

THE EVOLUTION OF FORM AND FUNCTION:  
MORPHOLOGY AND LOCOMOTOR PERFORMANCE IN  
WEST INDIAN *ANOLIS* LIZARDS

JONATHAN B. LOSOS

Museum of Vertebrate Zoology and Department of Zoology, University of California,  
Berkeley, CA 94720 USA

*Abstract.*—I tested biomechanical predictions that morphological proportions (snout–vent length, forelimb length, hindlimb length, tail length, and mass) and maximal sprinting and jumping ability have evolved concordantly among 15 species of *Anolis* lizards from Jamaica and Puerto Rico. Based on a phylogenetic hypothesis for these species, the ancestor reconstruction and contrast approaches were used to test hypotheses that variables coevolved. Evolutionary change in all morphological and performance variables scales positively with evolution of body size (represented by snout–vent length); size evolution accounts for greater than 50% of the variance in sprinting and jumping evolution. With the effect of the evolution of body size removed, increases in hindlimb length are associated with increases in sprinting and jumping capability. When further variables are removed, evolution in forelimb and tail length exhibits a negative relationship with evolution of both performance measures. The success of the biomechanical predictions indicates that the assumption that evolution in other variables (e.g., muscle mass and composition) did not affect performance evolution is probably correct; evolution of the morphological variables accounts for approximately 80% of the evolutionary change in performance ability. In this case, however, such assumptions are clade-specific; extrapolation to taxa outside the clade is thus unwarranted. The results have implications concerning ecomorphological evolution. The observed relationship between forelimb and tail length and ecology probably is a spurious result of the correlation between these variables and hindlimb length. Further, because the evolution of jumping and sprinting ability are closely linked, the ability to adapt to certain microhabitats may be limited.

Received May 30, 1989. Accepted December 1, 1989.

To test hypotheses about the adaptive significance of a phenotypic feature, an understanding of how it functions is essential. Only then can one understand how evolutionary change in that feature enhances or constrains an organism's ability to utilize its environment and, consequently, how the feature may have evolved in response to selective pressures (Bock and von Wahlert, 1965; Arnold, 1983, 1986). Recent approaches (Huey and Stevenson, 1979; Huey and Bennett, 1986; Arnold, 1983) have emphasized the importance of ecologically-relevant measures of performance capability, which directly affect how successful an organism will be in interacting with the environment. Further, comparative studies of adaptation explicitly concern the evolutionary history of a character or character complex within a clade, and must be conducted in a phylogenetic context (Lauder, 1981; Gould and Vrba, 1982; Ridley, 1983; Huey, 1987). Study of extant taxa, without consideration of their relationships, is likely to result in mistaken conclusions about evolutionary patterns and processes (Felsen-

stein, 1985; Huey and Bennett, 1987). These two perspectives (the performance and phylogenetic approaches) can be combined to rigorously test adaptive hypotheses by considering the ecological context in which the evolution, not only of a character, but also of its associated performance capability, has occurred (Greene, 1986; Wainwright and Lauder, in press; Losos, 1990a).

The radiation of *Anolis* lizards in the West Indies presents an opportunity to utilize this integrative approach. A set of species differing in body size, limb and tail proportions, body shape, and other characters exists on each of the Greater Antillean islands. In both intra- and inter-island comparisons, morphologically similar species (members of the same "ecomorph" type) are also similar in ecology and behavior (Rand and Williams, 1969; Williams, 1972, 1983). The phylogeny of *Anolis* indicates that each of the set of the "ecomorph" types has evolved independently several times within the Greater Antilles (Williams, 1972, 1983).

Although this widespread convergence strongly suggests an adaptive relationship

between morphology and "structural niche" (Clutton-Brock and Harvey, 1984; Luke, 1986), the lack of functional information prevents a more critical interpretation. In particular, one cannot determine why particular morphological features are associated with particular structural habitats. In this study, I consider two performance measures that are ecologically relevant to these arboreal saltatory species: jumping and sprinting capability. I investigate whether morphological variation among 15 species of Jamaican and Puerto Rican *Anolis* is related to variation in maximal jumping and sprinting capability and whether morphology and performance ability have evolved concordantly. The role that performance ability plays in determining ecological differences among these species is explored elsewhere (Losos, 1990a).

A functional analysis can also indicate which morphological features are responsible for variation in performance ability among taxa. With the effect of body size removed, limb and tail proportions and body shape (i.e., whether species are stout or slender) are strongly correlated among these 15 *Anolis* species (Losos, 1990a). Biomechanical models predict that each of these morphological variables should affect jumping and sprinting capability (see below). By holding other variables constant statistically, the relative importance of each variable in determining performance ability can be determined and the biomechanical models can be tested. In turn, this information suggests two hypotheses concerning the variables with relatively little impact on running and sprinting ability: either their correlation with ecology and behavior is an incidental by-product of their correlation with morphological variables directly affecting performance ability, or they are related to other ecologically relevant measures of performance.

#### *Biomechanical Models Jumping*

Distance jumped ( $d$ ) by a lizard should be:

$$d = (4klm_m/m_b)^{1/2} \sin^2 \theta g^{-1},$$

where  $k$  is the power produced per unit mus-

cle,  $l$  is the distance through which the lizard accelerates,  $m_b$  is mass,  $m_m$  is muscle mass of the hindlimb that is used in jumping,  $\theta$  is the angle of take-off, and  $g$  is acceleration due to gravity (Alexander, 1968; Pounds, 1988).

For most animals, hindlimb length is proportional to  $l$  (Alexander, 1968; Emerson, 1985). Consequently, two predictions about the effect of hindlimb length on jumping ability follow: (i) Because a tight allometric relationship usually exists between body size and limb length, larger animals should be able to jump farther; (ii) With the effect of size removed, longer-legged animals should be able to jump farther. The first prediction has been corroborated within species of frogs (Zug, 1972, 1978; Emerson, 1978) and lizards (Losos et al., 1989); the second prediction has been confirmed in comparisons among species of frogs (Rand, 1952; Zug, 1972; but see Emerson [1985]) and saltatory vertebrates (Emerson, 1985), but not within species of frogs (Emerson, 1978) or lizards (Losos et al., 1989). These predictions assume that the ratio of hindlimb muscle mass-to-body mass, power per unit muscle and take-off angle are constant. I have no information on muscle mass or power output, but, based on unquantified observations, the angle of takeoff in laboratory trials appears approximately constant among species. Ongoing studies will assess the degree to which interspecific variation in these parameters contributes to differences in jumping capability.

Biomechanical models also predict that body shape, forelimb length, and tail length might affect jumping ability by affecting the location of the center of gravity. Many jumping species have relatively short trunks, presumably to shift the center of balance over the hindlimbs, thus preventing pitching in a forward direction during the jump (Emerson, 1985). However, examination of 13 species (suitable preserved specimens were unavailable for *A. cuvieri* and *A. evermanni*) included in this study indicates that body shape (slender versus stocky, quantified as the residual of body mass regressed on snout-vent length) is not related to the position of the center of gravity (Losos, unpubl). Body shape also could affect jumping ability if stocky animals had rela-

tively large hindlimb muscles for their body mass. Unfortunately, this information is currently unavailable.

The forelimbs provide little, if any, propulsive force for most jumpers (Emerson, 1985). To the extent that the forelimbs shift the center of balance forward from over the hindlimbs and thus decrease the distance jumped, species with relatively shorter forelimbs for their size should be able to jump farther. Tail length may also affect the center of balance by acting as a counterbalance (Ballinger, 1973; Pounds, 1988); species with relatively long tails should be able to jump further. In support of this prediction, *Anolis carolinensis* with experimentally-removed tails had difficulty jumping in laboratory enclosures (Ballinger, 1973).

