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## MORPHOLOGICAL TRAIT VARIATION BETWEEN TWO POPULATIONS OF *CERCOSAURA SCHREIBERSII* IN SOUTHERN BRAZIL: INSIGHTS ON HABITAT-DRIVEN ADAPTATION

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**Abstract.**—Differences in morphological traits among organisms are a result of evolutionary processes and can increase performance in their habitat. Knowledge of the links between morphology and abiotic environmental composition is vital in understanding ecology and evolution of organisms. In this study, we evaluated the variation of morphological traits in specimens of the lizard Schreiber’s Many-fingered Teiid (*Cercosaura schreibersii*) collected from different environments in southern Brazil. We compared 14 morphological traits between two populations of this species located 400 km apart. We defined the two collection sites by the dominant substrate type: sand and cambisol. We found evidence of morphological variation between the two populations, with lizards from cambisol having longer forelimbs and front autopodia than those from sand habitat. The larger autopodia in cambisol individuals could improve climbing ability by increasing toepad area and facilitating movement over rocky substrates which are rich in organic matter and obstacles. Sand lizards presented longer back autopodia, that could represent advantages for moving in the loose sand substrate. Our results reveal key morphological differences between two populations of the same species that are concordant with predictions of the literature.

**Key Words.**—Brazil; ecology; evolution; natural selection; performance

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### INTRODUCTION

The relationship between morphology and habitat characteristics has been extensively studied and represents one of the central questions in ecology and evolution (Arnold 1998; Aerts et al. 2000; Collar et al. 2010). Environmental filters, such as physical habitats properties (e.g., substrate composition, climatic stability, topography) or biotic components (e.g., predation risk, food availability, competitors) affect how some morphological traits are selected. Selection is predicted to follow the ecomorphological paradigm, wherein morphological changes that result in increased performance, and consequently fitness of populations are under positive selection (Arnold 1983). Lizards are good models for ecomorphological studies due to their diversity in life histories (Elstrott and Irschick 2004; Losos 2009) because they are poikilothermic vertebrates and therefore are more sensitive to habitat changes by relying heavily on predictable environmental conditions (Garland and Losos 1994).

Lizards have evolved many habitat-specific adaptations for improved locomotor abilities (Lundelius 1957; Collette 1961; Moermond 1979; Kolbe 2015). The evolution of lizard locomotion is dependent

not only on body morphology, but also the physical interactions between morphology and environment, especially substrate (Garland and Losos 1994). Lizards are exposed to different levels of friction and adhesion depending on substrate composition, which can affect sprint speeds (Lejeune et al. 1998; Kerdok et al. 2002). In granular substrates, for example, foot impact during movement causes displacement of the substrate surface leading to greater energy expenditure and reduced sprint performance (Li et al. 2012). The same applies to substrate friction properties likely determining grip (Vanhooydonck et al. 2015), and subsequently energy expenditure, during locomotion (Zani 2000; Tulli et al. 2012). Despite environmental selection for morphological adaptations typically occurring over long periods of time, some studies have found evidence of such selection in species from recently transformed habitats (Zani 2000; Winchell et al. 2018). In the Puerto Rican Crested Anole (*Anolis cristatellus*) for example, morphological adaptations for climbing, such as larger toepad area, were observed in urban populations but not in natural areas where artificial obstacles were not present (Winchell et al. 2018).

