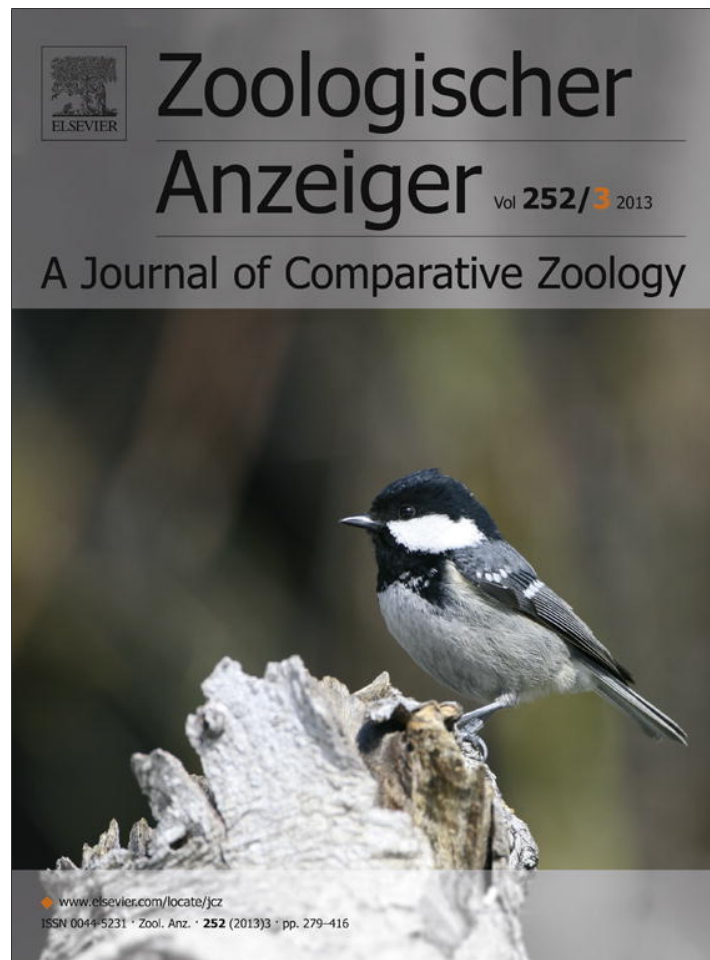


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Sexual size dimorphism and allometry in *Liolaemus* of the *L. laurenti* group (Sauria: Liolaemidae): Morphologic lability in a clade of lizards with different reproductive modes

María P. Cabrera^{a,*}, Gustavo J. Scrocchi^a, Félix B. Cruz^b^a Instituto de Herpetología - Fundación Miguel Lillo, Miguel Lillo 251, 4000 San Miguel de Tucumán, Tucumán, Argentina^b Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), CONICET-UNCOMA, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Río Negro, Argentina

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ABSTRACT

Sexual size dimorphism is a common aspect in animals and different hypotheses to this regard were generated. Additionally, Rensch's rule is an empirical pattern that states that the degree of sexual size dimorphism is more pronounced in species with larger males, and less pronounced in those with larger females. We studied the body size differences, Rensch's rule and sexual dimorphism in morphological features in 22 lizard species of the *Liolaemus laurenti* clade. We assessed sexual dimorphism using independent contrasts and gauged phylogenetic signal in all measured traits. We intend to answer the following questions: (a) what is the phylogenetic signal of body size and other morphological features?; (b) do the *Liolaemus* lizards of the *laurenti* clade follow the Rensch's rule pattern?, and (c) do fecundity advantage or sexual selection hypotheses explain the differences between sexes?. *Liolaemus* species show low phylogenetic signal in most of the measured traits. In this group, male-larger dimorphism is more common, and several species showed no sexual size dimorphism. Additionally, our results do not support Rensch's rule. Head shape and radius length showed sexual dimorphism suggesting sexual selection. Finally, no relationship was recovered between inter-limb length and reproductive output, thus fecundity advantage hypothesis was not supported.

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1. Introduction

Morphological differences between the sexes are a common feature in many animals (Fairbairn, 1997; Sinsch et al., 2002), including reptiles (Fairbairn, 1997; Zamudio, 1998; Kratochvíl and Frynta, 2002; Cox et al., 2003; Stuart Fox, 2008; Boretto and Ibagüengotyá, 2009; Frýdlová and Frynta, 2010). In lizards, males and females may differ in several traits, such as coloration, body shape, or size. However, most comparative studies on sexual dimorphism have focused on differences in body size (Butler and Losos, 2002), because this trait has profound effects on physiology, ecology, and life-history traits in general.

One particular pattern related to sexual size dimorphism (SSD) is called Rensch's rule where SSD is proposed to be more pronounced when males are the larger sex (hyperallometry; Fairbairn, 1997), conversely when females are the larger sex SSD decreases with SVL (hypoallometry). Independently of its variation with body size, several hypotheses have been proposed to explain the causes

of sexual dimorphism. For example, the sexual selection hypothesis that predicts that larger males will have higher reproductive success (Cox et al., 2003). According to this, males show larger body size or show allometric growth of structures that may be used in aggressive encounters with other males (Petrie, 1992; Fairbairn, 1997), or may be used by females to assess the quality of their partners (Carothers, 1984; Anderson and Vitt, 1990). Now, in the case of larger females, an alternative hypothesis proposed is the fecundity advantage hypothesis (or reproductive selection *sensu* Fairbairn, 1997) that states that female fecundity is proportional to body size, and selection will favor larger females (Koslowski, 1989; Zamudio, 1998; Cox et al., 2003). Together, these hypotheses may identify sexual selection on male size and fecundity (natural selection on female size as important influences on size dimorphism. Finally, if resources such as space or prey are limited, the niche segregation hypothesis (Pianka and Huey, 1978) predicts that size dimorphism may arise through competition avoidance, promoting a more efficient use of resources by the sexes (Perez-Mellado and de la Riva, 1993; Zamudio, 1998). These hypotheses, however, are not mutually exclusive. For example, SSD may result from sexual selection, but can be modulated by ecological factors (Shine, 1989).

