

Is Evolution Predictable? Evolutionary Relationships of Divergence in Ecology, Performance and Morphology in Old and New World Lizard Radiations

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Abstract

A central question in evolutionary biology concerns whether the direction of evolution proceeds in the same manner for groups of species from independent radiations. We investigated this general issue by examining two diverse lizard clades: Caribbean *Anolis* lizards and lizards from the family Lacertidae. Specifically, we asked: (1) For 13 Caribbean *Anolis* and 11 lacertid lizard species, whether divergence in habitat use is associated with divergence in morphology and performance, and whether the same associations are found in the two radiations. (2) For 46 species from both groups (92 species in all), do both groups show similar levels of variation in external morphology? In lacertid lizards, there is an evolutionary relationship between divergence in performance and habitat use, and between morphology and performance. By contrast, *Anolis* lizards show significant correlations between morphology and performance, and between morphology and habitat use. Morphological comparisons show that these differential relationships might be a consequence of differences in the degree of morphological divergence. Although, the mean evolutionary divergence in morphology is very similar for both groups, the anoles show a higher variance in external morphology. These findings suggest that one cannot assume that divergence in habitat use is associated with evolutionary divergence in morphology and performance in the same manner for different groups.

Key words: adaptive radiation; ecology; performance; morphology; lizards.

Introduction

Patterns of evolutionary change are influenced by three processes: natural selection, stochastic processes (e.g. genetic drift) and historical contingency (Travisano et al., 1995; Losos et al., 1998; Taylor and McPhail, 2000). Although researchers generally accept that all three play a role in shaping species diversity, the relative contribution of each factor is subject to intense debate (Travisano et al., 1995). On extended time scales, however, explicitly testing the repeatability of evolution and evaluating the importance of selection, chance and contingency is difficult, as rewinding the "tape of life" and replaying it over again is impossible (Gould, 1989). Nonetheless, by performing rigorous experiments of shorter duration and in simpler environments (e.g. Travisano et al., 1995), or by comparing the outcomes (i.e. populations, species, radiations) of evolutionary trajectories (e.g. Losos et al., 1998; Huey et al. 2000; Taylor and McPhail, 2000), one

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can test whether evolution is contingent or predictable. More specifically, if replicate populations or radiations in the same environmental context show convergent responses, one can gain evidence for the statement that evolution is predictable.

Whereas most studies have addressed the issue of convergent evolution at the 'design' (i.e. physiological, morphological traits) level (e.g. Cadle and Greene, 1993; Losos et al., 1998; Huey et al., 2000; Leal et al., 2002), few researchers have examined whether different types of characters (i.e. morphology, habitat use, functional capacities) have evolved in a similar manner in different groups. Documentation of such repeated evolutionary events would thus provide powerful evidence for the role of natural selection in structuring evolutionary patterns.

In this study we want to address the latter issue by comparing two distinct lizard radiations, i.e. Old World lacertids and New World anoles. Both radiations have diversified into a variety of habitats and phenotypes. Caribbean *Anolis* lizards have evolved into a series of ecologically and morphologically distinct forms, termed ecomorphs (Rand, 1964, 1967; Schoener, 1968; Williams, 1983; Losos 1990; Irschick and Losos, 1998). Although most *Anolis* lizards can be classified as 'arboreal', they occupy different microhabitats and substrates within that habitat. For instance some species occur primarily near the ground, whereas other species occur high in the canopy. Moreover, some unique radiations of *Anolis* lizards in the Caribbean include aquatic, saxicolous and ground-dwelling species (Leal et al., 2002). Thus, each ecomorph occupies distinct habitats and has unique combinations of morphology, behaviour and functional capacities. Caribbean *Anolis* lizards have been cited as a classic example of adaptive radiation, and comparative studies have shown that morphology, performance, habitat use and behaviour have co-evolved (Losos, 1990; Irschick and Losos, 1998, 1999; Irschick, 2000).

