

# Physiological correlates of locomotory performance in a lizard: an allometric approach

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GARLAND, THEODORE, JR. *Physiological correlates of locomotory performance in a lizard: an allometric approach*. Am. J. Physiol. 247 (Regulatory Integrative Comp. Physiol. 16): R806–R815, 1984.—Three measures of locomotory performance and a series of variables thought to affect performance were measured in the iguanid lizard *Ctenosaura similis*. Burst speed is mass independent; however, endurance time at 1 km/h (ENDUR) and maximal distance run (MAX DIS) scale as  $M^{0.3}$ . Standard and maximal rates of  $O_2$  consumption ( $\dot{V}O_{2\max}$ ) scale as  $M^{0.9}$ ;  $\dot{V}O_{2\max}$  averages 10-fold greater than standard metabolic rate (SMR). Three of ten enzyme activities measured exhibit significant scaling. After statistically removing the effects of body mass, multiple-regression analysis indicates that 1) 89% of the residual variation in ENDUR is correlated with variation among individuals in thigh muscle mass,  $\dot{V}O_{2\max}$ , heart mass, and liver citrate synthase (CS) activity; 2) maximal  $CO_2$  consumption ( $\dot{V}CO_{2\max}$ ) and thigh pyruvate kinase activity statistically explain 64% of the variation in MAX DIS; 3) heart and liver masses together predict 35% of the variation in SMR; 4) thigh and liver CS activity, heart lactate dehydrogenase (LDH) activity, and hematocrit account for 67% of the variation in  $\dot{V}O_{2\max}$ ; 5) 97% of the variation in  $\dot{V}CO_{2\max}$  is statistically related to variation in liver CS activity, thigh and heart masses, and heart LDH activity.

activity metabolism; exercise physiology; myofibrillar adenosine triphosphatase; scaling; treadmill

**VARIATION IN LOCOMOTORY PERFORMANCE** capacity exists among classes of terrestrial quadrupedal vertebrates, among orders or families within these classes (13, 14), and even among closely related species (23). Considerable variation in locomotory capacity also exists among individuals within a species; consider, for example, differences among humans, dogs, and horses. Presumably, variation in locomotory capacity occurs in populations of wild vertebrates as well, but such variation has apparently not been studied. The first objective of this study was to quantify variation in locomotory performance that exists in a natural population of lizards.

Differences among species are the evolutionary result of natural selection acting on phenotypic variation among individuals within populations. Therefore understanding the physiological bases of differences among individuals may offer valuable insights as to how the evolution of locomotory performance has occurred. Many previous studies have attempted to elucidate the mechanistic basis of interspecific differences in locomotory performance. Except in humans, however, there has been

no attempt to elucidate the basis of interindividual differences that exist in natural populations. The second objective of this study was to identify the physiological correlates of variation in locomotory performance among individual lizards.

Such an approach may offer new insights for physiologists as well as evolutionary biologists. Previous studies of exercise physiology have considered differences among species or among groups within a species that differ in their history of physical activity or training regime. A priori, it is unclear that such an approach should be more informative than examining differences among individuals, unless differences among individuals are so small as to preclude demonstrating statistically significant relationships, should they exist.

Three types of locomotory performance, measured in the laboratory, were chosen to include the range of locomotory activities engaged in by free-living animals. Variation in locomotory performance is first described and found to be substantial and to some extent explainable by differences in body size and age. After accounting statistically for the influence of body size, considerable residual variation in locomotory performance remains. Multivariate statistical analyses are employed to relate the residual variation in locomotory performance to a series of morphological, physiological, and enzymatic variables. These "predictor" variables were chosen as likely affectors of locomotory performance and/or metabolic rate, based on the exercise physiology literature and previous comparative studies of activity metabolism. The residual variation in performance is to a significant extent statistically explainable by variation among individuals in the predictor variables.

## MATERIALS AND METHODS

*Body temperature of lizards active in the field.* Because temperature affects locomotory performance (2), metabolic rate (3, 4), and enzyme activities measured in vitro, it was important to know the body temperatures ( $T_b$ ) of ctenosaurs active under natural conditions and to make measurements at an ecologically relevant  $T_b$ . Therefore  $T_b$  of ctenosaurs active in the field in Costa Rica were obtained during the summers of 1981 and 1982. Individuals were captured by hand or by slip noose and a Schultheis quick-registering mercury thermometer was inserted cloacally immediately after capture.

*Animal collection and maintenance.* *Ctenosaura similis*

were collected during early August, 1982, near Cañas, Guanacaste, Costa Rica, and were transported to the laboratory at the University of California, Irvine, within 10 days of capture. Individuals used in the present experiments ranged from 12.3 to 866 g. Individuals  $\leq 51$  g were young of the year, estimated to be  $\leq 3$  mo at time of killing. Individuals 110–240 g were assumed to be young of the previous year, hence  $\leq 15$  mo at time of killing; individuals  $> 500$  g were assumed to be at least 1 yr older. Other than these general categories, which were based on previous studies (7 and references cited therein), age could not be precisely determined.

Lizards were housed in glass or wood and wire terraria equipped with incandescent lights (permitting behavioral thermoregulation) set on a 12:12 h photocycle, approximately in phase with the natural (Costa Rican) day. Lizards were maintained in good health during the course of experiments. Juveniles ( $\leq 51$  g) fed on crickets; older lizards fed on fruit, vegetables, and dog food. Water was always available, and animals were misted daily.

**Locomotor performance.** The three measures of locomotor performance were chosen to include the extremes of locomotor behaviors exhibited by *C. similis* in the field. All measurements were made at  $T_b$  40°C. Protocols were designed to elicit maximal performance from individuals. Previous studies have shown similar protocols to yield highly repeatable measures of performance (2, 15, 25, H. B. John-Adler, unpublished, T. Garland, unpublished). Maximal running (burst) speed was measured by high-speed filming (60 frames/s) of lizards chased down a straight track (length 3–6 m, width 10–30 cm, depending on animal size). Reported burst speed is the highest speed ever attained over a 10- to 20-cm interval during any of two or three trials. Endurance time at 1 km/h (ENDUR) on a motorized treadmill (described in 25, 26, and H. B. John-Adler, unpublished) was recorded as the length of time an individual maintained tread speed with prodding and pinching as motivation. Trials were terminated when an individual did not maintain station after 10 consecutive pinches at  $< 1$ -s intervals; animals were usually exhausted at this point. Maximal distance run (MAX DIS) was recorded as individuals were chased continually and ultimately to fatigue around a circular track (circumference at center 5.3–6.7 m, width 10–30 cm, depending on lizard size). Trials were terminated when an animal made no progress after 10 consecutive prods. Each individual was tested twice for both ENDUR and MAX DIS, each trial being conducted on a different day; best performances were analyzed.

