

The Effect of Activity on Oxygen Consumption, Oxygen Debt, and Heart Rate in the Lizards *Varanus gouldii* and *Sauromalus hispidus*

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Summary. Oxygen consumption and heart rate were measured during rest and activity in the lizards *Varanus gouldii* and *Sauromalus hispidus*. Oxygen debt was calculated from postactive oxygen consumption. Standard metabolic rates of the two animals are similar but *Varanus* consumes much more oxygen during activity than does *Sauromalus* (Fig. 1–3). The latter has a constant active metabolic rate above 30°C and accumulates a large oxygen debt, which is repayed slowly (Fig. 4). *Varanus* recovers rapidly from activity (Fig. 5), presumably because of the smaller lactacid debt incurred. Heart rate increment in *Sauromalus* is high (Fig. 8). This variable cannot be responsible for the limitation of active oxygen consumption; calculations of oxygen pulse suggest that an inability to increase A-V difference and/or stroke volume are implicated (Fig. 9). *Varanus* have evolved mechanisms to sustain high levels of oxygen consumption superior to those of other reptiles investigated. The role of anaerobiosis in the biology of both animals is discussed.

Introduction

A considerable amount of data has been gathered on resting metabolic rate in reptiles, and this is summarized and discussed extensively elsewhere (Dawson, 1967; Templeton, 1970; Bennett and Dawson, 1971). The effects of controlled activity have been investigated in only a few species of large reptiles (*Amphibolurus*, Bartholomew and Tucker, 1963; *Iguana*, Moberly, 1968a, b; *Pituophis*, Greenwald, 1971; *Sphenodon*, Wilson and Lee, 1970; *Tiliqua*, Bartholomew *et al.*, 1965; *Varanus*, Bartholomew and Tucker, 1964). In most of these species, aerobic scope, the augmentation of oxygen consumption above resting levels during maximal activity (see Fry, 1947), is low and decreases with increasing body temperature (T_b) over the normal temperature range of activity. *Varanus*, however, is reported to have exceptional powers of oxygen utilization during activity (Bartholomew and Tucker, 1964). This study was undertaken to investigate oxygen transport and its functional bases in *Varanus gouldii*, the racehorse goanna, and an iguanid lizard of comparable size and thermal preferendum, *Sauromalus hispidus*, the spiny chuckwalla. This paper examines the capacities of the two species

to function aerobically during activity, and the contribution of heart rate to oxygen transport is also analyzed.

The monotypic family Varanidae (*Varanus*) is widespread throughout the Old World. All of its members are similar in body form and habits, differing chiefly in body size. *Varanus* are all carnivorous, preying principally on rodents and lizards. They maintain large territories, foraging over great distances, and are active and extremely wary animals, difficult to approach and capture. They normally flee at high speeds but will fight savagely if cornered (Cowles, 1930; Mertens, 1942; Bartholomew and Tucker, 1964; Pianka, 1970). Bartholomew and Tucker (1964), in an examination of several Australian species, reported that standard levels of metabolism were twice as high as those of other lizards at normal T_b 's, that T_b increased during activity, and that oxygen consumption during activity increased with increasing T_b . Subsequent speculation (Tucker, 1967; Greenwald, 1971) suggested that varanids possess aerobic capacities superior to those of other reptiles.

Varanus possess a morphological specialization suggestive of unusual capacities for aerobiosis. The lung structure has been examined extensively and is far more complex than that of other reptiles, possibly similar to that of primitive mammals or birds (Milani, 1893; Wolf, 1933; Mertens, 1942; Kirschfeld, 1970). Most saurian lungs are relatively simple sacs and have no intrapulmonary bronchi. The respiratory area is confined to the anterior portion of the lung and not developed extensively; the posterior portion is devoid of air cells. The entire organ is not considered efficient in its ability to extract oxygen from ventilated air (Wolf, 1933). *Varanus*, however, possess cartilage-lined intrapulmonary bronchi and extensive spongy, alveolar-like air cells throughout the lung. Wolf believed that oxygen exchange could be as efficient as that in avian lungs. Although Mertens (1942) maintained that the muscular ridge subdividing the ventricle in *Varanus* is better developed than in other lizards, other studies (Mathur, 1944; Copland, 1953) show no cardiovascular specializations that could be interpreted as facilitating oxygen transport or partitioning oxygenated from deoxygenated blood.

The family Iguanidae, with the relatively closely allied forms, the agamids and chameleons, forms one of the largest assemblages of lizards. They are probably not greatly morphologically different from the ancestors of the order Squamata (Romer, 1956). *Iguana iguana*, the only large representative of the family examined during activity, undergoes considerable lactate production and exhausts easily (Moberly, 1968a). Another large iguanid was chosen for examination to determine whether *Iguana* is highly specialized metabolically or is representative of the group in its reliance on anaerobiosis. *Sauromalus hispidus* is a large, herbivorous animal, similar in appearance to its congener, *S. obesus*

(Norris and Dawson, 1964). The thermal preferendum of *Sauromalus hispidus* is 37.1°C (K. Nagy, pers. comm.), of *S. obesus*, 37.9°C (Brattstrom, 1965). The active T_b of *Varanus gouldii* is reported as 37.1°C (Licht *et al.*, 1966) and 38.1°C (Pianka, 1970). Bartholomew and Tucker (1964) reported a mean T_b of 35.5°C for several species of *Varanus*, including *V. gouldii*. Both *Sauromalus* and *Varanus*, therefore, have activity temperatures of approximately 37–38°C.

