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GEOGRAPHIC BODY SIZE AND SHAPE VARIATION IN A MAINLAND *Anolis* (SQUAMATA: DACTYLOIDAE) FROM NORTHWESTERN SOUTH AMERICA (COLOMBIA)

Variación geográfica en tamaño y forma corporal en un *Anolis* (Squamata: Dactyloidae) continental del noroeste de Suramérica (Colombia)

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ABSTRACT

Anolis auratus is a widely distributed species, from Costa Rica in Central America, through northern South America, including Colombia, Venezuela, northern Brazil, Surinam and the Guyanas. In Colombia, its widespread distribution across different life zones suggests that these lizards occupy different environments and exhibit different microhabitat use in different geographic areas. On the other hand, some observations suggest that this species prefers open areas, selecting grasslands over brushy areas, and thus, an alternative hypothesis is that microhabitat use is similar among different populations. In *Anolis*, body variables related to locomotion (body size and shape) define structural microhabitat use, so two distinct patterns could be expected in this species: conservative or highly variable body size and shape throughout the species distribution. To test these predictions, we characterized geographic variation in morphometric traits of this species in Colombia. Females and males were similar in body size, but exhibited differences in some variables related to body shape. These characteristics also varied among males and females from different regions, suggesting heterogeneous use of structural microhabitat, between sexes and among populations. As an alternative, phylogenetic divergence among populations could also account for the observed differences. Absence of ecological and phylogenetic data limits our ability to identify the underlying causes of this pattern. However, we provide a general framework to explore hypotheses about evolution of body size and shape in this species.

Keywords: *Anolis auratus*, geographic variation, microhabitat use, morphometric variables.

RESUMEN

Anolis auratus se distribuye desde Costa Rica en Centro América, el norte de Sur América, incluyendo Colombia, Venezuela, norte de Brasil, Surinam y las Guyanas. En Colombia, su amplia distribución en distintas zonas de vida sugiere que estos lagartos ocupan distintos ambientes, y por tanto, posiblemente exhiben variación geográfica en el uso de microhabitat. Por otra parte, algunas observaciones sugieren que estos lagartos prefieren zonas abiertas, seleccionando pastizales y por tanto, una hipótesis alternativa es que usan el mismo microhabitat en toda su distribución. En *Anolis*, las variables corporales relacionadas con el movimiento (tamaño y forma corporal) definen el uso del microhabitat, así que pueden esperarse dos patrones en esta especie: tamaño y forma corporal conservativos o altamente variables a lo largo de su distribución. Caracterizamos la variación geográfica en variables morfométricas de esta especie en Colombia. Hembras y machos mostraron tamaño corporal similar, pero fueron distintos en la forma del cuerpo. La forma corporal varía también en machos y hembras de distintas regiones, sugiriendo un uso heterogéneo del microhabitat estructural. Como alternativa, la divergencia filogenética entre poblaciones podría explicar las diferencias observadas. La ausencia de datos ecológicos y filogenéticos para la especie limita las hipótesis sobre causas de este patrón. Proveemos un marco general para explorar hipótesis que expliquen la evolución de tamaño y forma corporal en esta especie.

Palabras clave: *Anolis auratus*, uso del microhábitat, variación geográfica, variables morfométricas.

INTRODUCTION

Anolis lizards represent one of the best few documented adaptative radiations in vertebrates (Losos *et al.*, 1997; Losos *et al.*, 2006; Losos *et al.*, 2007). High morphological diversification in Caribbean species of this genus involves convergent evolution of body variables, which are associated with ecological and behavioral characteristics, and together define ecomorphs (Williams, 1972; Losos, 2009). The convergent habitat specialists, (i.e. ecomorphs), are denominated according to structural microhabitat each mostly uses: Crown lizards, trunk-crown, trunk, trunk-ground, grass-bush and twig anoles (Losos, 1990, Losos, 2009; Irschick *et al.*, 1997). These Caribbean ecomorphs are not generally represented in mainland anoles, which apparently have been influenced by different selective and historical factors (Irschick *et al.*, 1997; Macrini *et al.*, 2003; Velazco and Herrel, 2007; Pinto *et al.*, 2008; Losos, 2009; Shaad and Poe, 2010). This would explain why Caribbean ecomorphs are usually not observed in mainland environments, and suggests that eco-morphological relationships in mainland species show different patterns than those described for island anoles.

