

# Metabolic rate and endurance capacity in Australian varanid lizards (Squamata; Varanidae; *Varanus*)

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In ecomorphological and ecophysiological studies, locomotor performance is often considered to be an intermediate step between the form of an organism and its environment. We examined this premise by measuring morphology, physiology and circular track endurance in the closely related group of Australian varanid lizards. Body size, body mass and relative body proportions were poor indicators of endurance. Body mass was not correlated with endurance and size-free lower forelimb length had only a weak relationship with endurance. Instead, maximal metabolic rate was positively correlated with endurance capacity in varanids. A comparison of varanids with other groups of lizards supported this result as varanids showed both elevated maximal metabolic rate and elevated endurance scores when compared with similar sized non-varanid lizards. There was support for a strong association between endurance with foraging mode and climate. Varanid species with higher endurance tended to be widely foraging and from xeric climates, while sit-and-wait and mesic species showed reduced endurance. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **97**, 664–676.

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## INTRODUCTION

Ecomorphological and ecophysiological analyses often seek to link an organism's structure and function to relevant aspects of the environment (Losos, 1990a, b; Miles, 1994; Bauwens *et al.*, 1995; Thompson & Withers, 2005; Thompson *et al.*, 2008; McElroy & Reilly, 2009). Arnold (1983) presented a paradigm proposing that differences in design were linked to differences in fitness through ecologically relevant performance traits. The suggestion was that differences in design would be functional and would translate into differences in the ability to undertake ecologically relevant tasks. This paradigm has been expanded to interspecific studies (Emerson & Arnold, 1989; Garland & Losos, 1994). Rather than testing the link between performance and fitness among individuals in a population, the relationship between performance and ecological traits (such as habitat) among

species is tested. Locomotor ability is a common example of a performance variable that may be related to habitat. The faster speed and greater endurance might be beneficial in certain environments.

The relationship between endurance with morphology, physiology and habitat has received less attention than other locomotory traits (for example, sprint speed), despite its potential ecological significance (Garland & Losos, 1994). Of the studies that have examined endurance, the results are varied. Some have reported that endurance generally increases with body mass (Garland, 1984; Autumn, Weinstein & Full, 1994; Garland, 1994), giving rise to the 'bigger is better' hypothesis (Bennett, 1987, 1990). Using 57 species of lizards, ranging in mass from 1.8 to 2885 g, Garland (1994) reported a positive correlation between body mass and endurance for both non-phylogenetically corrected and phylogenetically corrected data. A more recent study suggested a weaker relationship: for 12 species of lacertid lizards, endurance was not correlated with body mass, body size or other body dimensions, over a much smaller size

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range of 2.79–50.12 g (Vanhooydonck, VanDamme & Aerts, 2001).

The relationship between endurance and morphological variables other than body size has been infrequently examined. At the intraspecific level, residual hindlimb length was not related to endurance for *Sceloporus merriami* (Huey *et al.*, 1990); however, there was a significant correlation between treadmill endurance and residual tail length for hatchling *Sceloporus occidentalis* (Tsuji *et al.*, 1989). Further, when residuals were used to remove the effect of size, heart and thigh muscle mass were positively correlated with endurance in *Ctenophorus (Amphibolurus) nuchalis* (Garland, 1984; Garland & Else, 1987).

As endurance is largely thought to be an aerobic process, some studies have focused on the relationships between endurance and aerobic metabolism. Garland (1984) reported a positive relationship between maximal metabolic rate ( $VO_2$  max) and endurance for the iguanid lizard *Ctenosaura similis*. Garland & Else (1987) noted a similar result for the agamid lizard *Ctenophorus nuchalis*. Further, changes in endurance of the iguanid lizard, *Dipsosaurus dorsalis*, were found to parallel seasonal changes in  $VO_2$  max (John-Alder, 1984).

However, few studies have described both morphological and physiological variation with endurance across numerous closely related taxa. Varanidae is an ancient group of 'snake-like' lizards, often referred to collectively as monitors or goannas. They can differ in body size by almost four orders of magnitude (Pianka, 1995). Substantial variation in body shape, posture and locomotor ability among varanid species has also been previously reported (Thompson & Withers, 1997a; Thompson *et al.*, 2008; Clemente, Thompson & Withers, 2009; Schuett, Reiserer & Earley, 2009). Further, varanids appear to have a higher  $VO_2$  max than other lizards. The earliest work, by Bartholomew & Tucker (1964) showed that *Varanus gouldii* and *V. varius* had a higher  $VO_2$  max than 'typical' lizards. Since then, several studies have confirmed a higher  $VO_2$  max for varanids compared with other lizards, with the exception of two aquatic species *V. mertensi* and *V. salvator* (Gleeson, Mitchell & Bennett, 1980; Mitchell, Gleeson & Bennett, 1981; Bickler & Anderson, 1986; Christian & Conley, 1994; Thompson & Withers, 1997b).

Large differences in size, shape and a heightened metabolic rate make Varanidae an ideal group to examine the effect these morphological and physiological variables have on endurance and, in turn, any affect that endurance has on the fitness within different habitats. Our objective was to examine possible relationships with endurance, which we believe is an ecologically relevant performance trait for many

widely foraging varanids, with their morphology, metabolism and habitat traits.

## MATERIAL AND METHODS

### ANIMALS AND SAMPLE COLLECTION

One hundred and seven lizards from 18 species of Australian varanids were used in the analysis. All specimens used in the study were wild caught. Individuals that were sick, injured or obviously malnourished were not included. Juveniles were not included as they tended to show higher than expected endurance scores (Clemente, Withers & Thompson, 2008). Because of uncertainty in determining sex, both males and females were treated together.

### PHYLOGENY

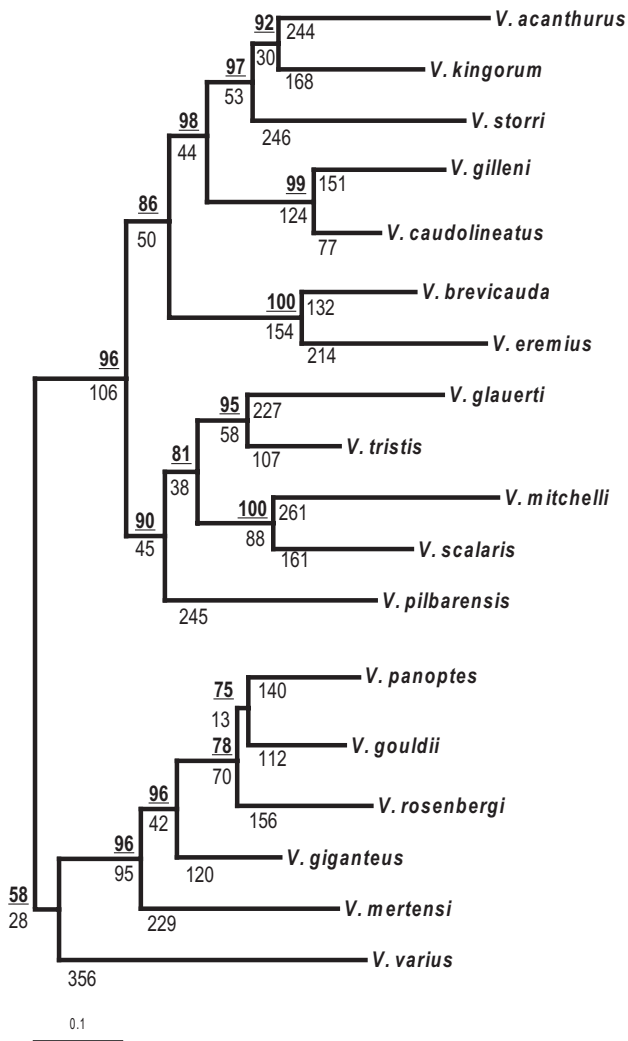
Phylogeny and environment both affect species variation. Interspecific comparisons are most commonly used to examine species adaptation to their environment (Harvey & Purvis, 1991). However, closely related species may be more similar. To characterize and account for this, we used a maximum likelihood tree of 18 species of *Varanus* based on 1038 base pairs of the NADH2-gene from Clemente (2006; Fig. 1).

