Evolutionary relationships of sprint speed in Australian varanid lizards

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Abstract

Ecomorphological studies often seek to link morphology and performance to relevant ecological characteristics. Varanid lizards are unique in that species can vary in body size by almost four orders of magnitude within a single genus, and a question of considerable interest is whether similar ecomorphological relationships exist when constraints on body size are reduced. We studied sprint speed in relation to size, shape and ecology for 18 species of varanid lizards. Maximal speed scaled positively with $mass^{0.166}$ using least squares regression, and $mass^{0.21}$ using reduced major-axis regression. However, a curvilinear trend better described this relationship, suggesting an optimal mass of 2.83 kg with respect to speed. Including data for the komodo dragon *Varanus komodoensis* moves the optimum mass to 2.23 kg. We use this relationship to predict the sprint speed of the Komodo's giant extinct relative *Varanus* (*Megalania*) *prisca* to be $2.6\text{--}3\,m\,s^{-1}$ similar to that of extant freshwater crocodiles *Crocodylus johnstoni*. When differences in speed were compared to ecological characteristics, species from open habitats were significantly faster than species from semi-open or closed habitat types, and remained so after correction for size and phylogeny. Thus, despite large variation in body size, varanids appear to share similar associations between performance and ecology as seen in other lizard groups. Varanids did, however, differ in morphological relationships with sprint speed. Differences in relative speed were not related to relative hindlimb length, as is commonly reported for other lizard groups. Instead, size-free forefoot length was negatively related to speed as was the size-free thorax–abdomen length. While shorter forefeet were thought to be an adaptation to burrowing, and thus open habitats, rather than speed *per se*, the reduction in the thorax–abdomen length may have significant advantages to increasing speed. Biomechanical models predicting this advantage are discussed in relation to a trade-off between speed and manoeuvrability.

Introduction

In ecomorphological and ecophysiological studies, locomotion is often thought to be an intermediatory step between form and function. Thus many studies now include ecologically relevant performance measures in analysing the relationship between morphology (or physiology) and ecology (Garland Jr & Losos, 1994; Irschick & Garland Jr, 2001). Originally this was proposed for intra-specific studies (Arnold, 1983), but it can be expanded to inter-specific studies. Rather than testing the link between performance and fitness among individuals in a population, the paradigm has been expanded to test the relationship between performance and habitat among species (Emerson & Arnold, 1989; Garland Jr & Losos, 1994). While several studies have compared sprint speeds species within closely related groups (e.g. Lacertidae: Bauwens *et al.*, 1995; Phrynosomatidae: Bonine & Garland,

1999; *Niveoscincus*: Melville & Swain, 2000, 2003), studies are often limited by a restricted range in body size. Varanids can differ in body size by almost four orders of magnitude (Pianka, 1995), no other study has examined sprint speeds over such a large size range within a single genus. This size ranges make varanids ideal for testing scaling of sprint speed across body size, and further, it is unclear whether biomechanical or ecological relationships will be similar to that reported for other groups of lizards where size appears more constrained. We have used an ecomorphological approach to compare morphology with speed, and then speed with ecological traits, for Australian varanid lizards.

Morphology and sprint speed

Of the morphological traits body mass is perhaps the most important determinant of speed. Speed tends to scale

positively with body size (Schmidt-Nielsen, 1972; Heglund, Taylor & McMahon, 1974; Garland Jr, 1983; Van Damme & Vanhooydonck, 2001), and several biomechanical models have been proposed to predict this relationship between body mass and speed including; the dynamic similarity model ($v \approx \text{mass}^{0.16}$, Günther, 1975); the elastic similarity model ($v \approx \text{mass}^{0.25}$, McMahon, 1973, 1975); the static stress similarity model ($v \approx \text{mass}^{0.40}$, McMahon, 1973, 1975); and more recently the unifying constructional theory ($v \approx \text{mass}^{0.167}$, Bejan & Marden, 2006).

The elastic similarity model was supported by Heglund et al. (1974) who reported that the relationship between speeds at the trot/gallop transition scaled with $\text{mass}^{0.24}$. Van Damme & Vanhooydonck (2001), using data for 94 species of lizard, found an exponent for ordinary least squares regression was $\text{mass}^{0.18}$, close to the value predicted by Günther's (1975) dynamic similarity model, or Bejan & Marden's (2006) unifying constructional theory. Garland Jr (1983), using 106 mammal species ranging in mass from 0.016 to 6000 kg obtained a similar exponent for speed using least squares regression, of $\text{mass}^{0.165}$.

Several authors have argued that ordinary least squares regression may not be the most appropriate technique for allometric studies since it does not consider measurement error along the x-axis, suggesting reduced major axis regression may be more suitable (Rayner, 1985; McArdle, 1988; Christian & Garland Jr, 1996; Van Damme & Vanhooydonck, 2001). When Van Damme & Vanhooydonck (2001) reanalysed their data using reduced major axis regression, the exponent for speed increased to $\text{mass}^{0.39}$, which was much closer to the relationship predicted by the static stress similarity model proposed by McMahon (1975).

