SPEED AND STAMINA TRADE-OFF IN LACERTID LIZARDS

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Abstract.—Morphological and physiological considerations suggest that sprinting ability and endurance capacity put conflicting demands on the design of an animal's locomotor apparatus and therefore cannot be maximized simultaneously. To test this hypothesis, we correlated size-corrected maximal sprint speed and stamina of 12 species of lacertid lizards. Phylogenetically independent contrasts of sprint speed and stamina showed a significant negative relationship, giving support to the idea of an evolutionary trade-off between the two performance measures. To test the hypothesis that the trade-off is mediated by a conflict in morphological requirements, we correlated both performance traits with snout-vent length, size-corrected estimates of body mass and limb length, and relative hindlimb length (the residuals of the relationship between hind- and forelimb length). Fast-running species had hindlimbs that were long compared to their forelimbs. None of the other size or shape variables showed a significant relationship with speed or endurance. We conclude that the evolution of sprint capacity may be constrained by the need for endurance capacity and vice versa, but the design conflict underlying this trade-off has yet to be identified.

Key words.—Ecomorphology, evolutionary trade-off, lizards, locomotion, performance.

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In recent years, students of ecomorphology have abandoned the traditional view that natural selection molds every character in isolation to serve one particular function (Rose and Lauder 1996). Instead, it is now realized that most characters serve multiple functions, and that altering one character will affect performance in all functions. If two (or more) functions pose conflicting demands on the same design trait, then simultaneous optimization becomes impossible and a trade-off will result in a compromise phenotype (Lewontin 1978). Trade-offs constrain the adaptation of individual traits.

The notion of a trade-off seems particularly relevant to the evolution of locomotion because the same design features (e.g., limb dimensions, muscle architecture, fiber types) affect several components of performance (e.g., sprint speed, stamina, maneuverability, climbing capacity), all of which seem ecologically relevant (e.g., Bulova 1994). In addition, physiological and biomechanical theory suggests that the design characteristics required to maximize different performance traits may be hard to reconcile within one phenotype (Bennett 1978; Peterson 1984; Cartmill 1985; Losos 1990; Losos et al. 1993; Garland and Losos 1994; Miles 1994; Alexander 1999). In accordance with this idea, trade-offs have been demonstrated between speed and surefootedness (in lizards: Losos and Sinervo 1989; Sinervo and Losos 1991; Macrini and Irschick 1998), between speed and clinging ability (in lizards: Losos et al. 1993), and between speed and maneuverability (in fish: Webb 1984; Domenici and Blake 1991; Kasapi et al. 1993; in bats: Aldridge and Rautenbach 1987; in tadpoles: Wassersug 1989; Brown and Taylor 1995).

Perhaps because of our familiarity with the obvious differences in body shape between human world-class sprinters and marathoners, the trade-off between maximal speed and endurance may seem the most obvious example of constraints in the evolution of locomotor capacity. The idea is supported by observations on muscle physiology: power athletes tend to have high proportions of fast-twitch muscle fibers, which have rapid contraction rates, but fatigue quickly; endurance

athletes have high proportions of slow-twitch muscle fibers, which are more resistant to fatigue but can only contract relatively slowly (Komi 1984; Esbjörnsson et al. 1993; Rivero et al. 1993). Given that the proportion of fiber types is at least partly under genetic control (Nakamura et al. 1993), a negative correlation between speed and endurance can be expected.

In spite of the apparent logic of the argument, surprisingly little empirical evidence shows a trade-off between speed and stamina. Speed and endurance do show a negative correlation when world-class sprinters and marathoners are compared (Heinrich 1985), but it is unclear whether this result can be extrapolated to more random samples of humans (Garland 1994a). Conclusions from intraspecific studies on other vertebrates are equivocal. Dohm et al. (1996) report a negative genetic correlation between running speed and swimming endurance in laboratory house mice, and Reidy et al. (2000) found evidence for a trade-off between stamina and burst speed in Atlantic cod. However, most other studies found no correlation or a positive correlation between the two performance traits (Bennett 1980; Garland and Else 1987; Garland 1988; Tsuji et al. 1989; Garland et al. 1990; Huey et al. 1990; Jayne and Bennett 1990; Secor et al. 1992; Brodie and Garland 1993; Garland 1994a; Sorci et al. 1995).

Extrapolating to an interspecific scale, a trade-off between speed and stamina should result in a gradient with at one extreme species that can run relatively fast but fatigue easily and species with limited speed capacity but great endurance at the other end. Surprisingly few studies have tested this hypothesis. Garland et al. (1988) found no evidence for a correlation between capacities for maximal sprint running speed and maximal aerobic speed among 18 species of mammals. Huey et al. (1984) showed that of two related species of Kalahari lizards, the one with the higher speed capacity had the lower endurance and vice versa. These differences reflected differences in natural foraging patterns.

In this study, we explore covariation between sprint speed

and stamina of 12 species of lacertid lizards. The family Lacertidae is distributed over much of Eurasia and Africa, and species inhabit a wide range of habitats (e.g., tundra, alpine meadows, heath lands, Mediterranean scrub, tropical forests, deserts). Within these habitats, lacertids occupy a wide range of microhabitats that differ greatly in substrate, openness, and inclination (for details see Vanhooydonck and Van Damme 1999). In spite of their extensive ecological radiation, lacertid lizards have retained the same general body shape (Arnold 1989; Vanhooydonck and Van Damme 1999). For instance, in contrast to some other lizard families, no major adaptations of the locomotor apparatus (e.g., development of toe pads, loss of limbs) have occurred. Also, although quantitative data are mostly missing, most lacertids are highly active animals that move frequently in search of food or mates and use short bouts of fast locomotion to evade predators (Arnold 1987, 1998; Avery et al. 1987). The family of lacertid lizards therefore provides good opportunities to test for the existence of trade-off between stamina and speed.

Materials and Methods

Animals

We collected eight of the 12 species during the summers of 1996–1999 at different sites in Western Europe and the Canary Islands. The four remaining species (*Acanthodactylus pardalis, A. scutellatus, Latastia longicaudata,* and *Takydromus sexlineatus*) were obtained from the pet trade. Only adult individuals were used in this study. We sampled both males and (nongravid) females. With a one-way ANCOVA (snout-vent length [SVL] entered as covariate) for each species separately, we tested whether performance differed between the two sexes (see Cullum 1998). Of the 12 species, males and females differed in sprint speed in *A. pardalis* ($P = 0.03$; males faster than females), whereas endurance differed between males and females in *Podarcis muralis* ($P = 0.03$; males more stamina than females) and *Podarcis sicula* ($P = 0.02$; females more stamina than males). Given the inconsistency of the foregoing differences, we pooled the data for both sexes in subsequent analyses. Number of male and female individuals per species, morphometrics, sprint speed, and endurance are given in Table 1.