An index 'k' was computed to quantify the strength of the phylogenetic signal (Blomberg, Garland & Ives, 2003). Here, the strength of the phylogenetic signal was described based on a comparison with analytical expectations using the tree structure (topology and branch lengths) and assuming Brownian motion character evolution. Blomberg *et al.* (2003) reported that *k* values do not vary systematically with tree size, but do vary with traits. Therefore, it can be used to compare the strength of phylogenetic signals from different traits and from different trees.

Two methods were used in this study to remove the effects of phylogenetic inertia; independent contrasts (Felsenstein, 1985) and autocorrelation (Cheverud & Dow, 1985; Rohlf, 2001). To calculate these, custom written visual basic programs were used (Philip Withers, University of Western Australia), based on the methods published in Garland, Harvey & Ives (1992), Blomberg *et al.* (2003) and Rohlf (2001). For size-free and phylogenetically corrected analyses, size was removed before phylogeny following Thompson & Withers (2005).

### MORPHOLOGY

Various morphological dimensions were measured for each lizard as shown in Figure 2: tail length (TAIL), head-neck length (HN), thorax-abdomen length (TA), upper fore-limb length (UFL), lower forelimb length (LFL), forefoot length (FFOOT), upper hindlimb



**Figure 1.** Phylogenetic relationships between 18 species of *Varanus* used in this study, based on 1038 base pairs from the NADH2-gene, showing the maximum likelihood hypothesis from Clemente (2006). Bootstrap values > 50% (percentages of 100 pseudoreplicates) are underlined and shown above branches, branch lengths are shown below the branches (substitution/site  $\times$  1000).

length (UHL), lower hindlimb length (LHL) and hind-foot length (HFOOT). Snout-to-vent length (SVL) is  $HN + TA$ . All measurements were made using digital calipers ( $\pm 0.05$  mm), with the exception of TAIL of large lizards ( $> 300$  mm SVL) for which a ruler was used ( $\pm 1$  mm). Each lizard was weighed using either a 5-kg spring balance for large varanids ( $> 2000$  g  $\pm 25$  g), kitchen scales for medium-sized varanids ( $< 2000$  g,  $> 1000$  g  $\pm 0.5$  g) or laboratory scales for small varanids ( $< 1000$  g  $\pm 0.05$  g). Each lizard was measured and weighed within 2 weeks of capture.

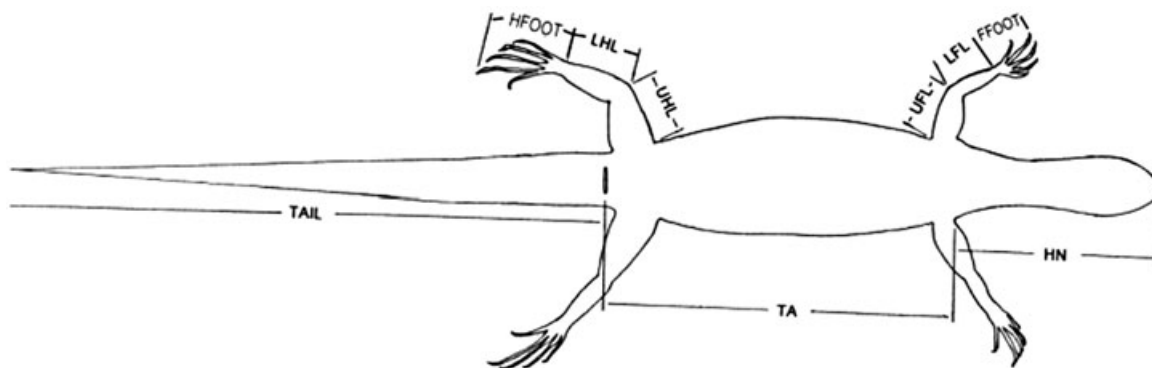
To test the effects of size on performance or habitat variables, both SVL and mass of an animal were used. In each case, both size and the characteristic were log-transformed. Somers' (1986) size-free analysis was used to obtain morphometric values that were independent of size. To perform this analysis, a custom-written visual basic program (Philip Withers, University of Western Australia) was used. This program was directly adapted from a BASIC program written by Somers (1986) based on the program PCAR in Orloci (1978). This process involves a principal component analysis size-constrained method, which extracts 'size' as the first component.

#### PHYSIOLOGY

Metabolic rates were recorded using a flow-through respirometry system based on methods used previously in Thompson & Withers (1997b) and Christian & Conley (1994).

Standard metabolic rates ( $VO_2$  std) were measured for eight species at both 25 and 35 °C, for which  $VO_2$  std was not available from the literature. Each lizard was weighed before being placed in an opaque plastic cylinder. Cylinder size varied according to the mass of the lizard, such that it restricted but did not prevent voluntary movement. The cylinders were placed in a controlled temperature chamber at 25 or 35 °C. Compressed ambient air flowed through the chamber at varying controlled flow rates (Brooks mass-flow controller) so that the excurrent  $O_2$  content was between 20.0 and 20.7%. For lizards  $< 50$  g, a flow rate of 50 mL  $min^{-1}$  was used; for lizards  $> 50$  but  $< 1000$  g, a flow rate of 100 mL  $min^{-1}$  was used; lizards weighing more than 1000 g had a flow rate of 500 mL  $min^{-1}$ . A Drierite column dried the excurrent air before it entered a paramagnetic  $O_2$  analyser (Servomex 184A). A Thurlby digital voltmeter with an RS232 interface recorded the differential output of the  $O_2$  analyser. The minimum (i.e. standard)  $VO_2$  was calculated as the average of the lowest continuous period of  $O_2$  consumption.

Maximal metabolic rate ( $VO_2$  max) was measured for individuals from nine species, using a flow-through respirometry system. Lizards were weighed before each trial. Body temperatures were measured cloacally to ensure that body temperature was at 35 °C ( $\pm 1.0$ ). Each experiment was conducted in a constant temperature room at 35 °C. A vacuum drew ambient air through a lightweight, transparent acetate mask placed over the lizard's head and approximately half the neck. A controlled air flow rate (Brooks mass-flow controller) was maintained at 500 mL  $min^{-1}$ . Excurrent air was dried in a Drierite column before passing through a paramagnetic  $O_2$  analyser (Servomex 184A). The output of the  $O_2$



**Figure 2.** Morphological measurements taken from Varanid specimens. Modified from Thompson & Withers (1997a). FFOOT, forefoot length; HFOOT, hindfoot length; HN, head-neck length; LFL, lower forelimb length; LHL, lower hindlimb length; TA, thorax-abdomen length; TAIL, tail length; UFL, upper fore-limb length; UHL, upper hindlimb length.

analyser was connected to a Promax XT microcomputer with Analog Device RT1800 A/D interface board or a Thurlby digital voltmeter connected with a RS232 interface. Data were collected every 3 s.

Lizards were first placed on a stationary treadmill and the mask fitted over the head and attached in place using Leucoplast surgical tape. The treadmill was then started and the belt speed increased to the maximum rate that each lizard could sustain for the duration of the experiment (typically  $1.0 \text{ km h}^{-1}$ ). Lizards that would not run spontaneously were encouraged to do so with gentle tapping on the tail.  $\text{VO}_2$  max was achieved when further exercise or higher speeds did not produce an increase in oxygen consumption, often within 5 min of the lizard commencing to run on the treadmill. A mean value of  $\text{VO}_2$  max was calculated from the longest continuous period of maximal oxygen consumption.

To analyse standard and maximal metabolic traces, a custom-written VB program (Philip Withers, University of Western Australia) was used. This program calculated the oxygen consumption based on the equations and procedures presented in Withers (1977). Least-squares regression was used to calculate the slopes. Results are presented in the form;  $\text{VO}_2$  ( $\text{mL h}^{-1}$ ) =  $a \text{ Mass}^b$ , where 'a' is the inverse log of the intercept and 'b' is the slope of the log-log relationship between  $\text{VO}_2$  and mass.

