Evolutionary Ecology Research, 1999, **1**: 785–805

Evolutionary relationships between body shape and habitat use in lacertid lizards

Bieke Vanhooydonck* and Raoul Van Damme

Department of Biology, University of Antwerp (UIA), Universiteitsplein 1, B-2610 Wilrijk, Belgium

ABSTRACT

The aim of this study was to determine if divergence in habitat use among lacertid lizards is paralleled by morphological differentiation. For 35 lacertid species, we measured body, head and limb dimensions. Habitat use was inferred from the literature: ground-dwelling on open terrain, ground-dwelling in vegetated areas, shrub-climbing, tree-climbing, saxicolous (i.e. rock-climbing). Traditional (i.e. non-phylogenetic) statistical analyses suggest morphological differences among species groups with different habitat use. Ground-dwelling species from open habitats tend to have longer femurs, tibiae and humeri (relative to body length) than other groups. Cursorial (i.e. level-running) species have relatively high heads and trunks compared to climbing species. These differences follow biomechanical predictions and it is tempting to consider them as adaptations to habitat use. However, phylogenetic analyses of the data fail to establish a clear relationship between habitat use and morphology in the data set considered. There is a weak indication that the differences in head and trunk height have evolved as an adaptation to different habitat use, but the differences in relative limb dimensions among species groups with different habitat use vanish. Either adaptation of limb dimensions to habitat use has not occurred in lacertid lizards, or our methods are unable to demonstrate such an adaptation. We show that uncertainties in the topology of the phylogenetic tree used are unlikely to influence the outcome of our study. We also address the fact that habitat use is often similar in different branches of the phylogenetic tree, and the consequences this may have for the power of our statistical analyses.

Keywords: adaptation, ecomorphology, habitat use, Lacertidae, phylogenetic analysis.

INTRODUCTION

The apparent match of organismal structure with ecological function has stimulated many leading historical figures in biology, from Aristotle to Darwin (Lauder, 1995), and the topic remains pivotal today in such disciplines as ecophysiology (Feder *et al.*, 1987) and ecomorphology (Wainwright and Reilly, 1994). However, recent studies have rendered the structure–function relationship more obscure than previously supposed. First, although the correlation between design and function may be obvious when structures are compared among distantly related taxa (e.g. wings in bats, flippers in dolphins, paddles in moles, legs in horses), the association can be very subtle (Moreno

---

* Author to whom all correspondence should be addressed. e-mail: vhooyd@uia.ua.ac.be

and Carrascal, 1993; Van Damme *et al.*, 1997) or even non-existent (Wiens and Rotenberry, 1980; Lederer, 1984; Wiens, 1989) *within* adaptive zones. Secondly, while some characteristics can change radically and relatively rapidly, others appear immune from selection or random fluctuation. For instance, differences in the structure of the fins and limbs of tetrapods directly reflect changes in habitat and lifestyle within and between each major group, but the number of digits on both fore limbs and hind limbs in extant species is the same as it was in the ancestral group of amniotes living 340 million years ago (Carroll, 1997). Thirdly, rates of evolutionary change appear extremely variable from one group of organisms to the next (and from one time period to another) both at levels of species and of higher taxa. For instance, cichlids adapted much faster to the new trophic environments than any other families of fish from the East African Great Lakes (Coulter, 1991). Finally, even within closely related groups, ecomorphological patterns may differ substantially between environments. For example, morphological variation in Caribbean island anoles correlates primarily with perch diameter, whereas among mainland anoles, morphology correlates primarily with perch height (Irschick *et al.*, 1997). These complexities impel biologists to investigate evolutionary pathways for a range of structural characteristics, in a variety of organisms and environments.

Caribbean *Anolis* lizards have been showpieces of ecomorphological studies for many years. On each of the Greater Antillean islands, different species of *Anolis* occupying similar microhabitats tend to be similar in body size, limb and tail proportions, and other characteristics (Collette, 1961; Rand and Williams, 1969; Williams, 1972), and the functional basis for this morphological differentiation is well understood (Moermond, 1979; Pounds, 1988; Losos and Sinervo, 1989; Losos, 1990a,b,c; Losos and Irschick, 1996). The phylogeny of *Anolis* indicates that similar anole communities have evolved independently at least four times in the West Indies (Williams, 1983; Burnell and Hedges, 1990; Losos, 1992; Irschick *et al.*, 1997; Losos *et al.*, 1998), suggesting a strong and highly predictable correlation between lizard ecology (habitat use) and general morphology.

However, studies of other groups of lizards do not confirm the patterns found in Caribbean *Anolis* (e.g. Jaksic *et al.*, 1980, on *Liolaemus*; Miles, 1994, on phrynosomatid lizards). Moreover, in a recent study, Irschick *et al.* (1997) showed that ecomorphological patterns found in Caribbean anoles differ dramatically from those in mainland habitats (see above). Thus the remarkable evolutionary radiation of the West Indian anoles may not constitute a good model for other lizard groups. This inconsistency prompted us to study the relationship between habitat use and general morphology in lizards of the family Lacertidae.

Distributed over much of Europe, Asia and Africa, lacertid lizards have radiated extensively into habitats ranging from tundra to alpine meadows, heathland and Mediterranean scrub, to tropical forests, semi-desert and desert. Within these habitats, lacertids occupy microhabitats and substrates that vary considerably in structure (Arnold, 1989a): some species are mainly cursorial, and live on very open or highly vegetated terrain; others frequently climb shrubs or even trees, and yet others are mainly saxicolous. In contrast to other lizard families, differences in habitat use among lacertid lizards have not produced distinctive modifications such as adhesive toe pads or loss of limbs. Moreover, at first glance, all species seem to share the same body shape. However, a thorough study of the relationship between habitat use and morphology is lacking for this family (but see Arnold, 1989b, 1998), and more subtle adaptations may have been overlooked.

Associations between limb proportions, general body shape and habitat use can be expected because of the high structural differences among the habitats occupied by lacertids. Moreover, requirements imposed by one lifestyle may conflict with those imposed by another. Specifically, fast-running lizards from open habitats should have relatively long hind limbs (Pianka and Pianka, 1976; Garland and Losos, 1994) and short fore limbs (Snyder, 1962; Losos, 1990c). In contrast, rock- or tree-climbing species should have short fore and hind limbs (Jaksic *et al.*, 1980; Pounds, 1988; Sinervo and Losos, 1991). The body shape of cursorial species, especially those living in vegetated areas, should be laterally compressed (Snyder, 1954; Van Damme *et al.*, 1997). A dorso-ventrally flattened body seems more appropriate for tree-climbing and saxicolous species (Cartmill, 1985; Pounds, 1988; Miles, 1994).

In this study, we test the hypothesis that the ecological radiation of lacertid lizard species has produced a concordant differentiation in relative limb dimensions and general body shape. Because evolutionary history may play an important role in shaping present-day patterns, we adopt a phylogenetic approach.

MATERIALS AND METHODS

Morphology

We took morphometric measurements on specimens from 35 lacertid species (Table 1). Fixed specimens (31 species) were obtained from the Natural History Museum in London (UK), the Museum of Central Africa in Tervuren and the Royal Belgian Institute of Natural Sciences in Brussels (Belgium). A preliminary analysis comparing fixed and live specimens of the same species showed no effect of fixation on the shape characteristics considered here. Therefore, we added measurements of live specimens from an additional four species to the data set. To eliminate effects of sex and age, we only considered adult males. Between six and 29 specimens were measured per species.

We took the following measurements to the nearest 0.01 mm using digital calipers (Mitutoyo CD-15DC): snout–vent length, head length, head width, head height, body length, body width, body height, femur length, tibia length, metatarsus length, length of the second toe of the hind foot, humerus length, radius length, metacarpus length and length of the fourth toe of the front foot (see Appendix for descriptions and raw data). Tail length was not included in the analysis because many specimens had partly regenerated tails.

Habitat use

We obtained information on the habitat use of the 35 species considered from the literature (Table 1). Each of the species was attributed to one of five classes of habitat use (Arnold, 1998): (1) ground-dwelling species that live on open, sparsely vegetated terrain, typically desert or semi-desert areas; (2) ground-dwelling species that occupy densely vegetated habitats, such as meadows, heathlands and Mediterranean maquis; (3) shrub-climbing species; (4) tree-climbing species, most often seen on the trunk of trees; and (5) saxicolous species, living on boulders, rocks or walls.

