( Q_{10} \) value of 2.19. At \( T_B = 25-35C \) the equation for active metabolism is:
Figure 3. Relation of metabolic rate to body temperature in room temperature acclimated R. septemvittata. Points indicate mean maximum and minimum rates. Adjacent numbers represent the number of determinations (= number of individuals). Rectangles indicate mean ±2 S.E. and vertical lines indicate ranges.
Figure 3
\[ \log \frac{W}{kg^{-1}} = -0.08 + 0.015 T_B \]
(N = 23; \( r = 0.67 \); 95% c.l. for \( b = 0.009-0.021 \))

and this corresponds to a \( Q_{10} \) of 1.43.

Comparison of Flow-through and Closed Systems for Measuring Oxygen Consumption.

Individual rates of oxygen consumption of several R. septemvittata at 25, 30, 35C collected using both the flow-through system and the closed system are presented in Table 4. The least squares mean values of the two systems at those temperatures were compared with the resulting \( F \) value of 0.00006 which indicates no significant difference between the two systems.

Heart Rate during Rest and Activity.

The relationship between heart rate and body temperature during rest and electrically stimulated activity at various body temperatures is plotted semilogarithmically in Figure 4. The appropriate breaking points of the lines in Figure 4 were determined as were those in Figure 3. Both active and resting heart rates rise with increasing \( T_B \). The line equating resting heart rate to body temperature at \( T_B = 10-20C \) corresponds to the equation:

\[ \log HR = 0.429 + 0.033 T_B \] (N = 23; \( r = 0.83 \); 95% c.l. for \( b = 0.025-0.041 \))

and that for \( T_B = 20-35C \) is:
Table 4. Comparison of oxygen consumption values (W·kg⁻¹) recorded for flowthrough and closed systems.

<table>
<thead>
<tr>
<th></th>
<th>(T_B^{35})</th>
<th>(T_B^{30})</th>
<th>(T_B^{25})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flowthrough</td>
<td>0.84</td>
<td>0.50</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>1.12</td>
<td>0.56</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>0.95</td>
<td>0.56</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>0.84</td>
<td>0.45</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>0.84</td>
<td>0.50</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>0.73</td>
<td>0.50</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>0.95</td>
<td>0.61</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>0.95</td>
<td></td>
<td>0.28</td>
</tr>
<tr>
<td>Closed</td>
<td>0.78</td>
<td>0.56</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>0.95</td>
<td>0.56</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>0.89</td>
<td>0.50</td>
<td>0.28</td>
</tr>
</tbody>
</table>

**Least Squares Mean**

- **Flowthrough** = 0.56
- **Closed** = 0.56

**F value** = 0.00006 N.S.
Figure 4. Relation of heart rate to body temperature in room temperature acclimated *P. septemvittata*. Points indicate mean maximum and minimum rates. Adjacent numbers represent the number of determinations (= number of individuals). Rectangles indicate mean ±2 S.E. and vertical lines indicate ranges. Since at 35°C means, standard errors, and ranges were similar the rectangle represents active mean +2 S.E. and resting mean -2 S.E.
\[ \log HR = 0.278 + 0.069T_B \] (N = 31; \( r = 0.98 \); 95% c.l. for \( b = 0.047-0.091 \))

Their slopes have \( Q_{10} \) values of 2.16 and 4.57 respectively.

Active heart rate at \( T_B = 10-20^\circ C \) is related to body temperature by the equation:

\[ \log HR = 0.654 + 0.053T_B \] (N = 21; \( r = 0.81 \); 95% c.l. for \( b = 0.047-0.059 \))

and at \( T_B = 20-35^\circ C \) the equation is:

\[ \log HR = 1.128 - 0.029T_B \] (N = 32; \( r = 0.94 \); 95% c.l. for \( b = 0.026-0.055 \))

The slopes of these lines have \( Q_{10} \) values of 3.2 and 1.98 respectively.

Rates of Change of Body Temperature at a 10°C Difference between Ambient and Body Temperatures in Air and Water.

Heating and cooling rates were compared by calculating the instantaneous change of body temperature at 20°C; which is the experimental ambient temperature at which the difference between \( T_B \) and \( T_A \) equals 10°C during both heating and cooling. The equation for instantaneous change of body temperature is

\[ \Delta T_B/\Delta t = 2.303 S \Delta T \]

where 2.303 is the base of the natural logarithms, \( S \) is the slope of the line relating the difference between \( T_B \) and \( T_A \) with time, and \( \Delta T \) is the \( T_B - T_A \) difference at the point of evaluation (\( \Delta T = 10^\circ C \) in this case). The value of \( S \) was
determined in each case from the semilogarithmic plot of the difference between $T_A$ and $T_B$ versus time by the method of least squares regression (Figures 5, 6 and 7).

Snakes heated faster than they cooled in all cases in both air and water regardless of acclimation as shown in Figures 5, 6, and 7. The equation of the line for heating in air after snakes were acclimated at room temperature (Figure 5) as determined by least square regression is:

$$\log \Delta T = 1.17 + (-0.052)t$$

(N = 113; $r = -0.60$; 95% c.l. for $b = -0.049$ to -0.054)

while that for cooling (Figure 5) is:

$$\log \Delta T = 1.22 + (-0.039)t$$

(N = 162; $r = -0.96$; 95% c.l. for $b = -0.038$ to -0.040)

The equation of the line for heating in air after 10C acclimation (Figure 6) is:

$$\log \Delta T = 1.22 + (-0.042)t$$

(N = 184; $r = -0.93$; 95% c.l. for $b = -0.041$ to -0.043)

and that for cooling after cold acclimation (Figure 6) is:

$$\log \Delta T = 1.13 + (-0.025)t$$

(N = 303; $r = -0.92$; 95% c.l. for $b = -0.024$ to -0.025)

The 95% confidence limits of the regression coefficients do not overlap for the lines representing $\Delta T$ versus time for room temperature acclimated queen snakes (Figure 5) or for those acclimated at 10C temperatures (Figure 6).
Figure 5. Relation of the difference between $T_B$ and $T_A$ ($\Delta T$) to time in *R. septemvittata* during heating and cooling in air after room temperature acclimation. Shaded circles represent the mean $\Delta T$'s of 6 snakes at 3 minute intervals while heating. Unshaded circles represent the mean $\Delta T$'s of 6 snakes at 3 minute intervals while cooling. During heating $T_A = 30^\circ C$; during cooling $T_A = 10^\circ C$. Lines fitted by least squares regression.
Figure 5

\[ \Delta T \text{ oC} \]

\[ \text{cooling: } \log \Delta T = 1.22 + (-0.039) t \]

\[ \text{heating: } \log \Delta T = 1.17 + (-0.052) t \]
Figure 6. Relation of the difference between $T_B$ and $T_A$ ($\Delta T$) to time in *R. septemvittata* during heating and cooling in air after 10C acclimation. Shaded circles represent mean $\Delta T$'s of 8 snakes at 3 minute intervals while heating. Unshaded circles represent the mean $\Delta T$'s of 8 snakes at 3 minute intervals while cooling. During heating $T_A = 30C$; during cooling $T_A = 10C$. Lines fitted by least squares regression.
Figure 7. Relation of the difference between $T_B$ and $T_A$ ($\Delta T$) to time in room temperature acclimated $R$. septemvittata during heating and cooling in water. Shaded circles represent the mean $\Delta T$'s of 10 snakes at 10 second intervals while heating. Unshaded circles represent the mean $\Delta T$'s of 10 snakes at 10 second intervals while cooling. During heating $T_A = 30C$; during cooling $T_A = 10C$. Lines fitted by least squares regression.
This indicates that the slopes of the lines representing heating and cooling under each set of experimental conditions are different, thus it can be said that in both cases the snakes heated significantly faster than they cooled.

