Morphological variation and sexual dimorphism in *Liolaemus wiegmannii* (Duméril & Bibron, 1837) (Squamata: Liolaemidae) from Uruguay

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Abstract. Intraspecific morphological variation is a relatively common pattern among lizards, where several selective factors have been suggested as responsible for this phenomenon. For instance, geographic variation could result from natural selection along with historical processes, whereas sexual dimorphism has usually been attributed to sexual selection, natural selection, and niche segregation. *Liolaemus wiegmannii* is a diurnal lizard distributed in the center, center-east and north-west of Argentina, as well as on the shores of south-west and south Uruguay. Information about morphological variation in this species is almost entirely limited to differences in mid-body scales between populations in the north and center of Argentina and some sex-based morphometric variation. Herein, we studied the geographic and sexual morphological variation of *Liolaemus wiegmannii* from Uruguay to test the hypothesis of morphological isolation by distance and morphological structuring by geographic barriers (rivers), as well as exploring the occurrence of sexual dimorphism in morphometry and lepidosis. Neither geographic distance nor rivers seem to play an important structuring role on the external morphology of *Liolaemus wiegmannii* in Uruguay. Multiple multivariate analyses support the hypothesis that most of the external morphological variation is probably due to sexual dimorphism. Natural and sexual selection acting on females and males, respectively, are the most plausible mechanisms underlying the dimorphism observed in this species.

Keywords. Morphometry, lepidosis, sexual dimorphism, *Liolaemus*, Uruguay.

INTRODUCTION

Intraspecific morphological variation can arise as the result of selective pressures, phenotypic plasticity or historical factors acting at a population level. Geographic variation in morphology is quite frequent among lizards and has been attributed to both genetic and non-genetic factors (Ballinger, 1983; Dunham et al., 1988; Qualls and Shine, 1998). Intersexual variation is also common, and at least three hypotheses have been proposed in order to explain its causes in lizards: sexual selection (Maynard

Smith, 1987; Carothers, 1984; Braña, 1996; Cox et al., 2003); fecundity advantage (Tinkle et al., 1970; Braña, 1996; Fairbairn, 1997; Blanckenhorn, 2005) and trophic niche segregation (Schoener, 1967; Pianka and Huey, 1978). Sexual selection as the main factor behind sexual dimorphism predicts higher reproductive success in larger males or in those that are more attractive to females. Consequently, those structures involved in male-male combat or related to female choice of male quality often become conspicuous (Carothers, 1984; Andersson, 1994; Andersson and Simmons, 2006). Alternatively, the fecun-

dity advantage hypothesis states that natural selection will favor larger females, and therefore, predicts a proportional increase of fecundity with body size (Tinkle et al., 1970; Kozlowski, 1989; Braña, 1996; Fairbairn, 1997; Zamudio, 1998; Cox et al., 2003; Blanckenhorn, 2005; Du et al., 2005). Otherwise, sexual dimorphism could also be a consequence of competition for trophic resources, where the resulting morphological differences between sexes allow a more efficient exploitation of the trophic niche (Schoener, 1967; Pianka and Huey, 1978; Herrel et al., 1999).

With about 240 recognized species, *Liolaemus* is one of the most widely distributed and species rich lizard genera worldwide (Lobo et al., 2010; Etheridge and Frost, 2010; Breitman et al., 2011, 2013; Avila et al., 2013). *Liolaemus* is distributed exclusively in South America, occurring in Bolivia, Paraguay, Peru, Chile, Argentina, Brazil and Uruguay, spanning different environments from the Andes Mountains to the Atacama Desert and from the Pacific Ocean shores to the Atlantic Ocean coasts (Lobo, 2001; Avila, 2003; Pincheira-Donosso et al., 2008). The systematics of the genus is quite complex, with several sections, series and groups being recognized (Schulte et al., 2000; Espinoza et al., 2004; Cruz et al., 2005; Fontanella et al., 2012; Olave et al., 2014). *Liolaemus wiegmannii* (Duméril and Bibron, 1837) is a member of the *L. wiegmannii* group, a species group that has been suggested as monophyletic based on molecular and morphological data (Etheridge, 2000; Schulte et al., 2000; Espinoza et al., 2004; Avila et al., 2006; Abdala, 2007; Pincheira-Donoso et al., 2008; but see Olave et al., 2014). It is a diurnal terrestrial lizard, which occupies a variety of habitats throughout its extensive and fragmented range, although it is often found in sand dunes and sandy soils (Etheridge, 2000). Its distribution in Argentina includes the Provinces of Río Negro, Buenos Aires, La Pampa, Entre Ríos, Santa Fé, Córdoba, San Luis, Mendoza, San Juan, Catamarca, Tucumán, Jujuy and Salta, whereas in Uruguay, this species occurs in the sandy shores of the Departments of Río Negro, Soriano, Colonia, San José, Montevideo, Canelones, Maldonado, and Rocha, to the west of Valizas Creek (Cei, 1986, 1993; Carreira et al., 2005; Carreira and Maneyro, 2013; Párraga, 2011, Avila et al., 2013; Stellatelli et al., 2014). Nonetheless, numerous authors have pointed out that *Liolaemus wiegmannii* is probably a species complex containing several disjunct populations that may represent separate species (Avila, 2003; Morando, 2004; Avila et al., 2006; Avila et al., 2009; Aiassa and Gorla, 2010; Olave et al., 2014).

Beyond its systematic complexity, the morphological variation of *Liolaemus wiegmannii* across its whole range has been poorly studied. Cei (1979), and Avila and Mar-

tori (1996), reported some geographic variation in the number of mid body scales from Argentina. Etheridge (2000) published data on snout-vent length, dorsal scales, supralabials, infralabials and precloacal pores. In addition, Avila et al. (2009) provided some morphological information about *L. wiegmannii*. However, the last two studies did not provide a geographically explicit analysis of the morphological variation.