Table 1. Species of lacertid lizards used in the analysis: Number of specimens measured of each species, their condition (1 = fixed, 2 = alive) and their habitat use

Species	Code	*n*	Condition	Habitat	References
Acanthodactylus aureus	AU	12	1	1	Arnold (1998)
Acanthodactylus boskianus	AB	23	1	1	Pérez-Mellado (1992), Arnold (1998)
Acanthodactylus longipes	AL	12	1	1	Pérez-Mellado (1992), Arnold (1998)
Acanthodactylus pardalis	AP	17	1	1	Arnold (1998)
Acanthodactylus scutellatus	AS	10	1	1	Pérez-Mellado (1992), Arnold (1998)
Eremias persica	EP	10	1	1	Minton (1966), Arnold (1998)
Eremias velox	EV	12	1	1	Terent'ev and Chernov (1949), Arnold (1998)
Ichnotropis capensis	IC	24	1	1	Branch (1988), Arnold (1998)
Lacerta parva	LP	9	1	1	Terent'ev and Chernov (1949), Arnold (1998)
Lacerta pater	PA	13	1	1	Schleich *et al.* (1996)
Mesalina brevirostris	MB	9	1	1	Arnold (1998)
Mesalina guttulata	MG	29	1	1	Pérez-Mellado (1992), Arnold (1998)
Adolfus africanus	AA	14	1	2	Arnold (1989b, 1998)
Adolfus jacksoni	AJ	21	1	2	Arnold (1989b, 1998)
Adolfus vauereselli	AV	10	1	2	Arnold (1989b, 1998)
Gallotia galloti	GG	7	2	2	Ashmole and Ashmole (1989)
Heliobolus spekii	HS	8	1	2	Arnold (1998)
Lacerta vivipara	VI	20	2	2	Dely and Böhme (1984), Arnold *et al.* (1978), Arnold (1998)
Ophisops minor	OM	9	1	2	Arnold (1998)
Podarcis sicula	PS	9	1	2	Arnold *et al.* (1978), Arnold (1998)
Podarcis taurica	PT	11	1	2	Kabisch (1986), Arnold (1998)
Takydromus sexlineatus	TS	11	1	2	Karsen *et al.* (1986), Arnold (1998)
Acanthodactylus haasi	AH	9	1	3	Leviton *et al.* (1992), Arnold (1998)
Algyroides nigropunctatus	AN	15	1	3	Arnold *et al.* (1978), Arnold (1998)
Lacerta viridis	LV	13	1	3	Nettmann and Rykena (1984), Arnold *et al.* (1978), Arnold (1998)
Holaspis guentheri	HG	18	1	4	Branch (1988), Arnold (1989b, 1998)
Lacerta chlorogaster	LC	13	1	4	Terent'ev and Chernov (1949), Arnold (1998)
Algyroides fitzingeri	AF	8	1	5	Forman and Forman (1981), in den Bosch (1986)
Lacerta bedriagae	BE	10	2	5	Arnold *et al.* (1978), Castilla *et al.* (1989), Arnold (1998)
Lacerta jayakari	LJ	10	1	5	Arnold (1998)
Lacerta oxycephala	LO	14	1	5	Bischoff (1984), Arnold (1998)
Podarcis erhardii	PE	12	1	5	Gruber (1986)
Podarcis filfolensis	PF	12	1	5	Bischoff (1986)
Podarcis muralis	PM	11	2	5	Arnold *et al.* (1978), Avery *et al.* (1987), Arnold (1998)
Podarcis tiliguerta	TI	12	1	5	Arnold *et al.* (1978), Van Damme *et al.* (1990)

Note: References are to studies describing habitat use. Species are classified as (1) ground-dwelling in open terrain, (2) ground-dwelling in vegetated areas, (3) shrub-climbing, (4) tree-climbing and (5) saxicolous. See text for details.

Non-phylogenetic analyses

All analyses are based on logarithmically transformed (log10) data. We evaluated size differences among species, and among species groups with different habitat use, with a nested analysis of variance (SPSSwin 5.0.1; species nested in habitat use). The among-habitat use mean squares were tested against the among-subgroups (species within habitat use) mean squares. Satterthwaite's approximation was used to calculate appropriate *F*-statistics and degrees of freedom (Sokal and Rohlf, 1994). To evaluate differences in shape, we calculated logarithms of individual trait values and regressed them against the logarithm of snout–vent length. The residuals of these relationships were used as input for further analyses.

We then performed a factor analysis on the residuals to identify morphological measures responsible for the overall variation in body shape and to test for differences in general body shape among species of the five classes of habitat use (Statistica 5.0). Factors were extracted using the varimax rotational strategy. The correlation (factor loading) between an original variable and the factors extracted was used to evaluate the importance of the original variable in the description of the overall morphological variation. We calculated factor scores on the two most important factors and used them as input for a nested analysis of variance (species nested in habitat use). We then performed *a posteriori* tests (Tukey Honest Significant Difference test for unequal *N*) to determine between which habitat use categories the differences lay.

Phylogenetic analyses

In recent years, it has been stressed repeatedly that evolutionary analyses should be conducted in an explicit phylogenetic context (Felsenstein, 1985, 1988; Harvey and Pagel, 1991; Garland *et al.*, 1993). Because species share parts of their evolutionary history, they cannot be considered independent data points. Hence, the statistical significance of differences among sets of species cannot be evaluated with standard tabular *F*-distributions (see Pagel, 1993). One way out of this impasse is to create an appropriate empirical null distribution – that is, one that takes the phylogenetic relationships among the species into account. In this study, we used the PDSIMUL and PDANOVA computer programs presented by Garland *et al.* (1993) to derive such a distribution.

In the PDSIMUL program, we used Brownian motion as a model of evolutionary change. The means and variances of the simulations were set to the means and variances of the original data. We repeated the procedure 1000 times. The analyses were run both with and without limits imposed and highly similar results were obtained. In the first case, the lower limit was set to 1 (log10) and the upper limit to 3.5 (log10) (see Arnold, 1989a). We only report the results from the unbounded simulations.

The PDANOVA program performs traditional one-way analyses of variance (ANOVA) on each of the simulated data sets. The *F*-statistics of these 1000 analyses of variance were used to create a null distribution against which the *F*-value from the actual data set can be compared. We considered differences among means of species with the respective habitat use significant if the *F*-value exceeded the upper 95th percentile of the empirical *F*-distribution.

The method described requires input 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 immunological (Lutz and Mayer, 1985; Mayer and Lutz, 1989, 1990; Mayer and Benyr, 1994) and morphological studies (Arnold, 1983, 1989a, 1998) to construct a 'currently best' tree (Fig. 1; see also Bauwens *et al.*, 1995). As few data are available on divergence times between species, all branch lengths were set to unity. It has been shown that the actual length of the branches does not usually affect the results of phylogenetic analyses substantially (Martins and Garland, 1991; Walton, 1993; Irschick *et al.*, 1996, Díaz-Uriarte and Garland, 1998).

We performed the phylogenetic analyses on a subset of morphological variables (means per species): (1) snout–vent length, (2) variables that had high (>0.7) loadings on any of the first two factors and (3) three limb proportions of alleged importance in locomotion (fore limb/hind limb, radius/humerus and tibia/femur). The latter variables were represented by the residuals of least squares linear regressions, all data log10-transformed. The currently available programs for phylogenetic analyses do not allow multivariate comparisons, so all variables were tested separately. To correct the level of significance for multiple testing, we used the Bonferroni correction (Hochberg, 1988).

Effect of uncertainties in tree topology

As already mentioned, parts of the topology of the phylogenetic tree we used are uncertain. This is the case for the relationships near the root of the tree and for some relationships within the Palaearctic and Oriental clade (Arnold, 1989a; Fig. 1). To estimate to what extent these uncertainties may influence our conclusions, we repeated our phylogenetic analyses on a subset of all possible trees for the 35 species. The subset consisted of 1000 trees that varied randomly from the original tree in the resolution of the tentative relationships (see Losos, 1994; Abouheif, 1998). For each of these 1000 trees, 1000 trait simulations (i.e. 1 million in total) were performed along the branches to obtain an empirical *F*-distribution, following the same procedure as in the PDSIMUL and PDANOVA programs (Garland *et al.*, 1993; see above). The distribution of the 1000 critical *F*-values thus obtained was used to evaluate the effect of the uncertain tree topology on our conclusions.

We performed these simulations for only one variable (residual head height), because they are very time-consuming. Moreover, the critical *F*-values obtained by simulation were very similar for all traits considered (see Results).

Effect of habitat use clustering

The distribution of habitat use over the phylogenetic tree is highly unequal (Fig. 1). Habitat use tends to 'cluster' in parts of the tree. For instance, most members of the genus *Acanthodactylus* belong to the 'ground-dwelling in open vegetation' group. To quantify the effect of this habitat use 'clustering' on the power of the phylogenetic statistical analysis, we generated a set of 1000 trees with topologies equal to the original tree, but with habitat use randomly assigned to each tip node. For each of these 1000 trees, we calculated the sum of the number of nodes between each pair of species using the same habitat. We considered this sum as a measure of habitat use 'clustering'. Then, following the same method as used in the computer programs PDSIMUL and PDANOVA (Garland *et al.*, 1993; see above), 1000 trait simulations were performed along the branches of each tree to obtain empirical *F*-distributions.

