The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropidurinae*: Liolaemini)

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Abstract

Phenotypic differences among species are known to have functional consequences that in turn allow species to use different habitats. However, the role of behaviour in this ecomorphological paradigm is not well defined. We investigated the relationship between morphology, ecology and escape behaviour among 25 species of the lizard clade *Liolaemus* in a phylogenetic framework. We demonstrate that the relationship between morphology and characteristics of habitat structure shows little or no association, consistent with a previous study on this group. However, a significant relationship was found between morphology and escape behaviour with the distance a lizard moved from a potential predator correlated with body width, axilla-groin length, and pelvis width. A significant relationship between escape behaviour and habitat structure occupation was found; lizards that occupied tree trunks and open ground ran longer distances from predators and were found greater distances from shelter. Behavioural strategies used by these lizards in open habitats appear to have made unnecessary the evolution of limb morphology that has occurred in other lizards from other clades that are found in open settings. Understanding differences in patterns of ecomorphological relationships among clades is an important component for studying adaptive diversification.

Introduction

In recent years, the field of ecological morphology has blossomed. Integrating state-of-the-art methods in functional morphology, behaviour, and ecology, synthesized and analysed in a phylogenetic context, studies of ecological morphology have provided important insights into the process of adaptation and evolutionary diversification (Wainwright & Reilly, 1994; Luczkovich *et al.*, 1995; Aerts *et al.*, 2002). The classic paradigm in ecological morphology of the phenotype → performance → environment relationship was formally articulated by Arnold (1983) and states that differences in phenotype (e.g. morphology, physiology) lead to

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differences in functional capabilities, which, in turn, are adaptive for the differing demands of different environments (Greene, 1986; Coddington, 1988; Emerson & Arnold, 1989; Arnold, 1994; Garland & Losos, 1994).

The role of behaviour in this paradigm is not straightforward (Garland & Losos, 1994; Huey *et al.*, 2003). On one hand, behavioural differences may promote evolutionary change; as populations or species find themselves in different habitats, they may exhibit different behaviours which in turn lead to selection for phenotypes that maximize the effectiveness of these behaviours (Mayr, 1963). As a result, comparative studies would find that interspecific differences in behaviour would be concordant with differences in morphology, performance ability, and habitat use. In Caribbean *Anolis* lizards, for example, species that use broad surfaces have long legs and can run rapidly, whereas species that use narrow surfaces have short legs and poor sprinting capabilities (Losos, 1990a). As one might predict,

behavioural differences parallel morphological, functional, and ecological ones: the long-legged species frequently make use of their great running capabilities, whereas short-legged species depend more on stealth to capture prey and escape predators (Losos, 1990b; Irschick & Losos, 1998).

Conversely, behavioural adjustments can prevent ecomorphological differentiation; a phenomenon recently termed the 'Bogert effect' (Huey *et al.*, 2003). If species are able to reduce the effect of environmental differences solely by altering their behaviour, then phenotypic differentiation may not result from differences in habitat use. For example, lizards of many species alter their escape behaviour when their running ability is compromised by internal conditions such as, gravidity, a full stomach, or low body temperature (Rand, 1964; Ballinger, 1973; Bauwens & Thoen, 1981; Hertz *et al.*, 1982; Dial & Fitzpatrick, 1984; Formanowicz *et al.*, 1990; Schieffelin & de Queiroz, 1991; Núñez, 1996). Lizards also may change their behaviour because of differences in external conditions, such as *Anolis* that adjust their basking behaviour with changes in average ambient temperature (Huey *et al.*, 2003). Thus, to the extent that morphologically similar lizards can use alternative behaviours in different contexts, one would not necessarily expect a relationship to exist between morphology and environment.

Squamate reptiles have been a model group for examination of ecomorphological relationships. Clades of a wide variety of lizards and a few snakes have been studied. Focusing primarily on the demands placed by the structural environment on locomotion and associated morphology, studies have been conducted in taxa from around the world living in a variety of habitats (Table 1). With very few exceptions, relationships between morphology and habitat use are apparent; many studies have also involved functional studies illustrating the role of performance capability as the mechanistic link between morphology and ecology (Table 1). However, few studies have examined the role of behaviour in lizard ecomorphological relationships.

The iguanid lizard clade *Liolaemus* is an ideal candidate for a comparative study of ecological morphology both for its exceptional diversity and because it is one of the few clades in which previous research did not find a relationship between ecology and morphology (Jaksic *et al.*, 1980), despite the fact that a relationship may exist between habitat use and behaviour (Jaksic & Núñez, 1979). Jaksic *et al.* (1980) examined the habitat use and limb and tail morphology of 12 species of Chilean *Liolaemus* finding almost no relationship. Species found on rocks, trees, or the ground showed few significant differences in forelimb, hind limb, and tail morphology (Jaksic *et al.*, 1980; see also Sage, 1973). However, in a comparison of the escape behaviour of two species, Jaksic & Núñez (1979) found that the species that escaped into the grass, *L. lemniscatus*, had significantly shorter limbs than the species which escaped into rocky areas, *L. fuscus.*

For several reasons, the relationship between ecology, morphology and behaviour in *Liolaemus* bears further scrutiny. First, the species studied by Jaksic *et al.* (1980) did not sample either the geographic or phylogenetic range of this clade. In particular, Jaksic *et al.*'s (1980) study was restricted to the region of Mediterranean scrub in central Chile (between 30 and 33°S) and all 12 were members of a single clade. However, the Chilean radiation of *Liolaemus* (subgenus *Liolaemus*) contains approximately 60 species that use a wide variety of habitats. Moreover, an independent radiation of *Liolaemus* primarily distributed in Argentina (subgenus *Eulaemus*) contains almost twice as many species. Thus, one possible explanation for Jaksic *et al.*'s (1980) finding is that the diversity of the clade was not sufficiently sampled. In addition, Jaksic et al.'s study was conducted before an

Table 1 Relationship between morphology and ecology in squamate reptiles.

