

Evolutionary trade-offs in locomotor capacities in lacertid lizards: are splendid sprinters clumsy climbers?

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Keywords:

climbing;
locomotion;
performance;
running;
trade-off.

Abstract

We tested the hypothesis that an evolutionary trade-off exists between the capacity to run on level terrain and the ability to climb inclined structures in lacertid lizards. Biomechanical and physiological models of lizard locomotor performance suggest that the morphological design requirements of a ground-dwelling vs. scansorial life style are difficult to reconcile. This conflict is thought to preclude simultaneous evolution of maximal locomotor performance on level and inclined terrain. This notion has been corroborated by comparative studies on lizard species from other groups (*Anolis*, *Chamaeleo*, *Sceloporus*), but is not supported by our data on 13 species from the family Lacertidae. We found no indication of a negative association between maximal sprint speed of lizards over a level racetrack (indicative of ground-dwelling locomotor performance), on an inclined stony surface (indicative of climbing performance over rock faces) and inclined mesh surface (indicative of clambering performance among vegetation). Moreover, morphological characteristics associated with fast sprinting capacities (e.g. long hind limbs) apparently enhance, rather than hinder climbing and clambering performance. We conclude that in our sample of lacertid lizards, the evolution of fast sprinting capacity on level terrain has not inflicted major restrictions on climbing and clambering performance.

Introduction

The concept of niche partitioning (Hutchinson, 1959; MacArthur & Levins, 1967; Schoener, 1974) is largely based on the understanding that a species can exclusively occupy a particular microhabitat by adapting its morphology, physiology and behaviour to suit that environment. Implicit in this notion is the principle that a species which is specialized to be excellent at exploiting one type of microhabitat will be inferior at utilizing others. This tenet is usually explained by the existence of trade-offs between traits that prevent simultaneous evolution of optimal performance in characteristics that require opposing biomechanical or physiological adaptations (Stearns, 1992). Therefore, identifying ecologically rele-

vant but conflicting performance traits is basic to our understanding of the evolution of species radiations.

Among the best examples of a trade-off between performance capabilities that is reflected in morphological and ecological differentiation, is the conflict between sprinting speed and climbing capacity in *Anolis* lizards (Losos & Sinervo, 1989; Losos & Irschick, 1996). *Anolis* with long limbs sprint relatively quickly on broad surfaces, but move awkwardly across narrow perches. In contrast, *Anolis* with short limbs sprint relatively slowly on broad surfaces but are 'surefooted' when moving across narrow perches. This differentiation of locomotor capacities among *Anolis* lizards is consistent with predictions on the biomechanics and physiology of lizards adopting an arboreal vs. ground-dwelling life style. Long, parasagittal limbs are thought to be advantageous to ground-dwelling lizards because they allow for larger strides and hence faster sprinting on flat surfaces (Cartmill, 1985; Pounds, 1988; Losos & Sinervo, 1989).

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In climbing lizards, however, long parasagittal limbs would hinder climbing by moving a lizard's centre of mass (and balance) away from the perch (Sinervo & Losos, 1991; Losos *et al.*, 1994; Van Damme *et al.*, 1997). Additionally, all else being equal, long limbs tend to result in a 'high gear' system of locomotion that is beneficial for lizards attaining high speeds on level terrain but may push lizards away from the substrate when climbing vertical perches (Arnold, 1998).

The relative lengths of limbs and their component parts and the musculature of limbs, is also predicted to vary according to the habitat specialization of lizard species. Ground-dwelling lizards are expected to have a relatively low fore limb to hind limb ratio, because (1) they are thrust forward from the hind limbs (Snyder, 1954) and (2) long fore limbs may interfere with the motion of hind limbs (Rewcastle, 1981). In contrast, climbing lizards are expected to have hind limbs and fore limbs that are of similar length because fore limbs are necessary for securely gripping perches (Cartmill, 1974, 1985; Autumn *et al.*, 1998; Zaaf *et al.*, 1999; Vanhooydonck *et al.*, 2000). It may also be important for climbing lizards to stride a similar length with fore and hind limbs and fore limbs are probably consequential for vertical locomotion (Arnold, 1998). Moreover, within the hind limbs, a high tibia length to femur length ratio results in a long moment arm, thereby promoting fast running on level ground. Climbers should have a low intralimb proportion in both limbs so as to enhance their capacity to grip perches (Moermond, 1979). Furthermore, appendicular flexors that are inserted proximally allow for rapid movement of limbs, whereas those inserted distally heighten the torque of limbs (Losos *et al.*, 1993). A relatively high proportion of tonic muscle fibres in limbs confers greater maximal force which probably is important for postural support when stationary and probably does not have a major function during rapid locomotion (Abu-Ghalyun *et al.*, 1988; Losos *et al.*, 1993).

