

Standard and Maximal Metabolic Rates of Goannas (Squamata: Varanidae)

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ABSTRACT

Standard metabolic rate and maximal metabolic rate during forced exercise are examined for nine species of goanna (genus *Varanus*), with body mass varying from 10 to 3,750 g. At 35°C, the common pooled mass exponent for standard metabolic rate is 0.97 and at 25°C it is 0.89, with considerable variation between species (0.43–1.20). Standard metabolic rate at 35°C scales interspecifically with body mass^{0.92} and at 25°C with body mass^{0.87}. The Q_{10} for standard metabolic rate is approximately 2.5 between 25° and 35°C. At 35°C, maximal metabolic rate scales intraspecifically with body mass^{0.79} and scales interspecifically with body mass^{0.72}. Factorial metabolic scope ranges from nine for the larger species to 35 for the smaller species; it scales with body mass^{-0.199} at 35°C. The maximal metabolic rate of 6.36 mL O₂ g⁻¹ h⁻¹ for *Varanus caudolineatus* is the highest recorded for any squamate. Variations from the interspecific regression line appear to have some ecological significance. *Varanus tristis* (a widely foraging arboreal goanna) and *Varanus eremius* (a widely foraging terrestrial goanna) have a higher standard metabolic rate than *Varanus acanthurus* (a sedentary terrestrial goanna). The three arboreal goannas (*Varanus caudolineatus*, *Varanus gilleni*, and *Varanus tristis*) have a higher maximal metabolic rate than the terrestrial species (*Varanus brevicauda*, *V. eremius*, *V. acanthurus*, *Varanus gouldii*, *Varanus rosenbergi*, and *Varanus panoptes*).

Introduction

The intra- and interspecific allometry of standard metabolic rate ($\dot{V}O_2$) for reptiles has been of recent interest to physiolo-

gists (e.g., Garland 1984; Andrews and Pough 1985; Reiss 1989; Beaupre et al. 1993; DeMarco 1993). The interspecific mass exponent reported by Andrews and Pough (1985) for the standard $\dot{V}O_2$ of 107 squamate species is 0.80 (SE ± 0.012) and the intercept is 0.013. The mean metabolic rate of Varanidae (the family with the highest standard $\dot{V}O_2$) is not statistically different from the mean metabolic rate of Boidae (the family with the lowest standard $\dot{V}O_2$), suggesting that there are no systematic differences in the level of standard $\dot{V}O_2$ for different taxa of squamates. Maximal $\dot{V}O_2$ of large varanids (Gleeson et al. 1980; Gleeson 1981; Gleeson and Bennett 1982; Christian and Conley 1994) appears to be generally higher than for other lizards, but it is not clear whether there are systematic differences in maximal $\dot{V}O_2$ of reptiles. Most studies of maximal $\dot{V}O_2$ for varanids have examined medium and large species. The only study of a small goanna, *Varanus gilleni*, indicates a remarkably high maximal $\dot{V}O_2$ and factorial aerobic scope (maximal $\dot{V}O_2$ /standard $\dot{V}O_2 \approx 28$; Bickler and Anderson 1986). To determine more accurately the interspecific allometry for both standard and maximal $\dot{V}O_2$ in *Varanus*, it would therefore be informative to measure standard and maximal $\dot{V}O_2$ for a number of other species of varying body mass.

Andrews and Pough (1985) report a mean intraspecific mass exponent for 17 species (28 data sets) of 0.67, ranging from 0.51 to 0.80. Wood et al. (1978) report intraspecific mass exponents for *Varanus exanthematicus* (0.57 at 25° and 30°C and 0.51 at 35°C) to be at the lower end of Andrews and Pough's (1985) range, whereas Thompson and Withers (1992, 1994) report intraspecific mass exponents for four species of *Varanus* to be toward the other end of the range (≈ 0.9 –1.0). Further investigation of the intraspecific mass exponent may explain this difference.

Pianka (1995) points out that the morphological conservatism of the various species in the genus *Varanus*, with a mass range of nearly five orders of magnitude, makes them ideal animals for an examination of the effects of body size. However, this potential was not realised in the review of Andrews and Pough (1985) because standard $\dot{V}O_2$ values had been measured almost exclusively for medium- and large-sized varanid lizards (Bartholomew and Tucker 1964; Bennett 1972; Louw et al. 1976; Wood et al. 1977a, 1977b, 1978; Gleeson 1981; Mitchell et al. 1981; Earll 1982; Mitchell and Gleeson 1985). Since the report of Andrews and Pough (1985), additional standard $\dot{V}O_2$'s have also become available (Bickler and Anderson 1986; Thompson and Withers 1992, 1994; Christian and Conley 1994; Thompson et al. 1995).

We extend the earlier studies of standard $\dot{V}O_2$ for medium-

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sized goannas by Thompson and Withers (1992) for *Varanus gouldii* and *Varanus panoptes*, by Thompson and Withers (1994) for the smaller *Varanus caudolineatus* and *Varanus acanthurus*, and by Thompson et al. (1995) for *Varanus giganteus*, the largest Australian goanna, and report standard $\dot{V}O_2$ for three additional species of small and medium-sized Western Australian goannas (*Varanus breviceauda*, *Varanus eremius*, and *Varanus tristis*). All of these studies, including the present one, use a similar research protocol. Additional standard $\dot{V}O_2$ data for *V. gouldii*, *V. panoptes*, *V. caudolineatus*, and *V. acanthurus* are combined with that reported by Thompson and Withers (1992, 1994) to provide a larger sample size for reanalysis. Thus, standard $\dot{V}O_2$ data are analysed for nine species, with mean mass varying from 16 g to 2,000 g. In addition, maximal $\dot{V}O_2$ has been measured for nine species of goanna (*V. breviceauda*, *V. caudolineatus*, *V. gilleni*, *V. eremius*, *V. acanthurus*, *V. tristis*, *V. gouldii*, *Varanus rosenbergi*, and *V. panoptes*) to determine the allometric scaling of both maximal $\dot{V}O_2$ and factorial aerobic scope for goannas. These data for standard and maximal $\dot{V}O_2$ of goannas allow a better analysis of the unusual allometry of goannas reported by Thompson and Withers (1992, 1994) and Thompson et al. (1995).

Material and Methods

Specimens of *Varanus breviceauda*, *Varanus caudolineatus*, *Varanus gilleni*, *Varanus eremius*, *Varanus acanthurus*, and *Varanus tristis* were collected from various locations in Western Australia (App. A). *Varanus caudolineatus* were collected from three different locations in Western Australia, and variation in the site-specific standard metabolic rates meant that these groups were analysed separately (Garland and Adolph 1991; Thompson and Withers 1994). These small goannas were maintained at 20°C in indoor aquaria with incandescent lighting as a heat source, enabling lizards to increase their body temperature (T_b) up to 44°C, for 12 h d⁻¹. These goannas were fed cockroaches, mealworms, and small mice, with an occasional mineral and vitamin supplement. The medium-sized goannas *Varanus rosenbergi*, *Varanus panoptes*, and *Varanus gouldii* were collected at a number of sites in Western Australia (App. A). These goannas were maintained in outdoor cages under natural light and temperature conditions; they were fed mice and raw meat. All of these goannas were able to achieve their preferred T_b on most days. Water was available at all times for all goannas.

Maximal $\dot{V}O_2$ values were measured for nine *V. breviceauda* (in September 1992 and November 1994), 10 *V. acanthurus* (in September 1992), two *V. gilleni* (in February 1994), 14 *V. caudolineatus* (in December 1992), five *V. tristis* (in November 1992, February 1994, and November 1994), 25 *V. gouldii* (between October 1992 and January 1993, and February 1994; nine from a captive colony and 15 fresh-caught from Karrakatta Cemetery, Perth, and one from Eurardy Station, Western Australia), six *V. panoptes* (in February 1994), five *V. rosenbergi* (in February 1994), and eight *V. eremius* (in November 1994).

Individual *V. breviceauda*, *V. caudolineatus*, *V. gilleni*, *V. eremius*, *V. tristis*, *V. acanthurus*, *V. panoptes*, and *V. rosenbergi* were each tested on two consecutive days with the highest recorded maximal $\dot{V}O_2$ used in all analyses. The captive group of *V. gouldii* was tested on three separate occasions, each 4 wk apart; the highest maximal $\dot{V}O_2$ for each goanna was subsequently used in all inter- and intraspecific analyses. Fresh-caught *V. gouldii* were tested twice on consecutive days, with the highest value for each lizard being used in all analysis. The data for the two *V. gilleni* measured here have been combined with data reported for four *V. gilleni* by Bickler and Anderson (1986) to increase the sample size for this species to six.

The O₂ and CO₂ analysers were regularly calibrated during the experiments against a precise gas mixture and with an ethanol burner (theoretical respiratory exchange ratio = 0.67).

Measurement of Standard Metabolic Rate

Food was withheld for at least 60 h before the measurement of standard $\dot{V}O_2$. Standard $\dot{V}O_2$ was measured after at least 3 wk of captivity for all goannas, except for some *V. caudolineatus* that were used in an experiment to examine the variation in standard $\dot{V}O_2$ between fresh-caught and long-term captive goannas (Thompson and Withers 1994). Standard $\dot{V}O_2$ and CO₂ production ($\dot{V}CO_2$) were measured only once for each lizard at each temperature, but not all individual lizards were measured at all temperatures. $\dot{V}O_2$ (mL O₂ h⁻¹) and $\dot{V}CO_2$ (mL CO₂ h⁻¹) were measured with a flow-through respirometry system. Each lizard was weighed before being placed in an opaque plastic cylinder. Cylinder sizes varied according to the mass of the goanna being measured so that they restricted but did not prevent voluntary activity. These cylinders were placed in a controlled temperature chamber at 15°, 20°, 25°, 35°, or 40°C (± 1°C; minor offsets and oscillations in ambient temperature < 1°C occurred in the controlled-temperature room). All standard $\dot{V}O_2$ values have been adjusted for the less than 1°C offset to a temperature of exactly 15°, 20°, 25°, 35°, or 40°C using a Q₁₀ value of 2.5 (see Discussion for justification). A comparison of the mean cloacal temperature for five *V. panoptes* (35.0°C, ± 0.12°) and the cylinder air temperature (35.2°C, ± 0.13°) confirmed that the T_b of even these large goannas had equilibrated with atmospheric conditions after a period of 5 h. Body heating trials for *Varanus giganteus* (N. Heger and T. Heger, unpublished data) confirmed expectations, based on Bartholomew and Tucker (1964), Brattstrom (1973), and McNab and Auffenberg (1976), that such large goannas require about 3 h for their T_b to increase from approximately 25°C to within 1°C of 35°C. As all standard metabolic rate values were taken after 0000 hours, the goannas would have had at least 4 h for T_b to equilibrate with the ambient temperature (T_a). It has therefore been assumed that the T_b of goannas was the same as that of the ambient air in the cylinders.