Taxon	Morphology	Ecology	Reference
Anolis – Island	Long limbs, heavy-bodied, Tail length	Perch type, perch height, perch diameter (neg.), closest perch distance	Losos, 1990a
Anolis – Mainland	Toepad size Tail length	Perch height perch diameter	Irschick *et al.*, 1997
Niveoscincus	Long limbs, heavy-bodied	Microhabitat openness	Melville & Swain, 2000
Tropidurines	Short tibia Short tail and hind limbs Long feet	Closed habitat Branch-dwelling Sand-dwelling	Kohlsdorf *et al.*, 2001
Ctenotus	Long limbs	Microhabitat openness	Pianka, 1969
Phrynosomatinae	Long limbs, broad pelvis Slender-bodied, long tail and toes	Terrestrial habitat Arboreal habitat	Miles, 1994; Herrel *et al.*, 2002
Bothrops	Long tail, slender body	Arboreal habitat	Martins *et al.*, 2001
Liolaemus	Short limbs	Escape into grasses	Jaksic & Núñez, 1979
Chameleons	Long tail, long limbs, Small head	Arboreal habitat	Bickel & Losos, 2002
Squamates	Slender head and body, long feet, short front legs	Microhabitat openness	Scheibe, 1987

explicit phylogenetic hypothesis for *Liolaemus* was available and before the importance of conducting comparative studies in a phylogenetic context was appreciated. Consequently, a study of ecomorphological relationships in *Liolaemus*, sampling the clade's diversity and rigorously analysed using modern comparative methods, is needed to determine the relationships between morphology, behaviour, and habitat occupation in *Liolaemus*.

Methods

Study species

Liolaemus lizards are diurnal heliotherms in the Iguanidae distributed throughout the Andes and adjacent lowlands of South America from Perú to Tierra del Fuego (Donoso-Barros, 1966; Cei, 1986, 1993; Etheridge, 1995). *Liolaemus* is found in almost every available habitat including coniferous forests, dry Chaco, Patagonian steppe, Monte semi-desert, and the driest region in the world, the Atacama Desert. As a result, species exhibit considerable ecological, physiological, and morphological variation. The clade comprises more than 160 species and has one of the largest latitudinal, elevational, and climatic distributions among lizards worldwide, with species found from sea level to over 5000 m (Donoso-Barros, 1966; Cei, 1986, 1993; Núñez, 1992; Etheridge, 1995). This study proposes to use multivariate statistics in an evolutionary framework to investigate whether morphological differences exist in *Liolaemus* and if this morphological variation is associated with microhabitat characteristics and behaviour. Table 2 contains the number of individuals per species sampled for the morphometric, ecological and ecobehavioural analyses.

Field work

Structural microhabitat and ecobehavioural characteristics were recorded at field sites in Argentina and Chile from mid-January to mid-March 1999–2001 (localities listed in Appendix). Field sites were chosen to provide a wide range of habitat types including temperate

Table 2 Species of *Liolaemus* lizards used in the analysis: number of specimens measured for morphological, habitat and ecobehavioural variables is indicated.

Species	Number individuals used in morphology	Number of individuals used in ecology	Number of individuals used in behaviour	Habitat occupation*
Liolaemus bellii	14	14	14	Ground-small shrubs
L. bibronii	12	11	8	Ground-small shrubs
L. buergeri	4	35	33	Saxicolous
L. chiliensis	16	33	33	Ground-dense vegetation
L. cyanogaster	20	10	5	Ground-dense vegetation
L. cf. hernani	11	19	19	Tree trunks
L. lemniscatus	16	47	45	Ground-dense vegetation
L. monticola	16	32	32	Saxicolous
L. nitidus	8	14	12	Saxicolous
L. petrophilus	3	8	6	Saxicolous
L. pictus	16	91	75	Tree trunks
L. robertmertensi	8	27	27	Ground-dense vegetation
L. schroederi	9	26	26	Ground-dense vegetation
L. tenuis	21	46	39	Tree trunks
L. manueli	5	16	14	Ground-large shrubs
L. albiceps	10	12	12	Ground-large shrubs
L. chacoensis	10	7	7	Ground-dense vegetation
L. darwinii	31	26	26	Ground-large shrubs
L. fitzingerii	8	21	19	Ground-large shrubs
L. irregularis	10	16	15	Ground-large shrubs
L. kingi	11	12	11	Ground-small shrubs
L. koslowskyi	14	43	43	Ground-large shrubs
L. laurenti	14	7	7	Ground-large shrubs
L. melanops	11	21	21	Ground-large shrubs
L. rothi	9	38	38	Ground-small shrubs

*Habitat occupation classifications are based on personal observations and correlate primarily with large-scale habitat characteristics in which each species was found. Ground dwelling species are subdivided into three largely, nonoverlapping vegetation categories: (1) species occupying open ground among small, sparse shrubs (Patagonian), (2) species living in dense vegetation and (3) species occupying open ground among large, sparse shrubs (Monte-Hermosan desert and Chaparral). *L. cf. hernani* refers to an undescribed species resembling *L. hernani*.

semi-desert, temperate and montane steppe, semi-arid temperate scrub, alpine or rock desert, tropical extreme desert, cool temperate forest, warm temperate evergreen forest, tropical thorn scrub and tropical grassland (Olson *et al.*, 1983). Ecological data were recorded by walking in haphazard transects throughout the field site from approximately 08.00 until 19.00 hours. Data were collected on sunny, warm days when lizards were assumed to be active at preferred daily body temperatures. Lizards were caught with the use of a noose or by hand. Only animals for which the original perch surface could be identified were included. Data were not recorded for lizards moving at the time of first sight.

