

Relationships among morphology, clinging performance and habitat use in Liolaemini lizards

M. J. TULLI*, V. ABDALA† & F. B. CRUZ‡

*CONICET-Instituto de Herpetología-Fundación Miguel Lillo, San Miguel de Tucumán, Argentina

†Fac. Cs. Naturales (UNT), CONICET, Instituto de Herpetología, Fundación Miguel Lillo, San Miguel de Tucumán, Argentina

‡Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA) CONICET-UNCOMA, S.C. Bariloche, Río Negro, Argentina

Keywords:

clinging;
ecology;
Liolaemini;
morphology;
performance.

Abstract

The central tenet of ecomorphological theory holds that different ecological requirements lead to different organismal designs (morphology). Here, we studied the relationships between performance (interlocking grasping) and forelimb morphological traits in species of lizards that exploit different structural habitats in a phylogenetic context. The performance (measured by the maximum force of clinging to substrate) was measured on different substrate types. After phylogenetically informed analyses, we found that arboreal and saxicolous species showed stronger resistance to mechanical traction in all substrates when compared to generalists and sand dweller lizards. These species showed a positive relationship between forelimb dimensions (humerus length and length of claw of toe 5) and maximum force exerted, on the contrary, hand width, claw height (CH) of digits III and IV and claw length of toe 4 showed a negative relationship. In addition, we observed a partial positive correlation between CH and maximal cling force on rough surfaces, but not on smooth surfaces.

Introduction

The relationship between 'design' (i.e. morphological traits) and functional capabilities has been studied by many researches (Collette, 1961; Odendaal, 1979; Peterson, 1984; Russell & Bauer, 1989; Carrillo de Espinoza *et al.*, 1990; Losos, 1990a–c, Losos, 2009; Irschick *et al.*, 1996; Van Damme *et al.*, 1997; Losos *et al.*, 1998; Zani, 2000; Huey *et al.*, 2003; Grizante *et al.*, 2010). In these investigations, a test of the functionality of phenotypic traits is performed, proposing that morphological traits should have ecological correlates. Concordantly, if traits are correctly defined, the recurrent fit between a trait and some environmental aspect provides evidence supporting that the trait is an adaptation to its current function (Pagel, 1994). Substantial effort has been devoted to deeply understand how morphology interacts with the environment or, more precisely, with the ecological context where species occur. In doing so, many studies analysed whether different suites of characters (i.e. mor-

phological, functional and ecological) evolved in a similar manner in different groups of species (Irschick *et al.*, 1996, 1997, 2005; Zaaf & Van Damme, 2001; Vanhooydonck & Irschick, 2002). Documenting such repeated evolutionary events would provide powerful evidence for the role of natural selection in structuring evolutionary patterns.

Many animal species, such as squirrels, woodpeckers and lizards, are able to climb vertical surfaces thanks to specialized features such as claws or tails. Lizards have evolved specializations (digital pads, claws) for moving effectively on heterogeneous surfaces, such as, small or large tree branches, boulders or rocks. To achieve a vertical position, the animals need to be in equilibrium by pulling their fore feet toward the substrate, while its hind feet push on the substrate. The friction between the animal and the bark must be enough to counter the upward force acting on the claws. The ability to balance over a support requires an animal maintain its centre-of-mass in line with its support. There are two basic means by which an animal can accomplish this: either it can achieve an interlocking surface with the substrate to generate a new nonvertical contact surface between itself and its support, or it can develop an adhesive or suction force between its body and the contact surface (Cartmill, 1985).

Correspondence: María José Tulli, Instituto de Herpetología, Fundación Miguel Lillo, Miguel Lillo 251 (4000), San Miguel de Tucumán, Argentina.
Tel.: +54 381 4230056; fax: +54 381 4330868;
e-mail: majotulli@gmail.com

Many lizards cling by performing an interlocking grip on rocks (Biewener, 2003). This involves the development of claws that may penetrate into the surface (or grip into small cracks) of the substrate creating a new nearly perpendicular contact surface to the gripping adductor force for the digits (Biewener, 2003). This aspect was studied in several lizard species, mainly aiming to explain how arboreal lizards perform it (Irschick *et al.*, 1996; Zani, 2000; Goodman *et al.*, 2008). From these studies, pad area in pad-bearing lizard species (Irschick *et al.*, 1996) and claw height (CH) and toe length (Zani, 2000) were considered the most important factors determining climbing ability. In a recent study, Tulli *et al.* (2009) observed that claws of climbing species (arboreal and saxicolous) are tall and sharply curved, whereas terrestrial species have long and gently curved claws. Similar associations between morphology and ecology were found in mammals. For example, arboreal squirrels have sharp and abruptly curved claws at the tip, whereas their terrestrial relatives have blunter, smoothly curved claws (Cartmill, 1985). Similar claw differences distinguish tree-climbing birds from their closest nonclimbing relatives (Bock & Miller, 1959).

Liolaemus is one of the most diverse and species-rich lizard genera in the world, comprising more than 200 species (Abdala & Quinteros, 2008; Quinteros *et al.*, 2008), and together with *Phymaturus* (with more than 25 species described) and *Ctenoblepharys* constitute the clade Liolaemini (Schulte *et al.*, 2003). These species use a variety of habitats and range from generalized ground dwellers to highly specialized forms that live exclusively on rock boulders or associated with loose sand (Schulte *et al.*, 2004; Pincheira-Donoso *et al.*, 2009; Tulli *et al.*, 2009). This ecological variety and the knowledge of their phylogenetic relationships make these lizards an ideal system to explore the proximate relationships between morphology and function in an ecological context.

In this work, we study the interspecific variation in functional capability (performance), morphology and habitat in *Liolaemus* species. An historical perspective allows us to test the expected evolutionary relationship between form and function. Our main questions are the following: (i) what is the degree of phylogenetic signal of morphological features and performance in this group of lizards? (ii) what is the relationship between performance (clinging ability) and morphology? and (iii) do animals occupying different habitats differ in morphology and performance?

We selected *Liolaemus* species, because these animals occupy a wide variety of habitats, and the proximate relationships between morphology and ecology have been scarcely been studied in this genus (Jaksic *et al.*, 1980; Halloy *et al.*, 1998; Etheridge, 2000; O'Grady *et al.*, 2005; Schulte *et al.*, 2004; Pincheira-Donoso *et al.*, 2009; Tulli *et al.*, 2009). Moreover, very few studies have explicitly addressed the question of locomotor specialization in these lizards (Tulli *et al.*, 2009).

In addition to the *Liolaemus* species considered, we include seven species of *Phymaturus*, *Diplolaemus sexcintus* and *Leiosaurus belli* for comparison. These were selected as they occupy very distinct and restricted habitats allowing us to test the generality of the results obtained for *Liolaemus* across other iguanians.