#### ENDURANCE

Two measures of endurance were recorded: maximum distance run at exhaustion (MAXDIS) and maximum time to exhaustion (ENDUR). Both measures were recorded simultaneously by encouraging lizards to run around a circular racetrack. The racetrack was 12.3 m in length, 0.8 m in width

and the sides were 1 m in height. Time elapsed since the beginning of each trial was measured using a stopwatch and recorded once the lizard was deemed to be exhausted. The point of exhaustion for each lizard was when the animal ceased to respond to repeated tapping on the hindlimbs or base of tail. This stimulus was found to induce escape behaviour in 'fresh' lizards and partially exhausted lizards. Once a lizard received ten taps in quick succession and failed to move forward, it was deemed to be 'exhausted'.

Previous experiments have used treadmill endurance to estimate endurance in lizards. However, there are several problems with this technique in addition to keeping large varanids on a treadmill for an extended period of time. Studies often use a treadmill running at a single speed, e.g.  $1.0 \text{ km h}^{-1}$  (Garland, 1994). Using a single speed is problematic when comparing lizards over a large size range as the maximum aerobic speed a lizard is capable of maintaining is likely to increase with size, as larger lizards need only take fewer steps to cover a similar distance as smaller-sized lizards. This may have the effect of causing a false-positive relationship between endurance and size as larger lizards maybe running at a speed much below their aerobic maximum and can therefore run further, while smaller lizards are running at a speed at or above their aerobic maximum and therefore may show reduced endurance as a result of anaerobic respiration. Circular racetrack endurance avoids this problem by running each lizard at its typical escape speed and may therefore provide an ecologically relevant measure of endurance. However, it should be noted that, as the speed of the lizard was not controlled, this measure of endurance may be the result of both aerobic and anaerobic metabolism and, as such, may not be com-

parable with treadmill endurance. Endurance speeds for each species was calculated by dividing MAXDIS by ENDUR for each individual and calculating species means.

#### ECOLOGICAL CHARACTERISTICS

Each species was classified based on six different ecological traits: habitat type, retreat site, foraging mode, climbing ability, climate and openness of its typical habitat. These data are summarized in Table 1. Habitat was based on categories reported in Thompson & Withers (1997a). Retreat sites were taken from Thompson *et al.* (2008). Foraging modes, climbing ability and climate were based on an extensive literature review of each species published in Clemente (2006). Foraging mode was inferred from the literature based on information concerning movement and activity. Species were classified as either sit-and-wait or widely foraging predators. Although this is generally considered to be a continuum (Perry, 1999), species were classified based on the foraging mode that best represented their activity. Climbing ability simply separated species that climb often, either while foraging or moving to a retreat site, from species that rarely climb. The climate where each species most commonly occurs was also recorded as xeric, mesic or tropical. Where species were found in multiple climatic zones, the one which represented where most of the individuals were collected from was

chosen. The 'openness' of habitat was classified for each species as either 'closed', meaning the species was rarely seen in the open, 'semi-open', meaning the species was occasionally encountered in the open, or 'open', where the species was often encountered in open areas with little cover.

#### RESULTS

Means for  $VO_2$  max and  $VO_2$  std of 18 species of varanid are shown in Tables 2 and 3, respectively.  $VO_2$  std ( $mLO_2 h^{-1}$ ) for 16 species at 25 °C scaled as  $0.12 M^{0.88}$  ( $r^2 = 0.98$ ,  $F_{15} = 625.42$ ,  $P < 0.001$ ), while at 35 °C  $VO_2$  std for 17 species scaled as  $0.31 M^{0.86}$  ( $r^2 = 0.96$ ,  $F_{16} = 515.01$ ,  $P < 0.001$ ). The interspecific mass exponent using the  $VO_2$  max values for 17 species was  $5.63 M^{0.74}$  ( $r^2 = 0.94$ ,  $F_{16} = 213.00$ ,  $P < 0.001$ ).

Residuals from a log–log plot of metabolic rate ( $mLO_2 h^{-1}$ ) with mass, were not significantly related to phylogeny for  $VO_2$  max ( $k = 0.55$ ,  $P = 0.50$ ),  $VO_2$  std at 25 °C ( $k = 0.52$ ,  $P = 0.23$ ) or  $VO_2$  std at 35 °C ( $k = 0.82$ ,  $P = 0.07$ ).

#### ENDURANCE

Species means for endurance are presented in Table 4. Generally, species that ran further ran for a longer period ( $r^2 = 0.53$ ,  $P = 0.001$ ). The mean circular

**Table 1.** Summary of the habitat characteristics of 18 species of Australian varanids

Species	Habitat (Thompson & Withers, 1997a)	Retreat type (Thompson <i>et al.</i> , 2008)	Foraging strategy	Climbing ability	Openness	Climate
<i>V. acanthurus</i>	Sedentary terrestrial	Spaces in rocks and trees	SW	NC	Closed	Xeric
<i>V. brevicauda</i>	Sedentary terrestrial	Burrows	SW	NC	Closed	Xeric
<i>V. caudolineatus</i>	Arboreal/rock	Spaces in rocks and trees	WF	Climber	Closed	Xeric
<i>V. eremius</i>	WF terrestrial	Burrows	WF	NC	Open	Xeric
<i>V. giganteus</i>	WF terrestrial	Burrows	WF	NC	Open	Xeric
<i>V. gilleni</i>	Arboreal/rock	Spaces in rocks and trees	WF	Climber	Closed	Xeric
<i>V. glauerti</i>	Arboreal/rock	Oblique rock crevices	WF	Climber	Semi-open	Tropical
<i>V. gouldii</i>	WF terrestrial	Burrows	WF	NC	Open	Xeric
<i>V. kingorum</i>	Sedentary terrestrial	Spaces in rocks and trees	SW	Climber	Closed	Tropical
<i>V. mertensi</i>	Aquatic	Burrows	WF	Climber	Semi-open	Tropical
<i>V. mitchelli</i>	Aquatic	Spaces in rocks and trees	SW	Climber	Closed	Tropical
<i>V. pilbarensis</i>	Arboreal/rock	Oblique rock crevices	WF	Climber	Semi-open	Xeric
<i>V. panoptes</i>	WF terrestrial	Burrows	WF	NC	Open	Tropical
<i>V. rosenbergi</i>	WF terrestrial	Burrows	WF	NC	Semi-open	Mesic
<i>V. scalaris</i>	Arboreal/rock	Spaces in rocks and trees	WF	Climber	Semi-open	Tropical
<i>V. storri</i>	Sedentary terrestrial	Burrows	SW	NC	Closed	Tropical
<i>V. tristis</i>	Arboreal/rock	Spaces in rocks and trees	SW	Climber	Semi-open	Xeric
<i>V. varius</i>	Arboreal/rock	Spaces in rocks and trees	WF	Climber	Semi-open	Mesic

NC, non-climbing; SW, sit-and-wait predator; WF, widely foraging predator.

**Table 2.** Maximal metabolic rates for Australian varanids

Species	<i>N</i>	Mass (g)	VO <sub>2</sub> max 35 °C mL O <sub>2</sub> h <sup>-1</sup>	Study
<i>V. acanthurus</i>	10	73.61 ± 6.25	170.00 ± 19.70	B
<i>V. brevicauda</i>	9	17.48 ± 1.31	56.40 ± 4.44	B
<i>V. caudolineatus</i>	14	14.95 ± 0.78	94.00 ± 6.20	B
<i>V. eremius</i>	8	39.97 ± 6.76	91.90 ± 17.00	B
<i>V. gilleni</i>	6	21.14	106.80	B
<i>V. glauerti</i>	5	34.19 ± 17.65	56.50 ± 23.90	A
<i>V. gouldii</i>	9	402.89 ± 80.68	313.83 ± 44.72	A
<i>V. kingorum</i>	4	17.81 ± 3.13	33.70 ± 6.98	A
<i>V. mertensi</i>	7	904.00	822.00	C
<i>V. mitchelli</i>	1	184.00	177.93	A
<i>V. panoptes</i>	6	2240.00 ± 583.00	2364.00 ± 494.00	B
<i>V. pilbarensis</i>	5	30.35 ± 10.36	54.08 ± 18.64	A
<i>V. rosenbergi</i>	5	1503.00 ± 239.00	1860.00 ± 321.00	B
<i>V. scalaris</i>	2	98.35 ± 17.65	124.62 ± 39.40	A
<i>V. storri</i>	6	24.00 ± 3.26	47.20 ± 7.00	A
<i>V. tristis</i>	4	71.64 ± 28.63	105.80 ± 27.07	A
<i>V. varius</i>	2	6800.00 ± 1100.00	4384.95 ± 1255.65	A

Values are mean ± standard error, with the sample size *N*.

