

AN ABSTRACT OF THE THESIS OF

GLENN R. STEWART for the Ph. D. in Zoology  
(Name) (Degree) (Major)

Date thesis is presented December 16, 1963

Title THERMAL ECOLOGY OF THE GARTER SNAKES

THAMNOPHIS SIRTALIS CONCINNUS (HALLOWELL) AND

THAMNOPHIS ORDINOIDES (BAIRD & GIRARD).

Abstract approved   
(Major Professor)

In recent years, studies dealing with temperature regulation, temperature sensitivity, and physiological responses to temperature in lizards and other reptiles have increased tremendously. It is notable that snakes have been largely ignored in such studies. This no doubt is due to their less direct relationship to ancestral endotherms. However, problems in the ecology of snakes themselves may be elucidated by studies of this kind.

The present study deals with two species of garter snakes (Thamnophis sirtalis concinnus and Thamnophis ordinoides) which are abundant in Oregon's Willamette Valley. The species sirtalis is the most wide ranging snake in the United States. It is commonly found near permanent water, though occasionally it is encountered in rather dry situations. In contrast to sirtalis, the monotypic species ordinoides is a strictly terrestrial northern Pacific Coast form,

which typically is associated with areas of dense vegetation.

T. s. concinnus is often seen basking on mild days of the coldest winter months (November-February) while T. ordinoides rarely emerges during these months.

The distinct differences in habitat preference and winter behavior exhibited by these snakes suggest differences in thermal preferences and critical levels. To examine this possibility, and the responses of the snakes to thermal acclimation, comparative data on the following variables have been sought: 1) Body temperature of snakes in the field and its relationship to environmental temperatures; 2) body temperature of snakes in a thermal gradient box; 3) critical thermal maximum and minimum; 4) metabolic rate; 5) the effect of thermal acclimation on items two, three, and four.

While more investigations are needed to confirm and clarify the results of this study, some tentative conclusions may be stated here: 1) T. s. concinnus and T. ordinoides are diurnal, heliothermic snakes which consistently maintain body temperatures higher than the air and substrate temperatures. 2) T. s. concinnus is more tolerant of seasonally extreme temperatures than T. ordinoides. 3) T. s. concinnus prefers slightly higher body temperatures than T. ordinoides. 4) If temperature tolerances and preferred temperatures are heritable characteristics developed in the phylogeny of the species, these differences probably are primarily related to the

difference in distribution of each species as a whole, and secondarily to differences in habitat preference and habit which have resulted from competitive interactions with other species. 5) There are sexual differences in the preferred temperatures of both species, the most significant of which is the relatively high preferred temperature of pregnant females. 6) Initially, the preferred temperatures of both species are inversely related to acclimation temperature. Later, they may be directly related to acclimation temperature. 7) The critical thermal maxima and minima are similar in both species and are directly related to acclimation temperature. However, reacclimation affects the original response differently in the two species. 8) Both species exhibit typical metabolic rate responses to thermal acclimation. 9) Since metabolic rate responses are the same in both species, the greater cold tolerance of T. s. concinnus cannot be attributed to a greater ability to compensate for low temperature.

THERMAL ECOLOGY OF THE GARTER SNAKES  
THAMNOPHIS SIRTALIS CONCINNUS (HALLOWELL) AND  
THAMNOPHIS ORDINOIDES (BAIRD & GIRARD)

by

GLENN R. STEWART

A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of  
the requirements for the  
degree of

DOCTOR OF PHILOSOPHY

June 1964

APPROVED:

[Redacted Signature]

\_\_\_\_\_  
Professor of Zoology

In Charge of Major

[Redacted Signature]

\_\_\_\_\_  
Chairman of the Department of Zoology

[Redacted Signature]

\_\_\_\_\_  
Dean of Graduate School

Date thesis is presented December 16, 1963

Typed by Nancy Kerley

## ACKNOWLEDGEMENTS

I wish to express sincere thanks to my major professor, Dr. Robert M. Storm, for the help, suggestions, and encouragement he so generously offered during the course of this investigation. I am indebted also to Dr. Austin W. Pritchard for providing the water bath and space to work in the physiology laboratory, to Mr. Orville O. Doerfler for permission to work on his property, to Dr. Donald R. Jensen for help in setting up statistical analyses of the data, and special thanks are due my friend, Mr. Chris Maser, for taking care of my animals and the preferred temperature experiment in my absence. Finally, I wish to thank my fiancée, Miss Julie Lingscheid, for her help and constant encouragement during the preparation of this manuscript.

## TABLE OF CONTENTS

	Page
INTRODUCTION	1
METHODS AND MATERIALS	12
BODY TEMPERATURE OF SNAKES IN THE FIELD, AND IN THE THERMAL GRADIENT BOX	29
ACCLIMATION OF PREFERRED TEMPERATURE	47
CRITICAL THERMAL MAXIMUM	52
CRITICAL THERMAL MINIMUM	57
METABOLIC RATE	63
SUMMARY AND DISCUSSION OF COMPARATIVE DATA ON <u>T. S. CONCINNUS</u> AND <u>T. ORDINOIDES</u>	66
CONCLUSIONS	74
BIBLIOGRAPHY	76
APPENDIX	85

## LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Habitat of <u>Thamnophis sirtalis concinnus</u> (and <u>Thamnophis ordinoides</u> ) at Doerfler's marsh.	8
2	Habitat of <u>Thamnophis ordinoides</u> at Willamette Park.	10
3	Thermal gradient box.	16
4	A volumetric respirometer.	24
5	Body temperatures of <u>T. s. concinnus</u> in field during summer.	33
6	Body temperatures of <u>T. ordinoides</u> in field during summer.	33
7	Body temperatures of <u>T. s. concinnus</u> in field during winter.	34
8	Body temperatures of <u>T. ordinoides</u> in field during winter.	34
9	Body temperatures of <u>T. s. concinnus</u> in a thermal gradient box.	36
10	Body temperatures of <u>T. ordinoides</u> in a thermal gradient box.	36
11	Preferred body temperature of <u>T. s. concinnus</u> and <u>T. ordinoides</u> acclimated at room temperature (x), 8° C. (·), and 32° C. (o) for five days.	48

## LIST OF TABLES

<u>Table</u>	<u>Page</u>
I    Distribution of body temperatures for <u>T. s. concinnus</u> .	30
II   Distribution of body temperatures for <u>T. ordinoides</u> .	31
III  Mean body temperature ( $^{\circ}$ C.) of three reproductive categories of <u>T. s. concinnus</u> and <u>T. ordinoides</u> in the field during summer and in a thermal gradient box.	32
IV   Critical thermal maximum ( $^{\circ}$ C.) of male <u>T. s. concinnus</u> and male <u>T. ordinoides</u> acclimated for five days at room temperature, $8^{\circ}$ C., and $32^{\circ}$ C.	52
V    Critical thermal minimum ( $^{\circ}$ C.) of male <u>T. s. concinnus</u> and male <u>T. ordinoides</u> acclimated for 12 days at room temperature, $8^{\circ}$ C. and $32^{\circ}$ C.	57
VI   Oxygen consumption (cc. /hr.) and metabolic rate (cc./kg. /hr.) of male <u>T. s. concinnus</u> and male <u>T. ordinoides</u> acclimated at $8^{\circ}$ C. for five and twelve days, and acclimated at $32^{\circ}$ C. for five and twelve days.	63
VII  Summary of ecologically significant thermal parameters estimated for <u>T. s. concinnus</u> and <u>T. ordinoides</u> .	70

THERMAL ECOLOGY OF THE GARTER SNAKES  
THAMNOPHIS SIRTALIS CONCINNUS (HALLOWELL) AND  
THAMNOPHIS ORDINOIDES (BAIRD & GIRARD)

INTRODUCTION

Temperature, because of its manifold physiological effects, has long been recognized as an environmental factor of utmost importance to all kinds of animals. The literature dealing with it is voluminous.<sup>1</sup> Generally, a distinction is made between animals which derive their body heat from metabolic processes within their bodies and those which derive their heat principally from external sources. Cowles (19) proposed that the terms "endothermic" and "ectothermic" be used to designate these two groups, rather than the terms "homiothermic" and "poikilothermic."<sup>2</sup> This proposal is gaining acceptance with more and more zoologists, and currently is used by nearly all herpetologists and environmental physiologists.

---

<sup>1</sup>For general reviews and guides to the literature see Carlson (11), Hensel (57), Prosser and Brown (78, pp. 238-284), and Smith (84). Reviews dealing more specifically with the temperature responses of aquatic groups of animals or various kinds of responses are: Brett (9), Bullock (10), Fry (49), Hutchison (59), Prosser (76, 77), and Roots (79).

<sup>2</sup>Within ectotherms Cowles distinguishes "heliotherms", or basking forms, and "thigmotherms", forms which derive heat principally from contact with the substrate and surrounding air.

This acceptance is a result of the now rapidly accumulating evidence that "homiotherms" do not necessarily maintain constant body temperatures, and that "poikilotherms" do not necessarily have body temperatures close to and fluctuating with that of the environment. Recognition of these facts has led to a great surge of investigation on all aspects of thermo-regulation in endotherms and ectotherms, and attempts have been made to reconstruct the evolution of endothermy.<sup>3</sup> It must be noted, however, that recognition of these facts was slow in coming. Thus it may be well to briefly review the principal investigations and concepts dealing with the influence of temperature on the animals of particular interest to herpetologists-- amphibians and reptiles.

Early in this century, various investigators recognized that terrestrial ectotherms occasionally had body temperatures higher than their surroundings (53). However, it was not until the publication of studies on desert reptiles by Cowles (18, 19), and particularly Cowles and Bogert (23), that the ability of these animals to regulate their body temperatures began to be appreciated. Besides demonstrating considerable thermo-regulatory ability in reptiles, these

---

<sup>3</sup>For reviews of the literature dealing with endothermy and its evolution see Bartholomew and Tucker (2), Bogert (5), Cowles (20, 22), Johansen (61), Kahl (63), and Lasiewski (65).

investigators properly emphasized that reptiles were quite sensitive to temperature extremes. As a result of their studies, the concepts of critical maxima and minima, voluntary maxima and minima, normal activity range, and preferred temperature were established.<sup>4</sup>

These concepts are widely accepted today and are being applied in the study of an ever-increasing number of amphibians and reptiles.<sup>5</sup> Although the concepts have been somewhat modified by various investigators, the criteria for determining the actual parameters have not been standardized. Hutchison (59) has thoroughly reviewed the literature concerning critical maxima and minima in fish and amphibians, and has discussed the effect of thermal acclimation on them. Moreover, he has listed conditions which should be taken into account if such concepts are to be of value in ecological studies on any animal. In both amphibians and reptiles, the critical maximum has received more attention than the critical minimum,

---

<sup>4</sup>The concept of preferred temperature was already established in work on fish (48), but was modified slightly by Cowles and Bogert (23) and Bogert (5).

<sup>5</sup>Some recent studies on body temperature and critical thermal levels in amphibians and reptiles are listed here. Amphibians: Bogert (6), Brattstrom (7), Brattstrom and Lawrence (8), Cunningham (25), Hutchison (59), and Scott and Carpenter (83). Reptiles: Carpenter (15, 16), Cowles (21), Edgren and Edgren (30), Fitch (36, 37, 38, 39), Hirth (58), Inger (60), Larson (64), Lee and Badham (66), Lowe and Vance (68), Mayhew (70), Norris (73), Pearson (74), Ruibal (80), Saint-Girons and Saint-Girons (81), Soulé (86), Wilhoft (96, 98), and Wilhoft and Anderson (99).

primarily because its symptoms are readily apparent (23, 59). So far as the present author is aware, data on the critical minimum is only in the form of casual observations (37, 39, 62, 74, 88, 91).

The voluntary maxima and minima are easily determined by field and laboratory observation, but determination of the normal activity range and preferred temperature presents problems. The difficulty stems from the recognition by Cowles and Bogert (23) and Bogert (5) of a "basking range" lying between the voluntary minimum and the normal activity range. They regard the normal activity range as the preferred range, the mean of which they call the "optimum." Temperature records for animals presumed to be within the "basking range" are not included in the calculation of the "optimum" which, by implication, is the preferred temperature.<sup>6</sup>

As pointed out by Mayhew (70), one rarely has any previous knowledge of the activities of an animal before it is captured. Designation of the "basking range" and the lower limits of the preferred range, therefore, becomes questionable. Furthermore, it becomes an arbitrary matter as to what temperature records are considered to be within the preferred range and suitable for calculation of the preferred temperature. Since the preferred temperature

---

<sup>6</sup>Because of its anthropomorphic connotation, some authors object to the word "preferred" and substitute "eccritic" (Gr. chosen). The word "optimum" is now rarely used in this sense.

is often a convenient parameter for comparing the body temperatures of different groups of animals, and since the greatest percentage of animals will be within the preferred range, some investigators choose to consider a mean calculated from all of the body temperature records as the preferred temperature. In the present author's view, this practice is acceptable so long as the following points are kept in mind: 1) Using body temperature records collected at times known to be thermally unfavorable for the animals being studied may bias the data toward a lower preferred temperature. 2) The preferred temperature must necessarily be a range, however narrow, due to the interaction of complex behavior patterns with an animal's thermoregulatory mechanism (66). 3) A fluctuating body temperature may actually be required for an animal's well-being (61, 97).

Concomitant with the tremendous increase in studies dealing with behavioral thermo-regulation and thermo-sensitivity in amphibians and reptiles, there has been a comparable, though somewhat later, increase in studies on the physiological adaptations of these animals. This is particularly true for reptiles, for as late as 1955 Bullock (10), in referring to thermal acclimation, could only "feel confident in predicting that reptiles will also yield examples of physiological adaptation." His prediction was correct as shown in a number of publications (27, 51, 52, 64, 68, 99). In addition to these

studies, several others should be listed because they represent the results of continued efforts to understand the nature and mechanisms of the physiological adjustments of reptiles to temperature. These papers are the following: Bartholomew and Tucker (2), Chew (17), Dawson (26), Dawson and Bartholomew (28), Dawson and Templeton (29), Heath (54), Moberly (71), Nielsen (72), Templeton (92), and Templeton and Dawson (93).

It is notable that snakes have been largely ignored in thermoregulatory and physiological studies. With respect to the latter, the classic work of Benedict (4) is the most important. Some effects of temperature on snakes have been studied by Lueth (69), and the body temperatures of snakes in the field have been recorded by Carpenter (15), Cowles and Bogert (23), and Fitch (37, 39). Saint-Girons and Saint-Girons (81) and, more recently, Ruibal (80) have discussed the relatively low body temperatures of snakes as compared to lizards.

The relative abundance of literature on lizards is no doubt due to their generally greater morphological, physiological, and behavioral complexity which probably more closely approximates that of ancestral endotherms. From this point of view, investigations on lizards will be more instructive than those on snakes. However, if one is seeking to understand snakes themselves and to elucidate

problems in the ecology of snakes, studies similar to those on lizards must be conducted.

The present study deals with two species of garter snakes which are abundant in Oregon's Willamette Valley, Thamnophis sirtalis concinnus (red-spotted garter snake) and Thamnophis ordinoides (northwestern garter snake). The species sirtalis is the most wide-ranging snake in the United States. It is absent only from the southwestern deserts comprising southeastern California and most of Nevada and Arizona. Its range extends northward well into Canada and southward into the Mexican states of Chihuahua and Coahuila.<sup>8</sup> The subspecies concinnus, however, is restricted to northwestern Oregon, ranging from the Cascades to the coast. As is usual for the species, concinnus is commonly found near permanent water, particularly marshes and ponds in the Willamette Valley (Figure 1), though it may be encountered some distance from water in grassy fields and meadows.

In contrast to sirtalis, the monotypic species ordinoides is strictly a northern Pacific Coast form. It ranges from extreme northwestern California to southwestern British Columbia, being confined to the region west of the Cascades. Here it inhabits dense

---

<sup>8</sup>See range maps in Stebbins (87, p. 505, 507) and Wright and Wright (100, p. 756, 834).



