Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards

THEODORE GARLAND, JR., AND PAUL L. ELSE
Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717; and Department of Biology, University of Wollongong, Wollongong, New South Wales 2500, Australia

GARLAND, THEODORE, JR., AND PAUL L. ELSE. *Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards.* Am. J. Physiol. 252 (Regulatory Integrative Comp. Physiol. 21): R439–R449, 1987.—Amphibolurus nuchalis were collected in central Australia during mid- (January) and late summer (March). Endurance time at 1 km/h on a motorized treadmill is greater in larger lizards, scaling as $M^{0.65}$. Maximal O_2 consumption ($\dot{V}O_{2max}$) scales as $M^{0.96}$; standard metabolic rate (SMR) scales as $M^{0.83}$. Factorial aerobic scope thus increases ontogenetically (9.4 at 1 g vs. 15 at 50 g). All organ masses scale allometrically; larger lizards have relatively smaller livers, but larger hearts and thigh muscles. Hematocrit and hemoglobin increase during early ontogeny, but are mass independent in adults. Maximal in vitro catalytic rates were determined for citrate synthase (CS) and pyruvate kinase (PK) in liver, heart, and thigh muscle and for lactate dehydrogenase (LDH) (lactate oxidation) in heart. All enzyme activities (expressed per g tissue) scale positively, except CS in heart. Females exhibit lower SMR and heart CS activity. March animals exhibit elevated endurance, $\dot{V}O_{2max}$, heart LDH, and thigh CS and PK activities. Individual variation in endurance correlates with individual differences in heart LDH and thigh CS and/or PK activities. Individual differences in $\dot{V}O_{2max}$ are partly related to variation in hematocrit.

Amphibolurus nuchalis (*ctenophorus*); allometry; citrate synthase; ecology; oxygen consumption; pyruvate kinase; scaling; treadmill running

LOCOMOTOR PERFORMANCE and activity metabolism have become of increasing interest to physiological ecologists during the past 15 yr (e.g., Refs. 2–4, 6, 7, 13–17, 19, 20, 23, 24, 28–36, and Refs. therein). Although the discipline began by examining the responses of resting animals to various environmental stresses, it is apparent that, in nature, many important selective events involve active animals. Interspecific differences in performance capacity and activity metabolism have been documented (3, 6, 15, 33), but only a single published study (13) has examined specifically the mechanistic bases of individual differences in metabolism and performance in a natural population (see also Ref. 36). Given the evolutionary significance of individual variation, this is an important but neglected aspect of comparative physiology.

The present study was undertaken to examine individual variation in locomotor performance and its physiological, biochemical, and morphological correlates in a natural population of lizards. Expanding on previous work (13, 24), we consider not only the consequences of patterns of ontogenetic allometry, but also differences between the sexes and seasonal variation. In a companion paper (17) we examine the responses of these lizards to captivity and to physical conditioning via daily treadmill running.

The study animal was *Amphibolurus nuchalis*, an omnivorous agamid lizard that is widely distributed in arid regions of central and western Australia. This species was chosen because it is relatively well known both ecologically and physiologically (8, 11, 14, 22, 26, and bibliography therein). In addition, *A. nuchalis* maintains body temperatures near 40°C while active in the field, thus facilitating comparisons with previous and ongoing work on other lizards (13, 15, 23, 24; Garland, unpublished observations).

MATERIALS AND METHODS

Animal collection and maintenance. Amphibolurus nuchalis were collected in central Australia as described elsewhere (14) and brought to the laboratory at the University of Wollongong. All measurements were completed, and animals were killed within 28 days of capture. Individuals captured during January 1984 included recent hatchlings and animals at least 1 yr older (>8 g), which could be sexed. During March 1984, young of the year had grown such that no individuals <4.5 g were captured, and large adults were apparently inactive. Thus, although we captured virtually every individual sighted during March, the body mass range of March animals (4.5–22 g) is much narrower than for January lizards (1.3–48 g). No gravid females were captured during March, and many of the smaller individuals were probably young of the year.

Lizards were maintained in cages on a 12:12-h photocycle (30°C days, 20°C nights), with incandescent lights allowing behavioral thermoregulation to >40°C. Water was always available, and food (fruit, vegetables, canned dog food, *Tenebrio* larvae) was provided in excess daily. All animals remained in apparent good health during the experiments.

Endurance. Endurance was recorded as the length of time individuals could maintain 1.0 km/h on a motorized treadmill. Trials were terminated when an individual did not maintain tread speed following 10 consecutive pinches and prods given at <1-s intervals (13, 15). Each animal was tested on 2 different days. Both performances

were analyzed for repeatability; the better performance of each individual was used to generate allometric equations and residuals and to test for sexual and seasonal differences.

Maximal aerobic speed. For a subset of adults the maximal aerobic speed was recorded as the tread speed above which O_2 consumption ($\dot{V}O_2$) did not continue to increase (4, 10, 15, 34). Each individual was tested twice, during the $\dot{V}O_{2max}$ step tests (next section); if maximal aerobic speeds could be estimated for both trials, higher values were analyzed.

Maximal O_2 consumption. $\dot{V}O_{2max}$ rates were determined by means of a step test, as previously described (13, 15, 23, 24). Individuals wearing lightweight transparent acetate masks were forced to run on a treadmill through an increasing series of speeds until percent O_2 in excurrent air failed to decrease further with increasing tread speed and/or the animal exhausted. Ambient air was drawn through the mask by a downstream pump at rates of ~200–1,000 ml/min STPD, depending on animal size. Air was sequentially dried and had CO_2 removed, then drawn through a calibrated Brook's rotameter, through a Taylor-Servomex type OA 272 oxygen analyzer, and into the pump. Individuals were tested on each of 2 days; values were analyzed as described above for endurance.

Standard metabolic rate. Standard metabolic rate (SMR, Refs. 1, 5) was measured using an open-flow system, similar to that described previously (13, 15, 24), but using the Taylor-Servomex oxygen analyzer. Individuals were fasted for 2 days, then placed in glass metabolic chambers inside a constant-temperature cabinet. Flow rates were ~20–200 ml/min STPD, depending on animal size. A continuous recording of percent O_2 in excurrent air was made on a Houston Omniscribe chart recorder. Each individual was sampled for >8 min/h, overnight (~12 h). The lowest stable trace (>8 min) of O_2 concentration in dried CO_2-free excurrent air was used to calculate SMR as described previously (13). All gas exchange rates are presented as STPD.

Hematocrit and hemoglobin. Animals were killed by decapitation, and blood samples were taken from the neck. Hematocrit tubes were centrifuged for 5 min at maximal speed in a clinical (benchtop) centrifuge. Hemoglobin was determined as cyanmethemoglobin following Sigma Technical Bulletin No. 525.

Organ masses. Following decapitation, heart, liver (minus contents of gallbladder), and the entire mass of thigh muscles were dissected free and weighed to the nearest 0.1 mg. Each tissue was then wrapped in aluminum foil, frozen in liquid N_2, and stored at −70°C until homogenization for enzyme assays.