* Corresponding author. Tel.: +54 381 4230056; fax: +54 381 4330868.

E-mail addresses: mpaucab@yahoo.com, mpaucab17@gmail.com (M.P. Cabrera).

Previous studies on lizards showed a mix of results in regard to sexual size dimorphism. Studies on some lizard groups show that females are the greater sex, for example phrynosomatid lizards and dwarf chameleons (Zamudio, 1998; Stuart Fox, 2008). Conversely eublepharid geckos and varanids show a male biased dimorphism (Kratovichil and Frynta, 2002; Frýdlová and Frynta, 2010). Additionally, two broader analyses of SSD using comparative data showed a majority of species with larger males (Fairbairn, 1997; Cox et al., 2003).

Besides sexual size dimorphism, several characteristics other than SVL show variation between sexes, especially in male biased sexually dimorphic taxa (Kratovichil and Frynta, 2002) but also in female biased species (Tubaro and Bertelli, 2003). In the case of male biased species, dimorphic these traits (e.g., head size) may be used during male–male combat (Kratovichil and Frynta, 2002) or signaling (Martins et al., 2004). Thus, shape dimorphism, or the allometric growth of some features (such as head size in males or axilla–groin distance in females) may rely on the hypotheses underlying the causal factors driving sexual size dimorphism.

We here explore these issues for the *Liolaemus laurenti* species group (*L. darwini* clade + *L. wiegmanni* clade; Abdala, 2007; Lobo et al., 2010). The *L. laurenti* group belongs to the series of *L. boulengeri* of the genus *Liolaemus* (Abdala, 2007). The *L. laurenti* group is composed of approximately 30 species (Lobo et al., 2010), of which we studied 22. Because this group forms a monophyletic clade (the *L. laurenti* group, *sensu* Abdala, 2007) and shares several ecological characteristics, such as habitat use (most of them are terrestrial generalists or sand dwellers, Tulli et al., 2009), this allows us to explore sexual dimorphism and sexually dimorphic features within a phylogenetic context. *Liolaemus* lizards as use several parts of their body for signaling as do many other iguanians (Martins et al., 2004). For example head bobs and push-ups are a common part of their communication system (Martins et al., 2004). Thus, head shape and forelimb characteristics are particularly interesting traits that may drive communication ability among these lizards. Additionally, within this group of species, two reproductive modes are observed: six out of the 22 species are viviparous and the rest oviparous. Viviparity may lead to a larger distance between axilla and groin because for a viviparous species carrying full developed embryos needs more space than in the case of oviparous species that lay smaller undeveloped eggs, in this sense we expect that the abdominal cavity (expressed in the inter-limb length, ILL) should be larger in viviparous species.

Our main questions are: (a) what is the phylogenetic signal of body size and other morphological features (head shape and fore limb sections)?; (b) do *Liolaemus* lizards of the *laurenti* clade follow the Rensch's rule pattern?; (c) what hypotheses explain better the differences between sexes, fecundity advantage hypothesis or sexual selection hypothesis?

2. Materials and methods

Biometric variables used in the analysis, (taken with Vernier calipers; Mitutoyo, to 0.02 mm) were as follows: snout–vent length (SVL), head length (HL) from end of rostral to anterior border of ear opening, head width (HW) measured at the edge of the ear opening, inter-limb length (ILL) the distance between axilla and groin, humerus length (HuL), radius length (RL), and manus length (ML) (Table 1). Because we compare the effect of body size of adult specimens, we calculated the arithmetic average of the largest one-third of the total sample of SVL and body measurements to obtain an indication of asymptotic size of the studied species (see Losos et al., 2003). We used museum specimens (Appendix 1) deposited in the Instituto de Herpetología of the Fundación Miguel Lillo, Tucumán, Argentina.

Among *Liolaemus* lizards, sex is identified from the shape of the cloacae (square shaped in males, rounded in females) and the presence of precloacal pores, which are always present in males, although females of some species also possess precloacal pores. There is also strong sexual dichromatism in most *Liolaemus* lizard species, thus we used these characters as diagnostic for sexing specimens. After using the larger third of the samples for each species, we are confident that only adult specimens were considered (see Table 1). We based adult stages on previous studies on reproductive biology of *Liolaemus* species (Ramírez Pinilla, 1989, 1991, 1994; Cruz and Ramírez Pinilla, 1996; Martori and Aun, 1997; Aun and Martori, 1998; Vega, 1999; Martori, 2005; Cánovas et al., 2006b; Valdecantos and Lobo, 2007; Cruz et al., 2011) and personal observations.

Within each species we tested for differences between sexes in the variables mentioned above by running *t*-tests or Mann–Whitney tests (depending on whether the data fulfilled assumptions of normality and homoscedasticity). We also modified our alpha levels using Bonferroni corrections to take into account the effect of multiple testing.

When examining data from phylogenetically related species, data points cannot be considered as statistically independent due to shared evolutionary history (Felsenstein, 1985; Harvey and Pagel, 1991). On the other hand, the importance of accounting for this evolutionary relatedness in comparative analyses depends partially if they show evidence of significant phylogenetic signal (Blomberg et al., 2003; Garland et al., 2005). For these reasons, we run independent contrasts analyses and tested for phylogenetic signal by using a total evidence phylogenetic tree for the studied species here (after Abdala, 2007). Because the Abdala (2007) study corresponds to a larger sample of *Liolaemus* species, it does not provide branch lengths. Therefore, we used a composite tree topology and arbitrarily set the branch lengths to unity as divergence times among the different species are unclear.