**Metabolic rate.** Standard metabolic rate (SMR) was recorded by using an open flow system as animals rested in the dark in a constant-temperature chamber at 40°C. Dry air was metered through metabolic chambers at flow rates of  $\sim 50$ –2,800 ml/min STPD, depending on animal size. An automatic sampling device incorporating a mechanical timer and solenoid switches allowed up to five animals to be continuously monitored through the night, each animal being sampled for at least 8 continuous min/h. A portion ( $\approx 1/3$ ) of the excurrent air was sampled by an Applied Electrochemistry model S-3A  $O_2$  analyzer,

and a continuous recording of percent  $O_2$  was produced on a Honeywell flatbed recorder. The lowest stable trace of  $O_2$  concentration in dried  $CO_2$ -free excurrent air from individual lizards was used to calculate SMR by using Hill's (20) Eq. 4.

Maximal rates of  $O_2$  consumption ( $\dot{V}O_{2\max}$ ) and  $CO_2$  production ( $\dot{V}CO_{2\max}$ ) were recorded with a flow-through system incorporating an Applied Electrochemistry model S-3A  $O_2$  analyzer, a Beckman model LB-2 infrared  $CO_2$  analyzer, a Brook's rotameter, and a diaphragm pump, as described in previous reports from this laboratory (25, 26, 28, H. B. John-Adler, unpublished). Lizards with lightweight transparent acetate masks through which room air was pulled at flow rates of 430–3,800 ml/min STPD were run on a motorized treadmill at speeds of 0.8–1.2 km/h in a stepwise sequence. Previous studies suggested that ctenosaurs would attain  $\dot{V}O_{2\max}$  within or below this range of speeds (3, 13, T. Garland, unpublished).  $\dot{V}O_2$  increased with increasing speed;  $\dot{V}O_{2\max}$  was considered to have been attained when further increments in speed resulted in no further increase in  $\dot{V}O_2$ . Respiratory exchange ratios (R) were always  $> 1$  as  $\dot{V}O_2$  peaked, and  $CO_2$  elimination generally continued to increase above the speed at which  $\dot{V}O_{2\max}$  was attained. Each individual was tested at least twice, and for each test the highest stable minute of  $\dot{V}O_2$  was calculated from the chart recording by polar planimetry (26). The highest rate of  $\dot{V}O_2$  ever attained is reported as  $\dot{V}O_{2\max}$ . The rate of  $\dot{V}CO_2$  attained during peak  $\dot{V}O_2$  of each step test was also noted, and the highest rate recorded during any of the two or more step tests is presented as  $\dot{V}CO_{2\max}$ . Note that for 12 of 18 individuals, the presented  $\dot{V}CO_{2\max}$  occurred during a different trial than did  $\dot{V}O_{2\max}$ . Calculation of rates of gas exchange followed those of John-Adler and Bennett (26). All gas exchange rates are presented as STPD.

**Morphology.** Hindlimb span (HLS) was measured to the nearest millimeter, immediately after decapitation, as the maximum distance from toe tip to toe tip (excluding claw length) with hindlimbs outstretched perpendicularly to the body. Liver (minus contents of gall bladder), heart (including atria), and the entire thigh muscle mass were dissected free and weighed. These tissues were then frozen and stored at  $-70^\circ C$  until homogenization for enzyme assays.

**Hematocrit and hemoglobin.** Heparinized microcapillary tubes were used to take blood samples from the neck of lizards immediately after decapitation. For measurement of hematocrit (Hct), tubes were centrifuged for 10 min at maximum speed in a clinical centrifuge. Hct was measured immediately after centrifugation. For measurement of hemoglobin (Hb) 25- $\mu$ l blood samples were added to 5 ml Drabkin's reagent and freeze-thawed three times to remove turbidity. Concentration of cyanmethemoglobin was determined spectrophotometrically at 540 nm. Hct and Hb were determined in duplicate; means were analyzed.

**Enzyme assays.** Citrate synthase (CS) activity was used as an indicator of the citric acid cycle (aerobic or oxidative) capacity of tissues (5, 12, 25, 36, 37, John-Adler, unpublished). Pyruvate kinase (PK) and lactate

dehydrogenase (LDH) activities were used as indicators of the anaerobic glycolytic capacity of tissues (8, 12, 36, John-Adler, unpublished). Myofibrillar adenosine triphosphatase (mATPase) activity was used as an indicator of the maximal rate at which skeletal muscle could catabolize high-energy phosphate compounds and may also correlate with maximal (intrinsic) contractile velocity (5, 9, 27). Samples of liver, heart, and thigh muscle were homogenized with a glass-glass homogenizer on ice in 19 or 49 vols of medium (100 mM potassium phosphate buffer containing 5 mM EDTA, pH 7.4); further dilutions were made as necessary. Homogenates were frozen and thawed twice before assaying for CS activity by the colorimetric method of Srere (37), following the appearance of mercaptide ion at 412 nm at reaction pH 8.0 at 40°C. Homogenates were centrifuged for 10 min at maximum speed in a clinical centrifuge, and the supernatant was used to assay PK activity as described by Somero and Childress (36) at pH 7.5 at 40°C. (Supernatants were also used for CS activity in thigh muscle and showed no loss of activity compared with whole homogenates.) Resuspended homogenates were used to assay LDH activity in the pyruvate reductase direction (characteristic of an anaerobically functioning tissue), following the method of Somero and Childress (36) (reaction pH 7.2 at 40°C). A separate sample of thigh muscle was used to assay mATPase activity exactly as described in Marsh and Wickler (27) and Ref. 5 and H. B. John-Adler, unpublished. Muscle samples used in the two separate homogenates (one for CS, PK, and LDH; one for mATPase) were taken from thoroughly minced and mixed thigh muscle to minimize variation due to heterogeneity of fiber type distributions within and among individual thigh muscles. All samples were run in duplicate, and means were analyzed.

Enzyme activities are expressed as micromoles product produced/(min  $\times$  g wet tissue mass) (U/g) at 40°C or as micromoles inorganic phosphate ( $P_i$ ) produced/(min  $\times$  mg myofibrillar protein). Acronyms for mass-specific enzyme activities are CSLIV for CS activity/g liver tissue, PKHRT for PK activity/g heart tissue, LDHTHI for LDH activity/g thigh muscle, and so forth. For CS, PK, and LDH, total organ enzyme activities were also calculated (i.e., U/organ) by multiplying the per gram activity by organ mass. Acronyms for total organ enzyme activities are LIVCS for total liver CS activity, HRTPK for total heart PK activity, THILDH for total thigh muscle LDH activity, and so forth.

*Statistical analyses.* Because any or all characters measured might scale allometrically with body mass ( $M$ ), all were log<sub>10</sub> transformed and regressed on log<sub>10</sub>  $M$  by using standard least-squares techniques. Thus for each variable, an equation of the form

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

was obtained or, in arithmetic form

$$Y = aM^b$$

where  $a$  is  $Y$ -intercept or position of the line (predicted value of  $Y$  at  $M = 1$  g, which is outside the range of  $M$ s

used) and  $b$  is slope of the log-log relationship or the scaling exponent. For those variables that exhibited significant scaling (i.e.,  $b$  significantly different from 0), allometric equations are given. For those variables that did not vary in relation to  $M$ , means of the untransformed data are presented. Analysis of covariance or  $t$  tests were used to compare  $a$  and  $b$  values.

