STANDARD METABOLIC RATES OF TWO SMALL AUSTRALIAN VARANID LIZARDS (*VARANUS CAUDOLINEATUS* AND *V. ACANTHURUS*)

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ABSTRACT: We measured standard metabolic rate (SMR) for two small monitor lizards (*Varanus caudolineatus* and *V. acanthurus*) between 2400–0900 h, after the lizards had rested for at least 8 h and fasted for 60 h. There were no significant differences in mass-specific VO_2 (ml g^{-1} h^{-1}) between freshly caught and long term captive *V. caudolineatus* from the same location, but there was a significant difference between SMR for *V. caudolineatus* caught at different locations. The intraspecific mass exponents for VO_2 values were generally higher than 0.75 for these small varanid species. The common mass exponent, for the three temperatures of 25, 35, and 40 C, was 0.86 for *V. caudolineatus* and 1.04 for *V. acanthurus*.

Key words: *Varanus caudolineatus*; *Varanus acanthurus*; Varanids; Allometry; Standard metabolic rate; Temperature

THE relationship between metabolic rate and body mass for animals has long been of interest to biologists (Benedict, 1938; Brody, 1945; Gunther, 1975; Kleiber, 1961; von Bertalanffy, 1957; Withers, 1992). The general form of the allometric relationship between standard metabolic rate (SMR: ml O_2 h^{-1}) and body mass (M: g) is a power curve, $SMR = aM^b$, where a is the mass coefficient and b is the mass exponent. The inter-species b value is generally about 0.75 for most vertebrates whereas the intra-species mass exponent is generally lower, at about 0.67 (Heusner, 1982; Withers, 1992). Despite the generally good allometric relationship between SMR and body mass, there remains residual deviation from the general relationship which may relate to the ecology or physiology of particular species.

There has recently been considerable interest in the intra- and interspecific allometry of standard metabolic rate (SMR) for lizards and other reptiles (Andrews and Pough, 1985; Beaupre et al., 1993; Chappell and Ellis, 1987; DeMarco, 1993; Reiss, 1989). Andrews and Pough (1985) reported a mean intraspecific mass exponent of 0.67 for 17 species of squamates, but the intraspecific scaling relationship appears to be different for varanid lizards. Wood et al. (1978) reported a mass exponent of

0.57 at 25 C and 30 C and 0.51 at 35 C for the large *V. exanthematicus* (172–750 g). In contrast, Thompson and Withers (1992) reported a high intraspecific mass exponent of approximately 1.1 for *V. gouldii* (20–555 g) and *V. panoptes* (227–3480 g) over the temperature range of 20–40 C.

Thompson and Withers (1992) reported a common slope of 1.1 for allometry of SMR in the medium sized varanids, *V. gouldii* and *V. panoptes*. If this value held constant with the inclusion of other varanid species, then the interspecific scaling exponent for the SMR of varanids would differ from the 0.8 (±0.012 SE) reported by Andrews and Pough (1985) for squamates. Galvão et al. (1965) also reported interspecific b values of 0.98 and 1.09 for two families of snakes, which are higher than that reported by Andrews and Pough (1985).

SMR values have been measured almost exclusively for medium and large sized varanids (Bartholomew and Tucker, 1964; Bennett, 1972; Earll, 1982; Gleeson, 1981; Louw et al., 1976; Mitchell and Gleeson, 1985; Mitchell et al., 1981; Wood et al., 1977a,b, 1978). One exception is the small *V. gilleni* (Bickler and Anderson, 1986). To determine more accurately the interspecies mass exponent for the relationship between SMR and body mass for *Varanus*,

it would be informative to measure SMR for more small species (e.g., *V. caudolineatus*, *V. brevicauda*, and *V. acanthurus*) and for very large species (*V. komodoensis* and *V. giganteus*).

This study is an extension of a previous study by Thompson and Withers (1992), of *V. gouldii* and *V. panoptes*. We determine SMR for two small varanid species, *V. caudolineatus* and *V. acanthurus*, using the same methods. This avoids problems associated with different research protocols and makes intraspecific and interspecific interpretations more meaningful. Allometric comparisons of data from various sources often have a low reliability due to the differing methodologies (Gunther, 1975).