Some authors have noted sexual dichromatism in *Liolaemus wiegmannii*, with males exhibiting conspicuous orange and blue scales in the reproductive season that in general are absent in females, although, a tenuous orange coloration can be occasionally observed on females (Cei, 1986, 1993; Etheridge, 2000; Carreira et al., 2005; Avila et al., 2009). Recently, Cabrera et al. (2013) studied the sexual size dimorphism of several species of the *Liolaemus laurentii* group (*sensu* Abdala 2007), and showed that *Liolaemus wiegmannii* has sexual differences in humerus length and axila-groin distance. However, sexual dimorphism in lepidosis and other morphometric traits have not been considered yet. In addition, because *L. wiegmannii* is a species complex, it is possible that the individuals analyzed by Cabrera et al. (2013) from Argentina could belong to a species different to the one occurring in Uruguay.

In this work, we studied the intraspecific morphological variation of *Liolaemus wiegmannii* throughout its range in Uruguay using meristic (lepidosis) and morphometric data. We hypothesized that the morphological variation between localities should show a geographic pattern due to isolation-by-distance. Alternatively, considering the influence of rivers on the variation of terrestrial organisms (Pound and Jackson, 1981; Gascon et al. 1998; Pellegrino et al., 2005; Geghring et al., 2012), three main rivers were considered as potential geographic barriers that could influence the structure morphological variation. Finally, we expected to find significant differences in lepidosis and other morphological traits between sexes, in addition to those sexually-dimorphic traits found in previous studies.

MATERIALS AND METHODS

Morphological variation of *Liolaemus wiegmannii* was studied through a set of eight classic morphometric and nine meristic variables (lepidosis) (Table 1) from 134 specimens housed in the vertebrate collection of the Faculty of Sciences, University of the Republic and the herpetological collection of the National Museum of Natural History (Montevideo, Uruguay) (Appendix 1). The geographic coverage of the specimens includes 40 localities spanning almost the whole range of this species in Uruguay (Fig. 1).

Table 1. Morphometric and meristic variable abbreviations and their corresponding meanings.

| MorphometricVariables	Detail	Meristic Variables	Detail
SVL	Snout-vent length	MBSc	Scales around mid-body
HL	Head length	DSc	Dorsal scales
HW	Head width	VSc	Ventral Scales
humL	Humerus length	PP	Precloacal pores
antbL	Forearm length	Lam3	Subdigital lamellae of third finger
FL	Femur length	Lam4	Subdigital lamellae of fourth toe
TibL	Tibia length	InfLab	Infralabial scales
A-G	Axilla-groin distance	SupLab	Supralabial scales
		LorLab	Lorilabials scales
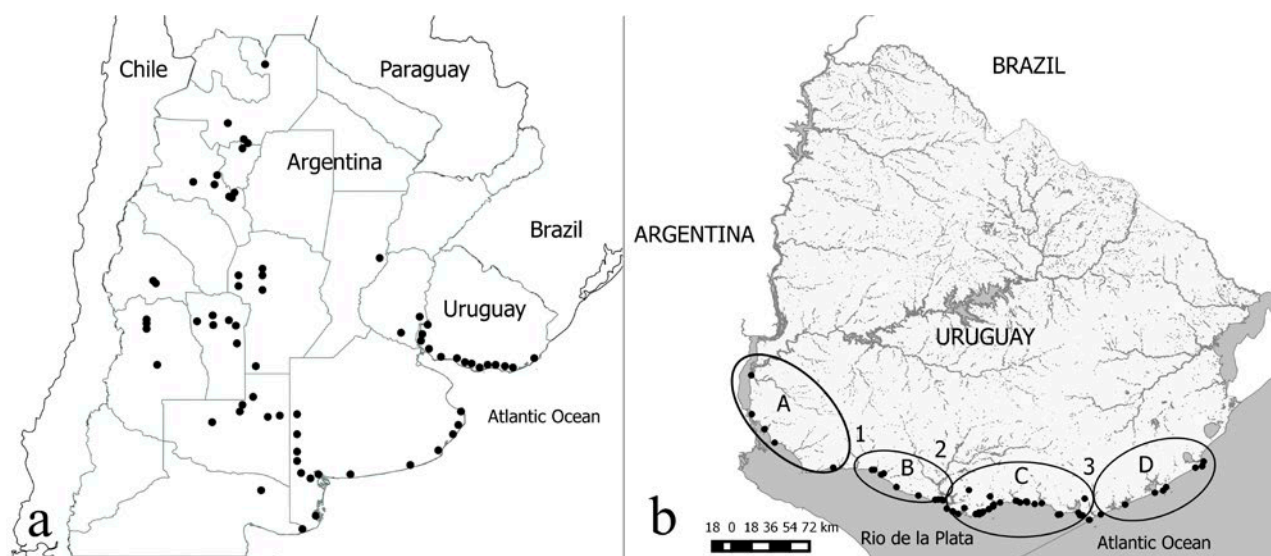
Fig. 1. (a) Distribution of *Liolaemus wiegmannii* after Etheridge (2000) and Avila et al. (2009). (b) Localities of Uruguay used for geographic analysis with perMANOVA. A and B: west and east of Rosario River (1) localities; C: east Santa Lucía River (2) localities; D: east Maldonado Stream (3) localities.

Variables were chosen based on Etheridge (2000), Verrastro et al. (2003), and Avila et al. (2009), and the lepidosis terminology followed Smith (1946). Morphometric measurements were taken with a digital caliper to the nearest 0.01 mm, whereas for meristic variables a stereoscopic microscope was used. Sex was determined based on the shape of the cloaca, which is squared-shaped in males and rounded in females (Cabrera et al., 2013).

In order to remove the effect of size from morphometric variables, each variable was transformed as

$$Z = Y_i (\overline{SVL} / SVL_i)^b \qquad (1)$$

following Lleonart et al. (2000), where Z represent the transformed value of the variable Y, which is the variable affected by size, represented in this case as the snout-vent length (SVL). The exponent b is the slope of the linear regression between logY and logSVL. This transformation completely removes all the information related to size by scaling individuals to the same size and adjusting their shape to that they would have at the new size according to allometry (Lleonart et al., 2000). To check that no size effect persisted after transformation, slopes of linear regression between each transformed variable and SVL were evaluated trough a Student's *t* test implemented in R 3.3.0 (R Core Team 2016) (see appendix 2). Under a successful size correction a slope of zero is expected.

