Temperature and energy characteristics of the sagebrush lizard in Yellowstone National Park
by Charles Frederick Mueller

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Zoology
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Abstract:
A study of the temperature and energy characteristics of Sceloporus graciosus graciosus in Yellowstone National Park was carried out during 1965 1966, and January to June, 1967. The mean cloacal temperature for 41 field measurements made with a Schultheis rapid reading thermometer was 30.9°Co This result strengthens the hypothesis by other workers that lizard populations at high altitudes have low mean preferred temperatures. Both the mean air temperature one inch above the ground(23.7°C) and the mean substrate temperature (25.7°C) were significantly lower than the mean cloacal temperature. When the cloacal temperatures of discrete spring, summer, and fall samples of lizards collected in 1966 were measured in a laboratory temperature gradient (N= 58, 70 and 60 respectively), all three mean cloacal temperatures were significantly different with the spring sample having the lowest mean (28»9 C) and the summer sample the highest (32.3°C. The mean critical thermal maximum of a sample of 14 lizards collected August, 1965, was significantly higher than the mean critical thermal maximum of a sample of 10 lizards collected in June, 1966 (43.6 vs 42.6°C). While the mean critical thermal maxima of three samples collected in 1966 were not significantly different, they, as well as the mean temperatures obtained from the samples in the thermal gradient, followed the general seasonal trend in temperatures. Oxygen consumption measured at 30°C with a Warburg apparatus was approximately 30% of the value indicated for most species of lizards. Mean fat storage by September 7, 1966, was approximately 23% of the total dry body weight for both juvenile and older lizards. A five gram lizard loses approximately .3 grams of fat during a hibernation period of 220 days, representing a loss of 2778 cal. Caloric utilization during hibernation based on oxygen consumption data extrapolated to 15°C is 2036 cal. The average energy assimilation measured in feeding experiments was 73 cal/g/day. Four age classes are discernible in the population: l) juveniles; 2) one year olds; 3) two year olds; and 4) three years old and older. Approximately 65% of the total growth occurs during the first year. A three year energy budget was constructed for a male lizard. Approximately 64,000 cal were utilized by the lizard during this period of which 6l% was consumed in metabolism.

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ABSTRACT

A study of the temperature and energy characteristics of Sceloporus graciosus graciosus in Yellowstone National Park was carried out during 1965, 1966, and January to June, 1967. The mean cloacal temperature for 41 field measurements made with a Schultheis rapid reading thermometer was 30.9 C. This result strengthens the hypothesis by other workers that lizard populations at high altitudes have low mean preferred temperatures. Both the mean air temperature one inch above the ground (23.7 C) and the mean substrate temperature (25.7 C) were significantly lower than the mean cloacal temperature. When the cloacal temperatures of discrete spring, summer, and fall samples of lizards collected in 1966 were measured in a laboratory temperature gradient (N = 58, 70 and 60 respectively), all three mean cloacal temperatures were significantly different with the spring sample having the lowest mean (28.9 C) and the summer sample the highest (32.3 C). The mean critical thermal maximum of a sample of 14 lizards collected August, 1965, was significantly higher than the mean critical thermal maximum of a sample of 10 lizards collected in June, 1966 (43.6 vs 42.6 C). While the mean critical thermal maxima of three samples collected in 1966 were not significantly different, they, as well as the mean temperatures obtained from the samples in the thermal gradient, followed the general seasonal trend in temperatures. Oxygen consumption measured at 30 C with a Warburg apparatus was approximately 30% of the value indicated for most species of lizards. Mean fat storage by September 7, 1966, was approximately 23% of the total dry body weight for both juvenile and older lizards. A five gram lizard loses approximately .3 grams of fat during a hibernation period of 220 days, representing a loss of 2778 cal. Caloric utilization during hibernation based on oxygen consumption data extrapolated to 15 C is 2036 cal. The average energy assimilation measured in feeding experiments was 73 cal/g/day. Four age classes are discernible in the population: 1) juveniles; 2) one year olds; 3) two year olds; and 4) three years old and older. Approximately 65% of the total growth occurs during the first year. A three year energy budget was constructed for a male lizard. Approximately 64,000 cal were utilized by the lizard during this period of which 61% was consumed in metabolism.