Sixteen structural microhabitat characteristics were recorded for each lizard caught see *Supplementary material*, Table S1. These variables were subdivided into three categories – perch characteristics, microhabitat openness and habitat substrate – representing different aspects of the lizard's ecology and chosen to overlap with variables used in previous studies (Losos, 1990a; Miles, 1994; Melville & Swain, 2000). Perch characteristics measured were: (1) perch surface, scored as either (a) open ground (exposed in the open away from cover), (b) closed ground (found in or under shelter), (c) rock surface, (d) grass cover (herbaceous vegetation), (e) litter (e.g. fallen dead branches, leaves, debris), (f) branch of tree or shrub, (g) tree trunk or log, (h) under shrub on ground and (i) surface interface (i.e. perched between two categories); (2) sun exposure (full sun = 0, filtered sun = 1 or shade = 2); (3) perch height in centimetre. Microhabitat openness variables followed Melville & Swain (2000). For each lizard, we measured: (1) estimate of percentage shrub cover in a 3-m^2 radius surrounding the lizard; (2) estimate of percentage ground cover or herbaceous vegetation in a 3-m^2 radius surrounding lizard; (3) estimate of percentage tree cover in a 3-m^2 radius surrounding lizard; (4) height of nearest vegetation; (5) estimate of percentage litter cover in a 3-m^2 radius surrounding lizard; (6) vegetative substrate type, scored as an ordered, categorical variable: none = 0, litter = 1, branch = 2, or trunk = 3. Habitat substrate was quantified by estimating the percentage of cover in the 3-m^2 area surrounding the lizard composed of rocks of the following sizes: (i) 0–5 cm in diameter; (ii) 5–20 cm; (iii) 20–50 cm; (iv) 50–100 cm; (v) 100–200 cm; (vi) >200 cm; (7) ground substrate type, broken into categories and given numerical values to represent a continuum of particle size: (nongranular substrate (vegetation) = 0, fine sand = 1, sand = 2, gravel = 3, heavy gravel = 4, rock = 5).

We also measured three variables related to the escape behaviour of lizards. The first is a behavioural measure: how far the lizards ran away from the predator. Lizards that did not move upon sight were induced to escape by approaching at a constant pace of ca. 80 m/min. toward the individual that is usually sufficient to evoke a behavioural response in *Liolaemus* or similar lizards

(Jaksic & Núñez, 1979; see Cooper, 1997a,b and references therein). The second two variables are aspects of the environment directly related to escape behaviour: distance of lizard to nearest shelter (shelter defined as location where a lizard would be hidden from a visually oriented predator) and height of nearest shelter (recorded as the height above ground of nearest object or cavity in which a lizard would be hidden from a visually oriented predator). These latter two variables differ from the other habitat measurements we took because they specifically reflect how the lizards interact with the environment in one particular context, avoiding predation. The other variables, by contrast, are more general measures of the structure of the habitat. Moreover, the distribution of shelters in an environment is likely to be much more heterogeneous than the other variables we measured. As a result, a lizard's location with respect to distance to a shelter and height of that shelter is more likely to represent specific habitat choice decisions by the lizard; i.e. 'rockiness' or extent of vegetation cover is likely to vary less at a particular locality; measures of these variables represent indices of the general habitat in which the lizard occurs, rather than the specific spot within that habitat in which the lizard chooses to perch.

Morphological measurements

External morphological measurements were taken from preserved museum specimens see *Supplementary material*, Table S2. Specimens were chosen from localities as close as possible to localities where ecological data were obtained and museum numbers are available from the first author on request. Only large adult males were used for morphological measurements. Measurements were chosen based on their ecological and behavioural importance in other lizard groups (Miles, 1994; Arnold, 1998; Beuttell & Losos, 1999; Vanhooydonck & Van Damme, 1999). The following measurements were taken in millimetres using Fowler (Newton, MA) Pro-Max digital calipers: Snout-vent length (SVL) – from tip of snout to anterior end of cloaca; Tail length – from anterior end of cloaca to tip of tail (tail measurements from individuals with regenerated or broken tails were not included); Head length – ventral measurement from tip of the lower jaw to immediately posterior to the jaw; Head width – the widest portion of the head anterior to the ear; Body width – widest portion of mid-body (poorly preserved specimens not included); Pelvic width – width of body immediately anterior to hind legs; Length of fourth finger – from distal end of manus to end of finger (not including claw); Length of fourth toe – from distal end of foot to end of toe (not including claw). Forelimb length was measured as the sum of the following measurements: Upper foreleg length – from insertion of foreleg into body to elbow; Lower foreleg length – from elbow to proximal end of manus; Metacarpal length – from proximal end of manus to proximal end of the longest finger (4th). Hind

limb length was measured as the sum of the following measurements: Upper hind leg length – from insertion of hind leg into body to knee; Lower hind leg length – from knee to proximal end of foot; Metatarsal length – from proximal end of foot to proximal end of longest toe (4th).

Statistical analyses

The mean value of each variable for each species was used in statistical analyses, except perch surface, which was the proportion of individuals per species using a particular perch type (see *Supplementary material*). Prior to analyses, all continuous variables were ln-transformed after addition of one and all percentage variables were arcsine square-root transformed after addition of 0.5 to adjust for nonnormality and reduce the effect of data heteroscedasticity (Zar, 1999).

To investigate the importance of body shape, regressing each variable on SVL and calculating residuals, which were used in subsequent analyses, removed the effect of size on morphological variables. SVL is a commonly used proxy for size among herpetologists and may be simpler to interpret biologically than a composite measure, such as the first principal components axis (Beuttell & Losos, 1999).

Two alternative statistical methods were used to compare differences in morphological shape between species in different microhabitats: phylogenetic analysis of variance (PDANOVA; Garland *et al.*, 1993) and canonical correlation analysis on phylogenetically independent contrasts. To conduct the phylogenetic ANOVA, each species was assigned to one of five general habitat categories (Table 2) and a nonphylogenetic ANOVA on each morphological variable was performed using PDSINGLE (Garland *et al.*, 1993). However, values for species in this analysis may not be statistically independent (Felsenstein, 1985); consequently, statistical significance cannot be evaluated with standard tabular *F*-statistic values (Pagel, 1993). An empirical null distribution of *F*-statistics that takes phylogeny into account was generated using PDSIMUL and analysed with PDANOVA (Garland *et al.*, 1993). For each morphological variable, simulations were repeated 1000 times using both a gradual and a speciational model of evolution. The gradual model assumes character changes along branches of the tree are proportional to branch length. The speciational model sets all branch lengths to one in PDSIMUL, thus assuming only one character change per branch (Martins & Garland, 1991). The means and variances of the simulations were set to the means and variances of the original data.

