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Notes on ....

Higher than predicted endurance for juvenile goannas (Varanidae; *Varanus*)

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Abstract. Endurance of juvenile Western Australian varanid lizards was compared with that of conspecific adults. Among adults, endurance generally increased intra-specifically with increasing body size. However, juvenile varanids have a higher than expected endurance. Possible causes for this heightened endurance are discussed, and probably result from a relatively high maximal metabolic rate, as has been previously described for juvenile varanids. Origins of relatively high metabolic rates are unknown, but may be caused by greater oxygen affinity of juvenile haemoglobin when compared to adult conspecifics.

Key words: endurance, locomotion, varanid, lizard

Introduction

Locomotion is considered to be an intermediate step between form and function and is therefore important in ecomorphological and ecophysiological studies (Arnold 1983; Irschick & Garland 2001). Endurance capacity has been studied in relation to both morphological and physiological factors. Many studies have reported that endurance increases with body size (Autumn *et al*. 1994; Garland 1984; 1994), and increases with a higher relative maximal metabolic rate (Garland 1984; Garland & Else 1987; John-Alder 1984). However, few studies have examined whether juvenile lizards conform to this general pattern. We explore this idea for four species of varanid lizard.

Materials and methods

Four varanid species were captured in the field; *Varanus gouldii* (n = 15), *V. mertensi* (n = 11), *V. mitchelli* (n = 7) and *V. panoptes* (n = 12). Each lizard was measured and weighed within two weeks of capture. Snout-to-vent length (SVL) was measured using either digital callipers (± 0.05 mm) for the smaller individuals or with a ruler (± 1 mm) for the large lizards (>300 mm SVL). Mass was recorded using a spring balance or scales. Juvenile lizards were identified by a prominent yolk scar on the abdomen.

We were unable to get large lizards to run at a constant speed on a treadmill. Instead two other measures of endurance were recorded; maximum distance to exhaustion (MAXDIST) and maximum time to exhaustion (ENDUR). Both measures were taken simultaneously by encouraging lizards to run around a circular racetrack. The racetrack was 12.3 m in circumference, 1.0 m in height and 0.8 m in width. Time elapsed for each trial was measured using a stopwatch, and recorded once the lizard was deemed to be exhausted. A lizard was deemed to be exhausted when it received ten taps in quick succession without showing any further forward movement. This stimulus was found to induce escape behaviour in 'fresh' lizards, and partially exhausted lizards. Each individual was run twice and the highest score for each measure of endurance was used. For analysis, both endurance data and size data were log-transformed. The average endurance scores for the juvenile lizards were tested against the 95% confidence interval of predicted endurance, calculated for juvenile SVL by backwards extrapolating the regression for adult varanids (Zar 1998).

As lizards were not run at constant speeds around the racetrack it is possible that these measures of endurance may be the result of both aerobic and anaerobic metabolism, and are therefore not directly comparable to treadmill endurance. However, this measure of endurance is still likely to be ecologically relevant, and is therefore a useful measure of endurance capacity.

Results

When all individuals were included in the analysis for each species, size (SVL) was significantly and positively related to MAXDIST for *V. gouldii* and *V. mertensi* (Table 1). For these species larger lizards ran further and for longer. However, removing juveniles from each data set generally increased the strength of the relationship between SVL and endurance (Table 1).

Table 1

Relationship between body size (snout-to-vent length) with two measures of endurance capacity, maximum time to exhaustion (ENDUR) and maximum distance to exhaustion (MAXDIST) for four species of Australian varanid lizard both including (above) and excluding juveniles (ex. juv.). Bold font indicated P < 0.05.