Lacertid lizards have also diversified tremendously. Lacertid lizards are distributed over most parts of Europe, Africa and Asia, and have radiated into habitats ranging from tundra to alpine meadows, heathland to tropical forests and deserts (Arnold, 1989, 1998). Within these habitats, lacertid lizards occupy microhabitats and substrates that vary considerably in structure (Arnold, 1989, 1998): some species are primarily ground-dwelling in open areas, others occur among patches of dense vegetation, or climb in shrubs or on steep rock faces, and yet others are strictly arboreal. Recent work on their phylogenetic relationships, habitat use, behaviour, and functional capacities has provided a rich source of material for comparison to New World *Anolis* lizards (Bauwens et al., 1995; Van Damme et al., 1997, 1998; Vanhooydonck and Van Damme, 1999, 2001, Vanhooydonck et al., 2001).

However, both lizard radiations do not segregate their habitat in the same manner: while anoles are mainly arboreal, lacertids are primarily terrestrial or saxicolous. A direct comparison of the evolutionary relationships between habitat use, performance and morphology in both groups is therefore irrelevant and practically impossible. Instead, we address the issue of whether ecological divergence correlates with the evolutionary divergence in morphology and functional capacities within each group. To do so, we selected those morphological and performance variables that were expected to be ecologically relevant for each specific radiation.

More specifically, we addressed the following issues: First, has divergence in habitat use resulted in divergence in morphology and locomotor performance, and are the same evolutionary relationships found in two distinct lizard radiations? To accomplish this goal, we reanalyzed previously published data for 13 Caribbean *Anolis* species and 11 lacertid lizard species (Losos, 1990; Vanhooydonck and Van Damme, 1999, 2001; Vanhooydonck et al., 2000, 2001, 2002). We derive multivariate measures of the three characteristics to determine whether the degree of divergence in habitat use correlated with the degree of evolutionary divergence in morphology, and locomotor performance across the two groups. Second, we explore one potential cause for not finding similar evolutionary relationships within each group, namely whether lacertid and *Anolis*

radiations display similar levels of variation in morphology. To address this question, we reanalyzed previously published and new data on the external morphology of 46 species from each radiation (92 species total; data taken from Beuttell and Losos 1999; Vanhooydonck and Van Damme, 2001). For anoles, we include 43 species of *Anolis* and 3 species that are labeled different genera, of which two (*Chamelionorops barbouri* and *Chamaeleolis chamaeleonides*) are nested within the larger *Anolis* radiation (Jackman et al. 1999).

Materials and Methods

Evolutionary relationships

We compiled data on morphology, performance and habitat use on 11 lacertid and 13 *Anolis* lizard species. For the lacertid lizards, data were taken from previously published papers (Vanhooydonck and Van Damme, 1999, 2001, Vanhooydonck et al. 2000, 2001, 2002) and included measurements on snout-vent length, mass, hindlimb length, length of the second toe of the hindfoot, forelimb length, and length of the fourth toe of the forefoot as morphological variables. For performance variables, we included sprint speed, climbing speed, clambering speed, endurance and manoeuvrability. Finally, as habitat variables, we used the proportion of time spent in open, vertical and densely vegetated microhabitats, as measured in an experimental set-up. For the 13 *Anolis* species (Losos, 1990), we used data on snout-vent length, mass, tail length, hindlimb length, forelimb length, and the number of lamellae as morphological variables. For performance, we used sprint speed, jumping distance and clinging ability. Finally, as habitat variables, we used perch height, perch diameter and the distance to the nearest perch, as measured in the field. For details on how each of these measurements was taken and the experimental set-ups used, we refer to the papers cited above. We calculated the means per species of all the variables and logarithmically (\log_{10}) transformed them.

All analyses were completed for the lacertid and *Anolis* group separately. We regressed the means per species of the morphological, and performance variables against the means per species of SVL and calculated residuals. We carried out this size-removal procedure because all of the above characteristics tend to change with size. We then performed a principal component analysis (PCA) on each set of residual variables. In each case, the first two principal components explained the majority of variation (>60%), so we only employed the first two principal components in subsequent analyses by using varimax rotation. The factor scores on the first two PC's of each data set were used as input for further statistical analyses.

Morphological divergence

For this analysis, we compiled data on the following morphological variables for 92 lacertid and *Anolis* species (46 species from each group): snout-vent length (SVL), head height, femur length, tibia length, metatarsus length, length of the second toe of the hindfoot, humerus length, radius length, and length of the fourth toe of the forefoot. Data were taken from published papers or from unpublished data sets (Beuttell and Losos, 1999; Losos, pers. comm.; Vanhooydonck and Van Damme, 1999; Vanhooydonck, unpubl. data). Details on how each measurement was taken can be found in the papers cited above. Only adult males were used in the analyses. We calculated the means per species of all morphological variables and logarithmically (\log_{10}) transformed them.

