

Morphometric differences between two sympatric species of *Anolis* (Reptilia: Squamata: Polychrotidae)

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Abstract. There has been a recent surge of interest in the study of evolutionary relationships between morphology and microhabitat use in lizards in general. Lizards of the genus *Anolis*, most notably the Caribbean species, have become a model system in this respect. Although the mechanisms of *Anolis* locomotion have received considerable attention, however, little is known regarding locomotor performance of species of mainland *Anolis* in nature, and their morphological diversity. The goal of this study was to investigate the differences in morphology between *Anolis humilis* and *Anolis limifrons*, sympatric species that exploit different structural microhabitats (arboreal vs. ground-dwelling) with different locomotion challenges. A principal components analysis was performed on morphometric data for the two species that illustrates differences between the species. A multivariate analysis of variance on selected variables suggested only three variables: manus length, tail length and forelimbs length showed significant differences with respect to microhabitat use. Lizards that occupy vertical habitats (arboreal) tend to have longer tails and longer hind limbs (included the longer fourth toe) whereas lizards in terrestrial habitats have wider and flatter bodies and head and longer forelimbs. These morphological characteristics may allow climbing lizards to keep their centre of mass close to the substrate, while in terrestrial lizards they would enhance maneuverability and support weight during level running.

Key words: morphology, locomotors habits, microhabitat use, *Anolis*.

Introduction

Ecologists have been interested in the differential use of the resources as a possible explanation for the determinants of the distribution, abundance, and diversity of organisms (Toft 1985). Three traditional categories of resource dimensions are habitat, food, and activity time (Pianka 1975) which can be further divided into the following six categories: macrohabitat, microhabitat, food type, food size, and diel and seasonal activity time (Schoener 1974, Toft 1985). Toft (1985) determined that, for amphibians and reptiles, the habitat is likely the most important resource.

Many authors have stressed that morphological differences may account for the diversity in locomotor behavior exhibited by many species, because living in different habitats may result in morphological differentiation (Arnold 1983, Rewcastle 1983, Lauder & Reilly 1991, Blob 2001). Biomechanical principles stress that, ground-dwelling lizards are expected to have relatively long and parasagittal hind limbs, with high shank to thigh ratios, and relatively short forelimbs to maximize acceleration during running and jumping, and generally elongated bodies to minimize the friction with the substrate (Vanhooydonk & Van

Damme 1999, Aerts et al. 2000, Herrel et al. 2002). However, tree dwellers or climbers should have relatively short limbs, with low shank-to-thigh ratios and equally long hind limbs and forelimbs, and relatively wide and flat bodies to keep their centre of mass close to the substrate (Ricklefs et al. 1981, Pianka 1986, Miles 1994, Vanhooydonk & Van Damme 1999). Thus, fast running species that live in open habitats should have long hind limbs and short forelimbs, with a shank to thigh ratio that is greater than that of climbing species with short fore and hind limbs (Pianka & Pianka 1976, Garland & Losos 1994). And body shape of the terrestrial species should be laterally compressed versus climbing species' dorso-ventrally flattened bodies.

Tails are functionally critical and versatile, serving primary roles in locomotion, balance and sexual display (Gillis et al. 2009). Additionally, the tail augments in-air stability during jumping (Gillis et al. 2009), acts as a counter balance to increase running speed in ground-dwelling species, and is used for balance while climbing in arboreal lizards (Ballinger & Tinkle 1979).

Another highly specialized trait characteristic mainly in *Anolis* lizards is the presence of specialized enlarged subdigital scales (lamellae) that fa-

cilitate climbing on vertical substrates. Consequently it could be expected that climbing lizards have more or broader lamellae than terrestrial lizards. As mentioned above, these simple biomechanical predictions have been confirmed by some, but not all, studies of lizard locomotion (Collette 1961, Moermond 1979, Losos & Sinervo 1989, Irschick et al. 1997, Bickel & Losos 2002). The general assumptions of ecomorphological studies to express that these measurements are ecologically-relevant aspects of the organisms under study (Arnold 1983, Hertz et al. 1988, Losos 2009, Garland & Losos 1994, Melville & Swain 2000, Goodman et al. 2008). Many authors have stressed that morphological differences may account for the diversity in locomotor behavior exhibited by many species, because living in different habitats may result in morphological differentiation (Arnold 1983, Rewcastle 1983, Lauder & Reilly 1991, Blob 2001).