The equation of the line for heating in water after room temperature acclimation (Figure 7) is:

\[ \log \Delta T = 1.32 + (-0.009)t \]

\( N = 158; \ r = -0.98; \ 95\% \ c.l. \ for \ b = -0.007 \ to \ -0.011) \]

and the equation for the cooling line (Figure 7) is:

\[ \log \Delta T = 1.26 + (-0.007)t \]

\( N = 162; \ r = -0.96; \ 95\% \ c.l. \ for \ b = -0.004 \ to \ -0.009) \]

Since the 95% confidence limits for the slope value overlap the regression lines do not differ so under these circumstances queen snakes appear to heat and cool at the same rate.

Heart rates at various body temperatures during heating and cooling in air at room temperature and cold acclimation and in water after room temperature acclimation are illustrated in Figures 8, 9, and 10. The equation for the line as determined by least squares regression which corresponds to the semilogarithmic plot of heart rate versus body temperature during heating in air after room temperature acclimation (Figure 8) is:
Figure 8. Relation of heart rate to body temperature of *R. septemvittata* during heating and cooling in air after room temperature acclimation. Shaded circles represent mean heart rates of 6 snakes at 3C T<sub>B</sub> intervals while heating. Unshaded circles represent mean heart rates of 6 snakes at 3C T<sub>B</sub> intervals while cooling. Lines fitted by least squares regression.
Figure 8
Figure 9. Relation of heart rate to body temperature of *R. septemvittata* during heating and cooling in air after cold acclimation. Shaded circles represent mean heart rates of 8 snakes at 3°C $T_B$ intervals while heating. Unshaded circles represent mean heart rates of 8 snakes at 3°C $T_B$ intervals while cooling. Lines fitted by least squares regression.
Figure 9
Figure 10. Relation of heart rate to body temperature of room temperature acclimated *R. septemvittata* during heating and cooling in water. Shaded circles represent mean heart rates of 10 snakes at 3C $T_B$ intervals while heating. Unshaded circles represent mean heart rates of 10 snakes at 3C $T_B$ intervals while cooling. Lines fitted by least squares regression.
Figure 10

Relation between heart beats per minute and body temperature. The graph shows a linear correlation between heart beats per minute and body temperature, with separate lines for heating and cooling conditions.
\[ \log HR = 0.96 + (0.036) T_B \]
(N = 45; \( r = 0.97; \) 95\% c.l. for \( b = 0.033-0.041 \))

and that for cooling (Figure 8) is:
\[ \log HR = 0.73 + (0.046) T_B \]
(N = 58; \( r = 0.95; \) 95\% c.l. for \( b = 0.045-0.047 \)).

The equation for the line representing heart rate versus body temperature during heating in air after 10C acclimation (Figure 9) is:
\[ \log HR = 0.99 + (0.0347) T_B \]
(N = 181; \( r = 0.91; \) 95\% c.l. for \( b = 0.0342-0.0352 \))

and that for cooling after 10C acclimation (Figure 9) is:
\[ \log HR = 0.75 + (0.0417) T_B \]
(N = 266; \( r = 0.85; \) 95\% c.l. for \( b = 0.0411-0.0423 \)).

The slopes of the lines representing the semilogarithmic plots of heart rate at various body temperatures during heating and cooling in air after room temperature acclimation (Figure 8) are significantly different since the 95\% confidence limits of the regression coefficients do not overlap. The same is true for snakes acclimated at 10C (Figure 9). Thus, under these sets of experimental conditions heart rate during heating exceeds that during cooling.

The equation determined by least squares regression for the line representing the semilogarithmic plot of
heart rate versus body temperature during heating in water (Figure 10) is:

\[ \log HR = 0.98 + (0.034) T_B \]

(N = 79; \( r = 0.95 \); 95\% c.l. for \( b = 0.031-0.037 \))

and that for cooling (Figure 10) is:

\[ \log HR = 1.005 + (0.034) T_B \]

(N = 77; \( r = 0.93 \); 95\% c.l. for \( b = 0.030-0.037 \))

In this case the 95\% confidence limits of both the regression coefficients and the y intercept values overlap indicating that the lines are not different.

**Optimum Temperature for Myosin ATPase Activity.**

The relationship between myosin ATPase activity expressed as a percent of maximum activity from four muscle homogenates at ten temperatures (15-45C) is illustrated in Figure 11. Maximum activity of all four homogenates occurred at 28C though it should be noted that activity was not tested at 26, 27 or 29C.
Figure 11. Myosin ATPase activity as a percent of maximum at various temperatures. Shaded circles represent the mean of 4 homogenates of room temperature acclimated R. septemvittata muscle while vertical bars represent ± S.E.
DISCUSSION

Analysis of Stomach Content during Spring.

The importance of crayfish as a preferred food item of the queen snake has been discussed by several authors (listed in the Introduction). The major studies for which seasonal data concerning gut content of the queen snake include that of Raney and Roecker (1947) in which data for spring, summer, and fall are not presented separately; and Branson and Baker (1974) which includes only summer analyses. This study attempts to determine if shifts in preferred food items or feeding frequency of the queen snake occur in the spring in central Ohio.

Strecker (1927) and Hall (1969) suggest that R. grahami, while preferring a diet of crayfish, shifts to small fish and amphibians when crayfish are not prevalent. Adult R. alleni also prefer crayfish (Franz, 1977) though 96% of the food of juveniles in south Florida was odonate naiads (Godley, 1976). During the colder spring and fall months in Ohio it is possible that adult queen snakes forage in terrestrial habitats in order to avoid low water temperatures.
Raney and Roecker (1947) state that 97.8% of the food material contained in 45 queen snake stomachs collected in spring, summer, and fall in New York was crayfish. Crayfish constituted 98.1% of the food material from 110 queen snakes during summer in Kentucky (Branson and Baker, 1974). The results of the present study offer no indication of a shift in food preference since 94.1% of the stomachs with food contained crayfish.

Branson and Baker (1974) state that 91.7% of the snakes analyzed for gut content during their summer study contained food material. Only 56.6% of the snakes in the present study contained food, which may suggest a lower feeding frequency in the spring.

Little is known about the spring ecology of this snake. Conant (1938b) reported that queen snakes in Lucas County, Ohio are not active until early May, while Branson and Baker (1974) list early April as the period of spring emergence in Kentucky. The present study shows that, at least in one year, queen snakes were active as early as late March in central Ohio, when water temperatures were well below the mean $T_B$ reported by Brattstrom (1965) of 25.6°C for all the snake species studied, the mean $T_B$ of 205 queen snakes of 25.6°C reported by Branson and Baker (1974), and the mean $T_B$ of 38 queen snakes of 27.2°C reported elsewhere in this paper. Since the snake has a limited diet,
more information is necessary to understand why it may be active during periods when thermal stress associated with aquatic feeding may be high and when snakes may feed less frequently or with lowered success (cf. Greenwald, 1974, on strike success with regard to body temperature in Pituophis).

One possible reason for early spring emergence may be that the queen snakes breed during this period before dispersal. Aleksiuk and Gregory (1974) described the spring courtship and mating behavior of extremely large aggregations of red-sided garter snakes (Thamnophis sirtalis parietalis) and they found an inverse relationship between feeding frequency and reproductive behavior in laboratory studies. Wood (1944) and Wood and Duellman (1950) have reported large aggregations of queen snakes in the fall. During the spring, I have encountered aggregations of 20 and 17 queen snakes on two rocky outcrops along the Olentangy River. These outcrops are probably queen snake hibernacula but no breeding behavior has been observed at either of them. Several captive queen snakes have bred during the spring in the laboratory. Hopefully, close observation of these two "hibernacula" will offer more information concerning early spring emergence, feeding, and reproductive behavior of this snake.
Eccritic and Preferred Body Temperatures.

