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Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*

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(With 1 figure in the text)

The present study investigates relationships among size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. Maximal running speed, body mass, snout-vent length, tail length, fore- and hind limb spans and thigh muscle mass were measured in 68 field-fresh individuals spanning the entire ontogenetic size range (1·3–48 g). Relative lengths of both fore- and hind limbs decrease with increasing body mass (= negative allometry), whereas relative tail length and thigh muscle mass increase with body mass (= positive allometry). Repeatable and significant differences in maximal running speed exist among individuals. Maximal running speed scales as (body mass)$^{0 \cdot 161}$, and 59% of the variation in maximal speed was related to body mass. Based on the results of the present and previous studies, data on scaling of body proportions alone appear inadequate to infer scaling relationships of functional characters such as top speed.

Surprisingly, individual variation in maximal speed is not related to individual variation in shape (relative limb, tail and body lengths). These components of overall shape are not independent; individuals tended to have either relatively long or relatively short limbs, tails and bodies for their body mass. Even the significant difference in multivariate shape between adult males and females has no measurable consequences for maximal speed. Speeds of field-fresh animals did not vary on a seasonal basis, and eight weeks of captivity had no effect on maximal running speeds. Gravid females and long-term (obese) captive lizards were both approximately 12% slower than field-fresh lizards.

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Introduction

Size is a fundamental character of any organism, and its correlates and consequences are manifold (Garland, 1982, 1983*a*, *b*; Peters, 1983; Calder, 1984; McMahon, 1984; Schmidt-Nielsen, 1984). Shape is another fundamental organismal property, and related organisms may or may not

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be of similar shape. Size and shape would both be expected to influence such whole-animal performance characters as maximal running speed, and several theories of biological similarity offer predictions concerning the relationships among size, shape and speed. Perhaps the simplest theory is that regarding geometric similarity (see Hill, 1950; Tenney, 1967; Maynard Smith, 1968; Gunther, 1975; McMahon, 1975, 1984; Alexander, 1982 and above references for details). Geometrically similar animals are scale models of each other; they differ only in size but not in shape, all linear body dimensions being proportional to or 'scaling as' (body mass)$^{1/3}$. Among geometrically similar tetrapods, maximal running speed is expected to be mass independent. Among species of quadrupedal mammals, body proportions approach geometric similarity (references in Alexander, 1982; Alexander & Jayes, 1983; Peters, 1983; Garland, 1983*b*, 1984), but maximal speeds are not mass independent (Garland, 1983*b*). Maximal speed is often mass independent within orders of mammals (Garland, 1983*b*), although limb proportions deviate from geometric similarity within one of these orders (McMahon, 1975, 1984; Alexander, 1982). Preliminary analyses indicate that limb bone lengths scale close to geometric similarity among species of lizards (Peterson & McDonald, 1982), whereas maximal speeds increase slightly but significantly with increasing size (Garland, 1982).

Other theories of biological similarity offer different predictions concerning the relationships among size, shape and speed, but none adequately predicts scaling relationships for both limb dimensions and maximal speed (static stress similarity, elastic similarity, dynamic similarity: see Gunther, 1975; McMahon, 1975, 1984; Alexander, 1982; Alexander & Jayes, 1983; Garland, 1983*b*). However, existing data on body proportions and speed have not generally been collected for the same set of animals, and the 'noise' so introduced might obscure congruence between theory and measurement. Furthermore, most studies to date have been interspecific comparisons, and hence suffer from the possible confounding influences of phylogeny (discussions and references in Harvey & Mace, 1982; Garland, 1983*b*; Bennett, Huey & John-Alder, 1984; Huey, Bennett, John-Alder & Nagy, 1984). For example, data on the scaling of speed at the trot-gallop transition, which McMahon (1975, 1984) cites as supporting his model of elastic similarity, have been criticized because the data set compares members of three different mammalian orders (Garland, 1983*b*), whose linear dimensions do not scale in accordance with elastic similarity (Alexander, 1982).

The present study was undertaken to quantify both body proportions and maximal running speeds within an ontogenetic series of a single species, measuring all characters on the same individuals. I first quantify the scaling relationships for both speed and body proportions, and ask whether form and function scale congruently. That is, could the scaling of a functional character such as maximal running speed be predicted solely from knowledge of the scaling of body proportions? If so, then the range of plausible inferences open to morphologists, ecologists and paleobiologists might be expanded significantly. After considering the allometry of speed, the confounding effects of size are eliminated statistically (Garland, 1984), and individual variations in maximal speed are related to individual differences in shape. Such correlations, if they could be shown to exist, would help to elucidate the selective importance of individual variations in shape as they occur in natural populations. Natural selection acts directly on functional characters, such as maximal running speed, and indirectly on morphological characters (e.g. relative limb lengths) only if such characters are correlated with aspects of whole-animal performance that affect fitness (e.g., Lundelius, 1957: 70; Huey & Stevenson, 1979; Arnold, 1983).

