Scaling of the sexual size and shape skull dimorphism in the sand lizard (*Lacerta agilis* L.)

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Abstract

Sand lizards (*Lacerta agilis*) exhibit a clear pattern of sexual dimorphism, both in coloration and body proportions, where males have larger heads and are longer-legged at a given snout-to-vent length (SVL). In this study we analyse allometry of skull growth with SVL and skull length (SL) as references. The sand lizard skull is basically sexually size dimorphic and there are only minor shape differences. When SVL is used as a reference point, it generates differences in all traits to be measured, presumably because SVL is subject to different and strong selection pressures in both sexes. When skull length is taken as a reference point, differences in skull shape are restricted only to the postorbital region, which is wider in males. This may reflect selection pressure on stronger bite force in males.

Key words

Reptilia: Sauria: Lacertidae: *Lacerta agilis*; sexual dimorphism; allometry; skull.

Introduction

Sexual dimorphism in size and shape is a widespread phenomenon among squamate reptiles (e.g. Pianka & Vitt 2003). It may result from different forces, which are not mutually exclusive and may act in concert or oppose each other, depending on ecological circumstances and the mating system. Sexual selection is often used to explain sexual dimorphism, like the evolution of male ornamentation and weapons, or attractiveness instead of camouflage coloration or in the case of females the increase in their abdomen size (e.g. Darwin 1871, Olsson *et al.* 2002). Another force that may drive the evolution of sexual dimorphism is natural selection. In this case, the evolution of sexual dimorphism may be used to reduce the intraspecific resource competition (Slatkin 1984, Shine 1986 a, b, Hierlihy *et al.* 2013).

The common pattern of sexual dimorphism in numerous lizard species involves larger head and longer limbs and tail in males together with their more intensive col-oration (e.g. Vitt 1983, Pianka & Vitt 2003, Nkosi *et al.* 2004). It is commonly assumed that larger male heads evolved because of their aggressive mating behaviour, enhancing changes in the male-male combats or copulatory-biting performance and thus fertilisation (Gvozdik & Van Damme 2003, Van Damme *et al.* 2008); longer limbs enhance locomotion abilities, enabling the male to control larger areas and thus increase the chance of meeting a mate (Schwarzkopf 2005); and a longer tail provides the necessary space for hemipenes and their musculature (Barbadillo & Bauwens 1997). However, all of these differences mentioned above can be relative: the head is larger and the limbs and tail are longer in males compared to females at a given snout-to-vent length (SVL). However, female SVL in most (if not all) studied lizard species grows with positive allometry as it is under fecundity selection (Braña 1996, Kratochvil *et al.* 2003, Scharf & Meiri 2013). Thus, the interpretation

of intersexual differences in body proportions may be in-accurate if the SVL is taken as a universal size indicator (Kratochvil et al. 2003, Scharf & Meiri 2013).

The sand lizard, *Lacerta agilis* L., is a medium-sized lacertid, which is common in Europe. This species shows very clear pattern of sexual dimorphism both in morphology and behaviour, with males being the smaller, but larger-headed sex (Bischoff 1984) (Fig. 1). Because there are no differences in the diet composition and prey size between males and females (Gvozdik & Boukal 1998), there must be other factor(s) responsible for the evolution of sexual dimorphism in head size and shape than the food niche divergence hypothesis. The sand lizard males are territorial and use their jaws during fights. They also use their jaws to grasp females during copulation (see Fig. 1A). Taking this in to account, we assume that the male head should differ from the female head, being better designed to provide a stronger bite (Lappin & Husak 2005). This can be achieved in three ways: the head can be bigger, can have a different shape or both. However, such dimorphism and its ontogeny have not been seriously studied in this species and, in general, sexual dimorphism in physical performance and associated morphology in squamates has been poorly documented (see Vincent & Herrel 2007, Ljubisavljević *et al*. 2010).

We analysed shape and size dimorphism in sand lizard skulls has using linear morphometrics. This method allows a pattern of differences in skull shape and size to be identified between sexes and the determination of how allometric (size-dependent) changes contribute to overall dimorphism.