A, this study; B, Thompson & Withers (1997b); C, Christian & Conley (1994).

**Table 3.** Standard metabolic rates for Australian varanids

Species	<i>N</i>	Mass (g)	VO <sub>2</sub> std 25 °C		VO <sub>2</sub> std 35 °C		Study
			<i>N</i>	Mass (g)	<i>N</i>	Mass (g)	
<i>V. acanthurus</i>	9	53.10 ± 8.31	2.80 ± 0.46	9	53.40 ± 8.50	6.24 ± 1.35	B
<i>V. brevicauda</i>	10	16.70 ± 1.12	1.12 ± 0.12	11	17.40 ± 0.94	2.71 ± 0.25	B
<i>V. caudolineatus</i>	31	13.10 ± 0.64	0.92 ± 0.03	27	13.10 ± 0.86	2.26 ± 0.14	B
<i>V. eremius</i>	14	36.40 ± 5.01	2.38 ± 0.32	14	35.90 ± 5.07	6.16 ± 0.91	B
<i>V. giganteus</i>	6	2499.00 ± 774.00	91.00 ± 27.00	6	2502.00 ± 782.00	237.00 ± 78.20	B
<i>V. gilleni</i>	6	20.00	1.92	6	20.00	3.58	B
<i>V. glauerti</i>	5	33.84 ± 17.75	3.40 ± 0.86	5	33.84 ± 17.75	12.59 ± 4.21	A
<i>V. gouldii</i>	8	420.75 ± 98.74	35.70 ± 12.45	7	443.86 ± 108.64	83.42 ± 24.43	A
<i>V. kingorum</i>	6	20.86 ± 2.61	2.06 ± 0.38	6	19.81 ± 2.47	3.37 ± 0.54	A
<i>V. mertensi</i>				7	904.00	72.00	C
<i>V. mitchelli</i>	1	189.00	17.58	1	184.00	32.94	A
<i>V. panoptes</i>	5	1896.00 ± 562.00	66.00 ± 15.60	12	1622.00 ± 313.00	179.00 ± 33.90	B
<i>V. rosenbergi</i>	7	2081.00 ± 313.00	90.00 ± 13.10	7	2074.00 ± 312.00	284.00 ± 43.00	B
<i>V. scalaris</i>	4	81.63 ± 7.02	7.47 ± 2.46	3	88.33 ± 13.54	19.33 ± 5.86	A
<i>V. storri</i>	5	26.90 ± 3.13	2.64 ± 0.35	6	27.63 ± 2.76	5.65 ± 0.65	A
<i>V. tristis</i>	5	76.81 ± 24.22	7.44 ± 1.10	4	56.42 ± 13.16	13.94 ± 2.05	A
<i>V. varius</i>	2	6800.00 ± 1100.00	398.75 ± 11.65	2	6800.00 ± 1100.00	492.20 ± 13.40	A

Values are mean ± standard error, with the sample size *N*.

A, this study; B, Thompson & Withers (1997b); C, Christian & Conley (1994).

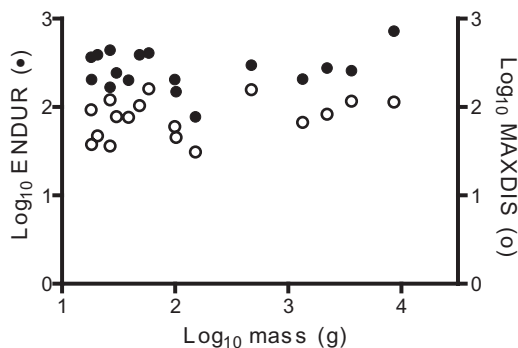
racetrack endurance speed for all varanid species was 1.17 km h<sup>-1</sup> (SE = 0.107, *N* = 17, Table 4). Endurance speed was not significantly related to size, either intraspecifically or interspecifically (i.e. interspecific relationship to mass  $F_{1,16} = 0.9664$ ,  $P = 0.341$ ). Nor was endurance speed (nor residuals from size of endurance speed) related to VO<sub>2</sub> max or VO<sub>2</sub> std.

The two measures of endurance differed in their relationship to phylogeny. MAXDIST was largely independent of phylogeny ( $k = 0.57$ ,  $P = 0.425$ ), whereas ENDUR had a significant phylogenetic signal ( $k = 0.93$ ,  $P = 0.019$ ).

Morphology (SVL, mass or size-free body dimensions) was a poor indicator of endurance. Neither SVL

**Table 4.** Species mean ( $\pm$ standard error) snout-to-vent length (SVL), mass and endurance parameters maximum distance run (MAXDIS), endurance time (ENDUR) and endurance speed (end speed) for Australian varanids

Species	<i>N</i>	SVL (mm)	Mass (g)	MAXDIS (m)	ENDUR (s)	End speed (km h <sup>-1</sup> )
<i>V. acanthurus</i>	4	131.8 $\pm$ 10.91	58.5 $\pm$ 18.39	160.7 $\pm$ 55.76	407.7 $\pm$ 176.11	1.57 $\pm$ 0.94
<i>V. brevicauda</i>	2	106.2 $\pm$ 0.75	20.6 $\pm$ 1.95	47.3 $\pm$ 0.50	389.5 $\pm$ 77.50	0.46 $\pm$ 0.10
<i>V. caudolineatus</i>	5	105.7 $\pm$ 6.36	18.1 $\pm$ 2.51	93.3 $\pm$ 15.93	366.0 $\pm$ 83.66	0.97 $\pm$ 0.10
<i>V. eremius</i>	4	155.8 $\pm$ 4.18	48.5 $\pm$ 3.91	103.8 $\pm$ 5.60	389.2 $\pm$ 61.62	1.07 $\pm$ 0.24
<i>V. giganteus</i>	2	719.0 $\pm$ 101.00	3625 $\pm$ 1575.00	116.5 $\pm$ 47.25	257.5 $\pm$ 22.50	1.58 $\pm$ 0.52
<i>V. gilleni</i>	12	133.0 $\pm$ 7.21	26.6 $\pm$ 2.20	120.3 $\pm$ 13.25	441.0 $\pm$ 56.33	0.97 $\pm$ 0.13
<i>V. glauerti</i>	4	144.8 $\pm$ 21.50	38.8 $\pm$ 22.00	76.6 $\pm$ 36.47	201.0 $\pm$ 97.90	1.36 $\pm$ 0.23
<i>V. gouldii</i>	14	310.1 $\pm$ 12.40	472.9 $\pm$ 64.36	156.9 $\pm$ 19.61	298.4 $\pm$ 56.36	2.28 $\pm$ 0.21
<i>V. kingorum</i>	7	98.2 $\pm$ 3.92	18.3 $\pm$ 2.70	37.7 $\pm$ 10.81	205.1 $\pm$ 54.27	0.73 $\pm$ 0.12
<i>V. mertensi</i>	8	439.1 $\pm$ 32.94	1342.8 $\pm$ 319.34	67.2 $\pm$ 13.30	207.2 $\pm$ 49.20	1.48 $\pm$ 0.39
<i>V. mitchelli</i>	7	232.7 $\pm$ 17.14	151.3 $\pm$ 36.69	30.9 $\pm$ 3.77	77.4 $\pm$ 7.53	1.43 $\pm$ 0.12
<i>V. panoptes</i>	10	498.1 $\pm$ 35.64	2208 $\pm$ 491.44	82.7 $\pm$ 9.57	276.2 $\pm$ 46.86	1.31 $\pm$ 0.19
<i>V. pilbarensis</i>	5	125.1 $\pm$ 12.06	30.3 $\pm$ 10.36	77.7 $\pm$ 7.25	243.4 $\pm$ 33.69	1.21 $\pm$ 0.14
<i>V. scalaris</i>	7	203.1 $\pm$ 5.21	102.1 $\pm$ 13.60	45.2 $\pm$ 4.28	149.3 $\pm$ 13.89	1.10 $\pm$ 0.07
<i>V. storri</i>	7	103.6 $\pm$ 2.86	26.6 $\pm$ 2.99	36.3 $\pm$ 5.50	167.4 $\pm$ 21.67	0.79 $\pm$ 0.08
<i>V. tristis</i>	7	190.2 $\pm$ 13.37	99.1 $\pm$ 27.24	60.1 $\pm$ 14.94	204.7 $\pm$ 50.59	1.11 $\pm$ 0.20
<i>V. varius</i>	2	655.0 $\pm$ 20.00	8625 $\pm$ 775.00	113.7 $\pm$ 50.52	724.0 $\pm$ 274.00	0.55 $\pm$ 0.04

**Figure 3.** Relationship between Log mass (g) and endurance parameters, time to exhaustion (ENDUR; s) and maximum distance to exhaustion (MAXDIS; m).