Brattstrom (1965) reports 27.5°C to be the mean field (eccritic) \( T_B \) of twelve natricine snakes representing three species and for all snakes \((N = 914)\) he lists a mean \( T_B \) of 25.6°C. Since during parts of its seasonal activity period the queen snake may be subjected to cold environmental temperatures when foraging for food, this study attempts to determine if the queen snake differs from other colubrid snakes with regard to eccritic or preferred temperatures.

The mean field body temperature of the queen snake found in this study is 27.2°C suggesting that the queen snake is similar to other colubrid snakes with regard to eccritic temperature. The regression line relating \( T_B \) and \( T_A \) in Figure 1 crosses the theoretical line \( T_B = T_A \) at 28.3°C. It has been suggested that the point at which the regression line crosses the theoretical line is the actual preferred ambient temperature of the animal. At ambient temperatures above this preferred level the snakes are believed to seek shelter (Dmi'el and Borut, 1972). The present data support this theory since only 3 snakes (7.8%) were captured at ambient temperatures in excess of 28°C.

Since all but 4 data points in Figure 1 lie above the theoretical line at which \( T_B \) would equal \( T_A \) it appears that the snakes are actively regulating their body
temperatures above ambient temperatures. The most obvious mechanism for this thermoregulation is basking and 71% of the captures listed in Table 2 are of basking snakes.

Several queen snakes were captured at $T_B$'s higher than the eccritic mean of 27.2C and the theoretical preferred ambient temperature of 28.3C. These snakes may be preparing to enter the water to cool, seek shelter, forage for food, or may be adjusting to some special physiological function such as digestion since studies have shown that for other reptiles the process of digestion increases with increasing temperatures (cf. Licht, 1964; Skoczylas, 1970).

The mean field body temperature of 205 queen snakes reported by Branson and Baker (1974) is 25.6C. This figure also supports the contention that the eccritic temperature of the queen snake is similar to other colubrid snakes. The fact that eccritic temperature reported in the present study is somewhat higher than that in the previous literature is probably reflective of the fact that a high percentage of the captures were of basking snakes.

It has been suggested that eccritic temperatures are not indicative of the temperatures which reptiles actually prefer for in the field they are subjected to higher temperatures than they would choose in a thermal gradient. Licht et al. (1966) defined the preferred body temperature
as the mean temperature selected by an animal under thermal gradient conditions. This preferred temperature is usually lower than the mean field body temperatures. The preferred body temperature of the queen snake (23.6°C) in a thermal gradient was found to be 3.6°C lower than the ectricitic temperature reported in this study.

When the points in Figure 2 which relates preferred body temperature to time of day are connected, a bimodal curve is produced which suggests a crepuscular activity cycle with peak activity periods occurring in early morning and late afternoon. The crayfish which are available to the queen snake in the Olentangy and Scioto Rivers are primarily nocturnally active (cf. Turner, 1926; Crocker and Barr, 1968). Thus, the crepuscular pattern of this snake may not appear to have selective advantage for feeding. But very little is known of the feeding habits of the queen snake. Perhaps crayfish are sought out from places of retreat thus limiting the possibility for an alert crayfish to escape. Another advantage of the crepuscular activity cycle is the avoidance of the very warm midday ambient temperatures while activity occurs during parts of the day when body temperature could still be effectively raised through basking.

**Thermal Acclimation of C T Min and C T Max.**

Several studies have demonstrated that thermal acclimation of some physiological parameters such as critical
temperatures, and aerobic metabolism does occur in some cold acclimated reptiles (Vance, 1953; Lowe and Vance, 1955; Dawson and Bartholomew, 1956; Stewart, 1965; Jacobson and Whitford, 1970; Dutton and Fitzpatrick, 1975). Since the queen snake is a temperate zone reptile exposed to cool temperatures in spring and fall, and warmer temperatures during summer it is reasonable to expect some variation in physiological requirements of this snake with season. A shift in C T Min and/or C T Max occurring after acclimation at varying temperatures is an index of the ability of an animal to thermally acclimate.

The results of the present study of the queen snake indicate that thermal acclimation of C T Min occurs but not of C T Max. (Possibly exposure to a temperature somewhat lower than 32C would have caused C T Max acclimation.) A more pronounced acclimation of C T Min than C T Max was reported for the red-sided garter snake (T. sirtalis concinnus) and the northwestern garter snake (T. ordinoides) by Stewart (1965), and for the western ribbon snake (T. proximus) and the diamond-backed water snake (N. rhombifera) by Jacobson and Whitford (1970). The possibility that acclimation of C T Min may be more important than that of C T Max in terms of geographic distribution and seasonal activity periods for temperate zone snakes was addressed by Jacobson and Whitford (1970). The
results of the present study are in agreement with this contention. The lower C T Min which accompanies cold acclimation probably allows the queen snake to be more active during cold periods such that it may be able to move to basking sites where preferred temperature can then be achieved.

Since queen snakes probably seek shelter during very warm parts of the day they would probably avoid temperatures near the C T Max. (See Discussion of Eccritic and Preferred Body Temperature.)

**Oxygen Consumption.**

**Effects of temperature on metabolic rate.** Both resting and active metabolic rates of the queen snake increase with increasing body temperatures (see Figure 3). The $Q_{10}$ value for metabolic rate of resting queen snakes between 10 and 20°C is 1.96; and that between 20 and 35 is 3.38. The lower $Q_{10}$ value between 10 and 20°C for resting metabolism may suggest that the rate of change of this metabolism is slowed which would allow the snake to be somewhat alert when subjected to cool temperatures. Several authors (Benedict, 1932; Buikema and Armitage, 1969; Jacobson and Whitford, 1970; and Aleksiuk, 1971a) have noted that some snakes exhibit a metabolic plateau occurring where metabolic rate remains somewhat constant over several degrees Celsius (i.e. $Q_{10}$ values are near 1.0).
This has been interpreted as a thermal independence of metabolism over these temperature ranges. While no such plateau exists for the queen snake during rest, it can be said that metabolic changes of this snake are more dependent on changes in body temperature at higher temperatures (20-35C) than at lower temperatures (10-20C).

During activity the $Q_{10}$ value for metabolic rate of the queen snake is 2.19 between 10 and 25C and 1.43 between 25 and 35C. This may indicate that near 25C the upper limit of active metabolic rate is being approached, and that metabolic changes are more temperature dependant at low than at high body temperatures during activity. Decreased heat production during activity with increasing body temperatures could allow the queen snake to remain at preferred temperature for a longer period.

Resting metabolism and body size. Bennett and Dawson (1976) combined all data from previous literature concerning metabolism of snakes and calculated the least squares regression of metabolic rate on body weight at 30C to be:

$$
cc \ 0_2 \ h^{-1} = 0.280g^{0.76}
$$

or

$$
cc \ 0_2 \ g^{-1}.h^{-1} = 0.280g^{-0.24}
$$

(N = 13; r = 0.91; 95% c.l. for b = 0.69 and 0.83).

That same relationship calculated for the queen snake in the present study is:
\[ cc \text{ O}_2 \cdot h^{-1} = 0.386g \cdot 0.68 \]

or

\[ cc \text{ O}_2 \cdot g^{-1} \cdot h^{-1} = 0.386g \cdot 0.32 \]

\((N = 7; r = 0.89; 95\% \text{ c.l. for } b = 0.53 \text{ and } 0.82)\)

The overlapping 95\% confidence limits for the \(b\) values indicates that they do not differ significantly. The relationship of metabolic rate to body weight of seven queen snakes at 30\(^\circ\)C is plotted in Figure 12. The mean weight of the seven queen snakes included here is 73g. If this figure is substituted in Bennett and Dawson's (1976) equation a metabolic rate of 0.10 \(cc \text{ O}_2 \cdot g^{-1} \cdot h^{-1} (0.56W\cdot kg^{-1})\) is calculated for the queen snake at 30\(^\circ\)C. The actual mean metabolic rate of the seven queen snakes at 30\(^\circ\)C determined in the present study is 0.09\(cc \text{ O}_2 \cdot g^{-1} \cdot h^{-1} (0.50W\cdot kg^{-1})\) which is about 11\% lower than the value predicted by Bennett and Dawson's equation.