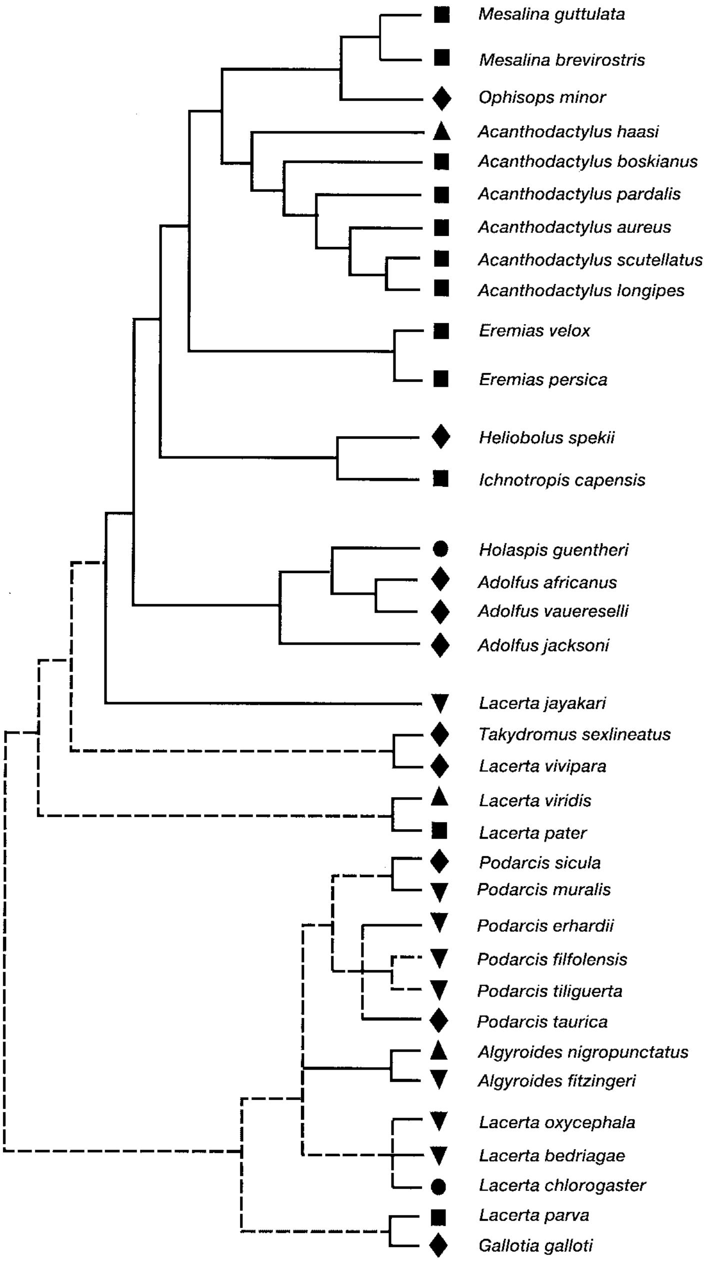

Fig. 1. Phylogenetic tree used in the analyses. The tree was constructed based on results from immunological and morphological studies (see text for references). It should be noted that the phylogeny is incompletely resolved and that the tree used should thus be considered a 'currently' best approximation. Tentative relationships are represented by the dashed lines. Symbols refer to habitat use (■, ground-dwelling in open habitats; ◆, ground-dwelling in vegetated habitats; ▲, shrub-climbing; ●, tree-climbing; ▼, saxicolous).

RESULTS

Non-phylogenetic analyses

The bulk of variation in snout–vent length was among species with the same habitat use (nested ANOVA: $F_{30,449} = 91.70$, $P < 0.0001$). Snout–vent length did not differ among species with different habitat use ($F_{4,30} = 0.59$, $P = 0.67$). In all five habitat use categories considered, average snout–vent length clustered mainly between 40 and 80 mm, but all groups using the same habitat (except the tree-climbing species) also contained species with much higher average snout–vent lengths (Fig. 2).

Factor analysis on the 14 size-free morphometric traits yielded two new variables (Fig. 3). The first factor showed high loadings for residual femur length, residual tibia length and residual humerus length (Table 2). A nested ANOVA on the factor scores revealed marginally significant differences among species groups with different habitat use ($F_{4,29.82} = 2.99$, $P = 0.048$). The *a posteriori* test separated ground-dwelling species living in open terrain (high scores) from the other four groups (low scores) (Table 3). This suggests that ground-dwelling lacertids from open terrain tend to have long femurs, tibiae and humeri for their body size. However, within the habitat use groups, differences among species also contributed significantly to the variation in factor scores (nested ANOVA: $F_{30,445} = 31.15$, $P < 0.0001$).

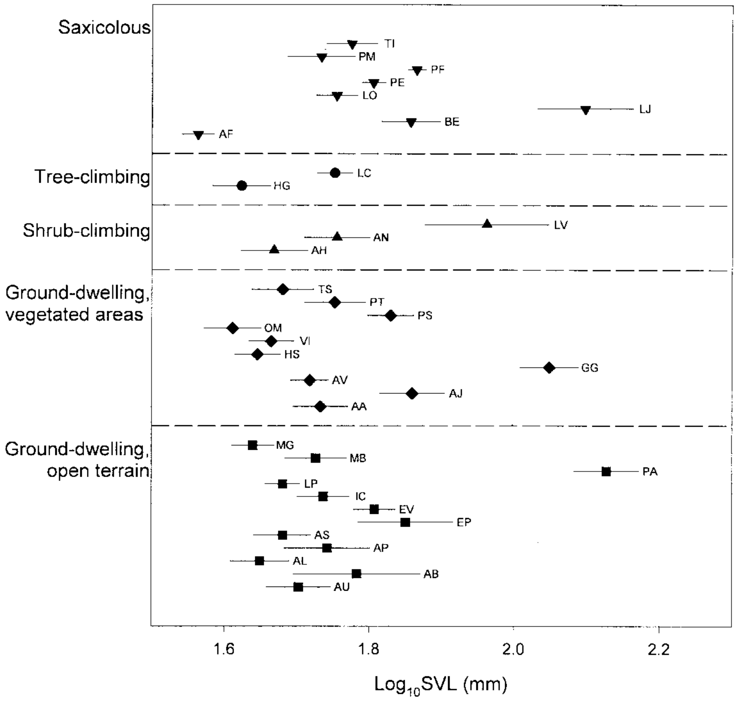

Fig. 2. The snout–vent length (SVL) of 35 species of lacertid lizards, grouped by habitat use (mean ± S.D.). Means are for adult males only; sample sizes vary between 7 and 24. See Table 1 for abbreviations. Symbols refer to habitat use (■, ground-dwelling in open habitats; ◆, ground-dwelling in vegetated habitats; ▲, shrub-climbing; ●, tree-climbing; ▼, saxicolous).

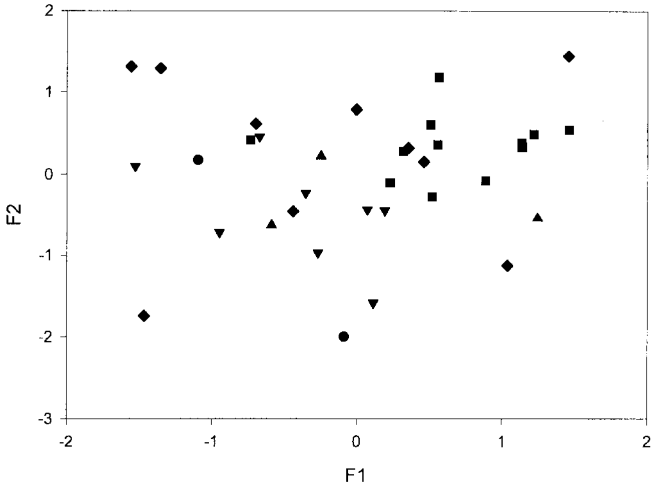

Fig. 3. Position of the 35 lacertid species in the 'morphospace' described by the first two factors. The first factor (F1) correlates with femur, tibia and humerus length, the second (F2) with head and body height. Species means are indicated. Symbols refer to habitat use (■, ground-dwelling in open habitats; ◆, ground-dwelling in vegetated habitats; ▲, shrub-climbing; ●, tree-climbing; ▼, saxicolous).

Table 2. Eigenvalues, percent variation explained and factor loadings of five factors in the factor analysis (only the first two were used in further analyses and discussion)

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Eigenvalue	4.44	1.72	1.27	1.19	1.06
% Variation accounted for	31.74	12.31	9.10	8.48	7.5
Head length	0.02	0.12	0.35	0.03	0.75
Head width	0.18	0.68	0.00	0.03	0.59
Head height	0.13	0.76	0.23	–0.07	0.07
Body length	–0.21	–0.04	–0.04	–0.07	–0.70
Body width	0.15	0.63	–0.15	0.12	0.28
Body height	–0.06	0.84	0.12	–0.04	–0.10
Femur length	0.79	0.05	0.06	0.24	0.25
Tibia length	0.88	0.25	0.11	0.15	0.01
Metatarsus length	0.37	0.49	0.50	0.32	0.04
Toe length (hind)	0.33	0.13	–0.18	0.72	0.04
Humerus length	0.73	–0.01	0.32	–0.24	0.19
Radius length	0.16	0.02	0.81	–0.07	0.16
Metacarpus length	0.20	0.28	0.58	0.33	0.17
Toe length (fore)	–0.12	–0.16	0.31	0.70	0.07

The second factor was positively correlated with residual head height and residual body height (Table 2), although its statistical significance is dubious according to the broken stick model (Jackson, 1993). Mean factor scores on this axis differed among habitat use groups (nested ANOVA: $F_{4,29.75} = 3.67$, $P = 0.015$). The *a posteriori* test revealed that species from

Table 3. *A posteriori* tests (Tukey HSD test for unequal *N*) on factor scores from the first two factors (mean factor scores per habitat are given)

Factor 1					
Habitat	1	2	3	4	5
Mean	0.63	–0.17	–0.28	–0.26	–0.26
1		0.00	0.00	0.00	0.00
2			0.87	0.96	0.75
3				1.00	1.00
4					1.00
Factor 2					
Habitat	1	2	3	4	5
Mean	0.38	0.37	–0.21	–1.24	–0.55
1		0.99	0.00	0.00	0.00
2			0.00	0.00	0.00
3				0.00	0.04
4					0.00

Note: Habitats are (1) ground-dwelling in open habitats, (2) ground-dwelling in vegetated habitats, (3) shrub-climbing, (4) tree-climbing and (5) saxicolous.

both ground-dwelling groups had relatively high factor scores compared with the other species, suggesting that relatively high heads and trunks are typical in cursorial species, or atypical in climbing species (Table 3). As for the first axis, variation among species within habitat use groups added significantly to the total variation in factor scores ($F_{30,449} = 22.51$, $P < 0.0001$).