To examine the relative variability of all characters, SD of residuals from allometric equations were compared. The SD of a log<sub>e</sub> transformed data set is approximately equivalent to the coefficient of variation (CV) of the untransformed data set. For variables that do not scale significantly, SD of residuals from a log<sub>10</sub>-log<sub>10</sub> regression on  $M$  (multiplied by 2.3026 to convert from base 10 to base  $e$ ) is equivalent to the CV of the untransformed data. For variables that do scale significantly, SD of residuals is equivalent to a CV of the untransformed data, after removing the variation in the data set that is statistically related to variation in  $M$ . Hence, comparing SD of residuals from allometric equations ( $\approx$ CV) allows conclusions to be drawn concerning the relative variability of different characters, after removing variation related to  $M$ . Comparing standard errors of estimate from log-log regressions gives qualitatively identical results, but CVs calculated as described above are more useful for comparison to literature values.

To determine the extent to which variation in locomotory performance and metabolic rate was related to variation among individuals in morphology or enzyme activities, residuals from allometric equations were used in regression and/or correlation analyses. Such a technique removes the confounding effects of  $M$ . First, residuals of locomotory performance were regressed on the metabolic, morphological, blood, and enzyme variables one at a time. Second, stepwise multiple-regression analysis was employed to determine the best predictive equations for residual locomotory performance by using all metabolic, morphological, blood, and enzyme residuals as independent (predictor) variables. Similarly, the residual metabolic rate variables were regressed on the morphological, blood, and enzyme residuals. In these multiple regressions, either mass-specific enzyme activities and organ masses or total organ enzyme activities were used as independent variables. Except in one case (prediction of MAX DIS, see Table 4), the former always yielded better predictive equations (higher  $r^2$  and/or more significant independent variables). Therefore multiple regressions with total organ enzyme activities are not presented. Statistical significance was judged at  $P < 0.05$  in all cases.

## RESULTS

### *Body Temperatures of Ctenosaurs Active in the Field*

The modal body temperature (27 of 104 individuals) of *C. similis* active in the field was 39.5 – 40.4°C [37.8  $\pm$  2.9 (SD) range 29.0–42.0]. Therefore 40°C was chosen for all measurements.

TABLE 1. Allometric equations or descriptive statistics for variables measured in *Ctenosaura similis*

Variable, U	Range	$a \pm 95\% \text{ CI}^*$	$b \pm 95\% \text{ CI}$	$R^2, \%$	SEE	CV, %†
<i>Locomotory performance</i>						
Burst, km/h	11.6–34.6	$22.3 \pm 6.1$ (27.2)				26.7
ENDUR, s	219–2,145	$151.5 \div \times 3.656$	$0.270 \pm 0.261$	24.4	0.28135	62.7
MAX DIS, m	25–103	$15.4 \div \times 1.601$	$0.265 \pm 0.099$	63.6	0.12680	28.4
<i>Metabolic rate</i>						
SMR, ml O <sub>2</sub> /h	3.17–148	$0.467 \div \times 1.184$	$0.858 \pm 0.036$	99.2	0.04866	10.9
$\dot{V}O_{2 \text{ max}}$ , ml O <sub>2</sub> /h	61.4–1,299	$3.381 \div \times 1.407$	$0.918 \pm 0.070$	98.0	0.07785	17.4
$\dot{V}CO_{2 \text{ max}}$ , ml CO <sub>2</sub> /h	85.0–1,941	$4.773 \div \times 1.488$	$0.945 \pm 0.081$	97.5	0.09062	20.2
<i>Morphology</i>						
HLS, mm	148–435	$63.0 \div \times 1.071$	$0.291 \pm 0.014$	99.3	0.01481	3.3
Liver, g	0.433–11.0	$0.0330 \div \times 1.437$	$0.866 \pm 0.073$	97.7	0.07812	17.4
Heart, g	0.054–1.96	$0.00394 \div \times 1.294$	$0.913 \pm 0.052$	99.0	0.05550	12.4
Thigh, g	0.485–19.6	$0.0216 \div \times 1.213$	$1.047 \pm 0.039$	99.6	0.04154	9.3
<i>Blood characters</i>						
Hct, %	19.3–33.5	$27.9 \pm 4.8$ (17.3)				18.1
Hb, g%	5.53–8.80	$7.06 \pm 0.94$ (13.3)				13.1
<i>Enzyme activities‡</i>						
CSLIV, U/g tissue	19.4–47.8	$31.5 \pm 8.3$ (26.3)				23.2
PKLIV, U/g tissue	11.6–22.4	$15.6 \pm 3.0$ (19.3)				16.4
LDHLIV, U/g tissue	102–290	$351 \div \times 1.667$	$-0.152 \pm 0.102$	40.2	0.10999	24.5
CSHRT, U/g tissue	101–185	$134 \pm 24$ (17.5)				16.3
PKHRT, U/g tissue	27.4–69.9	$75.8 \div \times 1.448$	$-0.094 \pm 0.074$	32.7	0.07967	17.8
LDHHRT, U/g tissue	110–207	$156 \pm 26$ (16.8)				17.2
CSTHI, U/g tissue	7.4–23.6	$17.0 \pm 4.7$ (27.9)				30.0
PKTHI, U/g tissue	155–376	$265 \pm 57$ (21.3)				20.3
LDTHI, U/g tissue	268–569	$238 \div \times 1.383$	$0.098 \pm 0.065$	40.5	0.06988	15.6
mATPase, U/mg myofibrillar protein	0.47–1.16	$0.774 \pm 0.213$ (27.5)				23.6

For all variables  $n = 17$  except burst  $n = 18$ , MAX DIS  $n = 20$ , SMR  $n = 22$ ,  $\dot{V}O_{2 \text{ max}}$   $n = 18$ . Equations in form of variable =  $a$  (body mass) <sup>$b$</sup> . SEE, standard errors of estimate of regressions in log 10 units. See text for other abbreviations. \*  $a$ , Antilog of estimated  $y$ -intercept (value at body mass = 1 g) from log-log regressions. Entry for 95% confidence interval (CI) denotes using ENDUR as an example, from  $151.5 \div 3.656$  to  $151.5 \times 3.656$ ; hence, on an arithmetic scale CIs are asymmetrical about the mean ( $a$ ). Values are means  $\pm$  SD; values in parentheses are CV. † CV =  $2.3026 \times$  SD of residuals from allometric equations, which is approximately equivalent to a CV (see text). ‡ Values determined at 40°C.