The equation describing the relationship of metabolism to body weight is:

\[
\text{metabolic rate} = a \cdot \text{body weight}^b
\]

where \(a\) is a proportionality constant characterizing that variable for the animal group, and \(b\) describes the effect of body size on the variable (cf. Bartholomew, 1977a). The \(b\) value reported here is similar to those reported for other snakes by Vinegar et al. (1970), Dmi'el and Borut (1972), and Dmi'el (1972) but differs from the findings of
Figure 12. Relation of oxygen consumption to body weight of seven *R. septemvittata* at 30°C.
Figure 12
Galvão et al. (1965). Hemmingson (1960) reviewed all data concerning energy metabolism and body size and concluded that a b value of 0.75 allows the best fit of all data for unicellular organisms, multicellular plants and metazoans. The value of b reported in this study is not significantly different from that of Hemmingson's.

Comparison with other snakes. Kleiber (1961) explains that large animals may have a lower metabolic rate on a per gram basis than those which are small. Of the temperate zone snakes that have been tested for metabolism the group of queen snakes in this study has a mean weight greater than Diadophis punctatus (Buikema and Armitage, 1969), Storeria dekayi (Clausen, 1936) and T. proximus (Jacobson and Whitford, 1970) and has a mean metabolic rate which is lower than these snakes by 46%, 85%, and 66% respectively at 30C. The group is similar in size to Salvadoria hexalepis (Jacobson and Whitford, 1971) and has a metabolic rate 18% lower at 30C. The metabolic rate reported by Greenwald (1971) for Pituophis catenifer affinis, nearly 8 times the mean weight of the queen snakes in the present study, is about one half that of the queen snake group at 30C. It is interesting to note that the mean metabolic rate of the queen snakes in this study is only 4% higher than that reported for a group of Natrix rhombifera at 30C (Jacobson and Whitford, 1970) which weigh over 3 times as much as the queen snakes. Both species are water
snakes of the subfamily Natricinae which may suggest similarities in this parameter at the subfamily level which may be linked to habitat preference (cf. McNab, 1970 for discussion of energetics of temperature regulation in relation to climate and food habits of birds and mammals). More information concerning metabolism of water snakes is necessary before such a relationship can be confirmed.

**Heart Rate**

Effect of temperature on heart rate. Both resting and active heart rates of queen snakes increase with increasing body temperatures (see Figure 4). The $Q_{10}$ value for resting heart rate between 10 and 20°C is 2.16, and between 20 and 35°C is 4.57. During activity the $Q_{10}$ value between 10 and 20°C is 3.2 and between 20 and 35 is 1.98. Though heart rate does not increase in exactly the same manner as oxygen consumption the fact that the $Q_{10}$ values for heart rate are greater than those for metabolism at all temperature ranges implicates heart rate changes as a strong contributor to increases in oxygen transport with temperature. Templeton (1970) reviewed heart rate and metabolic data for ten species of lizards and found that the $Q_{10}$ for heart rate between 20 and 40°C was lower than that for metabolism. Greenwald's (1970) data show that for the gopher snake the $Q_{10}$ of heart rate may be either higher or lower than that of oxygen consumption depending
on temperature and activity state. These authors suggest
that changes in heart rate alone are not sufficient to
explain differences in oxygen transport with temperature
and that changes in stroke volume and/or oxygen extraction
between arterial and venous blood are probably occurring
to account for some of this change. While changes in heart
rate of the queen snake with temperature appear to be
adequate to account for differences in metabolism the
possibility of changes in either of the other contributors
to oxygen transport cannot be discarded simply on the
basis of $Q_{10}$ values.

**Effect of body weight on heart rate.** Licht (1965)
collected heart rate data of several lizard species ranging
in weight from 70 to 400g and found that lizard heart rate
at 30C could be predicted with reasonable accuracy using
the equation:

$$\text{heart beats} \cdot \text{min}^{-1} = 153W^{-0.207}$$

I know of no such equation that has been calculated for
snakes. The mean weight of the seven snakes from which
resting heart rates were collected is 68.2g. If this
figure is used in Licht's equation for lizards a heart rate
of 64 beats $\cdot$ min$^{-1}$ is predicted which is quite similar to
the actual resting heart rate of the queen snake at 30C of
66 beats $\cdot$ min$^{-1}$. 
Comparison with other snakes. A mean heart rate of 58/min at 25C was reported by Mullen (1967) for 30 species of snakes representing four different families. The heart rate of the queen snake at 25C during rest is 26/min. The possibility that Mullen's data may be elevated since the snakes he used were anesthetized with pentobarbital was noted by Greenwald (1971). Heart rates of several other snakes at various body temperatures and at various levels of activity are presented in Table 5 as a percentage of those values for the queen snake. The data in the table suggest that at rest the heart rate of the queen snake is less than that of the other three snakes at temperatures between 10 and 25C except for that of the gopher snake at 20C. Above 25C the heart rate of the queen snake is slightly higher than that of the others. During activity queen snake heart rate is quite similar at 10 and 20C to the two snakes for which data are available, and slightly higher at temperatures above 20C. One might have expected the heart rate of the queen snake to be consistently higher than those of S. cliffordi or P. c. affinis since the queen snake is smaller than the latter two. (cf. Templeton, 1970; White, 1976.) The reverse may have been expected for queen snake heart rate in comparison to S. hexalepis since the queen snake is the larger. Since such relationships do not consistently occur body temperature
Table 5. Some snake heart rates expressed as a percentage of that of *R. septemvittata*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Wt range (g)</th>
<th>Condition</th>
<th>Heart rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>10</td>
</tr>
<tr>
<td><em>S. hexalepis</em></td>
<td>65</td>
<td>resting</td>
<td>175</td>
</tr>
<tr>
<td></td>
<td></td>
<td>active</td>
<td>-</td>
</tr>
<tr>
<td><em>S. cliffordi</em></td>
<td>100-500</td>
<td>resting</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>active</td>
<td>-</td>
</tr>
<tr>
<td><em>P. c. affinis</em></td>
<td>396-961</td>
<td>resting</td>
<td>150</td>
</tr>
<tr>
<td></td>
<td></td>
<td>active</td>
<td>106</td>
</tr>
</tbody>
</table>

1 From Jacobson and Whitford, 1971.
2 Mean weight at 30C taken from Bennett and Dawson, 1976 (Table 7).
3 From Dmi'el and Borut, 1972.
4 From Greenwald, 1971.
appears to have more of an effect on heart rate of the queen snake than does body size.

A slow heart rate at lower temperatures could reduce heat loss from the body when environmental temperatures drop. A fast heart rate at higher temperatures could help present more oxygen to the tissues when activities of digestion, foraging, or seeking shelter for example might occur. These changes could occur if changes in the other components of cardiac output do not affect the heart rate changes.

**Metabolic Scope, Heart Rate Increment, and Oxygen Pulse.**

The aerobic metabolic scope, first discussed by Fry (1947) is an indirect measure of the capacity of an animal for activity and is defined as the difference between maximal and minimal metabolic rates. Moberly (1968) suggests that since reptiles depend to a large extent on anaerobic processes one must realize that metabolic scope considers only aerobic energy expenditures. Several authors have attempted to relate the value of metabolic scope to preferred temperature with little success (Dawson, 1967; Tucker, 1967; Templeton, 1970). Since reptiles appear to prefer certain temperature ranges one might expect these preferences to be reflected in higher scope values as the animals may perform various daily activities at these temperatures. Wilson (1974)
reviewed some of the previous data concerning metabolic scope and preferred temperature and found that aerobic scope does appear to be maximal near preferred temperatures. Both Greenwald (1971) and Dmi'el and Borut (1972) found maximum scope values to be near the preferred temperatures of the snakes they studied. The metabolic scope values for the queen snake are plotted in Figure 13 (dashed line). The scope value does not peak for this snake but continues to rise throughout the temperature range that was studied. However, there is an obvious change in the slope of this curve above 25C where the curve appears to plateau. The plateau begins near the mean field body temperature (27.2C) and preferred temperature (23.6C) reported for the queen snake elsewhere in this study. This suggests that at 25C the scope of the queen snake is very near the maximum value.