Figure 1. Habitat of Thamnophis sirtalis concinnus (and Thamnophis ordinoides) at Doerfler's marsh. Note clumps of rose bushes in foreground.

thickets in valleys (Figure 2) and occurs in meadows, clearings, roadways, etc. in Douglas fir forests. Wherever it is found, it is rarely far from cover of some kind, and is not necessarily associated with water. While ordinoides is often collected at the same sites as other garter snakes occurring in the same region, its rather secretive habits appear to separate it effectively from competition with them (32, 55, present study).

During the course of a study on thermal acclimation in concinus (90), it was noted that concinus was occasionally seen out basking on mild winter days. Similar observations have been reported for this subspecies by Dr. Robert M. Storm (Professor of Zoology, Oregon State University) and for sirtalis sirtalis in Michigan (12). Carpenter (12) and Fitch (37) have also reported that sirtalis sirtalis may be the latest snake to enter hibernation sites and the earliest to emerge. This appeared to be the case for concinus with respect to ordinoides in the Willamette Valley, for the latter was never seen out during the winter in an area known to be inhabited by both forms (Figure 1). Furthermore, Hebard (56) indicated that mid-March to mid-October represented the period of activity for ordinoids in Washington and Wright and Wright (100, p. 806) listed only one winter record for it.

The distinct differences in habitat preference and winter



Figure 2. Habitat of Thamnophis ordinoides at Willamette Park. Note dense thicket at left side of road.

behavior exhibited by concinnus and ordinoides suggested that these snakes might have different thermal preferences and critical levels. To examine this possibility, and the responses of the snakes to thermal acclimation, comparative data on the following variables were sought: 1) Body temperature of snakes in the field and its relationship to environmental temperatures; 2) body temperature of snakes in a thermal gradient box; 3) critical thermal maximum and minimum; 4) metabolic rate; 5) the effect of thermal acclimation on items two, three, and four.

Incidental to the collection of data on these variables, considerable data on the natural history of concinnus and ordinoides was obtained. It will be reported elsewhere, except as it pertains to the problem just described. For general information on the natural history and ecology of garter snakes, the following references should be consulted: Wright and Wright (100), Stebbins (87), Carpenter (12, 13), Fitch (32, 34), Fox (43, 44, 45, 46), Hebard (55, 56) Tinkle (94), and Batts (3).

## METHODS AND MATERIALS

The present study was conducted from the fall of 1960 to the fall of 1962. Field data and animals for experimental work were collected principally in the Willamette Valley. T. s. concinnus was studied most extensively at a marsh six miles east of Corvallis owned by Mr. Orville O. Doerfler (Figure 1). This marsh area harbors a dense population of concinnus and a fair population of ordinoides. T. s. concinnus was also studied at "MacFadden's marsh" ten miles south of Corvallis. This marsh is inhabited by a somewhat less dense population of concinnus than Doerfler's marsh, and topographical conditions make it a less convenient place to work. T. ordinoides was rarely seen here. Until the spring of 1962, ordinoides was studied only at Doerfler's marsh and the Oregon Institute of Marine Biology laboratories at Charleston. However, in the spring of this year, a dense population of ordinoides was discovered at Willamette Park on the southern outskirts of Corvallis (Figure 2). Fair populations were also found some ten miles north of Corvallis in the "saddle" and Sulfur Springs areas of MacDonald Forest. With the discovery of these additional ordinoides populations, the investigator was able to obtain sufficient data for comparisons to be made with concinnus.

### Field Work

Approximately 200 hours were spent in the field. Of this time, 73 percent was logged during the "summer" (May -- September) and 27 percent during the "winter" (October -- April). All of the winter hours were logged in the afternoon, but during the summer, 40 percent of the hours were logged in the morning. Weather conditions were noted as follows: clear, partly cloudy, partly cloudy with showers, hazy sun, or overcast.

Snake cloacal temperatures, substrate temperatures, and air temperatures were recorded with a fast-reading Schultheis thermometer graduated in  $0.2^{\circ}$  C. intervals. Snakes were grasped by the tail away from the cloacal region and readings were taken within 10 to 15 seconds. Notations were made on the position of the snakes relative to sun and shade, and on their size, sex, and reproductive condition. Substrate temperatures for all snakes were recorded immediately after the cloacal temperatures, approximately at the locations where the snakes were first seen. In almost all cases, the "substrate" temperature was not a ground temperature, but was an air temperature recorded one to three inches above the ground in the shade of a blade of grass. Because grass was actually a snake's substrate, except in a few instances, such a temperature was a better

representation of thermal conditions in a snake's immediate environment than the temperature of the usually damp, shaded ground below. Air temperatures were recorded every 30 to 60 minutes four feet above the ground in the observer's shadow.

### Experimental Work

Snakes intended for experimental work were brought into the laboratory, weighed, measured, and given individual numbers by clipping the subcaudal scutes. They were kept in fish bowls (diameter nine inches), one or two per bowl. All snakes were kept at room temperature ( $18^{\circ}$  -  $24^{\circ}$ ), except during acclimation periods, and were given a photoperiod of approximately 12 hours. Snakes designated as "room temperature" in the various experiments were kept at room temperature for at least three days (average ten days) before they were used. Room temperature and warm-acclimating ( $32^{\circ}$  C.) snakes were continuously supplied with finger bowls of water. They were fed weekly,<sup>10</sup> but not for at least three days prior to an experimental run. Cold-acclimating ( $8^{\circ}$  C.) snakes were also supplied with water, but were not fed for at least three days before acclimation

---

<sup>10</sup>T. s. concinnus fed readily on tree frogs (Hyla regilla) and long-toed salamanders (Ambystoma macrodactylum). T. ordinoides was usually reluctant to eat, but sometimes could be induced to take slugs and earthworms.

was begun. Adult snakes were used in all experiments.<sup>11</sup> Some individuals were used in more than one kind of experiment, but never after being used in either of the critical temperature experiments. To eliminate possible variation due to sex, only males were used in critical temperature and metabolic rate experiments. Body temperatures were recorded with a Schultheis thermometer as previously described.

#### Body Temperature of Snakes in a Thermal Gradient Box

In order to determine the preferred temperatures of concinus and ordinoides under controlled conditions, a thermal gradient box was constructed in an air-conditioned laboratory. Stebbins (88) has described an elaborate photo-thermal gradient, and Stebbins and Eakin (89) have described a more simple model. The present thermal gradient box is somewhat different from these. Its essential features are shown in Figure 3.

The box is constructed of nine-inch by three-fourth-inch

---

<sup>11</sup> On the basis of a few dissections and examinations for sperm, it was found that minimum body length for adult male concinus was about 360 mm. (weight about 22 gms.) and about 320 mm. (weight about 15 gms.) for adult male ordinoides. Minimum body lengths for adult females were about 435 mm. and 360 mm., respectively. These measurements are similar to those reported by other investigators (13, 56).

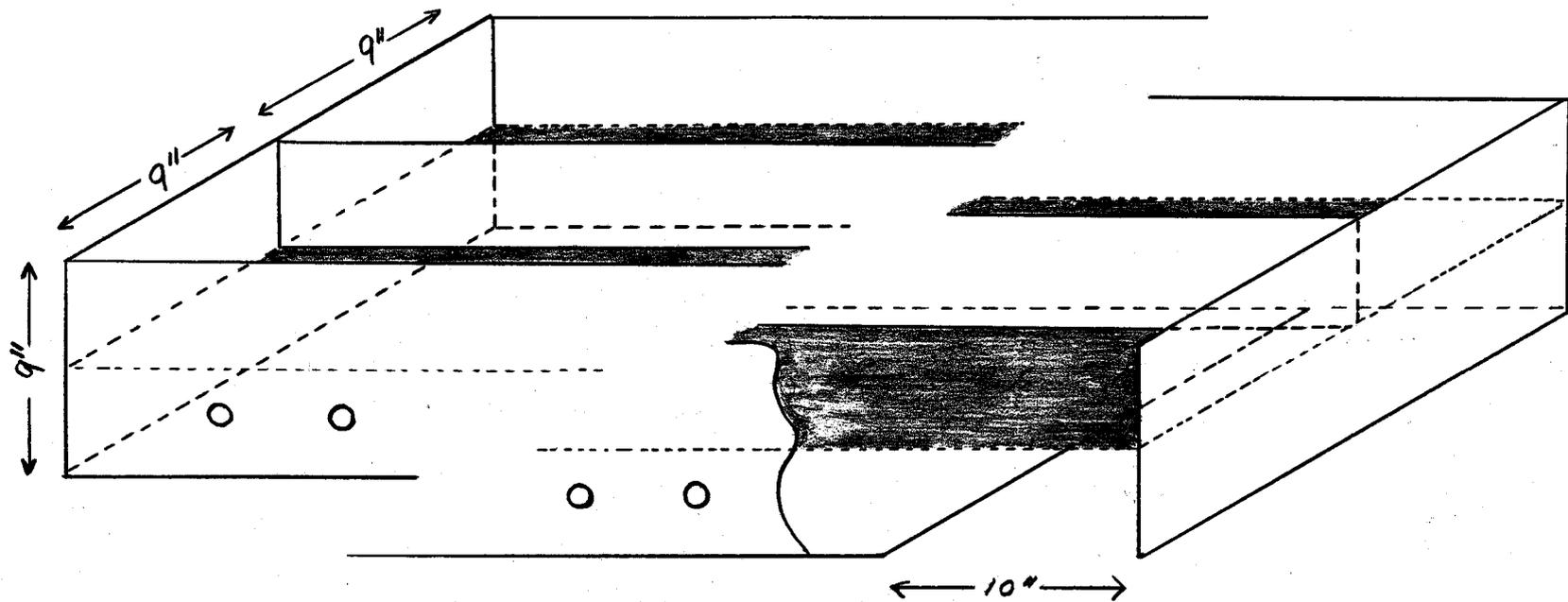


Figure 3. Thermal gradient box. Only the ends of the ten-foot-long box are shown. The shaded area and its associated dotted lines indicate the position of the galvanized metal sheet. The cutaway reveals the ten-inch gap at one end where a heat lamp irradiates the metal sheet. Legs which raise the bottom of the box 13 inches above the laboratory floor are not shown. See text for detailed description.

boards. It is ten feet long, 18 inches wide, and is equipped with three  $\frac{1}{4}$ -inch plywood lids of equal size. Two nine-inch-wide runways are formed by a plywood partition which runs the length of the box and fits snugly between the lids and a thin sheet of galvanized metal. The sheet of galvanized metal is fitted into the box  $4\frac{1}{2}$  inches above the bottom, and is held in place by  $\frac{1}{2}$ -inch by  $\frac{1}{2}$ -inch strips of wood nailed to the sides of the box. The metal sheet forms the substrate upon which the snakes rest. A ten-inch section of its underside is exposed to a 250 Watt infra-red heat lamp at one end of the box. Three evenly-spaced pairs of legs raise the bottom of the box 13 inches above the laboratory floor, and raise the metal sheet seven inches above the surface of the heat lamp. A smooth temperature gradient is achieved by almost completely closing off the air space below the metal sheet at a point immediately adjacent to the gap in the bottom of the box, and by ventilating this air space with holes at eight to ten inch intervals. The holes can be plugged as necessary to give the best gradient. The gradient ranges from above  $60^{\circ}$  C. directly over the heat lamp to slightly above room temperature ( $20^{\circ}$ -- $23^{\circ}$  C.) at the cool end where a thermometer indicates the temperature at any given moment. For inside illumination, the box is equipped with a 25 Watt light bulb centered at the hot end.

The preferred temperature experiment was run in September

and October of 1961, and from March to October of 1962. It was divided into two phases: 1) Preferred temperature of males, pregnant females, and non-pregnant females of both species after acclimation at room temperature; 2) preferred temperature of males and non-pregnant females of both species after acclimation for five days at 8° or 32° C. Room temperature controls were run during the same period as the 8° and 32° acclimated snakes.

A total of 51 concinus (22 males, 14 pregnant females, 15 non-pregnant females) and 46 ordinoides (18 males, 12 pregnant females, 16 non-pregnant females) were used in the first phase of this experiment. Twenty-eight snakes of each species were used in the second phase of the experiment. In this phase, the concinus were divided as follows: Room temperature controls--8 (5 males, 3 females); 8°-acclimated--10 (6 males, 4 females); 32°-acclimated--10 (6 males, 4 females). The ordinoides were divided as follows: Room temperature controls--10 (6 males, 4 females); 8°-acclimated--10 (6 males, 4 females); 32°-acclimated--8 (6 males, 2 females).<sup>12</sup>

Pairs of snakes were taken from their acclimation rooms and placed in the thermal gradient box (one in each runway) late in the

---

<sup>12</sup>The smaller number of females relative to males in phase 2 is due to the difficulty in obtaining non-pregnant females in June, July, and August, and to the lesser abundance of females during the winter.

evening. Beginning on the following morning and continuing for three days, the body temperatures of the snakes were recorded four times per day (morning, noon, early evening, late evening).<sup>13</sup> The snakes were given approximately a 12-hour photoperiod. Thus two body temperatures were recorded during a dark period (morning and late evening) and two during a light period (noon and early evening) each day. The temperature at the cool end of the box was recorded simultaneously with the body temperatures. Infrequently, the box temperature exceeded 25° C. At such times, the body temperature records were discarded. On the second day of their stay in the thermal gradient box, the snakes were briefly transferred to a fish bowl, allowed to drink (which most did readily), and then returned to the box.

#### Critical Thermal Maximum

The critical maximum experiment was run in a water bath made from an old Coca-Cola dispensing machine. The inside dimensions of the tub were: length, 46 inches; width, 21 inches; and

---

<sup>13</sup>An average of 11-12 observations per snake was recorded for the 8° - and 32°-acclimation groups and the pregnant female groups. However, the average number of observations per snake was somewhat higher than this for male and non-pregnant female room temperature groups because a few of the snakes in these groups were run more than once.

depth, 15 inches. One end of the tub was equipped with a thermostat, a 500 Watt heating element, and a water circulating pump. These were separated from the rest of the tub by a 15-inch by 21-inch "window screen type" framed screen which permitted water to be circulated throughout the tub. With the framed screen in place, the length of the tub's working area was reduced to 34 inches.

Thirty male snakes of each species were collected in May and June, 1962. They were divided into the following groups: Controls-- 10 (5 room-temperature-acclimated, 5 from the field); 8<sup>o</sup>-acclimated-- 10 (5 acute, 5 non-acute); 32<sup>o</sup>-acclimated-- 10 (5 acute, 5 non-acute). These groups require some further explanation. Animals "from the field" were kept overnight (10-12 hours) at room temperature before being started in an experimental run. "Acute" animals were taken from the acclimation rooms and left at room temperature for one hour before being started in a run. Within this time their body temperatures approached the room temperature. "Non-acute" animals were taken from the acclimation rooms and left overnight at room temperature before being started. The 8<sup>o</sup> and 32<sup>o</sup> acclimation periods were five days in length.

Following the treatments just described, three to ten snakes were put in wide-mouth gallon jars (no more than three per jar) which were immersed for one hour in 36<sup>o</sup> C. water standing five to six

inches deep in the tub. Then the snakes were dumped into the water at 36° and allowed to swim freely.<sup>14</sup> The temperature of the water was increased 0.5° C. every 30 minutes and body temperatures were taken at 30 minute intervals, 15 minutes after each temperature increase. At a point in their activity characterized by loss of coordination, wide opening of the mouth, and general limpness, the snakes were quickly removed from the water bath and their body temperatures were taken with 10-15 seconds. After their critical temperatures were recorded, the snakes were kept at room temperature for observation. All but one recovered their normal locomotor ability within 30 minutes.

