

Body size variation and sexual size dimorphism across climatic gradients in the widespread treefrog *Scinax fuscovarius* (Anura, Hylidae)

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Abstract Variation in body size represents one of the crucial raw materials for evolution. However, at present, it is still being debated what is the main factor affecting body size or if the final body size is the consequence of several factors acting synergistically. To evaluate this, widespread species seem to be suitable models because the different populations occur along a geographical gradient and under contrasted climatic and environmental conditions. Here we describe the spatial pattern of variation in body size and sexual size dimorphism in the snouted treefrog *Scinax fuscovarius* (Anura, Hylidae) along a 10° range in latitude, 25° longitude, and 2000 m in altitude from Argentina, Brazil and Paraguay using an information-theoretic approach to evaluate the support of the data for eight a priori hypotheses proposed in the literature to account for geographical body size, and three hypotheses for sexual size dimorphism variation. Body size of *S. fuscovarius* varied most dramatically with longitude and less so with latitude; frogs were largest in the northwestern populations. Body size was positively related with precipitation seasonality, and negatively with annual precipitation. Furthermore, the degree of sexual size dimorphism was greatest in the western populations with less annual precipitation, as the increase in body size was stronger for females. Our results on body size variation are consistent with two ecogeographical hypotheses, the starvation resistance and the water availability hypotheses, while our results on sexual size dimorphism in *S. fuscovarius* supports the differential-plasticity hypothesis but the inverse to Rensch's rule and the parental investment hypothesis. Due to the weak association between environmental variables and body size and sexual size dimorphism variation, we stress that there are other factors, mainly those related to the life history, driving the geographical variation of *S. fuscovarius*.

Key words: ecogeographic hypotheses, information-theoretic approach, intraspecific variation, precipitation, sexual dimorphism index.

INTRODUCTION

Body size is a fundamental property of animal form, related to behavior, ecology, morphology, and physiology (White *et al.* 2007). Based on this assumption, there are numerous studies from multiples disciplines that involve body size as the key aspect of evolutionary adaptation and diversification of organisms (e.g., Blanckenhorn 2000; Huang *et al.* 2017; Kruuk 2017). In this context, variation in body size represents one of the crucial raw materials for evolution to occur.

The existence of geographic clines in body size might reflect trade-offs that can be at least partially genetically determined (e.g., Marangoni & Tejedo 2008) and ultimately shaped by environmental

variation (e.g., Marangoni *et al.* 2008; Stillwell 2010). According to these authors, it is important to distinguish between genetic and environmental contributions to phenotypic variation in size because we may undervalue the role that plasticity plays in shaping geographic clines and whether these clines are adaptive.

The relationship between environmental gradients and patterns of geographic variation in body size has been studied for more than 150 years and several ecogeographic rules have been proposed (Bergmann 1847; Rensch 1938; Mayr 1956; James 1970; Gaston *et al.* 2008). However, there are still controversies about whether endothermic and ectothermic organisms follow the same patterns (e.g., Ashton 2002). The lack of a general pattern in ectotherms suggests that more than a single mechanism is necessary to explain the geographical variation in body size (Terribile *et al.* 2009). To further complicate matters, most

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species show some degree of sexual size dimorphism (SSD), and several climate gradients have been identified as important correlations of the SSD (Schäuble 2004; Blanckenhorn *et al.* 2006). This means that (i) body size variation among populations could be explained only by one or both sexes and/or (ii) body size variation in each sex may have its own explanation, genetic and/or environmentally induced (as explained in the differential-plasticity hypothesis; Angilletta & Dunham 2003).

Among amphibians, few studies on trends in body size variation have been carried out, including nearly 5% of total amphibian species around the world (Ashton 2002; Schäuble 2004; Laugen *et al.* 2005; Olalla-Tárraga & Rodríguez 2007; Adams & Church 2008; Marangoni & Tejedo 2008; Marangoni *et al.* 2008; Bidau *et al.* 2011; Liao & Lu 2012; Gouveia *et al.* 2013; Boaratti & Da Silva 2015; Liao *et al.* 2015; among others). However, there is a wide range of plausible explanations. In cross-species analyses among anurans species, Ashton (2002) reported the apparent absence of a general relationship between body size and temperature while Olalla-Tárraga *et al.* (2009) and Gouveia and Correia (2016) link body size variation to environmental water deficit, mainly in tropical regions. Boaratti and Da Silva (2015) compared different ecogeographic hypothesis between three Brazilian species and suggested that intraspecific variation in anuran body size is more dependent on species-specific response than on the region (i.e. temperate or tropical) where they occur. Therefore, more studies are needed to complete our knowledge of the environment–body size association among anuran species.