Compressed ambient air flowed through the chamber at varying controlled flow rates (Brooks mass-flow controller) so

that the excurrent O_2 content was greater than 19.5%. Airflow rates varied for each species at each temperature, between 50 and 500 mL min^{-1} . A 2-m length of copper tube in the in-current airflow line, located in the controlled temperature chamber, ensured that the temperature of the air passing into the cylinder containing the goanna was within $\pm 0.5^\circ\text{C}$ of the T_a within the chamber. A chromel-alumel thermocouple measured the T_a ($^\circ\text{C}$) in the metabolic chamber. A Drierite column removed water from the excurrent air before it passed through one channel of a paramagnetic O_2 analyser (Servomex 184A) and a CO_2 analyser (Hereus-Leybold Binos). A Promax XT microcomputer with Analog Device RTI800 A/D interface board (or a Thurlby digital voltmeter with an RS232 interface) recorded the differential output of the O_2 analyser (ambient air – excurrent air) and the analog outputs of the CO_2 analyser and thermocouple, and calculated the STPD $\dot{V}O_2$ and $\dot{V}CO_2$ every 60 s for 12–16-h periods, commencing between 1200 and 2000 hours. The microcomputer averaged the analog output of the $\dot{V}O_2$ and $\dot{V}CO_2$ signal for 25 consecutive values to determine each 60-s value and calculated $\dot{V}O_2$ and $\dot{V}CO_2$ (after Withers 1977). The minimum (i.e., standard) $\dot{V}O_2$ and $\dot{V}CO_2$ were calculated as the average of the lowest continuous period of O_2 consumption and CO_2 production (normally 10–20-min duration), between 0000 and 0800 hours. Brief periods of activity or transient low values were excluded from the period for the calculation of standard $\dot{V}O_2$.

Measurement of Maximal Metabolic Rate

Maximal $\dot{V}O_2$ and $\dot{V}CO_2$ were measured with a flow-through respirometry system. Each lizard was weighed, and those with a body mass greater than 300 g were held for at least 6 h at 35°C ($\pm 1.0^\circ\text{C}$) prior to being exercised on a treadmill, whereas those with a body mass less than 300 g were held at 35°C for at least 1 h prior to being exercised on a treadmill. A vacuum drew ambient air through a lightweight, transparent acetate mask placed over the lizard's head and approximately half of the neck. A controlled airflow rate (Brooks mass-flow controller) of either 300 or 500 mL min^{-1} for goannas less than 70 g or 800 mL min^{-1} for all other goannas maintained the excurrent O_2 content of air at between 17% and 20.5%. The T_a in the controlled-temperature chamber ($^\circ\text{C}$) was constantly measured with a chromel-alumel thermocouple. Excurrent air was dried by a Drierite column before passing through a CO_2 analyser (Hereus-Leybold Binos) and one channel of a paramagnetic O_2 analyser (Servomex 184A). The differential output of the O_2 analyser (ambient air – excurrent air) and the analog outputs of the CO_2 analyser and thermocouple meter were connected to a Promax XT microcomputer via either an Analog Device RTI800 A/D interface board or a Thurlby digital voltmeter with an RS232 interface. The computer system monitored T_a and excurrent O_2 and CO_2 content and calculated $\dot{V}O_2$ and $\dot{V}CO_2$ (STPD) after Withers (1977) every 10 or 15 s for 8–12 min; data were stored to disk for subsequent analysis.

Goannas were first placed on a stationary treadmill with their masks in place. The treadmill was then started and the belt speed adjusted in two or three steps to the maximum speed that each lizard could sustain for the duration of the experiment. Lizards were encouraged to run by being touched or prodded at the base of the tail or hind-limbs. The mean rate of the highest four successive $\dot{V}O_2$ recordings was used as the measure of maximal $\dot{V}O_2$. All goannas were run for a variable period of time between 5 and 12 min. However, $\dot{V}O_2$ values immediately after release of the lizard on the treadmill were excluded, and only scores after at least 30 s of running were used, as it was apparent that some goannas held their breath while being handled, and their measured $\dot{V}O_2$ and $\dot{V}CO_2$ values immediately after recommencing to breathe were occasionally higher than their subsequent maximal $\dot{V}O_2$ values when running. Most often, maximal $\dot{V}O_2$ was achieved within 5 min of the goanna commencing to run on the treadmill. The $\dot{V}CO_2$ reported corresponds to periods for the maximal $\dot{V}O_2$ recording, although later values for $\dot{V}CO_2$ were often higher. The maximum treadmill speed varied according to the mass of the individual goanna and ranged from 0.75 to 1.8 km h^{-1} .

Statistics

Differences between absolute metabolic rates were tested with ANCOVA and Tukey's multiple comparison procedure (Zar 1984). For judging statistical significance, we used $P < 0.05$. Means are reported with ± 1 SE, and \log_{10} is used throughout for logarithmic transformations. The allometry of metabolic rate was examined using the \log_{10} -transformed form of the normal power curve—that is, $\dot{V}O_2 = am^b$ or $\log_{10} \dot{V}O_2 = \log_{10} a + b \log_{10} m$, where m is body mass in grams.

Results

Standard Metabolic Rate

Mean absolute standard $\dot{V}O_2$ and $\dot{V}CO_2$, respiratory exchange ratio, and mean body mass values are summarised for each of the nine *Varanus* species in Table 1. The regression equations showing the relationship between absolute $\dot{V}O_2$ and $\dot{V}CO_2$ with the independent variables of T_b and body mass are given in Table 2. Data for *Varanus giganteus* from Thompson et al. (1995), originally measured at mean T_b of 25.9° and 34.7°C but recalculated to a T_b of 25° and 35°C using a Q_{10} of 2.5, are presented for comparative purposes (Tables 1 and 2) and have been used in all interspecific analyses, as they increase the sample size and mass range. Data from the four *Varanus gilleni* reported by Bickler and Anderson (1986) have been adjusted to a T_b of 25° and 35°C (using their Q_{10} value of 1.97) and combined with the data for the two *V. gilleni* measured in this study.

When the effect of body mass was removed by ANCOVA, there was a significant variation between absolute $\log \dot{V}O_2$ and $\dot{V}CO_2$ for the three site-specific groups of *Varanus caudolineatus*

Table 1: Standard metabolic rate ($\dot{V}O_2$ and $\dot{V}CO_2$) and respiratory exchange ratio for 10 *Varanus* species at a range of T_b 's from 15° to 40°C

| T_b (°C) | Mass (g) | $\dot{V}O_2$ (mL h ⁻¹) | $\dot{V}CO_2$ (mL h ⁻¹) | Respiratory Exchange Ratio | n |
|--|-------------|---------------------------------------|--|-------------------------------|---------|
| <i>Varanus breviceauda</i> : | | | | | |
| 20° | 16.2 ± 1.54 | .53 ± .071 | .43 ± .045 | .84 ± .0583 | 5 |
| 25° | 16.7 ± 1.12 | 1.12 ± .117 | .88 ± .080 | .80 ± .034 | 10 |
| 35° | 17.4 ± .94 | 2.71 ± .254 | 2.02 ± .200 | .75 ± .024 | 11 |
| <i>Varanus caudolineatus</i> : | | | | | |
| All: | | | | | |
| 15° | 16.3 ± 1.38 | .23 ± .025 | .15 ± .026 | .66 ± .081 | 5 |
| 20° | 18.4 ± 1.63 | .53 ± .078 | .48 ± .077 | .89 ± .041 | 5 |
| 25° | 13.1 ± .64 | .92 ± .034 | .68 ± .033 | .76 ± .021 | 29 (31) |
| 35° | 13.1 ± .86 | 2.26 ± .135 | 1.75 ± .099 | .78 ± .016 | 27 |
| 40° | 14.1 ± .76 | 3.46 ± .191 | 2.68 ± .151 | .78 ± .016 | 20 (21) |
| Atley: | | | | | |
| 15° | 16.3 ± 1.38 | .23 ± .025 | .15 ± .026 | .66 ± .081 | 5 |
| 20° | 18.4 ± 1.63 | .53 ± .078 | .48 ± .077 | .89 ± .041 | 5 |
| 25° | 14.7 ± .46 | .93 ± .047 | .69 ± .039 | .75 ± .021 | 16 (17) |
| 35° | 15.5 ± .78 | 2.47 ± .196 | 1.80 ± .121 | .74 ± .016 | 14 |
| 40° | 15.6 ± .55 | 3.44 ± .230 | 2.68 ± .186 | .79 ± .018 | 5 |
| Ajana: | | | | | |
| 25° | 11.4 ± 1.12 | .91 ± .006 | .67 ± .006 | .79 ± .060 | 6 (7) |
| 35° | 10.2 ± .87 | 2.33 ± .017 | 1.92 ± .013 | .84 ± .035 | 7 |
| 40° | 9.2 ± 1.44 | 3.54 ± .038 | 2.68 ± .042 | .76 ± .028 | 4 |
| Dead Horse Rocks: | | | | | |
| 25° | 10.8 ± 2.06 | .88 ± .068 | .66 ± .0621 | .76 ± .057 | 7 |
| 35° | 10.8 ± 2.59 | 1.78 ± .297 | 1.46 ± .261 | .81 ± .026 | 6 |
| <i>Varanus gilleni</i> (combined values): | | | | | |
| 25° | 20.0 | 1.92 | ... | ... | 6 |
| 35° | 20.0 | 3.58 | ... | ... | 6 |
| <i>Varanus eremius</i> : | | | | | |
| 25° | 36.4 ± 5.01 | 2.38 ± .324 | 1.91 ± .271 | .80 ± .029 | 14 |
| 35° | 35.9 ± 5.07 | 6.16 ± .906 | 4.74 ± .697 | .77 ± .015 | 14 |
| <i>Varanus acanthurus</i> : | | | | | |
| 25° | 53.1 ± 8.31 | 2.80 ± .463 | 1.94 ± .304 | .73 ± .033 | 8 (9) |
| 35° | 53.4 ± 8.50 | 6.24 ± 1.350 | 4.80 ± 1.080 | .76 ± .014 | 9 |
| <i>Varanus tristis</i> : | | | | | |
| 25° | 77 ± 34.2 | 5.3 ± 1.74 | 3.9 ± 1.31 | .75 ± .028 | 5 |
| 35° | 99 ± 30.8 | 15.7 ± 5.36 | 13.3 ± 5.12 | .80 ± .060 | 6 |
| <i>Varanus gouldii</i> : | | | | | |
| 25° | 411 ± 62.2 | 18.6 ± 3.60 | 14.6 ± 2.44 | .81 ± .031 | 7 |
| 35° | 303 ± 75.4 | 38.1 ± 9.66 | 25.9 ± 6.97 | .65 ± .047 | 9 |
| <i>Varanus rosenbergi</i> : | | | | | |
| 25° | 2,081 ± 313 | 90 ± 13.1 | 71 ± 10.2 | .79 ± .030 | 7 |
| 35° | 2,074 ± 312 | 284 ± 43.0 | 214 ± 32.7 | .77 ± .021 | 7 |
| <i>Varanus panoptes</i> : | | | | | |
| 25° | 1,896 ± 562 | 66 ± 15.6 | 49 ± 12.4 | .72 ± .020 | 5 |
| 35° | 1,622 ± 313 | 179 ± 33.9 | 135 ± 25.1 | .78 ± .022 | 12 |
| <i>Varanus giganteus</i> : | | | | | |
| 25° | 2,499 ± 774 | 91 ± 27.0 | 66 ± 20.8 | .71 ± .021 | 6 |
| 35° | 2,502 ± 782 | 237 ± 78.2 | 192 ± 66.4 | .80 ± .021 | 6 |