#### Critical Thermal Minimum

The critical minimum experiment was run from July to September, 1962. During this time, 50 male snakes of each species were collected and divided into groups as follows: Controls--10 (for concinus, 7 room-temperature-acclimated and 3 from the field; for ordinoides, 5 room-temperature-acclimated and 5 from the field);

---

<sup>14</sup>The snakes were prevented from climbing out of the tub by over-hanging plywood strips which were fitted tightly against the rim. The over-hang was about four inches on all sides. The framed screen kept the snakes out of the temperature control area.

8°-acclimated--20 (10 acute, 10 non-acute); 32°-acclimated--20 (10 acute, 10 non-acute). The terms "from the field," "acute," and "non-acute" refer to the same things as in the critical maximum experiment. However, in the critical minimum experiment, the 8° and 32° acclimation periods were 12 days in length rather than five.

A refrigerator with a 16-inch by 20-inch bottom area was used in this experiment. The inside was continuously illuminated by a 40 Watt refrigerator light and a thermometer indicated the temperature at the bottom. At the beginning of an experimental run, the refrigerator was at room temperature. Three to ten snakes were put in the bottom of the refrigerator and allowed to crawl freely. The refrigerator was started and cooled to between 0° and 7° C. within one hour. Thereafter, the temperature was maintained between -2° and +4° C. After the first hour, the refrigerator door was opened at five to ten minuted intervals, the temperature recorded, and the snakes checked for their ability to right themselves after being turned on their backs. The inability to turn over was considered to be the criterion of the critical minimum. When this point was reached, the snakes' temperatures were immediately taken. Then the snakes were removed from the refrigerator and kept at room temperature for observation. Most snakes recovered the righting reflex within ten minutes and all recovered it within 30 minutes.

### Metabolic Rate

Various types of respirometers have been devised to measure gaseous metabolism, a number of them being similar in principle to the direct-reading volumetric microrespirometers of Scholander (82). The modification described by Flemister and Flemister (41) was adapted for use in the present investigation. One of the two identical respirometers used is shown in Figure 4.

The animal chamber (1) is a small bowl  $5\frac{1}{2}$  inches in diameter and  $3\frac{1}{4}$  inches deep (volume approximately 1000 cc.). Another bowl of the same size serves as a compensation chamber (2). The lids of these chambers are made from a 0.312-inch-thick sheet of Plexiglas plastic. Three holes are drilled in the lid of the respiration chamber and two in that of the compensation chamber. The holes are fitted with rubber stoppers and glass tubing. A tube from one stopper in the lid of each chamber opens directly to the outside. Two millimeter bore capillary tubing from a second pair of stoppers links the two chambers via a "U" tube (3) of the same bore containing Brodie's manometer fluid. A "T" tube with a three-way stopcock (4) is thrust into the third stopper in the lid of the animal chamber and is connected to a 20 cc. syringe (5). The syringe is clamped to a Plexiglas block which is cemented to the lid.

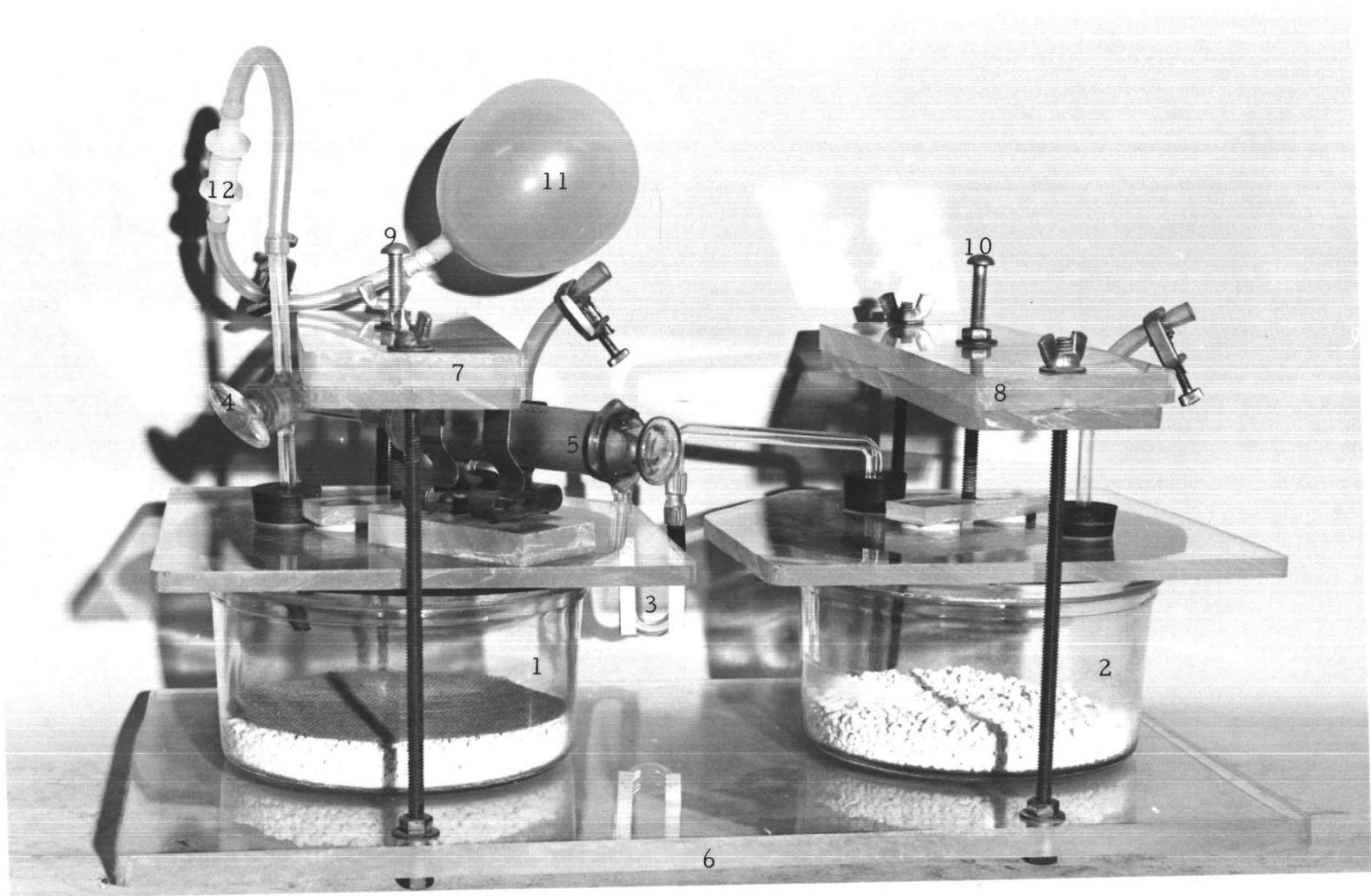


Figure 4. A volumetric respirometer.

The lids of the respiration and compensation chambers are held tightly in place by stirrup clamps. The principal components of the clamps are: 1) A 12-inch by 17-inch base of  $\frac{1}{2}$ -inch Plexiglas (6); 2) a pair of crossmembers (7 and 8), each consisting of strips of  $\frac{1}{2}$ -inch and 0.312-inch Plexiglas; 3) two pairs of  $\frac{1}{4}$ -inch threaded brass rods; 4) two  $\frac{1}{4}$ -inch wall screws (9 and 10). The base is drilled and tapped to take the brass rods which are securely bolted to it. The crossmembers are drilled at each end to pass the threads of the brass rods. In the center, the crossmembers are drilled and tapped to take the threads of the wall screws. The latter are securely bolted to the crossmembers. With crossmembers in position, pressure is applied by tightening wing nuts on the ends of the brass rods. The wall screws bear directly on blocks of Plexiglas supported by rubber washers. In this way, pressure is distributed over the lids. Gaskets of neoprene rubber between the lids and the rims of the bowls make air-tight seals.

Oxygen is stored in a balloon (11) which is attached to the top end of the "T" tube by a length of  $\frac{1}{4}$ -inch Tygon tubing. A Teflon junction (12) intervenes between the balloon and the "T" tube permitting the balloon to be easily detached for inflation. Tygon tubing is used for the "U" tube junctions and outside connections, the latter being closed when necessary by light-weight hose clamps. A  $\frac{3}{4}$ -inch layer of No. 4-8 mesh soda lime covers the bottoms of the respiration

and compensation chambers, serving as a carbon dioxide absorbent and desiccant. In the respiration chamber, two discs of plastic screen are laid over the soda lime to prevent the animal from coming in contact with it.

The metabolic rate experiment was run from June to August, 1962. During this time, 50 male snakes of each species were collected and divided as follows: Controls--10 from the field (i. e., kept overnight in the laboratory); 8°-acclimated--20 (10 acclimated for 5 days, 10 acclimated for 12 days). The mean body weight for snakes in each group of 10 ranged between 30.5 and 36.9 grams.

Following the treatments described above, the oxygen consumption of all snakes was measured at 25° C. Pairs of snakes were taken from their acclimation rooms, weighed, and placed in the respirometers. The lids of the respirometers were tightened in position and the manometers set in place. With both of their outside extensions open to maintain contact with the atmosphere, the respirometers were submerged in the water bath previously described. The balloons were filled with oxygen, attached to the respirometers, and the oxygen supply systems were flushed with ten cc. of oxygen. The syringes were then refilled with 15 cc. of oxygen.

The snakes were given one and one-half to two hours to adjust

to their new environment before oxygen consumption was measured. This seemed to be sufficient time for them to reach a constant temperature and stop their exploratory activity. At the end of the adjustment period, the outside extensions were closed and recording of oxygen consumption was begun. As oxygen was consumed, it was replaced by oxygen from the syringes, the plungers being advanced by hand just enough to maintain the menisci of the manometers at a constant level. The smallest change in pressure that could be read on the manometers was equivalent to a volume decrease of about  $\frac{1}{4}$  cc. The passages from the syringes to the respiration chambers were closed by the stopcocks except when oxygen was added.

Oxygen consumption was recorded at the end of every 30 minutes for one and one-half to three hours. If necessary, the syringes were refilled at the end of a measurement period without stopping the experimental run. When the snakes were quiet, oxygen consumption did not vary more than one-third cc. in the first three periods and the run was terminated. However, in some runs, the snakes were not perfectly quiet. Then the runs were continued until oxygen consumption was recorded for at least three inactive periods. An average rate of oxygen consumption per hour was calculated for each snake, and this value was used in calculating the metabolic rate.

Metabolic rate is expressed here in terms of the cubic centimeters of oxygen consumed per kilogram of body weight per hour (cc. /kg./hr. ).

BODY TEMPERATURE OF SNAKES IN THE FIELD,  
AND IN THE THERMAL GRADIENT BOX

The body temperature data for snakes in the field are presented in Tables I, II, and III (see also Appendix Tables). Figures 5, 6, 7, and 8 graphically present the field data in Tables I and II. Because the body temperature of very small snakes could not be accurately recorded, the field data are for adult and some subadult (at least nine-month-old) snakes. To facilitate direct comparisons among the reproductive categories of snakes, the frequency distributions are expressed as percent of the total number in each category. Body temperatures are lumped in three-degree groupings to eliminate degree to degree fluctuations which tend to obscure the significant trends.

Within each species, a difference in body temperature distribution is apparent among the three categories. The mode for pregnant females of both species is somewhat greater than that of the other categories and is in the  $29^{\circ}$ - $30^{\circ}$  range. Pregnant females also have the greatest percentage of observations in the  $26^{\circ}$  and above range, and have the highest mean body temperatures. Non-pregnant female concinus have a fairly even distribution of frequencies above 20 percent in the range  $26^{\circ}$ - $34^{\circ}$ , while the males have a more nearly normal distribution. The mode for males is the same as that for pregnant females. No observations are recorded for males in the

Table I. Distribution of Body Temperatures for *T. s. concinnus*. Number of observations and their percent of the total for each reproductive category of snakes in each temperature range.

Temperature Range ° C.	Summer						Winter				Thermal Gradient Box*						
	♂ N=160	♀P N=79	♀NP N=130	♂ N=95	♀NP N=44	♂ N=288	♀P N=158	♀NP N=199	♂	♀P	♀NP	♂	♀P	♀NP	♂	♀P	♀NP
13 and below	---	---	---	---	---	---	2	2.1	---	---	---	---	---	---	---	---	---
14-16	---	---	---	---	---	---	5	5.3	1	2.3	---	---	---	---	---	---	---
17-19	3	1.9	---	---	2	1.9	10	10.5	5	11.3	---	---	---	---	---	---	---
20-22	15	9.4	2	2.5	5	4.8	13	13.7	3	6.8	17	5.9	2	1.3	3	1.5	---
23-25	24	15.0	10	12.6	19	18.5	21	22.1	8	18.2	79	27.4	6	3.8	25	12.6	---
26-28	43	26.9	19	24.1	28	27.2	28	29.5	13	29.6	95	33.0	46	29.1	66	33.2	---
29-31	55	34.3	34	43.0	22	21.4	13	13.7	12	27.3	93	32.3	85	53.8	80	40.2	---
32-34	20	12.5	13	16.5	26	25.2	3	3.1	2	4.5	4	1.4	19	12.0	24	12.0	---
35 and above	---	---	1	1.3	1	1.0	---	---	---	---	---	---	---	---	1	0.5	---
26-32	108	67.5	60	76.0	62	60.2	43	45.2	25	56.8	190	66.0	144	91.1	164	82.4	---
25 and below	42	26.3	12	15.1	26	25.2	51	53.7	17	38.6	96	33.3	8	5.1	28	14.1	---
26 and above	118	73.7	67	84.9	77	74.8	44	46.3	27	61.4	192	66.7	150	94.9	171	85.9	---
33 and above	10	6.2	7	8.9	15	14.6	1	1.1	2	4.6	2	0.7	6	3.8	7	3.5	---

\*"N" is the number of observations on 22 males, 14 pregnant females, and 15 non-pregnant females. See footnote 13.

Table II. Distribution of body temperatures for *T. ordinoides*. Number of observations and their percent of the total for each reproductive category of snakes in each temperature range.

Temperature Range ° C.	Summer						Winter				Thermal Gradient Box*					
	♂	N=82	♀P	N=55	♀NP	N=36	♂	N=18	♀NP	N=6	♂	N=282	♀P	N=136	♀NP	N=212
17-19	2	2.4	1	1.8	1	2.8	5	27.8	3	50.0	---	---	---	---	---	---
20-22	10	12.2	7	12.7	5	13.9	2	11.1	---	---	26	9.2	3	2.2	2	0.9
23-25	18	22.0	9	16.4	13	36.1	6	33.3	1	16.7	83	29.4	18	13.2	59	27.8
26-28	29	35.4	11	20.0	8	22.2	4	22.2	2	33.3	80	28.4	29	21.3	43	20.4
29-31	16	19.5	20	36.4	8	22.2	---	---	---	---	85	30.2	65	47.8	91	42.9
32-34	7	8.5	6	10.9	1	2.8	1	5.6	---	---	8	2.8	21	15.5	17	8.0
35 and above	---	---	1	1.8	---	---	---	---	---	---	---	---	---	---	---	---
26-32	48	58.5	36	65.5	17	47.2	5	27.8	2	33.3	171	60.6	108	79.4	150	70.8
25 and below	30	36.6	17	30.9	19	52.8	13	72.2	4	66.7	109	38.6	21	15.4	61	28.7
26 and above	52	63.4	38	69.1	17	47.2	5	27.8	2	33.3	173	61.4	115	84.6	151	71.3
33 and above	4	4.9	2	3.6	---	---	---	---	---	---	2	0.8	7	5.2	1	0.5

\*"N" is the number of observations on 18 males, 12 pregnant females, and 16 non-pregnant females. See footnote 13.

Table III. Mean body temperature ( $^{\circ}$  C.) of three reproductive categories of T. s. concinnus and T. ordinoides in the field during summer and in a thermal gradient box. "Preferred Range" arbitrarily calculated from  $\pm$  one standard deviation of the mean. N for each group same as in Tables I and II.