We transported all lizards to the laboratory at the University of Antwerp, Belgium. Small species (SVL < 80 mm) were housed in groups of four or five individuals, with species kept apart, in glass terraria (100 x 50 cm) with a sandy substrate. To prevent possible effects of social dominance on performance (John-Alder and Joos 1991; John-Alder et al. 1996), lizards were offered access to many hiding places (flat stones) and to several basking spots (100-W light/bulbs, providing heat and light for 10 h a day). For similar reasons, the larger species (i.e., *Lacerta bilineata* and *Gallotia galloti*) were housed individually in identical terraria. We fed them live crickets dusted with calcium daily. Water was always present.

Morphometrics

We took the following external measurements on each individual to the nearest 0.01 mm, using digital calipers (Mi-

TABLE 1. Species (number of males, number of females), morphometrics, and performance measures of the animals used in this study. Data are means and standard deviations per species.

Species (N)	Snout-vent length (mm)	Body mass (g)	Hindlimb length (mm)	Forelimb length (mm)	Sprint speed (cm/s)	Endurance at 0.22 m/s (s)
Gallotia galloti (6, 9)	98.53 ± 16.24	50.12 ± 25.44	45.39 ± 8.61	30.90 ± 4.85	193.44 ± 51.84	311.38 ± 103.27
Lacerta oxycephala (9, 7)	56.77 ± 2.80	4.78 ± 0.74	24.72 ± 1.89	17.22 ± 1.66	201.57 ± 34.47	109.60 ± 39.34
Lacerta bedriagae (10, 5)	71.73 ± 6.11	9.56 ± 2.60	31.16 ± 3.21	21.61 ± 2.03	178.66 ± 59.64	437.60 ± 151.77
Lacerta vivipara (8, 12)	46.41 ± 3.18	3.84 ± 0.58	16.77 ± 1.63	12.76 ± 0.91	86.56 ± 23.46	370.33 ± 241.27
Podarcis sicula (10, 5)	68.23 ± 2.29	7.02 ± 1.10	30.89 ± 2.66	19.23 ± 1.37	166.91 ± 37.11	266.07 ± 94.89
Podarcis muralis (10, 11)	52.08 ± 5.24	3.17 ± 1.70	19.92 ± 3.15	13.39 ± 2.15	213.64 ± 97.13	184.9 ± 57.04
Podarcis tiliguerta (10, 4)	56.87 ± 2.55	4.77 ± 0.61	26.41 ± 1.64	16.89 ± 1.21	154.59 ± 47.02	194.79 ± 67.03
Lacerta bilineata (4, 2)	92.69 ± 11.16	28.44 ± 6.00	40.65 ± 2.40	26.35 ± 0.67	267.95 ± 55.95	276.60 ± 144.22
Takydromus sexlineatus (6, 3)	51.79 ± 2.61	2.79 ± 0.48	17.94 ± 1.05	14.45 ± 1.16	132.81 ± 38.81	93.56 ± 35.00
Acanthodactylus pardalis (9, 3)	59.22 ± 2.52	6.73 ± 0.84	27.77 ± 2.12	17.29 ± 1.01	261.67 ± 67.40	87.83 ± 19.24
Acanthodactylus scutellatus (2, 2)	67.70 ± 8.11	8.09 ± 4.02	33.96 ± 7.27	20.19 ± 4.08	279.51 ± 25.59	74.22 ± 27.79
Latastia longicaudata (4, 5)	73.83 ± 5.77	8.61 ± 2.43	34.55 ± 2.56	20.54 ± 1.73	334.45 ± 52.14	51.71 ± 18.62

tutoyo, Ltd., Telford, U.K., CD-15DC): SVL (measured from the tip of the snout to the posterior edge of the anal scale) and length of thigh (from the hip joint to the knee joint), calf (from knee joint to ankle), midfoot (from ankle to the base of the third toe), upper arm (from shoulder joint to elbow), lower arm (from elbow to wrist), and midhand (from the wrist to the base of the third finger). All measurements were done on live, unanesthetized animals. The limb measurements were always taken on the left limbs. All animals were weighed on an electronic balance to the nearest 0.01 g (A & D Instruments, Ltd., Abingdon, U.K. FX-3200). The sum of thigh, calf, and mid/foot length (hereafter referred to as total hindlimb length) and the sum of upper arm, lower arm, and mid/hand length (hereafter referred to as total forelimb length) were used in subsequent analyses. Thus, our measurement of limb length does not correspond to the measure of limb span (e.g., Bonine and Garland 1999), which takes variation in width of the pelvis into account.

We calculated the means per species of all morphological variables and logarithmically ($\log_{10}$) transformed them before statistical analyses.

Performance Testing

Sprint speed was quantified on a 2.5-m long racetrack with a cork substrate. The lizards were chased down the track toward a black cloth sack. Eight pairs of photocells, placed at 25-cm intervals in the middle part of the track, registered when a lizard passed. The elapsed time between passing two subsequent cells was stored in the computer and sprint speed over each interval was calculated. We tested each animal five times. Between two trials, lizards were allowed to recover for at least 1 h. Sprint speed was not consistently highest in the first trial, so a resting period of 1 h seems sufficient in these lizards. As an estimate of maximal sprint performance, we used the highest speed over any 25-cm interval. Following procedures outlined in van Berkum and Tsuji (1987), we eliminated bad-quality trials. This was seldom necessary, because most individuals readily ran down the track or did so after mild stimulation (a gentle tap on the base of the tail).

We measured endurance as the running time until exhaustion on a treadmill moving at a low and constant speed (0.22 m/s). This speed was imposed by the mechanic properties of the treadmill used, but it is not atypical for undisturbed lacertid lizards (see Huey and Pianka 1981; Avery et al. 1987). After a short burst at the beginning of the experiment (typically over the full length of the moving belt), most individuals quieted down and moved at speeds near the speed of the treadmill. A mild stimulation sufficed to keep them going. On rare occasions, lizards engaged in frantic activity for a longer period of time. In these cases, the experiment was stopped and the animals given another trial after a 1-h period of rest (see also Garland 1994b).

Animals were considered exhausted when they did not show a righting response after being placed on their backs (Huey et al. 1990). Each lizard was tested three times over two days. As an estimate of maximal endurance, we used the longest running time over the three trials.

Prior to experimentation and between trials, we placed the animals for at least 1h in an incubator set at the different species selected body temperatures (32°C for *Lacerta vivipara*; 35°C for *G. galloti, Lacerta bedriagae, Lacerta oxycephala, L. bilineata, P. muralis, P. sicula, Podarcis tiliguerta,* and *T. sexlineatus*; 38°C for *A. pardalis, A. scutellatus,* and *L. longicaudata*). These temperatures are within the range of field active temperatures, see review in Castilla et al. (1999). Sprint speed and endurance were measured on different days. All performance tests were carried out by the same person (B. Vanhooydonck) and within weeks after the animals were captured.