On the other hand, several authors have demonstrated a geographic trend in body size and SSD within species, some with some environmental variables as explaining factors, other with no relationship (Nevo 1973; Schäuble 2004; Laugen *et al.* 2005; Cvetkovic *et al.* 2008; Marangoni *et al.* 2008; Yu *et al.* 2010; Oromi *et al.* 2012; Hsu *et al.* 2014; Feng *et al.* 2015; Valenzuela-Sánchez *et al.* 2015; Davenport & Hossack 2016; Gouveia & Correia 2016). Also, differences in age at maturity, longevity, growth rates, or substrate could also account for population divergence (e.g. Bruce & Hairston 1990; Leclair *et al.* 2005; Marangoni *et al.* 2008; Hsu *et al.* 2014). On the other hand, temporal changes in average body size within populations in relation to density may be a significant component of phenotypic variation (Green & Middleton 2013). Within this framework, it is still arguable if there is a unique, main, factor affecting body size (often identified as being temperature or moisture) or if the final body size is the consequence of several factors acting synergistically. In this sense, a detailed study of body size variation among populations is necessary,

including a greater number of species, in order to obtain a general explanation across taxonomic levels (Fairbairn 1997).

To evaluate this, species with a wide geographic distribution seem to be suitable models because the different populations occur along a latitudinal, longitudinal, and altitudinal gradient and therefore under contrasted climatic and environmental conditions. The snouted treefrog *Scinax fuscovarius* (Hylidae, Anura) occurs throughout urban, periurban, and open non-forested lands of southeastern Brazil, northern Argentina, Paraguay, and Bolivia (Frost 2016). Throughout its wide geographic range, *S. fuscovarius* occurs in several ecoregions, being exposed to considerable variation in climatic and geographic conditions (Fig. 1).

Therefore, we explored the pattern of geographic variation in body size and SSD in *S. fuscovarius* along a 10° range in latitude, a 25° range in longitude and a nearly 2000 m range in altitude using an information theoretic-approach to investigate the relative support for a set of competing hypotheses that potentially influence the geographic pattern of the body size. These competing hypotheses being: (i) heat balance: this hypothesis predicts a negative relationship between body size and temperature (Olalla-Tárraga & Rodríguez 2007). The lower surface-to-volume ratio of larger animals implies higher heat conservation capacity; (ii) starvation resistance: this hypothesis predicts that in more seasonal environments, large-bodied species should be able to ride out longer periods of unfavorable conditions because energy stores increase with size faster than metabolic rate (Cushman *et al.* 1993); (iii) growing season length: predicts that season length has a considerable influence on body size because of constraints on resource availability, resulting in an increase in body size in less seasonal environments (Bidau & Martí 2007); (iv) water availability: predicts that a large body size is associated with dry climates because of higher desiccation tolerance (Ashton 2002); (v) Converse water availability: predicts large body sizes are associated with areas with greater precipitation because the activity of amphibians is often associated with high water availability or wet periods (Zug *et al.* 2001); (vi) Primary productivity: areas with higher productivity provide more food supply and thus permit the attainment of a larger size (Rosenzweig 1968); (vii) the water conservation: predicts that body size increase towards more dehydrating environments which does not necessary means warmer environments (Gouveia & Correia 2016); and (viii) the energy-water conservation: a large body provides greater heat conservation in cold macroclimates and greater water conservation in dry areas (Olalla-Tárraga *et al.* 2009).