Anolis is a predominantly Neotropical genus of nearly 400 species. It is widely distributed from the Caribbean to Central and South America (Losos 2009, Klütsch et al. 2007). On each major island in the Caribbean, different morphological groups, called "ecomorphs", have convergently diversified resulting in species that occupy a set of ecological niches. In the last decades, most of the ecomorphological studies (Irschick et al. 1997, Jackman et al. 1997, Velasco & Herrel 2007, Pinto et al. 2008, Johnson et al. 2009, Losos 2009, 2010, Mahler et al., 2010) have focused on *Anolis* of the Greater Antilles, and information about the ecology and behavior of mainland species is relatively scarce. Interestingly, the ecomorphological relationships among Costa Rican anoles are different from those described for Caribbean species (Losos 2009). Even more surprising, mainland anoles do not appear to fit into the same ecomorph categories as those observed in Greater Antillean *Anolis* lizards (Velasco & Herrel 2007, Pinto et al. 2008, Losos 2009, 2010).

This relationship between locomotor performances has been acquired through the study of Caribbean *Anolis*, and their ecomorphs; therefore, the information regarding other groups of lizards is necessary, mainly in mainland *Anolis*. Given the paucity of ecological and behavioral information on mainland anoles, the goal of this work was to investigate whether morphological variation among mainland anoles correlates with differences in ecology. This will allow testing of the hypothesis that habitat use is reflected in limb mor-

phology, even if the nature of their relationships is different between mainland and Caribbean anoles. Specifically, the present study evaluated the relationship between morphology and microhabitat use in two sympatric mainland species, *Anolis humilis* and *A. limifrons*, both of which are beta anoles (Etheridge 1959).

Anolis humilis is a diurnally active lizard, found in leaf litter, low vegetation, and on tree trunks, up to 1 m high (Talbot 1976). They are usually seen facing downward on the lower trunk of a tree. *Anolis limifrons* is also diurnal, and usually found on vegetation in the forest understory, on leaves or on trees, and have been seen leaping from perch to perch. On tree trunks they are seen facing upwards about two meters above the ground. Both species have relatively small territories and low dispersal rates (Talbot 1976).

Materials and methods

Study site

The study was carried out at the La Selva Biological Station (10° 26' N, 83° 59' W), located approximately 2 km east of the town of Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica during February and March of 2007. The station comprises 1,600 ha of tropical wet forests and disturbed lands. A total of 91 lizards, 52 *A. humilis* and 39 *A. limifrons*, were captured randomly by hand during their normal activity period. Lizards were transported to the laboratory where they were measured. Lizards were marked with white paint on the fourth toe of the right foot and the base of the tail (dorsal side) to avoid replication, and released at the place where they were captured. These species were selected because they were observed in wooded habitats at La Selva, Costa Rica, and these similar-sized anoles occupied two largely separate vertical zones (*A. limifrons* above *A. humilis*) (Talbot 1976, 1979, pers. obs.). Also, because the population densities of *A. humilis* and *A. limifrons* were higher here than those of other species of *Anolis*, this allowed the researchers to manipulate them at their discretion. They were captured randomly along the Three River Road for 500 meters until the cacao groves. This area was designated for research programs by OTS, as the grid arrangement and even spacing of cacao trees were useful in establishing a randomized design allowing independent observations of anole activities. For both species, only adult males were included in morphology assays to minimize the confounding effects of intraspecific allometric and sexual variation.

Morphological measurements

For each specimen, 13 external variables were measured with digital calipers (Mitutoyo CD-15B; ± 0.01 mm): snout-vent length (SVL), maximum body width (BW), interlimb length (ILL: distance between limbs), maximum head width (HW), head length (HL: from the anterior border of

the external auditory meatus to the tip of the snout), humerus length (LH), antebrachium length (AL), manus length (ML), thigh length (TL), shank length (SL), length of the longest toe of the hind limbs (T4), tail length (LT: from vent to tail tip), and tail width (WT: at the base of the tail). Forelimb length (FLL) was recorded as the sum of the humerus and antebrachium lengths and hind limb length (HLL) was considered as the sum of the thigh and shank lengths. All measurements were taken on the right side of the specimens. In the field the lizards were recorded as ground dwellers if they were observed on the ground and as arboreal if they were observed on tree trunks (Talbot 1976, 1979, Velasco & Herrel 2007).