Phylogenetic analyses

Table 4 summarizes the results of the phylogenetic analyses performed on snout–vent length and a set of shape variables. F-statistics from one-way ANOVAs on the respective traits were compared to empirical F-distributions, obtained by 1000 simulations of character evolution along the phylogenetic tree presented in Fig. 1. Although the F-statistics for some of these traits (residual humerus length, residual body and head height, and the tibia/femur and radius/humerus ratios) would be judged significant if compared to standard tables ($F_{0.05[4,30]} = 2.69$), most of them are not significant when weighed against the appropriate empirical F-distribution ($6.12 < F_{0.05} < 7.02$). Only head and body height showed marginally significant differences among habitat use categories, but even these vanished when the Bonferroni correction was applied. Thus, in contrast to traditional statistics, the phylogenetic analyses suggest little association between body shape and habitat use.

Effect of uncertainties in tree topology

The critical F-values obtained by the simulations along the 1000 new trees, in which the uncertain relations were reshuffled randomly, ranged between 4.5 and 9.0, with a median of 5.55 (Fig. 4). Even when compared to the lowest critical F-value (Table 4), the results from

Table 4. Morphological variation among species from different habitat types: Results of the phylogenetic analyses

Trait	$F_{4,30}$	P
Snout–vent length	0.49	0.91
Residual femur length	0.23	0.98
Residual tibia length	1.86	0.51
Residual humerus length	1.36	0.64
Residual head height	6.59	0.05
Residual body height	7.52	0.03
Forelimb/hindlimb ratio	1.91	0.48
Tibia/femur ratio	4.80	0.12
Radius/humerus ratio	5.25	0.08

Note: F-values were obtained from non-phylogenetic one-way ANOVAs. P-values were derived from empirical F-distributions, obtained from 1000 simulations of character evolution along the phylogenetic tree from Fig. 1. After Bonferroni correction, none of the results was significant.

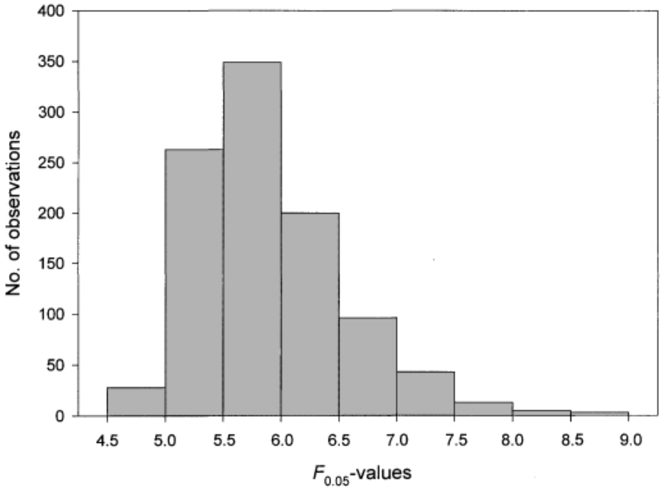

Fig. 4. Distribution of empirical critical F-values (at the 0.05 level of significance) obtained from 1000 simulations of character evolution along a subset of ‘all possible’ lacertid trees. This subset consisted of 1000 randomly generated trees that varied with respect to the original tree in the resolution of the tentative relationships (see Fig. 1). We compared the F-values from Table 4 with this distribution to evaluate the effect of uncertainties in tree topology.

the ANOVAs on most traits would remain non-significant. That is, for most traits, our conclusion (no differences among habitat use groups) holds.

The uncertainties in the tree topology may affect our conclusion concerning the relation between habitat use and head and trunk height, however. For head height, 12.6% of the alternative trees produced critical F-values above the observed value. The same was true for

1.8% of the 1000 trees in the case of trunk height. If these alternative trees describe the phylogenetic relationships among lacertids better than the tree used above, then we must conclude that the latter variables do not differ among habitat use groups. However, in general, it seems unlikely that our conclusions are faulty because of uncertain tree topology.

Effect of habitat use 'clustering'

The measure for clustering for the 1000 new sets, with topologies equal to the original tree but with habitat use randomly assigned to each tip node, ranged between 1224 and 1549 (median = 1455), while critical $F_{0.05}$-values ranged between 1.63 and 5.96 (median = 2.47). We also generated a set of trees with an exceptionally high clustering of habitat use. The worst case had a 'clustering' measure of 820 and produced an $F_{0.05}$-value of 23.83 (Fig. 5). Figure 5 clearly shows that habitat use clustering and the critical F-value are negatively related. In other words, when phylogenetically close species tend to exhibit identical habitat use, the critical values of the F-statistic increase dramatically, such that morphological differences must be extremely pronounced to reject the null hypothesis. The 'clustering' measure for our real tree was 1180, and is situated at the lower extreme of the 1000 trees with habitat use randomly assigned to the tip nodes (see Fig. 5). That is, the rather extreme 'clustering' of habitat use along the lacertids' phylogenetic tree places strong restrictions on our ability to find statistical support for the putative morphological differences among groups of species.

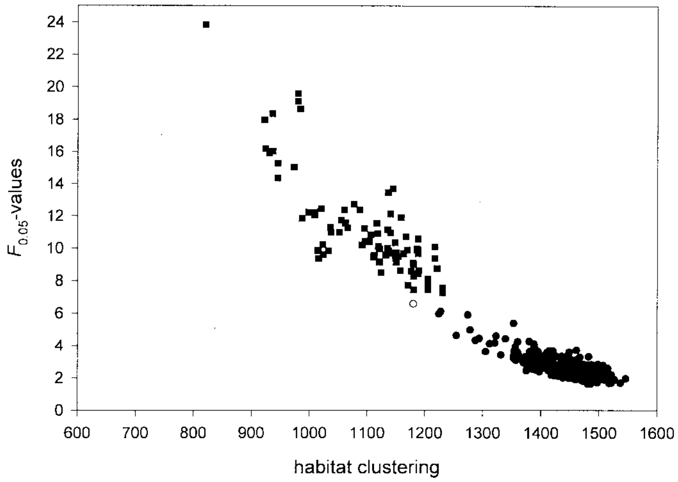

Fig. 5. Effect of 'habitat use clustering' on the empirical critical F-value against which the among-habitat use variation must be tested. 'Habitat use clustering' (tendency of habitat use to occur in the same part of the tree) was measured as the total number of nodes between all pairs of species with the same habitat use. A low number of nodes corresponds to a high level of habitat clustering, a high number of nodes to low habitat clustering. Each critical F-value was obtained from 1000 simulations of trait evolution along a tree with a topology as in Fig. 1. Values depicted were obtained for trees with habitat use randomly attributed to the extant species (●) and values for trees on which high 'clustering' was enforced (■). For reasons of clarity, only a representative subset is depicted in the plot. The open circle refers to the actual situation in lacertid lizards.

DISCUSSION

Non-phylogenetic analyses confirmed our expectations based on biomechanical models. However, appropriate phylogenetic methods failed to provide statistical support for an association between body size or shape and habitat use.

Non-phylogenetic analyses

Mean snout–vent length did not differ among lacertid lizards that occurred in the five habitat use categories considered. Adult males typically have snout–vent lengths between 45 and 80 mm, but all five habitat use groups contain species that are considerably larger. This suggests that, in lacertid lizards, body size does not constrain habitat use or vice versa (see also Losos, 1990a).

Traditional (i.e. non-phylogenetic) statistical analyses suggest that lacertid lizard species with different habitat use do vary in body shape. Some of these differences appear to be in line with the biomechanical predictions made, and thus it is tempting to see them as adaptations to habitat use.

First, relative head and body height differ among habitat use groups. Ground-dwelling species, both from open and from vegetated habitats, tend to be laterally compressed, whereas species that climb shrubs, trees or rocks are dorso-ventrally compressed. Dorso-ventral flattening lowers the body's centre of gravity, making it closer to the substrate. This may reduce the chances of toppling back while climbing (Jaksic *et al.*, 1980; Pounds, 1988; Sinervo and Losos, 1991). Moreover, a flat body plan could allow saxicolous species to hide in small cracks and crevices (Miles, 1994). A laterally compressed body shape seems adaptive for cursorial lizards, because it allows greater lateral flexion. This is thought to permit longer strides and thus a capacity for higher speeds (Snyder, 1954; Van Damme *et al.*, 1997). It may also enhance manoeuvrability.

Secondly, species with different habitat uses differ in limb morphology. The hind limbs (both femur and tibia) of species from horizontal, open habitats tend to be longer than those of species from other habitats. Long hind limbs are supposed to increase stride length and hence propulsion and sprint speed in open habitats (Pianka and Pianka, 1976; Garland and Losos, 1994). Species climbing shrubs, rocks and trees and ground-dwelling species from vegetated habitats tend to have short hind limbs. Short limbs may be effective in climbing species, as they place the centre of gravity closer to the substrate, thus increasing stability (Cartmill, 1985; Pounds, 1988; Miles, 1994). They may also be effective in highly vegetated areas, where long limbs tend to get tangled.