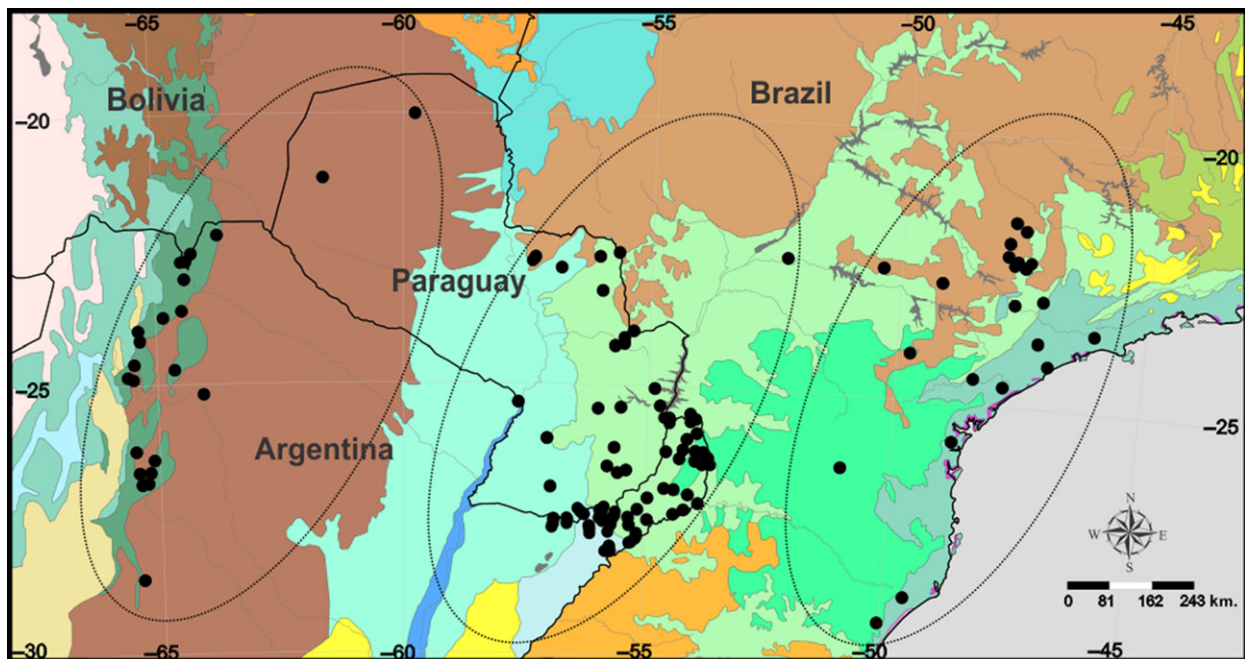


Fig. 1. Localities sampled (black circles) of *Scinax fuscovarius* populations separated into three major regions: western, central and eastern (dashed circles). Landscape colors indicate different ecoregions. We used Simplemappr (Shorthouse 2010) and Inkscape version 0.91 to plot each locality on a digital map of the area. [Colour figure can be viewed at wileyonlinelibrary.com]

A previous study considering a single population of *S. fuscovarius* from Central Brazil has shown that females are significantly larger than males in this species (Rodrigues *et al.* 2005). However, we ask: (i) does the SSD in this species show a geographic trend?, (ii) is it related to climatic variation?, and (iii) do males and females exhibit different patterns of clinal variation in body size across environmental gradients? These questions rely on a series of rules and hypothesis about the evolution of SSD to be discussed: (i) Rensch rule, SSD increases with body size when males are the larger sex, and decreases with body size when females are the larger sex; (ii) parental investment hypothesis: larger females can afford a greater parental investment (i.e. larger eggs or larger clutches). This hypothesis predicts that females are larger in cold climates, that is, sexual dimorphism increases in cold climates; and (iii) differential-plasticity hypothesis: sex-differential plasticity to environmental variables generates inter-population variation in the degree of sexual dimorphism.

In this study, we investigated whether these hypotheses can explain geographical variation of body size and SSD in the treefrog *S. fuscovarius*. The analysis of geographic and environmental factors that could influence body size will allow us not only to explore the possible variation of patterns in this species, but also to identify the best correlates of this variation.

METHODS

Scinax fuscovarius morphological data

We obtained the dataset after examined 798 vouchers stored at the herpetological collections: Célio F. B. Haddad (CFBH), Universidade Estadual Paulista 'Júlio de Mesquita Filho', Rio Claro, Brazil; Laboratorio de Genética Evolutiva (LGE), Instituto de Biología Subtropical, Misiones, Argentina; Museo Nacional de Historia Natural del Paraguay, Paraguay (MNHNP), Asunción, Paraguay; and Fundación Miguel Lillo (FML), Tucumán, Argentina (see Appendix S1 for detailed reference). Sex was determined by visual inspection of secondary sexual characters, such as nuptial pads or extended vocal sacs in males, and presence of ovarian follicles in females. Based on our observations and data from the literature (Goldberg 2015), we considered as adult, all specimens with more than 35 mm of snout-vent length. We analyzed the body size variation based on snout-vent length (SVL). Measurements were taken with digital calipers (precision 0.01 mm). For each hypothesis we predicted a priori a specific relationship between body size and environmental features as depicted in Table 1. We estimated SSD using the Lovich and Gibbons (1992) index, in which $SDI = (\text{size of larger sex} / \text{size of smaller sex}) \pm 1$, +1 if males are larger or -1 if females are larger, and arbitrarily defined as positive when females are larger than males and negative for the contrary. In order to analyze SSD in other morphometric variables we measured, following Duellman (1970), with digital calipers (precision 0.01 mm): head length (HL), head wide (HW), tibia length (TL), and total length of the arm (TAL), which

Table 1. Snout-vent length (SVL) of *Scinax fuscovarius* specimens. Measurements are given as mean $\pm$ SD (min–max) for all specimens, males and females