Structural microhabitat use, that is, type of vegetation most frequently used by *Anolis* lizards, is associated with lizard body size and shape and digital lamellae number and size, variables that determine optimal locomotion performance (Losos, 1990; Losos and Irschick, 1996; Irschick and Losos, 1999; Elstrott and Irschick, 2004; but see Irschick, 2002). Then, exploring variation in morphological traits involved in locomotion within a widespread species inhabiting heterogeneous environments may be useful to understand mechanisms and processes driving evolution of body size and shape in these lizards. Morphometric variation in these species ranged from very low in Amazonian *A. fuscoauratus*, which can be related to shallow genetic divergence, to very high in Andean anoles (e.g. *A. ventrimaculatus*) potentially related to differences in microhabitat use (Calderón-Espinosa *et al.*, 2012). Here we explore the morphological variation of a widely distributed mainland species, *Anolis auratus*.

Anolis auratus is a lowland species that ranges from Costa Rica to Ecuador, northern Brazil, Surinam and French Guyana (Avila-Pires, 1995). In Colombia, this species exhibit a widespread distribution at both sides of the Andean system (Ayala, 1986; Sánchez *et al.* 1995) and thus, it is potentially exposed to a wide range of microhabitats and then, might exhibit different microhabitat use. Despite being a relatively common anole, there is no detailed information about intraspecific variation in morphological traits related to microhabitat use. We provide a description of geographic patterns of morphometric variation in this species, in order to propose some preliminary hypothesis about factors shaping body size and shape characteristics that apparently determine structural microhabitat use in this anole.

METHODS

We obtained morphometric data from 217 adult (>40 mm snout vent length, SVL) individuals of *Anolis auratus* from the Reptile Collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN-R). Females (n = 86) and males (n = 131) were identified based on presence or absence of dewlap, or post-anal scales characteristic of males. We defined six geographic groups based on spatial distribution of samples (Appendix 1), using potential geographic barriers (river systems, mountain ranges) to determined these groups. Each group contained lizards collected over an altitudinal range of 1-1234 m.a.m.s.l. (Appendix 1).

We collected data on 17 variables from each individual, using a digital caliper (±0.1 mm precision). Variables were as follows: snout vent length (SVL), trunk length (TkL), tail length (TL), humerus length (HL), ulna length (UL), hand length (HnL), IV finger length (FgL), femur length (FL), tibia length (TbL), foot length (FtL), IV toe length (ToL), pelvis height (PH), pelvis width (PW), head length (HeL), head height (HeH), head width (HeW), mouth length (ML), lamellae width (LW) and lamellae number (LN). See Pinto *et al.* (2008) for variable descriptions.

Sexual size dimorphism (SSD) was evaluated at the species level and within four populations with large enough sample sizes (Table 1). These populations represened four of the six geographic groups included in the other analyses. In both cases, we used Mann-Whitney non-parametric tests.

We also compared body shape between males and females at the species level, and within these four populations; in this case, we used residuals from regression analyses of each log variable against log SVL. We first eliminated redundant correlated variables by Principal Component Analyses (PCA). Then, we performed a Discriminant Function Analysis (DFA) at the species level. Significant variables identified by DFA were compared within each population by univariate non-parametric tests.

Table 1. Sexual dimorphism in *Anolis auratus*. Variables with significant differences between sexes at each locality are accompanied by superscript numbers (groups). Average ± (Standard deviation). Values are given in mm.