Materials and methods

Study system

Twenty-nine *Liolaemus* species were collected during summer months of 2007–2009; together with seven *Phymaturus* species, *D. sexcintus* and *L. belli* (see Appendix S1 for species list). Specimens were captured during normal activity periods either by hand or by noose. Lizards were placed in cloth bags and transported to the laboratory in Bariloche, Argentina. The lizards were housed in glass terraria of (120 cm × 60 cm × 40 cm), divided in five 0.12-m lanes each. Lizards were fed *ad libitum* with live crickets or flower buds (depending on their diet type) and watered twice daily and were maintained in a climate-controlled room at 22 °C (±1.4 °C). Three 150 W infrared light bulbs at one end of the terraria provided light and heat. Temperature within the terrarium ranged from 44 °C to room temperature, allowing lizards to choose their preferred temperature. Voucher specimens of the species studied were deposited at the Herpetology Collection of the Fundación Miguel Lillo, Tucumán, Argentina (Appendix S1).

Habitat use

To test differences among species analysed in relation to habitat use, we classified each species as generalized terrestrial, arenicolous, saxicolous or arboreal. The assignment of habitat use in the lizards studied here (Table 1) is based on personal field observations and literature data (Ceí & Scolaro, 1983; Pereyra, 1985; Ceí, 1986; Medel *et al.*, 1988; Ceí & Scolaro, 1996; Scolaro & Ceí, 1997; Halloy *et al.*, 1998; Etheridge, 2000; Schulte *et al.*, 2000; Frost *et al.*, 2001; Ceí *et al.*, 2003; Avila *et al.*, 2004; Scolaro, 2005; Avila *et al.*, 2006; Abdala & Díaz Gómez, 2006; Abdala & Lobo, 2006; Abdala, 2007; Laspiur *et al.*, 2007; Lobo & Quinteros, 2005; Pincheira-Donoso *et al.*, 2007; Abdala & Quinteros, 2008; Tulli *et al.*, 2009).

Performance

We measured performance as the maximum grasping force needed to detach lizards from the surface in each trial. We test substrate dependence by measuring grasping force when pulling the lizard across three different substrate types: smooth rock, rough rock and tree bark (Fig. 1). Once lizards reach their preferred body

Table 1 Habitat use of the species examined in this study based on literature data (see text).

Species	Author	Function	Habits
<i>Diplolaemus sexcintus</i>	Cei <i>et al.</i> (2003)	Ground-dwelling	Terrestrial
<i>Liolaemus baguali</i>	Cei & Scolaro (1996)	Clinging ability	Saxicolous
<i>Liolaemus bibroni</i>	Schulte <i>et al.</i> (2000)	Ground-dwelling	Terrestrial
<i>Liolaemus canqueli</i>	Etheridge (2000)	Bury in the sand	Arenicolous
<i>Liolaemus ceii</i>	Cei (1986)	Clinging ability	Saxicolous
<i>Liolaemus coeruleus</i>	Pincheira-Donoso <i>et al.</i> (2007)		
<i>Liolaemus crepuscularis</i>	Abdala & Díaz Gómez (2006)	Ground-dwelling	Terrestrial
<i>Liolaemus dorbignyi</i>	Abdala & Quinteros (2008)	Clinging ability	Saxicolous
<i>Liolaemus elongatus</i>	Cei (1986)		
<i>Liolaemus escarchadosi</i>	Scolaro & Cei (1997)	Ground-dwelling	Terrestrial
<i>Liolaemus fitzingeri</i>	Etheridge (2000)	Bury in the sand	Arenicolous
<i>Liolaemus goestchi</i>	Abdala (2007)	Ground-dwelling	Terrestrial
<i>Liolaemus hatcheri</i>	Etheridge (2000)	Clinging ability	Saxicolous
<i>Liolaemus irregularis</i>	Abdala (2007)	Ground-dwelling	Terrestrial
<i>Liolaemus kingii</i>	Avila <i>et al.</i> (2006)	Clinging ability	Saxicolous
<i>Liolaemus koslowskyi</i>	Etheridge (2000)	Ground-dwelling	Terrestrial
<i>Liolaemus kolengh</i>	Abdala & Lobo (2006)		
<i>Liolaemus melanops</i>	Cei & Scolaro (1983)	Bury in the sand	Arenicolous
<i>Liolaemus multimaculatus</i>	Halloy <i>et al.</i> (1998)		
<i>Liolaemus olongasta</i>	Etheridge (2000)		
<i>Liolaemus ornatus</i>	Abdala (2007)	Ground-dwelling	Terrestrial
<i>Liolaemus petrophilus</i>	Avila <i>et al.</i> (2004)	Clinging ability	Saxicolous
<i>Liolaemus pictus</i>	Medel <i>et al.</i> (1988)		Arboreal
<i>Liolaemus poecilochromus</i>	Abdala field observations	Ground-dwelling	Terrestrial
<i>Liolaemus riojanus</i>	Halloy <i>et al.</i> (1998)	Bury in the sand	Arenicolous
<i>Liolaemus rothi</i>	Etheridge (2000)	Clinging ability	Saxicolous
<i>Liolaemus sarmientoi</i>	Cei & Scolaro (1996)	Clinging ability	Saxicolous
<i>Liolaemus scapularis</i>	Halloy <i>et al.</i> (1998)	Bury in the sand	Arenicolous
<i>Liolaemus tenuis</i>	Medel <i>et al.</i> (1988)	Clinging ability	Arboreal
<i>Liolaemus zullyi</i>	Cei & Scolaro (1996)	Ground-dwelling	Terrestrial
<i>Leiosaurus belli</i>	Laspiur <i>et al.</i> (2007)		
<i>Phymaturus antofagastensis</i>	Pereyra (1985)	Clinging ability	Saxicolous
<i>Phymaturus dorsimaculatus</i>	Lobo & Quinteros (2005)		
<i>Phymaturus excelsus</i>			
<i>Phymaturus spectabilis</i>			
<i>Phymaturus spurcus</i>			
<i>Phymaturus somuncurensis</i>			
<i>Phymaturus tenebrosus</i>			

temperature, we tied a harness to their hips which was attached to a dynamometer (accuracy: 0.1 g). Each lizard was placed on each of the selected substrates and allowed to grasp the substrate with both hands. Then, the lizard was dragged horizontally at a constant speed (lizards were not jerked) and at the maximum, force was measured at the moment when the lizard not increase the exerted force. On each surface, every lizard underwent three trials, qualified as good or bad (Bauwens *et al.*, 1995; Losos *et al.*, 2002). We included only those trials qualified as good, during which lizards exerted a maximum effort by extending both forelimbs. Only one investigator (FBC) conducted these trials to ensure consistency. Three trials, including at least three pull-offs each, were recorded for each animal on each surface ($N = 221$, $X = 5.81$, $SD = 2.43$) (Appendix S2). We used the best of these three attempts for further analyses.

Morphological variables

Before the experiments, all specimens were weighed with an Ohaus electronic balance (accuracy, 0.01 g). After experimental trials, specimens were euthanized with an overdose of Pentothal. Lizards were fixed with 10% formalin and preserved in 75% ethanol. Body dimensions were measured before preservation, with a digital caliper (Mitutoyo CD-15B; ± 0.01 mm) as follows: snout-vent length (SVL); maximum body width (BW); body length (BL) measured from the base of the neck until the vent; and inter limb length (ILL) which is the distance between the fore and hind limbs; forelimbs: humerus length (HL); radius length (RL); dorsum of the hand length (DHL); dorsum of the hand width (DHW); length of digits of the hand not including the claws; and longest toes length of the foot (d3, d4, and d5) not

(a) Tree bark



(b) Smooth rock



(c) Rough rock



Fig. 1 The pictures show the lizards in a resting position, placed on different substrates, before the trails. It can be observed the position of the harness. (a) *Liolaemus ceii*, (b) *Liolaemus cf. elongatus*, (c) *Phymaturus dorsimaculatus*.

including the claws. Following the same protocol in Tulli *et al.* (2009), we also calculated CH, claw length (CL) and claw curvature (CC) corresponding to digits III and IV of the hand, and 3, 4 and 5 of the foot. These toes were selected because they are the longest and presumably functionally the most important in push the lizard body on the substrate when lizards climb (Vrcibradic & Rocha, 1996; Teixeira-Filho *et al.*, 2001). Only adult specimens of both sexes were measured and used in experimental trials. Means and SDs for morphological traits and force exerted are presented in Appendix S2.