Statistical analysis

All morphometric variables were \log_{10} -transformed prior to analyses to meet requirements of normality (Zar 1999). Student test of independent samples by grouping was performed to determine if differences in SVL among species existed. The total tail length of lizards with broken or regenerated tails was estimated by using a species-specific linear regression relating tail length to SVL, obtained from lizards with intact tails. To reduce the dimensionality of the morphological data, a Principal Component Analysis (PCA) was conducted. To reduce the dimensionality of morphological space, the remaining morphological variables that were significant in the PCA were analyzed using a multivariate analysis of covariance (MANCOVA), using as categorical variables the habitat use, and continuous variable the SVL. Then, a False Discovery Rate (FDR) was performed to determine which means are significantly different from one another. This method increases the chances for detecting significant differences when multiple tests are applied simultaneously and tend to larger Type I error (Weller et al. 1998, Benjamini & Yekutieli 2001). This test was performed with R software (version 2.14.0 (2011)). Additionally, three variables important in locomotion (Garland & Janis 1993) were calculated: 1) a Reduced Major Axis Regression (RMA) of forelimb length against hind limb length (both \log_{10} -transformed), 2) a residual of regression major axis of shank on thigh and 3) antebrachium on humerus. Basic statistical methods were applied using the Statistica 6.0 (StatSoft Inc. 2001) statistical package and Software for Reduced Major Axis Regression (RMA, Bohonak & van der Linde 2004). Differences were considered significant if $p < 0.05$.

Results

For each species, Table 1 lists number of individuals used and the means and standard error of the morphological traits. There were no significant differences between species in SVL (t-value= 0.61; df= 89; $p < 0.54$). The PCA on morphological variables extracted two axes that together explained 88.76 % of the variation (Table 2). The first PC axis (74.02% of total variation) shows high and negative loads with all variables. The second PC axis

(14.74 % of total variation) showed high and positive loads with LH and AL. The PCA described a contrast between tail length and variables that describe the forelimbs (e.g. ML, LH and AL). *Anolis limifrons*, with long tails is at one end of this axis, whereas *A. humilis*, with largest manus, largest humerus and antebrachium, is positioned at the opposite end of this axis (Fig. 1). The traits that affected the second PC axis were mainly related to the forelimb, i.e. *A. humilis* had longer forelimb elements (e.g. humerus and antebrachium). The PC2 axis contrasted longer tails and shorter manus in *A. limifrons* with longer forelimbs in *A. humilis* (Fig. 1). Thus, the loading for the first two axes describes morphological traits that covary contrary to predictions by theoretical studies (Table 2). The

Table 1. Means and standard errors of morphological traits for each *Anolis* species.

Variables	<i>A. humilis</i> (N =52)	<i>A. limifrons</i> (N =39)
Snout-vent length	29.82±10.47	32.37±12.22
Tail	41.17±18.66	60.01±26.12
Tail width	1.56±1.59	1.816±1.54
Head length	8.59±3.07	9.32±3.10
Head width	5.27±1.97	5.04±1.87
Body width	6.27±2.63	5.42±2.64
Thigh length	8.05±2.99	9.03±3.47
Shank length	7.38±2.57	8.33±3.05
Antebrachium length	4.18±1.85	4.60±1.87
Humerus length	2.59±2.60	3.58±3.06
Fourth toe of pes	5.90±2.63	6.88±2.87
Manus length	0.69±0.72	0.82±0.76
Distance between limbs	6.14±6.74	8.03±7.22

means for *A. limifrons* and *A. humilis* were significantly different. The scores from each PC axis were used in a one-way ANOVA with microhabitat use as the main effect. The means for *A. limifrons* and *A. humilis* differed only on the first axis (PC1 $F_{(1, 89)} = 4.08$, $p = 0.04$; PC 2 $F_{(1, 89)} = 1.75$, $p = 0.18$; PC3 $F_{(1, 89)} = 1.23$, $p = 0.26$), illustrating that *A. limifrons* was significantly different from *A. humilis* along the first axis only. Conventional multivariate analysis of the covariance (MANCOVA) on selected variables demonstrated differences between arboreal and terrestrial species ($\lambda = 0.18$, $F_{(13, 76)} = 25.03$, $p < 0.00$). Only three variables (TW, BL and ILL) did not show significant differences with respect to microhabitat use. The FDR test demonstrated that both groups showed significant differences for all variables analyzed (q-values < 0.005).