These considerations suggest that an evolutionary trade-off should exist between climbing and sprinting capacity in lizards. In this paper, we test this hypothesis by comparing data on the morphology and locomotor performance of 13 species of lacertid lizards. This data set spans a range of lizard species that vary in the degree to which they climb in their natural habitat (Arnold, 1998; Vanhooydonck & Van Damme, 1999; references therein). We adopted two approaches: in one, we used traditional (i.e. nonphylogenetic) statistical analyses, in the other we accounted for phylogenetic relatedness among the species. Many species of Lacertidae climb wide rocks and walls, rather than the narrow trees or shrubs which are inhabited by climbing species used in previous comparative studies on this topic (e.g. *Anolis*, *Sceloporus*, *Chamaeleo*). Therefore, in addition to explicit testing for evolutionary trade-offs in locomotor performance, we compared trends among lizard groups that utilize different microhabitats. Our previous analyses

suggest that extrapolating findings across lizard groups may not be straightforward (Van Damme *et al.*, 1997; Vanhooydonck & Van Damme, 1999).

Materials and methods

Animals

During the summers of 1994–1999, we collected adults of nine species of lacertid lizards from various locations in western Europe and the Canary Islands. Adult individuals from four additional species (*Acanthodactylus pardalis*, *A. scutellatus*, *Latastia longicaudata* and *Takydromus sexlineatus*) were obtained from the pet trade. For each species, Table 1 lists the full scientific name, number of individuals used in the study and mean morphometric and speed measurements.

We transported all lizards to the lab at the University of Antwerp, Belgium. Animals from each species were housed together in groups of four or five individuals in glass terraria (100 × 50 cm) with a sandy substrate and stones and grass vegetation shelter. A 100-W light bulb provided heat and light for 10 h a day, enabling lizards to thermoregulate. Lizards were fed daily with live crickets dusted with calcium and provided with water *ad libitum*.

Morphometric measurements

For each lizard, we measured the following characteristics using digital callipers (Mitutoyo CD-15DC, precision 0.01 mm): snout vent length (SVL) and lengths of femur, tibia, metatarsus, humerus, radius and metacarpus. All measurements were taken on live animals. Hereafter, 'hind limb length' refers to the sum of femur, tibia and metatarsus lengths and 'fore limb length' refers to the sum of humerus, radius and metacarpus lengths.

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

Performance testing

We measured sprint speed on a 2 m long by 0.15 m wide electronic racetrack with a cork substrate. Eight pairs of photocells, placed at 0.25 m intervals along the runway, recorded the time taken for lizards to cross each successive infra-red beam. The time elapsed between triggering two consecutive cells was stored in a computer and recordings were expressed as cm s^{-1} for each interval. We tested each individual five times with at least 1 h rest between trials. Each run was scored as 'good' or 'bad' (cf. van Berkum & Tsuji, 1987; Tsuji *et al.*, 1989). 'Bad' trials were eliminated before further analysis. For each lizard, we used the fastest speed over any 0.25 m interval as an estimate of maximal sprint performance.

Climbing speed was measured on a 1 m long by 0.15 m wide electronic racetrack, tilted to an angle of 70°. We

Table 1 Full scientific name (*n* = number of individuals), morphological (all in mm, except for mass in g) and performance measures (in m s^{-1}) for each of the 13 lizard species used in this study. Values are untransformed means \pm SD per species.