Enzyme assays. Maximal in vitro catalytic rates (V_{max}) were determined spectrophotometrically with nonlimiting concentrations of substrates and cofactors (reaction velocity proportional to amount of homogenate added). Citrate synthase activity was used as an indicator of the aerobic capacity of tissues. Pyruvate kinase activity was used as an index of the anaerobic glycolytic capacity of tissues (9, 13). Preparation of homogenates and assay conditions for citrate and pyruvate kinase were as described previously (13). Lactate dehydrogenase activity was measured in the direction of lactate oxidation as described by Castellini et al. (Ref. 9; reaction pH = 7.2 at 40°C). All biochemicals were obtained from Sigma. All assays were conducted at 40°C in a thermostated Varian CARY dual-beam spectrophotometer. All samples were run in duplicate, and means were analyzed. Results are expressed as units per gram tissue at 40°C (μmol product produced·min^{-1}·g $tissue^{-1}$).

Statistical analyses. We conducted a repeated-measures analysis of variance to determine whether individuals differed significantly in speed (data from Ref. 14), endurance, or $\dot{V}O_{2max}$. For these measures of organismal performance, higher values for each individual were used in subsequent analyses. Least-squares linear regression analysis was used to calculate allometric equations to describe ontogenetic scaling relationships (13, 14). We also tested whether any of the log-to-log relationships were fit significantly better by a curvilinear relationship, by testing the significance of a $(\log_{10}$ body mass$)^2$ term as an additional independent variable. Except for endurance (see RESULTS), such was never the case.

We used analysis of covariance (ANCOVA) to test for sexual differences among those individuals that could be sexed (>8 g). Supplementarily, we compared females with all other individuals. After allowing for sexual differences, we tested for differences between January and March lizards. We compared March lizards ($n = 13$) to all nongravid January lizards ($n \leq 46$), rather than to January lizards of similar size only, because we believe the full data set provides the best estimate of January values, including scaling relationships. Finally, after allowing for both sexual and seasonal differences, we used ANCOVA to determine whether scaling relationships differed between adults and juveniles (e.g., whether there were break points on log-to-log plots).

We computed residuals from allometric equations presented in Table 1 (Table 3 for hemoglobin and hematocrit) as estimates of individual differences in characters, after removing the effects of body mass (13, 14, 24). We used these residuals in correlation and multiple regression analyses, to determine how characters were intercorrelated, and whether individual differences in morphology, physiology, or biochemistry could be used to predict individual differences in organismal performance or $\dot{V}O_2$. As an alternative multivariate statistical technique, we conducted a principal component analysis of all enzyme activities and of all characters combined.

RESULTS

Repeatability of organismal performance. Measurements of speed (see also Ref. 14), endurance, and $\dot{V}O_{2max}$ were highly repeatable. Correlations between log-transformed values on *trials 1* and *2* were 0.799 ($n = 68$), 0.874 ($n = 47$), and 0.971 ($n = 50$), respectively. Mass-corrected values were computed by dividing each value by body mass raised to the appropriate exponent (from Tables 1 or 3; cf., Ref. 29), then log transforming these values. Correlations between these "residual" values were 0.636, 0.777, and 0.538, respectively, all of which are highly significant ($P < 0.001$). We also conducted repeated-

TABLE 1. *Allometric equations or descriptive statistics for characters measured in Amphibolurus nuchalis*

Character, units	Range	$a \pm 95\%$ CI*	$b \pm 95\%$ CI	r^2, %	SEE	CV, %†
Speed, km/h	5.39–13.53	5.919÷/×1.106	0.161±0.036	58.7	0.06265	14.3
Endurance, s	100–10,169	387.1÷/×1.838	0.615±0.216	36.8	0.37049	84.6
Maximal aerobic speed, km/h	0.60–1.40	0.385÷/×1.886	0.293±0.193	28.1	0.08379	18.9
$\dot{V}O_{2\,max}$, ml O_2/h	6.219–179.7	3.839÷/×1.196	0.948±0.063	94.3	0.08835	20.2
SMR, ml O_2/h	0.504–11.41	0.4094÷/×1.147	0.830±0.047	95.7	0.06846	15.6
Liver, g	0.0181–1.523	0.03355÷/×1.464	0.905±0.158	81.5	0.15708	35.6
Heart, g	0.0045–0.189	0.00267÷/×1.135	1.105±0.052	98.4	0.05205	11.8
Thigh, g	0.0176–1.062	0.01314÷/×1.140	1.158±0.054	98.4	0.05405	12.2
Hct, %	7.00–34.86	10.16÷/×1.279	0.265±0.109	47.5	0.10132	23.0
Hb, g/100 ml	2.91–9.25	4.327÷/×1.267	0.181±0.098	31.3	0.09762	22.1
CS liver, U/g tissue	4.25–26.5	8.125÷/×1.407	0.224±0.142	25.1	0.14075	31.9
PK liver, U/g tissue	1.74–6.01	2.436÷/×1.357	0.192±0.127	23.6	0.12595	28.6
CS heart, U/g tissue	74.5–176.6	122.5±8.08 (18.6%)				19.0
PK heart, U/g tissue	31.0–58.8	30.85÷/×1.134	0.154±0.052	53.9	0.05180	11.7
LDH heart, U/g tissue	49.7–95.7	57.67÷/×1.176	0.108±0.067	26.8	0.06536	14.8
CS thigh, U/g tissue	7.30–37.8	10.32÷/×1.498	0.322±0.168	33.1	0.16673	37.8
PK thigh, U/g tissue	42.6–221	92.66÷/×1.383	0.161±0.135	16.2	0.13382	30.3
Liver CS, U/organ	0.209–40.3	0.2726÷/×1.617	1.129±0.199	81.1	0.19822	44.9
Liver PK, U/organ	0.073–6.78	0.08173÷/×1.503	1.098±0.169	85.0	0.16812	38.1
Heart CS, U/organ	0.448–26.2	0.3154÷/×1.285	1.115±0.104	93.9	0.10342	23.4
Heart PK, U/organ	0.139–11.1	0.08249÷/×1.175	1.259±0.067	97.9	0.06,641	15.1
Heart LDH, U/organ	0.225–13.35	0.1535÷/×1.261	1.215±0.096	95.5	0.09559	21.7
Thigh CS, U/organ	0.142–32.7	0.1536÷/×1.566	1.480±0.186	89.5	0.18485	41.9
Thigh PK, U/organ	0.750–130.0	1.2178÷/×1.525	1.320±0.175	88.4	0.17412	39.5

For all characters $n = 33$, except Speed, $n = 60$ (from Ref. 14); Endurance, $n = 58$; Maximal Aerobic Speed, $n = 27$; $\dot{V}O_{2\,max}$, $n = 57$; SMR, $n = 59$; LDH Heart and Heart LDH, $n = 32$. Equations in form of character = a(body mass)^b. * a, Antilog of estimated y intercept (value at body mass = 1 g) from log-to-log regressions. Entry for 95% confidence interval (CI) denotes, using Endurance as an example, from 387.1 ÷ 1.838 to 387.1 × 1.838; hence, on an arithmetic scale CIs are asymmetrical about mean (a). For CS Heart, the only character that did not vary with body mass, value is mean of raw numbers ± 95% CI (CV). † CV = 2.3026 × SD of residuals from allometric equations, which is approximately equivalent to a CV (see Ref. 14). For further definitions see text.

