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Towards a functional understanding of species coexistence: ecomorphological variation in relation to whole-organism performance in two sympatric lizards

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Summary

1. We examined intra- and interspecific variation in functional morphology and whole-organism performance in a sympatric lizard species pair, *Iberolacerta horvathi* and *Podarcis muralis*, in the area with a high potential for competition.

2. The biggest variation between species was found in two functional traits, bite force and climbing speed, linked with corresponding morphological traits.

3. The species with larger and taller heads, *P. muralis*, exhibited correspondingly stronger bite forces. The other species exhibited smaller and flatter head. Both traits may potentially promote segregation between species in trophic niche (stronger bites relate to harder prey) and in refuge use (flatter heads allow using narrower crevices, hence, influencing escaping from common predators). Stronger bites and larger heads also provide one species with a dominant position in interspecific agonistic interactions.

4. Females had longer trunks that impacted negatively on climbing speed, which may lower anti-predator escape abilities of the more trunk-dimorphic species, but positively influence reproductive effort.

5. Our results exemplify how the joint examination of morphological and functional traits of ecologically similar and sympatric species can provide a mechanistic background for understanding their coexistence, namely, syntopic populations that are frequent in the study area.

6. The identified roles of functional morphology in this system of sympatric rock lizards support the contribution of functional diversification for the complexity of community structure via coexistence.

Key-words: bite force, coexistence, community structure, functional diversity, locomotor performance, morphology

Introduction

Species within the same ecological guild use the same resources in a similar way (Root 1967) and often share morphological and functional characteristics (Schoener 1977). When resources are limited, a high potential for interspecific competition among such ecologically similar species is expected (Schoener 1977). Due to the costly nature of competitive interactions, species within the same guild will, under such conditions, eventually segregate in one or more dimensions of their ecological niche to minimize competition (e.g. Cody & Diamond 1975; Arnold 1987; Vrezec & Tome 2004). This type of segregation is a cornerstone element in determining community structure (Begon, Townsend & Harper 2006). Niche differentiation may have developed due to past competition that has been conserved (i.e. ghost of competition; Langkilde, Lance & Shine 2005), or may reflect current niche segregation in sympatry (Schoener 1977; Pacala & Roughgarden 1982). In particular, the ecomorphological paradigm has a central position in our understanding of how species interactions shape morphological and functional features to promote the utilization of different ecological resources (e.g. Losos & Sinervo 1989; Losos 1990). Moreover, whole-organism performance directly influences individual fitness and survival, and thus contributes to determining population success (e.g. Angilletta, Hill & Robson 2002; Irschick *et al.* 2008). Examining variation in functional morphology, and

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its link with whole-organism performance, within and among species, sheds light on how the functional capacity for exploiting ecological and social resources may shape ecological coexistence phenomena (e.g. Weiher, Clarke & Keddy 1998; Fountain-Jones, Baker & Jordan 2015).

Lizards are major model organisms in ecomorphological studies, thus extensive knowledge exists about the relationship between whole-organism performance and the functional morphology of different body parts (e.g. Garland & Losos 1994; Vanhooydonck & Van Damme 1999; Aerts *et al.* 2000; Irschick & Garland 2001; Husak & Fox 2008; Irschick *et al.* 2008). Head shape and size are known to be important determinants of lizard bite force, which has repercussions in multiple and highly relevant ecological and social activities, including feeding, mating and aggressive interactions (e.g. Herrel *et al.* 2001; Olsson *et al.* 2002; Perry *et al.* 2004; Husak *et al.* 2006; Herrel, McBrayer & Larson 2007; Kaliontzopoulou *et al.* 2012). In addition, head dimensions are directly associated with microhabitat and refuge use (e.g. Kaliontzopoulou, Carretero & Adams 2015). As a result, head morphology and bite force may be relevant in the context of species coexistence in several ways: by determining the outcome of aggressive interactions (higher bite force is competitively advantageous, e.g. Husak *et al.* 2006); by acting as a reproductive barrier preventing hybridization (differences in the way males bite female during copulation, e.g. Fabre *et al.* 2014a, b); by promoting spatial segregation in microhabitat use (head height determines the height of crevices used as refuges, e.g. Carretero *et al.* 2006) or by promoting trophic niche segregation (both gape and bite performance are known traits linked with maximal prey items consumed, e.g. Verwaijen, Van Damme & Herrel 2002).

Locomotor performance in lizards is involved in escape from predators, prey capture, habitat use and territory defence, therefore can be under strong interspecific and intraspecific (sexual) selective pressures (Husak 2006; Kaliontzopoulou, Bandeira & Carretero 2012). For example, it has been shown that locomotor performance directly enhances antagonistic capacity and reproductive fitness in males (Huyghe *et al.* 2005; Husak *et al.* 2006; Husak & Fox 2008). In a system of potentially competing sympatric species, differences in locomotor performance may determine behavioural dominance (e.g. Husak *et al.* 2006) and contribute to spatial segregation, as faster species could be more efficient at defending territories (e.g. Pacala & Roughgarden 1982). Selection on sprint speed may also be mediated directly by predator attacks, which will be relevant when species share common predators in syntopy (Holt 1977; Husak 2006; Žagar *et al.* 2015a). Finally, differences in locomotor capacities may translate into dietary segregation via different prey capture abilities (e.g. Edwards *et al.* 2013).