Note. Values are mean ± 1 SE; T_b is presumed to be the same as T_a ; n values in parentheses are values for $\dot{V}CO_2$ when they differ from $\dot{V}O_2$.

Table 2: The relationship between $\log \dot{V}O_2$ (mL h⁻¹) and $\dot{V}CO_2$ (mL h⁻¹), with T_a and body mass for specified T_a between 20° and 40°C, for nine species of *Varanus*

| | <i>a</i> | <i>b</i> | <i>c</i> | <i>r</i> ² | <i>n</i> | <i>F</i> | <i>P</i> | Mass (g) |
|---|--------------|-------------|-------------|-----------------------|----------|----------|----------|--------------------|
| <i>Varanus brevicauda</i> (20°–35°C): | | | | | | | | |
| $\dot{V}O_2$ | -2.35 ± .268 | 1.05 ± .216 | .043 ± .004 | .90 | 26 | 107.78 | .001 | 16.73 (10.12–22.1) |
| $\dot{V}CO_2$ | -2.30 ± .253 | .98 ± .204 | .040 ± .004 | .90 | 26 | 106.20 | .001 | |
| <i>Varanus caudolineatus</i> (25°–40°C): | | | | | | | | |
| $\dot{V}O_2$ | -1.46 ± .098 | .43 ± .757 | .038 ± .002 | .88 | 76 | 265.33 | .001 | 13.43 (5.3–22.8) |
| $\dot{V}CO_2$ | -1.66 ± .102 | .46 ± .080 | .039 ± .002 | .88 | 79 | 264.91 | .001 | |
| Atley (25°–40°C): | | | | | | | | |
| $\dot{V}O_2$ | -2.00 ± .223 | .91 ± .189 | .036 ± .002 | .88 | 49 | 178.75 | .001 | 15.26 (9.8–19.8) |
| $\dot{V}CO_2$ | -2.26 ± .216 | .99 ± .184 | .037 ± .002 | .90 | 48 | 212.97 | .001 | |
| Ajana (25°–35°C): | | | | | | | | |
| $\dot{V}O_2$ | -1.73 ± .235 | .52 ± .164 | .044 ± .003 | .94 | 17 | 96.08 | .001 | 10.45 (5.3–15.7) |
| $\dot{V}CO_2$ | -2.19 ± .262 | .75 ± .192 | .048 ± .004 | .90 | 18 | 75.78 | .001 | |
| Dead Horse Rocks (25°–35°C): | | | | | | | | |
| $\dot{V}O_2$ | -1.28 ± .169 | .48 ± .110 | .030 ± .004 | .86 | 13 | 33.54 | .001 | 10.82 (5.9–22.8) |
| $\dot{V}CO_2$ | -1.60 ± .153 | .57 ± .100 | .034 ± .004 | .92 | 13 | 54.12 | .001 | |
| <i>Varanus eremius</i> (25°–35°C): | | | | | | | | |
| $\dot{V}O_2$ | -2.12 ± .107 | .92 ± .050 | .042 ± .002 | .96 | 28 | 313.23 | .001 | 36.0 (8.7–68) |
| $\dot{V}CO_2$ | -2.21 ± .118 | .94 ± .055 | .040 ± .003 | .96 | 28 | 252.30 | .001 | |
| <i>Varanus acanthurus</i> (25°–40°C): | | | | | | | | |
| $\dot{V}O_2$ | -2.19 ± .199 | .99 ± .097 | .036 ± .003 | .92 | 25 | 115.64 | .001 | 51.14 (19.6–103.1) |
| $\dot{V}CO_2$ | -2.50 ± .181 | 1.04 ± .090 | .039 ± .003 | .94 | 26 | 162.87 | .001 | |
| <i>Varanus tristis</i> (25°–35°C): | | | | | | | | |
| $\dot{V}O_2$ | -1.55 ± .232 | .81 ± .072 | .032 ± .007 | .96 | 11 | 79.34 | .001 | 96 (10–191.5) |
| $\dot{V}CO_2$ | -1.76 ± .298 | .83 ± .091 | .033 ± .008 | .92 | 11 | 51.82 | .001 | |
| <i>Varanus gouldii</i> (25°–35°C): | | | | | | | | |
| $\dot{V}O_2$ | -2.78 ± .355 | 1.09 ± .955 | .045 ± .006 | .92 | 16 | 71.13 | .001 | 350.1 (53–706) |
| $\dot{V}CO_2$ | -2.95 ± .240 | 1.20 ± .064 | .039 ± .004 | .96 | 16 | 174.96 | .001 | |
| <i>Varanus rosenbergi</i> (25°–35°C): | | | | | | | | |
| $\dot{V}O_2$ | -2.53 ± .248 | .98 ± .069 | .050 ± .003 | .98 | 14 | 208.18 | .001 | 2,077 (485–3,210) |
| $\dot{V}CO_2$ | -2.41 ± .291 | .92 ± .081 | .048 ± .004 | .96 | 14 | 137.78 | .001 | |
| <i>Varanus panoptes</i> (25°–35°C): | | | | | | | | |
| $\dot{V}O_2$ | -2.78 ± .334 | 1.06 ± .080 | .045 ± .006 | .96 | 17 | 107.15 | .001 | 1,703 (228–3,754) |
| $\dot{V}CO_2$ | -2.88 ± .282 | 1.03 ± .675 | .048 ± .005 | .98 | 17 | 147.39 | .001 | |
| <i>Varanus giganteus</i> (25°–35°C): | | | | | | | | |
| $\dot{V}O_2$ | -2.13 ± .132 | .91 ± .027 | .040 ± .003 | .98 | 6 | 642.26 | .001 | 2,499 (84–5,660) |
| $\dot{V}CO_2$ | -2.46 ± .126 | .93 ± .026 | .045 ± .003 | .98 | 6 | 731.42 | .001 | |

Note. Equations are of the form $\log \dot{V}O_2 = a + b \log \text{mass} + c T_a$. Values are $a \pm 1$ SE, $b \pm 1$ SE, and $c \pm 1$ SE from the regression equation, *F* statistics, *P* values, the coefficient of determination (*r*²), and mean and range in body mass.

at 35°C (ANCOVA, $\dot{V}O_2$, $F_{2,23} = 4.34$, $P < 0.03$; $\dot{V}CO_2$, $F_{2,23} = 11.67$, $P < 0.001$) but not for the lower $\dot{V}O_2$ and $\dot{V}CO_2$ values at 25°C (ANCOVA, $\dot{V}O_2$, $F_{2,25} = 0.45$, $P = 0.65$; $\dot{V}CO_2$, $F_{2,27} = 1.50$, $P = 0.24$). Consequently, the three site-specific groups of *V. caudolineatus* have been treated as separate groups in subsequent analyses.

Intraspecific Allometry of Standard $\dot{V}O_2$

No significant variations in the mass exponents (b) were found for standard $\dot{V}O_2$ or $\dot{V}CO_2$ of each goanna species at either 25° or 35°C. The common (weighted) pooled mass exponents for standard $\dot{V}O_2$ and $\dot{V}CO_2$ at 25°C were both 0.89; the common (weighted) pooled mass exponents were 0.97 and 1.00, respectively, at 35°C. The three geographic groups of *V. caudolineatus* had different mean masses and intraspecific intercepts from the regression equations of standard $\dot{V}O_2$ with body mass, thereby reducing the common (weighted) pooled slope intraspecific mass exponent for the combined data for *V. caudolineatus* (Table 2), and so these three groups were treated separately in subsequent intraspecific analyses. The comparison of the elevations of the intraspecific regression equations for nine species of goannas (data for *V. gilleni* are insufficient) indicated significant variation in standard $\dot{V}O_2$ and $\dot{V}CO_2$ at 25°C (for standard $\dot{V}O_2$, $F_{10,78} = 2.82$, $P < 0.05$; for standard $\dot{V}CO_2$, $F_{10,81} = 3.67$, $P < 0.05$). A Tukey multiple comparison test found *Varanus tristis* to have a significantly higher standard metabolic rate than *Varanus acanthurus* at 25°C. At 35°C, there was a significant variation in the elevations for standard $\dot{V}O_2$ ($F_{10,89} = 3.91$, $P < 0.05$) but not for $\dot{V}CO_2$ ($F_{10,89} = 1.93$, $P > 0.05$); a Tukey's multiple comparison test indicated that *Varanus eremius* and *V. tristis* had a higher $\dot{V}O_2$ intercept than *V. acanthurus*.

