

Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length

Kevin E. Bonine and Theodore Garland, Jr

Department of Zoology, University of Wisconsin, 430 Lincoln Drive, Madison, WI 53706-1381, U.S.A.

(Accepted 19 September 1998)

Abstract

We measured sprint performance of phrynosomatid lizards and selected outgroups ($n=27$ species). Maximal sprint running speeds were obtained with a new measurement technique, a high-speed treadmill (H.S.T.). Animals were measured at their approximate field-active body temperatures once on both of 2 consecutive days. Within species, individual variation in speed measurements was consistent between trial days and repeatabilities were similar to values reported previously for photocell-timed racetrack measurements. Multiple regression with phylogenetically independent contrasts indicates that interspecific variation in maximal speed is positively correlated with hindlimb span, but not significantly related to either body mass or body temperature. Among the three phrynosomatid subclades, sand lizards (*Uma*, *Callisaurus*, *Cophosaurus*, *Holbrookia*) have the highest sprint speeds and longest hindlimbs, horned lizards (*Phrynosoma*) exhibit the lowest speeds and shortest limbs, and the *Sceloporus* group (including *Uta* and *Urosaurus*) is intermediate in both speed and hindlimb span.

Key words: comparative method, lizard, locomotion, morphometrics, phrynosomatidae, sprint speed

INTRODUCTION

Evolutionary physiologists and functional morphologists emphasize the importance of direct measurements of whole-animal performance (Arnold, 1983; Garland & Carter, 1994; Garland & Losos, 1994; Zani, 1996; Harris & Steudel, 1997). Selection is thought to act more directly on whole-animal performance capacities (e.g. maximal sprint running speed) than on lower-level morphological or physiological traits. Interspecific variation in performance abilities such as locomotor speed and endurance should, therefore, more clearly reflect the action of past natural selection and adaptive evolution than would such traits as leg length or heart mass. At the same time, variation in locomotor abilities results from multivariate interactions of underlying morphological or physiological traits. Here, we examine variation in sprint performance and its relationship with hindlimb span in North American phrynosomatid lizards and certain outgroups (see Fig. 1).

The family Phrynosomatidae is chosen as a model system for several reasons. First, most evolutionary biologists seem to agree that, for comparative studies, one should focus initially on a single clade (monophyletic group) of relatively closely related organisms that exhibits adequate diversity in the phenotypic traits of interest (Brooks & McLennan, 1991). Phrynosomatidae is comprised of three closely related mini-radiations (see

Fig. 1; Montanucci, 1987; de Queiroz, 1992; Wiens & Reeder, 1997) that exhibit large variation in locomotor morphology and performance, behaviour, and ecology (Stebbins, 1985; Conant & Collins, 1991; Garland, 1994; Miles, 1994a). Within Phrynosomatidae, the horned lizards are a highly derived group of flat-bodied, ant specialists (e.g. Sherbrooke, 1981). To avoid predation, they rely primarily on crypsis, defensive morphology (spines on body and head), and the unique ability to squirt blood from the orbital sinus (Middendorf & Sherbrooke, 1992). Their sister clade, the sand lizards, are relatively long-limbed and rely on speed to escape from predators (Dial, 1986; Bulova, 1994). The *Sceloporus* group is somewhat of an intermediate generalist in both morphology and behaviour. Second, the phylogenetic relationships within Phrynosomatidae are relatively well known (de Queiroz, 1992; Wiens, 1993; Changchien, 1996; Wiens & Reeder, 1997), which facilitates the use of phylogenetically based statistical methods (Harvey & Pagel, 1991; Martins & Hansen, 1996; Garland, Midford & Ives, 1999). Third, many species, including members of all three subclades, are readily accessible in the south-western U.S.A., a centre for phrynosomatid lizard diversity. Finally, phrynosomatid lizards are amenable to locomotor measurements (e.g. Huey *et al.*, 1990; Garland, 1994; Miles, 1994a, b; Autumn *et al.*, 1997).

To avoid comparing widely divergent locomotor

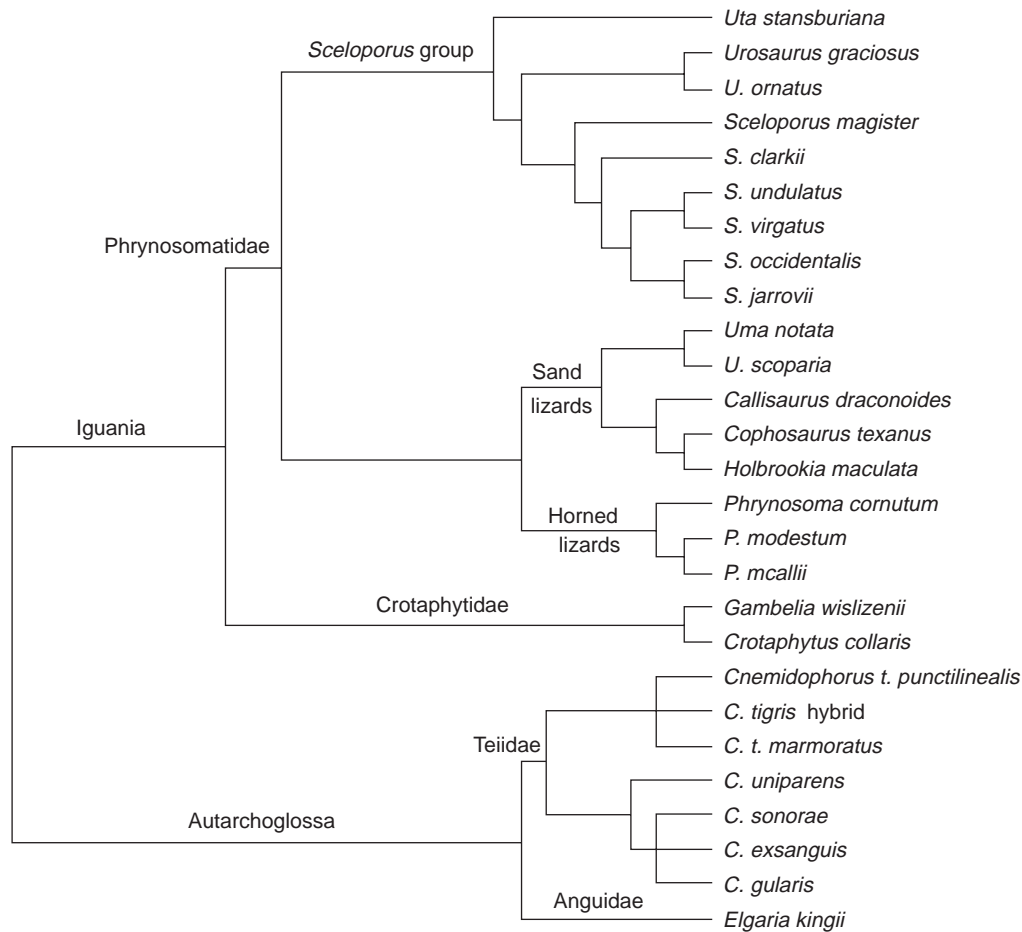


Fig. 1. Hypothesized phylogenetic relationships of the 27 lizard species (or subspecies) included in this study. Branch lengths are arbitrary. The two multifurcations are 'hard' polytomies (see Purvis & Garland, 1993), indicating what are essentially simultaneous, three-way splits: they represent two subspecies of *Cnemidophorus tigris* plus their hybrids (see Dohm *et al.*, 1998) and a parthenogenetic species (*C. exsanguis*) of hybrid origin (Dessauer & Cole, 1989). Branch lengths used for phylogenetic analyses are reported in Methods.

modes, we focused on species that are largely terrestrial and occur in arid or semi-arid habitats. We also included several sympatric 'outgroup' species that are similar to Phrynosomatidae in both body size and habitat. These species were included to enhance statistical power and to explore the phylogenetic generality of our findings. All lizard species included in this study are diurnal and primarily insectivorous (or carnivorous: *Gambelia*, *Crotaphytus*; Pietruszka, Weins & Pietruszka, 1981; Stebbins, 1985; Conant & Collins, 1991). Based on our own and published information on behaviour and habitat, we hypothesized that, within Phrynosomatidae, the horned lizards (*Phrynosoma*) would have the lowest maximal sprint speed, sand lizards would be fastest, and the *Sceloporus* group would be intermediate.