METHODS AND MATERIALS

We caught nine *V. caudolineatus* during 1990 and eight during December 1991 at Atley Station (119°07′ E, 28°25′ S; 55 km SW of Sandstone in Western Australia). In addition, we caught five more *V. caudolineatus* 40 km north of Ajana (114°45′ E, 27°35′ S) in July 1991. Six of the *V. acanthurus* that we used in this study came from 15 km WNW of Exmouth, Western Australia, and the other two were from 42 km NNE of Meekatharra, Western Australia. The mean mass of *V. caudolineatus* caught at Atley Station and kept in the laboratory for more than 2 mo was 15.72 g (±0.87, range = 13.4–18.65); the mean mass of the wild caught *V. caudolineatus* from Atley Station was 15.35 g (±1.25, range = 9.8–19.50), and the mean mass of the *V. caudolineatus* from Ajana was 8.3 g (±1.61, range = 3.73–12). The mean mass of *V. acanthurus* was 47.22 g (±6.67, range = 19.6–83.0).

We maintained all lizards in indoor cages with incandescent lighting, as the heat source, for 12 h/day. *Varanus caudolineatus* ate cockroaches and mealworms while *V. acanthurus* consumed cockroaches, baby mice, and raw meat; water was always available for all lizards. We withheld food from all lizards for at least 60 h before the measurement of standard metabolic rates. We measured oxygen consumption and carbon dioxide production only once for each lizard at each temperature, but we were unable to measure all individuals at all temperatures.

We measured the SMR of the eight freshly caught *V. caudolineatus* at 35 C within 13 days of capture. We measured SMR for the remaining *V. caudolineatus* and all of the *V. acanthurus* after holding them for at least 2 mo of captivity and some after periods >12 mo in captivity.

We measured oxygen consumption rate (VO_2; ml O_2 h^{-1}) and carbon dioxide production rate (VCO_2; ml CO_2 h^{-1}) using a flow-through respirometry system. We weighed all lizards before placing them in opaque plastic cylinders (lizards <20 g in a cylinder 20 mm diameter × 190 mm; lizards >21 g in a cylinder 28 mm diameter × 250 mm), which restricted but did not prevent voluntary activity. We placed these cylinders in a controlled temperature chamber at 25, 35, or 40 C (±1 C). Compressed ambient air flowed through the chamber at a controlled flow rate (Brooks mass flow meter; 50 ml min^{-1} for SMR measurements at 25 C and 100 ml min^{-1} at 35 and 40 C) so that the excurrent O_2 content was about 20.1%. A chromel-alumel thermocouple measured the temperature of the air in the metabolic chamber (T_a: in C). A drierite column dried the excurrent air before it passed through one channel of a paramagnetic oxygen analyser (Servomex 184A) and a CO_2 analyser (Hereus-Leybold Binos). A Promax XT microcomputer with Analog Device RTI800 A/D interface board recorded the differential output of the oxygen analyser (ambient air–excurrent air) and the analog outputs of the CO_2 analyser and thermocouple, and calculated STPD VO_2 and VCO_2 every 60 s, for 12–16 h periods commencing between 1200 and 2000 h. The microcomputer averaged the analog output of the VO_2 and VCO_2 signals for 25 consecutive values to determine each 60-s value, and calculated VO_2 after Withers (1977). We calculated minimum (i.e., standard) VO_2 and VCO_2 as the average of the lowest continuous period of O_2 consumption and VCO_2 production (normally 10–

TABLE 1.—Mass-specific standard metabolic rate (VO_2; ml g^{-1} h^{-1}) at various ambient temperatures for two species of varanids. Values are mean ± 1 SE with sample size in parentheses.

T_a	Mass	VO_2
V. caudolineatus (Ajana site)		
25.1	8.84 ± 1.64	0.086 ± 0.0069 (4)
35.3	8.30 ± 1.60	0.238 ± 0.0120 (5)
39.8	8.09 ± 1.55	0.395 ± 0.0403 (5)
V. caudolineatus (Atley site)		
26.0	14.67 ± 0.46	0.066 ± 0.0034 (16)
35.4	15.51 ± 0.78	0.156 ± 0.0076 (14)
40.0	15.64 ± 0.55	0.219 ± 0.0108 (16)
V. acanthurus		
26.3	46.74 ± 6.19	0.057 ± 0.0046 (7)
35.1	47.22 ± 6.67	0.116 ± 0.0088 (8)
40.4	46.53 ± 6.21	0.196 ± 0.0134 (8)

40 min duration). We did this to avoid the effect of brief periods of activity, or transient low VO_2 or VCO_2 values (due to short apneic respiratory periods) on the calculation of SMR.