In this study, we examined a gymnophthalmid lizard, Schreiber’s Many-fingered Teiid (*Cercosaura*

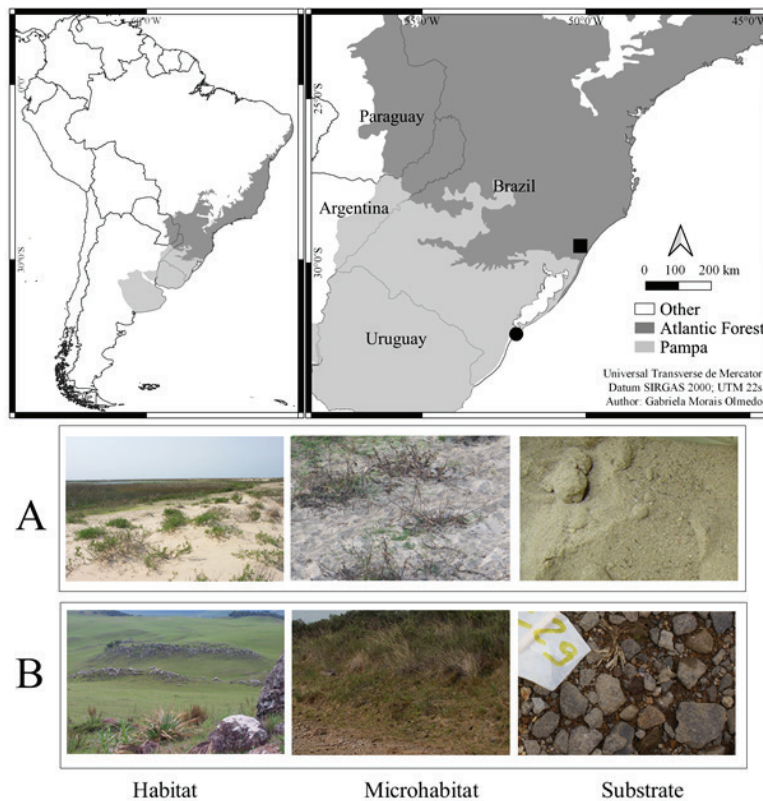
*schreibersii*), seeking to determine if there were morphological differences between populations. This species is distributed southeast of Peru, Bolivia, Paraguay, Argentina, meridional Brazil, and Uruguay (Lema 1984), typically inhabiting small, rocky outcrops in fields (Cei 1986; Lema 1984, 2002; Carreira et al. 2019). In southern Brazil, they occur in the Atlantic Forest and Pampas biomes (referred to in this study as northern and southern populations, respectively). Both populations inhabit comparable habitats in terms of vegetation cover (grassland-like habitat), but inhabit different biomes, elevations, and substrates. The southern population occurs over a wide area dominated by sandy substrates, while the northern population is in an area dominated by stony cambisol substrate.

We hypothesize that site-specific substrate composition will affect lizard morphology. By comparing the morphology of individuals from northern and southern population, we predict that lizards in the southern population, because they use sandy substrate, would have pronounced adaptations for moving across looser sediments including wider pelvises and shorter forelimbs, which could avoid lizards slipping in the loose sediment (Vanhooydonck and Van Damme 1999; Herrel et al. 2001). We also predict lizards will have longer rear autopodia in southern populations, which

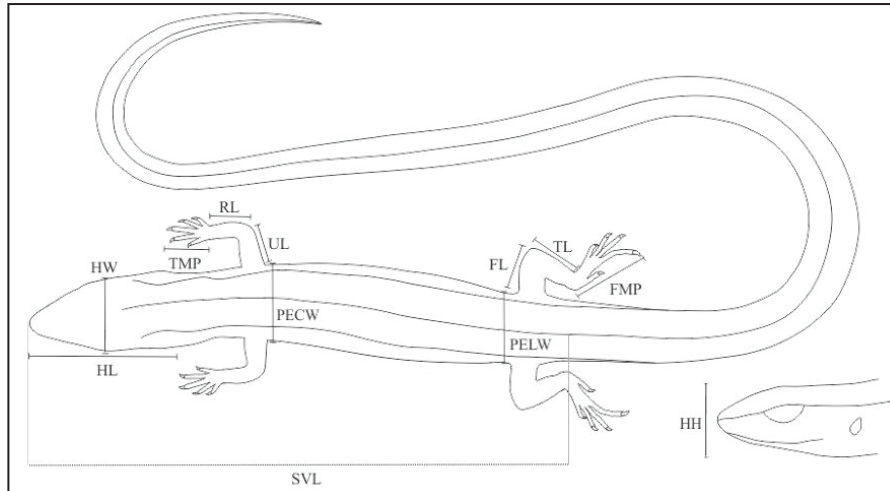
could minimize energy cost of moving on granular substrate (Bauwens et al. 1995; Li et al. 2012; Tulli et al. 2012), and smaller body size, which could improve thermoregulation by facilitating heat loss in the hotter climate of lower elevations (Huey and Slatkin 1976). In contrast, we predict that lizards in the northern population would have adaptations related to moving over obstacles, such as longer forelimbs and narrower bodies that could improve movement across obstacles (Zaaf and VanDamme 2001; Borges-Landáez and Shine 2003; Irschick et al. 2005). We also predict they will have larger bodies to maintain heat for a longer time in higher elevations where they experience lower mean temperatures than in the south (Huey and Slatkin 1976).

