

## Aerobic Metabolism of the Lizard *Varanus exanthematicus*: Effects of Activity, Temperature, and Size

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**Summary.** Oxygen consumption ( $\dot{V}_{O_2}$ ) was measured at rest and during spontaneous activity at body temperatures of 25 and 35 °C in 14 fasting Savanna monitor lizards, *Varanus exanthematicus* ranging in weight from 172 to 7500 g. The allometric relationship between metabolic rate at 25 °C and body weight ( $W$ ) is given by:  $\dot{V}_{O_2}$  (ml O<sub>2</sub> STPD · g<sup>-1</sup> · hr<sup>-1</sup>) =  $0.88 W^{-0.43}$  (Fig. 2). Although statistical comparisons are equivocal, this intraspecific size dependence exceeds that reported for interspecific comparisons among reptiles and other vertebrate groups (Fig 3). A reproducible diurnal pattern of activity was observed in undisturbed animals with minimum values of  $\dot{V}_{O_2}$  between 2400 and 0800 h (Fig. 1). Spontaneous activity and  $\dot{V}_{O_2}$  generally reached peak values between 1200 and 2000 hrs. The average ratio of active aerobic metabolic rate (AMR) to minimum (standard) aerobic metabolic rate (SMR) was 8.2. This voluntary AMR/SMR in *Varanus* exceeds the AMR/SMR for most reptiles stimulated to exhaustion. The high aerobic capacity is consistent with other evidence for efficient exchange and transport of respiratory gases in *V. exanthematicus*; e.g., low or absent intracardiac shunt flow resulting in high arterial saturation and low ventilation ( $\dot{V}/\dot{V}_{O_2}$ ) and perfusion ( $\dot{Q}/\dot{V}_{O_2}$ ) requirements.

### Introduction

Varanid lizards have a reputation for being active and aggressive predators with associated, high levels

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of aerobic metabolism (Bartholomew and Tucker, 1964; Bennett, 1972). Recent studies have also shown that varanids, unlike other reptiles studied, have (1) minimal or absent intracardiac shunt flow; (2) a high ratio of systemic to pulmonary arterial pressure; (3) a ventilation/perfusion ratio in the lung which is close to unity and independent of body temperature (Millard and Johansen, 1974; Wood et al., 1977a, b). These attributes, suggestive of efficient exchange and transport of respiratory gases, prompted the present study of aerobic metabolism in the Savannah monitor.

The objectives of this study were 1) to measure gas exchange at rest to test the hypothesis that standard metabolic rate is higher in varanids than in other reptiles; (2) to determine metabolic rate during voluntary activity and test the hypothesis that *Varanus exanthematicus* has a high capacity to increase O<sub>2</sub> uptake; (3) to determine the influence of body size and temperature on aerobic metabolism in *V. exanthematicus*.

### Methods and Materials

Savannah monitors ( $N=14$ ) were obtained in Kenya, East Africa and air-shipped to Denmark. They were maintained in cages having an aerial thermal gradient of 25 to 40 °C for at least 3 weeks before use. They were fed mice *ad lib.* and maintained or gained weight in captivity. Body weights ranged from 172 to 7500 g. Food was withheld before experiments until measured values of the respiratory exchange ratio at steady-state indicated a fasting condition ( $R=0.73$ ).

Oxygen uptake ( $\dot{V}_{O_2}$ ) and carbon dioxide production ( $\dot{V}_{CO_2}$ ) were measured at 25 and 35 °C using an open circuit system. The lizards were placed in plastic cylinders which restricted but did not prevent voluntary activity. A mass spectrometer (Med. Spect. II, Searle) sampled cylinder air at a constant rate (160 ml/min) and provided a continuous analysis of the O<sub>2</sub> and CO<sub>2</sub> content of the dry excurrent air.  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$  were calculated from the flow rate and changes in fractional concentrations of O<sub>2</sub> and CO<sub>2</sub> using a correction for  $R < 1$  (Hill, 1972). The mass spectrometer

was calibrated for O<sub>2</sub> and CO<sub>2</sub> using a Wösthoff gas mixing pump. The gas exchange of each animal was monitored continuously for 1–3 days at each body temperature. During this period the animals were not disturbed; sound level was minimum (recorder noise) as was illumination (heat lamps and low-level room light). The body temperature of the animals was controlled by a servocircuit consisting of 2 heat lamps activated when core temperature fell below a pre-set level. An indwelling cloacal probe (Thermistor, Yellow Springs Instrument Co.), inserted ca. 10 cm, measured core temperature.