Principal Component Analyses were computed separately for morphometric (excluding SVL) and meristic variables through a variance-covariance matrix with the purpose of understanding the structure of the morphological variation and the contribution of each variable to the components that explain most of the variation observed. The assumption of multivariate normality was evaluated through Mardia (Mardia, 1970) and Omnibus (Dornik and Hansen, 2008) tests implemented in PAST 3.07 (Hammer et al., 2001).

For testing the hypothesis of isolation by distance, a Mantel test between a morphological and geographical distance matri-

ces was conducted. The original dataset was divided into four matrices (one for each sex and class of variable, *i.e.* morphometric and meristic), which were independently analyzed using Mahalanobis and Correlation distances for morphometric and meristic data respectively and geographic distances obtained from coordinates. Correlation distances were obtained with Past software as 1-r, where r is the Pearson's coefficient.

To test for statistical differences between sexes and geography, morphometric and meristic variables were analyzed separately through a perMANOVA (Anderson, 2001), which was computed based on Mahalanobis and Correlation distances respectively, and one million permutations. This analysis uses a multivariate statistic analogous to Fisher's F-ratio constructed from sums of squared distances within and between groups and provides a p value that is calculated through permutations (Anderson, 2001). For testing geographic variation independently from sex, geographic arrangements were tested separately for males and females. Three main rivers were considered as potential barriers (Rosario River, Santa Lucía River, and Maldonado Stream), and therefore localities were grouped into four groups limited by these courses (Fig. 1b). Moreover, differences between localities west and east of the Santa Lucía River, and between all localities were also tested.

Sexual dimorphism was also explored through a Discriminant Function Analysis (DFA), considering morphometric and meristic measurements separately. Besides the discriminant function, Mann-Whitney and Student's t-test were performed to evaluate which variables show significant differences between sexes.

All the statistical analyses, except Student's t-test on slopes, were implemented in PAST 3.07 software (Hammer et al., 2001).

RESULTS

Descriptive statistics

Based on the descriptive statistics for each untransformed variable, there are several sexually-dimorphic variables (Table 2). Considering both sexes, individuals of *L. wiegmannii* from Uruguay exhibit a maximum snout-vent length of 60.82 mm. Although males reached larger maximum sizes than females, both mean and median of females were higher than males (SVL male mean: 38.84 mm; SVL female mean: 41.89 mm; SVL male median: 36.10 mm; SVL female median: 44.61 mm) (Table 2). Regarding lepidosis, the ranges observed were particularly broad except for the number of lorilabial scales, which was 2 for all specimens analyzed except one (not shown in Table 2). The number of scales around the mid-body (MBSc) was similar for both sexes (males: 41–58; females: 42–58), whereas the range of the number of dorsal scales (*DSc*) was broader in females (males: 41–59; females: 43–65). The number of ventral scales (VSc) shows overlapping ranges between sexes, although females exhibit a higher maximum value (males: 40–59;

females: 45–64). The number of precloacal pores ranged between 0 and 7 for males and between 0 and 6 for females. Although these intervals are quite similar, the median of males was 5 whereas that for females was 0. In addition, the frequency of males without precloacal pores (data not shown) was markedly lower than for females (males: 0.097; females: 0.325). The number of subdigital lamellae on both the third finger and the fourth toe had very similar intervals among sexes. The range (4-7) and the median (5) of supralabials were equal between sexes, whereas the infralabials differ in range (males: 5-8; females: 5-7), but have the same median (6).

Ordination analysis

Considering the transformed morphometric variables and excluding SVL, the PCA shows that 81% of the variance is comprised by the first three components with the first principal component (PCA1) accounting for 47% of the variation. On the other hand, 84% of the meristic variance is explained by the first three components with a 50% of variation accounted for in the first principal component (Table 3).

For morphometric variables, the correlation coefficients show that PCA1 has a very strong positive correlation with the axilla-groin distance (Fig. 2A), whereas PCA2 is mostly positively correlated with the tibia and femur lengths, and in a lesser way, with the head length (Fig. 2B). Regarding to meristic characters, PCA1 has a high positive correlation with ventral and dorsal scales. To a lesser extent, PCA1 shows a negative correlation with the number of precloacal pores, where the magnitude of this correlation is about half of the absolute value of the maximum correlation observed in PCA1 (Fig. 2C). Moreover, PCA2 is mainly linked with the number of scales around midbody, with which it shows a very strong positive correlation (Fig. 2D).

The bidimensional projection of the first two principal components shows a substantial overlap of sexes for both morphometric (Fig. 3A) and meristic data (Fig. 3B). However, from a morphometric point of view, it is possible to note that females tend to be located towards the positive values of PCA1 and negative values of PCA2, whereas males show the opposite tendency (Fig. 3A). Taking into account the variables that have the strongest correlation with these two components (Fig. 2A and B), this tendency might reflect that females have longer axilla-groin distances than males whereas males tend to have longer femur, tibia and head lengths. For meristic variables, females tend to be located toward the positive values of the PCA1 while males are principally located in the region of negative values (Fig 3B). Considering the

Table 2. Descriptive statistics for morphometric and meristic variables considered for *L. wiegmannii* from Uruguay. Min: minimum value; Max: maximum value; Me: median; X̄: mean; $S_{\bar{x}}$: standard error of the mean; S^2_{n-1} : variance; S_{n-1}: standard desviation. SVL: snout-vent length; HL: head length; HW: Head width; humL: humerus length; antbL: forearm length; FL: femur length; TibL: Tibial length; A-G: axilla-groin distance; MBsc: scales around mid-body; DSc: dorsal scales; VSc: ventral scales: PP: precloacal pores; Lam3: subdigital lamellaeof third finger; Lam4: subdigital lamellaeof fourth toe; SupLab: supralabial scales; InfLab: infralabial scales.