	Magdalena (Group 1)		Cordoba (Group 2)		Santander (Group 5)		Meta (Group 6)	
	Females	Males	Females	Males	Females	Males	Females	Males
SVL	50.59 (4.40)	53.49 (3.54)	45.72 (2.69)	48.01 (3.45)	46.28 (2.38)	43.87 (3.45)	46.86 (2.27)	42.19 (1.47)
TkL1,2,5,6	22.96 (2.63)	22.91 (1.68)	18.76 (1.58)	18.53 (1.97)	21.42 (2.25)	17.95 (1.47)	20.80 (1.95)	17.58 (1.00)
PW6	6.29 (1.08)	6.47 (0.59)	5.47 (0.48)	5.06 (0.40)	5.27 (0.54)	4.28 (0.30)	5.46 (0.65)	4.46 (0.39)
FL	9.08 (1.61)	10.93 (1.26)	8.67 (0.83)	9.52 (0.87)	8.45 (1.06)	8.79 (0.74)	8.66 (0.49)	7.96 (0.56)
TL	9.93 (0.79)	10.84 (0.93)	9.99 (0.61)	10.08 (0.90)	9.40 (0.73)	8.93 (0.79)	8.78 (2.28)	7.93 (0.74)
ToL1	9.61 (0.96)	10.68 (0.76)	8.61 (0.94)	9.15 (0.91)	9.16 (0.49)	9.38 (0.73)	8.49 (0.52)	7.93 (0.91)
HeL2	12.03 (0.92)	12.86 (0.98)	11.03 (0.47)	11.77 (0.82)	11.26 (0.34)	10.51 (0.81)	11.2 (0.42)	10.43 (0.39)
HeH2,6	5.94 (0.61)	6.56 (0.55)	5.44 (0.40)	6.04 (0.55)	5.28 (0.51)	5.13 (0.46)	5.07 (0.36)	4.97 (0.22)
HeW5	6.87 (0.69)	7.17 (0.63)	6.46 (0.47)	6.63 (0.45)	6.62 (0.28)	5.94 (0.39)	6.50 (0.18)	6.02 (0.24)
ML	9.84 (1.17)	10.02 (1.41)	9.46 (0.48)	10.16 (0.75)	9.02 (0.55)	8.64 (0.69)	9.26 (0.18)	8.63 (0.39)

We characterized body size (SVL) variation among geographic groups using Kruskal-Wallis tests.

Since males and females showed some degree of body shape dimorphism, we compared morphometric variables among groups or regions for each sex independently, through PCA and DFA. ANCOVA tests (SVL as covariate) were implemented to evaluate the direction of variation in variables detected as significant by DFA. Samples from group four (Antioquia and Tolima) were excluded from these comparisons due to the small sample size of this group.

All data were log10 transformed before statistical analyses in order to normalize distributions. We evaluated normality and homocedasticity for all data sets. Although SVL data were normalized after log10 transformation, homogeneity of variances test was significant and then, we analyzed this variable through non-parametric tests.

Statistical test were performed with Statistica Vr. 8, StatSoft.

RESULTS

Sexual Dimorphism

Males and females exhibited similar body sizes overall (Z = -1.093, $p = 0.2743$, 86 females, 131 males) and within each population ($p > 0.1$ in all cases, except $p = 0.039$ for Cis-Andean group) (Table 1).

Based on PCA analyses including all body shape variables and lamellae number (after correcting for the SVL effect on each variable) we selected nine: trunk length, pelvis width, mouth length, head length, head width, head height, femur length, tibia length and IV toe length, which appear non-correlated and IV toe length, from others that appear correlated and then might be redundant. These variables were contrasted between sexes, at the species level through DFA and within each population by Mann-Whitney tests. Males and females exhibited sexual shape dimorphism at the species level (Wilks' Lambda: 0.607 approx., F (9,207) = 14.84344, $p < 0.001$). Significant variables identified in DFA were trunk length, pelvis width and head height. Classification success was 70-86 % in females and 64-72 % in males. ANCOVA tests (with SVL as the covariate) indicated that trunk and pelvis were larger in females, and head height was larger in males ($p < 0.05$). Dimorphism also was observed within each population, with some minor differences among populations, although sexes were dimorphic in trunk length in all of them (Table 1).