However, the relationship between speed and mass may not necessarily be linear. For mammals, Garland Jr (1983) showed that $\log_{10}(\text{speed})$ does not increase linearly with $\log_{10}(\text{mass})$, but is curvilinear; a second-order polynomial best fitted the data, which had a maximum speed at a body mass of 119 kg. A similar curvilinear regression was fitted to the lizard data by Van Damme & Vanhooydonck (2001), who suggested that speed was maximal for lizards at a mass of 48 g. However, these authors noted that the dataset was limited by the inclusion of fewer speeds for larger lizards.

Several studies have also examined the relationship between body dimensions and speed. To remove the effects of size, most studies use relative body proportions and relative speeds. Biomechanical models predict a positive relationship between relative limb lengths and speed, as longer legs would allow the body to travel further with each step (Garland Jr, 1985; Marsh, 1988; Losos, 1990a; Vanhooydonck, Van Damme & Aerts, 2002). Many empirical studies have supported this prediction (Snell et al., 1988; Losos, 1990a; Sinervo, Hedges & Adolph, 1991; Sinervo & Losos, 1991; Bauwens et al., 1995; Bonine & Garland, 1999; Melville & Swain, 2000, 2003; Gifford, Herrel & Mahler, 2008). The relationship between tail length and speed has also been studied, though often in regard to tail loss (Arnold, 1988; Russell & Bauer, 1992). Many lizards with experimentally shortened tails run more slowly (Ballinger,

Nietfeldt & Krupa, 1979; Pond, 1981; Punzo, 1982; Arnold, 1984; Formanowicz, Brodie & Bradley, 1990), but there are several exceptions (Daniels, 1983, 1985; Jayne & Bennett, 1989; Huey et al., 1990).

Sprint speed and ecology

Variation in performance may affect an organism's ability to exploit specific ecological opportunities (Huey & Stevenson, 1979). The ecology of varanid species can be classified based on five major variables; climate, habitat type, climbing ability and openness of habitat. Climate may affect sprinting though environmental temperatures and therefore thermoregulatory opportunities. Several studies have shown a positive relationship between optimal body temperature and sprint speed (Garland Jr, 1994; Bauwens et al., 1995; Van Damme & Vanhooydonck, 2001). Species from hot xeric climates might then be expected to show higher sprint speeds, some evidence supports this hypothesis (Van Damme & Vanhooydonck, 2001).

Many lizards have a preferred habitat type, and it is generally assumed that specialization in one particular microhabitat type will occur at the cost of reduced fitness in another habitat type (Losos, 1990b; Garland Jr, 1994; Vanhooydonck, Van Damme & Aerts, 2000). Sprint speeds are typically measured on a flat surface without any obstacles, which is most similar to a terrestrial habitat, so based on biomechanical models terrestrial species may be expected to excel in this performance variable. However, contrary to this hypothesis, Melville & Swain (2003) reported Niveoscincus species from saxicolous habitats showed higher sprint speeds than both ground-dwelling and arboreal species.

Climbing species are expected to be disadvantaged in terrestrial running as the performance variables they are selected for in their habitat (e.g. climbing ability or sure-footedness) are often traded-off against high speed on flat surfaces. Studies in Anolis, Sceloporus and Chamaeleo support this hypothesis (Losos & Sinervo, 1989; Sinervo & Losos, 1991; Losos, Walton & Bennett, 1993; Losos & Irschick, 1996), however, studies on Lacertid lizards did not (Van Damme, Aerts & Vanhooydonck, 1997; Vanhooydonck & Van Damme, 2001). These latter studies suggested that the trade-off between climbing and terrestrial species may only exist where arboreal species climb on narrow structures (Vanhooydonck & Van Damme, 2001). As arboreal varanids appear to favour broad vertical structures (Christian et al., 1996; Sweet, 2004; Weavers, 2004), we may not expect a strong trade-off to exist, as optimal designs for both flat vertical and horizontal surfaces may be similar.

Species from open habitats should favour the evolution of traits that increase predator avoidance, such as longer legs and greater sprint speed. Conversely, such features may hinder locomotion in closed habitats (Pianka, 1969). This expectation was supported by several studies (Melville & Swain, 2000; Vanhooydonck & Van Damme, 2003; Gifford et al., 2008). Species that spent the most time in 'open habitats' had a higher sprint speed than species which spent

most time in vegetated or vertical habitat types. However, some studies have failed to find this association. Species from the lizard clade *Liolaemus* do not show a strong association between morphology and habitat openness (Jaksic, Núnez & Ojeda, 1980; Schulte *et al.*, 2004). Instead habitat openness was related to behaviour, lizards from open habitats ran longer distances from predators, which may have made the evolution of limb morphology unnecessary (Schulte *et al.*, 2004).