Since the work of Bennett, Huey, and Hertz (Bennett, 1980; Huey *et al.*, 1981; Huey, 1982; Huey & Hertz, 1982, 1984), measurement of maximal sprint running speed by photocell-timed racetracks has become a standard technique for lizards (e.g. Garland, 1985; Miles & Smith, 1987; Huey *et al.*, 1990; Losos, 1990a;

Miles, 1994a,b; Miles, Fitzgerald & Snell, 1995), snakes (e.g. Jayne & Bennett, 1990), and small mammals (Djawdan & Garland, 1988). During studies of both lizards and mammals, we obtained evidence that some species were not performing at maximal levels in racetracks. For example, *Dipsosaurus dorsalis* were reported to reach speeds exceeding 8 m s^{-1} both in timed field trials (Belkin, 1961) and when filmed running on a high-speed treadmill (J. A. Peterson, pers. comm.), but were slower in racetracks (e.g. Marsh, 1988, reports a maximum of about 5 m s^{-1}). Similarly, kangaroo rats were shown to reach substantially higher speeds when released directly into the field as compared with trials in racetracks (Djawdan & Garland, 1988).

Given the range of locomotor abilities that we expected to find within Phrynosomatidae, any tendency to underestimate speeds of the fast species, thus artificially reducing the range of variation, would constitute a potentially important bias. Therefore, we used a new method for measuring maximal sprint running speed in lizards, a high-speed treadmill (H.S.T.). Previously, Dohm *et al.* (1998) demonstrated for one of

the species included here (*Cnemidophorus tigris*) that measurement of maximal sprint speed on the H.S.T. may be as repeatable as is typical for racetrack measurements of lizards (e.g. Garland, 1985; Gleeson & Harrison, 1988; van Berkum *et al.*, 1989; Sorci *et al.*, 1995), a result that we extend to multiple species.

METHODS

Animal collection

We collected lizards in the south-western U.S. in 1991 and 1996, primarily in Arizona and New Mexico, using slip noose, modified drift fence (C. J. Cole, pers. comm.), and excavation. Sprint performance was measured at the American Museum of Natural History's Southwestern Research Station near Portal, Arizona on over 300 individuals of 27 species. We restricted collections to close proximity of SWRS in order to keep animals field-fresh. We excluded from analyses locomotor measurements of gravid females and juveniles. During captivity, we kept individual lizards isolated in cloth bags or plastic cups (depending on size), with periodic access to water but no food.

Sprint measurements

We measured maximal sprint speed on a high-speed treadmill (H.S.T.) constructed in the Department of Zoology shops at the University of Wisconsin-Madison. The treadmill had a total belt area of 155 cm long by 30 cm wide, with adjustable plexiglass walls (Dohm *et al.*, 1998). We used an effective running area of about 140 cm in length by 15 cm wide at the front and 25 cm wide at the rear. The textured rubber cloth belt (American Star International, Brighton, MI #IAR-PT) of the treadmill provided excellent traction. A 3.0-horsepower motor provided almost instant acceleration to a maximum speed of 12.5 m s⁻¹, twice the fastest lizard sprint speed measured here.

Following previous comparative studies (Garland, 1994; Zani, 1996), we made sprint speed measurements near the lizard's field-active body temperature. We placed animals in an environmental chamber for at least 2 h before measurements. We preheated some animals to 35 °C and others to 40 °C, consistent with their approximate field-active body temperature (except *Elgaria*, which prefers 30 °C, but was measured at 35 °C for logistical reasons and because Bennett (1980) found the highest speed of a related species, *E. multicaeratus*, at 37.5 °C). We removed lizards from the environmental chamber (they were kept in cloth bags or plastic cups) and placed them immediately on the rear of the horizontal treadmill. A light tap to the tail induced the animal to run toward the clear plexiglass front of the treadmill. As the lizard began to run, we rapidly accelerated the treadmill to match the speed of the running lizard. Some lizards required additional taps to the tail

to maintain sprinting, and we increased the belt speed until the animal reached an apparent maximum speed. We then held speed constant and the lizard tired quickly, came off the back of the moving belt, and was captured. We recorded body temperature (T_b) immediately after each trial with a quick-reading cloacal thermometer (Miller and Weber, Inc., Queens, NY). The treadmill apparatus was heated with overhead incandescent lamps before and during trials. A tachometer displayed the final speed. The total length of a trial was *c.* 5–15 s. Each trial was subjectively scored for the perceived effort that the lizard was making to run as fast as possible: Great, Good, OK, Fair, and Poor. Only trials that were scored at least OK were used in subsequent analyses. We measured maximal sprint running speed once on each of 2 consecutive days for a given individual, and we used the higher measure in subsequent analyses. We computed mean maximal sprint speed for each species using the maximum value recorded for each individual. Mean body temperature for each species was calculated using the temperature of the fastest trial for each individual.

Morphometric measurements

With a clear plastic ruler, we measured snout–vent length, tail length, and hindlimb span (toe-to-toe, excluding claws, with limbs stretched horizontally perpendicular to body; Garland, 1985) to the nearest 0.5 mm. We measured body mass on a Mettler balance (model PM200) to the nearest 0.001 g within 5 days after H.S.T. measurements. Mean body mass for each species was calculated using masses of those animals for which we had at least one usable sprint measurement. Mean hindlimb span was predicted from the mean body mass of each species using an allometric equation. This allometric equation was derived from a separate regression for each species of log hindlimb span on log body mass for all the individuals for which we had morphometric measurements (this was many more than for sprint data, and included juveniles).

