Ann. Zool. Fennici 52: 129–144 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 26 June 2015

Phenotypic diversity in female body shape is related to reproductive potential in *Tupinambis merianae* lizards

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Received 6 June 2014, final version received 7 Dec. 2014, accepted 8 Jan. 2015

Cardozo, G., Naretto, S., Blengini, C. S. & Chiaraviglio, M. 2015: Phenotypic diversity in female body shape is related to reproductive potential in *Tupinambis merianae* lizards. — *Ann. Zool. Fennici* 52: 129–144.

A major goal in evolutionary biology is to determine the mechanisms responsible for maintaining phenotypic variation. Species that have evolved intersexual differences provide an opportunity to increase our understanding of trait evolution. We hypothesize that phenotypic diversity is related to reproductive strategies of female lizards and therefore, to their reproductive potential. Consequently, we evaluated sexual dimorphism in several morphological traits and assessed phenotypic variability and selection on body traits of female lizards in a model species (*Tupinambis merianae*). The results support our hypothesis that certain phenotypic traits of body shape are sexually dimorphic and that females present large continuous variation in these traits. Moreover, some morphological traits in females favor the increment of energetic reserves and reproductive output. These results contribute to the identification of characters upon which selection may have acted and suggest that phenotypic variation in female lizards are related to a diversity of reproductive strategies. Therefore, we fill part of the knowledge gap on the proximate mechanisms that link maternal morphology and reproductive potential in female lizards.

Introduction

The mechanisms underlying intraspecific phenotypic diversity of species have evolutionary importance because they make diverse phenotypes visible to selection (Lee 2011, Shine *et al*. 2011). A major goal in evolutionary biology is to determine the mechanisms responsible for maintaining phenotypic variation (Calsbeek *et al*. 2010a). Moreover, an organism's phenotype is considered a causal link with its reproductive output and hence to its microevolutionary fitness (Brown & Shine 2005, Vergara *et al*. 2012). Therefore, assessing phenotypic diversity in the reproductive context of species might contribute to our understanding of microevolutionary processes.

Species that have evolved sexual dimorphism provide an opportunity to increase our understanding of trait evolution because dimorphic traits result from selective forces that act differentially on individuals of each sex (Cox *et al.* 2003, Corl *et al.* 2009). Sexual dimorphism in body size (Gienger & Beck 2007) as well as the relative size of different body parts (i.e. abdomen, tails and limbs) can be very informative of the selective pressures imposed (Butler & Losos 2002, Kratochvil *et al.* 2003). The causes of sexual dimorphism are complex, but most sexually dimorphic traits are believed to be directly linked to the reproductive role of each sex (Bulté *et al.* 2008, Naretto *et al.* 2014).

How females determine their reproductive output is an important question that has been scarcely studied (Du & Lu 2010). Fat reserves may constrain reproductive investment in Squamata (Shine 1992, Olsson & Shine 1997, Du *et al.* 2005, Lourdais *et al.* 2006) and body volume can determine the upper physical limit up to which females can fill themselves up with eggs (Du & Lu 2010). However, little is known about the proximate mechanisms that link maternal morphology and reproductive potential. Therefore analyzing how diverse phenotypic traits of female body shape are related to the storage of fat bodies and to clutch size may be an interesting approach to understand sexual selection mechanisms acting on the morphology of female lizards.

Selection for increasing female body size plays a central role in the evolution of fecundity, resulting in the evolution of female-biased sexual size dimorphism (Cox *et al.* 2003, Lourdais *et al.* 2006, Corl *et al.* 2009, Cardozo & Chiaraviglio 2011, Pincheira-Donoso & Tregenza 2011, Liao 2013). Accordingly, Brown and Shine (2005) found strong links between maternal phenotype and reproductive success using path analysis. Moreover, species with a high relative clutch mass that produce a single clutch per reproductive season are more constrained by body size than species with low relative clutch mass. Therefore, they are excellent subjects for exploring the phenotypic variation of female body morphology (Du *et al.* 2005, Du & Lu 2010).

The evolutionary dynamics of reproductive variation involves complex selection-mediated interactions among life-history traits that coevolve to increase reproductive success (Sinervo *et al.* 2000, Butler & Losos 2002, Lancaster *et al.* 2010). Accordingly, Karsten *et al.* (2009) showed that it is selection for multiple traits rather than for a single individual trait that best predicts reproductive success. For female lizards, trunk length, abdominal volume and tail robustness might be important phenotypic traits. A greater trunk length would provide females with more space to hold abdominal fat bodies and then eggs (Olsson *et al.* 2002, Kaliontzopoulou *et al.* 2007, Boretto & Ibargüengoytía 2009). Moreover, increased reproductive output may result from a relative increase in abdomen width (Goodman *et al.* 2009, Bastiaans *et al.* 2013, Sun *et al.* 2012, Scharf & Meiri 2013). In addition, in several lizard species fat reserves were also found to be stored in the proximate section of the tail; indeed, variations in tail circumference in mature females over the active season have been reported (Fitzgerald *et al.* 1993). Limb robustness may help to carry the weight of stout females (Dubey *et al.* 2011). Therefore, what traits are sexually dimorphic and how sexual selective pressures influence them are interesting questions that may help to understand phenotypic selection in female lizards. Although phenotypic variation related to reproductive strategies is often partitioned into discrete morphs (Calsbeek *et al.* 2010b), continuous phenotypic variation may also be related to reproductive potential and selection should benefit phenotypic traits that maximize energy storage and clutch size.

Procedures for phenotypic selection analysis within a generation are standardly used to reveal the relationship between phenotypic traits and reproductive success (Arnold & Wade 1984, Brodie *et al.* 1995). Functional correlates of trait evolution are important to understand phenotypic evolution (Irshick *et al.* 2007, Losos 2011, Galeotti *et al.* 2013). Accordingly, the model of Lande and Arnold (1983) is a suitable approach to estimate multivariate selection gradients. When direct measures of the offspring are unavailable or scarce, fitness-related traits are commonly used to estimate the reproductive success of individuals (Aubret *et al.* 2002, Molnar *et al.* 2012). Moreover, the relationship between these traits and reproductive output is useful to understand the proximate mechanisms underlying fecundity selection. In reptiles, body condition is commonly considered a measure of fitness (Bulté *et al.* 2008) and because body condition is influenced by fat body storage, it is a reliable predictor of the reproductive potential of individuals (Bertona & Chiaraviglio 2003, Cardozo & Chiaraviglio 2008). Fat storage is an indicator of the reproductive effort of females because of its close relationship with ovarian follicle development and vitellogenesis (Hans &Tinkle 1965, Smith 1968, Derickson 1976, Guillette & Casas-Andreu 1981, Guillete & Sullivan 1985, Amat *et al.* 2000, Aguilar-Kirigin & Naya 2013, Verrastro & Rauber 2013, Naretto 2014).

The form and strength of selection on morphological traits may also depend on the social context (Shine *et al.* 2006, Procter *et al.* 2012). The choice of a social context may depend on the relative attractiveness, given by the phenotype of competitors or potential mates (Gasparini *et al.* 2013). Temporal variation in the presence of females and males might be associated with the variation in social context over the reproductive season (Vercken *et al.* 2006, Lancaster *et al.* 2010, McLean *et al.* 2012, Hughes 2013). Therefore, analyzing patterns of reproductive phenotypes in relation to the temporal presence of potential mates may provide insights into how sexual selection influences phenotypic traits.

Squamata includes interesting model systems for examining evolutionary changes in body shape because of their strong intra- and interspecific variation in body size and shape. Although this variation could be explained by several ecological factors, evolutionary forces linked to the reproductive performance of individuals are likely to be responsible for phenotypic variability (Bulté *et al.* 2008, Goodman *et al.* 2009, Cardozo & Chiaraviglio 2011, Naretto *et al.* 2013). Our study model, *Tupinambis merianae*, a large teiid lizard, is particularly interesting because females invest greatly in a single clutch per reproductive season (Fitzgerald *et al.* 1993).