We tested differences in mass-specific SMR between freshly caught and long term captive *V. caudolineatus* from Atley Station and north of Ajana using ANOVA and Tukey's multiple comparison procedure (Kitchens, 1987) and ANCOVA (Zar, 1984). We tested the differences in SMR between species and temperatures by two-factor analysis of variance (unequal sample sizes; Statview software). We tested the difference between species regression equations by ANCOVA and Tukey's Q test (Zar, 1984). We used a statistically significant level of $P < 0.05$ throughout the analysis. Means are reported with ±1 SE throughout.

RESULTS

Standard Metabolic Rate

The metabolic rate of some lizards decreased to standard levels within a few hours after being placed in the chamber and remained at that level until we removed them in the morning. Others were not at their lowest level of metabolism until 2200 h or later. A few lizards had short periods of increased metabolism during the night. There was a spontaneous increase in metabolism about dawn for some *V. caudolineatus* and *V. acanthurus*, presumably reflecting a circadian rhythm.

Mass-specific VO_2 increased with temperature and decreased with body mass for *V. caudolineatus* from Atley Station and Ajana (Table 1). The VCO_2 showed a similar pattern and the mean RQ value was 0.76 (±0.01). There was a significant difference (ANOVA: $F = 15.44$, df = 2, 16) in the mass-specific VO_2 values for the freshly caught and long term captive *V. caudolineatus* for Atley Station and *V. caudolineatus* caught at a site north of Ajana. There was no significant difference (Tukey's multiple comparison procedure) between the freshly caught and long term captive *V. caudolineatus* from Atley Station (both groups had a similar mass). As a consequence, we grouped together all *V. caudolineatus* from Atley Station. The Ajana group (which had the lowest mean body mass) had a significantly higher mass-specific metabolic rate than the two Atley groups. We found a significant difference between the $\log_{10} VO_2$ for *V. caudolineatus* caught at the Atley and Ajana sites (ANCOVA), so we have treated the Atley and Ajana *V. caudolineatus* as separate groups for further analysis.

The mass-specific VO_2 values for *V. acanthurus* are generally lower than for *V. caudolineatus* and their body mass is higher (Table 1). Mass specific VO_2 of *V. acanthurus* increased with temperature and decreased with body mass. VCO_2 showed a similar pattern and the mean RQ value was 0.76 (±0.016).

Intraspecific Allometry for Standard Metabolic Rate

There was a consistently high correlation ($r > 0.80$) between $\log_{10}$ mass and $\log_{10}$ absolute SMR (ml O_2 h^{-1}) for the Ajana group of *V. caudolineatus* and *V. acanthurus* at T_a = 25, 35, and 40 C (Table 2). The lower correlation coefficient for the *V. caudolineatus* from Atley reflects the smaller mass range (see SE values, Table 1). This makes it difficult to establish a reliable intraspecific allometric relationship with SMR for the lizards from Atley.

There were no significant differences for

TABLE 2.—Relationship between $\log_{10} VO_2$ (ml h^{-1}) with $\log_{10}$ body mass (g) at 25, 35, and 40 C for *V. caudolineatus* and *V. acanthurus*. Equations are of the form $\log_{10} VO_2 = a + b \log_{10}$ mass. Values are $a \pm$ 1 SE, and $b \pm 1$ SE from the regression equation, with the F statistic, P values, and the correlation coefficient (r), mass as in Table 1 and sample size (n).