The fore limbs (i.e. humeri) in ground-dwelling species from open habitats and species that climb shrubs tend to be longer than in the other groups. The functional significance of this difference, if any, is unclear. It has been suggested that fast running species should not have long fore limbs, because they may interfere with the locomotor cycles of the hind limbs (Snyder, 1962; Sukhanov, 1968; Losos, 1990c). The limbs of climbers should be short to lower the centre of gravity (Cartmill, 1985; Pounds, 1988; Miles, 1994). These biomechanical predictions were not confirmed by our results. As the predictions are based on mammalian data, this may not come as a surprise. Clearly, much has yet to be learned about the biomechanics of climbing and running in lizards.

Phylogenetic analyses

As argued in the Introduction, inferring adaptation requires that the phylogenetic relationships among the species studied are taken into account. In this study, the phylogenetic analyses failed to show a close association between body size or shape and habitat use. This could mean that the resemblances among the members of one habitat use group have emerged via a common history, rather than through adaptation to the habitat use in question. Alternatively, methodological problems may have prevented us from demonstrating the putative adaptive relationship between morphology and habitat use.

A first methodological problem may be that we centred on the wrong morphological characters. Ecomorphological relationships may depend on more subtle differences in the musculoskeletal system than that studied here (Miles, 1994). Biomechanical considerations do predict differentiation in many of the characters we have examined, but the applicability of the models used to generate these predictions for lizards in general, and for lacertids in particular, has recently been questioned (Van Damme *et al.*, 1997, 1998; see above). Detailed kinematic studies and performance measurements of lizards moving on different substrates and at different angles of inclination are needed to refine these biomechanical models.

Another methodological problem is the topology of the tree used in the analyses. We tried to test the robustness of our conclusion by re-running the analysis on a subset of all possible trees that can be generated from the original tree, given the uncertainties indicated in Fig. 1. Our conclusions appear to remain valid, regardless of the tree used. Only for residual head and trunk height is there a small possibility that our conclusion without correcting for multiple testing ('association') is corrupted because of using the wrong tree. We did not assess the potential error that was introduced in our analyses by equating all divergence times to unity (but see Martins and Garland, 1991; Walton, 1993; Bauwens *et al.*, 1995; Irschick *et al.*, 1996; Díaz-Uriarte and Garland, 1998).

The 'clustering' of habitat use on our phylogenetic tree constitutes perhaps a more serious problem. The 'clustering' weakens the power of our phylogenetic analyses, in the sense that, among habitat uses, variation in morphology must be high to obtain significant results (Fig. 5). Garland *et al.* (1993) described a similar situation in their phylogenetic test of the hypothesis that, in two clades of mammals (i.e. Carnivora and ungulates), herbivores would have smaller home ranges than carnivores and omnivores. Like 'habitat use' in lacertid lizards, 'diet' in these mammals is highly clustered. Herbivores crop up at one side of the root of the tree, omnivores and herbivores at the other. Thus, a diet transition has occurred only once in the history of the Carnivora and ungulates, reducing the degrees of freedom to such an extent that proving an association between diet and home range becomes impossible. Compare this situation with that described by Losos (1990a,b,c) in Caribbean *Anolis* lizards. Because of the exceptional radiation pattern of *Anolis* lizards (with independent morphological and ecological diversification on each of the islands colonized), habitat use in these lizards does not cluster at all on the phylogenetic tree. It may not be coincidental that Losos was able to demonstrate an association between habitat use and morphology in Caribbean *Anolis.* The confounding of habitat use with phylogeny reduces the value of the family Lacertidae as a test case for ecomorphological relationships. In the future, different approaches may prove more fruitful. Detailed examination of particular species with 'atypical' habitat use (e.g. saxicolous species within a largely ground-dwelling clade) may provide interesting clues. However, few examples of such species can be found within the Lacertidae. Another avenue is to test for intraspecific morphological differentiation among populations that occupy different habitats (Van Damme *et al.*, 1997, 1998). Tracking morphological modifications in animals that have been introduced into new habitats (Losos *et al.*, 1997) is yet another option.

We have argued that the statistical properties of the data may have prevented us from identifying relationships between habitat use and morphology. This may be an overly adaptationist approach. An obvious alternative explanation for the lack of association between morphology and habitat use in lacertid lizards is that adaptation has not (yet) occurred. Adaptation of a trait requires heritable variation in the trait(s) considered, a selection gradient (*sensu* Arnold, 1983) and time.

We have no such information for the traits considered here, but it is generally acknowledged that morphological measures have relatively high heritabilities (Van Berkum and Tsuji, 1987; Tsuji *et al.*, 1989; Bennett and Huey, 1990), and therefore could respond quickly to selection. Williams (1992) has argued that, in theory, a bird's tibiotarsus might elongate from 1 to 100 cm in only 92 centuries. Moreover, it has been shown that, in novel or depauperate ecological conditions, adaptive radiation such as that expected for lacertids may have occurred in a period between 100 and 1000 years (see Losos *et al.*, 1994). Even more convincing, Losos *et al.* (1997) documented a change in average limb length in populations of *Anolis sagrei* that had been introduced in a novel habitat in just 10–14 years (although it is not yet clear whether this change is genetic or constitutes an example of phenotypic plasticity). Lacertid lizards radiated about 65 million years ago (Arnold, 1989a). Time, therefore, does not appear to be a real issue here.

The existence of a selection gradient, or its steepness, constitutes another matter. Although this has seldom been tested experimentally, it is likely that ground-dwelling lizards will benefit from traits that enable them to run faster on level ground, just as climbers will benefit from traits that enhance their speed on steep slopes. Specialization in one direction, however, may be at the expense of performance capacity in another (Van Damme *et al.*, 1997, 1998). Most lacertid species do not use one type of habitat. Although most seem to 'prefer' one of the habitat types used in this study, they usually also encounter, and make use of, one or several other habitat types. For instance, individuals of *Podarcis sicula* typically forage on the ground in highly vegetated areas, but now and then do dash across open, sandy patches, and occasionally climb on a rock to bask or in a tree to escape from predators (personal observation). In such circumstances, average performance in a variety of conditions may be more important for survival than high performance in one condition. That is, most lacertids may benefit from a generalized body plan (see also Jaksic *et al.*, 1980).

This hypothesis rests on a number of assumptions that remain to be tested. First, the relation between morphology and (locomotor) performance needs to be examined. If differences in morphology do not translate into differences in performance, their ecological significance becomes dubious and adaptive explanation will fail. Secondly, the hypothesis contains elements of the 'Principle of Allocation' (Levins, 1968; Huey and Hertz, 1984), stating that 'a jack of all substrates is a master of none'. This assumption has been validated by some authors (Losos *et al.*, 1993; Sinervo and Losos, 1991), but refuted by others (Van Damme *et al.*, 1997). Much will depend on the existence of trade-offs among locomotor styles (e.g. level-running *vs* climbing). Finally, the significance of locomotor performance for survival and reproduction in the field remains to be tested.

In summary, lacertid species with different habitat use tend to differ from one another, but we cannot reject the null hypothesis that the morphological differences are not adaptations to habitat use and that they emerged as a result of a common history.

ACKNOWLEDGEMENTS

We thank E.N. Arnold from the Natural History Museum in London (UK), D. Meirte from the Museum of Central Africa in Brussels (Belgium) and G. Lenglet from the Royal Belgian Institute of Natural History in Brussels (Belgium) for allowing us access to the collections of Lacertids. E.N. Arnold checked the phylogenetic tree used. Peter Aerts, Dirk Bauwens, Anthony Herrel and two anonymous referees provided constructive comments on an earlier draft of the manuscript. This study was supported by an IWT grant (no. 951359) to B.V., a FWO-VI grant (G. 0221.96) and a GOA-BOF project (University of Antwerp 1999) to R.V.D. R.V.D. is a senior research assistant at the National Science Fund-Flanders (FWO-VI).

REFERENCES

Abouheif, E. 1998. Random trees and the comparative method: A cautionary tale. *Evolution*, **52**: 1197–1204.

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

Arnold, E.N. 1989a. Towards a phylogeny and biogeography of the Lacertidae: Relationships within an Old-World family of lizards derived from morphology. *Bull. Br. Mus. Nat. Hist.* (*Zool.*), **55**: 209–257.

Arnold, E.N. 1989b. Systematics and adaptive radiation of Equatorial African lizards assigned to the genera *Adolfus*, *Bedriagaia*, *Holaspis* and *Lacerta* (Reptilia: Lacertidae). *J. Nat. Hist.*, **23**: 525–555.

Arnold, E.N. 1998. Structural niche, limb morphology and locomotion in lacertid lizards (Squamata: Lacertidae), a preliminary survey. *Bull. Nat. Hist. Mus. Lond.* (*Zool.*), **64**: 63–89.

Arnold, E.N., Burton, J.A. and Ovenden, D.W. 1978. *Reptiles and Amphibians of Britain and Europe*. London: Collins.

Arnold, S.J. 1983. Morphology, performance and fitness. *Am. Zool.*, **23**: 347–361.

Ashmole, M. and Ashmole, P. 1989. *Natural History Excursions on Tenerife*: *A Guide to the Countryside, Plants and Animals*. Peebles, UK: Kidston Mill Press.

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

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

Bennett, A.F. and Huey, R.B. 1990. *Studying the Evolution of Physiological Performance*. Oxford Surveys in Evolutionary Biology, Vol. 7, pp. 251–284. Oxford: Oxford University Press.