| Species (<i>n</i>) | SVL | Mass | Hind limb length | Fore limb length | Femur length | Tibia length | Sprint speed | Climbing speed | Clambering speed |
|--------------------------------------|-------------------|-------------------|------------------|------------------|------------------|------------------|-----------------|-----------------|------------------|
| <i>Acanthodactylus pardalis</i> (12) | 59.23 \pm 2.52 | 6.73 \pm 0.84 | 27.77 \pm 2.12 | 17.29 \pm 1.01 | 13.07 \pm 1.09 | 10.76 \pm 0.77 | 2.61 \pm 0.67 | 0.32 \pm 0.28 | 1.18 \pm 0.56 |
| <i>A. scutellatus</i> (4) | 67.70 \pm 8.11 | 8.09 \pm 4.02 | 33.96 \pm 7.27 | 20.19 \pm 4.08 | 16.60 \pm 3.97 | 12.74 \pm 2.19 | 2.79 \pm 0.26 | 0.14 \pm 0.30 | 1.30 \pm 0.18 |
| <i>Gallioia galloti</i> (15) | 98.53 \pm 16.24 | 50.12 \pm 25.44 | 45.39 \pm 8.61 | 30.90 \pm 4.85 | 21.47 \pm 4.64 | 17.19 \pm 2.79 | 1.93 \pm 0.52 | 0.34 \pm 0.23 | 1.57 \pm 0.76 |
| <i>Lacerta bedriagae</i> (15) | 71.73 \pm 6.11 | 9.56 \pm 2.60 | 31.16 \pm 3.21 | 21.61 \pm 2.03 | 14.65 \pm 1.82 | 11.83 \pm 1.10 | 1.79 \pm 0.60 | 0.99 \pm 0.31 | 1.49 \pm 0.32 |
| <i>L. viridis</i> (6) | 92.69 \pm 11.16 | 28.44 \pm 6.00 | 40.65 \pm 2.40 | 26.35 \pm 0.67 | 18.93 \pm 1.49 | 15.38 \pm 0.70 | 2.68 \pm 0.56 | 0.28 \pm 0.13 | 1.55 \pm 0.22 |
| <i>Podarcis muralis</i> (21) | 52.08 \pm 5.24 | 3.17 \pm 1.70 | 19.92 \pm 3.15 | 13.39 \pm 2.15 | 9.47 \pm 1.62 | 7.55 \pm 1.10 | 2.14 \pm 0.97 | 0.29 \pm 0.15 | 0.91 \pm 0.33 |
| <i>P. sicula</i> (15) | 68.23 \pm 2.29 | 7.02 \pm 1.10 | 30.89 \pm 2.66 | 19.23 \pm 1.37 | 14.40 \pm 1.53 | 11.81 \pm 0.96 | 1.67 \pm 0.37 | 0.47 \pm 0.17 | 1.19 \pm 0.21 |
| <i>P. tiliguerta</i> (14) | 56.78 \pm 2.55 | 4.77 \pm 0.61 | 26.41 \pm 1.64 | 16.89 \pm 1.21 | 12.63 \pm 0.86 | 9.87 \pm 0.61 | 1.55 \pm 0.47 | 0.45 \pm 0.24 | 1.25 \pm 0.33 |
| <i>Takydromus sexlineatus</i> (9) | 51.79 \pm 2.61 | 2.79 \pm 0.48 | 17.94 \pm 1.05 | 14.45 \pm 1.16 | 8.11 \pm 0.69 | 7.37 \pm 0.36 | 1.33 \pm 0.39 | 0.25 \pm 0.11 | 0.57 \pm 0.16 |
| <i>L. oxycephala</i> (16) | 56.77 \pm 2.80 | 4.78 \pm 0.74 | 24.72 \pm 1.89 | 17.22 \pm 1.66 | 12.11 \pm 1.24 | 8.83 \pm 0.76 | 2.02 \pm 0.34 | 1.25 \pm 0.30 | 1.62 \pm 0.22 |
| <i>Latastia longicaudata</i> (9) | 73.83 \pm 5.77 | 8.61 \pm 2.43 | 34.55 \pm 2.56 | 20.54 \pm 1.73 | 15.30 \pm 1.32 | 13.12 \pm 1.17 | 3.34 \pm 0.52 | 1.05 \pm 0.57 | 2.09 \pm 0.21 |
| <i>P. hispanica</i> (14) | 47.58 \pm 4.34 | 2.65 \pm 0.77 | 17.79 \pm 1.79 | 11.88 \pm 1.02 | 7.27 \pm 0.96 | 7.71 \pm 0.91 | 2.03 \pm 0.40 | 0.62 \pm 0.23 | 1.27 \pm 0.27 |
| <i>P. atra</i> (15) | 56.89 \pm 6.93 | 4.52 \pm 1.98 | 19.48 \pm 3.61 | 13.36 \pm 1.80 | 7.83 \pm 1.45 | 8.63 \pm 1.57 | 1.09 \pm 0.42 | 0.19 \pm 0.86 | 0.86 \pm 0.37 |