Sex	<i>n</i>	All specimens	West	Center	East
SVL					
Both sexes	797	44.90 $\pm$ 3.21 (36.00–55.46)	47.77 $\pm$ 3.41 (36.66–55.46)	44.11 $\pm$ 2.73 (36.60–53.84)	43.92 $\pm$ 2.35 (36.00–49.36)
Females	319	45.50 $\pm$ 3.57 (37.60–55.46)	48.62 $\pm$ 3.70 (38.26–55.46)	44.48 $\pm$ 2.99 (37.60–53.84)	44.35 $\pm$ 1.91 (40.73–47.33)
Males	478	44.49 $\pm$ 2.87 (36.00–54.26)	46.60 $\pm$ 2.93 (36.66–54.26)	43.87 $\pm$ 2.52 (36.60–52.61)	43.65 $\pm$ 2.58 (36.00–49.36)

was taken from the tip of finger IV to the beginning of the humerus.

Geographic and environmental variables

Geographic coordinates (latitude, longitude, and altitude) of each voucher analyzed, in most cases, were obtained from collection database. However, some altitudinal records were obtained from Google Earth. We used the WorldClim database Version 1.4 (Hijmans *et al.* 2005) at spatial resolution of 30 arc-seconds in the program Arc-GIS to obtain the four climatic variables for each collection point for a 50-year period (1950–2000). BIO1 = Annual Mean Temperature, BIO4 = Temperature Seasonality (standard deviation $\times$ 100), BIO12 = Annual Precipitation, BIO15 = Precipitation Seasonality (Coefficient of Variation). In addition, potential evapotranspiration (PET) for each point was obtained from CGIAR-CSI Global Soil-Water Balance Database (Trabucco & Zomer 2010) following Gouveia and Correia (2016) and Normalized Difference Vegetation Index (NDVI) of each site using images from 2000 (satellite Terra, MODIS sensor) with a spatial resolution of 1 km (https://reverb.echo.nasa.gov/reverb/#utf8=%E2%9C%93&spatial_map=satellite&spatial_type=rectangle). The NDVI provides values that are highly correlated with photosynthetic mass and primary productivity. We obtained images of the two mid-weeks of each month and the mean annual NDVI was subsequently calculated (https://lpdaac.usgs.gov/dataset_disc/overly/modis/modis_products_table/mod13a3_v006).

Statistical analyses

Data were analyzed with InfoStat 2012e (Di Rienzo *et al.* 2016). We used ARCGIS 10.0 to calculate Moran's *I*, as a measure of spatial autocorrelation of SVL. We also used a Monte Carlo permutation test (199 permutations) in SAM 3.0 to assess spatial autocorrelation of residuals (Lichstein *et al.* 2002; Rangel *et al.* 2010). SVL was log-transformed to meet normality and/or homogeneity of variance. Linear regression analyses were used to explore the relationships between body size and environmental variables following Valenzuela-Sánchez *et al.* (2015). We also used these analyses for evaluate each sex separately. To show the incidence of extreme geographic variation in body size along the environmental gradient, we categorized geographic variation in three regions: western, central, and eastern, in accordance with the

distribution of sampled specimens (Fig. 1). This does not mean the species has a disjunct distribution but reflects the specimens available in the herpetological collection studied, which are among the most important in the region (Appendix S1). In this sense, other geographical trends could emerge in other non-sampled regions. In any case, it reflects the different ecoregions that comprise each region, i.e., Dry Chaco and Southern Andean Yungas in the western region; Humid Chaco, Interior Atlantic forest, Southern Cone Mesopotamian savanna and, in a small proportion, Cerrado in the central; and Cerrado, Araucaria moist forest, and Serra do Mar coastal forest in the eastern region. ANOVA and post hoc Tukey's test were used to detect significant differences in SVL (whole sample, males, and females) and climate indexes among the three regions.

Sexual dimorphism was studied by different approaches. First, we examined dimorphism in overall body size of the whole sample using Student *t* test. Then, a 2×3 factorial ANOVA with SVL as the dependent variable was used to test for effects due to sex and region. A significant SEX $\times$ REGION interaction would demonstrate geographic variation in SSD (Lovich *et al.* 1998). Thereafter, we used the Student *t* test to assess the significance of overall size difference between the sexes in each region. Finally, to evaluate the amount of SSD variation that could be related to environmental variables we performed a regression analysis with SDI as the dependent variable. In order to include latitude, longitude, and climate in the same analysis, we calculated the mean value for each of the climate components for each one-degree block in which latitudinal and longitudinal gradients were categorically divided (Schäuble 2004). The direction of the relationship between body size and each of the climatic variables retained in the final regression model was determined from the sign of the correlation coefficients (Schäuble 2004).