Bischoff, W. 1984. *Lacerta oxycephala* – Spitzkopfeidechse. In *Handbuch der Reptilien und Amphibien Europas. Band 2/I Echsen II* (*Lacerta*) (W. Böhme, ed.), pp. 301–317. Wiesbaden: AULA-Verlag.

Bischoff, W. 1986. *Podarcis filfolensis* – Malta-Eidechse. In *Handbuch der Reptilien und Amphibien Europas. Band 2/II Echsen III* (*Podarcis*) (W. Böhme, ed.), pp. 50–64. Wiesbaden: AULA-Verlag.

Branch, B. 1988. *Snakes and Other Reptiles of Southern Africa*. Cape Town: Struik.

Burnell, K.L. and Hedges, S.B. 1990. Relationships of Caribbean *Anolis* (Sauria: Iguanidae): An approach using slow-evolving protein loci. *Caribb. J. Sci.*, **26**: 7–30.

Carroll, R.L. 1997. *Patterns and Processes of Vertebrate Evolution*. Cambridge: Cambridge University Press.

Cartmill, M. 1985. Climbing. In *Functional Vertebrate Morphology* (M. Hildebrand, D.M. Bramble, K.F. Liem and D.B. Wake, eds), pp. 73–88. Cambridge, MA: Harvard University Press.

Castilla, A.M., Bauwens, D., Van Damme, R. and Verheyen, R.F. 1989. Notes on the biology of the high altitude lizard *Lacerta bedriagae*. *Herpetol. J.*, **1**: 400–403.

Collette, B.B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern California. *Bull. Mus. Comp. Zool.*, **125**: 137–162.

Coulter, G.W. 1991. *Lake Tanganyika and Its Life*. Oxford: Oxford University Press.

Dely, O.G. and Böhme, W. 1984. *Lacerta vivipara* – Waldeidechse. In *Handbuch der Reptilien und Amphibien Europas. Band 2/I Echsen II* (*Lacerta*) (W. Böhme, ed.), pp. 362–393. Wiesbaden: AULA-Verlag.

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

Feder, M.E., Bennett, A.F., Burggren, W.W. and Huey, R.B. 1987. *New Directions in Ecological Physiology.* Cambridge: Cambridge University Press.

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

Felsenstein, J. 1988. Phylogenies and quantitative characters. *Ann. Rev. Ecol. Syst.*, **19**: 445–471.

Forman, F. and Forman, B. 1981. Herpetologische Beobachtungen auf Korsika. *Herpetofauna*, **10**: 12–16.

Garland, T. Jr and Losos, J.B. 1994. Ecological morphology of locomotor performance in Squamate reptiles. In *Ecological Morphology: Integrative Organismal Biology* (P.C. Wainwright and S.M. Reilly, eds), pp. 240–302. Chicago, IL: University of Chicago Press.

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

Gruber, U. 1986. *Podarcis erhardii* – Ägäische Mauereidechse. In *Handbuch der Reptilien und Amphibien Europas. Band 2/II Echsen III* (*Podarcis*) (W. Böhme, ed.), pp. 25–49. Wiesbaden: AULA-Verlag.

Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology.* Oxford: Oxford University Press.

Hochberg, Y. 1988. A sharper Bonferroni procedure for multiple tests of significance. *Biometrika*, **75**: 800–802.

Huey, R.B. and Hertz, P.E. 1984. Is a jack-of-all-temperatures a master of none? *Evolution*, **38**: 441–444.

in den Bosch, H.A.J. 1986. Beschränkte Freilandnahrungsanalysen an *Algyroides fitzingeri* (Wiegmann, 1834) auf Sardinien. *Salamandra*, **22**: 47–54.

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

Irschick, D.J., Vitt, L.J., Zani, P. and Losos, J.B. 1997. A comparison of evolutionary radiations in mainland and Caribbean *Anolis* lizards. *Ecology*, **78**: 2191–2203.

Jackson, D.A. 1993. Stopping rules in principal components analysis: A comparison of heuristical and statistical approaches. *Ecology*, **74**: 2204–2214.

Jaksic, F.M., Nunez, H. and Ojeda, F.P. 1980. Body proportions, microhabitat selection, and adaptive radiation of *Liolaemus* lizards in central Chile. *Oecologia* (*Berl.*), **45**: 178–181.

Kabisch, K. 1986. *Podarcis taurica* – Taurische Eidechse. In *Handbuch der Reptilien und Amphibien Europas. Band 2/II Echsen III* (*Podarcis*) (W. Böhme, ed.), pp. 343–362. Wiesbaden: AULA-Verlag.

Karsen, S.J., Wai-neng Lau, M. and Bogadek, A. 1986. *Hong Kong Amphibians and Reptiles*. Hong Kong: Urban Council.

Lauder, G.V. 1995. On the inference of function from structure. In *Functional Morphology in Vertebrate Paleontology* (J.J. Thomasen, ed.), pp. 1–18. Cambridge: Cambridge University Press.

Lederer, R.J. 1984. A view of avian ecomorphological hypotheses. *Ökologie der Vögel*, **6**: 119–126.

Levins, R. 1968. *Evolution in Changing Environments.* Princeton, NJ: Princeton University Press.

Leviton, A.E., Anderson, S.C., Adler, K. and Minton, S.A. 1992. *Handbook of Middle East Amphibians and Reptiles*. New York: Society for the Study of Amphibians and Reptiles.

Losos, J.B. 1990a. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: An evolutionary analysis. *Ecol. Monogr.*, **60**: 369–388.

Losos, J.B. 1990b. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. *Anim. Behav.*, **39**: 879–890.

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

Losos, J.B. 1992. A critical comparison of the taxon-cycle and character-displacement models for size evolution of *Anolis* lizards in the Lesser Antilles. *Copeia*, **1992**: 279–288.

Losos, J.B. 1994. An approach to the analysis of comparative data when a phylogeny is unavailable or incomplete. *Syst. Biol.*, **43**: 117–123.

Losos, J.B. and Irschick, D.J. 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: Laboratory predictions and field tests. *Anim. Behav.*, **51**: 593–602.

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

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

Losos, J.B., Irschick, D.J. and Schoener, T. 1994. Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. *Evolution*, **48**: 1786–1798.

Losos, J.B., Warheit, K.I. and Schoener, T.W. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature*, **387**: 70–73.

Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K. and Rodríguez-Schettino, L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, **279**: 2115–2118.

Lutz, D. and Mayer, W. 1985. Albumin evolution and its phylogenetic and taxonomic implications in several Lacertid lizards. *Amphibia-Reptilia*, **6**: 53–61.

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

Mayer, W. and Benyr, G. 1994. Albumin-Evolution und Phylogenese in der Familie Lacertidae. *Ann. Naturhist. Mus. Wien*, **96B**: 621–648.

Mayer, W. and Lutz, D. 1989. Chemosystematische Untersuchungen zur Phylogenese der Sammelgattung *Lacerta* (Reptilia: Sauria: Lacertidae). *Z. zool. Syst. Evolut.-forsch.*, **27**: 338–349.

Mayer, W. and Lutz, D. 1990. Albumin-immunologische Untersuchungen zur Phylogenese de Gattung *Algyroides* und ihrer systematischen Position gegenüber der Sammelgattung *Lacerta* (Reptilia: Sauria: Lacertidae). *Zool. Anz.*, **224**: 99–105.

Miles, D.B. 1994. Covariation between morphology and locomotory performance in Sceloporine lizards. In *Lizard Ecology: Historical and Experimental Perspectives* (L.J. Vitt and E.R. Pianka, eds), pp. 207–235. Princeton, NJ: Princeton University Press.

Minton, S.A. Jr. 1966. A contribution to the herpetology of West Pakistan. *Bull. Am. Mus. Nat. Hist.*, **134**.

Moermond, T.R. 1979. Habitat constraints on the behavior, morphology and community structure of *Anolis* lizards. *Ecology*, **60**: 152–164.

Moreno, E. and Carrascal, L.M. 1993. Leg morphology and feeding postures in four *Parus* species: An experimental ecomorphological approach. *Ecology*, **74**: 2037–2044.

Nettmann, H.K. and Rykena, S. 1984. *Lacerta viridis* – Smaragdeidechse. In *Handbuch der Reptilien und Amphibien Europas. Band 2/I Echsen II* (*Lacerta*) (W. Böhme, ed.), pp. 129–180. Wiesbaden: AULA-Verlag.

Pagel, M.D. 1993. Seeking the evolutionary regression coefficient: An analysis of what comparative methods measure. *J. Theor. Biol.*, **164**: 191–205.

Pérez-Mellado, V. 1992. Ecology of lacertid lizards in a desert area of eastern Morocco. *J. Zool.* (*Lond.*), **226**: 369–386.

Pianka, E.R. and Pianka, H.D. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia*, **1**: 125–142.

Pounds, J.A. 1988. Ecomorphology, locomotion, and microhabitat structure: Patterns in a tropical mainland *Anolis* community. *Ecol. Monogr.*, **58**: 299–320.

Rand, A.S. and Williams, E.E. 1969. The anoles of La Palma: Aspects of their ecological relationships. *Breviora*, **327**: 1–19.

Schleich, H.H., Kästle, W. and Kabisch K. 1996. *Amphibians and Reptiles of North Africa: Biology, Systematics, Field Guide*. London: NHBS.