We calculated the means per species of sprint speed and endurance, and logarithmically ($\log_{10}$) transformed them before statistical analyses.

Nonphylogenetic Analyses

The logarithmically transformed means per species of mass, total hindlimb length, total forelimb length, sprint speed, and endurance were regressed against the logarithmically transformed means per species of SVL and residuals were calculated. Hereafter, we will refer to these variables as residual mass, residual total hindlimb length, residual total forelimb length, residual sprint speed, and residual endurance, respectively.

Additionally, we regressed the logarithmically transformed means per species of total hindlimb length against the logarithmically transformed means per species of total forelimb length and calculated the residuals. Hereafter, we will refer to this variable as relative hindlimb length.

To test for a correlation between both performance measures, we performed a Pearson product moment correlation on residual sprint speed and residual endurance.

We performed a backward stepwise multiple regression with one of the performance measures (i.e., residual sprint speed or residual endurance) as dependent variable and the four morphological traits (residual mass, residual total hindlimb length, residual total forelimb length, and relative hindlimb length) as independent variables to test whether differences in performance can be explained by differences in morphology.

Phylogenetic Analyses

Because species share parts of their evolutionary history, they cannot be considered independent datapoints (Felsenstein 1985, 1988; Harvey and Pagel 1991; Garland et al. 1993). Independence of datapoints, however, is one of the basic assumptions in traditional statistical analyses. In recent years, various methods and computer programs have been developed to take phylogenetic relationships into account in statistical analyses (see Harvey and Pagel 1991; Garland et al. 1993; Losos and Miles 1994). We used the independent contrast approach (Felsenstein 1985, 1988) in the present study.

We calculated the independent contrasts of the logarithmically transformed means per species of SVL, mass, total hindlimb length, total forelimb length, sprint speed, and endurance using the PDTREE program (Garland et al. 1999). Subsequently, we regressed the contrasts (of the logarithmically transformed means per species) of mass, total hindlimb length, total forelimb length, sprint speed, and endur-

ance against the contrasts (of the logarithmically transformed means per species) of SVL and calculated residuals. Hereafter, we will refer to these variables as residual contrast of mass, residual contrast of total hindlimb length, residual contrast of total forelimb length, residual contrast of sprint speed, and residual contrast of endurance, respectively.

Also, we regressed the contrasts (of the logarithmically transformed means per species) of total hindlimb length against the contrasts (of the logarithmically transformed means per species) of total forelimb length and calculated the residuals. Hereafter, we will refer to this variable as relative contrast of hindlimb length.

The regressions on which the calculations of the residuals were based were forced through the origin (see Garland et al. 1992). To test for a correlation between the contrasts of both performance measures, we performed a Pearson product moment correlation on the residual contrasts of sprint speed and the residual contrasts of endurance through the origin using the PDTREE program (Garland et al. 1999).

We performed backward stepwise multiple regressions through the origin with the performance measures (i.e., residual contrasts of sprint speed or residual contrasts of endurance) as dependent variable and the morphological variables (i.e., residual contrasts of mass, residual contrasts of total hindlimb length, residual contrasts of total forelimb length, relative contrasts of hindlimb length) as independent variables. The *P*-value to remove a variable was set to 0.10.

The independent contrast method requires information on the topology and branch lengths of the phylogenetic tree. The phylogeny of the Lacertidae is incompletely resolved, and we had to use a combination of results from mitochondrial DNA (Harris et al. 1998; Harris and Arnold 1999) and morphological studies (Arnold 1983, 1989, 1998) to compile a tree that is the best approximation at the moment (Fig. 1). Some unresolved polytomies remain. However, all attempts of phylogeny reconstruction in lacertids, even the most recent ones using molecular techniques, have been unable to resolve these relationships and the polytomies might in fact represent explosive speciation events (Arnold 1989; Harris et al. 1998; Harris and Arnold 1999; Fu 2000). Therefore, we considered the unresolved nodes as hard polytomies (see Purvis and Garland 1993). Because few data are available on the divergence times within lacertids, we set all branch lengths to unity. It has been shown that the actual length of the branches does not usually have substantial effects on the results of phylogenetic analyses (Martins and Garland 1991; Walton 1993; Irschick et al. 1996; Díaz-Uriarte and Garland 1998). Moreover, checks of branch lengths with the PDTREE program did not show any significant correlation between the absolute values of the standardized contrasts and their standard deviations (Garland et al. 1992).

RESULTS

Nonphylogenetic Analyses

Residual sprint speed correlated negatively with residual endurance in the 12 species ($r = -0.79$, $t_{10} = -4.02$, $P = 0.002$; Fig. 2A). Species with relative high sprint capacities had the lowest endurance and vice versa.

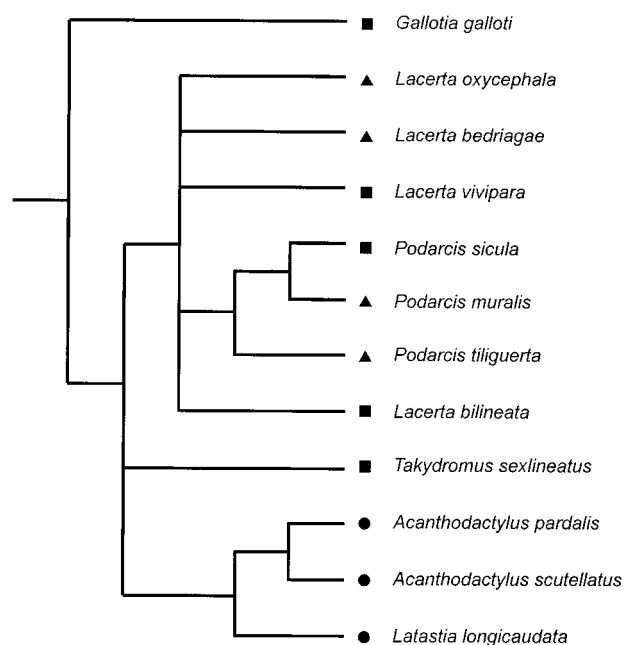Backward stepwise multiple regression with residual sprint

Figure 1.

FIG. 1. Hypothesized phylogenetic relationships among the 12 lacertid lizard species included in this study. The phylogeny is incompletely resolved and this tree should be considered a currently best approximation. However, polytomies were treated as hard for purposes of analyses with phylogenetically independent contrasts. Symbols refer to habitat use, as stated in the literature (see Arnold 1998; Vanhooydonck and Van Damme 1999): ●, ground-dwelling in open habitats; ■, ground-dwelling in vegetated habitats; ▲, saxicolous.

speed as dependent variable resulted in a significant model that included residual total hindlimb length and residual total forelimb length ($r = 0.72$, $F_{2,9} = 4.87$, $P = 0.037$; partial correlations: $r = 0.71$, $t_{10} = 3.00$, $P = 0.015$ and $r = -0.57$, $t_{10} = -2.06$, $P = 0.07$, respectively). Thus, species with long hindlimbs and short forelimbs, both relative to their SVL, are the fastest sprinters. Residual body mass and relative hindlimb length were not retained in the model (partial correlations: all $P > 0.35$). In bivariate analyses, residual total hindlimb length tends to be positively correlated with residual sprint speed ($r = 0.54$, $t_{11} = 2.01$, $P = 0.07$; Fig. 3A), whereas residual total forelimb length is not correlated with residual sprint speed ($r = -0.20$, $t_{11} = 0.63$, $P = 0.54$; Fig. 3B).