### Running

Sprint speed is determined by stride length and frequency (Sukhanov, 1968). Morphology may affect sprinting ability by altering these parameters. Currently, however, little evidence exists concerning the causal basis of among-species differences in maximum speed. Sukhanov (1968) suggested that differences among a sample of scincid, lacertid, and gekkonid lizards result solely from differences in stride length, but differences between this group and a sample of several agamid lizards are due to changes in both stride length and frequency.

Stride frequency is affected by a variety of physiological and biomechanical factors (e.g., proportion of muscle fiber types, relative muscle and limb mass, distance of muscle insertion from the point of rotation), and is inversely correlated with body size (Sukhanov, 1968; Marsh, 1988). However, the morphological variables I measure (other than overall body size) should not affect stride frequency. Consequently, I focus on differences in stride length and ignore stride frequency, which, with the effect of size removed, might not vary among closely related taxa (Sukhanov, 1968). Kinematic studies are needed to verify this assumption.

Stride length is determined by limb length, angle of limb swing, limb extension, pelvic rotation, and axial flexion (Barclay, 1946; Sukhanov, 1968; Garland, 1985). The hind-

limb is more important than the forelimb in determining stride length and propulsive force among most lizard species, particularly those, like *Anolis*, in which the hindlimb is longer than the forelimb (Snyder, 1952; Sukhanov, 1968). The forelimb often serves as little more than a prop and is not in contact with the substrate throughout much of the limb cycle. Bipedality, observed in numerous lizard taxa (Snyder, 1949, 1952; Sukhanov, 1968; including laboratory observations [as below] on *A. cristatellus* from Florida [J. B. Losos, unpubl.]), is an extension of this trend at high speeds (Snyder, 1952; Sukhanov, 1968).

The relationship between limb length and maximal speed leads to the prediction that larger animals, with consequently longer limbs, should run faster; at a given size, speed and limb length should also be correlated. The first prediction is generally true within species (e.g., Huey, 1982; Huey and Hertz, 1982; Garland, 1985; Marsh, 1988; Snell et al., 1988; Losos et al., 1989; but see Garland, 1984). Within orders of mammals and within families of lizards, however, sprint speed is independent of mass (Garland, 1983). With body size held constant, relatively longer-legged mammals generally run faster (Bakker, 1975; Coombs, 1978), which confirms the second prediction. Among lizards, however, a relationship between relative limb length and sprint speed has rarely been documented, despite the wealth of information linking leg length and ecology of lizards (Garland, 1985; but see Snell et al., 1988; Losos and Sinervo, 1989; Sinervo and Losos, in press).

The other factors affecting stride length in lizards have not received much attention. Most lizards, including *Anolis* (Schaeffer, 1941), extend their hindlimbs nearly completely at maximal running speed (Snyder, 1952; Sukhanov, 1968; Brinkman, 1981). Little information is available on among-species differences in angle of swing, axial flexion, or pelvic rotation (see Peterson, 1984).

Other morphological variables also might affect sprint speed. In some species, the forelimbs exert force only vertically and not anteriorly (Sukhanov, 1968). In other species, forelimbs impede the movement of the hindlimbs, decreasing stride length (Snyder,

TABLE 1. Predictions about the effect of morphological variables on sprinting and jumping ability, based on biomechanical models. (+) indicates a positive relationship, (-) indicates an inverse relationship.

	SVL	Hind-limb length	Fore-limb length	Tail length	Body shape*
Jump distance	+	+	-	+	?
Sprint speed	+	+	-	+	?

\* Stocky vs. slender-quantified as the residual of  $mass^{1/3}$  regressed on snout-vent length.

1962; Sukhanov, 1968). Consequently, independent of size, forelimb length and sprint speed might be inversely related.

The effect of body shape on sprint speed is difficult to predict, and probably depends on the relationship of muscle mass/body mass and the effect of shape on degree of axial rotation.

The tail serves as a counterbalance during running, particularly for lizards with long hindlimbs relative to their forelimbs (Snyder, 1949, 1952, 1962; Sukhanov, 1968). The tail also serves to balance the lateral forces generated in undulation by lizards (Sukhanov, 1968). Lizards with experimentally-reduced tails generally run more slowly (Ballinger et al., 1979; Pond, 1981; Punzo, 1982; Arnold, 1984). However, the gecko *Phyllodactylus marmoratus*, which does not use its tail as a counterbalance, runs faster when its tail is removed (Daniels, 1983), as does the skink *Sphenomorphus quoyii* (Daniels, 1985).

Predictions about the effect of morphological variables on jumping and sprinting performance are summarized in Table 1.

## MATERIALS AND METHODS

### *Performance and Morphological Measurements*

I measured maximum running and jumping capability for more than 15 adult males of 13 species of *Anolis* lizards from Jamaica and Puerto Rico, as well as for smaller samples (including females) of two relatively rare species, *A. occultus* (11 individuals) and *A. cuvieri* (6). The data are graphically presented in Figure 1 (raw data are presented in Losos, 1990a). Sprint capability was measured by placing lizards at the lower end of a 2.25-m trackway covered with a

rough rubber surface and angled at 37° (anoles raced on horizontal surfaces tend to hop [van Berkum, 1986; Losos, pers. obs.]) and inducing them to run by repeated taps to the tail (protocol following Huey, 1982, 1983; Garland, 1985; van Berkum, 1986; Losos et al., 1989). A running lizard interrupted light beams stationed every 0.25 m. The time elapsed during each interval was computed using a Compaq personal computer. Maximum speed for each lizard was the fastest single interval during five trials, conducted at hourly intervals. Jumping capability was measured by placing lizards on a flat board covered with a rough rubber surface 28 cm above the floor and inducing them to jump from a stationary position by a tap to the tail. This procedure was repeated twice at hourly intervals; the maximum horizontal distance jumped was recorded for each individual.

Most performance measurements were conducted at the El Verde Field Station (Luquillo Mtns., Puerto Rico). Puerto Rican lizards were tested within two (three for *A. poncensis*) days of capture. In 1987, Jamaican anoles were returned to Berkeley for sprint speed measurements, maintained at appropriate temperatures with food and water supplied ad libitum, and tested within three weeks of capture. In 1988, Jamaican anoles were transported to the El Verde Field Station and tested for sprinting and jumping within one week of capture. In most cases, jumping was measured on the first day and sprint speed on the second day. All performance measurements were conducted at a body temperature of 30°C, which is at or near the optimal temperature for sprint performance for these species (Huey and Webster, 1976; Huey, 1982; van Berkum, 1986; R. B. Huey, pers. comm.; the optimal temperature for jump performance is unknown). Sub-optimal trials, recognized by jump posture and trajectory and running gait, were excluded. Lizards with only one acceptable trial were not included in the sprint speed calculations; hence, no sprint data are available for *A. occultus*. Animals with at least one acceptable jump were included in jump calculations.