Material and Methods

Collection and Animal Maintenance

Fifteen adult *Sauromalus hispidus* (mean weight: 574 gm; range: 396–1061 gm) were collected on Isla Mejia, Baja California Norte, Mexico, and transported to The University of Michigan where all experiments were performed. They were maintained in wood and metal-screen pens equipped with incandescent lights and heat lamps set on a seven hour per day thermal period (1000–1700 EST). They were fed lettuce, dog food, and a weekly supplement of raw egg and vitamin mixture. Water was available at all times. All metabolic measurements were made between January and April.

Ten specimens of *Varanus gouldii gouldii* and *V. g. rosenbergi* (674 gm, 139–1280 gm) were collected from widely scattered sites in Western Australia. The lizards were housed in large, open-air pens at the University of Western Australia, where all metabolic measurements were made. The pens were equipped with heat lamps set on a seven hour per day cycle (0900–1600). The animals were exposed to ambient photoperiods. They remained healthy on a diet of live mice and rats and raw kangaroo meat. Water was always available. Experiments were run during January and February.

Measurements of Metabolism and Heart Rate

To measure metabolic rate during activity, it is necessary to monitor oxygen consumption continuously with little lag time or dilution of expired air. Such measurements are impossible in large metabolic chambers. Therefore, metabolic masks of small volume (100, 175, and 400 cc), which covered the entire head and neck, were fashioned from rubber "wet suit" material and fastened securely to the pectoral region of the animals with contact cement. The masks, which contained incurrent and excurrent air ports, admitted no light, were free from air leaks, and did not interfere with normal ventilation. A mask was generally left on an individual for three days, during which time three metabolic measurements at different T_b 's were made. No ill effects were observed after the mask was removed.

The animals were fasted for at least two days before the experiments. Preliminary measurements indicated a substantially lower metabolic rate at night (see also Roberts, 1968). Since minimal values were desired, all experimental determinations were made after 2000 local time. Masked animals were fitted with a rectal thermocouple and gold-plated safety pin leads in front and hind limbs for measurement of T_b and heart rate, respectively. The animal was tied to a restraining board and placed in a constant temperature cabinet (regulated at $\pm 0.5^\circ\text{C}$) before 1200 local time. The temperature of the cabinet was set between 15° and 42°C. Dry air was metered through the mask at 150–1000 cc/min. Body and ambient temperatures were monitored with thermocouples connected to a Brown Class 15 recording potentiometer. Heart rate was measured with a Sanborn EKG pre-

amplifier and recording oscillograph, Model 150 (*Sauromalus*) or a Grass A.C. pre-amplifier, Model P5B, and Sanborn 299 D.C. amplifier recorder (*Varanus*). Oxygen consumption was determined by monitoring the excurrent air line with a Beckman paramagnetic oxygen analyzer, Model G-2 (*Sauromalus*) or F-3 (*Varanus*), connected to a Brown Class 15 recording potentiometer. Carbon dioxide and water vapor were removed before oxygen analysis by Ascarite (sodium hydrate asbestos) and Drierite (anhydrous calcium sulfate), respectively. All gas volumes were corrected to standard conditions of temperature and pressure.

During the experimental period, oxygen consumption was monitored for one hour and heart rate was measured every fifteen minutes during that period. All observations were averaged to obtain standard values. To obtain maximum oxygen consumption, the temperature cabinet was opened and gold-plated safety pin electrodes were implanted in the hind limbs of the animal. It was first stimulated by general handling of the limbs and tail, which caused violent struggling. Sometimes a series of electric shocks (2-10 volts, 10 per sec) were delivered with a Grass stimulator, Model S4C for *Sauromalus* or Model S6C for *Varanus*, if the animal became refractory to further handling. The animal was stimulated for seven minutes. Oxygen consumption and T_b were monitored continuously; heart rate was measured at the end of the stimulation period. Oxygen consumption increased to a peak value during stimulation, maintained that level for 30 to 60 seconds, and slowly declined to resting levels. The return of oxygen consumption to resting levels was monitored for one hour after stimulation. The animals rarely, if ever, moved or struggled if left undisturbed during this recovery period. Occasionally an animal was restimulated during the recovery; it nearly always returned to the maximal level measured previously.

To determine whether the metabolic mask altered standard metabolism, the metabolic rate and heart rate of unmasked, unrestrained *Sauromalus* were determined. Animals were placed in large metal boxes before 1200 EST and left undisturbed until after 2000 EST. Oxygen consumption, heart rate, and T_b were measured as outlined above.

Statistics

All linear and polynomial equations calculated for this study are the best computed least squares fit to the data. If a function was not obviously linear after transformation, polynomial regressions of increasingly higher degree were computed until no further significant improvement ($p < 0.05$) was obtained. In practice, this never required more than a second-order regression. Standard errors are reported with mean estimates; 95% confidence limits are used to estimate significance.

Results

Oxygen Consumption and Scope

Metabolic rates are reported in cc oxygen consumed per gm body weight per hour. The results of all oxygen consumption experiments on *Sauromalus* are given in Fig. 1. No significant difference ($p = 0.68$ by analysis of covariance) was found between the metabolic rate of undisturbed animals in metabolic chambers and masked lizards tied to restraining boards. The data on resting animals were pooled and yielded the regression

$$\log \text{SMR} = -2.540 + 0.0396 T_b. \quad (1)$$

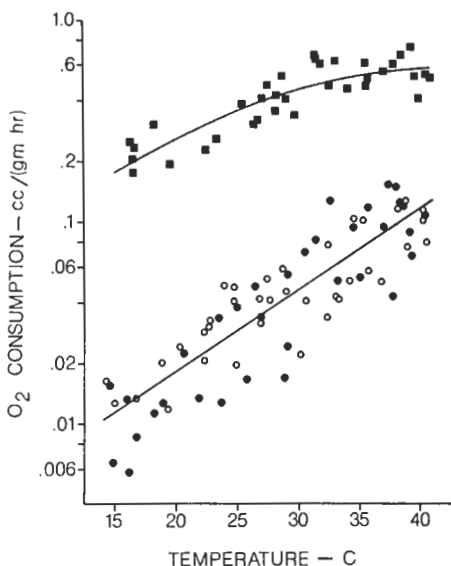


Fig. 1. Standard and active oxygen consumption in *Sauromalus hispidus*. Shaded circles represent resting animals with metabolic masks; unshaded circles, resting animals without masks; squares, active animals with masks