INTRODUCTION

In 1944 Cowles and Bogert published on the thermal requirements of reptiles and established criteria which have been used in studies of temperature characteristics of reptiles. Since then this has become an area of extremely active research, particularly the field of adaptations of lizards to environments with constantly changing temperatures. Bogert (1949a) felt that modifications producing control over the body temperature could be either physiological or behavioral and showed the importance of behavior in thermoregulation (Bogert, 1959). Larson (1961) reported on the critical thermal maximum of Sceloporus occidentalis and demonstrated that it could be altered by exposure to different temperature regimes. Lowe and Vance (1955) reported that the critical thermal maximum of Urosaurus ornatus was increased 1.4 C after 7-9 days at a constant 35 C. Acclimation of S. occidentalis to a high temperature resulted in selection of a lowered mean preferred body temperature (Wilhoft and Anderson, 1960). Several workers have tried to characterize various temperature criteria for members of the genus Sceloporus (Cole, 1943; Bogert, 1959; Licht, 1965; McGinnis, 1966). Brattstrom (1965) has recently summarized much of the known data on body temperatures of reptiles.

Recently much work has been done in attempts to correlate temperature patterns of lizards with their physiology. Oxygen consumption has been widely investigated. Bartholomew and Tucker (1964) evaluated the relationship between oxygen consumption and body weight in lizards at 30 C and presented the equation:

$$cc\ O_2/g/hr = 0.82\ W^{-.38},$$

where W is the weight in grams. Dawson (1960) and Dawson and Bartholomew (1958) investigated the oxygen consumption of Eumeces obsoletus and Crotaphytus collaris respectively. Moberly (1963) found that oxygen consumption in hibernating Dipsosaurus dorsalis was as much as 50% lower than that of nonhibernators in the 30-40 C range. Maher (1965) proposed that the thyroid gland in lizards has an effect on oxygen consumption which is dependent on temperature. To my knowledge the only work done on a lizard in a weight range similar to Sceloporus graciosus (ca. 5 g) is that of Hudson and Bertram (1966) on Lygosoma laterale.

Very little work has been done on energy studies in lizards. Dessauer (1952) demonstrated that there were marked seasonal variations in total lipid and liver glycogen in Anolis carolinensis. Dessauer and Fox (1957) concluded that both food consumption and growth in A. carolinensis was possibly under photoperiodic control. Johnson (1966) has estimated the energy assimilation for three species of lizards.

This study was initiated to determine the temperature and energy characteristics of Sceloporus graciosus graciosus Baird and Girard at Norris Geyser Basin, Yellowstone National Park, Wyoming. This location at an elevation of 2300 m (7552 ft.) is near the northern extreme of distribution for this species (Stebbins, 1954). The temperature characteristics investigated were the preferred temperature, critical thermal minimum, and critical thermal maximum. An investigation of the oxygen consumption, fat storage and utilization, growth rates, and caloric requirements were carried out to obtain a basic understanding of this animal's bioenergetics.

Norris Geyser Basin is an area of geysers, springs, and mudpots of varying degrees of activity. Boyd (1961) and Allen and Day (1935) have extensively discussed the geology and thermal features of the general area. The area is composed of hills of rhyolite eroded by the thermal waters which reach temperatures of 138 C. Low areas are covered with siliceous sinter resulting from the action of the hot water on the rhyolite outcrops. The thermal features are in a state of constant flux, with the appearance of new features occurring sporadically along with the disappearance or lessening in intensity of currently active features. Differential erosion rates of the rhyolite have produced a honeycombed effect in the rocks. These openings, along with fissures and vents remaining from extinct thermal features and rock piles resulting from slides, provide shelter for the lizards. The largest numbers of lizards were found on the eroded hillsides. *Pinus contorta* (lodgepole pine) and *Juniperus communis* (mountain common juniper) are the most conspicuous plants with the latter often forming dense clumps on the lower slopes. Herbaceous plants are limited, occurring mainly on the periphery of stands of lodgepole pine and juniper. Local changes in thermal features may result in the killing of plants or the appearance of plants in previously unsuitable areas.

METHODS AND MATERIALS

Field work was conducted May to September, 1965, April through October, 1966, April through May, 1967, and in February, 1967. Use of funnel traps and buried cans with drift fences to capture lizards was unsuccessful. Lizards were caught by hand. Cloacal temperatures of large lizards were taken with a Schultheis rapid reading thermometer immediately upon capture if no extended chase had ensued after the initial sighting. The thermometer was inserted with the right hand while holding the lizard with the thumb and forefinger of the left hand approximately one foot from the observer's body. This procedure minimized temperature increase in the lizard resulting from handling. The air temperature one inch above the ground and the substrate temperature at the place of first sighting were usually obtained. All lizards caught were toe-clipped for permanent identification. Sex was determined. The snout-vent and tail lengths were measured to the nearest mm and, starting in May, 1966, the lizards were weighed to the nearest 0.05 g. Except for those retained for laboratory studies, each lizard was released at the capture point.