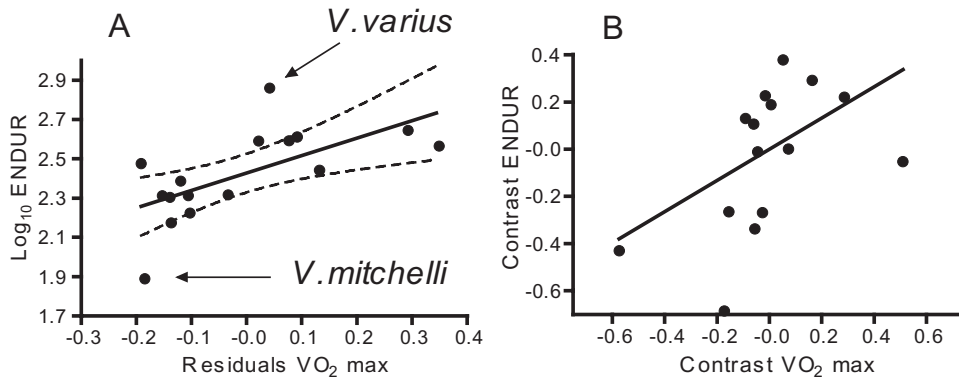
nor mass were significantly correlated with either endurance score using species averages (logENDUR vs. logMass  $r^2 = 0.54$ ,  $P = 0.539$ ; logMAXDIS vs. logMass  $r^2 = 0.11$ ,  $P = 0.201$ ; Fig. 3). The relationship between both size and mass with endurance remained non-significant when the effects of phylogeny were removed by regressing independent contrasts for size against independent contrasts of endurance. Body dimensions had little relationship to endurance. Size-free LFL had a marginally significant positive correlation with ENDUR ( $r^2 = 0.24$ ,  $P = 0.048$ ). This relationship was not significant when analysed in a phylogenetic context.

VO<sub>2</sub> max showed a stronger relationship with endurance than size or body dimensions. Residuals were used to remove the effect of mass from metabolic

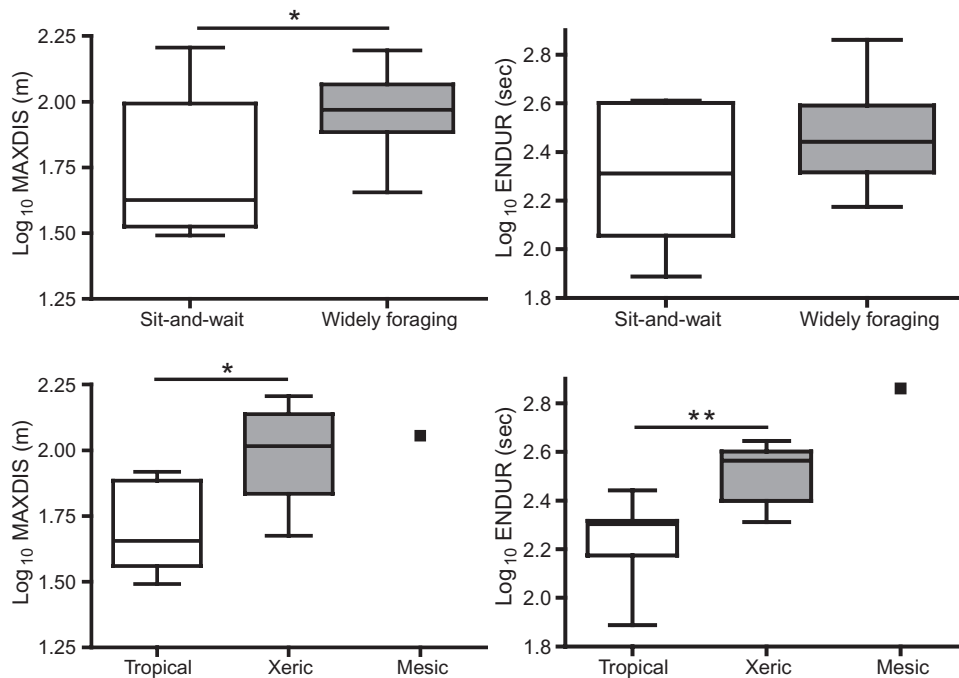
rates. As size was not correlated with endurance, the relationship with residual VO<sub>2</sub> max is with non size-corrected endurance scores (although a stronger relationship was obtained using residual endurance scores from mass). Residual VO<sub>2</sub> max was significantly and positively related to ENDUR ( $r^2 = 0.41$ ,  $P = 0.008$ ,  $N = 16$ ; Fig. 4A). This relationship suggests that species with relatively higher VO<sub>2</sub> max scores ran for longer than species with relatively lower VO<sub>2</sub> max scores. When independent contrasts for ENDUR were regressed against contrasts for VO<sub>2</sub> max, there was still a significant relationship between these variables ( $r^2 = 0.26$ ,  $P = 0.044$ ,  $N = 15$ ; Fig. 4B). Neither VO<sub>2</sub> std at 25 °C nor VO<sub>2</sub> std at 35 °C was correlated to endurance.

#### ENDURANCE AND ECOLOGY

Comparisons of endurance and ecology were significant for climate and foraging mode but not habitat type, retreat site, openness of habitat or climbing ability. Climate was related to both MAXDIS ( $F_{2,14} = 5.70$ ,  $P = 0.015$ ) and ENDUR ( $F_{2,14} = 11.91$ ,  $P = 0.001$ ; Fig. 5). When reassessed using size-corrected endurance scores, climate was still significantly related to endurance (MAXDIS  $F_{2,14} = 5.04$ ,  $P = 0.022$ ; ENDUR  $F_{2,14} = 6.21$ ,  $P = 0.012$ ). Generally, xeric varanids had greater endurance than tropical species. Mesic species had an even higher endurance, but this result should be interpreted with caution as there was only one mesic species (*V. varius*). When *V. varius* was removed from the analysis, a two-tailed Student's *t*-test confirmed that xeric species had



**Figure 4.** A, linear regression for residual  $\text{VO}_2$  max (from mass) and ENDUR showing 95% confidence intervals. B, independent contrasts for residual  $\text{VO}_2$  max and contrasts for ENDUR.



**Figure 5.** Maximum distance run (MAXDIS) and endurance time (ENDUR) with ecology for varanids. \* $P < 0.05$ , \*\* $P < 0.001$ . Boxes represent the median within the 25<sup>th</sup> and 75<sup>th</sup> percentiles. Whiskers represent the maximum and minimum values.

greater endurance than tropical species (MAXDIS  $t_{14} = 3.20$ ,  $P = 0.006$ ; ENDUR  $t_{14} = 3.73$ ,  $P = 0.002$ ).

Endurance data were then phylogenetically corrected using autocorrelation. When the effect of climate was reassessed using phylogenetically corrected endurance data, there was still a significant difference in endurance between climatic groups. After removing the single mesic species, a two-tailed  $t$ -test showed a significant difference between species from xeric and tropical climates

for phylogenetically corrected endurance scores (MAXDIS  $t_{14} = 2.15$ ,  $P = 0.049$ ; ENDUR  $t_{14} = 2.49$ ,  $P = 0.038$ ).

There was also a difference of MAXDIS with foraging strategy (Fig. 5). Widely foraging species ran further during endurance trials than sit-and-wait species ( $t_{15} = 2.51$ ,  $P = 0.024$ ). When MAXDIS scores were corrected for phylogenetic effects using autocorrelation and were analysed, widely foraging species still had significantly higher endurance than sit-and-



wait species ( $t_{15} = 2.68$ ,  $P = 0.012$ ). However, foraging mode was no longer related to endurance using size-corrected endurance scores (MAXDIS  $t_{15} = 1.39$ ,  $P = 0.184$ ).

