Standard metabolic rate of the largest Australian lizard, *Varanus giganteus*

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The intraspecific relationship between standard metabolic rate (VO_2; ml hr^{-1}) and body mass for *Varanus giganteus* is $0.0896\,g^{0.90}$ at 25°C and $0.126\,g^{0.96}$ at 35°C. The relationship between VCO_2 (ml hr^{-1}) and body mass is $0.052\,g^{0.92}$ at 25°C and $0.094\,g^{0.97}$ at 35°C. The common slope for the intraspecific mass exponent at the two body temperatures of 25 and 35°C was 0.93 for VO_2 and 0.95 for VCO_2. When these data for *V. giganteus* are considered in conjunction with those from recent studies of other varanids, the interspecific scaling exponent for *Varanus* is approximately 0.9; this is similar to the intraspecific scaling exponent for *V. giganteus* and other varanids.

Key words: *Varanus giganteus*; Standard metabolic rate; Temperature; Australian; Lizard; Metabolism.

Comp. Biochem. Physiol. 111A, 603–608, 1995.

Introduction

There has recently been considerable interest in the intra- and interspecific allometry of standard metabolic rate for groups of related species (Feldman and McMahon, 1983; Heusner, 1987; Reiss, 1989; Withers, 1992; Beaupre et al., 1993; DeMarco, 1993). The allometric relationship between standard metabolic rate (SMR; ml O_2 hr^{-1}) and body mass (M;g) is $SMR = aM^b$, where a is the mass coefficient and b is the mass exponent. In general, the metabolic rate of animals scales differently with body mass (M) for interspecific ($MR \propto M^{0.81}$) and intraspecific ($MR \propto M^{0.67}$) relationships (Withers, 1992; mode values for mass exponents).

After an extensive review of the squamate literature, Andrews and Pough (1985) estimated the interspecific mass exponent (b) for SMR of squamates to be 0.80 ($SE_b = 0.012$). Thompson and Withers (1992) reported a significantly

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higher interspecific mass exponent of 1.11 for the pooled SMR of *V. gouldii* and *V. panoptes* between 20 and 40°C. An interspecific mass exponent of 0.92 for SMR at 35°C for *V. caudolineatus*, *V. acanthurus*, *V. gouldii* and *V. panoptes* was demonstrated by Thompson and Withers (1994), lending further support to the prior suggestion that the interspecific mass exponent for varanids is higher than the general value of about 0.8 for other lizards. Although these additional data supported the suggestion that the interspecific mass exponent for varanids might be different from that of other squamates, information for larger varanid species is required for a confident prediction of interspecific scaling for *Varanus* to be made.

Andrews and Pough (1985) reported the mean intraspecific mass exponent for 17 species of squamates to be 0.67, with values ranging from 0.51 to 0.80. However, Thompson and Withers (1992) reported the common intraspecific mass exponents for the allometric relationship of SMR for *V. gouldii* (20–555 g) to be 1.12 and *V. panoptes* (227–3480 g) to be 1.10. Thompson and Withers (1994) reported a simi-

lar intraspecific mass exponent for *V. acanthurus* (20–80 g) of 1.04 and for the smaller *V. caudolineatus* (4–19.5 g) of 0.86 for VO_2. These values are appreciably higher than for most other reptiles (see review by Andrews and Pough, (1985). In contrast, Wood *et al.* (1978) report a lower mass exponent of 0.57 at 25 and 30°C and 0.51 at 35°C for the larger *V. exanthematicus* (172–7500 g). SMR data for other species of varanids, particularly large species, would enable a more general statement to be made about the intraspecific mass exponent for this genus.

The major purpose of this study was to measure the SMR of *V. giganteus*, of varying masses, to determine if the intraspecific allometry for Australia's largest varanid was similar to the high *b* values already reported for small and medium sized varanids using an identical research protocol. The second objective was to determine if the SMR data for this large species is consistent with a high (>0.90) interspecific mass exponent for varanids.

Methods and Materials

Six *V. giganteus* (two females, three males and one juvenile) with a mass range of 84–5660 g (snout-to-vent length range 226–735 mm), were caught in Cape Range National Park or just south of Exmouth in Western Australia during February 1992. These monitors were transported to the University of Western Australia where they were held in temporary cages for 15 days and occasionally fed. Water was provided at all times. All animals were fasted for at least 60 hr before the measurement of metabolic rate. Only one measure of minimal oxygen consumption and carbon dioxide production for each lizard at each temperature (25 and 35°C) was used for allometric calculations.