We tested for phylogenetic signal of SVL and other morphological features using a simple randomization test executed in the PHYSIG program (Blomberg et al., 2003). We calculated the *K* statistic ($K=0$ no phylogenetic signal, $K=1$ or higher indicate actual phylogenetic signal) to estimate the level of phylogenetic signal relative to Brownian motion evolution using the tree topology and branch lengths (Blomberg et al., 2003). For this analysis, we used constant branch lengths and two different branch lengths transformations with an Ornstein–Uhlenbeck model of evolution. Each one of these transformations represent the strength of stabilizing selection, where a low value of OU transformation index ($d=0.2$) turns the data toward a more “adaptive” scenario, meanwhile a close to 1 OU transformation ($d=0.8$) tend to Brownian motion (Blomberg et al., 2003). Thus, we set the *d*-value equal to 0.2, thus creating a more star-like topology, and equal to 0.8, resulting in a more hierarchical topology (Blomberg et al., 2003). In the case of snout–vent length, we introduced this variable in PHYSIG after \log_{10} transformation. All other morphological traits (i.e. head measurements and forelimb segments lengths) were size-corrected following the method in Blomberg et al. (2003). We calculated the *K* statistic to quantify the level of phylogenetic signal relative to what is expected for a character undergoing Brownian motion evolution considering the current topology and branch lengths (Blomberg et al., 2003). A *K*-value equal to or greater than 1 indicates that the trait shows an expected amount of phylogenetic signal among close relatives, conversely a *K*-value less than 1 indicates less phylogenetic signal than expected and possible selection or measurement error in the broad sense (including errors in estimates of phenotypes, branch lengths, and topology; Blomberg et al., 2003).

We ran simple regressions of IC for SVL as a measurement of sexual size dimorphism following Fairbairn (1997) taking males as the independent variable. We also tested for the relationship

Table 1
Mean and maximum values (\pm SE) of body measurements from females (\varnothing) and males (σ^7) of the studied species.

	Sex	Snout-vent length			Head length			Head width			Inter-limb length		
		Mean	Max	\pm SE	Mean	Max	\pm SE	Mean	Max	\pm SE	Mean	Max	\pm SE
<i>L. abaucan</i>	\varnothing	51.27	54.09	0.40	11.54	12.10	0.10	10.32	10.82	0.09	24.07	25.49	0.25
	σ^7	52.88	56.38	0.61	12.63	13.49	0.16	11.16	11.94	0.15	23.06	24.82	0.33
<i>L. albiceps</i>	\varnothing	69.52	71.22	1.43	14.88	15.47	0.30	13.13	13.64	0.23	33.78	35.24	0.83
	σ^7	79.32	81.45	2.18	17.77	18.18	0.44	16.42	16.85	0.51	35.55	35.84	1.03
<i>L. calchaqui</i>	\varnothing	56.96	59.02	0.94	12.02	12.05	0.14	9.89	9.75	0.26	26.83	28.46	0.69
	σ^7	51.92	55.16	1.58	12.02	12.77	0.35	9.88	10.54	0.25	21.51	22.42	0.36
<i>L. chacoensis</i>	\varnothing	45.90	49.91	0.42	10.16	10.56	0.06	7.44	7.69	0.05	21.65	24.28	0.29
	σ^7	42.98	46.58	0.33	10.22	10.84	0.07	7.50	7.90	0.05	18.49	20.22	0.20
<i>L. crepuscularis</i>	\varnothing	58.83	61.76	1.18	12.45	12.83	0.21	11.70	11.99	0.17	27.59	29.05	0.72
	σ^7	54.12	56.13	0.55	12.18	12.64	0.12	11.34	11.75	0.16	22.74	24.18	0.46
<i>L. darwini n</i>	\varnothing	53.67	56.25	0.51	11.84	12.27	0.15	10.47	10.89	0.13	25.54	26.41	0.30
	σ^7	54.99	58.05	0.52	12.79	13.24	0.12	11.10	11.59	0.09	24.22	25.78	0.35
<i>L. darwini s</i>	\varnothing	54.69	57.94	0.65	11.87	12.42	0.14	10.01	10.48	0.15	25.75	27.65	0.47
	σ^7	52.92	56.07	0.62	12.26	12.80	0.12	10.22	10.28	0.11	22.17	23.20	0.38
<i>L. espinozai</i>	\varnothing	55.16	60.82	0.85	11.94	12.89	0.16	10.37	11.11	0.15	26.44	29.85	0.54
	σ^7	53.69	58.95	0.77	12.71	13.94	0.20	10.77	11.71	0.16	23.72	26.97	0.48
<i>L. grosseorum</i>	\varnothing	49.38	51.47	0.45	11.30	11.63	0.20	8.54	8.96	0.16	23.65	25.26	0.45
	σ^7	50.56	53.38	0.63	11.72	13.08	0.29	9.22	9.33	0.16	22.42	23.60	0.38
<i>L. irregularis</i>	\varnothing	70.49	74.87	1.59	15.20	15.53	0.33	12.74	13.20	0.26	34.73	37.66	1.05
	σ^7	77.59	85.74	1.51	17.52	19.44	0.38	15.49	17.29	0.34	35.41	39.32	0.74
<i>L. koslowskyi</i>	\varnothing	56.35	60.39	0.57	12.31	12.76	0.19	10.50	11.31	0.13	27.29	30.68	0.76
	σ^7	60.25	66.30	0.89	14.16	16.34	0.34	12.08	12.98	0.16	27.62	29.74	0.39
<i>L. laurenti</i>	\varnothing	52.11	55.13	0.43	11.65	12.13	0.12	9.47	10.33	0.15	24.80	26.13	0.34
	σ^7	52.59	55.20	0.45	12.12	12.52	0.10	9.98	10.41	0.09	23.15	24.67	0.27
<i>L. lavillai</i>	\varnothing	57.20	59.59	0.56	12.24	12.73	0.13	10.84	11.01	0.12	27.62	28.85	0.36
	σ^7	59.20	61.49	0.44	13.43	13.88	0.13	11.92	12.35	0.12	26.10	27.29	0.35
<i>L. multimaculatus</i>	\varnothing	58.54	62.81	1.53	14.30	15.72	0.53	10.86	11.40	0.21	28.06	29.24	0.92
	σ^7	64.48	68.41	1.83	16.72	18.14	0.60	12.24	12.87	0.29	28.57	28.43	0.85
<i>L. olongasta</i>	\varnothing	50.40	57.13	2.50	10.72	11.28	0.35	8.20	9.29	0.36	19.21	–	–
	σ^7	55.49	59.21	1.56	12.98	13.19	0.39	9.89	10.15	0.39	24.18	25.69	0.83
<i>L. ornatus</i>	\varnothing	62.36	65.29	0.46	13.00	13.45	0.09	11.68	11.87	0.09	30.44	32.46	0.48
	σ^7	65.40	65.40	0.73	14.52	14.52	0.18	12.96	12.96	0.12	28.84	28.84	0.38
<i>L. quilmes</i>	\varnothing	51.45	54.74	0.33	11.50	12.03	0.07	8.92	9.29	0.06	23.99	25.51	0.22
	σ^7	54.66	58.72	0.41	12.89	13.69	0.10	9.92	10.50	0.08	23.27	25.03	0.25
<i>L. riojanus</i>	\varnothing	48.73	51.43	1.07	12.53	12.09	0.26	9.63	9.71	0.15	23.89	27.01	1.04
	σ^7	50.91	56.73	1.61	13.32	14.51	0.40	10.05	10.80	0.25	23.03	25.67	0.90
<i>L. salinicola</i>	\varnothing	58.19	62.09	0.70	13.56	14.49	0.18	10.86	11.10	0.11	27.70	30.03	0.46
	σ^7	69.13	73.49	0.95	16.05	16.52	0.31	13.37	14.01	0.21	29.64	31.39	0.50
<i>L. scapularis</i>	\varnothing	55.03	58.55	0.63	12.89	13.36	0.14	10.97	11.59	0.19	26.23	27.75	0.59
	σ^7	63.81	68.53	0.77	15.61	16.69	0.22	12.76	13.96	0.26	28.14	29.91	0.49
<i>L. uspallatensis</i>	\varnothing	58.50	62.51	0.98	13.02	13.53	0.25	11.25	11.54	0.18	28.12	30.26	0.56
	σ^7	57.58	60.91	1.21	13.44	13.72	0.21	11.25	11.89	0.33	25.66	28.82	1.04
<i>L. wiegmannii</i>	\varnothing	48.68	51.38	0.77	12.73	13.13	0.17	9.10	9.18	0.13	25.04	25.77	0.57
	σ^7	48.07	53.23	1.48	13.40	14.74	0.40	9.23	10.03	0.26	23.17	24.71	0.68