The RMA regression of forelimb length against hind limb length showed that hind limbs

Table 2. Component scores resulting from a Principal Component Analysis (PCA) performed on the morphological traits. All traits were log-transformed, and effects of body size were removed prior to analysis by computing residuals from regressions on SVL (except for SVL itself). Traits contributing most to each component are indicated in bold. The total amount of variance in the data explained by these first two principal components is 88.76%.

Character	PC1	PC2
SVL	-0.98751	-0.071134
Tail	-0.75292	-0.340289
BT	-0.94410	-0.152435
HL	-0.96811	-0.076690
HW	-0.98193	-0.004984
BW	-0.88581	-0.089142
TL	-0.98745	-0.085262
SL	-0.98211	-0.034197
LH	-0.32901	0.915308
AL	-0.34803	0.895590
IL	-0.97164	-0.028695
ML	-0.57447	0.493363
T4	-0.96311	-0.115418
Eigenvalues	10.36	2.06
Var Exp Cum %	74.02	88.76

are longer than forelimbs in both species (Table 3, Fig. 2). The RMA regression of antebrachium length against humerus length in both species suggested high antebrachium to humerus ratios. The RMA regression of shank length against thigh length in both species showed high shank: thigh ratios (Table 3).

Discussion

In general terms, species of this study show some consistent relationships between life style (climbing versus cursorial) and relative body dimensions. Contrary to expectations, the arboreal species has some traits (longest head, tail, hind limbs and fourth toe) that allow them to climb a vertical surface, while terrestrial species have the longest forelimbs (humerus, antebrachium, and manus), widest head, and body. This agrees with other studies (Irschick et al. 1997, Velasco & Herrel 2007) that stress that ecomorphological patterns found in mainland anoles differ from those in Caribbean habitats. Why arboreal species have longer limbs than terrestrial species is unclear. Considering the disagreement of these different comparative studies on the relationship between morphology and habitat use, it appears that the degree of these relationships and the features involved depend on

the taxonomic level and the taxonomic group (Zaaf & Van Damme 2001) and the features taken into account.

Table 3. Regressions of the major axis of the \log_{10} of the variables important in locomotion: forelimb length against hind limb length, shank length on thigh length and antebrachium length on humerus length. FLL: forelimb length, HLL: hind limb length, AL: antebrachium length, LH: humerus length, SL: shank length, TL: thigh length.

Variables (\log_{10})	$\log b_0$	$\log b_1$	SE	R ²
FLL/HLL	.010	0.897	0.01	0.975
AL/LH	-0.05	1.031	0.02	0.928
SL/TL	-0.01	1.06	0.01	0.976

According to this study, the ground-dwelling species was seen on the trunks of trees (Talbot 1976, 1979, pers. obs.) and its long legs are employed for hopping on the forest floor or for running swiftly about on the ground. Shorter forelimbs of the arboreal species lets them move more slowly in the trees than the terrestrial species do on the ground. Terrestrial species that are fast running and live in open habitats should have long hind limbs with short forelimbs, with a shank to thigh ratio that is greater than that of climbing species with short fore- and hind limbs (Pianka & Pianka 1976, Garland & Losos 1994). Moreover, the length of the whole limb (including femur and tibia) length is relevant in most of the ecomorphological studies undertaken thus far (Losos 2009, Miles 1994, Bauwens et al. 1995, Bonine & Garland 1999, Bauer et al. 1996, Higham & Russell 2010).

The body shape of the terrestrial species should be laterally compressed versus climbing species' dorso-ventrally flattened bodies. Interestingly, a ground-dwelling lizard, *A. humilis*, showed wider bodies, a trait that allows them to climb broad surfaces such as tree trunks (see text above) because it brings the center of mass close to the substrate. In contrast, *A. limifrons* is able to climb trees and twigs, and an elongated body helps them to avoid falling by placing the body alignment to the habitat; additionally, this trait allows them to enhance stability (Gillis et al. 2009).