tested lizards on two types of substrate: wire screen (mesh width 2 mm) and smooth slate. The former substrate mimicked climbing conditions in a vegetation matrix whereas the latter measured a lizard's capacity to climb rocks. Hereafter, we refer to these types of near-vertical locomotion as 'clambering' and 'climbing', respectively. Eight pairs of photocells positioned at 0.15 m intervals along the runway, recorded the time taken for lizards to cross each successive infra-red beam. Each animal was tested three times on each substrate with at least 1 h rest between trials. Each run was scored as 'good' or 'bad' (cf. van Berkum & Tsuji, 1987; Tsuji *et al.*, 1989). 'Bad' trials were eliminated before further analysis. For each lizard, we used the fastest speed over any 0.15 m interval as an estimate of maximal clambering and climbing capacity.

Prior to and in between all performance trials, lizards were placed for at least 1 h in an incubator at 38 °C (*A. pardalis*, *A. scutellatus* and *L. longicaudata*) or 35 °C (all other tested species). These temperatures approximate those preferentially selected by the animals and we therefore assume that lizards at these temperatures perform at near-maximal levels (see Castilla *et al.*, 1999). The three performance capacities (sprint speed, climbing speed, clambering speed) were measured on different days and the order in which animals were subjected to the three tests was randomized. All animals were tested within weeks after being captured.

We calculated the means per species of the three performance measures and logarithmically (\log_{10}) transformed them before statistical analyses.

Nonphylogenetic analyses

The logtransformed means per species of hind limb length, fore limb length, sprint speed, climbing speed and clambering speed were regressed against the logtransformed means per species of SVL, and residuals were calculated. Hereafter, we will refer to these variables as residual hind limb length, residual fore limb length, residual sprint speed, residual climbing speed and residual clambering speed, respectively.

We estimated two additional morphological characteristics for each species. The 'interlimb ratio' was calculated as the residuals from the regression of the logtransformed means per species of hind limb length against the logtransformed means per species of fore limb length. Species with long hind limbs relative to their fore limbs, have large values for this trait. The 'intra-limb ratio' was calculated as the residual from the regression of the logtransformed means per species of tibia length against the logtransformed means per species of femur length. Species with a large intra-limb ratio have long tibiae relative to femurs.

To test for correlations between the different performance traits, we performed Pearson correlations on residual sprint speed, residual climbing speed and residual

clambering speed. A negative relationship between residuals for different performance measures would indicate a trade-off between the two types of locomotion in question.

We performed a backward stepwise multiple regression with one of the performance measures (i.e. residual sprint speed, residual climbing speed, residual clambering speed) as dependent variable and three morphological variables (residual hind limb length, residual fore limb length and intralimb ratio) as independent variables to investigate associations between morphology and locomotor performance. Because interlimb ratio is calculated from two of the independent variables included in our multiple regression analysis, we did not incorporate it into the model. However, we tested whether this morphological variable was correlated with locomotor performance using Pearson correlation analyses (all with $n = 13$).

Phylogenetic analyses

Because closely related species have a common evolutionary history, they cannot be considered as independent data points in statistical analyses (Felsenstein, 1985, 1988; Harvey & Pagel, 1991; Garland *et al.*, 1993). However a basic assumption of traditional statistical methods is that data points are independent from each other. In recent years various computer programs have been developed that account for phylogenetic relationships in statistical analyses involving comparisons among closely related species (see Harvey & Pagel, 1991; Garland *et al.*, 1993; Losos & Miles, 1994). We used Felsenstein's (1985) approach of phylogenetically independent contrasts.

We calculated the independent contrasts of the logarithmically transformed means per species of SVL, hind limb length, fore limb length, femur length, tibia length, sprint speed, climbing speed and clambering speed using the PDTREE program (Garland *et al.*, 1999). Subsequently, we regressed the contrasts (of the logtransformed means per species) of hind limb length, fore limb length, sprint speed, climbing speed and clambering speed against the contrasts (of the logtransformed means per species) of SVL and calculated residuals. Hereafter, we will refer to these variables as residual contrast of hind limb length, residual contrast of fore limb length, residual contrast of sprint speed, residual contrast of climbing speed and residual contrast of clambering speed, respectively.