	Field During Summer			Thermal Gradient Box			Field and Box Combined		
	N for Reproductive Categories	Mean $\pm$ 1 Standard Deviation	"Preferred Range"	N for Reproductive Categories	Mean $\pm$ 1 Standard Deviation	"Preferred Range"	N for Reproductive Categories	Mean $\pm$ 1 Standard Deviation	"Preferred Range"
<u>T. s. concinnus</u>									
Male	160	27.7 $\pm$ 3.58	24.1-31.3	288	26.9 $\pm$ 2.84	24.1-29.7	---	---	---
Pregnant	79	28.8 $\pm$ 3.14	25.7-31.9	158	29.2 $\pm$ 2.20	27.0-31.4	---	---	---
Non-pregnant	103	28.2* $\pm$ 3.69	24.5-31.9	199	28.6* $\pm$ 2.58	26.0-31.2	---	---	---
All	342	28.1* $\pm$ 3.54	24.6-31.6	645	28.0* $\pm$ 2.62	25.4-30.6	987	28.0* $\pm$ 2.96	25.0-31.0
<u>T. ordinoides</u>									
Male	82	26.6 $\pm$ 3.36	23.2-30.0	282	26.7 $\pm$ 2.88	23.8-29.6	---	---	---
Pregnant	55	27.3 $\pm$ 3.76	23.5-31.1	136	28.9 $\pm$ 2.85	26.0-31.8	---	---	---
Non-pregnant	36	25.6* $\pm$ 3.22	22.4-28.8	212	27.9* $\pm$ 2.84	25.1-30.7	---	---	---
All	173	26.6* $\pm$ 3.48	23.1-30.1	630	27.6* $\pm$ 2.86	24.7-30.5	803	27.4* $\pm$ 2.98	24.4-30.4

\*Difference between these means for T. s. concinnus and T. ordinoides significant at the one percent level.

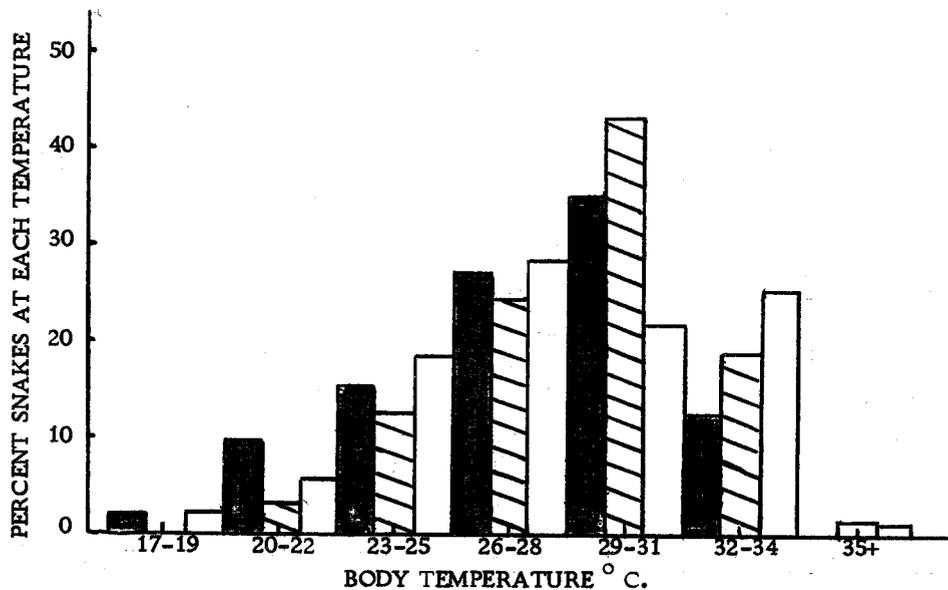


Figure 5. Body temperatures of *T. s. concinnus* in field during summer. Frequency in 3° groupings expressed as percent of total in each category of snakes, males (■ N = 160), pregnant females (▨ N = 79), and non-pregnant females (□ N = 103).

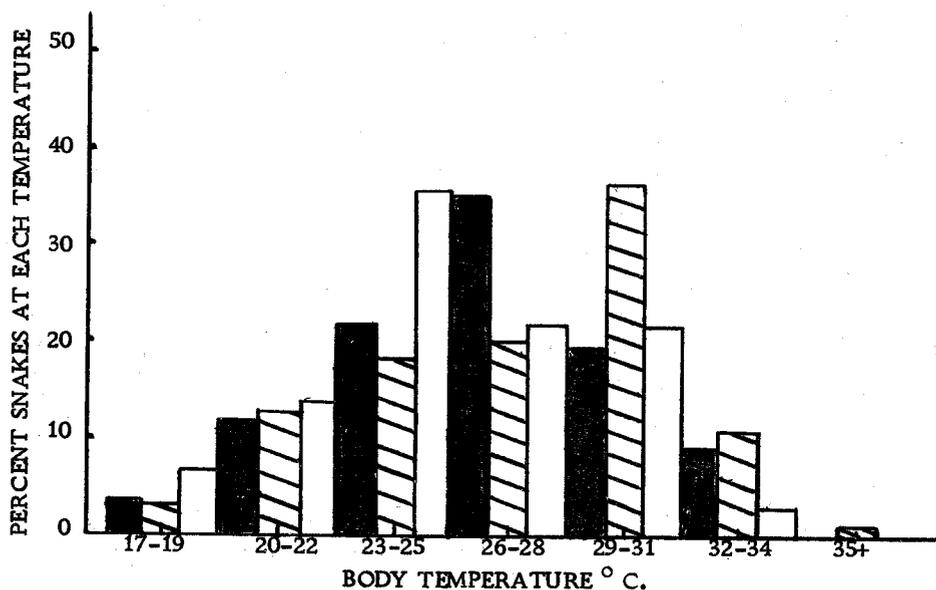


Figure 6. Body temperatures of *T. ordinoides* in field during summer. Frequency in 3° groupings expressed as percent of total in each category of snakes, males (■ N = 82), pregnant females (▨ N = 55), and non-pregnant females (□ N = 36).

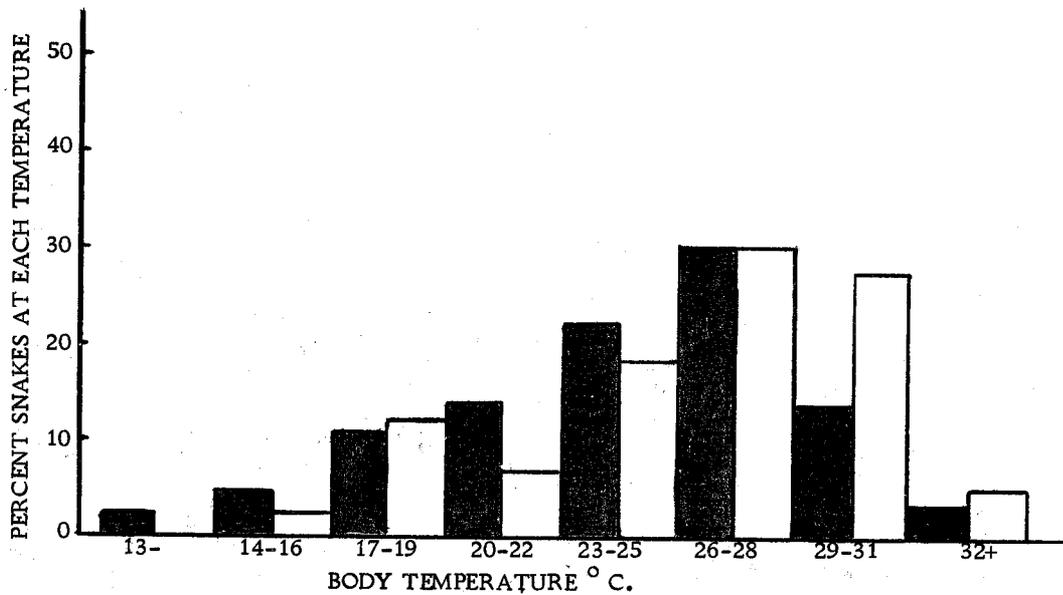


Figure 7. Body temperatures of *T. s. concinnus* in field during winter. Frequency in 3° grouping expressed as percent of total in each category of snakes, males (■ N = 95), and females (□ N = 44).

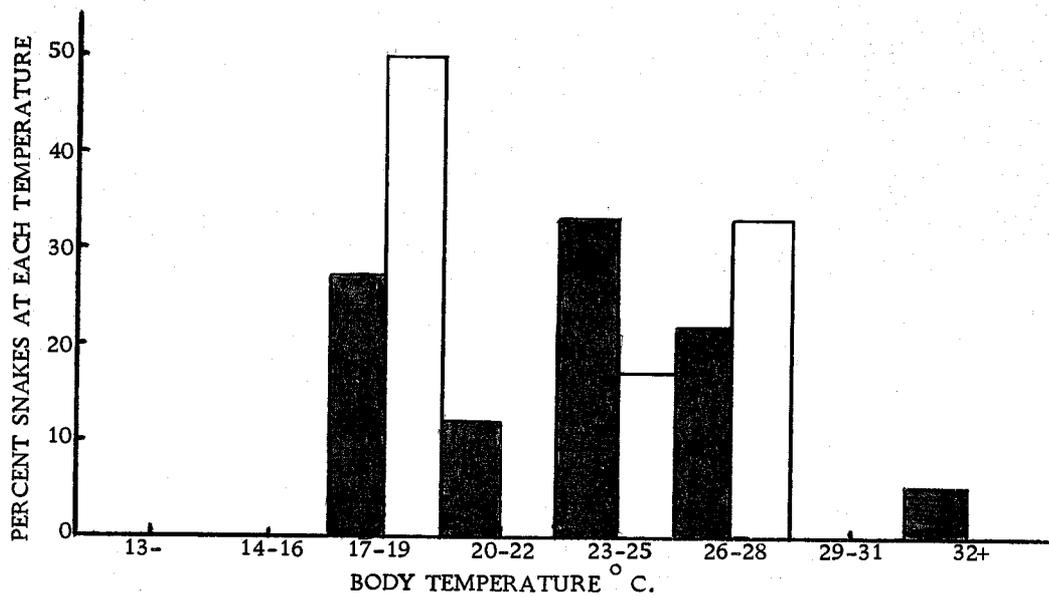


Figure 8. Body temperatures of *T. ordinoides* in field during winter. Frequency in 3° grouping expressed as percent of total in each category of snakes, males (■ N = 18), and females (□ N = 6).

35°+ range. The mean body temperature of non-pregnant female concinus is higher than that of the males. Non-pregnant ordinoides females exhibit a mode in the 23°-25° range with frequencies still above 20 percent in the 26°-31° range. Males of ordinoides have a nearly normal distribution with a mode in the range 26°-28° and, as in the concinus distribution, no observations in the 35°+ range. The mean body temperature of ordinoides non-pregnant females is lower than that of the males.

The field data for concinus in the winter show that females have greater frequencies than males in the range 29° and above, although the modes for the two are the same. Females also have a higher mean body temperature (Appendix Table II). Because of the small sample size, the winter field data for ordinoides are not particularly instructive. However, the mean body temperature for females of this species is again lower than that of males (Appendix Table II). Mean body temperatures of both species are lower in the winter than in the summer.

The body temperature data for the three reproductive categories of snakes in the thermal gradient box are presented in Tables I, II, and III (see also Appendix Tables), and in Figures 9 and 10. The lower end of the body temperature distribution is cut off and the frequencies in the 23°-25° range are increased because the

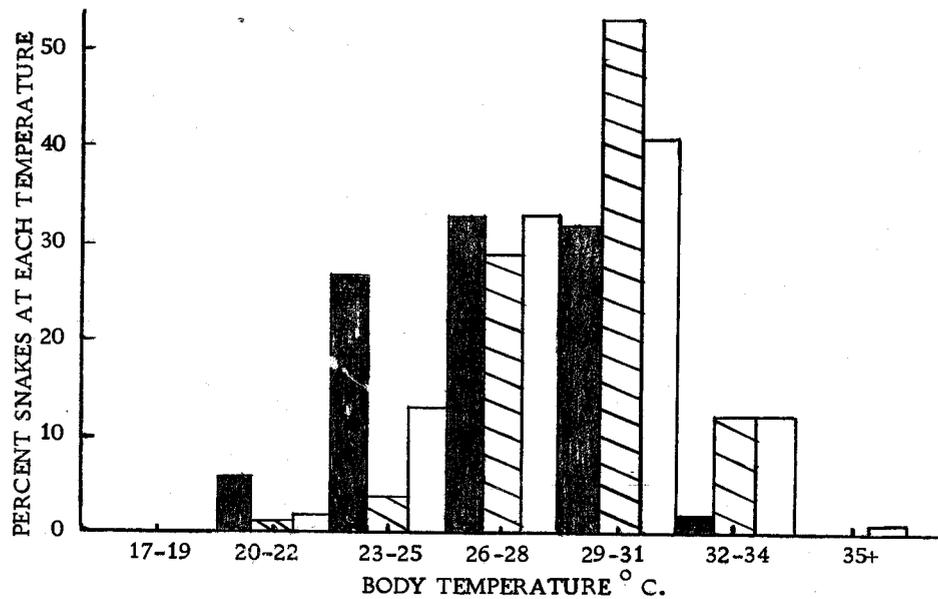


Figure 9. Body temperatures of *T. s. concinnus* in a thermal gradient box. Frequency in 3° groupings expressed as percent of total in each category of snakes, males (■ N = 288), pregnant females (▨ N = 158), and non-pregnant females (□ N = 199).\*

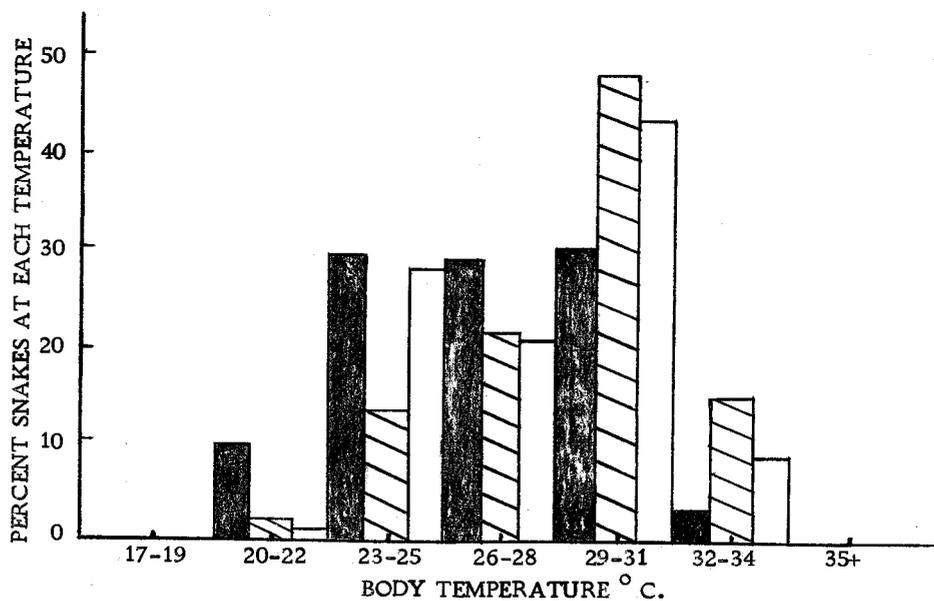


Figure 10. Body temperatures of *T. ordinoides* in a thermal gradient box. Frequency in 3° groupings expressed as percent of total in each category of snakes, males (■ N = 282), pregnant females (▨ N = 136), and non-pregnant females (□ N = 212).\*

\* See Tables I and II for explanation of N values.

temperature at the cool end of the box rarely dropped below 21° (mean 22.6°). While the cool end of the gradient box did not reach below the voluntary minimum (Table VII and Appendix Table IV) as it theoretically should to give the best results, it was consistently below what may be considered a good, if somewhat arbitrary, estimate of the "preferred range" (Table III). Furthermore, the data obtained in the gradient box rather closely approximate the summer field data. The gradient box data, therefore, may be considered valid.<sup>15</sup>

Pregnant females of both species again have the greatest modal frequency of any category, and again this is in the 29°-31° range. In the 26° and above range are found 94.9 percent of the observations for pregnant female concinus and 84.6 percent of those for pregnant female ordinoides. Pregnant females have the highest mean body temperatures. Non-pregnant females and males of both species bear essentially the same relationship to each other in the thermal gradient box, i. e., non-pregnant females have distinct modes

---

<sup>15</sup>Snakes of both species and all categories (except concinus non-pregnant females) were found to consistently have slightly lower body temperatures during dark periods than light periods. This difference was not tested statistically. However, since the difference was consistent, it is considered acceptable procedure to lump light and dark data together in the present discussions.

in the  $29^{\circ}$ - $31^{\circ}$  range while males are fairly evenly spread over the  $23^{\circ}$ - $31^{\circ}$  range. As in the summer field data, the frequency for males in the range above  $31^{\circ}$  is quite low. Mean body temperatures for non-pregnant females of both species are higher than those of males.