Standardized independent contrasts were calculated using PDTREE (Garland *et al.*, 1999) for each morphological and ecological variable. The effect of size was removed from morphological variables separately using the residuals of a regression analysis (through the origin) of the standardized independent contrast for SVL on the standardized independent contrast for the variable (Garland *et al.*, 1999). Principal components analyses (PCA) based on correlation matrices (calculated through the origin) were performed separately for standardized independent contrasts of each data set to reduce dimensionality of the data. Zani (2000) examined the statistical procedural order used here and alternatives finding no difference in results of that study. To determine the number of principal component axes to retain for further analyses we included all axes that were significant using the broken stick model (Guttman, 1954; Jackson, 1993; Legendre & Legendre, 1998) and that had eigenvalues >1.0.

Canonical correlation analysis was used to examine whether a relationship exists between: (1) morphology and ecology; (2) morphology and ecobehaviour; and (3) ecobehaviour and perch characteristics. In these analyses, the different categories of ecological variables (perch characteristics, microhabitat openness, and substrate) were analysed separately. Principal components axis scores for each set of variables were used in canonical correlation analysis rather than the original variables (Miles & Ricklefs, 1984; Losos, 1990a). The null hypothesis that the *i*th correlation axis and all that follow are zero was tested using Bartlett's approximation of Wilks' λ, which has a χ^2 distribution (Miles & Ricklefs, 1984). All factor and canonical correlation analyses were performed using Systat 10 or SPSS/Windows v. 10.1 (SPSS Inc., 2000, Chicago, IL, USA).

Branch lengths in the form of number of substitutions were calculated from a parsimony analysis of the mitochondrial DNA data set of Schulte *et al.* (2000, unpublished data) for the 25 *Liolaemus* species sampled (Fig. 1). Diagnostic checks were performed in PDTREE and indicated appropriate standardization of independent contrasts (Garland & Díaz-Uriarte, 1999).

Results

Morphology

Results of principal components analyses using standardized phylogenetic contrasts of size-adjusted morphological variables are presented in Table 3. The first three axes represent 80.4% of the variation. The first axis loads primarily for length of limb elements, head length, and head width. The next PC axis indicates that species with short tails also have short trunks and short fourth toes, and the third axis reveals an inverse relationship between body width and trunk length vs. pelvic width.

Habitat occupation and ecobehaviour

The first three principal component axes from analysis of standardized independent contrasts of the perch data explain 72.4% of the variation in these variables (Table 4a). The first perch axis reveals an inverse
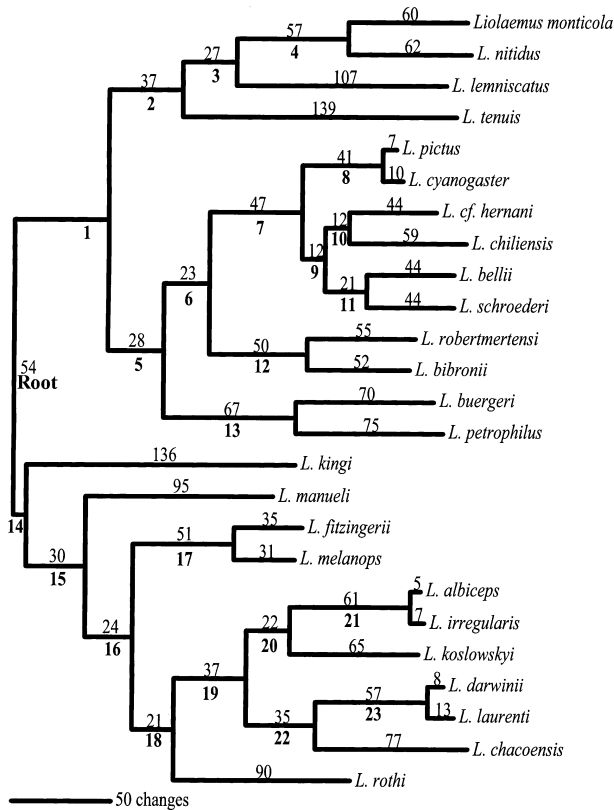
Fig. 1 Phylogenetic hypothesis used for comparative statistical analyses. Phylogeny based on the single overall most parsimonious tree from analysis of 1710 aligned mitochondrial DNA base pairs (558 parsimony informative characters) representing 25 species sampled (Schulte *et al.*, 2000, unpublished data). Tree length = 2204 steps. Branch lengths indicated above branches are number of DNA substitutions. Numbers in bold below branches correspond to independent contrasts for reference in Fig. 2.

Table 3 Loadings from the first three principal component axes based on size-adjusted morphological variables.

Variable	PC 1	PC 2	PC 3
Hindlimb length	0.884	0.006	0.003
Forelimb length	0.864	0.088	0.370
Head width	0.823	0.414	−0.071
Fourth finger	0.812	−0.094	0.403
Head length	0.759	0.234	−0.495
Fourth toe	0.731	−0.513	−0.050
Tail length	0.343	−0.826	−0.135
Axilla-groin length	−0.231	−0.593	0.668
Body width	0.434	0.367	0.632
Pelvis width	0.477	−0.336	−0.528
Eigenvalue	4.563	1.786	1.694
% of total variance	45.63	17.86	16.94

correlation between the use of perches with greater sun exposure, percentage of individuals in closed ground, shrubs and the interface between two perch categories

Table 4 Loadings from the significant principal component axes based on the four categories of ecological variables.