Phylogeny

We used the phylogeny shown in Fig. 1 for independent contrasts analyses (see next section). The general evolutionary relationships within Phrynosomatidae, including the topology within sand lizards and within the *Sceloporus* group, are well supported (de Queiroz, 1992; Wiens, 1993; Changchien, 1996; Reeder & Wiens, 1996). Within the *Sceloporus* group (*Uta*, *Urosaurus*, *Petrosaurus*, *Sceloporus*), we used the most recent topology as described by Wiens & Reeder (1997). The sand lizards, primarily inhabitants of open, sandy desert (e.g. de Queiroz, 1992; Howland, 1992; Bulova, 1994), are a closely related group of species that includes 4 recognized genera, *Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma* (fringe-toed lizards, which are

Table 1. Repeatability of sprint speeds for species that had at least three individuals with two acceptable trials. Pearson correlation between trial 1 and trial 2, and two-tailed *t*-test comparing values between the two trials are reported

Species	<i>n</i>	Correlation and <i>P</i> value		Two-tailed <i>t</i> -test and <i>P</i> value ^a	
<i>Uta stansburiana</i>	8	0.507	0.200	-0.08	0.938
<i>Urosaurus ornatus</i>	21	0.556	0.009	1.27	0.220
<i>Sceloporus magister</i>	10	0.258	0.471	-1.33	0.217
<i>Sceloporus undulatus</i>	14	0.918	<0.001	0.12	0.904
<i>Sceloporus virgatus</i>	19	0.590	0.008	0.48	0.635
<i>Sceloporus jarrovi</i>	13	0.772	0.002	-1.25	0.235
<i>Uma notata</i>	7	0.641	0.120	-2.07	0.084
<i>Callisaurus draconoides</i>	9	0.946	<0.001	-0.34	0.743
<i>Cophosaurus texanus</i>	9	0.235	0.542	0.51	0.624
<i>Holbrookia maculata</i>	6	0.560	0.247	-0.12	0.906
<i>Phrynosoma cornutum</i>	6	0.391	0.443	2.78	0.039
<i>Phrynosoma modestum</i>	4	0.855	0.145	1.00	0.389
<i>Phrynosoma mcallii</i>	3	0.966	0.167	1.02	0.414
<i>Gambelia wislizenii</i>	7	0.376	0.406	0.46	0.661
<i>Crotaphytus collaris</i>	11	0.778	0.005	-2.41	0.037
<i>Cnemidophorus uniparens</i>	14	0.535	0.049	-0.74	0.470
<i>Elgaria kingii</i>	7	0.385	0.393	-1.42	0.206

^a Negative *t*-value indicates trial 2 slower.

essentially restricted to sand dunes; Norris, 1958; Carothers, 1986; Jayne & Ellis, 1998). The *Phrynosoma* (horned lizards) topology follows Montanucci's (1987) cladistic analysis of morphology. Remaining within Iguania, we studied 2 species of Crotaphytidae, predators that occur in microsympatry with several species of Phrynosomatidae and often feed on them (Stebbins, 1985; Pianka, 1986). Moving to the other half of the lizard family tree (see Fig. 1), we sampled 2 families that occur in the U.S. and are similar to Phrynosomatidae in body size and habitat. Within Teiidae, we studied 7 species of *Cnemidophorus*, including 1 species (*C. tigris*) represented by 2 subspecies and their hybrids (see Dohm *et al.*, 1998) and 1 parthenogenetic species of hybrid origin (Dessauer & Cole, 1989). Both of these are treated as 'hard' polytomies for analyses with independent contrasts (see Purvis & Garland, 1993). We also studied 1 species of Anguidae, *Elgaria kingii*.

Statistical analyses

We regressed mean maximal sprint speed against 3 likely predictors of sprint speed: body temperature, log body mass, and log hindlimb span. Because sample size varied widely among species (see Table 2), we calculated regressions both unweighted and weighted by the square root of the sample size for sprint speed measurements. *Elgaria kingii* was a potential outlier and/or statistically influential data point (compare Fig. 4c in Garland & Janis, 1993) because it had the shortest legs, slowest speed, and lowest body temperature; therefore, we calculated regressions both with and without this species. Because body mass, hindlimb span, and body temperature were highly correlated, we also calculated regressions using residuals of speed, body temperature, and log hindlimb span regressed on log body mass.

Additionally, we performed regressions with both conventional statistical methods (equivalent to assuming a star phylogeny) and phylogenetically independent contrasts (Felsenstein, 1985; Garland, Harvey & Ives, 1992; Garland, 1994). Independent contrasts were computed with the PDTREE program (Garland *et al.*, 1999). Estimates of phylogenetic branch lengths in terms of divergence times, genetic distances, or some other common metric were not available for all of the 27 species included here. Therefore, following Clobert, Garland & Barbault (1998), we tried 3 different sets of arbitrary branch lengths (all = 1, Pagel's (1992), Grafen's (1989)) as well as transforms of the latter 2. In all cases, no intercept term was included in the model, as is required for independent contrasts (Felsenstein, 1985; Grafen, 1989; Garland *et al.*, 1992). We checked diagnostic plots as described previously (Garland *et al.*, 1992; Clobert *et al.*, 1998; Diaz-Uriarte & Garland, 1998). For all 4 characters, plots of the absolute values of the standardized independent contrasts versus their standard deviations showed no statistically significant linear trends when the following branch lengths were used: sprint speed (Grafen^{0.5}), log body mass and log hindlimb span (Grafen^{0.8}), body temperature (all = 1).

As with the conventional regression analyses, we conducted independent contrasts analyses both unweighted and weighted by the square root of speed sample size. To do this, we used PDTREE to enter the square root of sample size as a variable at the tips of the phylogeny shown in Fig. 1. We then collapsed the phylogeny to a star (a single hard polytomy) by setting all internode branch lengths to 0 and branches leading to tip species to 1. This use of a star phylogeny, with no hierarchical relationships, reflects the fact that sample size is not a characteristic of the species themselves, and hence is not inherited phylogenetically (see Wolf, Garland & Griffith, 1998, for other examples). We then

Table 2. Data for species comparisons: speed, size, temperature, and predicted \log_{10} hindlimb span from an allometric regression for each species

Species	Mean speed and body mass			Mean body temperature		Predicted \log_{10} hindlimb span	
	<i>n</i>	m s^{-1}	g	<i>n</i>	$^{\circ}\text{C}$	<i>n</i>	log mm
<i>Uta stansburiana</i>	10	2.55	3.79	9	35.72	33	1.902
<i>Urosaurus graciosus</i>	3	2.81	3.31	3	35.30	3	1.887
<i>U. ornatus</i>	26	2.42	3.14	26	35.73	41	1.829
<i>Sceloporus magister</i>	9	3.02	31.51	9	36.56	17	2.166
<i>S. clarkii</i>	2	3.00	37.94	2	37.80	2	2.166
<i>S. undulatus</i>	8	2.51	10.45	7	37.37	20	2.000
<i>S. virgatus</i>	9	1.64	6.12	9	35.10	26	1.959
<i>S. occidentalis</i>	30	2.88	14.31	30	34.99	19	2.026
<i>S. jarrovii</i>	9	1.62	15.74	9	36.09	27	2.083
<i>Uma notata</i>	9	3.49	22.36	9	39.44	19	2.177
<i>U. scoparia</i>	2	3.20	14.46	2	38.80	2	2.153
<i>Callisaurus draconoides</i>	6	5.72	13.47	6	39.45	34	2.192
<i>Cophosaurus texanus</i>	9	4.57	10.47	9	39.67	39	2.128
<i>Holbrookia maculata</i>	7	3.12	4.02	6	36.35	14	1.965
<i>Phrynosoma cornutum</i>	7	2.18	33.69	6	37.75	13	2.091
<i>P. modestum</i>	5	1.45	10.68	5	36.32	15	1.935
<i>P. mcallii</i>	5	1.60	9.09	5	35.14	8	1.988
<i>Gambelia wislizenii</i>	6	4.08	29.58	6	39.55	30	2.236
<i>Crotaphytus collaris</i>	11	4.62	22.33	11	37.65	12	2.226
<i>Cnemidophorus t. punctilinealis</i>	18	5.63	14.41	16	40.17	18	2.104
<i>C. tigris</i> hybrid	7	5.79	17.87	6	39.37	13	2.130
<i>C. t. marmoratus</i>	9	6.17	15.66	8	39.51	11	2.114
<i>C. uniparens</i>	9	3.58	5.40	9	37.93	26	1.992
<i>C. sonora</i>	2	3.94	15.15	2	39.45	3	2.093
<i>C. exsanguis</i>	2	4.03	13.77	2	40.45	4	2.107
<i>C. gularis</i>	2	5.06	13.68	2	38.25	2	2.117
<i>Elgaria kingii</i>	6	1.08	7.98	6	34.57	12	1.774

computed independent contrasts as for all other variables. As contrasts are calculated, an intermediate part of the computations is an estimate of the value at the base of each contrast (see Felsenstein, 1985). These are an estimate of the 'ancestral' value for each contrast or, equivalently, the mean of the 2 descendant species, weighted by branch lengths. We used these estimated nodal values to weight correlations or multiple regressions.