Also, we regressed the contrasts (of the logtransformed means per species) of hind limb length against the contrasts (of the logtransformed means per species) of fore limb length and calculated the residuals. Hereafter, we will refer to this variable as contrast of interlimb ratio. Lastly, we regressed the contrasts (of the logarithmically transformed means per species) of tibia length against the contrasts (of the logarithmically transformed means per species) of femur length and calculated residuals. Here-

after, we will refer to this variable as contrast of intralimb ratio. The regressions on which the calculation of the residuals were based, were forced through the origin (see Garland *et al.*, 1992).

We used (multiple) regression techniques to examine associations among the residual contrasts of the performance measures and between the residual contrasts of the performance measures and the morphological traits. We forced the regression line through the origin, as is required when regressing contrasts (see Garland *et al.*, 1992).

The independent contrast method requires information on the topology and branch lengths of the phylogenetic tree. The tree we used is depicted in Fig. 1 and is currently the 'best estimate' of phylogenetic relationships among the lacertid lizards used in our study. It is based on a combination of data from mitochondrial DNA (Harris *et al.*, 1998; Harris & Arnold, 1999) and morphological studies (Arnold, 1983, 1989, 1998). 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

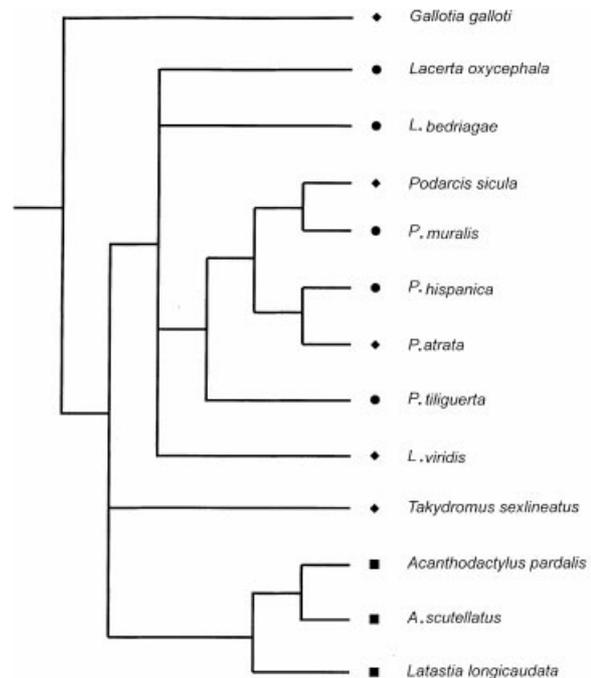


Fig. 1 Putative relationships among the 13 lacertid lizard species, used as input for the phylogenetic analyses. The tree is a 'currently best' working hypothesis, based on morphological characters and on mitochondrial DNA sequences (see text for references). The symbols indicate the habitat preference of the species (●: rock-dwelling; ■: ground-dwelling, open terrain; ◆: ground-dwelling in densely vegetated areas or climbing in shrubs).

(Fu, 2000). Therefore, we considered the unresolved nodes as 'hard' polytomies (Purvis & Garland, 1993; Garland, 1994a; Garland & Díaz-Uriarte, 1999). As few data are available on divergence times between species within the Lacertidae, we set all branch lengths to unity. Previous studies suggest that the actual length of

branches usually does not affect the main outcomes of phylogenetic analyses (Martins & Garland, 1991; Walton, 1993; Irschick *et al.*, 1996; Díaz-Uriarte & Garland, 1998). We inspected diagnostic graphs and statistics in the program PDTREE (Garland *et al.*, 1999) to verify that the branch lengths were adequate for all traits.