Variable	PC 1	PC 2	PC 3
(a) Perch characteristics			
% individuals in litter	−0.724	0.501	−0.025
% individuals in closed ground	0.672	0.234	0.377
% individuals on branches	−0.667	0.070	0.555
% individuals in shrubs	0.662	0.512	0.361
Sun exposure	0.628	0.663	0.273
% individuals on rocks	−0.580	0.196	−0.188
% individuals on ground cover	−0.558	0.549	−0.170
Perch height	−0.544	−0.374	0.527
% individuals at interface	0.542	0.093	−0.603
% individuals in open ground	0.162	−0.790	−0.334
% individuals on trunks	0.297	−0.705	0.512
Eigenvalue	3.61	2.62	1.74
% of total variance	32.79	23.84	15.78
(b) Microhabitat openness			
% litter cover	0.863	0.455	
% tree cover	0.860	0.077	
Substrate-vegetation type	0.856	0.200	
Height of near vegetation	0.671	−0.051	
% shrub cover	0.459	−0.727	
% ground cover	−0.304	0.860	
Eigenvalue	2.97	1.53	
% of total variance	49.53	25.41	
(c) Substrate			
% rock cover (50–100 cm)	0.837	−0.372	
Substrate – particle size	0.785	0.139	
% rock cover (20–50 cm)	0.755	0.197	
% rock cover (100–200 cm)	0.649	0.621	
% rock cover (5–20 cm)	0.460	0.743	
% rock cover (0–5 cm)	0.390	0.708	
% rock cover (>200 cm)	0.305	−0.528	
Eigenvalue	2.77	1.92	
% of total variance	39.50	27.36	
(d) Ecobehaviour			
Distance to near shelter	0.827		
Height of near shelter	0.685		
Distance moved	0.645		
Eigenvalue	1.569		
% of total variance	52.29		

on the one hand, vs. low perch height and the percentage of individuals found in litter, branches, rocks and ground cover. The second axis reveals a negative correlation for use of open ground and trunks vs. percentage of individuals in ground cover, shrubs and litter and perches with more full sun. PC axis 3 loads strongly and positive for high perch height and percentage of individuals on branches and trunks on the one hand and negatively for percentage of individuals at the interface of two perches.

The first two axes for microhabitat openness explain 74.9% of the variation in these variables (Table 4b). PC axis 1 loads strongly and positive for percentage tree cover and litter, greater height of the vegetative substrate
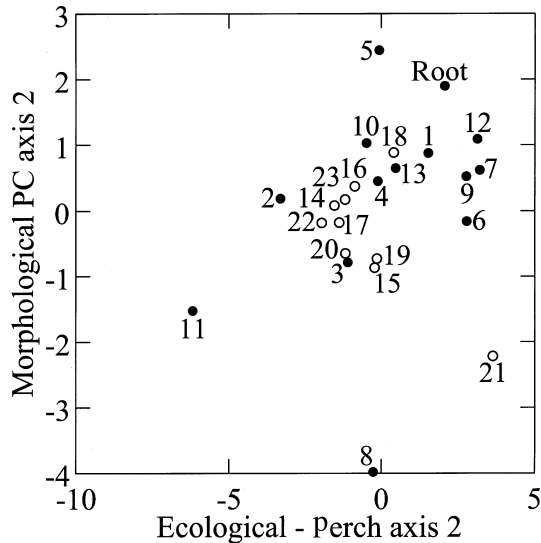
Fig. 2 Scatterplot of morphological principal components axis 2 and ecological – perch principal components axis 2 based on independent contrasts of *Liolaemus* species. This plot indicates the lack of relationship between morphology and structural habitat (perch) variables that has been shown to be significant in other squamate reptile studies. Numbers refer to independent contrasts as shown in Fig. 1. Filled circles are contrasts within the subclade *Liolaemus* (number 1 on Fig. 1) and open circles are contrasts within the subclade *Eulaemus* (number 14 on Fig. 1).

on which the lizard was perched, and the height of the nearest vegetation to the lizard. The second axis indicates an inverse relationship between percentage ground and shrub cover.

In the substrate category principal components analysis, the first two PC axes explain 66.9% of the variation (Table 4c). The first axis loads primarily for overall particle size and percentage rock cover in the categories 20–50, 50–100, and 100–200 cm. PC axis 2 loadings indicate a negative correlation between use of habitats

with high percentage rock cover in the categories <20 and 100–200 cm vs. habitats with high percentage rock cover in the category >200 cm.

Only the first axis is significant in the analysis of the ecobehavioural data (Table 4d). This axis loads strongly for all three variables, distance to nearest shelter, height of nearest shelter, and the distance the lizard fled from a potential predator.

Relationship between morphology, ecology and ecobehaviour

Canonical correlation analysis was used to test the hypothesis that position in morphological space was related to position in the spaces defined by each of the categories of habitat and ecobehavioural data. No relationship was found between morphology and any aspect of habitat occupation (Fig. 2; Table 5); this result was corroborated by phylogenetic ANOVAs with size-corrected morphological variables also indicating no relationship between morphology and habitat (Table 6). By contrast, canonical correlation analyses indicated highly significant correlations between position in ecobehavioural and morphological shape space. The first canonical correlation axis in this comparison was significant (Table 5). CC axis 1 indicates a relationship between long distance moved, long distance to shelter and tall shelter height (ecobehavioural PC 1, 100% of the variance in CC axis 1 is explained by this PC axis) with longer trunks, wider bodies, and a narrow pelvis (morphological PC 3, 73.8% of the variance in CC axis 1 is explained by this PC axis). A significant correlation also was found between position in ecobehaviour and perch characteristics space (Table 5). CC axis 1 in this comparison indicates that species with a large number of individuals occupying open ground and tree trunks or logs vs. low number of individuals in ground cover, shrubs and litter (perch characteristics PC 2, 66.3% of the variance in CC axis 1 is explained by this PC axis) is correlated with long distance