## DISCUSSION

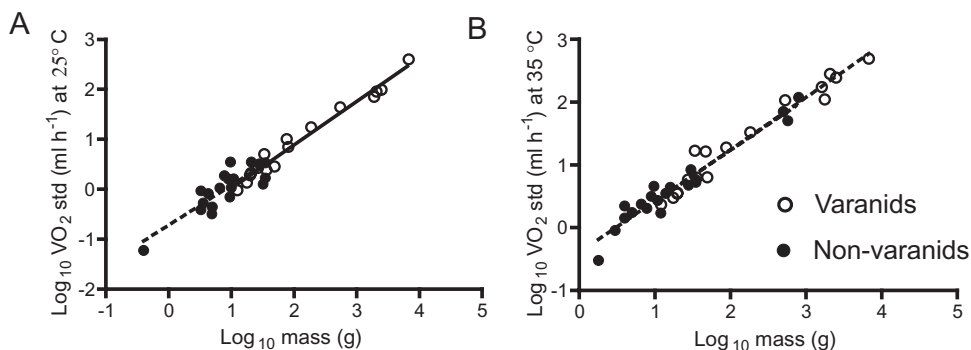
Both ecomorphological studies and ecophysiological studies can provide valuable insights into character trait evolution (Arnold, 1983; Irschick & Garland, 2001). The relationship between endurance and size is unclear for lizards. Within *Varanus* there was no relationship between mass or SVL with endurance, but interspecific relationships between mass and endurance have been previously reported for treadmill endurance by Garland (1994), even after the effects of body temperature and phylogeny had been removed. However, treadmill endurance scores may not be comparable with circular racetrack endurance scores (Garland, 1993), thus comparisons between the two experimental protocols may be difficult.

Garland (1993) provided a smaller data set for MAXDIS endurance scores of 10 species around a circular racetrack. When means were calculated for these species, there was no significant correlation between endurance and mass ( $r^2 = 0.04$ ,  $P = 0.565$ ), reflecting results obtained for varanids. Thus, for the two groups examined so far there appears to be no interspecific relationship between circular racetrack endurance and mass. This could be the result of low sample sizes for both Garland's (1993) data set ( $N = 10$ ) and varanids ( $N = 17$ ). Combining the data sets from both studies does result in a weak, but significant, positive correlation between endurance and mass ( $r^2 = 0.15$ ,  $P = 0.048$ ,  $N = 27$ ). However, a more robust interpretation cannot be made until these data can be analysed in a phylogenetic context, as it could reflect the generally higher MAXDIS and mass of varanids.

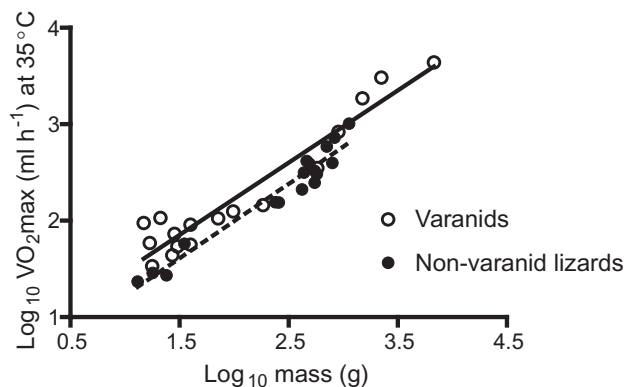
Relationships between body dimensions and endurance have received little investigation. Similar to previous studies (Tsuji *et al.*, 1989; Huey *et al.*, 1990), within varanids, size-free hindlimb length was not related to endurance, showing that, across all lizards studied, relative hindlimb length has little or no relationship with endurance. Relative tail length was also not correlated with endurance in varanids, in contrast to the previous findings for *Sceloporus* (Tsuji *et al.*, 1989).

Substantial variation in size, shape and ecology make varanids an ideal group for ecomorphological studies, but the large size variation also allows scaling comparisons to be made. Standard metabolic rates ( $VO_2$  std) across vertebrate species are generally thought to scale with a mass exponent of 0.75 (Heusner, 1982; Feldman & McMahon, 1983). However, squamates show a significantly higher mass exponent scaling as  $mass^{0.80}$  (Andrews & Pough, 1985), although the reasons for both scaling exponents are largely unknown. This study reports the interspecific mass exponent for  $VO_2$  std of 16 species ranging from 12.5 to 6800 g at 25 °C to be 0.88 ( $\pm 0.076$  95% CI), and for 17 species ranging from 12.2 to 6800 g at 35 °C to be 0.86 ( $\pm 0.081$  95% CI), confirming the higher mass exponent for squamates.

When the  $VO_2$  std of varanids are compared with non-varanid lizards reported in Andrews & Pough (1985), there was no significant difference between either the slope or the elevation at 25 or 35 °C (Fig. 6), supporting Bennett's (1972) suggestion that  $VO_2$  std of varanids does not differ from that of other lizards. However, there was a significant difference when maximal metabolic rates ( $VO_2$  max) are compared. Comparison of  $VO_2$  max of varanids with 17 other species of lizard cited by Bennett (1982) suggested that there was no significant difference in slope of the two regressions, but there was a significant difference in elevation ( $F_{1,32} = 15.7$ ,  $P < 0.001$ ). Varanids in this study tended to have a higher  $VO_2$



**Figure 6.** Standard metabolic rates of varanids (open circles – this study) and other non-varanid lizards (closed circles published in Andrews & Pough, 1985), at 25 °C (A) and at 35 °C (B).



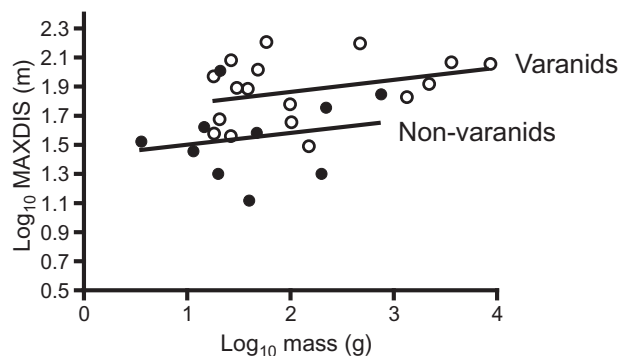
**Figure 7.** Relationship between maximal metabolic rate of varanids at 35 °C with other lizards published in Bennett (1982).

max than other lizards (Fig. 7). Higher  $\text{VO}_2$  max in varanids may have a significant positive effect on performance traits (e.g. endurance) when compared with other lizards.

Interspecific comparisons indicate a positive relationship between endurance and metabolism. The positive relationship between ENDUR and  $\text{VO}_2$  max supports previous findings (Garland, 1984, 1994) and suggests the ability to transport a greater volume of oxygen during peak activity has advantages for extending endurance.

Several reasons have been proposed for the higher aerobic capacity of varanids. Varanids can sustain higher levels of activity because their blood does not lose its capacity to transport oxygen during activity as quickly as that of other lizards (Bennett, 1973). Other features of varanid design may also contribute to their high  $\text{VO}_2$  max, many involving their respiratory system. For most lizards there is a trade-off between breathing and running, as the hypaxial muscles contribute to both functions (Carrier, 1987a, b, 1989, 1990). This means that, as speed of movement increases, ventilation and oxygen uptake decrease (Wang, Carrier & Hicks, 1997). Varanids partially overcome this trade-off using their 'gular pump'. The gular pump is the movement of the ventral section of the throat that forces air into the lungs rather than sucking air in by expanding the ribcage, as occurs in other lizards (Owerkowicz *et al.*, 1999). Therefore, varanids are able to effectively ventilate the lungs to match the increased metabolic rate during locomotion, at least at moderate speeds (Wang *et al.*, 1997).