Species	n	ENDUR		MAXDIST	
		r^2	P	r^2	P
V. gouldii	15	0.01	0.763	0.56	**0.001**
(ex. juv.)	13	0.29	0.054	0.40	**0.022**
V. mertensi	11	0.06	0.469	0.37	**0.046**
(ex. juv.)	8	0.27	0.190	0.53	**0.039**
V. mitchelli	7	0.48	0.084	0.19	0.325
(ex. juv.)	6	0.52	0.106	0.72	**0.034**
V. panoptes	12	0.18	0.174	0.25	0.095
(ex. juv.)	10	0.50	**0.021**	0.31	0.095

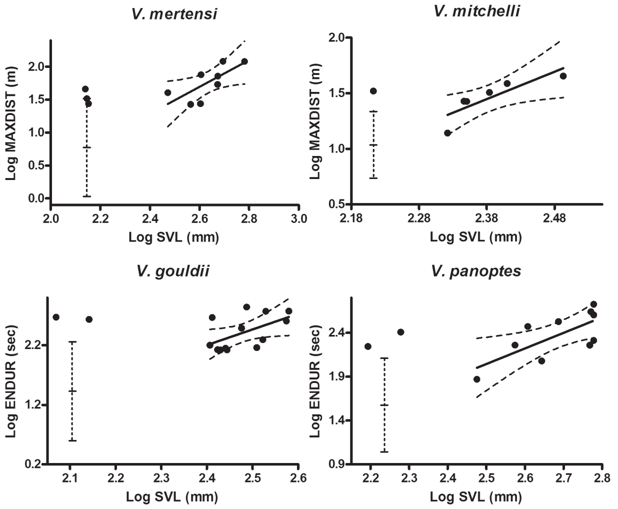

Figure 1. Endurance and SVL for four species of varanid, showing adult and juvenile scores. Regression ± 95% CI shown for regression line of adult lizards. Vertical dashed line shows mean ± 95% CI for predicted endurance of juvenile lizards based on backwards extrapolation of regression for adult lizards. Examples where juveniles have higher than expected endurance are shown. MAXDIST is plotted for *V. mertensi and V. mitchelli*, and ENDUR is plotted for *V. gouldii* and *V. panoptes*.

Removing juvenile *V. panoptes* resulted in a significant relationship for ENDUR with both mass and size. Removal of juvenile *V. mitchelli* resulted in a significant positive relationship for MAXDIST with mass and SVL. For *V. mertensi*, it had the effect of strengthening the relationship for MAXDIST with mass and SVL. *Varanus gouldii* was the only exception, showing a slightly weaker (but still significant) relationship for MAXDIST with size after juveniles were removed.

Each juvenile had a higher endurance than predicted from its SVL (Fig. 1, Table 2). Juvenile *V. mitchelli* and *V. mertensi* showed significantly higher endurance when MAXDIST was considered, but not when ENDUR was used. Conversely, juvenile *V. gouldii* and *V. panoptes* had significantly higher ENDUR than predicted from adults, but not MAXDIST. Similar results were obtained when mass was considered.

Discussion

Juveniles appear to have a higher than expected endurance, often higher than lizards many times their size. Why this occurs is unclear. Behavioural motivation is one obvious possibility; juveniles are more susceptible to predation (even by conspecific adults) and are therefore more likely to rely on their flight response. Such a reliance on flight may decline as the lizard grows larger, and predation pressure decreases. However, such an argument might predict a negative intra-specific relationship between mass and endurance for adults, which is not the case. Arguments concerning cost of transport or mass to weight ratios would also fail for similar reasoning.

One problem with interpreting results of this nature was the incomplete data set in relation to mass. There was often a substantial gap in mass between juveniles and the smallest 'adult' of a species. *Varanus mitchelli* had the smallest 'gap' between the juvenile and adults and still showed the characteristic elevated endurance for the juvenile (Fig. 1). This suggests that whatever the mechanism for enhanced endurance in juveniles (be it behavioural, morphological or physiological), it may not be a consistent change throughout development, but works rather like a switch, present only in juveniles but after some event (possibly ontogentically controlled – *i.e.* after the first year/season) it is switched off, and the lizard may not show such great endurance again until later in life (at a much larger size).

Table 2

95% confidence intervals of predicted juvenile endurance based on backwards extrapolation of regression for adult varainds. End type – Endurance type, Juv end – Measured juvenile endurance, Pred end – Predicted juvenile endurance based on backward extrapolation of regression for adults, P – significance on one-tailed t-test of measured juvenile endurance vs predicted juvenile endurance.