We hypothesize that phenotypic diversity of female lizards is related to reproductive strategies and therefore, we expect certain phenotypic traits to be sexually dimorphic and related to fat storage and reproductive potential. Consequently, we tested sexual dimorphism in total body size and body parts, and assessed the phenotypic diversity of body shape in females by analyzing the variability and correlation between morphological traits. Moreover, we tested how phenotypic selection shapes female traits in relation to fat storage and clutch size. We also evaluated temporal variation in the presence of female and male phenotypes throughout the reproductive period. Our findings may help to better understand the evolutionary dynamics of female body shape in the context of sexual selection.

Material and methods

Study species and data collection

The life history of *T. merianae* presents seasonal cyclic reproduction (Mercolli & Yanosky 1990, Noriega *et al.* 1996). The species spends the cold winter months sheltered in burrows in the ground (Andrade *et al.* 2004, Winck & Cechin 2008). Reproductive activities such as courtship and mating are restricted to spring (Fitzgerald *et al.* 1993).

The specimens were captured in central Argentina (31°25´59´´S, 63°41´04´´W to 31°40´55´´S, 63°22´30´´W), which corresponds to the southernmost distribution area of the species (Cardozo *et al.* 2012, Lanfri *et al.* 2013). *Tupinambis merianae* is included in Appendix II of the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES); commercial harvest is allowed in Argentina (Porini 2006). Scientific studies based on the examination of specimens collected for the international skin trade provide important knowledge of the biology of the species (Shine *et al.* 1999). During the reproductive season, we worked with authorized local people who harvest *Tupinambis* lizards from the wild to be killed in accordance with AVMA Guidelines on Euthanasia (AVMA 2007). Methods comply with the current laws of Argentina. We are authorized by the government environmental agencies for scientific capture.

Male and female lizards were captured near caves where they performed sexual activity, and sampling included the entire size range of mature individuals. To classify the individuals as mature, we set a minimum snout–vent length

(SVL) threshold, following the criterion of the smallest reproductive female and male, respectively (Madsen *et al.* 2006, Cardozo & Chiaraviglio 2011, Naretto *et al.* 2014). We included in the analyses receptive females during a 3-month period (October through December); therefore, we discarded females with calcareous eggs in oviducts or with signs of recent oviposition, such as conspicuous corpora lutea. A total of 199 mature females and 274 mature males were analyzed. We recorded the following variables from each specimen: total SVL; interlimb length considering the linear distance between the insertion of forelegs and hind legs; abdominal perimeter and proximate tail perimeter, measured at the respective widest transversal sections; foreleg and hind leg circumference measured at the middle of the upper arm and upper leg, respectively. All these variables were recorded to the nearest 0.5 cm using a ruler. Body mass was determined to the nearest 50 g using a balance. We dissected both abdominal fat bodies and weighed their masses to the nearest 0.1 g using an electronic balance (Traveler TA302; OHAUS; New Jersey, USA) following Fitzgerald *et al.* (1993) and Herrera and Robinson (2000). Clutch size was estimated based on the number of > 7 mm ovarian vitellogenic follicles.

Statistical analyses

A variety of parametric statistical tests were applied after checking data for normality and equality of variances. When these assumptions were not satisfied we applied nonparametric tests. To test sexual dimorphism, we examined if there were sexual differences in SVL, interlimb length, abdominal perimeter, tail perimeter, and foreleg and hind leg circumference. To do so, we applied a Dummy-Variable Regression Model with Interaction in order to compare the slopes of the linear regressions between the size of the morphological traits and SVL (SVL was the quantitative regressor; the factor sex was represented by the dummy regressor; and the interaction regressor was the product of the other two regressors; *p* value of interactions were reported) (Fox 2015).

To assess female morphological variability, we evaluated position and dispersion measures (mean, range and standard deviation for all quantitative variables). To compare the relative amount of variation in traits that had different measurement units we used the coefficient of variation. Statistical dispersion of the data was also measured by assessing kurtosis, considering that widely dispersed data present platykurtic distribution (kurtosis < 0), whereas data concentrated around the mean present leptokurtic distribution (kurtosis > 0). Spearman's (r_S) correlation was used to analyze the relationships between the morphological characters. Allometry of these characters with body size was tested with regression analysis. The ln-transformed body measurements were regressed on ln-transformed SVL. The slope (b) of these regressions estimated the relative relationships: for linear dimensions, a slope of 1 indicated isometry, a slope greater than 1.0 indicated positive allometry, and a slope less than 1.0 indicated negative allometry (Huxley 1932, Gayton 2000, Araujo & Tschinkel 2010, Cabrera *et al.* 2013). We applied a t-test to evaluate if the observed slopes were significantly different from $b = 1$.

To explore functional correlates of morphological traits we assessed for differences between sexes in the contribution of the aforementioned traits to fat storage for reproduction. To do this, we tested sexual dimorphism in the relationships between morphological trait size and weight of fat bodies using a Dummy-Variable Regression Model with Interaction (each morphological trait was used as quantitative regressor; the factor sex was represented by the dummy regressor; and the interaction regressor was the product of the other two regressors; *p* value of interactions were reported) (Fox 2015).

Differences in multiple phenotypic traits between males and females were evaluated using principal component analysis (PCA). We assessed how changes in multivariate morphology were associated with changes in fitness according to the capacity of individuals to store fat for reproduction and according to their reproductive output. Therefore, we correlated body condition, weight of fat bodies and clutch size with the scores of the principal components (PC) using Spearman's correlation (r_S). To obtain a measure of lizard's body condition (mass relative to length), we calculated residual scores from the general linear regression of ln-transformed body mass to SVL (Madsen & Shine 1999, Bertona & Chiaraviglio 2003). Then, we tested if body condition was influenced by body size using linear regression between the obtained residual scores and SVL.

We evaluated variations in the presence of female and male phenotypes by examining monthly temporal variations in multivariate morphology (October to December) with MANOVA using the scores on the first and second principal components. *A posteriori* Hotelling's test was also performed.

We evaluated phenotypic selection following Lande and Arnold's (1983) model, i.e. we estimated multivariate selection gradients on female morphological traits using a multiple regression linear model. We measured female fitness as body condition, since it is related to fat storage, which contributes to follicle development (Derickson 1976, Fitzgerald *et al*. 1993). We evaluated linear gradients, non-linear gradients and correlational gradients. Linear gradients for higher or lower phenotypic values assess the association between the mean of a trait and fitness; non-linear gradients assess the effect of selection on the variance of the trait producing stabilizing or disruptive patterns; and correlational gradients assess the covariance between two traits. To avoid over-parametrization of the model we used SVL, interlimb length, abdominal perimeter and tail perimeter as independent terms, considering their role in the increment of body space for fat storage (Fitzgerald *et al*. 1993, Olsson *et al*. 2002, Lourdais *et al*. 2006). Lande and Arnold's model was performed using R (R development core team 2013). Finally, we tested the relationship between the variables selected in this model and clutch size by applying a multiple linear regression model. All statistical analyses were conducted using Infostat (2013).

Results

Snout–vent length was a sexually dimorphic character (female mean = 37.8 cm, SD = 2.56, $n = 199$; male mean = 39.4 cm, SD = 3.58, $n = 274$; W = 38561.5; $p < 0.001$). Regression analyses between morphological traits and SVL also showed significant differences between sexes (Fig. 1) (interlimb length: slope: $F = 6.32$, $p = 0.013$; abdominal perimeter: slope: $F = 8.69$, $p = 0.003$; tail perimeter: slope: $F = 4.29$, $p = 0.039$; foreleg circumference: slope: $F = 10.38$, $p = 0.001$; hind leg circumference: slope: $F = 5.35$, $p = 0.021$).

Frequency distributions of morphological traits in females are presented in Fig. 2. Body mass and abdominal perimeter expressed the highest phenotypic variability based on the coefficient of variation, whereas SVL expressed the lowest variability (Table 1). Morphological traits often presented platykurtic distributions.