Other studies have failed to find relationships between speed and ecology. Miles (1994) compared morphology and performance for nine lizard species that exploit different substrate types, predicting that species which exploit substrates with different physical characteristics vary in morphology, which consequently results in differences in sprint speed. The results did not support this hypothesis. Van Damme & Vanhooydonck (2001) analysed sprint speed in relation to foraging mode, activity, microhabitat use and climate, using data for mass, speed and ecology of 129 species of lizard from the literature. Activity, microhabitat and climate all had significant relationships with sprint speed, but there was no difference between sit-and-wait predators and actively foraging species. Further, the relationships with activity, microhabitat and climate were no longer significant when analysed in a phylogenetic context. These authors concluded that differences in sprint speed reflect phylogeny rather than ecology *per se*.

Our objective was to examine possible relationships with sprint speed, which we believe is an ecologically relevant performance trait for many varanids, with their morphology and ecological traits. Large differences in size and shape make *Varanus* an ideal group to examine the effect morphological traits have on sprint speed, and in turn any affect that difference in sprint speed has on the fitness of lizards within different habitats.

Methods

Animals and sample collection

We collected 125 adult lizards from 18 species of Australian varanids for this study. All specimens used in the study were wild caught. Lizards were captured using a variety of techniques including pit trapping and hand foraging. Individuals that appeared sick, injured or obviously malnourished were not included. Owing to uncertainty in determining sex, males and females were not differentiated in the analysis.

Phylogeny

Phylogenetic history and environment both affect species variation. Inter-specific 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) shown in Fig. 1.

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 phylogenetically independent data, custom written visual basic programs (Philip Withers, University of Western Australia) were used, based on the methods published in Garland Jr, Harvey & Ives (1992), Blomberg, Garland Jr & Ives (2003) and Rohlf (2001).

Morphology

Various morphological dimensions were measured for each lizard as shown in Fig. 2: snout-to-vent length (SVL), tail length (TAIL), head–neck length (HN), thorax–abdomen length (TA), upper fore-limb length (UFL), lower fore-limb length (LFL), fore-foot length (FFOOT), upper hind-limb
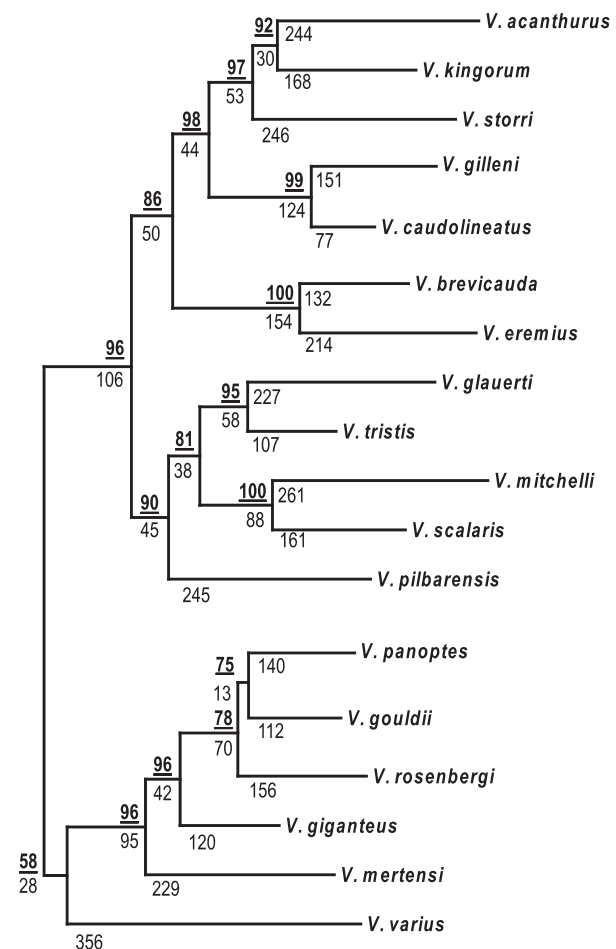

Figure 1 Phylogenetic relationships for 18 species of *Varanus* used in this study, based on 1038 base pairs from the NADH2-gene, showing the maximum likelihood hypothesis from Clemente (2006). Bootstrap values >50% (percentages of 100 pseudoreplicates) are underlined and shown above branches, branch lengths are shown below the branches (substitution/site × 1000).
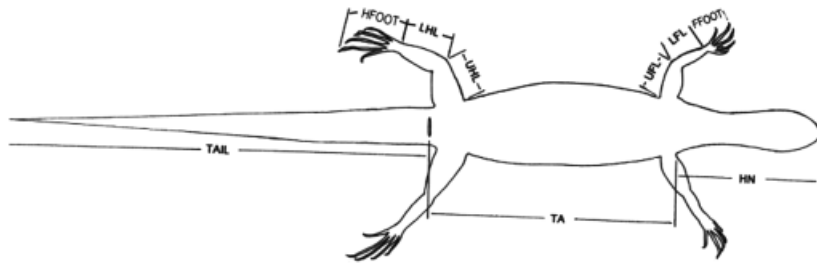
Figure 2 Morphological measurements taken from varanid specimens. Modified from Thompson & Withers (1997).