Preferred body temperature was determined by radiotelemetry (Mini-mitter Col, Evansville, In.) on unrestrained animals kept in a thermal gradient cage in which air temperature ranged from 20 to 40 °C.

## Results and Discussion

### Diurnal Pattern

The diurnal pattern of  $\dot{V}_{O_2}$  at 25 °C, reflecting circadian metabolic fluctuations and changes in voluntary physical activity, is shown in Figure 1. These data were obtained from 7 individuals left undisturbed in the metabolism chamber for 2–3 days. In the complete series of animals (N=14) the mean  $\dot{V}_{O_2}$  during maximum activity was somewhat higher,  $370.8 \pm 60.8$  (S.E.M.) ml STPD kg<sup>-1</sup>h<sup>-1</sup> (n=14), range 74.1–912.0 ml kg<sup>-1</sup>h<sup>-1</sup>. The minimum metabolic rate consistently occurred between 2400 and 0800 hrs. The mean resting  $\dot{V}_{O_2}$  was  $49.7 \pm 6.0$  (S.E.M.) ml STPD kg<sup>-1</sup>h<sup>-1</sup> (n=14), range 17.8–86.0 ml kg<sup>-1</sup>h<sup>-1</sup>. Between 0800 and 2400 hrs, the metabolic rate was consistently elevated. This was largely due to voluntary activity, but recordings of resting animals during the awake-sleep transition indicate a rather marked reduction of ventilation and  $\dot{V}_{O_2}$  during *sleep* (cf. Wood et al., 1977a). Similar patterns of reduced activity and metabolism at night have been reported for *V. gouldii* (Bennett, 1972) and *V. niloticus* (Cloudsley-Thompson, 1969).

It is reasonable that such a distinct diurnal rhythmicity in  $\dot{V}_{O_2}$  of an ectotherm in nature is tuned to have maximal values coinciding with the maximum potential for external heat uptake from solar radiation. It should be emphasized, however, that the diurnal variation in O<sub>2</sub> uptake recorded in the present experiments was independent of body temperature.

### Effects of Activity and Temperature

The increase in aerobic metabolism of *V. exanthematicus* during activity is 8.2 (±1.1)-fold, on the average (range 2.0–14.8; n=14). Previous studies have quantified this augmented  $\dot{V}_{O_2}$  in two ways. The aerobic “metabolic scope” (Fry, 1947) is the difference between active and standard metabolic rates (AMR–SMR). Alternatively, the ratio of maximal to standard

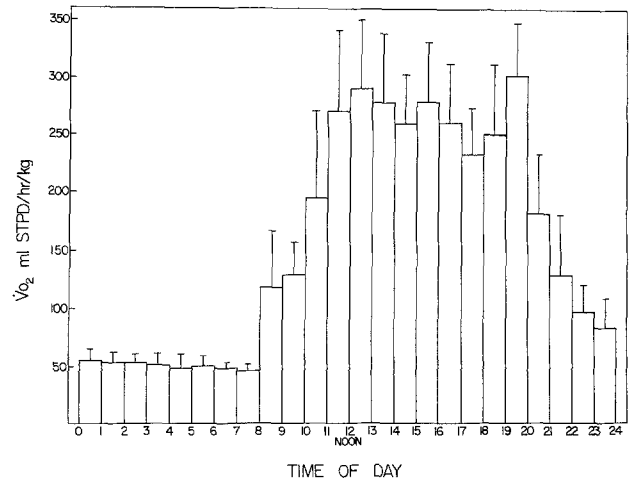


Fig. 1. Diurnal pattern of oxygen uptake in spontaneously active *Varanus exanthematicus* at 25 °C

