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
Montana State University
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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°C 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.
TEMPERATURE AND ENERGY CHARACTERISTICS OF THE SAGEBRUSH LIZARD IN YELLOWSTONE NATIONAL PARK

by

CHARLES FREDERICK MUELLER

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Approved:

[Signatures and signatures]

MONTANA STATE UNIVERSITY
Bozeman, Montana

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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 0.3 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:

\[
\text{cc } O_2/\text{g/hr} = 0.82 W^{0.38},
\]
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 gracilis* (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 gracilis* gracilis 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 hill-sides. 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 $\frac{1}{4}$
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 \( \frac{1}{4} \) 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 molitor*. Larvae 15 to 25 mm long were weighed individually to the nearest 0.001 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. gracilis*.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Mean</th>
<th>Range</th>
<th>SD</th>
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<td>Cloacal</td>
<td>41</td>
<td>30.9</td>
<td>21.7-36.8</td>
<td>±3.3</td>
</tr>
<tr>
<td>Air</td>
<td>23</td>
<td>23.7</td>
<td>16.0-33.4</td>
<td>±5.1</td>
</tr>
<tr>
<td>Substrate</td>
<td>27</td>
<td>25.7</td>
<td>15.8-36.4</td>
<td>±5.8</td>
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</table>

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. gracilis* in laboratory temperature gradient. Collection dates: Spring, 13-16 June; Summer, 23-28 July; Fall, 21-24 August.

<table>
<thead>
<tr>
<th></th>
<th>Mean preferred temperature</th>
<th>Range</th>
<th>SD</th>
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<tr>
<td>Spring</td>
<td>28.9</td>
<td>20.2-36.4</td>
<td>±3.8</td>
</tr>
<tr>
<td>Summer</td>
<td>32.3</td>
<td>24.6-36.9</td>
<td>±2.7</td>
</tr>
<tr>
<td>Fall</td>
<td>30.2</td>
<td>22.2-36.2</td>
<td>±3.6</td>
</tr>
</tbody>
</table>

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
Figure 2. Seasonal variation of the critical thermal maximum of *S. graciosus*. Horizontal bars on abscissa indicate collecting dates. Horizontal line = mean. Vertical line = range. Vertical bar = ± SD. Numbers = sample size.
any of the 1966 collecting periods, and since no temperature data were
collected at Norris Geyser Basin during 1965, it is difficult to compare
the data. However, the mean maximum temperature during the first 16 days
of August at West Yellowstone, Montana, was 26.3 in both 1965 and 1966
(U.S. Weather Bureau, 1965, 1966). The mean maximum temperature during
the collecting period in 1965 was 26.1 C while the mean maximum tempera­
ture during the same dates of 1966 was 25.0 C. If these temperatures are
indicative of conditions at Norris Geyser Basin, temperatures during the
early part of August, 1965, were similar to, or slightly above tempera­
tures during the comparable period of 1966.

There is greater variation in the spring, 1966, sample than in the
other three samples. This may possibly be due to varying degrees of
acclimation among the lizards. Lizards were first seen on May 2nd in
1966. However, the months of May and June are characterized by unpre­
dictable weather including heavy thunderstorms and snow. Lizards in
advantageous locations, such as south facing slopes, may be able to take
better advantage of what warm days occur by being able to achieve a
temperature permitting activity earlier than other lizards, and can emerge
for longer periods of activity. While lizards were collected during warm
periods when the lizards were usually fairly active, all lizards collected
did not necessarily have a uniform previous record of activity and might
exhibit varying degrees of temperature acclimation.

The mean air temperatures at which panting and loss of muscular
control occurred for all lizards was 44.4 and 48.0 C respectively. While
TABLE III. Air temperatures at which panting and muscular convulsions occur in *S. gracilis*. August, 1965, collection dates are 9-16 August. Other dates are as in Table II.