TABLE 2. *Consequences of allometry in Amphibolurus nuchalis*

Character, units	Value at 1 g	Value at 50 g	Value at 50 g / Value at 1 g
Speed, km/h	5.919	11.108	1.88
Endurance, s	387.1	4,295	11.10
Maximal aerobic speed, km/h	0.385	1.212	3.15
$\dot{V}O_{2\,max}$, ml O_2/h,	3.839	156.4	40.74
ml $O_2 \cdot g^{-1} \cdot h^{-1}$	3.839	3.128	0.815
SMR, ml O_2/h,	0.4094	10.53	25.72
ml $O_2 \cdot g^{-2} \cdot h^{-1}$	0.4094	0.2,106	0.514
$\dot{V}O_{2\,max}$/SMR	9.38	14.85	1.58
Hindlimb span/snout-vent length*	1.521	1.254	0.824
Liver, % body mass	3.36	2.32	0.690
Heart, % body mass	0.267	0.404	1.510
Thigh, % body mass	1.31	2.44	1.857
Hct, %	6.02	20.69	3.44
Hb, g%	2.53	6.95	2.75
CS liver†	8.13	19.5	2.40
PK liver	2.44	5.17	2.12
CS heart	122.5	122.5	1.00
PK heart	30.9	56.3	1.82
LDH heart	57.8	88.4	1.53
CS thigh	10.3	36.3	3.52
PK thigh	92.7	174.2	1.88

* From Ref. 14. † All enzyme activities are units/g tissue.

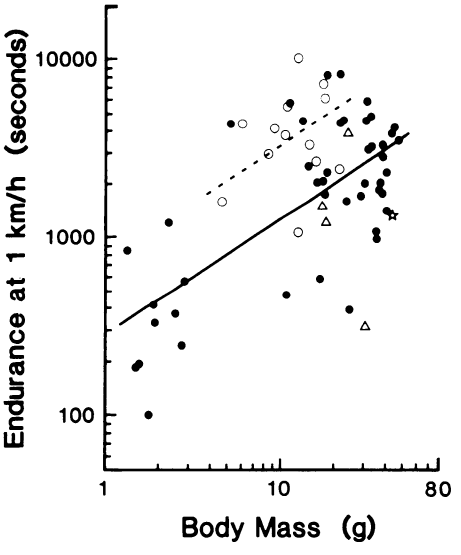

FIG. 1. Treadmill endurance at 1 km/h in *Amphibolurus nuchalis*. *Closed circles* and *solid regression line* (from Table 3) are January animals; *open circles* and *dashed line* are March animals. *Open triangles* represent 4 gravid females. *Star* is adult male captured missing lower portion of right leg below knee (see text).

measures analysis of variance on these mass-corrected values. For each character there was a highly significant component of variance attributable to individual differences in organismal performance ($F = 4.405$, 62.3% of total variance; $F = 7.940$, 77.5%; $F = 3.324$, 52.1%; for speed, endurance, and $\dot{V}O_{2\,max}$, respectively, all $P < 0.001$).

We also tested whether performances differed between *days 1* and *2*, assuming no individual by trial interaction. Neither speed nor endurance varied between trial days; $\dot{V}O_{2\,max}$ showed a small (−6.4%) but statistically significant ($P = 0.0412$) decrease from *days 1* to *2*. The fact that no performance measure increased significantly

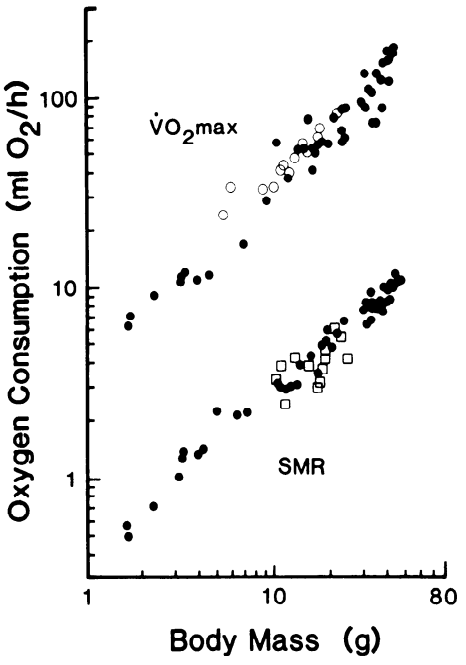

FIG. 2. Maximal ($\dot{V}O_{2max}$) and standard (SMR) rates of O_2 consumption. March animals (*open circles*) exhibited a significantly elevated $\dot{V}O_{2max}$. Females (*open boxes*) exhibited a significantly lower SMR (see Table 3 for regression equations).

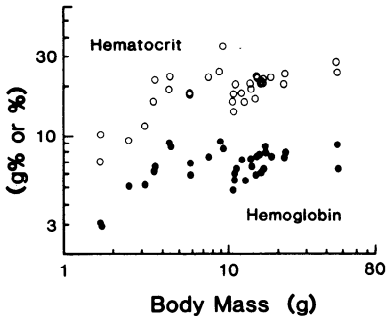

FIG. 3. Hematocrit and hemoglobin content of blood. See Tables 1 and 3 for descriptive statistics.

from *trials 1* to *2* suggests that two trials, conducted on successive days, are an adequate protocol for eliciting maximal performances (cf., Refs. 3, 14, 16).

Allometry. Allometric equations are presented in Table 1. Table 2 presents calculations indicating the magnitude of scaling effects, including the ratio of a character as measured in 50- vs. 1-g animals. The smallest individuals used in the present study were <1.3 g; presumably, some hatchlings are as small as 1 g. The largest lizards used were almost 50 g.

Larger lizards had greater endurance (Fig. 1 and Tables 1, 2) and higher sprint speeds (Tables 1, 2, results from Ref. 14). The adult male missing part of one hindlimb ran only 57% as long as predicted (Fig. 1). This same individual's maximal sprint speed was 66% of predicted (14). Maximal aerobic speeds were also higher for larger lizards (Tables 1 and 2).

Standard and maximal rates of $\dot{V}O_2$ scaled as $M^{0.830\pm0.047}$ and $M^{0.948\pm0.063}$, respectively, so larger lizards had lower mass-specific rates of $\dot{V}O_2$ (Fig. 2 and Tables 1, 2). These slopes are significantly different, and the ratio $\dot{V}O_{2max}$:SMR (factorial aerobic scope) is calculated to average 9.4 for 1-g juveniles, but almost 15 for 50-g adults (Table 2).

All organs scaled allometrically (Table 1). Larger lizards had relatively smaller livers, but relatively larger hearts and more massive thigh muscles. Hematocrit and hemoglobin content of the blood both increased with increasing body mass within juveniles (Fig. 3 and Tables 1–3), but were mass independent among adults.

Six of the seven enzyme activities measured exhibited positive scaling (Table 1 and Fig. 4); larger lizards exhibited higher mass-specific enzyme activities, except for citrate synthase activity in heart (Fig. 4*a*).

Sexual differences. Sexual differences were examined with ANCOVA, comparing only adults (>8 g), as well as comparing females vs. all other lizards. Significant differences existed for only two characters (Table 3). Females exhibited a standard metabolic rate that was 12% lower (on an arithmetic scale) than in males (Fig. 2; $F = 7.42$, $P = 0.0086$). Heart citrate synthase activity was 23% lower in females (Fig. 4; $F = 11.1$, $P = 0.0033$).