(or basal) oxygen uptake is calculated (AMR/SMR). The latter method, designated by Drabkin (1950) as the “index of expansibility of metabolism”, seems preferable when comparing species since it is not affected by differences in absolute values of oxygen uptake; e.g., due to size or temperature. For example, Table 1 shows that the ratio of active metabolic rate to standard (or basal) metabolic rate is almost identical for the mouse (AMR/BMR=7.2) and *Varanus gouldii* (AMR/SMR=7.4). However, because of different absolute values of  $\dot{V}_{O_2}$ , the scope (AMR–SMR) is 8.9 for the mouse and only 0.49 for *V. gouldii*. Even within a species, there is only a weak correlation between aerobic scope (AMR–SMR) and the ratio AMR/SMR. For *V. exanthematicus* the slope and intercept of the regression equation,  $AMR/SMR = 0.2 + (AMR-SMR)^{0.43}$ , are not significantly different from zero. When all the data in Table 1 are analyzed, the correlation between (AMR/SMR) and (AMR–SMR) is almost zero ( $r=0.04$ ).

How closely the  $\dot{V}_{O_2}$  during spontaneous activity approximates the maximum aerobic capacity is not presently known, although it is expected to be less than in animals electrically stimulated to exhaustion (cf., Bennett and Dawson, 1976). For example, the maximum values of  $\dot{V}_{O_2}$  in the lizard *Amphibolurus barbatus* following electrical stimulation (Wilson, 1974) were three times greater than values obtained from spontaneously active animals (Bartholomew and Tucker, 1963). Nevertheless, the average ratio of AMR/SMR measured during voluntary activity of *Varanus exanthematicus* exceeds that reported for most other reptiles which, in most cases, were electrically stimulated to exhaustion. The wide range of values of the ratio AMR/SMR in *V. exanthematicus* is expected since the AMR is due to spontaneous activity. Obviously, several of the animals spent little

**Table 1.** Standard (SMR) and Active (AMR) metabolic rates of various vertebrates

Species	T <sub>B</sub> (°C)	Body wt. (g)	SMR (ml STPD/g·h)	AMR	AMR/SMR	AMR-SMR	Reference
<b>Lizards</b>							
<i>Egernia cunninghami</i>	30	261	0.087	0.496	5.7	0.41	Wilson (1971, 1974)
<i>Iguana iguana</i>	30	795 <sup>a</sup>	0.081	0.400	4.9	0.32	Moberly (1968)
<i>Physignathus lesuerii</i>	30	504	0.080	0.459	5.7	0.38	Wilson (1971, 1974)
<i>Sauromalus hispidus</i>	30	574	0.052	0.450	8.6	0.40	Bennett (1972)
<i>Tiliqua scincoides</i>	30	493	0.090	0.252	2.8	0.16	Bartholomew et al. (1965)
<i>Trachydosaurus rugosus</i>	30	461	0.092	0.451	4.9	0.36	Wilson (1971, 1974)
<i>Varanus gouldii</i>	30	674	0.077	0.568	7.4	0.49	Bennett (1972)
<b>Turtles</b>							
<i>Chelydra serpentina</i>	20	1.637 <sup>a</sup>	0.019	0.058	3.0	0.04	Baldwin (1926 a, b)
<i>Testudo gigantea</i>	25	1.000	0.045	0.141	3.1	0.10	Hughes et al. (1971)
<i>Testudo gigantea</i>	25	100.000	0.020	0.122	6.1	0.10	Hughes et al. (1971)
<i>Pseudemys scripta</i>	30	305	0.031	0.684	21.8	0.65	Gatten (1974)
<i>Chelonia mydas</i>	25	735 <sup>a</sup>	0.070	0.245	3.5	0.18	Prange (1976)
<b>Snakes</b>							
<i>Coluber constrictor</i>	35	301 <sup>a</sup>	0.11	1.02	9.3	0.91	Ruben (1976)
<i>Crotalus viridis</i>	35	262 <sup>a</sup>	0.11	0.50	4.5	0.39	Ruben (1976)
<i>Lichamura roseofusca</i>	32	314 <sup>a</sup>	0.10	0.25	2.5	0.15	Ruben (1976)
<i>Masticophis flagellum</i>	35	262 <sup>a</sup>	0.11	1.02	9.3	0.91	Ruben (1976)
<b>Fish</b>							
<i>Oncorhynchus nerka</i>	15	50	0.05	0.63	12.6	0.58	Brett (1964)
<b>Mammals</b>							
<i>Mus musculus</i>	37	33 <sup>a</sup>	1.44	10.34	7.2	8.90	Pasquis et al. (1970)
<i>Cricetus auratus</i>	37	100 <sup>a</sup>	1.09	7.10	6.5	6.01	Pasquis et al. (1970)
<i>Rattus norvegicus</i>	37	376 <sup>a</sup>	0.78	5.42	6.9	4.64	Pasquis et al. (1970)
<i>Cavia cobaya</i>	37	841 <sup>a</sup>	0.64	4.02	6.3	3.88	Pasquis et al. (1970)
<i>Canis familiaris</i>	37	6.300	0.39	4.28	11.0	3.89	Chatonnet and Minaire (1966)
<i>Homo sapiens</i>	37	81.500	0.20	3.35	16.7	3.15	Astrand (1952)