Species	End type	Juv end	Pred end	95% CI	P
V. gouldii	ENDUR	1.83	1.48	± 0.48	0.109
	MAXDIST	2.65	1.43	± 0.83	**0.011**
V. mertensi	ENDUR	1.54	1.04	± 0.30	**0.013**
	MAXDIST	2.17	1.65	± 0.25	0.156
V. mitchelli	ENDUR	1.52	0.77	± 0.74	**0.046**
	MAXDIST	1.79	1.38	± 1.12	0.110
V. panoptes	ENDUR	1.75	1.49	± 0.40	0.129
	MAXDIST	2.32	1.58	± 0.53	**0.016**

What could cause the relatively higher endurance of juveniles? Increased endurance is often associated with increased maximal metabolic rates (VO_2 max) and standard metabolic rates (VO_{2std}; Garland 1984; Garland & Else 1987; John-Alder 1984). Thompson (1996) noted higher VO_2 max and VO_{2std} for juveniles than would be predicted from the intra-specific regression equation for adults, for six species of *Varanus*. The heightened metabolic rate may then explain the elevated endurance score of juveniles.

What causes this heightened metabolic rate remains unknown. One possible explanation may be found in the juvenile cardiovascular system. Frappell et al. (2002) noted that the parameters controlling the transfer of O_2 through the steps of the respiratory system of varanids, seemed to be limited by circulatory convection. This is determined by hemoglobin concentration, O_2 binding capacity of the hemoglobin, and the saturation of hemoglobin. In mammals, fetal blood has a higher affinity for O_2 than maternal blood (Petschow et al. 1978). Similar results have been reported for reptiles. Juvenile alligators have a higher percentage of alkali–resistant hemoglobin than adults (Ramsey 1941). The hemoglobin of embryonic Diamond Back terrapins also has a higher oxygen affinity than hemoglobin of adults (McCutcheon 1947), and similar fetal-maternal difference in the oxygen affinity of blood was observed in viviparous garter snakes *Thamnophis sirtalis* (Manwell 1960). Though reproductive strategies differ between these groups, it is possible that the blood of juvenile varanids has a similar higher affinity for oxygen than adults. Such an observation would predict that juveniles have a heightened metabolic rate since the limiting factor for the respiratory system will have been reduced, explaining the findings of Thompson (1996) of increased metabolic rates in juvenile varanids. A heightened metabolic rate may then explain the elevated endurance score of juveniles.

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References

Arnold S J 1983 Morphology, performance and fitness. Integrative and Comparative Biology 23:347–361.

Autumn K, Weinstein R B & Full R J 1994 Low cost of locomotion increases performance at low temperature in a nocturnal lizard. Physiological Zoology 67:238–262.

Frappell P B, Schultz T J & Christian K A 2002 The respiratory system in varanid lizards: determinants of O_2 transfer. Comparative Biochemistry and Physiology A 133:239–258.

Garland Jr T 1984 Physiological correlates of locomotory performance in a lizard: an allometric approach. American Journal of Physiology- Regulatory, Integrative and Comparative Physiology 247:806–815.

Garland Jr T 1994 Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In: Lizard Ecology: Historical and Experimental Perspectives, (eds E. R. Vitt and E. R. Pianka), pp. 237–259. Princeton: Princeton University Press.

Garland Jr T & 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.

Irschick D J & Garland Jr T 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 (T_3 and T_4) in an iguanid lizard. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 154:409–419.

Manwell C 1960 Comparative physiology: blood pigments. Annual Review of Physiology 22:191–244.

McCutcheon F 1947 Specific oxygen affinity of hemoglobin in elasmobranchs and turtles. Journal of Cellular and Comparative Physiology 29:333–344.

Petschow R., Petschow D, Bartels R, Baumann R & Bartels H 1978 Regulation of oxygen affinity in blood of fetal, newborn and adult mouse. Respiration Physiology 35:271–282.

Ramsey H J 1941 A comparative study of hemoglobin denaturation. Journal of Cellular and Comparative Physiology 18:369–377.

Thompson G 1996 Aspects of the Morphology and Metabolism of Western Australian Goannas (Reptilia: Squamata: Varanidae) with particular reference to the Effects of Body Mass and Shape. PhD thesis. University of Western Australia, Perth, Western Australia.

Zar J H 1998 Biostatistical Analysis. 4th Ed. Pearson Education, New Jersey, USA.