RESULTS

Repeatability

Speeds of individual lizards tended to be consistent from day to day. As shown in Table 1, Pearson correlations between days ranged from 0.235 to 0.966 and averaged 0.604 (unweighted). These repeatabilities are similar to published sprint-speed repeatabilities measured in photocell-timed racetracks (e.g. Garland, 1985, 0.771 for 68 *Ctenophorus nuchalis*; van Berkum *et al.*, 1989, 0.45 for 298 hatchling *Sceloporus occidentalis*; Garland *et al.*, 1990, 0.839 for 42 adult *S. occidentalis*; Sorci *et al.*, 1995, 0.492 for 386 *Lacerta vivipera*, day 1 faster; Gleeson & Harrison, 1988, 0.88 (intra-class correlation coefficient) for 20 *Dipsosaurus dorsalis*). Speeds were not significantly different on trial days 1 and 2,

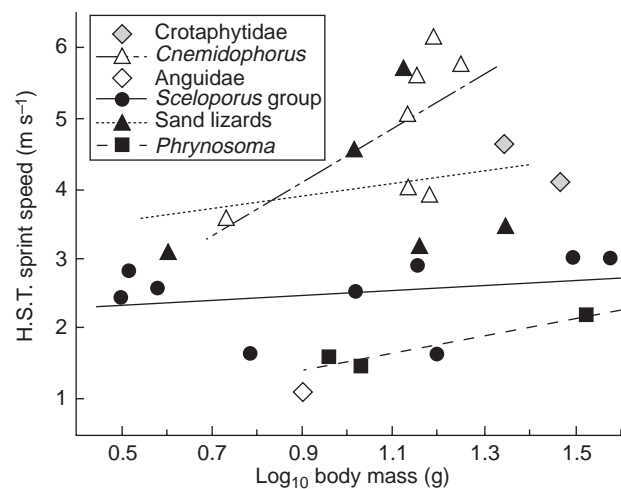


Fig. 2. Species' mean sprint speeds show a weak positive relation to \log_{10} body mass within each phrynosomatid subclade and within *Cnemidophorus* (lines are conventional least-squares linear regressions). Considering all 27 species, the relationship is statistically significant with independent contrasts analysis ($P < 0.05$, Table 3).

except for *Phrynosoma cornutum* and *Crotaphytus collaris* (paired *t*-tests, Table 1). Scatterplots for each species indicated no large deviations from bivariate normality.

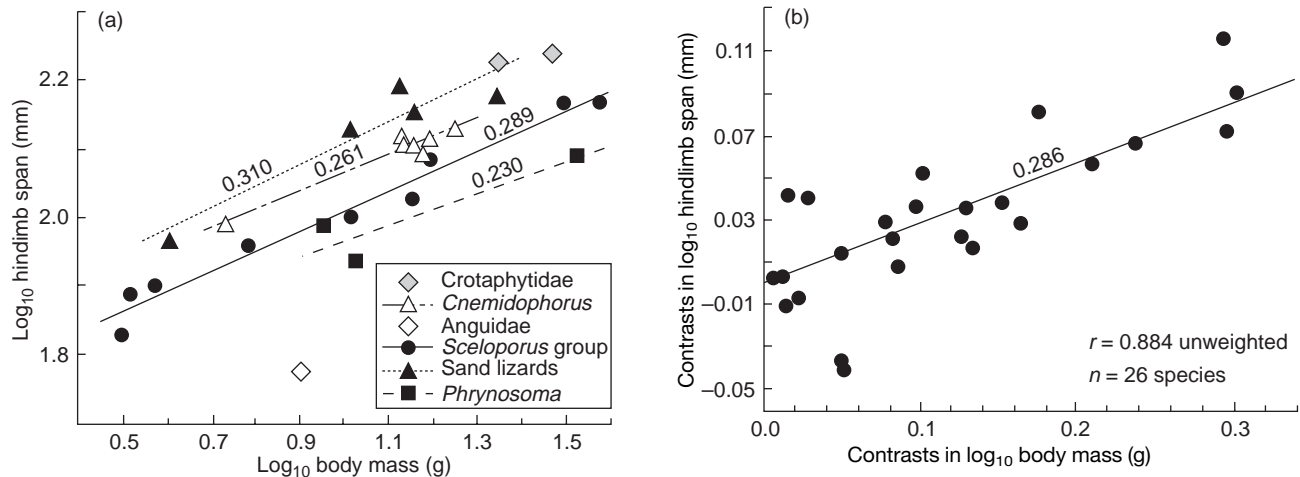


Fig. 3. Significant positive relationship between species' mean \log_{10} hindlimb span and \log_{10} body mass. The conventional regression slopes (unweighted) for four subclades (a) are similar to each other and to the overall independent contrasts slope (b). Note outlier *Elgaria kingii* (Anguinae) in (a), which was removed before independent contrasts computation in (b). In (b), contrasts are 'positivized' (Garland *et al.*, 1992) on body mass and the regression is constrained to pass through the origin.

Variability

Mean sprint speeds (unweighted) of the three subclades within Phrynosomatidae were in the order hypothesized (Fig. 2): 1.74 m s^{-1} for the horned lizards, 2.49 m s^{-1} for the *Sceloporus* group, and 4.02 m s^{-1} for the sand lizards. The crotophytids averaged 4.35 m s^{-1} and the *Cnemidophorus* 4.89 m s^{-1} (Table 2). Individual species' mean maximal sprint running speeds ranged from 1.08 (*Elgaria kingii*) to 6.17 m s^{-1} (*Cnemidophorus tigris*

marmoratus), which represents a 6-fold difference. Zani (1996) reports a range of $0.34\text{--}3.97 \text{ m s}^{-1}$, or 11.5-fold, for 39 species of lizards spanning a broader phylogenetic range than represented here. If we exclude the Scincidae, Gymnophthalmidae, Gekkonidae, and Polychrotidae, relatively slow families that are not included in the present study, then Zani's range reduces to $1.13\text{--}3.97 \text{ m s}^{-1}$, or 3.5-fold. Miles (1994a) reports a range of $1.73\text{--}2.48 \text{ m s}^{-1}$, or 1.4-fold, among eight species in the *Sceloporus* group. Considering only the nine *Sceloporus*-group species that we measured, our range of mean sprint speeds is similar, $1.62\text{--}3.02$, or 1.9-fold. Losos (1990a) reports a range of $1.49\text{--}2.48 \text{ m s}^{-1}$, or 1.7-fold, among 14 species of *Anolis*. Cullum (1997) reports a range of $1.89\text{--}3.15 \text{ m s}^{-1}$, also 1.7-fold, among 11 species of *Cnemidophorus*.

