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CHAPTER 11
PHYLOGENETIC ANALYSES OF LIZARD ENDURANCE CAPACITY IN RELATION TO BODY SIZE AND BODY TEMPERATURE

Theodore Garland, Jr.

The causes and consequences of variation in locomotor costs and capacities have received considerable attention from physiological ecologists and comparative physiologists during the last 20 years (reviews in Taylor et al. 1982; Bennett 1983; Bennett and Huey 1990; Bennett 1991; Full 1991; Gatten et al. 1992; MacMillen and Hinds 1992; Djawdan 1993; Garland 1993; Garland and Losos 1994; Miles this volume). Two main reasons for this attention are apparent. First, locomotor performance is known or thought to be causally related to success in many activities that affect fitness in nature, including foraging, courtship, and escape from predators (reviews in Bennett 1983; Hertz et al. 1988; Bennett and Huey 1990; Garland et al. 1990b; Jayne and Bennett 1990; Garland and Losos 1994; Bulova in press). Second, selection is thought to act more directly on whole-animal performance abilities (e.g., speed, stamina) than on lower-level morphological or physiological traits (e.g., limb proportions, muscle contractile properties, enzyme activities; see Fig. 11.1). Thus, many recent studies of locomotion by organismal biologists have focused on or at least included direct measures of performance abilities, rather than only isolated morphological, physiological, or biochemical characters.

Much of the work quantifying locomotor capacities has involved reptiles (citations above and Brodie and Garland 1993; Miles this volume). For several reasons, reptiles and lizards in particular are attractive groups for studying locomotor abilities. Even ignoring birds, extant Reptilia exhibit a great range of locomotor modes, including swimming (e.g., turtles and crocodilians), burrowing (e.g., amphisbaenians), and limbless crawling (e.g., snakes) (Zug 1993). Even excluding snakes, squamate reptiles offer an impressive array of locomotor types, also including limbless forms, arboreal forms with specialized toe pads, gliding forms, and bipedal species with toe fringes that aid locomotion on water or sand (references in Garland and Losos 1994). As compared with terrestrial mammals, lizards have limited stamina but not necessarily limited speed or acceleration, which raises both physiological and ecological questions (Bennett 1983, 1991). Lizards also experience relatively variable body temperatures when active and have a large range of body sizes (both within and among species), both of which may be expected to affect absolute locomotor abilities. Finally, lizards are relatively
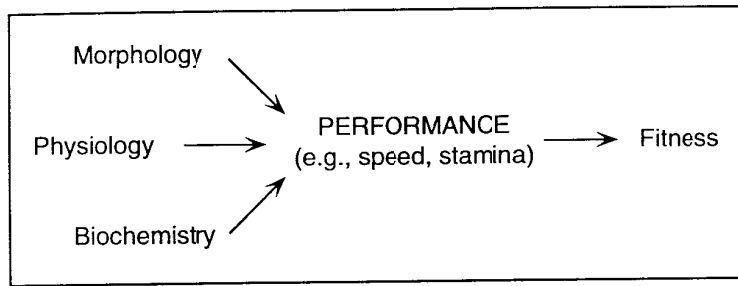
Figure 11.1. Conceptual relationships among individual variation in lower-level traits (morphology, physiology, biochemistry), organismal performance (e.g., various measures of locomotor abilities), and Darwinian fitness (modified from Arnold 1993; Garland 1994; Garland and Losos 1994; see also Huey and Stevenson 1979; Bennett 1980; Garland et al. 1990a). More complicated versions of this paradigm have also been proposed, sometimes inserting behavior between performance and fitness; it is also recognized that many of the relationships between levels are context dependent, and strongly affected by environmental circumstances (e.g., temperature; see Garland and Losos 1994) When considering interspecific variation, Darwinian fitness can be replaced by ecological factors and/or by measures of evolutionary success. The present comparative study is one of the first to begin with a survey of an organismal performance trait (treadmill endurance capacity) as the starting point for future studies of either the mechanistic bases of interspecific variation in performance or the behavioral and ecological correlates or consequences of variation in performance.

cooperative subjects for many measures of locomotor abilities (Bennett and Huey 1990; Garland and Losos 1994).

The most commonly measured aspects of lizard locomotor performance have been maximal sprint running speeds (e.g., Bennett 1980; Garland 1985; Huey et al. 1990; Losos 1990a; Bauwens et al. 1994; Miles this volume) and energetic costs of locomotion (Bennett and Gleeson 1979; John-Alder and Bennett 1981; John-Alder et al. 1983, 1986; Dial et al. 1987; Walton et al. 1990; Secor et al. 1992; Autumn et al. 1994). Far less information is available on variation in stamina (review in Garland and Losos 1994) or, at the other extreme, acceleration or jumping abilities (Huey and Hertz 1984; Carothers 1986; Losos 1990a). The purpose of the present study is to survey and quantify variation in treadmill-endurance capacities among species of lizards. The data set is one I have been accumulating since 1982, and the species included are opportunistically eclectic rather than a representative sample of all extant lizard clades. Nevertheless, the present study is the first broadly based comparative study of reptiles to begin with a survey of an organismal performance character as a starting point for future physiological or ecological studies (Fig. 11.1; see also Djawdan and Garland 1988; Garland et al. 1988; Djawdan 1993 on mammals). Chapters in each of the first two volumes on lizard ecology mentioned the general relationships between

activity capacities and behavior or ecology, but did not directly address quantitative interspecific variation in locomotor abilities (Tucker 1967; Bennett 1983).

In addition to documenting interspecific variation, I address whether stamina is related to body size and/or body temperature, using a recently developed statistical method–phylogenetically independent contrasts–that explicitly uses information on phylogenetic relationships. This analysis indicates that stamina has evolved in a positive fashion with both size and temperature. Further studies will be required to elucidate other factors underlying interspecific variation in stamina, as well as the selective forces that have shaped its evolution.

Methods

Data collection

Data presented herein were gathered from March 1982 through August 1993. Most animals were captured by hand or by hand-held slip noose and returned to the laboratory within 1–2 or at most a few days of capture. When possible, animals were tested immediately; otherwise, they were maintained with access to incandescent lamps for thermoregulation during the day and given ad libitum access to water and fed (mealworms, crickets, fruits, vegetables, dog food) approximately every other day.

All animals tested appeared to be in good health; obviously gravid females were excluded, because they may show reduced locomotor abilities (Shine 1980; Garland 1985; Garland and Else 1987; Sinervo et al. 1991; review in Garland and Losos 1994). Sample sizes ranged from one to 58 individuals per species (Table 11.1: $\bar{x}$ = 10.2 for 54 species, excluding *D. dorsalis*, *A. cristatus*, and *V. salvator*). For some species (especially *Pogona*, *Gambelia*, *Sauromalus*, *Phrynosoma*), some individuals tested refused to walk to exhaustion on the treadmill, instead biting or inflating their bodies (cf. Crowley and Pietruszka 1983; John-Alder et al. 1986; Mautz et al. 1992; refs. therein). Some *Phrynosoma* squirted blood from their suborbital sinuses. For some other species, such as *Cophosaurus texanus*, nearly one-half of the individuals tested exhibited frantic activity during each trial, resulting in rapid exhaustion. All such individuals were excluded from the analyses. All species' mean values are treated equally in statistical analyses, with no attempt to weight for sample size. As this is the first broad-scale comparative study of endurance capacities of lizards, I considered it appropriate to include all available data (e.g., including the four species represented by a single individual) and hence possibly err on the side of completeness.