energy in voluntary exercise or attempting to escape from the metabolism chamber. This also explains the lack of correlation of AMR with body size (Fig. 2). Presumably a better correlation during activity would be obtained if the activity level was standardized on a treadmill or the work level otherwise could be quantified. For example, Bennett and Dawson (1976) found a good correlation ( $r=0.81$ ) of AMR with body size in 14 species, most of which were electrically stimulated to exhaustion. Thus, the mean value of the ratio between AMR and SMR of spontaneously active *V. exanthematicus* (8.2) is all the more impressive in comparison with other vertebrates.

It should be noted that the ratio AMR/SMR does not indicate or limit the level of maximum activity or total metabolism for a particular species. For many reptiles, the added energy demands of activity are met primarily by anaerobic metabolism (cf., Bennett and Dawson, 1976). Iguanas are a dramatic example. The common iguana, when stimulated electrically to exhaustive exercise, obtain up to 77% of their total energy through anaerobic metabolism (with blood lactate levels reaching 160 mg %) while the ratio AMR/SMR reaches a maximum of only 4 (Moberly,

1968). The marine iguana depends even more heavily on anaerobic metabolism during maximal activity, with an estimated 97–99% of the carbohydrate utilized anaerobically (Bennet et al., 1975). Lactate elimination; i.e., repayment of oxygen debts incurred during anaerobic metabolism, is generally slower than lactate formation in reptiles (cf., Bennett and Dawson, 1976), resulting in long recovery times and further impeding prolonged activity. Thus, the advantages of high levels of aerobic activity are numerous. The ability of an animal to increase oxygen uptake and maintain aerobic metabolism during activity is an index of the maximum O<sub>2</sub> conductance to the tissues and a reflection of the effectiveness of all components of oxygen transport; e.g., ventilation, pulmonary diffusion, circulation, oxygen delivery to the tissues, and tissue diffusion. Bennett (1973a, b) compared many aspects of the respiratory physiology of the iguanid lizard, *Sauromalus hispidus* with *Varanus gouldii*. He noted relatively little reliance of *V. gouldii* on anaerobic metabolism during even sustained activity. He also found that the ventilation required for a given O<sub>2</sub> uptake ( $\dot{V}_E/\dot{V}_{O_2}$ ) was much lower in *Varanus* than *Sauromalus* (44 vs. 98 at 40 °C) and

the oxygen extracted from air was greater (13.4 vs. 6%). Bennett (1972) pointed out that *Sauromalus*, a herbivore as is the iguana, rarely engages in maximum activity and can easily get by on short bursts of anaerobically generated energy. In contrast, varanids occupy relative large territories, pursue prey actively and generally rely on sustained high levels of oxygen delivery to their tissues. The  $\dot{V}_{O_2}$  of active *V. exanthematicus* and other varanids (Bartholomew and Tucker 1964; Bennett, 1972) often exceeds the basal  $\dot{V}_{O_2}$  predicted for a similar-sized mammal, supporting the statement by Bartholomew and Tucker (1964) that varanids "bridge the metabolic gap" which had been assumed to exist between mammals and reptiles.