During the summer of 1966 air and soil surface temperatures were periodically taken on a north-east facing slope known from previous work to be utilized by lizards. Measurements were made with general purpose thermistors and a Yellow Springs Instrument Company Thermistor-Thermometer. One thermistor was placed one inch above the ground surface while the second was placed flush with the soil surface.

The critical thermal maximum (CTMax) was obtained following the technique of Larson (1961). Each lizard was placed on a platform of $\frac{1}{2}$

inch hardware cloth in a one pint jar. Moist paper toweling was placed under the platform. The jar was stoppered with a two-hole rubber stopper. One hole was fitted with 3/8 inch glass tubing bent in an L shape. A Schultheis thermometer was placed in the second hole. The apparatus with a lizard inside was immersed in a water bath with only the end of the bent glass tubing protruding above the surface. The bath was then warmed until the CTMax was obtained. The heating rate was controlled so that this process took approximately 30 minutes in each test. The CTMax was taken as the temperature at which trembling and loss of muscular control occurred and was usually quite obvious. The air temperature inside the bottle was then noted, the lizard was quickly removed from the bottle, placed on paper toweling under a 100 w bulb used to retard heat loss, and the cloacal temperature was obtained with a second Schultheis thermometer. The air temperature at the level of the paper varied from 35 to 40 C. Only one lizard failed to recover, and that record was deleted. Forty-six records, divided into four discrete samples, were obtained during 1965 and 1966.

Critical thermal minima (CTMin) were obtained for five lizards during the summer of 1966. Each lizard was exposed to decreasing ambient temperatures during the evening at Norris Geyser Basin. The cloacal temperature was continuously monitored with the Thermistor-Thermometer by inserting a small animal thermistor approximately 15 mm into the cloaca and taping the thermistor lead to the lizard's tail. With this arrangement the lizard was able to move normally, albeit slowly. That cloacal temperature at which the lizard was unable to right itself when placed on its back was considered the CTMin.

Preferred temperatures were obtained in 1966 for a total of 33 lizards comprising discrete spring, summer, and fall samples by utilization of an open-topped temperature gradient box. The inside dimensions were 6 feet long, 11 inches wide and 5 3/4 inches high. Polyethylene tubing (inside diameter ¼ inch) was tightly coiled at one end of the box but with increasing distances between the coils toward the center of the box where the tubing passed through a hole in the bottom and entered a drain. The other end of the tubing was attached to a cold water faucet. The other end of the box was heated from below with a 250 w infrared lamp. One inch of sand completely covering the tubing was placed in the box. The box was arranged so that it was parallel to an overhead bank of fluorescent lights which were always on during a test. A temperature gradient from 16 to 40 C was established one hour after beginning operation. One or two lizards were placed in the gradient box at 10:00 a.m. at least 30 minutes after the gradient had been established. Beginning at 11:00 a.m. the lizards were caught and the temperatures were measured to the nearest .1 C with a Schultheis thermometer. Readings were taken hourly through 4:00 p.m. If the lizard escaped capture on the first attempt or escaped after being caught and before measurement of the cloacal temperature, the measurement was not counted.

Lizards used for fat extraction were killed, weighed, placed in an oven at 30 C and dried to constant weight. The animals were then usually placed in a freezer at 0 C and stored for future work. The carcasses were pulverized by hand and placed in boiling ether for 10-15 minutes. The extract was then filtered, the ether evaporated, and the fat weighed.

Oxygen consumption was measured by placing lizards weighing over 1 g in a specially constructed 200 ml glass chamber equipped with a center well for KOH and using a Warburg Apparatus. Lizards weighing less than 1 g were placed in a standard 18 ml glass chamber. Lizards were fasted 72 hours before measurements, and measurements were taken at 25, 30, 35, and 40 C in that order. Lizards were allowed at least 30 minutes in the chamber before each series of readings were started. Readings were taken every five minutes until six consecutive readings of resting rate oxygen consumption were obtained. If readings fluctuated or the animal was apparently active in the chamber, the readings were discarded as not representing resting rates. All oxygen measurements were taken during August and September, 1966.