When the nine mass coefficients for each goanna species at 25° and 35°C were regressed against the log of mean body mass for each species, the regression equations were not significant, but there was a tendency for the intercepts to decrease with body mass—that is, the slopes were negative (at 25°C, $a = -0.59$ [SE, ± 0.308] $- 0.220$ [± 0.1389] $\log m$, $r^2 = 0.22$, $F_{1,9} = 2.51$, $P = 0.15$; at 35°C, $a = -0.38$ [± 0.246] $- 0.202$ [± 0.1112] $\log m$, $r^2 = 0.27$, $F_{1,9} = 3.31$, $P = 0.1$).

Interspecific Allometry of Standard $\dot{V}O_2$

The logarithmically transformed interspecific regression equations (using mean values for each species, Table 1) for standard $\dot{V}O_2$ and $\dot{V}CO_2$ of goannas at 25°C were: \log standard $\dot{V}O_2$ (mL h⁻¹) = -0.93 (± 0.082) + 0.87 (± 0.036) $\log m$ ($r^2 = 0.98$, $F_{1,8} = 589.00$, $P < 0.001$), and \log standard $\dot{V}CO_2$ (mL h⁻¹) = -1.07 (± 0.101) + 0.87 (± 0.043) $\log m$ ($r^2 = 0.98$, $F_{1,7} = 419.95$, $P < 0.001$), where m is body mass in grams. The $\dot{V}O_2$ slope is not significantly different from the general squamate value (Andrews and Pough 1985) of 0.8 (standard $\dot{V}O_2$, $t_8 = 1.89$; standard $\dot{V}CO_2$, $t_7 = 1.70$), although both standard

$\dot{V}O_2$ and $\dot{V}CO_2$ slopes are significantly different from 1.0 (standard $\dot{V}O_2$, $t_8 = 3.70$; standard $\dot{V}CO_2$, $t_7 = 3.00$).

At 35°C, the interspecific regression equations were: \log standard $\dot{V}O_2$ (mL h⁻¹) = -0.68 (± 0.057) + 0.92 (± 0.024) $\log m$, ($r^2 = 0.99$, $F_{1,8} = 1,381.34$, $P < 0.001$), and \log standard $\dot{V}CO_2$ (mL h⁻¹) = -0.82 (± 0.078) + 0.92 (± 0.032) $\log m$ ($r^2 = 0.99$, $F_{1,7} = 806.11$, $P < 0.001$). Both of these slopes were significantly different from 0.8 (standard $\dot{V}O_2$, $t_8 = 4.74$; standard $\dot{V}CO_2$, $t_7 = 3.80$) and 1.0 (standard $\dot{V}O_2$, $t_8 = 3.37$; standard $\dot{V}CO_2$, $t_7 = 2.34$).

Effect of Temperature on Standard $\dot{V}O_2$

Standard $\dot{V}O_2$ increased with increasing T_b 's (Table 1). The relationship of both standard $\dot{V}O_2$ and $\dot{V}CO_2$, with T_b 's of 25°, 35°, and 40°C, appears linear for *V. acanthurus* but not for *Varanus brevicauda* or *V. caudolineatus* between 15° and 40°C. Q_{10} values generally decrease with increasing T_b 's. This is particularly evident for *V. brevicauda*, where the Q_{10} between 20° and 25°C was 4.28 but declined to 2.35 between 25° and 35°C and also for *V. caudolineatus* (Q_{10} 25°–35°C was 2.51, 35°–40°C was 1.88). Standard $\dot{V}O_2$ and $\dot{V}CO_2$ showed no plateau between 35° and 40°C for *V. caudolineatus* (standard $\dot{V}O_2$ values differed significantly between 35° and 40°C; ANCOVA, $F_{1,44} = 31.22$, $P < 0.05$). The mean Q_{10} values for all goanna species measured from 25° to 35°C were 2.49 for $\dot{V}O_2$ and 2.59 for $\dot{V}CO_2$.

The interspecific regression equations relating absolute standard $\dot{V}O_2$ and $\dot{V}CO_2$ to the independent variables of body mass and temperature are: \log standard $\dot{V}O_2$ (mL h⁻¹) = -2.22 (± 0.095) + 0.044 (± 0.0029) T_b + 0.92 (± 0.023) $\log m$, ($r^2 = 0.98$, $F_{2,22} = 989.3$, $P < 0.001$), and \log standard $\dot{V}CO_2$ (mL h⁻¹) = -2.38 (± 0.101) + 0.045 (± 0.0031) T_b + 0.92 (± 0.025) $\log m$, ($r^2 = 0.98$, $F_{2,20} = 879.15$, $P < 0.001$). It can be seen from the r^2 values that these two variables account for almost all of the variation in standard $\dot{V}O_2$ and $\dot{V}CO_2$ and are therefore together very useful predictors of standard metabolism.

Maximal Metabolic Rate

The maximal $\dot{V}O_2$ and the corresponding $\dot{V}CO_2$ values for each of the nine species along with respiratory exchange ratios are shown in Table 3. The allometric regression equations for maximal $\dot{V}O_2$ and the corresponding $\dot{V}CO_2$ at a T_b of 35°C are shown in Table 4. The mean mass-specific maximal $\dot{V}O_2$ and the corresponding $\dot{V}CO_2$ values for the two *V. gilleni* (mean mass 8.42 g) were 5.1 and 11.2 mL g⁻¹ h⁻¹, respectively. The mean maximal $\dot{V}O_2$ of the four *V. gilleni* measured by Bickler and Anderson (1986) (27.5 g, 5.4 mL g⁻¹ h⁻¹ at 37°C) is 4.5 mL g⁻¹ h⁻¹ when corrected to a T_b of 35°C using a Q_{10} of 2.5. The combined mean mass and maximal $\dot{V}O_2$ for *V. gilleni* from these two studies (Table 3) has been used in subsequent interspecific analyses. The individual maximal $\dot{V}O_2$ and body mass values for each *V. gilleni* from the study by Bickler and

Table 3: Maximal metabolic rate for nine species of *Varanus* from this study and five species of squamates and other varanids used in the regression equations at 35°C

| Species/Study ^a | Mass (g) | $\dot{V}O_2$ (mL h ⁻¹) | $\dot{V}CO_2$ (mL h ⁻¹) | Respiratory Exchange Rate | <i>n</i> |
|---|--------------|---------------------------------------|--|---------------------------------|----------|
| <i>Varanus caudolineatus</i> | 14.95 ± .78 | 94.0 ± 6.20 | 126.3 ± 6.47 | 1.37 ± .059 | 14 |
| <i>Varanus brevicauda</i> | 17.48 ± 1.31 | 56.4 ± 4.44 | 74.3 ± 6.28 | 1.33 ± .074 | 9 |
| <i>Varanus gilleni</i> : | | | | | |
| This study | 8.4 | 43.5 | 94.4 | 2.2 | 2 |
| Combined data ^b | 21.14 | 106.8 | ... | ... | 6 |
| <i>Varanus eremius</i> | 39.97 ± 6.76 | 91.9 ± 17.0 | 112.9 ± 25.1 | 1.13 ± .083 | 8 |
| <i>Varanus acanthurus</i> | 73.61 ± 6.25 | 170 ± 19.7 | 205 ± 19.7 | 1.26 ± .0660 | 10 |
| <i>Varanus tristis</i> | 103.2 ± 28.3 | 310 ± 104.0 | 663 ± 288.0 | 1.88 ± .209 | 5 |
| <i>Varanus gouldii</i> | 401.8 ± 30.2 | 459 ± 43.6 | 632 ± 74.5 | 1.39 ± .062 | 25 |
| <i>Varanus rosenbergi</i> | 1,503 ± 239 | 1,860 ± 321.0 | 2,285 ± 204.0 | 1.41 ± .331 | 5 |
| <i>Varanus panoptes</i> | 2,240 ± 583 | 2,364 ± 494.0 | 3,276 ± 573.0 | 1.46 ± .160 | 6 |
| <i>Cyclura nubila</i> (Christian and Conley 1994) | 1,136 | 1,016 | ... | ... | ... |
| <i>Tupinambis nigropunctatus</i> (Bennett and John-Alder 1984) | 836 | 728 | ... | ... | ... |
| <i>Iguana iguana</i> (Gleeson et al. 1980) | 709 | 588 | ... | ... | ... |
| <i>Heloderma suspectum</i> (John-Alder et al. 1983) | 464 | 416 | ... | ... | ... |
| <i>Tiliqua rugosa</i> : | | | | | |
| John-Alder et al. 1986 | 438 | 316 | ... | ... | ... |
| Christian and Conley 1994 | 548 | 329 | ... | ... | ... |
| Various species of varanids (Bartholomew and Tucker 1964) | 714 | 122.7 | ... | ... | ... |
| <i>V. gouldii</i> and <i>V. rosenbergi</i> (Bennett 1972) | 674 | 44.5 | ... | ... | ... |
| <i>Varanus albigularis</i> (Louw et al. 1976) | 963 | 92.5 | ... | ... | ... |
| <i>Varanus salvator</i> : | | | | | |
| Gleeson 1981 | 505 | 44.9 | ... | ... | ... |
| Gleeson and Bennett 1982 | 458 | 42.9 | ... | ... | ... |
| Mitchell and Gleeson 1985 | 650 | 76.7 | ... | ... | ... |
| <i>Varanus exanthematicus</i> (Mitchell et al. 1981) | 1,040 | 122.7 | ... | ... | ... |
| <i>Varanus mertensi</i> (Christian and Conley 1994) | 904 | 70.5 | ... | ... | ... |
| <i>V. panoptes</i> (Christian and Conley 1994) | 931 | 122.9 | ... | ... | ... |
| <i>V. gouldii</i> (Christian and Conley 1994) | 1,086 | 97.7 | ... | ... | ... |
| <i>V. rosenbergi</i> (Christian and Conley 1994) | 1,287 | 169.9 | ... | ... | ... |

^a Data are for this study unless otherwise indicated.