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

Snyder, R.C. 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. *Am. J. Anat.*, **95**: 1–36.

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

Sokal, R.R. and Rohlf, F.J. 1994. *Biometry: The Principles and Practice of Statistics in Biological Research.* New York: W.H. Freeman.

Sukhanov, V.B. 1968. *General System of Symmetrical Locomotion of Terrestrial Vertebrates and Some Features of Movement of Lower Tetrapods*. Leningrad: Nauka Publications (translated to English, Amerinde Publishing Co., New Delhi).

Terent'ev, P.V. and Chernov, S.A. 1949. *Key to Amphibians and Reptiles.* Moscow: Gosudartvennae Izdatel'stvo 'Sovetskaya Nauka'.

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

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

Van Damme, R., Bauwens, D., Castilla, A.M. and Verheyen, R.F. 1990. Comparative thermal ecology of the sympatric lizards *Podarcis tiliguerta* and *Podarcis sicula. Acta Oecologica*, **11**: 503–512.

Van Damme, R., Aerts, P. and Vanhooydonck, B. 1997. No trade-off between sprinting and climbing in two populations of the lizard *Podarcis hispanica* (Reptilia: Lacertidae). *Biol. J. Linn. Soc.*, **60**: 493–503.

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

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

Wainwright, P.C. and Reilly, S.M., eds. 1994. *Ecological Morphology: Integrative Organismal Biology*. Chicago, IL: University of Chicago Press.

Wiens, J.A. 1989. *The Ecology of Bird Communities: Foundations and Patterns*. Cambridge: Cambridge University Press.

Wiens, J.A. and Rotenberry, J.T. 1980. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. *Ecol. Monogr.*, **50**: 287–308.

Williams, E.E. 1972. The origin of faunas: Evolution of lizard congeners in a complex island fauna. A trial analysis. *Evol. Biol.*, **6**: 47–89.

Williams, E.E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. In *Lizards Ecology: Studies of a Model Organism* (R.B. Huey, E.R. Pianka and T.W. Schoener, eds), pp. 326–370. Cambridge, MA: Harvard University Press.

Williams, G.C. 1992. *Natural Selection: Domains, Levels, and Challenges*. Oxford: Oxford University Press.

APPENDIX

*Measurements (mm) on 35 species of lacertid lizards: Body and head dimensions (mean ± S.D.)**

Species	Snout–vent length	Head length	Head width	Head height	Body length	Body height	Body width
A. aureus	50.69 ± 5.02	12.56 ± 1.18	8.47 ± 0.83	6.35 ± 0.77	25.37 ± 3.02	5.91 ± 0.43	14.76 ± 0.96
A. boskianus	61.83 ± 11.24	14.84 ± 2.30	10.37 ± 1.99	8.41 ± 1.78	28.64 ± 6.30	8.07 ± 2.02	5.72 ± 2.76
A. longipes	44.75 ± 4.14	10.91 ± 0.78	7.54 ± 0.67	5.69 ± 0.53	22.49 ± 2.63	4.92 ± 1.01	7.14 ± 0.94
A. pardalis	55.73 ± 7.56	13.27 ± 1.32	9.28 ± 1.41	7.10 ± 1.00	27.53 ± 5.37	6.84 ± 1.72	5.05 ± 2.88
A. scutellatus	48.10 ± 4.36	11.59 ± 0.86	8.07 ± 0.88	6.09 ± 0.60	24.67 ± 3.03	6.12 ± 1.02	10.80 ± 0.91
E. persica	71.57 ± 10.29	17.12 ± 2.22	11.96 ± 1.92	10.09 ± 1.63	35.05 ± 5.04	9.88 ± 2.04	26.53 ± 3.02
E. velox	64.30 ± 4.29	15.58 ± 1.24	10.60 ± 1.04	8.60 ± 0.80	31.41 ± 2.91	7.35 ± 0.69	8.91 ± 0.73
I. capensis	54.72 ± 4.73	12.70 ± 0.84	8.18 ± 0.52	7.26 ± 0.90	27.13 ± 3.75	7.45 ± 1.33	10.66 ± 1.45
L. parva	47.97 ± 2.60	10.96 ± 0.57	7.11 ± 0.43	5.72 ± 0.39	24.99 ± 1.87	5.48 ± 0.75	11.91 ± 0.50
L. pater	129.03 ± 23.59	36.15 ± 7.63	25.25 ± 5.57	21.97 ± 4.87	58.68 ± 11.02	22.38 ± 4.85	6.85 ± 5.54
M. brevirostris	53.46 ± 5.03	12.21 ± 0.89	8.48 ± 0.73	6.14 ± 0.55	26.49 ± 3.28	6.61 ± 1.21	9.41 ± 1.51
M. guttulata	43.68 ± 2.94	10.55 ± 0.68	6.51 ± 0.59	4.71 ± 0.42	22.70 ± 2.63	4.81 ± 1.30	6.42 ± 1.30
A. africanus	54.22 ± 4.46	13.47 ± 1.02	8.79 ± 0.86	6.29 ± 0.68	24.38 ± 2.32	7.17 ± 0.91	10.16 ± 2.10
A. jacksoni	72.70 ± 7.39	19.34 ± 2.21	14.07 ± 2.12	10.37 ± 1.54	30.45 ± 3.85	11.63 ± 1.93	14.79 ± 1.67
A. vauereselli	52.30 ± 3.13	13.29 ± 0.85	8.56 ± 0.58	6.77 ± 0.45	23.48 ± 2.85	6.89 ± 1.13	8.17 ± 1.32
G. galloti	112.18 ± 9.96	32.97 ± 3.61	22.05 ± 1.88	17.88 ± 1.29	63.20 ± 3.45	19.99 ± 2.87	26.51 ± 2.97
H. spekii	44.33 ± 3.26	10.99 ± 0.44	7.36 ± 0.43	5.59 ± 0.39	22.34 ± 1.82	6.38 ± 1.39	7.81 ± 0.51
L. vivipara	46.31 ± 3.28	10.81 ± 0.50	7.48 ± 0.35	5.94 ± 0.32	25.90 ± 1.91	6.50 ± 0.70	7.78 ± 1.10
O. minor	41.01 ± 3.93	10.65 ± 0.50	5.97 ± 0.49	4.79 ± 0.29	18.89 ± 2.02	4.95 ± 0.82	5.21 ± 0.73
P. sicula	66.36 ± 6.37	16.98 ± 1.95	10.68 ± 1.15	9.27 ± 1.13	32.53 ± 2.11	9.17 ± 1.51	9.89 ± 1.55
P. taurica	56.79 ± 5.38	13.47 ± 1.19	8.90 ± 0.94	7.56 ± 0.89	29.53 ± 3.52	7.42 ± 1.04	8.24 ± 1.18
T. sexlineatus	45.91 ± 4.14	10.89 ± 1.03	5.67 ± 0.52	4.87 ± 0.47	25.48 ± 2.49	4.70 ± 0.66	4.56 ± 0.78
A. haasi	46.83 ± 4.61	10.62 ± 0.90	6.83 ± 0.77	5.07 ± 0.58	24.26 ± 2.82	4.80 ± 0.92	6.62 ± 1.35
A. nigropunctatus	57.21 ± 5.79	14.97 ± 1.60	9.17 ± 1.15	6.88 ± 1.07	27.33 ± 2.96	6.23 ± 1.11	8.01 ± 1.34
L. viridis	93.22 ± 16.58	21.92 ± 3.59	14.99 ± 2.82	13.03 ± 2.81	49.48 ± 8.86	14.44 ± 3.07	14.76 ± 3.49
H. guentheri	42.17 ± 3.88	10.02 ± 1.13	6.06 ± 0.83	3.39 ± 0.45	21.02 ± 2.91	3.30 ± 0.58	5.72 ± 1.36
L. chlorogaster	56.59 ± 3.16	14.02 ± 0.62	8.92 ± 0.56	7.03 ± 0.41	28.11 ± 1.98	6.35 ± 0.33	7.14 ± 0.60
A. fitzingeri	36.63 ± 1.88	8.82 ± 0.33	5.41 ± 0.18	3.59 ± 0.32	19.19 ± 1.81	3.43 ± 0.33	5.05 ± 0.72
L. bedriagae	72.22 ± 6.47	19.52 ± 2.24	11.65 ± 1.37	7.47 ± 0.66	36.24 ± 3.33	6.75 ± 0.76	10.80 ± 1.52
L. jayakari	126.51 ± 19.67	31.70 ± 5.81	20.80 ± 5.09	16.64 ± 4.20	59.31 ± 10.97	18.08 ± 3.27	26.53 ± 5.22
L. oxycephala	56.98 ± 3.67	14.43 ± 1.03	9.23 ± 0.68	5.98 ± 0.67	26.87 ± 1.67	5.93 ± 0.88	8.91 ± 1.72
P. erhardii	63.93 ± 2.43	15.41 ± 0.61	10.32 ± 0.46	8.30 ± 0.33	34.38 ± 2.69	8.00 ± 0.71	10.66 ± 0.78
P. filfolensis	73.35 ± 2.06	17.54 ± 0.58	11.61 ± 0.53	9.17 ± 0.57	38.52 ± 3.42	8.60 ± 1.27	11.91 ± 1.94
P. muralis	54.42 ± 6.08	13.50 ± 1.36	7.66 ± 0.82	6.33 ± 0.87	29.11 ± 2.60	5.41 ± 0.50	6.85 ± 1.04
P. tiliguerta	61.69 ± 6.50	15.82 ± 1.88	9.81 ± 1.10	8.05 ± 0.85	31.64 ± 4.49	7.18 ± 1.03	8.92 ± 1.47

* Snout–vent length = measured from tip of snout to cloaca; head length = measured from tip of snout to occipital scale; head width = measured at widest point; head height = measured at highest point; body length = distance between fore and hind limbs measured between shoulder and pelvic joint; body width = measured at widest point; body height = measured at highest point.