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<thead>
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<td></td>
<td>Mean</td>
<td>Range</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>August, 1965</td>
<td>43.2</td>
<td>41.2-44.7</td>
<td>±1.3</td>
<td>47.2</td>
</tr>
<tr>
<td>Spring, 1966</td>
<td>46.3</td>
<td>43.8-48.0</td>
<td>±1.0</td>
<td>50.3</td>
</tr>
<tr>
<td>Summer, 1966</td>
<td>45.8</td>
<td>43.8-47.6</td>
<td>±1.3</td>
<td>48.1</td>
</tr>
<tr>
<td>Fall, 1966</td>
<td>42.7</td>
<td>41.6-43.9</td>
<td>±0.8</td>
<td>46.6</td>
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</tbody>
</table>

Air temperatures at which panting and muscular convulsions occurred exhibited very little variation within each sample (Table III), there was no correlation in the rank of these two factors with the CTMax. The spring, 1966, sample had the highest mean air temperatures at which panting and loss of muscular control occurred but had the lowest mean CTMax. The means of the two characters were similar in rank, that is a sample of given rank in panting had the same rank in the mean temperatures for muscular convulsions. The mean air temperature for all samples at which panting occurred was 3.6°C lower than the mean air temperature at which loss of muscular control occurred.

Lizards used in the CTMax experiments exhibited the normal color changes found in the genus *Sceloporus*. The lizards became lighter in color with increasing temperatures until the air temperature approached the temperature at which panting started. The color then began to darken, and when the lizards were removed from the jar for measurement the dorsal surface, axillary region and groin were often a subdued black in color.
Body Weight (Gms)

Figure 3. The relationship between oxygen consumption and body weight at four ambient temperatures in S. gracilisus. Lines were fitted to data by method of least squares. See Table IV for regression equations.

During the period of recovery from high temperatures the lizard would slowly regain its normal color.

Energy Characteristics

Oxygen consumption

The oxygen consumption of S. gracilisus at four different temperatures is shown in Figure 3. Data are plotted on a double logarithmic plot. All oxygen consumption data were corrected to STP. The regression equations, confidence intervals, and correlation coefficients are presented in Table IV. At all temperatures an inverse relationship between weight and oxygen
TABLE IV. Relationship of oxygen consumption to body weight in S. graciosus at four ambient temperatures.

<table>
<thead>
<tr>
<th>Ambient Temp. (C)</th>
<th>N</th>
<th>Regression Equation</th>
<th>Confidence Intervals 95% level</th>
<th>Correlation Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>a b</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>25</td>
<td>35</td>
<td>$y = .216 + .087(x-1.87)$</td>
<td>.174-.258</td>
<td>.063-.111</td>
</tr>
<tr>
<td>30</td>
<td>32</td>
<td>$y = .373 + .146(x-1.89)$</td>
<td>.326-.420</td>
<td>.119-.173</td>
</tr>
<tr>
<td>35</td>
<td>35</td>
<td>$y = .615 + .279(x-1.85)$</td>
<td>.478-.752</td>
<td>.199-.359</td>
</tr>
<tr>
<td>40</td>
<td>35</td>
<td>$y = .885 + .388(x-1.85)$</td>
<td>.694-1.076</td>
<td>.211-.505</td>
</tr>
</tbody>
</table>

consumption was present. For example at 30 C, a 1 g lizard consumed .24 cc O_2/g/hr while a 5 g lizard consumed .17 cc O_2/g/hr.

Since the data covered a weight range of approximately 4.8 g, it was necessary to choose one weight for the purpose of comparing temperature coefficients. To facilitate comparison with records in the literature temperature coefficients were based on the oxygen consumption of a 1 g lizard. Temperature coefficients were 2.99 for the interval 25-30 C, 2.40 for the interval 30-35 C, and 2.13 for the interval 35-40 C.