Spearman's correlations revealed that some traits covaried, being highly correlated ($r_S > 0.75$), whereas others were less correlated ($r_S < 0.75$) (Table 2). Abdominal perimeter showed positive allometry ($b = 1.35$; $p < 0.01$), whereas the other characters showed isometry (interlimb length $b = 1.07$, $p = 0.44$; foreleg circumference $b = 1.03$, $p = 0.72$; hind leg circumference $b = 0.88$, $p = 0.1$; tail perimeter $b = 0.86$, $p = 0.07$).

Females stored more fat mass than males (slopes: $F = 8.70$, $p = 0.003$). The size of the morphological traits was directly related to the

Table 1. Morphological traits estimated in mature females of *Tupinambis merianae* (Shapiro test: For SVL, AP and IL $p > 0.05$; for FLC, HLC, TP and BM $p < 0.05$).

Trait	*n*	Mean	SD	CV	Min	Max	Median	Kurtosis
Body mass (BM, kg)	199	1.76	0.45	25.74	0.95	3.10	1.70	–0.26
Snout–vent length (SVL, cm)	199	37.80	2.57	6.79	32.00	44.50	38.00	–0.40
Abdominal perimeter (AP, cm)	199	25.62	3.47	13.56	18.00	37.00	25.00	–0.25
Tail perimeter (TP, cm)	199	15.30	1.42	9.26	12.00	19.50	15.50	–0.24
Foreleg circumference (FLC, cm)	199	7.22	0.71	9.80	5.50	9.00	7.00	–0.11
Hind leg circumference (HLC, cm)	199	11.42	1.07	9.36	9.00	14.00	11.50	–0.38
Interlimb length (IL, cm)	116	17.81	1.63	9.13	13.00	22.50	18.00	0.37

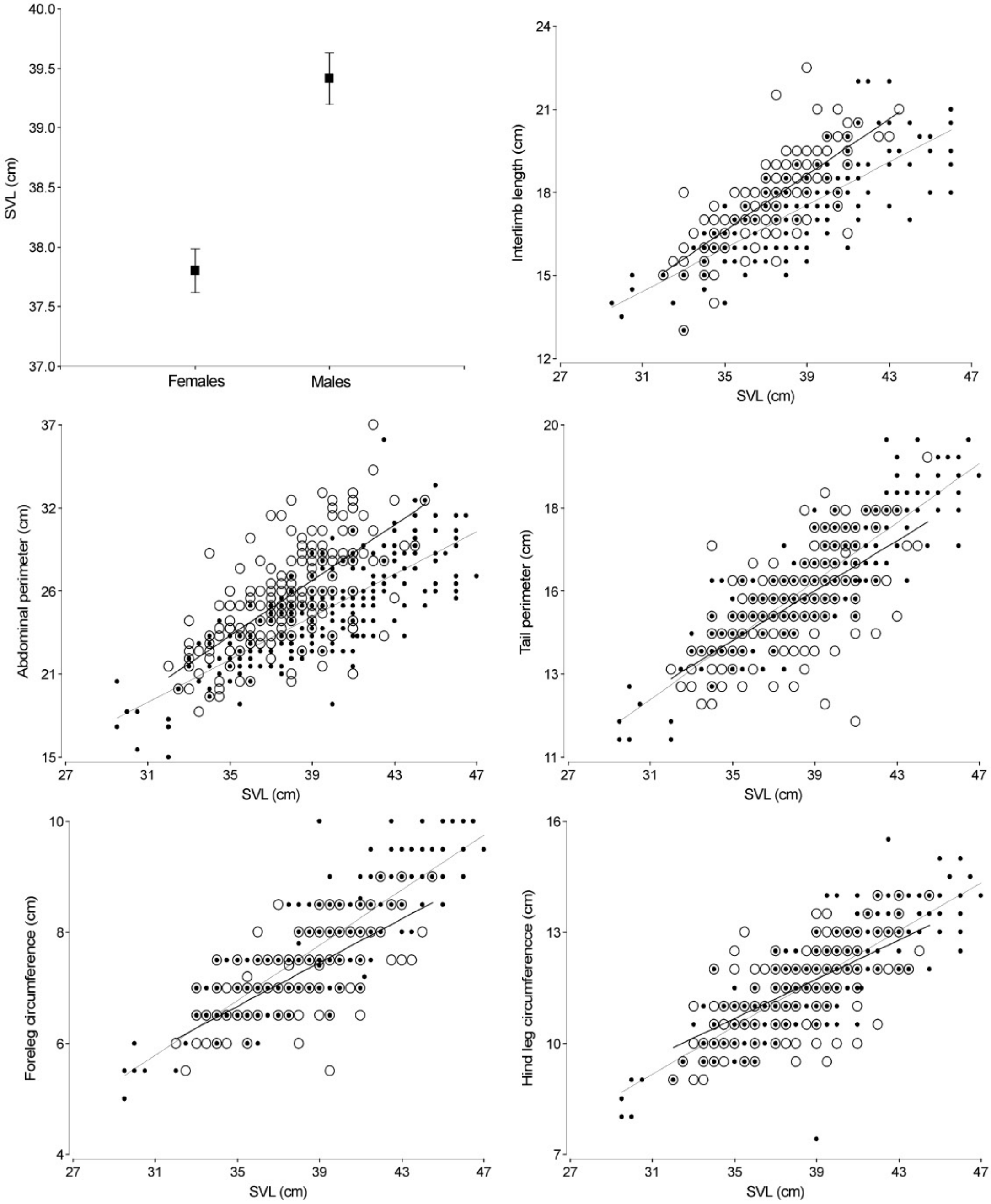

Fig. 1. Sexual dimorphism in morphological traits of *Tupinambis merianae*. Circles: females, black dots: males. Lines represent the adjusted models for females (solid line) and males (dotted line).

weight of fat bodies and these relationships were sexually dimorphic (abdominal perimeter: slope: $F = 4.18$, $p = 0.042$; tail perimeter: slope: $F = 42.13$, $p < 0.001$; foreleg circumference: slope: $F = 29.22$, $p < 0.001$; hind leg circumference: slope: $F = 26.81$, $p < 0.001$), except for interlimb length (slope: $F = 0.0008$, $p = 0.977$; intercept: $F = 0.08$, $p = 0.775$) (Fig. 3).

The principal component analyses performed on the original morphological variables yielded

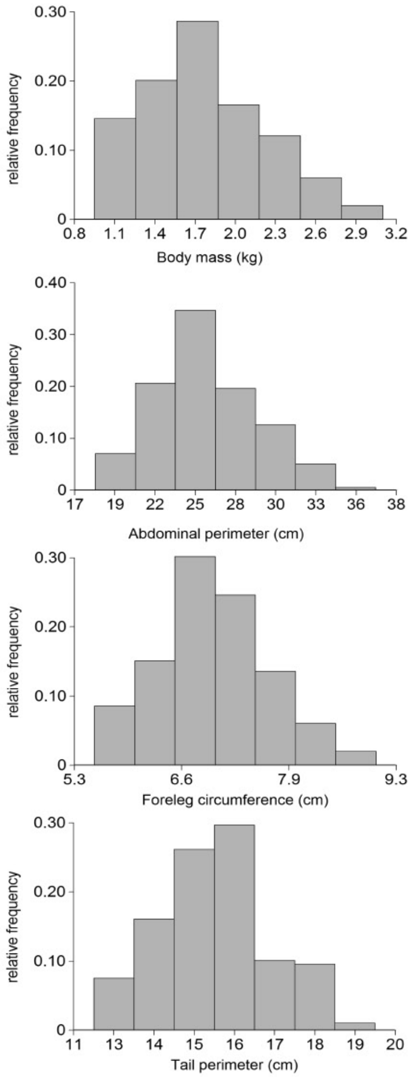

Fig. 2. Frequency distributions of morphological traits in mature females of *Tupinambis merianae*.

two significant factors both for females and males (Table 3). Female points in the biplot were more dispersed than male points, indicating greater phenotypic diversity in females than in males

Table 2. Spearman's correlation coefficients for correlations between morphological traits in mature females of *Tupinambis merianae*. All correlations are significant (at $p < 0.05$). BM = body mass, SVL = snout–vent length, AP = abdominal perimeter, TP = tail perimeter, FLC = foreleg circumference, HLC = hind leg circumference, IL = interlimb length.