Snout-vent length (svl), mass, forelimb and hindlimb length (from the tip of the most distal toe on the right side of the body

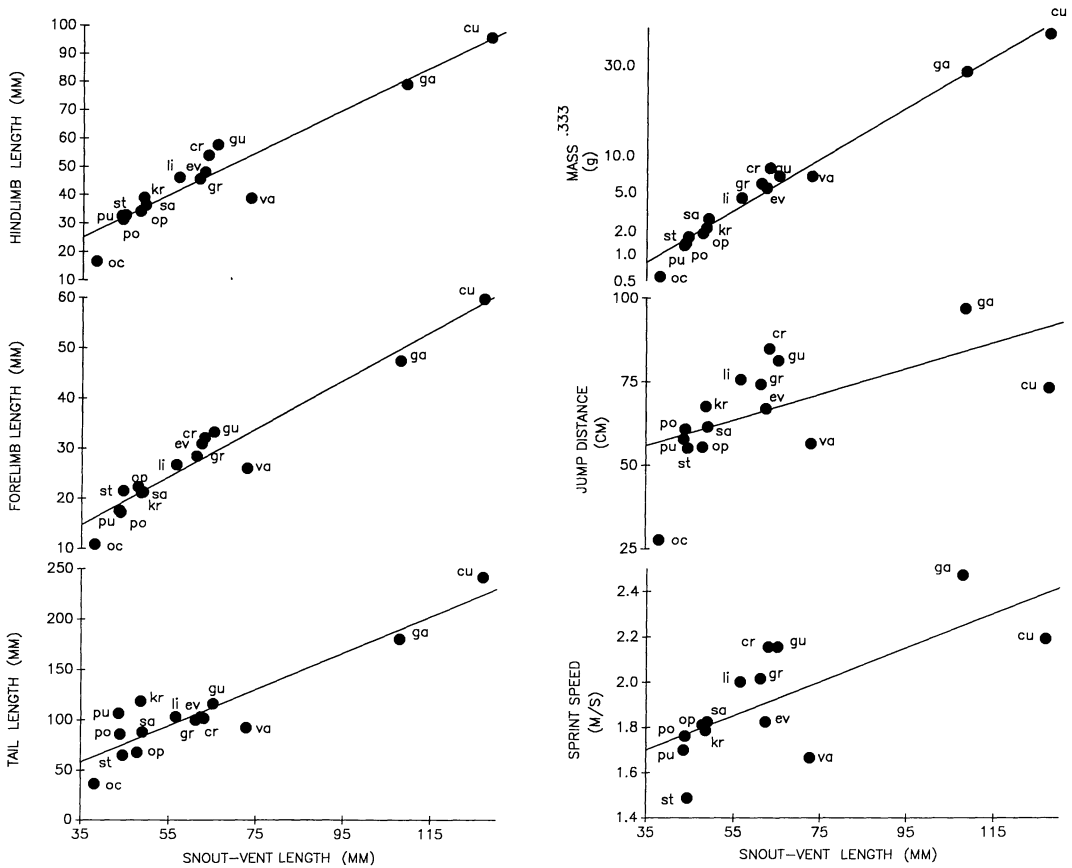


FIG. 1. The relationship of all variables regressed against svl. Original data from Losos (1990a). All points represent the mean for a species. Each species is indicated by the first two letters of its specific name. No sprint speed data are available for *A. occultus*. Numbers along the y-axis in the mass<sup>0.333</sup> - svl plot represent the mass, rather than mass<sup>1/3</sup> of species.

to the insertion of the limb in the body wall), and tail length (excluding regenerated tails) were measured on each individual.

Previous discussion of morphological differences among *Anolis* have focused on adult males (Rand and Williams, 1969; Williams, 1972, 1983). Considerable sexual dimorphism exists in most species; interspecific differences among females are much less pronounced than among males. Consequently, in all analyses, only relatively large adult males are used (with the exception of two relatively rare species, *A. cuvieri* and *A. occultus*, for which adult females were included as well. Excluding those females does not qualitatively alter the results.). Using only large adults minimizes the confounding effect of intraspecific allometric variation.

#### Phylogenetic and Statistical Analyses

Until recently, comparative analyses have asked whether variation in two traits is correlated among species. Such a relationship does not necessarily imply that the two traits have evolved concordantly; species may be similar for traits either because they have evolved them convergently or because the species are closely related and have inherited the traits from a common ancestor (Clutton-Brock and Harvey, 1984; Felsenstein, 1985, 1988; Huey, 1987). Further, potential similarity due to shared ancestry means that species do not represent statistically independent data points (Ridley, 1983; Clutton-Brock and Harvey, 1984; Felsenstein, 1985).

Two methods have been proposed to circumvent these difficulties and test whether two variables have evolved in tandem within a clade (see Losos [1990a] for a detailed discussion of these methods and their variants). Beginning with a phylogenetic hypothesis, the ancestor reconstruction approach (Larson, 1984; Sessions and Larson, 1987) assigns values to hypothetical ancestral taxa using one of several parsimony algorithms (e.g., Farris, 1970; Huey and Bennett, 1987; Swofford and Maddison, 1987; E. P. Martins and T. Garland, in press) that minimize the amount of change for a variable along the branches of a phylogeny. Here I use an algorithm that minimizes the sum of the evolutionary change squared along each branch (Huey and Bennett, 1987). Once all hypothetical taxa have been assigned values for both traits in question, one can calculate how much each trait changes along each branch of the phylogeny and then test whether evolutionary change in one trait is associated with evolutionary change in the other (Huey and Bennett, 1987; Losos, 1990a, b; Huey and Bennett [1987] used only branches leading to terminal taxa, but I use change along all branches of the tree). This approach has two difficulties: (1) The values assigned to hypothetical taxa are not independent; and (2) A tree with  $n$  species produces data for  $2n - 2$  branches (Felsenstein, 1988). Preliminary work indicates that these problems lead to a heightened risk of Type I error (Martins and Garland, in press). To minimize these problems, I have used the number of species (15 for jumping, 14 for sprinting), rather than the number of branches on the phylogenetic tree (28 for jumping, 26 for sprinting) as the sample size  $n$  in statistical analyses.

The contrast approach (Felsenstein, 1985) avoids these statistical problems. Every hypothetical ancestor in a phylogenetic tree has two immediate descendants. The degree to which these descendants differ in a given trait reflects the amount of evolution since their differentiation and is independent of change occurring elsewhere on the tree. For a tree with  $n$  extant species, there are  $n - 1$  independent contrasts. One can ask whether the calculated differences in these contrasts for one variable are related to differences in a second variable; i.e., is differ-

entiation in these variables associated? One can calculate  $n - 1$  independent contrasts for each trait and test whether the contrast values for one trait are related to those of a second trait (Felsenstein, 1985; Sessions and Larson, 1987; Losos, 1990a, b). If one assumes that random changes accumulate in time in a manner similar to Brownian motion (i.e., small and independent change between generations), then each contrast can be scaled by a function of the time elapsed since the two descendants differentiated; this transformation guarantees equal variance among contrasts (Felsenstein, 1985). This procedure is statistically robust (Martins and Garland, in press), but has one major drawback: it requires not only information on the phylogeny of a clade, but also on the amount of time elapsed along each branch of the phylogenetic tree. Thus, the contrast method is sensitive to mistakes in the assignment of branch lengths.

Because of these potential difficulties, I take a conservative approach and utilize both methods. In most of the analyses in this study, the two methods produce very similar statistical results. The phylogeny of the 15 species of *Anolis* in this study (Fig. 2) is based on osteological (Underwood and Williams, 1959; Williams, 1972), karyological (Gorman and Atkins, 1968), immunological (Gorman et al., 1980a; Shochat and Dessauer, 1981; Wyles and Gorman, 1980), and electrophoretic (Gorman et al., 1980b; Gorman et al., 1983) studies. I have added tentative estimates of branch lengths to the tree based on the immunological and electrophoretic analyses (for more detail on construction of the phylogenetic tree and assignment of branch lengths, see Losos [1990a]).