Backward stepwise multiple regression with residual endurance as dependent variable did not result in a significant model ($r = 0.58$, $F_{4,7} = 0.90$, $P = 0.51$). Differences in residual endurance cannot be adequately explained by any of the morphological variables (partial correlations: all $P > 0.12$).

Phylogenetic Analyses

The residual contrasts of sprint speed and the residual contrasts of endurance correlated negatively ($r = -0.75$, $t_{10} = -3.59$, $P = 0.005$; Fig. 2B).

Backward stepwise multiple regression with residual contrasts of sprint speed as dependent variable resulted in a model that included the residual contrasts of hindlimb length and
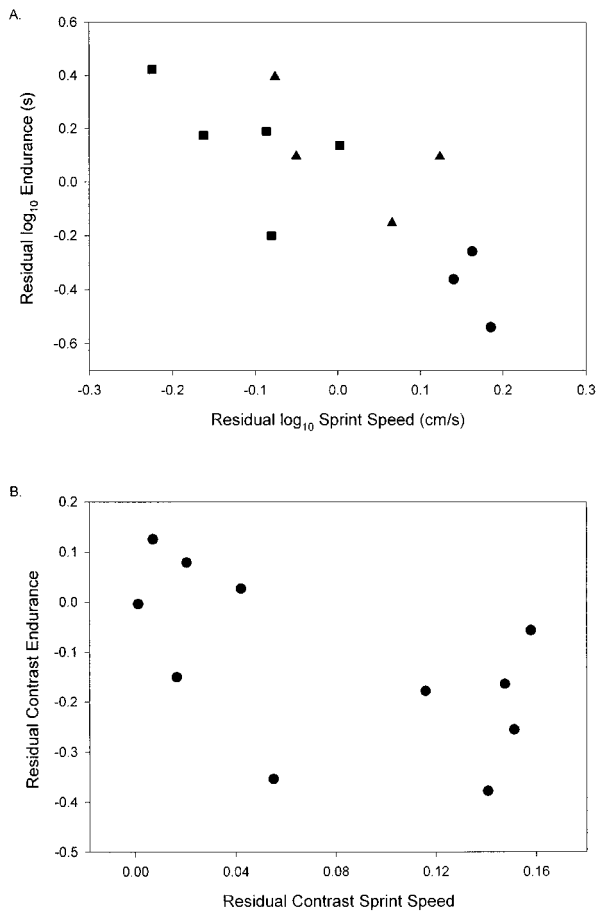
Figure 2.

FIG. 2. The negative correlation between sprint speed and endurance for the 12 species: (A) residuals of the logarithmically transformed means per species of sprint speed and endurance ($r = -0.79$); (B) residuals of the phylogenetic contrasts of the logarithmically transformed means per species of sprint speed and endurance (r through origin $= -0.75$). The symbols in (A) refer to habitat use ($\bullet$, ground-dwelling in open habitats; $\blacksquare$, ground-dwelling in vegetated habitats; $\blacktriangle$, saxicolous). The residual contrasts of sprint speed in (B) are positivized (see Garland et al. 1992).

residual contrasts of forelimb length, but that was not significant ($r = 0.59$, $F_{2,9} = 2.37$, $P = 0.15$; partial correlations: $r = 0.56$, $t_9 = 2.05$, $P = 0.07$ and $r = -0.53$, $t_9 = -1.88$, $P = 0.09$, respectively). In bivariate analyses, neither the residual contrasts of total hindlimb length ($r = 0.30$, $t_{10} = 0.99$, $P = 0.35$; Fig. 3C) nor the residual contrasts of sprint speed were correlated with the residual contrasts of forelimb length ($r = -0.20$, $t_9 = -0.65$, $P = 0.53$; Fig. 3D). Residual contrasts of mass and relative contrasts of hindlimb length were nonsignificant predictors of the residual contrasts in sprint speed (all partial correlations: $P > 0.46$).

None of the residual contrasts of the four morphological variables (i.e., residual contrasts of mass, residual contrasts of total hindlimb length, residual contrasts of total forelimb length, relative contrasts of hindlimb length) explained the variation in the residual contrasts of endurance (backward stepwise multiple regression; $r = 0.42$, $F_{4,7} = 0.38$, $P =$

0.82). Therefore, differences in the residual contrasts of endurance cannot be adequately explained by the differences in the residual contrasts of any morphological variable (partial correlations: all $P > 0.19$).

DISCUSSION

Our values for sprint speed are similar to those reported in the literature (*L. vivipara*: 90 cm/s [Van Damme et al. 1991]; *P. tiliguerta*: 216 cm/s [Van Damme et al. 1989]; *P. muralis*: 181 cm/s [Bauwens et al. 1995] and 176 cm/s [Avery et al. 1987]). Recently, studies using high-speed treadmills have shown that some large, fast species of lizards may not be able attain their maximal sprint speed on short racetracks like ours (Jayne and Ellis 1998; Bonine and Garland 1999). However, this seems unlikely for the lacertid species in our study. Preliminary data obtained by filming several lacertid species with high-speed video cameras suggest that sprinting in lacertids is explosive, with top velocities being reached within milliseconds after departure from rest (similar results were found for lizards of comparable size of other families; Huey and Hertz 1982; Irschick and Jayne 1999).

Our values for treadmill endurance are not directly comparable to any reported previously for lacertids (Garland 1994b; Sorci et al. 1995) because we used a different belt speed (cf. Garland 1994b) and a different criterion to judge whether animals were exhausted. Moreover, Sorci et al. (1995) measured stamina of hatchling *L. vivipara* only.

The species in our dataset are not randomly distributed across the speed-stamina performance space (the plane described by all possible combinations of the two performance traits; Miles 1994). Two regions of the space are left empty: no species score poorly on both tests (lower left corner in Fig. 2), and no species excel in both locomotor functions simultaneously (upper right corner in Fig. 2). Gaps in performance spaces can be explained by two general hypotheses: developmental constraint and natural selection (Raup 1966).