Table 11.1. Treadmill-endurance running times at 1.0 km/h for 57 species or subspecies of lizards. Listing order of species follows that of Figure 11.3.

Species	N	Temp. (°C)	Body Mass (grams)		Endurance (minutes)		Within-species log-log regression		Predicted $\log_{10}$ Endur. at Max. Mass
			Min	Max	Min	Max	intercept	slope	
Agaminae (5 species)									
Physignathus lesueuri	15	35.8	3.6	559.2	0.848	9.7	0.295	0.182	0.79486
Ctenophorus nuchalis	58	40	1.3	48.3	1.673	169.5	0.809	0.615*	1.84578
Ctenophorus fordi	9	37	0.7	3.9	1.825	9.4	0.402	0.713*	0.81999
Pogona vitticeps	10	37.7	4.1	421.4	8.053	189.9	0.692	0.370	1.66381
Pogona barbata	3	37.7	100.8	317.9	9.952	31.1	-0.024	0.510	1.25126
Polychridae (1 species)									
Anolis carolinensis	12	31.9	2.3	5.9	1.082	2.1	0.080	0.159	0.20255
Iguanidae (5 species)									
Dipsosaurus dorsalis		40		65					1.17609†
Amblyrhynchus cristatus		35		2885					1.30103†
Ctenosaura similis	17	40	21.4	760.1	3.643	35.7	0.402	0.270*	1.17887
Sauromalus obesus	1	39.5		192.0		7.8			0.88947
Sauromalus hispidus	2	38.4	443.5	530.5	10.9	16.8			1.13239‡
Crotaphytidae (2 species)									
Gambelia wislizenii	7	`38.7	15.4	31.8	3.3	53.0	-1.323	1.720	1.26058
Crotaphytus collaris	12	37.3	14.2	33.6	3.4	29.8	0.555	0.254	0.94287
Phrynosomatidae (17 species)									
Uta stansburiana	21	37.2	1.8	4.8	1.4	3.7	0.294	0.054	0.33050
Urosaurus ornatus	21	36.9	1.8	4.4	0.8	1.9	-0.164	0.602*	0.22313
Sceloporus undulatus	7	37.5	3.0	11.7	1.1	2.8	-0.141	0.477*	0.36763
Sceloporus virgatus	13	36.4	2.3	5.1	0.9	2.5	-0.239	0.795	0.32244
Sceloporus occidentalis	19	34.7	7.2	14.2	1.3	3.8	-0.716	1.023	0.46192
Sceloporus olivaceus	1	36.4		30.6		1.6			0.19875
Sceloporus jarrovi	8	37.6	5.5	23.4	0.9	1.7	-0.243	0.336*	0.21713
Sceloporus clarkii	1	37.6		43.1		3.0			0.47596
Sceloporus magister	2	39.4	46.9	65.8	5.8	77.5			1.32726‡
Uma inornata	3	38	7.3	17.3	1.3	7.7	-1.439	1.895	0.90897
Callisaurus draconoides	20	40	8.2	19.2	3.4	18.3	-0.022	0.748	0.93720
Cophosaurus texanus	8	40.3	4.2	14.3	2.8	4.7	0.672	-0.152	0.54184‡
Holbrookia maculata	11	37.9	2.1	6.4	0.9	3.3	-0.131	0.545	0.30724
Phrynosoma coronatum	3	37.7	28.0	38.0	2.4	8.7	-5.920	4.335	0.92862
Phrynosoma cornutum	13	37.0	21.2	49.9	1.7	11.2	-0.200	0.468	0.59553
Phrynosoma platyrhinos	1	39.3		19.1		3.0			0.47900
Phrynosoma modestum	11	36.4	3.7	16.6	1.6	6.3	0.384	-0.022	0.36510‡

Table 11.1 (cont.)

| Species | N | Temp. (°C) | Body Mass (grams) | | Endurance (minutes) | | Within-species log-log regression | | Predicted log₁₀ Endur. at Max. Mass |
			Min	Max	Min	Max	intercept	slope	
Gekkota (5 species)									
Coleonyx brevis	2	35	1.8	1.8	0.9	1.3			0.04336‡
Teratoscincus przewalskii	25	15		9.1					-0.10791†
Lepidodactylus lugubris	7	34	0.8	1.8	0.5	1.1	-0.148	0.681	0.01852
Hemidactylus turcicus	9	35	2.3	3.6	0.7	1.2	0.1463	0.223	-0.02144
Hemidactylus frenatus	10	34	2.5	4.3	1.0	1.7	-0.228	0.608*	0.15889
Scincidae (7 species)									
Ctenotus regius	10	36.8	1.0	5.7	2.1	19.7	0.350	1.036*	1.13192
Ctenotus leonhardii	5	36.8	1.3	8.4	6.3	38.8	0.983	0.203	1.17002
Egernia cunninghami	25	35.7	7.0	313.6	3.4	9.3	0.579	0.102	0.83277
Tiliqua rugosa	6	36.6	471.5	652.3	11.5	45.4	-1.388	0.082	1.37404
Tiliqua scincoides	6	36.1	16.3	552.0	5.6	96.3	0.032	0.678*	1.89014
Eumeces laticeps	9	35.6	23.2	37.8	6.1	44.7	-2.941	2.893	1.62406
Eumeces skiltonianus	3	35	1.4	7.8	2.0	3.8	0.286	0.205	0.46897
Teiidae (7 species)									
Cnemidophorus t. tigris	24	40	10.3	25.8					2.07918
Cnemidophorus t. gracilis	12	40.0	8.4	22.1	13.0	71.2	0.089	1.218*	1.72483
Cnemidophorus t. marmoratus	8	40.8	6.8	18.8	17.2	79.8	1.766	-0.122	1.62477‡
Cnemidophorus sexlineatus	5	38.7	4.1	6.8	27.6	77.8	1.448	0.189	1.60501
Cnemidophorus uniparens	9	38.9	2.6	8.0	2.8	9.4	0.672	0.101	0.76295
Cnemidophorus exsanguis	2	39.9	13.0	14.5	11.0	37.5			1.30709‡
Cnemidophorus gularis	3	40.4	13.0	14.4	18.7	22.9	3.486	-1.913*	1.31472‡
Lacertidae (3 species)									
Pedioplanis lineoocellata	11	38.6	2.7	4.3	2.1	22.4	0.661	0.002	0.66181
Lacerta agilis	9	33.3	3.1	19.7	1.3	2.9	-0.069	0.401*	0.45008
Lacerta vivipara	19	30.3	1.1	4.7	0.8	1.8	0.260	0.144	0.12203
Anguidae (2 species)									
Gerrhonotus multicarinatus	6	35	5.9	31.3	1.4	3.3	-0.230	0.489*	0.50181
Gerrhonotus coeruleus	4	35	0.8	8.8	0.7	2.1	-0.086	0.427*	0.31821
Varanidae (1 species)									
Varanus salvator		35		505					0.84510†
Helodermatidae (2 species)									
Heloderma suspectum	6	31	24.5	673	2.9	17.4	0.168	0.360	1.18580
Heloderma horridum	7	31	194	1220	5.08	45.3	0.597	0.227	1.29644