In sympatry, two ecologically similar species may compete for ecological resources when they come into contact and frequently occur in syntopy (coexist). Thus, the traits involved in the exploitation of these resources may be under evolutionary pressures due to ecological interaction (Schoener 1977). Theoretically, interspecific competition pressures would become relevant only when they outweigh pressures exerted due to intraspecific competition (Schoener 1977). On the other hand, sexual dimorphism reflects the main direction of intraspecific interactions, either competitive (between females and males for resources) or co-evolutionary (that influence morphological variation by favouring traits that enhance reproductive success (Andersson 1994; Aleksić & Ljubisavljević 2001; Olsson *et al.* 2002). For example, bite force and related head morphology in lizards are also under sexual selection due to male–male competition and mating, which translates into relatively larger heads in males than females (Olsson *et al.* 2002). In this context, ecomorphological and functional differentiation between sexes is relevant in species interaction studies when species coexist (occur in syntopic populations) and needs to be taken into account (e.g. Kaliontzopoulou, Carretero & Llorente 2007).

Here, we investigated the relationship between morphological and functional traits in a model system of two sympatric lizard species in an area with a high frequency of occurrence of syntopic populations (Žagar 2016) to understand how ecomorphological variation potentially shapes their coexistence pattern. The studied species (Fig. 1), *Iberolacerta horvathi* (Méhely 1904) and *Podarcis muralis* (Laurenti 1768), have overlapping distribution ranges at a geographic scale, where the range of *I. horvathi* completely overlaps with that of *P. muralis* (Sillero *et al.* 2014). Locally, *P. muralis* is more abundant at lower altitudes while *I. horvathi* is at higher altitudes and syntopic

Fig. 1. Studied species, *Iberolacerta horvati* (Méhely 1904) (a) and *Podarcis muralis* (Laurenti 1768) (b). (Photos courtesy of Miha Krofel).

populations are typically most frequently found at mid-altitudes (Lapini *et al.* 2004; Cabela, Grillitsch & Tiedemann 2007; Rassati 2010; Žagar, Kos & Vrezec 2013) but can also occur across all the altitudinal span as in the case of our study area (Žagar 2016). Phylogenetically, the two species belong to different genera, *Iberolacerta* and *Podarcis*, that diverged from other genera in the sub-family Lacertini about 16–12 million years ago (Mendes *et al.* 2016). Both genera then simultaneously radiated at around 8 million years ago and no hybridization of the two species has been recorded and is not likely due to their distant phylogenetic positions (Mendes *et al.* 2016).

In the study area, these two species are the only representatives of the lizard community sharing rocky habitats with scarce vegetation and are of similar size (Žagar, Kos & Vrezec 2013). Other lizards present are either much larger (*Lacerta viridis* complex; Marzahn *et al.* 2016) and/or are spatially segregated (*Zootoca vivipara*), and they exhibit different habitat use that is more associated with high vegetation cover vs. rocky and scarcely vegetated habitat of rock and wall lizards (Arnold 1987; Žagar, Kos & Vrezec 2013; Žagar, Vrezec & Carretero 2017), thus belong to a different ecological guild (Begon, Townsend & Harper 2006). It has been suggested that coexistence in this two-lizard study system is potentially mediated by variations in their thermal, hydric and metabolic physiology, behaviour and by indirect effects of common predators (Osojnik *et al.* 2013; Žagar *et al.* 2015a, b, c). In particular, the physiology of the species prevailing at higher altitudes, *I. horvathi*, reflects specialization to the thermally restrictive climate conditions typical of high-mountain environments. In detail, this species has a higher thermoregulatory precision, lower water-loss rates and higher metabolic potentials, which likely give it a competitive advantage over *P. muralis* at higher altitudes. However, at intermediate and lower altitudes precise thermoregulation is known to carry substantial time and energy costs (Huey & Slatkin 1976; Osojnik *et al.* 2013; Žagar *et al.* 2015b, c). As both species have been found to occur in syntopic populations across the altitudinal span (200–1100 m a.s.l.; Žagar 2016), apparently, physiology alone does not explain the existing spatial pattern of density-dependent altitudinal segregation together with frequent syntopy (coexisting populations). In fact, it has been shown that when sun patches for thermoregulation are limited, *P. muralis* has a dominant competitive position over *I. horvathi* via interspecific male–male agonistic interactions, which restricts the thermoregulatory ability of *I. horvathi* (Žagar *et al.* 2015b). This association between agonistic social interactions and physiology provides a better understanding of the processes behind the observed dynamics of species coexistence in the study area, but it lacks the knowledge of the functional morphology involved.

The studied species also show differences in escape responses to common predators (Žagar *et al.* 2015a). They face two different types of predators: snakes that are specialized in searching for inactive lizards in their refuges (e.g. Luiselli 1996) and avian or mammalian predators, which forage visually and capture active lizards in open areas (e.g. Castilla *et al.* 1999). *Iberolacerta horvathi*, which exhibited stronger anti-predator behavioural responses (i.e. stronger than the other species), could have short-term benefits (higher survival rates), but only under strong predator pressure because anti-predator behaviour is otherwise time and energy costly (Žagar *et al.* 2015a). However, the potential for an enhanced escape capability via using refuge sites needs more attention linked with functional morphology.

In this context, the main aim of this work is to understand the functional relationships between morphology and factors involved in interspecific interactions that occur in cases of syntopy (coexistence) in studied sympatric lizards. Specifically, we focus on the functional traits promoting higher success in potential agonistic encounters. Firstly, in bite force we predict that if both species differ in bite force, the one previously known to have the dominant position over the other in agonistic encounters (*P. muralis*) is expected to have stronger bites. If coexisting occurrence (syntopy) is facilitated by differential microhabitat use, we should observe variation in morphological and performance traits that can enhance the use of various microhabitats in the study area. In particular, we would expect interspecific differences in climbing and running abilities and limb dimensions correlated with the use of different substrates and variability in head height, if head height determines the minimal size of the crevices accessible as refuges (e.g. Carretero *et al.* 2006). Using smaller refuges may also enhance escape from the most specialized common predator – saurophagous snakes for the flatter species. Thus, the studied species potentially differ in their ability to escape common predators, which is expected to have an indirect effect on their coexistence (Holt 1977). Finally, we also consider the variation between sexes to account for intraspecific differences.