Fat Storage and Utilization

The lizards have been divided into juveniles and adults for purposes of comparing fat content, although sexual maturity is probably not achieved until the third spring after hatching. Lizards are considered as juveniles from time of hatching until first hibernation. If juveniles were included in the overall sample there would appear to be a decrease in
the average fat content when the juveniles enter the population in early August. No significant difference was found in mean percentage of fat content in adults for samples collected 7-16 August, 1965, and 13 August, 1966 (t test, P=.05). The data have been lumped. No significant difference was found in fat content between sexes for any sample except the 13-27 June, 1966, sample in which the mean fat content expressed as percentage of total dry body weight was 11.7% for females and 5.2% for males. This is to be expected since lipids are being deposited in the developing ova in the females at this time. For purposes of comparing trends in the entire population the data for both sexes have been grouped. The 7 September samples were not tested because of small sample size.

Fat content, expressed as percentage of total dry body weight, varied in adults from 8.8% in June, 1966, to 24.4% in early September, 1966, to 9.9% in May, 1967 (Fig. 4). Juvenile lizards, first sighted and collected on August 13, 1966, had an average fat content of 4.3% which must be approximately the fat content of newly hatched lizards. By September 6, or 24 days later, the average fat content had risen to 22.3%, or approximately the same percentage found in the adults at that time (Fig. 5).

The mean weight of lipids present in adults ranged from .083 g for the sample collected 13-27 June to .334 g for the sample collected 7 September (Table V). The sample collected 16-23 May, 1967, had a mean fat content of .065 g, or .269 g less than the mean fat content of the 7 September sample. Fat content of juvenile lizards ranged from .005 g for
Figure 4. Seasonal variation in the fat content of adult S. graciosus. Horizontal bars on abscissa indicate collecting dates. Horizontal line = mean. Vertical line = range. Vertical bar = + SD. Numbers = sample size. Vertical lines on abscissa indicate middle of month.
Figure 5. Seasonal variation in the fat content of juvenile S. graciosus. Horizontal bars on abscissa indicate collecting dates. Horizontal line = mean. Vertical line = range. Vertical bar = ± SD. Numbers = sample size.
TABLE V. Seasonal variation in fat content in adult and juvenile S. graciosus. Sample size is as in Figs. 4 and 5.

<table>
<thead>
<tr>
<th>Collection Dates</th>
<th>Adults Mean</th>
<th>Adults Range</th>
<th>Juveniles Mean</th>
<th>Juveniles Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>13-27 June</td>
<td>.083</td>
<td>.006-.218</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>24-28 July</td>
<td>.097</td>
<td>.004-.410</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>13 August</td>
<td>----</td>
<td>----</td>
<td>.005</td>
<td>.003-.006</td>
</tr>
<tr>
<td>7-16 Aug.</td>
<td>.194</td>
<td>.026-.383</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>21-30 Aug.</td>
<td>.211</td>
<td>.033-.404</td>
<td>.008</td>
<td>.002-.025</td>
</tr>
<tr>
<td>7 Sept.</td>
<td>.334</td>
<td>.158-.604</td>
<td>.059</td>
<td>.022-.084</td>
</tr>
<tr>
<td>16-23 May</td>
<td>.065</td>
<td>.004-.212</td>
<td>----</td>
<td>----</td>
</tr>
</tbody>
</table>

The sample collected 13 August to .059 g for the sample collected 7 Sept.

When sexually mature lizards, at least 46 mm in snout-vent length, are separated from subadult lizards 24 to 45 mm in snout-vent length, there is a difference in the percent fat content between the two groups with the adults having the higher percentage. The differences between the mean percent ranged from 8% for the 21-30 August sample (4 adults, 3 subadults) to 6% for the 16-23 May sample (3 adults, 14 subadults). Due to the relatively small sample sizes when the adult-subadult division is made it is hard to make meaningful comparisons, but in general there appears to be a greater proportion of fat stored as the length increases.

Energy assimilation

Energy assimilation for each lizard was determined by subtracting the total energy excreted by the lizard from the gross energy ingested. The
TABLE VI. Energy assimilation of _S. graciosus_ at room temperatures (21-33°C).

