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Variation in skull size and shape of the Common wall lizard (*Podarcis muralis*): allometric and non-allometric shape changes

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Abstract

We analysed patterns of skull size and shape variation among populations of the Common wall lizard (*Podarcis muralis*) in the Central Balkans, particularly the effecs of insularity and the presence of the ecologically similar lacertid lizard species *P. melisellensis*. Two components of shape variation were analysed – size dependent (allometric) and size independent shape changes. The observed shape differentiation relating to insularity was greatly size-dependent and concordant to allometric shape changes which explained over 20% of variation in the skull shape in the analysed sample. The explorative analysis of size-independent shape changes revealed that populations of *P. muralis* which share habitat with *P. melisellensis* diverge from populations which do not share habitat with potentially competing species. These changes related to the general shortening and widening of the skull and increase of the jaw adductor muscle chambers were more pronounced in males. We suppose that the observed pattern of shape changes is driven by competition among species (character displacement) and, possibly, is further modified by heterospecific aggression and trophic shift.

Contents

Introduction

Intraspecific variation in body size and shape results from numerous intrinsic and extrinsic factors that interact to drive patterns of phenotypic variation (Hallgrímsson and Hall, 2005). The variation in body shape *per se* is composed of two components: allometric and non-allometric shape components. Allometry is the shape change associated with size variation (*i.e.*, Gould, 1966), while the non-allometric component accounts for the changes in shape which are not simply a result of biological scaling, but are influenced by other factors and selective pressures (Klingenberg, 1996). Despite growing use of size-correction in morphology, studies on the separated allometric and non-allometric components of the intraspecific shape variation are relatively rare (Debat *et al.*, 2003; Gidaszewski *et al.*, 2009; Ljubisavljević *et al.*, 2010; Singleton *et al.*, 2011).

Numerous empirical studies on intraspecific morphological variation found that diversification in size and shape within species can arise via ecological character displacement due to interspecific competition (Brown and Willson, 1956; Pianka, 1973; Arnold, 1987; Losos, 2000; Schluter, 2000; Adams and Collyer, 2007; Stuart and Losos, 2013), different resource availability and environmental factors in habitats (*e.g.*, Meiri *et al.*, 2011), heterospecific aggressive interactions (Schoener, 1977) or phenotypic plasticity alone (Pfenning *et al.*, 2010). The most pronounced pattern of intraspecific variation in size in vertebrates could be related to the 'island rule', (Foster, 1964; Carlquist, 1965; Van Valen, 1973; Case, 1978; Pearson et al., 2002; Lomolino, 2005; but see also Meiri *et al.*, 2006, 2008; Meiri, 2007).

In this study, we analysed patterns of variation in skull size and skull shape of the Common wall lizard (*Podarcis muralis* (Laurenti, 1768)) among insular and mainland populations in the Central Balkans region (Serbia and Montenegro). Because insular gigantism was confirmed in wall lizards of the genus *Podarcis* (Radovanović, 1951; Cirer and Martínez-Rica, 1990; Crnobrnja *et al.*, 1994; Castilla *et al.*, 1998; Sá-Sousa *et al*., 2000; Arnold and Ovenden, 2002; Arntzen and Sá-Sousa, 2007; Herrel *et al*., 2008) we assumed that differences in size and shape between insular and mainland populations of *Podarcis muralis* could account for most of the size related variation in this species. We also explored and compared the populations from the same geographic region (Skadar Lake) in which *Podarcis muralis* is the sole lacertid species with the populations in which *P. muralis* co-occurs with the morphologically and ecologically similar species *Podarcis melisellensis* (Braun, 1877).

Populations of the common wall lizard from the Central Balkans are very suitable for such kind of study due to low levels of genetic differentiation (Crnobrnja *et al*., 1994). Using landbridge island populations of the Skadar Lake archipelago which are of relatively recent, postglacial origin (Stanković, 1976), it was ensured that only closely related genetic lineages are used and the effect of island age is minimized (Meiri, 2007).