### Scaling, Variation, and Covariation of Characters

**Locomotory performance.** Locomotory performance varied greatly among individuals. Burst speed of the fastest individual was almost three times that of the slowest (Table 1), but this variation was not related to M. ENDUR varied by almost an order of magnitude (Fig. 1), and 24% of this variation was explainable by M (Table 1). MAX DIS varied almost fourfold (Fig. 1), 64% of the variation being related to M (Table 1). MAX DIS trials lasted an average of  $\sim 70$  s (range 34–127 s). Both ENDUR and MAX DIS scaled approximately as  $M^{0.27}$ , so on the average larger lizards had greater stamina.

The untransformed performance measures were positively intercorrelated ( $r = 0.589$  for burst  $\times$  ENDUR,  $0.579$  for ENDUR  $\times$  MAX DIS,  $0.437$  for MAX DIS  $\times$  burst), with only the last correlation being nonsignificant ( $P = 0.070$ ). Residuals of the performance measures were all positively but not significantly intercorrelated.

**Metabolic rate.** Analysis of covariance (ANCOVA) indicated that the relation between metabolic rate and M did not differ between juvenile and older ctenosaurs. SMR and  $\dot{V}O_{2 \text{ max}}$  scaled as  $M^{0.86}$  and  $M^{0.92}$ , respectively (Fig. 2, Table 1); however, these slopes are not significantly different by ANCOVA ( $F = 3.02$ ,  $P = 0.091$ ). By using a pooled slope of  $0.883 \pm 0.036$ ,  $\dot{V}O_{2 \text{ max}}$  averaged

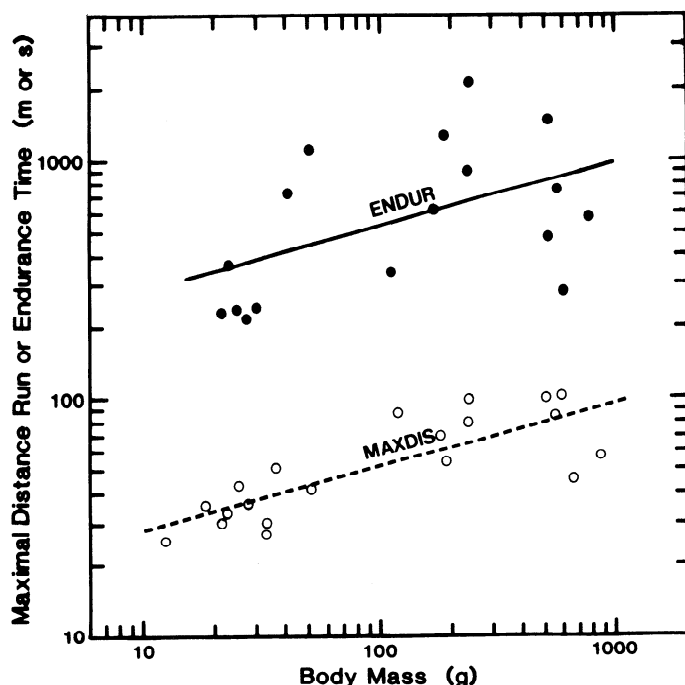


FIG. 1. Log-log plot of endurance time at 1 km/h (ENDUR; closed circles, solid line) and maximal distance run (MAX DIS; open circles, broken line) vs. body mass in ctenosaurs.

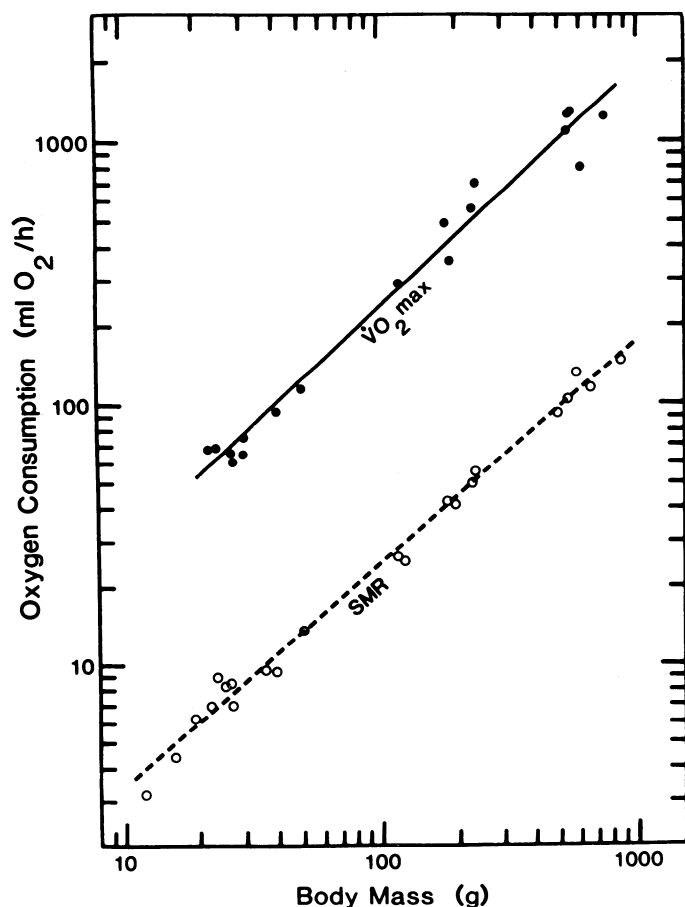


FIG. 2. Log-log plot of standard (SMR) and maximal ( $\dot{V}O_{2\max}$ ) rates of  $O_2$  consumption vs. body mass in ctenosaurs.

9.6 times greater than SMR.  $\dot{V}CO_{2\max}$  scaled as  $M^{0.95}$ , which is not significantly different from the exponent for scaling of  $\dot{V}O_{2\max}$  ( $F = 0.29$ ,  $P = 0.592$ ). By using a pooled slope of  $0.932 \pm 0.051$ ,  $\dot{V}CO_{2\max}$  averaged 1.6 times greater than  $\dot{V}O_{2\max}$ .

Residuals of SMR and  $\dot{V}O_{2\max}$  were not correlated ( $n = 18$ ,  $r = 0.122$ ,  $P = 0.630$ ). Residuals of SMR and  $\dot{V}CO_{2\max}$  were also uncorrelated ( $n = 18$ ,  $r = -0.152$ ,  $P = 0.548$ ). However, residuals of  $\dot{V}O_{2\max}$  and  $\dot{V}CO_{2\max}$  were positively correlated ( $n = 18$ ,  $r = 0.533$ ,  $P = 0.023$ ).

**Morphology.** Juvenile and adult ctenosaurs were not geometrically similar (Table 1). HLS scaled as  $M^{0.29}$ , significantly lower than the expected  $M^{0.33}$ , so larger lizards had relatively shorter hindlimbs. No organ scaled isometrically (Fig. 3, Table 1), all slopes being significantly different from one. Large lizards had relatively more massive thigh muscles but smaller hearts and livers, than small lizards. Residuals of the morphological variables were not significantly intercorrelated.

**Hematocrit and hemoglobin.** Neither Hct nor Hb varied with  $M$  (Table 1). The two measures were highly correlated ( $r = 0.771$ ,  $P < 0.001$ ).