		SVL	HL	HW	humL	antbL	FL	TibL	A-G	MBSc	DSc	VSc	PP	Lam3	Lam4	SupLab	InfLab
Min.	♂	23.21	6.07	5.38	3.37	2.25	3.75	3.2	9.3	41	41	40	0	13	16	4	5
	♀	22.4	5.79	5.22	3.17	2.28	3.56	2.79	8.68	42	43	45	0	12	17	4	5
Max.	♂	60.82	11.34	11.07	7.9	6.68	10.06	9.17	28.74	58	59	59	7	19	24	7	8
	♀	57.65	12.8	11.12	8.12	6.82	8.97	8.23	29.26	58	65	64	6	20	24	7	7
Me	♂	36.10	8.07	7.67	5.14	4.12	6.22	5.67	15.68	48	50	49	5	15	20	5	6
	♀	44,82	8.45	8.38	5.66	4.66	7.25	6.50	20.02	48	50	53	0	16	20	5	6
X̄	♂	38.84	8.24	7.90	5.30	4.35	6.43	5.91	16.59	48.24	49.28	48.69	4.06	15.36	19.89	5.43	6.19
	♀	42.05	8.41	8.35	5.62	4.61	6.75	6.07	19.47	48.16	50.40	53.51	1.71	15.38	20.54	5.33	6.15
$S_{\bar{x}}$	♂	1.18	0.17	0.19	0.15	0.13	0.19	0.19	0.53	0.37	0.45	0.48	0.27	0.11	0.18	0.08	0.08
	♀	1.03	0.15	0.16	0.13	0.11	0.16	0.16	0.55	0.36	0.41	0.38	0.23	0.13	0.19	0.06	0.06
S^2_{n-1}	♂	100.64	2.17	2.55	1.64	1.25	2.64	2.57	20.50	9.90	14.34	16.4	5.18	0.91	2.21	0.47	0.47
	♀	87.69	1.84	2.18	1.45	0.98	2.10	2.02	24.91	10.88	13.97	11.83	4.16	1.30	2.99	0.32	0.32
S_{n-1}	♂	10.03	1.47	1.60	1.28	1.12	1.62	1.60	4.53	3.15	3.79	4.05	2.28	0.95	1.49	0.69	0.17
	♀	9.36	1.36	1.47	1.20	0.99	1.45	1.42	4.99	3.30	3.74	3.44	2.04	1.14	1.73	0.57	0.57

Table 3. Principal components explaining most of the morphological variation of *Liolaemus wiegmannii* from Uruguay.

Variables	Principal Component	Eigenvalue	% of variance explained
Morphometrics	1	1.63446	46.52
	2	0.759644	21.621
	3	0.45371	12.913
Meristic	1	27.6334	50.226
	2	10.7795	19.593
	3	8.02788	14.591

correlation of each variable in PCA1 (Fig. 2C), this pattern might reflect that females have higher numbers of dorsal and ventral scales than males, whereas males have more precloacal pores than females. Dispersion among PCA2 axes is particularly high, so meristic data for this component do not show a conspicuous pattern among sexes (Fig. 3B).

DFA based on transformed morphometric variables correctly classified 72% of the analyzed individuals (75% of males and 71% of females, Table 6). The discriminant function obtained (DF = – 0.198Zhl – 0.029Zhw – 0.027ZhumL – 0.028ZantbL – 0.12Zfl – 0.24Ztl + 0.97Za-g) shows that the axilla-groin distance is the most influential variable on the equation; therefore, it is the morphometric variable that best discriminates between sexes. Other less important variables for morphometric sex discrimination are tibia and head length, which show

an opposite pattern: the sex with longer axilla-groin distance has a shorter head and tibia, and *vice versa*. For meristic variables, the DFA classified correctly 85% of the specimens with similar percentages between sexes (Table 4). In the discriminant function for these variables (DF = −0.046MBSc + 0.67DSc + 2.87VSc − 1.40PP + 0.010Lam3 + 0.39Lam4 − 0.060SupLab − 0.029InfLab) the number of ventral scales (*VSc*) and the numbers of precloacal pores are the most important variables for discriminating between sexes. Again, the sex with higher values for one of these variables has lower values for the other.

Multivariate tests

Multivariate normality of the entire dataset was rejected with a 95% confidence (Table 5).

According to the non-parametric multivariate analysis of variance (perMANOVA) there are significant differences between sexes for both morphometric (F = 6.31; P < 0.001) and meristic (F = 54.85; P < 0.001) data, whereas this analysis rejected geographic differences for all arranges of localities considering main rivers as barriers and also between localities individually treated (Table 6).