A much longer tail seems to be correlated with its use as a balancing organ, as *A. humilis* hops along the forest floor, or for use as a prop in climbing. The tail is adapted for holding up in the air as a balancing organ while the lizards hop (Collette 1961). On the contrary, *A. limifrons* that use verti-

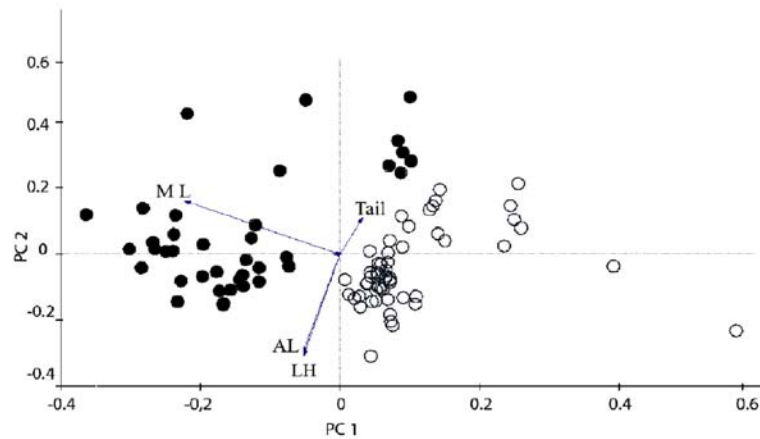


Figure 1. Distribution of two species of *Anolis* lizards in morphological space. The PCA used residuals of the regression between morphological variables and body size. The symbols indicate microhabitat use: dot white corresponds to species from arboreal habitats *Anolis limifrons*, and dot black species that use terrestrial habits *Anolis humilis*. TL: tail length, ML: manus length, AL: antebrachium length, LH: humerus length.

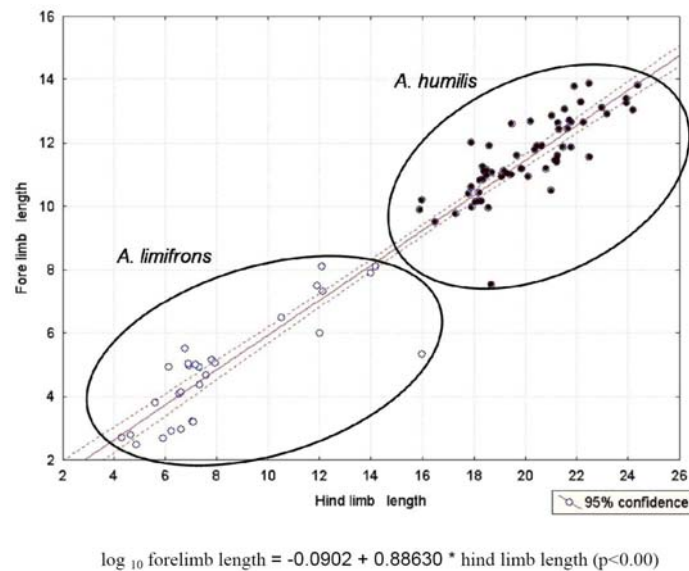


Figure 2. Simple linear regression (least squares) from \log_{10} forelimb length against \log_{10} hind limb length. The symbols indicate microhabitat usage: dot white corresponds to specimens from arboreal habitats, dot black species that use terrestrial habits. Graphic shows the model and the significance (b_0 and b_1) according to linear regression.

cal habitats tend to have long tails, which may enhance maneuverability (Ricklefs et al. 1981, Pianka 1986, Miles 1994, Vanhooydonck & Van Damme 1999).

The covariation pattern appears to be consistent with the predictions for adaptations to differ-

ent modes of life (arboreal vs. terrestrial). The fore- and hind limbs in lizards have differential roles during vertical versus horizontal movements (Zaaf et al. 2001a). Forelegs that mainly function to support body weight during level running provide propulsion and pull the body toward the sur-

face during climbing (Zaaf et al. 2001a). Hind legs that support weight during level running show a reduction of the normal forces by one-sixth during climbing (Autumn et al. 2006). These data indicate that the role of the forelimb should not be underestimated when climbing is considered.

Thus, this study identified multiple traits that suggest divergent morphological and habitat characteristics. The morphological differences suggested that the arboreal lizard *A. limifrons* have longer tails and hind limbs (including fourth toe), whereas a longer manus, wider body and long forelimbs are more common in the ground-dwelling species, *A. humilis*. These morphological characteristics may allow climbing lizards to keep their centre of mass close to the substrate, while in terrestrial lizards they would enhance maneuverability and support weight during level running. However, more studies are needed to understand the causes for the independence of evolutionary trajectories on the mainland and the Greater Antilles, and to obtain a better understanding of the ecological and evolutionary processes underlying the radiation of these faunas.

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