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Walking or hanging: the role of habitat use for body shape evolution in lacertid lizards

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Abstract

Differences in habitat use impose ecological constraints which in turn lead to functional and morphological differences through adaptation. In fact, a convergent evolutionary pattern is evident when species exhibit similar responses to similar environments. In this study, we examine how habitat use influences the evolution of body shape in lizards from the family Lacertidae. We divided our species into two categories: ground-dwellers and climbers, which encompasses the verticality and horizontality aspects of the habitat. We performed phylogenetic comparative analyses employing 186 species and seven linear morphological traits. Our results show contrasting patterns between head and limb shapes, which are considered distinct functional blocks. We observed differences in forelimb proportions, but not in hindlimb length, contrary to what was documented in other lizard groups, demonstrating a novel axis in the limb–locomotion–habitat relationship in this family. In addition, a clear effect of habitat use on head shape was detected. We observed that climbing species present on average flatter heads than ground-dwelling species, as well as different evolutionary trajectories. These findings suggest the complex interplay between habitat use and morphological evolution in lizards, highlighting how distinct selective pressures drive divergent adaptations in different functional traits.

Keywords: phylogenetic comparative methods, convergence, adaptation, Ornstein–Uhlenbeck, phenotypic evolution

Introduction

Understanding how species respond and adapt to their environment is central in evolutionary biology (Arnold, 1998; Collar et al., 2010; Elstrott & Irschick, 2004; Irschick & Garland, 2001; Kaliontzopoulou et al., 2010; Openshaw & Keogh, 2014; Outomuro et al., 2013). Habitat use imposes ecological restrictions and demands that may drive morphological and performance adaptations. Consequently, adaptation to similar environmental niches can result in evolutionary convergence (Collar et al., 2014; Stayton, 2006), as seen in exemplary evolutionary cases such as cichlid fishes of East African lakes (Muschick et al., 2012) or spider ecomorphs along the Hawaiian Islands (Blackledge & Gillespie, 2004). Convergence, examined under the ecomorphological paradigm (Aguilar-Puntriano et al., 2018; Collar et al., 2014; Friedman et al., 2016; Stayton, 2015)—where form and function (i.e., whole-organism performance, physiology) are the reflection of the adaptation to a specific ecological niche (Arnold, 1983)—, underscores the close relationship between functional performance, body size and shape, which reflects adaptation to specific ecological niches and environmental pressures (Herrel et al., 2002).

In particular, the shape of the body plays an essential role in the way organisms interact and survive in their environment. As such, body shape adaptations to the habitat have been recorded in various animal groups, including fishes (Friedman et al., 2020, 2021; Kolmann et al., 2020; Larouche et al., 2020; Martinez et al., 2021), dragonflies (Outomuro et al., 2013), frogs (Moen et al., 2016; Stepanova & Womack, 2020), salamanders (Baken & Adams, 2019), and lizards (Bedford & Christian, 1996; Thompson & Withers, 2005; Gray et al., 2019). Among these, lizards have been extensively used as model organisms in ecomorphology because they are very widespread and they utilize a great diversity of habitats (e.g., terrestrial, aquatic, semiaquatic, arboreal, fossorial, and desertic). Remarkably, among all the habitats that lizards occupy, there is a recurrent trend whereby ground-dwelling species transit and adapt to a type of habitat that requires extensive climbing (arboreal or saxicolous) (Collar et al., 2010, 2011; Melville & Swain, 2003; Revell et al., 2007). In this new habitat, selection on functional performance results in convergent evolution (Revell et al., 2007). The contrast between ground-dwelling and climbing environments revolves around how species navigate the structural dimension of the habitat. Saxicolous and tree-climbing species navigate upright and exploit the vertical axis of the habitat, whereas ground-dwellers predominantly use the horizontal axis of the habitat. Differences in habitat exploitation imply different biomechanical requirements species need to fulfil. Species that move vertically need to cope with the effect of gravity, jump

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between adjacent rocks or trees, move along vertical surfaces with sufficient efficiency to escape from predators or use small crevices and tree cavities to hide from them (Arnold, 1998; Revell et al., 2007; Vanhooydonck & Van Damme, 1999). By contrast, species that move horizontally, tend to favour speed to escape from predators or to feed on prey in open areas, as well as, a large visual field to better notice their surroundings when moving close to the ground (Herrel et al., 2002; Losos, 1990; Vanhooydonck & Van Damme, 2003). These functional requirements are expected to be reflected in the corresponding morphological traits (Goodman et al., 2008; Herrel et al., 2002). Indeed, many climbing lizards present shallower heads (Openshaw & Keogh, 2014; Paluh & Bauer, 2017; Revell et al., 2007) and shorter limbs, both beneficial in maintaining the centre of mass close to the substrate (Huie et al., 2021; Vanhooydonck & Van Damme, 1999, 2001). However, opposite patterns are also observed in some lizard groups regarding limb (Goodman et al., 2008; Revell et al., 2007) and head proportions (Kohlsdorf et al., 2001; Kulyomina et al., 2019; Miles, 2014; Zaaf & Van Damme, 2001). This discrepancy may arise because factors beyond habitat verticality, like substrate type or element broadness, could have influenced limb and head evolution (Aerts et al., 2000; Revell et al., 2007).

Ground-dwelling species, which occupy relatively simple and more open environments, generally present more robust heads and longer hindlimbs to favour sprint and speed over manoeuvrability (Herrel et al., 2002; Losos, 1990), as well as differences in fore to—hindlimb ratios (Goodman et al., 2008), but once again exceptions also exist (Jaksić et al., 1980; Kohlsdorf et al., 2008). Together, these contrasting patterns suggest that maybe there is no overarching trend in morphological adaptations to the use of vertical relative to horizontal substrates in lizards. Furthermore, these findings emphasize that the overall body shape does not always uniformly adapt in response to specific habitats. Different body components, such as the head, limbs, and trunk, serve distinct functional roles in ecological tasks and biomechanical functions, responding variably to environmental factors including habitat use but also, feeding, mating, and territory defence (Edwards et al., 2013; Herrel et al., 2002).

