

Speed versus manoeuvrability: association between vertebral number and habitat structure in lacertid lizards

Raoul Van Damme* and Bieke Vanhooydonck

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

(Accepted 12 December 2001)

Abstract

We tested the hypothesis that the number of presacral vertebrae in lacertid lizards has evolved to meet requirements set by the structural habitat. The idea was that lizards from cluttered habitats (densely vegetated areas, stony walls and hills, rocks) would be aided by a flexible backbone with many vertebrae, ensuring manoeuvrability, whereas lizards from open habitats would require stiffer vertebrate columns, with relatively few vertebrae, favouring speed and acceleration capacity. In contrast to earlier findings in fishes and snakes, evolution of vertebral number and body size was uncorrelated in lacertid lizards. Body size also did not differ between structural habitat types (open areas, densely vegetated areas, vertical elements). Traditional analysis of variance suggests strong differences in vertebral counts between species from open areas and cluttered areas, the latter having higher numbers of presacral vertebrae. When adequate phylogenetic analyses are used, differences remain significant although the level of significance is considerably lower. Tests of the mechanistic relationships between vertebral number, bending ability, and manoeuvrability, and assessment of the relative importance of manoeuvrability and speed in habitats with varying degrees of impediment are needed to reveal the evolutionary path that has led to the differences in vertebral number.

Key words: ecomorphology, habitat use, interspecific comparison, locomotion, phylogenetic analyses, lacertid lizards

INTRODUCTION

Trade-offs among different aspects of locomotor performance are often invoked to explain the covariation between body form and habitat use. The idea is that the specific locomotor skills needed to survive depend on the physical structure of the habitat, and that different skills require different, antagonistic morphologies (e.g. Losos & Sinervo, 1989; Sinervo & Losos, 1991; Losos, Walton & Bennett, 1993; Vanhooydonck, Van Damme & Aerts, 2001). Maximal speed (or acceleration) capacity and manoeuvrability constitute an example of such a pair of potentially conflicting performance traits. Causes and consequences of this particular trade-off have been explored extensively in swimming (e.g. Webb, 1984; Brown & Taylor, 1995) and flying animals (e.g. Leisler & Winkler, 1985; Norberg, 1994; Rayner, 1995), but less so in terrestrial animals (Garland & Losos, 1994).

One morphological variable that may mediate the trade-off between manoeuvrability and maximal speed capacity in terrestrial vertebrates is the number of

presacral vertebrae. Manoeuvrability typically requires a high degree of body flexibility, which is probably aided by a large number of vertebrae per unit body length (Jayne, 1982, 1985, 1988*a*; Gasc & Gans, 1990; Kelly, Arnold & Gladstone, 1997; E. N. Arnold, 1998). In contrast, a relatively stiff trunk (low number of vertebrae per unit body length) would benefit speed and acceleration capacity, as work spent to move the axial body parts with respect to each other (i.e. internal work) cannot be used to accelerate the centre of mass. Preventing flexion and torsion of the body reduces internal work, thus enhancing speed and acceleration capacity. Therefore, the prediction is that species living in cluttered habitats (densely vegetated areas, stony walls and rocks), where manoeuvrability is important, would tend to have more vertebrae for a given body length, than species living in open, unimpeded habitats, where speed and acceleration capacities are more meaningful (E. N. Arnold, 1983, 1998).

This idea was tested by comparing vertebral numbers between lacertid lizards from different habitats. Lacertid lizards occupy a wide variety of habitats and microhabitats (E. N. Arnold, 1989*a*; Vanhooydonck & Van Damme, 1999), ranging from highly cluttered

*All correspondence to: R. Van Damme.
E-mail: raoul.vandamme@ua.ac.be

(e.g. tropical forest, Mediterranean scrub, scree) to extremely open (e.g. mesic and arid savannah, sand dunes). Most species are active, agile animals that rely on relatively fast locomotor bouts to escape from predators and to capture prey (pers. obs.). Lacertid lizards typically have eight nuchal and five sternal vertebrae with ribs attached to the sternum, but the number of more posterior presacral vertebrae varies considerably (E. N. Arnold, 1998). An association between vertebral number and habitat use has been suggested in this family (E. N. Arnold, 1983, 1989*a,b*), but it has not been tested quantitatively.

MATERIAL AND METHODS

Number of presacral vertebrae

Data were collated on the number of presacral vertebrae in lacertid lizards from the literature (E. N. Arnold, 1973, 1983, 1989*a,b*, 1991, 1997; Salvador, 1982; Schleich, Kästle & Kabisch, 1996; Table 1). In most, but not all, lacertid species, females tend to have higher presacral counts than males (E. N. Arnold, 1998). To avoid confounding by intersexual variation, we only used information on adult male lizards. When different counts were given for the same species, the most frequently occurring number of presacralia in that species was used if mentioned in the paper; otherwise, the mean number of presacral vertebrae was used in subsequent statistical analyses.

Body size estimates

In many families of snake (Lindell, 1994; Shine, 2000) and fish (Lindsey, 1975), larger species tend to have more vertebrae. If such a relationship exists in lacertid lizards, snout–vent length (SVL) must be introduced in the analyses as a covariate. Mean SVLs for adult males of each species were taken from the literature (Pérez-Mellado, 1982; Machado, 1985; Böhme, 1986*a,b*; Molina-Borja & Barquin, 1986; Castilla, Bauwens & Llorente, 1991; Pérez-Mellado & Corti, 1993; Bauwens *et al.*, 1995; Schleich *et al.*, 1996; Vanhooydonck & Van Damme, 1999). Some studies report maximal, rather than mean SVLs. In these cases ($n = 38$), mean SVL was calculated from the following regular (i.e. non-phylogenetic) regression equation:

$$SVL_{(x)} = 11.109 + 0.666 * SVL_{(max)}$$

This empirical equation is based on 55 lacertid species in our database for which we have gathered data on both maximal and mean SVL. The coefficient of determination for this regression is 0.82.