The size and shape of the ventral part of the skull (upper jaw and palate) of lacertid lizards has proven to be a good model-system for ecomorphological and evolutionary studies due to its biomechanical roles related to foraging, diet, mating, anti-predatory behaviour and shelter use (Herrel *et al*., 2007; Ljubisavljević *et al*., 2010, 2011; Urošević *et al*., 2012, 2013). By using the geometric morphometric approach (Zelditch *et al*., 2012) we captured variation in ventral skull size and shape and we disentangled the allometric and non-allometric components of skull shape variation to assess whether shape changes among populations are attributable to change in size, or influenced by other sources of variation.

Material and methods

Study species and samples

Podarcis muralis is a small, insectivorous, saxicolous lizard which is found over a wide range in central and southern Europe (Arnold and Ovenden, 2002) including the Central Balkans.

The samples of *P. muralis* from two islands and northern shore of the Skadar Lake (Malo Starčevo island: 17 males and 20 females; Malo Beško island: 15 males and 15 females, shore locality of Zeta: 14 males and 15 females) and urban and sub-urban localities in Belgrade, Serbia (23 males and 25 females) were initially collected for other studies. All specimens were adults, which was determined by dissection and inspection of gonads.

In the Belgrade (mainland) and Malo Starčevo (island) habitats, *P. muralis* is the sole *Podarcis* species. Populations from the Zeta (mainland) and Malo Beško (island) share their habitat with *P. melisellensis*. In places where the two species occur in the same habitat, *P. melisellensis* is more terrestrial than *P. muralis* and opts for horizontal, vegetated microhabitats (Džukić, 1977; Arnold, 1987; Aleksić *et al*., 2009). More detailed information on the samples and localities was published earlier (Bejaković *et al*., 1996; Aleksić *et al*., 2009; Urošević *et al*., 2012). In the remainder of this paper, the populations in which *P. muralis* co-occurs with *P. melisellensis* are referred to as syntopic.

All specimens were deposited in the Herpetological Collections of the Institute for Biological Research 'Siniša Stanković', University of Belgrade, Serbia. De-

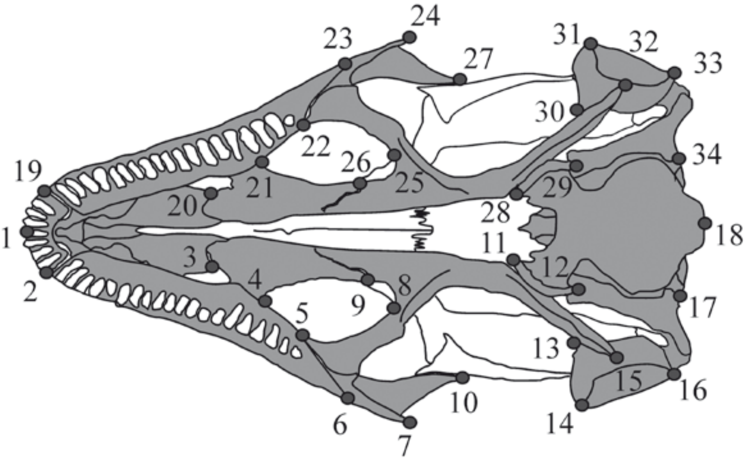

Fig. 1. Landmarks on the ventral side of the skull: 1 - Tip of premaxilla (tip of the snout); 2, 19 - Suture between premaxilla and maxilla; 3, 20 - Suture between vomer and palatine; 4, 21 - Anteriormost point of subocular foramen; 5, 22 - Anteriormost point of ectopterygoid; 6, 23 - Posterior tip of maxilla; 7, 24 - Lateralmost point of skull; 8, 25 - Posteriormost point of subocular foramen; 9, 26 - Suture between pterygoid and palatine; 10, 27 - Posterior tip of jugal; 11, 28 - Anterior tip of basipterygoid process; 12, 29 - Posterior tip of basipterygoid process; 13, 30 - Anteriormost point of quadrate; 14, 31 - Lateralmost point of quadrate; 15, 32 - Posterior tip of pterygoid process; 16, 33 - Posterior point of quadrate; 17, 34 - Posterior tip of otooccipital; 18 - Posteriormost point on the curve of the occipital condyle.

tails about specimens – locality coordinates, voucher numbers, sex, number of specimens and condition of syntopy with *P. melisellensis*, are given in the supplementary table (Table S1).