Table 3. Pearson product-moment correlations between variables (unweighted above diagonal, weighted below)

	Speed	Temp.	Mass	Hindlimb
Conventional				
<i>n</i> = 27 species				
Maximal sprint speed	1.0	0.792	0.287	0.628
Body temperature	0.810	1.0	0.495	0.737
Log body mass	0.317	0.472	1.0	0.808
Log hindlimb span	0.628	0.711	0.829	1.0
<i>n</i> = 26 species				
Maximal sprint speed	1.0	0.768	0.265	0.571
Body temperature	0.792	1.0	0.487	0.700
Log body mass	0.304	0.467	1.0	0.858
Log hindlimb span	0.580	0.680	0.873	1.0
Independent contrasts				
<i>n</i> = 27 species				
Maximal sprint speed	1.0	0.573	0.436	0.686
Body temperature	0.568	1.0	0.655	0.751
Log body mass	0.438	0.656	1.0	0.833
Log hindlimb span	0.689	0.751	0.835	1.0
<i>n</i> = 26 species				
Maximal sprint speed	1.0	0.432	0.452	0.587
Body temperature	0.432	1.0	0.697	0.673
Log body mass	0.453	0.697	1.0	0.884
Log hindlimb span	0.593	0.675	0.885	1.0

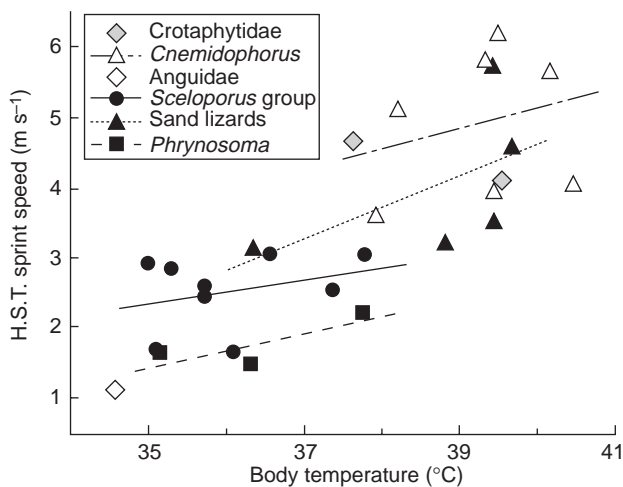
Correlates of sprint speed

Table 3 presents pairwise correlations for all variables. All were positively intercorrelated, with the correlation between log body mass and log hindlimb span the strongest ($r > 0.8$; Fig. 3). Because *Elgaria kingii* was an outlier with respect to relative hindlimb span (Fig. 3a; as well as having the slowest speed and lowest body temperature, Table 2), subsequent analyses were performed with both 27 and 26 (*E. kingii* removed) species: results were similar.

Within each phrynosomatid subclade, and within *Cnemidophorus*, sprint speed and log body mass show a weak positive relationship (Fig. 2). Independent contrasts analysis (Table 3) indicates that the overall correlation between sprint speed and log body mass is statistically significant (two-tailed $P < 0.05$). Losos (1990b) and Miles (1994a) also found a significant positive correlation between speed and log body mass.

Table 4. Multiple regressions to predict lizard sprint speed. Weighted regressions are weighted by (sample size)^{0.5} for each species

Regression	Independent variable	Standardized partial regression coefficient	F	P
Conventional multiple regression				
<i>n</i> = 27 species				
Unweighted	Log HLS	0.541	4.41	0.0468
	Log mass	-0.458	5.22	0.0318
	<i>T_b</i>	0.621	12.65	0.0017
Weighted	Log HLS	0.519	3.87	0.0613
	Log mass	-0.414	3.86	0.0615
	<i>T_b</i>	0.637	14.49	0.0009
<i>n</i> = 26 species				
Unweighted	Log HLS	0.673	4.92	0.0371
	Log mass	-0.599	5.84	0.0244
	<i>T_b</i>	0.590	10.96	0.0032
Weighted	Log HLS	0.616	3.83	0.0630
	Log mass	-0.521	3.99	0.0582
	<i>T_b</i>	0.617	12.61	0.0018
Independent contrasts multiple regression				
<i>n</i> = 27 species (26 contrasts)				
Unweighted	Log HLS	0.944	10.41	0.0037
	Log mass	-0.457	3.19	0.0873
	<i>T_b</i>	0.163	0.58	0.4545
Weighted	Log HLS	0.966	10.88	0.0031
	Log mass	-0.465	3.29	0.0828
	<i>T_b</i>	0.147	0.47	0.4979
<i>n</i> = 26 species (25 contrasts)				
Unweighted	Log HLS	0.825	5.09	0.0344
	Log mass	-0.374	0.98	0.3327
	<i>T_b</i>	0.138	0.34	0.5684
Weighted	Log HLS	0.854	5.49	0.0286
	Log mass	-0.394	1.11	0.3046
	<i>T_b</i>	0.130	0.30	0.5882

**Fig. 4.** Apparent relationship between sprint speed and body temperature, which is not statistically significant by independent contrasts (see text). Lines are conventional least-squares linear regressions.

For conventional regression analyses, body temperature was the best predictor of speed (results are presented in Table 4 for both weighted and unweighted analyses). For independent contrasts regressions, however, hindlimb span was the only significant predictor of speed. The main difference between the standard and independent contrasts multiple regressions was the loss of body temperature as a significant predictor of sprint speed. Figure 4 shows the raw relationship between speed and body temperature: across all 27 species measured, it is quite strong. Within each clade, however, the relationship is weaker. The independent contrasts estimate more closely reflects the within-clade relationships; thus, when phylogeny is taken into account, the strong overall relationship between speed and temperature (Fig. 4) appropriately diminishes.

Because body temperature, hindlimb span, and body mass are strongly intercorrelated, multicollinearity may be a problem. Therefore, we regressed speed contrasts, body temperature contrasts, and log hindlimb span contrasts on log mass contrasts and computed residuals. The potential problems of multicollinearity are further suggested because the sign of the partial regression

Table 5. Multiple regressions to predict sprint speed, using residuals from regressions on log body mass. Weighted regressions are weighted by (sample size)^{0.5} for each species

Independent contrasts regression	Variable (<i>r</i> between vars)	Standardized partial regression coefficient	<i>F</i>	<i>P</i>
<i>n</i> = 27 species (26 contrasts)				
Unweighted	Residual log HLS	0.581	10.86	0.0030
	Residual <i>T</i> _b (0.491)	0.137	0.60	0.4447
Weighted	Residual log HLS	0.592	11.35	0.0025
	Residual <i>T</i> _b (0.489)	0.124	0.50	0.4885
<i>n</i> = 26 species (25 contrasts)				
Unweighted	Residual log HLS	0.432	5.32	0.0305
	Residual <i>T</i> _b (0.168)	0.111	0.35	0.5596
Weighted	Residual log HLS	0.446	5.74	0.0251
	Residual <i>T</i> _b (0.175)	0.105	0.32	0.5796

coefficient for mass is negative for the independent contrasts multiple regression (Table 4), but becomes positive in the regression using residuals (Table 5). For these residuals, only hindlimb span was a significant predictor of sprint speed (Fig. 5, Table 5).

DISCUSSION

The purpose of our study was to measure maximal sprint speeds of lizards on a high-speed treadmill and to determine if speed correlates with leg length. Measurement of maximal sprint running speed was reproducible between days, and the values reported in Table 1 indicate that the H.S.T. method of sprint-speed estimation is as repeatable as reported previously for studies that used photocell-timed racetracks. However, as

shown in Table 6, and discussed below, the H.S.T. often yields higher estimates of maximal speed.