*. Slope significant at $P < 0.05$ (2-tailed test).
†. Data for four species are taken from the literature: *Amblyrhynchus cristatus* data estimated from Gleeson (1979, 1980); *Dipsosaurus dorsalis* data estimated from John-Alder and Bennett (1981), John-Alder (1983, 1984a,b)(see also Cannon and Kluger 1985; Gleeson 1985); *Teratoscincus przewalskii* prediction from Autumn et al. (1994); *Varanus salvator* data estimated from Gleeson (1981; see also Gleeson and Bennett 1982). For these four species, body mass listed under "maximum" column is actually mean of animals tested.
‡. Mean of log₁₀ endurance reported and analyzed (see text).

Endurance capacity was measured as the length of time lizards could maintain pace at 1.0 km/h on a motorized treadmill. Consistent with previous studies, trials were terminated when lizards failed to maintain pace following 10 consecutive taps or pinches (at < 1-s intervals) about the tail and hind limbs; this protocol yields repeatable measures of stamina (John-Alder and Bennett 1981; Garland 1988 unpubl.; John-Alder et al. 1986; Garland and Else 1987; Tsuji et al. 1989). The belt surface varied somewhat among laboratories, but was generally a type of rubberized cloth that provided good traction. The size of the area within which lizards could walk was varied in relation to lizard size (see Garland 1984; John-Alder et al. 1986; Garland and Else 1987).

Some species and individuals maintained pace more steadily than others, but every attempt was made to minimize any tendency to sprint forward and ride back on the belt, because this behavior may affect both the energetic cost of locomotion and stamina (cf. Thompson 1985; Full pers. comm.). At all times during a trial I used the mildest stimulation possible to keep a lizard moving but avoid having it become excessively frightened and engage in frantic activity, which usually leads to rapid exhaustion. All individuals were tested on two consecutive days, and the longer time was used as the measure of stamina. Notes were recorded at the end of each trial, and trials were repeated on an additional day if frantic activity occurred. If an individual never cooperated, its endurance time was excluded. Within species, individual differences in endurance time were generally repeatable from trial to trial. Some of the endurance data have been reported previously (Garland 1984, 1993; Garland and Else 1987; John-Alder et al. 1986; Beck et al. unpubl.).

All species were measured at or near the mean body temperature of animals when active in the field, as indicated in the literature (references in John-Alder and Bennett 1981; Avery 1982; Garland 1984; John-Alder et al. 1986; Garland and Else 1987; Hertz et al. 1988; Tsuji et al. 1989; Beck et al. unpubl.). Temperature was maintained by (1) placing the treadmill in an environmental chamber or (2) placing incandescent lights above the treadmill or by blowing warm air onto the belt surface with a portable hair dryer, controlled by a digital thermocouple temperature controller. In most cases, body temperatures of individuals were taken with a quick-registering mercury thermometer immediately after exhaustion; either the mean of these values or the maintained ambient temperature was used in data analysis. Body mass was recorded at the end of each trial.

For *Cnemidophorus tigris tigris* from Dale Dry Lake, San Bernardino Co., California, a mean endurance time of 2 hours was estimated from Garland (1993). Data for four additional species were taken from published sources. Three of these species were measured in the laboratory of

A. F. Bennett at the University of California-Irvine: *Amblyrhynchus cristatus* (20 min, estimated from Gleeson 1979, 1980), *Dipsosaurus dorsalis* (15 min, estimated from John-Alder and Bennett 1981; John-Alder 1983, 1984a,b: see also Cannon and Kluger 1985; Gleeson 1985), and *Varanus salvator* (seven min, estimated from Gleeson 1981; see also Gleeson and Bennett 1982). Endurance data for *Teratoscincus przewalskii* (0.78 min) were from a predictive equation for animals tested at 15°C (Autumn et al. 1994). Data on field-active body temperatures of these geckos range from 9.9°–21.5°C, with a mean of 15.3°C; endurance was measured at 15° and at 25°C (Autumn et al. 1994). I have therefore used the endurance value for 15°C rather than for 25°C. For all of the foregoing species, mean body masses for individuals tested were substituted for "Maximum" body mass in Table 11.1.

Statistical analyses

Lizards exhibit relatively indeterminate growth, at least as compared with birds or mammals. For many species, I tested a broad ontogenetic size range, and in 40 of 44 cases endurance correlated positively with body mass and/or age, although few of these correlations were statistically significant at $P < 0.05$ (Table 11.1; see also Garland 1984; Garland and Else 1987; Garland and Losos 1994). Using mean body mass or mean endurance would therefore be unrepresentative of typical adults for many species. Moreover, my sampling of juveniles versus adults was not consistent across species. For comparative analyses, I therefore analyzed the logarithm of the maximum body mass within my sample and the predicted log endurance at that mass, computed from a least-squares linear regression equation for each species (right-most column of Table 11.1). All regression analyses were performed using SPSS/PC+ Version 5.0 (Norusis 1992). For *Cophosaurus texanus*, *Phrynosoma modestum*, *Cnemidophorus tigris marmoratus*, and *Cnemidophorus gularis* ($N = 3$), regression slopes were negative (see Table 11.1). For these four species and for *Sauromalus hispidus*, *Sceloporus magister*, *Coleonyx brevis*, and *Cnemidophorus gularis* (all $N = 2$), I analyzed the log of the maximum mass and the mean log endurance.

Examination of univariate and bivariate distributions and of residuals from regressions indicated that transformations were appropriate. Endurance and body mass were $\log_{10}$ transformed prior to all analyses, as is common in allometric studies. Body temperature was strongly left-skewed, with a single species measured at 15°C and all other values falling between 30° and 40°C. Thus, values for this independent variable were not evenly spaced on the raw scale. Body temperature was therefore transformed by raising it to the 10th power (and then divided by 10^{14} to simplify labeling of graphs). This transformation achieved a more-or-less even spacing of body temperature (see Fig. 11.6), which should improve statistical power while avoiding

undue statistical influence by the single species measured at a very low (although ecologically realistic: Autumn et al. 1994) temperature.