	V. caudolineatus Atley site	*V. caudolineatus* Ajana site	*V. acanthurus*
25 C			
a	-0.797 ± 0.4474	-0.8917 ± 0.1478	-1.1875 ± 0.3733
b	0.663 ± 0.3839	0.8084 ± 0.1555	0.9597 ± 0.2263
r	0.42	0.96	0.88
n	16	4	7
F (df)	2.98 (1,14)	27.04 (1,2)	17.98 (1,5)
P	0.106	0.035	0.008
35 C			
a	-0.8007 ± 0.2996	-0.5364 ± 0.1014	-1.3691 ± 0.2343
b	0.9901 ± 0.2527	0.8990 ± 0.1126	1.2588 ± 0.1559
r	0.75	0.80	0.96
n	14	5	8
F (df)	15.35 (1,12)	63.75 (1,3)	78.68 (1,6)
P	0.002	0.004	0.001
40 C			
a	-0.7610 ± 0.4123	-0.2035 ± 0.1797	-0.4683 ± 0.3311
b	1.078 ± 0.3458	0.7615 ± 0.2018	0.8497 ± 0.2009
r	0.64	0.91	0.87
n	16	5	8
F (df)	9.72 (1,14)	14.23 (1,3)	17.89 (1,6)
P	0.008	0.033	0.006

either of the two species in the slope of their allometric VO_2 relationship for the three air temperatures (ANCOVA slope test: Atley *V. caudolineatus*, $F = 0.38$, df $= 2, 40$; Ajana *V. caudolineatus*, $F = 0.19$, df $= 2, 8$; *V. acanthurus*, $F = 1.31$, df $= 2, 17$). The common slope for the *V. caudolineatus* from Atley was 0.94 and for *V. caudolineatus* from Ajana was 0.82 (the common slope for the two groups of *V. caudolineatus* was 0.86). The common slope for *V. acanthurus* was 1.04. The slopes for VCO_2 were similar to those reported for VO_2, and RQ values were relatively constant at about 0.76 for all three temperatures.

Standard Metabolic Rate and Body Temperature

The curvilinear relationship between the mass-specific SMR and T_a can be best represented by the equation SMR $= a 10^{cT_a}$ (or $\log_{10}$SMR $= \log_{10}(a) + cT_a$). There were significant positive semilogarithmic correlations for mass-specific VO_2 with T_a (25–40 C) for the two groups of *V. caudoli-* *neatus* (Atley, $\log_{10}VO_2 = -2.15 + 0.037T_a$, $r = 0.93$, $F = 297.8$, df $= 1, 44$; Ajana, $\log_{10}VO_2 = -2.33 + 0.048T_a$, $r = 0.98$, $F = 299.8$, df $= 1, 12$) and *V. acanthurus* ($\log_{10}VO_2 = -2.24 + 0.037T_a$, $r = 0.93$, $F = 125.9$, df $= 1, 21$). There were no significant differences in the slopes of the regression equations for $\log_{10}VO_2$ with T_a (b from 0.037–0.048) for the two groups of *V. caudolineatus*, and *V. acanthurus* (ANCOVA: slope $F = 2.996$, df $= 2, 77$). There were, however, significant differences in the elevations between the two groups of *V. caudolineatus*, and *V. acanthurus*.

The multiple regression relationship for VO_2, mass and T_a is $VO_2 = a$ Mass$^b 10^{cT_a}$ (or $\log_{10}VO_2 = \log_{10}a + b \log_{10}$Mass $+ cT_a$). The multiple regression equations relating VO_2 to mass and T_a were highly significant. For *V. caudolineatus* from Atley, $\log_{10}VO_2 = -2.068 \ (\pm 0.22) + 0.923 \ (\pm 0.186) \log_{10}$Mass $+ 0.0399 \ (\pm 0.0022) \ T_a$ ($r = 0.94$); for *V. caudolineatus* from Ajana, $\log_{10}VO_2 = -2.183 \ (\pm 0.117) + 0.867 \ (\pm 0.072) \log_{10}$Mass $+ 0.0474 \ (\pm 0.0026) \ T_a$ ($r = 0.99$); and for *V. acanthurus*, $\log_{10}VO_2$

$$= -2.316 \ (\pm 0.227) \ + \ 1.047 \ (\pm 0.118) \ \log_{10}\text{Mass} + 0.0371 \ (\pm 0.0034) \ T_a \ (r = 0.95).$$

DISCUSSION

The analysis of intraspecific and interspecific allometry of SMR in varanids, and other lizards, can be complicated by differences amongst species in both in the allometric slope and intercept. Biological effects such as thermal acclimation, captivity, season, sex, temperature, reproductive state, and experimental protocols can also potentially affect the relationship between body mass and SMR of reptiles (Bennett and Dawson, 1976; Beuchat and Vleck, 1990; DeMarco, 1993, Niewiarowski and Waldschmidt, 1992; Tsuji, 1988a,b).