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

Sprint speed

Sprint speeds were measured by taking serial digital pictures at 25 Hz of each lizard as it ran along a 'racetrack'. Clear plastic or metal sheeting formed the sides of a racetrack 13.6 m long by 0.75 m wide. A canvas chute was placed at the end of the racetrack to catch running lizards. Both sand and canvas were used as substrates. A Sony MiniDV (ORADELL New Jersey, USA) digital Handycam (Model DCR-TRV27 PAL) was placed at the end of the racetrack facing down at about 45° to the centre. Each lizard's run was filmed and the images analysed frame-by-frame using custom built video analysis software (Philip Withers, University of Western Australia). Lizards were run four to five times during each trial, for a total of three trials, allowing 24-h rest between subsequent trials. Multiple runs for each individual were compared and the maximal speed for each individual was selected. Species means were then calculated by averaging the maximal performance values for each individual for each species. A body temperature range of 35–38 °C, measured cloacally, was used for all experiments.

Our experience is that lizards will often run sub-maximally during sprint trials. Including sub-maximal performance scores could change the interpretation of results, and therefore sub-maximal data should be excluded from analysis (Losos, Creer & Schulte, 2002). Following the advice of Losos et al. (2002) the criterion for excluding a run was based not on the speed the lizard obtained, but rather the manner in which the lizard ran. Runs were not included if the lizard did not lift its body off the substrate, moved in a jerky, start–stop fashion, ran into the walls of the racetrack or stumbled during the trial.

To normalize variability in speed and body mass scores, $\log_{10}$ values were used in all analyses. To remove the effects of size from body dimensions, Somer's (1986) size-free analysis was used. 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. When correlating size-free body dimensions with speed, the size effect was removed from speed by calculating residual speed from this size component. When relating performance scores to ecological variables, the size effect was removed using residuals from mass. Size-corrected numbers for speed were calculated from mass using curvilinear regression, using a linear regression did not change the outcome of results.

Species means were used to test the inter-specific differences in speed with mass, body dimensions and ecological characteristics. Where an ecological category consisted of more than two groups a full factorial ANOVA was used to test for statistical differences among groups, otherwise a two-tailed t-test was used. ANOVA (or t-tests) were performed on the original log-transformed data, on size-corrected data and on size and phylogenetically corrected data. If size-corrected analyses did not indicate a significant relationship with ecological characteristics, further phylogenetic correction was not undertaken.

Speed data for varanids were compared with Auffenberg's (1981) data for sprint speed of adult *Varanus komodoensis* (4.69 m s^{-1}, 8000 g), 136 species of non-varanid lizards published in Van Damme & Vanhooydonck (2001) and Zani (1996), and Garland's Jr (1983) dataset for 107 species of mammal.

Ecological characteristics

Each varanid was classified based on four different ecological traits: habitat type, climbing ability, climate and openness of its typical habitat. These data are summarized in Table 1. Habitat was based on categories reported by Thompson & Withers (1997). Climbing ability and climate were based on an extensive literature review of each species (Clemente, 2006). 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 categorized as xeric, mesic or tropical. Where species were found in multiple climatic zones, we chose the one that represented where most of the study individuals were collected from. 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 most often encountered in open areas with little cover.

Results

The highest species means for sprint speed of varanids (Table 2) was $8.77\,\mathrm{m\,s^{-1}}$ for *Varanus giganteus*, which may be the highest speed recorded for any squamate lizard. Sprint speed was positively related to mass across species (Fig. 3a) scaling with mass at an exponent of 0.166 using ordinary least squares regression (± 0.066, 95% CL for slope, $r^2 = 0.64$, $P < 0.001$). Reduced major axis regression produced a higher slope scaling with body mass to 0.208 (± 0.066, 95% CL).

Removing the effects of phylogeny, using independent contrasts, produced a similar but weaker result. When contrasts for body mass were regressed against contrasts for speed, there was a positive relationship. For the regression, forced through the origin, the slope of the line using least squares regression was 0.151 ($r^2 = 0.40$, $P < 0.005$; Fig. 3b).

However, the relationship between maximal sprint speed and mass was best represented not by a linear relationship but rather by a second order polynomial (Fig. 4). The polynomial was $\mathrm{Log(speed)} = -0.2516 + 0.5709$