#### MATERIAL AND METHODS

**Study species and localities.**—We studied specimens of *Cercosaura schreibersii* collected in the subtropical region of southern Brazil (Fig. 1; Supplemental Information Table S1) and preserved in natural history collections at Universidade Federal de Rio Grande - FURG and Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul - PUCRS. We selected individuals from two sites near the southern limit of the species distribution in Brazil; the northern



**FIGURE 1.** Map of collection localities with examples of habitat types. The black rectangle marks the cambisol habitat and the black circle marks the sand habitat. Images show (A) sand habitat and (B) cambisol habitat. (Habitats photographed by Alexandro M. Tozetti).



**FIGURE 2.** Schematic of morphological attributes measured in Schreiber's Many-fingered Teiid (*Cercosaura schreibersii*) lizards. Abbreviations are SVL = snout-vent length; HL = head length; HH = head height; HW = head width; PECW = pectoral width; PELW = pelvic width; TMP = third metacarpal and phalanx length; RL = radius length; UL = humerus length; FMP = fourth metatarsal and phalanx length; TL = tibia length; FL = femur length

population located in the Atlantic Forest biome and the southern population located in the Pampas biome. These sites were located 400 km apart. Although the sites were in different biomes, with differences in the general structure of the landscape, elevation, and temperature, the habitat used by individuals of each population was similar and was predominated by grasses (Fig. 1). We collected individuals of the southern population near the city of Rio Grande in a coastal area of sand dunes covered by natural grassy vegetation and sparse shrubs (32°09'47.37"S 52°06'45.81"W, 6 m elevation; Gayer et al. 1988) and from the northern population near the city of São Francisco de Paula in a landscape forming a mosaic of forest and natural grasslands (29°28'47.35"S 50°10'24.31"W, 907 m elevation; Veloso et al. 1991; Fig. 1).

Soil substrates from each location are visibly different based on their physical properties. Based on the Brazilian Soil Classification System, soil at the northern site is primarily cambisol (Santos et al 2018). Soil mapping (Figure S1) indicates that soil at the northern site is Brazilian Neossolo (from Greek neo = new, referring to the poor pedogenetic development of this soil). This soil consists of a thin layer of mineral material composed of coarse fragments (e.g., quartz gravel bed) with a diameter > 2 mm (gravel, pebbles, and rocks). All sampled regions are formed by Brazilian Neossolos Litólicos (Leptosols) soil (Lemos 1973; Pedron et al. 2009). Our southern site is predominantly sand dunes which are classified by Santos et al (2018) as a terrain type, not a true soil (Fig. 1). Sand dunes at the southern site were formed by accumulation of soilless small mineral particles where the pedogenetic horizons are not developed. We differentiate both sites based on the physical properties

of their substrate (soil), which could affect lizard grip and locomotion. Our own observations (supported by gray literature of soil penetration values) show that sites have quite different compaction levels (Associação Brasileira de Normas Técnicas 2001). Technical reports from local public engineering departments indicate that soil compaction at the northern site varies from 20N to 30N, which represents a medium/dense compaction level whereas at the southern site, substrate is lower than 4N, representing a very loose compaction level. We are comfortable to assert that on average, compaction of soil is about five times greater at the northern site compared to the southern site. To simplify habitat characteristics of sites, we use the following names based on soil properties: northern locality = cambisol habitat; southern locality = sand habitat. The key difference between the two habitats is their substrate composition: sand has exclusively sandy soil whereas cambisol has clay soil with small rocks (Fig. 1).