Skull preparation and landmarks

The skulls of *P. muralis* from Malo Starčevo island were prepared as dry skeletons – flesh was removed by dermestid beetles (Aleksić, 1997). The skulls of *P. muralis* from Malo Beško island, Zeta and Belgrade were cleared with trypsin and potassium hydroxide (Dingerkus and Uhler, 1977). All samples were stained with Alizarin Red S to better distinguish between skeletal elements and their articulations, and preserved in glycerol. Digital images of ventral skull were taken with Sony DSC F828 (resolution 8.0 MP; Sony Corp., Tokyo, Japan). Each skull was submerged in glycerol and placed in the centre of the optical field, with palate oriented parallel to the image plane. Camera setup and placement of the lens relative to the specimen (3 cm from the skull) were kept constant to minimize image error related to distortion and parallax (Mullin and Taylor, 2002). The 34 landmarks (16 symmetric and 2 median) on the ventral skull were digitized (by A.U.) using TpsDig 2 software (Rohlf, 2008). The landmark configuration was based on previous studies on the lacertid lizard skull morphology (Ljubisavljević *et al.*, 2010, 2011; Urošević *et al.*, 2012, 2013) (Fig. 1). The chosen landmarks were present on all specimens and they sufficiently summarize the morphology of the ventral skull symmetric structures - contact points between bones, tips of processes, or the point of maximum curvature of structures (Bookstein, 1991).

Statistical analyses

To obtain information on ventral skull shape with differences related to size, position and orientation removed (Rohlf and Slice, 1990; Bookstein, 1996; Dryden and Mardia, 1998), we performed a Generalized Procrustes Analysis (GPA) which yields a matrix of Procrustes coordinates – shape variables which can be further used as input variables in any conventional statistical analysis (Zelditch *et al.*, 2012). Shape analyses were done on the symmetric component of shape variation – the average of original and mirrored configurations of each specimen (Klingenberg *et al.*, 2002). The set of shape variables was obtained using MorphoJ software (Klingenberg, 2011). We used centroid size (CS), the square root of the summed squared distances of each landmark from the centroid of the landmark configuration, as a geometric measure of the ventral skull size (Bookstein, 1991; Zelditch *et al.*, 2012).

Size and shape variation

Since significant sexual dimorphism in skull size and shape was established in this species (Ljubisavljević *et al.*, 2010), we did all our analyses on separated sexes. To assess differences in skull size between populations, we employed ANOVA with CS as the dependent variable and population as factor. To explore variation in skull shape, we employed MANOVA with the symmetric component of the shape variation as the dependent variables and population as factor. To assess effects of insularity and syntopy, and their interaction, on size, we employed ANOVA with CS as the dependent variable and insularity and syntopy as factors. For effects of insularity and syntopy on shape, as well as insularity – syntopy interaction, we used MANOVA with symmetric components of shape variation as the dependent variables and insularity and syntopy as factors.

The differences in size among populations were obtained by comparing mean CS values of each population.

To explore variation in ventral skull shape among populations and to visualize skull shape changes, we conducted a PCA analysis on the covariance matrix of the shape variables (symmetric component). The PCA analysis was performed using MorphoJ software (Klingenberg, 2011).

Mean shape configuration was calculated for each population (females and males separately). Procrustes distances were calculated between mean shapes and permutation test was performed to estimate statistical significance of divergence among populations. The Procrustes distances among populations and statistical significance were assessed using MorphoJ software (Klingenberg, 2011).

Analysis of allometry and removing the effect of size

Static allometry denotes size-related shape changes measured in different individuals at the same developmental stage within a population or species (Klingenberg, 1998; Shingleton, 2010). To assess the effect of size on shape within and among populations, we explored the size-related shape changes within populations by regressing the shape variables on CS, and

Table 1. Effects of insularity and syntopy on ventral skull size.

sex	effect	SS	df	F	p
females	insularity	410.68	1	219.83	$<1.0 \times 10^{-4}$
	syntopy	25.03	1	13.4	4.8×10^{-4}
	insularity × syntopy	7.96	1	4.26	4.3×10^{-2}
males	insularity	568.15	1	163.84	$<1.0 \times 10^{-4}$
	syntopy	77.68	1	22.4	1.2×10^{-5}
	insularity × syntopy	43.34	1	12.5	7.5×10^{-4}