Geographic Morphometric Variation

Body size (males + females) varied among geographic groups (Kruskal-Wallis test: $H_{4,209} = 45.80247$ $p < 0.01$), with individuals from group six (eastern Andes) being the smallest, and individuals from the Caribbean region (groups one and two) and mid-Magdalena valley (group four) being the largest. Geographic variation of body shape and lamellae number for females and males was detected, particularly among some geographic groups. According to PCA analysis, 70 % of the variation was explained by eight components in both, females and males, which might suggest that differentiation among groups involved many variables. However, based on DFA (including the nine variables selected based on PCA analyses) we found that differences among geographic groups were significant (DF function for females: Wilks' Lambda: 0.42896 approx. F(36,260) = 1.8323 $p < 0.0040$; and males: Wilks' Lambda: 0.52486 approx. F(36,428) = 2.2365 $p < 0.0001$, (Fig. 1A, B). Variables involved in these differences were, for females: trunk and tibia length, and for males: trunk, femur and tibia length, pelvis width and head height (Tables 2 and 3). Classification success was (8-67 %) for males, and (14-73 %) in females; in both cases highest classification success (over 61 %) was observed for the Caribbean groups (one and two). Distance between groups indicates that patterns of variation are different for males and females. The most divergent female geographic groups were groups 2 (Western Caribbean) and 3 (Western Cordillera). In contrast, males from group 1 (Eastern Caribbean) and 5 (Eastern Cordillera) exhibited the greatest divergence.

Table 2. DFA for females. Significant differences among regions ($p < 0.05$) appear in bold.

Variable	Wilks'	Partial	F-remove	p-level	Toler.	1-Toler.
TkL	0,492297	0,871339	2,547119	0,046985	0,823646	0,176354
PW	0,465703	0,921098	1,477657	0,218442	0,856122	0,143878
FL	0,471918	0,908967	1,727587	0,153807	0,848854	0,151146
TL	0,492209	0,871495	2,543584	0,047229	0,745103	0,254897
ToL	0,462528	0,927419	1,350013	0,260368	0,768189	0,231811
HeL	0,477789	0,897798	1,963684	0,109741	0,610683	0,389317
HeH	0,458273	0,936031	1,178874	0,327796	0,73062	0,26938
HeW	0,464541	0,923401	1,430937	0,233018	0,770725	0,229275
ML	0,431806	0,993403	0,114558	0,976975	0,970154	0,029846

Table 3. DFA for males. Significant differences among regions ($p < 0.05$) appear in bold.

Variable	Wilks'	Partial	F-remove	p-level	Toler.	1-Toler.
TkL	0,573442	0,91528	2,638019	0,037512	0,973842	0,026158
PW	0,577147	0,909404	2,839221	0,027478	0,877805	0,122195
FL	0,570299	0,920324	2,467348	0,048782	0,80923	0,19077
TL	0,600067	0,874668	4,083797	0,003944	0,784119	0,215881
ToL	0,554868	0,945918	1,629448	0,171634	0,93256	0,06744
HeL	0,5361	0,979033	0,610372	0,655993	0,777235	0,222765
HeH	0,587102	0,893983	3,379788	0,011845	0,782324	0,217676
HeW	0,534744	0,981517	0,536691	0,709047	0,78595	0,21405
ML	0,543767	0,96523	1,026649	0,396683	0,900405	0,099595