<table>
<thead>
<tr>
<th>Sex</th>
<th>Weight (g)</th>
<th>Weight Change During Period</th>
<th>Days of Measurement</th>
<th>Cal/day</th>
<th>Cal/g/day</th>
</tr>
</thead>
<tbody>
<tr>
<td>M</td>
<td>4.13</td>
<td>+.25</td>
<td>39</td>
<td>346</td>
<td>84</td>
</tr>
<tr>
<td>F</td>
<td>3.40</td>
<td>0</td>
<td>21</td>
<td>249</td>
<td>73</td>
</tr>
<tr>
<td>M</td>
<td>3.85</td>
<td>+.50</td>
<td>17</td>
<td>337</td>
<td>88</td>
</tr>
<tr>
<td>M</td>
<td>3.93</td>
<td>+.35</td>
<td>24</td>
<td>327</td>
<td>83</td>
</tr>
<tr>
<td>F</td>
<td>4.93</td>
<td>-.25</td>
<td>26</td>
<td>286</td>
<td>58</td>
</tr>
</tbody>
</table>

1. Mean weight during measurement.

Cal/day utilized by each lizard was obtained by dividing the total calories assimilated by each lizard by the number of days it was measured. The cal/g/day utilized by each lizard was obtained by dividing the cal/day by the mean weight of the lizard during the period of measurement. All but two lizards kept at room temperature either maintained their initial weight or gained weight during the period of measurement.

Feces and nitrogenous waste combined had a mean caloric value of 3,144 cal/g. The mean caloric value of _Tenebrio molitor_ was 6,593 cal/g. Values are uncorrected for sulfur content.

One lizard which maintained a constant body weight during the period of measurement utilized 73 cal/g/day (Table VI). Three lizards that gained weight during the period of measurement utilized an average of 84 cal/g/day. One female not included in Table VI lost 1.25 g during a period
of 17 days. During this period she layed four eggs, in two clutches of two eggs each. Her average energy assimilation was 38 cal/g/day. She was losing weight rapidly at the conclusion of the measurements and died soon thereafter.

Growth

Ninety-three lizards were marked in the field during 1965 and 1966. Thirteen marked lizards were recaptured once, and two lizards were recaptured twice. In addition the snout-vent lengths of 132 lizards used in the laboratory were obtained. All snout-vent lengths were plotted against dates of capture to determine the age class composition of the population. Data from recaptured marked lizards were utilized to help delimit each age class and to aid in determining growth rates within each age class. Due to the comparatively small sample size and small return of marked lizards, no attempt was made to determine if any variation was present in growth rate between males and females.

Four age groups are discernible in the population during all or part of the summer; 1) juveniles, appearing near the middle of August; 2) one year olds; 3) two year olds; 4) three years and older lizards (Fig. 6). The curves in Fig. 6 indicate mean snout-vent length for the age class indicated at a given date. Juvenile lizards grow approximately 3 mm from the time of hatching until hibernation. The most rapid growth occurs during July and August of the first full summer with approximately 78% of the total summer growth occurring during this period (Fig. 7; a,b). Two-year-old lizards are clearly distinguishable from older lizards only
Figure 6. Average growth rates of different age classes discernible in the population of *S. graciosus*. The curves were fitted to data by sight.
Figure 7. Growth rates of individual *S. gracilis*. 
during the early part of the summer. Due to increased growth within the
age class, and the individual variation present, the two-year-old and older
lizards are indistinguishable by late summer. Growth decreases markedly
in the three years and older class (Fig. 7; c) with approximately a 3 mm
increase in length occurring. No growth apparently occurs during hiber­
nation.