	BM (kg)	SVL (cm)	AP (cm)	TP (cm)	FLC (cm)	HLC (cm)
SVL (cm)	0.80					
AP (cm)	0.89	0.67				
TP (cm)	0.85	0.64	0.71			
FLC (cm)	0.78	0.72	0.70	0.79		
HLC (cm)	0.79	0.62	0.68	0.87	0.83	
IL (cm)	0.64	0.77	0.54	0.43	0.46	0.44

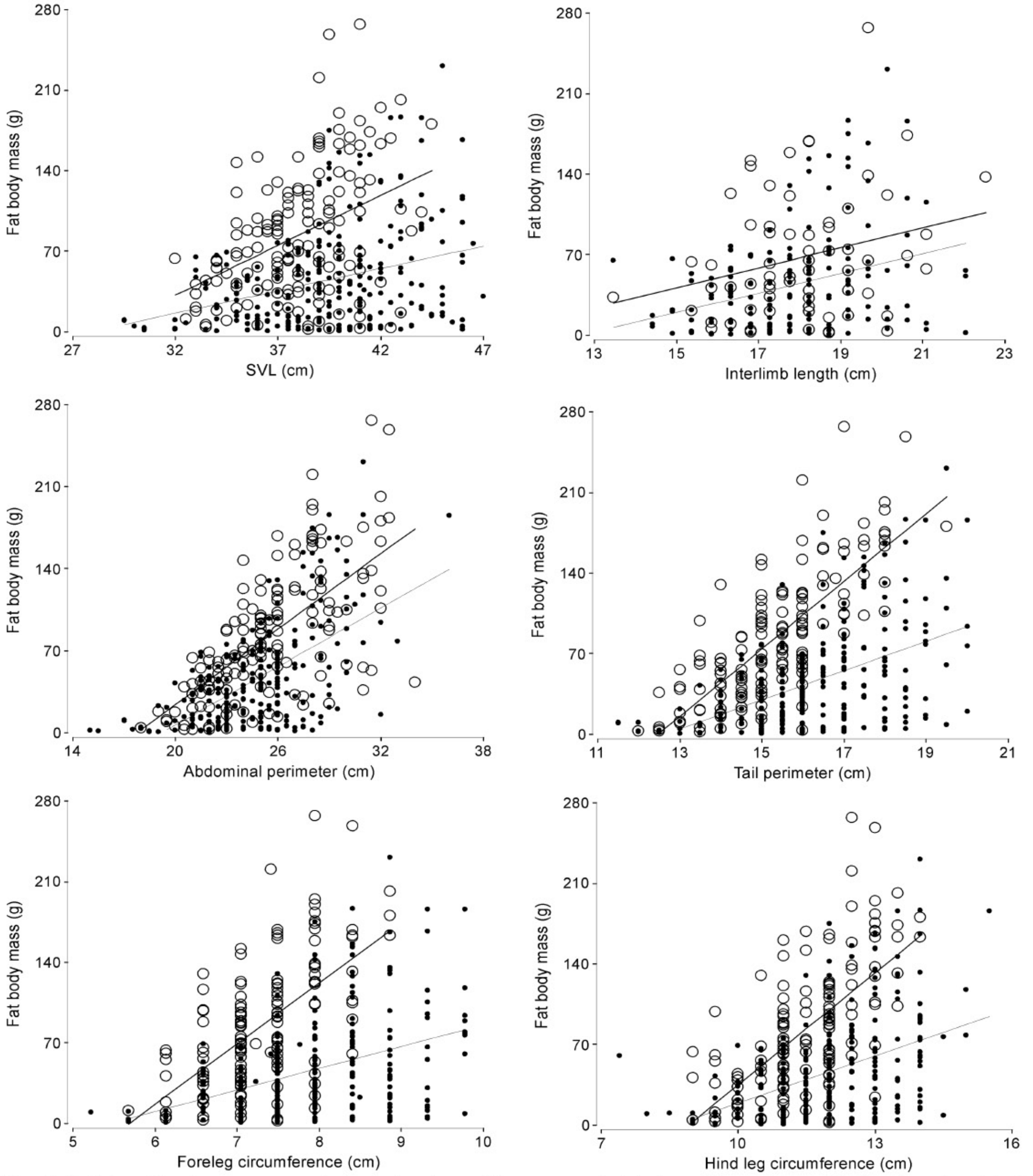

Fig. 3. Relationships between morphological traits and fat storage in *Tupinambis merianae*. Circles: females, black dots: males. Lines represent the adjusted models for females (solid line) and males (dotted line).

(Fig. 4). All morphological variables of females contributed similarly to PC 1. Abdominal perimeter was more related to PC 1 than to PC 2. According to PC 2, female phenotypic variation was also explained by interlimb length, tail perimeter, foreleg circumference and hind leg circumference. Phenotypic diversity in females was related to their body condition according to PC 1 and PC 2. Body condition was positively related to PC 1 ($r_S = 0.49$, $p < 0.01$), and negatively related to PC 2 ($r_S = -0.43$, $p < 0.01$). Body condition was not influenced by SVL ($F = 0$, $p > 0.999$). Fat body weight was also positively correlated to PC 1 ($r_S = 0.61$, $p < 0.01$) and negatively related to PC 2 in females ($r_S = -0.41$, $p < 0.01$). Finally, clutch size was influenced by PC 1

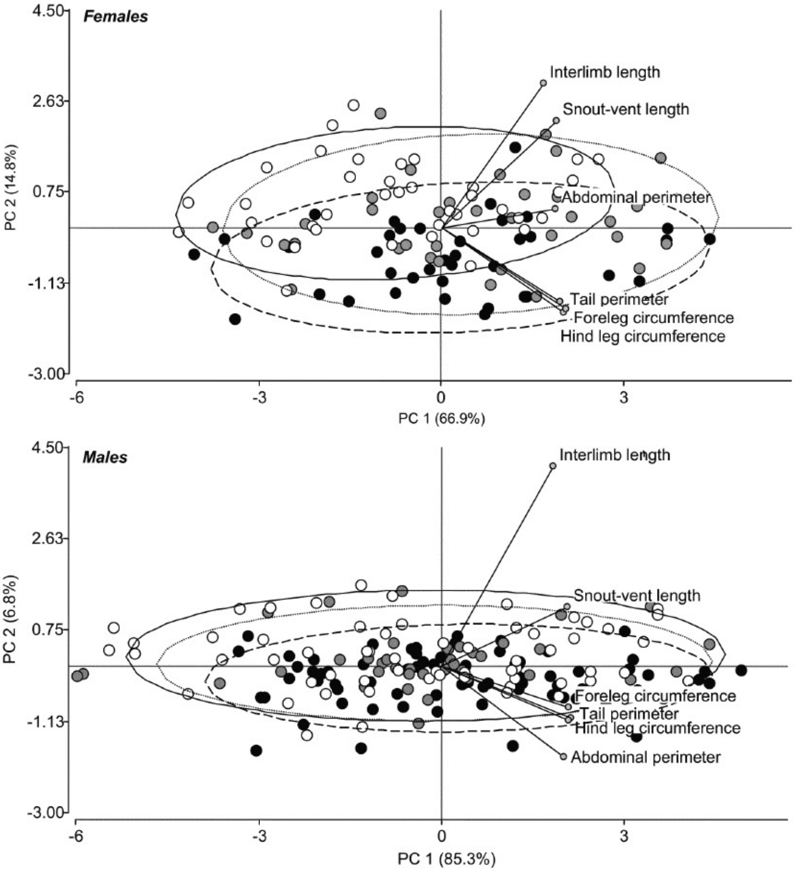

Fig. 4. Principal component analysis of morphological traits in mature females and males of *Tupinambis merianae*. Predictive ellipses are indicated (October: black dots and dashed line; November: gray dots and dotted line; December: circles and solid line).

($r_S = 0.53$, $p < 0.01$), with no relationship with PC2 being observed ($r_S = 0.25$, $p = 0.16$).