Materials and methods

STUDY SITE AND INDIVIDUALS USED IN EXPERIMENTS

The study was conducted in the Kočevsko region, SE Slovenia (lat. 45°38′N, long. 14°51′E, datum WGS1984), characterized by thick forest cover (Puncer 1980) and a mosaic of natural and anthropized open areas. The climate is temperate continental with an alpine trend at higher elevations (Kordiš 1993). Collection sites were similar in habitat structure and altitude (*P. muralis* site: 723 m a.s.l., and *I. horvathi* site: 986 m. a.s.l.), and were located at a distance of 9·4 km. All individuals were collected and experiments conducted in July 2013. To minimize any effects of ontogeny and reproduction, all experimental individuals were adults and we used only females that did not show signs of gravidity. Captured individuals were transported to the laboratory facilities to conduct performance experiments and quantify morphological traits. During the experimental period, lizards were housed in individual terraria with a wooden shelter, fed with meal worm larvae *ad libitum* and provided with water, also *ad libitum*. Lizards were kept under the natural light regime and suitable temperature maintained by infra-red lights which were connected for six daily hours, allowing active thermoregulatory behaviour.

MORPHOLOGICAL MEASUREMENTS

We quantified body size, head and limb dimensions of both species to the nearest 0·1 mm by using digital callipers. Specifically, we measured snout-vent length (SVL), trunk length (TRL), pileus length (PL), head length (HL), head width (HW), head height (HH), fore limb length (FLL), hind limb length (HLL) and we also measured mouth opening (MO) (Kaliontzopoulou, Carretero & Llorente 2007). All morphological traits were log-transformed prior to data analyses to ensure normality in the distribution. Head size was calculated as a geometric mean of HL, HW and HH, which in the logarithmic form becomes the arithmetic mean of log-transformed head dimensions (Kaliontzopoulou *et al.* 2012).

WHOLE-ORGANISM PERFORMANCE

Two days of acclimatization were allowed between arrival at the laboratory and the beginning of bite force and locomotion experiments. Before the experiments, lizards were allowed to thermoregulate in individual terraria to attain the body temperature at their average preferred body temperatures (Tp average ± SE for *I. horvathi* in summer was 30·5 ± 0·2 °C and for *P. muralis* 31·1 ± 0·2 °C, Osojnik *et al.* 2013). Individuals were used in an experimental trial immediately after taken out of their thermoregulatory boxes. All experiments were carried out at room temperature (~22 °C) and individual trials of locomotor or bite force performance lasted for less than 10 s. In this way, we ensured that lizards were tested at their optimal body temperature and did not cool down during the experiment due to its short duration. After each trial, we put each lizard back into its individual terrarium to continue with normal thermoregulatory behaviour. Bite forces were measured using a 20N force gauge (SAUTER GmbH, Balingen, Germany) mounted on a vertical holder. Bite force measurements were obtained by provoking the lizards to bite a pair of thin metal plates connected to the force transducer (Herrel *et al.* 2001). Each lizard was tested five times with a rest of at least 2 h between trials, and the maximal value recorded per individual was retained for statistical analysis.

Sprinting and climbing speed were measured on a 1-m-long and 15-cm-wide racetrack with cork substrate. To quantify climbing speed, we tilted the racetrack to an angle of 60°. All trials were filmed with a digital camera (Canon EOS 60D, Tokyo, Japan) at a filming speed of 50 fps. All animals were tested three times in each setting, to ensure that maximal performance capacity was recorded (Losos, Creer & Schulte Ii 2002; Adolph & Pickering 2008). Trials of each individual were randomized to make sure that all lizards were tested during different days and hours of the day, and to avoid sequential repeats of the same trial. A rest of at least 2 h between locomotor trials allowed physical recovery of the individuals. The position of the lizard in each trial was digitized using MaxTRAQ 2D motion analysis software (Innovision Systems Inc., Columbiaville, MI, USA, 2009). The maximum instantaneous speed per individual across trials was retained for statistical analysis. All performance traits were log-transformed prior to data analysis.

STATISTICAL ANALYSIS

To obtain a general view of morphological variation in our dataset we first performed a principal components analysis (PCA) of all morphological measurements (Klingenberg & Monteiro 2005; Mitteroecker & Bookstein 2011). To examine whether both species differed in their morphological properties and in whole-organism performance traits, we first conducted AN(C)OVA comparisons with species, sex and their interaction as categorical predictors. Two-way ANOVA comparisons were conducted in the case of total body size, as represented by SVL. To examine variation across both species and sexes in relative head size, TRL and fore and hind limb length, we performed ANCOVA comparisons using SVL as the covariate. Furthermore, we examined differences across species × sex groups in relative head dimensions using ANCOVA comparisons where head size was treated as the covariate. For bite force, we examined AN(C)OVA models with species, sex and their interaction as categorical predictors, and in addition including either SVL or head size as covariates. Finally, to investigate variation across species and sexes in locomotor performance, we performed AN(C)OVA comparisons with or without SVL as a covariate.

To investigate the association between morphological and performance traits, and examine how differences in morphology between species and sexes may translate into differences in whole-organism performance, we used two-block partial least squares (PLS). Specifically, we examined the association of maximal bite force with relative head dimensions, after correcting both blocks of traits for the effect of head size variation. In terms of locomotor performance, we only investigated climbing speed and examined its association to trunk and limb length, after correcting both sets of traits for variation due to SVL. As a measure of the association between blocks of traits we used the Pearson correlation between individual scores of the PLS vectors, and we tested the significance of this association using a permutation procedure with 1000 permutations (Rohlf & Corti 2000).