The weights of 163 lizards were obtained. The relationship between
snout-vent length and weight is described by the equation:

\[ \bar{y}_x = 2.40 + .17(x-37) \]

where \( \bar{y}_x \) is the weight in grams and \( x \) is the snout-vent length in mm
\((r = .98)\).
DISCUSSION

At Norris Geyser Basin *S. gracilis* appears to use radiant energy to raise its body temperature. This is based on the finding that the body temperatures were consistently higher than either the air or substrate temperatures. This relationship of cloacal temperatures to air and substrate temperatures does not seem to be the general case. Cowles and Bogert (1944) and Larson (1961) found that the mean cloacal temperature was intermediate between the mean air and substrate temperatures with the substrate temperature being higher. In this study the mean air temperature one inch above the ground and the mean substrate temperature were not significantly different. This may be due to the constant temperature heat source below the ground at Norris Geyser Basin and the extremely rough surface features which would allow little mixing of the air near the ground surface.

In the absence of a radiant heat source the lizards are capable of utilizing warm substrates to raise their body temperatures to the preferred temperature. The mean for all cloacal temperatures obtained in the thermal gradient box, where the heat source was below the substrate, was 30.6 °C in comparison to a mean cloacal temperature of 30.9 °C in the field. Cole (1943), working on the heat tolerance of 10 species of lizards, including *S. gracilis*, concluded that the substrate temperature was more important than air temperature in determining the body temperatures. In Cole’s work the substrate was heated from below.

While Norris Geyser Basin is an area of locally high temperatures due to hot springs, geysers, steam vents, etc., these features appear to
exert little influence on the lizards' body temperatures. Field observations indicate that areas of thermal activity which were observable on the surface of the ground were seldom if ever frequented by lizards. Lizards were never seen to assume positions in these areas which would indicate they were trying to use these heat sources to raise their body temperatures (e.g., flattening of the body against the substrate). The main importance of the thermal features to the lizards is probably in maintaining environmental temperatures such that the seasonal period of activity is longer than otherwise possible at that latitude and altitude. One result of the thermal features which could influence the lizards is an extension of the snow-free period. Insolation, directly striking the uncovered ground, would allow the soil to warm up faster in the spring and would maintain warm soil temperatures later in the fall than in snow covered areas. Warm soil temperatures would permit the lizards to achieve body temperatures allowing them to emerge on hot clear days in the spring and fall even though surrounding areas may be covered with snow.

The relative roles of behavior and physiology in control of body temperatures are unknown for *S. gracilis*. Panting, a strongly developed characteristic in this lizard, has been accepted as one source of heat elimination. *Crotaphytus collaris* (Dawson and Templeton, 1963) and *Dipsosaurus dorsalis* (Templeton, 1960), two lizards with strongly developed panting, can dissipate about 1.3 times their metabolic heat production at high temperatures. The relative importance of panting in *S. gracilis* is as yet unknown. Vasomotor changes in lizards which affect rates of heat
gain and loss have been discovered (Cowles, 1958; Bartholomew and Tucker, 1963). The question of the importance of metabolic heat production in raising body temperatures is undecided. Large $Q_{10}$ metabolism values at lower ambient temperatures have been interpreted as providing increased heat production in the temperature range where the animal would be warming up to activity temperature (Hudson and Bertram, 1966). The largest $Q_{10}$ values in this study were found at the lower temperature ranges. However, Templeton (1960) found that in the desert iguana metabolic heat production can only raise the body temperature approximately 1 C.

The mean preferred temperature reported for *S. gracilis* in this study is considerably lower than other recorded values. Brattstrom (1965) gave a mean temperature of 37.5 C for *S. g. vandenburghianus* and a mean temperature of 34.9 for *S. g. gracilis*. Licht (1965) reported 35.3 C as the mean temperature for *S. gracilis* in a laboratory temperature gradient. Bogert (1949b) gave a mean preferred temperature from field records of 36.0 C. The optimal temperature range for most diurnal lizards is 36-42 C (Cowles and Bogert, 1947). The mean temperature for all lizards in this study, both in the field and in the laboratory, was near 30.8 C, approximately 4-6 C lower than the other records. Brattstrom (1965), using the data of Bogert (1949b), showed an apparent inverse relationship in the genus *Sceloporus* between mean body temperature and increasing altitude. The mean body temperature of 30.8 C for *S. gracilis* from Norris Geyser Basin, at an altitude of 2300 m, fits the curve proposed by Brattstrom. He was not sure if the relationship indicated true differences between the
species or if it was a result of sample error or poor weather conditions at higher altitudes. Since the lizards in the thermal gradient box had the possibilities of choosing temperatures as high as 40.0°C, and yet chose temperatures giving a mean approximately that in the field (30.6 vs 30.9), neither the weather conditions nor sample error (N=229) are apparently factors. The question of whether the different mean body temperatures indicate a true genetic difference or are a result of acclimation is undetermined.