In Table III, the standard deviations of the mean body temperatures are presented for each category of snakes. These values have been used to calculate arbitrary "preferred ranges." The standard deviations for concinus pregnant females in the field and in the gradient box are considerably smaller than the same values for the other categories. However, pregnant female ordinoides have the greatest standard deviation of any category in the field and one in the gradient box that is very close to those of the other categories.

Using Student's t-test (67, p. 131-133), various comparisons for mean<sup>16</sup> body, substrate, and air temperatures have been made within and between reproductive categories, species, seasons, and the thermal gradient box. The results of most of these comparisons are presented in Table III and Appendix Tables I, II, and III. They are summarized here as follows:

---

<sup>16</sup>It must be emphasized that although the term "mean" will usually be omitted in describing the following comparisons, it is always the mean temperature to which reference is made.

Summer Field Data: 1) Within-species-differences in body temperature among the categories are significant at the five percent level (.05) only in the comparisons concinnus males versus pregnant females and ordinoides non-pregnant females versus pregnant females. 2) Body temperatures of all categories of concinnus are significantly higher than those of ordinoides at the five percent level (one percent level for non-pregnant females). 3) All categories of both species are significantly warmer than the substrate (.01). 4) There is no significant difference between the substrate temperatures for concinnus and ordinoides (.05). 5) Air temperature for concinnus is significantly higher than that for ordinoides (.01).

Winter Field Data: 1) Within-species-differences in body temperature between males and females are significant at the five percent level in concinnus but not in ordinoides. 2) Body temperature of female concinnus is significantly higher than that of female ordinoides, but the difference between the males is not significant (.05). 3) Both male and female concinnus are significantly warmer than the substrate (.01), but only male ordinoides are significantly warmer than the substrate (.05). 4) There is no significant difference (.05) between substrate temperatures for concinnus and ordinoides. 5) There is no significant difference (.05) between the air temperatures for these species.

Thermal Gradient Box: 1) Within-species-differences in body temperature among the categories are significant at the one percent level, except in the comparison concinnus pregnant versus non-pregnant females. This difference is significant at the five percent level. 2) In direct comparisons between the respective categories of the two species, a significant difference shows up only in the comparison of non-pregnant females (.01). When all categories of the respective species are considered together, however, a significant difference between the species is indicated at the one percent level.

Summer Versus Winter: 1) The body, substrate, and air temperatures for both species are significantly higher in the summer than in the winter (one percent level, except in the body temperature comparison for non-pregnant female ordinoides and the substrate temperature comparison for male ordinoides).

Summer Versus Thermal Gradient Box: 1) All categories considered, there is no significant difference (.05) between the body temperatures of summer field concinnus and concinnus in the gradient box. However, the body temperature of ordinoides is significantly higher (.01) in the gradient box than in the field.

Combined Summer and Thermal Gradient Box, concinnus  
Versus ordinoides: A comparison of the combined summer field and

gradient box data for each species indicates that the mean body temperature of concinus is significantly higher (.01) than that of ordinoides.

With respect to the mean body temperatures of each species as a whole, the summer field data and the gradient box data lead to the same conclusion: concinus prefers a slightly higher body temperature than ordinoides. The frequency distributions also suggest this. The fact that between-species-comparisons of the different reproductive categories in the gradient box are statistically significant only in the case of non-pregnant females does not invalidate this conclusion. A relatively small sample of individual snakes was run in the gradient box. If more were run, it is probable that a significant difference between each category of the respective species would be shown in the direction already indicated (Table III).

Carpenter (15) presented field data on the body temperatures of Thamnophis sirtalis sirtalis, T. sauritus, and T. butleri in Michigan. Mean body temperatures for these species during the period April-September were 25.6°, 26.0°, and 26.1°, respectively. Greater differences among these species were found during the months July-September. Mean body temperatures then were 28.4°, 26.8°, and 29.5°. These temperatures are probably better estimates of the actual preferred temperatures of the snakes because

more favorable environmental conditions prevailed. According to the present author's calculations, the difference between the last two means is significant at the five percent level.

Carpenter's data on garter snakes agree well with those of the present study, and they support the contention that related species (i. e. , species within a genus) may have different preferred temperatures. While the main thesis of Bogert's work (5) is that related species have similar temperature preferences, it is reasonable to expect that small but consistent differences between species do exist. No doubt, they are correlated with adaptations to specific microhabitats. With this in mind, Soulé (86) has suggested that the variance of mean body temperatures within a group of related forms may increase with the size of the group. The garter snakes seem to be a group which could profitably be included in investigations of this possibility. However, because of the difficulties in accurately estimating preferred temperatures in the field, it must be emphasized that such investigations will not lead to valid conclusions unless the field data are supported by data obtained under controlled conditions.

In the thermal gradient box, the differences among the mean body temperatures of the reproductive categories are shown to be significant in both species, the categories bearing the same

relationship to each other. In declining order of temperature preference the categories are: pregnant females, non-pregnant females, and males. As compared to the summer field data, ordinoides non-pregnant females have reversed their relationship to males; but this reversal may simply represent sampling error in the field, the true situation being that found in the gradient box.

The most interesting point revealed in the within-species-comparisons of reproductive categories is the consistent tendency for pregnant females of both species to maintain relatively high body temperatures. In most studies where the preferred temperatures of male and female reptiles have been compared, the conclusion has been that there was no significant difference (5, 70, 99). However, Fitch (36) noted a slight tendency for female collared lizards to have higher body temperatures than males, and Carpenter (15) noted a similar tendency in garter snakes. In fact, calculations based on Carpenter's data show the difference he found between T. s. sirtalis males and females to be significant at the one percent level. How many observations were on pregnant females is not known.

More important is the recent demonstration by Fitch (39) that pregnant female copperheads (Ancistrodon contortrix) tend to maintain higher temperatures than males by basking in the sun. The basking behavior of gestating female copperheads has been noted by a

number of investigators (31), but no data on the body temperatures of these snakes has been available. Thus, until his most recent data were compiled, even Fitch (40, p. 400, 413) was reluctant to suggest that pregnant females actually preferred higher temperatures.

On the basis of the data presented here and that of Fitch (39), it would seem likely that preference for relatively high body temperatures may not be uncommon for pregnant females of typically diurnal, viviparous reptiles. This is particularly true for temperate regions and the more extreme northern and southern latitudes. It is well known that viviparous reptiles are the only reptiles able to propagate in the most extreme latitudes, and the ability of these forms to properly incubate their embryos may be the reason for this. Fitch (40, p. 400) and Fox et al. (47) have noted delayed parturition and abnormal young to result from the maintenance of pregnant female copperheads and garter snakes at suboptimal temperatures. However, Pearson (74) found that the lizard Liolaemus multiformis gestates its young through the winter in the high mountains of southern Peru, and Fitch (40, p. 399) reported that pregnant female rattlesnakes (Crotalus viridis oreganus) are principally subterranean in habit at the San Joaquin Experimental Range in California. In view of these somewhat conflicting observations on gestating females, and the much less easily interpreted possibility of relatively high preferred

temperatures in non-pregnant females, a thorough investigation of sexual differences in the temperature preferences of reptiles seems warranted.

So far as the present study is concerned, the apparent preference of non-pregnant females for somewhat higher temperatures than males could be one reason why females are less abundant than males during the winter (October-April) and slightly more abundant during the summer (May-September). During the coldest winter months (November, December, January, February), only nine of 42 concinus seen were females. The only two ordinoides seen during these months were males (see summary and discussion of comparative data on concinus and ordinoides).<sup>17</sup>

From the standard deviation data presented in Table III, it appears that pregnant females of ordinoides are less efficient in maintaining their body temperatures at the preferred level than those of concinus. This is suggested in direct comparisons between the pregnant females, and in comparisons between the pregnant females and the other categories, both in the field and in the thermal gradient box. Another interpretation is possible, however.

Wilhoft (97) demonstrated that fence lizards needed relief from

---

<sup>17</sup>For a general discussion of seasonal activity in snakes, see Fitch (40, p. 396-414).

temperatures constantly at the preferred level. There is some evidence (to be discussed in later sections) that ordinoides is more heat sensitive than concinnus. Thus, the greater standard deviations for pregnant female ordinoides may be a reflection of their susceptibility to temperatures maintained at the relatively high level preferred by pregnant females. In this case, pregnant female ordinoides may need to spend more time at cooler temperatures than pregnant female concinnus, and the greater standard deviations for them may not be an indication of poor thermoregulatory ability. Further investigations are required to determine which, if either, of these interpretations is correct.

## ACCLIMATION OF PREFERRED TEMPERATURE

The effect of thermal acclimation on the preferred temperature of the snakes is best illustrated graphically as in Figure 11. The data for males and females are lumped because similar responses are shown by the two sexes. In both species, it is evident that on the first day 8°-acclimated snakes prefer higher temperatures than 32°-acclimated snakes, and that by the third day the two groups have essentially the same temperature preference. Male concinus kept in the thermal gradient box for six days (Figure 11c) instead of the usual three show the same response in the first three days. By the sixth day, however, 8°-acclimated animals prefer somewhat lower temperatures than 32°-acclimated animals. Thus, the initial response to acclimation at extreme temperatures is not a change of the preferred temperature toward the acclimation temperature. Such a change seems to appear only after six days. The room-temperature-acclimated control groups of concinus and ordinoides behave more like the 8°-acclimated groups than the 32°-acclimated groups. However, they tend to be somewhat lower on the temperature scale than the 8° groups (except in part c) and to have a less pronounced decline of preferred temperature through time.

The data for parts a, b, and c of Figure 11 were analyzed

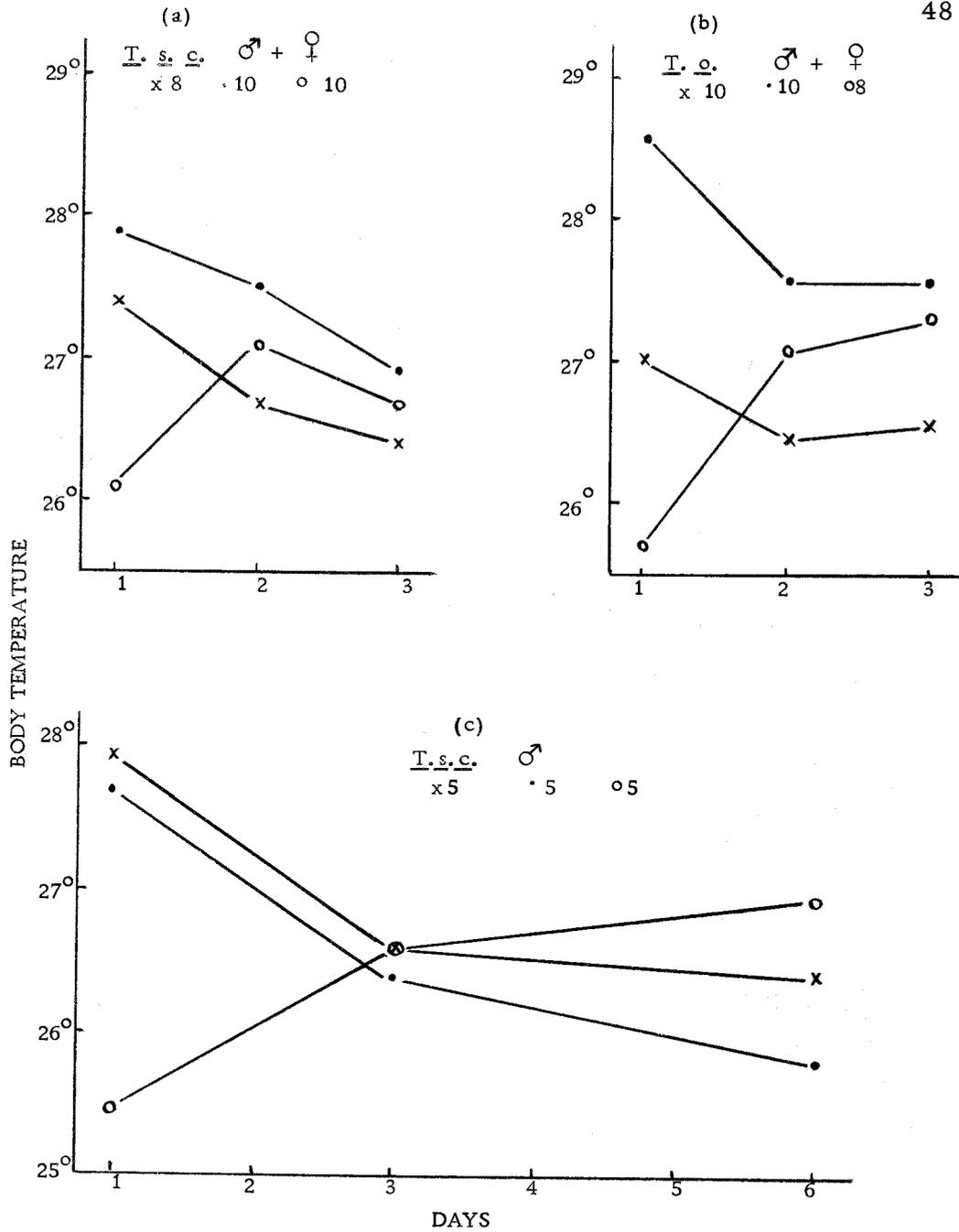


Figure 11. Preferred body temperature of T. s. concinnus and T. ordinoides acclimated at room temperature (x), 8° C. (·), and 32° C. (○) for five days. Number of snakes in each group indicated above. Body temperature of each snake recorded four times per day.

separately according to the method for analysis of variance using proportional numbers described by Snedecor (85, p. 386-387). This analysis gave the following information: 1) For each part as a whole, there is no significant difference among the mean body temperatures recorded on successive days (.05). 2) For parts a and c (concinnus males and females, and concinnus males), there is no significant difference among the mean body temperatures of the different acclimation groups (.05). For part b (ordinoides males and females), there is a significant difference among the acclimation groups (.01).<sup>18</sup> 3) For each part as a whole, there is a significant interaction between acclimation temperature and the preferred temperature on successive days (one percent level for parts a and c, five percent level for part b). While this analysis does not compare the mean body temperatures of different acclimation groups on specific days, the strong interaction indicates that there is a differential effect of the acclimation temperatures on preferred temperatures traced through time. It is likely that the trends shown in Figure 11 are a true representation of this differential effect.

Garside and Tait (50) demonstrated an inverse relationship between acclimation temperature and preferred temperature in

---

<sup>18</sup> At present, no importance should be attributed to the slight difference in behavior of ordinoides as compared to concinnus.

rainbow trout, noting that it was contrary to the usual direct relationship observed in studies on fish. Wilhoft and Anderson (99), studying the fence lizard (Sceloporus occidentalis), found that animals acclimated to 35° preferred lower temperatures than room-temperature-acclimated (21°-26°) controls, but 12°-acclimated animals did not differ significantly from the controls. In both of these studies, the animals were tested for their preferred temperatures within a few hours of their removal from the acclimation temperatures. Wilhoft and Anderson (99) did allow a 24-hour "rest period" for some of their lizards, but these showed no change as compared to the earlier tests.