All analyses for this part of the study were completed for the 92 species combined. We regressed the means per species of the morphological variables, other than SVL, against the means per species of SVL and calculated residuals. These residuals were then used as input for a principal component analysis (varimax rotation).

Phylogenetic analyses

Because species are related evolutionarily, they cannot be regarded independent data points in statistical analyses (Felsenstein, 1985, 1988; Harvey & Pagel 1991; Garland et al., 1993). In recent years, various methods and computer programs have been developed to take phylogenetic relationships into account in statistical analyses (Harvey and Pagel, 1991; Garland et al., 1993; Losos and Miles, 1994). In this analysis, we used the independent contrasts approach (Felsenstein, 1985). We calculated the unstandardized independent contrasts, and used these as a measure of evolutionary divergence between species.

The independent contrasts method requires information on the topology and branch lengths of the phylogenetic tree. The phylogenetic relationships within both lacertids and *Anolis* lizards are only partially resolved, and we had to create composite trees based on trees generated using mitochondrial DNA and morphology (lacertids: Arnold, 1989, 1998; Harris et al., 1998; Harris and Arnold, 1999, 2000; *Anolis*: references in Irschick et al., 1997; Jackman et al., 1999) (Fig. 1a, b). Because few data are available on the divergence times within each group, we set all branch lengths to unity. Previous work has shown that variation in branch lengths do not substantially affect the outcome of statistical analyses (Martins and Garland, 1991; Walton, 1993; Irschick et al., 1996; Díaz-Uriarte and Garland, 1998). Moreover, checks of branch lengths with the PDTREE program did not reveal any significant correlation between the absolute values of the standardized contrasts and their standard deviations (Garland et al., 1992).

To test whether divergence in habitat use is associated with divergence in morphology and performance we performed three sets of correlations: (1) between the unstandardized contrasts of the factor scores on PC1 and PC2 in morphological space and the unstandardized contrasts of the factor scores on PC1 and PC2 in performance space, (2) between the unstandardized contrasts of the factor scores on PC1 and PC2 in performance space and the unstandardized contrasts of the factor scores on PC1 and PC2 in habitat space, (3) between the unstandardized contrasts of the factor scores on PC1 and PC2 in morphological space and the unstandardized contrasts of the factor scores on PC1 and PC2 in habitat space (all through origin, see Garland et al. 1992). We used the Bonferroni correction to correct for the level of significance for multiple testing (Hochberg 1988).

To test whether the lacertid and *Anolis* group differ in degree of morphological divergence, we calculated the unstandardized independent contrasts of the means per species of SVL, and of the factor scores on PC1 and PC2 in morphological space (PCA on 92 species combined), using the PDTREE program (Garland et al. 1999). As, in this case, we were interested in the magnitude of the divergence, the absolute values of the contrasts were used in further analyses. We calculated the mean, variance, range, minimum and maximum contrast in SVL, PC1 and PC2 within each group. The means were statistically compared using a one-way ANOVA with 'group' as factor