Table 2. Effects of insularity and syntopy on ventral skull shape.

sex	effect	Wilks' λ	effect df	error df	F	p
females	insularity	0.077	32	35	13	$<1.0 \times 10^{-4}$
	syntopy	0.085	32	35	12	$<1.0 \times 10^{-4}$
	insularity × syntopy	0.091	32	35	11	$<1.0 \times 10^{-4}$
males	insularity	0.108	32	40	10	$<1.0 \times 10^{-4}$
	syntopy	0.124	32	40	9	$<1.0 \times 10^{-4}$
	insularity × syntopy	0.114	32	40	10	$<1.0 \times 10^{-4}$

evaluated the similarity of static allometric trajectories among populations by comparing regression slopes. To check linearity we visually inspected the scatter plots of the regression scores. These preliminary analyses showed clear, linear relationship between shape changes and increase in size. To test if the allometric slopes differ among populations, we employed a multivariate analysis of covariance (MANCOVA) with the symmetric component of shape variation as dependent variables, population as factor and CS as covariate. Significant population × CS interaction would indicate that size-dependent shape changes differ between populations.

In cases where multiple groups exhibit the same allometry, the multivariate regression can be done on pooled groups to assess the common allometric pattern (Klingenberg, 2011; Zelditch *et al*., 2012). We employed multivariate regression of the symmetric component of shape variation on CS to calculate the percentage of static allometry and statistical significance.

To explore variation between populations after correction for size, we carried out PCA on the covariance matrix of regression residuals. Multivariate regression and PCA analysis were performed using the MorphoJ program (Klingenberg, 2011).

Results

Size and shape variation

The differences in ventral skull size were statistically significant among populations, for each sex: ANOVA, F=88.22, df=3, p<0.0001 (females) and F=75.81, df=3, p<0.0001 (males). The effects of both insularity and

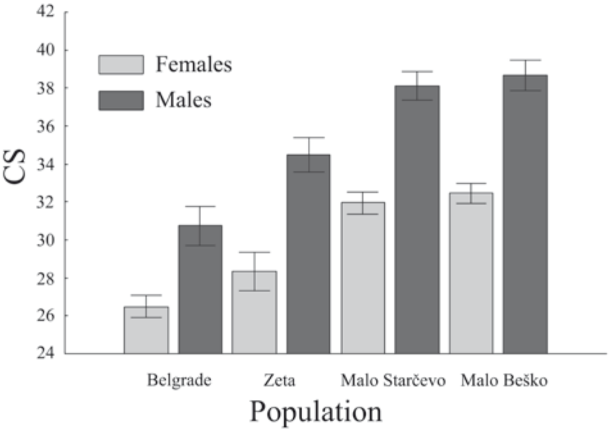

Fig. 2. Mean skull size (CS) values for females and males of all four studied populations, with 95% confidence intervals.

Table 3. Interpopulation size and shape divergence (in Procrustes distances) for females (above the diagonal) and males (below the diagonal). Statistical significance of the Procrustes distances after the permutation test (N=10000) is indicated by * ($p < 0.05$).

population	Belgrade	Zeta	Malo Starčevo	Malo Beško
Belgrade		0.0233*	0.0271*	0.0303*
Zeta	0.0287*		0.0301*	0.0257*
Malo Starčevo	0.0307*	0.0398*		0.0239*
Malo Beško	0.0319*	0.0266*	0.0346*	

Table 4. Allometric shape changes between populations for each sex, tested by multivariate analysis of covariance (MANCOVA). CS – centroid size.

sex	effect	Wilks' λ	effect df	error df	F	p
female	population	0.207	96	108.66	0.78	0.887
	CS	0.146	32	36	6.57	$<1.0 \times 10^{-4}$
	population × CS	0.215	96	108.66	0.76	0.915
male	population	0.109	96	93.69	1.07	0.372
	CS	0.134	32	31	6.24	1.0×10^{-6}
	population × CS	0.116	96	93.69	1.03	0.448

syntopy on skull size were statistically significant with significant insularity × syntopy interaction (marginal in females) (Table 1). The specimens from the two islands were similar in skull size and clearly larger than those from mainland populations (Fig. 2).