Habitat use

Each species was assigned to 1 of 3 habitat-type

classes: (1) ground-dwelling species living in open areas; (2) species occurring among or in vegetation patches; (3) species mainly occurring on vertical elements. Information on habitat use was based on descriptions in the literature (Minton, 1966; Schleich *et al.*, 1996; E. N. Arnold, 1997, 1998; Vanhooydonck & Van Damme, 1999).

Statistical analysis

In recent years, it has been repeatedly stressed that ‘traditional’ statistical analyses are generally invalid in interspecific comparisons (Felsenstein, 1985, 1988; Harvey & Pagel, 1991; Garland, Dickerman *et al.*, 1993). Because species share parts of their evolutionary history, they cannot be regarded as independent data points in statistical analyses. In this study, independent contrasts (Felsenstein, 1985, 1988) and phylogenetical ANOVAs (Garland, Dickerman *et al.*, 1993) are used to deal with the problem of non-independence.

Both methods require information on the topology and branch lengths of the phylogenetic tree. A ‘currently best’ tree was compiled based on literature (Fig. 1; Harris, Arnold & Thomas, 1998*a,b*, 1999; Harris & Arnold, 1999, 2000; Oliverio, Bologna & Mariottini, 2000). Preferably, data of molecular studies were used instead of information from morphological studies. Presacral number and phylogeny might be confounded because number of presacral vertebrae is sometimes used as taxonomic character (among dozens of others) in morphological studies. Even when using data from molecular studies, polytomies remain and not all lacertid relationships have been resolved. However, it has been argued that these polytomies might represent explosive speciation events (Harris *et al.*, 1998*b*; Harris & Arnold, 1999; Fu, 2000). Therefore, we considered the unresolved nodes as ‘hard’ polytomies (see Purvis & Garland, 1993).

As few data are available on the divergence times between species, all branch lengths were set to unity. It has been shown that the actual length of the branches does not affect the outcome of the statistical analyses to a great extent (Martins & Garland, 1991; Walton, 1993; Irschick *et al.*, 1996; Díaz-Uriarte & Garland, 1998). Moreover, checks of branch lengths with the PDtree program (Garland, Midford & Ives, 1999) did not show any significant correlation between the absolute values of the standardized contrasts and their standard deviations (Garland, Harvey & Ives, 1992).

In total, 96 lacertid species were retained for which we had vertebral counts, mean SVL, habitat use, and phylogenetic position. Presacral number and SVL were logarithmically (\log_{10}) transformed before statistical analyses.

The independent contrasts approach was used to test for a correlation between SVL and number of presacral vertebrae. Independent contrasts of both variables were calculated in the PDtree program (Garland, Midford *et al.*, 1999). Subsequently, the contrasts of number of presacral vertebrae were regressed against the contrasts