We observed that reproductive females and males were present coordinately according to their morphology during the reproductive season (Fig. 4). At the beginning of the season (October), the most robust males with big abdomen, tail and legs appeared consistently with females with the highest body condition, which were medium-large females with big abdominal perimeter (according to PC 1) and with short interlimb length and robust tail and legs (according to PC 2). Later in the reproductive season (November) males and females with intermediate traits were present (according to both PC 1 and PC 2). At the end of the reproductive season (December), females with small SVL, the largest interlimb length, the smallest circumference of tail and legs, and the smallest abdominal perimeter were the most frequent (Fig. 4). These variations among months were significant, according to the scores on PC 1 and PC 2 (Table 4).

The relationships between morphological traits of females and body condition, accord-

Table 3. First and second axes of the principal component analyses performed on morphological traits in mature females and males of *Tupinambis merianae*. For abbreviations *see* Table 2.

	Females		Males	
	PC1	PC2	PC1	PC2
Eigenvalue	4.02	0.89	5.12	0.85
Explained Variation	0.67	0.15	0.41	0.07
SVL	0.40	0.47	0.41	0.24
AP	0.40	0.08	0.40	–0.38
TP	0.43	–0.37	0.42	–0.21
FLC	0.42	–0.32	0.42	–0.17
HLC	0.44	–0.35	0.42	–0.22
IL	0.36	0.64	0.37	0.82

ing to the model of Lande and Arnold (1983), are presented in Table 5 (Multiple r^2: 0.840, F-statistic: 37.73, $p < 0.001$). Snout–vent length, tail perimeter and abdominal perimeter were selected directionally for increased body condition, whereas interlimb length was marginally selected. Snout–vent length had a significant negative effect on body condition, whereas abdominal perimeter and tail perimeter had a positive effect on body condition. We did not find effects of non-linear gradients or correlational gradients. We tested the relationship between the selected variables and clutch size in a multiple linear regression model and found that SVL and abdominal perimeter were the most important predictors of the reproductive output of females (SVL: coefficient: 0.36, $F = 15.12$, $p < 0.001$; abdominal perimeter: coefficient: 1.19, $F = 3.73$, $p = 0.0580$; tail perimeter: coefficient: 1.95, $F = 1.31$, $p = 0.257$; $r^2 = 0.25$; $n = 66$).

Discussion

Our study contributes to fill part of the knowledge gap on the relationship between phenotype and reproductive strategies in female lizards. The main results allowed us to identify characters upon which selection may have acted differentially between sexes and supported our hypothesis that continuous phenotypic variation in females may be related to variation in their reproductive potential. Moreover, we found correlates among morphological traits, energetic reserves (fat bodies) and reproductive output (clutch size).

Table 4. Monthly phenotypic variation of mature females and males of *Tupinambis merianae* based on scores on PC 1 and PC 2 (MANOVA). Different superscript letters indicate significant differences between months (*a posteriori* Hotelling's test).

	Month	n	Mean	SD	Median	F	p
Females							
PC 1	October^a	40	0.36	2.24	0.20	11.77	< 0.001
	November^b	36	0.58	2.20	0.81		
	December^c	40	–0.89	1.95	–0.87		
PC 2	October^a	40	–0.60	0.77	–0.55		
	November^b	36	0.09	0.93	0.07		
	December^c	40	0.52	0.78	0.45		
Males							
PC 1	October^a	73	0.28	2.09	0.23	5.42	< 0.001
	November^b	40	–0.11	2.25	–0.24		
	December^b	62	–0.26	2.46	–0.13		
PC 2	October^a	73	–0.23	0.56	–0.18		
	November^b	40	0.08	0.59	–0.05		
	December^b	62	0.23	0.68	0.20		

Table 5. Multivariate analysis of phenotypic selection in mature females of *Tupinambis merianae* with body condition as a measure of fitness (Lande & Arnold 1983). Standardized linear selection gradients (β), non-linear selection gradients (γ_{ii}), correlational selection gradients (γ_{ij}) and standard errors (in parentheses) are given. ** $p < 0.001$; * $0.05 < p < 0.1$. Abbreviations: snout vent length (SVL), abdominal perimeter (AP), tail perimeter (TP), interlimb length (IL).

Traits	β	γ_{ii}	γ_{ij}		
			TP	AP	IL
SVL	–0.23 (0.02)**	0.03 (0.06)	0.06 (0.04)	–0.05 (0.04)	–0.04 (0.03)
TP	0.14 (0.01)**	–0.002 (0.04)		–0.007 (0.02)	–0.03 (0.03)
AP	0.12 (0.01)**	0.007 (0.03)			0.02 (0.03)
IL	0.02 (0.01)*	0.03 (0.03)			

Morphological traits studied here differed between the sexes. Notable differences between sexes were detected in SVL, interlimb length and abdominal perimeter. Females were shorter than males but had larger interlimb length and bigger abdominal perimeter. These results suggest that different selective pressures have been acting on each sex, shaping the studied morphological traits as sexually dimorphic. Interpreting the proximate causes that lead to morphological differences between and within males and females is important to elucidate the evolutionary pressures acting on each sex (Kaliontzopoulou *et al*. 2007). It has been observed that large interlimb length and wide abdomen would provide females with larger body cavities for storing fat reserves that will be used during reproductive processes (Lourdais *et al*. 2006). We did not observe a differential contribution of interlimb length to fat storage between sexes but increments of abdominal capacity and leg robustness were associated with larger fat storage in females than in males. Therefore, according to the functional significance of these characters, the increment in their size might be favored in female lizards.

Although phenotypic variation involved in reproductive strategies is usually partitioned into discrete morphs (Calsbeek *et al*. 2010b), exploring continuous phenotypic variation linked to reproduction as observed in females of *Tupinambis merianae* may contribute to understand the biological meaning of phenotypic variability, which is a major question in evolutionary biology (Calsbeek *et al*. 2010a, Cox & Calsbeek 2011). Females showed phenotypic variability in diverse morphological traits that present platykurtic distributions, with values dispersed among the distribution classes. The evolution of polymorphisms in a population is probably an important consequence of the co-existence of diverse reproductive strategies (Gray & McKinnon 2006, Corl *et al*. 2009, Vercken *et al*. 2010, Cox & Calsbeek 2011, Galeotti *et al*. 2013). Similarly, the continuous variation of phenotypic traits might reveal variability of female reproductive tactics.

Whether or not the length reached by individuals is an advantage for fitness is a widely debated question in reptilian lineages (Fitch 1985, Cox *et al*. 2003, Shine 2005, Stephens & Wiens 2009, Pincheira-Donoso & Tregenza 2011). According to the tested sexual body size dimorphism, females were shorter than males. Moreover, considering the coefficient of variation, SVL was the trait that expressed the lowest variability in females. The SVL mean and median (ca. 38 cm) (Table 1) and the frequency histogram (Fig. 1) showed that the most frequent body size for females corresponds to the intermediate value within the SVL range. As Bonnet *et al*. (2000) suggested for viperids, an intermediate body size would balance ecological and reproductive advantages, maximizing reproductive output. Accordingly, Cardozo and Chiaraviglio (2011) showed that the optimum body size in boids might be shaped by trade-offs among life-history parameters to maximize fitness. Body size has a strong influence on reproductive output, but also on the ecological consequences for an organism, since overall energy balance is strongly affected by body size (Baird 2008).

By contrast, body mass and abdominal perimeter showed the highest variability, which supports the fact that females can differ greatly in the storage of energy reserves. Moreover, the close relationship between these traits (Spearman's correlation coefficient = 0.89) and the high contribution of abdomen size to fat storage in females suggest that the external morphology of females might work as an honest visual signal to males in the context of sexual selection (Irschick *et al*. 2007), reflecting their reproductive potential. Accordingly, given the high correlation observed between body mass and tail perimeter (Spearman's correlation coefficient = 0.85) and the association between tail perimeter and fat storage in females, tail appearance would provide additional evidence of the ability of females to store energetic reserves that might be allocated to reproduction. Moreover, the strong correlation obtained between tail perimeter and hind leg circumference, other significant correlations between limbs and body mass, and the dimorphic relationship between the circumference of legs and the weight of fat bodies suggest that limb robustness might play an important role in supporting the body of females when their fat reserves increase (Kaliontzopoulou *et al*. 2010, Lancaster *et al*. 2010, Dubey *et al*. 2011).