Materials and Methods

We measured skeletons (30 males and 30 females) of the sand lizard from the collection of the Institute of Environmental Biology at the University of Wrocław (males: IZK 00355, 00418–00423, 00427, 00430, 00432–00435, 00439–00443, 00446–00451, 00453, 00454, 00459, 00462 and two unnumbered specimens; females: IZK 00356, 00416, 00425, 00426, 00428, 00436–00438, 00444, 00445, 00452, 00455–00457, 00460, 00461, 00463, 00464, 00596–00606 and one unnumbered specimen). All specimens originally came from a population located near Wrocław. No lizard was killed for the purpose of this study.

We used 7 morphometric distances to quantify sexual dimorphism in skull shape: skull length (SL) (measured from the rostral tip of the premaxillare to the most caudal end of parietale), height (SH) (measured at the highest point of the skull) and widths: SW (measured as the distance between the jugular processes), SW1 (measured as the distance between the orbits) and SWPS (measured at the contact between postorbital and squamosal bones);

Fig. 1. (A) A pair of coupling sand lizards *Lacerta agilis* showing dimorphism in body proportions and colouration. Male is beating female tale base (photo courtesy of Rafał Robert Dudek). (B) Male (left, IZK 419, SVL 71.9 mm) and two females (middle, IZK 599, SVL = 74.4 mm and right, IZK 460, SVL = 46.2 mm) skulls of sand lizards *Lacerta agilis*.

the mandible length (MDBL) (measured from the most rostral tip of the dental bone to the end of the retroarticular process); and the maxilla length (MXL) (measured from the most anterior part of the maxillary bone to the end tip of the caudal process of the bone). As we were not interested in analysing asymmetry, all analyses used the mean values for right or left elements of paired bones where appropriate. Also, because we had already skeletonised specimens, we could not record other morphometric distances, such as the trunk length, except for SVL, which was recorded on the specific labels. All measurements were made with a digital calliper to the nearest 0.01 mm and the SVL data were recorded to the nearest 1 mm. One may suggest such accuracy is pseudoprecision, however, bones are firm, not flexible structures. We have randomly chosen 10 specimens and repeated the measurement to get each of the three subsequent measurements of given specimen differing ± 0.01 mm.

Kolmogorov-Smirnov tests were used to test the data for normal distribution. A principal component analysis (PCA) on correlation matrix was conducted to evaluate the pattern of size and shape variation in skull dimensions ($\log_{10}$-transformed data) between males and females. Because this procedure yielded only one axis (PC1) we reran PCA on the correlation matrix on the residuals from the skull measurements regressed on SVL and SL. Residuals are size-free indicators of shape and have been successfully used in analyses of shape differences (Reist, 1986). Discriminant Function Analysis (DFA) was also run on the residuals to evaluate which characters differentiated the sexes most effectively. All abovementioned

analyses have been done using Statistica v. 10.0 software (STATSOFT inc. 2011).

Scaling of each of the biometric variables with SVL and SL was done using reduced major axis regression (RMA). Because measurement error is present in both dependent and independent variables, the ordinary least-squares regression may produce skewed values for the allometry equations (SOKAL & ROHLF 1995). Thus, the RMA regression was applied using the *RMA* Software for Reduced Major Axis Regression v. 1.17 by BOHONAK (2004). Confidence intervals were calculated with 1000 bootstrap replications. Deviations from isometry and homogeneity of slopes between the sexes were examined by inspection of the 95% confidence intervals of the slope estimates.