Mantel tests did not find significant correlations and therefore rejected the hypothesis of isolation by distance for both males (morphometric data: R = −0.09, P = 0.895; meristic data: R = −0.08, *p* = 0.910) and females (morphometric data: R = 0.06, P = 0.159; meristic data: R = −0.01, P = 0.557).
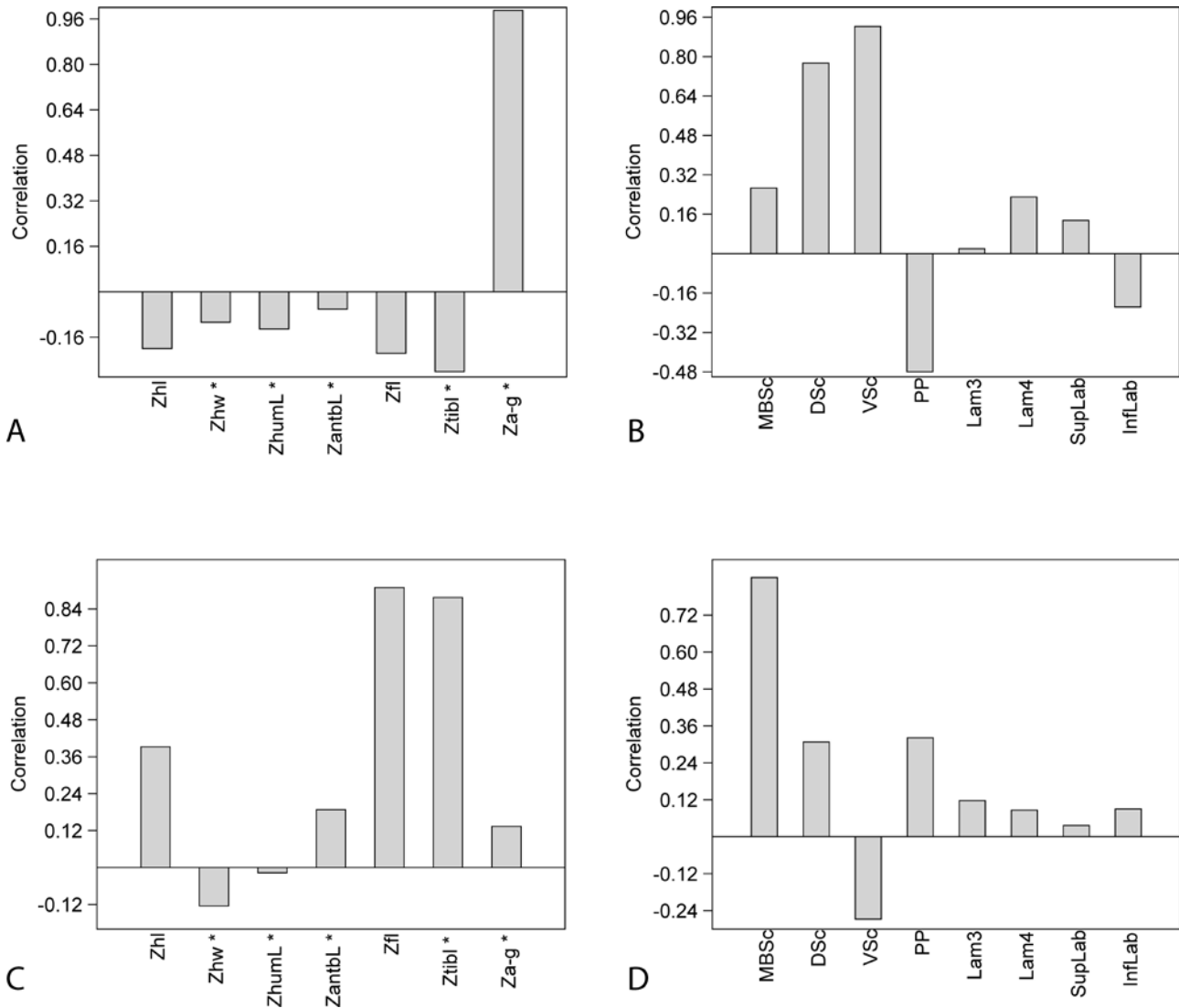
Fig. 2. Correlation coefficients of each variable in the first two principal components. A: morphometrics variables in the first principal component; B: morphometric variables in the second principal component; C: meristic variables in the first principal component; D: meristic variables in the second principal component. SVL: snout-vent length; HL: head length; HW: Head width; humL: humerus length; antbL: forearm length; FL: femur length; TibL: Tibial length; A-G: axilla-groin distance; MBsc: scales around mid-body; DSc: dorsal scales; VSc: ventral scales: PP: precloacal pores; Lam3: subdigital lamellae of third finger; Lam4: subdigital lamellae of fourth toe; SupLab: supralabial scales; InfLab: infralabial scales.

Univariate tests

Univariate tests (Mann-Whitney or t-test) show that those variables that are most influential for discriminating between sexes according to the DFA, also have highly significant sexual differences (P < 0.010 and P < 0.001) (i.e., axilla-groin distance; tibia length; head length; number of ventral scales, and number of precloacal pores) (Table 7). In addition, there are also significant differences (P < 0.05) in snout-vent length (SVL)

and number of subdigital lamellae of the fourth toe (Lam4). However, it is possible that an asymmetric distribution of juveniles and adults among sexes could be influencing this result for SVL. Unfortunately, given that data about minimum size at sexual maturity are only available for females (Ramirez Pinilla 1991; Martori and Aun 1997), the limit between juveniles and adults cannot be established for both sexes.
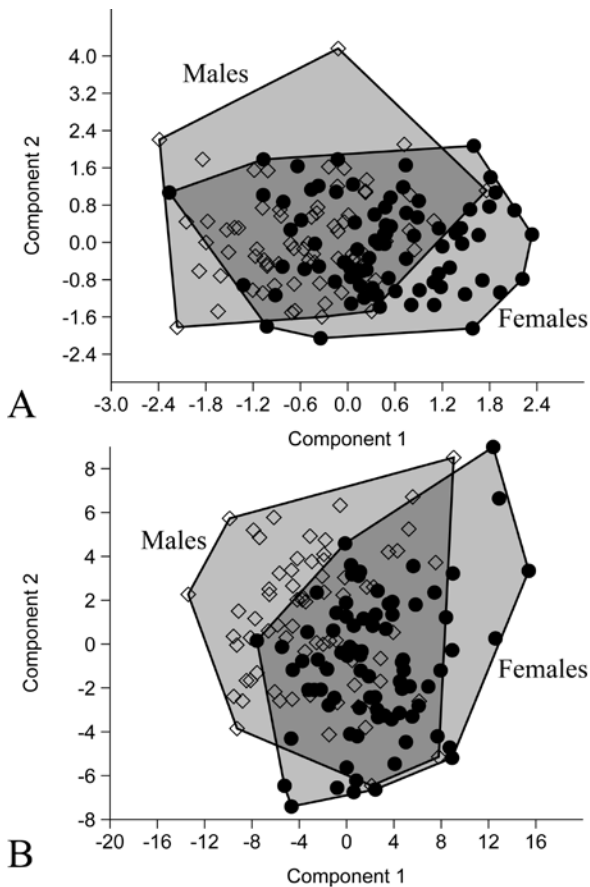
Fig. 3. Bidimensional projection of the morphological data of *Liolaemus wiegmannii* in the first two principal components. A: morphometric variables; B: meristic variables. Squares represent males whereas black full circles are females.

Table 4. Confusion matrix of the Discriminant Function Analysis for morphometric and meristic variables of *Liolaemus wiegmannii* from Uruguay. Values in the third and fourth column represent the number of individual assigned to each sex by the discriminant function.