Long-term captivity did not significantly affect the VO_2 of *V. caudolineatus* obtained from the Atley site. This is in contrast to the findings of Gleeson (1979) who found that captivity increased the resting VO_2 of *Sceloporus occidentalis* caught during spring, although there was no effect for lizards caught during winter. Garland et al. (1987) found that captivity decreased the SMR of *Amphibolurus nuchalis*. The levels of activity, or other uncontrolled conditions in captivity, or the difference in foraging mode (widely foraging versus sit-and-wait) between these lizards may account for this variation. The difference in SMR between the Atley Station and Ajana groups of *V. caudolineatus* is unexpected, and we have no explanation for this difference. There is a size difference between the two populations, but this did not account for the differences in SMR.

Intraspecific Allometry for Standard Metabolic Rate

The value of the intraspecific allometric slope (b) for SMR of animals is often about 0.67 (Heusner, 1982; Withers, 1992). Squamates appear to conform to this general pattern. For example, Andrews and Pough (1985) report an average intraspecific mean b value of 0.67 (range 0.51–0.80) for 17 squamate species. There is, however, considerable variation in the values of b reported for varanid lizards. Wood et al. (1978) reported low b values for *V. exanthematicus* (mass range 172–750 g) of 0.57 at 25 C and 30 C and 0.51 at 35 C (Fig. 1). In contrast, Thompson and Withers (1992) reported an unusually high b value of about 1.1 for both *V. gouldii* and *V. panoptes* (Fig. 1).

Small sample sizes and limited mass ranges often make it difficult to determine reliable intraspecific allometric relationships, but the results of our study for two small species support the suggestion that varanid species have high intraspecific b values. *Varanus acanthurus*, and the two groups of *V. caudolineatus*, have a common b value of 1.04 and 0.86 respectively for VO_2 at T_a = 25, 35, and 40 C. When we compared the VO_2 for *V. gouldii* and *V. panoptes* (Thompson and Withers, 1992) with the data from this study at 35 and 40 C, we found no significant differences in the slopes among the four species. Thus, the intraspecific mass exponent of varanids, as suggested by Thompson and Withers (1992), is high, at about 0.9–1.0 (Fig. 1).

It is not clear why the intraspecific b values for varanids are higher than for most other squamates (Andrews and Pough, 1985) and mammals (Heusner, 1982), but it may be for the same reasons that interspecific b values are also high (see below). It should, however, be noted that in recent years a number of studies have reported intraspecific b values significantly higher than the mean value reported by Andrews and Pough (1985)—0.858 for *Ctenotus similis* (juveniles and adults), Garland (1984); 0.83 for *Amphibolurus nuchalis* (juveniles and adults), Garland and Else (1987); 0.839 for *Dipsosaurus dorsalis* (adults only), John-Alder (1984); 0.93 for *Sceloporus merriami* (juveniles and adults), Beaupre et al. (1993); 1.13 for non-reproductive female *Sceloporus jarrovi*, De-Marco (1993). Bennett (1982) suggested that the mass exponents for SMR and maximal VO_2 are similar for most reptiles, and so it would therefore be interesting to determine if the intraspecific mass exponent for maximal VO_2 of varanids was also 0.9–1.0.
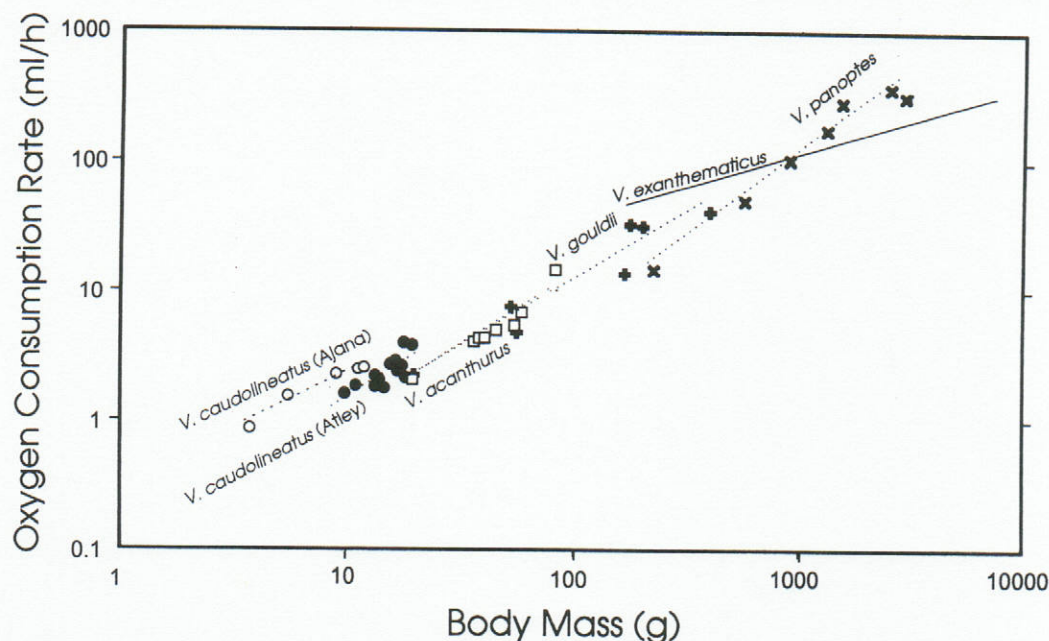
FIG. 1.—Intraspecific comparison of allometry for SMR of varanids. Data for *V. exanthematicus* from Wood et al. (1978), and for *V. gouldii* and *V. panoptes* from Thompson and Withers (1992). Open squares = *V. acanthurus*; closed circles = *V. caudolineatus* (Atley); open circles = *V. caudolineatus* (Ajana); + = *V. gouldii*; crosses = *V. panoptes*.