Felsenstein's (1985) method of phylogenetically independent contrasts was applied using the PDTREE program of Garland et al. (1993; this and other PC-based comparative method programs are available from the author on request in exchange for a formatted 3.5-inch, 1.44-megabyte disk). This method uses independently derived information on phylogenetic relationships (topology and branch lengths) of the species being analyzed in an attempt to transform the species' mean values to be statistically independent and identically distributed, thus permitting the use of conventional parametric statistics to address a variety of evolutionary questions (Felsenstein 1985; Harvey and Pagel 1991; Martins and Garland 1991; Garland 1992; Garland et al. 1992; Pagel 1993; Martins this volume).

An example of the computation of independent contrasts is presented in Fig. 11.2. The full phylogeny used for analyses is depicted in Fig. 11.3. A complete description of the sources used to construct this "best current compromise" phylogeny is available from the author on request (e.g., see Murphy et al. 1983; Wyles and Sarich 1983; Kluge 1987; Montanucci 1987; Estes and Pregill 1988; Good 1988a,b; Dessauer and Cole 1989; Mindell et al. 1989; de Queiroz 1992; Sites et al. 1992; Zug 1992; Wiens 1993; refs. therein). Relationships of major lineages within Iguania are uncertain. Thus, following recommendations of Frost and Etheridge (1989), these relationships are represented and analyzed as an unresolved polytomy including the subfamily Agaminae plus the families Polychridae (represented here only by *Anolis carolinensis*), Iguanidae, Crotaphytidae, and Phrynosomatidae.

In the face of the unresolved node for Iguania, recommendations of Purvis and Garland (1993) were followed for computing independent contrasts and for estimating statistical relationships between traits. Specifically, from the 57 taxa represented as the tips in Fig. 11.3, the full $N-1 = 56$ independent contrasts were computed. Unresolved nodes lead to uncertainty as to the degrees of freedom available for hypothesis testing; in the worst case, one degree of freedom is lost for each unresolved node (Purvis and Garland 1993). The polytomy for Iguania in Fig. 11.3 represents four unresolved nodes in comparison with a fully resolved, dichotomous tree. Thus, to be most conservative, four degrees of freedom (*df*) should be subtracted when testing for relationships between endurance contrasts and body mass and/or temperature contrasts. However, these relationships were highly significant (all $P < 0.001$), so reducing the *df* had no qualitative effect on the conclusions.

Checks of branch lengths as described in Garland et al. (1992), and again using the PDTREE program, indicated that for all three traits the absolute values of standardized contrasts showed significant negative relationships

millions of years			$\log_{10}$ Mass	$\log_{10}$ Endurance
15		*Egernia cunninghami*	2.496	0.833
	2.5	*Tiliqua rugosa*	2.814	1.375
12.5	node			
		Tiliqua scincoides	2.742	1.890

	Contrasts		Standard Deviation (years)	Standardized Contrasts	
	Mass	Endur.		Mass	Endurance
T. rugosa-T. scincoides	0.073	-0.515	2,236	0.00003243	-0.00023040
Egernia - node	-0.282	-0.800	5,362	-0.00005256	-0.00014916

Pearson Product-moment Correlation for tip data = 0.746
Correlation (through the origin) of Standardized Independent Contrasts = 0.022

Figure 11.2. Example of computation of phylogenetically independent contrasts (Felsenstein 1985), using data for three species of Australian skinks (from Table 11.1). "Contrasts" for mass and endurance are differences between species' mean values at the tips of the phylogeny; the value for the node is computed as a weighted average of its two descendants (in this example, the branch lengths from the node to the two tips are equal, so a simple average is the same as an average weighted by the reciprocal of the branch lengths). A "standard deviation" of an independent contrast is a square root of the sum of the branch lengths of the contrast; branch lengths leading to estimated nodal values are lengthened to reflect uncertainty, as described in Felsenstein (1985). "Standardized contrasts" are contrasts divided by their standard deviations; these values are used in statistical analyses, such as multiple regression through the origin. Note that branch lengths can be transformed prior to computation of contrasts (Garland et al. 1992); in the present analysis, branch lengths were log transformed for endurance and for body temperature, but were raised to the 0.6 power for body mass (computations in this figure use the untransformed branch lengths).

with their standard deviations ($r = -0.333$ for log body mass, $r = -0.449$ for log endurance, $r = -0.483$ for body temperature raised to the 10th power). Such relationships must be eliminated before testing for correlations between sets of independent contrasts. Independent contrasts are ratios representing an amount of difference for a given trait (divergence at the phenotypic level) divided by branch lengths (see Fig. 11.2 and Garland 1992). As is commonly the reason for computing ratios, division by the denominator is intended to standardize or "scale" the numerators so they can be compared directly. Thus, the ratio should not show any correlation with its denominator, or spurious correlations between sets of ratios will be introduced. Analogously, it is inappropriate to test for a correlation between, say, resting and maximal metabolic rates by correlating simple mass-specific
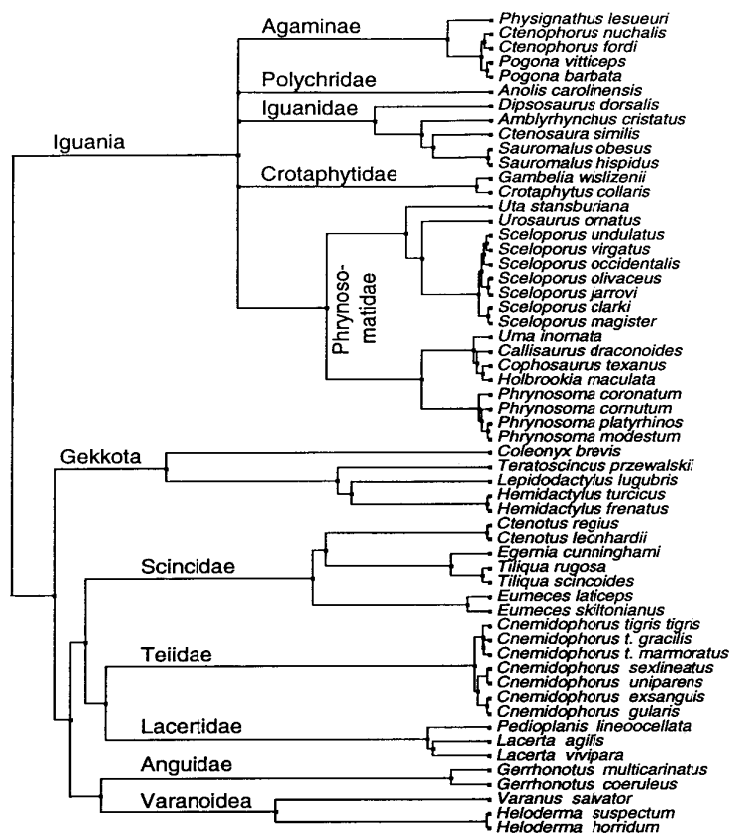
Figure 11.3. Phylogenetic topology and branch lengths estimated as divergence times for the 57 taxa of lizards studied herein. Basal split is at 190 million years. The unresolved polytomy at the base of the major lineages within Iguania (taxonomy follows Frost and Etheridge 1989) is arbitrarily placed at a depth of 100 million years.

values, because mass-specific metabolic rates typically show a negative relationship with body mass. Instead, metabolic rates can be divided by body mass raised to some appropriate power, determined empirically, or residuals from regressions on body mass can be computed (e.g., see Garland 1984, 1985; Garland and Else 1987; Garland and Losos 1994).