	Sex	Humerus length			Radius length			Manus length		
		Mean	Max	\pm SE	Mean	Max	\pm SE	Mean	Max	\pm SE
<i>L. abaucan</i>	\varnothing	5.27	5.75	0.10	6.70	7.02	0.05	8.93	8.97	0.07
	σ^7	5.54	6.07	0.12	7.02	7.39	0.10	9.05	9.39	0.13
<i>L. albiceps</i>	\varnothing	5.76	6.07	0.19	7.95	8.11	0.18	10.71	10.85	0.15
	σ^7	6.87	6.51	0.22	9.33	9.72	0.22	12.18	12.54	0.22
<i>L. calchaqui</i>	\varnothing	5.25	5.14	0.24	6.84	7.06	0.12	8.26	8.90	0.37
	σ^7	4.48	5.05	0.26	6.49	6.93	0.20	8.18	8.61	0.18
<i>L. chacoensis</i>	\varnothing	4.81	5.07	0.06	5.57	5.81	0.07	7.32	7.53	0.05
	σ^7	4.73	4.95	0.05	5.14	5.34	0.06	7.01	7.21	0.06
<i>L. crepuscularis</i>	\varnothing	5.27	5.17	0.22	6.81	7.00	0.15	8.20	8.47	0.21
	σ^7	4.99	5.27	0.10	6.68	6.89	0.09	8.17	8.29	0.11
<i>L. darwini n</i>	\varnothing	5.14	5.34	0.11	6.90	7.09	0.10	7.92	7.95	0.12
	σ^7	5.46	5.62	0.10	6.94	7.10	0.11	8.21	8.38	0.10
<i>L. darwini s</i>	\varnothing	5.27	5.81	0.14	6.97	7.11	0.09	8.32	8.31	0.11
	σ^7	5.05	5.17	0.10	6.93	7.13	0.11	8.25	8.47	0.12
<i>L. espinozai</i>	\varnothing	5.53	5.81	0.13	6.53	6.72	0.07	8.24	8.76	0.11
	σ^7	5.90	6.46	0.17	6.67	7.02	0.08	8.55	8.91	0.10
<i>L. grosseorum</i>	\varnothing	4.94	5.06	0.16	6.29	6.47	0.08	7.56	7.65	0.14
	σ^7	4.82	5.09	0.15	6.42	6.80	0.12	7.80	8.64	0.20
<i>L. irregularis</i>	\varnothing	6.52	6.57	0.18	8.51	8.66	0.24	11.31	11.01	0.48
	σ^7	7.01	7.33	0.27	9.67	10.34	0.16	12.49	12.85	0.17
<i>L. koslowskyi</i>	\varnothing	5.87	5.92	0.10	7.10	7.57	0.09	8.83	9.02	0.11
	σ^7	6.37	7.37	0.19	7.90	8.58	0.12	9.63	10.40	0.14
<i>L. laurenti</i>	\varnothing	5.61	5.77	0.13	6.66	7.08	0.11	7.97	8.28	0.10
	σ^7	5.46	5.62	0.10	6.80	6.98	0.07	7.94	8.11	0.08
<i>L. lavillai</i>	\varnothing	5.08	5.24	0.10	6.75	6.69	0.08	8.56	8.41	0.15
	σ^7	5.33	5.51	0.08	7.24	7.38	0.07	9.10	9.25	0.12

Table 1 (Continued)