There are some significant differences in the elevations (*a*) of the intraspecific scaling relationship for VO_2 for *V. gouldii*, *V. panoptes*, *V. caudolineatus*, and *V. acanthurus* (Fig. 1) despite the similarity of interspecific *b* values. For example, at about the preferred T_b of 35 C, the regression elevations for the smaller species are significantly higher than for the larger species, as we would expect if the interspecific *b* value were <1.

Interspecific Allometry for Standard Metabolic Rate

Small varanids have a higher mass-specific SMR than larger varanids. For example, *V. caudolineatus*, like *V. gilleni* (Bickler and Anderson, 1986), has a considerably higher mass-specific VO_2 than large varanids at 35 C (Table 3); *V. acanthurus*, the next smallest monitor for which standard VO_2 data is available, has a mass-specific SMR that is similar to that of larger monitors.

The interspecific mass exponent for metabolic rate of animals is generally about 0.75, although Andrews and Pough (1985) reported a slightly higher interspecific mass exponent of 0.8 for squamates. However, the interspecific mass exponent for the metabolic rate of varanids appears to be much higher than 0.80 (Fig. 2). We estimated the mass exponent for all available varanid data (mean SMR's and masses) at 35 C (Table 3) by assuming that resting metabolic rate is approximately 38% higher than SMR (Andrews and Pough, 1985), and we found that the interspecific mass exponent is 0.86 (±0.035): $VO_2 = 0.25M^{0.86}$. The interspecific slope for all species (0.86) is <1.0, indicating a lower mass-specific metabolic rate of the larger species compared to the smaller species. However, this slope is less than the intraspecific slopes that we have reported for varanids. This is in contrast to Heusner's (1982) finding that the mass exponents for comparisons within mammalian species are less than the mass exponents for comparison among species. It would therefore be informative

TABLE 3.—Comparison of mass-specific standard metabolic rates for varanids at about 35 C. Symbols are: a = this study; b = Bickler and Anderson (1986); c = Thompson and Withers (1992); d = Gleeson and Bennett (1982); e = Gleeson (1981); f = Mitchell and Gleeson (1985); g = Bennett (1972); h = Bartholomew and Tucker (1964); i = Louw et al. (1976); j = Mitchell et al. (1981).