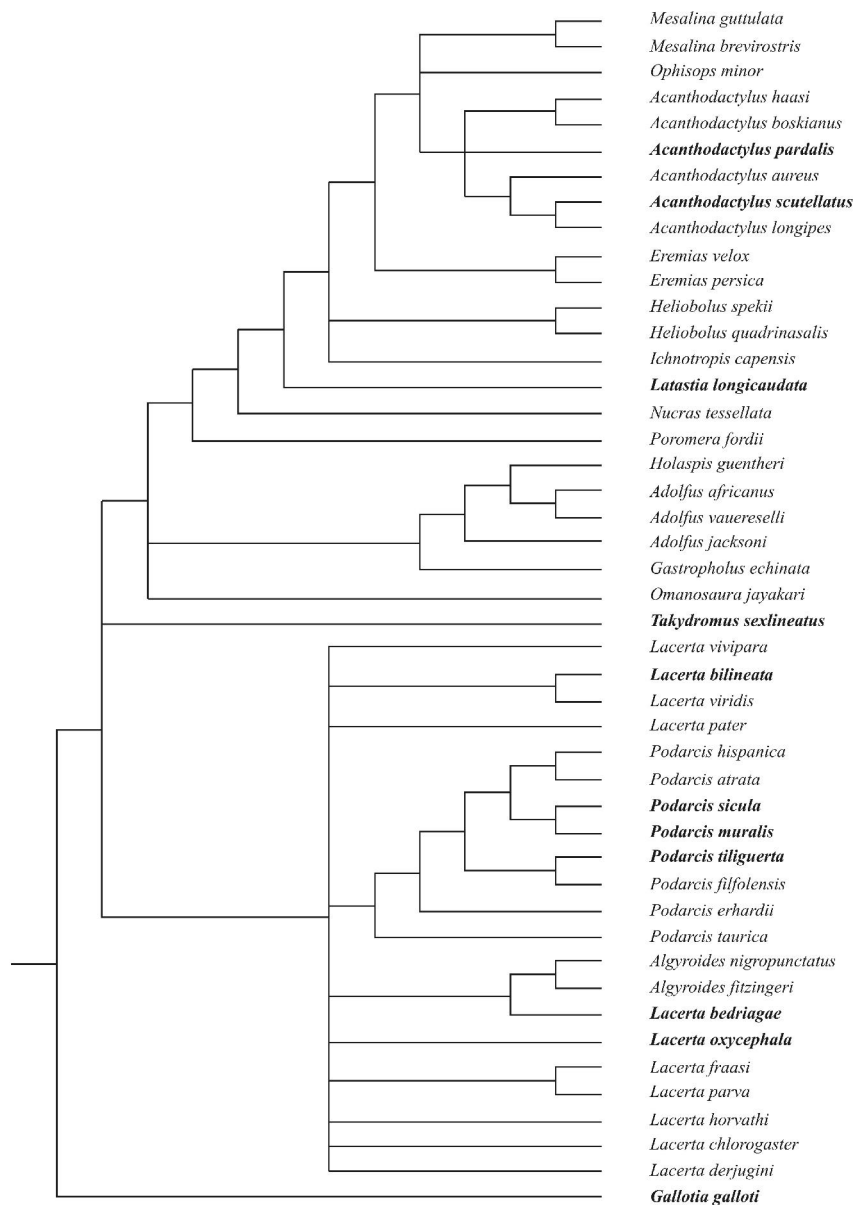


Figure 1a. Phylogenetic tree for the 46 lacertid species used in the analyses. The trees are constructed based on results from mitochondrial DNA and morphological studies (see text for references). It should be noted that the phylogenetic relationships are only partially resolved and these trees should be considered currently best approximations. The species in bold type are used in both parts of the study (i.e. 'Evolutionary relationships' and 'Morphological divergence').