DISCUSSION

Sexual Dimorphism

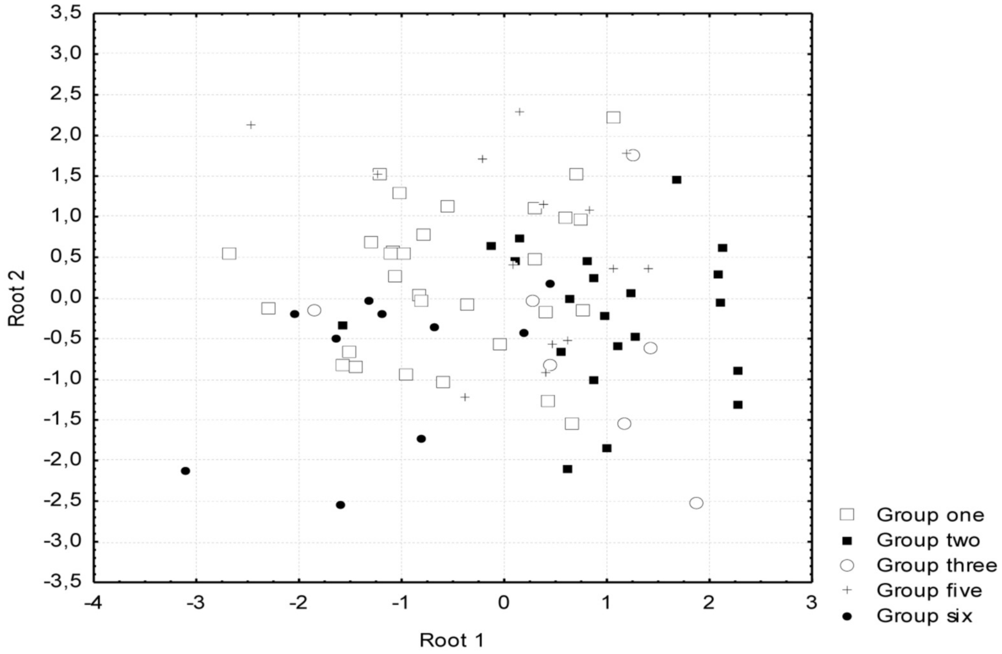
Patterns of sexual size dimorphism (SSD) vary among *Anolis* species (Butler *et al.*, 2000). For Antillean anoles, degree of size dimorphism is correlated with ecomorph type, with trunk-ground and trunk-crown species exhibiting the greatest differences between sexes, while trunk, crown-giant, grass-bush, and twig anoles exhibit low levels of SSD. The results also suggest that patterns of SSD are different between mainland *vs.* caribbean species, with males of many mainland species being smaller than females (Fitch, 1976, 1981 in Losos, 2009). However, considerable variation exists within mainland species, from species with strong male-biased or female-biased dimorphism, to species similar in size (Vitt *et al.*, 2003; Bock *et al.*, 2009; Steffen, 2009; Calderón-Espinosa *et al.*, 2010). SSD pattern in mainland *Anolis* is not explained by Rensch's Rule; it is, SSD increases with body size where one sex is consistently the larger sex (Steffen, 2009).

The absence of sexual size dimorphism in *A. auratus* suggests that feeding habits or structural microhabitat use are similar in both sexes, and that male interactions to access females are not determined by male body size, since those are the main factors that usually explain differences in body size in lizards (Butler *et al.*, 2000; Losos, 2009).

However, males and females of this species have different body shape, involving mainly trunk length, pelvis width and head variables. Dimorphism in trunk length is explained by differences in the reproductive role, with females exhibiting larger trunks to carry eggs (Trivers, 1976; Olsson *et al.*, 2002). Similarly, sex differences in pelvis width (wider in females) might be due to reproductive role, with wider pelvis required for oviposition, as suggested from studies on *A. carolinensis*, where egg mass varied among localities and was related to pelvis width (Michaud and Echternacht, 1995). Finally, variation in head dimensions might suggest differences in prey size or prey hardness (reviewed in Vincent and Herrel, 2007). It may also be explained by male-male competitive interactions, since bite force is important during these interactions (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005) and head size has been related to bite force in lizards (Herrel *et al.*, 1999, 2001a, b). Males of *Anolis auratus* are strongly territorial (Fleishman, 1988a; Fleishman, 1988b).