Endurance times of four gravid females (Fig. 1) were not significantly lower (average = ~52% lower) than those of other January lizards ($F = 3.385$, $P = 0.0710$, compared with *Eq. 2* from Table 3). Standard metabolic rates of two gravid females (4.73 and 3.39 ml O_2/h for 17.44- and 17.41-g lizards, respectively, not shown in Fig. 2) were similar to those of other females (cf., Ref. 25).

Seasonal differences. Seasonal variation was more pronounced than sexual dimorphism (Table 3). With regard to all lizards, endurance (Fig. 1) was 2.6-fold higher (on an arithmetic scale) in March lizards ($F = 45.4$, $P < 0.0001$; *Eq. 1* in Table 3). March lizards are also significantly higher (1.8-fold, $F = 4.34$, $P = 0.042$) when using a statistical model that allows $\log_{10}$ endurance to vary curvilinearly with $\log_{10}$ body mass (*Eq. 2* in Table 3; see next section, *Ontogenetic variation*). However, in comparison of the 13 March lizards with only January lizards of similar size ($n = 13$, see Fig. 1), the difference is insignificant ($F = 1.29$, $P = 0.2685$).

Four other characters were also higher in March than in January lizards (Table 3). $\dot{V}O_{2max}$ (Fig. 2) was 14% higher in March lizards ($F = 4.45$, $P = 0.0396$); lactate dehydrogenase activity in heart was elevated 17% ($F = 10.2$, $P = 0.0055$). Citrate synthase and pyruvate kinase activities in thigh muscle were elevated 48 and 31%, respectively, in March lizards ($F = 10.2$, $P = 0.0032$; $F = 6.843$, $P = 0.0138$, respectively: see Fig. 3 in Ref. 17).

Ontogenetic variation. Are there any nonlinearities in the log-to-log relationships between each character and body mass? After allowing for sexual and seasonal differences (i.e., including sex or season as covariates in the analysis), we used ANCOVA to examine whether scaling relationships differed in juvenile (<8 g) vs. adult lizards. We also tested whether a polynomial regression of $\log_{10}$ character on $\log_{10}$ body mass fit the data significantly better than a simple linear regression. With the following exceptions (Table 3), such was not the case.

A polynomial regression of $\log_{10}$ endurance on $\log_{10}$ body mass fits the data significantly better than does a linear regression ($F = 5.258$, $P = 0.0258$; Table 3), with March lizards remaining significantly higher ($F = 4.34$,

TABLE 3. *Seasonal, sexual, and ontogenetic variation*

$\log_{10}$ Character	=	$\log_{10}$ *y* Intercept	+ Independent Variables and Covariates	Multiple, r^2	SEE	CV, %
Endurance ($n = 58$)		2.458	+ 0.648 × $\log_{10}$ body mass + 0.413 if March animal	50.9	0.32973	74.6
Endurance ($n = 58$)	=	2.117	+ 1.810 × $\log_{10}$ body mass − 0.630 × ($\log_{10}$ mass)^2 + 0.259 if March animal	55.2	0.31766	71.2
$\dot{V}O_{2\ max}$ ($n = 57$)	=	0.559	+ 0.958 × $\log_{10}$ body mass + 0.058 if March animal	94.8	0.08571	19.4
SMR ($n = 59$)	=	−0.377	+ 0.831 × $\log_{10}$ body mass − 0.056 if Female	96.2	0.06490	14.7
($n = 48$)	=	−0.357	+ 0.815 × $\log_{10}$ body mass − 0.056 if Female	89.1	0.06453	14.5
Hct ($n = 33$)	=	1.316	if Adult (no scaling) or	61.6	0.08811	19.6
		0.779	+ 0.694 × $\log_{10}$ mass if Juv			
Hb ($n = 33$)	=	0.842	if Adult (no scaling) or	54.2	0.08102	18.1
		0.403	+ 0.630 × $\log_{10}$ mass if Juv			
CS heart ($n = 33$)	=	2.109	if Male or Juv or	27.1	0.07147	16.2
		2.017	if Female			
($n = 22$)	=	2.130	if Male or	35.8	0.07929	17.8
		2.017	if Female			
LDH heart ($n = 32$)	=	1.752	+ 0.089 × $\log_{10}$ body mass + 0.068 if March	46.6	0.05680	12.6
CS thigh ($n = 33$)	=	0.997	+ 0.270 × $\log_{10}$ body mass + 0.171 if March	50.1	0.14634	32.6
PK thigh ($n = 33$)	=	1.956	+ 0.126 × $\log_{10}$ body mass + 0.117 if March	31.8	0.12275	27.4
	=	2.102	if Adult or	59.0	0.09681	21.2
		1.650	+ 0.740 × $\log_{10}$ mass if Juv and for both Adults and Juv + 0.088 if March			

All independent variables were statistically significant ($P < 0.05$) in multiple regression equations.

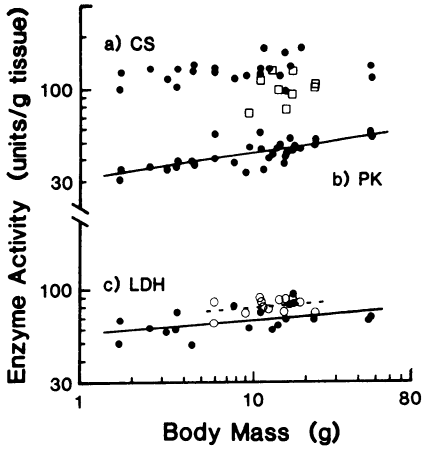

FIG. 4. Citrate synthase (CS) (*a*), pyruvate kinase (PK) (*b*), and lactate dehydrogenase (LDH) (*c*), (measured in direction of lactate oxidation) activities in heart. Both PK and LDH scale significantly with body mass (regression equations in Tables 1 and 3). Sexual differences are significant only for CS (females, represented by *open boxes*, are lower; see Table 3). Seasonal differences are significant only for LDH (March animals, represented by *open circles* and *dashed line*, are higher; see Table 3).

$P = 0.042$), but the multiple r^2 is improved only slightly (55.2% vs. 50.9%). The relationship can also be described as a sharp increase in endurance within juvenile lizards ($n = 13$), with no correlation between endurance and body mass among adults ($n = 45$): in this model March lizards are not significantly higher ($F = 3.59$, $P = 0.064$) than January lizards (multiple $r^2 = 57.1\%$ with March in the model, 53.9% without March in the model).

The slope of thigh muscle mass on body mass differed significantly for juveniles and adults ($F = 4.82$, $P = 0.0360$), but omitting the smallest juvenile from the calculations eliminates the statistical significance ($F = 2.24$, $P = 0.1454$). We therefore conclude that the relationship between $\log_{10}$ thigh muscle mass and $\log_{10}$ body mass is adequately described by a simple linear regression.

Both hematocrit and hemoglobin increased with increasing body mass among juveniles, at least up to a point, but were mass independent among adults (Fig. 3). Equations for these patterns are presented in Table 3.