We do not see how developmental constraints could prevent the evolution of a lizard with low sprint capacities and low stamina; a simple reduction of limb musculature would probably do the trick. Thus, the lack of such species is probably attributable to selection working on either or both performance traits. In the absence of quantitative data on habitat use, foraging modes, and antipredator behavior of the species examined, we can only speculate on the nature of these selective forces. Figure 2 suggests that relatively low running capacity can be tolerated in densely vegetated areas, but is selected against in open areas. This could be related to the tactics employed by lizards to evade predators in these two types of habitats. Lizards in open habitats must have the ability to dash quickly into hiding places that are typically several meters away, whereas lizards from more cluttered areas may rely more on crypsis or have to move only over a small distance. Figure 2 also suggests that relatively low endurance is perhaps permissible in open areas, but not in vegetated habitats. It is our experience that lacertid lizards usually do not run for extended periods when trying to escape predation and therefore, stamina is probably not an important aspect of their antipredator behavior. In these lizards, the ecological relevance of endurance capacity is more likely
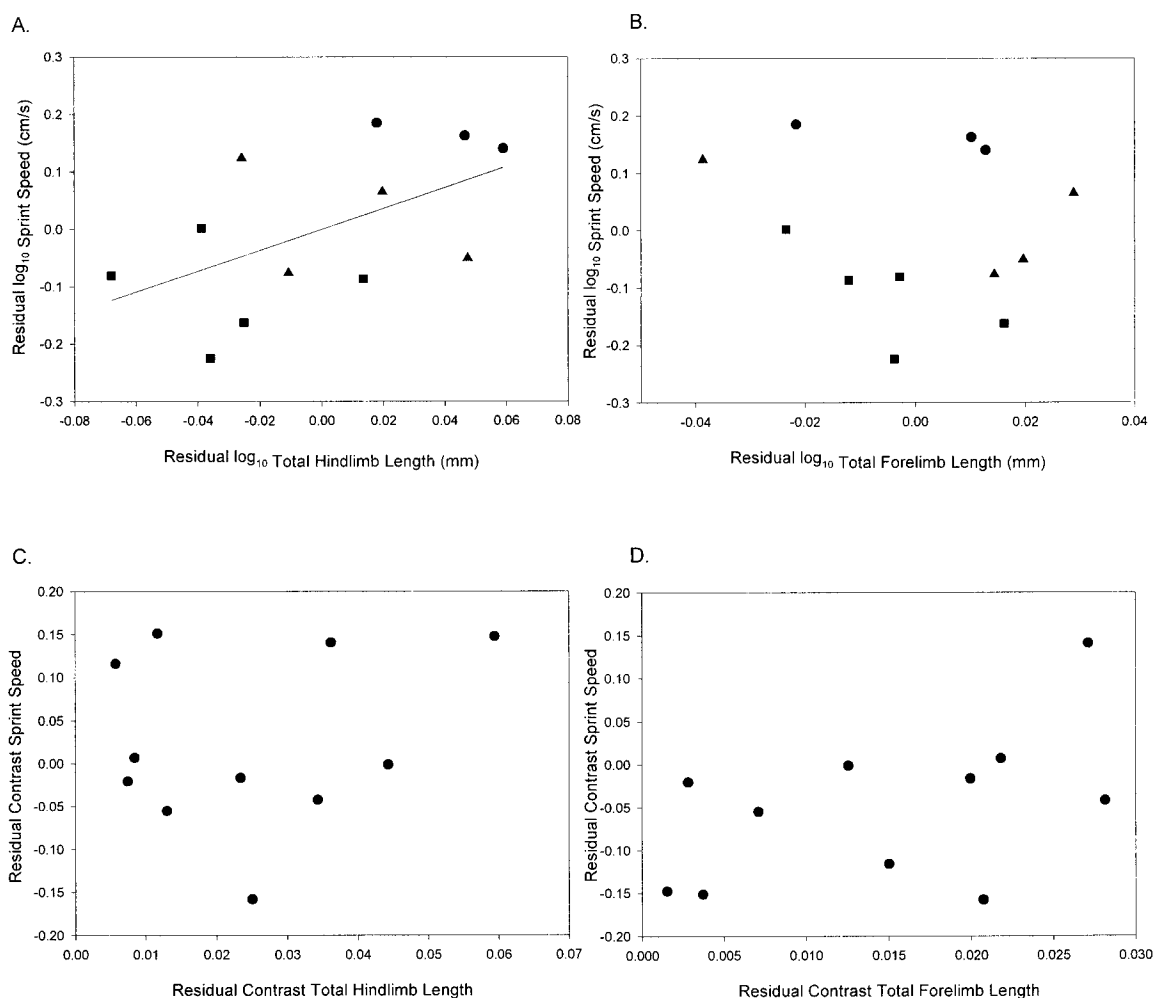
Figure 3.

FIG. 3. The bivariate relationships between the morphological traits and sprint speed: (A) the residuals of the logarithmically transformed means per species of total hindlimb length and sprint speed tend to be positively correlated ($r = 0.54$); (B) the residuals of the logarithmically transformed means per species of total forelimb length and sprint speed are not correlated ($r = -0.20$); (C) the residuals of the phylogenetic contrasts of the logarithmically transformed means per species of total hindlimb length and sprint speed are not correlated ($r = 0.30$); (D) the residuals of the phylogenetic contrasts of the logarithmically transformed means per species of total forelimb length and sprint speed are not correlated ($r = -0.20$). The symbols in (A) and (B) refer to habitat use (●, ground-dwelling in open habitats; ■, ground-dwelling in vegetated habitats; ▲, saxicolous). The residual contrasts of total hindlimb length and total forelimb length are positivized in (C) and (D), respectively (see Garland et al. 1992).

situated in foraging or social behavior (see also Garland 1999; Robson and Miles 2000). Most lacertids are actively foraging lizards (Stamps 1977; Pianka et al. 1979; Arnold 1989), and males of several species are known to defend territories against conspecifics (Edsman 1990; Olsson 1994; Salvador et al. 1996; Molina-Borja et al. 1998). Low visibility in densely vegetated habitats may require more extensive foraging and patrolling movements and, thus, higher endurance. However, these are only inferences. To test these hypotheses, we are currently gathering data on the ecology and behavior of these species.

A third explanation for the empty lower left corner in Figure 2 is incomplete sampling. With only 12 species in our dataset, we might easily have missed the species that are slow and easily fatigued. However, we think poor scores for both these performance traits could only be tolerated in circumstances with extremely low predation pressure, for instance, if species lived in predator-free environments, have developed a secretive lifestyle, or possess a highly effective armature (cf. molochs; Pianka and Pianka 1970), or when slow muscles appear to be very efficient in an energetic sense (cf. turtles; Alexander 1995). To our knowledge, these circumstances are found in no lacertid species.

How can we explain the absence of champion species (with high running capacities and high endurance; cf. *Cnemidophorus tigris,* Garland 1994b; Bonine and Garland 1999) within the lacertids? In this case, selection seems unlikely, unless a phenotype that simultaneously maximizes speed and stamina would compromise some other important function. Clearly, design components that affect stamina and speed

may affect other aspects of locomotion (e.g., climbing capacity, maneuverability) or other bodily functions (e.g., respiration, Carrier 1987, 1991; but see Wang et al. 1997). This would mean that the performance space is not adequately described by the two traits considered here, and more dimensions should be included (see also Bennett 1989).