The high aerobic capacity of varanids has both morphological and physiological correlates. *V. exanthematicus* lungs have maximum volumes twice that predicted for reptiles (Steven F. Perry, personal communication) and varanid lungs, in contrast to the sac-like lungs of many reptiles, are "alveolar" (Wolf, 1933; Mertens, 1942). Both features provide a greater surface area for diffusion, allowing higher rates of oxygen uptake than other reptiles. Physiological data are also consistent with high aerobic capacities. The cardiovascular system of varanids is unique among reptiles in that intracardiac shunts appear to be absent (Millard and Johansen, 1974; Wood et al., 1977b). The resulting high levels of arterial  $O_2$  saturation (ca. 94% in *V. exanthematicus*) provide varanids with a high arterial-venous  $O_2$  difference and, *pari passu*, a low blood convection requirement per unit  $\dot{V}_{O_2}$  (Wood et al., 1977b).

The acute effect of temperature was determined by measuring minimum (sleeping) rates of gas exchange at 25 and 35 °C, the normally encountered range of habitat temperature of *V. exanthematicus*. The mean temperature coefficient ( $Q_{10}$ ) is 2.1 ( $\pm 0.02$  (S.E.M.),  $n=7$ ). In one animal which survived an inadvertent heating for 15 min to a core temperature of 50 °C, the  $Q_{10}$  between 35 and 50 °C was 2.2. The preferred body temperature of *V. exanthematicus* determined by radiotelemetry using 6 animals was 36.5 °C. (S.D.  $\pm 1.1$ ).

Although 35 °C is close to the preferred body temperature of this species, there was very little spontaneous activity at this temperature. Obviously, in a natural habitat there are important stimuli to increased activity other than temperature per se.

#### Effects of Body Size

The influence of body weight ( $W$ ) on metabolic rate ( $M$ ) is given by the allometric equation,  $M = aW^b$  (Huxley, 1932), where  $b$  approximately 0.75 in mam-

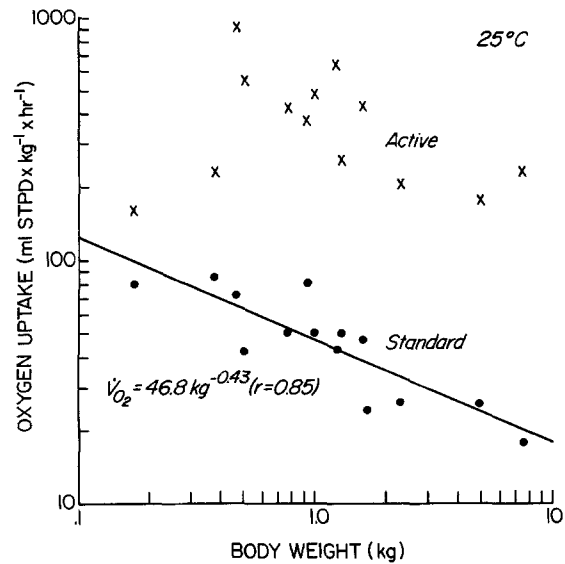


Fig. 2. Relationship of weight-specific oxygen uptake to body weight for *Varanus exanthematicus* at rest and during maximum spontaneous activity

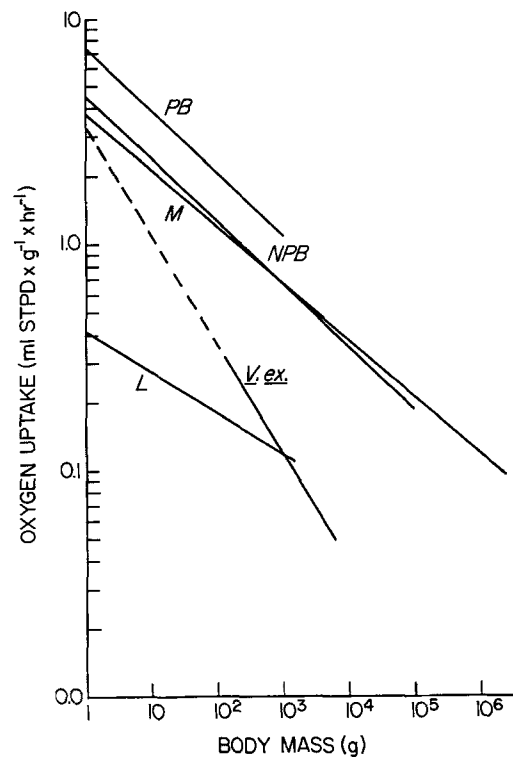


Fig. 3. Relationship of weight-specific oxygen uptake to body weight for *Varanus exanthematicus* (35 °C), other lizards (37 °C), mammals (37 °C), and passerine (PB) and non-passerine (NPB) birds (40 °C). See Table 2 for equations and references