Exploring the relationship between sexual morphological traits and allometry is an essential step toward understanding phenotypic diversification in a sexual selection context (Bonduriansky 2007) and, specifically, toward interpreting the biological meaning of the variability in female phenotypes. Abdominal perimeter presented positive allometry, indicating that females exacerbate this trait. Furthermore, although part of the sexual phenotypic variability is often explained by allometric relationships, the studied morphological traits are also combined, producing diverse non-allometric variability in female phenotypes. According to PCA results, PC 1 might be understood as body size variation, since all the morphological variables contributed similarly to this axis; however, PC 2 revealed another source of variation in the phenotypic variability of females, indicating a gradient of alternative phenotypes from females with enlarged interlimb and thin limbs and tail to females with shortened interlimb and robust limbs and tail. Although positive allometry is a typical attribute of some sexual traits, diversity of allometric patterns has been found in traits under sexual selection (Bonduriansky 2007).

Morphological trait variation has been frequently reported at a regional scale (Cardozo & Chiaraviglio 2011, Kelly *et al.* 2013). However, syntopic variation is likely to convey socially important information regarding reproductive behaviors (Vercken *et al.* 2006, Formica & Tuttle 2009, Roughgarden & Akcay 2010). In species in which sexual dimorphism is related to sexual selection, within-sex phenotypic variability is expected to be related to reproductive dynamics (Vercken *et al.* 2006). Accordingly, we observed that female and male phenotypes vary coordinately during the reproductive season. The syntopic temporal variations found could be expressing behavioral components in relation to sexual and social contexts of mate preference.

Direct measurements of selection or investigations of the functional correlates of trait evolution are important to understand phenotypic evolution (Irshick *et al.* 2007, Losos 2011, Galeotti *et al.* 2013). Reproductive tactics in female lizards are generally related to variation in yolk-provisioning strategies (Sinervo 1994), which depend on body condition and fat reserve mass (Bertona & Chiaraviglio 2003, Cardozo & Chiaraviglio 2008). Accordingly, we found an association between fat storage and morphological traits. Moreover, correlation of PC 1 and PC 2 with body condition showed a positive correlation of the former, indicating that, in general, larger females with wide abdomen have more capacity to accumulate energy reserves in fat bodies than smaller females. Probably these reserves favor reproductive success, since clutch size was also positively correlated with PC 1. In addition, the trade-off between growth and reproduction could be biased toward reproductive efficiency in larger females, in which growth has decreased (Cox & Calsbeek 2010; Cardozo & Chiaraviglio 2011). However, PC 2 explained that females can present alternatively enlarged or shortened interlimb phenotypes. These morphs vary in their capacity to store reserves, since females with enlarged interlimb and thin limbs and tail showed lower body condition than females with shortened interlimb and robust limbs and tail. Although we did not find a relationship between clutch size and PC 2, variation in energy stores associated with female phenotype variation explained by PC 2 may be revealing variability in other features of the reproductive strategies. Although selection would produce long trunk in some lizard species (Schwarzkopf 2005), our data suggest that body elongation might be associated with low body condition. Further research exploring the reproductive value of enlarged interlimb is necessary.

The phenotypic selection linear model obtained in this work, based on the model of Lande and Arnold (1983), helps to interpret the ultimate causes of phenotypic variation; indeed, the model revealed that selection is acting directionally on SVL, tail perimeter and abdominal perimeter of female *T. merianae*. The increment of SVL has a significant negative effect on body condition, suggesting that in large individuals energy storage might be lower than in short individuals, which is in agreement with the hypothesis of intermediate body size (Bonnet *et al.* 2000). Additionally, abdominal perimeter and tail perimeter have a positive effect on body condition, whereas selection influences interlimb length marginally. Therefore, considering the presented results, we suggest that although

T. merianae females present phenotypic diversity, selection would favor intermediate-sized females, with ample abdominal capacity and big tail perimeter. These findings are important to interpret how selection shapes female morphological traits to increase fitness.

Conclusion

Our results contribute to the identification of characters upon which selection may have acted, suggesting that phenotypic variation in female lizards would be related to diversity in reproductive strategies. We identified the phenotypic traits of body shape that are sexually dimorphic. Females present continuous variation in these traits. Moreover, we determined the morphological traits that contribute to increment energetic reserves, which are directly involved in vitellogenesis in lizards, and the traits that contribute to an increase in reproductive output. These results are interesting because they help to elucidate the proximate mechanisms that link maternal morphology and reproductive potential.

Acknowledgments

We are grateful to the local people from the study area for their invaluable assistance in the field. This study was funded by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) PIP 11420100100176, Fondo para la Investigación Científica y Tecnológica (FONCyT) PRESTAMO BID N° 2437 PICT N° 2010-2782, Ministerio de Ciencia y Tecnología de Córdoba (MinCyT) Préstamo BID-PID No. 013/2009, Secretaría de Ciencia y Tecnología (SeCyT) Res. Secyt 162/12, and Universidad Nacional de Córdoba, Argentina. We thank the anonymous reviewers and the editor for their constructive comments.

References

Aguilar-Kirigin, I. & Naya, D. 2013: Latitudinal patterns in phenotypic plasticity: the case of seasonal flexibility in lizards' fat body size. — *Oecologia* 173: 745–752.

Amat, F., Llorente, G. A. & Carretero, M. A. 2000: Reproductive cycle of the sand lizard (*Lacerta agilis*) in its southwestern range. — *Amphibia–Reptilia* 21: 463–476.

Andrade, D. V., Sanders, C., Milsom, W. K. & Abe, A. S. 2004: Overwintering in tegu lizards — In: Barnes, B. M. & Carey, H. V. (eds.), *Life in the cold: evolution, mechanisms, adaptation, and application*: 339–348. Institute of Arctic Biology, University of Alaska,Fairbanks.

Araujo, M. B. & Tschinkel, W. R. 2010: Worker allometry in relation to colony size and social form in the fire ant *Solenopsis invicta*. — *Journal of Insect Science* 10: 1–10.

Arnold, S. J. & Wade, M. J. 1984: On the measurement of natural and sexual selection: applications. — *Evolution* 38: 720–734.

Aubret, F., Bonnet, X., Shine, R. & Lourdais, O. 2002: Fat is sexy for females but not males: the influence of body reserves on reproduction in snakes (*Vipera aspis*). — *Hormones and Behavior* 42: 135–147.

AVMA 2007: *Guidelines on euthanasia. Formely report of the AVMA panel on euthanasia*. — American Veterinary Medical Association. [Available at http://www.avma.org/issues/animal_welfare/euthanasia.pdf].

Baird, T. A. 2008: A growth cost of experimentally induced conspicuous coloration in first-year collared lizard males. — *Behavioral Ecology* 19: 589–593.

Bastiaans, E., Méndez de la Cruz, F., Rodríguez Hernández, K., Flores Aguirre, C. & Sinervo, B. 2013: Female reproductive investment in the mesquite lizard (*Sceloporus grammicus*) species complex (Squamata: Phrynosomatidae). — *The Southwest Naturalist* 58: 335–343.

Bertona, M. & Chiaraviglio, M. 2003: Reproductive biology, mating aggregations and sexual dimorphism of the Argentine Boa Constrictor (*Boa constrictor occidentalis*). — *Journal of Herpetology* 37: 510–516.

Bonduriansky, R. 2007: Sexual selection and allometry: a critical reappraisal of the evidence and ideas. — *Evolution* 61: 838–849.

Bonnet, X., Naulleau, G., Shine, R. & Lourdais, O. 2000: Reproductive versus ecological advantages to larger body size in female snakes, *Vipera aspis*. — *Oikos* 89: 509–518.

Boretto, J. M. & Ibargüengoytía, N. R. 2009: *Phymaturus* of Patagonia, Argentina: reproductive biology of *Phymaturus zapalensis* (Liolaemidae) and a comparison of sexual dimorphism within the genus. — *Journal of Herpetology* 43: 96–104.