Q_{10} of the standard metabolic rate is 2.50. Oxygen consumption of active *Sauromalus* increased with increasing T_b up to approximately 30°C and remained constant between 30° and 41°C. Analyzed separately, the data at T_b greater than 30°C have no significant temperature trend. The second degree polynomial which best describes this relationship is

$$\log \text{AMR} = -1.456 + 0.0566 T_b - 0.000654 T_b^2 \quad (15^\circ\text{C} \leq T_b \leq 40^\circ\text{C}). \quad (2)$$

Q_{10} values of this function decrease continuously from 2.17 at 15–20°C to 1.08 at 35–40°C. The animals often exhausted during the activity period and ceased to respond to further stimulation.

The results of metabolic experiments on *Varanus* are reported in Fig. 2. The temperature dependence of standard metabolism decreased continuously from 15° to 40°C such that standard metabolic rate was essentially independent of T_b between 30° and 40°C. Two animals began hyperventilating at 40.4°C, although a third animal did not at 40.6°C. All individuals measured at 42°C or above actively hyperventilated. The thermoregulatory increase in ventilation rate resulted in a one- to three-fold increase in metabolic rate, and data on hyperventilating animals are consequently excluded from calculations of standard metabolic conditions. The best least squares description of the resting data is

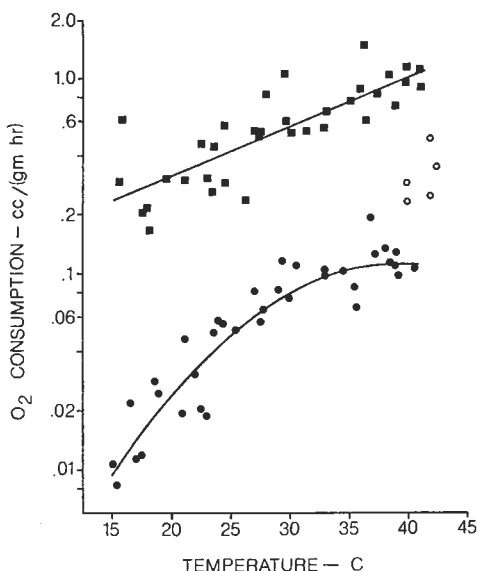


Fig. 2. Standard and active oxygen consumption in *Varanus gouldii*. Shaded circles represent resting animals; unshaded circles, hyperventilating animals; squares, active animals

$$\log \text{SMR} = -3.832 + 0.150 T_b - 0.00195 T_b^2 \quad (15^\circ\text{C} \leq T_b \leq 40^\circ\text{C}). \quad (3)$$

Q_{10} decreases from 6.61 at 15–20°C to 1.07 at 35–40°C. Oxygen consumption of active *Varanus* increased with increasing T_b with a constant Q_{10} of 1.78:

$$\log \text{AMR} = -0.996 + 0.0250 T_b. \quad (4)$$

Exhaustion was never observed during stimulation.

The aerobic metabolic scope of both species as a function of T_b is given in Fig. 3. Scope values were calculated from regression equations (Eqs. (1) and (2), *Sauromalus*; Eqs. (3) and (4), *Varanus*) and not determined directly from measurements of resting and active metabolism on an individual because of changes in T_b during activity. The metabolic increment is similar in both animals below 30°C; however, at 40°C, the aerobic scope of *Varanus* is double that of *Sauromalus*.

Body temperature increased slightly during activity in *Sauromalus* (mean change: $+0.4^\circ\text{C} \pm 0.1$). The maximum increase observed was 1.5°C . Increase in T_b was not correlated with ambient temperature. *Varanus* did not change T_b significantly during activity (mean change: $+0.2^\circ\text{C} \pm 0.2$). The maximum increase observed was 1.3°C .

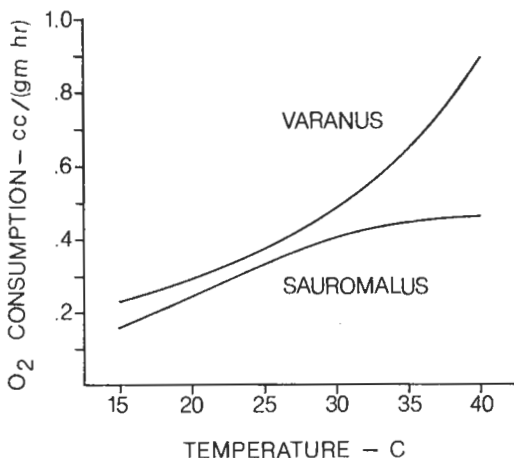


Fig. 3. Metabolic scope in *Sauromalus hispidus* and *Varanus gouldii*

Recovery

In order to determine how rapidly the animals recover standard metabolic levels after exercise, the oxygen consumption of each animal was measured after maximum oxygen consumption until 90% recovery had been reached. A smooth curve was fitted by eye to the recording of oxygen consumption, and the number of minutes required to reach 25, 40, 50, 60, 70, 75, 80, and 90% recovery of standard levels was measured. For each of these recovery percentages, a polynomial regression was computed for the time required to reach that percentage recovery as a function of T_b . These regressions were used to calculate recovery time at 5°C intervals between 15° and 40°C for each recovery percentage. The resulting relationships between percentage recovery, time, and T_b are given in Figs. 4 and 5 for *Sauromalus* and *Varanus*, respectively.