Oxygen consumption rate (VO_2; ml O_2 hr^{-1}) and carbon dioxide production rate (VCO_2; ml CO_2 hr^{-1}) were measured using a flow-through respirometry system. The lizards were weighed, then placed into varying sized opaque plastic cylinders that restricted, but did not prevent voluntary activity. These cylinders were placed in a controlled temperature chamber maintained at 25 or 35°C (± 1°C). Compressed ambient air was passed through the chamber at a controlled flow rate (Brooks mass flow meter for flows <1000 ml min^{-1}, GAP flow meter for flows >1000 ml min^{-1}) which kept the excurrent O_2 content at about 20.1%. The temperature of the air in the metabolic chamber (T_a; °C) was constantly measured with a chromel–alumel thermocouple. Excurrent air was dried using a drierite column before passing through one channel of a paramagnetic oxygen analyser (Servomex 184A) and a CO_2 analyser (Hereus-Leybold Binos). The differential output of the oxygen analyser (ambient air–excurrent air) and the analog outputs of the CO_2 analyser and thermocouple meter were connected to a Promax XT microcomputer with Analog Device RT1800 A/D interface board. The computer system monitored ambient temperature and excurrent O_2 and CO_2 content, and calculated STPD VO_2 and VCO_2 after Withers (1977), every 60 s for 12–16 hr periods commencing between 1200 and 2000 hr. The analog outputs of the O_2 and CO_2 analysers were averaged for 25 consecutive values to determine each 60 sec value, from which VO_2 and VCO_2 were calculated, and the values stored to disk for subsequent analysis. The minimum (i.e. standard) values of VO_2 and VCO_2 were calculated as the average of the lowest continuous period of VCO_2 production (normally 30–100 min duration). This ensured that the calculated SMR value was not affected by brief periods of activity, or transient low VO_2 or VCO_2 values due, presumably, to short respiratory apneic periods. Lizards attained their lowest VO_2 level within the period between 2400 and 0900 hr, which roughly corresponds to their normal period of inactivity. It was during this period that SMR was measured.

Temperatures reported are the ambient temperature (T_a) in the metabolic chamber near the lizard while SMR was being measured. It is presumed that the body temperature (T_b) of all lizards was the same as the ambient temperature, as all lizards were held at the specific temperature for at least 6 hr before their metabolism was recorded. Six hours' equilibration time was sufficient for the T_b of all lizards to reach ambient air temperature. For example, the T_b of the largest *V. giganteus* increased from 20 to 36°C in 3 hr and 50 min (N. Heger, unpublished data), (datum supported by McNab and Auffenberg (1976), Brattstrom (1973) and Bartholomew and Tucker (1964) for other varanids). Differences between species regression equations were tested by analysis of covariance and Tukey *Q* test (Zar 1984).

Results

The six *V. giganteus* had a mean mass-specific VO_2 of 0.043 ml g^{-1} hr^{-1} and VCO_2 of 0.030 ml g^{-1} hr^{-1} at 25°C, and at 35°C, the mean VO_2 was 0.095 ml g^{-1} hr^{-1} and VCO_2 was 0.076 ml g^{-1} hr^{-1} (Table 1). The respiratory quotient (RQ) was 0.71 (SE $\pm$ 0.021) at 25°C and 0.80 (SE $\pm$ 0.021) at 35°C. Metabolic rate did not decline to basal levels until 4–8 hr after the lizards were placed in the cylinders. In two of

Table 1. Mass-specific standard metabolic rate (VO_2 and VCO_2; ml g^{-1} hr^{-1}) at 25 and 35°C for *V. giganteus*

T_a°C	Mass (g)	VO_2 (ml g^{-1} hr^{-1})	VCO_2 (ml g^{-1} hr^{-1})	RQ	N
25.9	2496 ± 774	0.0429 ± 0.0034	0.0304 ± 0.0020	0.71	6
34.7	2502 ± 782	0.0953 ± 0.0054	0.0758 ± 0.0041	0.80	6

The values are mean ± SE with the sample size (N).

the 12 trials (both at 35°C), there was a spontaneous increase in metabolism around dawn.