Canonical variable	Canonical correlation	Canonical R^2	Statistical tests†		
			F	d.f.	P
(a) Perch characteristics–morphology	0.704	0.496	16.68	9	0.054
	0.286	0.082	3.31	4	0.508
	0.284	0.081	1.642	1	0.200
(b) Microhabitat openness–morphology	0.525	0.240	7.69	6	0.262
	0.244	0.057	1.22	2	0.542
(c) Substrate–morphology	0.377	0.142	3.24	6	0.778
	0.093	0.009	0.173	2	0.917
(d) Ecobehaviour–morphology	0.708	0.375	14.29	3	0.003*
(e) Ecobehaviour–perch characteristics	0.760	0.466	17.69	3	0.001*

Table 5 Canonical correlation analyses comparing position in morphological space vs. position in habitat or ecobehavioural spaces. Analyses used scores on axes generated in principal component analyses on independent contrasts.

*Significance below the 0.05 level. Results remain significant after sequential Bonferroni test (Holm, 1979; Rice, 1989).
†Tests of the null hypothesis that the correlation in the current row and all that follow within the same analysis are zero.

Table 6 Phylogenetic analyses of variance for each size-adjusted morphological variable among habitat types (Table 1). *F*-values, degrees of freedom, and *P*-values were obtained from nonphylogenetic one-way ANOVAs. Phylogenetic simulation values are the number of simulations in which the *F*-value was greater than that actually observed.

Morphological variable	d.f.	*F*	*P*	Phylogenetic simulations	
				Gradual model	Speciational model
Tail length	4,20	3.80	0.019	203/1000	221/1000
Forelimb length	4,20	1.24	0.325	662/1000	665/1000
Hindlimb length	4,20	4.00	0.015	174/1000	201/1000
Fourth finger	4,20	1.56	0.223	573/1000	590/1000
Fourth toe	4,20	2.88	0.049	331/1000	340/1000
Head length	4,20	2.41	0.083	385/1000	412/1000
Head width	4,20	2.53	0.073	372/1000	373/1000
Pelvis width	4,20	0.60	0.669	875/1000	884/1000
Body width	4,20	1.15	0.362	702/1000	663/1000
Axilla-groin length	4,20	1.99	0.134	483/1000	490/1000

moved, long distance to shelter and high shelter heights (ecobehavioural PC 1, 100% of the variance in CC axis 1 is explained by this PC axis).

Discussion

Our results confirm previous studies (Sage, 1973; Jaksic *et al.*, 1980) that found no relationship between morphology and habitat use among species of *Liolaemus*. Given the many differences in these studies in terms of species studied, field data collection and methods of analysis, the correspondence of results strongly suggests that an ecomorphological relationship does not exist for these lizards. Conversely, the significant relationship between escape behaviour and morphology found in this study and in the two-species comparison of Jaksic & Núñez (1979) suggests that some interspecific morphological variation in these lizards reflects adaptive responses to different predation pressures. We discuss each of these findings below.

Lack of a relationship between morphology and habitat occupation

Given the general similarity of *Liolaemus* to other iguanian lizard clades, such as the Phrynosomatinae and Tropidurini, for which studies have revealed ecomorphological relationships (Miles, 1994; Kohlsdorf *et al.*, 2001; Herrel *et al.*, 2002), the lack of a significant relationship between morphology and habitat characteristics in *Liolaemus* is surprising and suggests that patterns of adaptive diversification and community structure may be fundamentally different in these lizards.

In contrast to our findings with *Liolaemus*, numerous previous ecomorphological studies of squamate reptiles have detected a significant relationship between ecology and morphology (Losos, 1990a; Miles, 1994; Melville & Swain, 2000; Kohlsdorf *et al.*, 2001; Martins *et al.*, 2001; Bickel & Losos, 2002; Herrel *et al.*, 2002). One of the main factors producing significant ecomorphological differences is a correlation between aspects of morphol-

ogy and substrate diameter and orientation (Losos, 1990a; Irschick *et al.*, 1997; Irschick & Losos, 1999; Kohlsdorf *et al.*, 2001). For example, among *Anolis* lizards, a strong correlation exists between perch diameter and limb length (Losos, 1990a; see also Irschick *et al.*, 1997). Similarly, Kohlsdorf *et al.* (2001) detected significant differences in the morphology of *Tropidurus* species living on branches in contrast to those occupying trunks, rocks and sand. The cause for these correlations may be the relationship between limb morphology, locomotor capabilities, and the demands of moving on different surfaces. In *Anolis*, maximal sprinting capability is markedly affected by substrate diameter (Losos & Sinervo, 1989; Losos & Irschick, 1996; Irschick & Losos, 1999). As a result, species that use broad surfaces have long legs and use rapid movements to escape predators and, to a lesser extent capture prey. By contrast, on narrow surfaces, no species is able to run quickly, but short-legged species have greater agility.

One possible explanation, then, for the lack of a significant ecomorphological relationship in *Liolaemus* is that the habitats occupied by *Liolaemus* are relatively homogeneous, all being broad, flat and usually horizontal. As a result, the functional demands they place upon the lizards may be similar and, consequently, differences in habitat use do not lead to selective pressure for differences in morphology. In support of this hypothesis, a study of morphology and habitat use among primarily terrestrial lacertid lizards failed to find a significant relationship between the two (Vanhooydonck & Van Damme, 1999; Vanhooydonck & Irschick, 2002). Also, species of *Tropidurus* using trunks, rocks, and sand did not show large differences in limb morphology (Kohlsdorf *et al.*, 2001). On the other hand, several other studies of primarily terrestrial lizards have detected ecomorphological correlations (Pianka, 1969; Scheibe, 1987; Melville & Swain, 2000; Herrel *et al.*, 2002).