I chose a reptile for study for several reasons. Firstly, the post-natal ontogenetic size range exhibited by reptiles is typically at least one to three orders of magnitude in body mass, which is much greater than in most terrestrial endotherms. Secondly, since all reptiles must function independently, essentially without parental care, from birth, the ecological consequences of ontogenetic changes in performance (see Pough, 1983) should be more apparent than in birds or mammals. Finally, because of the indeterminate, essentially life-long, and slow (in comparison with endotherms) growth of reptiles (Case, 1978), and because reptiles begin breeding at sizes that are well below maximum, smaller ontogenetic stages of reptiles are considered to be significantly more important to their populations than are corresponding submaximal mammalian or avian stages (Dodson, 1975*b*: 444).

Methods

Study animal

Amphibolurus nuchalis, Central netted dragons (Heatwole, 1976; Cogger, 1983), were collected in extreme western New South Wales, Australia, in the vicinity of Fowlers Gap Arid Zone Research Station of the University of New South Wales. A total of 68 animals was collected at 3 different times: 13–16 Dec. 1983, 4 males, 2 females, 2 gravid; 19–21 Jan. 1984, 23 males, 6 females, 6 gravid, 12 juveniles; 9 March 1984, 9 males, 2 females, 2 juveniles. Animals smaller than 7 g could not be sexed and were classified as juveniles. Animals larger than 9 g were considered adults and were sexed by applying pressure to the base of the tail to determine the presence of hemipenes. Gravid females were determined by palpation. Seven animals that had been maintained in captivity for 22 months by Dr A. J. Hulbert were also measured. Most of these individuals were noticeably obese (see Results).

Measurement of maximal running speed

Maximal running (burst) speeds were measured on a microprocessor-controlled, photocell-timed racetrack (Huey, Schneider, Erie & Stevenson, 1981; Huey & Hertz, 1982; Hertz, Huey & Nevo, 1983; Huey *et al.*, 1984). The track was 3 m long and 0·2 m wide. It was constructed of cardboard with vertical slits in the walls (covered by acetate sheets) to allow passage of focused light beams across the track on to 12 sets of 6 vertically aligned phototransistors (vertical span of phototransistors was 60 cm). The sets of photocells were placed at intervals of 5, 5, 5, 10, 25, 25, 25, 25, 25, 25, 25 cm over the first 2 m of the track. Such a spacing allows the calculation of both initial acceleration (Huey & Hertz, 1984; Garland, unpubl.) and maximal speeds. The floor of the track was covered with a rough-surfaced rubber mat which provided excellent traction.

Lizards in individual cloth sacs were preheated to 41 °C in a constant temperature cabinet. Lizards were removed from the cabinet and quickly placed on the track with their nose immediately in front of the first set of photocells (such alignment was possible by observing the shadow of the nose falling on the track wall). Lizards either ran immediately on release from the hand or, after a pause of a few seconds, were induced to run by a grabbing motion and/or by a tap on the tail. Most individuals would accelerate smoothly (cf. Huey & Hertz, 1984; Huey *et al.*, 1984) and race to the end of the track into an open black cloth sac resembling a safe retreat. Two such trials were conducted in quick succession; then the animal was returned to the temperature box. At the end of such trials, body temperatures approximated 39 °C, so the effective body temperature is considered to be 40 °C, which is near the modal field body temperature of this species (Pianka, 1971; Heatwole, 1976). In any case, thermal sensitivity of sprint speed is expected to show a broad plateau around the mean (or modal) field body temperature (Bennett, 1980; Hertz *et al.*, 1983). After a rest of at least 2 hours, 2 more trials were conducted. On the following day, the entire sequence was repeated, so that each individual was raced a total of 8 times. For each trial, the fastest consecutive 0·5 m interval was computed. The fastest such interval ever recorded for an individual is reported as its maximal speed. All speed trials were completed within 9 days of capture (except for long-term captives), and animals were fasted during this interval.

Morphometric measurements

Body measurements were made on living animals immediately after the final-burst speed trial. Body mass (M) was measured to the nearest 0·001 g on an electronic balance. All linear measurements were recorded with a ruler to the nearest 0·5 mm. Snout-vent (SV) and total body lengths were measured, and tail length (TAIL) was calculated as their difference. Six individuals missing small portions of their tails were excluded from some analyses. Hind (HLS) and forelimb spans (FLS) were measured from toe tip to toe tip (excluding claws), with limbs outstretched perpendicularly to the body (Garland, 1984). The author made all measurements. On a subsample of lizards ($n = 33$), the mass of all thigh muscles (THIGH) was determined by dissection (Garland, 1984). Because some growth occurred between the times of measurement of body dimensions and THIGH, residuals of allometric equations (see below) were not compared.

Statistical analyses

All statistical analyses were performed on the University of California, Irvine Honeywell CP6 computer, using the Statistical Package for the Social Sciences (SPSS), version 7–9. Accounts of the techniques used herein are found in the SPSS manual (Nie, Hull, Jenkins, Steinbrenner & Bent, 1975; see also Dodson, 1975*a*, *b*; Sokal & Rohlf, 1981; Garland, 1983*b*, 1984). All data were $\log_{10}$ transformed before analysis.