Species	State	Mean mass (g)	VO₂ ml g⁻¹ h⁻¹
V. caudolineatus (Ajana)[a]	standard	8.3	0.238
V. caudolineatus (Atley)[a]	standard	15.5	0.156
V. gilleni[b]	standard	30	0.169
V. acanthurus[a]	standard	47.2	0.116
V. gouldii[c]	standard	154	0.123
V. salvator[d]	resting	458	0.093*
V. salvator[e]	resting	505	0.089*
V. salvator[f]	resting	650	0.118*
V. gouldii/rosenbergi[g]	resting	674	0.066*
"Australian varanids"[h]	resting	714	0.102*
V. albigularis[i]	resting	963	0.096*
V. exanthematicus[j]	resting	1040	0.118*
V. panoptes[c]	standard	1427	0.120

* Resting VO₂ reduced by 38% to equate with SMR values (see Andrews and Pough, 1985).
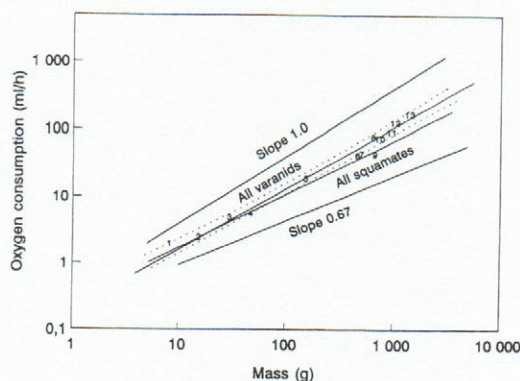

FIG. 2.—Comparison of interspecific allometry for SMR for varanids at 35 C (from this study and Thompson and Withers, 1992: with 95% confidence interval) with that for all squamates (Andrews and Pough, 1985). Numbers represent the mean values for 1 = V. caudolineatus (Ajana), 2 = V. caudolineatus (Atley), 3 = V. gilleni (Bickler and Anderson, 1986), 4 = V. acanthurus, 5 = V. gouldii (Thompson and Withers, 1992), 6 = V. salvator (Gleeson and Bennett, 1982), 7 = V. salvator (Gleeson, 1981), 8 = V. salvator (Mitchell and Gleeson, 1985), 9 = V. gouldii/V. rosenbergi (Bennett, 1972), 10 = Australian varanids (Bartholomew and Tucker, 1964), 11 = V. albigularis (Louw et al., 1976), 12 = V. exanthematicus (Mitchell et al., 1981), 13 = V. panoptes (Thompson and Withers, 1992).

to measure SMR of large varanids (i.e., V. giganteus and V. komodoensis) using the same research protocol to determine both the intra- and interspecific scaling relationships for varanids over as wide as possible a mass range.

We have no plausible biological explanation for the high interspecific mass exponent of varanids. However, the apparently conservative morphology and the widely foraging insectivorous/carnivorous habits of most Varanus (except V. olivaceus: Auffenberg, 1988) over a relatively large range of masses may be factors worth investigating. Similarly high interspecific mass exponents have been reported for two families of snakes (0.98 for Colubridae and 1.09 for Boidae: Galvão et al., 1965). Gunther (1975) attributed this unusual scaling to their filiform shape, serpentine locomotion, and warm habitat. The scaling of metabolic rate (power) might be expected to vary from mass$^{0.66}$ (kinematic or biological similarity) to mass$^{0.73}$ (biological similarity with operational-time concept) to mass$^{1.16}$ (mechanical or dynamic similarity) using various dimensional scaling arguments (Gunther, 1975). Whether there is any biological significance to varanids of mechanical similarity, and whether this

concept can explain their high interspecific mass exponent, is uncertain.

Standard Metabolic Rate and Body Temperature

SMR generally increases exponentially with an increase in body temperature for most terrestrial reptiles. Andrews and Pough (1985) reported the following equation to predict the oxygen consumption rate of lizards, taking into account body temperature, body mass, and metabolic state (ms; 0 = SMR, 1 = RMR): VO₂ (ml h⁻¹) = $0.013 \, g^{0.80} \, 10^{0.038(Tb)} \, 10^{0.14(ms)}$ (see Fig. 2 for regression line at 35 C). The corresponding equation that best predicts SMR for the two groups of V. caudolineatus and V. acanthurus in this study, together with the data for V. gouldii and V. panoptes from Thompson and Withers (1992), is VO₂ (ml h⁻¹) = $0.0074 \, g^{0.934} \, 10^{0.0391(Tb)}$ ($F = 2083$, df = 2, 134, $r = 0.98$: see Fig. 2 for regression line at 35 C). The temperature coefficient of 0.0391 for varanids is similar to the value of 0.038 reported by Andrews and Pough (1985) for squamates, but the

mass exponent of 0.934 for varanids is significantly higher than 0.8 for squamates.

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