	Sex	Humerus length			Radius length			Manus length		
		Mean	Max	±SE	Mean	Max	±SE	Mean	Max	±SE
<i>L. multimaculatus</i>	♀	8.18	8.15	0.53	6.12	6.49	0.43	7.88	7.47	0.30
	♂	8.19	8.78	0.39	6.81	8.23	0.46	9.50	9.65	0.34
<i>L. olongasta</i>	♀	5.82	6.44	0.63	4.79	–	–	7.56	–	–
	♂	6.73	7.26	0.28	7.32	8.54	0.70	9.60	10.16	0.70
<i>L. ornatus</i>	♀	5.11	5.25	0.09	7.56	7.65	0.06	8.77	8.82	0.09
	♂	5.57	5.57	0.07	8.22	8.22	0.08	9.49	9.49	0.10
<i>L. quilmes</i>	♀	4.73	4.79	0.05	5.15	5.40	0.05	7.57	7.83	0.05
	♂	5.13	5.17	0.06	5.78	6.01	0.05	8.20	8.51	0.07
<i>L. riojanus</i>	♀	6.08	6.64	0.26	5.31	4.89	0.22	7.33	6.41	0.47
	♂	6.21	6.52	0.27	5.57	5.57	0.26	7.54	7.72	0.29
<i>L. salinicola</i>	♀	5.66	6.27	0.15	7.26	7.49	0.10	9.24	9.82	0.16
	♂	6.57	6.67	0.16	8.41	8.75	0.14	10.62	10.66	0.18
<i>L. scapularis</i>	♀	5.47	5.70	0.13	6.71	7.15	0.13	8.70	9.11	0.12
	♂	6.62	6.82	0.22	7.97	8.38	0.11	10.15	11.01	0.23
<i>L. uspallatensis</i>	♀	5.85	6.33	0.29	8.04	8.24	0.15	10.25	10.36	0.12
	♂	5.91	6.14	0.17	8.07	8.15	0.12	10.41	10.67	0.25
<i>L. wiegmannii</i>	♀	6.22	5.93	0.21	6.41	6.23	0.27	7.58	8.32	0.26
	♂	5.55	5.36	0.22	6.06	6.33	0.17	7.70	8.01	0.20

between SSD and snout-vent length (SVL) of each sex. To test the different hypotheses that may explain sexual size dimorphism, we ran comparative regressions for the head, fore-limb and inter-limb measurements from each sex against the mean SVL of the largest one-third for each species. We used this traditional method for scaling to SVL; however, we are aware of the potential problems from using SVL as predicting variable especially in the case of ILL since it was suggested to be an artifact of inappropriate scaling to a sexually dimorphic trait (snout-vent length) (Kratovich et al., 2003). We used conventional statistics and we also calculated independent contrasts, since the trait values of related species are linked in a hierarchical fashion (Felsenstein, 1985) (Fig. 1). We calculated

independent contrasts (IC) for the log10 of every morphological trait measured. For calculating independent contrasts we used the PDAP 1.15 module (Midford et al., 2003) in Mesquite 2.74 (Maddison and Maddison, 2010), all regressions were forced through the origin (Garland et al., 1992). Particular attention was paid to slope in order to determine deviation from isometry.

Liolaemus species of the *L. laurenti* group show different reproductive modes (some species are oviparous and some viviparous). Cei et al. (2003) proposed that inter-limb length (ILL) may vary in relationship to the space necessary for eggs or larger full term embryos to be carried in *Liolaemus* lizards. Thus, we ran a phylogenetically based ANCOVA (PDANCOVA, Garland et al., 1993) with log₁₀ SVL as covariate, to investigate whether viviparous *Liolaemus* species show larger inter-limb length (ILL) than oviparous ones by using reproductive mode as the categorical variable. We also obtained brood and clutch size from 12 species of *Liolaemus* from the *L. laurenti* group (data from Ramírez Pinilla, 1991, 1994; Cruz and Ramírez Pinilla, 1996; Martori and Aun, 1997; Martori, 2005 and specimens from FML collection dissected by the authors). Thus, we evaluate if female ILL is an indicator of reproductive mode and if number of future offspring is an indicator of the volume needed for carrying eggs or embryos. In the case of phylogenetically based ANOVA or ANCOVA, an empirical null distribution of *F*-statistics was generated using PDSIMUL taking into account the phylogeny, then analyzed with PDANOVA (Garland et al., 1993). We ran 1000 simulations using a speciation model of evolution that sets all branch lengths equal to one.

3. Results

None of the *K* values obtained for the untransformed branch length analysis were greater than one for any of the variables studied, including SVL (Table 2). However, LH and LR of males and SSD of males showed significant results. Because branch length may influence the degree of phylogenetic signal, we ran Ornstein-Uhlenbeck (OU) transformations. In the case of OU transformations that mimic a star phylogeny like structure (*d* = 0.2), male humerus and radius length showed *K* scores greater than 1 in our data set, suggesting a trend for stabilizing selection in these features in males but not females (Table 1). None of the variables showed *K*-values greater than one for an OU transformation of 0.8. However, in the case of randomization tests, humerus and radius lengths and SSD of males showed significant *P*-values, indicating the presence of similarity among closely related species greater than what would be expected by chance (Blomberg et al., 2003).

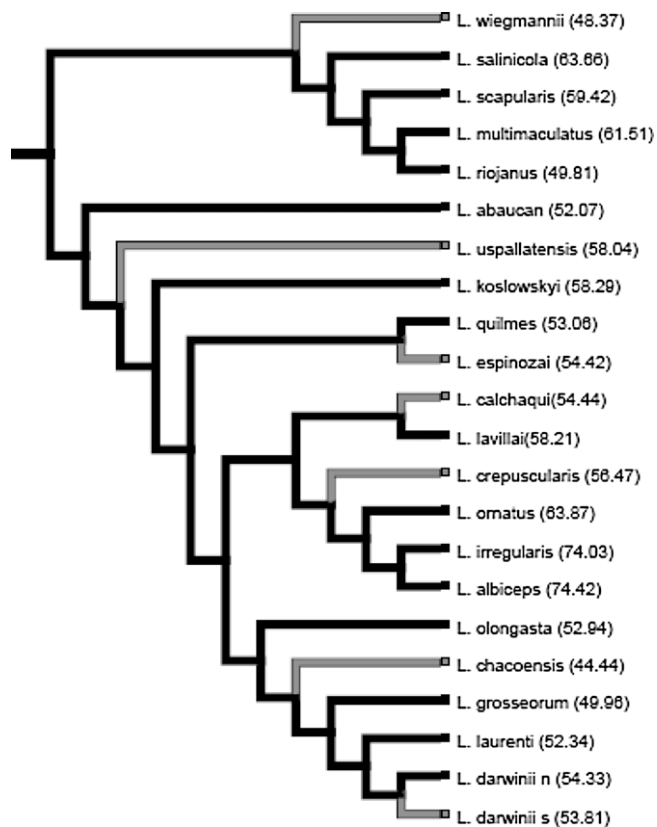


Fig. 1. Cladogram of *Liolaemus laurenti* group used in the analysis (after Abdala, 2007). Branches in gray: species with females with SVL greater than males.