Brattstrom (1965), quoting data from Mr. Don Mullally, gave the high lethal temperature of *S. g. vandenburghianus* as 45.0°C, while Cole (1943) reported a lethal temperature of 43.6°C for *S. graciosus*. It appears that the lethal temperature of *S. graciosus* in this study would be higher than that reported in the literature. This is based on the fact that the highest mean CTMax as determined in this study was 43.6°C. The lethal temperature would expectedly be several degrees higher than the CTMax (Cowles and Bogert, 1944).

Bogert (1959), speaking of spiny lizards in general (*genus Sceloporus*) indicated that lizards placed on their back could regain their normal position at temperatures as low as 7.0°C. The five CTMin values in this study were all slightly higher than 7.0°C. Since the sample size was small, the difference may not be significant. Future work should be conducted to determine if the CTMin undergoes acclimation during the course of the seasonal activity period.

The lizards appear to be able to acclimate to changing environmental
temperatures to a considerable degree. This is shown by the changes in both mean preferred temperature and CTMax which occur during the seasonal activity period and which follow the seasonal trends in temperature.

Previous work on acclimation of preferred temperatures have either indicated no acclimation occurring as a result of higher ambient temperatures (McGinnis, 1966) or the selection of a lowered mean preferred temperature after acclimation to high temperatures (Wilhoft and Anderson, 1960). Lowe and Vance (1955) and Larson (1961) have reported that the CTMax of Urosaurus ornatus and S. occidentalis respectively can be increased by exposure to higher temperature regimes. While the acclimation in U. ornatus was induced experimentally, the variation in the CTMax of S. occidentalis was apparently due to changing seasonal temperatures.

According to Cowles and Bogert (1944) "...one of the seemingly important requirements of reptiles is an effective extension of both their daily and seasonal hours of activity." The lizards at Norris Geyser Basin begin emerging from hibernation near the first week in May and begin disappearing in the middle of September with none apparently active after the end of September. However, during the month of May and at least the first two weeks of June the lizards have at best short periods of activity due to the normally inclement weather during this period. This means that in approximately 3-4 months the lizards must complete their reproductive cycle and also store enough fat to last through an extended period of hibernation. Any factor which would enable the lizards to extend their daily period of activity would increase their chances of survival.
Acclimation of the preferred temperature and CTMax resulting in higher temperature tolerances during the period of highest environmental temperatures would enable the lizards to extend their activity period to include temperatures previously avoided by them.

Most of the reported data on oxygen consumption at 30.0 C in lizards can be described by the equation \( \frac{O_2}{g/hr} = 0.82 W^{-0.38} \) (Bartholomew and Tucker, 1964). The oxygen consumption of a 1 g S. graciosus is .24 cc \( O_2/hr \), or approximately 30% of the predicted value. A 1 g Lygosoma laterale, another species with a small body weight, consumes .31 cc \( O_2/hr \), or approximately 40% of the predicted value (Hudson and Bertram, 1966).

The reasons for the large deviations from the predicted value are not known. As most data have been gathered from large lizards, more work must be done on small lizards to determine if this decreased oxygen consumption is characteristic of species with small body weights.

An apparent discrepancy is present between the May, 1967, and June, 1966, values of percent of stored fat. Assuming no sample error and similar variation in both samples the lowest fat content would normally be expected when the lizards emerge from hibernation, with the May value being lower than the June value. But, as mentioned, the period from May to the middle of June is characterized by inclement weather. During this period the lizards spend much of their time underground and presumably would use their stored fat as an energy source.

