

Variation in speed, gait characteristics and microhabitat use in lacertid lizards

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Summary

We quantified four gait characteristics (stride length, stride frequency, step length and floating distance) over a range of running speeds in 11 lacertid lizard species known to vary in maximal sprint speed and microhabitat use. For each species, we measured snout–vent length (SVL), body mass and hindlimb length. We tested which variables determine sprint speed, how each species modulates sprint speed and whether species occurring in different microhabitats differ in speed modulation strategy. In doing so, we aimed to test the assumption that sprint speed is correlated with hindlimb length through its effect on stride length. Variation in maximal sprint speed is determined by variation in both stride length and frequency, but those species that modulate their sprint speed mainly by altering stride length appear to attain the highest maximal speeds. At maximal sprint speed, long-limbed species take larger strides because of the positive effect of hindlimb length on step length and floating

distance. However, when hindlimb length is statistically controlled for, mass has a negative effect on step length. None of the three morphological variables explained the interspecific variation in stride frequency at maximal sprint speed. Possibly, differences in physiological properties (e.g. muscle contraction speed) underlie the variation in stride frequency. The 11 species modulate their speed in different ways. Lacertids often seen in vertical microhabitats do not seem to be either pronounced stride length or frequency modulators. These species alter their speed by combining the two strategies. However, species occurring mostly in open and vegetated microhabitats are, respectively, stride length and stride frequency modulators. This difference in running style is substantiated by interspecific morphological differences.

Key words: ecomorphology, gait characteristics, interspecific comparison, locomotion, Lacertidae, phylogenetic analysis.

Introduction

Locomotor performance varies considerably within and among species. In some cases, variation in locomotor performance has been linked to ecological differences (e.g. Garland et al., 1988; Garland and Losos, 1994; McPeck et al., 1996; Shipley et al., 1996; Garland, 1999; Perry, 1999; Melville and Swain, 2000). For instance, *Anolis* lizards that differ in sprint performance on dowels of different diameters use differently sized perches in nature (Irschick and Losos, 1999). The relationship between locomotor performance and ecological factors is generally interpreted in evolutionary terms, i.e. differences in selective pressures among species are considered to shape the tight correlation between the two variables. However, the variation in locomotor performance may also be explained by proximate factors. A large body of literature exists on the influence of morphological differences on the variation in performance (e.g. Garland, 1983; Heglund and Taylor, 1988; Emerson, 1991; Srygley and Dudley, 1993; Garland and Losos, 1994; Miles, 1994; Rayner, 1995; Kolok, 1999; Melville and Swain, 2000) and, for terrestrial locomotion, the positive correlation between (hind)limb length and speed seems self-evident (e.g. Garland and Janis, 1993; Garland and Losos, 1994; Bauwens et al., 1995; Bonine and

Garland, 1999; Melville and Swain, 2000). In all these cases, the underlying biomechanical assumption is that long limbs allow animals to take large strides, resulting in high sprint speeds.

We have three problems with the cause/effect assumption that hindlimb length affects stride length, which affects sprint speed. First, this often-cited assumption has never been explicitly tested. Second, stride length is not the sole determinant of sprint speed. Stride length is made up of two components: step length (or the distance the body moves forward during stance) and floating distance [or the distance the body moves forward when the (hind)limbs are not in contact with the substratum]. Moreover, sprint speed is the result of combining a particular stride length with a particular stride frequency. This implies that, in theory, species that are unable to lengthen their stride (for whatever reason) can ultimately attain identical sprint speeds solely by increasing their stride frequency. Moreover, interspecific variation in stride length and stride frequency at maximal sprint speed could originate in different ways. One possibility is that different species employ different speed modulation strategies, i.e. they alter stride length and frequency with speed to

different extents. Ultimately, maximal sprint speed will differ between species that alter stride length and frequency with speed in diverse ways because different speed modulation strategies place different limits on the maximal attainable speed. However, all species might employ the same speed modulation strategy, but the increase in stride length or frequency with speed might be limited at different points among species. How far each species can increase its stride length or frequency might be determined by its design (e.g. morphology, physiology, biochemistry). In this case, species will differ in maximal sprint speed. To elucidate the mechanistic basis of the variation in sprint speed, we therefore need information on how each species realises its maximal sprint speed (i.e. speed modulation strategy) and on the values of the gait characteristics at maximal sprint speed.

The third problem with the hindlimb length→stride length→sprint speed assumption is that the way in which animals realise their maximal sprint speed might differ among species occupying different microhabitats. To our knowledge, no quantitative data exist on the relationship between ecological variables and speed modulation. White and Anderson (1994) hypothesised that differences in gait characteristics with speed might reflect differences in foraging strategy (active *versus* ambush predators) among teiid lizards, and Van Damme et al. (1998) suggested that the way in which lizards realise their ultimate sprint speed may be influenced by predation pressure.