		Male	Female	Total	Correctly assigned (%)
Morphometric variables	Male	54	18	72	75.0
	Female	24	58	82	70.7
	Total	78	76	154	
Meristic variables	Male	61	11	72	84.7
	Female	12	70	82	85.4
	Total	73	81	154	

Table 5. Multivariate normality test results for the morphology of *Liolaemus wiegmannii* from Uruguay. All analyses were implemented in Past 3.07.

Test	Parameter	Coefficient	Statistic	d.f.	P(normal)
Mardia	Skewness	39.06	1003	680	8.62×10^{-15}
	Kurtosis	269.7	4.044		5.27×10^{-5}
Dornik & Hansen omnibus		124.5			1.78×10^{-13}

Table 6. perMANOVA results for morphometric and meristic data of *Liolaemus wiegmannii* from Uruguay considering three levels of variation. "A+B/C+D" tests differences between west and east Santa Lucía River localities. "A/B/C/D" evaluates differences between all the groups of localities divided by Rosario River, Santa Lucía River and Maldonado Stream and "Localities" considers the hypothesis of differences between each locality.

Groups tested	Data		F	P
A+B/C+D	*Morphometric*	♂	0.680	0.814
		♀	0.626	0.775
	Meristic	♂	-0.223	0.887
		♀	3.248	0.098
A/B/C/D	*Morphometric*	♂	0.970	0.505
		♀	0.825	0.705
	Meristic	♂	-0.064	0.861
		♀	1.277	0.341
Localities	*Morphometric*	♂	1.359	0.088
		♀	0.996	0.487
	Meristic	♂	0.722	0.589
		♀	1.954	0.175

DISCUSSION

Intraspecific and geographic variation

Considering both males and females, specimens of *Liolaemus wiegmannii* from Uruguay reach a maximum snout-vent length of 61 mm with females tending to be larger than males. This observed size is in the range of those reported in the literature for individuals from Argentina (Etheridge 2000; Avila et al. 2009).

Cei (1979) and Avila and Martori (1996) reported geographic variation in size and number of scales around mid-body in individuals from Argentina. The highest values were observed in Bahía Blanca (56-60), whereas the lowest were found in Tucumán (46-48), while Mendoza (48-50) had intermediate ranges. The range of this variable in individuals from Uruguay (41-58) is markedly broader than that observed in each one of these populations, being comparable with the whole interval reported for this species (Etheridge 2000; Avila et al. 2009). Unlike the number of scales around mid-body, information about other meristic variables in literature is scarce

Table 7. Morphological differences of *L. wiegmannii* between sexes, tested for each variable through a Mann-Whitney or *t* test, depending on the normality of each variable according to Shapiro-Wilk test. *Z* indicates transformed variables following the method proposed by Lleonart et al. (2000).

Variable	Shapiro-Wilk Test	Mann-Whitney Test	*t* Test
SVL*	W=0.95; P=0.0050	U=2381; **P=0.039**	
Z-HL**	W=0.98; P=0.015	U=2198; **P=0.0064**	
Z-HW	W=0.99; P=0.55		t=0.49; P=0.62
Z-humL	W=0.99; P=0.18		t=0.36; P=0.72
Z-antbL	W=0.99; P=0.78		t=0.48; P=0.64
Z-FL	W=0.98; P=0.017	U=2598; P=0.20	
Z-TibL**	W=0.99; P=0.39		t=2.99; **P=0.0031**
Z-A-G***	W=0.99; P=0.65		t=-6.72; **P=3.45x10^{-10}**
MBSc	W=0.97; P=0.0024	U=2888; P=0.82	
DSc	W=0.97; P=0.0091	U=2513; P=0.11	
VSc***	W=0.99; P=0.40		t=-7.98; **P=3.30x10^{-13}**
PP***	W=0.81; P=8.24x10^{-13}	U=1280; **P=2.95x10^{-10}**	
Lam3	W=0.86; P=1.12x10^{-10}	U=2817; P=0.60	
Lam4*	W=0.95; P=5.52x10^{-5}	U=2339; **P=0.023**	
SupLab	W=0.78 ; P=6.23x10^{-14}	U=2727; P=0.36	
InfLab	W=0.78; P=7.96x10^{-14}	U=2866; P=0.72	

P<0.05*; P<0.01**; P<0.001***.

and without specific geographic information, hampering the comparison with our data. Nevertheless, it can be observed that lepidosis in Uruguay shows broad ranges for almost all variables that overlap with the known variation across the whole distribution of the species (Etheridge, 2000).

Most of the morphological variation observed in Uruguay seems to be related to differences between sexes because most variables highly correlated with PCA1 and PCA2 are the same that statistically discriminate sexes. However, other variables are also highly correlated with the first two principal components (Fig. 2), but do not show significant differences between sexes (Table 7), suggesting that there is some morphological variation that is not explained by sexual dimorphism and accounts for the overlap seen in PCA space (Fig. 3). Nevertheless, this additional variation could not be attributed to geographic variability, given that morphological differences among groups of localities were rejected and there was no correlation between morphological and geographic distances. The absence of geographically-structured morphological variation in Uruguay contrasts with the differences in mid body scales found by Cei (1979) and Avila and Martori (1996) among several isolated populations in Argentina, which could actually represent separate species (Avila, 2003; Morando, 2004; Avila et al., 2006; Avila et al., 2009; Olave et al., 2014).

Sexual dimorphism

Sexual dimorphism in *L. wiegmannii* from Uruguay is strongly supported by several independent multi- and univariate analyses, which show that males have a longer head and tibia, and present a higher number of precloacal pores than females. On the other hand, females have a longer axilla-groin distance and exhibit a higher number of ventral scales. Based on seven morphometric variables, Cabrera et al. (2013) found that males and females differ only in axilla-groin distance and humerus length. Unlike the axilla-groin distance, the humerus length is not sexually dimorphic in specimens from Uruguay. Indeed, the humerus length is one of the variables with the lowest correlation coefficient with PCA1 and PCA2, and the least influential on the morphometric discriminant function. These discrepancies might suggest differences on the distribution of morphological variation among populations from Argentina and Uruguay.