This survey of patterns of ecomorphological evolution in squamates clearly raises as many questions as it answers. Further research is needed in several areas. On one hand, if not adaptation to habitat, what accounts for

the extensive morphological variation in *Liolaemus*, which includes variation in body size, limb and tail length, head dimensions, scale morphology, and colour. Three possibilities are:

(1) Species have adapted to similar habitats in different ways; in many cases, selection may favour different phenotypic solutions to the same environmental challenge. For example, *L. buergeri* and *L. monticola* in central Chile occupy very similar ecological niches. Both species are omnivorous and saxicolous, however *L. buergeri* is a large, robust-bodied species with relatively shorter limbs and tail and *L. monticola* is smaller, slender-bodied with relatively longer legs and tail. Why these ecologically similar species have evolved such different morphologies is not clear, but may be related to their different modes of reproduction: *L. buergeri* is viviparous, whereas *L. monticola* is oviparous, which may affect locomotor capabilities (Plummer, 1997; Miles *et al.*, 2000) and thus lead to different optimal solutions to the same ecological situation.

(2) Species may have adapted to environmental features other than those examined here. Possibilities include differences in humidity, predators and competitors. Similarly, other processes, such as sexual selection, may differ among species and select, either directly or indirectly, for different phenotypic features. For example, *L. koslowskyi* and *L. pseudoanomalus* both live on open ground and utilize shrubs and burrows in the Monte desert of north-central Argentina. Despite using the same structural habitat, the two species have adapted to very different ecological niches and, in the process, have responded to very different selective pressures. *L. koslowskyi* is broadly insectivorous (Aun & Martori, 1998), sexually dimorphic in colour, active throughout much of the day, and flees from predators into burrows or shrubs; by contrast, *L. pseudoanomalus* is myrmecophagous, sexually monomorphic in colour, active at a significantly lower body temperature than *L. koslowskyi*, and spends more time in the open, where it is exposed to predators frequently and often relies on crypsis to escape (F. Cruz, unpublished data). The species differ in morphology in ways (e.g. *L. pseudoanomalus* has a short, round head and pink and white dorsal spots resembling their substrate and *L. koslowskyi* has relatively longer limbs and a tail that is more easily automized) that may relate to either crypsis or behavioural differences, but would not be predicted based solely on their similar habitat use.

(3) Phenotypic differences among species may be random results of genetic drift and related phenomena.

Testing these hypotheses will require considerably more detailed studies of the ecology and behaviour of these species in their natural habitat, as well as laboratory studies to fully comprehend the functional significance of phenotypic differences. Such studies will also be necessary to understand why, even over a similar spectrum of habitat types, some clades exhibit ecomorphological relationships whereas others do not.

Role of behaviour in ecomorphological studies

Huey *et al.* (2003) make a strong argument for the complexity of behaviour in evolutionary studies (see also Garland & Losos (1994) on ecological morphology specifically). Huey *et al.* (2003) identify four possible functions behaviour may have in phenotypic evolution. In the short term, behaviour may either drive evolutionary change – the traditional view – or it may act to prevent change. Evolutionary changes also may result from a correlation between behaviour and a particular phenotypic trait (Brodie, 1992). In the longer term, behaviour may actually have a constraining or canalizing effect on directions of evolutionary diversification by constantly exposing taxa to only a subset of the possible selective factors in the environment. Each of these appears to have a role in the adaptive evolution among many of the squamate ecomorphological studies and *Liolaemus* in particular.

Among *Liolaemus* species, the significant relationship we found between perch variables and escape behaviour – that species in open and exposed habitats are further from shelter and move greater distances when approached – is scarcely surprising. On the other hand, the significant relationship between morphology and escape behaviour is harder to explain. Biomechanical predictions and previous studies (Table 1) suggest that lizard species occupying open ground should have longer limbs than those living in dense vegetation because of their need for greater speed to sprint to safety [this assumes that limb length correlates with sprint speed, which has been demonstrated in lizards (Bonine & Garland, 1999; Kohlsdorf *et al.*, 2001)].

However, we found neither that lizards using open habitats nor those fleeing longer distances have longer legs. This result suggests, contrary to many other lizard species (Pianka, 1969; Melville & Swain, 2000; Herrel *et al.*, 2002; but see Vanhooydonck & Van Damme, 1999), that variation in *Liolaemus* limb length does not result from more exposed lizards requiring longer limbs for more rapid bursts. In fact, our finding of a correlation between body width and the three ecobehavioural variables (distance moved, distance from shelter, and height of nearest shelter) suggests an alternative: species in exposed habitats far from shelter may rely more on crypsis than speed as a predator escape mechanism. For example, *L. pseudoanomalus* and *L. manueli* are highly cryptic and occupy open areas far from shelter with medium-sized gravel. Personal observations indicate that these lizards often remain motionless until the observer was at a relatively close distance before fleeing. Thus, a behavioural adjustment appears to have obviated the need for the evolutionary change in limb length observed in other lizard taxa, an example of the 'Bogert effect.'

Of course, as Bogert (1949) predicted, behaviour may prevent evolutionary change in one respect, and at the same time may lead to change in other aspects of the

phenotype. In this case, effective crypsis requires both the appropriate behaviour and the appropriate morphology that enhances the ability of the lizard to blend into its background, such as substrate-matching colour and a wide, flat body. Evolution of these traits has occurred in *Liolaemus*, as well as various iguanian lizard clades throughout the world, including *Phrynosoma* (North America), *Tympanocryptis* (Australia), and *Phrynocephalus* (Asia). In these cases, it seems that cryptic colouration and body shape have co-evolved with antipredator behaviour providing additional evidence for the phenomenon Brodie (1992) called 'correlational selection'.

The final role of behaviour discussed by Huey *et al.* (2003) is that it may act to constrain or canalize phenotypic traits. In the case of Tasmanian snow skinks, foraging mode may constrain the direction of evolutionary change in ecomorphological traits. Skinks, in general, tend to be more active foragers (Vitt *et al.*, 2003) than iguanian lizards and very rarely rely on crypsis to escape predators. Tasmanian snow skinks demonstrate a strong positive correlation between limb length and microhabitat openness (Melville & Swain, 2000), an expected result given the historical bias to rely on sprint speed rather than crypsis as a predator escape mechanism. Thus, the constraint of foraging behaviour may be restricting these skinks to adopt a single predator avoidance strategy and the morphology associated with increasing sprint speed.