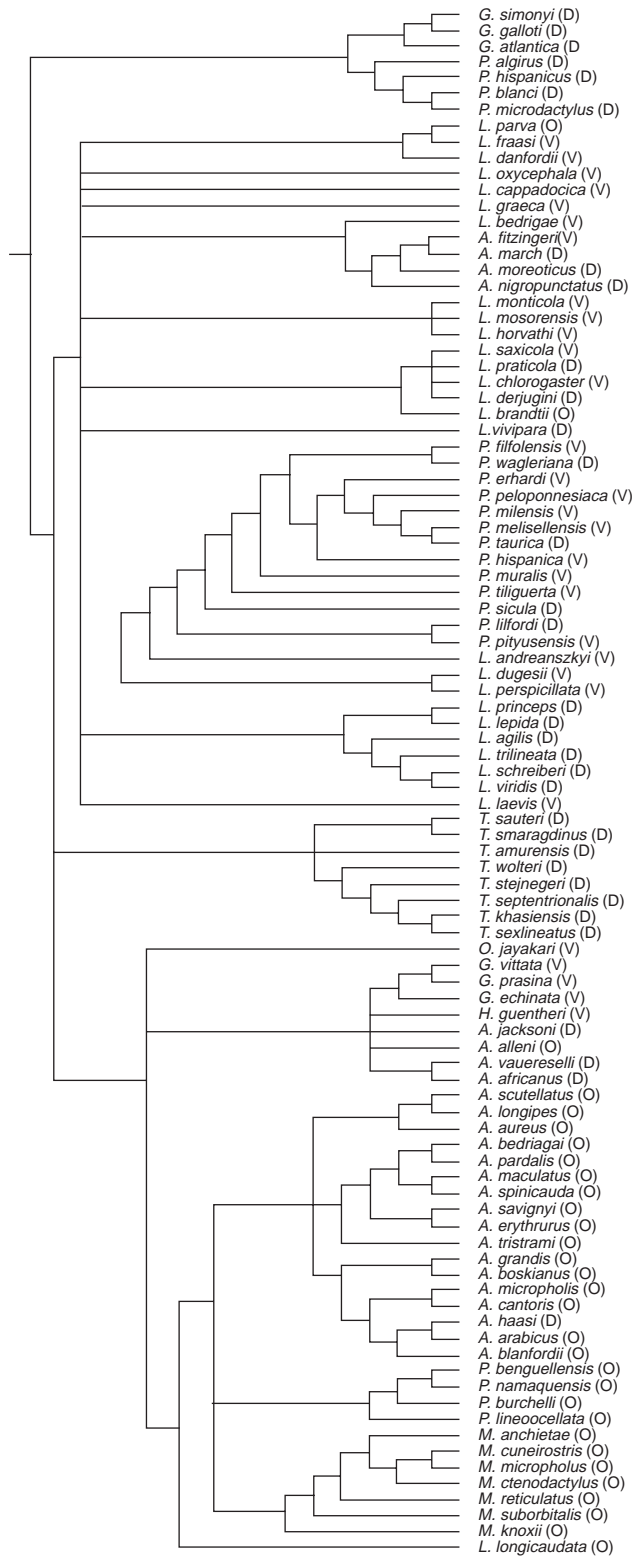


Fig. 1. Hypothesized phylogenetic relationships of the lacertid lizard species in this paper. Branch lengths shown are not indicative of actual divergence times and were put equal to one in the analysis. Structural habitat used by species in parentheses: O, open areas; D, densely vegetated areas; V, habitats with vertical elements. For sources, see text.

of SVL (regression forced through the origin; Garland, Harvey *et al.*, 1992).

The phylogenetic simulations were used to test whether the number of presacral vertebrae differed among species occurring in different habitat types. With the PDsimul program (Garland, Midford *et al.*, 1999) the evolution of number of presacral vertebrae along the phylogenetic tree of the 96 species under consideration was simulated. Brownian motion was used as the model of evolutionary change. Because all branch lengths equal 1, this is analogous to a speciation model of evolutionary change (see Garland, Dickerman *et al.*, 1993). The means and variances were set to the means and variances of the original data, and the procedure was repeated 1000 times. The analyses were run both with and without limits imposed, and highly similar results were obtained. For the analyses with limits, the lower limit was set to (\log_{10} of) 2 and the upper limit was set to (\log_{10} of) 500. Only the results from the unbounded simulations are reported. The PDANOVA program (Garland, Midford *et al.*, 1999) was then used to perform analyses of variance on the simulated values. The 1000 *F*-statistics were then used to set up an empirical null distribution against which the *F*-statistics of traditional analyses of variance (obtained with PDsingle program; Garland, Midford *et al.*, 1999) could be compared. The differences among the habitat groups were considered significant if the 'traditional' *F*-value exceeded the upper 95th percentile of the simulated *F*-distribution (i.e. the critical *F*-value).

RESULTS

Judging from traditional Pearson correlation analysis, the relationship between the number of presacral vertebrae and SVL was just not significant at the 0.05 level ($r = 0.20$, $P = 0.051$). The correlation between the independent contrasts of vertebral counts and SVL was

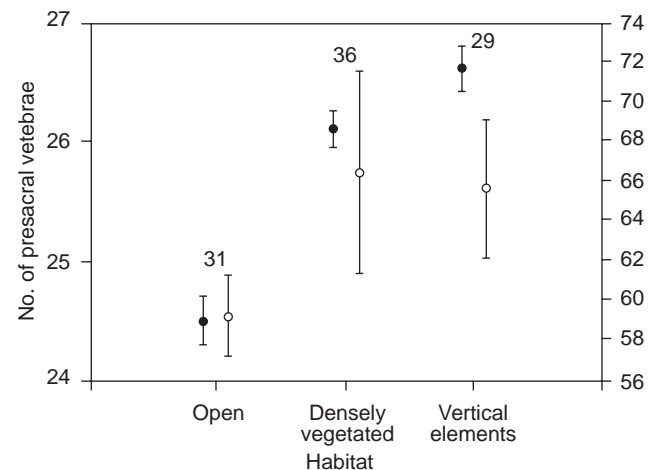


Fig. 2. Mean (\pm SE) snout-vent lengths (white symbols) and number of presacral vertebrae (black symbols) in lacertid lizards from different structural habitats. Numbers above the error bars indicate sample sizes (number of species).

Table 1. Raw data on presacral counts and mean SVL of 96 lacertid species used in the analyses. References are to papers from which data were collated