**Morphometric measurements.**—For morphometric analysis, we evaluated only adults of reproductive age; males > 21 mm snout-vent length (SVL) and females > 34.7 mm SVL (Diehl 2007). We measured 49 individuals: 24 (13 males and 11 females) from sand habitat and 25 (12 males and 13 females) from cambisol habitat (Table 1). We measured traits following previous studies that evaluated the relationship between substrate, habitat, and locomotor performance in lizards (Aerts et al. 2000; Meiri 2008; Galindo-Gil et al. 2015; Winchell 2018). The following attributes were measured (Fig. 2): head length (HL) from the snout to the caudal edge of the occipital scale; head width (HW) measured from the largest width of the jaws; head height (HH) from

**TABLE 1.** Mean values of morphologic attributes measured in *Cercosaura schreibersii* lizards in sand and cambisol habitats. Values presented as mean  $\pm$  standard deviation (mm). Abbreviations are SVL = snout-vent length; HL = head length; HH = head height; HW = head width; PECW = pectoral width; PELW = pelvic width; TMP = third metacarpal and phalanx length; RL = radius length; UL = humerus length; FMP = fourth metatarsal and phalanx length; TL = tibia length; FL = femur length.

Measures	Sand (all sexes)	Cambisol (all sexes)	Males (all habitats)	Females (all habitats)	Sand - F (n = 11)	Sand - M (n = 13)	Cambisol -F (n = 13)	Cambisol -M (n = 12)
SVL	37.58 $\pm$ 3.91	39.40 $\pm$ 4.03	35.59 $\pm$ 2.21	41.01 $\pm$ 4.07	39.35 $\pm$ 4.72	35.25 $\pm$ 2.21	42.41 $\pm$ 2.93	35.95 $\pm$ 2.32
HW	5.81 $\pm$ 0.71	6.04 $\pm$ 0.55	5.72 $\pm$ 0.57	5.66 $\pm$ 0.58	5.88 $\pm$ 0.86	5.8 $\pm$ 0.67	5.74 $\pm$ 0.56	5.63 $\pm$ 0.48
PECW	5.82 $\pm$ 0.68	6.1 $\pm$ 0.83	5.54 $\pm$ 0.56	5.47 $\pm$ 0.48	6.05 $\pm$ 0.62	6.18 $\pm$ 0.56	5.81 $\pm$ 0.72	5.63 $\pm$ 0.49
PELW	5.37 $\pm$ 0.61	5.75 $\pm$ 0.85	5.02 $\pm$ 0.39	5.13 $\pm$ 0.53	5.62 $\pm$ 0.73	5.36 $\pm$ 0.48	5.38 $\pm$ 0.97	5.32 $\pm$ 0.31
UL	14.14 $\pm$ 1.36	13.30 $\pm$ 1.16	3.35 $\pm$ 0.38	3.37 $\pm$ 0.40	3.5 $\pm$ 0.34	3.49 $\pm$ 0.38	3.41 $\pm$ 0.28	3.38 $\pm$ 0.40
RL	3.42 $\pm$ 0.37	3.49 $\pm$ 0.35	3.03 $\pm$ 0.34	3.09 $\pm$ 0.34	3.32 $\pm$ 0.39	3.19 $\pm$ 0.42	3.25 $\pm$ 0.23	3.18 $\pm$ 0.27
TMP	3.21 $\pm$ 0.41	3.17 $\pm$ 0.28	3.74 $\pm$ 0.44	3.77 $\pm$ 0.40	3.5 $\pm$ 0.24	3.5 $\pm$ 0.32	3.48 $\pm$ 0.39	3.39 $\pm$ 0.43
FLL	3.51 $\pm$ 0.30	4.15 $\pm$ 0.43	10.12 $\pm$ 0.86	10.23 $\pm$ 0.87	10.32 $\pm$ 0.74	10.18 $\pm$ 0.79	10.14 $\pm$ 0.62	9.95 $\pm$ 0.92