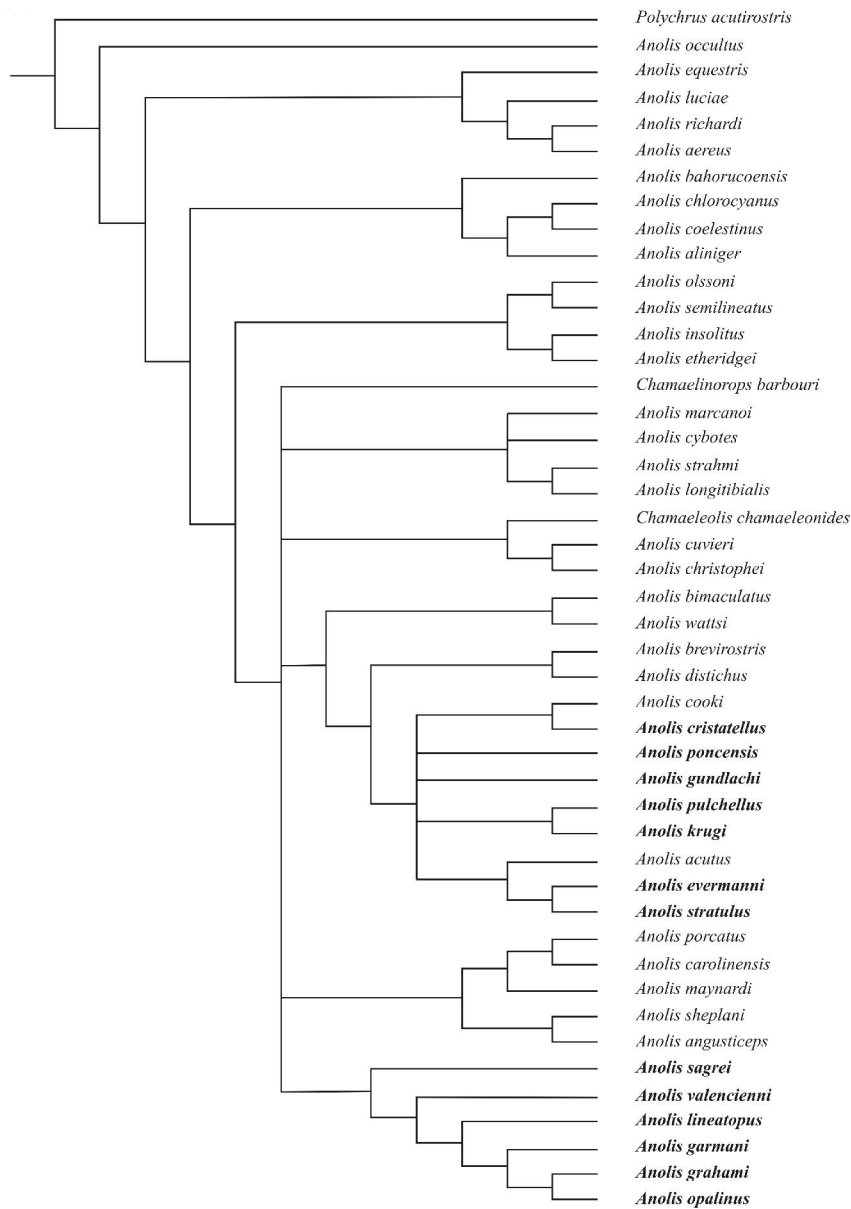


Figure 1b. Phylogenetic tree for the 46 *Anolis* lizard species used in the analyses. The trees are constructed based on results from mitochondrial DNA and morphological studies (see text for references). It should be noted that the phylogenetic relationships are only partially resolved and these trees should be considered currently best approximations. The species in bold type are used in both parts of the study (i.e. 'Evolutionary relationships' and 'Morphological divergence').

Results

Evolutionary relationships lacertids

Morphology

The first two principal components for the PCA on the five residual morphological variables explained 65.2% of the total variation. The first axis (33.5%) was positively correlated with residual mass (0.60), residual forelimb length (0.67) and residual length of the fourth toe of the forefoot (0.88). The second axis (31.7%) was positively correlated with residual hindlimb length (0.97) and the residual length of the second toe of the hindfoot (0.46).

Performance

The first two principal components for the PCA on the residual performance variables explained 78.9% of the total variation. The first axis (40.7%) was positively correlated with residual climbing speed (0.83), residual clambering speed (0.93) and residual manoeuvrability (0.63). The second axis (38.2%) was positively correlated with residual sprint speed (0.91) and negatively correlated with residual endurance (-0.87).

Habitat use

The first two principal components for the PCA on the habitat variables explained 99.8% of the total variation. The first axis (56.2%) was positively correlated with the proportion of time spent on vertical elements (1.0) and negatively correlated with the proportion of time spent in open microhabitats (-0.83). The second axis (43.6%) was positively correlated with the proportion of time spent in densely vegetated microhabitats (1.0).

Correlations

Only two correlations were significant. The contrasts of the factor scores on PC1 in morphological space appeared to be significantly correlated with the contrasts of the factor scores on PC2 in performance space. Also the correlation between the factor scores on PC1 in performance space and the contrasts of the factor scores on PC2 in habitat space proved to be significant (Table 1). After Bonferroni correction, none of the correlations were significant however.