Among *Liolaemus*, head dimensions and axilla-groin distance are sexually dimorphic in most of the species analyzed, suggesting that it is a relatively common pattern among these lizards (Villavicencio et al., 2003; Verrastro, 2004; Laspiur and Acosta, 2007; Cabrera et al., 2013; Astudillo et al., 2015).

Taking into account the main hypotheses regarding the causes of sexual dimorphism in lizards, sexual selection might adequately explain the differences in head and

tibia length and the number of precloacal pores found in this work. Longer heads in males of *L. wiegmannii* could suggest the existence of agonistic encounters between them, where individuals with longer heads would have an advantage in combats getting greater access to females (Carpenter and Fergusson, 1977; Carothers, 1984; Anderson and Vitt, 1990; Herrel et al., 1999; Verrastro, 2004; Huyghe et al., 2005; Vanhooydonck et al., 2010). In this sense, although scarcely documented, some male-male agonistic encounters have been observed among *Liolaemus* species (Halloy, 1996; Martins et al., 2004; Verrastro, 2004; Labra et al., 2007; Cabrera et al., 2013; Halloy et al., 2013). Additionally, males of some species of *Liolaemus* show hierarchical structure according to the size of their home range, suggesting the occurrence of male-male interactions, and therefore a potential evidence of sexual selection (Halloy and Robles, 2002; Frutos and Belver, 2007; Robles and Halloy, 2009; Cabrera et al., 2013). Moreover, Martins et al. (2004) has pointed out that the head and limbs are structures that play an important role in communication in *Liolaemus* lizards, and consequently, it is possible that sexual differences in these traits could be related to their use in this context. Head-bobbing seems to be a common behavior for signaling among *Liolaemus* males, both in aggressive interactions and courtship (Martins et al., 2004; Labra et al., 2007; Halloy, 2012; Halloy et al., 2013; Vicente and Halloy, 2015). In addition, several species displaying these behaviors, also show sexual dimorphism in head size, where males are always the sex with larger heads (Villavicencio et al., 2003; Laspiur and Acosta, 2007; Cabrera et al., 2013; Astudillo et al., 2015). This might suggest, at least for some species, a possible relationship between head-bobs and sexual dimorphism in head size that deserve further study. Although little is known about the behavior of *L. wiegmannii*, Achaval and Olmos (2007) have mentioned that head movements are observed during courtship, suggesting the possibility that head size differences could be related to its use in courtship or for warning other males during territory defense.

Alternatively, sexual dimorphism in head length observed in *L. wiegmannii* could also be the result of trophic niche segregation. However, Vanhooydonck et al. (2010) pointed out that bite force and consequently head dimension differences in male *Liolaemus* lizards is better explained by sexual selection rather than natural selection (i.e., niche segregation). Therefore, considering the phylogenetic context, head length sexual dimorphism found in *L. wiegmannii* is more likely to be the result of sexual selection than trophic niche segregation. Even so, given that information about the intersexual diet variation in *L. wiegmannii* remains scarce (see Aun et

al., 1999), the role of niche segregation on sexual dimorphism still demands further research.

Several lizard species show a strong positive correlation between hindlimb length and sprint speed (Snell et al., 1988; Losos, 1990; Miles, 1994; Bauwens et al., 1995; Bonine and Garland, 1999). Additionally, some studies have suggested that variation in sprinting ability can affect survival probabilities within populations of reptiles (Christian and Tracy, 1981; Jayne and Bennett, 1990; Miles, 2004, Vervust et al., 2007). In this sense, Bauwens et al. (1995) pointed out that the evolution of longer hindlimbs relative to body size is one of the main factors driving the evolution of high maximum sprinting ability in lizards. In this context, considering the notorious sexual differences in coloration observed in *L. wiegmannii*, where males are clearly less cryptic than females and thus, probably more detectable, it is reasonable to think that predation might play a more important role as a selection pressure in males, favoring faster runners, and therefore longer tibia. Alternatively, it should be taken into account that sprint speed could be also important for a more effective territory defense, where faster males are expected to defend a larger territory and/or more females through exclusion of slower rival males that still can usurp mates (Husak et al., 2006, 2008; Peterson and Husak, 2006). Consequently, if territorial defense occurs in *Liolaemus wiegmannii*, as in other species of the genus, and if the longer tibia (and thus, hindlimb) of males provide them an advantage for faster movements around territory boundaries, sexual selection could also have favored a longer tibia in males. On the other hand, given that among *Liolaemus* only the forelimbs are known to be implicated in communication (Martins et al., 2004; Halloy and Castillo, 2006; Halloy, 2012), it seems unlikely that differences in hindlimb dimensions are related to a communication use in this species.

Precloacal pores allow for the external exudation of chemical secretions by integumentary glands (Valdecantos et al., 2014), which in *Liolaemus* species have been suggested as important for stimulating copulation (Rocha 1996). Other authors think that these secretions play a role in territorial defense and recognition contexts similar to those in which head-bob displays are observed (Labra and Niemeyer, 1999; Martins et al., 2004). In addition, the use of chemical secretions by some male lizards allows them to reduce the cost of territory defense (Labra and Niemeyer, 1999 and references therein). In this scenario, the presence of more and bigger precloacal pores in males of *Liolaemus wiegmannii* could suggest that these might play a more important role in males than females, for instance, for territorial defense. If this is the case, it is possible that sexual selection could be underly-

ing the observed dimorphism in the number of precloacal pores. Moreover, the presence of precloacal pores in both male and female individuals suggests that the role of these glands on communication is not only for male territorial defense. It is known that chemical recognition of females during reproductive season occurs in *Liolaemus tenuis*, a species with precloacal pores present in both sexes (Labra and Niemeyer, 1999). Therefore, although the dimorphism in the number of precloacal pores found in this study may have evolved for male-male defense, we cannot discard their role in male-female communication, or even both roles as the drivers of sexual selection.