Given the correlations noted above, various transformations of branch lengths were applied in an attempt to reduce or eliminate them. For log body mass, branch lengths raised to the 0.6 power yielded a correlation of –0.065; for log endurance, log transformed branch lengths yielded $r = -0.108$; for body temperature raised to the 10th power, log branch

lengths yielded $r = -0.081$: all of these correlations are statistically insignificant. The foregoing transformations were therefore used for computing independent contrasts (see Fig. 11.4). Residuals from the independent contrasts multiple regression of endurance on mass and temperature were well behaved, further justifying the transformations. It is important to note that the decisions to transform branch lengths (or the phenotypic traits) are empirically based for the purpose of satisfying assumptions of parametric statistical tests and do not represent arbitrary attempts to induce correlations between variables (Garland et al. 1992).

Results

Species varied tremendously in their endurance capacities (Table 11.1; Figs. 11.5–11.7). For example, range of endurance running times in the three largest species of Scincidae (*Egernia cunninghami, Tiliqua [Trachydosaurus] rugosa, Tiliqua scincoides*) was 10-fold (see also table 1 of John-Alder et al. 1986), even though they are of similar body size and body temperature. The three largest species of Agaminae (*Physignathus lesueuri, Pogona vitticeps, Pogona barbata*) showed a similar range in stamina with minor differences in size and temperature. Even populations of *Cnemidophorus tigris* exhibited substantial differences in stamina (Table 11.1).

The foregoing comparisons demonstrate that body size and body temperature do not explain all of the intra- or interspecific variation in stamina. Nonetheless, Figs. 11.5–11.7 do indicate an overall positive interspecific relationship of $\log_{10}$ treadmill endurance with both $\log_{10}$ body mass ($r = 0.531$) and body temperature[10] ($r = 0.512$). A conventional nonphylogenetic, stepwise multiple regression was highly significant ($F_{2,54} = 31.14$; $P < 0.0001$; multiple $r^2 = 0.536$), with the partial regressions for both $\log_{10}$ body mass ($F_{1,54} = 31.75$; $P < 0.0001$; partial $r^2 = 0.282$) and body temperature[10] ($F_{1,54} = 29.48$; $P < 0.0001$; partial $r^2 = 0.254$) being highly significant. Residuals from this multiple regression were reasonably well behaved, and none of the standardized residuals was more than three standard deviations from the mean. In this multiple regression (Fig. 11.7), the partial regression coefficient for $\log_{10}$ body mass estimates the allometric scaling exponent: 0.364 ± 0.130 ($\pm$ 95% confidence interval). Such nonphylogenetic analyses generally yield unbiased, although inefficient, estimates of scaling relationships; however, the significance tests and confidence intervals must be treated with caution owing to the nonindependence of species' mean values (Harvey and Pagel 1991; Martins and Garland 1991; Pagel 1993).

The phylogenetic analysis indicated that standardized independent contrasts in endurance were positively correlated (Fig. 11.8) with contrasts in both body mass ($r = 0.501$) and body temperature ($r = 0.440$). A stepwise
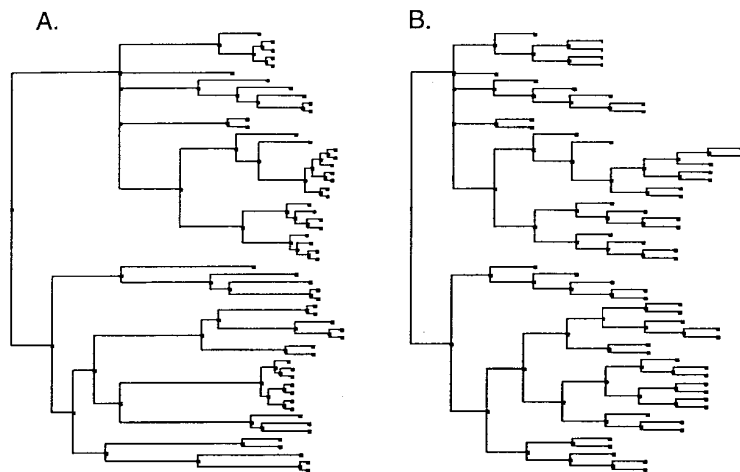
Figure 11.4. Phylogeny of Figure 11.3 with branch lengths (A) raised to the 0.6 power and (B) $\log_{10}$ transformed (cf. Garland et al. 1992). These transformations were used when computing phylogenetically independent contrasts (see text).

multiple regression through the origin showed that both contrasts in mass (partial $F_{1,54} = 19.78$; $P < 0.0001$; partial $r^2 = 0.251$) and contrasts in body temperature (partial $F_{1,54} = 14.53$; $P = 0.0004$; partial $r^2 = 0.159$) were highly significant predictors of contrasts in endurance (multiple $F_{2,54} = 18.75$; $P < 0.0001$; multiple $r^2 = 0.410$). Note that r^2 values for regressions through the origin are not directly comparable to regression models including an intercept, as were used for the nonphylogenetic analyses above. With regression through the origin, as must be used with independent contrasts (Garland et al. 1992), r^2 indicates the proportion of variability in the Ys about the origin that is explained by regression (Norusis 1992).

Residuals from the multiple regression using independent contrasts were approximately normally distributed. Only one of the standardized residuals was more than three standard deviations from the mean, that for the contrast between *Cnemidophorus sexlineatus* (with relatively high stamina) and *Cnemidophorus uniparens* (with the lowest stamina for any measured *Cnemidophorus*; see Table 11.1). As the inclusion of unisexual species of *Cnemidophorus* (here, *uniparens* and *exsanguis*) in a bifurcating phylogeny with the sexual species and subspecies is an extreme oversimplification at best (e.g., see Dessauer and Cole 1989), I would refrain from interpreting anything about this. Other checks of the residuals (e.g., see Norusis 1992) did not indicate any notable outliers, leading to the general interpretation that after accounting for divergence in body mass, divergence in body temperature, and estimated divergence times, no unusually rapid evolutionary divergences in stamina are apparent.
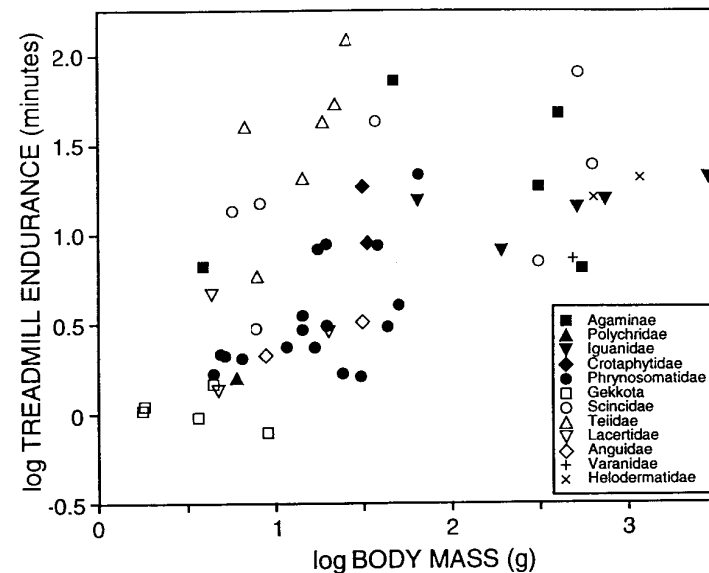
Figure 11.5. Positive log-log relationship between treadmill endurance running capacity and body mass for 57 species or subspecies of lizards (data from Table 11.1). Note that all solid symbols represent species within Iguania, whereas open symbols, +, and x represent species within Scleroglossa (represented here by Gekkota, Scincidae, Teiidae, Lacertidae, Anguidae, Varanidae, and Helodermatidae).