^b Data are combined with those of Bickler and Anderson (1986).

Table 4: Allometric regression equations for maximal $\dot{V}O_2$ (mL h⁻¹) and $\dot{V}CO_2$ (mL h⁻¹) of eight species of *Varanus*

| | <i>a</i> | <i>b</i> | <i>r</i> ² | <i>F</i> | <i>P</i> |
|--|-------------|-------------|-----------------------|----------|----------|
| <i>Varanus caudolineatus</i> (<i>n</i> = 14): | | | | | |
| $\dot{V}O_2$ | 1.12 ± .402 | .72 ± .343 | .27 | 4.36 | .059 |
| $\dot{V}CO_2$ | 1.91 ± .358 | .16 ± .306 | .02 | .27 | .612 |
| <i>Varanus brevicauda</i> (<i>n</i> = 9): | | | | | |
| $\dot{V}O_2$ | .81 ± .434 | .75 ± .351 | .40 | 4.60 | .069 |
| $\dot{V}CO_2$ | .85 ± .462 | .82 ± .373 | .40 | 4.78 | .065 |
| <i>Varanus eremius</i> (<i>n</i> = 8): | | | | | |
| $\dot{V}O_2$ | .28 ± .129 | 1.05 ± .082 | .96 | 162.10 | .001 |
| $\dot{V}CO_2$ | -.05 ± .211 | 1.28 ± .132 | .94 | 93.71 | .001 |
| <i>Varanus acanthurus</i> (<i>n</i> = 11): | | | | | |
| $\dot{V}O_2$ | -.24 ± .279 | 1.32 ± .150 | .88 | 76.87 | .001 |
| $\dot{V}CO_2$ | .21 ± .199 | 1.12 ± .107 | .92 | 109.71 | .001 |
| <i>Varanus tristis</i> (<i>n</i> = 5): | | | | | |
| $\dot{V}O_2$ | .42 ± .282 | 1.02 ± .145 | .94 | 49.59 | .006 |
| $\dot{V}CO_2$ | .25 ± .503 | 1.25 ± .258 | .88 | 23.27 | .019 |
| <i>Varanus gouldii</i> (<i>n</i> = 25): | | | | | |
| $\dot{V}O_2$ | 1.02 ± .48 | .62 ± .184 | .35 | 11.48 | .003 |
| $\dot{V}CO_2$ | 1.49 ± .56 | .49 ± .216 | .18 | 5.20 | .032 |
| <i>Varanus rosenbergi</i> (<i>n</i> = 5): | | | | | |
| $\dot{V}O_2$ | .36 ± .491 | .91 ± .156 | .92 | 34.34 | .01 |
| $\dot{V}CO_2$ | 3.18 ± .759 | .05 ± .241 | .02 | .05 | .83 |
| <i>Varanus panoptes</i> (<i>n</i> = 6): | | | | | |
| $\dot{V}O_2$ | 1.90 ± .652 | .44 ± .120 | .55 | 4.89 | .09 |
| $\dot{V}CO_2$ | 2.01 ± .386 | .45 ± .118 | .77 | 14.67 | .02 |

Note. The equations are in the form of $\log \dot{V}O_2$ (or $\dot{V}CO_2$) = $\log a + b \log \text{mass (g)}$; values are $a \pm 1 \text{ SE}$, $b \pm 1 \text{ SE}$, coefficient of determination (r^2), F and P values, and sample size (n).

Anderson (1986) are not available, and so it was not possible to calculate any intraspecific allometric relationship for maximal $\dot{V}O_2$.

The intraspecific mass exponents for maximal $\dot{V}O_2$ ranged widely from 0.44 for *Varanus panoptes* to 1.32 for *V. acanthurus* (Table 4); the common (weighted) pooled intraspecific slope for maximal $\dot{V}O_2$ of all eight goanna species (excluding *V. gilleni*) was 0.79. The interspecific regression equations determined using mean maximal $\dot{V}O_2$ and $\dot{V}CO_2$ values for each of the nine species at 35°C are: $\log \text{maximal } \dot{V}O_2 \text{ (mL h}^{-1}\text{)} = 0.95 (\pm 0.125) + 0.72 (\pm 0.057) \log m$ ($r^2 = 0.96$, $F_{1,7} = 158.87$, $P < 0.001$); and $\log \dot{V}CO_2 \text{ (mL h}^{-1}\text{)} = 0.99 (\pm 0.187) + 0.77 (\pm 0.082) \log m$ ($r^2 = 0.94$, $F_{1,6} = 85.94$, $P < 0.001$) where m is the body mass in grams. Inspection of Figure 1 indicates some interspecific variability in maximal $\dot{V}O_2$ values, particularly for the smaller species. However, if the mean maximal $\dot{V}O_2$ values for the nine species are grouped as terrestrial goannas and arboreal goannas and separate regression lines are determined (Fig. 1), then it appears that maximal $\dot{V}O_2$ values are different for these two goanna groups. The equations for each of these two groups are: arboreal, $\log \text{maximal } \dot{V}O_2 \text{ (mL h}^{-1}\text{)} = 1.24 (\pm 0.074) + 0.61 (\pm 0.048) \log m$ ($r^2 = 0.98$, $F_{1,1}$

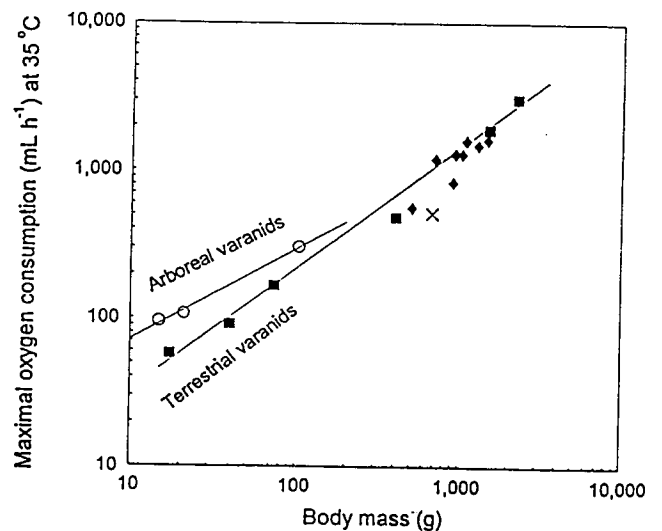


Figure 1. Interspecific mean maximal $\dot{V}O_2$ for all species of varanids at 35°C, with regression lines for the terrestrial and arboreal species from this study. Filled squares are for terrestrial species and open circles are for arboreal species from this study; diamonds are for varanids from other studies; cross is for nontreadmill data (Bennett 1972).

= 163.69, $P = 0.05$); terrestrial, $\log \dot{V}O_2$ (mL h^{-1}) = $0.69 (\pm 0.101) + 0.81 (\pm 0.041) \log m$ ($r^2 = 0.98$, $F_{1,4} = 386.53$, $P < 0.001$), where m is the body mass in grams. A significant difference exists between the maximal $\dot{V}O_2$ for the two groups (ANCOVA, $F_{1,6} = 12.49$, $P > 0.02$).

Factorial Aerobic Scope

The slopes of the interspecific regression equations for standard $\dot{V}O_2$ and body mass and for maximal $\dot{V}O_2$ and body mass at 35°C are not the same (Fig. 2); that is, the allometric slope of factorial scope is not 0 (Garland and Adolph 1994). Rather, factorial scope declines with increasing body mass from about 35 at about 15 g, to between 8 and 13 for the larger species (Table 5). The regression equation that best represents the interspecific factorial aerobic scope for goannas is as follows: $\log \text{factorial scope} = 1.629 (\pm 0.1195) - 0.199 (\pm 0.0549) \log m$, ($r^2 = 0.65$, $F_{1,7} = 13.16$, $P < 0.01$), where m is body mass in grams. When detransformed, factorial scope is $42.56 m^{-0.199}$.

Discussion

Andrews and Pough (1985) indicated for squamates that ecological factors are probably a greater determinant of standard $\dot{V}O_2$ than phylogenetic relationships, but phylogenetic effects should nevertheless be examined (Harvey and Pagel 1991; Garland et al. 1993). Unfortunately, this is not possible in the present study because a complete and rooted phylogenetic tree is not available for the *Varanus* species studied here (see Baverstock et al. 1993). However, the 10 goanna species studied

Table 5: Factorial aerobic scope for 12 species of *Varanus* at 35°C

| Species | Mean Mass (g) | Factorial Scope |
|---|---------------|--------------------|
| <i>Varanus caudolineatus</i> ^a | 14.9 | 35.04 |
| <i>Varanus breviceauda</i> ^a | 17.4 | 20.95 |
| <i>Varanus gilleni</i> ^a | 20.0 | 28.37 |
| <i>Varanus eremius</i> ^a | 38.0 | 12.98 |
| <i>Varanus acanthurus</i> ^a | 73.6 | 19.96 |
| <i>Varanus tristis</i> ^a | 100.0 | 18.10 |
| <i>Varanus gouldii</i> ^a | 349.2 | 9.61 |
| <i>Varanus salvator</i> ^b | 505 | 11.83 ^c |
| <i>V. gouldii/Varanus rosenbergi</i> ^d | 674 | 11.52 ^c |
| <i>Varanus mertensi</i> ^c | 904 | 11.85 |
| <i>Varanus panoptes</i> ^c | 931 | 10.50 |
| <i>Varanus exanthematicus</i> ^f | 1,025 | 10.68 ^c |
| <i>Varanus gouldii</i> ^c | 1,086 | 16.27 |
| <i>Varanus rosenbergi</i> ^c | 1,287 | 8.73 |
| <i>Varanus rosenbergi</i> ^a | 1,503 | 9.06 |
| <i>Varanus panoptes</i> ^a | 2,240 | 12.60 |

^a This study.

^b Gleeson 1981.

^c Factorial scope calculated using adjusted standard (38% lower; see Andrews and Pough 1985) rather than resting metabolic rate.

^d Bennett 1972.

^e Christian and Conley 1994.

^f Wood et al. 1978.