The results of MANOVA showed statistically significant differences in skull shape among populations: Wilks' Lambda=0.002176, F=8, p<0.0001 (females) and Wilks' Lambda=0.001028, F=10, p<0.0001 (males). The variation in skull shape among populations was also influenced by both insularity and syntopy, and the insularity × syntopy interaction was significant (Table 2).

The position of the specimens in the morphospace defined by the first two axes obtained by PCA analysis of skull shape variables and visualisation of related skull shape changes are presented in Fig. 3. In females, the first two PC axes accounted for 45.04% of the total shape variation. The PC1 described the transition from insular to mainland populations. Females from insular populations Malo Starčevo and Malo Beško had proportionally reduced skull base, shortened quadrates, enlarged jaw adductor muscle chambers, elongated jaw-closing in-lever (distance from the posterior edge of the postorbital bar to the quadrate) and elongated rostrum, while females from Belgrade and Zeta (mainland populations) had enlarged skull base, elongated quadrates, reduced jaw adductor muscle chambers, shortened jaw-closing in-lever and shorter rostrum. The PC2 described shape differences between allotopic and syntopic populations. Individuals from syntopic populations Zeta (mainland) and Malo Beško (island) with reduced skull base, quadrates shifted laterally, reduced subocular foramina, enlarged jaw adductor muscle chambers, skull widened in the jugal region and shorter rostrum, separated from allotopic Belgrade (mainland) and Malo Starčevo (island) individuals with enlarged skull base, quadrates shifted medially, enlarged subocular foramina, reduced jaw adductor muscle chambers, skull narrowed in the jugal region and elongated rostrum (Fig. 3A).

The pattern observed in males was similar to the one observed in females (Fig. 3B). The first two PCs accounted for 51.15% of the total shape variation. The PC1 axis described changes in skull shape in island populations Malo Starčevo and Malo Beško, with medially shifted quadrates, narrower skull and elongated rostrum, comparing to mainland Belgrade and Zeta populations, with laterally shifted quadrates, wider skull and shortened rostrum. The PC2 axis described differences between allotopic and syntopic populations, from Malo Beško and Zeta individuals, with