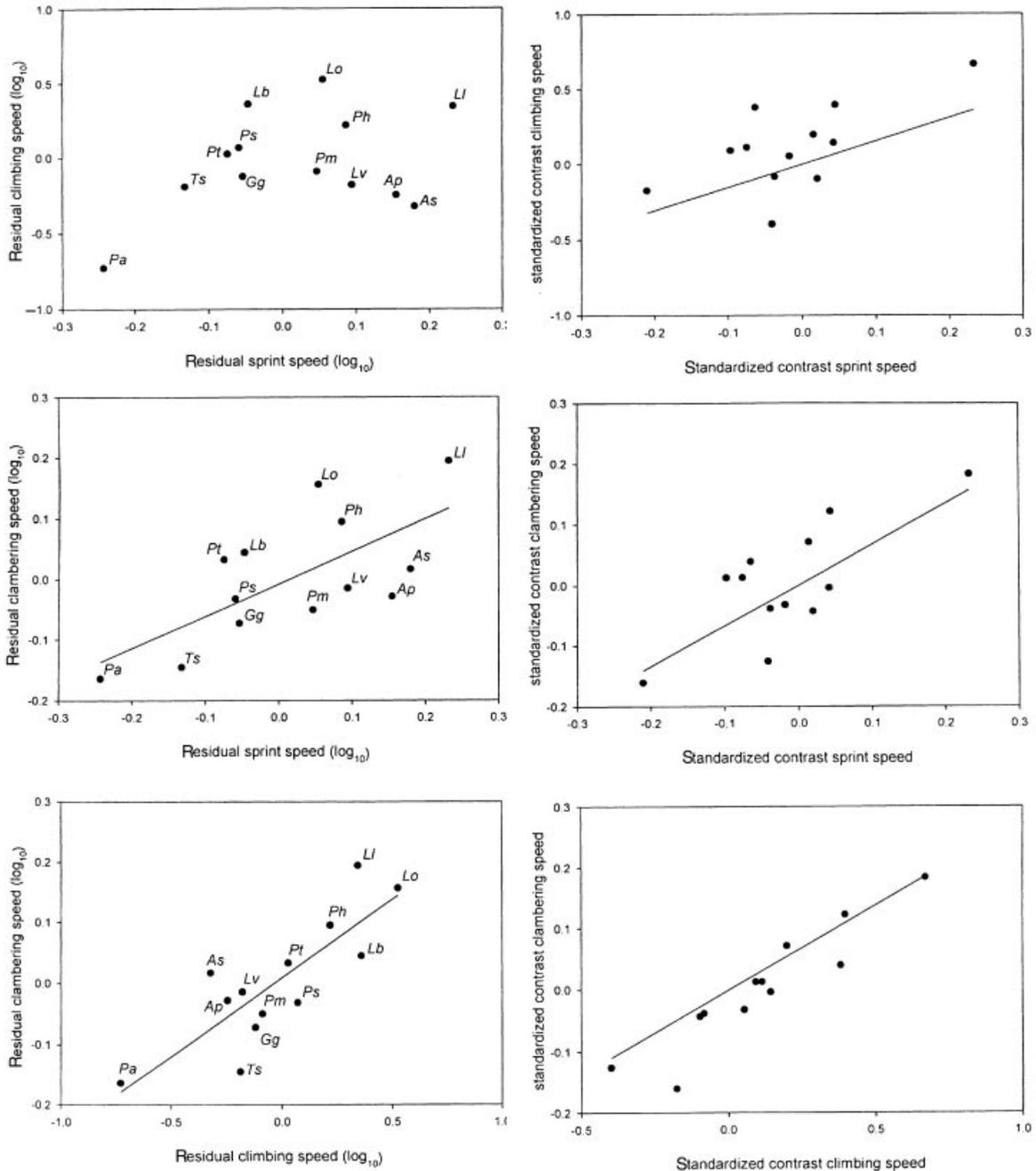


Fig. 2 Relationships among the three performance variables (sprinting, clambering and climbing speed). On the left: residuals of logarithmically transformed means per species. The point labels refer to the species (first letter of genus and species name). On the right: residuals of the phylogenetically independent contrasts.

Results

Nonphylogenetic analyses

Traditional correlation analyses revealed significant positive associations between residual sprint speed and residual clambering speed (Fig. 2, $r = 0.60$, $P = 0.03$), and between residual clambering speed and residual climbing speed (Fig. 2, $r = 0.72$, $P = 0.005$). The correlation between residual sprint and climbing speed was also positive but not statistically significant (Fig. 2, $r = 0.20$, $P = 0.50$).

Values for correlations between residual morphological and performance measures are given in Table 2. A stepwise multiple regression model with residual sprint speed as the dependent variable and residual hind limb length, residual fore limb length and intralimb ratio as independent variables revealed a marginally significant effect of morphology, in which hind limb length was the only significant contributor ($r = 0.59$, $P = 0.04$). Hind limb length was also the only independent variable retained in the model using clambering speed as the dependent variable ($r = 0.59$, $P = 0.04$). None of the morphological variables significantly contributed to variation in climbing speed.