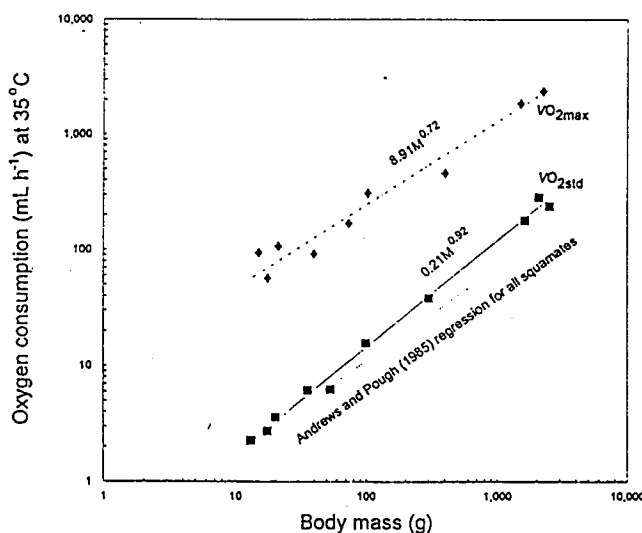


Figure 2. Interspecific standard ($n = 10$) and maximal ($n = 9$) metabolic rates for varanids measured in this study. Filled squares are for mean standard $\dot{V}O_2$; filled diamonds are for mean maximal $\dot{V}O_2$. The interspecific regression line from Andrews and Pough (1985) for squamate standard $\dot{V}O_2$ is shown as a dotted line.

are divided between the two Australian subgenera, *Odatia* (*Varanus caudolineatus*, *Varanus gilleni*, *Varanus breviceauda*, *Varanus eremius*, *Varanus acanthurus*, and *Varanus tristis*) and *Varanus* (*Varanus gouldii*, *Varanus rosenbergi*, *Varanus panoptes*, and *Varanus giganteus*), and a phylogenetic comparison can be made at this level.

Intraspecific Allometry of Standard $\dot{V}O_2$

The value of the intraspecific allometric slope for standard $\dot{V}O_2$ of vertebrates has often been reported to be about 0.67 (Heusner 1982a; Withers 1992). Andrews and Pough (1985) found that the mean intraspecific value determined from 28 data sets (17 species) is 0.67 for squamates; however, they concluded that Heusner's prediction of an intraspecific mass exponent of 0.67 is not generally applicable for lizards due to the wide variation in mass exponents. Similarly, Zari (1991, 1993), using the same research protocols in both studies, showed a variation between the intraspecific mass exponent for *Uromastyx microlepis* ($b \approx 0.80$), a relatively large herbivorous desert lizard, and *Chamaeleo calytratus* ($b \approx 0.65$), a much smaller desert chameleon. Small sample sizes and limited mass ranges often make it difficult to reliably determine intraspecific

allometric relationships, particularly as regression equations are sensitive to values at the extremes of the independent data set, and as a consequence many intraspecific mass exponents have high standard errors.

Wood et al. (1978) report unusually low intraspecific mass exponents for *Varanus exanthematicus* (0.57 at 25° and 30°C and 0.51 at 35°C), whereas Thompson and Withers (1992, 1994) and Thompson et al. (1995) report unusually high mass exponents (≈ 0.9 –1.1) for various varanid species. It is not surprising that the intraspecific mass exponents across a range of T_b 's in this study varied widely, from 0.43 for *V. caudolineatus* to 1.2 for *V. gouldii* (Table 2), but the common (weighted) pooled intraspecific mass exponent for all goannas at 35°C was 0.97 for standard $\dot{V}O_2$ and 1.00 for standard $\dot{V}CO_2$. Intraspecific mass exponents greater than 0.8, the highest recorded by Andrews and Pough (1985), have recently been reported for a number of other squamates: 0.86 for *Ctenosaura similis* (Garland 1984); 0.83 for *Ctenophorus nuchalis* (Garland and Else 1987); 0.84 for *Dipsosaurus dorsalis* (John-Alder 1984); 0.93 for *Sceloporus merriami* (Beaupre et al. 1993); and 1.13 for nonreproductive female *Sceloporus jarrovi* (DeMarco 1993). Variable mass exponents are also evident for snakes, with Dmi'el (1986) reporting intraspecific b values for seven species of snakes ranging from 0.56 to 0.68, and Chappell and Ellis (1987) reporting intraspecific values from 0.56 to 0.89. It therefore appears that there is little conformity among snakes or lizards in the intraspecific mass exponents for standard $\dot{V}O_2$, although *Varanus* species appear to have an unusually high value.

Heusner (1982a) and Feldman and McMahon (1983) suggest that the intraspecific mass coefficient should increase for a series of species with increasing mass. Data of Chappell and Ellis (1987) for 13 species of snakes (Boidae) support this hypothesis of a significant positive relationship between mass coefficients and body mass. In this study the slope of the regression equation between mass coefficient values and mean body mass was negative (but not significant) for the nine species of goannas (and *V. caudolineatus* treated as three separate groups, i.e., $n = 11$).

Thompson and Withers (1994) reported a significant difference in the standard $\dot{V}O_2$ for *V. caudolineatus* from Atley and Ajana based on small samples. The analysis in this study using larger samples, and a third geographic group from Dead Horse Rocks, confirms the earlier variation in $\dot{V}O_2$ from geographically separate groups (ANCOVA, $F_{2,23} = 4.34$, $P = 0.025$). Garland and Adolph (1991) report that geographic variation in morphological or meristic traits is common, whereas few studies report geographic variation in physiological traits. It is unknown whether this variation in standard $\dot{V}O_2$ of *V. caudolineatus* is of a genetic or environmental origin, and this may be an area worthy of further investigation.

Interspecific Allometry of Standard $\dot{V}O_2$

The interspecific mass exponent for metabolism is generally about 0.75 for vertebrates (Kleiber 1947; Heusner 1982b; Feldman and

McMahon 1983; Withers 1992). However, as Heusner (1987) explains, no satisfactory biological explanation for this interspecific mass exponent exists (Benedict 1938; Brody 1945; von Bertalanffy 1957; Kleiber 1961; Gunther 1975; Heusner 1982a, 1982b, 1984, 1987; Feldman and McMahon 1983; Iberall 1984). Gunther (1975) suggested that the scaling of metabolic rate 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), depending on which dimensional scaling argument is accepted.

Andrews and Pough (1985) report an interspecific mass exponent of 0.80 for squamates, with no family of reptiles having a standard $\dot{V}O_2$ that was statistically different from the overall regression equation. The interspecific mass exponents determined here for goanna species ranging in mass from 14 to 2,500 g were approximately 0.87 at 25°C and 0.92 at 35°C, with the latter being significantly higher than 0.8. When the standard $\dot{V}O_2$ data for other goanna species (various species, 714 g, 0.102 mL g⁻¹ h⁻¹ [Bartholomew and Tucker 1964]; *V. gouldii* and *V. rosenbergi*, 674 g, 0.066 mL g⁻¹ h⁻¹ [Bennett 1972]; *Varanus albigularis*, 963 g, 0.096 mL g⁻¹ h⁻¹ [Louw et al. 1976]; *Varanus salvator*, 505 g, 0.089 mL g⁻¹ h⁻¹ [Gleeson 1981]; *V. exanthematicus*, 1,040 g, 0.118 mL g⁻¹ h⁻¹ [Mitchell et al. 1981]; *Varanus salvator*, 458 g, 0.093 mL g⁻¹ h⁻¹ [Gleeson and Bennett 1982]; *V. salvator*, 650 g, 0.118 mL g⁻¹ h⁻¹ [Mitchell and Gleeson 1985]; *Varanus mertensi*, 904 g, 0.078 mL g⁻¹ h⁻¹, *V. panoptes*, 931 g, 0.132 mL g⁻¹ h⁻¹, *V. gouldii*, 0.090 mL g⁻¹ h⁻¹, *V. rosenbergi*, 1,287 g, 0.132 mL g⁻¹ h⁻¹ [Christian and Conley 1994]) were included with the data from this study, the equation for interspecific standard $\dot{V}O_2$ at 35°C is as follows: $\log \dot{V}O_2$ (mL h⁻¹) = $-0.63 (\pm 0.062) + 0.88 (\pm 0.024) \log m$, or $\dot{V}O_2$ (mL h⁻¹) = $0.23 m^{0.88}$ ($r^2 = 0.98$, $F_{1,21} = 1317$, $P < 0.001$); it was assumed for this analysis that resting $\dot{V}O_2$ values were 38% higher than standard $\dot{V}O_2$ (see Andrews and Pough 1985). The slope of this regression equation (0.88) was significantly higher than 0.8 ($t_{21} = 3.35$) and lower than 1.0 ($t_{21} = 4.91$).

A comparison of the interspecific standard $\dot{V}O_2$ regression equations for goannas and other squamates suggests that there should be minimal differences in the standard $\dot{V}O_2$ values of small goannas and other small squamates of the same mass (Fig. 2). In contrast, larger goannas generally have a higher standard $\dot{V}O_2$ than other squamates of the same mass. Christian and Conley (1994) found no difference in the standard $\dot{V}O_2$ at a T_b of 35°C of four large goannas (*V. gouldii*, *V. panoptes*, *V. rosenbergi*, and *V. mertensi*) and a slow moving, heavy-bodied skink (*Tiliqua rugosa*), which they described as a typical lizard. However, this skink's mean standard $\dot{V}O_2$ is considerably higher (96 mL h⁻¹) than that predicted by the squamate regression line (43 mL h⁻¹; Andrews and Pough 1985), suggesting that it may not be a "typical" lizard and therefore may not have been a good choice for comparison with goannas. However, John-Alder et al. (1986) report that the standard $\dot{V}O_2$ for *T. rugosa* is 42 mL h⁻¹, which is about the predicted value.