FL	10.15 $\pm$ 0.76	10.81 $\pm$ 0.87	3.74 $\pm$ 0.44	3.78 $\pm$ 0.37	3.79 $\pm$ 0.21	3.69 $\pm$ 0.43	3.75 $\pm$ 0.37	3.59 $\pm$ 0.43
TL	3.69 $\pm$ 0.35	3.99 $\pm$ 0.40	3.33 $\pm$ 0.27	3.36 $\pm$ 0.30	3.71 $\pm$ 0.24	3.57 $\pm$ 0.22	3.55 $\pm$ 0.33	3.52 $\pm$ 0.32
FMP	3.52 $\pm$ 0.31	3.42 $\pm$ 0.33	5.61 $\pm$ 0.57	5.66 $\pm$ 0.48	5.61 $\pm$ 0.33	5.47 $\pm$ 0.48	5.47 $\pm$ 0.61	5.38 $\pm$ 0.51
HLL	5.48 $\pm$ 0.44	6.03 $\pm$ 0.56	12.68 $\pm$ 1.01	12.8 $\pm$ 0.87	13.11 $\pm$ 0.66	12.73 $\pm$ 0.85	12.77 $\pm$ 1.20	12.49 $\pm$ 0.99
HH	12.69 $\pm$ 0.89	13.44 $\pm$ 1.12	3.88 $\pm$ 0.38	3.87 $\pm$ 0.44	3.83 $\pm$ 0.55	3.88 $\pm$ 0.37	3.84 $\pm$ 0.47	3.7 $\pm$ 0.30
HL	3.81 $\pm$ 0.44	4.15 $\pm$ 0.40	7.74 $\pm$ 0.54	7.74 $\pm$ 0.56	7.97 $\pm$ 0.49	7.98 $\pm$ 0.49	7.87 $\pm$ 0.59	7.86 $\pm$ 0.61

the head lower and higher points; third metacarpal and phalanx length (TMP) from the top of the third toe of the forelimb to the distal edge of radius; radius length (RL) from the wrist until the proximal edge of radius; humerus length (UL) from the proximal edge of the radius to the connection of the arm with the body; fourth metatarsal and phalanx length (FMP) from the top of the forelimb fourth toe to the distal edge of tibia; tibia length (TL) from the ankle to the proximal edge of tibia; femur length (FL) from the tibia proximal edge to the connection of the leg with the body; pectoral width (PECW) the body width directly below the arms connection; pelvic width (PELW) the body width directly above legs connection. We measured total body size using snout-vent length (SVL). We obtained the total length of the forelimbs (FLL) from the sum of UL, RL and TMP, and the total length of the hindlimbs (HLL) by the sum of FL, TL, and FMP. We made all measurements using electronic calipers with 0.01 mm precision (Supplemental Information Table S1).

**Statistical analyses.**—To test whether sex and site affect morphology of our lizards, we performed a Permutational Multivariate Analysis of Variance (PerMANOVA; 999 permutations) with randomization tests, based on a matrix of Euclidian distances between individuals calculated using the morphological variables, previously centered and normalized within variables (Pillar and Orlóci 1996). We then used Multivariate Analysis of Variance (MANOVA) to

determine which body measurements were significantly responsible for the differences between sites. We visualized these differences by plotting principal components axes.