Phylogenetic analyses

Correlation analyses based on the residual contrasts of the performance traits, revealed significant positive associations between the residual contrasts of sprint speed and clambering speed (Fig. 2, $r = 0.66$, $P = 0.01$) and between the residual contrasts of climbing speed and clambering speed (Fig. 2, $r = 0.72$, $P = 0.006$). The correlation between the residual contrasts of sprint speed and climbing speed was also positive but not significant (Fig. 2, $r = 0.37$, $P = 0.21$).

Values for correlations among the residual contrasts of the morphological variables and performance measures are listed in Table 2. Multiple regression analysis (forced through the origin) shows that only variation in residual contrasts for hind limb length contributes to the variation in residual contrasts of clambering speed ($r = 0.69$, $P = 0.008$). None of the contrasts of the morphological variables significantly contributed to variation in residual contrasts of sprint speed and climbing speed.

Discussion

Our results do not support the notion of an evolutionary trade-off between sprinting and climbing or clambering ability in lacertid lizards. Of those performance measures that were significantly correlated, the relationship between variables was always positive. Moreover, the morphological traits that were measured in our study apparently did not affect the three types of locomotor performance in opposing ways. Biomechanical and physiological considerations predict that optimal designs for horizontal and near-vertical locomotion are incompatible (see Introduction). Our results suggest that these models are inappropriate or of minor importance for the evolution of locomotor performance in lacertid lizards. One exception may be that faster species have longer hind limbs and high interlimb ratios (i.e. long hind limbs relative to fore limbs) than do slower species. However, statistical support for this trend was only weak and it is not possible to assess the individual contributions of these two morphological attributes because of our relatively small sample of species and the high level of intercorrelation among variables. Certainly, the prediction that lizards with high intralimb ratios (i.e. long tibiae and short femurs) are good runners on level ground does not hold.

Table 2 Values for correlations among the measured performance and morphological variables. Pearson correlation coefficients are shown for the residuals against SVL for each species ($n = 13$, above) and the correlation coefficients for the phylogenetically independent contrasts ($n = 12$, in bold type).

| | Climbing speed | Clambering speed | Hind limb length | Fore limb length | Interlimb ratio | Intralimb ratio |
|------------------|----------------|------------------|------------------|------------------|-----------------|-----------------|
| Sprint speed | 0.20 | 0.60* | 0.59* | 0.18 | 0.60* | -0.24 |
| | 0.37 | 0.66* | 0.41 | 0.002 | 0.59* | -0.25 |
| Climbing speed | | 0.72** | 0.22 | 0.30 | -0.007 | -0.20 |
| | | 0.72** | 0.36 | 0.33 | 0.16 | -0.08 |
| Clambering speed | | | 0.59* | 0.21 | 0.57* | -0.13 |
| | | | 0.69* | 0.34 | 0.64* | -0.28 |
| Hind limb length | | | | 0.66* | 0.66* | -0.48 |
| | | | | 0.73** | 0.66* | -0.55* |
| Fore limb length | | | | | -0.12 | -0.71* |
| | | | | | 0.04 | -0.66* |
| Interlimb ratio | | | | | | 0.08 |
| | | | | | | -0.07 |

* $0.05 > P > 0.01$; ** $0.01 > P > 0.001$. After Bonferroni correction for multiple testing, none of these bivariate correlations is significant.

In sharp contrast with biomechanical predictions and findings in *Anolis*, *Sceloporus* and *Chamaeleo* (Losos & Sinervo, 1989; Sinervo & Losos, 1991; Losos *et al.*, 1993; Losos & Irschick, 1996), lacertid species with longer limbs were able to mount inclined surfaces better (especially those mimicking clambering through vegetation). Long hind limbs are thought to be maladaptive in arboreal species of lizards because they prevent climbers from maintaining their centre of mass (and balance) close to an inclined substrate. This may be especially the case for species that use perches which are narrow, relative to the animal's body size. For such lizards, sure-footedness is likely to be inversely related to limb length, because even a small lateral force exerted on the animal's body will result in a large momentum. However, for species that climb broad steep surfaces, long hind limbs may be extended laterally to maintain centre of mass (and balance) close to the substrate. Indeed, long limbs may actually be advantageous in such circumstances by providing opportunities to grasp available points of support (Kramer, 1951) or jump from one location to another (Losos *et al.*, 1989; Losos, 1990). It thus seems probable that the optimal design for nonhorizontal locomotion may strongly depend on the width of the structures being climbed. Optimal locomotion on narrow supports such as twigs, branches or stems (as performed by some *Anolis*, *Sceloporus* and *Chamaeleo* species) places different stresses on the appendicular skeleton than does optimal locomotion on wider rocks or tree trunks (as performed by some lacertid species). Also, 'clambering' through vegetation, as exhibited by many lacertid lizards probably is not comparable with the typical locomotion of twig *Anolis* or that of arboreal *Sceloporus occidentalis* and *Chamaeleo* populations. We are not aware of studies that examined movement of lacertids through vegetation, but our anecdotal observations in the field indicate that these lizards frequently shift from one perch to another rather than remaining sedentary for long periods on the same perch. In structurally complex environments, the ability to bridge gaps between successive supports (which can be satisfied by long limbs) may be more important than the skill of maintaining centre of mass close to the perch substrate.