The results obtained on the first day (i. e. , recorded within 24 hours of removal from the acclimation temperatures) in the present experiment agree with those described by the above authors. However, the inverse relationship of acclimation temperature to preferred temperature seems to be lost by the third day, and possibly reversed to the expected direct relationship by the sixth day. More experiments must be run to confirm the reversal, but if it actually occurs, the effects of thermal acclimation on preferred temperature are more long-lasting than on critical thermal levels (see sections on critical thermal maxima and minima).

Wilhoft and Anderson (99) suggested that the inverse

relationship observed in lizards might represent a behavioral thermoregulatory response closely associated with the reduced rate of oxygen consumption reported in warm-acclimated lizards by Dawson and Bartholomew (27). These responses were interpreted as manifestations of homeostatic mechanisms designed to keep the animal from physiologically burning itself out. Such an interpretation might be applied to the initial inverse response observed in the present study, for a relatively low rate of oxygen consumption has been demonstrated in warm-acclimated garter snakes also (see section on metabolic rate). Additional studies should seek to establish the validity of this interpretation.

## CRITICAL THERMAL MAXIMUM

The results of the critical thermal maximum experiment are presented in Table IV.

Table IV. Critical thermal maximum ( $^{\circ}$  C.) of male T. s. concinnus and male T. ordinoides acclimated for five days at room temperature, \*  $8^{\circ}$  C., and  $32^{\circ}$  C. N = 10 for each group. Least significant difference at five percent level =  $0.5^{\circ}$  C.

	Room Temperature	$8^{\circ}$	$32^{\circ}$
<u>T. s. concinnus</u>	38.9	38.6	39.2
<u>T. ordinoides</u>	38.9	38.2	38.3

\* Room temperature group is the control group. It consists of five snakes acclimated at room temperature and five from the field.

Acute and non-acute groups were lumped to give larger, numerically equal samples for comparisons among the three acclimation groups. An analysis of variance (67, p. 167-169, 226-233) showed that there is a significant difference between the species as a whole (.01), and that there is a significant difference (.05) among the acclimation groups. However, there is no significant interaction (.05) between acclimation temperature and species, i. e., both species respond in the same way. So that more specific comparisons could be made among the groups, a least significant difference was calculated

(67, p. 233-238). Using this value ( $0.5^{\circ}$  at the five percent level), the following differences are shown to be significant: 1) concinus,  $8^{\circ}$ -acclimated versus  $32^{\circ}$ -acclimated; 2) ordinoides, room-temperature-acclimated versus  $8^{\circ}$ -acclimated or  $32^{\circ}$ -acclimated; 3) concinus versus ordinoides in the  $32^{\circ}$ -acclimated group.

Until additional data are obtained, most of these results must be considered inconclusive. Hutchison (59) and Brattstrom and Lawrence (8) have recently shown that many amphibians can significantly change the level of their critical maximum in just a few hours after being moved to a new temperature. Considerable reacclimation was no doubt occurring in the non-acutely treated snakes in the present experiment. This probably explains why, in concinus, the differences between the control group and the others was not significant. The significant difference between  $8^{\circ}$ - and  $32^{\circ}$ -acclimated concinus is what would be expected, and it shows up in spite of the reacclimation of non-acutely treated animals.

The critical maximum for  $8^{\circ}$ -acclimated ordinoides bears the expected relationship to that of the control group, but that of the  $32^{\circ}$ -acclimated group does not. However, the very low critical maximum obtained for  $32^{\circ}$ -acclimated ordinoides probably can be partly attributed to the 16.1 percent weight loss suffered by these

snakes during acclimation.<sup>19</sup> Larson (64) has reported that the loss of 18-49 percent (average about 30 percent) of body weight in Sceloporus occidentalis reduced resistance to high temperatures.

With regard to the 8° and 32° acclimation groups, ordinoides seems to have a lower critical maximum than concinus. In view of the weight loss and reacclimation factors just discussed, however, this cannot be stated with certainty. The fact that control groups of concinus and ordinoides have identical critical maxima indicates that ordinoides does not have a lower critical maximum before acclimation to extreme temperatures. The identity of these critical maxima may be purely coincidental, but more experiments are needed to test this possibility.

The critical maxima observed in the present study fall within the range of values (37.0° - 41.8°) determined for several desert snakes by Cowles and Bogert (23). They also agree with the data presented by Lueth (69) for survival times of Thamnophis sirtalis, T. radix, and Natrix sipedon kept at temperatures between 37° and 42°. <sup>20</sup> The magnitude of the difference among the acclimation groups,

---

<sup>19</sup>Individuals of ordinoides were reluctant to eat, but those of concinus ate readily. The latter lost only 0.5 percent of their body weight by comparison (Appendix Table V).

<sup>20</sup>One 32°-acclimated ordinoides in the present experiment died upon reaching a body temperature of 38.7°.

however, is not as great as has been demonstrated in lizards (68) and many amphibia (8, 59). This may well be due to the reacclimation already discussed. Reacclimation during the determination itself probably was negligible because total elapsed time for each run was only four to five hours. This length of time was necessary due to the relatively large size of the snakes. At least ten to fifteen minutes were required for their body temperatures to increase by  $0.5^{\circ}$  following a similar increase in water temperature. Since the snakes consistently maintained body temperatures  $0.5^{\circ}$  to  $1.5^{\circ}$  below the water temperature, an additional 15 minutes were deemed necessary to insure that all snakes were reaching about the same level of body temperature.

Cowles and Bogert (23, Plate 27) described angular bends of the body and wide open mouth as characteristic of the critical maximum in desert snakes. No angular bends of the body were noted in the present study. As the body temperature of the snakes approached the critical level, the snakes became increasingly active. Bursts of rapid swimming were spaced by periods of floating with their heads dangling in the water. A peculiar gasping behavior became frequent (see below). At the critical level, a wide open mouth seemed to be a final, exaggerated gasp in the garter snakes. It lasted for several seconds and was accompanied by general loss of coordination and

limpness. Limpness proceeded from posterior to anterior and was occasionally accompanied by spasmodic contractions and trembling.

In gasping, a snake opened its mouth about  $\frac{1}{4}$  to  $\frac{1}{2}$  the maximum gape for two to three seconds and made an audible hiss. It could not be determined if the hiss was due to inhalation or exhalation. However, gasping might be interpreted as analogous to the panting reaction of lizards. Fewer individuals of ordinoides were seen to gasp, and gasping in them was less frequent and less audible than in con-  
cinnus. If the gasping reaction can correctly be considered a vestigial temperature regulating response, it appears that ordinoides has lost the response to a greater degree than concinnus. This might be correlated with the generally cooler climates and habitats in which ordinoides occurs.

## CRITICAL THERMAL MINIMUM

The results of the critical minimum experiment are presented in Table V.

Table V. Critical thermal minimum ( $^{\circ}$  C.) of male T. s. concinnus and male T. ordinoides acclimated for 12 days at room temperature, \*  $8^{\circ}$  C. and  $32^{\circ}$  C. N = 10 for each group. Least significant difference at five percent level =  $0.7^{\circ}$  C.

	Room Temp.	$8^{\circ}$		$32^{\circ}$	
		Acute	Non-acute	Acute	Non-acute
<u>T. s. concinnus</u>	4.2	3.4	2.5	5.9	3.9
<u>T. ordinoides</u>	4.2	3.8	4.2	7.0	4.9

\*Room temperature group is the control group. For T. s. concinnus it consists of seven snakes acclimated at room temperature and three from the field; for T. ordinoides, five acclimated at room temperature and five from the field.

An analysis of variance provided the following information: 1) considering concinnus and ordinoides together, there is no significant difference between the room temperature groups and the other acclimation groups as a whole (.05). However, there is a significant difference (.01) between the  $8^{\circ}$  and  $32^{\circ}$  acclimation groups. 2) Both species and acclimation temperatures ( $8^{\circ}$  and  $32^{\circ}$ ) considered, there is a significant difference (.01) between acute and non-acute groups. 3) There is no significant difference (.05) between the room

temperature groups of the two species. 4) Considering the 8° and 32° acclimation groups for each species as a whole, the difference between concinnus and ordinoides is significant (.01). 5) There is no significant interaction (.05) between species and acclimation temperature, i. e., both species respond the same way to the acclimation temperatures. 6) There is no significant interaction (.05) between species and acute treatment, i. e., both species respond the same way in acute treatments with respect to non-acute treatments. 7) There is a significant interaction (.01) between acute treatment and acclimation temperature, i. e., acute treatments do not have the same effect with respect to non-acute treatments in the 8° and 32° acclimation groups. 8) There is no significant interaction (.05) among the factors species, acclimation temperature, and acute treatment.

To facilitate direct comparisons between various pairs of groups, a least significant difference (0.7°) was calculated at the five percent level. Pertinent comparisons showing significant differences not brought out in the analysis of variance are the following:

1) Room-temperature-acclimated concinnus versus each 8°-acclimated group and the acute 32° group; 2) Room-temperature-acclimated ordinoides versus each 32°-acclimated group; 3) 8°-acclimated concinnus, acute versus non-acute treatments.

Much of the discussion of the critical maximum experiment is also applicable to the critical minimum experiment. The acute versus non-acute treatments in the 32<sup>o</sup> acclimation groups of both species show that considerable reacclimation has taken place in about 12 hours. T. s. concinnus and T. ordinoides appear to reacclimate at the same rate. As in the critical maximum experiment, ordinoides lost more weight than concinnus (Appendix Table V), so this may be partly responsible for its greater susceptibility to low temperature.

The situation after acclimation at 8<sup>o</sup> is somewhat different, however. Here, non-acutely treated ordinoides have reacclimated, though not significantly, and have a higher critical minimum than acutely treated animals as expected. But non-acutely treated concinnus have a significantly lower critical minimum than acutely treated ones. This may indicate that concinnus responds to short-term cold acclimation in such a way as to prepare it for prolonged exposure to cold. Acclimation in amphibians (8, 59) and possibly in a lizard (95) has been shown to occur more rapidly at high temperatures than at low temperatures (at least acclimation to high temperatures occurs more rapidly than to low temperatures). Perhaps the 12 hours non-acutely treated concinnus spent at room temperature allowed them to rapidly continue acclimation in the direction initiated

by the exposure to cold. In view of the winter emergence habits of concinnus, this type of response would have survival value.

It should be pointed out that reacclimation may be regarded as a loss of acclimation to a previous temperature. However, such an interpretation ignores the premise that, under most circumstances, the most beneficial response animals can make to a change in temperature is to rapidly acclimate to the new temperature. In this way, they can best survive temperature changes which chance to catch them in unfavorable situations. The response of concinnus described above probably constitutes an exception to the rule.

The differences between ordinoides and concinnus in the 8<sup>0</sup> acclimation groups, which suggest that the former may have a higher critical minimum, cannot be attributed to excessive weight loss. In view of this, it is remarkable to find the control groups again having identical critical levels. These results are inconclusive, but if species differences in the "standard" critical levels are not indicated, species differences in degree and type of response to various acclimation treatments are. In further investigations, it will be desirable to obtain data on females as well as males, for sexual differences corresponding to those in preferred temperatures may be found. Such data will provide a more complete picture of what may be species differences in the critical levels, and will facilitate interpretation of

the seasonal differences in abundance of males and females noted in the present study.

Since no controlled study of the critical minimum in reptiles has been reported, the following comments on the present experiments are warranted. During an experimental run, the snakes crawled continuously. The amount of heat produced by this activity was sufficient to keep some cold-acclimated snakes from reaching the critical minimum for two or three hours, even though the refrigerator temperature was near  $0^{\circ}$ . As the critical temperature was reached, the snakes stopped crawling and were unable to right themselves. This was not a condition characterized by general limpness as in the critical maximum. Rather, the snakes were very stiff. Similar stiffness has been noted in cold reptiles by Fitch (37, 39), Pearson (74), and Stebbins (88).

That a condition of limpness could be achieved, however, without apparent harm to the animal, was demonstrated by one concinus which was taken to a body temperature of  $-0.5^{\circ}$ . This snake could still turn its head sideways with the anterior two and one-half inches of its neck, but the rest of the body, except for a twitch that could be induced in the tail, was completely limp. Within 30 minutes, full coordination was restored in the anterior one-half of the body and partial muscle tone was present in the posterior part. When

examined again in three and one-half hours, the snake had fully recovered.

Fitch (39) found that copperheads cooled to  $-1.0^{\circ}$  or  $-1.5^{\circ}$  became limp. While several of his snakes died at these temperatures, others revived with slow warming. On this basis, he believed that  $-1.0^{\circ}$  to  $-1.5^{\circ}$  represented the critical minimum for copperheads. The present author feels that these temperatures are actually below the critical minimum. The critical minimum as recognized in the present paper closely follows the definition given by Cowles and Bogert (23), i. e., the temperature at which cold narcosis prevents locomotion and an animal is helpless to escape enemies or remedy its thermal impasse. Thus, Fitch's observation that copperheads at ambient temperatures of  $5.5^{\circ}$  to  $5.7^{\circ}$  could barely move and were unable to defend themselves suggests a critical minimum in the one to four degree range.

Fitch (37) has also reported one observation on a garter snake (T. s. sirtalis) which was probably near its critical minimum. This snake was a large female found entangled in a wire bird trap at an air temperature of  $4.5^{\circ}$ . The snake was hardly able to crawl and unable to strike, but it could open its mouth.

## METABOLIC RATE

The results of the metabolic rate experiment are presented in Table VI.<sup>21</sup>

Table VI. Oxygen consumption (cc. /hr. ) and metabolic rate (cc. /kg. / hr. ) of male T. s. concinnus and male T. ordinoides acclimated at 8° C. for five and twelve days, and acclimated at 32° C. for five and twelve days. N = 10 for each group. O<sub>2</sub> consumption measured at 25° C.

	8°-acclimated				32°-acclimated			
	5 days		12 days		5 days		12 days	
	MR	O <sub>2</sub>	MR	O <sub>2</sub>	MR	O <sub>2</sub>	MR	O <sub>2</sub>
<u>T. s. concinnus</u>	111.3	4.10	102.1	3.55	75.8	2.69	72.8	2.56
<u>T. ordinoides</u>	117.0	3.65	115.8	3.54	72.1	2.35	77.6	2.36

Metabolic rates (cc. /kg. /hr. ) and rates of oxygen consumption (cc. / hr. ) are both given. The mean body weight for each group ranged between 30.5 and 36.9 grams. An analysis of variance showed that there was no significant difference (.05) among the mean body weights of the various groups. Further comparisons, therefore, are valid,

<sup>21</sup>Data for the control group comprising animals from the field are not given because they are extremely variable. This is attributed to the "specific dynamic action" of proteins in some of the snakes. Such snakes did not have food in the stomach (all snakes were checked for this), but the metabolism of food probably consumed some 48 hours earlier evidently was sufficient to raise the metabolic rate far above the normal resting level.

even though the small differences in body weight may change the difference between any two groups from positive to negative, depending upon whether one compares oxygen consumption values or metabolic rate values. Analyses of variance on both oxygen consumption and metabolic rate data revealed the following: There is no significant difference (.05) between 5 and 12 day acclimation groups after acclimation at 8° or 32°. 2) There is no significant difference (.05) between species after 8° or 32° acclimation. 3) There is a significant difference (.01) between 8° and 32° acclimation groups. 4) There is no significant interaction (.05) between duration of acclimation and acclimation temperature; between duration of acclimation and species; between acclimation temperature and species; or among the factors species, duration of acclimation, and acclimation temperature.

With respect to the first three comparisons listed above, the same conclusions may be drawn using a least significant difference calculated at the five percent level. This value is 0.58 cc./hr. for oxygen consumption data and 15.0 cc./kg./hr. for metabolic rate data.