Speed is here considered to be a character which depends functionally on body mass (cf. Garland, 1983*b*), so standard least squares regression estimates of the relation between speed and size seem most appropriate (see below). Analysis of covariance (ANCOVA) was employed to determine if speed differed, using mass as the covariate, or if the relation between speed and size differed in relation to date of capture or among males, females and juveniles. To determine whether individual variations in shape components were independent, and to determine whether differences in speed were related to individual differences in shape, independent of size (M), I performed 2 analyses. Firstly, I calculated residuals from allometric equations (see below) for all 60 non-gravid, field-fresh individuals and looked for correlations among these residual (individual) variations in shape and speed (cf. Garland, 1984). Secondly, I conducted a principal component analysis (PCA) of speed, mass and the 4 linear body dimensions, with and without speed, using either log transformed data or the residuals from allometric equations.

Adult males attained larger sizes than did females (see Fig. 1) and males and females appeared to differ in shape. To determine whether the relationship between a given linear body dimension and M differs between males, females and juveniles, ANCOVA was employed. However, even if ANCOVA reveals no significant differences in bivariate shape, significant differences may exist in multivariate shape. Therefore, discriminant analysis was performed on the log transformed morphometric data and on residuals from allometric equations.

Because ANCOVA revealed no significant differences among males, females and juveniles (see Results), the 60 field-fresh lizards were pooled for calculation of allometric equations. The data presented herein are 'mixed cross-sectional' (Cock, 1966: 136; Sweet, 1980); they do not represent the allometric growth trajectories of individual lizards. Nevertheless, it may be argued that such cross-sectional data are reasonable estimates of the average ontogenetic (growth) trajectory, assuming that natural selection has not biased the sample systematically in relation to size. To determine whether lizards deviated from geometric similarity, which is here considered a null hypothesis (cf. Sweet, 1980) for size-related changes in shape, the following analyses were performed. Firstly, regression analysis was used to generate allometric equations of the form:

$$\log_{10} \mathrm{Y} = \log_{10} \mathrm{a} + \mathrm{b} \log_{10} \mathrm{M}$$

which can be converted to arithmetic form as:

$$\mathrm{Y} = \mathrm{aM}^{\mathrm{b}}$$

where M = body mass in g. The choice of body mass as the measure of size against which to quantify scaling relationships is justifiable on functional grounds (cf. Dodson, 1975*a*: 324; Garland, 1983*b*), because the mass of an animal must be accelerated and kept in motion at top speed. Furthermore, measurement of M can be

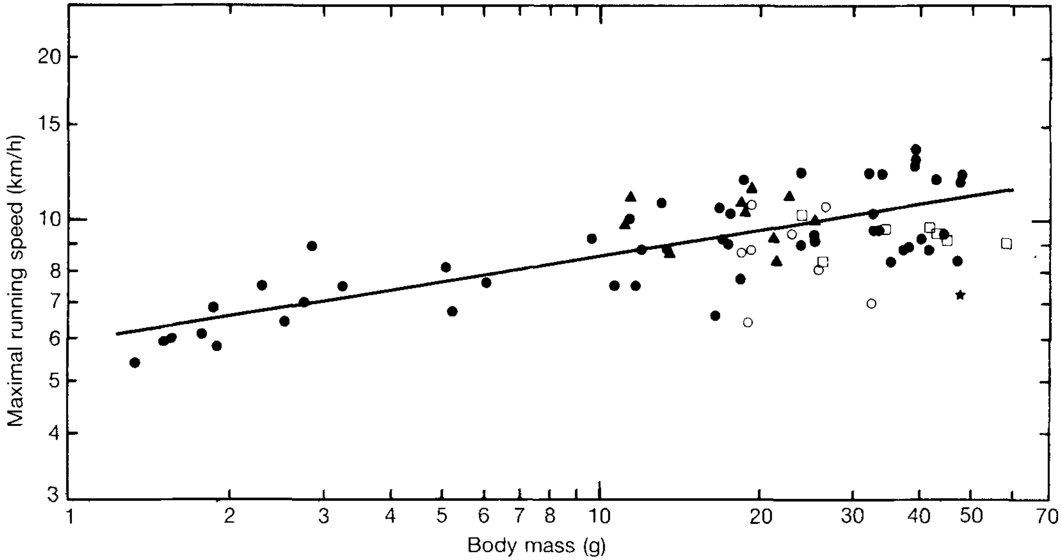

FIG. 1. Log-log plot of maximal running speed vs. body mass in the agamid lizard *Amphibolurus nuchalis*. Solid line is least squares regression of $\log_{10}$ speed on $\log_{10}$ mass (slope = 0·161) for 60 field-fresh animals; closed circles (●) are juveniles (< 7 g) and adult males, closed triangles (▲) are females. Open circles (○) are gravid females, open squares (□) are long-term captive individuals; both groups were approximately 12% slower than the 60 field-fresh lizards. Star (★) represents adult male missing one hind leg (see text).

highly accurate and precise with modern electronic balances. Finally, body mass had the greatest range of any character (Table I), varying by 36-fold, which reinforces its use as the character against which scaling relationships are judged (Dodson, 1975*a*: 324). Regression equations and their confidence intervals were obtained from SPSS using Student's *t* distribution. Because M cannot be measured entirely without error, including both measurement and biological components (e.g. day-to-day variations in body mass, see Ricker, 1973), regression analysis should tend to underestimate the true structural relationships (e.g. see Ricker, 1973; Sokal & Rohlf, 1981; Harvey & Mace, 1982) between body dimensions and M. Based on the recommendations of Ricker (1973) and others, I have therefore also calculated reduced major axis (RMA) slopes as the ratio of standard deviations (S.D.) or, equivalently, b/r, where b = slope from linear regression analysis and r = correlation coefficient. Confidence intervals (CI) for RMA slopes are identical to those determined for linear regression slopes (Kermack & Haldane, 1950); however, because they are asymmetrical around the RMA slope (Ricker, 1973), such CIs may be misleading if one uses them to test whether a RMA slope is significantly different from an expected (theoretical) value. Reduced major axis slopes were therefore compared with expected values ($\frac{1}{3}$ for scaling of linear dimensions), using the test statistic provided by Clarke (1980: 442) with degrees of freedom computed from his Equation 5.1. To faciliate comparisons with some previous studies, allometric equations with SV as the independent variable were also calculated.