Using the mean adult body size per site or SDI per one-degree block as dependent variables and bioclimatic and NDVI data as independent variables, we calculated Akaike's information criterion (AIC) for body size and AIC corrected for small sample sizes (AICc) for SSD, and Akaike weight (*w*; Burnham & Anderson 2002). To evaluate the strength of support for each model, we compared the models within a set based on Δ AIC or Δ AICc (difference between the AIC of a given model and the lowest AIC model in the set) and Akaike weight (a measure of the support for a given model relative to the other models in the set; Burnham & Anderson 2002). We considered a model to be well supported by the data if it had a Δ AIC < 2 and/or *w* > 0.8.

RESULTS

Mean values for SVL variation of the whole sample are detailed in Table 1. There was a significant difference between specimens from the three regions ($F = 94.39$; $P < 0.001$). Post hoc comparisons using the Tukey test indicated that the specimens from the west were significantly different from those from the central and the eastern regions. SVL was not spatially autocorrelated (Moran's $I = -0.07$, $P = 0.69$), indicating that the pattern of values distribution does not appear to be significantly different from random.

Within the set of models which examined the influence of environmental variables on body size variation, the precipitation seasonality and annual precipitation received the most support from the data (Table 2). Although the temperature plus precipitation seasonality model also received support, the relationship between body size and temperature seasonality was not significant. The independent contribution of each environmental variable is depicted in Table 2. Body size was positively related with precipitation seasonality and negatively with annual precipitation. The residuals of the best model were not spatially autocorrelated (Monte Carlo permutation test, $P > 0.1$), indicating that spatial autocorrelation did not bias our results.

Sexual dimorphism

Overall, *S. fuscovarius* females were significantly larger than males (all specimens, $t = 5.85$; $P < 0.001$), although body size ranges overlapped considerably (Fig. 2). In this sense, examination of the means of

other measures indicated that for all variables, females were larger by 0.5–1 mm (Fig. 2).

A 2×3 factorial ANOVA that compared body size between sexes and among our three regions demonstrated that the degree of SSD differed significantly among regions, pointing to a significant interaction between sex and region (Table 3). Mean body size in females were significantly greater than males in the western region ($t = 5.57$; $P < 0.001$) and in the central ($t = 4.22$; $P < 0.001$), but not in the eastern ($t = 1.76$; $P = 0.0823$). A trend for SSD to vary across a geographic cline is given by the SDIs on each region ($SDI_{\text{western}} = 0.043$; $SDI_{\text{central}} = 0.016$; $SDI_{\text{eastern}} = 0.014$), which indicate that SSD is well defined in the west and disappears going towards the east. This cline in sexual dimorphism appears to be due to gender differences in the slope of the longitudinal cline; the cline in female size ($R^2 = 0.44$; $\beta = -0.35$; $P = 0.0037$) was steeper than the cline in male size ($R^2 = 0.22$; $\beta = -0.12$; $P < 0.0487$).

Within our models, which examined the influence of temperature, precipitation, and productivity on

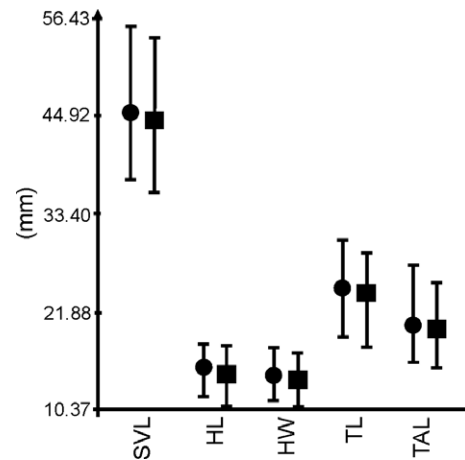


Fig. 2. Mean, maximum and minimum length of the five morphometric variables: snout-vent length (SVL), head length (HL), head width (HW), tibia length (TL), and total length of the arm (TAL) in females (black circles) and males (black squares) of *Scinax fuscovarius*. Note females are always larger. In all cases differences were highly significant ($P < 0.0001$).