A more commonly held standpoint would be that developmental constraints preclude the combination of high speed and stamina within a single phenotype. A trade-off between the two performance traits can be expected on simple biomechanical (Alexander 1999) and physiological grounds (Bennett 1978). Massive muscles, especially around the limbs, would aid animals in attaining high sprint speeds, but this could come at the expense of increased costs of locomotion and, thus, decreased stamina (McMahon 1984; also compare the muscular appearance of world class sprinters to the slender build of marathoners). Limb length, through its effect on stride length, should correlate positively with sprint speed (Pianka and Pianka 1976; Tsuji et al. 1989; Garland and Losos 1994; Bauwens et al. 1995; Bonine and Garland 1999), but may correlate negatively with the economy of running (McMahon 1984; Tsuji et al. 1989; Van Damme et al. 1998). High hindlimb:forelimb ratios could be beneficial to sprinting species, because the short forelimbs do not impede the movement of the long hindlimbs (Snyder 1962; Sukhanov 1968; Losos 1990); sustained locomotion at low speeds with unequal hind- and forelimb lengths might be energetically more demanding.

Our data give very limited support to these ideas. Among the 12 lacertid species, the tendency is for fast-sprinting species to have long hindlimbs and short forelimbs for their body size. None of the body shape characteristics measured affect endurance capacity. It should be noted, however, that the statistical power of the multiple regressions used are small, because the sample size is only 12. Also, our analysis of shape differences is limited to a small number of external characteristics that were easy to measure on live animals. We did not estimate masses of individual muscles, lever arms, or other aspects of the muscular-skeletal architecture that could mediate a trade-off between speed and stamina. Identifying the specific morphological characteristics responsible for the negative correlation (if any) is not an easy task, because many candidates exist. Moreover, previous studies indicate that subtle shifts in morphology may suffice to explain important differences in ecology (Moreno and Carrascal 1993; Van Damme et al. 1998). In an attempt to direct our search, we are currently examining gait characteristics (stride length, stride frequency, duty factor, step length) of the species in this study.

More likely, however, a trade-off between sprint speed and endurance would result from constraints at the physiological level. Physiologists predict a trade-off between speed and stamina because different muscle fiber types (i.e., fast-twitch and slow-twitch) enhance different performance traits (i.e., speed capacity and endurance, respectively) and because the total amount of muscle fibers may be limited (Komi 1984; Esbjörnsson et al. 1993; Rivero et al. 1993). Moreover, in a comparison of two lacertid species, differences in locomotor capacity were reflected in differences in physiological characteristics (see also Bennett et al. 1984; Huey et al. 1984).

Unfortunately, we have no data on the composition of muscle fiber types in our species (typifying muscle fibers requires sacrificing animals and many of the species used are protected), so we cannot test this idea at the moment. Recently, Bonine et al. (2000) have reported a negative relationship between the percentage of fast glycolytic and fast oxidative-glycolytic fibers in the iliofibularis muscle of phrynosomatid lizards.

Our results contradict intraspecific studies on snakes and lizards (Bennett 1980; Garland and Else 1987; Garland 1988, 1994a; Tsuji et al. 1989; Garland et al. 1990; Huey et al. 1990; Jayne and Bennett 1990; Secor et al. 1992; Brodie and Garland 1993; Sorci et al. 1995). Possibly, the design and performance variation among individuals within a population is too small to detect a trade-off. Moreover, other characteristics of individual animals (e.g., condition, motivation) may influence stamina and speed in the same direction, further masking the negative relationship. Differences in ecology are obviously much larger among species than among individuals, which should result in more clear-cut differences in design and performance. Interestingly, the one study of lizards that looked at this issue on an interspecific scale did find indications of a trade-off (Bennett et al. 1984; Huey et al. 1984). Of two species of Kalahari lacertids, the widely foraging *Heliobolus lugubris* had greater stamina but lower sprint capacity than the sit-and-wait predator *Pedioplanis lineoocellata*. The former also had higher rates of oxygen consumption, lower anaerobic scope, and greater relative heart mass and hematocrit than the latter. No differences were found in relative hindlimb muscle mass, myoglobin concentration, muscle enzyme activity, or contractile properties of the iliofibularis muscle.

LITERATURE CITED

Aldridge, H. D. J. N., and I. L. Rautenbach. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. J. Anim. Ecol. 56:763–778.

Alexander, R. M. 1995. Exploring biomechanics: animals in motion. Scientific American Library, New York.

———. 1999. Energy for animal life. Oxford Univ. Press, Oxford, U.K.

Arnold, E. N. 1983. Osteology, genitalia and the relationships of *Acanthodactylus* (Reptilia: Lacertidae). Bull. Brit. Mus. (Nat. Hist.) Zool. 44:291–339.

———. 1987. Resource partition among lacertid lizards in southern Europe. J. Zool. (Lond.) 1:739–782.

———. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. Bull. Brit. Mus. Nat. Hist. (Zool.) 55: 209–257.

———. 1998. Structural niche, limb morphology and locomotion

in lacertid lizards (Squamata, Lacertidae); a preliminary survey. Bull. Brit. Mus. (Nat. Hist.) Zool. 64:63–89.

Avery, R. A., C. F. Mueller, S. M. Jones, J. A. Smith, and D. J. Bond. 1987. Speeds and movement patterns of European lacertid lizards: a comparative study. J. Herpetol. 21:324–329.

Bauwens, D., T. Garland Jr., A. M. Castilla, and R. Van Damme. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. Evolution 49: 848–863.

Bennett, A. F. 1978. The thermal dependence of activity in lizards. Am. Zool. 18:653.

———. 1980. The thermal dependence of lizard behavior. Anim. Behav. 28:752–762.

———. 1989. Integrated studies of locomotor performance. Pp. 191–202 in D. B Wake and G. Roth, eds. Complex organismal functions: integration and evolution in vertebrates. John Wiley and Sons, Chichester, U.K.

Bennett, A. F., R. B. Huey, and H. John-Alder. 1984. Physiological correlates of natural activity and locomotor capacity in two species of lacertid lizards. J. Comp. Physiol. B 154:113–118.

Bonine, K. E., and T. Garland Jr. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. J. Zool. Lond. 248:255–265.

Bonine, K. E., T. T. Gleeson, and T. Garland Jr. 2000. Fiber-type variation in the iliofibularis muscle of phrynosomatid lizards. The Physiologist 43:356.

Brodie, E. D., III, and T. Garland Jr. 1993. Quantitative genetics of snake populations. Pp. 315–362 in R. A. Seigel and J. T. Collins, eds. Snakes: ecology and behavior. McGraw-Hill, Inc., New York.