		PC1 perf	PC2 perf	PC1 hab	PC2 hab
Lacertidae					
PC1 morph	r	-0.20	-0.67	-0.08	0.08
	p	0.56	0.03	0.81	0.81
PC2 morph	r	0.59	0.11	-0.15	-0.46
	p	0.06	0.75	0.67	0.15
PC1 perf	r			0.37	-0.72
	p			0.27	0.01
PC2 perf	r			-0.29	-0.37
	p			0.38	0.26
Anolis (including twig anole)					
PC1 morph	r	0.74	-0.27	0.68	-0.13
	p	0.004	0.37	0.01	0.68
PC2 morph	r	0.68	0.25	0.07	-0.26
	p	0.01	0.40	0.82	0.40

		PC1 perf	PC2 perf	PC1 hab	PC2 hab
PC1 perf	r			0.44	-0.25
	p			0.13	0.41
PC2 perf	r			-0.21	0.19
	p			0.50	0.53
Anolis (excluding twig anole)					
PC1 morph	r	-0.04	-0.51	0.12	0.46
	p	0.90	0.09	0.70	0.14
PC2 morph	r	0.79	-0.31	0.13	0.25
	p	0.002	0.33	0.69	0.44
PC1 perf	r			0.05	-0.07
	p			0.87	0.83
PC2 perf	r			0.15	-0.29
	p			0.65	0.35

Table 1. Correlations between the unstandardized contrasts of the factor scores on PC1 and PC2 in morphological (PC morph), performance (PC perf), and habitat (PC hab) space for the lacertids ($N = 10$ contrasts) and the *Anolis* radiation ($N = 12$ contrasts). Significant correlations are given in bold type. Note that only one correlation (PC1 morph with PC1 perf in *Anolis*) is still significant after Bonferroni correction. All analyses were redone for the *Anolis* group without the twig anole, *A. valencienni*, to test whether the presence of the twig ecomorph influences the results (see text for discussion).

Evolutionary relationships *Anolis*

Morphology

The first two principal components for the PCA on the residual morphological variables explained 78.2% of the total variation. The first axis (49.4%) was positively correlated with residual mass (0.91), residual forelimb length (0.96), and residual hindlimb length (0.85). The second axis (28.8%) was positively correlated with residual tail length (0.87) and negatively correlated with the residual number of lamellae (-0.66).

Performance

The first two principal components for the PCA on the residual performance variables explained 97.2% of the total variation. The first axis (63.3%) was positively correlated with residual sprint speed (0.98) and residual jumping distance (0.97). The second axis (33.9%) was positively correlated with residual clinging performance (1.0).

Habitat use

The first two principal components for the PCA on habitat use explained 91.6% of the total variation. The first axis (49.5%) was positively correlated with perch diameter (0.73) and distance to the nearest perch (0.95). The second axis (42.1%) was positively correlated with perch height (0.96).

Correlations

Three correlations proved to be significant. Both the contrasts of the factor scores on PC1 and PC2 in morphological space are significantly correlated with the contrasts of the factor scores on PC1 in performance space. Also, the correlation between the contrasts of the factor scores on PC1 in morphological space and the contrasts of the factor scores on PC1 in habitat space is significant.

After Bonferroni correction, however, only the correlation between the contrasts of the factor scores on PC1 in morphological space and the contrasts of the factor scores on PC1 in performance space was significant (Table 1).

Morphological divergence

The first two principal components for the PCA on the eight residual morphological variables explained 84.6% of the total variation. The first axis (57.9%) was positively correlated with residual head height (0.69), residual femur length (0.91), residual tibia length (0.85), residual metatarsus length (0.91), residual humerus length (0.92) and residual radius length (0.91). The second axis was positively correlated with residual length of the second toe of the hindfoot (0.95) and residual length of the fourth toe of the forefoot (0.90).

The mean unstandardized contrasts of SVL differ significantly between the lacertid and *Anolis* group (one way ANOVA: $F = 6.09$, $df = 1, 88$, $P = 0.02$). The contrasts of PC1 and PC2, on the other hand, do not differ significantly between the two groups (one way ANOVA: $F = 0.13$, $df = 1, 88$, $P = 0.72$ and $F = 0.92$, $df = 1, 88$, $P = 0.34$). The variance for all three variables is larger in *Anolis* than in lacertids (Table 2). Also, the ranges of the contrasts in SVL and both PC's are greater in *Anolis* than in lacertids (Table 2).