Effects of Temperature on Standard $\dot{V}O_2$

T_b has a profound effect on standard $\dot{V}O_2$ (Bennett and Dawson 1976; Bennett 1982; Al-Sadoon and Abdo 1988; Zari 1991, 1993; Withers 1992). In some species, Q_{10} values are relatively constant over a wide range of T_b 's (Prieto and Whitford 1971; Snyder 1975; Al-Sadoon and Abdo 1988), and the relationship between standard $\dot{V}O_2$ and T_b is semilogarithmic, expressed in the general form $\dot{V}O_2$ ($\text{mL g}^{-1} \text{h}^{-1}$) = $j 10^{k(T_b)}$. However, Q_{10} values often decrease with an increase in T_b (Bennett and Dawson 1976; Snyder and Weathers 1976; Earll 1982; Loumbourdis and Hailey 1985; Zari 1991, 1993) with values over 5 being reported for some species at low T_b and declining to between 1 and 2 for T_b 's above 30°C (Earll 1982; Al-Sadoon 1986a, 1986b; Zari 1991); the relationship between $\dot{V}O_2$ and T_b is positive but with decreasing slope. The semilogarithmic relationship between the mass specific log standard $\dot{V}O_2$ and $\dot{V}CO_2$ with T_b is not linear for *V. breviceauda* ($Q_{10} = 4.28$ to 2.35) or *V. caudolineatus* ($Q_{10} = 2.51$ to 1.88), but it is almost linear for *V. acanthurus* ($Q_{10} = 2.29$).

In regressing the mean log mass-specific $\dot{V}O_2$ and $\dot{V}CO_2$ values at 25° and 35°C with temperature for goanna species reported in this study (including *V. giganteus*), the equations that best represent the data are: standard $\dot{V}O_2$ ($\text{mL g}^{-1} \text{h}^{-1}$) = $0.0062 \times 10^{0.039(T_b)}$; and standard $\dot{V}CO_2$ ($\text{mL g}^{-1} \text{h}^{-1}$) = $0.0041 \times 10^{0.040(T_b)}$. The mean Q_{10} value for all goannas between 25° and 35°C, 2.49 for standard $\dot{V}O_2$ and 2.59 for $\dot{V}CO_2$, is similar to that for other goannas and squamates.

A significant positive relationship exists between the mean body mass of goanna species and Q_{10} values, with the regression equation that best represents the relationship being $Q_{10} = 1.84 (\pm 0.300) + 0.29 (\pm 0.130) \log m$ ($r^2 = 0.38$, $F_{1,8} = 5.10$, $P = 0.05$); that is, the standard $\dot{V}O_2$ of larger goannas is more sensitive to changes in T_b than is the standard $\dot{V}O_2$ of smaller species. Chappell and Ellis (1987) also found a weak positive relationship between Q_{10} values and log body mass ($r = 0.2$) between 20° and 30°C, and 30° and 34°C, for a large sample of boid snakes. The reason for this mass dependence of Q_{10} values is unknown.

Body Mass and Temperature as Combined Predictors of Standard $\dot{V}O_2$

Andrews and Pough (1985) reported the best regression equation predicting standard and resting metabolic rate (MR, $\text{mL O}_2 \text{h}^{-1}$) for squamates was $\text{MR} = 0.013m^{0.80} \times 10^{0.038T_b} \times 10^{0.14ms}$, where m is body mass (g), T_b is body temperature in °C, and ms is 0 for standard $\dot{V}O_2$ and 1 for resting $\dot{V}O_2$. The comparable equations for goannas are standard $\dot{V}O_2$ (mL h^{-1}) = $0.011m^{0.89} \times 10^{0.038T_b}$ ($r^2 = 0.99$, $F_{2,17} = 1,072$, $P < 0.001$) and standard $\dot{V}CO_2 = 0.007m^{0.90} \times 10^{0.040T_b}$ ($r^2 = 0.99$, $F_{2,15} = 807$, $P < 0.001$) between 25° and 35°C. The very high correlation coefficients and F statistics indicate that T_b and body mass account for most of the variation in standard $\dot{V}O_2$

over a wide mass range and T_b 's between 25° and 35°C. It is also apparent that the regression equation of Andrews and Pough (1985) is not appropriate for estimating the mean standard $\dot{V}O_2$ values for goannas, particularly the larger species.

Maximal Metabolic Rate

The maximal $\dot{V}O_2$ determined here (Table 3) for *V. caudolineatus* of 6.36 $\text{mL g}^{-1} \text{h}^{-1}$ at 35°C is the highest recorded for any reptile, but it is only slightly higher than the combined data for the slightly larger *V. gilleni* of 5.05 $\text{mL g}^{-1} \text{h}^{-1}$. The maximal $\dot{V}O_2$ values determined here for the larger goannas are similar to those reported by Gleeson et al. (1980) and Gleeson and Bennett (1982) for *V. exanthematicus*, Gleeson (1981) for *V. salvator*, and Christian and Conley (1994) for *V. mertensi*, *V. panoptes*, *V. gouldii*, and *V. rosenbergi*.

The intraspecific mass exponents for maximal $\dot{V}O_2$ are quite variable, ranging from 0.44 to 1.3 with relatively high standard error values for a number of the b values, in particular for the two smaller species (with small mass ranges) *V. caudolineatus* and *V. breviceauda* (Table 4). However, the common (weighted) pooled intraspecific mass exponent of 0.79, which is a good estimate of the average intraspecific exponent for goannas, is significantly higher than 0.67. Garland (1984) and Garland and Else (1987) also report high intraspecific maximal $\dot{V}O_2$ mass exponents of 0.92 for *C. similis* (compared with the standard $\dot{V}O_2$ mass exponent of 0.86) and 0.95 for *C. nuchalis* (compared with the standard $\dot{V}O_2$ mass exponent of 0.83). It therefore appears there is considerable variability between intraspecific mass exponents for maximal $\dot{V}O_2$ for lizards, and it is not possible to suggest a general intraspecific relationship between maximal $\dot{V}O_2$ and body mass for squamates or even to make a conclusive statement for a single genus (goannas).

Interspecific Allometry of Maximal $\dot{V}O_2$ for Goannas

Bennett (1982) reports an interspecific mass exponent for maximal $\dot{V}O_2$ of lizards varying from 0.81 at 20°C to 0.64 at 40°C. Cragg (1978) indicates that the intrageneric standard $\dot{V}O_2$ and maximal $\dot{V}O_2$ mass exponents for *Lacerta* are about 0.76 and 0.75, respectively. The interspecific mass exponent for the means of all goanna species measured in this study was 0.72 for maximal $\dot{V}O_2$ and 0.77 for $\dot{V}CO_2$. The regression equation using all available maximal $\dot{V}O_2$ data for goannas measured on a treadmill (*V. exanthematicus*, 1,025 g, 1.26 $\text{mL g}^{-1} \text{h}^{-1}$ [Gleeson et al. 1980]; *V. salvator*, 505 g, 1.10 $\text{mL g}^{-1} \text{h}^{-1}$ [Gleeson 1981]; *V. mertensi*, 904 g, 0.92 $\text{mL g}^{-1} \text{h}^{-1}$, *V. panoptes*, 931 g, 1.39 $\text{mL g}^{-1} \text{h}^{-1}$, *V. gouldii*, 1,086 g, 1.46 $\text{mL g}^{-1} \text{h}^{-1}$, and *V. rosenbergi*, 1,287 g, 1.15 $\text{mL g}^{-1} \text{h}^{-1}$ [Christian and Conley 1994]; and this study) is as follows: $\log \text{maximal } \dot{V}O_2$ (mL h^{-1}) = $0.97 (\pm 0.094) + 0.71 (\pm 0.037) \log m$ ($r^2 = 0.96$, $F_{1,13} = 358.4$, $P < 0.001$, 15 means, 12 species).

The maximal $\dot{V}O_2$ values for three species of large goannas (*V. salvator* [Gleeson 1981]; *V. gouldii*/*V. rosenbergi* [Bennett

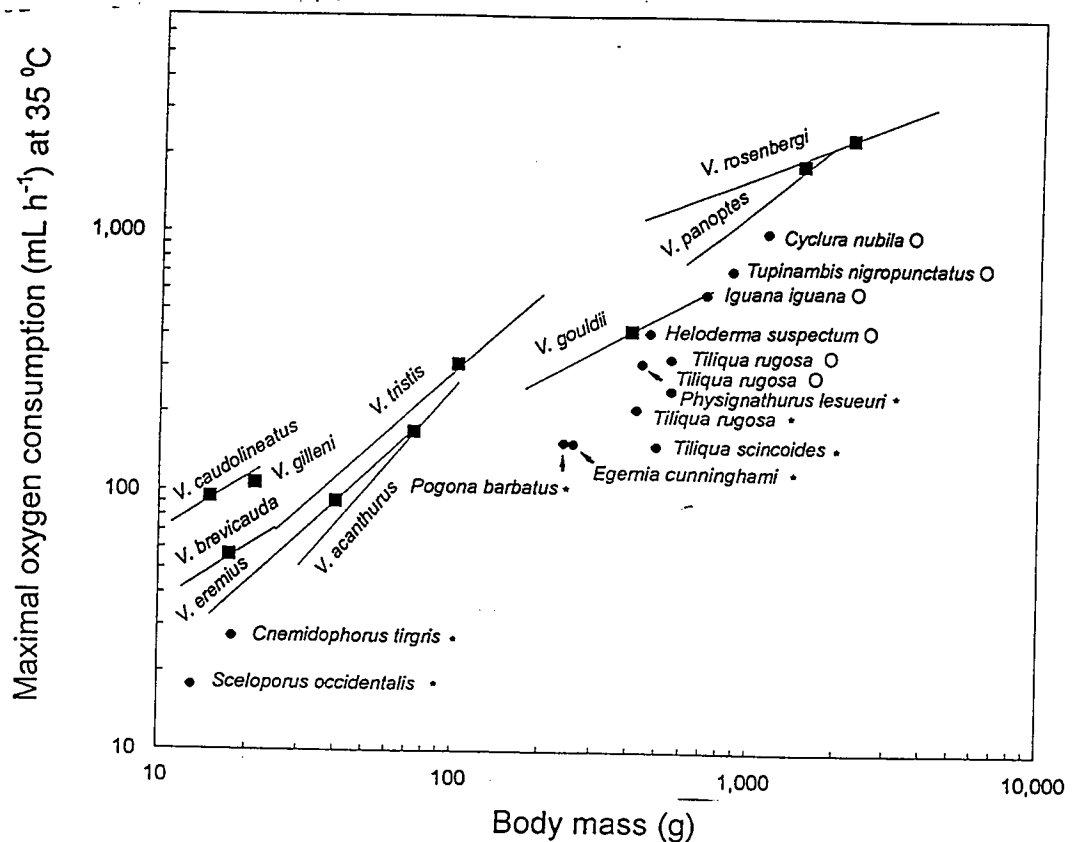


Figure 3. Intraspecific regression lines for maximal $\dot{V}O_2$ for eight species of varanids, compared with the mean maximal $\dot{V}O_2$ for a number of other species of lizards at 35°C. *Sceloporus occidentalis*, Gleeson 1979; *Physignathus lesueuri*, Egernia cunninghami, *Tiliqua rugosa*, *Pogona barbatus*, Wilson 1974; *T. rugosa*, *Cyclura nubila*, Christian and Conley 1994; *T. rugosa*, John-Alder et al. 1986; *Tiliqua scincoides*, Bartholomew et al. 1965; *Tupinambis nigropunctatus*, Bennett and John-Alder 1984; *Cnemidophorus tigris*, Asplund 1970; *Iguana iguana*, Gleeson et al. 1980; *Heloderma suspectum*, John-Alder et al. 1983. Values marked with an asterisk are not calculated from lizards running on a treadmill; values marked with open circles have been used to calculate the regression equation for nonvaranid lizards. Values are in Table 3.