Among lizards, the family Lacertidae, with over 360 species (Uetz, 2023), is a particularly suitable system to investigate the morphological implications of differential habitat-axis utilization. Through this transcontinental radiation, Lacertids have colonized an extraordinary number of ecosystems throughout the Old World. Even though they present a highly conservative morphology (Arnold, 1987, 1989), several macro- and micro-evolutionary studies have examined functional performance and morphology to understand phenotypic evolution in this group. Although the single study that investigated the consequence of habitat use on general body shape at the macroscale in lacertid lizards, could not establish an evolutionary effect (Vanhooydonck & Van Damme, 1999), other findings hint at the complexity of the relationship between morphological diversity and habitat use. Indeed, climbing and ground-dwelling lacertids present discrepancies in terms of locomotor performance (Van Damme et al., 1998; Vanhooydonck & Van Damme, 2003; Vanhooydonck et al., 2000), the tactics to boost speed (stride length vs. stride frequency) (Vanhooydonck et al., 2002), and the number of vertebrae and their function in manoeuvring (Van Damme & Vanhooydonck, 2002). However, those differences do not translate into limb proportion differences or a trade-off between horizontal-running and climbing abilities (Aerts et al., 2000; Vanhooydonck & Van Damme, 1999, 2001). Nevertheless, a recent study found differences in claw morphology between ground-dwelling and vertical-climbing lacertid species (Baeckens et al., 2020). This supports the hypothesis of limb adaptations to habitat in this group and provides further evidence that the use of vertical surfaces may favour the evolution of morphological traits associated with climbing (Hipsley et al., 2014). In contrast with these mixed patterns of limb shape evolution, several studies have established evolutionary links between head shape and microhabitat both within and across lacertid species, where climbers present flatter and narrower heads (Arnold, 1998; Gomes et al., 2016; Kaliontzopoulou et al., 2010, 2012, 2015; Urošević et al., 2013). Furthermore, species inhabiting arid environments have been shown to exhibit convergent evolution of cranial structures (Edwards et al., 2012; Harris et al., 1998; Hipsley & Müller, 2017).

These results highlight the need for a comprehensive approach to clarify how the contrast between using predominantly vertical versus horizontal habitats has contributed to body shape evolution in lacertid lizards. Here, we use the most complete Lacertidae phylogeny to date (Garcia-Porta et al., 2019), a comprehensive morphological dataset and state-of-the-art phylogenetic comparative tools to investigate the tempo and mode of body shape evolution as a response to these two structural habitat use axes, as well as adaptation trends using a comparison between Ornstein–Uhlenbeck (OU) vs Brownian motion models of evolution (Cressler et al., 2015). The implementation of appropriate phylogenetic comparative methods is imperative in untangling the unknowns of body shape evolution in the family Lacertidae, as well as significantly updating the existing background on this topic. To this end, we divide species into two categories: ground-dwelling and climbing. We expect climbing species to have evolved towards having shorter limbs and longer trunks on the one hand, and flattened, longer, and narrower heads on the other, to cope with the functional demands that vertical habitat imposes. We also predict that ground-dwelling species will present longer hindlimbs and a lower forelimb over hindlimb ratio, which are advantageous for sprinting in open areas. In addition, we expect a more robust body with taller heads as it is expected to be favourable in ground-dwelling habitats. We also anticipate ground-dwelling species to exhibit a higher diversity of forms, since they are adapted to a more diverse habitat what are expected to have less evolutionary constraints in comparison to habitats occupied by climbing species. Finally, we test for convergent evolution within each of the two habitats, with the prediction of a lower level of convergence in ground-dwelling species. Assuming that climbing habitat imposes high selective pressures on morphological evolution, we predict a convergent pattern for species that move vertically..

Material and methods

Morphology and habitat use

We collected linear measurements of a total of 956 adult male specimens for 186 lacertid species, using different datasets (specimens from collections and field campaigns) covering 52.2% of the described species and including at least one species per genus of the family (Uetz, 2023). We measured eight ecologically and evolutionarily relevant linear features in order to capture general body shape, understood as the relative proportions of different body parts. Those measurements are: snout-vent length, head length, head width, head height, mouth length, hindlimb length, forelimb length, and trunk length (Figure 1). All measurements were taken to the closest 0.01 mm, employing electronic callipers and following the protocol in (Kaliontzopoulou et al., 2007), and we computed the mean value of each morphological trait per species (Supplementary Table S1). For downstream analyses, we log10-transformed all data and used snout-vent length as a measure of body size to obtain size-corrected linear biometric measurements as the residuals from a phylogenetic regression using all species (Revell, 2009), as implemented in the function phyl.resid in the package "phytools" (Revell, 2012). This method allows to correct by size morphological data while accounting for species relatedness, which has been shown to avoid downstream type I error when working with phylogenetic comparative methods (Revell, 2009).

To explore the role of habitat use in the evolution of body shape, we divided the species into two groups: ground-dwellers and climbers. To classify species into one of the two habitat use groups, we conducted an extensive qualitative analysis, employing bibliographic review, consulting specific articles as well as general sources such as the reptile database (Uetz, 2023) and the IUCN red list (IUCN, 2022), among others (Supplementary Table S2). We classified as ground-dwelling lacertid species that spend most of their time on the ground, utilizing the horizontal axis of their habitat, independently of the type of substrate. The majority of *Acanthodactylus*, *Eremias*, *Lacerta*, and *Timon* species, among others, were placed in this category. This group also includes species that may use other structures such as rocks or shrubs on occasion, but not predominantly. The second type, climbers, refers to species that mainly employ the vertical axis of the habitat. Climbers are lizards that spend most of their time climbing and moving over vertical surfaces such as trees, shrubs, and rocky surfaces. We collapse all types of habitats that imply movements in the vertical axis, including both saxicolous and tree-climbing species, since lacertid species mainly use trunks rather than branches, which means that species primarily use