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

Species	Habitat (Thompson & Withers, 1997)	Climbing ability	Openness	Climate
Varanus acanthurus	Sedentary terrestrial	NC	Closed	Xeric
Varanus brevicauda	Sedentary terrestrial	NC	Closed	Xeric
Varanus caudolineatus	Arboreal/rock	Climber	Closed	Xeric
Varanus eremius	WF terrestrial	NC	Open	Xeric
Varanus giganteus	WF terrestrial	NC	Open	Xeric
Varanus gilleni	Arboreal/rock	Climber	Closed	Xeric
Varanus glauerti	Arboreal/rock	Climber	Semi-open	Tropical
Varanus gouldii	WF terrestrial	NC	Open	Xeric
Varanus kingorum	Sedentary terrestrial	Climber	Closed	Tropical
Varanus mertensi	Aquatic	Climber	Semi-open	Tropical
Varanus mitchelli	Aquatic	Climber	Closed	Tropical
Varanus pilbarensis	Arboreal/rock	Climber	Semi-open	Xeric
Varanus panoptes	WF terrestrial	NC	Open	Tropical
Varanus rosenbergi	WF terrestrial	NC	Semi-open	Mesic
Varanus scalaris	Arboreal/rock	Climber	Semi-open	Tropical
Varanus storri	Sedentary terrestrial	NC	Closed	Tropical
Varanus tristis	Arboreal/rock	Climber	Semi-open	Xeric
Varanus varius	Arboreal/rock	Climber	Semi-open	Mesic

WF terrestrial, widely foraging terrestrial; NC, non-climbing.

Table 2 Species mean ($\pm$ SE) for maximum speed, body mass and snout–vent length of 18 species of Australian varanids

| Species	n	Max Speed ($\mathrm{m\,s^{-1}}$)	Mass (g)	SVL (mm)
Varanus acanthurus	6	3.05 ± 0.32	58.9 ± 11.7	137.5 ± 19.3
Varanus brevicauda	2	1.59 ± 0.03	20.6 ± 1.9	106.2 ± 1.1
Varanus caudolineatus	5	2.34 ± 0.22	18.1 ± 2.5	105.7 ± 14.2
Varanus eremius	4	3.71 ± 0.40	48.5 ± 3.9	153.3 ± 9.2
Varanus giganteus	3	8.77 ± 0.55	2966.7 ± 1122.6	679.3 ± 122.2
Varanus gilleni	12	2.23 ± 0.11	27.1 ± 1.9	126.2 ± 8.6
Varanus glauerti	7	3.09 ± 0.21	35.7 ± 12.2	145.3 ± 31.6
Varanus gouldii	14	5.72 ± 0.19	429.4 ± 56.1	307.5 ± 45.8
Varanus kingorum	7	2.60 ± 0.16	18.3 ± 2.7	98.2 ± 10.4
Varanus mertensi	11	3.57 ± 0.33	1032.3 ± 280.0	409.7 ± 105.5
Varanus mitchelli	7	3.43 ± 0.19	151.3 ± 36.7	232.7 ± 45.4
Varanus panoptes	17	5.90 ± 0.26	2425.0 ± 358.9	526.8 ± 110.0
Varanus pilbarensis	5	2.83 ± 0.08	30.3 ± 4.2	125.1 ± 27.0
Varanus rosenbergi	2	5.27 ± 2.36	1025.0 ± 435.0	418.8 ± 72.4
Varanus scalaris	7	2.76 ± 0.19	102.1 ± 13.6	203.1 ± 13.8
Varanus storri	8	2.55 ± 0.10	26.9 ± 2.6	103.4 ± 8.5
Varanus tristis	6	3.95 ± 0.32	98.3 ± 32.2	190.2 ± 35.4
Varanus varius	2	4.03 ± 0.01	7700.0 ± 1700.0	655.0 ± 28.3
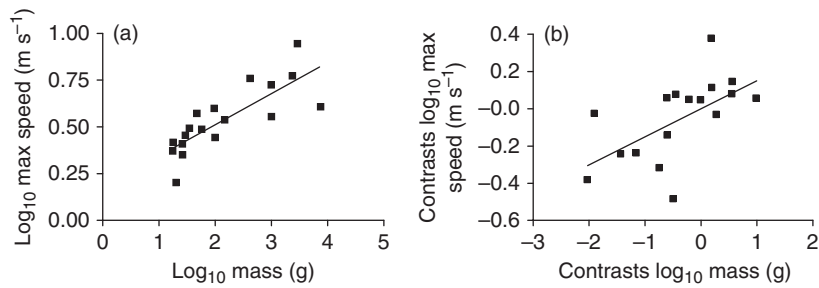
Figure 3 Effect of body mass on maximal sprint speed in varanids. (a) Non-phylogenetically corrected analysis for maximum sprint speed, with ordinary least squares regression. (b) Phylogenetically corrected analysis for maximum sprint speed, using independent contrasts, with ordinary least squares regression forced through the origin.
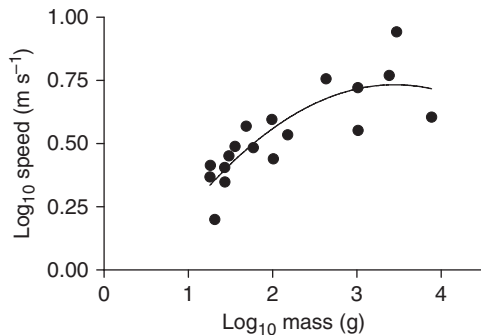

Figure 4 Curvilinear regression between maximum sprint speed and mass. The equation is $\log(\text{speed}) = -0.0827(\log \text{ mass})^2 + 0.5709(\log \text{ mass}) - 0.251$ ($r^2 = 0.71$, $P = 0.001$).