Scaling relationships were calculated by regressing change in one variable along branches of the tree against change in a second variable (usually  $svl$ ). For these calculations, each datum was the amount of evolutionary change in a variable along a branch of the tree. These relationships represent the evolutionary linkage between two variables, i.e., how evolutionary change in the two variables is correlated. They are thus analogous to the commonly reported non-evolutionary allometric relationships. However, instead of calculating allometric

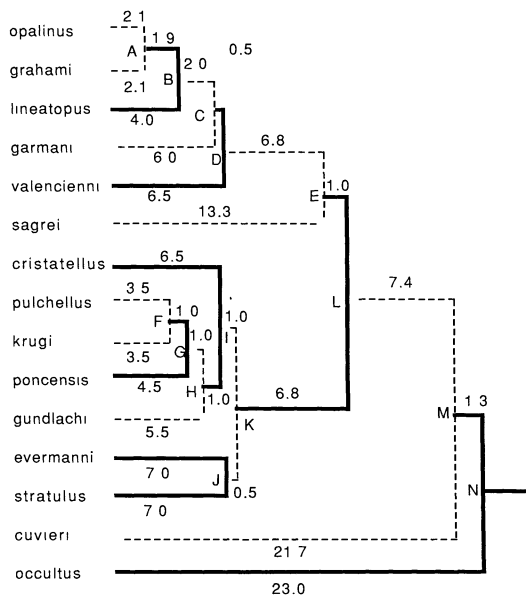


FIG. 2. (Adapted from Losos, 1990b) Phylogenetic relationships among Jamaican and Puerto Rican *Anolis* (from Losos, 1990a). This phylogenetic tree does not imply that the Jamaican and Puerto Rican anole radiations are sister taxa or monophyletic in the strict sense of including all descendant taxa. Numbers represent the relative length of each branch. The 14 independent contrasts are indicated by the line shading. Each contrast is identified by the letter corresponding to the ancestor of the two taxa.

relationships using values for two variables for each extant taxon, the evolutionary approach uses as variables the amount of change in the variables on each branch of the phylogenetic tree. Data were not log-transformed because many evolutionary changes were negative. The cube-root of mass was used in statistical analyses to make it comparable to the linear dimensions of the other variables. The contrast approach

does not estimate values for hypothetical ancestral taxa and thus cannot be used to calculate evolutionary scaling relationships. Because contrast values are scaled by a function of time (see above), they would be useful if one wanted to compare the scaling of rate of evolutionary change in two variables.

I used partial correlation (Sokal and Rohlf, 1981) to remove the pervasive effect of body size (see below). I consider svl as a proxy variable for body size; comparisons with the effect of svl statistically removed thus constitute "Standard-Length-Allometry-Free-Shape" comparisons (sensu Bookstein, 1989). Previous analysis (Losos, 1990a) indicated that the morphological variables were correlated even when the effect of size was removed. To assess the effect of each variable independent of correlations with other variables, I used partial correlations removing the effect of two or more variables simultaneously (e.g.,  $r_{\text{jump, tail}^* \text{svl, hindlimb, forelimb}}$ , which is the correlation of evolution in jumping ability and in tail length with the effects of evolution in svl, hindlimb length and forelimb length statistically removed).

## RESULTS

Evolutionary change in all morphological and performance variables scales strongly with change in svl (Table 2). The slopes (b) of the regressions of change in sprinting and in jumping ability against change in svl are greater for the evolutionary analysis than the conventional allometric relationships, which are calculated using data only from extant species, but the differences are not significant (Jumping: evolutionary analysis  $b = 0.493$ , conventional scaling  $b = 0.392$ , analysis of covariance, difference of slopes,  $F_{1,39} = 0.68$ ,  $P < 0.45$ ; Running: evolution-

TABLE 2. Evolutionary scaling\* of morphological and performance variables with snout-vent length. All morphological measurements are in mm, jump is measured in cm, and spring speed is in m/sec.

Scaling relationship	$r^2$	$F$	$df$	$P$
Forelimb = $0.129 + 0.504^* \text{svl}$	0.956	590.3	1,26	<0.001
Hindlimb = $0.311 + 0.820^* \text{svl}$	0.933	379.6	1,26	<0.001
Mass <sup>1/3</sup> = $-0.373 + 0.103^* \text{svl}$	0.852	53.6	1,26	<0.001
Tail = $1.281 + 2.025^* \text{svl}$	0.924	327.0	1,26	<0.001
Sprint = $0.000 + 0.008^* \text{svl}$	0.522	28.3	1,24	<0.001
Jump = $0.964 + 0.493^* \text{svl}$	0.582	38.6	1,26	<0.001

\* Relationship of evolutionary change in a variable to change in body size. Each datum is the amount of change for both variables along one branch of the phylogeny (see text for details). Data were not log-transformed because many evolutionary changes were negative.

TABLE 3. Partial correlations. For each correlation, the results of using the ancestral reconstruction values are reported on the first line and the results using independent contrasts on the second line.

Variables removed	Correlation			
	<i>r</i>	<i>t<sub>s</sub></i>	<i>df</i>	<i>P</i>
<b>svl</b>				
<i>r</i> <sub>jump,hindlimb*svl</sub>	0.739	3.80	12	< <b>0.01</b>
	0.751	3.77	11	< <b>0.01</b>
<i>r</i> <sub>jump,forelimb*svl</sub>	0.602	2.78	12	< <b>0.02</b>
	0.555	2.21	11	< <b>0.05</b>
<i>r</i> <sub>jump,mass<sup>1/3</sup>*svl</sub>	0.480	1.90	12	<0.10
	0.606	2.53	11	< <b>0.05</b>
<i>r</i> <sub>jump,tail*svl</sub>	0.265	0.95	12	<0.40
	0.134	0.45	11	<0.90
<i>r</i> <sub>sprint,hindlimb*svl</sub>	0.719	3.43	11	< <b>0.01</b>
	0.802	4.24	10	< <b>0.01</b>
<i>r</i> <sub>sprint,forelimb*svl</sub>	0.553	2.20	11	< <b>0.05</b>
	0.615	2.47	10	< <b>0.05</b>
<i>r</i> <sub>sprint,mass<sup>1/3</sup>*svl</sub>	0.572	2.31	11	< <b>0.05</b>
	0.677	2.91	10	< <b>0.02</b>
<i>r</i> <sub>sprint,tail*svl</sub>	0.194	0.66	11	<0.60
	0.129	0.41	10	<0.80
<b>svl, hindlimb</b>				
<i>r</i> <sub>jump,forelimb*svl,hindlimb</sub>	-0.401	1.45	11	<0.20
	-0.399	1.38	10	<0.20
<i>r</i> <sub>jump,mass<sup>1/3</sup>*svl,hindlimb</sub>	0.365	1.30	11	<0.25
	0.222	0.72	10	<0.50
<i>r</i> <sub>jump,tail*svl,hindlimb</sub>	-0.361	1.28	11	<0.30
	-0.229	0.74	10	<0.50
<i>r</i> <sub>sprint,forelimb*svl,hindlimb</sub>	-0.468	1.67	10	<0.20
	-0.378	1.22	9	<0.30
<i>r</i> <sub>sprint,mass<sup>1/3</sup>*svl,hindlimb</sub>	0.505	1.85	10	<0.10
	0.327	1.04	9	<0.40
<i>r</i> <sub>sprint,tail*svl,hindlimb</sub>	-0.366	1.24	10	<0.30
	-0.277	0.86	9	<0.50
<b>svl, hindlimb, mass<sup>1/3</sup></b>				
<i>r</i> <sub>jump,forelimb*svl,hindlimb,</sub>	-0.464	1.66	10	<0.20
	-0.383	1.31	9	<0.30
<i>r</i> <sub>jump,tail*svl,hindlimb,</sub>	-0.324	1.08	10	<0.40
	-0.240	0.74	9	<0.50
<i>r</i> <sub>sprint,forelimb*svl,hindlimb,</sub>	-0.520	1.93	10	<0.10
	-0.363	1.17	9	<0.30
<i>r</i> <sub>sprint,forelimb*svl,hindlimb</sub>	-0.250	0.82	10	<0.50
	-0.305	0.96	9	<0.40
<b>svl, hindlimb, tail</b>				
<i>r</i> <sub>jump,forelimb*svl,hindlimb,tail</sub>	-0.592	2.32	10	< <b>0.05</b>
	-0.721	3.12	9	< <b>0.02</b>
<i>r</i> <sub>jump,mass<sup>1/3</sup>*svl,hindlimb,tail</sub>	0.275	0.90	10	<0.40
	0.236	0.73	9	<0.50
<i>r</i> <sub>sprint,forelimb*svl,hindlimb,tail</sub>	-0.723	3.14	10	< <b>0.02</b>
	-0.776	3.48	9	< <b>0.01</b>
<i>r</i> <sub>sprint,mass<sup>1/3</sup>*svl,hindlimb,tail</sub>	0.442	1.56	10	<0.20
	0.350	1.12	9	<0.40
<b>svl, hindlimb, forelimb</b>				
<i>r</i> <sub>jump,mass<sup>1/3</sup>*svl,hindlimb,forelimb</sub>	0.389	1.34	10	<0.25
	0.193	0.59	9	<0.70



TABLE 3. Continued.