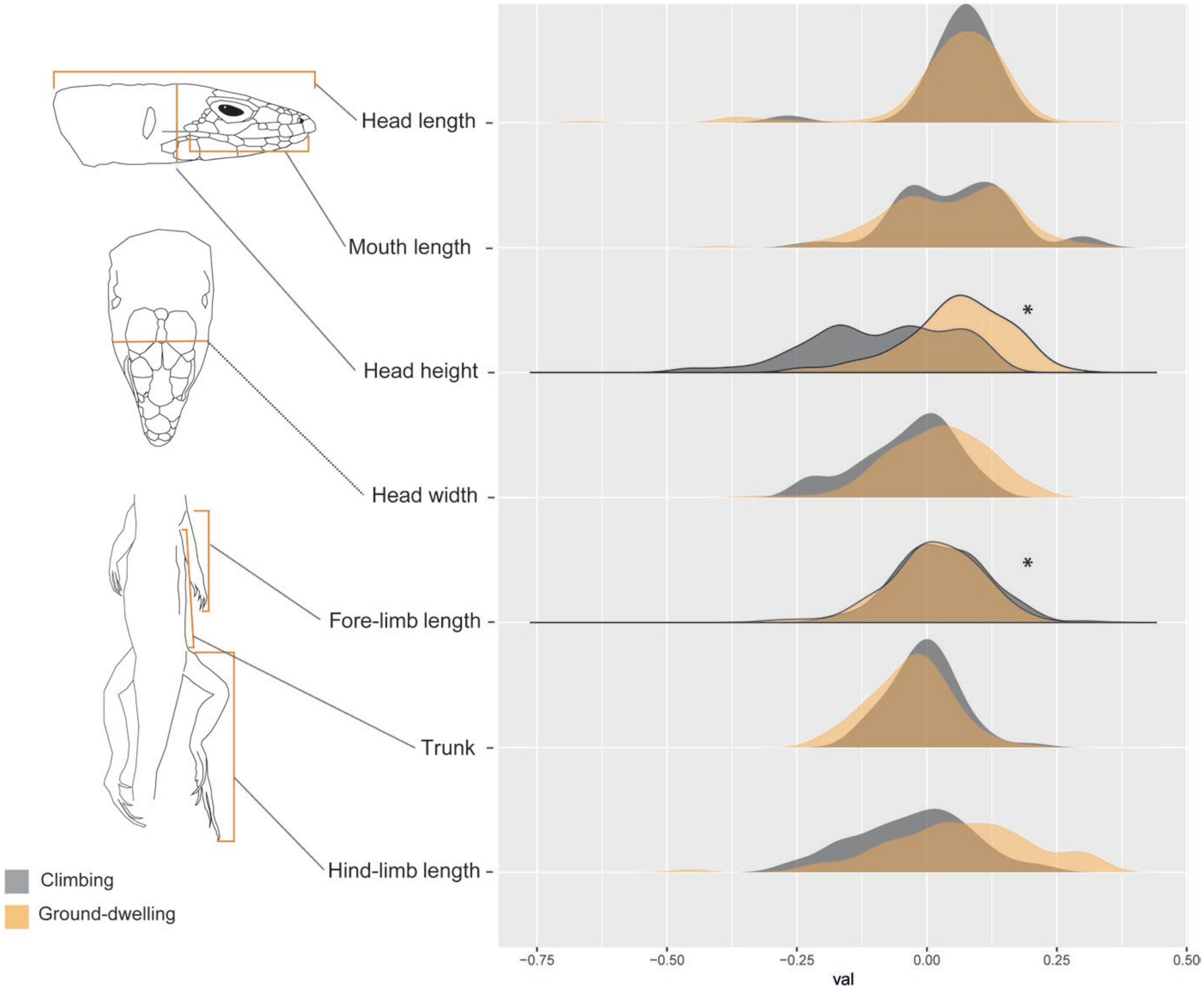

Figure 1. Generalized lacertid lizard outline (left) illustrating the seven morphological measurements considered and distribution of the log-transformed and size-corrected data coloured by habitat use category. The density curves with black outlines and asterisk are those that differed significantly in the phylogenetic ANOVAs.

broader surfaces. Therefore, both types of climbing structures are predicted to impose similar functional demands on lacertid morphologies (Foster et al., 2018; Tulli et al., 2011). These animals can use the ground in some circumstances, such as when escaping from predators, but it is not their preferred habitat. Species of the genera *Gastropholis*, *Takydromus*, *Algyroides*, *Dalmatolacerta*, some *Podarcis*, and others were considered as members of this category.

Comparative analyses

To perform comparative analyses, we used the most complete and dated phylogeny of lacertid lizards published to date (Garcia-Porta et al., 2019) (Supplementary Figure S1). This dated phylogeny combines genomic and genetic data and reconstructs the evolutionary relationships of 246 species (see Garcia-Porta et al., 2019 for further information). We discarded the tips for which we had no morphological data for downstream morphological analyses (but see further on for how habitat use was reconstructed using the full phylogeny).

Phylogenetic signal

To explore morphological patterns of body shape evolution, we first evaluated the degree of phylogenetic signal in size-corrected morphological traits, by calculating Pagel's λ statistic (Pagel, 1999) using the *phylosig* function in the R package "phytools" (Revell, 2010). This parameter is a measure of the scaling of the phylogeny that is necessary to better fit the data to a Brownian motion model. We opted for this statistic due to its good performance and low level of type I error (Münkemüller et al., 2012). Values near 0 represent phylogenetic independence, whereas values closer to 1 indicate that traits are as similar as expected under a Brownian motion model of evolution. To test if the λ values were significantly different from 1, we performed a likelihood ratio test between the lambda model and a Brownian motion model. The code to perform the comparison is available in the Github repository (). We would expect to find lower phylogenetic signal values for putative convergent traits, since high levels of phylogenetic signal would mean species resemble each other more because of their shared ancestral history rather than other external factors.

Morphospace occupancy

In order to describe morphological variation and morphospace occupancy across species we performed two principal component analyses (PCAs), where we separately considered two functional blocks of traits: head relative dimensions and body-limb shape (i.e., considering size-corrected traits of low collinearity, as described above). Then, we plotted the first and second components and projected the phylogeny onto PC space to form a phylomorphospace (Sidlauskas, 2008) using the function geom_phylomorpho implemented in the "deeptime" package (Gearty, 2023). Posteriorly, convex polygons were created for climbers and ground dwellers and for both PCAs using the *chull* function of the same R-package. To evaluate whether morphological disparity differed between habitat groups, as expected if ground dwellers are under less restrictive selective pressures in comparison to climbers, and therefore displaying higher morphological disparity, we used the function *morphol.disparity* in the package "geomorph" (v.4.0.5) (Adams et al., 2022; Baken et al., 2021) and we tested its significance using a permutation procedure of 999 iterations.

Phylogenetic analyses of variance

To investigate if habitat use had an effect on the diversification of body shape in lacertid lizards, we first performed two phylogenetic multivariate analyses of variance (pMANOVA) to examine the effect of habitat use on head shape and the shape of the locomotor apparatus. We fitted linear models using the corresponding morphological traits per functional groups using the function *lm.rrpp* and *manova.update* implemented in the package "RRPP" (Collyer & Adams, 2018, 2023). Subsequently, in order to investigate whether habitat use has an effect on individual morphological traits, and whether significant differences exist in the fore-hind limb ratio between climbers and ground dwellers, we performed phylogenetic analysis of variance (pANOVA). We used each of the morphological traits separately as the dependent variable and habitat use as a predictor in the first case; and we compared forelimb length vs hindlimb length, with habitat use as an interactive effect in the second case. We fitted linear models and evaluated their significance using residual randomization (RRPP), as implemented in the function *lm.rrpp* of the R package "RRPP" (Collyer & Adams, 2018, 2023).

Mode of evolution

To investigate how habitat use has influenced the tempo and mode of shape evolution, we first used stochastic character mapping as implemented in the function *make.simmaps* of the package "phytools" (Revell, 2012) to reconstruct the ancestral states of habitat preference across the phylogeny. Here, we used the complete phylogeny (before trimming it down to the species for which morphological data were available) to obtain a more accurate reconstruction. We fitted discrete trait evolutionary models based on two unordered state transition matrices (Supplementary Table S3). The first assumes transitions of equal frequency between trait states (equal rates: ER), while the second allows a different rate for each transition (all-rates-different: ARD). Based on the log-likelihoods of these models, we identified ARD as the best model to describe habitat use evolution in lacertids (Supplementary Table S4; see also *Results* section). Using this model, we produced 1,000 simmaps to explore transitions between states and infer which state was the most probable ancestral habitat use for this lizard family.