Results

Measurement of maximal running speed was highly repeatable and individuals differed significantly in maximal speed. Mean speeds on day 1 (8·849 km/h) and day 2 (8·562 km/h) were not significantly different (paired *t*-test; $t = -1{\cdot}856$, $n = 68$, $P = 0{\cdot}0678$); 37 individuals were faster on day 1, 31 were faster on day 2. The correlation (r) between maximal speeds of individuals

TABLE I

Descriptive statistics and correlations

	Maximal running speed (km/h)	Body mass (g)	Snout-vent length (mm)	Tail length (mm)	Hind limb span (mm)	Forelimb span (mm)
Range	5·39–13·53	1·33–48·02	36–123	39–178	55–154	43–117
Mean*	0·956	1·141	1·900	1·990	2·026	1·918
S.D.*	0·097	0·460	0·160	0·178	0·138	0·132
Correlations*						
Mass	0·766					
SV	0·771	0·994				
TAIL	0·766	0·988	0·989			
HLS	0·769	0·992	0·992	0·988		
FLS	0·763	0·992	0·993	0·987	0·998	

* Mean, S.D. and correlations are for $\log_{10}$ transformed data

$n = 60$ except $n = 54$ for TAIL

Thigh muscle mass ranged from 0·018 to 1·062 g ($n = 33$; mean of logs = −0·737, S.D. = 0·420)

TABLE II

Allometric equations with body mass as independent variable

Character	a ÷/× 95% C.I.	b ±95% C.I.	r^2 (%)	SEE	CV*	RMA	Significance**
	Linear regression estimates of $Y = a(\text{Mass})^b$						
Speed	5·92 ÷/× 1·106	0·161 ± 0·036	58·7	0·06265	14·30	0·210	——
SV	31·98 ÷/× 1·029	0·346 ± 0·010	98·8	0·01800	4·10	0·349	$P < 0·10$
TAIL	37·59 ÷/× 1·046	0·377 ± 0·016	97·6	0·02767	6·31	0·381	$P < 0·02$
HLS	48·66 ÷/× 1·029	0·297 ± 0·010	98·3	0·01800	4·12	0·299	$P < 0·01$
FLS	39·26 ÷/× 1·028	0·284 ± 0·010	98·4	0·01700	3·89	0·286	$P < 0·01$
THIGH	1·317‡ ÷/× 1·140	1·160 ± 0·054	98·4	0·05407	12·25	1·169	$P < 0·01$

SEE = standard errors of estimate of regressions in $\log_{10}$ units

* CV = 230·26 × S.D. of residuals from allometric equation (see Garland, 1984)

** Significance of two-tailed *t*-tests (Clarke, 1980) comparing reduced major axis slope vs. $\frac{1}{3}$ or, for THIGH, vs. unity

‡ $\times 10^{-2}$

$n = 60$ except $n = 54$ for tail, $n = 33$ for THIGH

on day 1 and 2 was 0·771 ($P \ll 0·001$). As part of another study, seven of the adult males were kept in captivity for 55 days, then retested. A two-way ANOVA (see Sokal & Rohlf, 1981: 354–359) indicated that maximal speed did not change significantly ($F = 0·0063$, *d.f.* = 1, 6, $P > 0·75$), but that individuals differed significantly in maximal speed ($F = 45·389$, *d.f.* = 6, 6, $P \ll 0·001$). The correlation between speeds (single fastest 0·5 m intervals) measured eight weeks apart was 0·967 ($P < 0·001$).

Maximal running speed varied by a factor of 2·5 (Table I) and, on average, large lizards were faster than small lizards (Fig. 1). Speed scaled as $M^{0·161}$ (Table II), and body mass accounted for 59% of the total variation in speed. The fastest individual (a 39·42 g male) attained a speed of 13·53 km/h. Visual inspection of Fig. 1 suggests a curvilinear relation between $\log_{10}$speed and $\log_{10}$M (cf. Garland, 1983*b*), but a second-degree polynomial does not significantly improve the fit ($P = 0·151$).