Variables removed	Correlation			
	<i>r</i>	<i>t<sub>s</sub></i>	<i>df</i>	<i>P</i>
<i>r</i> <sub>jump,tail*svl,hindlimb,forelimb</sub>	-0.572	2.21	10	<0.053
	-0.677	2.76	9	<0.05
<i>r</i> <sub>sprint,mass<sup>1/3</sup>*svl,hindlimb,forelimb</sub>	0.552	2.09	10	<0.07
	0.308	0.97	9	<0.40
<i>r</i> <sub>sprint,tail*svl,hindlimb,forelimb</sub>	-0.686	2.83	10	<0.02
	-0.756	3.27	9	<0.02
svl, hindlimb, forelimb, tail				
<i>r</i> <sub>jump,mass<sup>1/3</sup>*svl,hindlimb,forelimb,tail</sub>	0.205	0.63	9	<0.70
	0.216	0.63	8	<0.70
<i>r</i> <sub>sprint,mass<sup>1/3</sup>*svl,hindlimb,forelimb,tail</sub>	0.450	1.51	9	<0.20
	0.405	1.25	8	<0.30

ary analysis  $b = 0.0084$ , conventional scaling  $b = 0.0076$ , analysis of covariance, difference of slopes,  $F_{1,36} = 1.66$ ,  $P < 0.21$ ).

With the effect of evolution in svl removed, evolution in fore- and hindlimb length is related to both sprint and jump performance (Table 3; Fig. 3). Forelimb and hindlimb length evolution (svl independent) are strongly correlated ( $r_{\text{forelimb,hindlimb*svl}} = 0.940$ , using ancestor-reconstruction values). To verify that hindlimb length affects performance independent of forelimb length, I removed the effects of changes in both svl and forelimb length. Evolution of hindlimb length is still significantly related to change in both performance parameters (Ancestor Reconstruction Analyses:  $r_{\text{jump,hindlimb*svl,forelimb}} = 0.640$ ,  $t_s = 2.76$ ,  $df = 11$ ,  $P < 0.02$ ;  $r_{\text{sprint,hindlimb*svl,forelimb}} = 0.675$ ,  $t_s = 2.89$ ,  $df = 10$ ,  $P < 0.02$ ; Contrast Analyses:  $r_{\text{jump,hindlimb*svl,forelimb}} = 0.686$ ,  $t_s = 2.98$ ,  $df = 10$ ,  $P < 0.02$ ;  $r_{\text{sprint,hindlimb*svl,forelimb}} = 0.713$ ,  $t_s = 3.05$ ,  $df = 9$ ,  $P < 0.02$ ).

Given that the evolution of svl, hindlimb length, and performance capability are related, I then removed the effect of both morphological variables to assess whether performance evolution is related to evolution of any of the other variables. None of the correlations were significant (Table 3). Similarly, when the effect of svl, hindlimb length, and  $\text{mass}^{1/3}$  were removed, evolution in neither tail or forelimb length were related to evolution in sprinting or jumping ability (Table 3).

With the effect of change in svl, hindlimb

length, and tail length removed, however, evolution in jumping and sprinting ability is inversely related to evolution in forelimb length (Table 3). Similarly, with the effect of change in svl, hindlimb length, and forelimb length removed, evolution in both performance measures is inversely related to change in tail length (Table 3). In general, no significant relationships exist between change in performance and  $\text{mass}^{1/3}$  (with one, possibly spurious, exception: evolution in jumping ability vs.  $\text{mass}^{1/3}$ , effects of svl, hindlimb length, and forelimb length removed, ancestor reconstruction analysis), even when the effects of change in all other morphological variables are removed (Table 3).

Sprinting and jumping ability evolve in concert both when the effect of size is included (ancestor reconstruction,  $r = 0.928$ ,  $df = 12$ ,  $P \ll 0.001$ , contrast  $r = 0.962$ ,  $df = 10$ ,  $P \ll 0.001$ ) or removed (ancestor reconstruction:  $r_{\text{sprint,jump*svl}} = 0.877$ ,  $t_s = 6.05$ ,  $df = 11$ ,  $P < 0.001$ ; contrast:  $r_{\text{sprint,jump*svl}} = 0.871$ ,  $t_s = 5.61$ ,  $df = 10$ ,  $P < 0.001$ ).

## DISCUSSION

This analysis indicates that functional and biomechanical models can be integrated in a phylogenetic context to successfully elucidate the coevolution of morphology and performance ability. Evolutionary change in svl is strongly related to change in performance ability. When the effect of svl (a proxy for body size) is removed, evolution

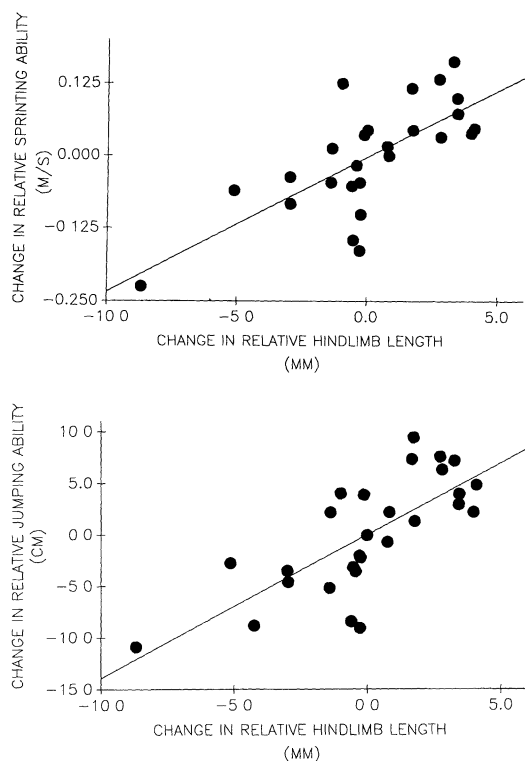


FIG. 3. Evolution in hindlimb length against (a) evolution in relative sprint speed and (b) relative jumping ability (all variables with the effect of size removed by regressing the variable against evolution in svl and using the residuals).

in hindlimb length and performance are correlated. When further variables are statistically removed, evolution of both forelimb and tail length exhibit correlations with performance ability.

#### *Size and Shape as Determinants of Performance*

Evolution of body size (represented by svl) is the most important variable affecting the evolution of jumping and sprinting ability, accounting for 52% of the variance in sprinting ability evolution and 58% of the variance in jumping ability evolution. Evolution in hindlimb length is the most important shape variable, explaining an additional 26% of the sprinting ability variance and 24% of the jumping ability variance (based on multiple regressions using ancestor reconstruction values). The additional inclusion of any of the three other variables (change in forelimb length, tail

length, or  $mass^{1/3}$ ) only explains a further 3–6% of sprint ability evolution and 1–3% of jump ability evolution.

Two important conclusions can be drawn from these results. First, the evolution of size is of overwhelming importance in determining the evolution of performance ability. By itself, evolution of svl explains more than half of the change in sprinting and jumping ability in the evolution of the 15 lizard species included in this study. Recent treatments (e.g., Peters, 1983; Calder, 1984) have emphasized size as the most important determinant of organismal structure and function. Previous studies have demonstrated that size accounts for much of the variation in sprinting (Huey, 1982; Huey and Hertz, 1982; Garland, 1985; Snell et al., 1988) and jumping (Losos et al., 1989) ability within several lizard species. This study confirms these views in an explicitly evolutionary context.