## RESULTS

We found that lizard morphometrics were influenced by sex (PerMANOVA:  $F_{1,47} = 26.11$ ,  $P = 0.001$ ,  $r^2 = 0.36$ ), site (PerMANOVA:  $F_{1,47} = 4.04$ ,  $P = 0.045$ ,  $r^2 = 0.08$ ), and their interaction (PerMANOVA:  $F_{3,45} = 11.64$ ,  $P = 0.001$ ,  $r^2 = 0.44$ ). Specifically, values of PC1 were higher in females and lizards from the northern population (cambisol), while values of PC2 were higher in females and lizards from the southern population (sand; Supplemental Information Tables S2, S3). Sex and site combined explained 27% of the total morphological variation recorded. All variables were positively associated with the first PC axis (Fig. 3; Supplemental Information Tables S2, S3) representing body size. Body measurements differed significantly between the populations ( $F_{14,34} = 6.97$ ,  $P < 0.001$ ). TMP, FLL, FMP, and HH were significantly different between the two sites (Table 2). Cambisol lizards had longer TMP lengths than those from sand habitats (4.15  $\pm$  0.43 [standard deviation] mm vs. 3.51  $\pm$  0.29 mm, respectively), longer FLL (10.81  $\pm$  0.87 mm vs. 10.08  $\pm$  0.77 mm, respectively), longer FMP (6.03  $\pm$  0.56 mm vs. 5.45  $\pm$  0.43 mm, respectively) and greater HH (4.15  $\pm$  0.40 mm vs. 3.76  $\pm$  0.46 mm, respectively).

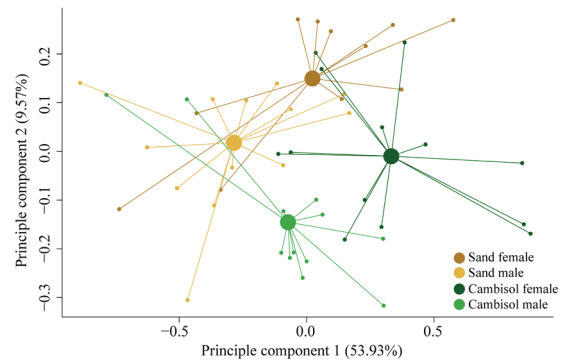
**TABLE 2.** Results of the MANOVA comparing body measurements between the two locations. Bonferroni corrected alpha value for 15 comparisons is 0.0033. Bolded values are significant after *P*-value correction. Abbreviations are SVL = snout-vent length; HL = head length; HH = head height; HW = head width; PECW = pectoral width; PELW = pelvic width; TMP = third metacarpal and phalanx length; RL = radius length; UL = humerus length; FMP = fourth metatarsal and phalanx length; TL = tibia length; FL = femur length; df = degrees of freedom.

	Estimate	<i>F</i> -Value	df	<i>P</i> -Value
Whole Model	2.868	6.965	14,34	< <b>0.001</b>
SVL	0.073	3.412	1,47	0.071
HW	0.061	2.880	1,47	0.096
PECW	0.045	2.100	1,47	0.154
PELW	0.014	0.656	1,47	0.422
UL	0.015	0.728	1,47	0.398
RL	< 0.001	0	1,47	0.998
TMP	0.786	36.94	1,47	< <b>0.001</b>
FLL	0.208	9.756	1,47	<b>0.003</b>
FL	0.172	8.098	1,47	0.007
TL	0.021	1.003	1,47	0.322
FMP	0.343	16.13	1,47	< <b>0.001</b>
HLL	0.162	7.594	1,47	0.008
HH	0.216	10.14	1,47	<b>0.003</b>
HL	0.001	0.054	1,47	0.817

## DISCUSSION

Our results reinforce the hypothesis that substrate type used by lizards could affect its morphology. Here we present key morphological differences between *Cercosaura schreibersii* individuals captured at two distinct locations that could be linked to local substrate differences, suggesting regional adaptation. We found that lizards from the site with cambisol substrates had longer limb lengths (TMP, FLL, and FMP) and greater head heights than conspecifics from the site with sand substrates. Although we have not experimentally tested lizard grip on substrates from the two habitats, it seems plausible that sandy substrates offer less grip than rocky cambisol based on compaction levels and previous literature (Tulli et al. 2012). In a recent experiment, Brandt et al (2015) showed that the lizards have better movement performance in coarse sand, leaf litter, and rocky substrates than in loose sand.