One of the most obvious potential ecological factors likely to influence locomotor style is microhabitat use because different substrata (e.g. open, sandy, patches of vegetation, inclined substrata) will impose different or even conflicting demands on steady-running style. Species from open areas can increase sprint speed by increasing both stride length and frequency; the former by including large floating distances in the stride cycle. Species living among patches of vegetation, in contrast, would be expected to modulate speed by altering stride frequency. Because these species will often have to move around obstacles, they must be able to change direction fast and frequently. In this context, it seems beneficial to increase the number of ground contact phases (and thus stride frequency) as these present the only possibilities for altering the direction of motion. Species occurring on inclined surfaces can increase speed by increasing stride frequency or stride length; in the latter case, only if the change in stride length is due to an increase in step length alone. No floating phases can be incorporated in the stride cycle because losing contact with the surface may have disastrous consequences, for climbing animals

In this study, we aimed to test the hindlimb length→stride length→sprint speed assumption for 11 lacertid lizard species known to vary considerably in maximal sprint speed and microhabitat use. Specifically, we test the following hypotheses: (i) that differences in both stride length and frequency contribute to variation in maximal sprint speed; (ii) that differences in both step length and floating distance contribute to differences in stride length at maximal sprint

speed; (iii) that differences in morphology (snout–vent length, SVL, mass, hindlimb length) explain differences in step length, floating distance and stride frequency at maximal sprint speed; (iv) that the variation in maximal sprint speed is due to differences in modulation strategies (stride length *versus* frequency); (v) that the way in which stride length changes with speed depends on the way in which both step length and floating distance change with speed; (vi) that morphological differences explain the way in which step length, floating distance and stride frequency change with speed and (vii) that species occurring in different microhabitats use different speed modulation strategies.

Materials and methods

Animals

We collected nine of the 11 species during the summers of 1994–1999 at different sites in Western Europe and the Canary Islands (see Table 1 for a list of species). *Latastia longicaudata* and *Takydromus sexlineatus* were obtained commercially. Adult males and non-gravid females were used in this study. We transported all lizards to the laboratory at the University of Antwerp, Belgium. Small species (<80 mm SVL) were housed in groups of four or five, with species kept apart, in glass terraria (100 cm×50 cm) with a sandy substratum, some stones and patches of vegetation. Multiple refuges and basking spots were available in each terrarium, and two light bulbs (100 W each) provided light and heat for 10 h per day, enabling the lizards to thermoregulate. The larger species, *Gallotia galloti* and *Lacerta bilineata*, were housed individually in identical terraria. We fed the animals live crickets dusted with calcium daily. Water was always present.

Morphometrics

We took the following external measurements with digital

Table 1. Species used in this study, number of individuals for which we obtained data on gait characteristics, number of digitised sequences and maximal sprint speed

Species	Number of individuals	Number of sequences	V_{\max} (m s ⁻¹)
<i>Gallotia galloti</i> (Oudart)	8	41	1.93
<i>Lacerta oxycephala</i> (Dumeril & Bibron)	8	47	2.02
<i>Lacerta bedriagae</i> (Camerano)	10	46	1.79
<i>Podarcis sicula</i> (Rafinesque)	9	43	1.67
<i>Podarcis muralis</i> (Laurenti)	10	48	2.14
<i>Podarcis hispanica</i> Steindachner	8	40	2.03
<i>Podarcis atrata</i> Steindachner	8	40	1.09
<i>Podarcis tiliguerta</i> Gmelin	10	47	1.55
<i>Lacerta bilineata</i> Daudin	4	26	2.68
<i>Takydromus sexlineatus</i> Daudin	8	24	1.33
<i>Latastia longicaudata</i> (Reuss)	6	31	3.34

Data are taken from Vanhooydonck and Van Damme (2001) and Vanhooydonck et al. (2001).

callipers (Mitutoyo, CD-15DC) to the nearest 0.01 mm: snout–vent length (SVL), measured from the tip of the snout to the posterior edge of the anal scale; femur length, measured from the hip to the knee joint; tibia length, measured from the knee joint to the ankle; and metatarsal length, measured from the ankle to the base of the third toe. All animals were weighed on an electronic balance (A&D Instruments, FX-3200) to the nearest 0.01 g. The sum of femur length, tibia length and metatarsal length (hereafter referred to as hindlimb length) was used in subsequent analyses. Thus, our measurement of hindlimb length does not correspond to the measure of hindlimb span (e.g. Bonine and Garland, 1999), which takes variation in the width of the pelvis into account.

We calculated the mean values for each species of the three morphological variables (SVL, mass, hindlimb length) and logarithmically (\log_{10})-transformed them before statistical analyses.

Performance

Data on maximal sprint speed of the 11 species are taken from our previous studies (Vanhooydonck and Van Damme, 2001; Vanhooydonck et al., 2001) and given in Table 1. We calculated the logarithm (\log_{10}) of the mean maximal sprint speed for each species and used these values in subsequent analyses.

Microhabitat use

We observed lizards in a large (4 m×4 m) terrarium containing the following eight types of microhabitat: (i) a dense stand of purple moor grass (*Molinia caerulea*), with a total area of 3 m²; (ii) a strip of grass (*Poa annua*), with an area of 3 m²; (iii) a patch of moss with a surface area of 3 m²; (iv) an area of approximately 3 m² closely planted with shrubs (*Lonicera* spp.); (v) a strip of sand, also 3 m² in surface area; (vi) a wall of piled stones, 0.5 m high and with a top surface area of 0.5 m²; (vii) a series of logs, loosely stacked to a height of 0.3 m; and (viii) a tree trunk of 20 cm diameter, cut off at a height of 40 cm. Eight 500 W lamps, one above each type of microhabitat, provided heat and light throughout the experiment.