Subsequently, we used the OUwie package (Beaulieu et al., 2012) and 100 simmaps randomly selected out of the 1,000 simulations to fit and compare different evolutionary models. First, we fitted a single-rate Brownian motion (BM1) that represents the null hypothesis of non-directional morphological evolution under a single evolutionary rate (σ^2), we also fitted a multiple rate Brownian motion (BMS), which allows for different evolutionary rates for ground-dwellers and climbers. Then, we fitted a second group of models that included a new parameter, θ. This parameter indicates the evolutionary tendency or optima of the data and has been used as evidence of adaptation (Cressler et al., 2015). We fitted a single-optimum OU, which has the same evolutionary peak (θ) for both habitats categories (OU1); a multiple optima Ornstein–Uhlenbeck (OUM), that allows for different evolutionary peaks for ground-dwellers and climbers; and finally, a multiple optima and multiple rate Ornstein–Uhlenbeck (OUMV), which allows both the optima and the evolutionary rate to vary depending on habitat use. Among OU-variant of the models, there is a parameter α, which represents the strength of the pull towards the evolutionary peak, that can be allowed to vary. We decided not to consider models that encompass variation in this parameter (i.e., OUMA and OUMVA) as the estimation of this parameter can affect others parameter estimations and can lead to model non-identifiability (Cooper et al., 2016; Friedman et al., 2021; Kaliontzopoulou & Adams, 2016). After fitting the models, we discarded model runs that presented negative eigenvalues, as these produce unreliable estimates (Beaulieu et al., 2012; Kolmann et al., 2020; Price & Hopkins, 2015). To compare model fit, we used the modified Akaike information criterion (AICc). When more than one model was equally supported ($\Delta\text{AICc} < 2$), we chose the model with the least number of parameters as the best-supported model. Note that models with similar AICc values often provide qualitatively similar results because the same mode of evolution can be characterized by different sets of parameters (Grabowski et al., 2023). Finally, we generated 97.5% confidence intervals for all model parameters of the best-fit model using parametric bootstrapping as implemented in the *OUwie.boot* function in OUwie package (Beaulieu et al., 2012). Due to computational limitations, we selected 10 random simmaps and performed 10 bootstrap replicates for OUMV and OUM models, while we performed 100 bootstrap replicates for BM1 and OU1 models.

Convergence

Finally, to test for convergent evolution among species belonging to each habitat type, we used pattern-based estimates to quantify the number of lineages that evolved independently towards the same phenotypic space. We used the package “convevol” (Stayton, 2015) to obtain different statistics which measure phenotypic similarity using distance-based approaches and we employed the statistics Ct1, Ct2, Ct3, and Ct4. This method is an updated version of the previous C1-4 (Stayton, 2015), to detect convergent patterns, but in this case, accounting for the time between tips. This method measures the phenotypic distance between species in specific moments in a time-scaled phylogeny. Ct1 measures the distance between two lineages in a specific time, as a proportion of the distance between the tips and the longest distance between the shared evolutionary trajectory. Ct2 captures the absolute magnitude of convergent change. Ct3 and Ct4 are standardized versions of Ct2, which divide this value by the total amount of phenotypic change in the convergence group (Ct3) or the total amount of phenotypic change in the entire clade (Ct4). We ran the analyses separately for each trait and in a multivariate manner for the two functional blocks (e.g., head and limbs) and both for ground-dwelling and climbing species. We created coherent groups by collapsing species to account only for the independent instances of the appearance of the character of interest (e.g., climbing and ground-dwelling), in order to avoid pairwise comparisons between sister taxa with the same state, as recommended by the authors (Grossnickle et al., 2024). We performed the analyses with 50 simulations using BM as an evolutionary model to test if each of the calculated Ct values was greater than expected by chance. The values of this parameter can range from negative to positive values, indicating divergence or convergence respectively (Grossnickle et al., 2024).

Results

We found that all morphological variables presented significant values of phylogenetic signal (Supplementary Table S5). Values for all variables ranged from 0.7 to 0.9, with all of them significantly different from 1, except for hindlimb length, which was not statistically distinguishable from 1.

The PCA performed with the head relative dimensions accounted for 74.75% of morphological variation in the first two PC axes (Figure 2A, Supplementary Table S6a). The first principal component (PC1) is related to head relative size, since the magnitude and direction of the components are very similar, with head width being the most strongly correlated. The second principal component (PC2) captured a contrast between head length and mouth length, on one side, and head height and head width, on the other. The second PCA, focusing on the locomotor apparatus (limbs and trunk) (Figure 2B, Supplementary Table S6b), accounted for 89.2% of the variance in the first two PC axes. The first component (PC1), captured a negative correlation between trunk and limb relative lengths, correlating positively with the limbs and negatively with the trunk (Supplementary Table S6b). Across both trait morphospaces, the multivariate morphological disparity did not differ significantly between ground-dwellers and climbers (Supplementary Table S7).

The phylogenetic MANOVAs on functional shape blocks (head vs. body) showed that climbing and ground-dwelling species differed when considering the multivariate set of head morphological traits, but not the locomotor apparatus (Supplementary Table S8). When investigating the effect of habitat use on individual morphological traits, we found that head height and forelimb length were significantly different between climbers and ground-dwellers (Table 1). Climbers present flatter heads and longer forelimbs than ground-dwellers. Finally, we observed no significant difference between habitat groups in forelimb to hindlimb ratio.

The ancestral state reconstruction of habitat occupation indicated that the most probable ancestral state for the root of the family Lacertidae was a climber, being reconstructed in 86% of the stochastic character maps (Figure 3). Accordingly, we found that the most common transition was from climbing habitat to ground-dwelling habitat. Regarding the mean total time spent in each state, we observed that the ground-dwelling state presented almost twice the time spent in the phylogeny than the climbing state (Supplementary Table S9).

Examination of evolutionary models of body shape evolution revealed different evolutionary regimes for different morphological traits (Supplementary Table S10). For mouth length and hindlimb length, the best-supported model was a single-rate Brownian motion. For forelimb length and trunk length, the best-fit model was a single-optimum Ornstein–Uhlenbeck (OU1). For head height and head width the best-fit model was a multiple optima Ornstein–Uhlenbeck. Finally, head length followed a multiple-rate and multiple-optima Ornstein–Uhlenbeck model (OUMV). Examination of model estimates revealed that ground-dwelling species are evolving towards larger values of head length, head height, and head width as compared to climbers (Table 2). In addition, ground-dwellers exhibited higher evolutionary rates than climbers for head length (Table 2).

Finally, when testing for convergence, according to Ct1-4 results, we found no significant signs of convergence or divergence neither in climbing nor in ground-dwelling species considering head morphology. Similarly, we did not find significant levels of convergence or divergence in ground-dwelling or climbing limb proportions (Supplementary Table S11).