Results

In total, we captured 51 individuals of *I. horvathi* (25 females and 26 males) and 52 individuals of *P. muralis* (24 females and 28 males). Examination of general patterns of morphological variation in our sample through PCA indicated a clear differentiation of three groups across the first PC axis: females of *I. horvathi*, females of *P. muralis* and males of both species (Fig. 2). This axis explained about 43% of variance in the sample and was mainly associated with variation in SVL, TRL and PL (Table 1). Males of the two species were weakly differentiated across the second PC axis (31·50% of variance), which mainly captured variation in head dimensions (Table 1). The third principal component explained 13·7% of morphological variation, and it was strongly associated with variation in limbs (fore and hind limb length) as well as head height (Fig. 2, Table 1).

The ANOVA considering variation in SVL showed that sexes, but not species, differed in total body size, and females of both species were larger than respective males (Table 2, Fig. 3a). The interaction between species and sex was not significant. ANCOVA comparisons with SVL as a covariate indicated that TRL and head size scaled allometrically with SVL, following different allometric slopes in different species × sex groups (Table 2, Fig. 3b,c). In contrast, fore- and hind limb length followed the same allometric slope in all groups, but differed significantly both between species and between the sexes once variation in

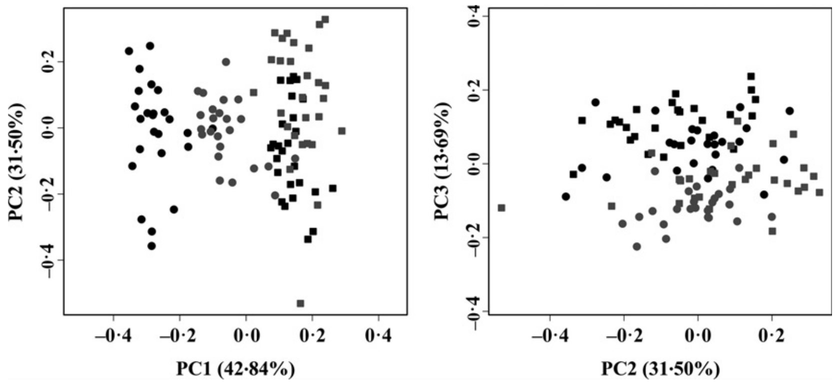

Fig. 2. Variation across species and sexes in morphological traits represented as principal component scores. Black: *Iberolacerta horvati*, grey: *Podarcis muralis*, circles: females, squares: males.

Table 1. Variance explained by the three principal component axes (% exp.) and correlations of each to the measured morphological traits

	PC1	PC2	PC3
% exp.	0·428	0·315	0·137
SVL	**−0·508**	**0·725**	−0·062
TRL	**−0·942**	0·326	−0·041
HL	0·367	**0·750**	0·206
PL	**0·559**	**0·751**	0·037
HW	0·273	**0·833**	0·250
HH	0·461	**0·640**	**−0·558**
MO	0·396	**0·771**	0·061
FLL	−0·005	0·324	**0·791**
HLL	0·251	0·360	**0·712**

Correlations >0·5 are highlighted in bold.
SVL, snout-vent length; TRL, trunk length; HL, head length; PL, pileus length; HW, head width; HH, head height; FLL, fore limb length; HLL, hind limb length; MO, mouth opening.

body size was taken into account (Table 2). Specifically, males of both species had relatively longer limbs than respective females, and individuals of *I. horvathi* had longer limbs than *P. muralis* of the same sex (Fig. 3d). Furthermore, all relative head dimensions differed between species, whereas only PL, HW and HH differed between sexes (Table 2). Two head dimensions, HW and HH, exhibited an inverse relationship to head size in the two species. Namely, *P. muralis* had a relatively narrower head, which increased in width with increasing head size at a higher rate than that of *I. horvathi* (Fig. 3e). In contrast, *I. horvathi* had a flatter head, which increased in height with increasing head size at a higher rate than that of *P. muralis* (Fig. 3f).

Whole-organism performance also exhibited significant variation between species and sexes. Males of both species were able to exert higher bite forces than respective females, and *P. muralis* exerted higher bite forces than *I. horvathi* of the same sex, both in absolute terms and when taking head size variation into account (Table 3, Fig. 4). Interestingly, SVL did not have a significant contribution in explaining variation in biting performance in our sample (Table 3). Sprinting performance did not differ between either species or sexes, but climbing speed did, both in absolute terms and relative to body size (Table 4). Remarkably, the interaction between species and sex was also significant in this case, where climbing speed differed between sexes in *I. horvathi*, but not in *P. muralis*. This resulted in a pattern where females of *I. horvathi* exhibited lower climbing speeds than respective males, or individuals of *P. muralis* of either sex (Fig. 4).

The observed variation across groups in whole-organism performance was in part attributable to their morphological differences. Interestingly, though, differences across species and sexes in biting and climbing performance remained after accounting for variation in head size and body size, respectively. As revealed by partial least squares analysis, once size effects are taken into account, there was still a significant association between morphology and performance. Specifically, we found a significant PLS vector of association between size-corrected bite force and relative head dimensions ($r_{\mathrm{PLS}} = 0{\cdot}42$, $P = 0{\cdot}002$). This association was mainly mediated by an inverse relationship between relative head height and head width. Individuals of the two species were clearly differentiated in the function–morphology space of association, where *P. muralis* occupied an area with relatively higher but narrower heads, associated with increased biting performance (Fig. 5, left). A different pattern was observed in the case of climbing performance, which was significantly associated with trunk and limb length variation ($r_{\mathrm{PLS}} = 0{\cdot}41$, $P = 0{\cdot}001$). In this case, higher climbing speed was associated with longer limbs and shorter trunks, a pattern that was mainly related to sexual dimorphism and a clear differentiation of females of *I. horvathi*, which occupy the area of the function–morphology space with long trunks, short limbs and a lower climbing capacity (Fig. 5, right).