The smaller species (SVL < 80 mm) were introduced into the test terrarium in groups of no more than eight individuals, the larger species in groups of no more than five individuals. Species were always kept apart. To avoid disturbance, all observations were made from behind a blind. After an initial habituation period of 1 h, we recorded the microhabitat occupied by each individual lizard in the terrarium at 30 min intervals. To facilitate interpretation, we decided to pool the types of microhabitat described above into three classes that clearly differ in structural features: an ‘open’ microhabitat [a combination of low grass (ii), moss (iii) and sandy (iv) patches], a ‘vegetated’ microhabitat [a combination of moor grass (i) and shrub (v) patches] and a ‘vertical’ microhabitat [stone wall (vi), logs (vii) and tree trunk (viii)].

For each species, we measured the proportion of time spent in each of the three microhabitats (open, vertical or vegetated).

We arcsine-transformed all proportions before subsequent statistical analyses. We used the arcsine transformation because it is the most appropriate when dealing with proportions (Sokal and Rohlf, 1995).

We were unable to make observations on microhabitat use in *Podarcis hispanica* and *Podarcis atrata* because the experimental arrangement described above was not available when we performed the morphological, performance and kinematic measurements on these two species. All analyses concerning microhabitat use are thus for nine species only.

Gait analysis

To obtain estimates of gait characteristics, we filmed all lizards with a high-speed video camera (NAC 1000) at 500 frames s⁻¹ in dorsal view while they were running on a moving treadmill belt. To facilitate subsequent digitisation, we marked the lizards with small white dots (of non-toxic paint) mid-dorsally on the pelvis and on the dorsal and ventral sides of the second toe of the hindlimb. After marking, the lizards were placed in an incubator set at the different species-selected body temperatures (38 °C for *L. longicaudata*, 35 °C for the other species) (see Castilla et al., 1999) for at least 1 h. The lizards were then placed, one at a time, on the belt moving at a low speed. Once the animals started running, the speed of the belt was increased slowly but steadily. We therefore obtained video sequences of each individual lizard at a wide range of running velocities.

In an initial analysis, the speed attained during each recorded running bout was assessed by digitising (using a NAC-1000 XY coordinator) a marker on the moving belt, as a reference, and the pelvic marker on the first and last frame of potentially useful sequences. A sequence was considered ‘potentially useful’ only if the lizard took at least five sequential steps at a constant speed and moved in a straight line. For each individual, we then aimed to select (at least) five sequences evenly spread throughout the range of speeds for further detailed analyses. For practical reasons (e.g. narrow range of speeds), this was not always possible. On these sequences, we digitised a marker on the moving belt and the pelvic and toe markers every third frame (i.e. with a time interval of 0.006 s). We chose to digitise a hindfoot because the posterior limbs generate most of the propulsive power in these animals (Snyder, 1952). The numbers of individuals and sequences used for complete digitisation and determination of maximal sprint speed (see Vanhooydonck and Van Damme, 2001; Vanhooydonck et al., 2001) are given in Table 1. The speeds at which lizards ran for each digitised sequence and species are presented in Fig. 1.

We obtained the following variables from the digitised images using the method described by Van Damme et al. (1998): (i) stride length, the distance travelled by the centre of mass during one complete cycle of limb movements (cf. Alexander, 1977a,b, 1982), here measured as the distance travelled from the time the hindfoot touches the ground until the time when that same hindfoot touches the ground in the following cycle; (ii) stride frequency, the number of complete

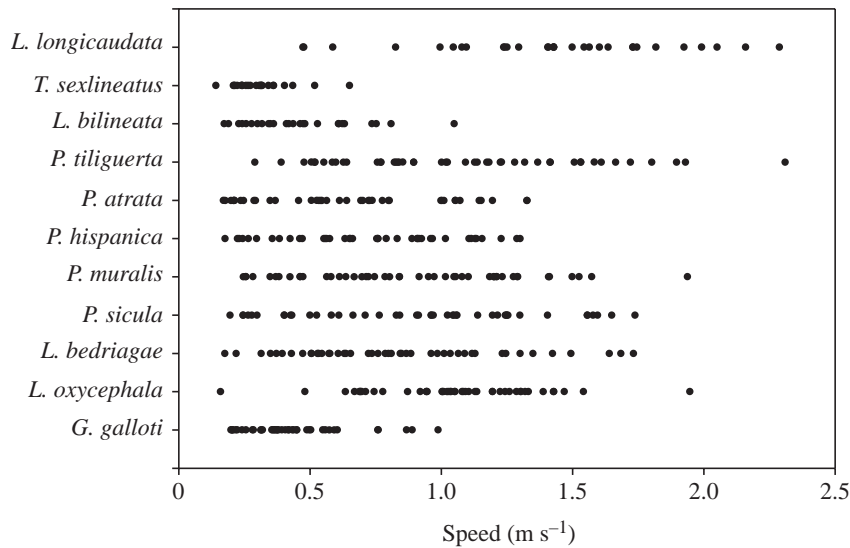


Fig. 1. Speeds at which the lizards ran on the treadmill for each species. Each dot represents a digitised sequence. Full species names are given in Table 1.

cycles per second; (iii) step length, the distance travelled by the centre of mass during the stance of a particular leg (Alexander, 1977a; McMahon, 1984), here measured as the distance travelled from the time the hindfoot touches the ground until the time that same hindfoot loses contact with the substratum in the same cycle; (iv) floating distance, the distance travelled by the centre of mass when neither of the hindfeet is in contact with the ground [(calculated as stride length minus 2(step length)], here measured as the distance travelled from the time both hindfeet lose contact with the substratum until the time one of the hindfeet touches the ground again.