We found that hindlimb span was a significant predictor of maximal sprint speed. This finding is consistent with other published interspecific comparisons of lizards. Losos (1990*b*) found within one genus (*Anolis*) that hindlimb length was positively correlated with sprint speed. Miles (1994*a*) found, for members of the *Sceloporus* group, that species with longer limbs were faster than short-limbed species. Bauwens *et al.* (1995) found that hindlimb length was positively correlated with sprint speed within European lacertids. Here, using a different measurement technique, we find that the correlation between speed and hindlimb size holds across a wide diversity of lizards. Thus, the positive relationship between speed and relative hindlimb length now seems well established for lizards, both within and among phylogenetic lineages (and see Garland & Janis, 1993, on mammals). Future studies should, therefore, attempt to determine what other morphological, physiological or mechanical (e.g. Farley & Ko, 1997) factors may account for additional variation in sprint speed. Zani (1996), for example, found that sprint speed correlated positively with the length of the caudifemoralis longus muscle across an even broader phylogenetic range of lizard species than studied here. Our preliminary data suggest that speed may be related to muscle fibre type composition (Bonine, Garland & Gleeson, 1997; see also Gleeson & Harrison, 1988).

In empirical studies, conventional and phylogenetically based statistical analyses sometimes yield rather different results (e.g. Harvey & Pagel, 1991; Garland *et al.*, 1992, 1999), although estimates of correlations between the two methods are generally consistent across many studies (Ricklefs & Starck, 1996; Price, 1997). Examination of our results with conventional statistics and independent contrasts illustrates both possibilities. Considering all species, the bivariate correlation between sprint speed and log body mass (Fig. 2) is not statistically significant unless phylogeny is taken into

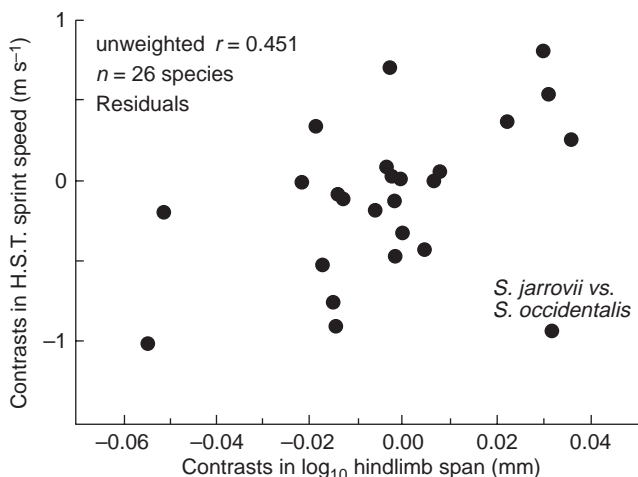


Fig. 5. Significant positive relationship between contrasts in species' mean sprint speed and log₁₀ hindlimb span. If the contrast including *Sceloporus jarrovii* is excluded (extreme lower right), the correlation increases to 0.633 (see Discussion). Both variables were positivized on body mass before computation of residuals.

Table 6. Comparison of maximal sprint running speeds (mean values for species, m s^{-1})

Species	This study	Previous values
<i>Uta stansburiana</i>	2.55	1.85 ^a
<i>Urosaurus graciosus</i>	2.81	1.77 ^a
<i>Urosaurus ornatus</i>	2.42	2.11 ^a
<i>Sceloporus clarkii</i>	3.00	1.89 ^a
<i>Sceloporus undulatus</i>	2.51	1.65 ^b
<i>Sceloporus occidentalis</i>	2.88	3.23 ^c
<i>Sceloporus jarrovi</i>	1.62	1.73 ^a
<i>Uma notata</i>	3.49	1.38 ^d
<i>Uma scoparia</i>	3.20	2.79 ^e
<i>Cophosaurus texanus</i>	4.57	1.40 ^d
<i>Callisaurus draconoides</i>	5.72	3.54 ^e , 3.53 ^f
<i>Phrynosoma cornutum</i>	2.18	1.06 ^f
<i>Gambelia wislizenii</i>	4.08	3.30 ^g
<i>Crotaphytus collaris</i>	4.62	2.09 ^{f*} , 7.15 ^h
<i>Cnemidophorus tigris punctilinealis</i>	5.63	2.81 ⁱ
<i>Cnemidophorus tigris marmoratus</i>	6.17	2.67 ⁱ
<i>Cnemidophorus uniparens</i>	3.58	2.60 ⁱ
<i>Cnemidophorus exsanguis</i>	4.03	3.01 ⁱ
<i>Cnemidophorus gularis</i>	5.06	3.02 ⁱ

^a Miles, 1994a, used sand on 2 m track.

^b Crowley, 1985, used 2 m track, values are for 0.25 m, rubberized surface.

^c Marsh & Bennett, 1986, used 3 m track with movie camera and stopwatch.

^d Punzo, 1982, used 8 m wooden runway, timed over 3 m with stopwatch.

^e Jayne & Ellis, 1998; Irschick & Jayne, 1998, used sand and video on 1.5 m of 3 m track.

^f Zani, 1996, used 1.00–2.25 m hardwood track, * *Crotaphytus bicinctores*.

^g Crowley & Pietruszka, 1983, used 1.0 m section of 2 m racetrack, fine gravel and sand.

^h Snyder, 1962 for *C. collaris*, reports a max. of 7.15 m s^{-1} (substantially greater than previously reported for lizards measured on racetracks) using film speed and distance travelled over at least a 3-foot section of sand-covered track; our two fastest individuals were 5.40 m s^{-1} .

ⁱ Cullum, 1997, used a 3 m, photocell-timed (last 2 m) track with rubberized substrate.

account (Table 3). An opposite example is provided by the relationship between speed and temperature (Fig. 4), wherein the strength of the relationship diminishes with phylogenetic analyses (Tables 3 & 4). Bauwens *et al.* (1995) report a marginally significant positive relationship between speed and optimal body temperature for independent contrasts analyses of 13 species of lacertid lizards.

Maximal sprint running speeds reported here are higher than values reported previously for 16 of 19 species (Table 6). All of these previous studies used racetracks, with timing performed by photocells, filming or hand-held stopwatches. Several factors may account for these differences. For example, populations may differ in sprinting abilities (e.g. Sinervo & Huey, 1990; Sinervo, Hedges & Adolph, 1991; Sinervo & Losos, 1991; Miles, 1994b), but these seem unlikely to account for the consistency or the magnitude of some of the differences reported in Table 6. Second, some of the

racetrack studies used sand, which may reduce speeds (Carothers, 1986). Third, lizards may be unable to reach top speeds in short tracks. Jayne & Ellis (1998) found that *Uma scoparia* (one of the species included in our study) increased stride length for the first 10–15 strides (acceleration) during sprinting. They reported that mean stride length was 21.9 cm (range 4.7–39.8) and that many lizards in the field did not reach maximal stride length for 5 m or more. Most of the studies reported in Table 6 used short racetracks. Fourth, lizards, especially some of the faster species, may be behaviourally inhibited from obtaining maximal speeds in relatively short racetracks (Jayne & Ellis, 1998). In future studies, we will compare directly the two techniques by measuring the speed of each individual on both the H.S.T. and in a long photocell-timed racetrack.