**Enzyme activities.** Of 10 enzyme activities, only three exhibited significant scaling (Table 1). LDHLIV and PKHRT scaled as  $M^{-0.15}$  and  $M^{-0.09}$ , respectively. LDHTHI, however, was greater in larger lizards, scaling as  $M^{0.10}$ .

**Total organ enzyme activities.** Allometric equations for

total organ enzyme activities are presented in Table 2.

**Correlations among enzyme activities.** Table 3 presents correlations among enzyme activities both for raw data and for residuals from allometric equations. In either case there are 45 possible intercorrelations; judging significance at  $P < 0.05$  ( $r > 0.481$ ), fewer than 2.25 correlations might be expected to appear statistically significant due to chance alone (i.e., a type I error). This is unlikely to be a problem for interpretation here, however, since most of the significant correlations are significant

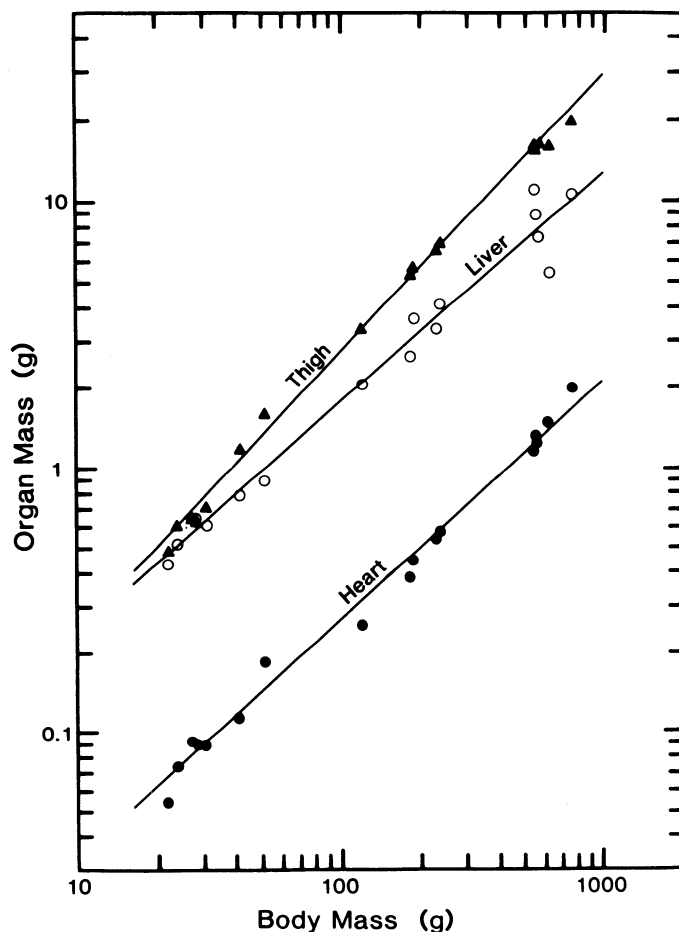


FIG. 3. Log-log plot of organ mass vs. body mass in ctenosaurs.

TABLE 2. Allometric equations

Organ Enzyme	$a \pm 95\% \text{ CI}$	$b \pm 95\% \text{ CI}$	$R^2, \%$	SEE	CV, %
Liver					
CS	$0.655 \pm 1.771$	$0.955 \pm 0.115$	95.5	0.12304	27.4
PK	$0.369 \pm 1.764$	$0.953 \pm 0.114$	95.3	0.12222	27.2
LDH	$11.59 \pm 1.810$	$0.713 \pm 0.119$	91.6	0.12773	28.5
Heart					
CS	$0.438 \pm 1.361$	$0.950 \pm 0.062$	98.6	0.06639	14.8
PK	$0.299 \pm 1.433$	$0.819 \pm 0.072$	97.5	0.07737	17.2
LDH	$0.664 \pm 1.426$	$0.895 \pm 0.071$	98.0	0.07642	17.0
Thigh					
CS	$0.485 \pm 1.959$	$0.980 \pm 0.135$	94.1	0.14479	32.3
PK	$4.254 \pm 1.563$	$1.104 \pm 0.090$	97.9	0.09619	21.4
LDH	$5.147 \pm 1.463$	$1.145 \pm 0.076$	98.6	0.08195	18.3

Equations in form of total enzyme activity =  $a$  (body mass) <sup>$b$</sup> ; values expressed in  $\mu\text{mol}$  product produced/(min  $\times$  organ) at  $40^\circ\text{C}$ . See Table 1 and text for explanation of parameters and abbreviations.

TABLE 3. *Correlations among enzyme activities*

	Liver			Heart			Thigh			
	CS	PK	LDH	CS	PK	LDH	CS	PK	LDH	ATP
Liver										
CS	1	0.326	−0.405	<b>0.549</b>	0.006	0.374	−0.324	0.001	0.072	−0.041
PK	0.221	1	<b>−0.643</b>	0.117	−0.302	−0.040	−0.188	−0.170	0.005	−0.405
LDH	−0.158	<b>−0.574</b>	1	−0.187	0.444	0.096	<b>0.525</b>	0.205	−0.092	0.225
Heart										
CS	0.472	0.045	−0.083	1	0.446*	<b>0.703</b>	−0.398	0.093	0.171	−0.078
PK	0.352	0.000	0.011	<b>0.832</b>	1	<b>0.639</b>	0.079	−0.120	−0.301	0.328
LDH	0.464	0.031	−0.030	<b>0.784</b>	<b>0.732</b>	1	−0.325	−0.264	−0.246	0.072
Thigh							0			
CS	−0.206	−0.143	0.410	−0.378	−0.189	−0.414	1	0.446	0.220	−0.070
PK	−0.117	−0.467	<b>0.527</b>	0.001	0.115	−0.232	<b>0.577</b>	1	<b>0.878</b>	−0.297
LDH	−0.251	−0.475	<b>0.496</b>	−0.004	0.085	−0.206	<b>0.551</b>	<b>0.890</b>	1	−0.320
ATP	0.234	−0.298	0.055	0.084	0.107	0.108	−0.167	−0.138	−0.046	1

Values above diagonal based on raw data; values below diagonal based on residuals from allometric equations. Correlations > 0.481 in magnitude are significant at  $P < 0.05$  and appear in **boldface** ( $n = 17$ ). See text for abbreviations. \* Significant for log 10 transformed data ( $r = 0.491$ ,  $P = 0.045$ ).