It has been argued that trade-offs between performance measures are more likely to be revealed when only extreme habitat specialists are incorporated into analyses. For instance, Garland (1994b) suggested that a trade-off between endurance and speed capacity in humans, although obvious when comparing world class sprinters and marathon runners, would not show up when comparing individuals were not specialized in these fields of athletics. Our failure to detect a trade-off between performance measures in lacertid lizards could reflect the inclusion of habitat generalist species in our comparative analysis. Some of the species that we categorize as being 'ground-dwelling' undoubtedly climb in vegetation or among stones to some extent. Lacertid

lizards are not large animals and small size itself demands a certain degree of scansorial ability because to a small animal, the world is full of obstacles (Robinson, 1975). Likewise, individuals of the species described as 'vegetation climbers' or 'rock-dwellers' are likely to journey to the ground to forage, find partners and disperse. Therefore, it seems plausible that in most lacertid lizards, natural selection would favour a phenotype that is generalized to enable locomotion on a variety of substrates and inclines. However, this does not seem to be the case for the more habitat specialist species included in our study. The two species of *Acanthodactylus* and *L. longicaudata* are clearly specialist ground-dwellers living in open, flat areas with few vertical structures. As predicted by the habitat matrix model (Moermond, 1979; Pounds, 1988), these species excel in sprinting on level surfaces when compared with the other lacertids. However, this ability apparently does not counteract a lizard's capacity to climb or clamber. Similarly, *Lacerta oxycephala* occurs almost exclusively on stony vertical structures and is specialized at this rock-dwelling style of life. Yet, in addition to a good ability to climb inclined surfaces, this species sprints well on level surfaces.

A complementary explanation for our main result is that a lizard's sprinting, climbing and clambering performances are genetically correlated in a positive way. Studies on locomotor performance in garter snakes demonstrated a positive genetic correlation between sprint speed and endurance capacity (Garland, 1988; Brodie, 1989, 1993; Jayne & Bennett, 1990; Brodie & Garland, 1993; Garland, 1994b; but see Tsuji *et al.*, 1989; Sorci *et al.*, 1995 on lizards). Obviously, quantitative genetic studies can only be conducted at an intraspecific rather than interspecific scale. Our work in progress on one of the species tested this study (*Gallotia galloti*) suggests that a positive genetic correlation may exist between sprinting, climbing and clambering performance (unpublished data).

We conclude that in our sample of lacertid lizards, the evolution of sprinting capacity on level substrates has not hindered the ability to climb in shrubs or mount steep rock faces. This finding contrasts those found for other groups of lizards and thereby warns against premature extrapolation of ecomorphological inferences from one group of animals to another (see also Irschick *et al.*, 1997). Most people categorize animals as being arboreal, ground-dwelling, etc. and extrapolate this between groups of animals when in fact 'arboreal' in one group may imply something very different from 'arboreal' in another group. Detailed analyses of performance capacities and behaviours of animals are required to fully understand how evolution may shape their locomotor systems.

Acknowledgements

We would like to thank Jan Scholliers for taking care of the animals. Sharon Downes, Peter Aerts and two

anonymous reviewers provided valuable comments on an earlier draft of the manuscript. B.V. is a scholarship student at the I.W.T. (grant no. 951359) and R.V.D. a senior research assistant of the Science Fund – Flanders (FWO-VI). This research was supported financially by a GOA-BOF project (University of Antwerp 1999–2002).

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Received 14 July 2000; revised 20 October 2000; accepted 6 November 2000.