Pyruvate kinase activity in thigh muscle can be described in several ways (Table 3, and see Fig. 3 in Ref. 17): *1*) activity scales positively, and March lizards exhibit higher activities; *2*) activity increases with mass among juveniles, but is mass independent among adults; *3*) activity increases with mass in juveniles, is mass independent among adults, and March animals show higher activities. Given that pyruvate kinase and citrate synthase activities in thigh muscle are positively correlated (see below and Table 4) and that citrate synthase

TABLE 4. *Product-moment correlation coefficients among enzyme activities*

	Liver		Heart			Thigh	
	CS	PK	CS	PK	LDH	CS	PK
Liver							
CS	1	**0.522**	−0.052	**0.523**	−0.005	**0.492**	0.085
PK	**0.368**	1	−0.153	0.305	0.234	**0.453**	0.090
Heart							
CS	−0.084	−0.197	1	−0.060	0.280	0.300	0.282
PK	0.264	−0.087	−0.131	1	**0.487**	**0.506**	0.282
LDH	−0.344	−0.001	0.278	0.190	1	**0.448**	**0.411**
Thigh							
CS	0.288	0.243	0.339	0.152	0.175	1	**0.644**
PK	−0.147	−0.132	0.291	−0.021	0.220	**0.551**	1

Values above diagonal are for $\log_{10}$ transformed data; values below diagonal are for residuals from allometric equations, presented in Table 1. $n = 33$; correlations > 0.344 are significant at $P < 0.05$. For LDH Heart, $n = 32$; correlations > 0.349 are significant at $P < 0.05$. Significant correlations appear in boldface. See text for definitions.

clearly exhibits *pattern 1* (above), we conclude that *pattern 1* is biologically the most realistic.

Correlations among characters. In agreement with two previous studies on lizards (3, 13), residual (individual) variation in speed and endurance were not correlated ($n = 58$, $r = 0.00001$, $P = 0.9999$). Sprint speed and maximal aerobic speed were also uncorrelated ($n = 27$, $r = 0.059$, $P = 0.771$). Endurance and maximal aerobic speed were positively but not significantly correlated ($n = 27$, $r = 0.276$, $P = 0.164$).

Residual variations in standard and maximal rates of $\dot{V}O_2$ were not significantly correlated ($n = 56$, $r = 0.219$, $P = 0.105$). Neither residual variation in SMR nor $\dot{V}O_{2\,max}$ were correlated with endurance ($n = 56$, $r = 0.189$, $P = 0.163$; $n = 56$, $r = 0.155$, $P = 0.255$, respectively).

Residual variations in organ masses were not significantly intercorrelated. Liver mass was significantly correlated with hematocrit ($r = 0.529$, $P = 0.002$) and thigh pyruvate kinase activity ($r = 0.346$, $P = 0.049$). Heart mass was marginally correlated with heart lactate dehydrogenase activity ($r = 0.341$, $P = 0.052$). Thigh muscle mass was significantly correlated with thigh pyruvate kinase activity ($r = 0.656$, $P < 0.001$) and hematocrit ($r = -0.379$, $P = 0.029$) and marginally correlated with heart citrate synthase activity ($r = 0.342$, $P = 0.052$).

Hematocrit and hemoglobin were correlated ($n = 33$, $r = 0.805$, $P < 0.001$ for raw values; $r = 0.857$, $P < 0.001$ for $\log_{10}$ transformed values). Residuals of the two blood characters (from equations in Table 3) were also correlated ($r = 0.695$, $P < 0.001$). Residual variation in hemoglobin was correlated with residual variation in heart lactate dehydrogenase activity ($r = -0.348$, $P = 0.047$). The biological significance of this latter correlation and of the correlations with organ masses mentioned in the previous paragraph is unclear, but they are important to note because they may confound interpretation of multiple regression analyses (below, cf., Ref. 14).

Several of the enzyme activities showed intercorrelations (Table 4). Citrate synthase and pyruvate kinase activities were positively correlated within both liver and thigh muscle, but not within the heart. Pyruvate kinase and lactate dehydrogenase activities were positively correlated within heart. Most enzyme activities that showed significant correlations among tissues (Table 4, above diagonal) showed correlations of lower magnitude and significance when considering residuals from allometric equations (Table 4, below diagonal). Such a pattern suggests that some of the correlations are attributable to both enzyme activities being positively correlated with body mass.

A principal components analysis (not shown) of all enzyme activities (not residuals) plus body mass yielded a first component (accounting for 44.9% of the total variation) on which all characters [except heart citrate synthase (CS)] loaded positively and significantly. This component is thus interpreted as a general body size/scaling factor. *Factors 2–5* accounted for 19.4, 11.2, 8.4, and 8.2% of the variation, respectively and had significant loadings for 5, 3, 2, and 2 enzyme activities, respectively. Thus, not all of the intercorrelations among enzymes are attributable entirely to similar scaling patterns. In particular, citrate synthase and pyruvate kinase are correlated within both liver and thigh muscle in all analyses (Table 4).

Correlation of locomotor performance and metabolic rate with suborganismal characters. Because the measures of whole-animal performance are sensitive enough to show significant individual differences, it is then appropriate to ask whether these individual differences in performance are related to individual differences at lower levels of biological organization. The following analyses are based on 33 individuals for which complete data sets existed and employ residuals from the allometric equations presented in Tables 1 or 3 (Hct and Hb).

Individual differences in sprint speed were unrelated to any character in the present study, or to limb or tail dimensions (14). Residual variation in endurance, however, was significantly correlated with residual variation in heart lactate dehydrogenase activity ($r = 0.519$, $P = 0.002$), thigh pyruvate kinase activity ($r = 0.457$, $P = 0.008$), thigh citrate synthase activity ($r = 0.408$, $P = 0.019$), and hemoglobin ($r = -0.387$, $P = 0.026$; correlation between endurance and hematocrit residuals was -0.340, $P = 0.053$). A stepwise multiple regression analysis of residual variation in endurance on residual variation in $\dot{V}O_{2\,max}$, SMR, organ masses, blood characters, and enzyme activities yielded a highly significant predictive equation ($r^2 = 47.1\%$), including three significant independent variables (Table 5). Whether citrate synthase or pyruvate kinase activity in thigh is actually the better predictor of endurance is unclear because the two are positively correlated (Table 4). Excluding thigh pyruvate kinase activity from the analysis leads to a predictive equation including only heart lactate dehydrogenase and thigh citrate synthase activity as significant predictors (Table 5).

Individual variation in maximal aerobic speed was significantly related to standard metabolic rate ($n = 27$, $r = 0.444$, $P = 0.020$), but not to $\dot{V}O_{2\,max}$ ($r = 0.015$) or hindlimb span ($r = 0.001$). Most of the individuals for which maximal aerobic speeds were recorded were subsequently used in the companion study of training effects (17), so small sample sizes precluded attempting to correlate this performance measure with the suborganismal

TABLE 5. *Results of multiple regression analyses*

Dependent Variable = Independent Variables (partial r^2)			Multiple r^2	Overall F	Overall Significance
Endurance (n = 33)	=	+ heart lactate dehydrogenase (27.0) + thigh pyruvate kinase (12.3) − liver mass (7.9)	47.1	8.62	0.0003
Endurance (n = 33)	=	+ heart lactate dehydrogenase (27.0) + thigh citrate synthase (10.4)	37.3	8.94	0.0009
Endurance (n = 18)	=	− liver citrate synthase (22.1) + thigh citrate synthase (18.2)	40.3	5.05	0.0210
$\dot{V}O_{2\,max}$ (n = 18)	=	+ hematocrit (24.8) − thigh pyruvate kinase (12.9) − liver mass (9.5)	47.2	4.17	0.0264
Standard metabolic rate (n = 33)	=	+ thigh citrate synthase (16.4) + liver mass (12.4)	28.7	6.05	0.0062

Based on residuals from allometric equations, presented in Table 1. Only signs of partial regression coefficients are given; all were significant at $P < 0.05$ by partial F tests.

characters.