Discussion

Results presented herein indicate, unsurprisingly, that species of lizards with larger body size tend to have greater absolute stamina. After accounting for the effect of body size, body temperature also accounts for a significant amount of the remaining variance in treadmill endurance (all species were measured at temperatures representative of active lizards in the field). Multiple-regression analyses using phylogenetically independent contrasts confirm that stamina has evolved in a correlated fashion with both body size and body temperature; thus, in an evolutionary sense, it appears that bigger is better and warmer is better (cf. Bennett 1987b, 1990). The latter result indicates that evolution has not been able to compensate fully for the general Q_{10} effect on biochemical and physiological rate processes. An alternative approach would have been to measure each species at its optimal temperature for stamina (cf. Bauwens et al. 1994 on sprint speed), but this information is available for only a handful of species (see Bennett 1990). Moreover, measuring each species at its physiologically optimum temperature would have been ecologically unrealistic for those species (e.g., *Gerrhonotus*,
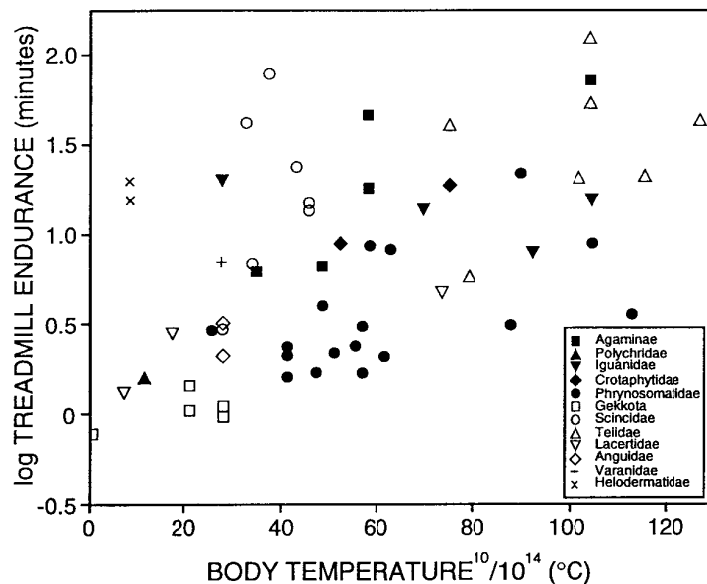
Figure 11.6. Positive relationship between $\log_{10}$ treadmill endurance and body temperature[10].

Figure 11.7. Three-dimensional plot showing positive relationship of $\log_{10}$ treadmill-endurance running capacity with both $\log_{10}$ body mass and body temperature[10] (data from Table 11.1; symbols as in Fig. 11.5). Plane represents the multiple regression of endurance on both mass and temperature (see text). Note that $\log_{10}$ body mass and body temperature[10] are uncorrelated ($r = 0.017$).

Teratoscincus przewalskii; Bennett 1980; Autumn et al. 1994) which are typically active at body temperatures considerably below their optimum for stamina.

The present comparative data suggest that if selection favors increased stamina in a lineage, one consequence may be increased body size and/or increased body temperatures while active. This hypothesis would be further supported by data indicating that within-population genetic correlations of stamina with size and with temperature tend to be positive in lizards (references in Brodie and Garland 1993; Garland and Losos 1994). Because stamina is probably mechanistically linked to both body temperature and body size (through its differential effects on limb cycling frequencies in relation to muscle mass and fuel and waste product storage capacities), positive genetic correlations seem likely to be both present and persistent over evolutionary time.