Our study sheds light on the role of substrate characteristics on lizard locomotor performance. Substrate characteristics such as texture, sand granulometry, presence of rocks, leaf litter, and vegetation all influence the way an animal may affect performance. As locomotion is a basic component in successfully finding mates, avoiding predation, and obtaining food, morphological adaptations that increase



**FIGURE 3.** Lizard morphometric ordination calculated using Principal Component Analysis based on Euclidean distances. Colors define groups and large circles indicate centroids for each group.

locomotor performance should be under positive selection (Garland and Losos 1994). A classic example of morphological adaptation to a specific substrate is the presence of toe fringes in the Mojave Fringe-toed Lizard (*Uma scoparia*), a sand dune specialist (Carothers 1986). The flatter head (low HH), shorter forelimbs (low FLL) and autopodia (low TMP) observed in lizards from sand habitats in our study are likely favorable in maintaining a lower center of mass which assists with balance and may offer stability when climbing dunes and general locomotion in looser sediments, offering a fitness advantage in movement (Vanhooydonck and Van Damme 1999; Herrel et al. 2001; Aerts et al 2003).

Motor performance also depends on the mechanical functioning of the upper hind limb muscles (Li et al. 2012), which are more effective in translating force to movement with larger forelimbs or toes. As the looser sandy substrate is more likely to shift with the application of force, movement over this substrate results in a greater energy cost than on cambisol substrates (Tulli et al. 2012). Selection would therefore act to minimize this energy loss through the evolution of longer limbs and toes. As expected, sand lizards do have larger toes (FMP), however, we found larger front autopodia (TMP) and forelimbs (FLL) in individuals from cambisol, not sand. An alternative explanation is that larger autopodia provide an increase in climbing ability through an increase in toepad area, which would be advantageous in cambisol habitat where more obstacles to movement exist (Zaaf and VanDamme 2001; Borges-Landáez and Shine 2003; Irschick et al. 2005).

Predation risk varies between the two population sites. Both habitats have a high predation rate as indicated by Ávila et al. (2019) in an experiment with snakes, but crypsis would be more important to avoid predation in sandy habitats as hiding locations like rocks are scarcer. In environments like sand habitat where predators have a clearer line of sight (Denno et al. 2005), lizards would

likely be highly exposed while sunning and foraging, so shorter limbs could offer a thinner silhouette (elongated body shape) and flatter heads that favors crypsis. This along with the smaller body size found in the sand dwelling lizards could provide animals a fitness advantage by reducing their shadows, making them less visible to avian predators (Lockard and Owings 1974; Kotler 1984).

Our results suggest adaptive morphological variation between northern and southern populations of *Cercosaura schreibersii*. Based on the linkage between key habitat characteristics and measured morphological traits, we assert that the morphological differences observed suggest evidence of morphological adaptation to the abiotic habitat among these populations. In addition, we were unable to test whether our findings had real impacts on lizard performance, and using just two populations, although we cannot exclude effects of others processes that we did not measure. Our findings are consistent with the literature of what is expected as a result of habitat adaptation by animals. This study highlights the importance of microhabitat characteristics in guiding adaptation of populations in relatively close proximity. Future studies measuring lizard performance on different substrates would be of value in understanding whether these morphological differences are truly adaptive.

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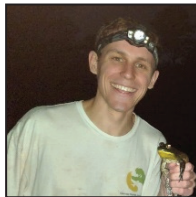
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