Species	Presacralia Mean	Reference	SVL Mean	Reference
<i>Gallotia simonyi</i>	26	E. N. Arnold, 1973	162.50	Machado, 1985
<i>Gallotia galloti</i>	26	E. N. Arnold, 1973	112.18	Vanhooydonck & Van Damme, 1999
<i>Gallotia atlantica</i>	26	E. N. Arnold, 1973	60.00	Molina-Borja & Barquin, 1986
<i>Psammodromus algirus</i>	26	E. N. Arnold, 1973	73.02	Bauwens <i>et al.</i> , 1995
<i>Psammodromus hispanicus</i>	26	E. N. Arnold, 1973	40.27	Bauwens <i>et al.</i> , 1995
<i>Psammodromus blanci</i>	26	E. N. Arnold, 1973	38.00	Schleich <i>et al.</i> , 1996
<i>Psammodromus microdactylus</i>	26	E. N. Arnold, 1973	58.00	Schleich <i>et al.</i> , 1996
<i>Lacerta parva</i>	28	E. N. Arnold, 1973	47.97	Vanhooydonck & Van Damme, 1999
<i>Lacerta fraasi</i>	28	E. N. Arnold, 1973	56.57	pers. obs.
<i>Lacerta danfordi</i>	26	E. N. Arnold, 1973	64.00	Valakos, 1987
<i>Lacerta oxycephala</i>	25	E. N. Arnold, 1973	56.98	Vanhooydonck & Van Damme, 1999
<i>Lacerta cappadocica</i>	26	E. N. Arnold, 1973	61.73 ^a	
<i>Lacerta graeca</i>	27	E. N. Arnold, 1973	53.07 ^a	
<i>Lacerta bedriagae</i>	26	E. N. Arnold, 1973	72.22	Vanhooydonck & Van Damme, 1999
<i>Algyroides fitzingeri</i>	26	E. N. Arnold, 1973	36.63	Vanhooydonck & Van Damme, 1999
<i>Algyroides marchi</i>	25	E. N. Arnold, 1973	46.41 ^a	
<i>Algyroides moreoticus</i>	25	E. N. Arnold, 1973	44.41 ^a	
<i>Algyroides nigropunctatus</i>	25	E. N. Arnold, 1973	57.21	Vanhooydonck & Van Damme, 1999
<i>Lacerta monticola</i>	26	E. N. Arnold, 1973	69.38	Bauwens <i>et al.</i> , 1995
<i>Lacerta mosorensis</i>	26	E. N. Arnold, 1973	64.39 ^a	
<i>Lacerta horvathi</i>	26	E. N. Arnold, 1973	52.44	pers. obs.
<i>Lacerta saxicola</i>	27	E. N. Arnold, 1973	69.72 ^a	
<i>Lacerta praticola</i>	27	E. N. Arnold, 1973	51.74 ^a	
<i>Lacerta chlorogaster</i>	27	E. N. Arnold, 1973	56.93	Vanhooydonck & Van Damme, 1999
<i>Lacerta derjugini</i>	26	E. N. Arnold, 1973	51.51	pers. obs.
<i>Lacerta brandtii</i>	26	E. N. Arnold, 1973	63.75	pers. obs.
<i>Lacerta vivipara</i>	26	E. N. Arnold, 1973	46.31	Vanhooydonck & Van Damme, 1999
<i>Podarcis filfolensis</i>	26	E. N. Arnold, 1973	73.35	Vanhooydonck & Van Damme, 1999
<i>Podarcis wagleriana</i>	27	E. N. Arnold, 1973	61.73 ^a	
<i>Podarcis erhardi</i>	27	E. N. Arnold, 1973	63.93	Vanhooydonck & Van Damme, 1999
<i>Podarcis peloponnesiaca</i>	27	E. N. Arnold, 1973	76.00	Böhme, 1986a,b
<i>Podarcis milensis</i>	27	E. N. Arnold, 1973	54.40 ^a	
<i>Podarcis melisellensis</i>	27	E. N. Arnold, 1973	62.40	Böhme, 1986a,b
<i>Podarcis taurica</i>	27	E. N. Arnold, 1973	56.79	Vanhooydonck & Van Damme, 1999
<i>Podarcis hispanica</i>	26.5	E. N. Arnold, 1973	49.00	pers. obs.
<i>Podarcis muralis</i>	26	E. N. Arnold, 1973	54.42	Vanhooydonck & Van Damme, 1999
<i>Podarcis tiliguerta</i>	26	E. N. Arnold, 1973	61.69	Vanhooydonck & Van Damme, 1999
<i>Podarcis sicula</i>	27	E. N. Arnold, 1973	67.70	Vanhooydonck & Van Damme, 1999
<i>Podarcis lilfordi</i>	26	E. N. Arnold, 1973	67.02	Bauwens <i>et al.</i> , 1995
<i>Podarcis pityusensis</i>	26	E. N. Arnold, 1973	75.40	Pérez-Mellado & Corti, 1993
<i>Lacerta andreanszkyi</i>	27	E. N. Arnold, 1973	50.60	Schleich <i>et al.</i> , 1996
<i>Lacerta dugesii</i>	26	E. N. Arnold, 1973	56.00	Böhme, 1986a,b
<i>Lacerta perspicillata</i>	26.5	E. N. Arnold, 1973	59.80	Böhme, 1986a,b
<i>Lacerta princeps</i>	27	E. N. Arnold, 1973	54.40 ^a	
<i>Lacerta lepida</i>	27	E. N. Arnold, 1973	165.20	Pérez-Mellado, 1982; Castilla <i>et al.</i> , 1991
<i>Lacerta agilis</i>	27.5	E. N. Arnold, 1973	68.45	Bauwens <i>et al.</i> , 1995
<i>Lacerta trilineata</i>	27	E. N. Arnold, 1973	126.99 ^a	
<i>Lacerta schreiberi</i>	27	E. N. Arnold, 1973	92.60	Bauwens <i>et al.</i> , 1995
<i>Lacerta viridis</i>	27	E. N. Arnold, 1973	93.22	Vanhooydonck & Van Damme, 1999
<i>Lacerta laevis</i>	26	E. N. Arnold, 1973	114.34 ^a	
<i>Takydromus sauteri</i>	24.5	E. N. Arnold, 1997	47.74 ^a	
<i>Takydromus smaragdinus</i>	26.5	E. N. Arnold, 1997	48.41 ^a	
<i>Takydromus amurensis</i>	24.5	E. N. Arnold, 1997	56.40 ^a	
<i>Takydromus wolteri</i>	24.5	E. N. Arnold, 1997	49.74 ^a	
<i>Takydromus stejnegeri</i>	26.5	E. N. Arnold, 1997	52.40 ^a	
<i>Takydromus septentrionalis</i>	26.5	E. N. Arnold, 1997	61.06 ^a	
<i>Takydromus khasiensis</i>	26.5	E. N. Arnold, 1997	45.08 ^a	
<i>Takydromus sexlineatus</i>	26.5	E. N. Arnold, 1997	45.91	Vanhooydonck & Van Damme, 1999
<i>Omanosaura jayakari</i>	25	E. N. Arnold, 1973	126.51	Vanhooydonck & Van Damme, 1999
<i>Gastropholis vittata</i>	29	E. N. Arnold, 1989a,b	66.39 ^a	
<i>Gastropholis prasina</i>	29	E. N. Arnold, 1989a,b	84.37 ^a	
<i>Gastropholis echinata</i>	29	E. N. Arnold, 1989a,b	78.77	pers. obs.
<i>Holaspis guentheri</i>	26.5	E. N. Arnold, 1989a,b	42.17	Vanhooydonck & Van Damme, 1999