We logarithmically (\log_{10})-transformed running speed and

the kinematic variables. For each species, we then regressed each of the four gait characteristics against running speed (see Table 2 for regression equations). We used the regression equation to estimate the values of the four gait characteristics (i.e. stride length, stride frequency, step length and floating distance) at maximal sprint speed (as measured on the moving belt) for each species. These estimated values at maximal sprint speed and the slopes (a in Table 2) of each regression equation were used in subsequent analyses, the former to test which variables determine maximal sprint speed and the latter to test how species realise their maximal sprint speed and whether speed modulation strategies differ among species occupying different microhabitats.

Statistical analyses

Because species share parts of their evolutionary history, they cannot be regarded as independent data points in statistical analyses (Felsenstein, 1985, 1988; Harvey and Pagel, 1991; Garland et al., 1993). A fundamental assumption in traditional statistical analyses, however, is that data points are independent of each other. In recent years, various computer programs have been developed to take phylogenetic relationships into account in statistical analyses (Harvey and Pagel, 1991; Garland et al., 1993; Losos and Miles, 1994). In the present study, we used the phylogenetic independent contrasts approach (Felsenstein, 1985, 1988).

The independent contrasts method requires information on the topology of the phylogenetic tree. The phylogeny of the Lacertidae is incompletely resolved, and we had to use a

Table 2. Regression equations describing the relationships between the gait characteristics and running speed of lizards running on the moving belt

Species	Stride length		Stride frequency		Step length		Floating distance	
	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>
<i>Gallotia galloti</i>	0.40	-1.01	0.60	1.01	0.26	-1.34	0.009	0.001
<i>Lacerta oxycephala</i>	0.35	-1.09	0.65	1.09	0.27	-1.38	<i>0.006</i>	<i>-0.001</i>
<i>Lacerta bedriagae</i>	0.42	-0.94	0.58	0.94	0.33	-1.19	<i>0.003</i>	<i>-0.006</i>
<i>Podaras sicula</i>	0.48	-0.95	0.52	0.95	0.36	-1.24	0.009	0.0001
<i>Podaras muralis</i>	0.46	-1.11	0.54	1.11	0.43	-1.34	<i>-0.003</i>	<i>-0.006</i>
<i>Podaras hispanica</i>	0.33	-1.15	0.67	1.15	0.29	-1.41	<i>0.00001</i>	<i>-0.004</i>
<i>Podaras atrata</i>	0.25	-1.17	0.75	1.17	0.25	-1.40	<i>-0.001</i>	<i>-0.005</i>
<i>Podaras tiliguerta</i>	0.53	-0.98	0.47	0.98	0.41	-1.23	<i>0.005</i>	<i>-0.006</i>
<i>Lacerta bilineata</i>	0.38	-0.96	0.62	0.96	0.24	-1.26	0.010	-0.001
<i>Takydromus sexlineatus</i>	0.31	-1.11	0.69	1.11	0.18	-1.33	<i>0.004</i>	<i>-0.007</i>
<i>Latastia longicaudata</i>	0.53	-0.97	0.47	0.97	0.37	-1.26	0.015	-0.001

We pooled all sequences per species.

All regressions were significant, except the regressions of floating distance against running speed in some species (given in italic type).

Equations are of the form $\log y = a \log x + b$, where x is running speed and y is the gait characteristic. On the basis of these regression equations, we estimated stride length, stride frequency, step length and floating distance at maximal sprint speed.

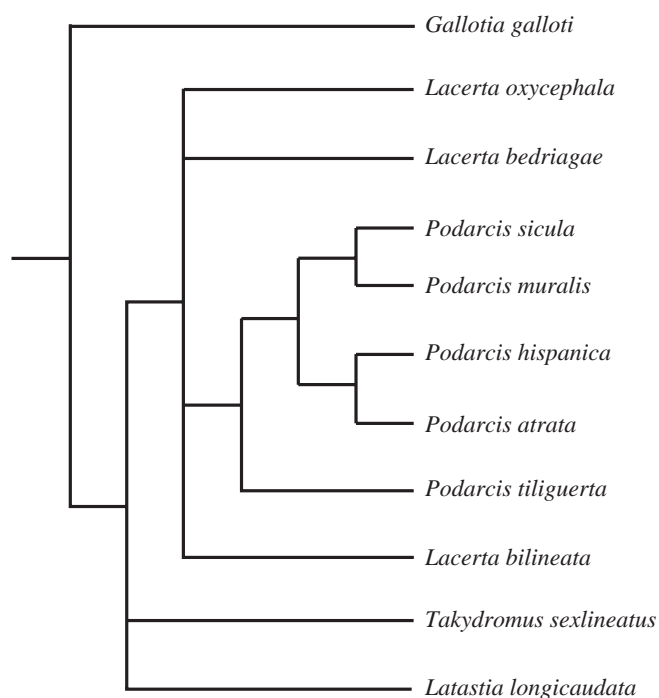


Fig. 2. Hypothesised phylogenetic relationships among the 11 lacertid lizard species under study. The phylogeny is incompletely resolved, and this tree should be considered a best approximation. Polytomies are treated as 'hard' for the purposes of phylogenetic analyses (see text).

combination of results from mitochondrial DNA (Harris et al., 1998; Harris and Arnold, 1999) and morphological studies (Arnold, 1989, 1998) to compile a tree that is the best approximation currently available (Fig. 2). Some unresolved polytomies remain. However, all attempts at phylogeny reconstruction in lacertids, even those using molecular techniques, have been unable to unravel these relationships, and the polytomies may, in fact, represent explosive speciation events (Arnold, 1989; Harris et al., 1998; Harris and Arnold, 1999; Fu, 2000). We therefore considered the unresolved nodes to be 'hard' polytomies (see Purvis and Garland, 1993). All branch lengths were set to unity, because few data are available on divergence times within lacertids. It has been shown that the actual length of the branches does not usually greatly affect the outcome of phylogenetic statistical 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 (Garland et al., 1999) did not show any significant correlation between the absolute values of the standardised contrasts and their standard deviations, implying that branch lengths were adequate for all traits.