Therefore, those species that live in terrestrial, open microhabitats seem to utilize two alternative behavioural strategies: (1) run long distances at high speed to a potential shelter; or (2) remain motionless, flattening the body against the ground. These alternatives result in different morphologies (Fig. 3). Lizards utilizing the first strategy evolve long hind limbs and short forelimbs to maximize sprint speed over long distances, as in *Callisaurus* and *Uma* in the North American deserts (Herrel *et al.*, 2002). On the other hand, species such as *L. pseudoanomalus* and *Phrynosoma modestum* tend to remain motionless when first spotted and have evolved a morphology that includes a relatively short, flat head and body, but does not require evolutionary change in limb length. What determines which evolutionary course a particular lineage takes is an important question requiring further investigation (Vanhooydonck & Irschick, 2002).

An additional alternative explanation for the discordance between our results and those for many other lizard ecomorphological studies needs to be mentioned. Our discussion assumes that the relationship between limb length and sprint speed documented in other lizard taxa also holds for *Liolaemus*. One possibility is that this relationship for some reason does not hold in *Liolaemus*. Thus, further work should examine whether limb length and sprint speed is related among *Liolaemus*. Assuming that it is, more detailed studies of anti-predator behaviour, perhaps including experimental manipulations (Cooper, 1997a,b, 1999; Leal & Rodriguez-Robles, 1997;
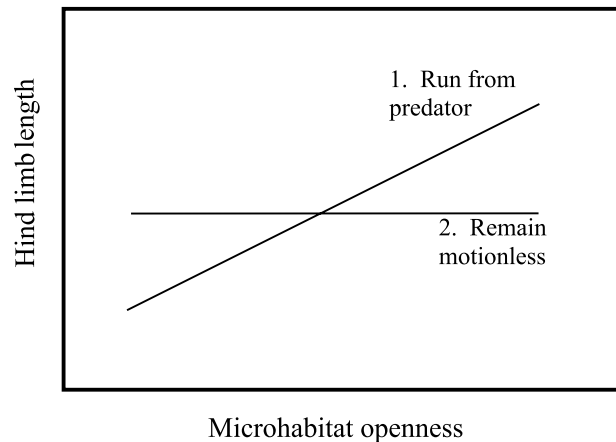

Fig. 3 Hypothetical impact of predator avoidance strategies on evolutionary changes in the hind limb morphology of lizards. Predator avoidance strategy 1, running away from predators, will result in longer hind limbs as lizards occupy more open habitats. Predator avoidance strategy 2, remain motionless, results in no change in hind limb length. These relationships assume there is a direct relationship between lizard sprint speed and hind limb length.

Leal, 1999), will provide insight into the genesis of these relationships.

Factors involved in the origin of phenotypic differences between closely related species are complex. The study of ecological morphology is not a simple one-to-one correlation between morphology and ecology. As demonstrated here, behaviour must be taken into account. To understand the adaptive basis of diversification requires the integration of field and laboratory studies of performance capabilities, their physiological basis, life history, thermal biology, and behavioural ecology. *Liolaemus* exhibits extensive phenotypic, ecological and behavioural variation, yet patterns of relationship among these variables differ from most other squamate groups studied. Consequently, further work on this diverse genus will provide important insights into patterns of adaptive evolutionary diversification.

Acknowledgments

Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/jeb/jeb659/jeb659sm.htm
Table S1 Ecobehavioural data for *Liolaemus spp*. Data are mean values with standard deviations for all individuals of a species in parentheses.
Table S2 Morphological measurements (mm) for *Liolaemus spp*. Data are mean values with standard deviations for all individuals of a species in parentheses.

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Appendix

Field localities

Argentina: San Antonio de Los Cobres and Tastil, Prov. Salta *(L. albiceps, L. irregularis);* near Anillaco, Prov. La Rioja *(L. chacoensis, L. koslowskyi, L. robertmertensi);* 5 km E Los Baldecitos, Prov. La Rioja *(L. darwinii, L. laurenti);* Puerto Madryn and Trelew, Prov. Chubut *(L. bibronii, L. darwinii, L. fitzingerii, L. melanops);* road between Dos Pozos and Trelew, Prov. Chubut *(L. bibronii, L. fitzingerii);* National Route 25, Los Altares and Las Chapas, Prov. Chubut *(L. bibronii, L. petrophilus);* road between Lago Musters *(Sarmiento)* and Comodoro Rivadavia, Prov. Chubut *(L. bibronii, L. kingii).*

Chile: Diego de Almagro, Region III (*L. manueli*); Lampa, Region V (*L. lemniscatus*); Farellones, Region V (*L. lemniscatus, L. nitidus, L. tenuis*); Road to El Volcán and Lo Valdes; Region V (*L. bellii, L. nitidus, L. tenuis*); Coya, Region VI (*L. lemniscatus, L. tenuis*); Vilches, Altos del Lircay, Region VII (*L. chiliensis, L. lemniscatus, L. pictus, L. monticola, L. schroederi, L. tenuis*); Laguna del Laja, Region VIII (*L. buergeri, L. monticola, L. rothi*); PN Nahuelbuta, Region VIII (*L. cyanogaster, L. pictus, L. tenuis*); Villarrica, Region IX (*L. pictus, L. tenuis*); PN Villarrica, near Curarrehue, Region IX (*L. hernani, L. pictus*); PN Vicente Perez Rosales, Region X (*L. cyanogaster, L. pictus*); Ancud, Isla de Chiloe, Region X (*L. cyanogaster, L. pictus*); PN Chiloe, Isla de Chiloe, Region X (*L. pictus*).