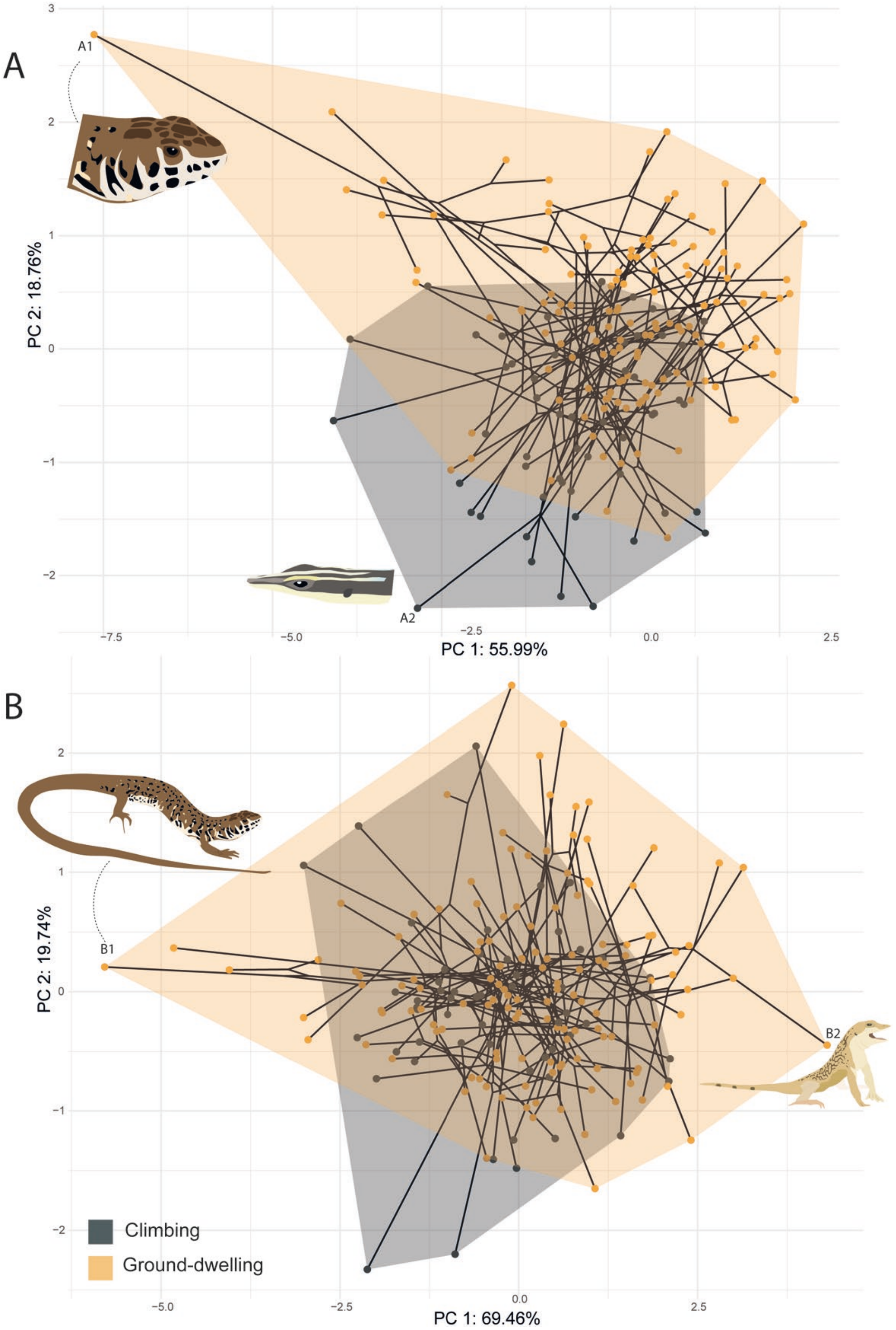

Figure 2. Phylomorphospace for the functional morphological trait blocks of head relative dimensions (A), and trunk and limb relative lengths (B). Each point represents a single species coloured by the correspondent habitat category. Illustrations represent the specific morphology in that part of the morphospace. A1: *Nucras lalandii*; A2: *Holaspis guentheri*; B1: *Nucras lalandii*; B2: *Meroles anchietae*.

Table 1. Results of the phylogenetic ANOVAs conducted to test for differences across habitats in size-corrected morphological variables and to examine if the relationship between fore and hindlimb lengths varied between climbers and ground-dwellers (fore-limb ratio). d.f.: degrees of freedom; R^2: R squared; F: F-value; Z: Z-score. *p*-values are based on 1,000 residual permutations and significant *p*-values (at α = 0.05) are highlighted in bold.

		d.f.	SS	MS	R^2	F	Z	*p*-value
Head length	Habitat	1	0.001	0.001	0.009	1.599	0.927	0.182
	Residuals	184	0.165	0.001	0.991			
	Total	185	0.166					
Head width	Habitat	1	0.001	0.001	0.019	3.488	1.442	0.074
	Residuals	184	0.066	0.000	0.981			
	Total	185	0.067					
Head height	Habitat	1	0.012	0.012	0.109	22.469	3.314	**0.001**
	Residuals	184	0.100	0.001	0.891			
	Total	185	0.112					
Mouth length	Habitat	1	0.000	0.000	0.002	0.396	−0.019	0.522
	Residuals	184	0.061	0.000	0.998			
	Total	185	0.061					
Forelimb length	Habitat	1	0.001	0.001	0.027	5.131	1.851	**0.024**
	Residuals	184	0.049	0.000	0.973			
	Total	185	0.050					
Hindlimb length	Habitat	1	0.000	0.000	0.005	0.860	0.424	0.360
	Residuals	184	0.087	0.000	0.995			
	Total	185	0.088					
Trunk	Habitat	1	8.69E-05	8.69E-05	0.002	0.427	−0.001	0.515
	Residuals	184	0.037	0	0.998			
	Total	185	0.038					
Fore-hind limb ratio	HLL * Habitat	1	0.000	0.000	0.006	1.862	0.978	0.170
	Residuals	182	0.028	0.000	0.562			
	Total	185	0.050					

Discussion

How habitat use influences morphological evolution through demands on functional performance has been a major theme in evolutionary biology (Garland & Losos, 1994). In this study, we explored morphological responses to the requirements imposed by different habitats depending on the structural axis along which species move. We investigated the distinction between lacertid lizards that predominantly use vertical vs. horizontal habitat axes considering two morpho-functional trait blocks: the head and the locomotor apparatus. Although macroevolutionary inferences have been made using about half of the species in the Lacertidae family, our results suggest mixed effects of habitat use on body shape macroevolutionary patterns. We did not find support for the broad hypotheses of limb dissimilarities based on biomechanical expectations regarding the locomotor apparatus (Kaliontzopoulou et al., 2010). Instead, we only uncovered differences in the length of the forelimbs between climbers and ground-dwellers, in a direction opposite to our expectations. By contrast, habitat use had a major effect on the evolution of head shape in lacertids, where we found morphological adaptations to climbing, in accordance with those previously reported from other groups (Openshaw & Keogh, 2014; Revell et al., 2007), as well as adaptations to navigate in the horizontal axis of the habitat. Indeed, we showed that the morphological features of the head follow different evolutionary trajectories for climbers and ground dwellers.