1972]; *V. mertensi* [Christian and Conley 1994]) are below the values predicted by our common regression equation for goannas' maximal $\dot{V}O_2$. The lower values for *V. salvator* and *V. mertensi* may be related to the different ecology of these particular species, as both are semiaquatic. The maximal $\dot{V}O_2$ determined for *V. gouldii*/*V. rosenbergi* by Bennett (1972) are presumably lower because goanna activity in this study consisted of struggling in a tethered position, stimulated by handling or electrical shock.

Gleeson (1981) suggests that the capacity of varanids for sustained activity may be no greater than that of some lizards of other families when their body mass is taken into account. More recently, Christian and Conley (1994) report that the maximal $\dot{V}O_2$ values for *V. rosenbergi*, *V. panoptes*, and *V.*

gouldii are higher than for *Cyclura nubila* and *T. rugosa*, while maximal $\dot{V}O_2$ values for *V. mertensi* are only higher than *T. rugosa*. A comparison of the intraspecific regression equations for the goanna species with the mean maximal $\dot{V}O_2$ values for other species of lizards suggests that the maximal $\dot{V}O_2$ for most goannas are generally higher than that of most other lizards (Fig. 3). A comparison of the interspecific regression equations for the mean maximal $\dot{V}O_2$ values for 12 species of goannas (given above) with that of five (six means) other lizard species (*T. rugosa*, 438 g, 0.72 mL g⁻¹ h⁻¹ [John-Alder et al. 1986]; 548 g, 0.60 mL g⁻¹ h⁻¹ [Christian and Conley 1994]; *C. nubila*, 1,136 g, 0.89 mL g⁻¹ h⁻¹ [Christian and Conley 1994]; *Tupinambis nigropunctatus*, 865 g, 0.84 mL g⁻¹ h⁻¹ [Bennett and John-Alder 1984]; *Iguana iguana*, 709 g, 1.35 mL g⁻¹ h⁻¹ [Gleeson et al. 1980]; *Heloderma suspectum*, 464 g, 0.90 mL g⁻¹ h⁻¹ [John-Alder et al. 1983]; log maximal $\dot{V}O_2 = -0.63 [\pm 0.542] + 1.19 [\pm 0.186] \log m$) showed a significant difference (ANCOVA, $F_{1,18} = 24.08$, $P < 0.001$).

Factorial Aerobic Scope

Two measures of the aerobic energy available during activity relative to rest are the difference between maximal $\dot{V}O_2$ and standard $\dot{V}O_2$ (absolute scope) and the ratio of maximal $\dot{V}O_2$ to standard $\dot{V}O_2$ (factorial scope) (Withers 1992). Factorial scope decreases for goannas as body mass increases, according

to a negative power curve (factorial scope = $42.56m^{-0.199}$, where m is body mass in grams; cf. the slopes in Fig. 2). The relatively low factorial scope for *V. eremius* (13) and the high value for *V. acanthurus* (20) reflect the difference in their standard $\dot{V}O_2$ values more than the difference in their maximal $\dot{V}O_2$ values. *Varanus eremius* has a relatively high standard $\dot{V}O_2$ ($0.18 \text{ mL g}^{-1} \text{ h}^{-1}$) compared with *V. acanthurus* ($0.11 \text{ mL g}^{-1} \text{ h}^{-1}$) at 35°C , whereas their maximal $\dot{V}O_2$ values are similar, at 2.27 and $2.25 \text{ mL g}^{-1} \text{ h}^{-1}$, respectively. The difference in standard $\dot{V}O_2$ and factorial scope might have an ecological basis. Pianka (1968) suggests that *V. eremius* is an active widely foraging goanna, with a large home range, compared with *V. acanthurus*, which is relatively sedentary (G. Thompson, personal observation). It might be expected that a widely foraging, active goanna would have a higher standard $\dot{V}O_2$ than a more sedentary one (Beck and Lowe 1994).

The difference between factorial scopes determined for *V. gouldii* in this study (9.6) compared with the value of 16.3 determined by Christian and Conley (1994) reflects a much higher standard $\dot{V}O_2$ value and slightly lower maximal $\dot{V}O_2$ value (when corrected for the mass differences) in our study. The higher factorial scope for *V. panoptes* measured in this study (12.6) compared with 10.5 determined by Christian and Conley (1994) reflects a slightly lower standard $\dot{V}O_2$ and a higher maximal $\dot{V}O_2$ measured by us. These differences in standard $\dot{V}O_2$ and maximal $\dot{V}O_2$ values and therefore the factorial scopes may be due to different research protocols used to measure either standard $\dot{V}O_2$ or maximal $\dot{V}O_2$ or may reflect seasonal or geographical variations in metabolism (Garland and Else 1987; Tsuji 1988; Christian and Conley 1994; Garland and Adolph 1994; Thompson and Withers 1994).

It is evident that the factorial scope measured here for small goannas far exceeds that reported for other lizards (Cragg 1978; Bennett 1982, 1983; Al-Sadoon 1986a) and is similar to the very high value of 27.7 reported for *V. gilleni* (Bickler and Anderson 1986). The physiological basis for this exceptionally high aerobic scope of small goannas is not known and is worthy of further investigation. However, a number of studies provide an indication of anatomical and physiological differences between goannas and other lizards that could contribute to their high aerobic capacity (Moberly 1968; Webb et al. 1971; Millard and Johansen 1974; Gleeson et al. 1980; Burggren and Johansen 1982; Johansen and Burggren 1984; Ishimatsu et al. 1988; Hopkins et al. 1995). The cardiopulmonary system's capacity to deliver oxygen to working muscles could, along with a number of other organs and biochemical processes, act as a limiting factor to maximal $\dot{V}O_2$ and determine factorial scope. From the information available, it is evident that the cardiopulmonary system and lung structure of goannas is superior to that found in other squamates in the delivery of oxygen to muscle mitochondria (Bartholomew and Tucker 1964; Bartholomew et al. 1965; Moberly 1968; Webb et al. 1971; Bennett 1972; Millard and Johansen 1974; Wood et al. 1977b; Gleeson et al. 1980; Burg-

gren and Johansen 1982; Johansen and Burggren 1984; Ishimatsu et al. 1988; Perry 1989; Hopkins et al. 1995).

Bennett and Ruben (1979) and Pough (1979) suggested that thermoregulatory considerations are inadequate by themselves to account for the evolution of endothermy. They suggested that a large metabolic response to exercise might have evolved into a capacity to produce thermally significant endogenous heat at rest. It is also presumed that a high level of sustained activity metabolism requires an elevated resting metabolic rate (Taigen 1983). Therefore, an important consideration in this hypothesis for the evolution of endothermy is a link between elevated activity and resting metabolic rates. Bennett and Ruben (1979) suggested that the factorial scope of vertebrates was surprisingly constant and provided evidence that resting metabolism and maximal $\dot{V}O_2$ are linked. However, there was no significant intraspecific correlation between the residuals of standard $\dot{V}O_2$ and the residuals of maximal $\dot{V}O_2$ values when regressed with body mass for the eight individual *V. eremius* measured in this study ($r = -0.014$, $P = 0.49$), and there was no relationship between the residuals of mean standard $\dot{V}O_2$ and the residuals of mean maximal $\dot{V}O_2$ for the nine species of goanna ($r = 0.044$, $P = 0.45$). Therefore, the intraspecific data for *V. eremius* and the interspecific data for all goannas do not support the basic assumption of Bennett and Ruben (1979) and Pough (1979) of a constant factorial scope. Hayes and Garland (1995) report that the available intraspecific data for terrestrial vertebrates support a positive phenotypic correlation between resting and maximal $\dot{V}O_2$, whereas their analyses provide mixed results for a positive interspecific phenotypic correlation.

Phylogenetic and Ecological Correlates with $\dot{V}O_2$

Both phylogeny and ecology might be expected to influence standard $\dot{V}O_2$ and maximal $\dot{V}O_2$. For example, Andrews and Pough (1985) report a significant variation among eight families of squamates in standard $\dot{V}O_2$ values, although an a posteriori Tukey test showed no difference between Varanidae, the family with the highest mean standard $\dot{V}O_2$, and Boidae, the family with the lowest mean standard $\dot{V}O_2$. However, there is a significant difference in standard $\dot{V}O_2$ between four ecological groups: day-active predators, herbivores, reclusive predators, and fossorial predators. In contrast, Chappell and Ellis (1987) report a phylogenetic difference in resting metabolic rates for snakes, with pythons having a significantly higher resting $\dot{V}O_2$ than boas. They also found significant differences in resting $\dot{V}O_2$ among the seven genera of pythons and the 10 genera of boas when the snakes were grouped according to the ecological categories; fossorial, arboreal, semiaquatic, and terrestrial groups. Beck and Lowe (1994) report that the sedentary and carnivorous lizards *Heloderma horridum* and *H. suspectum* have a lower standard metabolic rate than the widely foraging *Varanus*. In lizards, species with reclusive, fossorial, or restricted foraging movement habits generally have a low standard $\dot{V}O_2$ (Mautz 1979; Putnam and Murphy 1982; Beck and Lowe 1994).

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