For each species, we calculated the independent contrasts of the log-transformed mean values of the morphological (SVL, mass, hindlimb length) and performance (maximal sprint speed) variables, of the arcsine-transformed proportions of the observations on microhabitat use (open, vertical, vegetated

microhabitat) and of the species-specific slopes of the regressions of the four gait characteristics (stride length, stride frequency, step length, floating distance) against running speed and of the same gait characteristics at maximal sprint speed (extrapolations based on regression equations, see above).

The independent contrasts were then used as input for a series of backward stepwise multiple regressions through the origin (see Garland et al., 1992). A graphical representation of the different regression analyses, apart from those concerning microhabitat use, is shown in Fig. 3A. In the regressions in which we used the contrasts of the slopes of the gait characteristics against speed, we never introduced the contrasts of the slopes of stride length against speed and the contrasts of the slopes of stride frequency against speed simultaneously in the analyses because these two variables are, by definition, inversely related. To test for the context-dependency of speed modulation among the 11 lizard species, we correlated the contrasts of the three microhabitat variables with the contrasts of the slopes of stride frequency against speed. By definition, introducing the contrasts of the slopes of stride length against speed in the analyses gives the opposite result.

Results

Gait characteristics at maximal sprint speed

The variation in contrasts of maximal sprint speed is explained, by definition, by the variations in contrasts of stride length and frequency (Fig. 3B). Species that attain a high sprint speed do so by taking larger (standardised regression coefficient $r=0.90$) and more frequent ($r=0.69$) strides.

The variation in contrasts of stride length, in turn, is largely (97%) explained by the variations in contrasts of step length and floating distance (Fig. 3B). In other words, large strides are accomplished by taking large steps ($r=0.80$) and having long floating phases ($r=0.37$).

The variation in contrasts of step length is largely explained by the variations in contrasts of mass and hindlimb length (Fig. 3B). The variation in contrasts of SVL does not contribute significantly to the variation in contrasts of step length. Species that take large steps have relatively long hindlimbs ($r=1.92$) and are relatively light ($r=-1.45$).

Only the variation in contrasts of hindlimb length contributes significantly to the variation in contrasts of floating distance (Fig. 3B). The variations in contrasts of SVL and mass do not contribute significantly to the variation in contrasts of floating distance. Thus, species with long hindlimbs have long floating phases.

Variation in none of the contrasts of the three morphological variables (SVL, mass and hindlimb length) explains the variation in contrasts of stride frequency ($r=0.50$, $F_{3,7}=0.76$, $P=0.55$).

Speed modulation

The variation in contrasts of maximal sprint speed is marginally explained ($P=0.075$) by the variation in contrasts