TABLE 4. *Results of multiple-regression analyses*

Dependent Variable = Independent Variables	Multiple $r^2$ , %	Overall $F$	Overall Significance
ENDUR = + thigh + $\dot{V}O_{2\max}$ + heart + CSLIV (54.0) (18.7) (8.6) (8.0)	89.4	25.2	<0.0001
MAXDIS = + $\dot{V}CO_{2\max}$ + PKTHI (40.5) (17.7)	58.2	9.8	0.0022
SMR = + heart + liver (18.7) (16.3)	35.0	3.8	0.0490
$\dot{V}O_{2\max}$ = + CSTHI + CSLIV + LDHHRT + Hct (22.8) (20.7) (13.6) (10.1)	67.2	6.1	0.0063
$\dot{V}CO_{2\max}$ = + CSLIV + thigh − LDHHRT − heart (60.3) (23.0) (7.8) (6.2)	97.3	106.8	<0.0001

Only signs of partial regression coefficients are given; all were significant at  $P < 0.05$  by partial  $F$  tests ( $n = 17$ ). Values in parentheses indicate partial  $r^2$ . See text for abbreviations and results of simple linear regressions. \* Step-wise multiple regression of MAX DIS on total organ enzyme activities produced a slightly better predictive equation including  $\dot{V}CO_{2\max}$  and THIPK (multiple  $r^2 = 63.7\%$ ;  $F = 12.3$ ;  $P = 0.0008$ ).

at  $P \ll 0.05$ .

Considering the raw data, six enzyme intercorrelations are significant. Within tissues, PK and LDH are positively correlated in heart and thigh but negatively correlated in liver. LDHHRT and CSHRT are also positively correlated. Among tissues, CSHRT and CSLIV are positively correlated as are CSTHI and LDHLIV. Considering residuals, nine intercorrelations are significant, four of these corresponding to raw data correlations. Residuals of CSHRT, PKHRT, and LDHHRT are highly positively intercorrelated. Residuals of CSTHI, PKTHI, and LDHTHI are also positively intercorrelated. Finally, PKTHI and LDHTHI are positively correlated with LDHLIV. In summary, the most striking pattern that emerges is that enzymes concerned with energy production (CS, PK, LDH) are positively intercorrelated within both heart and thigh.

Relative Variation of Characters

Tables 1 and 2 include approximate CVs for all variables. Locomotory performance was generally the most variable (CV = 27–63%). Metabolic rates were less variable (CV = 11–20%). Mass- (or protein-) specific enzyme activities had CVs of 16–30%. Hct and Hb had CVs of 18 and 13%, respectively. Hindlimb span and thigh were

the least variable (CV = 3.3 and 9.3%, respectively) of all characters.

Correlation of Locomotory Performance and Metabolic Rate with Other Characters

No significant amount of the variation in burst speed residuals could be explained by any other variable.

ENDUR residuals were significantly positively related to thigh ( $r^2 = 0.540$ ),  $\dot{V}O_{2\max}$  ( $r^2 = 0.355$ ), and THICS ( $r^2 = 0.236$ ; CSTHI alone did not explain a significant amount of the variation in ENDUR,  $r^2 = 0.088$ ,  $P = 0.248$ ). Step-wise multiple-regression analysis (Table 4) indicates that four independent variables (thigh,  $\dot{V}O_{2\max}$ , heart, CSLIV) explain significant amounts of the variation in ENDUR (multiple  $r^2 = 89.4\%$ ).

MAX DIS residuals were positively related to  $\dot{V}CO_{2\max}$  ( $r^2 = 0.406$ ),  $\dot{V}O_{2\max}$  ( $r = 0.340$ ), LIVCS ( $r^2 = 0.305$ ), and THIPK ( $r^2 = 0.285$ ). However, multiple-regression analysis (Table 4) includes only  $\dot{V}CO_{2\max}$  and PKTHI (or THIPK) as significant predictors of MAX DIS (multiple  $r^2 = 58.2\%$ ).

Simple regression analysis yielded no single variable as a significant predictor of SMR residuals. However, a multiple regression of SMR residuals on heart and liver residuals is significant (Table 4, multiple  $r^2 = 0.350$ ),

although neither partial  $F$  value is significant ( $F = 3.884$ ,  $P = 0.069$  for heart;  $F = 3.515$ ,  $P = 0.082$  for liver).

In univariate analyses,  $\dot{V}O_{2\max}$  residuals are related positively only to LIVCS ( $r^2 = 0.327$ ). Multiple-regression analysis (Table 4), however, includes CSTHI, CSLIV, LDHRT, and Hct as significant predictors of  $\dot{V}O_{2\max}$  (multiple  $r^2 = 67.2\%$ ).

$\dot{V}CO_{2\max}$  residuals are related positively to CSLIV ( $r^2 = 0.603$ ), LIVCS ( $r^2 = 0.578$ ), and ATPTHI ( $r^2 = 0.281$ ) and negatively to heart ( $r^2 = 0.460$ ). Stepwise multiple regression (Table 4) includes CSLIV, thigh, LDHRT, and heart as significant predictors (multiple  $r^2 = 97.3\%$ ), the latter two independent variables being negatively related to  $\dot{V}CO_{2\max}$ .

## DISCUSSION

Many variables measured in this study scaled allometrically with body mass. Larger lizards are, on average, also older than smaller lizards, so it is difficult to know whether scaling patterns are attributable to the effects of body size per se or to age-related differences among individuals. Because *C. similis* could not be aged independently of body size, my discussion regarding scaling effects is related in terms of body mass. Although juvenile male and female ctenosaurs are externally indistinguishable, adult ctenosaurs are sexually dimorphic in size and shape (see Ref. 7). Due to small sample size (6 females vs. 4 males older than 1 yr and exhibiting external dimorphism) and because there was no apparent sexual dimorphism in any variable measured, males and females were treated together.

**Locomotor performance.** Burst speed was mass independent in ctenosaurs. Mass independence of burst speed has also been found in the smaller iguanid lizard *Sceloporus undulatus* (S. Crowley, personal communication) and in *Agama aculeata* (22). In contrast, burst speed scales positively in the iguanid *Dipsosaurus dorsalis* (R. L. Marsh, personal communication), in *Stellio sellio* (24), and in three *Eremias* species (22). Within families of lizards (13), as within orders of mammals (14), burst speed is generally mass independent. The fastest ctenosaur (230 g) attained a speed of 34.6 km/h, which is the highest speed yet reported for a lizard (13, and T. Garland, in preparation). Variation in burst is similar to that reported previously for lizards (2, 22–24, 35).

Both ENDUR and MAX DIS scaled positively in ctenosaurs. Endurance capacity is also greater in larger and older garter snakes and water snakes (29) and in some amphibians (e.g., 38). This increase in endurance capacity in snakes has been attributed to an ontogenetic increase in Hct, Hb, and blood  $O_2$  capacity (BOC), which enhances  $O_2$  transport and delivery. In addition, there is a less important ontogenetic increase in anaerobic capacity, as evidenced by greater whole-body lactic acid concentrations in larger snakes following maximal exertion. Neither Hct nor Hb is greater in larger ctenosaurs, which suggests that BOC is not increased in larger ctenosaurs. Furthermore, relative heart mass is lower in large ctenosaurs, so increased  $O_2$  transport and delivery capacity seem unlikely to account for the greater endurance of

larger ctenosaurs.