During June, July, and August, 1966, feeding experiments were carried out utilizing adult lizards 49 to 55 mm in snout-vent length. Lizards were individually housed in 8 x 10½ x 8 inch plastic cages with 3/8 inch hardware cloth covers. To insure that no unmeasured food source reached the lizards, a sheet of 1/16 inch wire screening was placed between the cover and the cage, making a snug fit. To prevent small organisms from possibly crawling up the cage and under the cover, a two inch band of vaseline was placed completely around the outside of the cage approximately two inches below the cover. No unwanted organisms were ever found in the cages. Lizards were fed only mealworms, the larval form of *Tenebrio moliter*. Larvae 15 to 25 mm long were weighed individually to the nearest .001 g and placed one at a time in a cage. All feedings were started at 1:00 p.m., and larvae were placed in the cage until it was either obvious that the lizard would not feed or the lizard was sated. Larvae were offered every other day. After each feeding the weight of *Tenebrio* eaten by each lizard was recorded. Every sixth day the cages were cleaned, all feces and nitrogenous wastes from each cage were collected separately, weighed, dried, and stored for calorimetric determinations. At each cleaning lizards were weighed to the nearest 0.05 g. Room temperatures varied from 21 to 33 C. All lizards were exposed to ambient photoperiods, and no water was supplied. Caloric values were determined for *Tenebrio* and combined lizard feces and nitrogenous wastes by using a Parr oxygen bomb calorimeter.

All tests of temperature characteristics were performed on lizards within seven days after arrival in the laboratory. Oxygen consumption measurements were carried out within four days, and all lizards used for fat extractions were killed within 10 days.

Statistical procedures follow Li (1964) and Steel and Torrie (1960).

RESULTS

Temperature Characteristics

Field Temperature studies

The mean cloacal temperature for 41 lizards measured in the field was 30.9 C, mean air temperature was 23.7 C and the mean substrate temperature was 25.7 C (Table I). Due to the difficulty of knowing where a lizard had been before being sighted, substrate and air temperatures were not always recorded. The mean cloacal temperature was significantly higher than either the main substrate temperature or the mean air temperature (t test, $P = .05$). The mean air and substrate temperatures were not significantly different. The sex of the lizard was known in 29 of 41 instances. There was no significant difference in the mean temperatures for 14 males (29.7 C) and 15 females (30.2 C). The data have been lumped in Table I. The mean snout-vent length of lizards used in the experiment was 45 mm, and the lengths ranged from 32 to 52 mm.

Environmental temperatures were higher than the corresponding cloacal temperatures in only four of 50 instances (Fig. 1). The substrate temperature more often approximated the cloacal temperature than did the air temperature, and mean substrate temperature was closer to the mean cloacal temperature. Over a wide range of environmental temperatures cloacal temperatures remained fairly constant, between 27 and 35 C.

Temperature gradient studies

The mean snout-vent lengths of all lizards used in the laboratory temperature gradient was 46 mm (33-54 mm), and the mean weight was 3.72 g (1.35-5.60 g). The mean weight for individual samples varied from 2.95 g