Brown, R. M., and D. H. Taylor. 1995. Compensatory escape mode trade-offs between swimming performance and maneuvering behavior through larval ontogeny of the wood frog, Rana sylvatica. Copeia 1995:1–7.

Bulova, S. J. 1994. Ecological correlates of population and individual variation in antipredator behavior of two species of desert lizards. Copeia 1994:980–992.

Carrier, D. R. 1987. Lung ventilation during walking and running in four species of lizards. J. Exp. Biol. 47:33–42.

———. 1991. Conflict in the hypaxial musculo-skeletal system: documenting an evolutionary constraint. Am. Zool. 31:644–654.

Cartmill, M. 1985. Climbing. Pp. 73–88 in M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds. Functional vertebrate morphology. The Belknap Press, Cambridge, MA.

Castilla, A. M., R. Van Damme, and D. Bauwens. 1999. Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards. Natura Croatica 8: 253–274.

Cullum, A. 1998. Sexual dimorphism in physiological performance of whiptail lizards (genus Cnemidophorus). Physiol. Zool. 71: 541–552.

Díaz-Uriarte, R., and T. Garland Jr. 1998. Effects of branch lengths errors on the performance of phylogenetically independent contrasts. Syst. Biol. 47:654–672.

Dohm, M. R., J. P. Hayes, and T. Garland Jr. 1996. Quantitative genetics of sprint running speed and swimming endurance in laboratory house mice (Mus domesticus). Evolution 50: 1688–1701.

Domenici, P., and R. W. Blake. 1991. The kinematics and performance of the escape response in the angelfish (Pterophyllum eimekei). J. exp. Biol. 156:187–205.

Edsman, L. 1990. Territoriality and competition in wall lizards. Ph.D. diss., University of Stockholm, Stockholm, Sweeden.

Esbjörnsson, M., C. Sylvén, I. Holm, and E. Jansson. 1993. Fast twitch fibres may predict anaerobic performance in both females and males. Int. J. Sports Med. 14:257–263.

Felsenstein, J. 1985. Phylogenies and the comparative method. Am. Nat. 125:1–15.

———. 1988. Phylogenies and quantitative characters. Ann. Rev. Ecol. Syst. 19:445–471.

Fu, J. 2000. Toward the phylogeny of the family Lacertidae: why 4708 base pairs of mtDNA sequences cannot draw the picture. Biol. J. Linn. Soc. 71:203–217.

Garland, T., Jr. 1988. Genetic basis of activity metabolism. I. Inheritance of speed, stamina, and antipredator displays in the garter snake Thamnophis sirtalis. Evolution 42:335–350.

———. 1994a. Quantitative genetics of locomotor behavior and physiology in a garter snake. Pp. 251–276 in C. R. B. Boake, ed. Quantitative genetic studies of behavioral evolution. Univ. of Chicago Press, Chicago.

———. 1994b. Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. Pp. 237–259 in L. J. Vitt and E. R. Pianka, eds. Lizard ecology: historical and experimental perspectives. Princeton Univ. Press, Princeton, NJ.

———. 1999. Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. Anim. Behav. 57:77–83.

Garland, T., Jr., and P. L. Else. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. Am. J. Physiol. 252:R439–R449.

Garland, T., Jr., and J. B. Losos. 1994. Ecological morphology of locomotor performance in squamate reptiles. Pp. 240–302 in P. C. Wainwright and S. M. Reilly, eds. Ecological morphology: integrative organismal biology. Univ. of Chicago Press, Chicago.

Garland, T., Jr., F. Geiser, and R. V. Baudinette. 1988. Comparative locomotor performance of marsupial and placental mammals. J. Zool. (Lond.) 215:505–522.

Garland, T., Jr., A. F. Bennett, and C. B. Daniels. 1990. Heritability of locomotor performance and its correlates in a natural population. Experientia 46:530–533.

Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst. Biol. 41:18–32.

Garland, T., Jr., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Syst. Biol. 42:265–292.

Garland, T., Jr., P. E. Midford, and A. R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral states. Am. Zool. 39: 374–388.

Harris, D. J., and E. N. Arnold. 1999. Relationships of wall lizards, Podarcis (Reptilia: Lacertidae) based on mitochondrial DNA sequences. Copeia 1999:749–754.

Harris, D. J., E. N. Arnold, and R. H. Thomas. 1998. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. Proc. R. Soc. London B 265:1939–1948.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford Univ. Press, Oxford, U.K.

Heinrich, B. 1985. Men vs. women, marathoners vs. ultramarathoners. Ultrarunning 1985:16–18.

Huey, R. B., and P. E. Hertz. 1982. Effects of body size and slope on sprint speed of a lizard (Stellio (Agama) stellio). J. Exp. Biol. 97:401–409.

Huey, R. B., and E. R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 62:991–999.

Huey, R. B., A. F. Bennett, H. John-Alder, and K. A. Nagy. 1984. Locomotor capacity and foraging behavior of Kalahari lacertid lizards. Anim. Behav. 32:41–50.

Huey, R. B., A. E. Dunham, K. L. Overall, and R. A. Newman. 1990. Variation in locomotor performance in demographically known populations of the lizard Sceloporus merriami. Physiol. Zool. 63:845–872.

Irschick, D. J., and B. C. Jayne. 1999. A field study of the effects of incline on the escape locomotion of a bipedal lizard, Callisaurus dracanoides. Physiol. Biochem. Zool. 72:44–56.

Irschick, D. J., C. C. Austin, K. Petren, R. N. Fisher, J. B. Losos, and O. Ellers. 1996. A comparative analysis of clinging ability among pad-bearing lizards. Biol. J. Linn. Soc. 59:21–35.

Jayne, B. C., and A. F. Bennett. 1990. Scaling of speed and endurance in garter snakes: a comparison of cross-sectional and longitudinal allometries. J. Zool. (London) 220:257–277.

Jayne, B. C., and R. V. Ellis. 1998. How inclines affect the escape behaviour of a dune-dwelling lizard, Uma scoparia. Anim. Behav. 55:1115–1130.

John-Alder, H. B., and B. Joos. 1991. Interactive effects of thyroxine and experimental location on running endurance, tissue masses, and enzyme activities in captive versus field-active lizards (*Sceloporus undulatus*). Gen. Comp. Endocrinol. 81: 120–132.

John-Alder, H. B., S. McMann, L. S. Katz, A. Gross, and D. S. Barton. 1996. Social modulaton of exercise endurance in a lizard (*Sceloporus undulatus*). Physiol. Zool. 69:547–567.

Kasapi, M. A., P. Domenici, R. W. Blake, and D. Harper. 1993. The kinematics and performance of escape responses of the knifefish *Xenomystus nigri.* Can. J. Zool. 71:189–195.