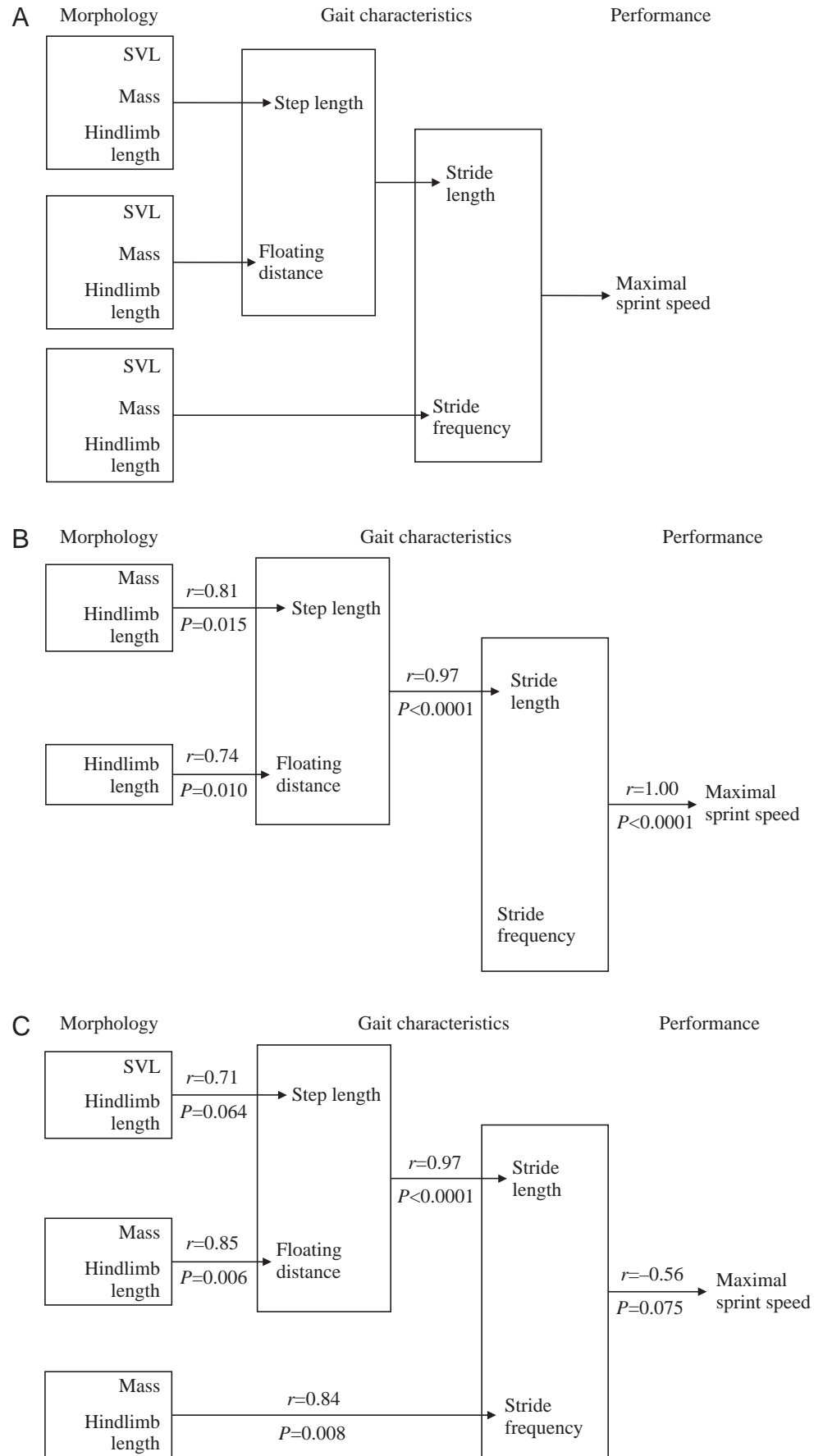


Fig. 3. Graphical representations of the multiple regression analyses we performed on the morphological, gait characteristics and performance data in the 11 lacertid lizard species. (A) All potential relationships. Each arrow represents one analysis. Independent variables introduced into the same multiple regression are boxed. Arrows are drawn from the independent variables box to the dependent variable box. We performed two series of analyses: one that included the (contrasts of the) values for the four gait characteristics at maximal sprint speed, and the second on the (contrasts of the) slopes of each of the four gait characteristics against speed. (B) Significant relationships in the multiple regression analyses including the contrasts of the estimated values of the four gait characteristics at maximal sprint speed. (C) Significant relationships in the multiple regression analyses including the contrasts of the slopes of each gait characteristic against speed. By definition, the contrasts of the slopes of stride length and stride frequency against speed are inversely related so we never introduced them simultaneously into the analyses. Instead, we included only the contrasts of the slopes of stride frequency against speed in the analysis; including the contrasts of the slopes of stride length against speed gives the opposite result ($r=0.56$; $P=0.075$).

of the slopes of stride length against speed (Fig. 3C). Because the contrasts of the slopes of stride frequency and stride length against running speed are inversely related (by definition), the opposite relationship is obtained for the contrasts of the slopes of stride frequency and maximal sprint speed. This means that species attain a higher maximal sprint speed if they modulate their speed mainly by increasing stride length rather than stride frequency.

The variation in contrasts of the slopes of stride length, in turn, is explained by the variations in contrasts of the slopes of step length and floating distance against speed (Fig. 3C). Lizards modulate their stride length by changing both step length ($r=0.83$) and, to a lesser extent, floating distance ($r=0.37$).

The variation in contrasts of SVL and hindlimb length explains the variation in contrasts of the slopes of step length against speed (Fig. 3C). The variation in contrasts of mass does not contribute to this variation. Species in which step length changes with speed have relatively long hindlimbs ($r=2.30$) and a relatively small SVL ($r=-2.16$).

The variation in contrasts of the slopes of floating distance against speed is explained by the variations in contrasts of mass and hindlimb length (Fig. 3C). The variation in contrasts of SVL does not contribute significantly to the variation in contrasts of the slopes of floating distance against speed. Species with relatively long hindlimbs ($r=1.77$) and a relatively small mass ($r=-1.12$) alter their floating distance with speed.

The variations in contrasts of mass and hindlimb length explain a significant proportion of the variation in contrasts of the slopes of stride frequency against speed (Fig. 3C): relatively heavy species ($r=1.78$) with relatively short hindlimbs ($r=-2.14$) alter stride frequency with speed. The variation in contrasts of SVL does not contribute significantly to the variation in contrasts of the slopes of stride frequency against speed.

The variation in contrasts of time spent in the open microhabitat is explained by the variation in contrasts of the slopes of stride frequency against speed (Fig. 4A). As mentioned above, the contrasts of the slopes of stride length and stride frequency are inversely related, so the opposite is true for the relationship between the contrasts of time spent in the open microhabitat and the contrasts of the slopes of stride length against running speed. This means that species occurring mostly in open microhabitats increase their speed mainly by increasing stride length and less by increasing stride frequency.

The variation in contrasts of time spent in the vertical microhabitat is not explained by the variation in contrasts of the slopes of stride frequency against speed ($r=0.20$, $F_{1,7}=0.30$, $P=0.60$). The variation in contrasts of time spent in the vegetated microhabitat is, however, explained by the variation in contrasts of the slopes of stride frequency against speed (Fig. 4B). In other words, species occurring mostly amongst vegetation increase their speed mainly by increasing stride frequency and less by increasing stride length.