Allometric relationship between standard metabolic rate and body mass

Log$_{10}$ body mass is a highly significant predictor of log VO_2 and VCO_2 for *V. giganteus* at 25 and 35°C ($F_{1,4} > 468$ for all four allometric equations; $P < 0.001$; $r > 0.99$). The regression coefficients for the relationship between log$_{10}VO_2$ and log$_{10}VCO_2$ with log$_{10}$body mass (given in Table 2) for *V. giganteus* are significantly higher than 0.8 (VO_2 at 25°C $t_5 = 2.92$, $P < 0.05$; at 35°C $t_5 = 3.62$, $P < 0.05$; VCO_2 at 25°C $t_5 = 3.54$, $P < 0.05$; at 35°C $t_5 = 3.97$, $P < 0.05$). We found no significant difference between the slopes of the regression equations for VO_2 at 25 and 35°C (ANCOVA; slope test $F_{1,8} = 1.313$, $P < 0.05$); the common slope was 0.93. Similarly, we found no significant difference between the slopes of the two regression equations for VCO_2 at 25 and 35°C (ANCOVA; slope test $F_{1,8} = 0.668$, $P < 0.05$); the common slope was 0.95.

Relationship between mass-specific standard metabolic rate and body temperature

There was a significant positive semilogarithmic relationship between mass-specific VO_2 and T_a from 25 to 35°C for *V. giganteus*, represented by the equation: log$_{10}VO_2$ (ml g^{-1} hr^{-1}) $= -2.39 + 0.039T_a$ ($P < 0.001$, $r = +0.92$), with SE for coefficients of ±0.158 and ±0.0051, respectively. There was also a significant positive correlation between mass-specific VCO_2 and T_a between 25 and 35°C; log$_{10}VCO_2$ (ml g^{-1} hr^{-1}) $= -2.68 + 0.045T_a$ ($P < 0.001$, $r = +0.95$), with SE for coefficients of ±0.14 and ±0.0046, respectively. The Q_{10} value determined from the average VO_2 was 2.5 between 25 and 35°C.

Relationship between metabolism, body mass, and temperature

The multiple regression equations that best predict SMR (ml hr^{-1}) for *V. giganteus* using the two independent variables of body mass (*M*, in grams), and temperature are log$_{10}VO_2 = -2.125 + 0.911$ log$_{10}$ *M* $+ 0.040T_a$ ($P < 0.001$, $r = +0.99$); with SE for coefficients of ±0.14, ±0.0276 and ±0.0037, respectively; log$_{10}$ $VCO_2 = -2.469 + 0.927$ log$_{10}M +$ $0.0455T_a$ ($P < 0.001$, $r = +0.99$), with SE for coefficients of ±0.1334, ±0.0264 and ±0.0036, respectively.

Varanus giganteus required at least 6 hr for the metabolic rate to decline to a standard level, with lowest metabolic rates usually achieved only in the early hours of the morning. Most lizards then remained at this minimal level until they were removed from the cylinder between 0800 and 0900 hr.

Discussion

Intraspecific allometry

Andrews and Pough (1985) calculated the mean intraspecific *b* value for 17 species of squamates as 0.67, but pointed out that the values ranged from 0.51 to 0.80. However, in recent years a number of studies have reported intraspecific *b* values above this range for lizards (0.858 for *Ctenosaura similis*: Garland (1984); 0.83 for *Amphibolurus nuchalis*: Garland and Else (1987); 0.839 for *Dipsosaurus dorsalis*; John-Alder (1984): 0.93 for *Sceloporus merriami*: Beaupre *et al.* (1993); and 1.13 for non-reproductive female *Sceloporus jarrovi*: DeMarco (1993) and snakes (Chappell and Ellis, 1987)). In contrast, Wood *et al.* (1978) reported low intraspecific *b* values for *V. exanthematicus* of 0.57 at 25 and 30°C and 0.51 at 35°C over the mass range of 172–7500 g.

