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The Influence of Habitat on the Morphology of *Liolaemus* Lizards

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Abstract

The morphology of an organism reflects its lifestyle (and that of its ancestors). Biomechanical theory predicts the existence of clear relationships between morphology and habitat use, given that the physical demands acting on the locomotor system are different in different habitats. Accordingly, the phenotype provides valuable information about the relationship between morphology and habitat structure and how these associations evolve as a response to changing environment. Here, present a study about relationship between morphology and habitat use in 37 species of *Liolaemus* lizards females and males that exploit different habitats. The main goal is to investigate if the general morphology of the locomotor apparatus (limbs and digits) in male and female *Liolaemus* reveals complex relationships with their ecology. The main results were head length and interlimb length, showed differences between sexes. Males presented bigger heads and females more distance between limbs. Meanwhile, for the habitat use arenicolous and terrestrial species showed shorter digits, arm, and crus. Arboreal species showed a larger interlimb. These results provide valuable insights into the morphological variation and sexual dimorphism within the *Liolaemus* genus.

Keywords: External Traits; Apparatus Locomotor; Substrate; *Liolaemus*

Introduction

The general theoretical principle of adaptive variation based on natural selection [1] predicts that there should be a correlation between the design and ecology of organisms, such that the mechanical demands imposed by ecological factors are reflected in the morphological changes of the system involved. This is a generalized point of view that the morphology of an organism reflects its lifestyle (and that of its ancestors) [2-4]. Biomechanical theory predicts the existence of clear relationships between morphology and habitat use, given that the physical demands acting on the locomotor system are different in different habitats [5]. Accordingly, the phenotype provides valuable information about the relationship between morphology and habitat structure [6-8], and how these associations evolve as a response to changing environments [9-11].

Lizards exhibit diverse locomotor abilities, including swimming, running, jumping, and flying, essential for various physiological functions such as foraging, predator avoidance, and reproduction [12]. The success of these functions, and ultimately survival, depends on factors related to the locomotor system, such as running speed, endurance, and maneuverability [13,14]. These factors are, in turn, influenced by a combination of characteristics, including morphology, biochemistry, and physiology, which vary significantly among organisms. This suggests that individual variation in locomotor ability can be both repeatable and heritable in some animal species (e.g., lizards, and mammals) [15]. This highlights the importance of investigating the evolution of the locomotor system to understand the mechanisms driving the diversity of organismal functions. Traditionally, have been suggested that variations in locomotion modes are correlated with variations in the anatomy of the locomotor apparatus, specifically the limbs and digits [16-19]. Based on this premise, several studies have explored the evolutionary relationships between morphology and microhabitat use in lizards *Liolaemus* [20-23], *Anolis* [24], Sceloporines [25], Lacertidae [26], *Niveoscincus* [27,28], *Tropidurus* [29-31], Gekkonidae [32,33].

Species of the genus *Liolaemus* represent an excellent model system for exploring the relationships between morphology, ecology, and behavior. As one of the world's most diverse and species-rich lizard genera, *Liolaemus* boasts approximately 285 described species [34]. Widely distributed across South America's arid and semi-arid regions, from Tierra del Fuego in southern Argentina to central Peru, *Liolaemus* inhabits a broad range of habitats, including open. Terrestrial environments with rocky or gravelly surfaces, loose or firm aeolian sand, and even areas with denser vegetation such as grasses, herbs, shrubs, and trees [22,23]. While some researchers posit that lizard morphology should exhibit significant interspecific variation to accommodate different ecological niches [24], *Liolaemus* species demonstrate remarkable morphological versatility. This adaptability enables them to thrive in diverse environments, effectively performing various tasks across different substrates, as long as they remain at ground level. However, studies on sexual dimorphism in size and shape within the genus are relatively scarce [35-37]. In this context, this study aims to investigate if the general morphology of the locomotor apparatus (limbs and digits) in male and female *Liolaemus* reveals complex relationships with their ecology. Additionally, the sexual dimorphism hypothesis was tested based on the main proposed hypothesis. Sexual selection theory predicts that larger males will have higher reproductive success due to advantages in competition for mates [38]. This is larger body sizes or allometric growth of structures used in male-male competition, such as large heads [39,40]. For females, an alternative hypothesis is the fecundity advantage hypothesis. This proposes that female fecundity is correlated with body size, leading to selection for larger females [41,42]. Thus the hypothesis of this work is hypothesize that male saxicolous species will exhibit more robust limbs and larger heads related to those inhabiting sandy habitats and females. Conversely, it is expected that females to display a more robust body and slender limbs. This research will contribute significantly to our understanding of *Liolaemus*, filling critical knowledge gaps regarding the relationships between morphology, locomotor abilities, and sexual dimorphism within this diverse genus.