Table 2
Phylogenetic signal based on *k* values and simulations (*P* value). *K* values higher than one or *P* values lower than 0.05 indicate the presence of phylogenetic signal.

	No transformation		OU transformation			
	<i>k</i> value	<i>P</i>	<i>d</i> = 0.8 <i>k</i> value	<i>P</i>	<i>d</i> = 0.2 <i>k</i> value	<i>P</i>
SVLf	0.203	0.987	0.383	0.958	0.867	0.679
SVLm	0.245	0.962	0.454	0.927	0.876	0.641
HLf	0.549	0.070	0.874	0.088	0.951	0.306
HLm	0.483	0.412	0.734	0.673	0.846	0.785
HWf	0.224	0.890	0.413	0.897	0.871	0.638
HWm	0.351	0.316	0.629	0.32	0.871	0.690
ILLf	0.413	0.282	0.642	0.622	0.878	0.674
iILLm	0.283	0.643	0.601	0.314	1.034	0.108
LHf	0.345	0.467	0.693	0.243	1.001	0.193
LHm	0.446	0.008	0.808	0.009	1.093	0.028
LRf	0.286	0.628	0.540	0.559	0.931	0.409
LRm	0.372	0.042	0.773	0.005	1.149	0.004
LMf	0.331	0.771	0.622	0.586	0.880	0.580
LMm	0.347	0.834	0.647	0.888	0.728	0.599
Ssd vs f	0.503	0.094	0.765	0.257	0.908	0.531
Ssd vs m	0.554	0.043	0.819	0.176	0.886	0.671

After comparison of body size and morphological variables between males and females within each species, we observed significant differences in several cases (Table 3). Among the 22 species studied, ten species showed to be male biased, five were significantly female biased species in SVL and seven species showed no significant different, although males were the larger sex in six of them (Table 3). Additionally, across species in this group, males tend to show larger HL, HW, HuL, RL and ML and females tend to show a relatively larger ILL (Table 3).

We observed a positive and significant relationship between male and female snout-vent length (males as determining factor) in overall (Table 4). A positive relationship was also observed for the 10 male-biased and the six female-biased species (Table 4). Additionally, our results show that IC SSD is positively related to IC body size ($r^2 = 0.432$; slope = 0.297; d.f. = 20; $P < 0.009$). Rensch's rule pattern is not supported because the slope of these regression were lower than 1. Thus, This *Liolaemus* lizards show a significant sexual size dimorphism among species, but Rensch's rule pattern is absent.

Table 3
Body size, body measurements, and sexual size dimorphism index (SDI, *sensu* Gobbons and Lovich, 1990) comparisons between sexes for each species. Boldface denotes significant differences when males are larger than females, boldface and italics significant with females as the larger sex. $t = t$ -test; *U* Mann–Whitney test.

Species	SVL		HL		HW		HuL		RL		ML		ILL		SDI	
	<i>t</i> or <i>U</i>	<i>P</i>	<i>t</i> or <i>U</i>	<i>P</i>	<i>t</i> or <i>U</i>	<i>P</i>	<i>t</i> or <i>U</i>	<i>P</i>	<i>t</i> or <i>U</i>	<i>P</i>	<i>t</i> or <i>U</i>	<i>P</i>	<i>t</i> or <i>U</i>	<i>P</i>	<i>t</i> or <i>U</i>	<i>P</i>
<i>L. abaucan</i>	t3.16	0.002	t6.29	0.000	t5.42	0.000	t0.39	0.696	t1.73	0.086	t0.356	0.722	t-6.4	0.000	0.0103	
<i>L. albiceps</i>	U11.00	0.008	U11.00	0.007	U14.50	0.020	U28.00	0.236	U13.00	0.014	U18.00	0.042	U15.50	0.025	0.0314	
<i>L. calchaqui</i>	U2.00	0.028	U2.00	0.028	U12.00	0.104	U4.00	0.075	U8.00	0.347	U10.50	0.676	U4.00	0.009	–0.0168	
<i>L. chacoensis</i>	t-5.52	0.000	t6.12	0.000	t4.74	0.000	U35.00	0.491	t-2.07	0.039	U3204.50	0.109	t-7.16	0.000	–0.0179	
<i>L. crepuscularis</i>	U8.00	0.002	U30.00	0.048	U44.00	0.118	U34.00	0.362	U39.50	0.634	U44.00	0.905	U2.00	0.000	–0.0237	
<i>L. darwini</i> N	t1.80	0.047	t4.72	0.000	t3.66	0.000	t1.66	0.102	t-0.45	0.653	t1.43	0.158	t-5.09	0.000	0.0078	
<i>L. darwini</i> S	t1.96	0.049	t7.35	0.000	t2.12	0.039	t-0.16	0.869	t0.99	0.323	t-0.40	0.690	t-5.71	0.000	–0.0081	
<i>L. espinozai</i>	t-1.44	0.153	t8.36	0.000	t6.93	0.000	t1.28	0.204	t2.99	0.003	t2.65	0.009	t-7.07	0.000	–0.0076	
<i>L. grosseorum</i>	t 0.69	0.490	U68.00	0.174	t2.47	0.020	t0.28	0.778	t-1.08	0.289	t0.488	0.629	t0.59	0.001	0.0092	
<i>L. irregularis</i>	U27.00	0.022	t2.96	0.006	U20.00	0.007	U61.00	0.750	t2.71	0.012	t2.29	0.031	U18.00	0.005	0.0314	
<i>L. koslowskyi</i>	t2.02	0.047	t8.06	0.000	t8.06	0.000	t0.42	0.674	t3.92	0.000	t4.52	0.000	U103.00	0.000	0.0227	
<i>L. laurenti</i>	t0.79	0.427	t7.13	0.000	t1.52	0.133	t-0.42	0.672	t0.09	0.928	t-0.18	0.850	U118.00	0.000	0.0002	
<i>L. lavillai</i>	t2.82	0.007	U51.00	0.000	U60.00	0.000	t0.97	0.335	t2.98	0.004	t2.84	0.007	t-6.01	0.000	0.0076	
<i>L. multimaculatus</i>	t5.94	0.038	t2.81	0.015	t1.38	0.004	t1.10	0.987	t1.06	0.313	t3.33	0.005	t0.51	0.697	0.0088	
<i>L. ornatus</i>	U206.00	0.000	U105.00	0.000	t6.35	0.000	t2.52	0.014	t4.33	0.000	t3.67	0.000	t-6.39	0.000	–0.0063	
<i>L. olongasta</i>	t1.72	0.40	t4.27	0.001	t1.98	0.023	t1.48	0.183							0.0004	
<i>L. quilmes</i>	t6.04	0.000	t9.22	0.000	t6.73	0.000	t3.19	0.001	t5.83	0.000	U2503.00	0.000	t-8.42	0.000	0.0175	
<i>L. riojanus</i>	t1.06	0.303	t1.55	0.141	t1.34	0.199	t0.35	0.731	t0.73	0.475	t0.39	0.698	t0.69	0.537	0.0206	
<i>L. salinicola</i>	t9.26	0.000	U21.50	0.004	U4.00	0.000	t-0.66	0.507	t0.98	0.330	U9.00	0.000	t3.54	0.001	0.0248	
<i>L. scapularis</i>	t8.42	0.000	t2.54	0.014	t0.95	0.345	t0.22	0.826	t1.19	0.239	U287.00	0.473	t2.96	0.004	0.0408	
<i>L. uspallatensis</i>	U38.00	0.963	U67.00	0.000	U34.00	0.683	U25.00	0.221	U35.50	0.785	U34.00	0.683	U10.00	0.009	0.0386	
<i>L. wiegmannii</i>	t0.39	0.695	U40.00	0.229	t0.49	0.629	t2.34	0.045	t0.99	0.334	t0.34	0.736	t0.21	0.049	0.0089	