On the other hand, geographic variation in shape dimorphism might be explained by differences in sample size or could be a result of real variation in selective or sexual pressures that generate a mosaic pattern of dimorphism. Butler and Losos (2002) found in some Antillean species that sexual shape dimorphism varied among ecomorphs, and suggested that

A



B

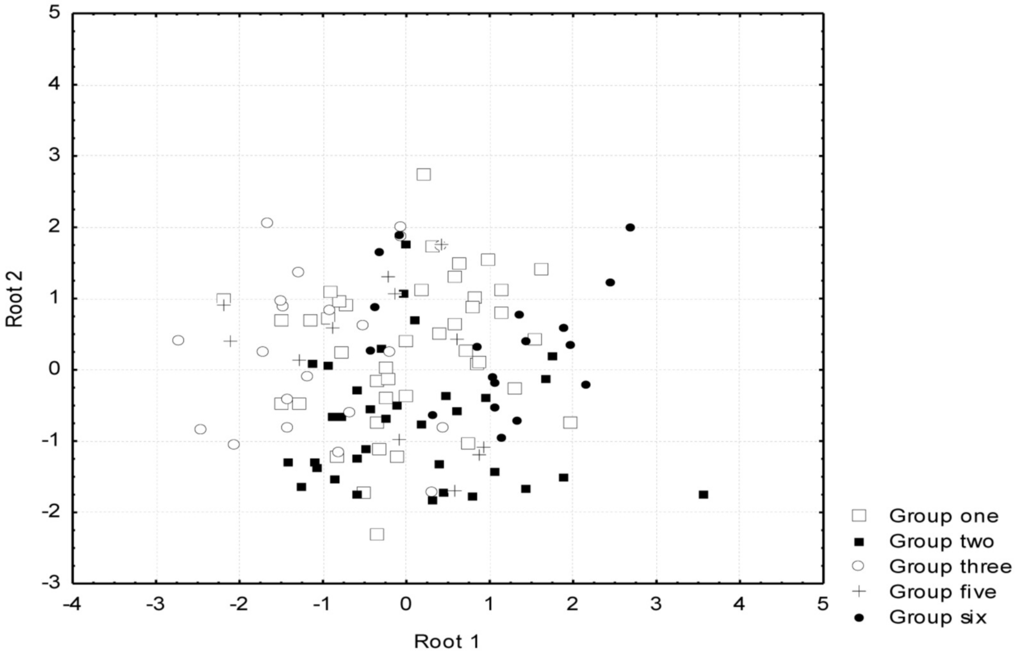


Figure 1. A. DFA females. B. DFA Males.

different selective pressures (natural or sexual) could operate differently among habitats. Most populations of *A. auratus* exhibited dimorphism in trunk length and variables related to head dimensions, except for population one (Magdalena), that displayed sexual differences in trunk and toe length, but not in head variables. This minor variation could be related to small sample size for each locality, but since most localities exhibited the species level pattern of shape dimorphism (larger trunk in females and larger heads in males), we consider that potential variation in selective pressures affects body shape differentially in males and females and should be explored within this species.

Geographic Variation

Individuals of *Anolis auratus* exhibited differences in body size among geographic groups. Smaller lizards were recorded throughout eastern Andes localities, and larger lizards in the Caribbean region. Geographic body size variation may be due to several ecological and/or historical factors in this species. Environmental variables have been linked to variation in lizard body size (Anguilleta, 1998; Horváthová *et al.*, 2013). For instance, microgeographic body size variation in *A. mariarum* appears to be due to differences in precipitation levels among localities (Bock *et al.*, 2009). Similarly, the relationship between body size and precipitation may be a consequence of productivity levels, as suggested for Tropidurine lizards (Brandt and Navas, 2013). Variation in lizard body size, particularly in females, also may be related to differential selective regimens on hatchling size, as suggested for *A. carolinensis* (Michaud and Echternacht, 1995). Intraspecific variation in island anoles has been correlated to geographic differences in habitat, and then, is explained by differential effects of natural selection forces (Malhorta and Thorpe, 1991a, b; Malhorta and Thorpe, 1994; Malhorta and Thorpe, 1997). Then, within species variation in *A. auratus* might also be a response to different selective regimens through its distribution.

It is noteworthy, however, that body size extremes within *A. auratus* involved populations separated by the Andes. This pattern might reveal possible historical factors as causal agents of this variation, an aspect that also could affect variation in other morphometric characteristics in this species. Smaller body size of *A. carolinenesis* from Florida also has been related to historical factors of isolation and local body size adjustments (Goodman *et al.*, 2013).