Table 2. Relationship between log$_{10}VO_2$ and log$_{10}VCO_2$ with log$_{10}$ body mass at 25.9 and 34.7°C for *V. giganteus*

	T_a°C	a ± SE	b ± SE	r	N
VO_2 (ml hr^{-1})	25.9	−1.047 ± 0.1074	0.897 ± 0.0333	0.99	6
VCO_2 (ml hr^{-1})	25.9	−1.283 ± 0.1136	0.925 ± 0.0352	0.99	6
VO_2 (ml hr^{-1})	34.7	−0.900 ± 0.1433	0.961 ± 0.0444	0.99	6
VCO_2 (ml hr^{-1})	34.7	−1.028 ± 0.1383	0.970 ± 0.0429	0.99	6

Equations are of the form log$_{10}VO_2 = a + b$log$_{10}$ mass. Values are a ± SE and b ± SE from the regression equation, with the correlation coefficient (r) and sample size (N).
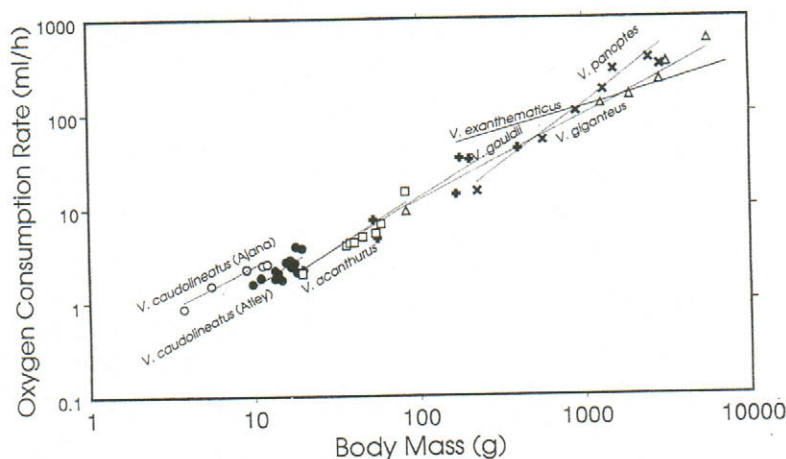
Fig. 1. The relationship of absolute oxygen consumption to body mass at 35°C for, ○ and ● *V. caudolineatus* (at two sites) and □ *V. acanthurus* (Thompson and Withers 1994), + *V. gouldii* and × *V. panoptes* (Thompson and Withers 1992) and △ *V. giganteus* in this study all determined using the same research protocol and *V. exanthematicus* (Wood *et al.*, 1978, solid line).

However, Thompson and Withers (1992) reported common *b* values across the temperature range 25–40°C of 1.12 for *V. gouldii* and 1.10 for *V. panoptes*, and Thompson and Withers (1994) reported *b* values for 0.86 for *V. caudolineatus* and 1.04 for *V. acanthurus* for the T_a of 25, 35 and 40°C. For *V. giganteus*, the common mass exponent was 0.93 for VO_2 and 0.95 for VCO_2. These more recent data confirm that the intraspecific mass exponent for varanids lies between 0.9 and 1.1, even for the large species (Fig. 1). This is in contrast to the lower *b* values observed for other reptiles (e.g. Andrews and Pough, 1985), other vertebrates, and most other animals (Heusner, 1987; Withers, 1992). This indicates that the intraspecific mass-specific

metabolism for any given species of *Varanus* is essentially independent of body mass. The reason for this unusually high intraspecific *b* value of varanids is not clear.