Table 1 (continued)

<i>Adolfus jacksoni</i>	27	E. N. Arnold, 1989a,b	72.70	Vanhooydonck & Van Damme, 1999
<i>Adolfus alleni</i>	27	E. N. Arnold, 1989a,b	48.75	pers. obs.
<i>Adolfus vauereselli</i>	25	E. N. Arnold, 1989a,b	52.30	Vanhooydonck & Van Damme, 1999
<i>Adolfus africanus</i>	25	E. N. Arnold, 1989a,b	54.22	Vanhooydonck & Van Damme, 1999
<i>Acanthodactylus scutellatus</i>	23.5	Salvador, 1982	63.00	Schleich <i>et al.</i> , 1996
<i>Acanthodactylus longipes</i>	24	Salvador, 1982	44.75	Vanhooydonck & Van Damme, 1999
<i>Acanthodactylus aureus</i>	24	Salvador, 1982	50.69	Vanhooydonck & Van Damme, 1999
<i>Acanthodactylus bedriagai</i>	26	Salvador, 1982; Schleich <i>et al.</i> , 1996	64.00	Schleich <i>et al.</i> , 1996
<i>Acanthodactylus pardalis</i>	24.5	Salvador, 1982; Schleich <i>et al.</i> , 1996	55.70	Schleich <i>et al.</i> , 1996
<i>Acanthodactylus maculatus</i>	24	Salvador, 1982; Schleich <i>et al.</i> , 1996	55.00	Schleich <i>et al.</i> , 1996
<i>Acanthodactylus spinicauda</i>	24	Salvador, 1982; Schleich <i>et al.</i> , 1996	55.00	Schleich <i>et al.</i> , 1996
<i>Acanthodactylus savignyi</i>	25	Salvador, 1982	71.00	Schleich <i>et al.</i> , 1996
<i>Acanthodactylus erythrurus</i>	25	Salvador, 1982	65.06 ^a	
<i>Acanthodactylus tristrami</i>	25.5	Salvador, 1982	71.05 ^a	
<i>Acanthodactylus grandis</i>	24	Salvador, 1982	79.71 ^a	
<i>Acanthodactylus boskianus</i>	24	Salvador, 1982	78.00	Schleich <i>et al.</i> , 1996
<i>Acanthodactylus micropholis</i>	24	Salvador, 1982	49.74 ^a	
<i>Acanthodactylus cantoris</i>	24	Salvador, 1982	59.06 ^a	
<i>Acanthodactylus haasi</i>	24	Salvador, 1982	46.83	pers. obs.
<i>Acanthodactylus arabicus</i>	24	Salvador, 1982	62.39 ^a	
<i>Acanthodactylus blanfordi</i>	24	Salvador, 1982	59.06 ^a	
<i>Pedioplanis benguelensis</i>	24	E. N. Arnold, 1991	43.74 ^a	
<i>Pedioplanis namaquensis</i>	24	E. N. Arnold, 1991	47.74 ^a	
<i>Pedioplanis burchelli</i>	25	E. N. Arnold, 1991	52.40 ^a	
<i>Pedioplanis lineocellata</i>	24	E. N. Arnold, 1991	54.40 ^a	
<i>Meroles anchietae</i>	23.5	E. N. Arnold, 1991	85.70 ^a	
<i>Meroles cuneirostris</i>	23.5	E. N. Arnold, 1991	49.74 ^a	
<i>Meroles micropholidotus</i>	24	E. N. Arnold, 1991	56.40 ^a	
<i>Meroles ctenodactylus</i>	23	E. N. Arnold, 1991	75.71 ^a	
<i>Meroles reticulatus</i>	24	E. N. Arnold, 1991	46.74 ^a	
<i>Meroles suborbitalis</i>	23	E. N. Arnold, 1991	57.73 ^a	
<i>Meroles knoxii</i>	24	E. N. Arnold, 1991	46.64	pers. obs.
<i>Latastia longicaudata</i>	27	pers. obs.	75.20	pers. obs.

^a Mean SVL recalculated from maximum SVL, using the regression equation $SVL_{(x)} = 11.109 + 0.666 * SVL_{(max)}$.

much lower ($r = 0.02$, $P = 0.45$). Analysis of variance showed no effect of habitat on SVL, whether the F -value ($F = 2.37$) was compared to traditional tabular values ($P = 0.5$) or against empirically obtained F -distributions ($P = 0.7$). Therefore SVL was not used as a covariate in our tests for the effect of habitat on vertebral counts.

Traditional analysis of variance suggested highly significant differences in mean vertebral counts between species from open habitats and species from densely vegetated and vertical habitats (Fig. 2; $F_{2,93} = 35.09$, $P < 0.0001$). As predicted, lizards from open habitats tended to have fewer vertebrae. However, this result may be confounded because many lizards from open habitats are closely related (see Fig. 1). The traditional ANOVA therefore does not show whether a low pre-sacral count is an adaptation to open habitats, or must be seen as a heritage shared by a clade of lizards that occupies open areas.