Lacertid ancestry

The preferred habitats of the assumed closest relatives of lacertids had led researchers to hypothesize that the common ancestor of this family was a ground-dweller (Arnold, 1998). Indeed, the families Teiidae and Gymnophtalmidae have been considered the sister clades of the Lacertidae, and both present the typical ground-dwelling lifestyle (Vitt & Pianka, 2004; Zweifel, 1998). Our results, nonetheless, based on an ML-based reconstruction of habitat use, point in a different direction, and support the hypothesis that lacertids evolved from a climbing ancestor (Figure 3). This does not seem unreasonable, as species diversification of teiids and gymnophthalmids, on the one hand, and of lacertids, on the other, has occurred in very distant regions (New World vs Old World). Indeed, although these families share part of their evolutionary history (Vitt & Pianka, 2004) they diverged from each other 180 million years ago (Zheng & Wiens, 2016). Moreover, a recent phylogenomic inference of the deeper relationships of reptiles indicates that the sister clade of the Lacertidae is the Amphisbaenia, a group of limbless lizards (Zheng & Wiens, 2016) which presents mostly burrowing behaviours (Longrich et al., 2015). As such, the diversification of the Lacertoidea seems to have been dominated by frequent and radical ecological, morphological, and performance changes, making the estimation of the ancestral habitat use of lacertids from their relatives questionable. Nevertheless, a ground-dwelling common ancestor for amphisbaenians and lacertids, with an early adaptation to a climbing habitat for

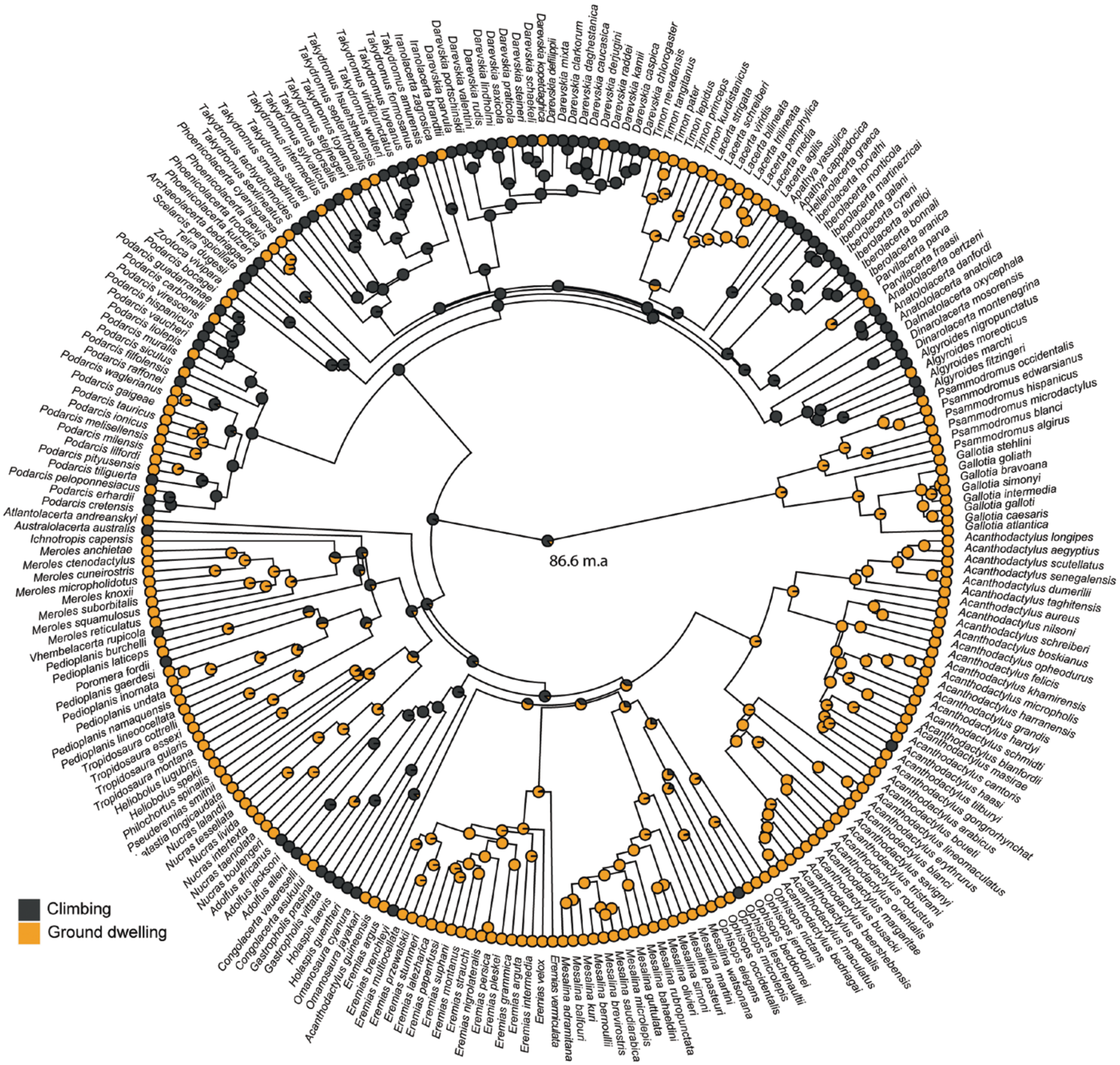

Figure 3. Evolution of habitat use in lacertid lizards reconstructed on the most recent phylogeny of the family with 246 species (obtained from Garcia-Porta et al., 2019) using the all-rates-different (ARD) transition matrix. The fraction of assignment to each state over the 100 simulations is represented by pie charts on the internal nodes. The circles at the tips represent the species' habitat use. The age of the node is presented. For further information, see Garcia-Porta et al. (2019).

the Lacertidae ancestor, followed by a secondary occupation of the ground, also seems to be a plausible scenario.

Interestingly, the ancestral state reconstruction for lacertids suggests different dynamics of evolutionary transitions between habitat types than that observed in other lizards. A recurrent trend whereby species shift from a ground-dwelling to a climbing habitat has been implicitly observed in several groups (Collar et al., 2010, 2011; Melville & Swain, 2003; Revell et al., 2007). In these transitions, morphology undergoes specific modifications to cope with vertical requirements (Collar et al., 2010, 2010; Goodman et al., 2008; Revell et al., 2007). However, the directionality, frequency, and implications of these transitions have never been addressed in detail but have rather been a tacit product of morphological analyses. In these studies, most groups present a ground-dwelling ancestor and, therefore, adaptation typically occurs towards climbing. By contrast, our results highlight that, in lacertids, transitions from the vertical to the horizontal axis have occurred at least six times more often than the reverse (Supplementary Table S9). Climbing habits are known to be biomechanically quite demanding and restrictive (Revell et al., 2007). As such, novel morphological adaptations to ground-dwelling could be acting as an evolutionary dead-end (Day et al., 2016). Such cases of the reverse transition—from climbing to the ground—have also been observed in particular species in other lizard groups (Collar et al., 2010), but they otherwise seem to be quite rare,

Table 2. Estimated parameters and confidence intervals (2.5%, 97.5%) of the best evolutionary model (see Supplementary Table S10) fitted to each of the seven morphological traits examined. θ: evolutionary optima; α: pull towards the evolutionary optima; σ^2: evolutionary rates. Different parameters for climbers (CL) and ground-dwellers (GD) are included when the model allows the parameters to change between habitat use categories.