In the range of T_b between 20° and 40°C, *Sauromalus* recovers most rapidly from a bout of activity at 25–30°C: recovery is slower at 40°C than at 20°C (Fig. 4). In contrast, the rate of recovery of *Varanus* continues to increase with increasing T_b and is most rapid at 40°C (Fig. 5). *Sauromalus* recovers slightly more rapidly than *Varanus*, at least in the initial phases of the process, between 15° and 30°C, but more slowly at 35° and 40°C, temperatures which are closer to the activity range of the animals. At 40°C, *Varanus* recovers more than three times as rapidly as *Sauromalus*. These calculations in terms of percentage recovery obscure the even greater difference in recovery rates between the two animals in terms of decrease in the rate of oxygen consumption, since metabolic scope is higher in *Varanus*.

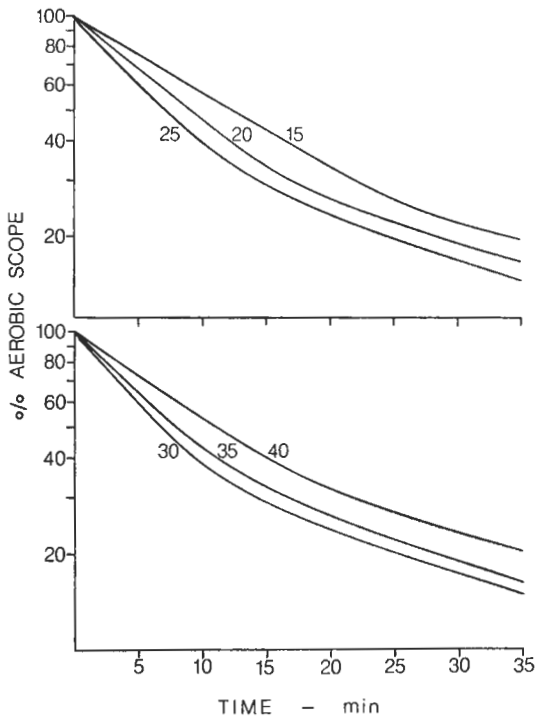


Fig. 4. The effect of body temperature on recovery of standard levels of metabolism after maximal oxygen consumption in *Sauromalus hispidus*. Body temperature ($^{\circ}\text{C}$) is given beside each regression

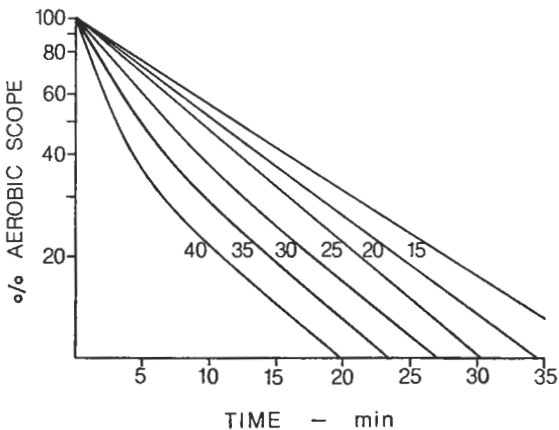


Fig. 5. The effect of body temperature on recovery of standard levels of metabolism after maximal oxygen consumption in *Varanus gouldii*. Body temperature ($^{\circ}\text{C}$) is given beside each regression

If the logarithm of an equilibration rate is plotted as a function of time, a linear relationship between the variables indicates that a single process is operating during the equilibration. Systematic deviations from linearity may indicate that two or more processes are operating with different equilibration rates. The latter is the case when the logarithm of the percentage of recovery is plotted as a function of time for both lizards, as is apparent in Figs. 4 and 5. For *Sauromalus* at all T_b 's and for *Varanus* at 30°–40°C, the recovery function may be separated into fast and slow components, and the contribution of each to the total increment may be estimated according to the relation:

$$\% \text{ aerobic scope} = K_1 e^{-\frac{1}{T_1}t} + K_2 e^{-\frac{1}{T_2}t} \quad (5)$$

where T_1 and T_2 are the time constants (time in minutes to 63% recovery) of the fast and slow components, K_1 and K_2 are the intercepts of the fast and slow components, e is the base of the natural logarithms, and t is the time in minutes (see Atkins, 1969, for the method of estimation).

Real physiological analogues have been attributed to these fast and slow mathematical components, designated as the alactacid and lactacid debts respectively (Henry, 1951; Henry and De Moor, 1956; Karpovich, 1959). The former consists of the rapid resynthesis of creatine phosphate and reoxygenation of the respiratory pigments and the latter represents the catabolism of lactate built up during activity. The total amount of oxygen consumed to repay each of these "debts" may be estimated by integrating the product of the aerobic scope and the intercept of the component over three time constants (to 95% recovery) for each T_b . Time constants, intercepts, and oxygen debts are reported in Tables 1 and 2 for *Sauromalus* and *Varanus*, respectively. The contribution of the fast (alactacid) component is nearly constant in *Sauromalus* at all T_b 's. The alactacid debt in *Varanus* cannot be analyzed by this procedure at 15°–25°C but is strongly temperature dependent between 30° and 40°C. Lactacid debt is highly temperature dependent in *Sauromalus*, much less so in *Varanus*. The total oxygen debt is much higher in *Sauromalus* than in *Varanus* over the range of active T_b 's, a consequence of its low aerobic scope.