The maximum scope value for the queen snake (1.92 W·kg\(^{-1}\) at \(T_B = 35C\)) is 82% of the maximum scope value reported by Greenwald (1971) for \(P. c. affinis\), 130% of that reported by Dmi'el and Borut (1972) for \(S. cliffordi\), and 384% of that reported by Hutchison et al. (1966) for brooding \(Python molurus\).

Heart rate increment is calculated as the difference between active and resting heart rates at a given temperature. The heart rate increment for the queen snake is
Figure 13. Relation of metabolic scope and heart rate increment to body temperature in room temperature acclimated R. septemvittata. Metabolic scope is represented by the dashed line, and heart rate increment by the solid line. Data points represent differences between mean active and resting oxygen consumption and heart rate values from Figures 3 and 4 respectively.
HEART RATE INCREMENT
BEATS/MIN.

50 40 30 20 10 8 6 5

0.5 0.6 0.7 0.8 0.9 1.0 2.0 3.0 35

BODY TEMPERATURE °C

METABOLIC SCOPE

6 W·K\(^{-1}\)·m\(^{-2}\)

Figure 13
plotted in Figure 13 (solid line) and a peak occurs at 25°C which is near this snake's mean field body temperature and preferred temperature. Similar peaks in heart rate increment near preferred body temperatures have been reported for lizards (Bartholomew et al., 1965; Moberly, 1968), and for one snake (Dmi'el and Borut, 1972).

It is apparent in Figure 13 that heart rate increment changes with temperature are somewhat similar to metabolic scope changes between 10 and 25°C which may implicate heart rate as a major factor in increased oxygen transport during activity.

The Fick equation states that:

\[ \text{Oxygen consumption} = \text{Heart rate} \times \text{Stroke volume} \times \text{A-V difference} \]

In the present study of the queen snake both oxygen consumption and heart rate were measured, thus by rearranging the Fick equation such that:

\[ \frac{\text{Oxygen consumption}}{\text{Heart rate}} = \text{Stroke volume} \times \text{A-V difference} \]

a quantification of \((\text{Stroke volume} \times \text{A-V difference})\) is possible. This parameter is called the oxygen pulse and the values of oxygen pulse for the queen snake during rest and activity are listed in Table 6. These values change very little with temperature while the queen snake is at rest indicating that increases in heart rate alone are probably sufficient to meet the increased metabolic demands. During activity changes in oxygen pulse are greater at each
Table 6. Oxygen pulse at various body temperatures for *R. septemvittata* acclimated at room temperature.

<table>
<thead>
<tr>
<th>TB</th>
<th>$\text{O}_2\text{Pulse (x 10}^{-5}\text{)}$</th>
<th>Contribution of heart rate to increased $\text{O}_2$ transport</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>cc $\text{O}_2$ g$^{-1}$:beat$^{-1}$</td>
<td>Rest</td>
</tr>
<tr>
<td>10</td>
<td>3.62</td>
<td>11.72</td>
</tr>
<tr>
<td>15</td>
<td>3.44</td>
<td>8.44</td>
</tr>
<tr>
<td>20</td>
<td>3.28</td>
<td>8.19</td>
</tr>
<tr>
<td>25</td>
<td>2.93</td>
<td>7.56</td>
</tr>
<tr>
<td>30</td>
<td>2.44</td>
<td>6.57</td>
</tr>
<tr>
<td>35</td>
<td>2.07</td>
<td>5.96</td>
</tr>
</tbody>
</table>
temperature than at rest. Since both metabolic scope and heart rate increment have been calculated, a value for the percent contribution of heart rate to the increased oxygen transport with activity can be calculated (see Gatten, 1974b for derivation of this equation). Table 6 shows that increases in heart rate account for between 4.1% and 33.5% of the increased oxygen transport during activity. Thus the increased oxygen demands of activity are met by changes in stroke volume and/or A-V difference.

The oxygen pulse value reported for the queen snake at 30°C is within the range limits of $1.0 \times 10^{-5}$ to $5.0 \times 10^{-5}$ cc O$_2$ ·g$^{-1}$·beat$^{-1}$ for resting reptiles (Dawson, 1967; Jacobson and Whitford, 1970, 71; Templeton, 1970; Vinegar et al., 1970; Wilson and Lee, 1970; Greenwald, 1971; Wilson, 1971; Bennett, 1972; Dmi'el and Borut, 1972; Gatten, 1974a). The active oxygen pulse value at 30°C reported here is within the range of $3 \times 10^{-5}$ to $16.31 \times 10^{-5}$ cc for that of active reptiles (Bartholomew & Tucker, 1963; Bartholomew et al., 1965; Licht, 1965; Moberly, 1968; Wilson and Lee, 1970; Greenwald, 1971; Wilson, 1971; Bennett, 1972; Bennett and Dawson, 1972; Dmi'el and Borut, 1972; Gatten, 1974a).

The oxygen pulse increment is the difference between resting and active oxygen pulse values at a given temperature (Gatten, 1974a) and these values for the queen snake
are included in Table 6. At 30C this value for the queen snake is similar to that reported for the gopher snake of 6.55 (Greenwald, 1971) and for *S. cliffordi* of 3.79 (Dmi'el and Borut, 1972) at 30C. The oxygen pulse increment values indicate that changes in stroke volume and/or A-V difference are more important as contributors to oxygen transport at low than at high temperatures for the queen snake.

**Ecological implications.** Values of active oxygen consumption and heart rate expressed as multiples of resting values for *P. c. affinis* were presented by Greenwald (1971). The greatest increase of oxygen consumption with activity occurred at 30C. In a more recent study (Greenwald, 1974) strike success and prey capture by gopher snakes was highest at body temperatures between 27C and 33C. Greenwald suggests that the ability to increase active metabolism over resting metabolism at this temperature may be responsible for the greater success of strike and capture.

Values of these parameters for the queen snake and the two other snakes for which data are available are listed in Table 7 and illustrated in Figure 14. *S. cliffordi* and *P. c. affinis* are both desert snakes while the queen snake is semi-aquatic. The data for *S. cliffordi* was estimated from Dmi'el and Borut (1972) and
Table 7. Values of active oxygen consumption ($O_2$ cons.) and heart rate (H.R.) of several snakes expressed as multiples of resting values.