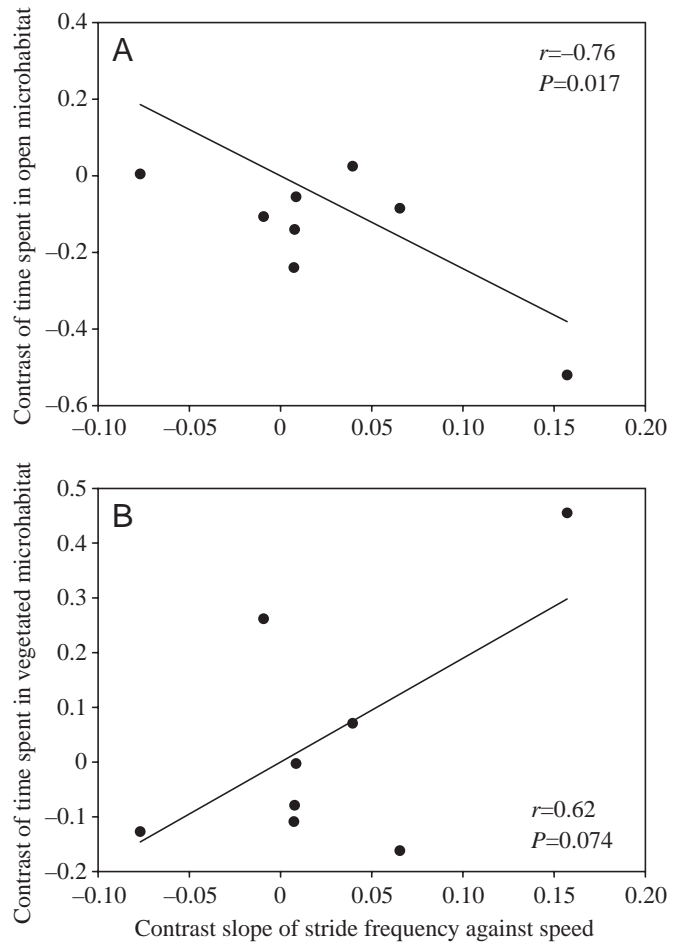


Fig. 4. Bivariate correlations between the contrasts of microhabitat use and the contrasts of the slopes of stride frequency against speed (forced through the origin). (A) Relationship between the contrasts of time spent in the open microhabitat and the contrasts of the slopes of stride frequency against speed. (B) Correlation between the contrasts of time spent in the vegetated microhabitat and the contrasts of the slopes of stride frequency against speed. In both cases, including the contrasts of the slopes of stride length against speed gives the opposite result ($r=0.76$, $P=0.017$; $r=-0.62$, $P=0.074$, respectively).

Discussion

Among the 11 lacertid lizards under study here, it is clear that the variation in maximal sprint speed is determined by variation in both stride length and stride frequency. The highest sprint speeds are, however, achieved by those species that modulate their speed mainly by increasing stride length. This is not surprising because stride frequency cannot be increased indefinitely. The dynamics, such as the force/velocity relationships, of the muscles involved and the inertial properties of the musculo-skeletal system at the moment of maximal performance (i.e. maximal activation of muscles) set the potential maximal frequency. Because of the great overall resemblance between lacertid lizards, it can be assumed that the maximal attainable stride frequencies for the different species will be of the same order of magnitude. When

comparing stride frequencies at maximal sprint speed among species, the lowest stride frequency is more than half the highest (the lowest stride length is one-third of the highest). If species were to employ a stride frequency modulation strategy, they would reach their respective stride frequency limit earlier (i.e. at a lower speed) than if they were to employ a stride length modulation strategy. In the latter case, they can therefore continue to increase sprint speed for longer, resulting in a higher maximal sprint performance.

Stride length, in turn, is determined by step length and floating distance. In this case, speed-dependent changes in step length have a greater effect on changes in stride length than does variation in floating distance with speed. Hindlimb length correlates positively (for a given body mass) both with step length and with floating distance. The positive effect of hindlimb length on step length is expected if the joint angles at touch-down and take-off are equal in short-limbed and long-limbed lizards. In this case, the distance the body moves forward during stance will be greater in species with longer limbs. Long-legged birds and mammals appear to be able to take longer steps (Hoyt et al., 2000), but Irschick and Jayne (1999) found no correlation between limb length and step length among five species of lizards.

The positive effect of hindlimb length on floating distance is in agreement with biomechanical predictions. A stride cycle that includes a floating phase can be regarded as two single leg jumps in sequence. The distance an animal can jump is determined, amongst other factors, by the distance through which it accelerates during push-off (Alexander, 1972). In this case, the latter distance relates to hindlimb length. Thus, long-limbed animals are predicted to perform the longest jumps. Quantitative data on jumping performance in *Anolis* lizards (Losos, 1990) and tree frogs (Emerson, 1991) substantiate this prediction.

Among the 11 lacertid species under study, mass has a negative effect on step length for lizards with equally long hindlimbs. If we assume that muscle mass scales proportionally with body mass (m) and that force (F) scales proportionally with the cross-sectional area of the muscles, thus with $m^{2/3}$, the acceleration (a) of the centre of mass will be lower for a given muscle activation pattern ($F=ma$). This will then result in a smaller forward displacement of the body and, thus, a shorter step length. Hoyt et al. (2000) also found that relative step length (i.e. expressed in units of leg length) is smaller in larger mammals and birds than in smaller ones.