These results indicate that thermal acclimation produces a fairly rapid response in metabolic rate as well as in the critical maxima and minima. Snakes are fully acclimated within five days and probably less. Further studies are needed to determine just how fast

metabolic compensation for temperature can be achieved. The observation that cold-acclimated animals have higher metabolic rates than warm-acclimated ones is consistent with data presented for lizards (27, 52, 95) and many other ectotherms (10, 75, 78, p. 238-284).

Since concinus had earlier been shown to increase its metabolic rate after cold-acclimation (90), it was of interest to determine if ordinoides could make similar compensatory adjustments. The results of the present study show that it can. Thus, a lesser ability to compensate for low temperature by increasing metabolic rate is not a factor preventing winter emergence of ordinoides.

SUMMARY AND DISCUSSION OF COMPARATIVE DATA  
ON T. S. CONCINNUS AND T. ORDINOIDES

Both concinus and ordinoides are diurnal, heliothermic snakes. They characteristically bask fully exposed to the sun's rays until their body temperatures are within the preferred range. Body temperatures then are maintained above air and substrate temperatures (see Appendix Tables I and II). Basking sites of concinus may be at the base of a rose bush, on some old boards, in a pile of rocks, in open grass, etc., but the shelter of thick vegetation, a hole, or other place of refuge is usually nearby. T. ordinoides may bask in open grass close to a thicket or in open patches of sunlight within the thicket itself. Its secretive habits make it much less conspicuous than concinus. Even though there is some difference in the basking sites chosen by these snakes, it is interesting to note that there is no significant difference in the temperatures of the corresponding substrates. However, air temperature records indicate that the types of habitats in which ordinoides is found are significantly cooler (.01) in summer than those of concinus (see Appendix Table I).

On clear summer days, both species seem to reach their preferred temperatures by midmorning and thereafter retire to more shaded spots. Foraging in both species evidently occurs during the mid-morning hours and again in the late afternoon. On partly cloudy

days, basking snakes may be seen periodically throughout the day. They are particularly conspicuous for a few minutes after the sun has reappeared from behind a slow-drifting cloud, especially if the cloud has dropped some rain. Overcast days may permit fair numbers of snakes to bask and forage between the hours of 12 Noon and 4 P. M. (Standard Time), but if the cloud cover is heavy, few snakes may emerge at all. Activity during the cooler seasons is appropriately adjusted to make use of the warmer afternoon hours. The concinus observed during the period November-February were either basking or, in February, exhibiting preliminary courtship behavior. None of the 42 examined during this period were found to have food.

Several investigators (1, 14, 24, 69) have found garter snakes and related forms (Natrix sp. ) to survive prolonged periods of freezing or near freezing temperatures. At present, not enough is known about the hibernation sites of concinus and ordinoides to say if it is common for them to experience subfreezing temperatures during the winter. Storm (Professor of Zoology, Oregon State University) has reported finding ordinoides at elevations above 5,000 feet in the Oregon Cascades.<sup>22</sup> In at least one location, the snakes were found

---

<sup>22</sup>The two locations reported are Scott Lake and Potholes Meadow. Observations were recorded in July.

closely associated with stony ridges which probably provided hibernation sites. Specimens of both ordinoides and concinnus have been collected for the author in the Green Peter area some 20 miles east of Lebanon at elevations approaching 4,000 feet. These areas have considerable winter snow, and they represent rather unusual, cold regions of habitation for these snakes.

On March 6, 1955, in the foothills bordering the Willamette Valley near Buena Vista, Storm found a hibernaculum containing four concinnus and one Coluber constrictor. The snakes were 20-30 inches down in the moist sandy rocks of a gravel pile. Environmental temperatures ( $^{\circ}$  C.) were: air,  $9.8^{\circ}$ ; rock surface,  $30.8^{\circ}$ ; gravel at depth of two inches,  $5.0^{\circ}$ . Body temperatures of the snakes ranged from  $5.4^{\circ}$  to  $8.2^{\circ}$ . It was Storm's impression that the snakes were beginning to emerge from hibernation.

In the present study, no attempt was made to excavate hibernation sites. At Doerfler's marsh, it appeared that both concinnus and ordinoides used the burrows of meadow mice (Microtus sp.) as hibernation sites and nightly shelters. Many of these burrows were located in thick clumps of rose bushes (Figure 1) among the roots of the plants. The sites at which concinnus were observed during mid-winter were about 100 feet from the closest water and about five feet above the water level. It is not known how deep the hibernation

burrows were or to what extent they were filled with water.

Carpenter (14) noted that garter snake hibernacula at the marsh where he worked were located at ground level close to the water table. Many of the hibernating snakes were actually submerged in the water. The habitats in which ordinoides usually occurs in the Willamette Valley and elsewhere are much more sheltered by thick vegetation than the habitat at Doerfler's marsh. It seems likely, therefore, that this species normally is not exposed to such extreme winter conditions as is concinus.

So far as winter emergence is concerned, it may unequivocally be stated that ordinoides, in the Willamette Valley at least, rarely emerges during the coldest winter months (November-February). This finding confirms the author's earlier observations. Only two ordinoides were found in the vicinity of Corvallis during these months, both at Doerfler's. One of these individuals does not constitute a valid record because it was in unfamiliar territory, probably unable to find an acceptable hibernation site. This snake (a large male) was originally captured in Willamette Park on October 20, 1962. After being run in the critical minimum experiment on October 28, it was released at Doerfler's. On October 31, and again on December 4, the same snake was recaptured. The other individual (a small male) was found on January 21, 1961.

In contrast to these observations on ordinoides, it was not uncommon to find concinus basking on mild days of the coldest months. During the three winters included in the present study, 42 concinus were captured and a number of others were seen. The season of greatest activity for concinus runs from mid-February through October, that of ordinoides from mid-March also through October. These observations on seasonal activity of the snakes agree with those of other investigators already mentioned in the introduction.

Because a primary objective of this investigation was to compare concinus and ordinoides with respect to certain ecologically significant thermal parameters, the data discussed in the foregoing sections have been summarized in Table VII.

Table VII. Summary of ecologically significant thermal parameters estimated for T. s. concinns and T. ordinoides.  
Temperatures given in ° C.

	<u>T. s. concinns</u>	<u>T. ordinoides</u>
Critical Minimum	4.2	4.2
Voluntary Minimum	10.4	16.6
Preferred Range	25.0-31.0	24.4-30.4
Mean Body Temperature	28.0	27.4
Voluntary Maximum	35.5	34.3
Critical Maximum	38.9	38.9

The voluntary maxima and minima are the highest and lowest body temperatures recorded for snakes exposed on the ground surface in winter or summer, or in the thermal gradient box (see Appendix Table IV). It is notable that the values given for T. s. concinnus are very close to those given for T. s. sirtalis by Carpenter (15). Carpenter's figures are  $9.0^{\circ}$  and  $35.0^{\circ}$ , at least  $3.4^{\circ}$  lower and  $1.0^{\circ}$  higher, respectively, than the voluntary minima and maxima recorded for the other species he studied. As compared to ordinoides, concinnus also has lower and higher extremes.

Although the values given for the critical maxima and the critical minima are the same for both species, it is not certain that such identity actually exists. The results of the critical temperature experiments indicate differences in the responses of the species to thermal acclimation, and it is felt that better controlled experiments will also reveal significant differences in the critical levels. The direction in which these differences may be expected is suggested by the voluntary maxima and minima, i. e., ordinoides may have a lower critical maximum and a higher critical minimum than concinnus.<sup>23</sup> If temperature tolerances have been fixed in the

---

<sup>23</sup>A significant difference in the critical minimum (ordinoides being higher) could explain why ordinoides does not emerge during the coldest winter months.

phylogeny of the species T. sirtalis and T. ordinoides, it is reasonable to expect such differences in view of the distribution, habitat preference, and habits of these species as discussed in this paper.

In support of this expectation, another interesting set of observations should be mentioned. T. ordinoides and T. s. concinnus are closely related to T. elegans terrestris and T. s. tetrataenia, forms which live in the rather similar, cool climate of Coastal California. Here, Fox et al. (47) have found considerable natural variation in the scutellation patterns of terrestris which, on the basis of laboratory experiments, they attribute to periodic chilling of the embryos during critical periods of development. The fact that tetrataenia living in the same region does not exhibit similar variability is felt to represent a difference between the two species in susceptibility to low temperature.

It is rather difficult to predict beforehand what kind of relationship the preferred temperatures of concinnus and ordinoides might bear to habitat preferences and temperature tolerances. Regarding the activity of concinnus in cool weather, one might expect that concinnus would have a lower preferred temperature than ordinoides. On the other hand, the relatively cool, sheltered habitat in which ordinoides occurs might suggest a lower preferred

temperature for it. The results of this investigation indicate that the preferred temperatures of these snakes are more closely related to heat sensitivity than to cold tolerance. Soulé (86) has discussed similar cases in which preferred temperature differences parallel heat sensitivity differences. It would not be surprising if this should often be the case, for reptiles normally operate precariously close to their thermal maxima.

## CONCLUSIONS

While more investigations are needed to confirm and clarify the results of this study, some tentative conclusions may be stated here:

- 1) T. s. concinnus and T. ordinoides are diurnal, heliothermic snakes which consistently maintain body temperatures higher than the air and substrate temperatures.
- 2) T. s. concinnus is more tolerant of seasonally extreme temperatures than T. ordinoides
- 3) T. s. concinnus prefers slightly higher body temperatures than T. ordinoides.
- 4) If temperature tolerances and preferred temperatures are heritable characteristics developed in the phylogeny of the species, these differences probably are primarily related to the difference in distribution of each species as a whole, and secondarily to differences in habitat preference and habit which have resulted from competitive interactions with other species.
- 5) There are sexual differences in the preferred temperatures of both species, the most significant of which is the relatively high preferred temperature of pregnant females.
- 6) Initially, the preferred temperatures of both species are

inversely related to acclimation temperature. Later, they may be directly related to acclimation temperature.

7) The critical thermal maxima and minima are similar in both species and are directly related to acclimation temperature. However, reacclimation affects the original response differently in the two species.

8) Both species exhibit typical metabolic rate responses to thermal acclimation.

9) Since metabolic rate responses are the same in both species, the greater cold tolerance of T. s. concinnus cannot be attributed to a greater ability to compensate for low temperature.

## BIBLIOGRAPHY

1. Bailey, Reeve M. Temperature toleration of garter snakes in hibernation. *Ecology* 30:238-242. 1949.
2. Bartholomew, George A. and Vance A. Tucker. Control of changes in body temperature, metabolism, and circulation by the agamid lizard, *Amphibolurus barbatus*. *Physiological Zoology* 36:199-218. 1963.
3. Batts, Billy S. Intertidal fishes as food of the common garter snake. *Copeia* 1961, p. 350-351.
4. Benedict, Francis G. The physiology of large reptiles, with special reference to the heat production of snakes, tortoises, lizards and alligators. 1932. 539 p. (Carnegie Institution of Washington. Publication no. 425)
5. Bogert, Charles M. Thermoregulation in reptiles, a factor in evolution. *Evolution* 3:195-211. 1949.
6. \_\_\_\_\_ . Relative abundance, habits, and normal thermal levels of some Virginia salamanders. *Ecology* 33:16-30. 1952.
7. Brattstrom, Bayard H. Thermal control of aggregation behavior in tadpoles. *Herpetologica* 18:38-46. 1962.
8. Brattstrom, Bayard H. and Penny Lawrence. The rate of thermal acclimation in anuran amphibians. *Physiological Zoology* 35:148-156. 1962.
9. Brett, J. R. Thermal requirements of fish--three decades of study, 1940-1970. *Transactions of the Second Seminar on Biological Problems in Water Pollution, Cincinnati, Ohio, United States Public Health Service, April 20-24, 1959.* 8 p.
10. Bullock, Theodore Holmes. Compensation for temperature in the metabolism and activity of poikilotherms. *Biological Reviews* 30:311-342. 1955.

11. Carlson, Loren D. Temperature. Annual Review of Physiology 24:85-108. 1962.
12. Carpenter, Charles C. Comparative ecology of the common garter snake (Thamnophis s. sirtalis), the ribbon snake (Thamnophis s. sauritus), and Butler's garter snake (Thamnophis butleri) in mixed populations. Ecological Monographs 22: 235-258. 1952.
13. \_\_\_\_\_ . Growth and maturity of three species of Thamnophis in Michigan. Copeia 1952, p. 237-243.
14. \_\_\_\_\_ . A study of hibernacula and hibernating associations of snakes and amphibians in Michigan. Ecology 34:74-80. 1953.
15. \_\_\_\_\_ . Body temperatures of three species of Thamnophis. Ecology 37:732-735. 1956.
16. \_\_\_\_\_ . Temperature relationships of two Oklahoma lizards. Proceedings of the Oklahoma Academy of Science 41:72-77. 1961.
17. Chew, Robert M. Water metabolism of desert-inhabiting vertebrates. Biological Reviews 36:1-31. 1962.
18. Cowles, Raymond B. Possible implications of reptilian thermal tolerance. Science 90:465-466. 1939.
19. \_\_\_\_\_ . Additional implications of reptilian sensitivity to high temperatures. American Naturalist 74:542-561. 1940.
20. \_\_\_\_\_ . Fur and feathers: A result of high temperatures? Science 103:74-75. 1946.
21. \_\_\_\_\_ . Notes on natural history of a South African agamid lizard. Herpetologica 12:297-302. 1956.
22. \_\_\_\_\_ . Possible origin of dermal temperature regulation. Evolution 12:347-357. 1958.

23. Cowles, Raymond B. and Charles M. Bogert. A preliminary study of the thermal requirements of desert reptiles. Bulletin of the American Museum of Natural History 83:261-296. 1944.
24. Criddle, S. Snakes from an ant hill. Copeia 1937, p. 142.
25. Cunningham, John D. Additional observations on the ecology of the Yosemite toad, Bufo canorus. Herpetologica 19:56-61. 1963.
26. Dawson, William R. Physiological responses to temperature in the lizard Eumeces obsoletus. Physiological Zoology 33: 87-103. 1960.
27. Dawson, William R. and George A. Bartholomew. Relation of oxygen consumption to body weight, temperature, and temperature acclimation in lizards Uta stansburiana and Sceloporus occidentalis. Physiological Zoology 29:40-51. 1956.
28. \_\_\_\_\_ . Metabolic and cardiac responses to temperature in the lizard Dipsosaurus dorsalis. Physiological Zoology 31:100-111. 1958.
29. Dawson, William R. and James R. Templeton. Physiological responses to temperature in the lizard Crotaphytus collaris. Physiological Zoology 36:219-236. 1963.
30. Edgren, Richard A. and Margery K. Edgren. Thermo-regulation in the musk turtle, Sternotherus odoratus Latreille. Herpetologica 11:213-217. 1955.
31. Finneran, Leo C. Aggregation behavior of the female copperhead, Agkistrodon mokeson, during gestation. Copeia 1953, p. 61-62.
32. Fitch, Henry S. A biogeographical study of the Ordinoides Artenkreis of garter snakes (genus Thamnophis). University of California Publications in Zoology 44:1-150. 1940.
33. \_\_\_\_\_ . Geographic variation in garter snakes of the species Thamnophis sirtalis in the Pacific Coast region of North America. The American Midland Naturalist 26:570-592. 1941.