If size and/or temperature evolved as a correlated response to selection on stamina per se, this would have ramifications for food requirements, because both size and temperature affect total metabolic rate. Given that stamina might initially be subject to natural selection because of its relevance for foraging abilities (see Bennett 1983, 1991; Garland 1993; Cooper
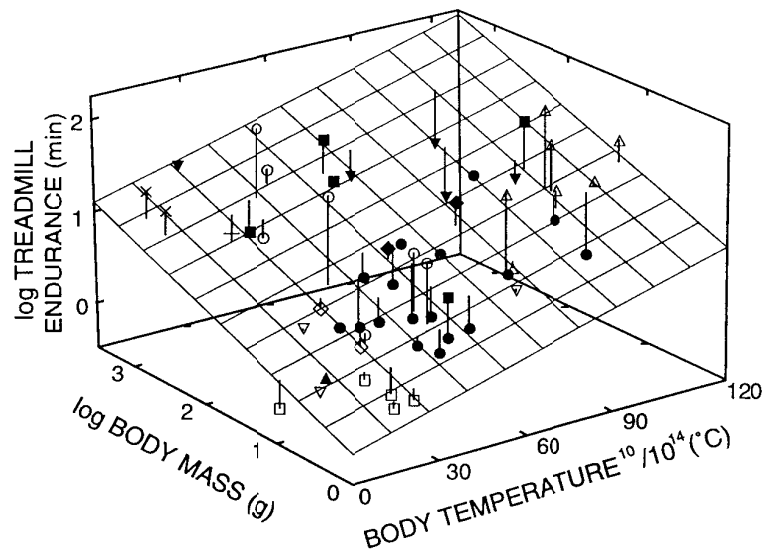
this volume), among other things, one can envision complicated scenarios involving positive feedback of selection, correlated response, and further selection. Moreover, stamina might be linked mechanistically with maximal sprinting abilities (Djawdan 1993; Garland and Losos 1994; but see Garland 1988; Garland et al. 1988), because these two aspects of locomotor abilities share some common morphological and physiological bases. Given that sprinting abilities can also affect foraging abilities, the situation becomes even more complicated. One can imagine, for example, that the high body temperatures of active *Cnemidophorus* both enhance stamina and increase food requirements; the former permits foraging widely, whereas the latter may necessitate it. Wide foraging in turn diminishes territoriality and leads to a mating system in which males may pursue females for hours during courtship, thus creating a predisposition for sexual selection to act on stamina (see also Stamps 1983; Garland 1993; Martins this volume). Wide foraging and conspicuous courtship (e.g., in open desert habitats characteristic of many *Cnemidophorus* species) would place a premium on antipredator mechanisms that include high sprint speed and/or the ability to run long distances when pursued by a predator (i.e., high stamina; for distance running
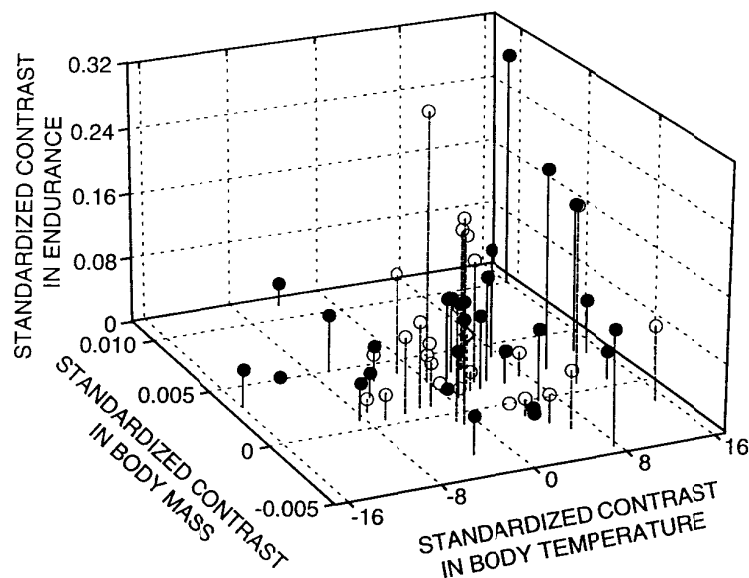
Figure 11.8. Three-dimensional plot showing positive relationship of standardized independent contrasts in $\log_{10}$ treadmill endurance capacity with contrasts in both $\log_{10}$ body mass and body temperature[10] (see text for statistics: contrasts in body mass and in body temperature were uncorrelated [$r = 0.086$], so multicollinearity was not a problem). Solid circles represent contrasts within the Iguania; open circles are contrasts within Scleroglossa (the bottom half of the phylogeny shown in Fig. 11.3); open diamond represents the basal contrast between these two clades. The fact that the basal contrast is not unusual indicates that these two clades do not differ in mean endurance, after accounting for effects of body mass and temperature (see Garland et al. 1993). Note that all contrasts in endurance have been set to positive while switching signs for mass and temperature contrasts accordingly (see Garland et al. 1992).

capacities, see Fig. 2 in Garland 1993); indeed, the *Cnemidophorus* studied herein also possess relatively high maximal sprinting abilities (Garland unpubl.). Phylogenetic comparative studies of *Cnemidophorus* and its relatives might be used to test such ideas (Brooks and McLennan 1991; Harvey and Pagel 1991). In any case, the foregoing scenarios emphasize the need to consider the evolution of whole organisms–not just single characters–in the appropriate behavioral, ecological, and phylogenetic context (e.g., Bennett and Huey 1990; Losos 1990a; Bauwens et al. 1994). Charles Darwin clearly appreciated this view, and it has been emphasized by many recent physiological ecologists, although some laboratory-oriented comparative physiologists and biochemists seem occasionally to have forgotten it.

Might the positive correlation with body mass be an artifact of the measurement protocol, which involved testing all species at the same absolute speed of 1.0 km/h? Probably not; consider other possible measures of stamina. One alternative would be to determine the maximum speed that each individual could maintain for some arbitrary length of time, perhaps 5 or 15 minutes. This would require measuring each individual at a series of speeds, and thus maintaining animals for extended periods of time in the laboratory, given that only one run to exhaustion per day is appropriate to allow for sufficient physiological recovery between trials (see Gleeson 1991). Such a protocol was logistically impossible in the present study. Moreover, even if it were undertaken, it would almost certainly show that larger individuals and species could maintain higher speeds for a given length of time, i.e., that stamina correlates positively with body size. Another index of stamina is the maximal aerobic speed, defined as the speed at which the maximal rate of oxygen consumption ($\dot{V}O_{2max}$) is attained (John-Alder and Bennett 1981; Taylor et al. 1982). Although ontogenetic data are limited to a single species (Garland and Else 1987), and comparative data for adults are limited to about 15 species of lizards (Fig. 23 in Garland 1993), in both cases the correlation with body mass seems to be positive. Thus, irrespective of what protocol might be used to measure the running endurance of lizards of different sizes, I am confident that it would show species with larger body sizes to have generally higher absolute stamina.

Why choose 1.0 km/h as the speed at which to measure stamina? This speed was chosen for two primary reasons. First, preliminary studies (e.g., John-Alder and Bennett 1981; Garland 1984) had indicated this to be a speed at which most individuals of most species would exhaust within a reasonable length of time, e.g., several minutes. This makes the measurement of many individuals per day feasible. But more importantly, most lizards do not engage in locomotor activity for more than a few minutes at a time, except in some unusual circumstances (Hertz et al. 1988; Garland 1993). Second, a survey of normal walking speeds of undisturbed lizards in nature showed that 1.0 km/h is not atypical for many species (appendix I of Garland 1993); certainly, it is only about 1/10 of the maximal sprint speed of many species (references in Garland and Losos 1994).

What about expressing locomotor performance on a per unit body length basis, as is commonly done in the literature on fishes? Might such an expression of stamina for lizards, or perhaps testing lizards at a speed that was a constant number of body length per second, be more "ecologically relevant?" I think not. What evidence have we that performance relative to body size–as opposed to absolute performance–is the more important determinant of success in foraging, courtship, or escaping from predators? None of which I am aware. Rather, absolute locomotor abilities (e.g., sprint speed in

meters per second or stamina in minutes) would seem to be the behaviorally and ecologically relevant measure of performance. In my opinion, a potential predator or prey organism does not "care" about a lizard's relative sprint speed, only how fast it can move in absolute terms! I do not believe that animals live on a per unit size basis (cf. Garland 1983). In fact, however, we have essentially no direct empirical evidence on this point (Hertz et al. 1988; Bennett and Huey 1990; Garland et al. 1990b; Jayne and Bennett 1990; Garland and Losos 1994).

Although locomotor abilities per unit size may have no special ecological relevance, it is of interest to compare the scaling of locomotor abilities with indices of movement in nature. In terrestrial mammals, daily movement distances (actual distances walked) scale approximately as body mass$^{0.3-0.6}$ (Garland 1983; Goszczynski 1986; Altman 1987). A positive scaling of daily movement distance probably also applies to lizards, although the scaling exponent has not been described (see Fig. 1 in Garland 1993). If daily movement distance scales to an exponent similar to that for the scaling of endurance at 1.0 km/h (estimated as about 0.36 in the present nonphylogenetic multiple regression), then endurance relative to typical daily movements would be similar in lizards of different size. Comparisons of the scaling of stamina with the scaling of home range area or of typical walking speeds should also prove interesting (see Stamps 1983; Christian and Waldschmidt 1984; Hertz et al. 1988; appendix I of Garland 1993).