Komi, P. V. 1984. Physiological and biomechanical correlates of muscle function: effects of muscle structure and stretch shortening cycle on force and velocity. Exercise Sport Sci. Rev. 12: 81–121.

Lewontin, R. C. 1978. Adaptation. Scient. Am. 239:156–169.

Losos, J. B. 1990. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. Evolution 44:1189–1203.

Losos, J. B., and D. B. Miles. 1994. Adaptation, constraint, and the comparative method: phylogenetic issues and methods. Pp. 60–98 *in* P. C. Wainwright and S. M. Reilly, eds. Ecological morphology: integrative organismal biology. Univ. of Chicago Press, Chicago.

Losos, J. B., and B. Sinervo. 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. J. Exp. Biol. 245:23–30.

Losos, J. B., B. M. Walton, and A. F. Bennett. 1993. Trade-offs between sprinting and clinging ability in Kenyan chameleons. Funct. Ecol. 7:281–286.

Macrini, T. E., and D. J. Irschick. 1998. An intraspecific analysis of trade-offs in sprinting performance in a West Indian lizard species (*Anolis lineatopus*). Biol. J. Linn. Soc. 63:579–591.

Martins, E. P., and T. Garland Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. Evolution 45:534–557.

McMahon, T. A. 1984. Muscles, reflexes and locomotion. Princeton Univ. Press, Princeton, NJ.

Miles, D. B. 1994. Covariation between morphology and locomotory performance in Sceloporine lizards. Pp. 207–235 *in* L. J. Vitt and E. R. Pianka, eds. Lizard ecology: historical and experimental perspectives. Princeton Univ. Press, Princeton, NJ.

Molina-Borja, M., M. Padron-Fumero, and T. Alfonso-Martin. 1998. Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (Family Lacertidae). Ethology 104:314–322.

Moreno, E., and L. M. Carrascal. 1993. Ecomorphological patterns of aerial feeding in oscines (Passeriformes: Passeri). Biol. J. Linn. Soc. 50:147–165.

Nakamura, T., S. Masui, M. Wada, H. Katoh, H. Mikami, and S. Katsuta. 1993. Heredity of muscle fibre composition estimated from a selection experiment in rats. Eur. J. Appl. Physiol. 66: 85–89.

Olsson, M. 1994. Nuptial color in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. Anim. Behav. 48:607–613.

Peterson, J. A. 1984. The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. J. Zool. 202:1–42.

Pianka, E. R., and H. D. Pianka. 1970. The ecology of *Moloch horridus* (Lacertilia: Agamidae) in western Australia. Copeia 1970:90–103.

———. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the western Australian desert. Copeia 1:125–142.

Pianka, E. R., R. B. Huey, and L. R. Lawlor. 1979. Niche segregation in desert lizards. Pp. 67–115 *in* D. J. Horn, G. R. Stairs, and R. D. Mitchell, eds. Analysis of ecological systems. Ohio State Univ. Press, Columbus.

Purvis, A., and T. Garland Jr. 1993. Polytomies in comparative analyses of continuous characters. Syst. Biol. 42:569–575.

Raup, D. M. 1966. Geometric analysis of shell coiling. J. Paleontology 40:1178–1190.

Reidy, S. P., S. R. Kerr, and J. A. Nelson. 2000. Aerobic and anaerobic swimming performance of individual Atlantic cod. J. Exp. Biol. 203:347–357.

Rivero, J. L., A. L. Serrano, P. Henckel, and E. Agüera. 1993. Muscle fiber type composition and fiber size in successfully and unsuccessfully endurance-raced horses. J. Appl. Physiol. 75: 1758–1766.

Robson, M. A., and D. B. Miles. 2000. Locomotor performance and dominance in male tree lizards, *Urosaurus ornatus.* Funct. Ecol. 14:338–344.

Rose, M. R., and G. V. Lauder. 1996. Post-spandrel adaptationism. Pp. 1–8 *in* M. R. Rose and G. V. Lauder, eds. Adaptation. Academic Press, San Diego, CA.

Salvador, A., J. Martín, P. López, and J. P. Veiga. 1996. Long-term effect of tail loss on home-range size and access to females in male lizards (*Psammodromus algirus*). Copeia 1996:208–209.

Secor, S. M., B. C. Jayne, and A. F. Bennett. 1992. Locomotor performance and energetic cost of sidewinding by the snake *Crotalus cerastes.* J. Exp. Biol. 163:1–14.

Sinervo, B., and J. B. Losos. 1991. Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. Ecology 72:1225–1233.

Snyder, R. C. 1962. Adaptations for bipedal locomotion of lizards. Am. Zool. 2:191–203.

Sorci, G., J. G. Swallow, T. Garland Jr.,and J. Clobert. 1995. Quantitative genetics of locomotor speed and endurance in the lizard *Lacerta vivipara.* Physiol. Zool. 68:698–720.

Stamps, J. A. 1977. Social behavior and spacing patterns in lizards. Pp. 265–334 *in* C. Gans and D. W. Tinkle, eds. Biology of the reptilia. Vol. 7. Ecology and behavior. Academic Press, New York.

Sukhanov, V. B. 1968. General system of symmetrical locomotion of terrestrial vertebrates and some features of movement of lower tetrapods. Nauka Publications, Leningrad. (Translated to English, Amerinde Publishing Co., New Delhi.)

Tsuji, J. S., R. B. Huey, F. H. Van Berkum, T. Garland Jr.,and R. G. Shaw. 1989. Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. Evol. Ecol. 3:240–252.

van Berkum, F. H., and J. S. Tsuji. 1987. Inter-familiar differences in sprint speed of hatchling *Sceloporus occidentalis* (Reptilia: Iguanidae). J. Zool. (Lond.) 212:511–519.

Van Damme, R., D. Bauwens, A. M. Castilla, and R. F. Verheyen. 1989. Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta.* Oecologia 80: 516–524.

Van Damme, R., D. Bauwens, R. F. Verheyen. 1991. The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. Funct. Ecol. 5:507–517.

Van Damme, R., P. Aerts, and B. Vanhooydonck. 1998. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. Biol. J. Linn. Soc. 63:409–427.

Vanhooydonck, B., and R. Van Damme. 1999. Evolutionary relationships between body shape and habitat use in lacertid lizards. Evol. Ecol. Res. 1:785–805.

Walton, B. M. 1993. Physiology and phylogeny: the evolution of locomotor energetics in hylid frogs. Am. Nat. 141:26–50.

Wang, T., D. R. Carrier, and J. W. Hicks. 1997. Ventilation and gas exchange in lizards during treadmill exercise. J. Exp. Biol. 200:2629–2639.

Wassersug, R. J. 1989. Locomotion in amphibian larvae (or ''why aren't tadpoles built like fishes?''). Amer. Zool. 29:65–84.

Webb, P. W. 1984. Body form, locomotion and foraging in aquatic vertebrates. Am. Zool. 24:107–120.

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