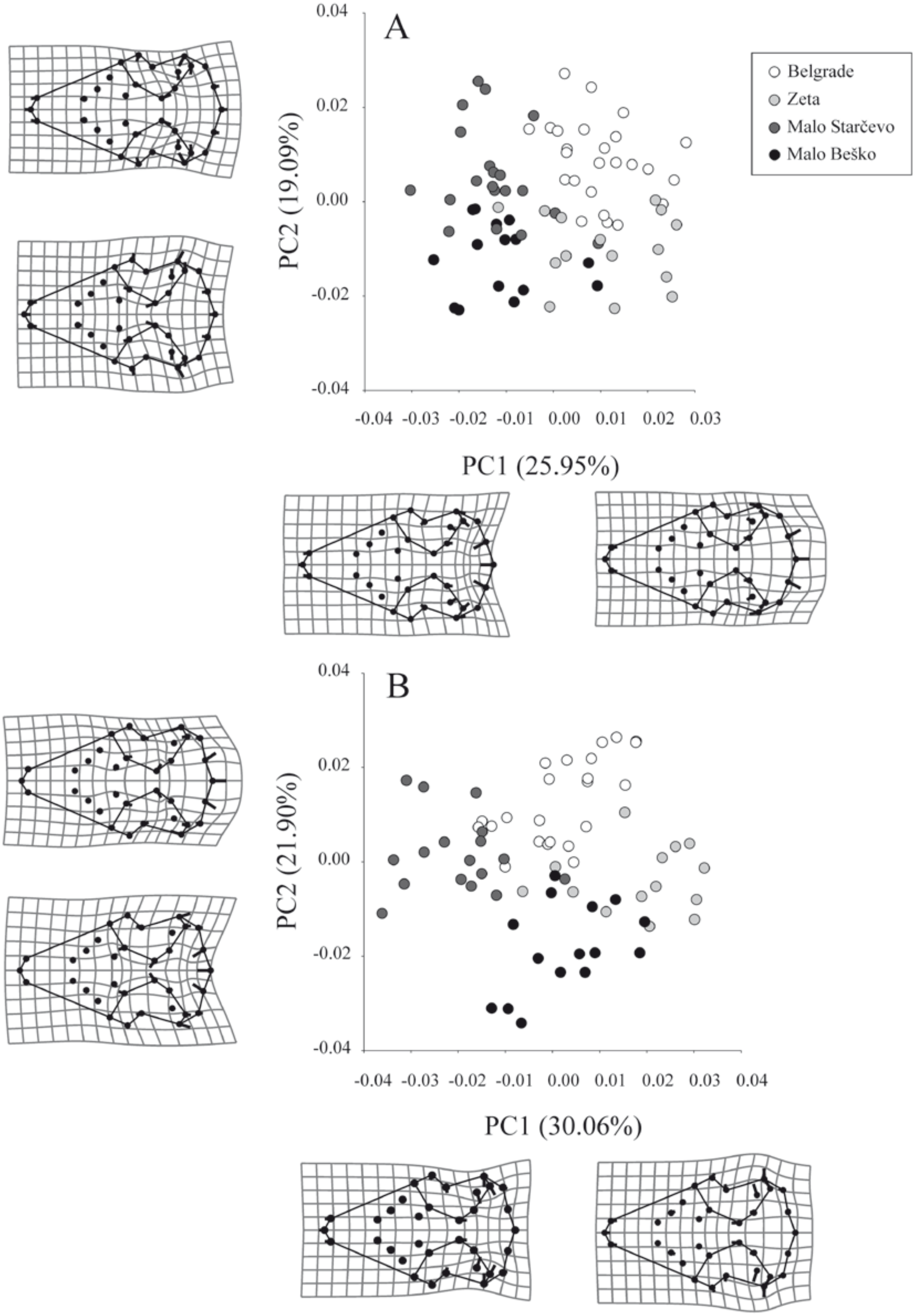

Fig. 3. The positions of the specimens from four populations of *P. muralis* in the morphospaces of the ventral skull shape defined by first two PC axes. Deformation grids illustrate shape changes associated with first two PC axes. The lines between landmarks 6, 7, 8, 10, 11, 12, 14 and 15 as well as 23, 24, 25, 27, 28, 29, 31, and 32 define the jaw adductor muscle chambers.

reduced skull base, shorter quadrates, wider crania, enlarged jaw adductor muscle chambers and reduced subocular foramina, to Malo Starčevo and Belgrade individuals, with enlarged skull base, longer quadrates, narrower crania, reduced jaw adductor muscle chambers and enlarged subocular foramina (Fig. 3B).

Interpopulation distances were higher for males than for females, and statistically significant in all cases (p<0.0001). Females were clustering according to insularity, and continental populations were the most similar regarding to the ventral skull shape. In males, syntopic populations from Zeta and Malo Beško island clustered together (Table 3).

Analysis of allometry and removing the effect of size

The MANCOVA results (Table 4) indicated that populations have a common static allometric slope (population × CS interaction was insignificant). The results of multivariate regression of shape variables on CS revealed that 21.48% (females) and 18.90% (males) of shape variation could be explained by allometry. The regressions were statistically significant in both cases (p<0.0001).

The positions of individuals in the allometry-free morphospace (first two PC axes obtained on residual data set) are presented in Fig. 4. For females, the first two PCs accounted for 40.02% of allometry-free shape variation. Along the first axis specimens from Belgrade and Malo Starčevo (with elongated snouts and reduced jaw adductor muscle chambers), gradually separated from Malo Beško and Zeta animals (with shorter snouts, wider crania and enlarged jaw adductor muscle chambers). Most of the shape changes described by the second axis were related to within-population variation (Fig. 4A). For males, the first two PCs described 49.58% of the total non-allometric shape variation, with the same pattern as observed in females. Along the PC1 axis, Malo Beško and Zeta animals, with enlarged jaw adductor muscle chambers, wider crania and shorter and narrower snout, gradually separated from Belgrade and Malo Starčevo animals with reduced jaw adductor muscle chambers, narrower crania and elongated and wider rostrum. Along the PC2, there was some separation between animals from Malo Beško and Belgrade, with crania narrower in the jugal region, reduced skull base, enlarged jaw adductor muscle chambers and shortened quadrates, and animals from Malo Starčevo and Zeta, with crania wider in the jugal region, enlarged skull base, reduced jaw adductor muscle chambers and elongated quadrates (Fig. 4B).