Morphological trait	Best model	$\theta_{(CL)}$	$\theta_{(GD)}$	α	$\sigma^2_{(CL)}$	$\sigma^2_{(GD)}$
Head length	OUMV	0.0551 (0.0331,0.0665)	0.0533 (0.0254,0.0672)	0.1930 (0.1071,0.3503)	3.39E-03 (1.71E-03,4.74E-03)	5.45E-03 (3.12E-03,1.21E-02)
Head width	OUM	−0.0245 (−0.0823, −0.0200)	0.0190 (0.0109, 0.0873)	0.0324 (0.0221,0.0433)	6.41E-04 (4.26E-04,8.38E-04)	
Head height	OUM	−0.0883 (−0.2017, −0.0591)	0.0413 (0.0403–0.1719)	0.0391 (0.0221, 0.0528)	1.08E-03 (7.20E-04,1.44E-03)	
Mouth length	BM1	–		–	3.27E-04 (2.57E-04,3.98E-04)	
Forelimb length	OU1	0.0070 (−0.0667, 0.0653)		0.0184 (0.0083, 0.0399)	3.90E-04 (2.84E-04, 5.63E-04)	
Hindlimb length	BM1	–		–	4.71E-04 (3.71E-04,5.92E-04)	
Trunk	OU1	−0.0164 (−0.0496, 0.0122)		0.0275 (0.0182, 0.0508)	3.35E-04 (2.64E-04,4.99E-04)	

making lacertids a unique example of this kind of evolutionary shift in habitat use.

Effects of habitat on phenotypic evolution

Demands of the climbing habitat type include elements such as the effect of gravity when climbing, vertical movements, jumping between adjacent rocks or branches, and hiding in small crevices when escaping from predators. These requirements are expected to affect performance and morphology (Arnold, 1983). Although previous studies found no morphological differences in limb proportions in lacertid lizards at different scales (Cordero et al., 2021; Gomes et al., 2016; Vanhooydonck & Van Damme, 1999), we identified significant variation in forelimb length but not in hindlimbs, the hindlimb to forelimb ratio, or trunk length, between climbers and ground-dwellers (Table 1). Although this result does not follow biomechanical expectations (Kaliontzopoulou et al., 2010), it is not striking for this group. Previous results illustrate a complex and not straightforward relationship in habitat–performance–morphology in lacertid lizards (Gomes et al., 2016). Accordingly, differences in limb length and body morphology associated with locomotor performance have not been observed (Aerts et al., 2000; Gomes et al., 2016; Vanhooydonck & Van Damme, 1999, 2001). In this study, we show that, when accounting for the phylogeny, climbing species present slightly longer forelimbs than ground-dwelling ones, which could be linked to locomotor mode. Nevertheless, the assessment of this relationship would require the analysis of quantitative performance data (e.g., speed, sprint speed, and climbing speed). In addition, other selective pressures could be acting on forelimb length evolution, such as the broadness of the surface (Revell et al., 2007) or the quantity of rocks in the habitat (Goodman et al., 2008).

In contrast with this limited differentiation of the locomotor apparatus, our results support the predictions made regarding the evolution of head shape in response to habitat use (Table 1). Climbing species present the typical flat head which helps them to, first, maintain the centre of mass of the body closer to the surface when climbing and, second, hide in small refugia when escaping from predators (Gomes et al., 2016; Goodman et al., 2008; Kaliontzopoulou et al., 2015; Kohlsdorf et al., 2008; Openshaw & Keogh, 2014; Revell et al., 2007). Since climbing species have the tendency to escape towards "known structures" such as holes and small crevices, and usually remain in the surroundings of the shelters (Diego-Rasilla, 2003; Vanhooydonck & Van Damme, 2003), escape behaviour is known to be a major determinant of morphological diversity in this group (Gomes et al., 2016; Husak & Fox, 2006). Therefore, natural selection would favour flatter heads for climbing lizards, which matches the observed patterns (Figure 1) and is also supported by evolution towards a lower evolutionary optimum for this morphological trait (Table 2). Ground-dwelling species, by contrast, present taller and more robust heads, which can be advantageous in horizontal habitats to have a broader vision to detect predators.

In addition to this apparently adaptive differentiation between climbers and ground-dwellers, where most head morphological traits follow a directional evolutionary model with two different adaptive optima (i.e., OUM, OUMV; Table 2, Supplementary Table S10), we also found evidence that habitat use has influenced the tempo of head shape evolution. Indeed, despite a lack of global differentiation in raw head shape disparity, when taking phylogeny into account we found that head length indeed evolved under different evolutionary rates (Table 2). Interestingly, the evolutionary optima estimated under this model for climbers and ground-dwellers are very similar, which translates into a lack of significant differences between present phenotypes (Figure 1). The apparent discrepancy between the evolutionary model in head length (OUMV) and the expected morphological output from it (i.e., no significant differences between groups in the phylogenetic ANOVA), may be a result of assuming a BM evolutionary model for ANOVAs, which is different from the best model. In terms of evolutionary rates, though, ground-dwelling species seem to have followed a faster pace of evolution for this morphological trait. This is expected as the ground-dwelling category encompasses species that explore a wide variety of structural habitats (deserts, forests floors, grasslands, dunes, etc.), potentially affecting the diversification of this morphological trait (Collar et al., 2010). This pattern also matches the expectation that climbing species may present a narrower adaptive peak, and therefore a lower phenotypic rate, due to the restrictive nature of moving vertically (Collar et al., 2010; Kaliontzopoulou et al., 2015).

Convergence

Convergence can emerge due to constraints, random changes, or natural selection (Stayton, 2015). A typical convergent pattern of many lizard groups is observed in body shape among species adapted to climbing (Goodman & Isaac, 2008; Losos, 1992; Openshaw & Keogh, 2014; Revell et al., 2007), while a few cases of ground-dwelling convergence have also been reported (Gray et al., 2019; Huie et al., 2021). These convergence patterns can be performance-mediated, since the same ecological requirements in a specific habitat can lead to convergence in performance and also trigger convergence in morphology (Edwards, 2011). While this phenomenon was found in other lizard groups (Elstrott & Irschick, 2004; Losos, 1990), we did not identify indices of convergence in lacertid lizards.