None of the morphological variables that we introduced in the regression analysis explained a significant proportion of the interspecific variation in stride frequency at maximal sprint speed. Among seven teiid lizard species, however, stride frequency appeared to be negatively affected by body mass at body-length-equivalent speeds (White and Anderson, 1994), and stride frequency at burst running speed decreased with body mass in the lizard *Dipsosaurus dorsalis* (Johnson et al., 1993). In contrast, mass had no effect on stride frequency in painted turtles *Chrysemys picta* (Zani and Claussen, 1995). The physiological properties of the limb muscles may determine

stride frequency. For example, limb cycling frequency increases with increasing body temperature in *D. dorsalis* (Swoap et al., 1993). It has been suggested that the positive relationship between frequency and temperature is due to the thermal dependence of muscle contraction speed (e.g. Bauwens et al., 1995). However, the seemingly straightforward link between muscle contractile properties and maximal stride frequency remains obscure because muscle cycling frequency for maximal power output largely exceeds maximal limb cycling frequency in *D. dorsalis* (Johnson et al., 1993; Swoap et al., 1993).

Speed modulation strategy during steady locomotion differs among lacertid species occurring in different microhabitats. Species that occur mainly in open microhabitats increase sprint speed mainly by increasing stride length, while species occurring in patches of vegetation mainly increase stride frequency. This is as expected. In an open microhabitat, species can include a floating phase in their stride cycle to increase stride length. A vegetated microhabitat, in contrast to an open one, poses conflicting demands on running style. Lizards occurring among patches of vegetation need to change direction fast and frequently. They can do so only when their feet are touching the ground. Therefore, it seems logical for these animals to increase speed mainly by increasing stride frequency. This reasoning is based on our data on steady-speed locomotion. In contrast, during unsteady locomotion, such as when accelerating, some lizard species are known to increase speed by increasing stride frequency initially and by subsequently increasing stride length (Irschick and Jayne, 1998).

Each steady-running style (stride length *versus* stride frequency modulation) seems to place specific demands on the locomotor apparatus of the lizards. While stride-length-modulating species appear to be long-limbed (for a given mass or SVL) and light or small (for a given hindlimb length), stride-frequency-modulating species are short-limbed (for a given mass) and heavy (for a given hindlimb length). Long-limbed lizards are able to change stride length over a greater range because limb length sets the upper limit on step length (in theory, maximal step length equals twice leg length) and floating distance (as argued above). Because, at a given speed, stride length and frequency are inversely related, long-limbed lizards have lower stride frequencies at any speed than short-limbed animals.

It is unclear why stride-length-modulating species should be light or small and stride frequency modulators heavy (all relative to hindlimb length). In Mammalia, the opposite effect was found (Strang and Steudel, 1990): larger mammals change speed mainly by altering stride length, while smaller mammals do so mainly by increasing stride frequency. However, Strang and Steudel (1990) state that it is not clear how the interrelationship between size and hindlimb length affects their results. Therefore, the morphological basis for the differences in how species change their sprint speed is far from clear. Data are needed on the physiology and architecture of the musculo-skeletal system to determine the factors that affect the way in which animals modulate sprint speed.

Species occurring mainly in vertical microhabitats do not seem to be either pronounced stride length or frequency modulators. They alter their speed by combining the two strategies. Neither stride length nor frequency can be indefinitely increased in this context. When climbing up vertical surfaces, animals need to establish a secure grip on the surface because slipping could be disastrous. This is in sharp contrast to locomotion on the level, where slipping does not constitute such a major hazard. Taking time to get a good grip and to position the legs precisely potentially constrains stride frequency. Taking larger strides in the same context can only be done by increasing step length; floating phases will cause the animals to fall from a vertical surface. We tested this idea by correlating the contrasts of the slopes of floating distance against speed with the contrasts of time spent in the vertical microhabitat. The relationship between the two variables was negative ($r=-0.65$; $P=0.057$) and therefore appears to substantiate our hypothesis. The inability to include floating phases into the stride cycles greatly limits stride length in lizards living on steep inclines.

By employing a stride length modulation strategy, species from open microhabitats are able to attain faster maximal sprint speeds than species occurring mainly in the other two microhabitats. Being able to escape fast in an open environment appears to be 'ecologically relevant', while high sprint speeds might be less important in enclosed environments (see B. Vanhooydonck and R. Van Damme, in preparation). On the basis of these results, it is tempting to conclude that the speed modulation strategy of lizards has been shaped by natural selection to fulfil the specific requirements set by the environmental context. However, we realise that sprint speed might be confounding the relationship between microhabitat use and speed modulation strategy. The sole objective of a lizard living in open areas might be to attain high sprint speeds. The way to maximise level sprinting speed is to modulate speed mainly by increasing stride length (see above). Because sprint capacity is correlated with occurrence in an open microhabitat (B. Vanhooydonck and R. Van Damme, in preparation), the latter might be correlated indirectly to speed modulation strategy. Theoretically, this could be tested by comparing species with the same maximal sprint speeds but from different microhabitats. In practice, this is impossible because the lacertid lizards studied here seem to differ in locomotor capacity depending, amongst other factors, on their microhabitat use (B. Vanhooydonck and R. Van Damme, in preparation).

Fundamental to this study are the assumptions that natural selection moulds the way in which lizards adapt their speed to their life style (open, vegetated or vertical microhabitat) and that running style is fixed within species. In other words, we assumed that, if species use a running style 'adapted' to life in their natural surroundings, the same animal will use the same speed modulation strategy in different contexts. Data on locomotor styles of level-running and climbing geckoes substantiate this assumption (Zaaf et al., 2001). However, to test explicitly whether running style in the lacertid lizards

studied here is plastic, we need quantitative data on their speed modulation strategies on different, ecologically relevant, substrata (e.g. level *versus* inclined surfaces, open areas *versus* patches of vegetation).

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