Table 2. Ranking of candidate linear regression models for mean adult body size (snout-vent length) in *Scinax fuscovarius*. Models are arranged according to fit, from the best to the worst model. Predictor variable names (with the regression coefficient sign or ns as non significant), R^2 , number of estimated parameters (k), AIC values, AIC differences (Δ) and Akaike weights (w), are presented. Environmental variables included in models were: annual mean temperature (BIO1), temperature seasonality (BIO4), annual precipitation (BIO12), precipitation seasonality (BIO15), the 'Normalized Difference Vegetation Index' (NDVI), and potential evapotranspiration (PET)

Model	R^2	k	AIC	Δ AIC	w
BIO15(+)	0.08	3	-960.35	0.00	0.40
BIO15 (+), BIO4(ns)	0.08	4	-959.97	0.38	0.33
BIO12 (-)	0.07	2	-958.47	1.93	0.15
BIO12 (-), BIO1 (ns)	0.07	3	-957.36	2.99	0.40
NDVI (ns)	0.02	2	-954.44	5.91	0.02
BIO4 (ns)	0.01	3	-945.62	14.73	0.00
PET (ns)	0.01	2	-945.53	14.82	0.00
BIO1 (ns)	0.002	2	-943.59	16.76	0.00

Table 3. ANOVA results for the effects of sex and region on body size in *Scinax fuscovarius*

Source	SQ	df	MS	F	P
Model	1050.14	5	210.03	76.70	<0.0001
Sex	94.36	1	94.36	34.46	<0.0001
Region	905.65	2	452.83	165.36	<0.0001
Sex * Region	27.12	2	13.56	4.95	0.0073
Error	2108.52	770	2.74		
Total	3158.67	775			

Table 4. Ranking of candidate linear regression models for sexual size dimorphism in *Scinax fuscovarius*. Models are arranged according to fit, from the best to the worst model. Predictor variable names (with the regression coefficient sign), number of estimated parameters (k), AICc values, AICc differences (Δ) and Akaike weights (w), are presented. Environmental variables included in models were: annual mean temperature (BIO1), annual precipitation (BIO12), and the 'Normalized Difference Vegetation Index' (NDVI)

Model	k	AICc	Δ AICc	w
BIO12 (–)	2	–53.35	0.00	0.93
BIO1 (+)	2	–47.89	5.46	0.06
NDVI (–)	2	–43.80	9.55	0.00

Table 5. Results of regression tests of relationships between environmental variables and male and female body size of *Scinax fuscovarius*. Environmental variables included were: annual mean temperature (BIO1), annual precipitation (BIO12), and the 'Normalized Difference Vegetation Index' (NDVI).

Sex	Coeff.	BIO1	BIO12	NDVI
Females	R^2	0.22	0.52	0.11
	F	4.12	16.00	1.68
	P	0.06	0.0012	0.2160
	β	0.07	–0.001	–0.001
Males	R^2	0.02	0.13	0.02
	F	0.33	2.27	0.24
	P	0.5728	0.1530	0.6330
	β	0.01	–0.001	0.0002

SSD, the annual precipitation model received the most support from the data (Table 4). However, the independent contribution of each environmental factor on SSD revealed that it was positively correlated with annual mean temperature ($F = 4.83$; $R^2 = 0.24$; $P = 0.0440$) and inversely affected by annual precipitation ($F = 12.34$; $R^2 = 0.45$; $P = 0.0031$) and productivity ($F = 4.61$; $R^2 = 0.25$; $P = 0.0498$).

When we examined the environmental variables that affected the clines in female and male size separately (Table 5), we found that females were significantly negatively affected by annual precipitation while in males it had no significant effect. The other two variables, annual mean temperature and productivity, had no significant effect on either sex.

DISCUSSION

Body size variation

We found evidence of geographic variation in body size of *S. fuscovarius* across the sampled area with precipitation seasonality being the best supported,

and annual precipitation as predictor variables. The same pattern, its inverse, and its absence have been described at the intraspecific and interspecific level (Nevo 1972; Schauble 2004; Olalla-Tárraga *et al.* 2009; Yu *et al.* 2010; Bidau *et al.* 2011; Oromi *et al.* 2012; Boaratti & Da Silva 2015; Oyamaguchi *et al.* 2016).

The comparison among alternative models supports two hypotheses. Populations with larger body size were associated with dryer and more (precipitation) seasonal environments in agreement with the predictions of the starvation resistance and water availability hypotheses (Cushman *et al.* 1993; Ashton 2002). On the other hand, the growing season length hypothesis predicted a pattern opposed to that observed in our dataset. The remaining hypotheses examined here did not receive substantial support.

Body size in *S. fuscovarius* increased with increasing seasonality. Larger specimens are found to the west where seasonality is higher. The starvation hypothesis explains increasing body size in more seasonal environments based on the fact that metabolic rate is reduced further and longer during extended winters or dry periods, leading to decreased energy depletion during hibernation, improved survival and increased longevity (Cushman *et al.* 1993). This explanation has also been discussed by Valenzuela-Sánchez *et al.* (2015) considering the temperature seasonality under the 'hibernation hypothesis'. This hypothesis predicts that post-overwinter body condition should be better in animals from areas with lower mean winter temperatures. Among anurans, several works support this hypothesis (Reading 2007; Jönsson *et al.* 2009; Valenzuela-Sánchez *et al.* 2015). We do not have data about body condition after hibernation, but data from the literature (Bertolucci 1998; Toledo *et al.* 2003; Oda *et al.* 2009), collecting dates (of those adult specimens measured here), and personal observations revealed that the inactive period of *S. fuscovarius* is about seven months throughout its distribution. Therefore, it seems that it is not the duration of the hibernation period but other seasonality variables of the environments where the species inhabit that could be related to a larger size.