Observing our results and contrary to expectations, we did not find any signs of convergence in the locomotor apparatus, neither in climbing nor in ground-dwelling lacertids (Supplementary Table S11). Nevertheless, taking into account the complex relationship between locomotor morphology and performance in this group (Gomes et al., 2016), the absence of limb convergence is far from surprising. It seems that locomotor performance and body shape are not responding in concert with similar selective pressures in lacertids. Rather, the selective pressures imposed by habitat may be acting on different performance and morphological aspects (Baeckens et al., 2020). For example, when examining the morphospace occupancy of the species (Figure 2B), we observe that, although both groups share the majority of the morphospace, some ground-dwelling species appear to be evolving towards different directions. One group, located in the left part of the morphospace, exhibits longer trunks and shorter limbs, while another group, in the right part, shows the opposite pattern with shorter trunks and longer limbs. This variation may be related to substrate type and escape strategies of ground-dwellers. Species on the right, such as those of the genera *Meroles*, *Eremias*, and *Acanthodactylus* are typically associated with sandy environments and are adapted to fast running (Edwards et al., 2016; MartÍn & López, 2003). In contrast, species like *Nucras* and *Atlantolacerta*, found on the opposite extreme of the morphospace, are typically associated with rocky habitats and use short bursts of running to hide among rocks as their escape strategy (Huey et al., 1984, pers. observ). This suggests that, rather than climbing or ground-dwelling movement alone, other selective pressures may be influencing locomotor morphology in lacertid lizards.

In agreement with these results, our predictions regarding convergence in the shape of the head were neither confirmed by Ct measurements (Grossnickle et al., 2024). We expected both climbing and ground-dwelling heads to present significant levels of convergence, since the biomechanical constraints, stronger in climbing environments, would drive head morphology in the same direction for both groups. However, no signs of convergence were found in lacertid lizards (Table 2; Supplementary Table S11). This result is supported by the high levels of the phylogenetic signal of different morphological traits (Supplementary Table S5), which suggest that species resemble each other because of their shared evolutionary history rather than due to convergence processes. Moreover, disparity analyses showed no significant differences between the groups, further supporting the absence of convergence. Since neither group is converging towards a specific part of the morphospace, thereby reducing its disparity, no significant disparity differences were observed between both groups.

In contrast, we found that head-related traits follow a multi-optima Ornstein–Uhlenbeck model, which has been used as evidence of adaptation. In this case, ground-dwelling and climbing species evolve in different directions, each reaching an optimal head shape for their respective habitat use. However, the strength of selection exerted by each structural habitat does not seem sufficient to drive head shape evolution to be similar for all species occupying a specific habitat, as observed in other groups (Goodman & Isaac, 2008; Gray et al., 2019; Huie et al., 2021; Losos, 1992; Openshaw & Keogh, 2014; Revell et al., 2007). The level of specialization may be an important factor to consider, as in lacertid lizards, we observe highly specialized climbing and ground-dwelling species that may be driving morphological trends towards distinct optima. However, there is also a large group of species that fall between these two "putatively fully converged" morphologies (Figure 2A). Therefore, although the habitat imposes an adaptive regime on ground-dwelling and climbing heads, species may not have had enough time to converge. Alternatively, our classification of habitat use diversity in lacertids, which is quite complex, into two distinct categories, may underlie these results. Although obtaining continuous habitat use data for such a wide number and diversity of species is at present not practically possible, the possibility remains that a future reanalysis of our data using continuous habitat-use data may further enhance evolutionary inferences. Nevertheless and more likely, according to our results, species are adapting to the same structural habitat (e.g., climbing or ground-dwelling) but are modifying different aspects of head shape, resulting in different morphologies that perform the same function (Thompson et al., 2017). Indeed, it has been demonstrated that head shape is involved in several ecological activities that can act on its evolution such as feeding, mating, or territory defense (Gomes et al., 2018; Herrel et al., 2001; Verwaijen et al., 2002). These ecological constraints could also affect head shape evolution. For example, while a climbing environment should drive heads to be narrower, sexual selection on males may act in the opposite direction to enhance bite force, thereby increasing mating success or success in male-male competition (Kaliontzopoulou et al., 2012). This highlights how different parts of morphology, although participating in the same functional task, can be selected differently to fulfil various ecological functions.

Conclusion

In conclusion, our findings highlight how lacertid lizards present specific but clear ecomorphological adaptations. They also show how similar selective pressures can act differently and produce different effects over different parts of an organism's body (Herrel et al., 2002). Indeed, the presence of different evolutionary rates and modes depending on the traits, highlights how different body regions can evolve differently even when they form part of the same functional block (Smith et al., 2016). Because of habitat-specific pressures, climbers and ground-dwelling species exhibit distinct head evolutionary trends, which become tangible when looking at head height differences. By contrast, the relationships between habitat, locomotor performance, and limb morphology remain complex for this lizard family. One element that appears to blur the relationship between form and function is the presence of a few highly specialized forms in response to habitat use among lacertids (Aerts et al., 2000). We find such species in both habitat categories. For example, *Dalmatolacerta oxycephala*, *Hellenolacerta graeca*, or species of the genus *Gastropholis* are extensively adapted to vertical locomotion. On the other hand, species within genera such as *Acanthodactylus* or *Eremias* are found strictly in horizontal, open habitats. However, the bulk of lacertid lizards consists of species that, while displaying a clear preference for one habitat over another, may use other structures, such as the genus *Podarcis*. In this regard, the level of ecological specialization appears to be a determinant factor in morphological diversification and may also influence the detection of convergence in this study, since the broad habitat-use categories we have used may obscure real convergent patterns within the Lacertidae family. Lacertid lizards do not present a locomotor form clearly adapted to one habitat or another, instead, an all-purpose Bauplan appears to be selected for (Kaliontzopoulou et al., 2015). To meet particular locomotor requirements, some groups have developed specific structures, such as fringed toes in sand dwellers like some species within *Acanthodactylus*, prehensile tails in species of *Gastropholis*, rib expansion in species of *Holaspis* and longer tails in species of *Takydromus* (Hipsley et al., 2014). Thus, as is the case in geckos, these morphological structures may be blurring differentiation into distinct ecomorphs (Kulyomina et al., 2019; Zaaf & Van Damme, 2001). Ultimately, our study underscores that lacertid lizards embody an adaptable form, capable of both specialized and generalized responses to ecological pressures, contributing to a nuanced understanding of ecomorphological evolution in reptiles.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

Data and codes are available on Dryad repositories (10.5061/dryad.280gb5mxk).

Author contributions

Pablo Vicent-Castelló (Conceptualization [equal], Data curation, Formal analysis [lead], Investigation [equal], Methodology, Visualization, Writing—original draft [lead]), Antigoni Kalionzopoulou (Conceptualization [equal], Formal analysis, Investigation [supporting], Methodology, Resources, Supervision [lead], Writing—original draft [supporting], Writing—review & editing [lead]), Anthony Herrel (Data curation, Supervision, Writing—review & editing [supporting]), and D. James Harris (Supervision, Writing—review & editing [supporting])

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Conflicts of interest

None declared.

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