At least three factors are suggested to account for positive scaling of ENDUR and MAX DIS. First, even among geometrically similar tetrapods, endurance is predicted to scale as  $M^{0.33}$  (9, 20), mainly due to lower limb cycling frequencies in larger animals. Second, ctenosaurs are not geometrically similar but exhibit positive scaling of relative thigh muscle mass as well as mass-specific thigh LDH activity. Therefore total thigh LDH and PK activities scale as  $M^{1.14}$  and  $M^{1.10}$ , respectively (both exponents significantly  $>1$ ). Finally, mass-specific aerobic capacity (CS activity) is maintained in larger ctenosaurs, whereas the mass-specific cost of transport scales negatively among species of lizards (3) and presumably during ontogeny in ctenosaurs.

Variation in MAX DIS is similar to that reported previously for distance running ability of several small lizards (2, 23, 35). Similar variation in lizard ENDUR has also been reported (23, 26, H. B. John-Adler, unpublished).

**Metabolic rate.** SMR scaled as  $M^{0.86}$  in *C. similis*, which is within the range of variation reported previously for intraspecific scaling of SMR in lizards (4).  $\dot{V}O_{2\max}$  scaled as  $M^{0.92}$ , the exponent being not significantly different from that for SMR. Intraspecific scaling of  $\dot{V}O_{2\max}$  has not been reported previously for any species of reptile. Among species of lizards,  $\dot{V}O_{2\max}$  scales as  $M^{0.70-0.80}$  (3). Several workers have scaled  $\dot{V}O_{2\max}$  to body mass within amphibian species, their scaling exponents bracketing that reported here (38 and references cited therein).

Slope of the relation between metabolic rate (resting and/or  $\dot{V}O_{2\max}$ ) and body mass may change with age within species of fish, amphibians, birds, and mammals (e.g., Refs. 11 and 38) such that “break points” occur on a log-log plot. However, no such break points occur for SMR,  $\dot{V}O_{2\max}$ , or  $\dot{V}CO_{2\max}$  in *C. similis*. Apparently break points in metabolic rate-body mass relationships have not been reported to occur during postembryonic growth for any reptilian species.

$\dot{V}O_{2\max}$  averaged almost 10-fold greater than SMR in ctenosaurs. Such a differential is typical within the range of variation exhibited by lizards and among vertebrates in general (3), although there is considerable variation in the ratio  $\dot{V}O_{2\max}$  to SMR.

$\dot{V}CO_{2\max}$  averaged 1.6-fold greater than  $\dot{V}O_{2\max}$ , which is within the range of respiratory exchange ratios reported previously for lizards walking at nonsustainable speeds (17, 26).

**Morphology.** Scaling of the morphometric variables measured herein has been little studied in reptiles. In the alligator, heart mass scales approximately as  $M^{0.82}$ , and liver mass scales approximately as  $M^{0.86}$  (data from Table 1.4 of Ref. 10). These scaling patterns are similar to those found in ctenosaurs. Heart mass also scales negatively within some mammalian species (e.g., 6) but scales as  $M^{0.98 \pm 0.02}$  ( $\pm 95\%$  confidence interval) among mammalian species (31). Liver mass scales as  $M^{0.89}$  among species of mammals, but intraspecific scaling exponents vary and may show break points (6, 33). Relative limb muscle mass tends to be larger in larger species of mammals (1), scaling exponents being similar to the 1.05



found within *C. similis*.

**Hematocrit and hemoglobin.** As mentioned above, Hct and Hb increase with size and age in some snakes (29, 30). Neither scales in ctenosaurs. Among mammalian species, Hct scales as  $M^{-0.01}$ , the exponent, according to Prothero (32), being significantly different from zero. Hct and Hb and their CVs in ctenosaurs are similar to values reported previously for lizards (5, 30, 35).

**Enzyme activities.** The well-known mouse-elephant curve indicates that mass-specific metabolic rate scales as  $M^{-0.25}$ . Several previous studies have shown that mass-specific tissue oxidative capacity, as indicated by tissue  $O_2$  uptake, activities of Kreb's cycle or electron transport enzymes, or mitochondrial or cytochrome contents generally also decreases with increasing body mass both within and among mammalian species (e.g., 12) and within species of fish (36). Mass-specific metabolic rate scales as  $M^{-0.082}$  or  $M^{-0.142}$  in ctenosaurs (both exponents significantly  $<0$  but  $>-0.25$ ), depending on whether one considers  $\dot{V}O_{2\max}$  or SMR. It was therefore expected that mass-specific CS activity, being an indicator of tissue oxidative capacity, would also scale negatively with *C. similis*. Such was not the case in any tissue. Alternatively, it was expected that total organ CS activity (Table 2) might scale to exponents similar to that for whole-animal metabolic rate (Table 1). LIVCS and HRTCS scale with exponents that are not significantly different from those for scaling of SMR (two-tailed *t* tests comparing exponents,  $P > 0.2$  and  $P > 0.05$ , respectively). THICS and HRTCS both scale with exponents that are not significantly different from that for scaling of  $\dot{V}O_{2\max}$  ( $P > 0.10$ ,  $P > 0.50$ , respectively). Therefore, in ctenosaurs total organ oxidative capacities scale approximately in parallel with whole-animal metabolic rates.

In contrast to the scaling of oxidative enzymes, glycolytic enzymes in muscle scale positively (on a mass-specific basis) within species of fish (36) and among mammalian species (12). In agreement with these studies, LDH and PK activities in thigh muscle scale positively in ctenosaurs, although only the scaling exponent for the former is significant. The adaptive and mechanistic significance of the discrepancy in scaling of oxidative vs. glycolytic enzymes has been related to differences in power requirements of sustained vs. burst locomotion (12, 36).

Among geometrically similar tetrapods (20), exhibiting mass independence of burst speed, mATPase is expected to scale as  $M^{-0.33}$  (9). mATPase scaled as  $M^{-0.093 \pm 0.099}$  in ctenosaurs, the exponent being not significantly different from zero ( $P = 0.063$ ).

Enzyme activities and their CVs reported herein are similar to those reported previously for the desert iguana at 40°C (25, H. B. John-Adler, unpublished) and for two small agamid lizards measured at 37°C (5). CVs of enzyme activities presented here are also similar to those calculated from other studies that used similar assay procedures (e.g., 8, 27, 36).

**Correlation of locomotory performance and metabolic rate with other characters.** It was expected that variation in burst speed would be positively related to HLS, thigh, and/or mATPase (e.g., Refs. 2 and 9). No significant

relations were found, however. Recent theoretical and empirical studies suggest that mATPase may not be limiting for contractile velocity (I. Johnston, personal communication). In addition, Bennett et al. (5) found no difference in mATPase activities between two agamid lizards that differed significantly in burst speed. Perhaps some component of neuromuscular transmission affects burst speed more importantly than the characters measured herein (cf. discussions in Refs. 5 and 23).