Table 3 Correlation between size-free body dimensions and size-corrected speed for 18 species of Australian varanids

Residual dimension	Max speed	
	R	P
HN	0.14	0.572
TA	−0.33	0.177
TAIL	0.29	0.247
FFOOT	−0.60	**0.009**
LFL	−0.52	**0.026**
UFL	0.20	0.424
HFOOT	−0.15	0.565
LHL	0.44	0.070
UHL	0.19	0.457

HN, head–neck length; TA, thorax–abdomen length; TAIL, tail length; FFOOT, fore-foot length; LFL, lower fore-limb length; UFL, upper fore-limb length; HFOOT, hind-foot length; LHL, lower hind-limb length; UHL, upper hind-limb length.

(log mass) $-0.0827(\log \text{ mass})^2$ (with speed in m s^{-1} and mass in g). This suggested an optimal mass with respect to speed of 2.83 kg. The polynomial fit had a higher correlation coefficient ($r^2 = 0.71$) than the linear regression (0.64). However, the variance for the residuals based on the polynomial (0.009), was not significantly less than the variance for the residuals based on linear regression (0.011), by F-test ($F_{17,17} = 1.23$, $P = 0.340$).

There was a significant relationship between body dimensions and speed. To remove the effects of size from body dimensions, size-free body dimensions were regressed against size-corrected performance variables. Faster speed was associated with varanids that had relatively shorter forefeet and shorter lower forelimbs lengths (Table 3).

When phylogenetically independent contrasts of size-free body dimensions were regressed against contrasts of size-free performance values, the relationships are similar (Table 4). Faster sprint speed was still associated with shorter forefeet, but the lower fore limb was no longer significantly related with speed. A negative relationship between thorax–abdomen length and speed became stronger.

Sprint speeds were not significantly related to climate ($F_{2,15} = 0.54$, $P = 0.591$) or climbing abilities ($t_{7.86} = 1.48$, $P = 0.194$) in these lizards. Speed was significantly different among habitat types when actual speed scores were exam-

ined ($F_{3,14} = 9.64$, $P = 0.001$; Fig. 5). However, the relationship between speed and habitat was no longer significant when size-corrected speed scores were examined ($F_{3,14} = 3.30$, $P = 0.052$), suggesting a relationship between size and habitat type.

Speed varied more consistently with habitat openness ($F_{2,15} = 12.96$, $P < 0.001$; Fig. 5). Species from open habitat types ran faster than species from both semi-open and closed habitat types (SNK *post hoc* test open vs. semi-open $P = 0.022$, open vs. close $P < 0.001$), while species from semi-open habitat types were faster than closed habitat species ($P = 0.011$). This was true for both absolute speeds and size-corrected speeds ($F_{2,15} = 4.92$, $P = 0.038$; Fig. 5), suggesting that species from open habitat types not only ran faster, but ran relatively faster than species from semi-open and closed habitat types. Phylogeny has the potential to confound the analysis since most of the species from open habitats belong to a single clade, so differences in speed may be due to a tendency for high speeds to be inherited in this group. However, when the possibly confounding effect of phylogeny was removed from size-corrected speed scores using autocorrelation, habitat openness was still significantly related to speed ($F_{2,15} = 4.14$, $P = 0.037$).

Discussion

Among Australian varanids, sprint speed scaled with a significant mass exponent of 0.166 using ordinary least squares regression. Auffenberg's (1981) data for sprint speed of adult *V. komodoensis* (4.69 m s^{-1}, 8000 g) is similar to the largest species used in this study, *Varanus varius*, and when the Komodo dragon speed is included with our data for *Varanus*, the mass exponent is 0.15. In either case, the exponent closely resembles the expected value predicted by Günther's (1975) dynamic similarity model (0.17), or Bejan

& Marden's (2006) unifying constructional theory (0.167). Van Damme & Vanhooydonck (2001) also found a similar exponent of 0.18 for other lizards, and Garland Jr (1983) obtained an exponent of 0.165, for 106 mammal species ranging from 0.016 to 6000 kg. However, reduced major axis regression may be a more suitable tool for analysis as it allows for error in both *X* and *Y*. Using reduced major axis regression, the exponent for speed and mass in varanids becomes 0.21 (0.19 including *V. komodoensis*), still close to the dynamic similarity model and unifying constructional theory.

Combining data for all other lizards species from Van Damme & Vanhooydonck (2001), with *V. komodoensis* (Auffenberg, 1981), and our data for varanids gives an exponent of 0.205 (lower 95% CL = 0.18; upper 95% CL = 0.25) by standard least squares regression and 0.31 (lower 95% CL = 0.27; upper 95% CL = 0.34) by reduced major axis regression. While the exponent for ordinary least squares regression is close to the dynamic similarity model and unifying constructional theory, the exponent obtained using reduced major axis regression is not convincingly close to any of the models.