variable	statistic	including twig ecomorph		excluding twig ecomorph	
		Lacertidae (N=45)	Anolis (N= 45)	Lacertidae (N = 45)	Anolis (N = 38)
SVL	mean	0.098	0.128	0.098	0.113
	variance	0.007	0.014	0.007	0.011
	minimum	0.011	0.000	0.011	0.002
	maximum	0.336	0.441	0.336	0.442
PC1	mean	0.423	0.576	0.607	0.510
	variance	0.132	0.362	0.296	0.201
	minimum	0.019	0.009	0.004	0.005
	maximum	1.551	2.453	2.301	1.686
PC2	mean	0.446	0.608	0.687	0.515
	variance	0.145	0.458	0.408	0.140
	minimum	0.000	0.004	0.002	0.001
	maximum	1.547	2.801	2.736	1.654

Table 2. Descriptive statistics for absolute values of unstandardized contrasts of SVL and the factor scores on PC1 and PC2. Values are given for the lacertids and the *Anolis* radiation, including and excluding the twig and twig-like anoles.

Discussion

Our comparisons of Old and New World lizard radiations reveal a striking result, namely the divergence in habitat use has not resulted in similar levels of divergence in morphology and performance in the two groups. In lacertid lizards, there is an evolutionary relationship between overall (i.e. multivariate) divergence in performance and habitat use and between divergence in morphology and performance. *Anolis* lizards, on the contrary, exhibit a strong correlation between the divergence in morphology and performance, and between the divergence in morphology and

habitat use, but there is no evolutionary relationship between divergence in performance and habitat use. What factors, or combination of factors, could explain these differential findings between lacertid lizards and anoles?

Morphological divergence

One possible explanation for why lacertid and *Anolis* lizards exhibit different evolutionary patterns is that the degree of evolutionary divergence differs between the clades, thus reducing the statistical power for detecting significant evolutionary relationships. If this were correct, then we expect to find greater evolutionary divergence in one clade relative to another. Our comparison of the morphology of 92 species of lacertid and *Anolis* lizards shows that morphological divergence in size (SVL) is greater in anoles than in lacertids, while the mean divergence in shape (PC1 and PC2) is similar in the two groups. In contrast, the variance in both the size and shape variables is much greater in anoles than in lacertids. When plotting the factor scores on PC1 and PC2 for all 92 species, it is clear that the twig anoles (i.e. *A. occultus*, *A. insolitus*, *A. sheplani*, *A. angusticeps*, *A. valencienni*; see Beuttel and Losos, 1999) and the anoles with a twig ecomorph-like habitus and behaviour (i.e. *Polychrus acutirostris* and *Chamaeleolis chamaeleonides*) are morphologically very different from all other anoles (see figure 2).

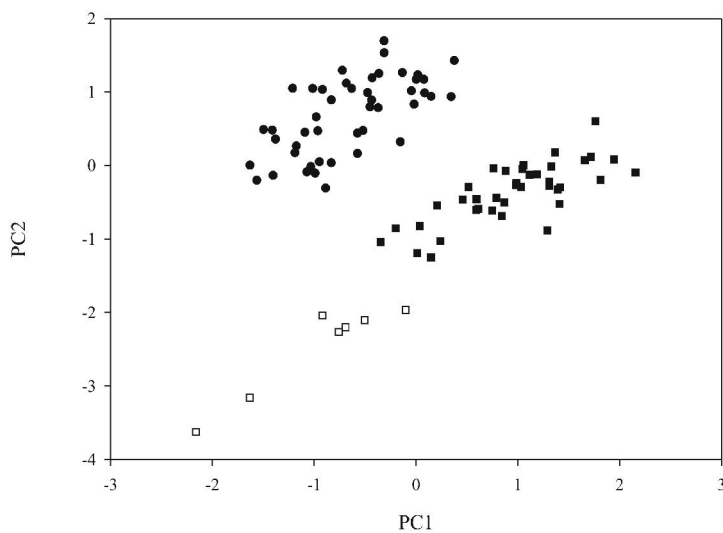


Figure 2. Position of the 46 lacertid and 46 *Anolis* species in the morphological space described by the first two principal components. PC1 correlates positively with residual bead height, residual femur length, residual tibia length, residual metatarsus length, residual humerus length, and residual radius length. PC2 correlates positively with residual length of the second toe of the hindfoot and residual length of the fourth toe of the forefoot. Symbols refer to the species (circles: lacertids; squares: Anolis); the open symbols represent twig or twig-like ecomorphs.