Any measure of locomotor performance can be affected by motivational factors in addition to morphology and physiology (Garland and Losos 1994). The recent emphasis on direct measures of locomotor performance (see Introduction; Fig. 11.1), however, is generally based on the assumption that the latter are more important than the former. A number of previous studies have been successful at identifying mechanistic correlates of individual variation in locomotor abilities in reptiles (e.g., John-Alder 1983, 1984a,b; Garland 1984; Garland and Else 1987; Tsuji et al. 1989; Garland et al. 1990a; Huey et al. 1990; reviews in Bennett and Huey 1990; Bennett 1991; Garland and Losos 1994)—performance gradients sensu Arnold (1983)—but comparable studies of interspecific variation have lagged behind (Bennett and Huey 1990; Losos 1990a; Bennett 1991; Garland 1993; Garland and Losos 1994). Apparently, motivation alone cannot account for all of the interspecific differences discovered in the present study because body size and temperature statistically explain about one-half of the variation among species. From a physiological perspective, future studies should attempt to determine what other factors are associated with variation in stamina (e.g., maximal oxygen consumption, relative heart size or muscle mass, blood oxygen carrying capacity; see Tucker 1967; Bennett 1983, 1991; Gleeson 1991; Garland 1993). Examination of the present data set would allow one to choose for

study species which vary relatively widely in stamina but which are relatively closely related, of similar size, and active at similar body temperatures (e.g., within Agaminae, Phrynosomatidae, *Cnemidophorus*, or Scincidae; see Table 11.1). Also of importance will be determining whether constraints or trade-offs may exist that affect the joint evolution of different aspects of locomotor abilities, such as speed versus stamina (Garland 1988; Garland et al. 1988; Losos 1990a; Djawdan 1993; Garland and Losos 1994).

Direct inspection of species' mean values indicates that stamina can vary by 10-fold even among related species that have similar body sizes and similar active body temperatures (e.g., the three largest species of Scincidae and the three largest species of Agaminae). Both body size and body temperature, as independent variables, fall on the left side of Fig. 11.1; they represent proximate, mechanistic determinants of stamina, assuming that the present correlations actually reflect causal relationships. What might be the ultimate, evolutionary causes of interspecific variation in stamina?

One might hypothesize that interspecific or interpopulation variation in stamina would correlate with typical walking speeds, general movement rates, or perhaps home range area (cf. Bennett 1983; John-Alder et al. 1983, 1986; Hertz et al. 1988; Autumn et al. 1994), which might reflect such environmental factors as habitat heterogeneity, availability of cover, or predator or prey abundance (Bulova in press; on mammals see also Garland et al. 1988; Djawdan 1993). Hertz et al. (1988) compiled data for nine lizard species suggesting a positive correlation between treadmill endurance at 1.0 km/h and average daily movement distance, but quantitative field data on such traits are scarce (see Stamps 1983; Christian and Waldschmidt 1984; Pietruszka 1986; McLaughlin 1989; Garland 1993; Garland and Losos 1994) and presently limiting to further comparative analyses. Some anecdotal observations may be relevant here. The Australian water dragon, *Physignathus lesueuri*, lives in forested areas and rarely strays far from water, into which it often retreats when approached by humans and presumably by other predators. This species also shows the lowest stamina of the five Agaminae tested, the other four of which occur in more open and more arid habitats. Similarly, the Australian skink, *Egernia cunninghami*, seems rarely to stray far from the cover of exfoliating granite boulders; except for the much smaller *Eumeces skiltonianus*, it possesses the lowest stamina of the seven Scincidae tested. Finally, *S. magister* has the highest stamina of the seven species of *Sceloporus* tested, also occupies relatively open, arid habitats, and probably moves relatively great distances (Lowe pers. comm.).

Even in the absence of quantitative and comparable data on field activities, conventional wisdom identifies certain entire clades of lizards as generally having high activity levels (e.g., Scincidae, Teiidae, Lacertidae, Varanoidea in Fig. 11.3; Cooper this volume). The genus *Cnemidophorus* is

a case in point (Garland 1993). Present data suggest that the genus *Cnemidophorus* appears to be characterized by generally high stamina, even after accounting for their relatively high body temperatures (see Fig. 11.7; Garland 1993; Cullum, pers. comm.; but see Bennett and Gleeson 1979 on *C. murinus*). Scincidae also have a reputation for being relatively active, widely foraging animals, and most of the species tested herein do have relatively high stamina; the same applies to the two species of *Heloderma* (Fig. 11.7).

Comparing the stamina of entire sets of species, such as species within different clades, is typically addressed by analysis of covariance. Garland et al. (1993) discuss several alternative phylogenetically based methods for ANCOVA. From the analytical perspective of phylogenetically independent contrasts (see "Methods"), hypotheses about whether clades show significant differences in some aspect of the phenotype are tested by asking whether the contrasts at their bases are unusual. For a priori hypotheses about differences between two clades, the (residual) independent contrast connecting the bases of the two clades can be tested for statistical significance. In the present study, I had no strong a priori hypotheses about clade differences. Also, the clades with reputations for being relatively highly active also are relatively closely related, i.e., the Scincidae, Teiidae, Lacertidae, and Varanoidea (see Fig. 11.3). Therefore, I simply examined the residuals from the independent contrasts multiple regression of endurance on body size and body temperature (see Fig. 11.8). Using standard criteria (e.g., Norusis 1992), none of the residual contrasts was a strong outlier (see last paragraph of "Results" section).

Therefore, based on the present data, after accounting for phylogenetic topology, estimated divergence times, evolutionary divergence in body size, and divergence in body temperature, I see no strong evidence that any of the clades discussed above experienced an unusual event during the evolutionary history of its stamina. By unusual event I mean a substantial change in stamina underlaid by change in something other than body size or body temperature, and perhaps caused by selection. Of course, general examination of all residual contrasts is not a very powerful test as compared with a priori hypotheses about specific contrasts (e.g., at the bases of clades). Larger sample sizes and more thorough sampling of clades may thus alter the foregoing conclusion. For example, the only species of *Varanus* in the present data base is *V. salvator*, a riparian species, which is almost certainly less active than are species which dwell in more open, arid habitats. However, a more powerful way to test hypotheses about the evolution of endurance capacity will be to obtain quantitative data on behavior and ecology, thus allowing each species to be fully used in a multiple correlation, regression, or path analysis, rather than having to lump and compare cladistically or ecologically defined groups of species (cf. Garland et al. 1993). In such an

endeavor, differences among populations within species should not be overlooked (e.g., *Cnemidophorus tigris* in the present study; see also Bulova in press). Studying population as opposed to species-level differences allows a more direct examination of microevolutionary processes (Huey et al. 1990; Garland and Adolph 1991; Sinervo et al. 1991; Garland et al. 1992; Garland and Losos 1994; Niewiarowski this volume).

Acknowledgments

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