Garland Jr (1983) noted that none of these models described the relationship between speed and mass very well for mammals, because speed did not increase monotonically with mass. Instead the relationship was better described by curvilinear regression. For mammals, this relationship reached an optimum speed at a body mass of about 119 kg (Garland Jr, 1983). Van Damme & Vanhooydonck (2001) found that a similar curvilinear path better described the relationship between speed and mass for lizards, reaching an optimum at 48 g. The second order polynomial fit to the

Table 4 Correlations between phylogenetically independent contrasts of size-free body dimension (from mass) and independent contrasts of size-corrected (from mass) performance variables for 18 species of Australian varanids

Contrasts size-free dimension	Contrast max speed	
	R	P
HN	0.08	0.750
TA	−0.51	**0.035**
TAIL	0.38	0.136
FFOOT	−0.53	**0.028**
LFL	−0.36	0.156
UFL	0.01	0.977
HFOOT	−0.01	0.974
LHL	0.44	0.081
UHL	0.19	0.464

HN, head–neck length; TA, thorax–abdomen length; TAIL, tail length; FFOOT, fore-foot length; LFL, lower fore-limb length; UFL, upper fore-limb length; HFOOT, hind-foot length; LHL, lower hind-limb length; UHL, upper hind-limb length.
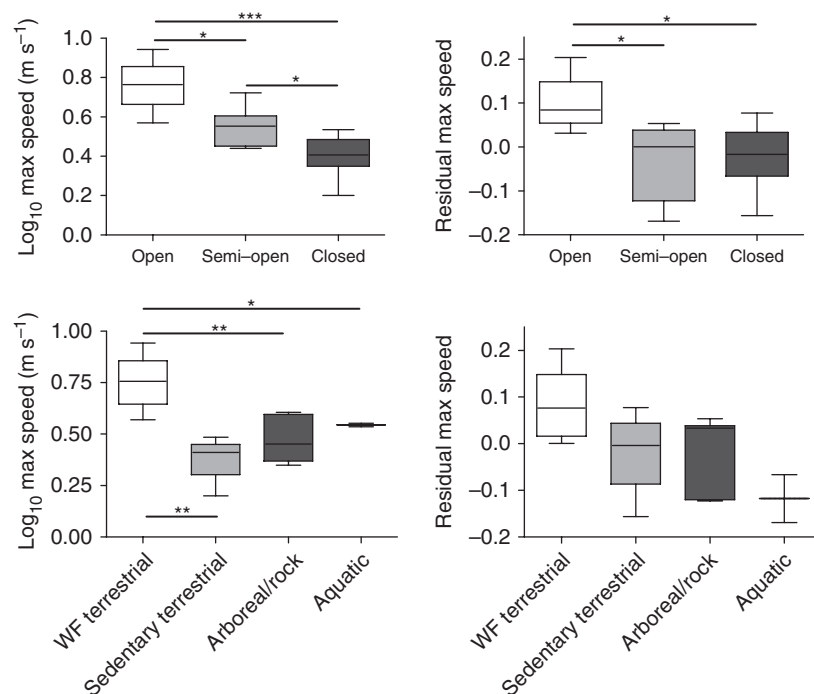

Figure 5 Maximum sprint speed and residual (size-corrected for mass) speed categorized by ecological types for varanids. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ (by SNK *post hoc* test). Boxes represent the median within the 25 and 75% percentiles. Whiskers represent the maximum and minimum values.

varanid data (including *V. komodoensis*) of log(speed) $=-0.2813+0.6014\log_{10}(\text{mass})-0.0898\log_{10}(\text{mass})^2$ indicates an optimal mass in relations to speed at 2.23 kg. If all three groups are placed on one plot there is evidence for three different systems with three different optima (Fig. 6).

It is difficult to decide which biomechanical model best fits these empirical data for sprint speed, as all the models examined here predict speed to continue increasing with increasing size. Instead there seems to be a maximum in all groups tested, suggesting that none of the models work particularly well. The concept of an optimal mass in respect to speed has not received enough attention in the literature. The reason for this probably lies in the small number of species with a mass above the maximum, which results in a lack of strong statistical support for a curvilinear regression over a linear fit. However, the repetition of an optimal mass in relation to speed among different taxa does lend strong support for a non-linear relationship between these variables.

The nature of the relationship between mass and speed becomes important when we wish to use these data to make predictions about speeds for species of which direct measurement of speed is not possible. For example, the ecology of the Komodo dragon's gigantic extinct relative, *Varanus* (*Megalania*) *prisca*, is contentious, in particular whether or not it was primarily a predator or scavenger, and whether it co-existed with humans remains an open question (Wroe, 2002; Wroe & Field, 2006). Estimates for the sprint speed of this species may be central in predicting aspects of its ecology. Body mass estimates for *V. prisca* vary up to 600 kg (Hecht, 1975), but more recent estimates of average body mass for adults of this species is between 97 and 158 kg (Wroe, 2002). Using these body mass estimates and linear regression for varanids, sprint speeds of *V. prisca* is predicted to be between 9 and 9.6 m s^{-1} (32–34 km h^{-1}), while curvilinear regression predicts sprint speeds for *V. prisca* of 2.6–3 m s^{-1} (9.5–10 km h^{-1}) the latter estimate being more similar to speeds reported for similar-sized crocodiles

Crocodylus johnstoni (Webb & Gans, 1982; Renous *et al.*, 2002). Thus favouring a curvilinear relationship between speed and mass may result in a different interpretation of the paleoecology of this species, from a top predator to a scavenger, from hunter of humans, to prey.