Pattern of body shape variation was different for males and females, with variation in both sexes being only marginally significant, as suggested by low values of assignation probabilities derived from DFA. We suspect this result is due to the low sample size for some geographic groups, where we obtained the lowest assignation values. If historical factors (represented here as potential physical barriers separating geographic groups) were the main factor accounting for morphometric variation observed within *A. auratus*, variation in both males and females would have exhibited a similar geographic pattern. In contrast, our results suggest that differences in body shape observed among geographic groups of this species might be explained by differential microhabitat use (variation in limb lengths in both sexes, and pelvis width in males), differences in the reproductive output in females (variation in trunk length), and in prey size and male-male interactions (differences in head height). However, variation in some of these traits also might be influenced by phylogeny (Poe, 2005), and it would be desirable to evaluate the pattern observed within a phylogenetic framework.

Finally, our results do not support the hypothesis of similar structural microhabitat use for this “open area”-dwelling lizard, if we assume that there is a strong link between body dimensions and optimal performance in structural microhabitat in *Anolis* species, and that open habitats offer similar structural microhabitats throughout the species distribution. However, the absence of ecological, behavioral and phylogenetic data for this species limits our ability to draw conclusions about the factors and processes underlying body size and shape evolution within this taxon.

CONCLUSIONS

Populations of *Anolis auratus* distributed throughout Colombia exhibit geographic variation in body size and shape, with males and females exhibiting different patterns. Potential differences in microhabitat use could explain minor differences in body shape; however, ecological and phylogenetic data are needed to test this hypothesis in a phylogenetic framework.

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Appendix 1. Geographic groups of *Anolis auratus* included in this study.

Group	Geographic distribution	Altitudinal range in m.	Vouchers (ICN-R, FBA, JDL, MLC, POE)*
1	Cesar, Guajira, Magdalena (Eastern Caribbean)	56 - 290	ICN-R: 2338-2342, 2345, 2348-2350, 2355-2358, 2360, 3832-3838, 3840-3843, 3845, 3848-3851, 3853-3854, 3856-3858, 3863-3877, 3883, 3908-3912, 3914, 3938-3944, 3946, 4021, 5961. FBA: 32-34, 51.
2	Antioquia, Córdoba, Atlántico, Bolívar (Western Caribbean)	1 - 370	ICN-R: 2957, 2959, 3880, 3884, 3886-3892, 3898-3901, 3907, 3915, 3916, 3921, 3925, 3927, 3929, 3930, 3932, 3945, 4025, 4026, 4029, 5832, 5836, 8491-8493, 8571, 8572, 8576-8578, 8581, 8582, 8587, 8588, 8590, 8594, 10138. FBA: 19, 21, 53, 54, 56.
3	Antioquia, Valle del Cauca (Western Cordillera)	512 -1066	ICN-R: 3814, 3822, 3835, 3937, 3952, 3953, 3955-3957, 3959-3968, 3970-3973, 6006-7, 6010-6012.
4	Antioquia, Tolima (Central Cordillera)	69 - 1234	ICN-R: 2768-2771, 3846,3969. POE: 4471, 4481.
5	Cundinamarca, Tolima, Huila, Santander (Magdalena Lowlands)	181 - 785	ICN-R: 2491, 2494, 2497, 2500, 3816, 3818-3821, 3954. FBA 24, JDL: 28581-28583, 28627, 28737-28739, 28786-28791, 28856, 28857.
6	Vichada, Meta, Casanare (Orinoquia region)	93 - 241	ICN-R: 2813, 3825-3827, 3829-3831, 3933, 3934, 6536, 9476-9478, 9482, 9484, 9485, 12037, 12056, 12062, 12063, 12278, 12280, 12290, 12292. MLC: 723, 732, 857, 858.

* ICN-R (Instituto de Ciencias Naturales, Reptile collection); FBA (Faidith Bracho Altamirano); JDL (John Douglas Lynch); MLC (Martha Lucía Calderón); POE (Steve Poe).