TABLE III

Allometric equations with snout-vent length as independent variable

	Linear regression estimates of $Y = a(SV)^b$						
Character	a ÷/× 95% C.I.	b ±95% C.I.	r^2 (%)	SEE	CV*	RMA	Significance**
Speed	1·181 ÷/× 1·556	0·465 ± 0·101	59·5	0·06200	14·16	0·603	——
Mass	0·5290‡ ÷/× 1·446	2·851 ± 0·084	98·8	0·05164	11·80	2·869	$P < 0·20$
TAIL	0·9002 ÷/× 1·218	1·079 ± 0·045	97·8	0·02674	6·10	1·091	$P < 0·10$
HLS	2·551 ÷/× 1·134	0·852 ± 0·029	98·4	0·01759	4·01	0·859	$P < 0·01$
FLS	2·335 ÷/× 1·121	0·816 ± 0·026	98·6	0·01594	3·64	0·822	$P < 0·01$

SEE = standard errors of regressions in $\log_{10}$ units
* CV = 230·26 × S.D. of residuals from allometric equation
** Significance of two-tailed *t*-tests (Clarke, 1980) comparing reduced major axis slope vs. unity or, for mass, v.s. 30
‡ $\times 10^{-4}$
$n = 60$ except $n = 54$ for tail

TABLE IV

Correlations among residuals from allometric equations. Mass residuals are above diagonal, snout-vent length residuals are below. Correlations > 0·254 (> 0·268 for TAIL correlations) are significant at ***P*** *< 0·05 and are in* **boldface**

	Speed	Mass	SV	TAIL	HLS	FLS
Speed	1	——	0·144	0·080*	0·119	0·041
Mass	−0·010	1	——	——	——	——
SV	——	——	1	**0·389**	**0·454**	**0·502**
TAIL	0·020**	**0·303**	——	1	**0·396**	**0·369**
HLS	0·052	**0·410**	——	**0·328**	1	**0·857**
FLS	−0·037	**0·387**	——	**0·276**	**0·845**	1

$n = 60$ except $n = 54$ for all TAIL correlations
* $r = 0·055$ for $n = 60$
** $r = 0·007$ for $n = 60$

Amphibolurus nuchalis are not geometrically similar (Tables II and III). Large individuals have relatively longer tails and more massive thigh muscles, but shorter fore- and hind limbs than do small individuals. The relationship between linear body dimensions and M (both log transformed) did not differ in relation to capture date, between males and females, or between juveniles and adults (results of ANCOVA). Furthermore, in no case did a polynomial equation fit the relationship between a linear body dimension and M better than did a simple linear regression. Therefore, pooled allometric equations based on all non-gravid, field-fresh animals ($n = 60$) are adequate descriptors of average ontogenetic changes in bivariate shape.

None of the correlations between speed residuals and shape residuals is significant, but all shape residuals are positively and significantly correlated (Table IV). The correlation between HLS and FLS residuals is the strongest ($r = 0·845$ or 0·857, $P \ll 0·001$). A stepwise multiple regression of speed residuals on all shape residuals yielded no significant predictive equation.

Principal component analyses further illustrate these patterns and reinforce the conclusion that individual variation in speed is unrelated to individual variation in shape. Using residuals (Table V), all four shape characters load heavily on the first factor, which is interpreted as a general body stoutness factor. In other words, the major axis of variation indicates that, for their body

TABLE V

Principal component analysis of mass residuals

		Component correlations with factors				
		I	II	III	IV	V
Mass residuals	SV	0·758	–	+	0·646	–
	TAIL	0·621	–	0·742	–	+
	HLS	0·889	–	–0·280	–	–**
	FLS	0·888	–	–0·316	–	0·272
	Speed	+	0·964	+	–	+
Eigenvalue		2·606	0·965	0·737	0·546	0·146
% of variance explained		52·1	19·3	14·7	10·9	2·9
Cumulative % explained		52·1	71·4	86·2	97·1	100·0

* Only correlations $> 0{\cdot}268$ in magnitude are listed. These may be considered significant at $P < 0{\cdot}05$. Only sign (+) is given for non-significant component correlations. $n = 54$

** component correlation $= 0{\cdot}264$

mass, individuals tend to have either a long body, long tail and long limbs, or a short body, short tail and short limbs. Residual variation in speed is the only character significantly related to factor II. Factor III contrasts TAIL with HLS and FLS, and further indicates the tight correlation between residual HLS and FLS. SV loads heavily on factor IV. Factor V accounts for only 2·9% of the variation in residuals, but tends to contrast HLS with FLS. The first factor of a PCA of the log transformed characters (not residuals) accounted for 99·3% of the total variation; component correlations for M, SV, TAIL, HLS and FLS were all $> 0{\cdot}95$ and that for speed was 0·775. Only speed was significantly correlated with the second factor ($-0{\cdot}631$), and no other factor loadings on any other factor were significant (all $< 0{\cdot}25$ in magnitude). Deleting speed from either of the PCAs (on residuals or log transformed data) did not qualitatively change the pattern of factor loadings for the morphometric characters.

Although ANCOVA revealed no significant differences in bivariate shape, males and females do differ in multivariate shape. A multivariate analysis of variance of the five morphometric characters was significant ($n = 40$, Wilks' lambda $= 0{\cdot}515$, $F = 6{\cdot}42$, $d.f. = 5$ and 34, $P = 0{\cdot}0003$). Univariate F-ratios indicate significant differences in TAIL, HLS and FLS ($P = 0{\cdot}023$ to $0{\cdot}046$), but not in M or SV ($P > 0{\cdot}07$). *A posteriori* classification probabilities are correct for 88% of the individuals (29 of 32 males, 6 of 8 females). Judging from the magnitudes of the normalized canonical vectors, SV is the character most strongly related to the canonical discriminant function (cosine of angle between factor and original character, $SV = -0{\cdot}822$; an absolute value of 1 indicates a perfect relation, 0 would indicate no relation). Hind limb span was the second most strongly related character to the discriminant function (0·433). Thus, size *per se* (body mass in the present study) is not the best discriminator. Note the complete overlap in body mass between males and females (Fig. 1). Significant discrimination between males and females was also accomplished using only residuals from allometric equations ($P = 0{\cdot}0002$; 83% of individuals classified correctly; other results not presented). This result demonstrates further that males and females differ significantly in multivariate shape independent of size.