Discussion

We have revealed that in the studied sympatric rock lizards a significant variation in functional traits both across species and between sexes exists. Interestingly, we have found that the degree of sexual dimorphism in some morphological traits was unequal between species, which in turn differentially affected the locomotor abilities of the lizards studied. The biggest variation between species was found

Table 2. Results of AN(C)OVA comparisons on SVL (top), body parts in relation to SVL (middle) and head dimensions relative to head size (bottom), considering the effect of species (sp), sex and their interaction

	SVL		
	d.f.	*F*	*P*
sp	1	0·85	0·362
Sex	1	32·82	**0·001**
sp × sex	1	1·93	0·174
Residuals	99		
Total	102		

		HS		TRL		FLL		HLL	
	d.f.	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
SVL	1	48·12	**0·001**	396·47	**0·001**	10·01	**0·002**	0·59	0·429
sp	1	112·45	**0·001**	57·54	**0·001**	49·02	**0·001**	21·80	**0·001**
Sex	1	180·21	**0·001**	210·35	**0·001**	34·13	**0·001**	65·08	**0·001**
SVL × sp	1	1·62	0·209	7·75	**0·010**	0·02	0·906	0·03	0·882
SVL × sex	1	1·01	0·319	0·06	0·827	1·37	0·247	1·83	0·161
sp × sex	1	0·04	0·859	70·54	**0·001**	0·28	0·588	0·56	0·448
SVL × sp × sex	1	4·91	**0·038**	0·93	0·325	0·11	0·747	0·11	0·753
Residuals	95								
Total	102								

		HL		PL		HW		HH		MO	
	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
HS	1	163·94	**0·001**	683·07	**0·001**	487·43	**0·001**	717·13	**0·001**	189·11	**0·001**
sp	1	27·00	**0·001**	6·85	**0·022**	132·67	**0·001**	94·06	**0·001**	8·60	**0·010**
Sex	1	1·58	0·207	30·03	**0·001**	5·33	**0·026**	4·97	**0·038**	1·38	0·243
HS × sp	1	0·13	0·702	2·41	0·122	9·98	**0·003**	10·49	**0·002**	0·16	0·696
HS × sex	1	5·35	**0·020**	0·14	0·725	0·43	0·516	0·49	0·472	2·06	0·167
sp × sex	1	7·45	**0·012**	1·20	0·266	0·95	0·291	0·01	0·928	0·33	0·541
HS × sp × sex	1	3·15	0·075	2·33	0·123	0·01	0·905	0·99	0·331	0·37	0·566
Residuals	95										

Significant effects are marked in bold.

d.f., degrees of freedom; *F*, *F*-statistic; *P*, corresponding *P*-value; PL, pileus length; SVL, snout-vent length; HL, head length; HW, head width; HH, head height; FLL, fore limb length; HLL, hind limb length; TRL, trunk length; HS, head shape; MO, mouth opening.

in two functional traits, bite force and climbing speed, linked with corresponding morphological traits. These traits have a potential to be involved in promoting segregation between species on a microhabitat scale that would promote syntopic occurrences in the study area via different mechanisms and across different aspects of their ecological niche. Our study extended the available knowledge on the potential links between functional traits and species coexistence patterns, which are among the main drivers of community structure (e.g. Díaz & Cabido 2001; Kearney & Porter 2006; McGill *et al.* 2006).

The effect of morphological sexual dimorphism on performance has been described frequently in lizard species (e.g. Olsson *et al.* 2002; Husak & Fox 2008; Irschick *et al.* 2008; Kaliontzopoulou, Bandeira & Carretero 2012; Fabre *et al.* 2014a, b; Brandt *et al.* 2016), but its significance in the context of potential effect of variable sexual dimorphism on species coexistence has been previously mostly neglected. In our study, females of both species were larger than conspecific males, similar to several previous findings on these species (De Luca 1989; Aleksić & Ljubisavljević 2001; Žagar *et al.* 2012). *Iberolacerta horvathi* females were also larger than *P. muralis* females, whereas males of both species were similar. The other sexually dimorphic trait was limb length. Males had longer limbs than females of the same species, in accordance with previous observations for other lacertids (e.g. Garland & Losos 1994; Kaliontzopoulou, Bandeira & Carretero 2012). Yet again, limb sizes were different between species in both sexes; *I. horvathi* had relatively longer limbs than *P. muralis* of the same sex.

Relative limb length and body size are known to be among the morphological traits that contribute the most to sprint speed in lizards, where larger lizards with longer limbs are faster (Garland & Losos 1994). Our results were not as straightforward as in some other studies where larger and longer-limbed individuals had the highest performance in sprint speed (e.g. Vanhooydonck, Van Damme & Aerts 2001; Kaliontzopoulou, Bandeira & Carretero 2012) because we did not find any differences in sprint speed among species and sexes. This can be most likely explained by a counter-balance between two morphological traits