Phylogeny and phylogenetic signal

Because a complete phylogenetic tree for all the species studied here is not available, we used a composite tree topology based on Lobo (2001, 2005); Lobo & Quinteros (2005); Abdala (2007) and Frost *et al.* (2001) for Leiosaurine species. We arbitrarily set the branch lengths to unity as divergence times among the different species are unclear because of the diverse nature of the original phylogenetic analyses. We ran all analyses using constant branch lengths and branch lengths transformed using an Ornstein-Uhlenbeck (OU) model of evolution. In the latter transformation, we set the d -value equal to 0.2, thus creating a topology with less structure and more star-like, or equal to 0.8, resulting in a more hierarchical topology (Blomberg *et al.*, 2003). Because species show different degrees of relatedness as a result of common evolutionary history, they cannot be regarded as independent data (Felsenstein, 1985; Harvey & Pagel, 1991). However, although it is necessary to conduct analyses within a phylogenetic framework, whether hypotheses based on phylogenetic or conventional statistics will be considered more informative depends on whether data show evidence of significant phylogenetic signal (Blomberg *et al.*, 2003; Garland *et al.*, 2005; Goodman, 2006). SVL was introduced in PHYSIG after \log_{10} transformation. All other morphological traits (i.e. CL, CH, forelimb length as well as its segments) were size-corrected (we used the residuals of \log_{10} morphometric variable vs. \log_{10} SVL) following the method suggested by Blomberg *et al.* (2003). Performance variables were corrected using \log_{10} body mass (Blomberg *et al.*, 2003). We used body mass as the independent variable because some of the species are heavier than other Liolaemini species at the same SVL as the case of stocky *Phymaturus* species compared to the more slender *Liolaemus* species Cruz *et al.*, 2009, in press). We calculated the K -statistic as an estimate of phylogenetic signal relative to Brownian motion evolution considering the topology and branch lengths (Blomberg *et al.*, 2003). K equal to 1 indicates that a trait shows an expected amount of phylogenetic signal among close relatives, whereas K -values < 1 indicate a trait is less similar among close relatives and therefore has less phylogenetic signal than expected. A $K > 1$ suggests there is more phylogenetic signal than expected. We tested for phylogenetic signal in all traits by a randomization test (PHYSIG, Blomberg *et al.*, 2003).

Conventional statistical and independent contrast analyses

We ran multiple regression analyses, as the dependent variable we used the residuals of \log_{10} of performance on each surface on the \log_{10} body mass. Residuals of the \log_{10} of mean morphological variables calculated on the \log_{10} mean SVL were used as independent variables.

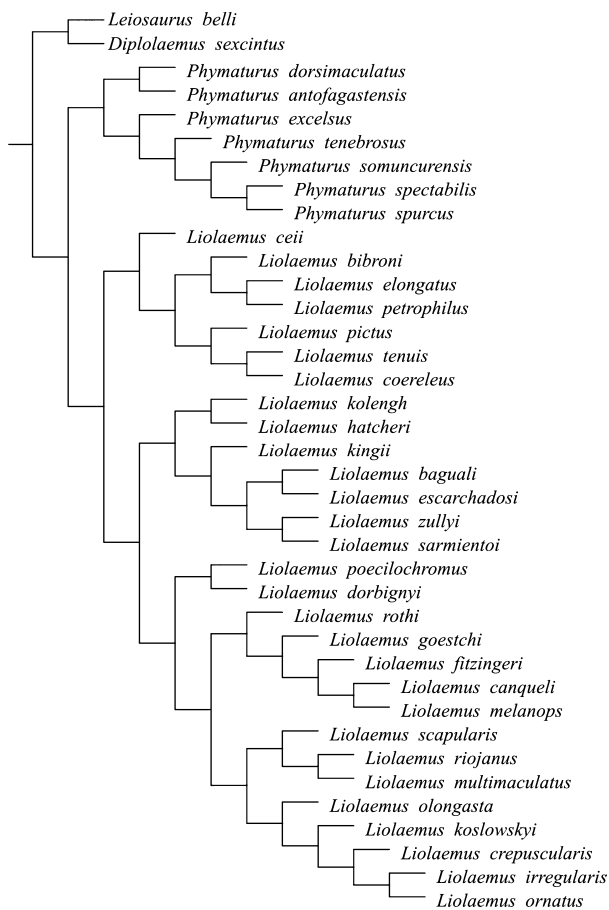


Fig. 2 Tree topology based on a combination of morphological and mitochondrial DNA analyses based on Lobo (2001, 2005); Lobo & Quinteros (2005); Abdala (2007) and Frost *et al.* (2001).

Many of the residuals of the morphological variables were considered redundant in the multiple regression analyses because of colinearity and were not used in the analyses. We ran multiple regressions for both conventional statistics as well as independent contrasts (IC) analyses (Felsenstein, 1985, 1988). For further analyses, IC of all morphological variables were regressed on the IC of SVL (forced through the origin; see Garland *et al.*, 1992), except for CC (size independent) and calculated the residuals. In the case of performance variables, each IC was regressed to IC of body mass; we used body mass because for several species at the same SVL body mass was quite different, besides strength may be more related to body mass rather than SVL. We used the topology showed in Fig. 2 and *MESQUITE* program v 2.72 (Maddison & Maddison, 2009) to calculate IC.

For each test, we recorded the peak grasp force for each individual and then calculated the mean value for each species for each surface. This variable was included in subsequent analyses. The performance variables were corrected by \log_{10} to test whether species analysed

exerted different forces on each of the different substrates. Then, we used a univariate analysis of covariance (ANCOVA), using the mass as covariate and habitat use as categorical variable. For phylogenetically based ANCOVA, an empirical null distribution of *F*-statistics taking into account the phylogeny was generated using PDSIMUL and analysed with *PDA*NOVA (Garland *et al.*, 1993). For each variable, we ran 1000 simulations using a speciation model of evolution. The speciation model sets all branch lengths to one in PDSIMUL (Martins & Garland, 1991). The means and variances of the simulations were set to the means and variances of the original data.

Results

Phylogenetic signal

K-values were not higher than one in any of the variables studied, including SVL (Table 2) which is an unexpected result in light of the results of Blomberg *et al.* (2003) for several taxa. However, randomization tests showed that CH presents significant *P*-values for all fingers and toes, indicating the presence of a pattern among closely related species (Blomberg *et al.*, 2003). Branch length may influence the degree of phylogenetic signal as well as *k*-statistics, indicating some features may be sensitive to model specification in branch length transformations. *K*-values after OU transformation equal to 0.2 indicate a tendency for a better fit of star-like structure for our data set, contrary to a stabilizing selection model expected for high *K*-values for OU transformation higher than 0.8. However, these values are intermediate and preclude us to make stronger statements.