<table>
<thead>
<tr>
<th>Species</th>
<th>Parameter</th>
<th>10</th>
<th>15</th>
<th>20</th>
<th>25</th>
<th>30</th>
<th>35</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. catenifer</em></td>
<td>$O_2$ cons.</td>
<td>4.1</td>
<td>-</td>
<td>8.3</td>
<td>-</td>
<td>11.6</td>
<td>3.8</td>
<td>[Greenwald (1971)]</td>
</tr>
<tr>
<td></td>
<td>H.R.</td>
<td>1.7</td>
<td>-</td>
<td>3.1</td>
<td>-</td>
<td>2.4</td>
<td>3.8</td>
<td></td>
</tr>
<tr>
<td><em>S. cliffordi</em></td>
<td>$O_2$ cons.</td>
<td>-</td>
<td>4.1</td>
<td>4.2</td>
<td>3.8</td>
<td>2.1</td>
<td>2.7</td>
<td>[Dmi'el &amp; Borut (1972)]</td>
</tr>
<tr>
<td></td>
<td>H.R.</td>
<td>-</td>
<td>1.4</td>
<td>1.7</td>
<td>1.5</td>
<td>1.4</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td><em>R. septemvittata</em></td>
<td>$O_2$ cons.</td>
<td>8.2</td>
<td>8.5</td>
<td>9.6</td>
<td>7.9</td>
<td>4.3</td>
<td>3</td>
<td>[Present study]</td>
</tr>
<tr>
<td></td>
<td>H.R.</td>
<td>2.5</td>
<td>3.3</td>
<td>3.8</td>
<td>3</td>
<td>1.6</td>
<td>1.1</td>
<td></td>
</tr>
</tbody>
</table>
Figure 14. Relation of active oxygen consumption expressed as multiples of resting oxygen consumption to body temperature of 3 snakes. Data points for *P. catenifer* from Greenwald (1971) and for *S. cliffordi* from Dmi'el and Borut (1972).
Figure 14
there is some doubt that maximum activity was induced for these snakes (cf. Bennett and Dawson, 1976).

The capacity of the queen snake to increase metabolism at 10C is twice that of P. c. affinis. Since resting oxygen consumption is similar at 10C this increase is absolute and indicates that the queen snake can be more active at 10C temperatures than the gopher snake. There is little change in this value for the queen snake through 25C. The fact that this value at 30C is less than half that for the gopher snake may be misleading when presented in this manner. At 30C the active metabolic rates for the two snakes are quite similar although the resting rate for the queen snake is much higher than that of the gopher snake.

The maximum aerobic metabolic scope of the gopher snake occurs at the same temperature as the maximum value of active oxygen consumption expressed as a multiple of that of resting (Greenwald, 1971). This situation does not occur with the queen snake since maximum aerobic scope value occurs at a body temperature of 35C and the values of the multiples are highest at the four lowest temperatures.

Since the queen snake must forage for food in waters that are cooler than air temperature, especially in the spring and fall, the capacity to increase metabolic rate during activity at low temperatures may have selective value. Such a suggestion is reasonable if this capacity
for activity is linked to strike or capture success.

Rate of Change of Body Temperature.

In a study of the control of body temperature of *Amphibolurus barbatus* Bartholomew and Tucker (1963) discussed the evolution of homeothermy in relation to rates of temperature change in reptiles. The fact that these animals can heat fast and cool slowly enables them to spend more time near their preferred body temperatures. The difference in rate of heat loss or gain by these animals is accomplished partially by metabolic alterations in response to temperature change but primarily through peripheral vasodilation during heating and vasoconstriction during cooling. This, they suggest, may have been an early step in the evolution of constant body temperature maintenance.

The rates of heating and cooling of the queen snake at various acclimation temperatures and in different media are presented in Table 8. When heated and cooled in water the rate of change of body temperature during both heating and cooling of room temperature acclimated queen snakes is over ten times those tested in air which is expected due to the differences in conductive properties of the two media. However, the ratios of heating rate to cooling rate are similar in both air and water.

The rates of heating, and cooling, and the ratio of cooling to heating of 10C acclimated queen snakes tested
Table 8. Heating and cooling rates (°C/min) of R. septemvittata in air and water.*

<table>
<thead>
<tr>
<th>T&lt;sub&gt;B&lt;/sub&gt; °C</th>
<th>ΔT</th>
<th>AIR (Room temperature acclimation)</th>
<th>AIR (10° acclimation)</th>
<th>WATER (Room temperature acclimation)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Heating Cooling Heating</td>
<td>Heating Cooling Heating</td>
<td>Heating Cooling Heating</td>
</tr>
<tr>
<td>20</td>
<td>10</td>
<td>1.198 0.898 0.750</td>
<td>0.967 .576 .595</td>
<td>12.44 9.26 0.744</td>
</tr>
</tbody>
</table>

* Instantaneous rate = 2.303 m ΔT
Figure 15. Relation of the difference between $T_B$ and $T_A$ ($\Delta T$) to time in *R. septemvittata* during heating (h) and cooling (c) in air after both room temperature (solid lines) and 10C (dashed lines) acclimation. Ambient conditions as in Figures 5 and 6. Lines fitted by least squares regression.
in air are respectively 19, 36, and 21% lower than those of room temperature acclimated snakes tested in air. This suggests that with cold acclimation heat flow during both heating and cooling is slowed. The effect of this phenomenon on the slopes of the heating and cooling curves is illustrated in Figure 15. The slopes of the heating lines for room temperature and 10°C acclimated snakes in Figure 15 are different since the 95% confidence limits of the regression coefficients do not overlap. This is also true of the cooling lines in Figure 15.

Changes in heart rate during heating and cooling for the two acclimation groups are illustrated in Figure 16. The slopes of the lines representing heart rates during cooling for room temperature and 10°C acclimated queen snakes are significantly different since no overlap occurs between the 95% confidence limits of the regression coefficients. However, an F-test reveals that the slopes of the lines representing heart rates during heating for room temperature and cold acclimated queen snakes are not different [P (F.05,1,222) = .34]. Thus, while changes in heart rate may facilitate slow cooling with cold acclimation, there is no such relationship which explains the slower heating rates. Possibly some component of the factors which limit heat loss during cooling after cold acclimation also limits heat gain during heating. The
Figure 16. Relation of heart rate to body temperature of *R. septemvittata* during heating (h) and cooling (c) in air after both room temperature (solid lines) and 10C (dashed lines) acclimation. Ambient conditions as in Figures 8 and 9. Lines fitted by least squares regression.
Figure 16
possibility of some type of physiological or biochemical adaptations to cold acclimation such as cell or cell membrane compositional changes, metabolic changes, insulatory changes, and other cardiovascular changes needs to be considered for adequate interpretation of this finding.

Slower cooling of the queen snake after cold acclimation would be advantageous during cold periods of activity but it is difficult to see that slow heating would be beneficial. Perhaps this situation represents a selective tradeoff which may be ultimately beneficial to this snake when active at cold temperatures.

Ecological implications. The Galapagos marine iguana (A. cristatus) is somewhat ecologically similar to the queen snake in that it is an underwater forager (though vegetarian) and feeds in waters that are quite cool compared to its preferred temperature. Studies by Bartholomew and Lasiewski (1965) and Bartholomew (1965) show that heat flow from the marine iguana to the cool water is slowed to such an extent that theoretically this animal could forage for about 20 minutes before its body temperature reaches that of ambient.

Up to now the marine iguana is the only reptile to be tested for rates of temperature change in water. The ecological similarities of the semi-aquatic habits of the queen snake and the marine iguana warrant a comparison of
heating and cooling rates of these species in both air and water.

All workable data concerning the ratio of cooling to heating rates of reptiles is presented in Table 9. This ratio for room temperature acclimated queen snakes tested in both air and water appears to be more similar to those of terrestrial reptiles than to the marine iguana. It is important to note that ratios of cooling to heating rates of the marine iguana are similar in both air and water, as are those of the room temperature acclimated queen snake.