Heart Rate and Heart Rate Increment

Heart rates are reported in beats per minute. Heart rates during rest and activity for *Sauromalus* are given in Fig. 6. No difference ($p=0.96$ by analysis of covariance) was found between resting animals in chambers and resting masked animals. The data were, therefore, pooled to produce the equation for stand heart rate:

$$\log \text{SHR} = 0.0059 + 0.0473 T_b. \quad (6)$$

Table 1. Oxygen debt acquired during activity by *Sauromalus hispidus*. See text for explanation and method of calculation

	Body temperature (C)					
	15	20	25	30	35	40
Alactacid debt						
T_1 (min)	8.3	6.0	5.0	3.8	3.8	5.7
K_1 (% scope)	64	63	61	56	45	46
Oxygen debt (cc O ₂ /kg)	14.5	15.0	16.5	14.2	12.8	19.8
Lactacid debt						
T_2 (min)	57.3	46.2	37.6	30.2	26.0	33.1
K_2 (% scope)	36	37	39	44	55	54
Oxygen debt (cc O ₂ /kg)	55.8	66.3	76.5	87.6	105	134
Total oxygen debt (cc O ₂ /kg)	70.3	81.3	93.0	102	118	154

Table 2. Oxygen debt acquired during activity by *Varanus gouldii*. See text for explanation and method of calculation

	Body temperature (C)					
	15	20	25	30	35	40
Alactacid debt						
T_1 (min)	—	—	—	4.1	3.2	2.1
K_1 (% scope)	—	—	—	23	39	52
Oxygen debt (cc O ₂ /kg)	—	—	—	7.5	13.2	15.8
Lactacid debt						
T_2 (min)	16.9	14.9	13.9	12.9	12.7	12.6
K_2 (% scope)	100	100	100	77	61	48
Oxygen debt (cc O ₂ /kg)	62.6	72.2	78.5	80.4	83.5	86.6
Total oxygen debt (cc O ₂ /kg)	62.6	72.2	78.5	87.9	96.7	102

Q_{10} for this relationship is 2.74. The regression for heart rate of active *Sauromalus* is

$$\log \text{AHR} = 0.740 + 0.0361 T_b. \quad (7)$$

Q_{10} for this regression is 2.30.

Heart rates of resting and active *Varanus* are given in Fig. 7. Hyper-ventilating animals are excluded from both regressions; they are, however,

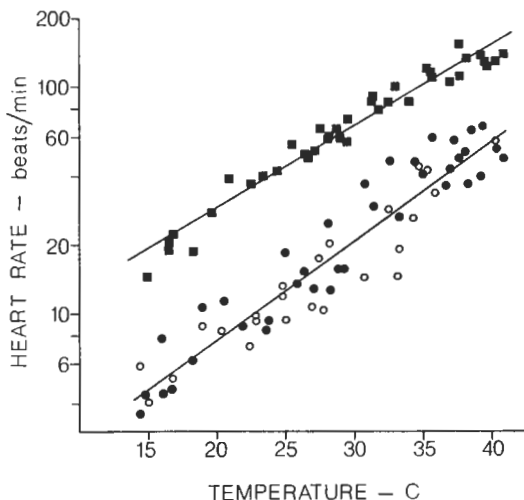


Fig. 6. Standard and active heart rate in *Sauromalus hispidus*. Symbols are explained in Fig. 1

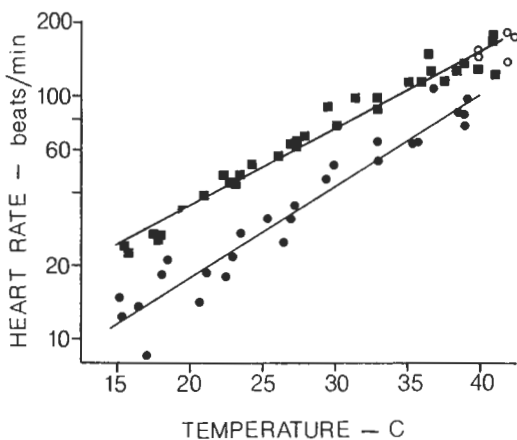


Fig. 7. Standard and active heart rate in *Varanus gouldii*. Symbols are explained in Fig. 2

indistinguishable from the rates of active animals. The equation describing standard heart rate is

$$\log \text{SHR} = 0.499 + 0.0373 T_b. \quad (8)$$

Q_{10} is 2.36. For active heart rate the regression equation is

$$\log \text{AHR} = 0.908 + 0.0317 T_b. \quad (9)$$

The corresponding Q_{10} is 2.08.

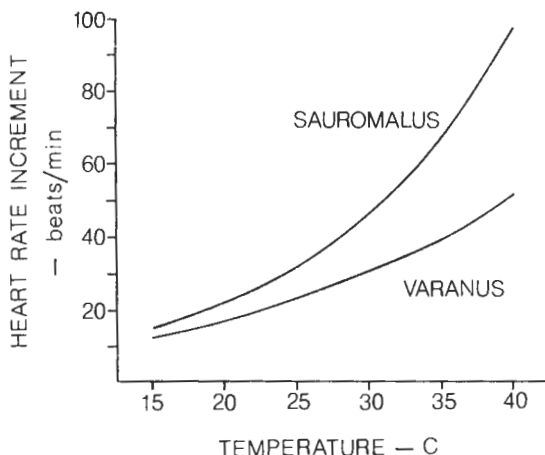


Fig. 8. Heart rate increment during activity in *Sauromalus hispidus* and *Varanus gouldii*

Values for heart rate increment, the difference between active and standard heart rates, are shown for both lizards in Fig. 8. The increments are calculated from regression equations (Eqs. (6) and (7), *Sauromalus*; Eqs. (8) and (9), *Varanus*). The functions for both animals increase with increasing T_b . The heart rates of both species when active are almost identical, but the lower standard heart rate of *Sauromalus* produces a far greater increment. At 37.5°C, *Sauromalus* nearly triples its heart rate during activity; heart rate in *Varanus* increases only by half.

