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Misinterpretation of character scaling: a tale of sexual dimorphism in body shape of common lizards

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Abstract: Male-biased sexual dimorphism in head, limbs, and tail scaled to snout–vent length has been reported in many lizard species. Consequently, various hypotheses have been proposed to explain observed body-shape dimorphism. According to the majority of them, the proportions of body components are adaptively related to sexual differences in ecology as well as in reproductive behaviour. Our study shows an alternative, much more parsimonious explanation in the common lizard (*Lacerta vivipara*). According to our analyses, the exaggeration of a single trait, specifically trunk length in females, may explain the whole pattern of sexual differences in body shape. The only consistent adaptive hypothesis, then, is that females with a larger abdominal cavity, and consequently a longer trunk, have a reproductive advantage. Size-adjusted heads, limbs, and tails traditionally reported to be larger in males than in females, features ascribed to numerous evolutionary mechanisms, thus appear to be just an artifact of inappropriate scaling to a sexually dimorphic trait (snout–vent length). As scaling to a single trait has been routinely used in many studies carried out in animals, we warn against quick interpretations based on such analyses and recommend more cautious inspection of allometries.

Résumé : On signale un dimorphisme sexuel des tailles de la tête, des membres et de la queue corrigées par rapport à la longueur museau–évent chez plusieurs espèces de lézards, dimorphisme qui favorise les mâles. Diverses hypothèses ont été avancées pour expliquer ce dimorphisme de la forme du corps. La plupart d'entre elles concluent que les proportions des segments du corps sont adaptées aux différences sexuelles d'écologie et de comportement reproducteur. Notre étude met de l'avant une explication de rechange, beaucoup plus parcimonieuse, chez le lézard vivipare (*Lacerta vivipara*). Selon nos analyses, l'exagération d'un seul caractère, spécifiquement la longueur du tronc chez les femelles, peut expliquer l'ensemble des différences sexuelles de la forme du corps. La seule hypothèse adaptative conséquente est alors que les femelles qui ont une plus grande cavité abdominale, et donc un tronc plus allongé, possèdent un avantage reproductif. Les tailles corrigées de la tête, des membres et de la queue, qui sont alors décrites comme plus grandes chez les mâles que chez les femelles et rattachées à divers mécanismes évolutifs, semblent alors n'être que des artéfacts causés par une correction impropre par rapport à la longueur museau–évent, un caractère à dimorphisme sexuel. Comme la correction par rapport à un seul caractère est couramment utilisée dans plusieurs études sur les animaux, nous mettons en garde contre l'interprétation hâtive des résultats et nous recommandons un examen plus attentif des allométries.

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Introduction

As genetic correlation between the sexes is very high for most morphological traits, it is often believed that long periods of time are required to overcome genetic constraints and to evolve sexually dimorphic morphological traits (e.g., Lande 1980; Hedrick and Temeles 1989). Moreover, the evolution of sexual dimorphism may be limited by physiological and ecological constraints as well (see Andersson 1994). Nevertheless, a growing body of literature reports sexual differences in the proportions of nearly every body component in many animal species. In the case of lizards, many authors have repeatedly reported that males possess elongated tails and limbs and larger heads compared with females of the same body size (e.g., Vial and Stewart 1989; Anderson and Vitt 1990; Castilla and Bauwens 1991; Mouton and van

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Wyk 1993; Vitt and Colli 1994; Barbadillo et al. 1995; Hews 1996; Smith et al. 1997; Shine et al. 1998; Kratochvíl and Frynta 2002). These findings have usually been interpreted as the outcome of natural and (or) sexual selection for particular traits, and numerous post-hoc hypotheses have been proposed to explain the observed pattern.