34. \_\_\_\_\_ . The feeding habits of California garter snakes. *California Fish and Game* 27(2):1-32. 1941.
35. \_\_\_\_\_ . Further remarks concerning Thamnophis ordinoides and its relatives. *Copeia* 1948, p. 121-126.
36. Fitch, Henry S. An ecological study of the collared lizard (Crotaphytus collaris). University of Kansas Publications, Museum of Natural History 8:213-274. 1956.
37. \_\_\_\_\_ . Temperature responses in free-living amphibians and reptiles of northeastern Kansas. University of Kansas Publications, Museum of Natural History 8:417-475. 1956.
38. \_\_\_\_\_ . Natural history of the six-lined racerunner (Cnemidophorus sexlineatus). University of Kansas Publications, Museum of Natural History 11:11-61. 1958.
39. \_\_\_\_\_ . Autecology of the copperhead. University of Kansas Publications, Museum of Natural History 13:85-288. 1960.
40. \_\_\_\_\_ . Longevity and age-size groups in some common snakes. In: *Vertebrate speciation*, ed. by W. Frank Blair. Austin, University of Texas Press, 1961. p. 396-414.
41. Flemister, Launce J. and Sarah C. Flemister. Chloride ion regulation and oxygen consumption in the crab Ocypode albicans (Bosq). *Biological Bulletin* 101:259-273. 1951.
42. Fox, Wade. The relationships of the garter snake Thamnophis ordinoides. *Copeia* 1948, p. 113-120.
43. \_\_\_\_\_ . Notes on feeding habits of Pacific Coast garter snakes. *Herpetologica* 8:4-8. 1952.
44. \_\_\_\_\_ . Seasonal variation in the male reproductive system of Pacific Coast garter snakes. *Journal of Morphology* 90:481-553. 1953.

45. \_\_\_\_\_ . Genetic and environmental variation in the timing of the reproductive cycles of male garter snakes. *Journal of Morphology* 95:415-450. 1954.
46. \_\_\_\_\_ . Seminal receptacles of snakes. *The Anatomical Record* 124:519-539. 1956.
47. Fox, Wade, Charles Gordon, and Marjorie H. Fox. Morphological effects of low temperatures during the embryonic development of the garter snake, Thamnophis elegans. *Zoologica* 46:57-71. 1961.
48. Fry, F. E. J. Effects of the environment on animal activity. University of Toronto Studies, Biological Series 55:5-62. 1947.
49. \_\_\_\_\_ . Temperature compensation. *Annual Review of Physiology* 20:207-224. 1958.
50. Garside, E. T. and J. S. Tait. Preferred temperature of rainbow trout (Salmo gairdneri Richardson) and its unusual relationship to acclimation temperature. *Canadian Journal of Zoology* 36:563-567. 1958.
51. Gelineo, S. and A. Gelineo. La Consommation d'oxygène chez différentes espèces de lézards à habitats différents. *Comptes Rendus de la Société de Biologie* 149:565-568. 1955.
52. \_\_\_\_\_ . Les Échanges respiratoires des lézards noirs de Dalmatie adaptés à différentes températures. *Comptes Rendus de la Société de Biologie* 149:387-389. 1955.
53. Gunn, D. L. Body temperature in poikilothermal animals. *Biological Reviews* 17:293-314. 1942.
54. Heath, James E. Temperature regulation and diurnal activity in horned lizards. Doctor's thesis. Los Angeles, University of California at Los Angeles, 1962. 135 numb. leaves.
55. Hebard, William B. Notes on the life history of the Puget Sound garter snake, Thamnophis ordinoides. *Herpetologica* 7:177-179. 1951.

56. \_\_\_\_\_ . Notes on the life history of the Puget Sound garter snake, Thamnophis ordinoides. *Herpetologica* 7:177-179. 1951.
57. Hensel, Herbert. Heat and cold. *Annual Review of Physiology* 21:91-116. 1959.
58. Hirth, Harold F. Cloacal temperatures of the green and hawksbill sea turtles. *Copeia* 1962, p. 647-648.
59. Hutchison, Victor H. Critical thermal maxima in salamanders. *Physiological Zoology* 34:92-125. 1961.
60. Inger, R. F. Temperature responses and ecological relations of two Bornean lizards. *Ecology* 40:127-136. 1959.
61. Johansen, Kjell. Temperature regulation in the nine-banded armadillo (Dasypus novemcinctus mexicanus). *Physiological Zoology* 34:126-144. 1961.
62. \_\_\_\_\_ . Observations on the wood frog, Rana sylvatica, in Alaska. *Ecology* 43:146-147. 1962.
63. Kahl, M. Philip. Thermoregulation in the wood stork, with special reference to the role of the legs. *Physiological Zoology* 36:141-151. 1963.
64. Larson, Mervin W. The critical thermal maximum of the lizard Sceloporus occidentalis occidentalis Baird and Girard. *Herpetologica* 17:113-122. 1961.
65. Lasiewski, Robert C. Oxygen consumption of torpid, resting, active, and flying humming birds. *Physiological Zoology* 36: 122-140. 1963.
66. Lee, Anthony K. and Judith A. Badham. Body temperature, activity, and behavior of the agamid lizard, Amphibolurus barbatus. *Copeia* 1963, p. 387-394.
67. Li, Jerome C. R. Introduction to statistical inference. Ann Arbor, Michigan, Edwards Brothers, 1957. 553 p.

68. Lowe, Charles H. and Velma J. Vance. Acclimation of the critical thermal maximum of the reptile Urosaurus ornatus. *Science* 122:73-74. 1955.
69. Lueth, F. X. Effects of temperature on snakes. *Copeia* 1941, p. 125-132.
70. Mayhew, Wilbur W. Temperature preferences of Sceloporus orcutti. *Herpetologica* 18:217-233. 1963.
71. Moberly, Walter R. Hibernation in the desert iguana, Dipsosaurus dorsalis. *Physiological Zoology* 36:152-160. 1963.
72. Nielsen, Bodil. On the regulation of the respiration in reptiles. I. The effect of temperature and CO<sub>2</sub> on the respiration of lizards (Lacerta). *Journal of Experimental Biology* 38: 301-314. 1961.
73. Norris, Kenneth S. The ecology of the desert iguana, Dipsosaurus dorsalis. *Ecology* 34:265-287. 1953.
74. Pearson, Oliver P. Habits of the lizard Liolaemus multi-  
formis multiformis at high altitudes in southern Peru. *Copeia* 1954, p. 111-116.
75. Precht, H. Concepts of the temperature adaptation of unchanging systems of cold-blooded animals. In: *Physiological adaptation*, ed. by C. Ladd Prosser. Washington, American Physiological Society, 1958, p. 50-78.
76. Prosser, C. Ladd. *Physiological variation in animals*. *Biological Reviews* 30:229-262. 1955.
77. \_\_\_\_\_ (ed.). *Physiological adaptation*. Washington, American Physiological Society, 1958. 185 p.
78. Prosser, C. Ladd and Frank A. Brown, Jr. *Comparative animal physiology*. 2d ed. Philadelphia, Saunders, 1961. 688 p.
79. Roots, Betty I. and C. Ladd Prosser. Temperature acclimation and the nervous system in fish. *Journal of Experimental Biology* 39:617-629. 1962.

80. Ruibal, Rodolfo. Thermal relations of five species of tropical lizards. *Evolution* 15:98-111. 1961.
81. Saint-Girons, M. C. and H. Saint-Girons. Cycle d'activité et thermorégulation chez les reptiles, (lézards et serpents). *Vie et Milieu* 7:133-226. 1956.
82. Scholander, P. F. Volumetric microrespirometers. *Review of Scientific Instruments* 13:32-33. 1942.
83. Scott, George W. and Charles C. Carpenter. Body temperatures of Bufo w. woodhousei. *Proceedings of the Oklahoma Academy of Science* 35:84-85. 1955.
84. Smith, Audrey U. The resistance of animals to cooling and freezing. *Biological Reviews* 33:197-253. 1958.
85. Snedecor, George W. *Statistical methods applied to experiments in agriculture and biology*. 5th ed. Ames, The Iowa State College Press, 1956. 534 p.
86. Soulé, Michael. Aspects of thermoregulation in nine species of lizards from Baja California. *Copeia* 1963, p. 107-115.
87. Stebbins, Robert C. *Amphibians and reptiles of western North America*. New York, McGraw-Hill, 1954. 528 p.
88. \_\_\_\_\_ . An experimental study of the "third eye" of the tuatara. *Copeia* 1958, p. 183-190.
89. Stebbins, Robert C. and Richard M. Eakin. The role of the "third eye" in reptilian behavior. *American Museum Novitates* 1870:1-40. 1958.
90. Stewart, Glenn R. Observations on respiratory metabolism in the red-spotted garter snake, Thamnophis sirtalis concinnus (Hallowell). Master's thesis. Corvallis, Oregon State University, 1960. 45 numb. leaves.
91. Stuart, L. C. The distributional implications of temperature tolerances and hemoglobin values in the toads Bufo marinus (Linnaeus) and Bufo bocourti Brocchia. *Copeia* 1951, p. 220-229.

92. Templeton, James R. Respiration and water loss at the higher temperatures in the desert iguana, Dipsosaurus dorsalis. *Physiological Zoology* 33:136-145. 1960.
93. Templeton, James R. and William R. Dawson. Respiration in the lizard Crotaphytus collaris. *Physiological Zoology* 36: 104-121. 1963.
94. Tinkle, Donald W. Ecology, maturation, and reproduction of Thamnophis sauritus proximus. *Ecology* 38:69-77. 1957.
95. Vance, Velma J. Respiratory metabolism and temperature acclimation of the lizard Urosaurus ornatus linearis (Baird). Master's thesis. Tucson, University of Arizona. 1953.
96. Wilhoft, Daniel C. Observations on preferred body temperature and feeding habits of some selected tropical iguanas. *Herpetologica* 14:161-164. 1958.
97. \_\_\_\_\_ . The effect of temperature on thyroid histology and survival in the lizard, Sceloporus occidentalis. *Copeia* 1958, p. 265-276.
98. \_\_\_\_\_ . Temperature responses in two tropical Australian skinks. *Herpetologica* 17:109-113. 1961.
99. Wilhoft, Daniel C. and J. D. Anderson. Effect of acclimation on the preferred body temperature of the lizard Sceloporus occidentalis. *Science* 131:610-611. 1960.
100. Wright, Albert Hazen and Anna Allen Wright. Handbook of snakes. vol. 2. Ithaca, N. Y., Comstock, 1957. 540 p.

Appendix Table I. Mean body, substrate, and air temperatures ( $^{\circ}$  C.) for three reproductive categories of T. s. concinnus and T. ordinoides in the field during summer with pertinent comparisons. N for body and substrate temperatures same as in Tables I, II, and III. NS = difference not significant, .05 = difference significant at five percent level, .01 = difference significant at one percent level.

		Reproductive Categories			Within Species Comparisons			Between Species Comparisons		
		Male	Pregnant	Non-pregnant	Male- Pregnant	Male- Non-pregnant	Pregnant- Non-pregnant	<u>T. s. c. -T. o.</u>	<u>T. s. c. -T. o.</u>	<u>T. s. c. -T. o.</u>
								Male	Pregnant	Non-pregnant
Body Temperature	<u>T. s. c.</u>	27.7	28.8	28.2	.05	NS	NS	.05	.05	.01
	<u>T. o.</u>	26.6	27.3	25.6	NS	NS	NS			
Substrate Temperature	<u>T. s. c.</u>	23.8	24.1	23.5	---	---	---	NS	NS	NS
	<u>T. o.</u>	23.8	23.4	23.4						
Body Temp. minus Substrate Temp.	<u>T. s. c.</u>	3.9	4.7	4.7	Difference between body and substrate temperatures significant for all at one percent level.					
	<u>T. o.</u>	2.8	3.9	2.2						
Air Temperature All Categories*	<u>T. s. c.</u>	20.8	Difference significant							
	<u>T. o.</u>	19.5	at one percent level.							

\*N for T. s. concinnus = 147; N for T. ordinoides = 178.

Appendix Table II. Mean body, substrate, and air temperatures ( $^{\circ}$  C.) for two reproductive categories of T. s. concinnus and T. ordinoides in the field during winter with pertinent comparisons. N for body and substrate temperatures same as in Tables I and II. Symbols NS, .05, and .01 same as in Appendix Table I.

	<u>Reproductive Categories Within Species Comparisons</u>			<u>Between Species Comparisons</u>		
		Male	Non-pregnant	Male-Non-pregnant	<u>T. s. concinnus-T. ordinoides</u> Male	<u>T. s. concinnus-T. ordinoides</u> Non-pregnant
Body Temperature	<u>T. s. c.</u>	24.3	26.0	.05	NS	NS
	<u>T. o.</u>	23.3	22.1	NS		
Substrate Temperature	<u>T. s. c.</u>	20.3	21.5	---	NS	NS
	<u>T. o.</u>	20.2	19.9			
Body Temperature minus Substrate Temp.	<u>T. s. c.</u>	4.0	4.5	Differences between body and substrate temperatures significant for <u>T. s. c.</u> at one percent level, but significant only for male <u>T. o.</u> (five percent level).		
	<u>T. o.</u>	3.1	2.2			
Air Temperature All Categories*	<u>T. s. c.</u>	15.9	Difference not significant			
	<u>T. o.</u>	16.5				

\* N for T. s. concinnus = 58; N for T. ordinoides = 49.

Appendix Table III. Mean body temperatures ( $^{\circ}$  C.) for three reproductive categories of T. s. concinnus and T. ordinoides in a thermal gradient box\* with pertinent comparisons. N for each group same as in Tables I, II, and III. Symbols NS, five percent, and one percent same as in Appendix Table I.

	<u>Reproductive Categories</u>			<u>Within Species Comparisons</u>			<u>Between Species Comparisons</u>		
	Male	Pregnant	Non-pregnant	Male- Pregnant	Male- Non-pregnant	Pregnant- Non-pregnant	<u>T. s. c. - T. o</u> Male	<u>T. s. c. - T. o</u> Pregnant	<u>T. s. c. - T. o</u> Non-pregnant
<u>T. s. concinnus</u>	26.9	29.2	28.6	.01	.01	.05	NS	NS	<sup>LOI</sup> <del>NS</del>
<u>T. ordinoides</u>	26.7	28.9	27.9	.01	.01	.01			

\* Mean box temperature  $22.6^{\circ}$  C.

Appendix Table IV. Ranges of body temperatures (voluntary maxima and minima) and associated environmental temperatures ( $^{\circ}$  C.) for three reproductive categories of T. s. concinnus and T. ordinoides in the field and in a thermal gradient box.

	Summer						Winter				Thermal Gradient Box					
	Male		Pregnant		Non-pregnant		Male		Non-pregnant		Male		Pregnant		Non-pregnant	
<u>T. s. concinnus</u>																
Body Temperature	16.8*	34.4*	19.6	34.8	19.4	35.5	10.4*	33.2	16.3	32.9*	19.6	33.0	21.2	33.7	22.3	34.6
Substrate Temperature	14.5	33.4	14.6	31.8	14.6	31.8	8.6	31.5	11.4	29.7	--	--	--	--	--	--
Air Temperature All Categories	13.3	31.8	--	--	--	--	7.3	23.7	--	--	--	--	--	--	--	--
<u>T. ordinoides</u>																
Body Temperature	17.9*	33.6	19.5*	32.6	17.9*	32.2	16.6	31.7	17.0	27.8	20.1	34.0	20.6	34.3	22.1	33.5
Substrate Temperature	16.8	31.7	15.3	34.5	17.4	29.4	14.1	27.8	17.3	23.1	--	--	--	--	--	--
Air Temperature All Categories	12.0	26.3	--	--	--	--	12.8	23.7	--	--	--	--	--	--	--	--

\* Body temperature corresponds to the substrate temperature. i. e., was recorded for the same individual.

Appendix Table V. Percent weight loss in T. s. concinnus and T. ordinoides used in critical temperature experiments. \*

	Critical Maximum			Critical Minimum		
	Room Temperature	8°	32°	Room Temperature	8°	32°
<u>T. s. concinnus</u>	4.7	+4.1	0.5	2.7	5.5	8.0
<u>T. ordinoides</u>	5.9	6.0	16.1	0.4	6.1	13.5

\*Snakes weighed when collected and again just before experimental runs. Values for 8° and 32° acclimation groups represent means for the acute plus non-acute groups which had essentially the same weight loss.