The heart, lungs and skeletal muscles of varanids are also structured differently from other lizards. Varanids have a more complete ventricular septum, resulting in higher blood pressure and cardiac output (Millard & Johansen, 1974). The lungs allow more efficient gas exchange, through better mechanics and

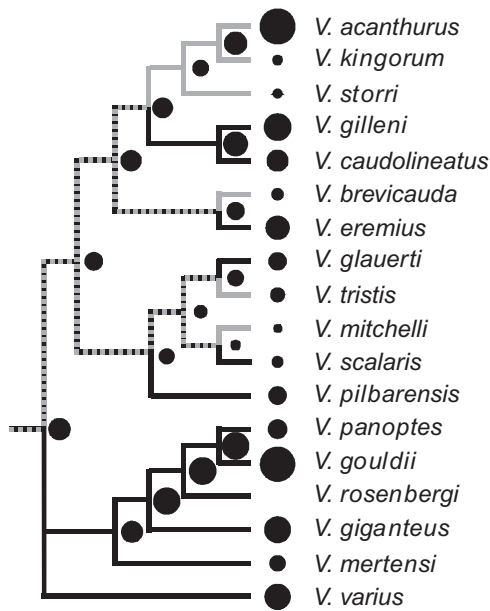


**Figure 8.** MAXDIS circular racetrack endurance scores for varanids compared with scores of Garland (1993) for 10 species of iguanids and teiids. Regression lines are shown. Neither slope was significantly different from 0.

architecture (Perry & Duncker, 1978), low diffusion limitation and good ventilation-perfusion (Mitchell *et al.*, 1981; Hopkins *et al.*, 1995). This is presumed to be advantageous for activity, as they can more effectively supply oxygen to their tissues during exercise (Burggren & Johansen, 1982; Regal, 1983; Garland, 1993). Further, the skeletal muscles of varanids have been shown to have higher levels of myoglobin than other lizards, which facilitates the rapid transfer of oxygen from the blood into the muscle fibres (Bennett, 1973). The higher  $\text{VO}_2$  max, gular pumping capacity and other morphological changes to the heart, lungs and skeletal muscles all suggest that varanids could maintain locomotion for a longer time than similar-sized non-varanids.

A comparison of the results from this study and those of Garland (1993) support this hypothesis. Varanids typically have equivalent or greater endurance than non-varanid lizards of similar size. While the slope for the relationship between MAXDIS and body mass for varanids and other lizards are similar, varanids appear to have a higher intercept (Fig. 8).

Some authors have observed the high locomotor endurance of varanids in the wild (Auffenberg, 1981; Phillips, 1995; King & Green, 1999). When endurance for varanids was compared with ecological characteristics there was a strong association. Endurance within varanids significantly differed with foraging mode, even after phylogenetic effects were removed. This suggests that endurance capacities of varanids have evolved in synchrony with foraging mode. This conclusion is appealing as it agrees with the intuitive relationship between these variables, such that widely foraging species that travel further each day would benefit from greater foraging success, and hence fitness, as a result of higher endurance. Sit-and-wait strategists would not be selected for high endurance.



**Figure 9.** Phylogenetic relationship for varanids used in this study with both endurance and foraging strategy mapped over. The size of the circles at tips indicates relative MAXDIS for each species (relative to the species with the largest MAXDIS), circles at nodes represent intermediate relative endurance based upon averaging the tips. Solid black line indicates predominately widely foraging species, solid grey line indicates predominately sit-and-wait species. Dashed line indicates ambiguous foraging strategy.

Garland (1999) recorded a similar result to this study, finding a significant relationship between treadmill endurance and both the percentage of time moving in the field and the daily distance moved. This largely supports the findings of this study and strengthens the concept of a relationship between endurance and foraging mode.

The co-evolution of endurance and foraging mode within Australian varanids is shown in Figure 9. The group at the base of the tree containing *V. gouldii* all show relatively high endurance and are widely foraging species, providing some evidence that the varanids which crossed over to Australia from Asia may have already been widely foraging varanids with high endurance. Supporting the link between endurance and foraging strategy, there are some examples where closely related species show a difference in foraging strategy and a corresponding difference in endurance capacity; for example, *V. brevicauda* and *V. eremius* and, to a lesser extent, *V. glauerti* and *V. tristis*. The group of spiny-tailed rock goanna at the top containing *V. storri* are typically sit-and-wait predators, which show low endurance scores. *Varanus acanthurus* is one obvious exception and the reason for this disparity is unknown.

There appears to be at least some size effect between endurance capacity and foraging mode in varanids. Widely foraging species tend to be much larger than sit-and-wait species [mass (g); widely foraging mean  $1273 \pm 584$ , sit-and-wait mean  $62 \pm 22$ ;  $t = 2.41$ ,  $P = 0.029$ ,  $N = 18$ ] and, although there is no significant relationship between size and endurance capacity interspecifically, removing the effects of size from endurance weakens the relationship between endurance capacity and foraging mode. This suggests that at least some of the relationship between foraging mode and endurance is because of the relationship of both of these variables to size.

The difference in endurance capacity with climate appears to be more robust. Xeric species have higher endurance than tropical species, even after correction for size and phylogeny. This has not been reported before and the reason for this difference is largely unknown. It may be a combination of climate-related foraging behaviours (xeric species may tend to be widely foraging) or it may reflect differences in behavioural motivation between the lizards from climatic regions. For example, xeric species may show greater flight response, while tropical species show a greater fight response.

Studies attempting to resolve the relationship between performance and ecology often suffer from a lack of quantitative data on variables such as habitat use and foraging mode. This study acknowledges this limitation but has shown how even a simple classification of a taxa's ecology may produce useful insights into the relationship between performance and ecology and provide directions for further research.

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#### REFERENCES

- Andrews R, Pough F. 1985. Metabolism of squamate reptiles: allometric and ecological relationships. *Physiological Zoology* **58**: 214–231.