Material and Methods

Data Collection

In this study, 761 adult specimens from 37 species, males and females of lizards belonging to the *Lioalemus* genus (Table S1). The species selected to explore a diversity of habitats arenicolous, saxicolous, arboreal, and terrestrial. All specimens belong to systematic collections and are in Table 1.

Species	Habitat use
Liolaemus albiceps	2
Liolaemus baguali	3
Liolaemus bibroni	2
Liolaemus canqueli	2
Liolaemus cei	3
Liolaemus coeruleus	3
Liolaemus crepuscularis	2
Liolaemus cuyanus	1
Liolaemus darwini	2
Liolaemus dorbignyi	4
Liolaemus elongatus	4
Liolaemus escarchadosi	3
Liolaemus fitzingeri	2
Liolaemus goetschi	2
Liolaemus hatcheri	3
Liolaemus hermannunezi	2
Liolaemus inacayali	2
Liolaemus irregularis	2
Liolaemus kingii	3
Liolaemus kolengh	3
Liolaemus koslowskyi	2
Liolaemus kriegi	4
Liolaemus lineomaculatus	2
Liolaemus magellanicus	2
Liolaemus melanops	2
Liolaemus multimaculatus	2
Liolaemus ornatus	2
Liolaemus petrophilus	4
Liolaemus pictus	5
Liolaemus poecilochromus	3
Liolaemus rothi	2
Liolaemus salinicola	1
Liolaemus sarmientoi	2
Liolaemus scapularis	1
Liolaemus tenuis	5
Liolaemus xanthoviridis	2
Liolaemus zullyi	3

Table 1: List of the species used in this study. Numbers of the habitat use the literature cited and personal observations: 1: arenicolous, 2: terrestrial, 3: saxicolous, 4 arboreal.

Measurements

We used Twenty one linear measurements from the body and limbs of each specimen were taken (Table 2). The following morphological traits were measured directly from lizards using digital calipers (Mitutoyo CD-15B; ±0.01 mm) on the right side of the body: body size (snout-vent length – SVL), the distance between limbs (interlimb length – ILL), maximum head width (HW), head length (HL: from the anterior border of the external auditory meatus to the tip of the snout), tail length (LT: from vent to tail tip), and tail width (WT: at the base of the tail); and elements of fore and hind limbs [forelimbs: arm length (ArmL), antebrachium length (AL), dorsum of manus length (ML), dorsum of manus width (MW), and lengths of the digits (DI-II-III-IV and V); hind limbs: thigh length (TL), crus length (CL), foot length (FL; distance from the ankle until the base of the toes), and lengths of the toes 3 (T3), 4 (T4), and 5 (T5) (Table S1).

Variables	PC1	PC2
ILL	-0.041	**0.624**
HL	-0.37	**-0.615**
HW	-0.56	0.004
TL	-0.222	-0.497
TW	-0.467	-0.273
ArmL	**-0.737**	0.102
AL	**-0.692**	0.057
ML	-0.594	**0.617**
MW	-0.565	0.457
DI	**-0.743**	0.294
DII	**-0.808**	0.235
DIII	**-0.898**	0.127
DIV	**-0.798**	0.214
DV	**-0.733**	0.166
T3	**-0.815**	-0.208
T4	-0.6	-0.485
T5	**-0.777**	-0.134
TL	-0.587	-0.225
CL	**-0.711**	-0.485
FL	**-0.669**	-0.113

Table 2: Coefficients representing the association of each morphological variable with the first two principal components (PC). Variables that contributing most each component are indicated in bold. Abbreviations are shown in the text.

Statistical Analyses

The data was log-transformed and assessed using Kolmogorov-Smirnov tests to determine if the morphological variables met the normality assumption. Homoscedasticity was evaluated through a visual examination of the data. To account for size effects, size-corrected morphological variables were analyzed using multiple regressions with snout-vent length (SVL) as the independent variable and morphological data as the dependent variable. Residuals from this regression were then used in subsequent analyses. A Principal Component Analysis (PCA) was performed to reduce the dimensionality of the morphological data.