In many lizard species, females are under fecundity selection for larger abdomen size, suggesting that this is probably the most frequent mechanism underlying the widespread pattern of sexual dimorphism in axilla-groin distance (Scharf and Meiri, 2013). An increase in axilla-groin distance, and therefore in abdomen size, provides to females the possibility of enlarging the space for storing eggs and, consequently, increasing their fecundity, which easily becomes a target of natural selection (Tinkle et al., 1970; Kozlowski, 1989; Braña, 1996; Fairbairn, 1997; Zamudio, 1998; Cox et al., 2003; Blanckenhorn, 2005; Du et al., 2005). Based on the fecundity advantage hypothesis, it is reasonable to think that the larger abdomen found in females of *L. wiegmannii* is a result from fecundity selection. In addition, it is possible that the enlargement of the female's abdomen could have led to an increase in the number of ventral scales observed in this sex. However, there is a reduction in the size of the ventral scales of females toward the cloacae, which might also contribute to the sexual differences found.

Finally, it is important to see that although sexual dimorphism seem to be a widespread pattern among lizards, where head (larger in males) and abdomen (larger in females) are the most frequent traits that differ between sexes, studies that test explicitly the hypotheses behind this phenomenon remain scarce (Scharf and Meiri, 2013). In this sense, the potential mechanisms proposed here for explaining the occurrence of sexual dimorphism in *Liolaemus wiegmannii*, should be taken as tentative. Further research is needed to explore and test explicitly the role of fecundity, behavior, and niche segregation on the sexual dimorphism observed on this species.

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APPENDIX 1

Individuals of *Liolaemus wiegmannii* used in the analysis and their respective localities from Uruguay. ZVC: vertebrate collection of the Faculty of Sciences, University of the Republic; MNHN: collection of the Museum of Natural History, Uruguay. *Excluded from geographical analysis.

Locality	Individuals
Arazatí, San José	ZVC 303, ZVC 324, ZVC 1229-1233, ZVC 1223, ZVC 6876, ZVC 6877, MNHN 5838, MNHN 5839
Artilleros, Colonia	MNHN 3346, MNHN 3348
Balneario Argentino, Canelones	ZVC 2498
Bello Horizonte, Canelones	MNHN 5662
Boca del Cufré, San José	ZVC 3761
Boca del Mauricio, San José	ZVC 6869, ZVC 6870, ZVC 6872-6875
Boca del San Salvador, Soriano	MNHN 154
Brisas del Plata, Colonia	ZVC 2105
Cabo Polonio, Rocha	ZVC 1499, ZVC 1863, ZVC 2504, ZVC 3387, ZVC 1839, ZVC 1932, ZVC 1497, ZVC 1497, ZVC 1864, ZVC 646, ZVC 1224, ZVC 6621, ZVC 6625, ZVC 6626, ZVC 6855-6857, MNHN 3425, MNHN 3427, MNHN 5671
Carrasco Stream, Canelones	ZVC 1939
Carrasco, Montevideo	ZVC 3549, ZVC 5153, MNHN 149, MNHN 165, MNHN 3304
Coast of Rio Negro River, in front of Villa Soriano, Soriano	ZVC 774*
Cuchilla Alta, Canelones	MNHN 3361
El Pinar, Canelones	ZVC 5050, ZVC 6859
La Floresta, Canelones	MNHN 168
La Paloma, Rocha	ZVC 914, MNHN 3127
Lagomar, Canelones	ZVC 6023, ZVC 6227, ZVC 3712, ZVC 2824, ZVC 2825, ZVC 3711, ZVC 3764
Laguna de Garzón, Rocha	MNHN 157, MNHN 3338, MNHN 3339
Laguna de Rocha	ZVC 5366
Laguna del Diario	MNHN 3344
Las Cañas, Río Negro	MNHN 3308*
Las Vegas, Canelones	ZVC 6860, ZVC 6861
Lomas de Carmelo, Colonia	ZVC 6878- 6881
Los Titanes, Canelones	ZVC 2435
Malvin, Montevideo	MNHN 1064, MNHN 1065, MNHN 3349, ZVC 595, ZVC 876 ZVC 585
Manantiales, Maldonado	ZVC 2442
Médanos de Solymar, Canelones	ZVC 3570
Nueva Palmira, Colonia	ZVC 1967, ZVC 1968, ZVC 1969
Pajas Blancas, Montevideo	ZVC 4357, ZVC 4361, ZVC 4362, ZVC 6845-6849
Pando, Canelones	MNHN 196, MNHN 199
Pinamar, Canelones	ZVC 1342
Playa Pascual, San José	MNHN 2445, MNHN 3310, MNHN 3311, MNHN 3312, MNHN 3313, MNHN 3314, MNHN 3337, ZVC 5152, ZVC 6865-6868, ZVC 6871
Portezuelo, Maldonado	MNHN 176
Punta Espinillo, Montevideo	ZVC 6850-6854
Punta Negra, Maldonado	MNHN 266, MNHN 3306, MNHN 3340, MNHN 3342, MNHN 3343, ZVC 6308
Rio de la Plata, 3 km east of Martin Chico, Colonia	ZVC 2164
San Gregorio Stream, San José	ZVC 970
San Luis, Canelones	ZVC 3307
Tigre Stream, San José	ZVC 1506-1508
West side of Cerro de Montevideo, Montevideo	ZVC 1385

APPENDIX 2

Results of the Student's t-test on the slopes of linear regressions between each transformed variable and snout-vent length (SVL). Z indicates transformed variables; hl: head length, hw: head width, humL: humerus length, antbL: forearm length, fl: femur length, tibl: tibia length, a-g: axilla-groin distance.

	Zhl vs SVL	Zhw vs SVL	ZhumL vs SVL	ZantbL vs SVL	Zfl vs SVL	Ztibl vs SVL	Za-g vs SVL
Slope	0.001163	6.53×10^{-5}	-3.798×10^{-5}	-0.0008418	-0.001766	-0.001699	-0.0005518
t value	0.236	0.017	-0.008	-0.222	-0.322	-0.326	-0.053
p(slope=0)	0.813	0.986	0.994	0.825	0.748	0.745	0.958