Capture date had no significant effect on the relation between speed and M for males. Due to small sample sizes (total $n = 10$), the effect of capture date was not tested for females. Pooling the 36 males for comparison with the 10 females, ANCOVA revealed no significant differences between males and females. Therefore, the 46 adults were pooled for comparison with the

14 juveniles. Again, ANCOVA revealed no significant differences. The visual impression that the relation between speed and size might differ for juveniles smaller than 4g vs. all others is also unsupported by ANCOVA. Finally, I compared speeds of all non-gravid lizards with regard to capture date. Four of the six December lizards fell above the regression line for all 60 lizards, which was reflected in a significantly ($P = 0{\cdot}041$) higher slope ($b = 0{\cdot}197$ vs. $b = 0{\cdot}156$) for the six December lizards. Due to the small sample size of the December group, as well as the marginal level of statistical significance, I consider this result to be of doubtful biological significance.

Gravid females were approximately 12% (on an arithmetic scale) slower for their body mass than the other 60 field-fresh lizards (ANCOVA, $P = 0{\cdot}029$; see Fig. 1). Long-term captives were also 12% slower than the 60 field-fresh lizards ($P = 0{\cdot}037$). For their snout-vent length, gravid females and long-term captives averaged 13% and 24%, respectively, heavier than other lizards. One adult male (47·44 g) captured was missing the distal portions of the right leg from about 5 mm below the knee; the wound was well healed and appeared old. This animal was not used in the analyses, but it ran surprisingly well on the racetrack and attained a top speed of 7·26 km/h, which is 66% of the speed predicted for a lizard of its mass (see Fig. 1).

Discussion

Central netted dragons do not remain geometrically similar during ontogeny. Large lizards have significantly longer tails, more massive thigh muscles, shorter limbs, and slightly thinner bodies. Although these lizards deviate from geometric similarity, they do not do so in a way consistent with any other theory of biological similarity (Table VI). Linear body dimensions scale on M with exponents ranging from 0·286 for FLS to 0·381 for TAIL (Table II), and these exponents differ significantly from each other. In contrast, theoretical expectations are, for a single scaling exponent, ranging from 0·200 for static stress similarity to 0·333 for geometric similarity, applicable to all linear dimensions (but see Rashevsky, 1960, cited in McMahon, 1984). Thigh muscle mass does not remain a constant proportion of total body mass, scaling as $M^{1\cdot169}$. Thigh

TABLE VI

Predictions of four theories of biological similarity versus ***Amphibolurus nuchalis***

	Scaling exponent*					
	Linear body dimensions	Body or muscle diameter	Stride (hind limb) length	Body or muscle cross-sectional area	Natural (stride) frequency	Speed
Geometric	0·333	0·333	0·333	0·667	−0·333	0
Elastic	0·250	0·375	0·375	0·750	−0·125	0·250
Static stress	0·200	0·400	0·400	0·800	0	0·400
Dynamic	0·333	0·333	0·333	0·667	−0·167	0·167
Amphibolurus nuchalis	0·286 for FLS to 0·381 for TAIL	0·326 for Body or 0·435 for THIGH	0·299* to 0·435	0·651 for Body or 0·870 for THIGH	−0·089* to −0·274	0·161 or 0·210 for RMA

* See text for references and method of calculation of *A. nuchalis* exponents

muscle cross-sectional area may scale approximately as thigh muscle mass/hind limb span and hence as $M^{1\cdot169}/M^{0\cdot299} = M^{0\cdot870}$, which is greater than predicted by any theory (Table VI). Thigh diameter would scale as $M^{0\cdot435}$, also greater than expected. In contrast, body cross-sectional area is estimated to scale as body mass/snout-vent length, or as $M^{1\cdot000}/M^{0\cdot349} = M^{0\cdot651}$; with body diameter scaling as $M^{0\cdot326}$, both exponents being close to the expectation for geometrically similar animals.

McMahon (1975: 624) argues that stride length (at the trot-gallop transition) should be associated with the diameter dimension of the similarity models. If it is assumed that stride length at maximal speed is a constant multiple of the value at the trot-gallop transition, then stride length of *A. nuchalis* at top speed would be predicted to scale as $M^{0\cdot435}$ (= thigh muscle diameter) or $M^{0\cdot326}$ (= body diameter). Both of these values are substantially different from the scaling exponent (0·299) for hind limb span, which might be presumed to correlate with stride length, and taken together the three exponents span the range of values predicted by the models (Table VI). Assuming speed = stride length × stride frequency, then stride frequency in *A. nuchalis* is expected to scale as anywhere between $M^{0\cdot161}/M^{0\cdot435} = M^{-0\cdot274}$ to $M^{0\cdot210}/M^{0\cdot299} = M^{-0\cdot089}$, which again spans the range of predicted values (Table VI).