Performance-morphology relationships

The informative features under conventional analyses were CH of digits III and IV and CL of digit III and toe 3 (Table 3a). CH of digit III and CL of toes 3 were positively correlated with performance for the three contact surfaces substrates, whereas CL of digit III and CH of digit IV were negatively correlated with performance (Table 3b). When multiple regression of IC residuals of morphological variables were used as independent variables and grasping forces used as dependent variables for the three type of surfaces under experimentation (Table 3a), results were different. Partial correlations show six morphological variables were informative in all experimental trails: CL of toe 4, CH and length of toe 5, HL, interlimb length and hand width (Table 3b). HL and CL of toe 5 correlated positively with interlocking grasp force, whereas CL toe 4, CH of toe 5, interlimb length and hand width correlated negatively with performance on the three surfaces under study (Table 3a). Interestingly, CH DIII and CH DIV correlated positively and strongly with performance on rough rock and tree bark surfaces,

Table 2 Summary of analyses calculating phylogenetic signal and using constant BL and Ornstein-Uhlenbeck (OU) transformed branch lengths.

	BL = 1		OU transformation = 0.2		OU transformation = 0.8	
	<i>K</i>	<i>P</i>	<i>k</i>	<i>P</i>	<i>k</i>	<i>P</i>
SVL	0.274	0.571	0.893	0.841	0.481	0.834
Mass	0.263	0.564	0.901	0.746	0.469	0.782
DIII	0.356	0.299	0.898	0.877	0.698	0.565
CH DIII	0.373	0.119	0.965	0.397	0.639	0.206
CC DIII	0.272	0.517	1.032	0.104	0.564	0.292
CL DIII	0.285	0.677	0.947	0.764	0.51	0.9
DIV	0.267	0.799	0.877	0.982	0.69	0.988
CH DIV	0.393	0.097	0.968	0.471	0.662	0.191
CC DIV	0.265	0.545	1.003	0.161	0.532	0.352
CL DIV	0.283	0.544	0.962	0.694	0.501	0.222
d3	0.27	0.619	0.789	0.75	0.436	0.744
CH d3	0.353	0.02	0.958	0.471	0.612	0.173
CC d3	0.247	0.506	1.017	0.071	0.598	0.246
CL d3	0.3	0.724	0.923	0.824	0.515	0.931
d4	0.289	0.888	0.567	0.783	0.621	0.85
CH d4	0.376	0.042	0.975	0.269	0.653	0.057
CC d4	0.227	0.927	0.945	0.472	0.474	0.738
CL d4	0.258	0.852	0.937	0.795	0.476	0.943
d5	0.271	0.333	0.769	0.756	0.477	0.73
CH d5	0.36	0.066	0.969	0.474	0.618	0.181
CC d5	0.318	0.673	1.048	0.052	0.678	0.21
CL d5	0.258	0.834	0.919	0.829	0.469	0.963
RL	0.287	0.12	0.845	0.945	0.472	0.881
HL	0.249	0.869	0.812	0.976	0.426	0.986
BL	0.255	0.72	0.812	0.982	0.425	0.975
BW	0.199	0.422	0.655	0.735	0.643	0.43
ILL	0.25	0.287	0.853	0.842	0.856	0.467
DHL	0.265	0.585	0.843	0.951	0.448	0.886
DHW	0.247	0.587	0.769	0.763	0.663	0.876
Smooth rock	0.293	0.248	0.749	0.551	0.541	0.335
Rough rock	0.276	0.344	0.921	0.679	0.494	0.608
Tree bark	0.302	0.158	0.973	0.357	0.538	0.304

BL, branch length; BW, body width; CH, claw height; CC, claw curvature; CL, claw length; HL, humerus length; RL, radius length; SVL, snout-vent length.

Significant values ($P < 0.05$) and presence of phylogenetic signal ($k > 1$) are indicated by bolded values.

All traits were log-transformed, and effects of SVL were removed prior to analysis as described in Blomberg *et al.*, 2003.

respectively. But no manus features correlated positively with performance on smooth rock surface (Table 3a).

Ecological groups and performance

We found significant differences between ecological groups (arboreal, saxicolous, arenicolous and generalized terrestrial) in performance (body mass residual strength to detach lizards from surface). The significant differences we found in both for conventional (Trad) and for phylogenetically informed analysis of covariance (Phy) (Table 4). Arboreal and saxicolous species needed more force to be detached from all substrate surfaces (Fig. 3). Residuals of the force exerted by arboreal and saxicolous lizards were positive, whereas residuals of force exerted

by arenicolous and generalized terrestrial were negative (Fig. 3). Our data show that arenicolous species exerted the weakest force whereas arboreal species exerted the maximum force relative to body weight (Fig. 3). These results are consistent with the expected hypothesis of higher clinging ability for those species occurring on vertical surfaces, such as rocky boulders and trees.

Discussion

An assumption of performance studies is that performance measures reflect ecologically relevant aspects of the organisms under study (Losos, 1990a–c, 2009; Melville & Swain, 2000; Goodman *et al.*, 2008). It is interesting that many other studies (Jaksic *et al.*, 1980;

Table 3 (a) Results of multiple regression of residuals of morphological variables were used as independent variables and grasping forces used as dependent variables for the three type of surfaces under experimentation. (b) Results for multiple regressions of the residuals independent contrasts (IC) of performance as dependent variable and residuals of IC of morphological data.

Dependent	<i>r</i>	d.f.	<i>F</i>	<i>P</i> -value	Independent	Partial <i>R</i>					
(a)											
Residual cling smooth	0.92	3.37	12.28	0.000	HL	0.66					
					CL d3	0.57					
					CH DIII	0.51					
					CL d5	0.47					
					CL DIV	0.32					
					CH d5	-0.35					
					RL	-0.36					
					CH DIV	-0.47					
					CL d4	-0.54					
					CL DIII	-0.62					
					CC d3	-0.69					
					Residual cling rough	0.92	3.37	9.81	0.000	CLd3	0.58
										DHL	0.48
										CHDIII	0.47
CHd3	0.42										
BL	0.40										
CLd5	0.36										
d 3	-0.35										
CL d4	-0.36										
BW	-0.44										
CH d4	-0.46										
CH DIV	-0.53										
CC DIV	-0.66										
CL DIII	-0.71										
Residual tree bark	0.92	3.37	11.98	0.000						CL d3	0.71
					D III	0.57					
					CH d3	0.55					
					BL	0.53					
					CH DIII	0.39					
					CH d5	0.39					
					d 3	-0.49					
					BW	-0.51					
					CH DIV	-0.53					
					CH d4	-0.64					
					CC DIV	-0.67					
					CL DIII	-0.74					
					(b)						
					Residual IC smooth rock	0.94	3.36	3.03	0.035	CL d5	0.80
HL	0.76										
BW	0.69										
d 3	0.64										
CL d3	0.63										
d 4	-0.63										
DHW	-0.68										
ILL	-0.73										
CH d5	-0.77										
CL d4	-0.79										
Residual IC rough rock	0.96	3.36	5.03	0.005						CL d5	0.76
										CH DIII	0.69
										HL	0.67
										CL d3	0.67
					d 5	0.67					
					D III	-0.61					
					CC d5	-0.61					
					DHW	-0.65					