Among extant varanids speed and habitat openness are closely linked. Species from open habitats ran significantly faster than species from either semi-open or closed habitats. For varanids much of the increase in speed associated with open habitats is due to large size; species from open areas are bigger than species from semi-open or closed habitat types (ANOVA on log transformed mass values, $F_{2,15}=5.03$, $P=0.021$). However, when we remove the effects of size from speed, using residuals from mass, there is still a significant difference between habitat openness, species from open habitats are not only absolutely quicker, but they are also relatively quicker. Similar associations between speed and habitat openness have been reported among *Niveoscincus* species (Melville & Swain, 2000), Lacertid lizards (Vanhooydonck & Van Damme, 2003) and *Leiocephalus* species (Gifford *et al.*, 2008), thus despite varanids showing a remarkable range in body sizes, similar constraints seem to apply.

However varanids appear to differ from other groups of lizards in the morphological associations with speed. Several studies have shown that sprint speeds are typically associated with relatively longer hindlimb dimensions (Snell *et al.*, 1988; Losos, 1990*a*; Sinervo *et al.*, 1991; Sinervo & Losos, 1991; Bauwens *et al.*, 1995; Bonine & Garland, 1999; Melville & Swain, 2000, 2003; Gifford *et al.*, 2008). For varanids there was only a weak non-significant positive relationship between hindlimb length and speed, instead a negative relationship between forefoot length and speed was much stronger. Based upon biomechanical predictions, shortening of the forelimbs is unlikely to be the cause of increased speed, but may be co-correlated with another performance trait often associated with animals with occupy open environments, burrowing. Although biomechanical models for burrowing species have been poorly studied, it is possible that the shortening of the lower forelimb is associated with increased strength and stability of the distal portion of the limb (Hildebrand, 1985). As varanids typically burrow head-first, shortening of the limbs in response to burrowing may only be associated with the fore-limbs.

Instead, the length of the body (thorax–abdomen length) was related to speed after phylogenetic correction. Species with a relatively shorter thorax–abdomen length were associated with faster speeds while species with relatively longer thorax–abdomen lengths were slower. This is consistent with predictions based on a biomechanical model (Van Damme & Vanhooydonck, 2002). Size-free thorax–abdomen length is significantly and positively related to the number of presacral vertebrae in varanids (Clemente, 2006), and speed may be negatively related to the number of presacral vertebrae, since this constitutes a trade-off between manoeuvrability and performance (Van Damme & Vanhooydonck, 2002). Manoeuvrability typically requires a high degree of body flexibility, which is probably aided by a
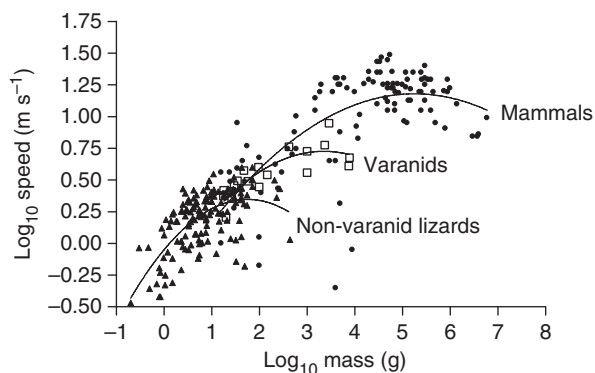

Figure 6 Curvilinear regressions between speed in mass in three different groups. Circles are mammal data from Garland (1983), squares are varanid data (from this study and Auffenberg, 1981), and triangles are data for non-varanid lizards (Zani, 1996; Van Damme & Vanhooydonck, 2001).

large number of vertebrae per unit body length (Jayne, 1982, 1988a,b; Arnold, 1988; Gasc & Gans, 1990). In contrast, a relatively stiff trunk (the result of fewer vertebrae per unit body length) would increase speed because less internal work would be needed to move axial body parts in respect to each other (Van Damme & Vanhooydonck, 2002). Preventing flexion and torsion of the body reduces internal work, therefore benefiting speed.

Differences in relative sprint speeds of Australian varanid lizards are likely due not only to differences in relative limb lengths as is the focus of this paper, but may also include several different aspects of morphology simultaneously. Further understanding of the relationship between morphology and ecology in relation to performance variables in varanids, may require examination of the interaction of the muscular–skeletal system as a whole by measuring the body kinematics during locomotion.

Acknowledgements

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