Discussion

The studied populations of *P. muralis* in the Central Balkans significantly varied in skull size and skull shape. In the analysed samples, most of the variation in skull size was accounted for by the effect of insularity, which was expected (Crnobrnja *et al*., 1994; Castilla *et al*., 1998; Sá-Sousa *et al*., 2000; Arntzen and Sá-Sousa, 2007). The skull shape significantly varied among populations. Almost all observed variation in skull shape among populations is attributable to allometric shape changes. These shape changes described differences between smaller mainland and large insular populations. Non-allometric, size-independent shape changes suggested character displacement between populations of *P. muralis*, possibly due to interspecific competition with *P. melisellensis*.

Although some recent studies showed that allometry can be very variable in lizards and influenced by different ecological traits, mainly different habitat type or diet (Kaliontzopoulou *et al*., 2008; Ljubisavljević *et al*., 2011), our results indicated that, despite high variation in skull shape between populations, the static allometry in the ventral skull of *P. muralis* was conserved, and the allometry related shape changes accounted for high percent of variation in skull shape within sample. Allometric shape changes among populations involved reduction of the skull base, posterior widening of the skull and elongation of the rostrum in the larger (insular) populations, which is largely similar to ontogenetic shape changes (Emerson and Bramble, 1993; Urošević *et al*., 2013).

Interestingly, when corrected for allometry, positions of specimens in non-allometric morphospace indicated that allotopic populations and populations which share habitat with *P. melisellensis* differ in skull shape. As noted before, the changes in ventral skull shape, especially jaw adductor muscle chamber, could be related to change in bite force, and skull biomechanics. The question is why the populations that share habitat with *P. melisellensis* differ in skull shape? The microhabitat shift between *P. muralis* and *P. melisellensis* in habitats where these species occur together is well documented (Arnold, 1987; Aleksić *et al*., 2009). Both species tend to be habitat generalists. However, in places where they co-occur, there is a ‘specialization’ of *P. melisellensis* for horizontal, vegetated and of *P. muralis* for vertical, rocky microhabitats (Arnold, 1987; Aleksić *et al*., 2009). In this case, ecological character displacement is a likely explanation for the observed morphological variation (Losos,