This is also the case for the common lizard, *Lacerta vivipara* Jacquin, 1787 (e.g., Barbadillo et al. 1995; Šmajda and Majláth 1999; Herrel et al. 2001), the well-known Palaearctic species that has the largest range among terrestrial reptiles (Bannikov et al. 1977). According to Herrel et al. (2001), the larger head of male *L. vivipara* could reflect natural selection leading to food-niche divergence; it could be an adaptation for holding onto the female during copulation, or it could have served as armament in combats between ancestral males and been retained in this nonterritorial, nonaggressive species. The longer tail was assumed to be the result of morphological constraints imposed by the male copulatory organs on tail autotomy, or it may have evolved as a result of improved escape abilities in the sex more likely subjected to heavier predation pressure (Barbadillo et al. 1995; Barbadillo and Bauwens 1997). Finally, the longer limbs in males could mirror a difference between the sexes in the position of the centre of gravity, and so may have evolved under selection for effective locomotion (Barbadillo et al. 1995). The majority of these hypotheses imply that sexual dimorphism in a particular body component reflects different selective forces operating in males and females, i.e., that body shape is ideally adapted for different ecological, social, or reproductive roles.

One widespread complication is that all the above-mentioned sexual differences were reported when a single trait, snout–vent length (SVL), was taken as a measure of body size. Naturally, SVL also includes the length of the abdomen, which determines the size of the abdominal cavity. Therefore, SVL can be affected by selection favouring a larger volume of the total clutch (Cooper and Vitt 1989; Shine 1989; Braña 1996; Olsson et al. 2002). The positive allometric growth of the female abdomen ensures that we would find all other body components to be dimorphic relative to body length (Braña 1996; Reyes-Gavilán et al. 1997), i.e., we would find them to be larger relative to SVL in males.

The aim of this paper is to examine the relationships among morphometric traits in *L. vivipara* and to demonstrate that traditional analyses showing sexually dimorphic allometries in the head, tail, and limbs are not justified. It is our purpose to demonstrate the pitfalls of using “standard” size measures in studies of allometry, and to warn against quick adaptive interpretations based on such analyses.

Materials and methods

Preserved specimens of *L. vivipara* from museum collections in Central Europe (Czech Republic and Slovak Republic) were examined. Three hundred and two specimens considered to be adults (SVL > 43 mm) were included in the analyses. Eight variables were measured to the nearest 0.05 mm with a digital caliper by M.F. in the standardized manner: SVL (from the tip of the snout to the anterior margin of the cloacal lips); head length (HL; from the tip of the snout to the posterior margin of the skull); head width (HW; the largest width of the head); head height (HH; the largest height of the head); distance between the extremities (DEX; from the posterior margin of the front leg to the anterior margin of the hind leg); tail length (TL; from the anterior margin of the cloacal lips to the tip of the tail; only in specimens with intact tails); upper-leg length (UL; from the anterior base of the fully extended forelimb to the end of the longest digit without the claw); and lower-leg length (LL; see UL). Sex was recorded according to external characters (femoral pores). Variables were measured blindly with respect to the present analysis. Although the specimens came from different localities, discriminant function analysis among well-represented populations showed no significant effect of geographic variation within single-sex samples. Therefore, we assume that interpopulational variation did not affect the results.

Differences between the sexes in the original measurements were tested using an unpaired Student’s *t* test. Data were natural-log-transformed before subsequent analyses. Principal component analysis (PCA) was applied as an exploratory procedure. Relationships among measurements were illustrated by a plot of PC coefficients, and PC scores were used to assess and quantify overall sexual differences in general body size and shape. Next we performed a series of bivariate analyses to explicitly compare our results with those from previously published papers. We performed analyses of covariance (ANCOVAs) with HL, HW, HH, DEX, TL, UL, and LL as dependent variables, sex as a factor, and SVL as a covariate, and searched for sexual differences in both slopes and intercepts. Then, we repeated ANCOVAs using a better predictor of general body size (HL) as a covariate.

Because of the possible unreliability of least-squares regressions in ANCOVAs, we employed a reduced major axis (RMA) regression model (Harvey and Pagel 1991). Differences between the sexes were tested using *t* tests and discriminant function analysis carried out on residuals from RMA regressions of traits against HL.

Whenever parametric statistics were applied, we checked the normality of distribution in each variable. Both graphical methods by eye and the Kolmogorov–Smirnov tests were applied.