mals (cf. Schmidt-Nielsen, 1975) and most other organisms (cf. Hemmingsen, 1960). Metabolic rate per unit body weight, given by  $M/W = aW^{b-1}$ , for *V. exanthematicus* is shown in Figure 2. A comparison of the allometric equations for *V. exanthematicus* with

**Table 2.** Equations relating weight-specific metabolic rate to body weight in *Varanus exanthematicus*, other reptiles, mammals, and birds. Equation is:  $\log \dot{V}_{O_2}$  (ml O<sub>2</sub> STPD g<sup>-1</sup> h<sup>-1</sup>) = log a - b log body weight

Species	Body wt. (g)	Body temp. (°C)	ml O <sub>2</sub> STPD/g·h (a=intercept at 1 g)	ml O <sub>2</sub> STPD/kg·h (a=intercept at 1 kg)	Slope (b)	Reference
V. exanthematicus (N=14)	172-7,500	25	0.88	46.8	-0.43	This study
					95% CL ±0.15	
V. exanthematicus	172-7,500	30*	1.38	72.5	-0.43	This study
V. exanthematicus	172-7,500	35	3.39	114.8	-0.49	This study
Australian varanids (N=10)	16-4,400	30	0.23	66.3	-0.18	Bartholomew and Tucker (1964)
Other lizards (N=23)	2-4,410	30	0.82	59.4	-0.38	Bartholomew and Tucker (1964)
					±0.08	
Other lizards (N=15)	2-1,250	30	1.33	118.5	-0.35	Templeton (1970)
	1-4,410	30	0.24	74.1	±0.09	
Other lizards (N=24)	1-4,410	30	0.24	74.1	-0.17	Bennett and Dawson (1976)
					±0.04	
Other lizards (N=19)	1-1,250	37	0.42	120.2	-0.18	Bennett and Dawson, (1976)
					±0.07	
Alligators	1150-8,780	25	0.83	97.5	-0.31	Smith (1975)
Mammals	5-3,833,000	37	3.80	676.1	-0.25	Schmidt-Nielsen (1975)
Passerine birds	6-866	40	7.54	1089.8	-0.28	Lasiewski and Dawson (1967)

other reptiles and other vertebrates is presented in Table 2 and Figure 3.

The reliability of statistical comparisons is diminished by many factors (cf. Gunter, 1975). First, the data come from different authors using different methods. Second, intraspecific relationships (*V. exanthematicus* and Alligators) are compared with interspecific relationships. Finally, when different authors compile data from the literature, even though much of the data is common, grossly different results are often obtained. For example, in "other lizards" at 30°C (Table 2) the allometric equations range from  $M=0.82 W^{-0.38}$  (Bartholomew and Tucker, 1964) to  $M=1.33 W^{-0.35}$  (Templeton, 1970) to  $M=0.24 W^{-0.17}$  (Bennett and Dawson, 1976). The difficulty of comparing groups and testing hypotheses about relative aerobic metabolic rates is compounded because of differing slopes of the regressive lines. Consequently, *V. exanthematicus* has a resting  $\dot{V}_{O_2}$  which exceeds that of other reptiles only in individuals smaller than 1 kg (Fig. 3). In a recent review of metabolism in reptiles, Bennett and Dawson (1976) conclude that there are no significant differences among reptiles in resting  $\dot{V}_{O_2}$  in either ordinal or subordinal comparisons; i.e., all species fall on a common regression line of  $\dot{V}_{O_2}$  vs. body weight, where ml O<sub>2</sub>/g·h =  $0.278 g^{-0.23}$ . The present data suggest that within a species the effect of body weight may deviate markedly from that observed in interspecies or inter-order comparisons.

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