A consequence of the hibernation hypothesis predicts that in those individuals living in a more seasonal areas the rate of depletion of energy reserves is lower, leading to a decrease in the mortality rate and consequently to a greater longevity which permits growth over a longer period of time (Valenzuela-Sánchez *et al.* 2015). In the literature, different age structures and longevity have been described between populations of a single species exposed to different environmental conditions and revealed that age increased as the duration of activity period decreased, i.e., when seasonality is greater (Miaud *et al.* 1999; Lu *et al.* 2006; Cvetkovic *et al.* 2008). Currently, we

lack age data from all populations except the western ones, subjected to a greater seasonality. There, the oldest males and females of *S. fuscovarius* are seven years old (Goldberg 2015). We would expect a shorter longevity to the east.

A prospect to be analyzed is that more seasonal environments are exploited by relatively fewer species which, as a result, can acquire more of the available resources, and therefore grow to a larger body size (Zevuloff & Boyce 1988), called the resource availability hypothesis (Blackburn *et al.* 1999). This hypothesis could, in fact, explain why our results contradict the predictions of the growing season length hypothesis that expects an increase in body size in less seasonal environments because of resource availability.

The negative relationship observed between annual precipitation and adult size in *S. fuscovarius* is in accordance with the water availability hypothesis which suggests that there is a selective advantage for larger anurans under high water deficit conditions due to the increase of surface/volume ratio which can minimize the effects of desiccation (Farrell & Macmahon 1969).

Several studies have shown that moisture can be more correlated with intraspecific variation in body size of animals than temperature, and anurans usually follow this trend (McDiarmid 1968; Nevo 1972, 1973; Yom-Tov & Geffen 2006; Castellano & Giacoma 1998; Olalla-Tárraga *et al.* 2009; Gouveia & Correia 2016; Oromi *et al.* 2012; Oyamaguchi *et al.* 2016; this study). Among anurans, it is expected that because they need to keep their skin moist in order to breathe a simple mechanism to achieve this is decreasing the surface-to-volume ratio by increasing body size, a mechanism analogous to the conservation of heat. However, it is important to distinguish the pattern (larger body size in dryer areas) from the process (water conservation) because they do not invalidate each other (Ashton 2002). In *S. fuscovarius* a body size gradient is consistent with precipitation variation, but moisture conservation needs to be proved. To support this idea, a positive correlation between body size and aridity in some frog species has been demonstrated (Nevo 1973; Marangoni *et al.* 2008); sandy substrates may limit growth by reducing activity or foraging efficiency, limiting availability of food resources or through reproductive outputs that affect body size such as mean clutch mass, egg size, and clutch size (Gomez-Mestre & Tejedo 2005; Marangoni *et al.* 2008).

Our results on body size variation revealed a geographical trend of increasing body size, which is partially attributable to environmental conditions, i.e., larger size towards seasonal, drier areas. The same pattern has also been observed in other species that share a similar wide distribution, *Leptodactylus*

bufonius and *Dermatonotus muelleri*, where individuals of populations of both species from the Dry Chaco (seasonal and dry area) are bigger than those from the Humid Chaco, suggesting a longitudinal cline (Marangoni, pers. com.). However, the weak association between these environmental variables and body size indicated that there are other factors driving the geographical variation that need to be clearly identified. Some of them have been mentioned and include the age at maturity, longevity, clutch size, egg size, larval period, food availability, substrate, etc. (Morrison & Hero 2003; Marangoni & Tejedo 2008; Marangoni *et al.* 2008; Sinsch *et al.* 2010; Oromi *et al.* 2012; Hsu *et al.* 2014; Davenport & Hossack 2016).

Sexual size dimorphism

The direction of SSD towards one sex or the other sex has been widely discussed and linked to three major selection processes: (i) sexual selection through both intrasexual male-male competition and intersexual female choice (Darwin 1871; Woolbright 1983; Andersson 1994), (ii) natural selection when the sexes use the resources or respond to environmental conditions in different ways and when populations experience different environments (differential-plasticity and parental investment hypotheses; Katsikaros & Shine 1997; Angilletta & Dunham 2003; Laiolo *et al.* 2013; Zhang & Lu 2013), and (iii) fertility selection, in which large female body size confers a reproductive advantage due to a positive relationship between clutch volume, egg size and body size (Crump 1974; Liao 2009; Han & Fu 2013). Additionally, SSD can also be a consequence of differences in age, growth rate, and age at maturity between sexes (Monnet & Cherry 2002; Fairbairn *et al.* 2007; Feng *et al.* 2015; Stănescu *et al.* 2016).