Oxygen Pulse

Division of the metabolic rate by the heart rate yields the oxygen pulse, the amount of oxygen transported per heart beat. The values for resting and active oxygen pulse for both lizards are reported in Fig. 9. These functions are calculated from Eqs. (1), (2), (6), and (7) for *Sauromalus* and Eqs. (3), (4), (8), and (9) for *Varanus*. Standard oxygen pulse is similar in both animals. Active oxygen pulse in *Sauromalus* declines precipitously above 30°C and is only double resting pulse at 40°C. In *Varanus*, active oxygen pulse remains high, nearly six times the resting pulse.

The percentage contribution of the increase in heart rate observed during activity to the total increment in oxygen transport can be

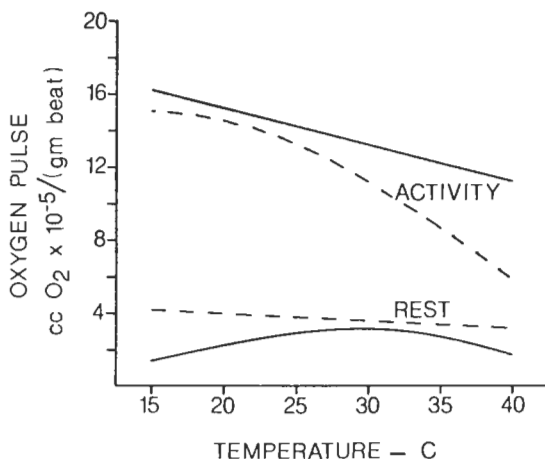


Fig. 9. Oxygen pulse during rest and maximal activity in *Sauromalus hispidus* (dashed lines) and *Varanus gouldii* (solid lines)

Table 3. Percentage contribution of increased heart rate to increased oxygen transport during activity in *Sauromalus hispidus* and *Varanus gouldii*. Calculations are based on Eq. (10)

Body temperature (° C)	Percentage contribution	
	<i>Sauromalus</i>	<i>Varanus</i>
15	55	10
20	51	15
25	49	20
30	51	19
35	56	15
37.5	60	12
40	65	10

calculated according to the formula given by Bartholomew and Tucker (1963), modified from the Fick principle:

$$\% \text{ contribution} = \frac{\text{AHR} - \text{SHR}}{\text{SHR}} \div \left(\frac{\text{AHR} - \text{SHR}}{\text{SHR}} + \frac{\text{AOP} - \text{SOP}}{\text{SOP}} \right) \quad (10)$$

in which AHR, SHR, AOP, and SOP are active and standard heart rates and oxygen pulses, respectively. The percentage contribution of heart rate to increased oxygen transport during activity is calculated for *Sauromalus* and *Varanus* in Table 3. It is clear that the former relies

much more heavily on heart rate increment to supply oxygen during activity than does the latter.

Discussion

Oxygen Consumption and Scope

The standard metabolic rates of both species at their preferred T_b , 37.5°C, are nearly equal: *Sauromalus*, 0.088 cc O₂/(g × hr); *Varanus*, 0.111 cc O₂/(g × hr). The varanid, however, consumes nearly twice the amount of oxygen during peak activity as does the iguanid. These experiments confirm the conclusions of Bartholomew and Tucker (1964) that *Varanus* possess an aerobic scope superior to comparably-sized reptiles. A separate series of experiments determined that the low aerobic scope of *Sauromalus* is accompanied by extensive production of lactic acid during activity. *Varanus* experiences only moderate anaerobiosis under identical experimental conditions (Bennett, 1971). The total work performed during stimulation was not measured and may not be equal in the two species. It is the pattern of maximal activity, however, which is of interest: low aerobic scope, high lactate production and exhaustion in *Sauromalus*; high scope and moderate anaerobiosis in *Varanus*.

The metabolic capacities reported here may be compared to those reported for other reptiles. According to the relation calculated by Templeton (1970) for metabolic rate of lizards at 37°C, *Sauromalus hispidus* has a metabolic rate 60% and *Varanus gouldii*, 80% of expected metabolic rate on the basis of body size. These lower rates are probably due more to circadian differences than to genuinely depressed metabolism; most of Templeton's data are based on diurnal observations. Metabolic rates of 0.087 and 0.312 cc O₂/(g × hr) have been reported for *Sauromalus obesus* at 35°C (Boyer, 1967; Crawford and Kampe, 1971). The plateau in active oxygen consumption in *Sauromalus hispidus* is virtually identical to that reported for *Iguana iguana* (Moberly, 1968a), the only other large iguanid for which scope has been examined. Metabolic rates are reported for several species of varanids, including *Varanus gouldii*, by Bartholomew and Tucker (1964). Their data were gathered only at 20°, 30°, and 40°C, and consequently do not include the plateau of metabolic rate between 30° and 40°C. Their animals began hyperventilating at 38°C, and although they state that gular pumping did not usually occur during the quiet periods at 40°C, their data are identical to those for resting animals at 20° and 30°C and hyperventilating animals at 40°C in this study. Their conclusion that the standard metabolic rate of *Varanus* at 38°C is one-third that of a comparably-

sized homeotherm is, therefore, an overestimation: at rest, the energy expenditure of this lizard is no greater than that of other saurians. Data gathered in these experiments indicate that the standard metabolic rate of *Varanus* is one-sixth that of a mammal of the same size, according to the relationship proposed by Kleiber (1961). The metabolic rates of active *Varanus* reported by Bartholomew and Tucker are lower than those presented here, but the temperature dependence is the same.