Table 4
Regression of major axis (RMA) between Independent contrasts (IC) of snout-vent length (SVL) of males and females (males as predictive variable). Regressions were run for all the 22 species in the *L. laurenti* group studied here (g.l. 20), for species where male are the larger sex (10 species, d.f. 8) and species female as the larger sex (6 species, d.f. 4).

	Variable	r^2	Slope	<i>P</i>
All species	SVL	0.846	0.631	<0.000
Male biased	SVL	0.971	0.786	<0.000
Female biased	SVL	0.910	0.696	<0.009

Table 5
Regressions of \log_{10} transformed body measurements versus \log_{10} transformed SVL from the species studied. We used raw data and independent contrasts, in the later case the regression was forced through the origin.

Variable	Raw data			Independent contrasts		
	r^2	Slope	<i>P</i>	r^2	Slope	<i>P</i>
HLf	0.74	0.673	<0.001	0.799	0.692	<0.001
HLm	0.774	0.978	<0.001	0.899	1.002	<0.001
HWf	0.772	0.969	<0.001	0.805	0.888	<0.001
HWm	0.934	1.367	<0.001	0.939	1.336	<0.001
ILLf	0.899	1.196	<0.001	0.935	1.002	<0.001
ILLm	0.742	0.902	<0.001	0.804	0.986	<0.001
LHf	0.139	0.357	0.087	0.077	0.236	0.209
LHm	0.365	0.725	0.003	0.286	0.525	0.011
LRf	0.475	0.788	<0.001	0.632	0.877	<0.001
LRm	0.811	1.138	<0.001	0.823	1.310	<0.001
LMf	0.709	0.803	<0.001	0.792	0.799	<0.001
LMm	0.837	1.103	<0.001	0.831	1.239	<0.001

The analyses of the relationship of body parts between sexes after conventional as well as phylogenetically based analyses (IC) reveal that; limb sections (except for humerus length for females after Bonferroni correction), head measurements and ILL were significantly greater with SVL. Interestingly, HW, radius and manus length of males, and ILL of females, showed a slope greater than one (Table 5), supporting the hypothesis of allometry (all *t*-test values were higher than 7.52, $P < 0.001$ indicating differences from isometry). The rest of the variables exhibit slopes lower than one (Table 5) and therefore negative allometry presumption was observed for these variables.

Table 6

Phylogenetically informed analysis of variance (ANOVA), and phylogenetically informed analysis of covariance (ANCOVA, SVL as covariate) comparing oviparous and viviparous species within the *L. laurenti* clade.

Analysis	Variable	$F_{(20;1)}$	P
ANOVA	SVLf	24.35	0.263
ANOVA	SVLm	24.40	0.502
ANOVA	SSD	23.13	0.779
ANCOVA	ILLf	124.99	0.899
ANCOVA	ILLm	93.50	0.979

SVL: snout-vent length; SSD: sexual size dimorphism; ILL: inter-limb length; f: females; m: males.

The analysis testing for the potential differences between oviparous and viviparous species of the *L. laurenti* species group showed no significant differences after phylogenetically informed ANOVAS/ANCOVAS for SVL, SSD or ILL (reproductive mode as response variable, Table 6). Additionally, there was no relationship between IC of clutch or brood size and IC of \log_{10} ILL for the twelve species for which we have complete data ($r^2 = 0.22$; d.f. 11; $P = 0.102$).