The F -value ($F = 35.09$) was therefore compared to an empirically scaled null distribution of F -statistics, obtained by repeated simulations of the evolution of vertebral count ($n = 1000$) over the phylogenetic tree

presented in Fig. 1. The level of significance was markedly lower, but remained significant ($P = 0.039$).

DISCUSSION

In many families of snakes (Klauber, 1956; Saint-Girons, 1978; Lindell, Forsman & Merilä, 1993; Lindell, 1994; Shine, 2000) and fish (Lindsey, 1975), vertebral number is positively correlated with body size, a phenomenon termed 'pleomerism' by Lindsey (1975). Although traditional regression suggests a similar relationship in lacertid lizards, our phylogenetically informed analysis refutes the idea that the evolution of vertebral count is correlated with that of body size. This may be because the range of body sizes spanned by lacertid lizards is relatively small (36–165 mm in this data set), especially when compared to that covered by families of snakes or fish. Possibly, the effects of relatively minor differences in body length among lacertid species can be compensated by changes in the size and shape of the vertebrae, and do not necessitate a change in vertebral number.

In snakes, vertebral count has been shown to have a strong genetic basis (S. J. Arnold & Bennett, 1988; Jayne, 1988*b*; Dohm & Garland, 1993). It therefore bears evolutionary potential. Accordingly, comparisons of vertebral counts in juvenile and adult snakes have suggested a directional or stabilizing selection on the trait (Linsdale, 1936; Stuart, 1941; Dunn, 1942; Inger, 1943; Beatson, 1976; Lindell *et al.*, 1993; Lindell, 1996; but see Klauber, 1945). Agents that have been suggested to promote evolutionary changes in snake vertebral number include shifts in body size (Lindell *et al.*, 1993), climate (species from warmer areas have more vertebrae: Klauber, 1941; but see Lindell, 1994), feeding behaviour (constricting species have more vertebrae than non-constricting ones; Jayne, 1982), prey choice (species feeding on larger prey have lower vertebral counts; Pough & Groves, 1983), habitat use (burrowing species have less vertebrae than terrestrial and arboreal species; Lindell, 1994) and locomotor habits (species with more vertebrae are better at concertina locomotion, snakes with less are better at lateral undulation; Jayne, 1988*a,b*). In lacertid lizards, vertebral count was predicted to vary between structural habitats (E. N. Arnold, 1983, 1998). Our results are consistent with this prediction. Lizards from open habitats tend to have fewer presacral vertebrae than lizards from cluttered habitats (E. N. Arnold, 1983, 1998). Species from vertical habitats tend to have vertebral counts similar to those of densely vegetated areas, suggesting that both habitats require high flexibility of the vertebral column. This may be related to the actual climbing, during which limbs are often moved in awkward positions in search of grips, or to the habits of these animals to hide in narrow crevices or between piled stones.

In concert with these remarks, it should be noted that our analysis is merely correlative and reveals little of the evolutionary path that has led to the differences in vertebral numbers among species occupying various habitats. Future research should further explore the performance gradient (*sensu* S. J. Arnold 1983) by correlating vertebral counts with bending ability of the vertebral column (cf. Gasc & Gans, 1990; Moon, 1999). Apart from the number of vertebrae, many other aspects of the axial skeleton (e.g. design of individual vertebrae, of the girdles) and musculature may contribute to the flexibility of the body. Also, the assumption that flexibility helps manoeuvrability but impairs rectilinear speed or acceleration capacity requires further empirical evidence. For instance, a high lateral flexibility of the body may help increase step length, and thus running speed, in lizards, rather than impede velocity (e.g. Daan & Belterman, 1968; Brinkman, 1981). On the other hand, work spent to move the axial body parts with respect to each other (i.e. internal work) cannot be used for accelerating the centre of mass. Finally, the ecological relevance of manoeuvrability and rectilinear speed should be compared in lizards from open and cluttered habitats.

Acknowledgements

We thank Peter Aerts for helpful discussions and constructive comments on an earlier draft of the manuscript. RVD is a senior research assistant at the Science Fund-Flanders (FWO-VI.). This work was supported financially by a GOA-BOF project of the University of Antwerp (1999–2002).