Table 3 (Continued)

Dependent	<i>r</i>	d.f.	<i>F</i>	<i>P</i> -value	Independent	Partial <i>R</i>
Residual IC tree bark	0.96	3.36	5.12	0.005	DM	-0.67
					CHd5	-0.71
					CLd4	-0.73
					LH	0.84
					d 5	0.70
					CL d5	0.69
					CC DIV	0.64
					CH d3	0.63
					CH DIV	0.60
					CC d3	-0.60
					ILL	-0.64
					DHW	-0.64
					CC DIII	-0.70
CL d4	-0.71					
CH d5	-0.79					

BW, body width; CH, claw height; CC, claw curvature; CL, claw length; DHL, dorsum of the hand length; DHW, dorsum of the hand width; HL, humerus length; ILL, inter limb length; RL, radius length.

All traits were log-transformed, and effects of snout-vent length and mass were removed prior to analysis. Bold values indicated the results on significant models and significant independent variables and their partial correlations (partial *r*) are given. Significant values ($P < 0.05$) are indicated by bolded values.

Table 4 Conventional analysis of covariance and phylogenetic ANCOVA simulation results of the force exerted on four habitat types (arboreal, saxicolous, arenicolous and ground dwellers). The analysis shows the significant differences among the four groups. *F* and *P*-values are for conventional non-phylogenetic ANCOVA and phylogenetic ANCOVA with mass as the covariate and habitat type as factor.

Variables	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i> phy	<i>P</i> phy
Smooth rock	3.33	7.238	<0.001	3.32	7.113	<0.048
Rough rock	3.33	5.507	<0.004	3.32	7.036	0.102
Tree bark	3.33	8.953	<0.000	3.32	7.372	<0.023

Significant differences among habitat groups are shown in bold.

Bold values are significant at $\alpha = 0.05$.

Zaaf & Van Damme, 2001; Schulte *et al.*, 2004) failed to find evolutionary relationships between some of these components (habitat use, morphology or performance). Thus, a study comparing gecko species from two habitats (climbing vs. terrestrial) that require very different modes of locomotion identified no difference in limb length, suggesting habitat-induced shifts in limb morphology are not inevitable (Zaaf & Van Damme, 2001). In general, Liolaemini lizards exhibited a clear relationship between morphology and performance considering the type of habitat they explore. For example, lizards that exploit vertical surfaces (arboreal and saxicolous) exerted greater force than terrestrial groups such as generalist and arenicolous species, suggesting that those traits considered in this study are relevant to performance.

Phylogenetic signal analyses often show importance of phylogenetic structure and branch lengths (Blomberg *et al.*, 2003). Our results showed that for most variables (gross morphology, claws and performance) *K*-statistics were lower than one, exhibiting less signal than expected given the topology and branch lengths, indicating a deviation from Brownian motion because of adaptation

or measuring error. Interestingly, *K* statistic values lower than one seem to be a common aspect in analyses that include Liolaemini lizards (Vanhooydonck *et al.*, 2010; Cruz *et al.*, in press). Our results are similar to Kohlsdorf *et al.* (2008), who studied tropidurine lizards. These authors obtained a phylogenetic signal lower than one in all the traits analysed, including SVL. Thus, these results indicate the traits examined are evolutionary labile. It has been shown that hand morphology and even SVL are evolutionary labile in tropidurine and Liolaemini lizards (Kohlsdorf *et al.*, 2008 and this study); in contrast with other studies on these same phylogenetic groups (for example Jaksic *et al.*, 1980; Schulte *et al.*, 2004; Tulli *et al.*, 2009). Apparently, species sampling and features considered have an important impact of the phylogenetic signal, at least for these iguanian lizards.

There was disagreement between conventional and phylogenetically informed multiple regression analyses. It is true that both analyses show a main effect for the several morphological features studied, but partial correlations were significant for different features depending the nature of the analysis. Interestingly, CH showed to be

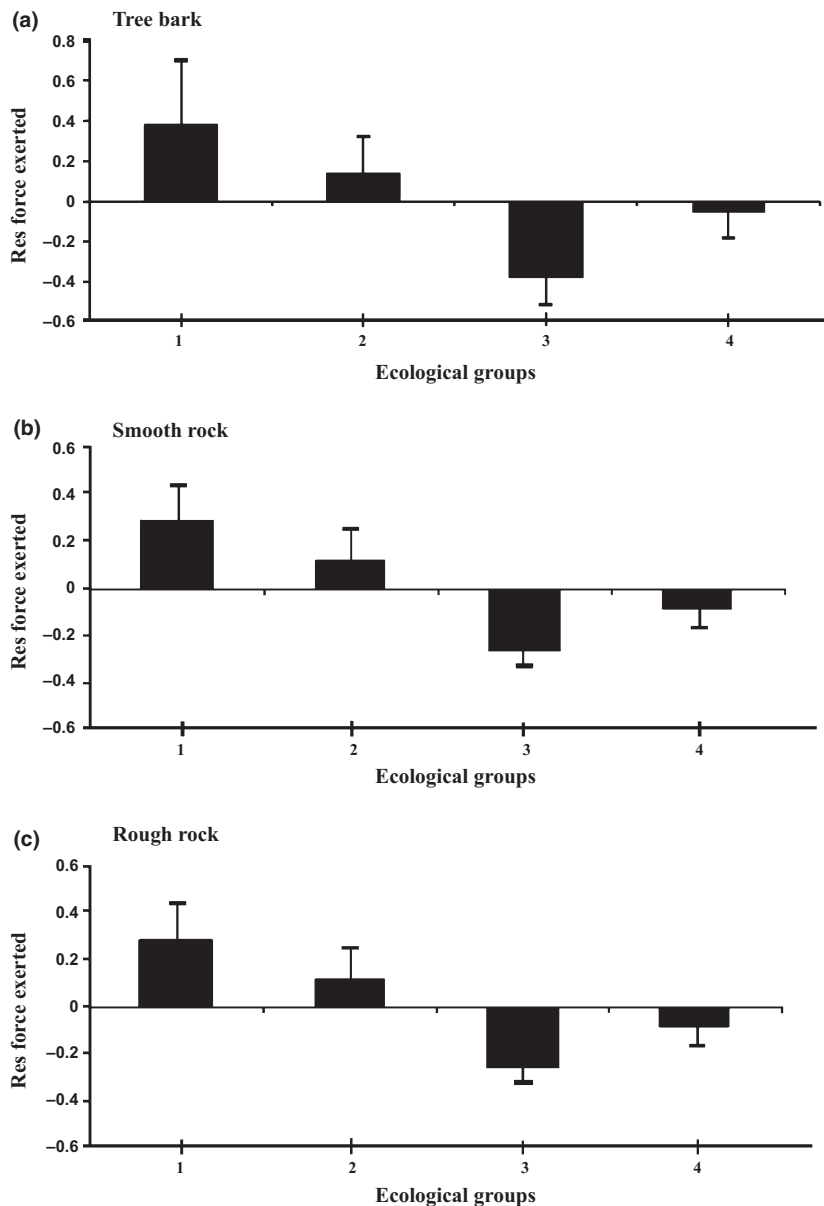


Fig. 3 Comparisons among mean residual of force measurements (bars, \pm one standard error) of the 38 species of Liolaemini lizards by habitat use (1: arboreal, 2: saxicolous, 3: arenicolous, 4: terrestrial generalist). Trials were made on three different substrates (a) Tree bark, (b) Smooth rock, (c) Rough rock.