The phylogenetically independent contrast which includes *Sceloporus jarrovi* is a noticeable outlier (Fig. 5). It is our belief, given the sprint speeds reported here and by Miles (1994a; see Table 6), that *S. jarrovi* may not have sprinted to its maximum ability in either study. If this is true, then the relationship between hindlimb span and speed may be more accurately represented by excluding this species. To recalculate the appropriate correlation for the contrast residuals without *S. jarrovi* in Fig. 5, this species would need to be deleted, the phylogeny redrawn, and all of the contrasts recomputed. However, as a rough approximation of the correlation without *S. jarrovi*, we removed that one contrast and *r* increased from 0.451 to 0.633. This is more similar to the value of 0.740 from Losos (1990a, as reported in Garland & Adolph, 1994, bottom right panel of their Fig. 3) and to the standardized partial regression coefficients reported in Fig. 3 of Bauwens *et al.* (1995).

The speed reported by Snyder (1962) for *Crotaphytus collaris* is substantially greater than reported here or by Zani (1996). However, Snyder's methods are unclear: he reported sprint speeds calculated from film footage discussed in a paper a decade earlier (Snyder, 1952) and did not distinguish between maximal or mean speed estimates. Our fastest two individual *C. collaris* attained speeds of 5.4 m s^{-1} on the H.S.T., still slower than the speed of 7.2 m s^{-1} reported by Snyder (1962).

Acknowledgements

We thank Wade C. Sherbrooke and the staff and volunteers at the AMNH Southwestern Research Station for assistance and support; Cindy Hayford for field assistance in Arizona; Tony Ives, Bill Karasov, John Swallow, Jennifer Klug, Suzanne Peyer, Dawn Dittman, Peter Midford, and Tom O'Keefe for helpful comments. Collecting permits were issued by the Arizona Department of Game and Fish and the New Mexico Department of Game and Fish to KEB. This project was supported in part by a Wisconsin Alumni Research Foundation Fellowship, a SWRS Student Support Grant, and a U.S. National Science Foundation Graduate Student Fellowship to KEB; and by NSF grant IBN-9723758 to TG.

REFERENCES

- Arnold, S. J. (1983). Morphology, performance and fitness. *Am. Zool.* **23**: 347–361.
- Autumn, K., Farley, C. T., Emshwiller, M. & Full, R. J. (1997). Low cost of locomotion in the banded gecko: a test of the nocturnality hypothesis. *Physiol. Zool.* **70**: 660–669.
- Bauwens, D., Garland, T., Jr, Castilla, A. M. & Van Damme, R. (1995). Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* **49**: 848–863.
- Belkin, D. A. (1961). The running speeds of the lizards *Dipsosaurus dorsalis* and *Callisaurus draconoides*. *Copeia* **1961**: 223–224.
- Bennett, A. F. (1980). The thermal dependence of lizard behaviour. *Anim. Behav.* **28**: 752–762.
- Bonine, K. E., Garland, T., Jr & Gleeson, T. T. (1997). Muscle fiber-type variation and locomotion in phrynosomatid lizards. *Am. Zool.* **37**: 104A.
- Brooks, D. R. & McLennan, D. A. (1991). *Phylogeny, ecology, and behavior. A research program in comparative biology*. Chicago: University of Chicago Press.
- Bulova, S. J. (1994). Ecological correlates of population and individual variation in antipredator behavior of two species of desert lizards. *Copeia* **1994**: 980–992.
- Carothers, J. H. (1986). An experimental confirmation of morphological adaptation: toe fringes in the sand-dwelling lizard *Uma scoparia*. *Evolution* **40**: 871–874.
- Changchien, L.-L. (1996). *A phylogenetic study of sceloporine lizards and their relationships with other iguanid lizards based on DNA/DNA hybridization*. Unpublished PhD dissertation, University of Wisconsin, Madison.
- Clobert, J., Garland, T., Jr & Barbault, R. (1998). The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. *J. Evol. Biol.* **11**: 329–364.
- Conant, R. & Collins, J. T. (1991). *A field guide to reptiles and amphibians: eastern and central North America*. 3rd edn. Boston: Houghton Mifflin.
- Crowley, S. R. (1985). Insensitivity to desiccation of sprint running performance in the lizard, *Sceloporus undulatus*. *J. Herpetol.* **19**: 171–174.
- Crowley, S. R. & Pietruszka, R. D. (1983). Aggressiveness and vocalization in the leopard lizard (*Gambelia wislizenii*): the influence of temperature. *Anim. Behav.* **31**: 1055–1060.
- Cullum, A. (1997). Comparisons of physiological performance in sexual and asexual whiptail lizards (genus *Cnemidophorus*): implications for the role of heterozygosity. *Am. Nat.* **150**: 24–47.
- de Queiroz, K. (1992). Phylogenetic relationships and rates of allozyme evolution among lineages of sceloporine sand lizards. *Biol. J. Linn. Soc.* **45**: 333–362.
- Dessauer, H. C. & Cole, C. J. (1989). Diversity between and within nominal forms of unisexual teiid lizards. In *Evolution and ecology of unisexual vertebrates*: 49–71. Dawley, R. M. & Bogert, J. P. (Eds). Albany: New York State Museum.
- Dial, B. E. (1986). Tail display in two species of iguanid lizards: a test of the 'predator signal' hypothesis. *Am. Nat.* **127**: 103–111.
- Díaz-Uriarte, R. & Garland, T., Jr (1998). Effects of branch length errors on the performance of phylogenetically independent contrasts. *Syst. Biol.* **47**: 654–672.
- Djawdan, M. & Garland, T., Jr (1988). Maximal running speeds of bipedal and quadrupedal rodents. *J. Mammal.* **69**: 765–772.
- Dohm, M. R., Garland, T., Jr, Cole, C. J. & Townsend, C. R. (1998). Physiological variation and allometry in western whiptail lizards (*Cnemidophorus tigris*) from a transect across a persistent hybrid zone. *Copeia* **1998**: 1–13.
- Farley, C. T. & Ko, T. C. (1997). External mechanical power output in lizard locomotion. *J. exp. Biol.* **200**: 2177–2188.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.
- Garland, T., Jr. (1985). Ontogenetic and individual variation in size, shape, and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool. (Lond.)* **207**: 425–439.
- Garland, T., Jr (1994). Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In *Lizard ecology: historical and experimental perspectives*: 237–259. Vitt, L. J. & Pianka, E. R. (Eds). Princeton, NJ: Princeton University Press.
- Garland, T., Jr & Adolph, S. C. (1994). Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiol. Zool.* **67**: 797–828.
- Garland, T., Jr & Carter, P. A. (1994). Evolutionary physiology. *Ann. Rev. Physiol.* **56**: 579–621.
- Garland, T., Jr, Hankins, E. & Huey, R. B. (1990). Locomotor capacity and social dominance in male lizards. *Funct. Ecol.* **4**: 243–250.
- Garland, T., Jr, Harvey, P. H. & Ives, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**: 18–32.
- Garland, T., Jr & Janis, C. M. (1993). Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? *J. Zool. (Lond.)* **229**: 133–151.
- Garland, T., Jr & Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological morphology: integrative organismal biology*: 240–302. Wainwright, P. C. & Reilly, S. M. (Eds). Chicago: University of Chicago Press.
- Garland, T., Jr, Midford, P. E. & Ives, A. R. (1999). An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *Am. Zool.*
- Gleeson, T. T. & Harrison, J. M. (1988). Muscle composition and its relation to sprint running in the lizard *Dipsosaurus dorsalis*. *Am. J. Physiol.* **255**: R470–R477.
- Grafen, A. (1989). The phylogenetic regression. *Phil. Trans. Roy. Soc. Lond. B* **326**: 119–157.
- Harris, M. A. & Steudel, K. (1997). Ecological correlates of hind-limb length in the Carnivora. *J. Zool. (Lond.)* **241**: 381–408.
- Harvey, P. H. & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Howland, J. M. (1992). Life history of *Cophosaurus texanus* (Sauria: Iguanidae): environmental correlates and interpopulational variation. *Copeia* **1992**: 82–93.
- Huey, R. B. (1982). Phylogenetic and ontogenetic determinants of sprint speed performance in some diurnal Kalahari lizards. *Koedoe* **25**: 43–48.
- Huey, R. B., Dunham, A. E., Overall, K. L. & Newman, R. A. (1990). Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiol. Zool.* **63**: 845–872.
- Huey, R. B. & Hertz, P. E. (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. & Hertz, P. E. (1984). Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). *J. exp. Biol.* **110**: 113–123.
- Huey, R. B., Schneider, W., Erie, G. L. & Stevenson, R. D. (1981). A field-portable racetrack and timer for measuring acceleration and speed of small cursorial animals. *Experientia* **37**: 1356–1357.
- Irschick, D. J. & Jayne, B. C. (1998). Effects of incline on speed, acceleration, body posture, and hindlimb kinematics in two species of lizard *Callisaurus draconoides* and *Uma scoparia*. *J. exp. Biol.* **201**: 273–287.
- Jayne, B. C. & Bennett, A. F. (1990). Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* **44**: 1204–1229.