Brodie, E. D. III, Moore, A. J. & Janzen, F. J. 1995: Visualizing and quantifying natural selection. — *Trends in Ecology and Evolution* 10: 313–318.

Brown, G. P. & Shine, R. 2005: Female phenotype, life history, and reproductive success in free-ranging snakes (*Tropidonophis mairii*). — *Ecology* 86: 2763–2770.

Bulté, G., Irschick, D. J. & Blouin-Demers, G. 2008: The reproductive role hypothesis explains trophic morphology dimorphism in the northern map turtle. — *Functional Ecology* 22: 824–830.

Butler, M. A. & Losos, J. B. 2002: Multivariate sexual dimorphism, sexual selection, and adaptation in greater antillean *Anolis* lizards. — *Ecological Monographs* 72: 541–559.

Cabrera, M., Scrocchi, G. & Cruz, F. 2013. 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. — *Zoologischer Anzeiger* 252: 299–306.

Calsbeek, B., Hasselquist, D. & Clobert, J. 2010a: Multivariate phenotypes and the potential for alternative phenotypic optima in wall lizard (*Podarcis muralis*) ventral color morphs. — *Journal of Evolutionary Biology* 23: 1138–1147.

Calsbeek, R., Bonvini, L. & Cox, R.M. 2010b: Geographic variation, frequency-dependent selection, and the maintenance of a female-limited polymorphism. — *Evolution* 64: 116–125.

Cardozo, G. & Chiaraviglio, M. 2008: Landscape changes influence the reproductive behavior of a key capital breeder snake (*Boa constrictor occidentalis*) in the Gran Chaco region. — *Biological Conservation* 141: 3050–3058.

Cardozo, G. & Chiaraviglio, M. 2011: Phenotypic plasticity of life history traits in relation to reproductive strategies in *Boa constrictor occidentalis*. — *Evolutionary Ecology* 25: 1163–1177.

Cardozo, G., Naretto, S., Zak, M. & Chiaraviglio, M. 2012: The role of landscape in contact zones of lizard sister species. — In: Tiefenbacher, J. (ed.), *Perspectives on nature conservation — patterns, pressures and prospects*: 161–176. Intech, Croatia.

Corl, A., Davis, A. R., Kuchta, S. R., Comendant, T. & Sinervo, B. 2009: Alternative mating strategies and the evolution of sexual size dimorphism in the side-blotched lizard, *Uta stansburiana*: a population-level comparative analysis. — *Evolution* 64: 79–96.

Cox, R. M. & Calsbeek, R. 2010: Severe costs of reproduction persist in *Anolis* lizards despite the evolution of a single-egg clutch. — *Evolution* 64: 1321–1330.

Cox, R. M. & Calsbeek, R. 2011: An experimental test for alternative reproductive strategies underlying a female-limited polymorphism. — *Journal of Evolutionary Biology* 24: 343–353.

Cox, R. M., Skelly, S. L. & John-Alder, H. B. 2003: A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. — *Evolution* 57: 1653–1669.

Derickson, W. K. 1976: Lipid storage and utilization in reptiles. — *American Zoologist* 16: 711–723.

Du, W., Ji, X. & Shine, R. 2005: Does body volume constrain reproductive output in lizards? — *Biological Letters* 1: 98–100.

Du, W. & Lu, D. 2010: An experimental test of body volume constraint on female reproductive output. — *Journal of Experimental Zoology* 313A: 123–128.

Dubey, S., Chevalley, M. & Shine, R. 2011: Sexual dimorphism and sexual selection in a montane scincid lizard (*Eulamprus leuraensis*). — *Austral Ecology* 36: 68–75.

Fitch, H. S. 1985: Variation in clutch and litter size in New World reptiles. — *Miscellaneous publication — University of Kansas, Museum of Natural History* 76: 1–72.

Fitzgerald, L. A., Cruz, F. B. & Perotti, G. 1993: The reproductive cycles and the size at maturity of *Tupinambis rufescens* (Sauria: Teiidae) in the Dry Chaco of Argentina. — *Journal of Herpetology* 27: 70–78.

Formica, V. A. & Tuttle, E. M. 2009: Examining the social landscapes of alternative reproductive strategies. — *Journal of Evolutionary Biology* 22: 2395–2408.

Fox, J. 2015: *Applied regression analysis and generalized linear models*, 3rd ed. — Sage Publications, London.

Galeotti, P., Sacchi, R., Pellitteri-Rosa, D., Bellati, A., Cocca, W., Gentilli, A., Scali, S. & Fasola, M. 2013: Colour polymorphism and alternative breeding strategies: effects of parent's colour morph on fitness traits in the common wall lizard. — *Evolutionary Biology* 40: 385-394.

Gasparini, C., Serena, G. & Pilastro, A. 2013: Do unattractive friends make you look better? Context-dependent male mating preferences in the guppy. — *Proceedings of the Royal Society of London B*: 280: 20123072.

Gayton, J. 2000: History of the concept of allometry. — *American Zoologist*. 40: 748–758.

Gienger, C. M. & Beck, D. D. 2007: Heads or tails? Sexual dimorphism in helodermatid lizards. — *Canadian Journal of Zoology* 85: 92–98.

Goodman, B. A., Hudson, S. C., Isaac, J. L. & Schwarzkopf, L. 2009: The evolution of body shape in response to habitats: is reproductive output reduced in flat lizards? — *Evolution* 63: 1279–1291.

Gray, S. M. & McKinnon, J. S. 2006: Linking color polymorphism maintenance and speciation. — *Trends in Ecology and Evolution* 22: 71–79.

Guillette, L. J. Jr. & Casas-Andreu, G. 1981: Seasonal variation in fat body weights of the Mexican high elevation lizard *Sceloporus grammicus microlepidotus*. — *Journal of Herpetology* 15: 366–371.

Guillette, L. J. & Sullivan, P. 1985: The reproductive and fat body cycles of the lizard, *Sceloporus formosus*. — *Journal of Herpetology* 19: 474–480.

Hans, W. E. & Tinkle, D. W. 1965: Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. — *Journal of Experimental Zoology* 158: 79–86.

Herrera, E. & Robinson, M. 2000: Reproductive and fat body cycles of the Tegu lizard, *Tupinambis teguixin*, in the Llanos of Venezuela. — *Journal of Herpetology* 34: 598–601.

Hughes, A. 2013: Female reproductive effort and sexual selection on males of waterfowl. — *Evolutionary Biology* 40: 92–100.

Huxley, J. S. 1932: *Problems of relative growth*. — Methuen, London.

Irschick, D. J., Herrel, A., Vanhooydonck, B. & Van Damme, R. 2007: A functional approach to sexual selection. — *Functional Ecology*. 21: 621–626.

Kaliontzopoulou, A., Carretero, M. A. & Llorente, G. A. 2007: Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. — *Journal of Morphology* 268: 152–165.

Kaliontzopoulou, A., Carretero, M. A. & Llorente, G. A 2010: Sexual dimorphism in traits related to locomotion: ontogenetic patterns of variation in *Podarcis* wall lizards. — *Biological Journal of the Linnean Society* 99: 530–543.

Karsten, K. B., Andriamandimbiarisoa, L. N., Fox, S. F. & Raxworthy, C. J. 2009: Sexual selection on body size and secondary sexual characters in two closely related, sympatric chameleons in Madagascar. — *Behavioral Ecology* 20: 1079–1088.

Kelly, C., Folinsbee, K. E., Adams, D. & Jennions, M. 2013: Intraspecific sexual size and shape dimorphism in an australian freshwater fish differs with respect to a biogeographic barrier and latitude. — *Evolutionary Biology* 40: 408–419.

Kratochvil, L., Fokt, M., Rehák, I. & Frinta, D. 2003: Misinterpretation of character scaling: a tale of sexual dimorphism in body shape of common lizards. — *Canadian Journal of Zoology* 81: 1112–1117.

Lancaster, L. T., McAdam, A. G. & Sinervo, B. 2010: Maternal adjustment of egg size organizes alternative escape behaviors, promoting adaptive phenotypic integration. — *Evolution* 64: 1607–1621.