Individual variation in $\dot{V}O_{2\,max}$ was not significantly correlated with any character for n = 33. Individual variation in standard metabolic rate was significantly correlated with thigh citrate synthase activity (r = 0.405, P = 0.020) and marginally correlated with liver mass (r = 0.339, P = 0.053) and thigh pyruvate kinase activity (r = 0.323, P = 0.067). A multiple regression analysis indicated that individual variation in liver mass and thigh citrate synthase activity together explain almost one-third of the individual variation in SMR (Table 5).

With regard to all 33 animals there is tremendous (>100-fold; Fig. 1 and Table 1) variation in the length of time individuals could maintain a treadmill speed of 1 km/h. We therefore felt that looking for correlates of individual differences using all individuals might be misleading, because some individuals were clearly engaging in submaximal exercise, i.e., below their maximal aerobic speed (which averaged 1.0 km/h among adults) and/or below their anaerobic threshold, whereas other individuals exceeded these limits. It is generally believed that, at least in mammals, these two contrasting domains of exercise elicit fundamentally different physiological processes (Ref. 35; see also Refs. 6, 32). Thus correlates of individual differences in performance might be obscured if subsets of individuals were, in effect, engaging in fundamentally different types of endurance exercise. We therefore repeated the analysis on only adult lizards that had an endurance time of at least 30 min, assuming that such individuals (n = 18) were engaging in "submaximal" exercise.

For these 18 individuals the best predictive multiple regression equation, based on residuals from allometric equations, accounts for 40% of the individual variation in endurance (Table 5). As in the entire sample, thigh citrate synthase activity is a significant predictor. About 47% of the individual variation in $\dot{V}O_{2\,max}$ was related statistically to three independent variables, with hematocrit accounting for 25%. There were no significant predictors of residual variation in SMR in the reduced sample.

Principal component analysis of character correlations. We conducted a principal component analysis of log-transformed values (not residuals) of 16 characters (n = 33), including body mass, but excluding speed and hindlimb span, since they were unrelated to any other characters. The first factor accounted for 58.7% of the overall variation and represents a general body size and scaling factor. All characters (except citrate synthase activity in heart, the only character that does not scale allometrically, Tables 1, 3) loaded positively and significantly on *factor 1*, with component correlations ranging from 0.53 (liver citrate synthase) to 0.96 (body mass, heart, and thigh masses, standard metabolic rate). A first factor representing overall size variation is typical of studies of morphometric characters alone (Ref. 14 and bibliography therein).

Up to six subsequent factors are interpretable as representing correlations among characters, after removing the confounding effects of variation in overall body size. *Factor 2* is interpreted as an enzyme factor, with five of seven enzyme activities loading significantly (component correlations >0.344). *Factor 3* is interpreted as a hematological factor, with hematocrit and hemoglobin, and at a lower level thigh pyruvate kinase activity, loading significantly. Three, 3, 2, and 1 enzymes load significantly on *factors 4, 5, 6,* and *7*, respectively. Endurance loads significantly on *factors 1* and *5* and fairly strongly on *factors 2* and *3*. Neither standard nor maximal rates of $\dot{V}O_2$ load strongly on any factor except the first. Thus, in agreement with results of the multiple-regression analyses, endurance appears unrelated to $\dot{V}O_2$, relative organ sizes, hematocrit, or hemoglobin, but is related to individual differences in tissue oxidative and/or glycolytic capacities.

DISCUSSION

Individual variation. Demonstrating the existence of significant individual differences in organismal performance is, of course, a prerequisite for asking what are the correlates of individual variation in performance. Significant individual differences in speed, stamina, and/or $\dot{V}O_2$ have apparently been demonstrated whenever they have been tested for in lizards (Refs. 3, 13, 14, 29; this study; T. Garland, unpublished observations), snakes (Ref. 16; S. J. Arnold and A. F. Bennett, personal communication; T. Garland, unpublished observations), and anuran amphibians (28, 36). These differences may be

stable for considerable periods of time, both in the laboratory (e.g., 8 wk, Refs. 14, 17) and in free-living animals (e.g., 1 yr in *Sceloporus merriami*, R. B. Huey and A. E. Dunham, personal communication). Temporal stability of individual differences increases the likelihood of a partial genetic basis for these differences (cf., Ref. 29). Ongoing analyses of variance within vs. among families indicate that sprint speeds and stamina in the lizard *Sceloporus occidentalis* (F. H. van Berkum, J. Tsuji, and R. B. Huey, personal communication), and in two species of garter snakes (*Thamnophis*, S. J. Arnold, A. F. Bennett, and T. Garland, unpublished data) are significantly heritable. Future studies should attempt more detailed quantitative genetic analyses of variation in performance and activity metabolism to address the question: relatively how important are genetic differences vs. the effects of "natural training" (17, 19) and other environmental factors in determining individual differences?

Ontogenetic allometry. Juvenile and adult *Amphibolurus nuchalis* are neither geometrically nor functionally similar. These size-related changes in the components of activity metabolism are reflected in ontogenetic changes in the capacity for locomotor performance. Larger *A. nuchalis* run both faster (14) and longer (Fig. 1) than do small individuals. Which factors, at lower levels of biological organization, are responsible for the ontogenetic increases in locomotor performance? The answers suggested here are only tentative, because many other characters that may affect performance were not measured (e.g., lung volumes, pulmonary diffusing capacities, maximal heart rates, muscle contractile properties, glycogen stores, blood and muscle buffering capacities). Moreover, it is unclear whether ontogenetic increases in endurance (Fig. 1), hematocrit and hemoglobin (Fig. 3), and thigh citrate synthase and pyruvate kinase activities (Table 3, Fig. 3 in Ref. 17) represent simple allometric scaling (linear increases with increasing body mass) or increases within juveniles followed by mass independence in adults.

Theoretical expectations suggest a positive scaling of endurance capacity ($M^{0.33}$), even among geometrically similar animals (Refs. in 13, 14). *Amphibolurus nuchalis* deviate from geometric similarity in several ways that should favor an even greater than expected positive scaling of endurance. First, maximal (and standard) rates of $\dot{V}O_2$ scale with exponents that are significantly greater than would be expected for either geometrically or elastically similar animals (0.948 and 0.830, respectively, vs. 0.667 or 0.75; Refs. and discussion in Refs. 12–14). Second, relative heart and thigh muscle masses increase with increasing body mass. Third, hematocrit and hemoglobin are higher in adults than in the smaller juveniles. Finally, tissue oxidative and glycolytic capacities, as indicated by maximal in vitro catalytic rates of representative enzymes, increase in six of seven cases (theoretical expectations would be for negative scaling of aerobic enzymes, when expressed on a per gram basis, approximately in parallel with the negative scaling of per gram $\dot{V}O_2$; discussion in Ref. 13).

Positive scaling of sprint speed may be accounted for by the positive scaling of thigh muscle mass: relative thigh muscle mass almost doubles as body mass changes from 1 to 50 g (Table 2). Another possibly important factor may be the increase in relative tail length in larger animals (see Ref. 14 for results and discussion).