Results

Males and females differed significantly (two-tailed *t* test, $P < 0.00001$ in all cases) in all of the original measurements: females had larger SVL and DEX and males had larger HL, HW, HH, TL, UL, and LL (details not shown). Both PC1 and PC2 scores were higher in males than in females ($t = 4.87$ and $t = 17.08$, respectively, both $P < 0.0001$). Based on PC coefficients (Fig. 1), PC1 reflects general size, as all variables show positive coefficients on this component. We interpret PC2 as indicating a relative proportion of the abdomen (DEX and SVL contributing most to the PC2 axis). In summary, the multivariate analysis clearly supports splitting the variables into two groups: the first group includes all head, limb, and tail measurements and the second just the variables involving abdomen length (DEX and SVL).

Next we performed traditional procedures to control for body size, ANCOVAs with SVL as the covariate. We found exactly the same pattern as that reported by earlier authors: females in our sample possessed a larger DEX but a smaller

Fig. 1. Coefficients for the first two principal components of body measurements of the common lizard, *Lacerta vivipara*. SVL, snout–vent length; HL, head length; HW, head width; HH, head height; DEX, distance between the extremities; TL, tail length; UL, upper-leg length; LL, lower-leg length.

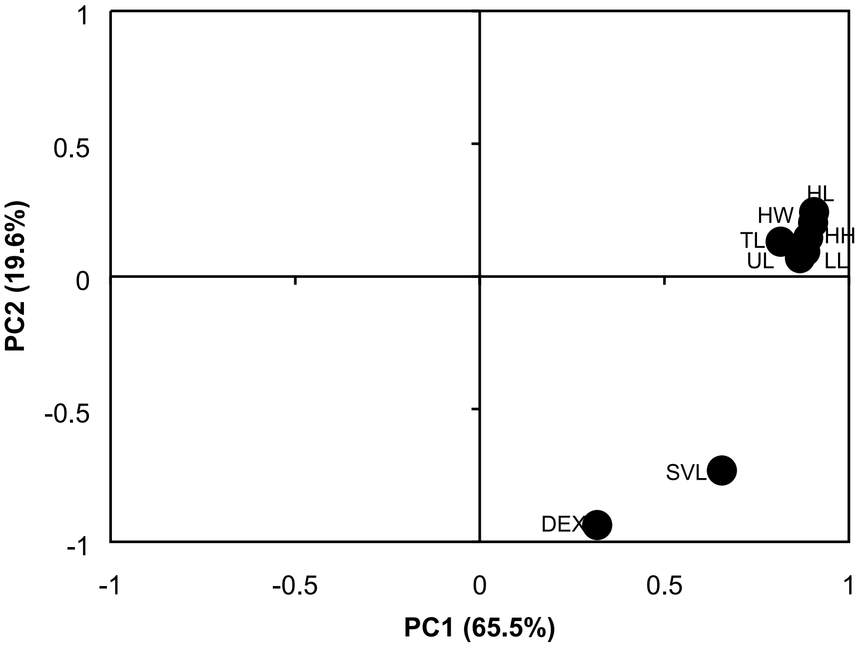


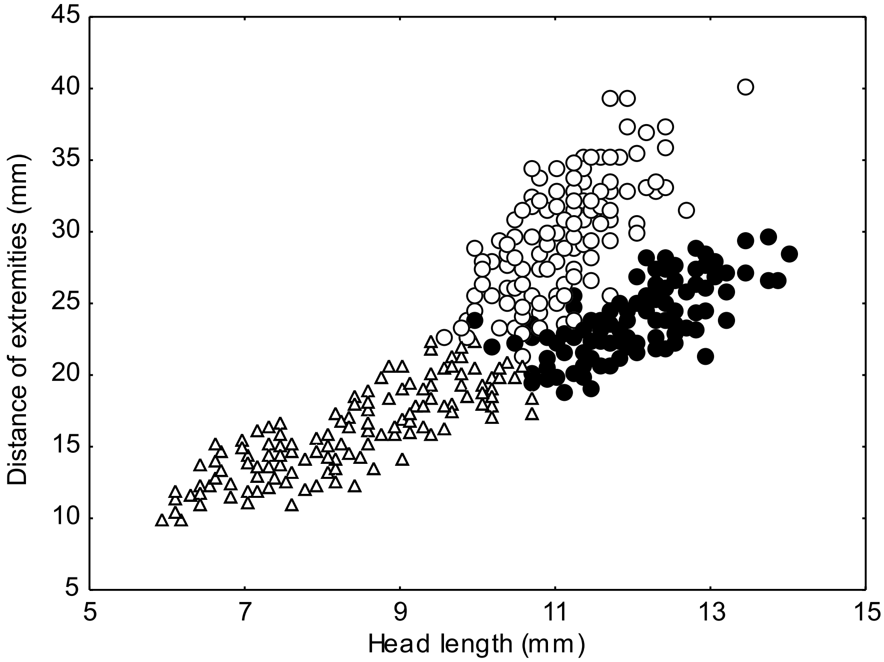
Table 1. Results of ANCOVAs on differences between the sexes in the measurements of the common lizard, *Lacerta vivipara*, under study.