Results

PCA performed on the skull measurements yielded only one significant axis (eigenvector value 6.58), explaining 93.93% of the total variation. The second axis explained only 2.92 % of variation (eigenvector value 0.2). The one-way ANOVA on the individual score loadings on the first PC axis (which is interpreted as size vector) showed statistically significant differences between the two sexes (MS = 27.58, F = 4.44, P = 0.0395). When PCA was run on the residuals from regression of skull dimensions on the SVL, it yielded two axes (PC1: 67.72%, eigenvector value 4.74; PC2: 14.29%, eigenvector value 1.00). The MANOVA on the individual score loadings showed statistically significant differences between the sexes (Wilks' Lambda = 0.465, P < 0.00001) on the PC1 (MS = 146.28, F = 63.6; P < 0.00001) but no differences for PC2 (MS = 0.716, F = 0.712, P = 0.4). When PCA was run on the residuals from regression on SL, it yielded three axes: PC1 (34.78%, eigenvector value 2.09), PC2 (22.17%, eigenvector value 1.33) and PC3 (14.64%, eigenvector value 0.88). However, tests for the sex differences are somewhat vague. MANOVA showed no sex differences on the three axes (Wilks' Lambda = 0.926, P = 0.227), but further ANOVA for each of the PCs show no statistically significant differences for PC1 and PC2 (MS = 0.001, F = 0.0004, P = 0.98 and MS = 0.104, F = 0.08, P = 0.78 respectively), but statistically significant differences for PC3 (MS = 3.76, F = 4.54, P = 0.04) (see Table 1). However, due to the fact that the P-value for the PC3 is close to the significance level, the results should be taken with caution.

The discriminant analysis based on residuals from regression on SVL yielded a much better classification than that conducted on residuals from regression on SL. The analysis based on residuals from traits regressed on SVL allowed the correct classification of 88.33% of individuals (90% of males and 86.66% of females), whereas the same analysis using the residuals from regression

Table 1. Variable loadings for principal component analysis of skull measurements (see text for the explanation of acronyms) of sand lizard (*Lacerta agilis*) calculated from log10-transformed data; residuals from regression of skull dimensions on SVL and SL.

Character	PC1	PC2	PC3
Log10-transformed			
SL	0.993	0.001	—
SW	0.971	−0.161	—
SW OC	0.933	0.327	—
SW PS	0.966	0.138	—
SH	0.979	−0.036	—
MXL	0.949	−0.223	—
MDBL	0.992	−0.038	—
Residulas from regression on SVL			
SL	0.000	1.000	—
SW	0.927	−0.001	—
SW OC	0.754	0.001	—
SW PS	0.910	−0.001	—
SH	0.921	0.001	—
MXL	0.839	−0.001	—
MDBL	0.965	0.001	—
Residulas from regression on SL			
SW	0.771	−0.289	−0.276
SW OC	−0.528	−0.543	−0.069
SW PS	−0.334	−0.706	−0.457
SH	0.519	−0.583	0.388
MXL	0.586	0.261	−0.610
MDBL	0.701	−0.214	0.257

Table 2. Discriminant function classification matrix for male and female sand lizards (*Lacerta agilis*). The table shows percentage and numbers of correctly classified specimens into their assumed sex based on analysis of residuals produced by regression of skull characters on SVL or SL.

	SVL			SL		
	% correct	M	F	% correct	M	F
M	90.00	27	3	70.00	21	9
F	86.66	4	26	73.33	8	22
Total	88.33	31	29	71.66	29	31

on SL only correctly classified 71.66% (70% of males and 73.33% of females) (Table 2). The statistically significant variable for discrimination between the sexes was MDBL when residuals from the regression on SVL were used (P = 0.015), whereas SWPS and SH were significant when residuals from regression on SL were used (P = 0.012 in both cases) (Table 3).

The intercept, slope and confidence intervals for each of the sexes are given in Table 4. In males, all features except SH grew isometrically when scaled against SVL (the slope is always above 1 but the confidence intervals overlap this value in those cases); the SH of males showed

Table 3. Summary of the discriminant function analysis of the male and female sand lizards (*Lacerta agilis*) based on residuals of log_{10}-transformed biometric variables in their regression with log_{10}-transformed SVL or log_{10}-transformed SL.