The only previous study of the ontogenetic allometry of activity metabolism in a lizard (13) found some similar and some contrasting patterns. The reader is referred to that study for discussions of comparisons with intra- and interspecific data for other vertebrates; here we focus on comparisons between *A. nuchalis* and *Ctenosaura similis*, a larger (12.3–866 g in Ref. 13) iguanid lizard from Central America. One point of caution is to note that the complete ontogenetic size range (~3–3,000 g) was not studied in *C. similis*; hence, potentially nonlinear scaling relationships (cf., Hct and Hb in the present study, Fig. 3) may have gone undetected.

Sprint speed scaled positively in *A. nuchalis* but was mass independent in *C. similis* (13). Positive ontogenetic scaling of sprint speed is the more common pattern in lizards (Ref. 14, T. Garland, unpublished observations).

Endurance at 1 km/h increased ontogenetically in both lizards. Studies in several other lizards (T. Garland, unpublished observations), snakes and anuran amphibians (Refs. 28, 30, and Refs. therein), and fishes (2) suggest that ontogenetic increase in endurance capacity is a general phenomenon in ectothermic vertebrates. However, endurance capacity is mass independent when considering adults only in both *A. nuchalis* (see RESULTS, Fig. 1 and Table 3) and *C. similis* (see Fig. 1 in Ref. 13). Similar pattens are seen within some species of anuran amphibians (Ref. 30 and Refs. therein). It should be noted that correlation coefficients and slopes of regression equations are partially dependent on the range of the independent variable (body mass), and lower and possibly insignificant correlations and scaling exponents would be expected when examining any subsample of an ontogenetic series.

Maximal aerobic speed was also higher in larger lizards. There are no other data on ontogenetic scaling of this character. Although there is wide variation in maximal aerobic speed among species of lizards, there is no clear relationship with body mass (4, 15).

Standard metabolic rate scaled as $M^{0.830\pm0.047}$ in *A. nuchalis*, similar to the exponent in *C. similis* ($M^{0.858\pm0.036}$). Andrews and Pough (1) have reviewed the literature on intra- and interspecific scaling of standard metabolism in lizards. Most previously reported intraspecific scaling exponents are lower than for these two species, perhaps in part because most previous studies did not include as wide an ontogenetic size range. This cannot explain all of the differences, however, and as Andrews and Pough (1) note, there are real and significant differences among species of lizards and snakes in the ontogenetic allometry of resting metabolism. As in *C. similis* (13), there is no evidence for "break points" in the postembryonic ontogenetic relationship between SMR (or $\dot{V}O_{2max}$) and body mass in *A. nuchalis* (cf., Ref. 5, p. 174–175).

$\dot{V}O_{2max}$ scaled as $M^{0.948\pm0.063}$, which is not significantly different from the exponent in *C. similis* ($M^{0.918\pm0.070}$). In *A. nuchalis*, but not in *C. similis*, the exponent for scaling of $\dot{V}O_{2max}$ is significantly greater than that for SMR; thus

factorial aerobic scope increases ontogenetically in netted dragons. An ontogenetic increase in factorial scope occurs also in some amphibians (30, 33) and fishes (2). Furthermore, among species of mammals, $\dot{V}O_{2max}$ seems to scale with an exponent greater than does basal metabolic rate (12, 34). These results may at first seem surprising. However, there is actually little reason to expect that minimal and maximal rates of $\dot{V}O_2$ must scale in parallel. Standard or basal $\dot{V}O_2$ is an indication of the minimal energetic maintenance cost of all tissues combined. $\dot{V}O_{2max}$, in contrast, is the maximal rate of $\dot{V}O_2$ that can be attained during vigorous exercise and must be limited by one or more factors, perhaps in the cardiovascular system and/or at the level of tissue utilization of O_2 (13, 15, 34, 35). Moreover, not all tissues are metabolizing maximally at $\dot{V}O_{2max}$, and the relative proportion of $\dot{V}O_2$ attributable to various tissues is very different under maximal vs. resting conditions.

Relative liver mass scales negatively and relative thigh muscle mass scales positively in both *A. nuchalis* and *C. similis* (13). Heart mass, however, scales positively in the former and negatively in the latter. Interspecific differences in ontogenetic allometry of relative heart mass are also found in amphibians (28, 30). Hematocrit and hemoglobin were lower in the smallest juveniles than in larger *A. nuchalis*. An ontogenetic increase in these characters occurs also in several snakes (28) and amphibians (30).

Patterns of enzyme scaling in *A. nuchalis* are quite different from those observed in *C. similis* (13). In *C. similis*, only 3 of 11 enzymes assayed exhibited significant scaling (2 negative, 1 positive); in *A. nuchalis*, 6 of 7 enzymes scaled positively; the other was mass independent.

Despite the fact that both standard and maximal rates of $\dot{V}O_2$ decrease on a mass-specific basis in both species, in neither species does citrate synthase activity (an indicator of tissue oxidative capacity) decrease in any tissue. Furthermore, in *A. nuchalis*, total organ citrate synthase activities scale with exponents that are significantly greater than those for the scaling of whole-animal $\dot{V}O_2$ (Table 1). This lack of correspondence between the scaling of tissue oxidative capacities and organismal $\dot{V}O_2$ is in marked contrast to the general agreement seen among species of mammals and reptiles (12, 34).

Sexual differences. Male *A. nuchalis* attain maximal sizes about twofold heavier than females, and in the present study adult males averaged about twofold heavier than adult females (see Fig. 4*a* and Ref. 14). Furthermore, males and females differ significantly in multivariate shape, based on measurements of limb, body, and tail proportions (14). Perhaps surprisingly, however, male and female *A. nuchalis* differ significantly in only two characters, SMR and heart citrate synthase activity (Figs. 2, 4 and Table 3), after allowing for differences in body mass. Where examined, female lizards have often been reported to have lower resting metabolic rates than males (Ref. 5, p. 175; but see Refs. 21, 25). Sexual differences in locomotor performance and activity metabolism of reptiles have previously been examined only incidentally or not at all. Bennett (3), Gratz and Hutchison (20), and John-Alder (24) all reported no significant sexual differences. Sexual differences in $\dot{V}O_{2max}$ have been reported in toads (28). Not surprisingly, gravid females are slower than other lizards of similar size (Ref. 14 and Refs. therein) and may have reduced endurance (Fig. 1).

Seasonal differences. Although seasonal variations in a variety of characters have been documented in reptiles (8, 18, 25), activity metabolism has rarely been examined in this context (4). March *A. nuchalis* appear to exhibit higher endurance, $\dot{V}O_{2max}$, heart lactate dehydrogenase, and thigh citrate synthase and pyruvate kinase activities than do January lizards; the latter four characters all may have functional significance for endurance. John-Alder (24) also found significant seasonal differences in endurance, $\dot{V}O_{2max}$, SMR, liver and muscle citrate synthase activity, and thyroid function in *Dipsosaurus dorsalis*, and a seasonal shift in O_2 affinity has been described previously in this species (27). Seasonal variation in SMR (Ref. 21, J. Tsuji, personal communication), sprint speed (3), $\dot{V}O_{2max}$, lactate production, and possibly distance running ability (19) has been reported in *Sceloporus occidentalis*. Thus, in each of three species that have been examined, seasonal differences in organismal performance appear to reflect seasonal changes in physiology and/or biochemistry.