		Covariate SVL			Covariate HL		
		F	*P*	Larger sex	*F*	*P*	Larger sex
SVL	Slope	—	—		18.815	<0.0001	
	Intercept	—	—	—	—	—	F
HL	Slope	35.175	<0.0001		—	—	
	Intercept	—	—	M	—	—	—
DEX	Slope	3.175	0.076		10.444	0.001	
	Intercept	252.194	<0.0001	F	—	—	F
TL	Slope	1.687	0.196		0.156	0.693	
	Intercept	150.066	<0.0001	M	0.889	0.347	None
HH	Slope	10.673	0.001		0.268	0.605	
	Intercept	—	—	M	0.164	0.685	None
HW	Slope	13.154	<0.001		0.013	0.909	
	Intercept	—	—	M	1.439	0.231	None
UL	Slope	2.480	0.116		2.596	0.108	
	Intercept	222.732	<0.0001	M	0.981	0.323	None
LL	Slope	10.673	0.001		1.209	0.272	
	Intercept	—	—	M	0.131	0.718	None

Note: *n* = 302 (150 females and 152 males), except for TL, where *n* = 155 (80 females and 75 males). Snout–vent length (SVL) or head length (HL) was used as a covariate. M, male; F, female; for an explanation of other abbreviations see Fig. 1.

head, a shorter tail, and shorter limbs than males at the same SVL (Table 1). However, SVL is a poor predictor of general body size (see Fig. 1). Therefore, we repeated the ANCOVAs with the simple, better predictor (HL) of general body size as a covariate to minutely explore relationships among variables using comparable bivariate analyses. Of course, there is no perfect single measurement that represents the size of an animal independently of its shape, hence our choice of HL is necessarily arbitrary. However, HL seems to be the best of all accessible candidates: it is easily measurable, it has the largest PC1 coefficient (Fig. 1), and there is some evidence that the size and shape of the skull are rather conservative among lizards (Stokely 1947; Wiens and Slingluff 2001). The use of HL as a size measure in ANCOVAs is even better than the use of the PC1 score. The latter approach, often recommended (e.g., Crespi and Bookstein

Fig. 2. Scatterplot of distances between the extremities versus head length for the common lizard, according to sex and maturity. Juveniles from Central Europe (n = 211) were added to show the ontogenetic trajectory of component development (●, males; ○, females; △, juveniles).



1989) and quite commonly used, would obviously be misleading in our case. The PC1 is a line of the best fit in a least-squares sense to the scatter of data points in the space of all measurements. Therefore, PC1 is automatically influenced by the variables expressing body shape as well (DEX and SVL in our case; this is graphically exemplified in Fig. 1). On the contrary, less variation can be expected in the case of HL. Using HL as a covariate, the ANCOVA results changed dramatically. When values were corrected for HL, females and males differed significantly only in DEX and SVL (larger in females again; see Table 1). Analysis of RMA regression model residuals of measurements on HL confirmed these results. Except for measurements involving abdomen size, no sexual dimorphism in residuals was detected by t tests, and discriminant function analysis based on residuals of head, limb, and tail measurements failed to discriminate between the sexes (Wilks' λ = 0.982, P = 0.740; n = 155). Based on our discussions on this topic, we feel it is important to note again that we do not insist that HL is non-problematic and the only correct expression of body size. However, using HL as a covariate in ANCOVAs allowed us to explore mutual relationships among head, tail, and limb measurements. The results support the conclusion that the reciprocal relative sizes of head, limbs, and tail do not show intersexual differences.