One-way ANOVA was conducted on each principal component with habitat use as a factor to test sex-specific habitat use. After that, a multivariate analysis of variance (MANOVA) was performed with those variables with high loading in the PCA using habitat use and sex as categorical variables. Then to determine which means are significantly different from one another *a* False Discovery Rate (FDR) was performed. This method increases the chances for detecting significant differences when multiple tests are applied simultaneously and tend to larger Type I error [43,44]. All analyses were performed in the R Environment [45] using appropriate packages.

Results

All morphological traits correlated positively with SVL in males and females. Principal Component Analysis (PCA) revealed that the first two principal components (PC1 and PC2) captured a substantial portion of the morphological variation explaining 67% of the total variance. PC1, which accounted for 42.8% of the variation showed a strong and negatively association with digits and limb proportions (Table 1). PC2 explained 12% of the morphological variation, explaining a smaller proportion of the variance, was positively associated with interlimb and manus length and negatively with head length (Table 1).

The scores from each PC axis were used in a one-way ANOVA with habitat use as the main effect differed only on the first axis (PC1 $F_{(1, 146)}$= 226.2, p= 0.00001; PC 2 $F_{(1, 146)}$= 311.2, p= 0.90); showing a gradient of decreasing from terrestrial, and saxicolous with higher values to arenicolous until arboreal species with lesser values (Figure 1). The MANOVA analysis revealed significant sexual dimorphism in head length and interlimb distance (Sex: λ=0.34, $F_{(60, 141.06)}$ =1.022, $p<0.44$; Habitat use: λ=0.03, $F_{(60, 141.06)}$ =5.05, $p<0.00$). After MANOVA only two variables, head length and interlimb length, showed differences between sexes. Males presented bigger heads (λ=0.56, $F_{(20, 52)}$ =2.04, $p<0.02$; (Figure 2a) and females more distance between limbs (Figure 2b). However, using habitat use as a categorical factor arenicolous and terrestrial species showed shorter digits, arm, and crus. Meanwhile, the arboreal showed a larger interlimb.

Discussion

The results of this study provide valuable insights into the morphological variation and sexual dimorphism within the *Liolaemus* genus. As expected, a strong positive correlation was observed between morphological traits and SVL in both sexes, indicating significant allometric scaling. This pattern is consistent with previous studies on lizards and suggests that body size plays a crucial role in shaping overall morphology [12]. Males exhibited larger heads, which may be related to sexual selection or differences in feeding ecology. Females, on the other hand, had longer interlimb distances, which could be associated with reproductive strategies or differences in foraging behavior [46]. These findings support the hypothesis of sexual selection favoring larger males and potentially different ecological roles for males and females.

Furthermore, the results also highlighted the influence of habitat use on morphological variation. These findings underscore the importance of habitat-specific adaptations in shaping the morphology of *Liolaemus* lizards. Arenicolous and terrestrial species exhibited shorter digits, arms, and crus, while arboreal species had longer interlimb distances. Sandy substrates can be unstable and energy-consuming to traverse having shorter limbs and digits may provide better stability and traction, and reducing energy expenditure during locomotion provides greater agility and maneuverability, allowing these lizards to quickly change direction and avoid predators even in terrestrial environments involve navigating over uneven terrain, rocks, and vegetation. Also, shorter digits can provide a broader base of support when the lizard is pushing against the sand to move forward or backward. This enhances stability in the loose, shifting substrate and providing better leverage for excavating burrow construction. Scansorial species as those arboreal *Liolaemus* showed a relative longer body (IIL) that could allow them for greater reach, enabling the lizard to grasp trunks that would otherwise be out of reach. Also, reach into crevices and narrow spaces in tree bark to access insects and other prey. Additionally, longer digits could provide a larger surface area for interlocking grasping onto vertical surfaces as trunks of trees, enhancing stability and preventing falls, and could be used to pry open bark or leaves to uncover hidden food sources.

Conclusion

This study provides a comprehensive understanding of morphological variation and sexual dimorphism within the *Liolaemus* genus. The results emphasize the role of allometry, locomotor adaptations, habitat use, and sexual selection in shaping the morphology of these lizards. Further research is needed to investigate the functional significance of these morphological differences and their impact on the ecology and behavior of *Liolaemus* species.

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