	Character	Wilks' Lambda	Partial Lambda	F-remove (3.106)	P-level	Tolerance	1-Toler. (R^2)
Residuals from regression on SVL	MdbL	0.461	0.892	6.302	0.015	0.196	0.804
	MxL	0.412	0.998	0.085	0.772	0.452	0.548
	SL	0.423	0.971	1.535	0.221	0.983	0.017
	SW	0.411	0.999	0.003	0.955	0.241	0.760
	SWOC	0.414	0.993	0.371	0.545	0.514	0.486
	SWPS	0.432	0.953	2.581	0.114	0.359	0.641
	SH	0.417	0.987	0.706	0.405	0.285	0.715
	Character	**Wilks' Lambda**	**Partial Lambda**	**F-remove (1.53)**	**P-level**	**Tolerance**	**1-Toler.** (R^2)
Residuals from regression on SL	MdbL	0.772	0.987	0.684	0.412	0.745	0.255
	MxL	0.766	0.995	0.269	0.606	0.796	0.204
	SW	0.789	0.967	1.851	0.179	0.599	0.401
	SWOC	0.791	0.963	2.018	0.161	0.765	0.235
	SWPS	0.857	0.887	6.726	0.012	0.769	0.231
	SH	0.859	0.887	6.779	0.012	0.721	0.279

Table 4. Intercepts, slopes and their 95 % confidence intervals of RMA-regression of skull measurements regressed on SVL or SL of male (M, *n*=30) and female (F, *n*=30) sand lizards *Lacerta agilis*.

Baseline	Character	Sex	Itercept	Intercept 95 % confidence intervals		Slope	Slope 95 % confidence intervals		R^2
SVL	SL	M	−0.701	−0.986	−0.535	1.025	0.934	1.181	0.889
		F	−0.212	−0.518	−0.083	0.731	0.660	0.896	0.891
	MDBL	M	−0.746	−1.033	−0.539	1.059	0.949	1.216	0.891
		F	−0.350	−0.585	−0.236	0.814	0.752	0.941	0.918
	MXL	M	−0.961	−1.452	−0.708	1.012	0.836	1.366	0.771
		F	−0.674	−1.206	−0.444	0.829	0.704	1.113	0.776
	SW	M	−1.044	−1.482	−0.784	1.120	0.980	1.358	0.798
		F	−0.741	−1.149	−0.551	0.919	0.814	1.142	0.796
	SWOC	M	−1.740	−2.349	−1.473	1.143	0.995	1.472	0.813
		F	−1.466	−2.173	−1.180	0.967	0.812	1.348	0.718
	SWPS	M	−1.193	−1.786	−0.842	1.152	0.961	1.473	0.849
		F	−0.649	−1.150	−0.451	0.818	0.711	1.083	0.756
	SH	M	−1.467	−1.825	−1.241	1.234	1.112	1.432	0.872
		F	−0.941	−1.265	−0.798	0.919	0.842	1.093	0.895
SL	MDBL	M	−0.021	−0.065	0.041	1.033	0.981	1.070	0.990
		F	−0.114	−0.173	−0.033	1.114	1.044	1.165	0.982
	MXL	M	−0.269	−0.474	−0.165	0.987	0.897	1.160	0.894
		F	−0.434	−0.778	−0.259	1.133	0.979	1.434	0.834
	SW	M	−0.278	−0.421	−0.193	1.093	1.018	1.212	0.926
		F	−0.474	−0.660	−0.349	1.257	1.147	1.423	0.891
	SWOC	M	−0.959	−1.251	−0.834	1.115	1.003	1.358	0.895
		F	−1.185	−1.561	−0.985	1.323	1.140	1.656	0.769
	SWPS	M	−0.405	−0.677	−0.263	1.124	1.000	1.350	0.928
		F	−0.411	−0.709	−0.283	1.119	1.005	1.374	0.883
	SH	M	−0.624	−0.723	−0.548	1.203	1.137	1.284	0.958
		F	−0.675	−0.854	−0.514	1.257	1.114	1.413	0.908