Our results showed that *S. fuscovarius* exhibits SSD, but with a significant geographical variation in the extent of this dimorphism. Females are larger than males, which is consistent with a widespread pattern among amphibians (e.g. Shine 1979; Kupfer 2007; Wells 2007). A significant correlation between female body size and fecundity related traits such as egg size and clutch size has been extensively described among anurans, suggesting fertility selection is the leading selecting force in shaping female-biased SSD in the group (Monnet & Cherry 2002; Han & Fu 2013). We have no data to support the male-male competition or female choice hypotheses. *Scinax fuscovarius* has been described as having a prolonged reproduction pattern (i.e., duration of the reproductive activity 4 months) but with characteristics typical of species with explosive reproduction in which males and females occurs synchronously, males form choruses to attract females, and almost

no interaction among males occurs (Rodrigues *et al.* 2005). In fact, in a cross-species analysis of more than 500 species, Han and Fu (2013) did not detect any significant correlations between SSD and any male combat behavioral traits, except in the super-family Dendrobatoidea.

Rensch's rule describes that SSD increases with body size (hyperallometry) when males are larger, but decreases with body size (hypoallometry) when males are smaller (Rensch 1950). In *S. fuscovarius*, body size in both sexes increases with longitude but female size exhibited a steeper longitudinal cline which is opposite to Rensch's rule but consistent with other anuran species (Liao & Chen 2012; Liao 2013; Lu *et al.* 2014; Liao *et al.* 2015). Therefore, it seems that in anurans the inverse of Rensch's rule is a constant or at least for species with a females-biased dimorphism.

Relatively larger females than males to the west could be explained by different traits related to the life history of *S. fuscovarius* as well. It has been stated that different age at maturity and growth rate between sexes can be related to size variation. However, we know that for western populations, males and females reach sexual maturity at 2 years old (Goldberg 2015) and growth rate up to the end of metamorphosis shows no difference (J. Goldberg, unpublished data, 2014). Therefore, other factors driving the longitudinal variation in SSD observed in this study need to be identified.

The differential-plasticity hypothesis states that sex-differential plasticity in response to environmental variables generates differences between both sexes and inter-population variations in the degree of sexual dimorphism (Angilletta & Dunham 2003). In *S. fuscovarius* where males and females have overlapping ecological niches, and thus experience similar selective pressures (Cadeddu *et al.* 2012), the degree of SSD (expressed as SDI) was significantly correlated with ambient temperature, precipitation, and primary productivity. In this sense, females were likely to be increasingly larger than males as precipitation and primary productivity decreased, and temperature increased to the west, as predicted by the differential-plasticity hypothesis; but inversely to the predictions of the parental investment hypothesis. This means that the variation in SSD results from females being more sensitive to climatic factors. In other anuran species with females-biased dimorphism, intraspecific variation in SSD was only related to latitude, increasing to the south like in *Limnodynastes tasmaniensis* (Schäuble 2004), temperature as in *Bufo andrewsi* (Liao 2009), or without any correlation at all with geographic and climatic variables like in *B. bufo*, *Nanorana parkeri*, *Rana temporaria* and *R. kukunoris* (Schäuble 2004; Cvetkovic *et al.* 2008; Lu *et al.* 2014; Feng *et al.* 2015). Differently, in species with

male-biased dimorphism SSD appears related to precipitation but with contrasting results; SSD was greater where precipitation is higher such as in *L. peronii* (Schäuble 2004) or lower as in *Paa spinosa* (Yu *et al.* 2010). Therefore, intraspecific variation in SSD seems to be a species-specific characteristic with each sex being capable of adjusting their body size more plastically than the other.

Because body size is a consequence of a plethora of ecological, physiological, and developmental variables acting synergistically, we consider two different approaches to be fully addressed in the future: (i) assess at the interspecific level if a different species with a similar distribution (e.g., *Leptodactylus gracilis*) exhibits a similar or dissimilar pattern with respect to environmental conditions (see Boaratti & Da Silva 2015) and, (ii) studies that describe spatial patterns in different variables related to the life history of *S. fuscovarius* because, even though this is a very common species with a wide distribution across South America, we know very little about its life cycle and possible variation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Names of the scientific collections and registry numbers of all individuals measured for this study.