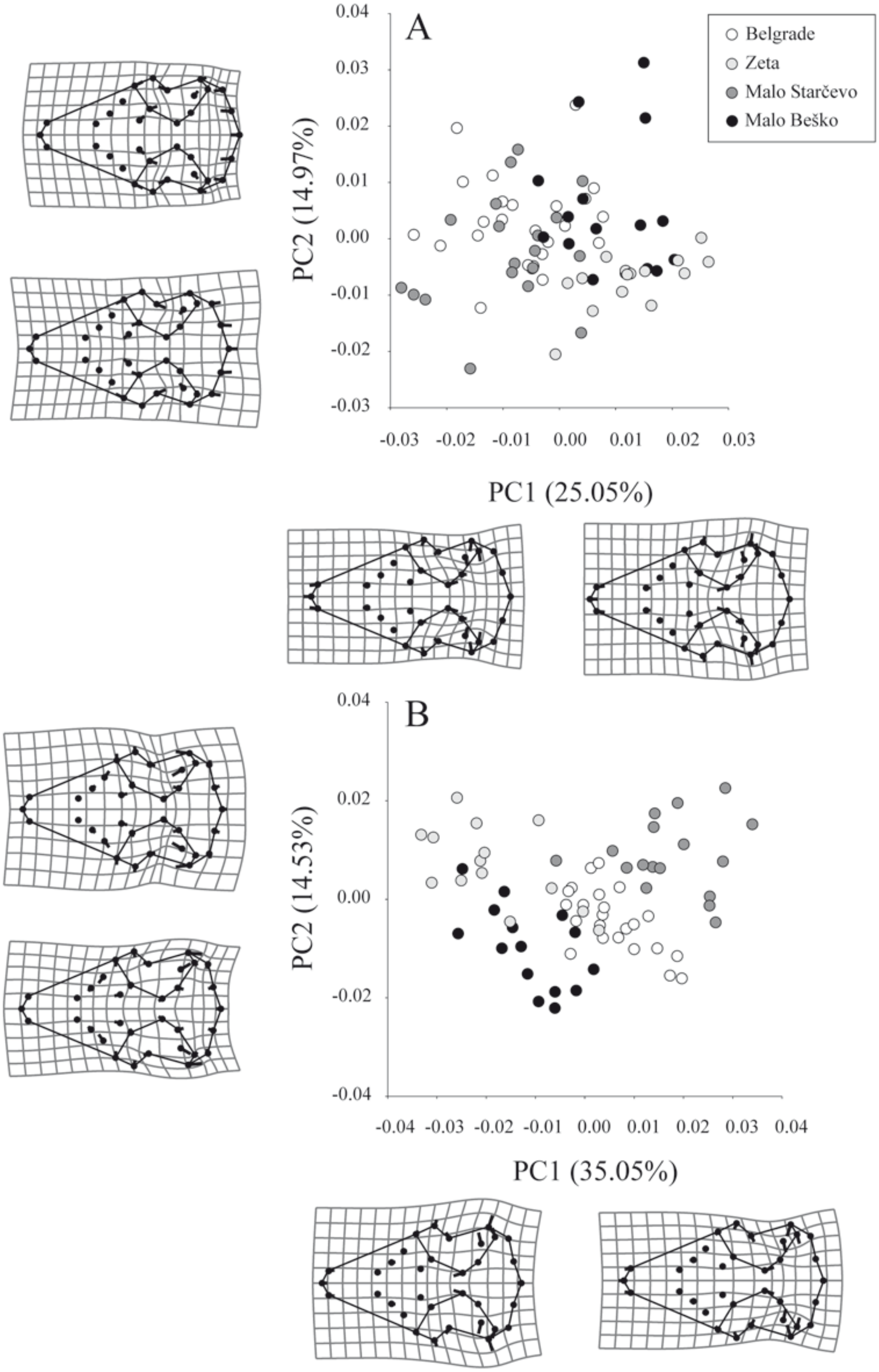

Fig. 4. The position of the specimens from four populations of *P. muralis* in the morphospaces of the ventral skull shape after the correction for size. Deformation grids illustrate shape changes associated with first two PC axes. The lines between landmarks 6, 7, 8, 10, 11, 12, 14 and 15 as well as 23, 24, 25, 27, 28, 29, 31, and 32 define the jaw adductor muscle chambers.

2000; Corse *et al*., 2009; Stuart and Losos, 2013). Alternative explanations could be heterospecific aggression and trophic shift. Both *P. muralis* and *P. melisellensis* are aggressive, territorial species (Herrel *et al*., 2001; Sacchi *et al*., 2009; Lailvaux *et al*., 2012) and heterospecific male-male interactions between the two species could be expected in the microhabitat contact zones (Peiman and Robinson, 2010; Lailvaux *et al*., 2012). It was shown that aggressive male behaviour can have positive effect on bite force and enlargement of the jaw adductor muscles in lizards (Herrel *et al*., 2001, 2007). Also, cases of trophic shifts relating to insularity and the presence of competing lizard species have been observed in *Podarcis* lizards (Zuffi and Giannelli, 2013) and differences in diet also have implications on bite force potential and head morphology (Verwaijen *et al*., 2002).

However, we lack field observations of aggressive interaction between these two species or trophic shift among *P. muralis* populations in the Skadar Lake region, so these explanations remain hypothetical. The analysis of the size – independent shape changes revealed an intricate pattern of shape variation which can be influenced by various external factors, and further field studies are needed to correctly assess the sources of the complex intraspecific shape variation in *Podarcis muralis*.

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On-line Supplementary Information (SI)

S1. The *Podarcis muralis* specimens included in the study. Material is deposited in the Herpetological Collection of the Institute for Biological Research 'Siniša Stanković', University of Belgrade, Serbia. N - number of specimens per population. Syn - populations share habitat with *P. melisellensis*.