The greatest amount of fat stored in Anolis carolinensis was only 7% of the dry body weight (Dessauer, 1953), compared to approximately 23% in
S. graciosus. However A. carolinensis is a subtropical species having no extended period of hibernation. Presumably it would not need large fat deposits since it can feed throughout the entire year.

When the oxygen consumption data found in this study for a 5 g lizard are extrapolated to 15 C, the average hibernation temperature for lizards (Cowles, 1941), an average value of .08 cc O₂/hr is obtained. Assuming a R.Q. of 0.82 and a caloric equivalent of 4.82 cal/cc O₂ consumed (Brody, 1945), a 5 g lizard would use 2036 cal during a hibernation period of 220 days. The average loss in fat content during hibernation for sexually mature lizards (ca. 5 g) is .302 g. Utilizing the value of 9.2 Cal/g found for Poor-will fat (Bartholomew et al., 1957) this would mean a loss of 2779 cal. Considering the difficulties in extrapolation of oxygen consumption data, and that both the fat loss and oxygen consumption data represent mean values, and the hibernation temperature may not be exactly 15 C, the two figures are remarkably close.

Values of energy assimilation obtained from the feeding experiment are comparable to the estimates by Johnson (1966) for S. undulatus, S. magister, and Cnemidophorus tigris. The estimated energy assimilated by the three lizards was 55, 72, and 71 cal/g/day, respectively. A S. graciosus in this study which maintained constant body weight averaged 73 cal/g/day.

McNab (1963) has discussed the arguments for construction of energy budgets and has shown the relative simplicity of using oxygen consumption as a measure of energy utilization as opposed to feeding experiments. By utilizing the results found in this study, a three-year energy budget for.
TABLE VII. Calculation of a three year energy budget for a male S. graciosus.

<table>
<thead>
<tr>
<th></th>
<th>Energy Utilized in Metabolism (cal)</th>
<th>Energy Stored (cal)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Summer</td>
<td>Winter</td>
<td>Growth</td>
</tr>
<tr>
<td>Juvenile (Juv.)</td>
<td>1,232</td>
<td>764</td>
<td>2,262</td>
</tr>
<tr>
<td>1 year (1 yr.)</td>
<td>8,282</td>
<td>1,018</td>
<td>11,312</td>
</tr>
<tr>
<td>2 year (2 yr.)</td>
<td>11,944</td>
<td>2,036</td>
<td>4,525</td>
</tr>
<tr>
<td>3 year (3 yr.)</td>
<td>13,705</td>
<td>----</td>
<td>2,262</td>
</tr>
</tbody>
</table>

A male S. graciosus was constructed. Measurement of oxygen consumption is based on the following assumptions: 1) the mean activity temperature is the same for all sizes of lizards; 2) metabolism during activity is three times greater than resting rate metabolism (Licht, 1965); 3) during the summer lizards not active were at a temperature of 18°C; and 4) lizards are active seven hours a day. The summer activity period was divided into three sections, May 10–June 27, June 28–August 14, August 15–September 30, with mean activity temperatures of 28.9, 32.3, and 30.2°C, respectively. The average weight during each period was used for computation of oxygen consumption. The calories stored in growth were obtained by multiplying the average increase in weight in grams by 4,436 cal/g, the average caloric content of fat-free whole lizards (this study, unreported).

Approximately 64,000 cal are utilized by the lizard in three years, 61% of which is consumed in metabolism (Table VII). Assuming that the efficiency of utilization in the field is similar to that in the laboratory...
(83%), the lizard would have to ingest approximately 78,000 cal during the three years. If the caloric content of the organisms eaten in the field was similar to *Tenebrio* larvae, 26.8 g of food would be eaten.
LITERATURE CITED


Temperature of desert reptiles.


Mueller, C.F. M887
Temperature and energy characteristics of the sagebrush lizard in Yellowstone National Park.

D378
M887
Cop. 2