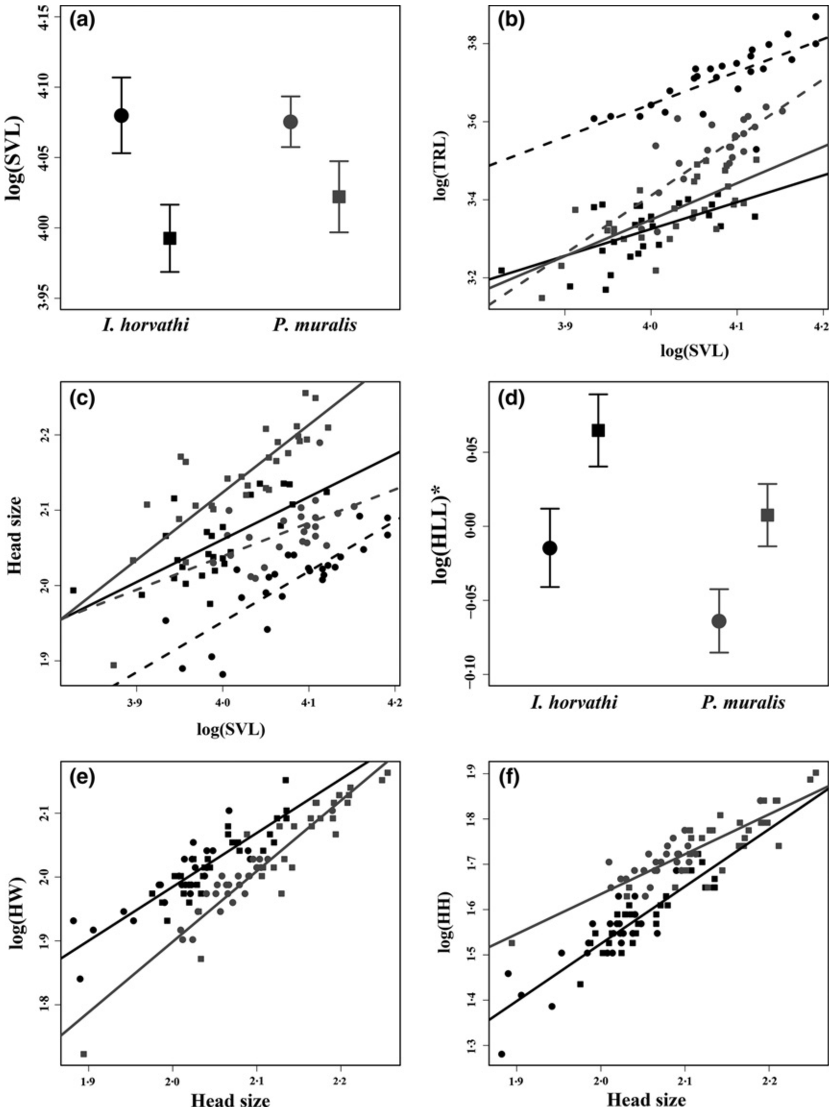

Fig. 3. Variation across species and sexes in morphological traits. (a) Means and 95% confidence intervals for snout-vent length (SVL); (b, c) Relationship of trunk length (TRL) and head size with SVL in different groups; (d) Means and 95% confidence intervals for hind limb length, after correction for SVL effects; (e, f) Relationship of head width (HW) and head height (HH) with head size in different groups; Black: *Iberolacerta horvati*, grey: *Podarcis muralis*, circles: females, squares: males.

involved in sprint speed, limb and TRL (Garland & Losos 1994), i.e. in both studied species, but particularly in *I. horvathi,* trunks were longer in females. Longer trunks of *I. horvathi* females may be balancing out the effect of relative limb length on running performance traits in females. While in similar sized males it is more difficult to understand found results as no differences between species in running speed was found notwithstanding that *I. horvathi* had longer limbs and that trunk lengths were similar.

Moreover, in climbing performance *I. horvathi* females were the slowest climbers and a negative association was found between longer trunks and shorter legs and climbing performance. Regarding limb length, these results match biomechanical predictions, as longer legs may help lizards to climb faster by enabling it to keep their centre of mass closer to the vertical surface (Vanhooydonck & Van Damme 1999; Van Damme *et al*. 2003). On the other hand, the result of negative association between TRL and climbing is intriguing as TRL is likely to be subject to selection by non-locomotor forces in females, i.e. reproductive effort (Ji & Braña 2000; Olsson *et al*. 2002; Roitberg *et al*. 2013, 2015). Other species of the genus *Iberolacerta* exhibit small clutch size, delayed sexual maturation and prolonged egg retention, which have been interpreted as an advanced stage in the tendency towards viviparity (e.g. Arribas & Galán 2005), but a specific comparative study providing adequate reproductive data for our species is still lacking. Because we have also showed that longer trunks negatively affect climbing speeds, our results suggest that fecundity selection negatively influences climbing performance but only in *I. horvathi* and not in *P. muralis*. Consequent differences in the climbing performance can potentially affect coexistence (syntopic occurrence) because climbing ability can influence the extent of use of vertical surfaces [such direct links between morphological variation and microhabitat use have previously been identified in different lizard groups (e.g. Losos 1990; Garland & Losos 1994; Aerts *et al*. 2000; Irschick & Garland 2001)]. In conclusion, this is an evidence of inter-connecting pressures; fecundity selection pressure impairing

Table 3. Results of AN(C)OVA comparisons on bite force considering the effect of species (sp), sex and their interaction, using SVL (middle) or head size (bottom) as a covariate

	BITE FORCE		
	d.f.	*F*	*P*
sp	1	159·10	**0·001**
Sex	1	107·01	**0·001**
sp × sex	1	0·01	0·906
Residuals	99		
Total	102		
	d.f.	*F*	*P*
SVL	1	2·46	0·116
sp	1	255·19	**0·001**
sex	1	234·67	**0·001**
SVL × sp	1	0·03	0·874
SVL × sex	1	0·41	0·545
sp × sex	1	1·30	0·266
SVL × sp × sex	1	2·04	0·161
Residuals	95		
Total	102		
	d.f.	*F*	*P*
HS	1	510·54	**0·001**
sp	1	45·53	**0·001**
Sex	1	62·65	**0·001**
HS × sp	1	0·76	0·421
HS × sex	1	0·03	0·880
sp × sex	1	0·20	0·652
HS × sp × sex	1	1·43	0·233
Residuals	95		
Total	102		

Significant effects are marked in bold.
d.f., degrees of freedom; *F*, *F*-statistic; *P*, corresponding *P*-value; SVL, snout-vent length; HS, head shape.