All studies of rate of change of body temperature of reptiles from previous literature are of animals acclimated at room temperature or recently captured in the field. When queen snakes are acclimated at 10°C and tested for rate of change of body temperature in air the ratio of cooling to heating becomes more similar to that of the marine iguana (Table 9). Furthermore, if the ratio of cooling to heating of cold acclimated queen snakes tested in water is similar to that in air, as is the case with the marine iguana and the room temperature acclimated queen snake, then cold acclimated queen snakes may be able to spend more time foraging for crayfish when water temperatures are cool. Room temperature acclimated queen snakes cool to ambient water temperatures from 30°C to 10°C in about 3 minutes in the laboratory (see Figure 7). A
Table 9. The ratio of cooling to heating rates (C/H) of several reptiles.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Temp. Range Tested °C</th>
<th>Wt Gm</th>
<th>C/H Air</th>
<th>C/H Water</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lizards</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. barbatus</em></td>
<td>2</td>
<td>40-20</td>
<td>442-482</td>
<td>0.64-0.71</td>
<td>-</td>
<td>Bartholomew &amp; Tucker, (1963)</td>
</tr>
<tr>
<td><em>Varanus sp.</em></td>
<td>9</td>
<td>40-20</td>
<td>16-4008</td>
<td>x = 0.88</td>
<td>-</td>
<td>Bartholomew &amp; Tucker, (1964)</td>
</tr>
<tr>
<td><em>A. cristatus</em></td>
<td>1</td>
<td>40-20</td>
<td>652</td>
<td>0.52</td>
<td>0.48-0.55</td>
<td>Bartholomew &amp; Lawiewski, (1965)</td>
</tr>
<tr>
<td><em>T. scincoides</em></td>
<td>2</td>
<td>40-20</td>
<td>512-420</td>
<td>0.85-0.90</td>
<td>-</td>
<td>Bartholomew et al., (1965)</td>
</tr>
<tr>
<td><em>D. dorsalis</em></td>
<td>19</td>
<td>39-20</td>
<td>x = 54</td>
<td>0.88</td>
<td>-</td>
<td>Weathers, (1970)</td>
</tr>
<tr>
<td>Snakes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. cliffordi</em></td>
<td>21</td>
<td>35-15</td>
<td>106-508</td>
<td>0.82</td>
<td>-</td>
<td>Dmi'el &amp; Borut, (1972)</td>
</tr>
<tr>
<td><em>R. septemvittata</em></td>
<td>8</td>
<td>30-10</td>
<td>56-101</td>
<td>0.75</td>
<td>0.74 (N=10)</td>
<td>Present study</td>
</tr>
<tr>
<td>(room temp. acclim.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R. septemvittata</em></td>
<td>8</td>
<td>30-10</td>
<td>48-66</td>
<td>0.60</td>
<td>-</td>
<td>Present study</td>
</tr>
<tr>
<td>(cold acclim.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
cooling to heating ratio of 0.60 for cold acclimated queen snakes tested in water would represent a 19% increase (about 34 seconds) in the length of time the animal could spend under these laboratory conditions before cooling to ambient temperature. Such an adaptation to cold may have high selective value to an animal such as the queen snake whose survival may be limited by cold temperature feeding behavior.

**Thermal conductance.** Several mechanisms for physiological regulation of body temperature of lizards during heating and cooling were discussed by Bartholomew and Tucker (1965). Of these mechanisms, changes in surface area, color, and rates of evaporative water loss with ventilation were considered insignificant, and the most important factors were changes in metabolic rate and blood flow.

Newton's Law of Cooling which states that change in heat content of a body per unit time \( \frac{\Delta H}{\Delta t} \) is proportional to the difference between its temperature and that of ambient:

\[
\frac{\Delta H}{\Delta t} = C \left( T_B - T_A \right)
\]

where \( C \) is thermal conductance, which is the rate of heat transfer per degree centigrade difference between \( T_B \) and \( T_A \). When the specific heat of the organism (see Morrison and Tietz, 1957) and its metabolic heat production are
known, $C$ can be calculated with the equation

$$C = C' - \frac{M}{T_B - T_A}$$

where $C'$ is the apparent thermal conductance which can be calculated with the slopes of the heating and cooling curves and $M$ is metabolic rate (see Bartholomew and Tucker, 1963 for derivation of this equation).

Values of thermal conductance of room temperature acclimated queen snakes tested in air and water are listed in Tables 10 and 11. Heart rates for room temperature acclimated queen snakes during heating and cooling in both air and water were always more similar to those measured during electrically stimulated activity than to those of resting snakes. Heart rate during heating and cooling has been used as an index of metabolic rate in previous studies (Bartholomew and Tucker, 1963; Bartholomew and Lasiewski, 1965; Bartholomew et al., 1965); however, the only one that reported them to be similar during both heating and cooling is Bartholomew and Tucker (1964). Thus for calculation of thermal conductance corrected for metabolism in Tables 10 and 11 during both heating and cooling, active metabolic rates measured at the various constant body temperatures were used in the equation. Since the ratios of thermal conductance during cooling to those during heating when corrected for metabolic heat production in Tables 10 and 11 do not approach unity
Table 10. Thermal conductance of *R. septemvittata* in air after room temperature acclimation.

<table>
<thead>
<tr>
<th>Body temperature</th>
<th>Uncorrected for metabolism</th>
<th>Corrected for metabolism</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Heating</td>
<td>Cooling</td>
</tr>
<tr>
<td>15</td>
<td>1.110</td>
<td>0.833</td>
</tr>
<tr>
<td>20</td>
<td>1.110</td>
<td>0.833</td>
</tr>
<tr>
<td>25</td>
<td>1.110</td>
<td>0.833</td>
</tr>
<tr>
<td>( \bar{x} )</td>
<td>1.110</td>
<td>0.833</td>
</tr>
</tbody>
</table>

* The absolute values have been presented in cc/gm/hr°C. To convert to calories multiply by 4.7.
Table 11. Thermal conductance of *R. septemvittata* in water after room temperature acclimation.

<table>
<thead>
<tr>
<th>Body temperature</th>
<th>Uncorrected for metabolism</th>
<th>Corrected for metabolism</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Heating</td>
<td>Cooling</td>
</tr>
<tr>
<td>15</td>
<td>11.536</td>
<td>8.972</td>
</tr>
<tr>
<td>20</td>
<td>11.536</td>
<td>8.972</td>
</tr>
<tr>
<td>25</td>
<td>11.536</td>
<td>8.972</td>
</tr>
<tr>
<td>$\bar{x}$</td>
<td>11.536</td>
<td>8.972</td>
</tr>
</tbody>
</table>

* The absolute values have been presented in cc/gm/hr°C. To convert to calories multiply by 4.7.
metabolic heat production cannot account for the differences in rates of heating and cooling. When corrected for metabolism the differences between mean values of C' and C in air and water are reduced by only 20 and 2.3% respectively.

Slow rates of change of body temperature for dead lizards led Bartholomew and Tucker (1963) to suggest that differences in conductance between live and dead lizards are related to cardiovascular changes. Queen snake heart rates change with temperature during heating and cooling experiments while values of thermal conductance are quite similar at all temperatures tested in both air and water. Similar findings in studies of other reptiles (Bartholomew and Tucker, 1963, 1964; Bartholomew and Lasiewski, 1965; Bartholomew, et al., 1965; Weathers, 1970) have led these authors to suggest that circulatory factors other than heart rate such as vasodilation, vasoconstriction, or stroke volume changes may be involved.

Values of thermal conductance for 10C acclimated queen snakes tested in air are listed in Table 12. Though data for oxygen consumption and heart rates at constant body temperatures for 10C acclimated queen snakes are not presented in the present study, I have measured these parameters at several temperatures which allows calculation of corrected thermal conductance (C) for this group.
Table 12. Thermal conductance of *R. septemvittata* in air after 10°C acclimation.