The independence of metabolic rate with increasing T_b near the activity range, as reported for *Varanus*, is not unusual in reptiles (see, for instance, Cook, 1949; Dawson and Templeton, 1963; Mayhew, 1965) although the most common pattern is that of constant Q_{10} as observed for *Sauromalus hispidus*. The possession of a temperature-independent metabolic pattern would free an organism from fluctuations in energy expenditure with minor changes in T_b and "perhaps . . . indicates a tendency towards homeostasis in these species" (Dawson and Bartholomew, 1956).

The 2.0°C increment in T_b during activity reported for *Varanus* (Bartholomew and Tucker, 1964) is not exceptional for a large reptile (see Benedict, 1932) and is not indicative of special metabolic capacities. Body temperature of *Sauromalus* increased more in these experiments than did that of *Varanus*. This increment is highly dependent upon experimental conditions: the insulating quality of the metabolic chamber and temperature cabinet, the rate of air movement, etc.

A declining aerobic scope with increasing T_b may be the result of a rapidly increasing standard metabolic rate or a constant or declining active metabolic rate. For all reptiles examined except *Varanus* and *Tiliqua scincoides* (Bartholomew *et al.*, 1965), the active metabolic rate has a low Q_{10} value at higher T_b . Scope in the latter animal is low. Declining scope, therefore, appears to be a result of a limitation of oxygen consumption during activity in reptiles. Brett (1964) found a similar situation in sockeye salmon, which he interpreted as an oxygen limitation in the fluid medium. When the oxygen content of the water was artificially increased, oxygen consumption during activity increased, revealing a constant Q_{10} relationship between active metabolism and T_b . Oxygen limitation appears to be an unlikely hypothesis for airbreathing organisms, since the relative concentration is much higher than in water. However, many physiological systems are involved in procuring and transporting oxygen before it reaches the site of utilization within the cells. It is possible that one or more of these systems is saturated at a relatively low T_b in most reptiles and is unable to increase oxygen delivery or utilization with further increments in T_b . Additional energy would have to be derived from anaerobic sources.

Recovery

At 40°C, *Varanus* recovers from activity more than three times as rapidly as *Sauromalus*. Its total oxygen debt is only two-thirds that of the iguanid, presumably because of the smaller lactacid component of the debt. If the fast and slow recovery components do represent alactacid and lactacid debts, respectively, an interesting pattern of aerobiosis and anaerobiosis emerges for both species. The constancy of the alactacid debt of *Sauromalus* at all T_b , comparable to the highest debt observed in *Varanus*, suggests that the iguanid exhausts its non-glycolytic energy reserves during activity and relies heavily on anaerobic metabolism. *Varanus*, however, undergoes moderate anaerobiosis at all T_b 's and depletes its non-glycolytic energy sources only at higher T_b . Moderate lactate buildup is common in man even at low levels of activity (DeLanne *et al.*, 1959; Karpovich, 1959). The validity of the recovery model has not been tested for reptiles. Satisfactory testing would involve the estimation of the total non-glycolytic energy reserves of an animal and measurement of total lactate produced during activity and the time course of its elimination. Blood lactate content after activity is highly temperature dependent in *Sauromalus* but is independent of T_b in *Varanus* (Bennett, 1971). This observation is in accord with the thermal dependence of the slow (lactacid) recovery component of oxygen consumption in both animals.

It is rather surprising that no other studies of oxygen debt or recovery time have been made in reptiles, since these variables are easily measured. The effects of T_b , length of activity, and body size on oxygen debt would all be of interest in view of the anaerobiosis undergone by some animals. Moberly (1968a) monitored the concentration of blood lactate after activity in *Iguana*. Lactate is removed most rapidly at 35°C and the rate of removal at 40°C is intermediate to that at 25° and 30°C. This condition is paralleled by the recovery rates of the lactacid component of oxygen debt for *Sauromalus*. The time constants for lactate elimination are nearly twice those predicted on the basis of oxygen consumption in *Sauromalus*: 30°C, 64 min; 40°C, 73 min.

Heart Rate

An inability to increase heart rate to meet oxygen demands during activity is obviously not the causal factor of the low aerobic scope of *Sauromalus*. In fact, increased heart rate is the principle means of adjusting cardiac output during activity. In *Varanus*, as Bartholomew and Tucker (1964) suggest, changes in stroke volume and arterial-venous difference (A-V difference) are more important than changes in heart rate in supplying oxygen to active tissues. The large heart rate increment

of the iguanid is the result of a very low standard heart rate, since the active heart rates of the two animals are nearly identical. Resting heart rate in *Sauromalus hispidus* is only three-fifths the average rate reported for other large lizards (*Amblyrhynchus*, Bartholomew and Lasiewski, 1965; *Iguana*, Tucker, 1966, Moberly, 1968a; *Tiliqua*, Bartholomew *et al.*, 1965, Licht, 1965; *Varanus*, Bartholomew and Tucker, 1964). Whether particularly low standard heart rates are characteristic of the genus *Sauromalus* is unclear: the heart rate of *S. obesus* is reported as 95 beats/min (Templeton, 1964) and 58 beats/min (Boyer, 1967) at 37°C. Resting heart rates reported for several species of *Varanus* (Bartholomew and Tucker, 1964) are three-fourths those determined for *V. gouldii*; active heart rates also differ by this factor.