Without the twig and twig-like anoles, the lacertid and *Anolis* radiation exhibit similar levels of morphological divergence (see Table 2). This suggests that the radiation into the twig microhabitat has caused the anoles to become more morphologically divergent than the lacertids. Moreover, when leaving out *A. valencienni* in the correlational analyses, two of the three significant correlations become non-significant (Table 1). Without the twig anole, neither the divergence in habitat use or performance (PC1) is associated with the morphological divergence. These results give further

support to the hypothesis that the evolutionary relationships between the divergence in habitat use, performance and morphology in the two lizard groups might differ because of the difference in morphological (and ecological) divergence, which, in turn, is due to the presence of the twig ecomorph in the *Anolis* radiation.

Historical contingency and clade-specific factors

As evolutionary methods have begun to take root in studies of community ecology, some researchers have suggested that historical contingency, chance events that influence the direction of evolution (Gould, 1989), may play an important role in shaping communities. In the current study, the differing evolutionary relationships among the divergence in morphology, performance and habitat use in the two lizard radiations suggests that evolution is partly contingent, which is in concordance with results from other studies (Cadle and Greene, 1993; Travisano et al., 1995; Losos et al., 1998; Huey et al., 2000; Taylor and McPhail, 2000; Emerson, 2001). Losos et al. (1998) compared the evolutionary radiations of *Anolis* lizards on four islands of the Greater Antilles, and found that whereas the same ecomorphs are produced on each island, the sequence by which they have evolved differs among islands. Thus, the importance of historical contingency seems to depend on the frame of reference: when comparing among islands, historical contingencies can be overcome, whereas within each island, prior evolutionary events limit the options available to particular species, and thus influence the direction in which evolution proceeds (Losos et al., 1998). Clade-specific factors might cause taxa to respond differently to similar selective pressures (Harvey and Pagel, 1991; Losos et al., 1998). For instance, the thermal sensitivity of sprint speed has evolved to match preferred body temperatures in *Anolis* lizards (van Berkum, 1986), whereas thermal physiology in other lizard groups is evolutionary conservative (Hertz et al., 1983; Crowley, 1985; Van Damme et al., 1989, 1990; Autumn et al., 1994). Moreover, both the fact that different characters may respond to similar forces, and that the same character may respond to meet different selective pressures, can cause taxa to show different adaptive responses (Harvey and Pagel, 1991). A classic example of how taxa have evolved different solutions to the same problem is the evolution of different "weapons" for male combat within mammals. Whereas antlers and horns have evolved to serve this purpose in cervids and bovids, respectively, primates use their enlarged canines when fighting for partners (Harvey and Pagel, 1991). We tried to circumvent this problem by comparing those traits that we believed were relevant for each particular radiation (i.e. lacertid versus *Anolis*), instead of comparing the exact same traits in both groups. At this moment, however, our understanding of which of the measured traits is ecologically relevant is incomplete, because of a lack of information on how these traits relate to fitness. The lack of an evolutionary relationship between the divergence in performance and the divergence in habitat use in *Anolis* lizards might thus be due to our choice of the performance traits (see Losos, 1990). Incorporating other performance variables, such as sprint sensitivity (i.e. how sprint speed is affected by differently sized substrates; see Losos and Sinervo, 1989; Losos and Irschick, 1996; Irschick and Losos, 1999; Irschick, 2000), might shed a different light on this issue. Similarly, one might argue that in lacertids, the weak correlation between morphological divergence and performance or habitat divergence, might also be due to our choice of morphological variables. The expectation of a 1:1 relationship between performance capacity or habitat use and morphological variation may be overly simplistic. Instead, performance capacity is likely influenced by a suite of design traits (i.e. morphological, physiological, and biochemical variables). For instance, variation in physiological traits, such as muscle fiber type, has been shown to correlate with variation in endurance capacity in lizards (e.g. Bennett et al., 1984; Bonine et al., 2001).

In sum, our analysis shows that levels of multivariate evolutionary divergence are correlated within both *Anolis* and lacertid lizards, but that the exact nature of the relationship differs between the two

groups. While the exact mechanistic reasons for this difference are unclear, future studies that investigate similar morphological, performance and habitat traits in different taxa would be useful.

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