Second, numerous non-morphological factors can have an important effect on sprinting and jumping performance. These factors include enzyme activity, muscle composition and histochemistry, orientation of lever arms, degree of axial flexion, posture, and behavior (e.g., Snyder, 1954; Sukhanov, 1968; Brinkman, 1981; Peterson, 1984; Garland, 1984, 1985; Gleeson and Harrison, 1988; Abu-Ghalyun et al., 1988). During the evolution of the 15 species of *Anolis* in this study, however, change in these variables has not played a major role in the evolution of sprinting and jumping performance ability; only 18–22% of the variation in performance evolution remains to be explained after the effects of svl and hindlimb length are removed and some of this variation may be accounted for by other morphological variables.

#### *Assessment of the Biomechanical Models*

Biomechanical models predict that hindlimb length should be the most important morphological variable determining jumping and sprinting performance, once the effect of size is removed. The analyses confirm that evolution of hindlimb length has been associated with evolution of performance capability, regardless of correlation with other variables. Kinematic studies are

in progress to assess whether the underlying assumptions (e.g., that hindlimb length is directly related to stride length and time of acceleration during a jump) in these analyses are correct.

Biomechanical models do not predict the observed positive relationship between change in forelimb length and changes in running speed and jumping ability. The forelimbs of *Anolis* are considerably shorter than their hindlimbs (54.0–67.2%) and should contribute little to propulsive force or stride length. In fact, reduced forelimb length would be expected in better jumpers and sprinters (see Introduction, Biomechanical Models). The positive effect of forelimb length on performance results from the correlation between evolution in forelimb and hindlimb length. With the effect of hindlimb evolution removed, the predicted negative relationship between evolution in forelimb length and performance is observed.

The models are less clear with regard to how body shape (the residual of  $\text{mass}^{1/3}$  regressed on  $\text{svl}$ ) should affect performance. If the degree of axial rotation or the ratio of hindlimb muscle mass-to-body mass are not altered, then change in shape would not be expected to affect the evolution of sprinting and jumping ability. The analyses, in fact, found no relationship between change in body shape and change in either sprinting or jumping ability.

Tail length is negatively related to performance evolution when the effects of change in  $\text{svl}$ , hindlimb length, and forelimb length are removed. This result is counterintuitive because short-tailed species (e.g., *A. valencienni*, *A. occultus*) tend to exhibit relatively low performance abilities, whereas some long-tailed species (e.g., *A. krugi*) sprint and jump relatively well. However, this positive relationship probably results from the correlation of evolution of hindlimb length and of tail length, with the effect of  $\text{svl}$  removed (Losos, unpublished). Examination of 13 species of *Anolis* confirms that the center of gravity of species is inversely correlated with tail length with the effect of either  $\text{svl}$  or of all other morphological variables removed (i.e., the center of gravity of longer-tailed species is nearer to the hindlimbs [Losos, unpubl.]). Conse-

quently, biomechanical models predict that the evolution of tail length should be positively correlated with the evolution of performance ability. Further work is required to understand the cause of the negative correlation.

#### *Relevance to Ecomorphological Evolution*

With the effect of change in  $\text{svl}$  removed, evolution in forelimb, hindlimb, and tail length are correlated with each other and with evolutionary changes in the ecology and behavior of the *Anolis* species in this study (Losos, 1990a, b). Elsewhere, I have shown that evolution in sprinting and jumping performance is an intermediate link between the evolution of morphology and of ecology and behavior (Losos, 1990a). However, of the morphological variables measured in this study, only evolution in hindlimb length has affected evolution in performance ability when the effect of change in  $\text{svl}$  is removed. The positive correlation between change in forelimb and tail length and change in ecology and behavior probably results incidentally from the correlation of all of these variables with evolution in hindlimb length.

When the effect of hindlimb evolution is removed, a negative relationship exists between evolution in forelimb and tail length and in performance. The ecological relevance of this inverse correlation is uncertain, however, because little of the variance in performance evolution remains after the effects of  $\text{svl}$  and hindlimb length evolution are accounted for (see above). For example, forelimb length evolution explains only an additional 4.9% of sprinting and 2.9% of jumping evolution variation. Nevertheless, these effects on performance evolution may be relevant to the evolution of locomotor behavior; species that jump more frequently in nature have shorter forelimbs (relative to their hindlimbs) than less frequent jumpers (Losos, 1990b).

#### *Constraints on Adaptation*

Evolutionary change in jumping and sprinting capability are tightly coupled, even when the effect of body size evolution is removed. The models and results discussed above suggest that both performance pa-

rameters are dependent on hindlimb length; hence, their correlation is expected. This linkage indicates that, at least within this clade, species will have difficulty specializing morphologically as either runners or jumpers, despite considerable differences among species in locomotor behavior (Moermond, 1979a, 1979b; Pounds, 1988; Losos, 1990b).

Further, the constraint that jumping and running ability must evolve together may set limits on how well species can adapt to some microhabitats. For example, on narrow rods, several similar-sized *Anolis* (*A. grahamsi*, *A. gundlachi*, *A. lineatopus*, and *A. valencienni*) can run at approximately the same speed, even though they vary greatly in hindlimb length. However, the short-legged *A. valencienni* moves with considerably greater facility than the longer-legged species, which frequently stumble or fall off the rods (Losos and Sinervo, 1989). The evolution of short legs in *A. valencienni* appears to be an adaptation for moving on narrow surfaces. This adaptation has not only involved a trade-off in running performance between stability when running on narrow surfaces and speed when running on broader surfaces (Losos and Sinervo, 1989 and above), but also has resulted in reduced jumping capabilities. Consequently, these *Anolis* apparently cannot adapt to both move on narrow surfaces and to utilize habitats requiring long jumps. In fact, *Anolis valencienni* jumps much less frequently and makes considerably shorter jumps than the other species in this study (except, probably, the short-legged *A. occultus*, for which little behavioral data are available [Losos, 1990b]).

#### *Evolutionary vs. Traditional Allometry*

Most physiological and organismal processes, including performance capabilities, exhibit an allometric relationship within and among extant taxa (see above). To my knowledge, the present study is the first to have documented explicitly how the evolution of such variables is affected by evolutionary change in body size (represented by *svl*). In this case, the traditional allometric relationships, based solely on extant

species, conform to the evolutionary scaling relationships. However, this will not always be the case. For example, *Anolis occultus* (the smallest species in this study) is an extreme low outlier in the *svl*-jumping regression using extant species. If *A. occultus* had numerous sibling species (it doesn't, as far as is known), and if I had included them all, the allometric slope using extant species would have been considerably higher than the true evolutionary scaling relationship. Implicit in non-phylogenetic comparative approaches are the assumptions that the characteristics of each species are determined solely by current selective conditions with little or no effect of ancestry and hence represent independent points (Felsenstein, 1985, 1988). The sample of *Anolis* included here demonstrates widespread convergence in morphology, behavior, and performance ability (Williams, 1972, 1983; Losos, 1990a, b) and, to a large extent, fulfills this assumption. Often, however, this will not be true.