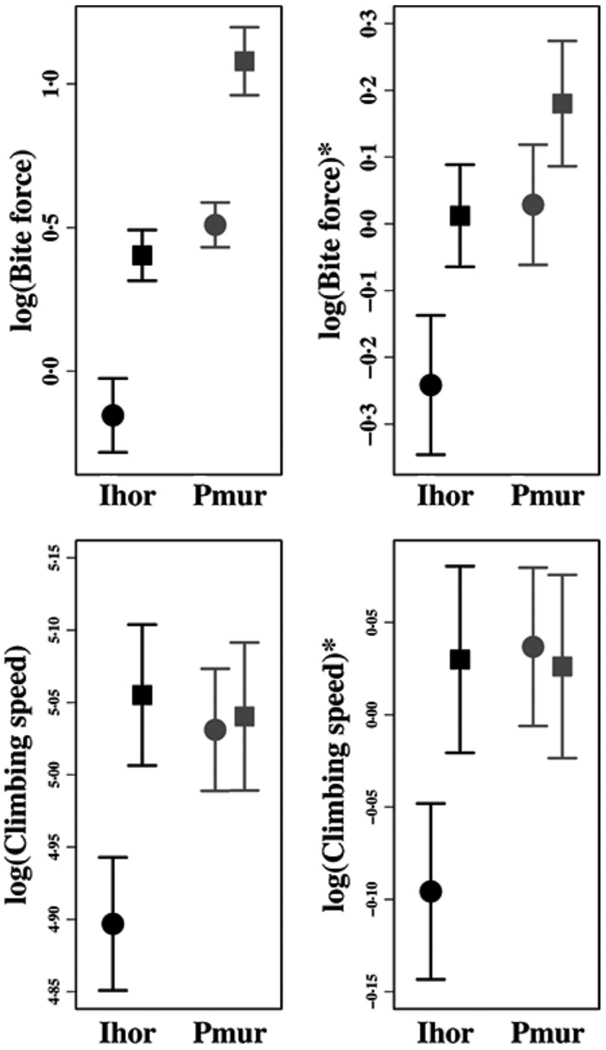

Fig. 4. Variation across species and sexes in bite force (top) and climbing speed (bottom) before (left) and after (right) correction for effects of the covariate (head size in the case of bite force and snout-vent length in the case of climbing speed). Black: *Iberolacerta horvati*, grey: *Podarcis muralis*, circles: females, squares: males.

locomotor abilities, i.e. negatively influence the climbing speed. Ecological implication of lower performance in climbing ability is that it may lower anti-predator escape abilities on steep surfaces, but on the other hand allow allocating larger single clutch sizes thus positively influencing reproductive effort (Ji & Braña 2000; Olsson *et al.* 2002).

Furthermore, morphological differentiation of the head closely matched biting performance, as is frequently the case in lizards (e.g. Kaliontzopoulou *et al.* 2012); *P. muralis* had larger heads and exhibited stronger bite forces than *I. horvathi* that had flatter heads. Enhanced biting performance may confer a competitive advantage in agonistic social interactions between males (e.g. Huyghe *et al.* 2005) and in agonistic encounters involved in territory defence (Langkilde, Lance & Shine 2005). In our study system, the species with greater bite force, *P. muralis*, is expected to displace *I. horvathi* in agonistic interactions (see also Introduction). Moreover, it has been also shown that in lizards (head) size can serve as a direct visual signal reducing aggressive interference to which other males respond by retreat (Langkilde, Lance & Shine 2005; Lailvaux & Irschick 2007); the higher heads of *P. muralis* may also scare the opponent away (Žagar *et al.* 2015b). Thus, in bite forces and head size the performance traits followed the morphology and are in consensus with the dominant competitor role of male *P. muralis* over male *I. hrovathi* (Žagar *et al.* 2015b).

Variation in the head morphology and the bite force can contribute to ecological segregation between species in lizards, such as segregation in trophic spectrum (Herrel *et al.* 2001; Kaliontzopoulou *et al.* 2012) or microhabitat use (Arnold 1987). Differences in bite force might translate into differences in maximal prey size taken (e.g. Herrel *et al.* 2008) thus *P. muralis* should have the potential to handle larger and harder prey than *I. horvathi*. However, these predictions are not in concordance with available diet studies, where a high overlap in the dietary niches of the two species was observed in sympatric populations

Table 4. Results of ANOVA (top) and ANCOVA (bottom) comparisons on locomotor performance considering the effect of species (sp), sex and their interaction, and using SVL as a covariate

		SPRINT		CLIMB	
	d.f.	*F*	*P*	*F*	*P*
sp	1	1·09	0·371	5·80	**0·012**
Sex	1	0·06	0·797	11·70	**0·001**
sp × sex	1	0·24	0·635	9·38	**0·004**
Residuals	99				
Total	102				
	d.f.	*F*	*P*	*F*	*P*
SVL	1	0·63	0·437	4·69	**0·041**
sp	1	1·22	0·306	6·61	**0·016**
Sex	1	0·61	0·449	6·56	**0·016**
SVL × sp	1	0·33	0·564	0·10	0·753
SVL × sex	1	0·46	0·530	0·95	0·325
sp × sex	1	0·01	0·948	9·51	**0·006**
SVL × sp × sex	1	0·41	0·524	0·64	0·428
Residuals	95				
Total	102				

Significant effects are marked in bold.
d.f., degrees of freedom; *F*, *F*-statistic; *P*, corresponding *P*-value; SVL, snout-vent length.