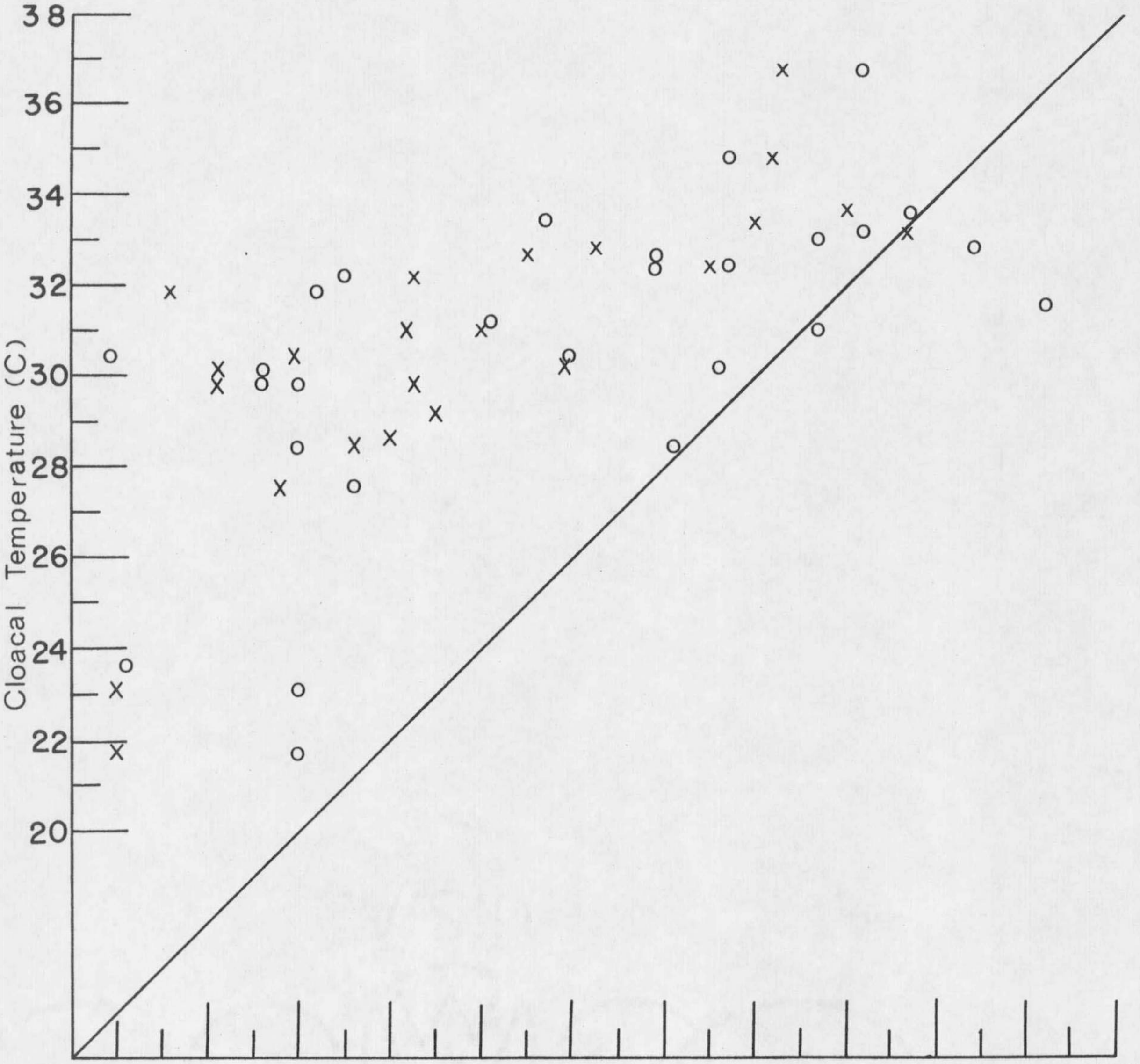

Figure 1. Correlation of cloacal and environmental temperatures for S. graciosus. X = cloacal-air correlation, O = cloacal-substrate correlation.

TABLE I. Field temperature records (C) for S. graciosus.

	N	Mean	Range	SD
Cloacal	41	30.9	21.7-36.8	±3.3
Air	23	23.7	16.0-33.4	±5.1
Substrate	27	25.7	15.8-36.4	±5.8

for the summer sample to 4.52 for the spring sample. The mean snout-vent lengths varied from 41 mm to 51 mm. When lizard weights were plotted against cloacal temperatures achieved within each sample in the laboratory gradient, no relationship between weight and cloacal temperature was observed. The mean preferred temperatures for spring, summer, and fall samples respectively were 28.9, 32.3, and 30.2 C (Table II). All three sample means are significantly different (Duncan's new multiple range test with unequal sample sizes, $P=.05$). The general mean for all samples was 30.6 C. The females had a significantly lower temperature for all samples combined than the males, but when the individual samples were tested only the fall sample indicated a significant difference (t test, $P=.05$). The mean cloacal temperature was 29.2 C for six females and 31.4 C for five males in the fall sample.

Critical Thermal Minimum

The mean CTMin was 9.1 C for five lizards. Individual CTMin ranged from 7.2 to 11.8 C. Snout-vent lengths ranged from 42 to 51 mm, and body weights ranged from 2.70 to 4.85 g.

TABLE II. Mean preferred body temperatures of S. graciosus in laboratory temperature gradient. Collection dates: Spring, 13-16 June; Summer, 23-28 July; Fall, 21-24 August.

	N	Mean preferred temperature	Range	SD
Spring	58	28.9	20.2-36.4	±3.8
Summer	70	32.3	24.6-36.9	±2.7
Fall	60	30.2	22.2-36.2	±3.6

Critical Thermal Maximum

Mean CTMax for the August, 1965, and spring, summer, and fall samples for 1966 were 43.6, 42.6, 43.4, and 42.9 C respectively (Fig. 2). The August, 1965, sample was significantly higher than the spring, 1966, sample (Duncan's new multiple range test with unequal sample size, P=.05). There was no significant difference between the sexes within any sample. While the three sample means for 1966 were not significantly different, they followed the general seasonal trend in environmental temperatures. Mean noon air temperatures measured one inch above the ground during the collecting periods were 24.2, 38.0, and 30.9 C for spring, summer, and fall. Thus the air temperatures showed the same patterns as the CTMax with the spring temperature being the lowest, the summer temperature highest, and the fall temperature intermediate. According to Lee Dalton, naturalist at Norris Geyser Basin, the weather the week preceding the fall, 1966, collecting period was characterized by snow, sleet, and heavy rain. Because the August, 1965, sample was not collected at a time comparable to