4. Discussion

Tests for phylogenetic signal generally confirm the relevance of taking into account phylogenetic structure and branch lengths in comparative analyses (Blomberg et al., 2003). Our results showed that for all variables, K statistic values were lower than one and generally non significant. Interestingly, K values lower than one seem to be a common aspect in analyses that include Liolaemini lizards (Vanhooydonck et al., 2010; Tulli et al., 2011, this study), similar to what was observed by Kohlsdorf et al. (2008) for tropidurine lizards. Apparently, morphology is generally evolutionarily labile in these two Neotropical clades. Nonetheless, some analyses indicate that phylogenetic signal is not always absent in Liolaemini lizards (for example, Tulli et al., 2009, 2012). It is possible that the scant SVL variation within each one of the two subclades in the *L. laurenti* group (Fig. 1; Abdala, 2007) may influence the results of the present study. Interestingly, after branch length manipulation, we observed that as OU transformations ' d ' values decrease from untransformed ($d = 1$) to $d = 0.8$ and then to $d = 0.2$, the phylogenetic signal becomes higher than one in several traits (ILL of males, LH of males and females and finally RL of males, but only limb sections of males were significant). This pattern indicates that it is likely stabilizing selection in these features. Nevertheless, we have to be cautious because the sample size is 22 species, and sample size problems may still exist in this kind of analysis (Blomberg et al., 2003).

Our results for sexual dimorphism and sexual size dimorphism index (SDI, *sensu* Gibbons and Lovich, 1990; Table 2) indicate that in overall, males are larger than females. From individual species 16 of the 22 species showed larger males, but only ten showed significant differences. Females are the larger sex in six of the species, but only five are significantly larger than males. Previous studies of sexual size dimorphism in lizards show both cases, female as well as male-biased groups of species (e.g., *Phrynosoma* Zamudio, 1998; geckos Kratochvíl and Frynta, 2002; dwarf chameleons Stuart Fox, 2008; varanids Frýdlová and Frynta, 2010). A broader analysis of SSD in near of 500 species indicates that sexual size dimorphism is a common feature in this group of animals (Cox et al., 2003). With regard to macroevolutionary pattern called Rensch's rule (defined as the increase of SSD with SVL in male-biased species or the decrease of SSD with SVL in female biased species; Fairbairn, 1997; Stuart Fox, 2008), the literature show mixed results in lizards. For example, some species show no relationship between SSD and SVL (Zamudio, 1998), while others do (Kratochvíl and Frynta, 2002; Stuart Fox, 2008; Frýdlová and Frynta, 2010). Despite our

expectations of hyperallometry in SVL based on the differences found in some species of *Liolaemus* lizards (Villavicencio et al., 2003; Cánovas et al., 2006a; Laspiur et al., 2006; Laspiur and Acosta, 2007) our results do not support this hypothesis. Noticeably, one seminal paper on Rensch's rule (Fairbairn, 1997) mentions that male biased iguanian lizards show a lower than one slope when testing allometry in accordance with our results for SVL. These results indicate the need of further and deeper analyses on the role of body size in iguanian lizards, since there is at least one entire group that shows female biased dimorphism (*Phrynosoma*; Zamudio, 1998).

Ecological and evolutionary implications may be important for snout-vent length (e.g., metabolism, predator-prey interactions, mate choice, male-male interactions, fecundity) and therefore may have an effect on sexual size dimorphism. Interestingly, and despite of being the second most speciose genus in the world, *Liolaemus* show quite simple assembly compositions (Videla, 1983; Vega and Bellagamba, 1990; Vega, 1993; Schulte et al., 2004), probably as a consequence of low levels of habitat structuring and limited resource availability (which may affect some aspects such as growth). These latter aspects may be important selective pressures for small body size in Liolaemini lizards (Espinoza et al., 2004). If this is the case, it is possible that the limitations imposed by small body size have implications on other aspects of life-history, for example sexual size dimorphism. The evolution of SVL in Liolaemini (SVL ranges from 40 to 105 mm) appears thus less variable compared to other lizard taxa, such as the tropical genera *Anolis* (Losos, 2009; Thomas et al., 2009) as well as *Varanus* lizards (Frýdlová and Frynta, 2010; Collar et al., 2011), both showing a wide range of body sizes and a different SSD evolution.

Most morphological traits correlated positively with SVL in males and females; however, only some of them showed allometric slopes (head length and width, radius length and manus length, Table 5) and particularly these allometric variables were only observed for the males of the *Liolaemus laurenti* clade. Theoretically, two important functions have been attributed to favor allometry of head size: ecological segregation in diet (Schoener, 1971; Camilleri and Shine, 1990; Shine, 1991; Perez-Mellado and de la Riva, 1993) and sexual selection involving male-male interactions (male contest competition; Kratochvíl and Frynta, 2002; Reaney and Whiting, 2002). Additional evidence leads us to suggest sexual selection in *Liolaemus* head and distal limb dimensions, head-bobs and push-ups displays (Martins et al., 2004) and male-male interactions, although these remain poorly documented (Kozykariski, 2010). Additionally, studies on the home range of some *Liolaemus* species indicate that males show some hierarchic structure according to the size of their home range (Frutos and Belver, 2007; Robles and Halloy, 2009), suggesting male-male interactions and therefore evidence of sexual selection. Finally, our results are concordant with Vanhooydonck et al. (2010) who also suggested that head shape and bite force in males of *Liolaemus* species are more related to sexual selection than to natural selection. In a previous study, Cei et al. (2003) suggested that the distance between fore and hind legs (ILL) is related and viviparous species should have larger ILL. Our results show that females are highly dimorphic in ILL suggesting support for the fecundity advantage hypothesis (Fairbairn, 1997). However, we found no differences in SVL nor in ILL between oviparous and viviparous species within the *L. laurenti* clade. Additionally, there was not positive relationship between ILL and fecundity (number of eggs or embryos) in this group of lizards either. It is important to notice that these variables do not fully represent fecundity. For example, few fully developed embryos may need more space and maternal investment than many early developing eggs.

Liolaemus are highly conservative in some attributes (morphology, Tulli et al., 2009, 2011; metabolic rate, Cruz et al., 2011) and less conservative in some others (bite force, Vanhooydonck et al.,

2010; clinging ability, Tulli et al., 2011). In our study, *Liolaemus* lizards showed a phylogenetically variable morphology and offered evidence leading us to suggest sexual selection for head and distal limb (radius and manus lengths) dimensions based on the observed dimorphism. Finally, resource scarcity in habitats where *Liolaemus* occur may have lead to a small body size in these lizards (Espinoza et al., 2004), this probably constrained body size evolution and perhaps brood or clutch size.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jcz.2012.08.003>.

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