(De Luca 1992; Richard & Lapini 1993; Capizzi 1999). This is likely due to the generalistic prey habits of most lacertid lizards, which mainly consume prey items much smaller than their mouth opening (Carretero 2004) and much softer than that allowed by their bite force (Herrel *et al.* 1999). Moreover, flatter heads of *I. horvathi* could have an effect on interspecific differences in microhabitat use and predator escape, i.e. allowing *I. horvathi* to enter narrower and deeper endolithic crevices than *P. muralis*. The degree of head flattening in lizards of the genus *Iberolacerta* is further accentuated via an incomplete ossification of the dorsal part of the orbit (Arnold, Arribas & Carranza 2007). This makes the skull very flexible, which probably allows these rock specialists to squeeze through extremely narrow spaces inside rocks, which they also use as refuge sites inaccessible to saurophagous snakes (Luiselli, Capula & Shine 1996; Cooper, Van Wyk & Le 1999). In sympatric species, predators common to both study species can play a mediator role thus influencing the interaction outcome of prey species in an indirect way (Holt 1977). We suggest that *I. horvathi,* having flatter heads than *P. muralis*, are able to utilize smaller crevices and are therefore better able to escape snake predation and consequently should be in advantage by greater ability to avoid specialized predators. However, whether observed flatness of the head is a consequence of current selection pressures related to predator escape has previously not been tested in lizards and should be done in future.

It is important to take into account that the individuals used in this study were collected in non-syntopic sites (due to logistic and practical limitations of acquiring good sample sizes, see also Materials and methods for details), which may raise doubts on the generality of the results obtained. Importantly, however, the localities sampled belong to a homogenous population that inhabits a common geographical area (mountain) and are located in a relatively short distance from each other, which is very likely within the dispersal ability range of lizards. Genetic analyses using mitochondrial and nuclear markers seem to confirm this assumption, as populations from this area are genetically quite homogenous, suggesting the existence of contemporary gene flow and mixing of individuals across sites (C. Walter, Ž. Anamarija, C.A. Miguel, K. Miha, L. Martina, P.L. Martina, T. Nikola & C. Angelica, unpublished data). In this sense, the individuals

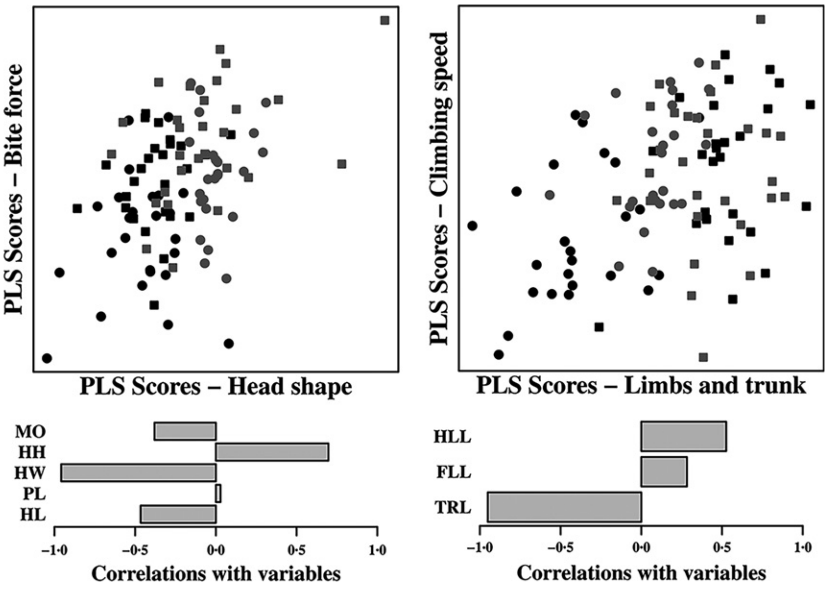

Fig. 5. Association between morphology and whole-organism performance for bite force and head dimensions (left), and climbing speed and trunk and limb lengths (right) visualized as a scatterplot of individual scores of the produced partial least squares (PLS) vectors. Bar plots below each scatterplot represent the strength of the correlation between morphological traits and the corresponding PLS vector. Black: *Iberolacerta horvati*, grey: *Podarcis muralis*, circles: females, squares: males.

examined here can in fact be considered representative of their corresponding species in this area, as they likely belong to a common population divided in several subpopulations where frequent interchange occurs.

Overall, although the observed species traits are shaped by past and current conditions, by observing them in the area of sympatry, we have showed that their functional morphology shaped by different evolutionary pressures, may also have repercussions for community structure influencing the dynamics of species coexistence. In summary, variation in the head shape in connection with bite forces may influence success in agonistic encounters between males where *P. muralis* has superior competitive position. It is less likely that it contributes to trophic segregation between species, but it probably influences segregation in the use of crevices or deep endolithic shelters. Flatness of the head and body may also provide better thermoregulatory ability to *I. horvathi* which exhibits better physiological performance in thermally restrictive environments compared to *P. muralis* (Osojnik *et al.* 2013; Žagar *et al.* 2015c). This contribution may represent another step for a better understanding of the role of functional diversification in structuring ecological communities (Kearney & Porter 2006; McGill *et al.* 2006). Jointly, results of our study highlight that functional morphology provides relevant information for understanding mechanisms shaping species coexistence and local biodiversity patterns. Certainly, further studies of these two species are needed to complete the picture, in particular, to test the local effect of direct competition on morphological and functional traits designed to include study populations from true allotopy and syntopy (isolated populations out of the dispersal ability of lizards).

Authors' contributions

A.Ž. and K.D. have conducted all the field work and conducted experiments and data processing, A.Ž., A.K. and M.A.C. led the design of the study and A.K. conducted statistical analyses, all authors contributed to design the study hypothesis and layout of the manuscript, manuscript writing has been divided into parts: initially A.Ž. and K.D. prepared Introduction and Materials and methods, A.K. – Results and A.Ž., A.K., M.A.C. and A.V. – Discussion. All authors several times revised the manuscript to prepare the final version, which was coordinated by A.Ž.

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Data accessibility

Data deposited in the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.jn14f (Žagar *et al.* 2017).

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