<table>
<thead>
<tr>
<th>Body temperature</th>
<th>Heating</th>
<th>Cooling</th>
<th>Uncorrected for metabolism</th>
<th>Heating</th>
<th>Cooling</th>
<th>Corrected for metabolism</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Cooling/Heating</td>
<td></td>
<td></td>
<td>Heating/Heating</td>
</tr>
<tr>
<td>15</td>
<td>0.897</td>
<td>0.534</td>
<td>0.595</td>
<td>0.884</td>
<td>0.543</td>
<td>0.614</td>
</tr>
<tr>
<td>20</td>
<td>0.897</td>
<td>0.534</td>
<td>0.595</td>
<td>0.871</td>
<td>0.538</td>
<td>0.618</td>
</tr>
<tr>
<td>25</td>
<td>0.897</td>
<td>0.534</td>
<td>0.595</td>
<td>0.855</td>
<td>0.539</td>
<td>0.694</td>
</tr>
<tr>
<td>$\bar{x}$</td>
<td>0.897</td>
<td>0.534</td>
<td>0.595</td>
<td>0.870</td>
<td>0.540</td>
<td>0.642</td>
</tr>
</tbody>
</table>

* The absolute values have been presented in cc/gm/hr°C. To convert to calories multiply by 4.7.
Heart rates during heating for this group are similar to those measured during electrical stimulation, though those during cooling are more similar to heart rates during rest. This suggests that during heating 10C acclimated queen snakes are metabolizing at active levels, and during cooling they are metabolizing at resting levels. Thus active metabolic rates at various temperatures were used in calculating C during heating, while resting rates were used during cooling. The heart rate differences between heating and cooling suggest that during heating cardiovascular changes assist heat gain and during cooling these changes impede heat loss.

The ratios of cooling to heating for this group when corrected for metabolism do not approach unity (Table 12), and only 8.4% of the mean difference between C' and C can be attributed to metabolic changes for this group. Thus, again other circulatory mechanisms are implied as major mechanisms in the control of thermal conductance.

Optimum Temperature for Myosin ATPase Activity.

The range of animal body temperatures in nature is between about 0C to 50C. At 0C some components of animal tissues crystallize and near 50C most proteins denature. Homeothermic animals characteristicly maintain body temperatures which are near the upper limit of this range and it has been suggested that this phenomenon is the
result of natural selection since most biochemical processes operate more efficiently as temperature increases (see Bartholomew, 1977b for discussion). Reptiles also appear to prefer temperatures near the upper limits of their activity ranges (cf. Templeton, 1970) which may be linked to optimum temperatures for some enzyme activities.

Within a muscle sarcomere the ATP of myosin is split by the enzyme myosin ATPase to release energy used for contraction. Licht (1964 and 1967) found that myosin ATPase of several lizard species is most active near their preferred body temperatures. The optimum temperature for myosin ATPase activity of the queen snake is 28C (see Figure 11) which is 103% of eccritic (27.2C) and 119% of preferred (23.6C) body temperatures reported for this snake elsewhere in this study.

One might have expected an optimum activity temperature for this enzyme to be somewhat lower for the queen snake since at times it actively forages for crayfish in water which is cooler than its preferred temperature. Though optimum activity of this enzyme occurs near 28C the enzyme is quite active over the entire range of temperatures tested and is about 45% of maximum at 15C. Possibly activity of this enzyme at this level is sufficient for adequate muscle contraction.
Future Physiological Studies of the Queen Snake.

More information concerning the capacity of the queen snake for physiological and biochemical acclimation to cold temperatures may facilitate interpretation of its spring ecology. Previous studies have demonstrated that compensation in several physiological parameters such as critical temperatures and aerobic metabolism does occur in some cold-acclimated reptiles (Vance, 1953; Lowe and Vance, 1955; Dawson and Bartholomew, 1956; Stewart, 1965; Jacobson and Whitford, 1970; Dutton and Fitzpatrick, 1975).

I am now studying resting and active metabolism of 10C acclimated queen snakes and preliminary data suggest that nearly complete compensation of resting metabolic rate occurs at the low temperatures tested thus far since this value at 10C for 10C acclimated snakes is similar to that at 20C for room temperature acclimated snakes. Metabolism during electrically stimulated activity does not appear to change at lower temperatures with cold acclimation from those values reported herein for room temperature acclimated queen snakes. The advantages of a phenomenon such as this are unclear since the snake would be using more energy during rest and possess less of a capacity for increase with activity at these temperatures at times of the year when, presumably, energy resources are scarce or at least more difficult to acquire.
Changes in rates of heat gain and loss between cold and room temperature acclimated snakes in air are reported in this study. If differences in heating and cooling between room temperature and cold acclimated queen snakes occur when they are tested in water, this may suggest that queen snakes possess the capacity to forage for longer periods during spring and fall than in summer. Since this may have selective value to the queen snake when food is scarce, preparations are being made to test rates of change of body temperature of cold acclimated queen snakes in water.

Biochemical acclimation of reptiles to cold is not well-documented. Although some fish possess isoenzyme systems that allow them to be active over a wide range of temperatures after acclimation (Hochachka and Somero, 1968; Baldwin and Hochachka, 1970), Ushakov (1964) suggests an absence of seasonal temperature acclimation of some cellular and enzymatic systems of lizards. It is generally accepted that terrestrial reptiles, at least, have not been pressured to evolve temperature-dependent isoenzyme systems due to the wide variety of microhabitats available in terrestrial environments and because reptiles may behaviorally thermoregulate (Bogert, 1949; Templeton, 1970). However, an isoenzymatic basis for differential tissue metabolism and heart rate with varying states of thermal
and photoperiodic acclimation are known for the red-sided garter snake (Aleksiuk, 1971b; Hoskins and Aleksiuk, 1973; Aleksiuk, 1976).

Since the queen snake is subjected to relatively cold temperatures when aquatically foraging for food in the spring, it may possess some biochemical adaptations that facilitate this function. The capacity for cold acclimation of muscle ATPase (apyrase) has been demonstrated in some insects (Mutchmore and Richards, 1961). In the future, I intend to determine if the optimum temperature for queen snake myosin ATPase activity shifts with cold temperature acclimation. Such a shift may indicate quantitative or qualitative changes in myosin ATPase production.
SUMMARY

1. It is shown that queen snakes do not shift from their dietary preference for crayfish even when water temperatures are cold since 94.1% of food items found in early spring were crayfish. Feeding frequency may be lower in the spring since only 56.6% of the snake stomachs contained food. This figure is lower than for queen snakes captured during summer as reported in previous literature.

2. The mean field body temperature for 38 queen snakes is 27.2°C while preferred body temperature of 58 body temperatures collected from 18 snakes in a thermal gradient is 23.6°C. These temperatures are similar to those reported in previous literature for temperate zone colubrid snakes.

3. The queen snakes in this study exhibit thermal acclimation of the CTMin since when acclimated at 32°C the CTMin is 9.7°C and at 8°C acclimation CTMin is 4.2. These two figures are significantly different. No acclimation of CTMax occurs at the temperatures tested.
4. Oxygen consumption and heart rate of queen snakes increase with body temperature during both rest and activity. Resting metabolic rate of queen snakes at 30°C is similar to that of other snakes for which data are available. Aerobic metabolic scope for the queen snake is greatest at a body temperature of 35°C though the rate of change of this value slows above 25°C which is near their ecratic and preferred temperatures. Heart rate increment peaks at 25°C. Oxygen pulse of the queen snake at rest changes very little with increasing body temperatures suggesting that changes in heart rate are the major factor in meeting increased metabolic demands. However, changes in stroke volume or A-V difference are of major importance in meeting these demands during activity. At low temperatures queen snakes increase oxygen consumption with activity more than two desert snakes for which appropriate data are available.

5. Both room temperature and cold acclimated queen snakes heat faster than they cool in air. Cold acclimated snakes heat and cool slower than those acclimated at room temperature. Since both heating and cooling of queen snakes are affected by cold acclimation a physical barrier to heat gain and loss is suggested.
Room temperature acclimated snakes tested in water heated and cooled at essentially the same rate. Corrected thermal conductance values suggest that circulatory factors other than heart rate such as stroke volume, vasodilation, or vasoconstriction are major contributors to rates of heat gain and loss.

6. Optimum activity of queen snake myosin ATPase occurs at 28°C though the enzyme is quite active throughout the entire temperature range that was tested (15C-45C).
LIST OF REFERENCES