#### *Generality of the Results*

The biomechanical predictions in this paper involved assumptions that other important variables did not differ to a great extent during the diversification of *Anolis*. The success of these predictions indicates that these assumptions are probably correct. Similar assumptions about the determinants of sprinting in several closely related lizard families were borne out (Sukhanov, 1968). That such predictions might be clade-specific, however, must be emphasized; further, the more distantly related the taxa, the more likely it will be that differences in biomechanical properties other than those being examined will contribute to performance differences (Huey and Bennett, 1986). A relevant example involves *Polychrus*, a genus of slow-moving tropical lizards closely allied to *Anolis* (Etheridge and de Queiroz, 1988). I measured the performance capability of a small *P. gutturosus* in Panama. Based on its size (84 mm *svl*) and hindlimb length (57 mm), this individual should have been able to run 1.85 m/sec and jump 66 cm (based on scaling relationships for *Anolis* using extant taxa). In fact, the performance measurements were considerably less

than these expectations (sprinting: 70.6% of predicted; jumping: 38.8% of predicted). The explanation is obvious; species of *Polychrus* move in a very slow, chameleon-like manner (Gorman et al., 1969; Vitt and Lacher, 1981; Greene, 1986; pers. obs.) and have spindly legs, with greatly reduced limb musculature (pers. obs.). Consequently, they cannot generate the force required to run or jump as well as their size and hindlimbs would predict. The relevant point, however, is that biomechanical predictions are only as good as their underlying assumptions; evolutionary biomechanical analyses must ensure the homogeneity of their included taxa with respect to variables not under direct examination, and must limit the breadth of their conclusions to taxa for which the same assumptions are likely to apply.

#### ACKNOWLEDGMENTS

For invaluable assistance in Jamaica and Puerto Rico, I thank N. Hess, S. Myers, D. Wagner, G. Vilela, R. Trivers, R. Thomas, R. Waide, J. Woodley, the staff and researchers at the Discovery Bay Marine Laboratory and El Verde Field Station, the residents of Southfield, Jamaica, J. Bloomberg, and D. Silverman. For advice and assistance on various aspects of this work, I gratefully acknowledge J. Beck, E. Dilworth, S. Emerson, M. Frelow, H. Fujishige, R. Full, T. Garland, Jr., H. Greene, R. Huey, B. Jayne, R. Jones, K. Klitz, E. Kwan, A. Larson, W. Maddison, E. Martins, G. Mayer, C. Meacham, S. Naeem, J. Patton, W. Rainey, S. Rand, J. Smith, R. Tokarz, and D. Wake. D. Carrier, S. Emerson, R. Full, H. Greene, R. Huey, C. Schneider, P. Wainwright and D. Wake provided helpful comments on prior drafts. The McDonalds Corp. kindly provided lizard containers. This research was supported by grants from the Museum of Vertebrate Zoology, the University of California at Berkeley (Chancellor's Patent Fund, Graduate Division, and Center for Latin American Studies), the Tinker Foundation, the American Museum of Natural History (Theodore Roosevelt Fund), the Explorer's Club, Sigma Xi (local and national), and a pre-doctoral fellowship from the Smithsonian Tropical Research Institution.

#### LITERATURE CITED

- ABU-GHALYUN, Y., L. GREENWALD, T. E. HETHERINGTON, AND A. S. GAUNT. 1988. The physiological basis of slow locomotion in chameleons. *J. Exp. Biol.* 245:225-231.
- ALEXANDER, R. M. 1968. *Animal Mechanics*. Univ. Washington Press, Seattle.
- ARNOLD, E. N. 1984. Evolutionary aspects of tail shedding in lizards and their relatives. *J. Natur. Hist.* 18:127-169.
- ARNOLD, S. J. 1983. Morphology, performance, and fitness. *Amer. Zool.* 23:347-361.
- . 1986. Laboratory and field approaches to the study of adaptation, pp. 157-179. In M. E. Feder and G. V. Lauder (eds.), *Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates*. Univ. Chicago Press, Chicago, IL.
- BAKKER, R. T. 1975. Experimental and fossil evidence for the evolution of tetrapod bioenergetics, pp. 365-399. In D. M. Gates and R. B. Schmerl, (eds.), *Perspectives of Biophysical Ecology*. Springer-Verlag, N.Y.
- BALLINGER, R. E. 1973. Experimental evidence of the tail as a balancing organ in the lizard, *Anolis carolinensis*. *Herpetologica* 29:65-66.
- BALLINGER, R. E., J. W. NIETFFELDT, AND J. J. KRUPA. 1979. An experimental analysis of the role of the tail in attaining high running speed in *Cnemidophorus sexlineatus* (Reptilia: Squamata: Lacertilia). *Herpetologica* 35:114-116.
- BARCLAY, O. R. 1946. The mechanics of amphibian locomotion. *J. Exp. Biol.* 23:177-203.
- BOCK, W. J., AND G. VON WAHLERT. 1965. Adaptation and the form-function complex. *Evolution* 19: 269-299.
- BOOKSTEIN, F. L. 1989. "Size and shape": A comment on semantics. *Syst. Zool.* 38:173-180.
- BRINKMAN, D. 1981. The hind limb step cycle of *Iguana* and primitive reptiles. *J. Zool., Lond.* 181: 91-103.
- CALDER, W. A. 1984. *Size, Function and Life History*. Harvard Univ. Press, Cambridge.
- CLUTTON-BROCK, T. H., AND P. H. HARVEY. 1984. Comparative approaches to investigating adaptation, pp. 7-29. In J. R. Krebs and N. B. Davies (eds.), *Behavioural Ecology: An Evolutionary Approach*. Sinauer, Sunderland, MA.
- COOMBS, W. P., JR. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Q. Rev. Biol.* 53: 398-418.
- DANIELS, C. B. 1983. Running: An escape strategy enhanced by autotomy. *Herpetologica* 39:162-165.
- . 1985. The effect of tail autotomy on the exercise capacity of the water skink, *Sphenomorphus quoyii*. *Copeia* 1985:1074-1077.
- EMERSON, S. B. 1978. Allometry and jumping in frogs: Helping the twain meet. *Evolution* 32:551-564.
- . 1985. Jumping and leaping, pp. 58-72. In M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake (eds.), *Functional Vertebrate Morphology*. Belknap Press, Cambridge, MA.
- ETHERIDGE, R., AND K. DE QUEIROZ. 1988. A phylogeny of Iguanidae, pp. 283-367. In R. Estes and