positive allometry. In females, all features except SL and MDBL grew isometrically; however, the slope coefficients were always slightly below 1, which is overlapped by the confidence intervals. The SL and MDBL grew with negative allometry. This pattern changed when characters were scaled against skull length (SL). In this case, both
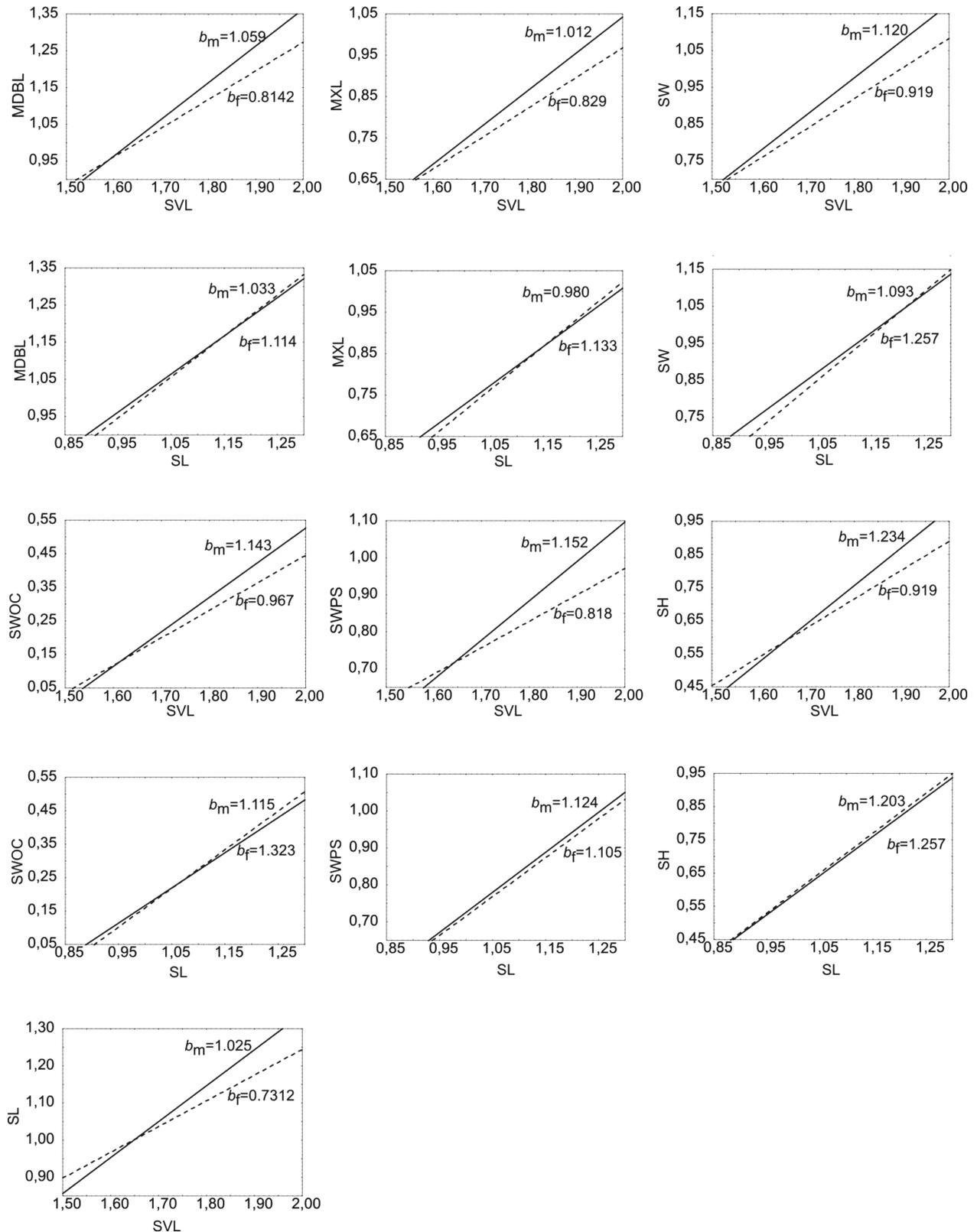
Fig. 2. Patterns of growth of skull dimensions scaled against the snout-vent length (SVL) or skull length (SL) in the sand lizard *Lacerta agilis*. The allometric coefficients for males (b_m) and females (b_f) are given on each diagram. For the skull measurements acronyms see the text.

sexes showed very similar patterns of skull growth: positive allometry for SW, SW1, SWPS and SH, and isometry for MXL; only MDBL differed in the growth pattern, being isometric in males and positively allometric in females. Interestingly, in all variables except SWPS, females had higher slope values (see Fig. 2).