Interspecific allometry

Andrews and Pough (1985) estimated the mass-exponent for all lizards to be 0.80 (SE ± 0.012). Bartholomew and Tucker (1964) reported the mass exponent for four species of Australian monitors as 0.82 at 30°C. However, Thompson and Withers (1992) reported the scaling exponent for VO_2 of *V. gouldii* and *V. panoptes* as 1.05 and for VCO_2 as 1.1 between 20 and 40°C. When the data for *V. gouldii* and *V. panoptes* (Thompson and Withers 1992), and
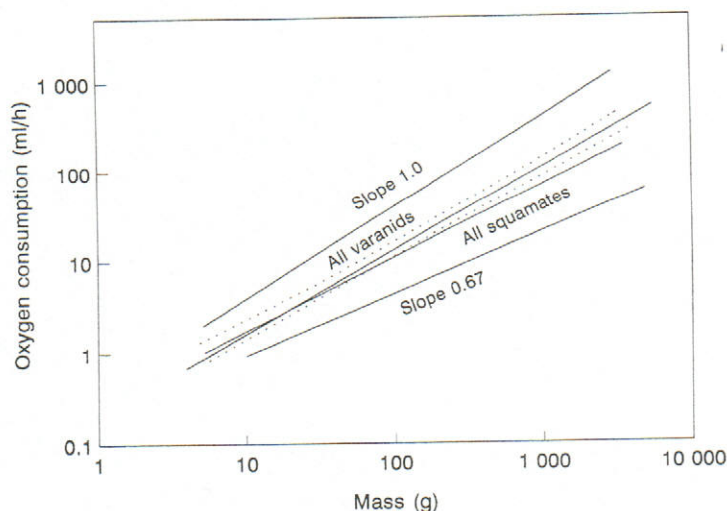

Fig. 2. A comparison of absolute oxygen consumption rate to body mass at 35°C for all varanids and all squamates (Andrews and Pough, 1985). 95% confident limits are shown for all varanids, and lines with a slope of 0.67 and 1.0 are shown for comparative purposes.

V. caudolineatus and *V. acanthurus* (Thompson and Withers, 1994) are combined with the data for *V. giganteus* at 35°C, then the regression equations that best predict SMR are as follows: $\log_{10} VO_2$ (ml hr^{-1}) $= -0.713 + 0.912 \log_{10}M$ and $\log_{10} VCO_2$ (ml hr^{-1}) $= -0.853 + 0.918 \log_{10}M$. The slopes of both of these regression equations are significantly different from 0.8 and from 1.0 (for VO_2 and VCO_2, $P < 0.01$). It would appear, therefore, that the general interspecific scaling exponent for varanids is approximately 0.9. This is higher than that estimated for all squamates by Andrews and Pough (1985, Fig. 2). It can be seen from Fig. 2 that the SMR of a small (25 g) varanid is approximately the same as for other squamates of a similar mass, except that larger varanids have a higher metabolism than other sizeable squamates.

Effect of temperature on metabolism

In general, SMR $= j10^{k(T_a)}$, where j is a proportionality coefficient and k is a temperature coefficient. The value of k for *V. giganteus* was 0.039 for VO_2 and 0.045 for VCO_2. These values are similar to values reported for *V. gouldii* and *V. panoptes* (Thompson and Withers, 1992), and for *V. caudolineatus* and *V. acanthurus* (Thompson and Withers, 1994). When the data for *V. caudolineatus*, *V. acanthurus*, *V. gouldii* and *V. panoptes* (Thompson and Withers, 1992, 1994) are combined with the data for *V. giganteus*, the equations that best predict the influence of T_a on mass-specific SMR are $VO_2 = 0.00437 \cdot 10^{0.042T_a}$ ($r^2 = 0.79$) and $VCO_2 = 0.00398 \cdot 10^{0.040T_a}$ ($r = 0.74$). These equations can be used to predict the mass-specific metabolism of varanids at temperatures between 25 and 35°C.

The Q_{10} value for *V. giganteus* for the temperature range 25–35°C was 2.5, which is similar to the values reported for *V. gouldii* and *V. panoptes* (Thompson and Withers, 1992), *V. caudolineatus* and *V. acanthurus* (Thompson and Withers, 1994), and *V. exanthematicus* (Wood *et al.*, 1977) but higher than those reported for *V. gouldii* (Bartholomew and Tucker, 1964) and *V. bengalensis* (Earll, 1982).

The data now available suggest that the intraspecific relationships between SMR and body mass for small, medium, and large varanids have mass exponents of approximately 1.0. These mass exponents are considerably higher than those reported for other reptiles (Andrews and Pough, 1985). Furthermore, the interspecific relationship between SMR and body mass also has a mass exponent of approximately 0.9. This is also higher than that reported for most other reptiles. The reasons why standard metabolism scales to body mass differently for varanids is unclear. The obvious

similarity of small and large varanid lizards in body shape, diet, activity and foraging behaviour is striking, and unlike the considerable allometric change in shape and activity apparent for other reptiles. The different metabolic allometry may be associated with one of these factors.

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