- Arnold SJ. 1983.** Morphology, performance and fitness. *Integrative and Comparative Biology* **23**: 347–361.
- Auffenberg W. 1981.** *The behavioral ecology of the komodo monitor*. Gainesville: University Presses of Florida.
- Autumn K, Weinstein RB, Full RJ. 1994.** Low cost of locomotion increases performance at low temperature in a nocturnal lizard. *Physiological zoology* **67**: 238–262.
- Bartholomew G, Tucker V. 1964.** Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. *Physiological zoology* **37**: 341–354.
- Bauwens D, Garland T Jr, Castilla A, Damme R. 1995.** Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. *Evolution* **49**: 848–863.
- Bennett AF. 1972.** The effect of activity on oxygen consumption, oxygen debt, and heart rate in the lizards *Varanus gouldii* and *Sauromalus hispidus*. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* **79**: 259–280.
- Bennett AF. 1973.** Blood physiology and oxygen transport during activity in two lizards, *Varanus gouldii* and *Sauromalus hispidus*. *Comparative Biochemical Physiology* **46**: 673–690.
- Bennett AF. 1982.** The energetics of reptilian activity. In: Gans C, Pough FH, eds. *Biology of the reptilia*. New York: Academic Press, 155–199.
- Bennett AF. 1987.** Interindividual variability: an underutilized resource. In: Feder ME, Bennett AF, Burggren WW, Huey RB, eds. *New directions in ecological physiology*. Cambridge: Cambridge University Press, 147–169.
- Bennett AF. 1990.** Thermal dependence of locomotor capacity. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* **259**: 253–258.
- Bickler E, Anderson R. 1986.** Ventilation, gas exchange, and aerobic scope in a small monitor lizard *Varanus gilleni*. *Physiological zoology* **59**: 76–81.
- Blomberg SP, Garland T Jr, Ives AR. 2003.** Testing for phylogenetic signal in comparative data: behavioural traits are more labile. *Evolution* **57**: 717–745.
- Burggren W, Johansen K. 1982.** Ventricular haemodynamics in the monitor lizard *varanus exanthematicus*: pulmonary and systemic pressure separation. *Journal of Experimental Biology* **96**: 343.
- Carrier DR. 1987a.** Lung ventilation during walking and running in four species of lizards. *Journal of Experimental Biology* **47**: 33–42.
- Carrier DR. 1987b.** The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. *Paleobiology* **13**: 326–341.
- Carrier DR. 1989.** Ventilatory action of the hypaxial muscles of the lizard *Iguana iguana*: a function of slow muscle. *Journal of Evolutionary Biology* **143**: 435–457.
- Carrier DR. 1990.** Activity of the hypaxial muscles during walking in the lizard *Iguana iguana*. *Journal of Experimental Biology* **152**: 453–470.
- Cheverud JM, Dow MM. 1985.** An autocorrelation analysis of genetic variation due to lineal fission in social groups of rhesus macaques. *American Journal of Physical Anthropology* **67**: 113–121.
- Christian KA, Conley KE. 1994.** Activity and resting metabolism of varanid lizards compared with 'typical' lizards. *Australian Journal of Zoology* **42**: 185–193.
- Clemente CJ. 2006.** *Evolution of locomotion in Australian varanid lizards (Reptilia: Squamata: Varanidae): ecomorphological and ecophysiological considerations*. PhD: University of Western Australia.
- Clemente CJ, Withers PC, Thompson GG. 2008.** Higher than predicted endurance for juvenile goannas (Varanidae; Varanus). *Journal of the Royal Society of Western Australia* **91**.
- Clemente CJ, Thompson GG, Withers PC. 2009.** Evolutionary relationships of sprint speed in Australian varanid lizards. *Journal of Zoology (London)*. DOI: 10.1111/j.1469-7998.2009.00559.x
- Emerson SB, Arnold SJ. 1989.** Intra- and interspecific relationships between morphology, performance, and fitness. In: Wake DB, Roth G, eds. *Complex organismal functions: integration and evolution in vertebrates*. Chichester: John Wiley and Sons, 295–314.
- Feldman HA, McMahon TA. 1983.** The 3/4 mass exponent for energy metabolism is not a statistical artifact. *Respiratory Physiology* **52**: 149–163.
- Felsenstein J. 1985.** Phylogenies and the comparative method. *American Naturalist* **125**: 1–15.
- Garland T Jr. 1984.** Physiological correlates of locomotor performance in a lizard: an allometric approach. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* **247**: 806–815.
- Garland T Jr. 1993.** Locomotor performance and activity metabolism of *Cnemidophorus tigris* in relation to natural behaviors. In: Boake CRB, ed. *Biology of whiptail lizards (genus cnemidophorus)*. Chicago, IL: University of Chicago Press, 163–210.
- Garland T Jr. 1994.** Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In: Vitt ER, Pianka ER, eds. *Lizard ecology: historical and experimental perspectives*. Princeton, NJ: Princeton University Press, 237–259.
- Garland T Jr. 1999.** Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Animal Behaviour* **58**: 77–83.
- Garland T Jr, Else P. 1987.** Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* **252**: 439–449.
- Garland T Jr, Harvey PH, Ives AR. 1992.** Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic biology* **41**: 18–32.
- Garland T Jr, Losos JB. 1994.** Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright PC, Reilly SM, eds. *Ecological morphology: integrative organismal biology*. Chicago, IL: University of Chicago Press, 240–302.

- Gleeson TT, Mitchell GS, Bennett AF. 1980.** Cardiovascular response to graded activity in *Varanus* and *Iguana*. *American Journal of Physiology- Regulatory, Integrative and Comparative Physiology* **239**: R174–R179.
- Harvey PH, Purvis A. 1991.** Comparative methods for explaining adaptations. *Nature* **351**: 619–624.
- Heusner A. 1982.** Energy metabolism and body size. I. Is the 0.75 mass exponent of Kleiber's equation a statistical artifact. *Respiration Physiology* **48**: 1–12.
- Hopkins SR, Hicks JW, Cooper TK, Powell FL. 1995.** Ventilation and pulmonary gas exchange during exercise in the savannah monitor lizard (*Varanus exanthematicus*). *Journal of Experimental Biology* **198**: 1783–1789.
- Huey RB, Dunham AE, Overall KL, Newman RA. 1990.** Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiological zoology* **63**: 845–872.
- Irschick DJ, Garland T Jr. 2001.** Intergrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annual reviews of Ecology and Systematics* **32**: 367–396.
- John-Alder H. 1984.** Seasonal variations in activity, aerobic energetic capacities, and plasma thyroid hormones (T3 and T4) in an iguanid lizard. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **154**: 409–419.
- King DR, Green B. 1999.** *Goanna: the biology of varanid lizards*. Kensington, NSW: New South Wales University Press.
- Losos JB. 1990a.** The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**: 1189–1203.
- Losos JB. 1990b.** Ecomorphology, performance capacity and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* **60**: 369–388.
- McElroy EJ, Reilly SM. 2009.** The relationship between limb morphology, kinematics, and force during running: the evolution of locomotor dynamics in lizards. *Biological Journal of the Linnean Society* **97**: 634–651.
- Miles D. 1994.** Covariation between morphology and locomotor performance in Sceloporine lizards. In: Vitt ER, Pianka ER, eds. *Lizard ecology: historical and experimental perspectives*. Princeton, NJ: Princeton University Press, 207–235.
- Millard RW, Johansen K. 1974.** Ventricular outflow dynamics in the lizard, *Varanus niloticus*: responses to hypoxia, hypercarbia and diving. *Journal of Experimental Biology* **60**: 871–880.
- Mitchell GS, Gleeson TT, Bennett AF. 1981.** Ventilation and acid-base balance during graded activity in lizards. *American Journal of Physiology- Regulatory, Integrative and Comparative Physiology* **240**: 29–37.
- Orlowski L. 1978.** *Multivariate analysis in vegetation research*, 2nd edn. The Hague, The Netherlands: Junk Publishers.
- Owercowicz T, Farmer CG, Hicks JW, Brainerd EL. 1999.** Contribution of gular pumping to lung ventilation in monitor lizards. *Science* **284**: 1661–1663.
- Perry G. 1999.** The evolution of search modes: ecological versus phylogenetic perspectives. *The American Naturalist* **153**: 98–109.
- Perry SF, Duncker HR. 1978.** Lung architecture volume and static mechanics in five species of lizards. *Respiration Physiology* **34**: 61–81.
- Phillips J. 1995.** Movement patterns and density of *Varanus albigularis*. *Journal of Herpetology* **29**: 407–416.
- Pianka ER. 1995.** Evolution of body size: varanid lizards as a model system. *The American Naturalist* **146**: 398–414.
- Regal PJ. 1983.** The adaptive zone and behavior of lizards. In: Huey RB, Pianka ER, Schoener TW, eds. *Lizard ecology: studies of a model organism*. Cambridge: Harvard University Press, 105–118.
- Rohlf F. 2001.** Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* **55**: 2143–2160.
- Schuetz GW, Reiserer RS, Earley RL. 2009.** The evolution of bipedal postures in varanoid lizards. *Biological Journal of the Linnean Society* **97**: 652–663.
- Somers K. 1986.** Multivariate allometry and removal of size with principal components analysis. *Systematic Zoology* **35**: 359–368.
- Thompson G, Withers PC. 1997a.** Comparative morphology of Western Australian varanid lizards (squamata: Varanidae). *Journal of Morphology* **233**: 127–152.
- Thompson G, Withers PC. 1997b.** Standard and maximal metabolic rates of goannas (squamata: Varanidae). *Physiological zoology* **70**: 307–323.
- Thompson G, Withers PC. 2005.** The relationship between size-free body shape and choice of retreat for Western Australian *Ctenophorus* (Agamidae) dragon lizards. *Amphibia-Reptilia* **26**: 65–72.
- Thompson GG, Clemente CJ, Withers PC, Fry BG, Norman JA. 2008.** Is body shape of Varanid lizards linked with retreat choice? *Australian Journal of Zoology* **56**: 351–362.
- Tsuji JS, Huey RB, van Berkum FH, Garland T Jr, Shaw RG. 1989.** Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. *Evolutionary Ecology* **3**: 240–252.
- Vanhooydonck B, VanDamme R, Aerts P. 2001.** Speed and stamina trade-off in lacertid lizards. *Evolution* **55**: 1040–1048.
- Wang T, Carrier DR, Hicks J. 1997.** Ventilation and gas exchange in lizards during treadmill exercise. *Journal of Experimental Biology* **200**: 2629–2639.
- Withers PC. 1977.** Measurement of VO<sub>2</sub>, VCO<sub>2</sub>, and evaporative water loss with a flow-through mask. *Journal of Applied Physiology* **42**: 120–123.