- Jayne, B. C. & Ellis, R. V. (1998). How inclines affect the escape behaviour of a dune-dwelling lizard, *Uma scoparia*. *Anim. Behav.* **55**: 1115–1130.
- Losos, J. B. (1990a). Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol. Monogr.* **60**: 369–388.
- Losos, J. B. (1990b). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**: 1189–1203.
- Marsh, R. L. (1988). Ontogenesis of contractile properties of skeletal muscle and sprint performance in the lizard *Dipsosaurus dorsalis*. *J. exp. Biol.* **137**: 119–139.
- Marsh, R. L. & Bennett, A. F. (1986). Thermal dependence of sprint performance of the lizard *Sceloporus occidentalis*. *J. exp. Biol.* **126**: 79–87.
- Martins, E. P. & T. F. Hansen. (1996). The statistical analysis of interspecific data: a review and evaluation of comparative methods. In *Phylogenies and the comparative method in animal behavior*: 22–75. Martins, E. P. (Ed.). Oxford: Oxford University Press.
- Middendorff, G. A., III & Sherbrooke, W. C. (1992). Canid elicitation of blood-squirting in a horned lizard (*Phrynosoma cornutum*). *Copeia* **1992**: 519–527.
- Miles, D. B. (1994a). Covariation between morphology and locomotor performance in sceloporine lizards. In *Lizard ecology: historical and experimental perspectives*: 207–235. Vitt, L. J. & Pianka, E. R. (Eds). Princeton, NJ: Princeton University Press.
- Miles, D. B. (1994b). Population differentiation in locomotor performance and the potential response of a terrestrial organism to global environmental change. *Am. Zool.* **34**: 422–436.
- Miles, D. B., Fitzgerald, L. A. & Snell, H. L. (1995). Morphological correlates of locomotor performance in hatchling *Amblyrhynchus cristatus*. *Oecologia* **103**: 261–264.
- Miles, D. B. & Smith, R. G. (1987). A microcomputer-based timer and data acquisition device for measuring sprint speed and acceleration in cursorial animals. *Funct. Ecol.* **1**: 281–286.
- Montanucci, R. R. (1987). A phylogenetic study of the horned lizards, genus *Phrynosoma*, based on skeletal and external morphology. *Contributions in Science, No. 390, Nat. Hist. Mus. Los Angeles County*.
- Norris, K. S. (1958). The evolution and systematics of the iguanid genus *Uma* and its relation to the evolution of other North American desert reptiles. *Bull. Am. Mus. Nat. Hist.* **114**: 251–326.
- Pagel, M. D. (1992). A method for the analysis of comparative data. *J. theor. Biol.* **156**: 431–442.
- Pianka, E. R. (1986). *Ecology and natural history of desert lizards*. Princeton, NJ: Princeton University Press.
- Pietruszka, R. D., Wiens, J. A. & Pietruszka, C. J. (1981). Leopard lizard predation on *Perognathus*. *J. Herpetol.* **15**: 249–250.
- Price, T. (1997). Correlated evolution and independent contrasts. *Phil. Trans. Roy. Soc. Lond. B* **352**: 519–529.
- Punzo, F. (1982). Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. *J. Herpetol.* **16**: 329–331.
- Purvis, A. & Garland, T., Jr. (1993). Polytomies in comparative analyses of continuous characters. *Syst. Biol.* **42**: 569–575.
- Reeder, T. W. & Wiens, J. J. (1996). Evolution of the lizard family Phrynosomatidae as inferred from diverse types of data. *Herpetol. Monogr.* **10**: 43–84.
- Ricklefs, R. E. & Starck, J. M. (1996). Applications of phylogenetically independent contrasts: a mixed progress report. *Oikos* **77**: 167–172.
- Sherbrooke, W. C. (1981). *Horned lizards: unique reptiles of western North America*. Globe, Arizona: Southwest Parks and Monuments Association.
- Sinervo, B., Hedges, R. & Adolph, S. C. (1991). Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variation among populations. *J. exp. Biol.* **155**: 323–336.
- Sinervo, B. & Huey, R. B. (1990). Allometric engineering: an experimental test of the causes of interpopulational differences in performance. *Science* **248**: 1106–1109.
- Sinervo, B. & Losos, J. B. (1991). Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. *Ecology* **72**: 1225–1233.
- Snyder, R. C. (1952). Quadrupedal and bipedal locomotion of lizards. *Copeia* **1952**: 64–70.
- Snyder, R. C. (1962). Adaptations for bipedal locomotion of lizards. *Am. Zool.* **2**: 191–203.
- Sorci, G., Swallow, J. G., Garland, T., Jr. & Clobert, J. (1995). Quantitative genetics of locomotor speed and endurance in the lizard *Lacerta vivipara*. *Physiol. Zool.* **68**: 698–720.
- Stebbins, R. C. (1985). *A field guide to western reptiles and amphibians*. 2nd edn. Boston: Houghton Mifflin.
- van Berkum, F. H., Huey, R. B., Tsuji, J. S. & Garland, T., Jr (1989). Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird & Girard). *Funct. Ecol.* **3**: 97–105.
- Wiens, J. J. (1993). Phylogenetic relationships of phrynosomatid lizards and monophyly of the *Sceloporus* group. *Copeia* **1993**: 287–299.
- Wiens, J. J. & Reeder, T. W. (1997). Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. *Herpetol. Monogr.* **11**: 1–101.
- Wolf, C. M., Garland, T., Jr & Griffith, B. (1998). Avian and mammalian translocations: reanalysis with phylogenetically independent contrasts. *Biol. Conserv.* **86**: 243–255.
- Zani, P. A. (1996). Patterns of caudal-autotomy evolution in lizards. *J. Zool. (Lond.)* **240**: 201–220.