REFERENCES

- Arnold, E. N. (1973). Relationships of the palaeartic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammadromus* (Reptilia: Lacertidae). *Bull. Br. Mus. (Nat. Hist.) Zool.* **25**: 291–366.
- 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. (1989*a*). 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. (1989*b*). 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. (1991). Relationships of the South African lizards assigned to *Aporosaura*, *Meroles* and *Pedioplanis* (Reptilia: Lacertidae). *J. nat. Hist.* **25**: 783–807.
- Arnold, E. N. (1997). Interrelationships and evolution of East Asian grass lizards, *Takydromus* (Squamata: Lacertidae). *Zool. J. Linn. Soc.* **119**: 267–296.
- Arnold, E. N. (1998). Structural niche, limb morphology and locomotion in lacertid lizards (Squamata Lacertidae); a preliminary survey. *Bull. Br. Mus. (Nat. Hist.) Zool.* **64**: 63–89.
- Arnold, S. J. (1983). Morphology, performance, and fitness. *Am. Zool.* **23**: 347–361.
- Arnold, S. J. & Bennett, A. F. (1988). Behavioural variation in natural populations. V. Morphological correlates of locomotion in the garter snake *Thamnophis radix*. *Biol. J. Linn. Soc.* **34**: 175–190.
- Bauwens, D., Garland, T. Jr, Castilla, A. M. & Van Damme, R. (1995). Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. *Evolution* **49**: 848–863.
- Beatson, R. R. (1976). Environmental and genetical correlations of disruptive coloration in the water snake, *Natrix s. sipedon*. *Evolution* **30**: 241–252.
- Böhme, W. (1986*a*). *Handbuch der Reptilien und Amphibien Europas 2/I Echsen II (Lacerta)*. Wiesbaden: AULA-Verlag.
- Böhme, W. (1986*b*). *Handbuch der Reptilien und Amphibien Europas 2/II Echsen III (Podarcis)*. Wiesbaden: AULA-Verlag.
- Brinkman, D. (1981). The hind limb step cycle of *Iguana* and primitive reptiles. *J. Zool., (Lond.)* **181**: 91–103.
- Brown, R. M. & Taylor, D. H. (1995). Compensatory escape mode trade-offs between swimming performance and maneuvering behavior through larval ontogeny of the wood frog, *Rana sylvatica*. *Copeia* **1995**: 1–7.
- Castilla, A. M., Bauwens, D. & Llorente, G. A. (1991). Diet composition of the lizard *Lacerta lepida* in central Spain. *J. Herpetol.* **25**: 30–36.
- Daan, S. & Belterman, T. (1968). Lateral bending in locomotion of some lower tetrapods. *Proc. K. Ned. Akad. Wet. Ser. C Biol. Med. Sci.* **71**: 245–266.
- Díaz-Uriarte, R. & Garland, T. Jr (1998). Effects of branch length

- errors on the performance of phylogenetically independent contrasts. *Syst. Biol.* **47**: 654–672.
- Dohm, M. R. & Garland, T. Jr (1993). Quantitative genetics of scale counts in the garter snake *Thamnophis sirtalis*. *Copeia* **1993**: 987–1002.
- Dunn, E. R. (1942). Survival value of varietal characters in snakes. *Am. Nat.* **76**: 104–109.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.
- Felsenstein, J. (1988). Phylogenies and quantitative characters. *Annu. Rev. Ecol. Syst.* **19**: 445–471.
- Fu, J. Z. (2000). Toward the phylogeny of the family Lacertidae – why 4708 base pairs of mtDNA sequences cannot draw the picture. *Biol. J. Linn. Soc.* **71**: 203–217.
- Garland, T. Jr, Dickerman, A. W., Janis, C. M. & Jones, J. A. (1993). Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* **42**: 265–292.
- Garland, T. Jr, Harvey, P. H. & Ives, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**: 18–32.
- Garland, T. Jr & Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological morphology*: 240–302. Wainwright, P. C. & Reilly S. M. (Eds). Chicago: University of Chicago Press.
- Garland, T. Jr, Midford, P. E. & Ives, A. R. (1999). An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *Am. Zool.* **39**: 374–388.
- Gasc, J. P. & Gans, C. (1990). Tests on locomotion of the elongate and limbless lizard *Anguis fragilis* (Squamata: Anguidae). *Copeia* **1990**: 1055–1067.
- Harris, D. J. & Arnold, E. N. (1999). Relationships of wall lizards, *Podarcis* (Reptilia: Lacertidae) based on mitochondrial DNA sequences. *Copeia* **1999**: 749–754.
- Harris, D. J. & Arnold, E. N. (2000). Elucidation of the relationships of spiny-footed lizards, *Acanthodactylus* spp. (Reptilia: Lacertidae) using mitochondrial DNA sequence, with comments on their biogeography and evolution. *J. Zool. (Lond.)* **252**: 351–362.
- Harris, D. J., Arnold, E. N. & Thomas, R. H. (1998a). Rapid speciation, morphological evolution, and adaptation to extreme environments in South African sand lizards (*Meroles*) as revealed by mitochondrial gene sequences. *Mol. Phylogenet. Evol.* **10**: 37–48.
- Harris, D. J., Arnold, E. N. & Thomas, R. H. (1998b). Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proc. R. Soc. London B Biol. Sci.* **265**: 1939–1948.
- Harris, D. J., Arnold, E. N. & Thomas, R. H. (1999). A phylogeny of the European lizard genus *Algyroides* (Reptilia: Lacertidae) based on DNA sequences, with comments on the evolution of the group. *J. Zool. (Lond.)* **249**: 49–60.
- Harvey, P. H. & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. New York: Oxford University Press.
- Inger, R. F. (1943). Further notes on differential selection of variant juvenile snakes. *Am. Nat.* **77**: 87–90.
- Irschick, D. J., Austin, C. C., Petren, K., Fisher, R. N., Losos, J. B. & Ellers, O. (1996). A comparative analysis of clinging ability among pad-bearing lizards. *Biol. J. Linn. Soc.* **59**: 21–35.
- Jayne, B. C. (1982). Comparative morphology of the semispinalis-spinalis muscle of snakes and correlations with locomotion and constriction. *J. Morphol.* **172**: 83–96.
- Jayne, B. C. (1985). Swimming in constricting (*Elaphe g. guttata*) and nonconstricting (*Nerodia fasciata pictiventris*) colubroid snakes. *Copeia* **1985**: 195–208.
- Jayne, B. C. (1988a). Muscular mechanisms of snake locomotion: an electromyographic study of the sidewinding and concertina modes of *Crotalus cerastes*, *Nerodia fasciata* and *Elaphe obsoleta*. *J. exp. Biol.* **140**: 1–33.
- Jayne, B. C. (1988b). Muscular mechanisms of snake locomotion: an electromyographic study of lateral undulation of the Florida banded water snake (*Nerodia fasciata*) and the yellow rat snake (*Elaphe obsoleta*). *J. Morphol.* **197**: 159–181.
- Kelly K. C., Arnold, S. J. & Gladstone, J. (1997). The effect of substrate and vertebral number on locomotion in the garter snake *Thamnophis elegans*. *Funct. Ecol.* **11**: 189–198.
- Klauber, L. (1941). The correlation between scalation and life zones in San Diego county snakes. *Bull. zool. Soc. S. Diego* **17**: 73–75.
- Klauber, L. (1945). Herpetological correlations. I. Correlations in homogeneous populations. *Bull. zool. Soc. S. Diego* **21**: 5–101.
- Klauber, L. (1956). *Rattlesnakes. Their habits, life histories, and influence on mankind*. Berkeley, CA: University of California Press.
- Leisler, B. & Winkler, H. (1985). Ecomorphology. *Curr. Ornithol.* **2**: 155–186.
- Lindell, L. E. (1994). The evolution of vertebral number and body size in snakes. *Funct. Ecol.* **8**: 708–719.
- Lindell, L. E. (1996). Vertebral numbers in adders, *Vipera berus*: direct and indirect effects on growth. *Biol. J. Linn. Soc.* **59**: 69–85.
- Lindell, L. E., Forsman, A. & Merilä, J. (1993). Variation in number of ventral scales and survival in the adder, *Vipera berus*. *J. Zool. (Lond.)* **230**: 101–115.
- Lindsey, C. C. (1975). Pleomerism, the widespread tendency among related fish species for vertebral number to be correlated with maximum body length. *J. Fish. Res. Bd Can.* **32**: 2453–2469.
- Linsdale, J. (1936). Variation in the dotted burrowing snake, *Chilomeniscus stramineus*. *Copeia* **1936**: 232–234.
- Losos, J. B. & 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. & Bennett, A. F. (1993). Trade-offs between sprinting and clinging ability in Kenyan chameleons. *Funct. Ecol.* **7**: 281–286.
- Machado, A. (1985). New data on the Hierro giant lizard and the lizard of Salmor (Canary Islands). *Bonn. Zool. Beitr.* **36**: 429–470.
- Martins, E. P. & Garland, T. Jr (1991). Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* **45**: 534–557.
- Minton, S. A. J. (1966). A contribution to the herpetology of West Pakistan. *Bull. Am. Mus. Nat. Hist.* **134**: 27–184.
- Molina-Borja, M. & Barquin, E. (1986). On the consumption of *Launaea arborescens* flowers by the lizard *Gallotia atlantica* in Lanzarote, Canary Islands. *Vieraea* **16**: 233–236.
- Moon, B. R. (1999). Testing an inference of function from structure: snake vertebrae do the twist. *J. Morphol.* **241**: 217–225.
- Norberg, U. M. (1994). Wing design, flight performance and habitat use in bats. In *Ecological morphology*: 205–239. Wainwright, P. C. & Reilly S. M. (Eds). Chicago: University of Chicago Press.
- Oliverio, M., Bologna, M. A. & Mariottini, P. (2000). Molecular biogeography of the Mediterranean lizards *Podarcis* Wagler, 1830 and *Teira* Gray, 1838 (Reptilia, Lacertidae). *J. Biogeogr.* **27**: 1403–1420.
- Pérez-Mellado, V. (1982). Estructura en una taxocenosis de Lacertidae (Sauria, Reptilia) del Sistema Central. *Mediterránea Ser. Biol.* **6**: 39–64.
- Pérez-Mellado, V. & Corti, C. (1993). Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). *Bonn. Zool. Beitr.* **44**: 193–220.
- Pough, F. D. & Groves, J. D. (1983). Specialization of the body form and food habits of snakes. *Am. Zool.* **23**: 443–454.
- Purvis, A. & Garland, T. Jr (1993). Polytomies in comparative analyses of continuous characters. *Syst. Biol.* **42**: 569–575.