Up to 89% of the residual variation in ENDUR was statistically related to variation among individuals in the physiological and morphological characters measured. The significant positive relationship between ENDUR and thigh,  $\dot{V}O_{2\max}$ , and heart is generally consistent with the mammalian exercise physiology-training literature. Davies et al. (summarized in Ref. 11) conclude the following for rats: 1) muscle oxidative capacity is the major determinant of submaximal endurance capacity, and 2)  $\dot{V}O_{2\max}$  is strongly related to the maximal intensity of work that can be attained aerobically. ENDUR was not submaximal, because 1 km/h is at or above the speed at which ctenosaurs attain  $\dot{V}O_{2\max}$ . Endurance at 1.1 km/h correlates with both  $\dot{V}O_{2\max}$  and muscle CS activity in the desert iguana (H. B. John-Adler, unpublished data).

After statistically removing the effects of body mass, relative thigh muscle mass is the single best predictor of ENDUR in ctenosaurs. Perhaps individuals with relatively massive thigh muscles experienced a lower energy expenditure (aerobic + anaerobic power input) per gram muscle (because there was more total thigh muscle to share the work) and hence fatigued less rapidly than individuals with smaller locomotory muscles.

$\dot{V}CO_{2\max}$ ,  $\dot{V}O_{2\max}$ , LIVCS, and THIPK were significant predictors of MAX DIS in simple linear regressions. In a multiple regression, about 60% of the residual variation in MAX DIS was accountable for by  $\dot{V}CO_{2\max}$  and PK activity in the thigh. MAX DIS trials lasted on average only a little over 1 min and were presumably fueled primarily by anaerobic production of ATP with concomitant lactate production (3, 10), by endogenous stores of ATP and creatine phosphate, and to a lesser extent by oxidative processes. It is therefore not surprising that the anaerobic glycolytic indicator enzyme PK correlates with MAX DIS. A relatively weak correlation between MAX DIS and  $\dot{V}O_{2\max}$  might also be expected (cf. Ref. 35).  $\dot{V}O_{2\max}$  is not a statistically significant predictor of MAX DIS in a multiple regression when  $\dot{V}CO_{2\max}$  is included in the model, but this result must be interpreted with caution because the two gas exchange variables are significantly correlated (hence the problem of multicollinearity in multiple regression analysis). Similarity among individuals in substrate utilization for aerobic metabolism would be expected to result in a positive correlation between residuals of  $\dot{V}O_{2\max}$  and  $\dot{V}CO_{2\max}$ . The functional basis for a positive correlation between  $\dot{V}CO_{2\max}$  and MAX DIS is less apparent.

Heart and liver account for a relatively large fraction of the resting metabolic rate in mammals and presumably in lizards. Hence it is not surprising that about one-third of the interindividual variation in ctenosaur SMR was explainable by variation in relative heart and liver



masses. John-Alder (25) found a significant correlation between hepatic CS activity and SMR in desert iguanas.

In mammals, particularly humans and rats, it is now generally believed that  $\dot{V}O_{2\max}$  is limited by cardiovascular parameters rather than by tissue oxidative capacity (11, 34 and refs. therein). Saltin and Rowell (34) caution, however, that "limitations in the consumption of oxygen may reside in different systems in different species." Of the indexes of cardiovascular function measured in ctenosaurs (Hct, Hb, relative heart mass, heart oxidative and glycolytic capacities), LDHRT (13.6%) and Hct (10.1%) account for significant amounts of the residual variation in  $\dot{V}O_{2\max}$  (Table 4). Why LDHRT correlates with  $\dot{V}O_{2\max}$  is unclear, since it is unknown what LDH activity indicates about cardiac function in lizards (see also below). It should be noted that significant intercorrelations among the heart enzymes, between Hct and Hb, and an almost significant correlation between CSTHI and Hb residuals ( $r = 0.469$ ,  $P = 0.058$ ) may confound statistical analyses. Schall et al. (35) report a significant correlation between  $\dot{V}O_{2\max}$  and Hb in a small iguanid lizard. In ctenosaurs, CS activity in the thigh and liver together explain 44% of the residual variation in  $\dot{V}O_{2\max}$ . John-Alder (25) reported a similar significant correlation between mass-specific  $\dot{V}O_{2\max}$  and gastrocnemius CS activity. It may also be relevant that CS activity in lizard muscle or heart is lower than in mammalian muscle or heart (cf. this study, 5, 12, and 25).

The foregoing raises the question: why is heart positively related to ENDUR, if the effect is not mediated through enhanced  $O_2$  delivery? Relative heart mass should correlate with stroke volume and hence be one determinant of maximal cardiac output (18). Substrate delivery to, and/or removal of metabolites from, exercising muscles may be partially limited by cardiac output, which could in turn account for the positive relationship between heart mass and ENDUR.

Almost all residual variation in  $\dot{V}CO_{2\max}$  was statistically related to CSLIV, thigh, LDHRT, and heart (Table 4). LDHRT and heart were negatively related to  $\dot{V}CO_{2\max}$ . If the heart is actively taking up lactate (cf. 8, 17, 19 and refs. therein) during nonsustainable activity, as during the latter stages of the  $\dot{V}O_{2\max}$  step tests, then individuals with higher LDHRT activities and/or relatively larger hearts might be eliminating less  $CO_2$  to maintain (28) blood pH.

Residual CSLIV is a statistically significant predictor of residual MAX DIS,  $\dot{V}O_{2\max}$ , and  $\dot{V}CO_{2\max}$  in simple linear regressions and a significant predictor of ENDUR,  $\dot{V}O_{2\max}$ , and  $\dot{V}CO_{2\max}$  in multiple regressions. Deleting

CSLIV invariably resulted in less satisfactory multiple-regression equations. These results suggest that liver oxidative capacity plays a significant role in the activity metabolism of ctenosaurs, although the nature of its involvement is unknown. Perhaps the liver plays an important role in conversion of metabolites during (and after) activity, and its capacity to do so depends on its oxidative capacity. The liver may be an important site of lactate oxidation and/or gluconeogenesis (10, 16, 19).

Alternatively, CSLIV may be correlated with ENDUR,  $\dot{V}O_{2\max}$ , and  $\dot{V}CO_{2\max}$  because they have common causes. Interestingly, John-Alder (25, unpublished data) found the following in desert iguanas. 1) CSLIV, ENDUR, and  $\dot{V}O_{2\max}$  respond similarly to thyroid manipulation. 2) All (including plasma thyroid hormone levels) undergo similar seasonal cycles. 3) There is a significant correlation on an individual basis between plasma thyroxine and mass-specific liver CS activity.

In conclusion, this study has demonstrated that performance variations in wild lizards, as measured in the laboratory, are considerable and appear to reflect physiological, morphological, and biochemical differences among individuals. Multivariate statistical analyses (Table 4) have been employed to identify factors, at lower levels of biological organization, that are significant predictors of variation in locomotory performance and metabolic rate. Some of these relationships were expected, based on previous studies of activity metabolism and exercise physiology. Others, in particular the role of liver oxidative capacity in activity metabolism, are not presently understandable. Whether these statistical relationships reflect underlying biological mechanisms, and hence causality, can only be determined through further comparative and experimental studies.

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