To summarize, morphological scaling relationships in this lizard are more complex than allowed by any single theory of biological similarity. Furthermore, no existing theory would accurately predict the scaling of maximal speed, given only the scaling of body proportions (cf. Gunther, 1975; Garland, 1983*b*).

Several previous workers have attempted to infer the ecological significance of ontogenetic deviations from geometric similarity in lizards. Negative allometry of hind limbs is more common than positive allometry (Kramer, 1951; Laerm, 1974; Pounds, Jackson & Shivley, 1983; Garland, 1984; this study). Kramer (1951: 205) related negative allometry to the attainment of 'immediate efficient locomotion' in hatchlings. Laerm (1974: 409) argued that 'allometric decrease in functional size of limb . . . show(s) good . . . correlation with . . . differences in habitat association, as well as correlations with differences in behavioral preferences for running on water [in Basilisk lizards] and the functional ability to do so.' Dodson (1975*b*: 421, 446) noted that 'positive allometry of limb length correlates with increased size of home range during ontogeny' and suggested that 'increased relative length of the limbs is the skeletal basis of the adaptation to increased movement.' Pounds *et al.* (1983: 1101) suggested that positive allometric growth of hind limbs (1) 'could be related to the use of vertical perches' (cf. Kramer, 1951), or (2) might represent 'an adaptive temporal patterning of energetic investments in morphology in relation to a behavioral change during ontogeny. Specifically, (if) juvenile(s) . . . rely more on passive crypsis as an antipredator tactic than do the adult(s) . . .'

As argued above, however, (and see Garland, 1984 for similar results in another lizard) knowledge of the scaling of limb proportions alone appears insufficient to allow accurate predictions as to the scaling of maximal running speed. Therefore, the arguments of Kramer (1951), Dodson (1975*b*) and Pounds *et al.* (1983) must be viewed with caution, because, lacking measures of function, they have relied on the assumption that scaling of limb dimensions determines, to a significant extent, the scaling of ecologically important locomotor capacities. Even the interspecific relationship between relative limb length and maximal speed has yet to be quantified for lizards, although species with more cursorial tendencies do tend to possess longer limbs (e.g., Snyder, 1962; Urban, 1965; Pianka, 1969; Pianka & Parker, 1972; Jackson, 1973; Moermond, 1979; Jaksić, Núñez & Ojeda, 1980; but see Huey, 1982). Among mammals, relative hind limb length correlates with cursorial tendencies and top running speed (Bakker, 1975;

Coombs, 1978). It should be noted that limb length may be related to functions other than locomotion (e.g., see Pianka, 1966: 1057; Muth, 1977: 718). Furthermore, limb configuration has no measurable effect on the energetic cost of transport (Taylor, Shkolnok, Dmi'el, Baharav & Borut, 1974; Bakker, 1975; Taylor, Heglund & Maloiy, 1982), and any relationship between relative limb size and mobility (e.g., Garland, 1983*a*) is undescribed.

Why might scaling of limb proportions be decoupled from the scaling of maximal running speed? Hind limb span is presumed to correlate with stride length; however, there are several reasons why HLS may not be directly proportional to stride length. This is possible if the degree of limb extension (see Snyder, 1954, fig. 1) and/or the amount of pelvic rotation (Daan & Belterman, 1968; Peterson, 1984) change in relation to M. If such is the case, then measurements of limb components (e.g., thigh or shank length, femur length, cf. Dodson, 1975*b*; Pounds *et al.*, 1983) would be even less reliable correlates of stride length. The hind limbs provide the majority of the power for locomotion in lizards (Snyder, 1954, 1962; Urban, 1965). However, muscle contractile properties and/or the mechanical advantage of individual locomotory muscles may change during ontogeny (e.g., Dodson, 1975*a*; Sperry, 1981; Witthames & Walker, 1982; Carrier, 1983). Direct measurement of stride length and frequency (Huey, 1982), lengths of limb segments, HLS, and FLS, muscle contractile properties and speed, will be necessary to determine why maximal running speed scales as it does in any group of animals.

The tail functions in lizard locomotion (Snyder, 1954, 1962; Urban, 1965; Daan & Belterman, 1968), especially in bipedal forms, where the tail tends to be better developed. Experimentally, tail loss decreases maximal speed in several bipedal lizards (Pond, 1981; references in Daniels, 1983), but has no significant effect in the quadrupedal iguanid *Sceloporus merriami* (R. B. Huey & A. E. Dunham, pers. comm.), and actually increases speed in a quadrupedal gecko (Daniels, 1983). Positive allometry of tail length may indicate that large individuals are better suited to bipedality. Some individual *A. nuchalis* ran bipedally on the racetrack, others appeared to run quadrupedally at top speed; unfortunately, these observations were not quantified.

Variations in the components of shape are not independent (Tables IV & V). Individuals tend to have either long or short limbs, bodies *and* tails, for their size. Fore- and hind limb spans are the most tightly intercorrelated, and their scaling exponents (0·286 and 0·299, respectively) are not significantly different. Thus the ratio FLS/HLS does not change ontogenetically. These intercorrelations suggest the existence of factors, either genetic or environmental (Cock, 1966), which have organism-wide effects on body stoutness. Interestingly, Jaksić *et al.* (1980) found that, although they differed significantly in absolute or relative (to body length) limb lengths, none of 12 species of *Liolaemus* lizards differed in the ratio forelimb/hind limb. Jaksić and co-workers suggested that 'this ratio has a functional significance for locomotion that constrains the independent development of both limbs'. Moreover, Kramer (1951) found that, interspecifically, relative lengths of tail and hind limbs are correlated, although he could not establish a significant correlation within populations.