important when tree bark and rough rock were used in the experimental trails, even under phylogenetically based analyses (Table 3b), but did not show a correlation with clinging ability on smooth surface. Disagreement between our conventional and phylogenetically informed analysis with regard to CH may be related to the higher k -statistic values observed for this feature and that hierarchic structure (after OU transformations) showed to be affected in the different analyses. Therefore, CH may be clustered in different clades that use similar habitats (Vanhooydonck *et al.*, 1999). Clinging by interlocking is the simplest and most familiar of the nonfrictional grip mechanisms. It is exemplified by any animal that clings to a support (Cartmill, 1974) mainly

rough surfaces (such a tree bark or a rough rock) because both offer a more complex structure where claws can get a better grip by gripping adductor force of their digits (Biewener, 2003). This adduction force depends on the claws curvature and depth to which they may penetrate (Cartmill, 1974). Thus, the type of surface in terms of roughness is a relevant performance factor to consider, which also explains the significant correlation between the IC of each digit CH and CL. In addition, claw morphology of digit III and IV was positively correlated with performance on rough surfaces. This result is consistent with our expectations, because lizards use their hand claws to exert the interlocking grasp. The importance of digit III and IV in locomotion have been

highlighted by Teixeira-Filho *et al.* (2001), who stressed that digit IV is mainly used as support and digit III seems to be the one driving clinging. With regard to CL of toe 3, the common location of toe 3 during clinging (Fig. 1) allows us to infer that it is being used as support, that is having a longer claw would increase the stability of the lizard during performance.

Biomechanical predictions posit that lizards that have some degree of vertical use of habitat tend to have shorter limbs (relative to SVL) and shorter and heavy distal limb segments, to bring the centre-of-mass closer to the substrate and broaden the plane of support (Van Damme *et al.*, 1997). Most of the saxicolous Liolaemini live in volcanic and basaltic tablelands in Patagonian Argentina (Lobo & Quinteros, 2005). These plateaus are rocky with deep crevices that are used as permanent or occasional refuges by *Phymaturus* or *Liolaemus* species, where these lizards are frequently observed in a vertical position. Species can often be found living in sympatry and often live beneath rocks. The challenge that this particular milieu represents for the lizards is solved by having similar features, because all of them have not only longer forelimb, but also higher claws, and shorter interlimb length, traits also shared with arboreal species. Finally, both ecological groups exhibit significantly better clinging performance than generalists and sand-dweller Liolaemini species.

In Caribbean *Anolis* lizards, longer hind limbs and shorter forelimbs are associated with evolution of performance traits, such as, clinging, running and jumping (Losos, 1990a–c; but see Irschick *et al.*, 2005). On the contrary, saxicolous scincid lizards use longer forelimbs to increase clinging ability using an increased base of support and frictional force, improving contact on irregular surfaces (Goodman, 2006; Goodman *et al.*, 2008). Our analysis of forelimb length in a phylogenetic context showed that arboreal and saxicolous species present a positive relationship between the interlocking grasping force and proximal segment of limb length (HL). Thus, arboreal and saxicolous species have a longer humerus, in agreement with Goodman (2006). It is possible that the controversies in these results are explained by considering that the relevance of limb size is small compared to other adaptations. It has been argued that the presence of 'key adaptations' may free organisms from some of the constraints imposed by the environment (Zaaf & Van Damme, 2001). It is possible that environment may have constrained claw morphology and conversely limb size show a relaxed response in different lineages.

Having a narrower hand is shown here to be important and positively related to strength. Liolaemini species which are harder to detach live on vertical surfaces and tend to have narrow hands (Table 3b). The hands of most lizards show a tendinous palmar structure with a large palmar sesamoid, and in lizards with this condition, the hand moves as a single rigid functional unit (Abdala

et al., 2009). The presence of a large sesamoid bone in the tendinous flexor plate may prevent buckling of this tendon (Abdala *et al.*, 2009) and tend to maintain a flattened hand. It seems that to maintain the hand flat is not as important for climbing. In ground dwelling lizards, the rigid unit of the hand may be beneficial during terrestrial over-ground locomotion as it allows the animal to effectively use its entire hand as a pivot (Abdala *et al.*, 2009). Remarkably, Grizante *et al.* (2010) found that tropidurid species with narrower foot soles were associated with a frequent use of rocks and branches. Likewise, they found that species that utilize trunks exhibit longer femora. The similarity of our results and those from Grizante *et al.* (2010), with respect to the feet in relation to the hands, suggest that both fore and hind limbs may be functionally constrained in tropidurine and Liolaemini lizards.

A strong correlation was found between shorter bodies, as expressed by a lower interlimb length, and clinging force. This result is consistent with observations made on scincids by Goodman *et al.* (2008). For these lizards, shorter bodies are associated with saxicolous habits. It is possible that interlimb length is a trait related to sexual dimorphism (Ceï *et al.*, 2003; Goodman, 2006), where a relatively longer distance between fore and hind limbs concurs with a larger volume for egg bearing; however the relationship with performance remains unclear for Liolaemini.

In conclusion, our data suggest that a relationship among morphology, performance and habitat use is present in Liolaemini lizards. Several traits were adaptive with arboreal and saxicolous Liolaemini exerting more strength than other Liolaemini that exploit horizontal substrates. Further study on the kinematics and biomechanics of these morphologically conservative lizards are needed to better understand the complex relationship between their morphology, physiology and environment.

Acknowledgments

We are very grateful to C. Abdala for his invaluable help in the field and suggestions for this study, and to S. Quinteros, J. C. Stazonelli, G. Scrocchi for help in the field. We appreciate the comments of D. Irschick and J. A. Schulte on early versions of the manuscript. M.J.T. was supported by a Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET) fellowship. Grants CONICET PIP 112-200801-00225; PIP-CONICET 6347 to V.A. and 6287 to F.B.C. and PICT 01205 to FBC partially supported this work.

References

- Abdala, C.S. 2007. Phylogeny of the *boulengeri* group (Iguania: Liolaemidae, *Liolaemus*) based on morphological and molecular characters. *Zootaxa* **1538**: 1–84.