Discussion

The skull dimensions which discriminate males and females of the sand lizard in the DFA are skull width at the postorbital-squamosum contact and skull height. These two dimensions are the most contributory to the bite force (Herrel *et al*. 2001, Lappin *et al*. 2006). The increase in skull width in the postorbital region is in fact an increase of the insertion surface for jaw closing musculature. It results in higher muscle volume, and thus higher generated force. It also changes the direction of fibres to more vertical, which increases the muscle force transmission when the lower jaw is adducted (Lappin *et al*. 2006). The result is greater and better oriented muscle mass in males acting on the same sized jaw compared to females of the same head size. A similar pattern of sexual dimorphism has been found in many other lizard species which indicates that main changes in the skull/head shape take place in the postorbital region where the jaw adductor attaches (e.g. Bruner *et al*. 2005, Ljubisavljević *et al*. 2010). One could explain the differences in head shape by inter-sexual differences in the diet; however, there are no such differences in the studied species (Gvozdik & Boukal 1998) and lizard bite force is usually much higher than the minimal force necessary for crushing the hardest exoskeletons of insects eaten by lizards (Herrel *et al*. 1996).

Here is an interesting pattern of scaling of the head dimensions. Male skull traits grow faster than female ones when scaled against SVL and their skulls became relatively bigger in respect of all studied variables. When male allometric coefficients are always above 1, females show negative allometry and isometry, with allometric coefficients below 1 for all of the studied features (see table 4 and fig. 2). This pattern of growth is similar in other species (e.g. Molina-Borja 2003, Kaliontzopoulou *et al*. 2006, 2008, Ljubisavljević *et al*. 2008, Žagar *et al*. 2012). However, it changes when the skull dimensions are scaled to the SL. In such cases, both sexes show a similar pattern of skull growth and most of the variables show positive allometry. In other words, the skulls become relatively higher and wider in bigger lizards of both sexes. Although male skull dimensions are bigger for any skull size, female slope values are higher and their skull dimensions grow at slightly faster rates, thus showing an opposite pattern to that of the same variables scaled against SVL. SVL is under strong fecundity selection, as the number and size of offspring is positively correlated to female body size (e.g. Cox *et al*. 2003, Scharf & Meiri 2013) and the sand lizard females have more trunk vertebrae compared to males (Porkert & Grosseova 1986). Thus, it is a kind of rule, that females evolve longer bodies as a result of their reproductive roles (Kratochvil *et al*. 2003, Scharf & Meiri 2013). In this case, the relative shape changes of skulls between males and females are due to scaling them against highly sexually dimorphic traits (Kratochvil *et al*. 2003).

The similar pattern of skull shape changes (when scaled against SL) may suggest some developmental restrictions, as is common among other lizard species (e.g. Barahona & Barbadillo 1998, Bruner *et al*. 2005, Kaliontzopoulou *et al*., 2007, 2008, Ljubisavljević *et al*. 2010, Urošević *et al*. 2013). Both sexes follow very similar skull growth trajectories when scaled against skull length and thus only minor shape changes are detectable among the sexes. It may be that their skull shape follows the optimal shape trajectory for most effective bite or prey handling (or both) at a given skull size. However, to get more general conclusions on the subject further studies should be focused on comparative analyses, possibly using some other techniques like geometric morphometrics. Also more comparative studies combining the ontogenetic changes in skull/head shape and size, and the changes in biting performance are desirable.

Acknowledgements

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