Oxygen Pulse

According to the Fick principle, the amount of oxygen consumed by an organism must be equal to the product of the blood flow (the product of heart rate and stroke volume) and the difference in the oxygen content of the blood entering and leaving the metabolizing tissue (A-V difference). Organismal oxygen consumption and heart rate are readily accessible factors, the A-V difference is less so, and the stroke volume is almost always estimated by measurement of the other factors. The oxygen pulse, the amount of oxygen transported per heart beat, can easily be calculated from metabolic and heart rates. Through the Fick equivalence, oxygen pulse is equal to the product of stroke volume and A-V difference; consequently, it is a valuable calculation for examining changes in these variables. An increase in oxygen pulse, as observed during activity, is the result of an equal increase in the product of stroke volume and A-V difference. Likewise, a declining oxygen pulse, as observed in both animals, particularly in *Sauromalus*, during activity with increasing T_b , must reflect a fall in stroke volume and/or a decrease in A-V difference. The latter might occur by a rise in the oxygen concentration of venous blood or a decrease in the saturation of arterial blood, a failure to load adequate quantities of oxygen in the lung.

The constancy of standard values of oxygen pulse between lizard species is impressive. The values generally approximate 3×10^{-5} to 4×10^{-5} cc O₂/(g × beat) (Dawson, 1967; Templeton, 1970); the values for *Varanus* and *Sauromalus* conform to this range. Oxygen pulse values for active reptiles are given in Table 4. The oxygen pulse during activity exceeds 10×10^{-5} cc O₂/(g × beat) in all but the most sluggish animals. Increased T_b decreases this quantity in all species except *Varanus*. This pulse value of *Varanus* is exceptionally high and reflects an ability to increase stroke volume or A-V difference during activity which greatly exceeds other reptiles investigated.

Table 4. Oxygen pulse in active reptiles

Species	Maximum O ₂ pulse		Pulse at high T _b		Reference
	T _b (°C)	cc O ₂ × 10 ⁻⁵ / (gm × beat)	T _b (°C)	cc O ₂ × 10 ⁻⁵ / (gm × beat)	
<i>Amphibolurus barbatus</i>	20	12.2	40	3.7	Bartholomew and Tucker (1963)
<i>Iguana iguana</i>	30	10.4	40	6.1	Moberly (1968a)
<i>Pituophis catenifer</i>	20	10.2	35	7.5	Greenwald (1971)
<i>Sauromalus hispidus</i>	15	15.0	40	6.3	Present study
<i>Sphenodon punctatus</i>	5	9.2	35	2.0	Wilson and Lee (1970)
<i>Tiliqua scincoides</i>	20	6.3	40	5.4	Bartholomew <i>et al.</i> (1965)
<i>Varanus</i> spp.	40	10.7	40	10.7	Bartholomew and Tucker (1964)
<i>Varanus gouldii</i>	15	16.5	40	11.3	Present study

Determinations of A-V difference or stroke volume in reptiles are few (Templeton, 1964; Tucker, 1966). From the information available, it appears that stroke volume is not greatly modified during activity or change in T_b, so that oxygen pulse must principally reflect adjustment of the A-V difference in reptiles. The rapid decline in active oxygen pulse of *Sauromalus* between 30° and 40°C is probably due to a decrease in the saturation of arterial blood, since it is highly doubtful that the oxygen content of the venous blood is increasing with increased metabolic demands.

Conclusions

Varanus gouldii is shown in this study to possess a standard metabolic rate equal to that of comparably-sized lizards. However, its capacities for transporting oxygen during activity are high and maximal oxygen consumption exceeds resting levels of homeotherms of equal size. Consequently, oxygen debt acquired during activity is low and is rapidly repayed. The high active oxygen pulse indicates a great capacity for increasing either stroke volume or A-V difference during activity.

Sauromalus hispidus conforms closely to the metabolic pattern established for *Iguana iguana* (Moberly, 1968a, b), an animal which relies heavily on anaerobiosis during activity and exhausts easily. Active oxygen consumption in *Sauromalus* does not increase with increasing T_b above 30°C, and, therefore, aerobic scope remains low. Oxygen debt

is high, presumably because of its large lactacid component, and recovery of standard metabolic levels is slow. A low heart rate increment is not responsible for this limitation of oxygen uptake during activity. Calculations of oxygen pulse suggest that A-V difference cannot be greatly increased to meet oxygen demands during activity due to low saturation of arterial blood.

From the evidence available, iguanid lizards appear to have a high tolerance of anaerobiosis. Iguanids survive twice as long as other lizards in an atmosphere of pure nitrogen (Belkin, 1963). *Sauromalus* and *Dipsosaurus* have high levels of muscle phosphofructokinase activity (Bennett, 1972); this enzyme controls the rate-limiting reaction in glycolysis and a high activity indicates a large anaerobic capacity. Moberly (1968b) emphasized anaerobiosis in *Iguana iguana* as an adaptation to diving and found it rather remarkable in an arboreal animal which dives only infrequently. It appears, however, that a considerable reliance on anaerobiosis may be primitively characteristic of the Iguanidae and that several of its members (*Iguana*, *Amblyrhynchus*, *Basiliscus*, and *Anolis*) have exploited this tolerance of anoxia for escape or feeding purposes.

It should be emphasized that the metabolic physiology of each of these lizards is highly adapted to its behavior and mode of existence. *Sauromalus*, an herbivore, engages in maximal activity only rarely, e.g., when pursued (an unlikely occurrence in its natural habitat) or perhaps during mating or territorial defense. Short bursts of anaerobically generated energy are quite adequate for such circumstances, and it is difficult to imagine the selective advantage of increased aerobic dependence. On the other hand, a varanid generally has a very large home range, is extensively active, and often pursues its prey. A large lactate buildup, with its disruptive physiological effects and consequent long recovery period, would be distinctly disadvantageous to such an animal. It appears that *Varanus* has evolved mechanisms to sustain high levels of oxygen delivery to its tissues even during the most strenuous activity.

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