- Rayner, J. M. V. (1995). Flight mechanics and constraints on flight performance. *Israel J. Zool.* **41**: 321–342.
- Saint-Girons, H. (1978). Morphologie externe comparée et systématique des Vipères d'Europe (Reptilia, Viperidae). *Rev. Suisse Zool.* **85**: 565–595.
- Salvador, A. (1982). A revision of the lizards of the genus *Acanthodactylus* (Sauria: Lacertidae). *Bonn. Zool. Beitr.* **16**: 1–167.
- Schleich, H. H., Kästle, W. & Kabisch, K. (1996). *Amphibians and reptiles of North Africa. Biology, systematics, field guide.* Koenigstein: Koeltz Scientific.
- Shine, R. (2000). Vertebral numbers in male and female snakes: the roles of natural, sexual and fecundity selection. *J. evol. Biol.* **13**: 455–465.
- Sinervo, B. & Losos, J. B. (1991). Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. *Ecology* **72**: 1225–1233.
- Stuart, L. C. (1941). Studies of neotropical Colubrinae. VIII. A revision of the genus *Dryadophis* Stuart, 1939. *Misc. Publ. Mus. Zool. Univ. Mich.* **49**: 1–106.
- Vanhooydonck, B. & Van Damme, R. (1999). Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evol. Ecol. Res.* **1**: 785–805.
- Vanhooydonck, B., Van Damme, R. & Aerts, P. (2001) Speed and stamina trade-off in lacertid lizards. *Evolution* **55**: 1040–1048.
- Walton, B. M. (1993). Physiology and phylogeny: the evolution of locomotor energetics in hylid frogs. *Am. Nat.* **141**: 26–50.
- Webb, P. W. (1984). Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.* **24**: 107–120.