- Abdala, C.S. & Díaz Gómez, J.M. 2006. A new species of the *Liolaemus darwini* group (Iguania: Liolaemidae) from Catamarca Province, Argentina. *Zootaxa* **1317**: 21–33.
- Abdala, C.S. & Lobo, F. 2006. Nueva especie del grupo de *Liolaemus darwini* (Iguania: Liolaemidae) del Noroeste de Argentina. *Cuad. Herpetol.* **19**: 3–18.
- Abdala, C.S. & Quinteros, S. 2008. Una nueva especie de *Liolaemus* (Iguania: Liolaemidae) endémica de la Sierra de Fiambalá, Catamarca, Argentina. *Cuad. Herpetol.* **22**: 35–47.
- Abdala, V., Manzano, A.S., Tulli, M.J. & Herrel, A. 2009. The tendinous patterns in the palmar surface of the lizard manus: functional consequences for grasping ability. *Anat. Rec.* **292**: 242–253.
- Avila, L.J., Morando, M., Perez, C.H.F. & Sites, J.W. Jr 2004. Phylogenetic relationships of lizards of the *Liolaemus petrophilus* group (Squamata, Liolaemidae), with description of two new species from western Argentina. *Herpetologica* **60**: 187–203.
- Avila, L.J., Morando, M. & Sites, J.W. Jr 2006. Congeneric phylogeography: hypothesizing species limits and evolutionary processes in Patagonian lizards of the *Liolaemus boulengeri* group (Squamata: Liolaemini). *Biol. J. Linn. Soc.* **89**: 241–275.
- 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.
- Biewener, A.A. 2003. *Animal Locomotion*. Oxford University Press, New York.
- Blomberg, S.P., Garland, T. Jr & Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–745.
- Bock, W.J. & Miller, W.D. 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. *Am. Mus. Novit.* **1931**: 1–45.
- Carrillo de Espinoza, N., Rothenstein, D., Salas, A. & Werner, Y.L. 1990. Radiation and convergence among desert geckos: *Phyllodactylus* species resembling both *Ptyodactylus* and *Stenodactylus*. *Amphibia-Reptilia* **11**: 275–284.
- Cartmill, M. 1974. Pads and claws in arboreal locomotion. In: *Primate Locomotion* (F.A. Jenkins Jr, ed.), pp. 45–83. Academic Press, New York.
- Cartmill, M. 1985. Climbing. In: *Functional Vertebrate Morphology* (M. Hildebrand, D.M. Bramble, K.F. Liem & D.B. Wake, eds), pp. 73–88. Harvard University Press, Cambridge.
- Cei, J.M. 1986. Reptiles del centro, centro-oeste y sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas. *Monografía VI. Mus. Reg. Sci. Nat. (Torino)* **4**: 1–527.
- Cei, J.M. & Scolaro, J.A. 1983. Un nuevo arreglo taxonómico para los *Liolaemus* del grupo *fitzingeri*. *Bol. Asoc. Herpetol. Arg.* **1**: 15–16.
- Cei, J.M. & Scolaro, J.A. 1996. A new species of *Liolaemus* of the *archeforus* group from the precordilleran valley of the Zeballos River, Santa Cruz Province, Argentina (Reptilia: Tropicoduridae). *Mus. Reg. Sci. Nat. Monogr. (Torino)* **14**: 389–401.
- Cei, J.M., Scolaro, J.A. & Videla, F. 2003. A taxonomic revision of recognized argentine species of the leiosaurid genus *Diplolaemus* (Reptilia, Squamata, Leiosauridae). *Facena* **19**: 87–106.
- Collette, B.B. 1961. Correlation between ecology and morphology in anoline lizards of Havana, Cuba and southern of Florida. *Bull. Mus. Comp. Zool.* **125**: 137–162.
- Cruz, F.B., Belver, L., Acosta, J.C., Villavicencio, H.J., Blanco, G. & Canovas, M.G. 2009. Thermal biology of *Phymaturus* lizards: evolutionary constraints or lack of environmental variation? *Zoology* **112**: 425–432.
- Cruz, F.B., Antenucci, D., Luna, F., Abdala, C.S. & Veja, L.E. in press. Energetics in Liolaemini lizards: implications of a small body size and ecological conservatism. *J. Comp. Physiol. B*, doi 10.1007/s00360-010-0524-4.
- Etheridge, R.E. 2000. A review of the *Liolaemus wiegmanni* group (Squamata, Iguania, Tropicoduridae), and a history of morphological change in the sand-dwelling species. *Herpetol. Monogr.* **14**: 293–352.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* **126**: 1–25.
- Felsenstein, J. 1988. Phylogenies and quantitative methods. *Annu. Rev. Ecol. Syst.* **19**: 445–471.
- Frost, D.R., Etheridge, R., Janies, D. & Titus, T.A. 2001. Total evidence, sequence alignment, evolution of polychrotid lizards and a reclassification of the Iguania (Squamata, Iguania). *Am. Mus. Novit.* **3343**: 1–38.
- Garland, T. Jr, Harvey, P.H. & Ives, A.R. 1992. Procedures for the analysis of comparative data using phylogenetic independent contrasts. *Syst. Biol.* **41**: 18–32.
- 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, 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.
- Goodman, B. 2006. Ecomorphology, Microhabitat Use, Performance and Reproductive Output in Tropical Lygosomine lizards. Unpublished PhD Thesis, James Cook University, Queensland.
- Goodman, B.A., Miles, D.B. & Schwarzkopf, L. 2008. Life on the rocks: habitat use drives morphological and performance evolution in lizards. *Ecology* **89**: 3462–3471.
- Grizante, M.B., Navas, C.A., Garland, T. Jr & Kohlsdorf, T. 2010. Morphological evolution in Tropicodurinae squamates: an integrated view along a continuum of ecological settings. *J. Evol. Biol.* **3**: 98–111.
- Halloy, M., Etheridge, R.E. & Burghardt, G.M. 1998. To bury in sand: phylogenetic relationships among lizard species of the *boulengeri* group, *Liolaemus* (Reptilia: Squamata: Tropicoduridae), based on behavioral characters. *Herpetol. Monogr.* **12**: 1–37.
- Harvey, P.H. & Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Huey, R.B., Hertz, P.E. & Sinervo, B. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* **161**: 357–366.
- Irschick, D.J., Austin, C., Petren, K., Fisher, R., Losos, J.B. & Eilers, O. 1996. A comparative analysis of clinging ability among pad-bearing lizards. *Biol. J. Linn. Soc.* **59**: 21–35.
- Irschick, D.J., Vitt, L.J., Zani, P. & Losos, J.B. 1997. A comparison of evolutionary radiations in mainland and Caribbean *Anolis* lizards. *Ecology* **78**: 2191–2203.
- Irschick, D.J., Carlisle, E., Elstrott, J., Ramos, M., Buckley, C., Vanhooydonck, B. et al. 2005. A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biol. J. Linn. Soc.* **85**: 223–234.
- Jaksic, F., Nuñez, H. & Ojeda, F. 1980. Body proportions, microhabitat selection, and adaptive radiation in *Liolaemus* lizards in Central Chile. *Oecologia* **45**: 178–181.