Discussion

The combination of multivariate (PCA) and bivariate analyses supports the conclusion that the measurements which involve abdomen length (DEX and SVL) are responsible for all substantive differences between the sexes with regard to body shape. By contrast, the measurements of other body components, i.e., head, limbs, and tail, are highly correlated, and follow in principle the same allometric rules in both male and female *L. vivipara*. Consequently, SVL is a sexually dimorphic trait, and taking it as a scale when searching for sexual dimorphism in a particular body component is confusing. Sexual dimorphism in size-adjusted head, limb, and tail measurements traditionally reported for species examined by other authors (Barbadillo et al. 1995; Barbadillo and Bauwens 1997; Šmajda and Majláth 1999; Herrel et al. 2001) can be attributed to an artifact of the adoption of SVL for scaling to body size. Most remarkably, previous authors proposed a number of evolutionary (mostly adaptive) scenarios explaining observed sexual differences in body shape in *L. vivipara*. Their scenarios seem to be countered by the principles of parsimony. According to our analyses, the whole pattern of sexual differences in *L. vivipara* can be explained most parsimoniously by exaggeration of a single trait, i.e., trunk proportions.

There is additional independent evidence that trunk size differs between the sexes in *L. vivipara*. First, in the ontogenetic trajectory of DEX, mature females depart strongly from both immature individuals and mature males (see Fig. 2). The breakpoint estimated using piecewise linear regression concerning immature individuals and females occurs in SVL at around 42 mm, close to the reported mean SVL at maturity (Bauwens and Díaz-Uriarte 1997). According to Emerson (2000), a trait showing such an allometric pattern may be interpreted as a hypertrophic secondary sexual character. However, this hypertrophy is preceded by hyperplasy in early ontogeny. It arises out of sexual dimorphism in pholidosis (the number of scales in *L. vivipara* does not increase with age; Lecomte et al. 1992). In *L. vivipara*, like most lacertids (e.g., Boulenger 1920), females have a considerably larger number of transverse rows of ventral scales covering the abdomen (Wermuth 1955; our data:

Kruskal–Wallis ANOVA, $F = 170.6$, $P < 0.0001$, $n = 302$) and a considerably larger number of scales in the lengthways dorsal row (our data: $F = 79.7$, $P < 0.0001$, $n = 302$). In contrast, we found no sexual dimorphism in numbers of head and neck scales (number of infralabials, supralabials, collar scales, and scales in a single lengthways row from gular to collar; Kruskal–Wallis ANOVA, all ns, $n = 302$). The pholidotic pattern, traditionally studied by taxonomists but often neglected by ecologists and evolutionary biologists (but see Shine 2000, 2002), could be unusually useful in determining sexually dimorphic traits in lizards and snakes. The exaggeration of abdomen size in females is likely to be the result of strong selection for fecundity in *L. vivipara*, which is a small viviparous species that oviposits just one relatively large clutch per year (Bauwens and Díaz-Uriarte 1997), and clutch size increases with female SVL (Braña 1996). However, these arguments supporting the fecundity-selection hypothesis are, regrettably, too indirect. For conclusive evidence, we must have data showing that the females with a long abdomen relative to their general size lay more eggs.

By its nature, the study of body shape is a multivariate problem (e.g., Zamudio 1998; Malmgren and Thollesson 1999). Nevertheless, a single trait has been used as the expression of body size for the purpose of scaling in most morphometric studies carried out in lizards, snakes, and other reptiles, as well as in other animals, in both intra- and interspecific comparisons (recently, e.g., Iwaniuk 2001; Madden 2001; Martins et al. 2001; Vanhooydonck and Van Damme 2001). The case of *L. vivipara* shows nicely how misleading this intuitively correct approach can be. We caution against an adaptive explanation for allometry in a particular trait unless the whole body-shape pattern is examined and independent data are available.

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