- G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*. Stanford Univ. Press, Stanford, CA.
- FARRIS, J. S. 1970. Methods for computing Wagner trees. *Syst. Zool.* 19:83-92.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *Amer. Natur.* 125:1-15.
- . 1988. Phylogenies and quantitative characters. *Ann. Rev. Ecol. Syst.* 19:445-471.
- GARLAND, T., JR. 1983. The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool., Lond.* 199:157-170.
- . 1984. Physiological correlates of locomotory performance in a lizard: An allometric approach. *Amer. J. Physiol.* 247:R806-R815.
- . 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool., Lond. (A)* 207:425-439.
- GLEESON, T. T., AND J. M. HARRISON. 1988. Muscle composition and its relation to sprint running in the lizard *Dipsosaurus dorsalis*. *Amer. J. Physiol.* 255:R470-R477.
- GORMAN, G. C., AND L. ATKINS. 1968. New karyotypic data for 16 species of *Anolis* (Sauria: Iguanidae) from Cuba, Jamaica, and the Cayman Islands. *Herpetologica* 24:13-21.
- GORMAN, G. C., D. BUTH, M. SOULÉ, AND S. Y. YANG. 1980a. The relationship of the *Anolis cristatellus* species group: Electrophoretic analysis. *J. Herpet.* 14:269-278.
- . 1983. The relationships of the Puerto Rican *Anolis*: electrophoretic and karyotypic studies, pp. 626-642. In A. G. J. Rhodin and K. Miyata (eds.), *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams*. Mus. Comp. Zool., Cambridge, MA.
- GORMAN, G. C., D. BUTH, AND J. S. WYLES. 1980b. *Anolis* lizards of the eastern Caribbean: A case study in evolution. III. A cladistic analysis of albumin immunological data, and the definition of species groups. *Syst. Zool.* 29:143-158.
- GORMAN, G. C., R. B. HUEY, AND E. E. WILLIAMS. 1969. Cytotaxonomic studies on some unusual iguanid lizards assigned to the genera *Chamaeleolis*, *Polychrus*, *Polychroides*, and *Phenacosaurus*, with behavioral notes. *Breviora* 316:1-17.
- GOULD, S. J., AND E. VRBA. 1982. Exaptation—A missing term in the science of form. *Paleobiology* 8:4-15.
- GREENE, H. W. 1986. Diet and arboreality in the emerald monitor, *Varanus prasinus*, with comments on the study of adaptation. *Fieldiana, Zoology (New Series)* 31:1-12.
- HUEY, R. B. 1982. Phylogenetic and ontogenetic determinants of sprint performance in some diurnal Kalahari lizards. *Koedoe* 25:43-48.
- . 1983. Natural variation in body temperature and physiological performance in a lizard (*Anolis cristatellus*), pp. 485-490. In A. G. J. Rhodin and K. Miyata (eds.), *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams*. Mus. Comp. Zool., Cambridge, MA.
- . 1987. Phylogeny, history, and the comparative method, pp. 76-101. In M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey (eds.), *New Directions in Ecological Physiology*. Cambridge Univ. Press, Cambridge.
- HUEY, R. B., AND A. F. BENNETT. 1986. A comparative approach to field and laboratory studies in evolutionary biology, pp. 82-98. In M. E. Feder and G. V. Lauder (eds.), *Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates*. Univ. of Chicago Press, Chicago, IL.
- . 1987. Phylogenetic studies of coadaptation: Preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41:1098-1115.
- HUEY, R. B., AND P. E. HERTZ. 1982. Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *J. Exp. Biol.* 97:401-409.
- HUEY, R. B., AND R. D. STEVENSON. 1979. Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *Amer. Zool.* 19:357-366.
- HUEY, R. B., AND T. P. WEBSTER. 1976. Thermal biology of *Anolis* lizards in a complex fauna: The *cristatellus* group on Puerto Rico. *Ecology* 57:985-994.
- LARSON, A. 1984. Neontological inferences of evolutionary pattern and process in the salamander family Plethodontidae. *Evol. Biol.* 17:119-217.
- LAUDER, G. V. 1981. Form and function: Structural analysis in evolutionary morphology. *Paleobiology* 7:430-442.
- LOSOS, J. B. 1990a. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: An evolutionary analysis. *Ecol. Mon.* 60:369-388.
- . 1990b. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. *Anim. Behav.* 39:879-890.
- LOSOS, J. B., T. J. PAPPENFUSS, AND J. R. MACEY. 1989. Correlates of sprinting, jumping, and parachuting performance in the butterfly lizard, *Leiolepis bellianii*. *J. Zool., Lond.* 217:559-568.
- LOSOS, J. B., AND B. SINERVO. 1989. The effects of morphology and perch diameter on sprint performance in *Anolis* lizards. *J. Exp. Biol.* 145:23-30.
- LUKE, C. 1986. Convergent evolution of lizard toe fringes. *Biol. J. Linn. Soc.* 27:1-16.
- MARSH, R. L. 1988. Ontogenesis of contractile properties and sprint performance in the lizard *Dipsosaurus dorsalis*. *J. Exp. Biol.* 137:119-139.
- MARTINS, E. P., AND GARLAND, T. JR. Phylogenetic analyses of the Evolution of continuous characters: A simulation study. *Evolution In press*.
- MOERMOND, T. C. 1979a. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecology* 60:152-164.
- . 1979b. The influence of habitat structure on *Anolis* foraging behavior. *Behaviour* 70:141-167.
- PETERS, R. H. 1983. *The Ecological Implications of Body Size*. Cambridge Univ. Press, Cambridge.
- PETERSON, J. A. 1984. The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. *J. Zool., Lond.* 202:1-42.
- POND, C. M. 1981. Storage, pp. 190-219. In C. R. Townsend and P. Calow (eds.), *Physiological Ecology—An Evolutionary Approach to Resource Use*. Blackwell Scientific Publications, Oxford.
- POUNDS, J. A. 1988. Ecomorphology, locomotion, and microhabitat structure: Patterns in a tropical

- mainland *Anolis* community. *Ecol. Mon.* 58:299–320.
- PUNZO, F. 1982. Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. *J. Herpet.* 16:329–331.
- RAND, A. S. 1952. Jumping ability of certain anurans with notes on endurance. *Copeia* 1952:15–20.
- RAND, A. S., AND E. E. WILLIAMS. 1969. The anoles of La Palma: Aspects of their ecological relationships. *Breviora* 327:1–19.
- RIDLEY, M. E. 1983. The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating. Clarendon Press, Oxford.
- SCHAEFFER, R. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bull. Amer. Mus. Nat. Hist.* 78:395–472.
- SESSIONS, S. K., AND A. LARSON. 1987. Developmental correlates of genome size in plethodontid salamanders and their implications for genome evolution. *Evolution* 41:1239–1251.
- SHOCHAT, D., AND H. C. DESSAUER. 1981. Comparative immunological study of the albumins of *Anolis* lizards of the Caribbean islands. *Comp. Biochem. Physiol.* 68A:67–73.
- SINERVO, B., AND J. B. LOSOS. Walking the tight-rope: A comparison of arboreal sprint performance among populations of *Sceloporus occidentalis*. *Ecology. In press.*
- SNELL, H. L., R. D. JENNINGS, H. M. SNELL, AND S. HARCOURT. 1988. Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: The interaction of sexual and natural selection. *Evol. Ecol.* 2:353–369.
- SNYDER, R. C. 1949. Bipedal locomotion of the lizard *Basiliscus basiliscus*. *Copeia* 1949:129–137.
- . 1952. Quadrupedal and bipedal locomotion in lizards. *Copeia* 1952:64–70.
- . 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. *Amer. J. Anat.* 95:1–36.
- . 1962. Adaptations for bipedal locomotion of lizards. *Amer. Zool.* 2:191–203.
- SOKAL, R. R., AND P. J. ROHLF. 1981. *Biometry*, 2nd Ed. W. H. Freeman, N.Y.
- SUKHANOV, V. B. 1968. General System of Symmetrical Locomotion of Terrestrial Vertebrates and Some Features of Movement of Lower Tetrapods. Nauka Pub., Leningrad (translated into English by Amerind Publishing Co., New Delhi, 1974).
- SWOFFORD, D. L., AND W. P. MADDISON. 1987. Reconstructing ancestral character states under Wagner parsimony. *Mathematical Biosciences* 87:199–229.
- UNDERWOOD, G., AND E. E. WILLIAMS. 1959. The anoline lizards of Jamaica. *Bulletin of the Institute of Jamaica, Science Series* 9:1–48.
- VAN BERKUM, F. H. 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution* 40:594–604.
- VITT, L. J., AND T. E. LACHER, JR. 1981. Behavior, habitat, diet, and reproduction of the iguanid lizard *Polychrus acutirostris* in the caatinga of northeastern Brazil. *Herpetologica* 37:53–63.
- WAINWRIGHT, P. C., AND G. V. LAUDER. The evolution of feeding biology in sunfishes (Centrarchidae), pp. —. In R. Mayden (ed.), *Systematics, Historical Ecology and North American Freshwater Fishes*. Stanford Univ. Press, Stanford, CA. *In press.*
- WILLIAMS, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. *Evol. Biol.* 6:47–89.
- . 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*, pp. 326–370. In R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), *Lizard Ecology: Studies of a Model Organism*. Harvard Univ. Press, Cambridge.
- WYLES, J. S., AND G. C. GORMAN. 1980. The albumin immunological and Nei electrophoretic distance correlation: A calibration for the saurian genus *Anolis* (Iguanidae). *Copeia* 1980:66–77.
- ZUG, G. R. 1972. Anuran locomotion: Structure and function. I. Preliminary observations on relation between jumping and osteometrics of appendicular and postcranial skeleton. *Copeia* 1972:613–624.
- . 1978. Anuran locomotion—Structure and function, 2: Jumping performance of semiaquatic, terrestrial, and arboreal frogs. *Smith. Cont. Zool.* 276:1–31.

Corresponding Editor: R. B. Huey