Measurements (*mm*) *on 35 species of lacertid lizards: Limb dimensions* (*mean* ± S.D.)*

Species	Femur length	Tibia length	Metatarsus length	Toe (hind)	Humerus length	Radius length	Metacarpus length	Toe (fore)
A. aureus	11.80 ± 1.11	10.16 ± 1.01	2.93 ± 0.27	9.95 ± 0.93	7.15 ± 0.66	4.76 ± 0.53	1.82 ± 0.30	5.43 ± 0.51
A. boskianus	13.63 ± 2.73	12.49 ± 2.18	4.54 ± 1.09	11.91 ± 1.66	9.08 ± 1.75	6.91 ± 1.43	2.78 ± 0.50	5.97 ± 0.98
A. longipes	9.79 ± 1.28	9.45 ± 0.94	3.31 ± 0.37	10.11 ± 0.74	6.81 ± 0.47	4.76 ± 0.48	1.83 ± 0.26	4.51 ± 0.36
A. pardalis	11.40 ± 1.59	10.52 ± 1.44	4.20 ± 0.81	10.64 ± 0.87	7.67 ± 1.08	5.94 ± 0.83	2.30 ± 0.43	5.80 ± 0.53
A. scutellatus	9.86 ± 1.18	9.26 ± 1.05	3.36 ± 0.31	8.38 ± 3.04	6.65 ± 0.62	4.61 ± 0.50	1.84 ± 0.32	4.91 ± 0.61
E. persica	16.71 ± 2.30	14.69 ± 2.47	4.87 ± 0.81	12.82 ± 1.54	10.52 ± 1.60	8.00 ± 1.33	3.11 ± 0.65	8.28 ± 0.90
E. velox	14.33 ± 1.60	11.67 ± 1.00	3.79 ± 0.28	11.13 ± 1.31	8.89 ± 0.82	6.76 ± 0.57	2.81 ± 0.30	7.14 ± 0.77
I. capensis	11.01 ± 1.46	10.36 ± 0.96	3.23 ± 0.52	8.37 ± 2.17	7.66 ± 0.60	6.46 ± 0.47	2.23 ± 0.28	4.96 ± 0.40
L. parva	9.00 ± 0.72	7.12 ± 0.49	2.73 ± 0.37	7.32 ± 0.64	5.48 ± 0.30	5.25 ± 0.47	1.97 ± 0.16	4.46 ± 0.24
L. pater	26.37 ± 4.91	21.12 ± 3.95	7.93 ± 1.04	18.41 ± 3.00	16.33 ± 3.06	14.79 ± 2.78	5.77 ± 1.13	12.41 ± 2.18
M. brevirostris	10.97 ± 1.10	9.97 ± 0.65	3.33 ± 0.15	10.17 ± 0.64	7.25 ± 0.58	5.49 ± 0.44	2.36 ± 0.40	6.09 ± 0.64
M. guttulata	8.97 ± 0.93	8.16 ± 0.66	2.84 ± 0.51	8.88 ± 0.86	5.88 ± 0.61	4.70 ± 0.40	1.84 ± 0.25	4.99 ± 0.53
A. africanus	11.82 ± 1.44	9.89 ± 0.81	4.70 ± 0.95	10.56 ± 0.56	8.30 ± 0.99	7.65 ± 0.76	2.65 ± 0.54	6.70 ± 0.77
A. jacksoni	13.87 ± 1.32	11.19 ± 0.99	6.16 ± 0.88	12.28 ± 1.12	9.19 ± 1.29	8.78 ± 1.26	3.67 ± 0.52	8.15 ± 0.97
A. vauereselli	11.06 ± 1.14	9.49 ± 0.69	4.73 ± 0.49	9.65 ± 0.97	8.12 ± 0.48	7.33 ± 0.47	2.58 ± 0.15	6.35 ± 0.57
G. galloti	25.93 ± 2.02	19.98 ± 1.13	7.95 ± 0.81	20.44 ± 1.90	15.24 ± 0.98	14.97 ± 1.45	5.47 ± 0.46	11.94 ± 0.73
H. spekii	10.15 ± 0.59	10.06 ± 0.54	4.42 ± 0.80	10.29 ± 0.63	6.49 ± 0.45	5.58 ± 0.49	2.04 ± 0.28	4.69 ± 0.22
L. vivipara	8.06 ± 0.71	6.67 ± 0.41	2.49 ± 0.35	7.09 ± 0.37	5.74 ± 0.38	5.48 ± 0.45	1.79 ± 0.25	4.72 ± 0.46
O. minor	9.39 ± 1.04	8.53 ± 0.53	2.97 ± 0.36	7.72 ± 1.07	5.73 ± 0.57	5.18 ± 0.40	1.95 ± 0.25	4.29 ± 0.57
P. sicula	14.52 ± 1.78	11.78 ± 1.06	4.45 ± 0.57	12.34 ± 1.48	8.29 ± 1.10	7.01 ± 0.89	3.19 ± 0.39	7.52 ± 0.76
P. taurica	10.95 ± 1.35	9.14 ± 0.92	3.17 ± 0.43	9.88 ± 1.16	6.89 ± 0.68	5.44 ± 0.61	2.19 ± 0.34	5.73 ± 0.55
T. sexlineatus	7.61 ± 1.02	6.47 ± 0.75	2.06 ± 0.35	7.73 ± 1.08	6.12 ± 0.90	4.75 ± 0.72	1.45 ± 0.31	5.26 ± 0.72
A. haasi	10.42 ± 1.05	9.66 ± 1.24	2.81 ± 0.48	9.88 ± 1.40	6.65 ± 0.77	4.88 ± 0.62	2.02 ± 0.36	5.36 ± 0.71
A. nigropunctatus	11.92 ± 1.50	8.84 ± 0.91	2.87 ± 0.26	10.95 ± 1.25	7.48 ± 0.82	5.92 ± 0.71	2.18 ± 0.30	6.54 ± 0.81
L. viridis	17.94 ± 2.86	14.90 ± 2.75	5.27 ± 0.92	14.99 ± 2.14	11.95 ± 2.25	9.71 ± 1.79	3.55 ± 0.65	8.22 ± 0.98
H. guentheri	8.10 ± 1.01	6.33 ± 0.73	1.62 ± 0.37	5.60 ± 1.52	6.02 ± 0.69	4.63 ± 0.66	1.39 ± 0.21	3.89 ± 0.48
L. chlorogaster	11.88 ± 0.77	9.29 ± 0.36	3.90 ± 0.39	11.29 ± 0.63	7.44 ± 0.50	7.10 ± 0.32	2.69 ± 0.24	6.94 ± 0.58
A. fitzingeri	6.63 ± 0.37	5.08 ± 0.22	1.91 ± 0.22	5.55 ± 0.45	4.05 ± 0.39	3.42 ± 0.39	1.43 ± 0.24	3.32 ± 0.13
L. bedriagae	15.31 ± 1.81	12.23 ± 1.13	4.95 ± 0.59	11.68 ± 4.23	10.26 ± 1.07	8.82 ± 0.56	3.43 ± 0.34	8.23 ± 0.73
L. jayakari	30.12 ± 5.69	23.76 ± 3.75	8.26 ± 1.44	21.07 ± 3.10	17.90 ± 2.89	16.90 ± 3.34	5.46 ± 1.06	14.65 ± 2.34
L. oxycephala	12.05 ± 0.98	9.36 ± 0.75	2.73 ± 0.36	9.86 ± 0.52	7.49 ± 0.65	5.93 ± 0.52	2.11 ± 0.28	6.79 ± 0.71
P. erhardii	13.25 ± 0.72	10.52 ± 0.68	3.99 ± 0.25	11.68 ± 0.94	7.50 ± 0.45	6.50 ± 0.36	3.11 ± 0.42	7.06 ± 0.69
P. filfolensis	14.91 ± 0.90	12.28 ± 0.43	4.48 ± 0.66	8.72 ± 6.50	8.80 ± 0.69	7.29 ± 0.67	3.11 ± 0.40	8.12 ± 0.67
P. muralis	10.59 ± 1.34	8.34 ± 0.72	3.25 ± 0.47	9.80 ± 1.05	6.39 ± 0.92	6.03 ± 0.75	2.34 ± 0.33	5.77 ± 0.74
P. tiliguerta	13.66 ± 1.63	11.24 ± 1.22	4.65 ± 0.39	13.09 ± 1.21	8.01 ± 1.09	6.84 ± 0.80	2.99 ± 0.48	7.71 ± 0.70

* Femur length = measured from pelvis to knee joint; tibia length = measured from knee to ankle joint; metatarsus length = measured from ankle to toe joint; length second toe (hind) = measured from toe joint to tip of toe; humerus length = measured from shoulder to elbow joint; radius length = measured from elbow to ankle joint; metacarpus length = measured from ankle to toe joint; length fourth toe (fore) = measured from toe joint to tip of toe.