What accounts for individual variation in maximal speed? The present study found no correlation between individual variations in maximal speed and individual variations in body shape, including limb lengths. This lack of correlation between speed and shape is even more surprising considering that individual components of shape are not independent. Garland (1984) also found no individual correlates of maximal speed in the iguanid lizard *Ctenosaura similis*. In that study, thigh muscle mass and myofibrillar ATPase activity were measured in addition to HLS. Bennett *et al.* (1984) found no differences in myofibrillar ATPase or in contractile speeds of hind limb muscles between two congeneric lacertid lizards of the same size, but found that they differed significantly in maximal speed. Future studies might look for correlations with individual variation in stride length and frequency or contractile properties of important locomotory muscles.

Male and female *A. nuchalis* did not differ in maximal running speed. Nor did ANCOVA reveal any significant sexual dimorphism in components of bivariate shape. Males and females did, however, differ in multivariate shape, but this sexual dimorphism apparently does not affect maximal speed. Dodson (1975*b*) also employed discriminant analysis to demonstrate slight but significant morphological sexual dimorphism in two species of *Sceloporus*. Jackson (1973: 751) found sexual dimorphism in several characters in another *Sceloporus* species, and suggested 'the longer limbs of males are probably connected with greater male cursorial activity involved in territoriality.' Sex differences in relative length of hind limbs are already pronounced in hatchling *Lacerta* (Kramer, 1951). Sex differences in maximal running speed or any other measure of locomotory performance have yet to be demonstrated in lizards.

Maximal running speeds of *A. nuchalis* did not vary seasonally. The only previous study to look for seasonal variations in locomotory performance in a reptile is John-Alder (1984). He found that endurance capacity on a motorized treadmill, as well as the physiological correlates maximal oxygen consumption, tissue oxidative capacity, and thyroid hormone levels, all varied seasonally in the iguanid lizard *Dipsosaurus dorsalis* (maximal running speed was not measured). This species is, in some ways, ecologically convergent with *A. nuchalis* (Pianka, 1971). Burst activities, such as maximal running speed, may be less plastic than are more prolonged locomotory activities, which, unlike burst speed, involve the mobilization of aerobic metabolic sources of ATP.

Gravid females, averaging 13% heavier for their snout-vent lengths, were significantly (12%) slower than were field-fresh animals. Reduced speed in gravid females has been reported in two other families of lizards (Shine, 1980; Bauwens & Thoen, 1981). Whether the reduced maximal speed of gravid animals is attributable solely to mass loading is unclear (see Garland & Arnold, 1983). Long-term (22 month) captives, averaging 24% heavier for their snouth-vent length, were also only 12% slower. This comparison of gravid vs. obese lizards agrees with Pond's (1981) experiments, showing that the distribution of a mass load, in addition to its magnitude and nature, may influence its affect on running speed. Small lacertid lizards force fed meals averaging 23% of body mass showed no significant decrease in maximal speed (Huey *et al.*, 1984), a result also obtained by Garland & Arnold (1983) for small snakes.

Eight weeks of captivity had no significant effect on maximal running speeds of seven adult males. Furthermore, the above comparison of relative speeds of gravid vs. 22-month captive lizards that were obese suggests that captivity *per se* had little effect on maximal speed. Gleeson (1979) found that six or eight weeks of captivity or physical conditioning had no apparent effect on distance-running capacity in the lizard *Sceloporus occidentalis* (maximal running speed not measured).

Summary

Examination of an ontogenetic series of the Australian agamid lizard *Amphibolurus nuchalis* (1·3–48 g) revealed that geometric similarity is not maintained. Both fore- and hind limbs are relatively shorter but the tail is relatively longer in large individuals, and thigh muscles make up a greater proportion of total body mass in large animals. Although *A. nuchalis* deviate from geometric similarity, they do so in a way that is inconsistent with the predictions of any other theory of biological similarity (Table VI).

Large *A. nuchalis* are faster than juveniles, and maximal running speed scales as (body mass)$^{0.161}$. Judging from the results of the present and previous studies (Garland, 1982, 1983*b*), knowledge of the scaling of body proportions alone appears inadequate to infer how maximal speed scales.

Variation in shape and speed also do not coincide at two other levels. Individual differences in maximal running speed are significant and highly repeatable; however, individual differences in speed are unrelated to individual differences in body shape. This lack of correlation is even more surprising because the components of multivariate shape do not vary independently; individuals tend to have *either* relatively long *or* relatively short bodies, tails, forelimbs, and hind limbs. Although adult male and female *A. nuchalis* differ significantly in multivariate shape, they do not differ in maximal speed.

Maximal running speeds of field-fresh animals did not vary on a seasonal basis, and eight weeks of captivity had no effect on speed. Gravid females and obese, 22-month captive animals were both approximately 12% slower than were field-fresh individuals.

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