Correlates of individual differences in endurance and $\dot{V}O_2$. Endurance varies greatly among species of lizards (3, 13, 15, 24, T. Garland, unpublished observations). For example, endurance time at 1 km/h is predicted to be >52 min for a 30-g *A. nuchalis* (Fig. 1 and Table 1) and >1–2 h in adult *Cnemidophorus tigris* (20–25 g; Ref. 15), but only 6.3 min in a 30-g *Ctenosaura similis* (13). In other lizards (7) and in humans (35) and amphibians (32), the work rate (e.g., treadmill speed) associated with the attainment of $\dot{V}O_{2max}$ can only be sustained for minutes. Clearly then, some species (and/or individuals), when run on a treadmill at 1 km/h, are engaging in "submaximal" exercise, i.e., below the anaerobic threshold (35) and/or below the maximal aerobic speed (= speed at which $\dot{V}O_{2max}$ is attained; Refs. 7, 15, 34), whereas others are engaging in maximal or supramaximal exercise (i.e., at or above the $\dot{V}O_{2max}$). The physiological responses and hence the factors leading ultimately to exhaustion during these different regimes appear to be quite different (32, 35). Therefore factors that correlate with individual differences in endurance at 1 km/h would be expected to differ among species, dependent in part on whether this work rate is submaximal, maximal, or supramaximal for the group of individuals in question.

This expectation is supported by comparing the present results with those obtained for *C. similis* (13). In consideration of all 33 field-fresh *A. nuchalis*, individual differences in endurance time were statistically related to individual differences in heart lactate dehydrogenase activity, thigh citrate synthase and/or pyruvate kinase activities, and possibly liver mass. Since lactate dehydrogenase was measured in the direction of lactate oxidation, it presumably reflects individual differences in the ability of the heart to take up lactate from the blood (9). With regard to only the 18 adult *A. nuchalis* with endurance

times ≥30 min, liver and thigh citrate synthase activities together account for 40% of the variation in endurance. Thus tissue oxidative capacity is a significant predictor of interindividual differences in submaximal endurance in *A. nuchalis*, but, notably, $\dot{V}O_{2max}$ is not. In agreement with this conclusion *1*) endurance more than doubles in March compared with January lizards (Fig. 1), whereas $\dot{V}O_{2max}$ increases by only 14% (Fig. 2), and *2*) 8 wk of captivity decreased $\dot{V}O_{2max}$ by 24%, whereas endurance increased by 87% (17).

In *C. similis*, individual variation in endurance at 1 km/h ($\geq\dot{V}O_{2max}$) correlates with thigh muscle mass, $\dot{V}O_{2max}$, heart mass, and liver citrate synthase activity (13). Endurance at 1.1 km/h in *D. dorsalis* (>maximal aerobic speed) correlates with individual variation in $\dot{V}O_{2max}$ and muscle citrate synthase activity, and this speed is maintained for times (24) similar to those maintained by *C. similis* at 1.0 km/h. In summary, $\dot{V}O_{2max}$ appears generally to correlate with individual differences in endurance in lizards, when treadmill speed is approximately equivalent to or above the maximal aerobic speed. When speed is submaximal, on the other hand, as in the present study, $\dot{V}O_{2max}$ does not correlate with endurance capacity; rather, tissue oxidative capacity is a better predictor of individual differences. This pattern is in agreement with conclusions for mammals (summarized in Ref. 10).

Individual variation in $\dot{V}O_{2max}$ is related to individual differences in hematocrit in *A. nuchalis* (Table 5). $\dot{V}O_{2max}$ correlates with hematocrit in *C. similis* (13) and with hemoglobin in *S. occidentalis* (31). Individual differences in standard metabolic rate are related to relative organ sizes and tissue oxidative capacities in *A. nuchalis*, as has been found in two other species of lizards (13, 23).

Ecological and evolutionary considerations. The capacity for various kinds of locomotor performance generally differs between juvenile (small) and adult (large) vertebrate ectotherms (Refs. 2, 13, 14, 28, 30, this study, T. Garland, unpublished observations). However, the precise pattern of ontogenetic change (e.g., the slopes of scaling relationships) of organismal performance and its physiological correlates varies among species. Ecological correlates of ontogenetic changes in performance appear not to have been quantified in lizards and should be the subject of future studies (cf., Refs. 28, 30).

Sexual dimorphism in external morphological characters is common in lizards, with males often attaining larger sizes than females. The limited available data suggest that sexual dimorphism in locomotor performance and activity metabolism is less common.

It appears that seasonal differences in performance and metabolism may be common in lizards and may relate to patterns of natural activity (Refs. 21, 24, 25, this study). Activity patterns of *A. nuchalis* vary seasonally at our collection sites (R. E. MacMillen, personal communication; cf., Refs. 8, 26, and Refs. therein), but the ecological significance of seasonal variation in endurance is unclear.

Individual differences in $\dot{V}O_{2max}$ do not reflect individual differences in standard metabolic rate in *A. nuchalis*, which agrees with the results of previous studies on three distantly related species of lizards (13, 24, 29). This lack of correlation offers no support for the hypothesis that standard and maximal rates of $\dot{V}O_2$ are functionally and hence evolutionarily linked characters (DISCUSSION and bibliography in Ref. 29).

Summary. Patterns of ontogenetic allometry in speed, endurance, and activity metabolism in the agamid lizard *Amphibolurus nuchalis* differ substantially from those reported for a much larger iguanid lizard (13). Unlike in *C. similis*, factorial aerobic scope increases ontogenetically in *A. nuchalis*. Hemoglobin, hematocrit, relative heart and thigh muscle masses, and six of seven enzyme activities also increase ontogenetically in *A. nuchalis*; all of the foregoing may contribute to the ontogenetic increase in endurance. Relative liver mass shows negative allometry in both species. In *A. nuchalis*, sexual differences occur in only two characters, standard metabolic rate and heart citrate synthase activity, and appear to be of little biological significance. Seasonal variation is more common, however, with endurance, $\dot{V}O_{2max}$, heart lactate dehydrogenase activity, and thigh citrate synthase and pyruvate kinase activities all being higher in March (late summer) than in January lizards.

Significant repeatable differences in speed, endurance, and $\dot{V}O_{2max}$ exist among individual *A. nuchalis*, independent of differences in body mass. Individual differences in speed and endurance are uncorrelated in *A. nuchalis*, as are individual differences in $\dot{V}O_{2max}$ and SMR: both observations agree with the results of previous studies on lizards (3, 13, 24, 29). In both *A. nuchalis* and *C. similis*, many enzyme activities show significant intercorrelations, some of which reflect scaling relationships. As in *C. similis* and two other lizards (13, 23, 24, 31), individual differences in endurance, $\dot{V}O_{2max}$, and standard metabolic rate are predictable in part by individual differences in relative organ sizes, enzyme activities, and hematocrit. However, the details of these correlations differ among species, suggesting that factors limiting individual performance also differ among species. These differences result in part because endurance capacity varies greatly among species and among individuals, such that testing stamina at any given work load (e.g., endurance time at 1 km/h) may result in testing stamina under fundamentally different physiological regimens.

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Present address of T. Garland, Jr.: Dept. of Zoology, NJ-15, Univ. of Washington, Seattle, WA 98195.

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