Lande, R. & Arnold, S. J. 1983: The measurement of selection on correlated characters. — *Evolution* 37: 1210–1226.

Lanfri, S., Di Cola, V., Naretto, S., Chiaraviglio, M. & Cardozo, G. 2013: Understanding the environmental niche to elucidate the spatial strategies of the southernmost *Tupinambis* lizards. — *Amphibia–Reptilia* 34: 551–565.

Lee, M. S. Y. 2011: Macroevolutionary consequences of "spatial sorting." — *Proceedings of the National Academy of Sciences USA* 108, E347, doi:10.1073/pnas.1105702108.

Liao, W.B. 2013: Evolution of sexual size dimorphism in a frog obeys the inverse of Rensch's rule. — *Evolutionary Biology* 40: 493–499.

Lourdais, O., Shine, R., Bonnet, X. & Brichoux, F. 2006: Sex differences in body composition, performance and behaviour in the Columbian rainbow boa (*Epicrates cenchria maurus*, Boidae). — *Journal of Zoology* 269: 175–182.

Losos, J. B. 2011: Convergence, adaptation, and constraint. — *Evolution* 65: 1827–1840.

Madsen, T. & Shine, R. 1999: The adjustment of reproductive threshold to prey abundance in a capital breeder. — *Journal of Animal Ecology* 68: 571–580.

Madsen, T., Ujvari, B., Shine, R. & Olsson, M. 2006: Rain, rats and pythons: climate-driven population dynamics of predators and prey in tropical Australia. — *Austral Ecology* 31: 30–37.

McLean, M. J., Bishop, P. J. & Nakagawa, S. 2012: Male quality, signal reliability and female choice: assessing the expectations of inter-sexual selection. — *Journal of Evolutionary Biology* 25: 1513–1520.

Mercolli, C. & Yanosky, A. A. 1990: Répertoire des comportements du Téju (*Tupinambis teguixin*). Sauria: Teiidae. — *Revue française d'Aquariology et Herpetologie* 16: 123–130.

Molnar, O., Bajer, K., Török, J. & Herczeg, G. 2012: Individual quality and nuptial throat colour in male European green lizards. — *Journal of Zoology* 287: 233–239.

Naretto, S. 2014: Estrategias reproductivas de lagartos (*Tupinambis merianae* y *Tupinambis rufescens*): perspectiva ecológica y evolutiva de los sistemas de apareamiento. — Ph.D. thesis, University of Cordoba, Argentina.

Naretto, S., Cardozo, G., Blengini, C. & Chiaraviglio, M. 2014: Sexual selection and dynamics of jaw muscle in *Tupinambis* lizards. — *Evolutionary Biology* 41: 192–200.

Noriega, T., Fogliatto, O., Mignola, L. & Manes, M. E. 1996: Ciclo biológico y patrones de comportamiento en una población de iguanas overas *Tupinambis teguixin* (L) (Sauria, Teiidae) adaptada al cautiverio. — *Revista Agronómica del Noroeste Argentino* 28: 109–127.

Olsson, M. & Shine, R. 1997: The limits to reproductive output: offspring size versus number in the sand lizard (*Lacerta agilis*). — *American Naturalist* 149: 179–188.

Olsson, M., Shine, R., Wapstra, E., Ujvari, B. & Madsen, T. 2002: Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. — *Evolution* 56: 1538–1542.

Pincheira-Donoso, D. & Tregenza, T. 2011: Fecundity selection and the evolution of reproductive output and sex-specific body size in the *Liolaemus* lizard adaptive radiation. — *Evolutionary Biology* 38: 197–207.

Porini, G. 2006: Proyecto *Tupinambis*. Una propuesta para el manejo de *Tupinambis rufescens* y *Tupinambis merianae* en la Argentina. — In: Bolkovic, M. & Ramadori, D. (eds.), *Manejo de fauna silvestre en la Argentina. Programa de uso sustentable*: 65–75. Dirección de Fauna Silvestre, Secretaría de Ambiente y Desarrollo Sustentable, Buenos Aires, Argentina.

Procter, D. S, Moore, A. J. & Miller, C. W. 2012: The form of sexual selection arising from male–male competition depends on the presence of females in the social environment. — *Journal of Evolutionary Biology* 25: 803–812.

R Core Team 2013. *R: a language and environment for statistical computing*. — R Foundation for Statistical Computing, Vienna, Austria. [Available at http://www.R-project.org/].

Roughgarden, J. & Akcay, E. 2010: Do we need a sexual selection 2.0? — *Animal Behavior* 79: e1–e4.

Scharf, I. & Meiri, S. 2013: Sexual dimorphism of heads and abdomens: different approaches to "being large" in female and male lizards. — *Biological Journal of the Linnean Society* 110: 665–673.

Schwarzkopf, L. 2005: Sexual dimorphism in body shape without sexual dimorphism in body size in water skinks (*Eulamprus quoyii*). — *Herpetologica* 6: 116–123.

Shine, R. 1992: Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? — *Evolution* 46: 828–833.

Shine, R. 2005: Life-history evolution in reptiles. — *Annual Review of Ecology, Evolution and Systematics* 36: 23–46.

Shine, R., Ambariyanto, Harlow, S. & Mumpuni 1999: Reticulated pythons in Sumatra: biology, harvesting and sustainability. — *Biological Conservation* 87: 349–357.

Shine, R., Webb, J. K., Lane, A., Mason, R. T. 2006: Flexible mate choice: a male snake's preference for larger females is modified by the sizes of females encountered. — *Animal Behavior* 71: 203–209.

Shine, R., Brown, G. P., Phillips, B. L. 2011: Reply to Lee: Spatial sorting, assortative mating, and natural selection. — *Proceedings of the National Academy of Sciences USA* 108, E348, doi:10.1073/pnas.1108240108.

Sinervo, B. 1994: Experimental tests of reproductive allocation paradigms. — In: Vitt, L. J. & Pianka, E. R. (eds.), *Lizard ecology: historical and experimental perspectives*: 73–90. Princeton University Press, Princeton.

Sinervo, B., Svensson, E. & Comendant, T. 2000: Density cycles and an offspring quantity and quality game driven by natural selection. — *Nature* 406: 985–988.

Smith, R. E. 1968: Experimental evidence for a gonadal-fat body relationship in two Teiid lizards (*Ameiva festiva, Ameiva quadrilineata*). — *Biological Bulletin* 134: 325–331.

Stephens, P. R. & Wiens, J. J. 2009: Evolution of sexual size dimorphisms in emydid turtles: ecological dimorphism, Rensch's rule, and sympatric divergence. — *Evolution* 63: 910–925.

Sun, Y.-Y., Du, Y., Yang, J., Fu, T.-B., Lin, C.-X. & Ji, X. 2012: Is the evolution of viviparity accompanied by a relative increase in maternal abdomen size in lizards? — *Evolutionary Biology* 39: 388–399.

Vercken, E., Clobert, J. & Sinervo, B. 2010: Frequency-dependent reproductive success in female common lizards: a real-life hawk-dove-bully game? — *Oecologia* 162: 49–58.

Vercken, E., Massot, M., Sinervo, B. & Clobert, J. 2006: Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. — *Journal of Evolutionary Biology* 20: 221–232.

Vergara, P., Martinez-Padilla J., Mougeot, F., Leckie, F. & Redpath, S. M. 2012: Environmental heterogeneity influences the reliability of secondary sexual traits as condition indicators. — *Journal of Evolutionary Biology* 25: 20–18.

Verrastro, L. & Rauber, R. 2013: Reproducción de las hembras de *Liolaemus occipitalis boulenger*, 1885, (Iguania, Liolaemidae) en la región sur de Brasil. — *Boletín de la Sociedad Zoológica de Uruguay* 22: 84–98.

Winck, G. R. & Cechin, S. Z. 2008: Hibernation and emergence pattern of *Tupinambis merianae* (Squamata: Teiidae) in the Taim Ecological Station, southern Brazil. — *Journal of Natural History* 42: 239–247.