- Kohlsdorf, T., M. B. Grizante, M.B., Navas, C.A. & Herrel, A. 2008. Head shape evolution in Tropicurinae lizards: does locomotion constrain diet? *J. Evol. Biol.* **21**: 647–917.
- Laspiur, A., Acosta, J.C. & Abdala, C.S. 2007. A new species of *Leiosaurus* (Iguania: Leiosauridae) from central-western Argentina. *Zootaxa* **1470**: 47–57.
- Lobo, F. 2001. A phylogenetic analysis of lizards of the *Liolaemus chilensis* group (Iguania: Tropicuridae). *Herpetol. J.* **11**: 137–150.
- Lobo, F. 2005. Las relaciones filogenéticas en el grupo *chilensis* de *Liolaemus* (Iguania: Liolaemidae). Sumando nuevos caracteres y taxa. *Acta Zool. Lilloana* **49**: 67–89.
- Lobo, F. & Quinteros, S. 2005. A morphology-based phylogeny of *Phymaturus* (Iguania: Liolaemidae) with the description of four new species from Argentina. *Pap. Av. Zool. (São Paulo)* **45**: 143–177.
- Losos, J.B. 1990a. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**: 1189–1203.
- Losos, J.B. 1990b. Ecomorphology, performance capability and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol. Monogr.* **60**: 369–388.
- Losos, J.B. 1990c. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* Lizards. *Anim. Behav.* **39**: 879–890.
- Losos, J.B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation in Anoles*. California University Press, Berkeley.
- Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K. & Rodríguez-Schettino, L. 1998. Historical contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**: 2115–2118.
- Losos, J.B., Creer, D. & Schulte, J.A. II 2002. Cautionary comments on use of maximal sprint performance. *J. Zool. Lond.* **258**: 57–61.
- Maddison, W.P. & Maddison, D.R. 2009. Mesquite: a modular system for evolutionary analysis. Version 2.6, <http://mesquiteproject.org>.
- Martins, E.P. & Garland, T. Jr 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* **45**: 534–557.
- Medel, R.G., Marquet, P.A. & Jaksic, F.M. 1988. Microhabitat shifts of lizards under different contexts of sympatry: a case study with South American *Liolaemus*. *Oecología* **76**: 567–569.
- Melville, J. & Swain, R. 2000. Evolutionary relationship between morphology, performance and habitat openness in the lizard genus *Niveoscincus* (Scincidae: Lygosomidae). *Biol. J. Linn. Soc.* **70**: 667–683.
- Odendaal, F.J. 1979. Notes on the adaptive ecology and behaviour of four species of *Rhoptropus* (Gekkonidae) from the Namib desert with special reference to a thermoregulatory mechanism employed by *Rhoptropus afer*. *Modoqua* **11**: 255–260.
- O'Grady, S.P., Morando, M., Avila, L.J. & Dearing, M.D. 2005. Correlating diet and digestive tract specialization: examples from the lizard family Liolaemidae. *Zoology* **108**: 201–210.
- Pagel, M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. Lond. B* **255**: 37–45.
- Pereyra, E.A. 1985. Nuevo iguanido del género *Phymaturus* del noroeste argentino. *Bol. Asoc. Herpetol. Arg.* **2**: 4.
- Peterson, J.A. 1984. The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. *J. Zoology* **202**: 1–42.
- Pincheira-Donoso, D., Scolaro, J.A. & Schulte, J.A. II 2007. The limits of polymorphism in *Liolaemus rothi*: molecular and phenotypic evidence for a new species of the *Liolaemus boulengeri* clade (Iguanidae, Liolaemini) from boreal Patagonia of Chile. *Zootaxa* **1452**: 25–42.
- Pincheira-Donoso, D., Hodgson, D.J., Stipala, J. & Tregenza, T. 2009. A phylogenetic analysis of sex-specific evolution of ecological morphology in *Liolaemus* lizards. *Ecol. Res.* **24**: 1223–1231.
- Quinteros, S., Abdala, C.S. & Lobo, F. 2008. Redescription of *Liolaemus dorbignyi* Koslowsky, 1898 and description of a new species of *Liolaemus* (Iguania: Liolaemidae). *Zootaxa* **1717**: 51–67.
- Russell, A.P. & Bauer, A.M. 1989. The morphology of the digits of the golden gecko, *Calodactylodes aureus* and its implications for the occupation of rupicolous habitats. *Amphibia-Reptilia* **10**: 125–140.
- Schulte, J.A. II, Macey, J.R., Espinoza, R.E. & Larson, A. 2000. Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. *Biol. J. Linn. Soc.* **69**: 75–102.
- Schulte, J.A. II, Valladares, J. & Larson, A. 2003. Phylogenetic relationships within Iguanidae inferred using molecular and morphological data and a phylogenetic taxonomy of Iguanid lizards. *Herpetologica* **59**: 399–419.
- Schulte, J.A. II, Losos, J.B., Cruz, F.B. & Núñez, H. 2004. The relationship between morphology, escape behavior, and microhabitat occupation in the iguanid lizard genus *Liolaemus*. *J. Evol. Biol.* **17**: 408–420.
- Scolaro, J.A. 2005. *Reptiles Patagónicos Sur*. Una Guía de Campo. Universidad Nacional de la Patagonia, Trelew.
- Scolaro, J.A. & Ceí, J.M. 1997. Systematic status and relationships of *Liolaemus* species of the *archeforus* and *kingii* groups: a morphological and taxonumerical approach (Reptilia: Tropicuridae). *Bull. Mus. Reg. Sci. Nat. (Torino)* **15**: 369–406.
- Teixeira-Filho, P.F., Rocha-Barbosa, O., Paes, V., Ribas, C.S. & de Almeida, J.R. 2001. Ecomorphological relationships in six lizard species of Restinga da Barra de Maricá, Rio de Janeiro, Brazil. *Rev. Chil. Anat.* **19**: 45–50.
- Tulli, M.J., Cruz, F.B., Herrel, A., Vanhooydonck, B. & Abdala, V. 2009. The interplay between claw morphology and habitat use in neotropical iguanian lizards. *Zoology* **112**: 379–392.
- Van Damme, R., Aerts, P. & Vanhooydonck, B. 1997. No trade-off between sprinting and climbing in two populations of the lizard *Podarcis hispanica* (Reptilia: Lacertidae). *Biol. J. Linn. Soc.* **60**: 493–503.
- Vanhooydonck, B. & Irschick, D.J. 2002. Is evolution predictable? Evolutionary relationships of divergence in ecology, performance and morphology in old and new world lizard radiations. In: *Topics in Functional and Ecological Vertebrate Morphology* (P. Aerts, K. D'Août, A. Herrel & R. Van Damme, eds), pp. 191–204. Shaker publisher, Maastricht.
- Vanhooydonck, B., Cruz, F.B., Abdala, C.S., Moreno Azócar, D.L., Bonino, M.F. & Herrel, A. 2010. Sex-specific evolution of bite performance in *Liolaemus* lizards (Iguania: Liolaemidae): the battle of the sexes. *Biol. J. Linn. Soc.* **101**: 461–475.
- Vrcibradic, D. & Rocha, C.F.D. 1996. Ecological differences in tropical sympatric skinks (*Mabuya macrorhyncha* and *Mabuya agilis*) in southeastern Brazil. *J. Herpetol.* **30**: 60–67.

- Zaaf, A. & Van Damme, R. 2001. Limb proportions in climbing and ground-dwelling geckos (Lepidosauria, Gekkonidae): a phylogenetically informed analysis. *Zoomorphology* **121**: 45–53.
- Zani, P.A. 2000. The comparative evolution of lizard claw and toe morphology and clinging performance. *J. Evol. Biol.* **13**: 316–325.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Institutional abbreviations where voucher specimens of the species studied are deposited.

Appendix S2 Mean (\pm SD) for morphological traits and force exerted values.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Received 26 October 2010; revised 13 December 2010; accepted 15 December 2010